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Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests

Edited by:

J.C. Grégoire
A.M. Liebhold
F.M. Stephen
K.R. Day
S.M. Salom

Vallombrosa, Italy
September 1-3, 1996

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The photograph on the cover is of the Monastery of Vallombrosa, Vallombrosa, Italy (Photo by A. Liebhold).

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Proceedings

Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests[1]

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Edited by:

J.C. Grégoire
Laboratoire de Biologie animale et cellulaire, Universite Libre de Bruxelles, 50 av. FD Roosevelt, B-1050 Bruxelles, Belgium

A.M. Liebhold
USDA Forest Service, Northeastern Forest Experiment Station, 180 Canfield St. Morgantown, WV 26505, USA

F.M. Stephen
Department of Entomology, University of Arkansas, Fayetteville, Arkansas 72701, USA

K.R. Day
Environmental Research, University of Ulster, Coleraine, N.Ireland, BT52 1SA UK

S.M. Salom
Department of Entomology, Virginia Tech., 216 Price Hall
Blacksburg, Virginia 24061-0319, USA

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[1] A meeting sponsored by the International Union of Forestry Research Organizations (IUFRO) working parties S7.03.03 "Insects affecting reforestation", S7.03.05 "Integrated control of scolytid bark beetles", S7.03.07 "Population dynamics of forest insects".

PREFACE

This proceedings results from a conference held at the Monastery of Vallombrosa, near Florence, Italy, on September 1st - 3rd 1996. The meeting, held under the guidelines of the International Union of Forestry Research Organizations, gathered three IUFRO Working Parties: S7.03.03 (Insects Affecting Reforestation), S7.03.05 (Integrated Control of Scolytid Bark Beetles) and S7.03.07 (Population Dynamics of Forest Insects). Forty-nine participants, from 15 countries, presented 33 papers and 8 posters. These figures understate the contributors' input; considerable sharing of expertise and enthusiasm also occurred between the sessions, and links for present or future co-operation were renewed or established.

The organizers wish to express their gratitude to the Italian colleagues who helped to organize locally the meeting: Prof. Riziero Tiberi and Dr. Franco Cerchiarini (Istituto di Patologia e Zoologia Forestale e Agraria, Universita degli Studi, Firenze), Dr. Andrea Battisti and Mr. Massimo Faccoli (Istituto di Entomologia Agraria, Universita' degli Studi, Padova).

We also thank Dr. Rose-Marie Muzika for helping in various aspects of organizing this meeting and preparing the proceedings.

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The editors also thank Becky J. Squires who performed an excellent job of bringing these manuscripts together and was responsible for the outstanding appearance of this report.

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Pheromone mass trapping: does it protect windfalls from attack by *Ips typographus* L. (Coleoptera: Scolytidae)?

JEAN-CLAUDE GRÉGOIRE[1,2], LAURENT RATY[1], ALAIN DRUMONT[1] AND NATHALIE DE WINDT[1]

[1]Laboratoire de Biologie animale et cellulaire, CP 160/12, Université Libre de Bruxelles,
50 av. FD Roosevelt, B-1050 Bruxelles, Belgium
[2]Fonds National Belge de la Recherche Scientifique

ABSTRACT Five sites containing windfalls were selected in Southern Belgium in the winter 1992-93. Trees in each site had been attacked in 1992 (total: 168 trees attacked during the second flight). These trees had shed a large amount of infested bark before their removal in the winter, leaving therefore a large residual overwintering bark-beetle population. Traps and/or trap-trees were set up in each site. After the first flight, in late spring, a model was first established from the sampling of six trees. It yielded a function describing the number of entrance holes to be expected at each position along the trunks, permitting estimation of total numbers of entrance holes per tree and per site. Sex-ratio per site was also estimated. Combining estimates of total numbers of holes per tree and sex-ratios, total numbers of beetles colonising the windfalls could be estimated at each site. A total of ca 202,000 beetles colonised 38 windfalls over 6 sites and therefore escaped trapping. At one of the sites, total catches in trap trees were also estimated: they amounted to ca 32,000 *Ips typographus* whilst at the same site 5 windfalls out of 8 were attacked by a total of 28.000 beetles. A significant relationship was found between windfall protection and trapping effort (ratio trap trees: trees attacked on previous year), suggesting that adequate trapping effort could provide efficient protection.

KEY WORDS *Ips typographus*; mass trapping; pheromones; trap trees; windfalls

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HIGH NUMBERS OF pioneer *Ips typographus* beetles and their symbiotic fungi are necessary to overcome the defenses of healthy spruce trees (Mulock and Christiansen 1986), while poorly defended hosts such as windfelled trees can be easily colonised. If this kind of breeding material becomes abundant, bark beetle populations may increase beyond epidemic threshold, and healthy, standing trees can be successfully attacked (Christiansen and Bakke 1988). Recurrent field observations illustrate this sequence. For example, Figure 1 (M. Dolmans unpublished) shows the progress of an outbreak at Mellier (Southern Belgium), where 70 trees had been windfelled in February 1990 and were left lying during the whole year. The beetles attacked first all the windfalls and then, during the flight of the first generation of the year, they turned to neighbouring live trees. One classical way to minimise these disastrous events is to remove or peel susceptible material before it can yield a new generation. However, as in the previous example, *Saubere Wirtschaft* (clean forestry) is not always implemented, due to either shortage in manpower or limited site accessibility.

Pages 1-8 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

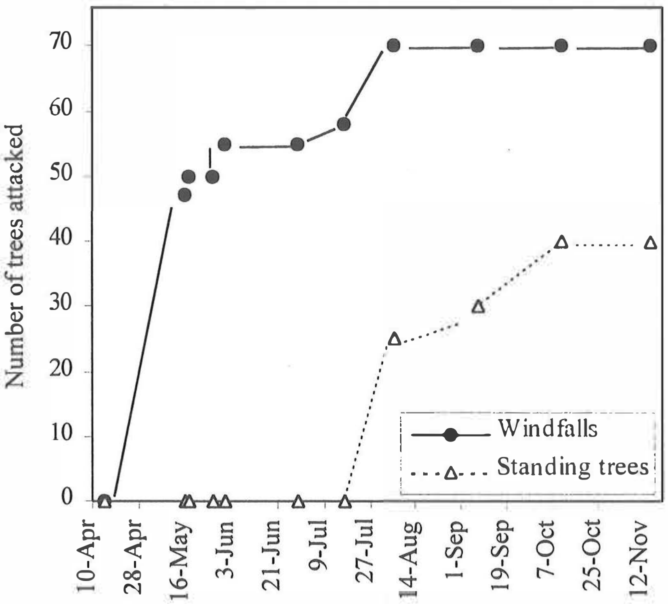

Figure 1. Shift of *Ips typographus* from windfalls to standing trees (Mellier 1990: M. Dolmans, unpublished)

Pest management would be greatly facilitated if pheromone mass-trapping could provide an alternative to forest hygiene under these conditions. Abgrall and Schvester (1987) tested this approach in the French Alps, where they surrounded several large windblown areas (ca 100 ha each) with high numbers of pheromone traps (49 to 108) and with felled, pheromone-baited poisoned trap trees. Millions of beetles were counted in the traps and trap trees, but the windfalls were nevertheless attacked and, in the two following years, live trees were killed.

In the experiments which are reported here, we tried to analyse further the potential of mass-trapping to protect windfalls. The following point were considered:

- How many insects attacked the windfalls?
- What proportion of the windfalls were protected by pheromone trapping?
- If windfalls were attacked, did this competition affect the performances of traps and trap trees?

To answer these questions, the following steps were followed: a) select windfall areas in winter; b) establish traps or trap trees; c) sample trees attacked in spring, to determine attack density and sex-ratio; d) model density of attacking beetles on an individual tree trunk; e) estimate how many beetles established on windfalls and, when possible, compare with trap catches; f) count how many windfalls escaped from attack; g) estimate how many windfalls were potentially protected by trapping.

Table 1. Characteristics of the five experimental sites in Saint-Hubert

Sites	Number of trees killed (summer 1992) [1]	Number of windfalls (winter 1992-93)	Number of trap trees [2]	Number of traps [3]	Ratio ([2]+[3]): [1]
A - "Ortho dh"	20	8	6 (standing)	6	0.36[1]
B - "Ortho db"	8	14	3 (lying)[2]	-	0.38
C - "Ortho gh"	8	13	5 (lying)	-	0.63
D - "Ortho gb"	26	24	6 (lying)	-	0.23
E - "Mochamps"	106	18	13 (lying)	-	0.12
Total	168	77	33	6	

[1] In site A, the six traps have been converted into "trap-tree equivalents" counting 5.42 traps for 1 trap tree

[2] Previous experiments (unpublished) showed no differences in catches between standing and lying trap trees.

Materials and Methods

Experimental set-up. Five sites containing windfalls (large trees of ca 1.5 m^3) were selected at Saint-Hubert (Southern Belgium) in the winter 1992-93. Each site had been attacked in 1992 (total: 168 trees attacked during the second flight in 1992). These trees had shed much infested bark before their removal in the winter, leaving therefore a large residual overwintering bark-beetle population. In early April, traps (Theysohn) and/or insecticide-treated, pheromone-baited traps-trees (Drumont et al. 1992, Raty et al. 1995) were set up in each site (Table 1). Each trapping device was equipped with one *Pheroprax* pheromone dispenser (Shell Agrar).

Sampling. After the first flight in late spring, six attacked windfalls were randomly selected (one in sites A and D; two in sites B and E). 30 x 30 cm phloem samples were taken on each tree along two lateral lines, one on each side, following two patterns: a) on both ends of the trees, 10 samples side by side over 3 m starting at the point on the trunks where infestation began or stopped, b) on the central portion of the infested part of the trunks, one sample every 1.5 m, starting from the end of the lower 3 m portion (Figure 2). The numbers of entrance holes were counted on each sample. Trunk circumference along the sampled trees was also recorded. On four trees, the numbers of maternal galleries were counted, to establish a sex-ratio. As sex-ratio did not significantly vary between sites (Chi^2 = 0.253; $p > 0.05$; 3 df), an average sex-ratio f:m of 2.12 was used for all sites. Trunk circumference at lower and upper ends of the attacked portion of the trunk, as well as total length of attack were also

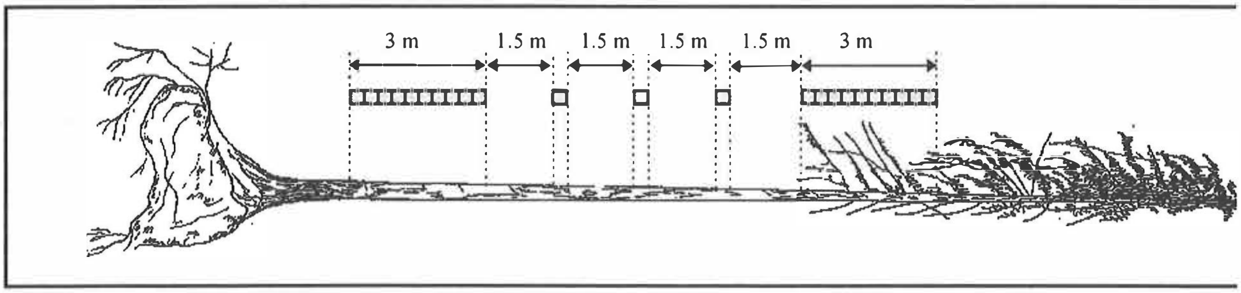

Figure 2. Sampling design for assessing densities of entrance holes per tree

measured on all unsampled trees.

Catches in site A. Numbers of insects caught in site A were determined by direct counting in the traps. In the trap trees, the numbers of insects caught in four funnels (diam. 30 cm) nailed to the base of the trunk (one just under the pheromone dispenser, the three others at right angle to each other) were used to estimate total catches following the method described by Raty et al. (1995). Comparing catches in traps to those in trap trees, a "trap-tree equivalent" ["TTE", ratio of the catches (trap:trap tree)] was calculated: 5037/27322 = 1:5.42.

Results

Table 2. Attacked windfalls in the experimental sites

Sites	Attacked	Unattacked
A	5	3
B	6	8
C	4	9
D	10	14
E	13	5
Total	38	39

Windfalls escaping from attack. Total protection failed in all five sites (Table 2).

Numbers of insects attacking the windfalls. A function describing the distribution of attacks along the infested part of the trunks was established (Figure 3). This function is similar to the one developed by Mayyasi et al. (1976) for *Dendroctonus frontalis*:

$$d = [(a+b(h/H)].[h/H-(h/H)^2]^c$$

where:
d: number of entrance holes/dm^2
h: height in the attacked portion of trunk (cm)
H: total length of attacked portion of trunk (cm)

The values for parameters a, b and c were established using the least squares method (a: 1.324557; b: -0.31153; c: 0.112154).

The trunk circumference was found to vary linearly along the trunks and could adequately be determined at each point on the trunks using the function:

$$C = C_0+(C_1-C_0).(h/H)$$

where:
C: circumference at height h (cm)
C_0: circumference where attacks start
C_1: circumference where attacks end

Integrating the product of these two functions on the total attacked trunk length, an equation was obtained, giving the total number of penetration holes (N) of each windfall according to its characteristics:

$$N = H(0.487822\ C_0+0.449375C_1)$$

The total number of insects per tree was then established by taking the females into account via the calculated sex-ratio: $N_{tot.} = 3.12N$. Total figures for each site are given in Table 3. An estimated 202,278 beetles attacked the windfalls.

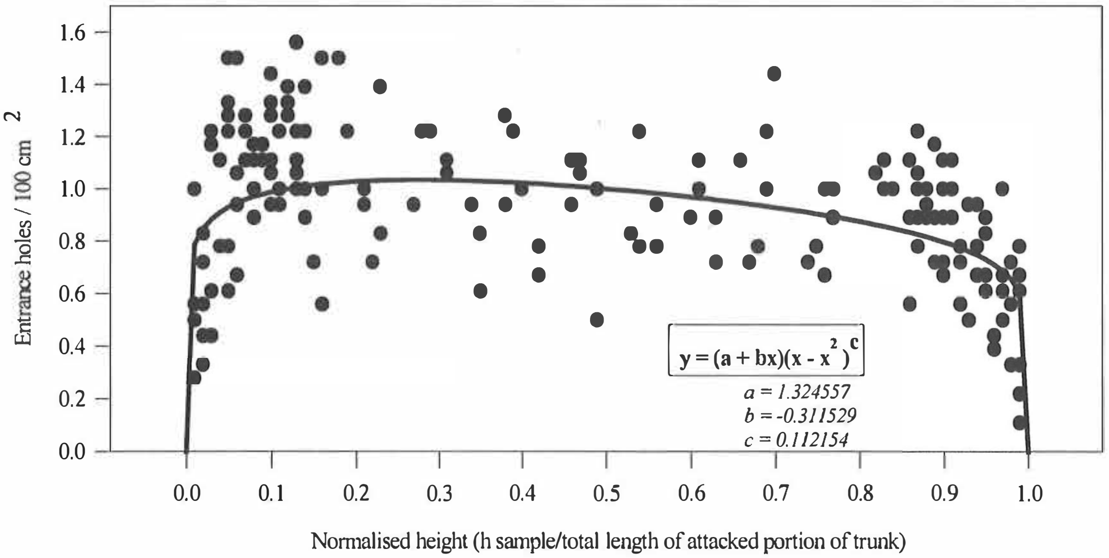

Figure 3. Estimated numbers of entrance holes of *Ips typographus* on each tree

Trapping efficiency. In site A, total estimated catches were 32,359 beetles while 28,067 insects attacked the windfalls. Working with trap-tree equivalents [n = 7.107, i.e. 6 trap trees + (6 traps/5.42)], the average number (± SD) of insects caught per TTE was 4,548.9 ± 2,051.9 . The average number of insects per windfall in site A was 5,613.6 ± 1548.4 . These figures suggest that, in site A, each trap tree prevented attack of one windfall.

In another location nearby (Chanly) with comparable past history (ca 30 trees attacked in the summer of 1992) but devoid of windfalls, 8 trap trees caught an average 4,445.9 ± 1,638.8 beetles. These catches are not significantly different from those in site A (t-test; t = 0.09; p = 0.93; 13 d.f.). Trapping efficiency therefore does not appear to be influenced by competition from the windfalls.

Table 3. Estimated numbers of *Ips typographus* that attacked the windfalls

Site	Mean per tree (± S.D.)	Total per site
A	5613.6 ± 1548.4	28,067
B	4819 ± 2560.2	28,914
C	6443.3 ± 1318	25,773
D	5220.9 ±1729.4	52,210
E	5177.9 ± 2024.8	67,314
Total	5323.1 ± 1881.9	202,278

As the experimental set-up had not taken into account any estimate of the beetle population in the sites, partial failure to protect the windfalls could have been due to deployment of inadequate numbers of trap trees. Since the trees in all five sites were nearly of the same age, and of comparable size (ANOVA on basal circumferences of the windfalls in the five sites: F = 1.41; p = 0.25; 4 d.f.), and since they had been attacked at the same time on the previous year and taken out of the stand at the same period and by the same manner, we used the numbers of trees attacked in each site during the summer 1992 as a measure of beetle populations. We also used the ratios: *[number of trap trees 1993]:[number of trees killed 1992]* or, in site A, *[number of trap-tree equivalents 1993]:[number of trees killed 1992]* as a measure of the trapping effort to protect the windfalls in each site. In Figure 4 these values were plotted against the numbers of windfalls attacked in 1993. The significant relationships observed suggests that, if the trapping effort is high enough, windfalls could be effectively protected.

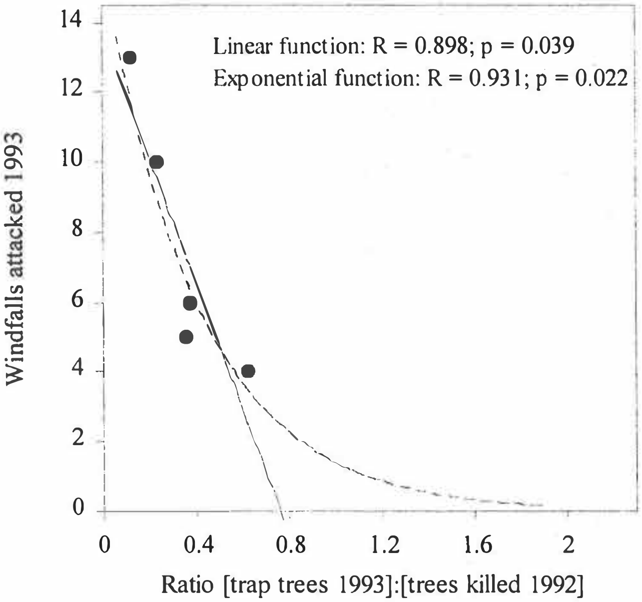

Figure 4 Relationship between numbers of windfalls attacked and trapping effort

Discussion

Windfalls offer no resistance to *Ips typographus*. As soon as a pioneer beetle lands on anyone of them it can start attracting conspecifics and the tree under attack competes with the protective traps or trap trees. Moreover, the windfalls possibly emit primary attractants not produced by the standing trap trees or the artificial traps: Austarå et al. (1986) report an enhanced effect of synthetic pheromones in the presence of logging waste. In our experiments, windfalls were attacked in all sites, as considerable numbers of insects escaped from trapping. However, competition from the windfalls did not seem to reduce the performances of the trap trees which, in site A, each caught as many beetles as each trap tree in another site where no windfall was present. On the other hand, over the whole trapping period considered (15 April to 30 July), the total numbers of beetles caught by the poisoned, pheromone-baited trap trees were not higher than those of insects establishing on the windfalls. This is intriguing, as the effect of insecticide is supposed to prevent the bark beetles from establishing on the trap trees and producing anti-aggregation pheromones, which should result in protracted attractivity of the pheromones and thus in larger catches.

When trapping effort is taken into account, it seems that windfalls could be protected by mass-trapping, provided that sufficient investments are made. In our experiments, this effort would have amounted to 0.8 - 2 TTE per tree attacked on the previous year (Figure 4). If the trees attacked in 1992 had not been removed during the winter 1992-93, local beetle populations would have been larger, and trapping efforts would have had to be higher. The trapping effort required for windfall protection can thus be prohibitive if large amounts of trees have been attacked during the previous year. However, if clean forestry cannot be implemented, especially in cases where windfalls have been preceded by few or no attacks, mass-trapping might constitute an efficient option.

In this perspective, further work is still needed to confirm and expand these first results. In particular, it would be important to know what is the temporal sequence of beetle colonisation (successive or simultaneous response to trap trees and windfalls ?), in order to establish whether pheromone trapping in a site so far devoid of *Ips typographus* might increase the risks for the windfalls to be colonised. Another priority would be to determine an optimal relationship between trapping efforts and the stand's past history.

Acknowledgements

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Silvicultural methods of *Lymantria dispar* L. management: effects on *Agrilus bilineatus* (Weber) populations

ROSE-MARIE MUZIKA, ANDREW LIEBHOLD, AND KURT GOTTSCHALK

USDA Forest Service, Northeastern Forest Experiment Station, 180 Canfield St.,
Morgantown, WV, 26505 USA

ABSTRACT The abundance of twolined chestnut borer, *Agrilus bilineatus* (Weber), adults were sampled using sticky panels over a 6-year period in a mixed hardwood forest in West Virginia. Sixteen stands (average size 10.5 ha) were used in the study; eight of these were silviculturally thinned in 1989, the remainder were uncut. During 1990 and 1991, populations of gypsy moth, *Lymantria dispar* L., reached outbreak levels. Densities of *A. bilineatus* adults peaked in 1992, the year following the second defoliation year (1992), and were always greater in thinned than unthinned stands, however overstory mortality was greater in unthinned stands. Correlations between twolined chestnut borer abundance and tree mortality were not strong, nor were the relationships between defoliation and twolined chestnut borer.

KEY WORDS *Agrilus bilineatus*; silviculture; mortality; *Quercus*; defoliation

FOR AT LEAST the past 100 years, the two-lined chestnut borer, *Agrilus bilineatus* (Weber), has been recognized as a significant source of mortality to oaks(*Quercus* spp.) and to American chestnut, *Castanea dentata* (Chittenden, 1909, Haack and Acciavatti 1992). *Agrilus bilineatus* is frequently associated with trees that have been stressed through defoliation. As a major cause of defoliation for hardwood trees in the Northeastern United States, *Lymantria dispar* L. (gypsy moth), provides an initial stress to its preferred hosts, i.e. *Quercus,* and has been followed by *A. bilineatus* and *Armillaria mellea* as secondary mortality agents (Wargo 1977).

Silvicultural approaches to managing gypsy moth impacts have been proposed several times over the last 100 years (Fisk 1913, Clement and Munro 1917, Behre 1939, Bess et al. 1947, Gottschalk 1993). The intent of this approach is to minimize damage if defoliation does occur or reduce the likelihood of defoliation. Few studies have examined the effect of silviculture on the secondary mortality agents of gypsy moth host trees. The objective of this study was to determine if silvicultural treatments affected *A. bilineatus* adult population densities. Because portions of the study area was defoliated by the gypsy moth, we were also able to examine the relationships among *A. bilineatus* abundance, defoliation, and tree mortality.

Pages 9-14 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

Methods

The study took place on the West Virginia University Forest (WVUF), located in Monongalia and Preston Counties, West Virginia. This oak-mixed hardwood forest (ca. 3075 ha) is along the Chestnut Ridge anticline, in the Appalachian Plateau physiographic province (Fenneman 1938). Average elevation of the WVUF is 591 m, but ranges from 318 m to 796 m. Overstory vegetation ranges from stands with a diverse assemblage of mixed-hardwood species to those dominated by oak. Variation in composition of overstory tree species corresponds in part to elevation -- percentage of oak increases with elevation. The 16 forest stands studied ranged in size from 7.8 to 12.6 ha, with an average size of 10.5 ha. The stands were physically selected to be arranged as eight pairs; one of each pair was thinned.

Within each stand, square plots (0.4 ha) were located within a stratified grid; each plot was separated by at least 100 m . Stands had 10 to 19 plots, depending on their size. The boles of two oaks associated with each stand were wrapped with a cardboard band impregnated with resin and coated with Tanglefoot™. Bands were 22.9 cm wide and were place at 1.4 m above ground. The bands were placed on trees in mid-May, and the diameter, species and vigor condition of the tree were recorded at that time. Bands were removed in mid-August at which time all adult *A.bilineatus* were removed and counted. The number of *A.bilineatus* adults / m^2 were calculated to adjust for the diameter of the tree.

Bands were first deployed in 1989 and the study continued until 1994. No data were collected in 1990, however. During the winter of 1989-90, 8 of the 16 stands were thinned to reduce susceptibility or vulnerability to the gypsy moth. During 1990 and 1991, six stands (three thinned and three unthinned) were defoliated by gypsy moth. Each of the six stands incurred more than 50% defoliation of preferred species and more than 40% defoliation of all species for 2 years. Defoliation in the other stands, i.e. background defoliation level, was less than 15% of all species, including preferred. The data on *A. bilineatus* from 1989, then, represents base-line information prior to treatment or defoliation effects.

Results and Discussion

When grouped by treatment, it is apparent that 1989 levels of *A. bilineatus* were similar among all stand types (Table 1). However, following defoliation in 1990 and 1991, the abundance of *A. bilineatus* increased significantly in the defoliated stands. Relative to control stands, the thinned stands also showed an increase in *A. bilineatus* populations in 1991, presumably due to the thinning effect, i.e. thinning may have damaged or stressed some trees, thereby attracting the insect (Dunn et al. 1986). Despite an increase in *A. bilineatus* in thinned stands, mortality of overstory species was minimal for stands that were not defoliated.

Table 1. Average number of *Agrilus bilineatus* in each of four treatments in West Virginia University Forest. The first year of defoliation was 1990, and silvicultural thinnings took place during the winter of 1989 - 1990.

Treatment	1989 #/m^2	1991 #/m^2	1992 #/m^2	1993 #/m^2	1994 #/m^2
Thinned	8.68	30.36	50.87	19.14	2.82
Control	12.33	3.27	16.96	20.19	6.90
Defoliated	5.69	85.78	533.34	92.89	4.47
Defoliated and Thinned	11.91	111.23	899.31	65.64	7.65

Figure 1 describes the temporal pattern of defoliation, abundance of *A. bilineatus* and overstory mortality. These data represent the pair of stands that was most heavily defoliated, but the trend resembles that of the other defoliated stands. Although defoliation was comparable in both thinned and unthinned stands, the abundance of *A. bilineatus* was greater in the thinned stand, however, overstory mortality was greater in the unthinned stand. One possibility for the lower mortality in thinned stands is the overall increased vigor of the trees. Because the objective of the thinning was to remove trees of low vigor, residual overstory trees generally were more healthy in thinned than unthinned stands. Attacks of *A. bilineatus* may not have been successful in healthy trees, thus there was no resulting increase in mortality. Further, the greater number of borers in thinned stands also may represent a higher concentration of *A. bilineatus*, i.e., more borers but on fewer trees.

Abundance of *A. bilineatus* reached a maximum in 1992, but most of the overstory mortality occurred in 1991. The high population level resulted from the tree stress as a result of high levels of defoliation in 1990 and 1991. The pulse in mortality in 1991 reflected an increase in successfully attacked trees, that is, the large number of trees from which adult borers emerged. As a result of the mortality, the number of available hosts declined in subsequent years, contributing to a decrease in *A. bilineatus* abundance.

To understand the relationship between *A. bilineatus* and defoliation and the relationship between the insect and overstory mortality, we derived correlation coefficients using 1992 data on *A. bilineatus* with defoliation and mortality data for various years. The relationships between the borer and defoliation (Table 2) generally were weak, and often inverse. Correlations between 1992 levels of *A. bilineatus* and defoliation in were relatively strong only for stand 8 in the three defoliation years.

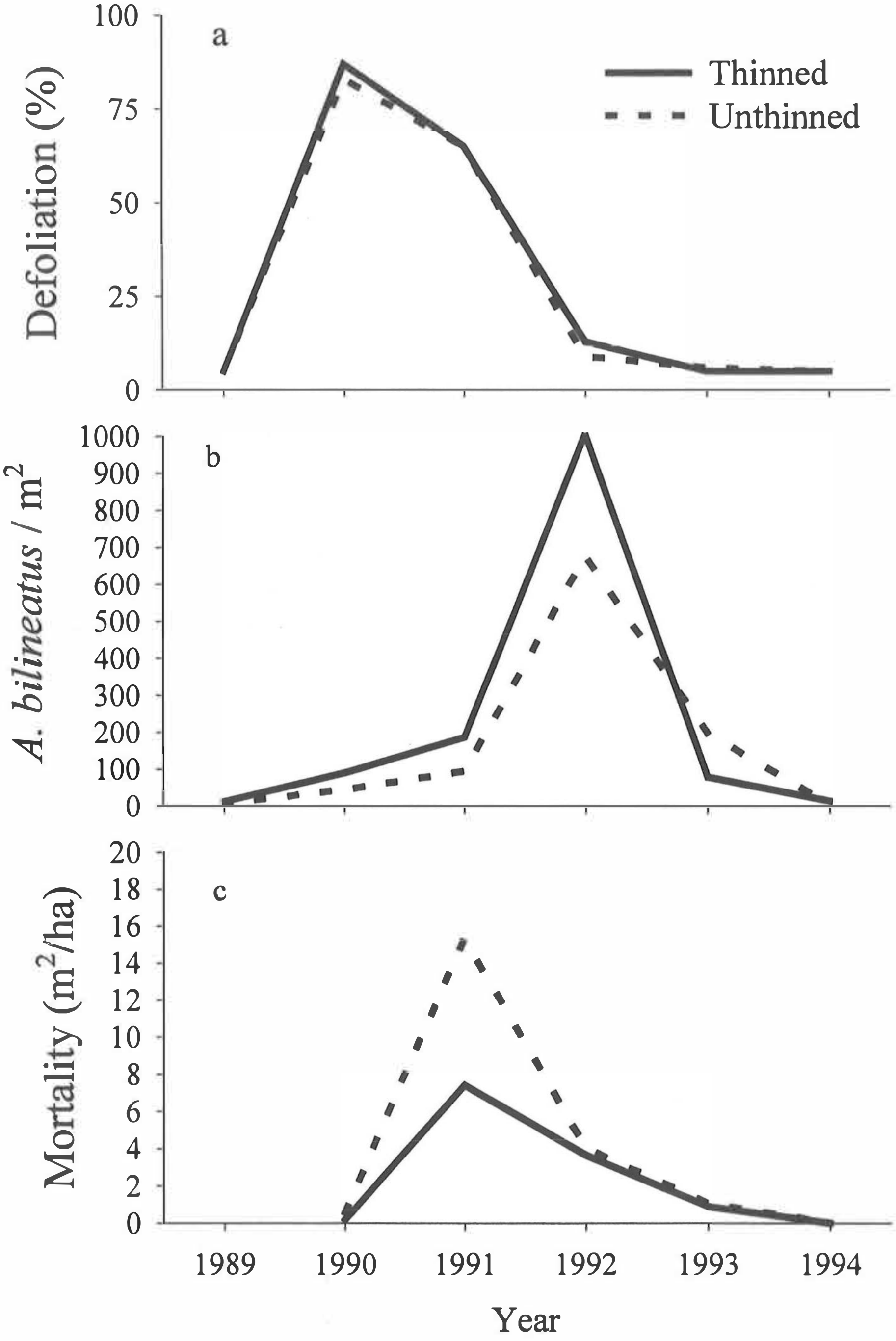

Figure 1. Trends in a pair of defoliated stands from 1989 to1994 on the West Virginia University Forest in (a) defoliation of overstory trees (b), abundance of *Agrilus bilineatus* (c), and overstory mortality.

Table 2. Pearson correlation coefficients of 1992 plot-level abundance of *Agrilus bilineatus* and defoliation.

	Defoliation year		
Stand No.	1990	1991	1992
7	-0.143	-0.549	-0.185
8	0.409	0.801	0.630
13	0.093	-0.155	0.072
14	-0.103	-0.529	-0.275
15	-0.252	0.084	0.268
16	-0.141	0.190	0.065

The relationship between *A. bilineatus* and overstory mortality generally was better than those with defoliation (Table 3). The highest correlations were between 1992 *A. bilineatus* and 1993 mortality in stand 8, and between 1992 *A. bilineatus* and 1992 mortality in stand 15. Given the life history characteristics of the insect, it is not surprising to find a good relationship between *A. bilineatus* abundance in one year and with overstory mortality in the next. However, *A. bilineatus* abundance rarely accounted for mortality in the same year unless populations have been increasing in the previous year. In stand 15 there was a strong relationship between 1992 borer abundanse and tree mortality for all three years: 1991, 1992, 1993. Some trees may take up to 3 years to die following inital attack by *A. bilineatus* (Haack and Acciavatti 1992). Thus, the pattern could be consistent for several years in succession. The most notable finding was the lack of a relationship between *A. bilineatus* and overstory mortality in most stands, for most years. These coefficients were generated using plot-level data, so it is possible that the plot-level relationship is insufficient to explain the dynamics of *A. bilineatus* in these stands. The plot and stand-level correspondence of borer abundance with defoliation and mortality may have more to do with attraction, dispersal, and aggregation – variables not addressed here.

Table 3. Pearson correlation coefficients of 1992 plot-level abundance of *Agrilus bilineatus* and mortality for stands that were defoliated.

	Mortality Year				
Stand No.	1990	1991	1992	1993	1994
7	-0.348	-0.417	0.186	-0.371	0.000
8	-0.302	0.368	0.715	0.895	-0.231
13	-0.341	-0.246	0.211	0.017	-0.203
14	0.330	0.016	0.446	-0.405	0.381
15	-0.393	0.550	0.752	0.555	-0.231
16	-0.140	-0.091	-0.001	-0.332	0.006

The abundance of *A. bilineatus* was consistently greater in thinned than in unthinned stands. The likely reason for this is stress from the logging operation, namely damage to residual trees or soil compaction. Several studies have shown that injured oaks attract more adult borers than uninjured oaks (Dunbar and Stephens 1975, Cote and Allen 1980, Haack and Benjamin 1982). Another possible explanation for an increase in *A. bilineatus* abundance in thinned stands is an increase in light in the canopy which in turn caused an increase in adult activity in thinned stands. Although thinning may promote activity of adult *A. bilineatus* and subsequent population buildup, it does not result in corresponding overstory mortality. Under circumstances where stress is minimal, and defoliation is not imminent, reducing overstory trees of low vigor and low starch reserves (Dunn *et al.* 1990), may keep populations of twolined chestnut borer low, in addition to reducing overstory mortality.

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Augmentation of *Dendroctonus frontalis* parasitoid effectiveness by artificial diet.

F.M. STEPHEN, M.P. LIH, AND L.E. BROWNE

University of Arkansas, Fayetteville, AR, and Entopath, Inc. Easton, PA

ABSTRACT *Dendroctonus frontalis* (Coleoptera: Scolytidae) is native to southeastern, USA, pine forests and has a rich complex of insect parasitoids. Natural enemies, and especially parasitoids, do not currently appear effective in regulating *D. frontalis* populations within rapidly expanding infestations. We believe forest stand structure, coupled with improper forest management strategies, are the primary reasons for this apparent lack of regulation.

We monitored *D. frontalis* and parasitoid populations over an 18-month period in a large infestation in east Texas and noted that although parasitoid numbers tracked *D. frontalis* population growth and decline, percent parasitism never exceeded 10% and averaged 5 to 6%. Why were parasitoids not able to better respond to increasing *D. frontalis* host populations? Our data suggest that both longevity and fecundity of parasitoid adults are severely constrained when food is not available.

Our research with a synthetic food, Eliminade™, developed by Entopath Inc., substantiates our hypothesis that longevity and egg production of adult *D. frontalis* parasitoids is increased when they are fed a nutrient-rich diet. We are currently testing field applications of this diet as an applied biological control tactic for southern pine beetle.

During the past 2 years we have been studying the role of adult nutrition in the biology of parasitoids of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, to test whether an artificial source of nutrition for the adult parasitoids will enhance their effectiveness as mortality agents of *D. frontalis*. The impetus for this research is based on a hypothesis (Stephen 1995) that the parasitoid complex of *D. frontalis*, when deprived of nutrition, is not successful in the control of beetle populations. The key point of this hypothesis is that parasitoids currently are not effective in regulating *D. frontalis* populations because parasitoid adults, in improperly managed southern pine forests (those which are overstocked, homogeneous in age and species composition and protected from fire), are limited in reproductive capacity and longevity by lack of suitable nutrition from natural sources. In this paper we summarize evidence that we believe supports this hypothesis.

Years of field-based observations of rapidly growing *D. frontalis* infestations, supported by a variety of published research, leads us to some specific observations about their dynamics (Table 1). Of particular interest to us is the fact that in all actively expanding infestations the rapid within-tree development of *D. frontalis* immatures, coupled with continuously re-emerging parent adults and emerging brood adults (Coulson et al. 1979; 1980; 1985), results in cohesive "spots" that contain a multitude of *D. frontalis* larvae that can serve as hosts for parasitoids.

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Table 1. Summary of pertinent information about large, rapidly growing southern pine beetle infestations.

A rich complex of *D. frontalis* parasitoids is always present.
A continuous supply of beetles, from brood adult emergence combined with re-emerging parent adults, produce an almost constant source of pheromone around trees under attack.
Continuous, rapid colonization of new trees yields overlapping beetle generations with all life stages present within the infestation.
Synchronous beetle development within neighboring trees results in thousands of fourth-stage larvae/pupae concentrated in closely adjacent trees.
Parasitoid host-selection behavior enables identification of and aggregation on those trees with susceptible hosts.
Parasitoid life cycles can be completed in approximately one-half the time of their hosts.

Also, our collection records indicate that there are eight common species of parasitoids (Table 2). We have sampled intensively in a wide variety of infestations between 1975 and 1992, and a cursory examination of those collection data (Fig. 1) suggest that most of those species are nearly always present (Berisford 1980; Goyer & Finger 1980; Moser et al. 1971; Stephen et al. unpublished) in these infestations. It is also commonly observed that those parasitoid adults aggregate at trees with susceptible hosts (Camors & Payne 1973; Dixon & Payne 1979; Berisford et al. unpublished); and that during summer, most species can complete development in about two weeks, or one-half the time of their *D. frontalis* hosts (Jones and Stephen 1994). This suggests that parasitoids should have a greater opportunity to numerically respond to growing *D. frontalis* populations than we observe in large infestations.

Table 2. Common Guild of *D. frontalis* Parasitoids

Family	Species
Braconidae	*Coeloides pissodis*
	Dendrosoter sulcatus
	Spathius pallidus
	Meteorus species
Chalcidoidea	*Roptrocerus xylophagorum*
	Dinotiscus dendroctoni
	Heydenia unica
	Eurytoma species

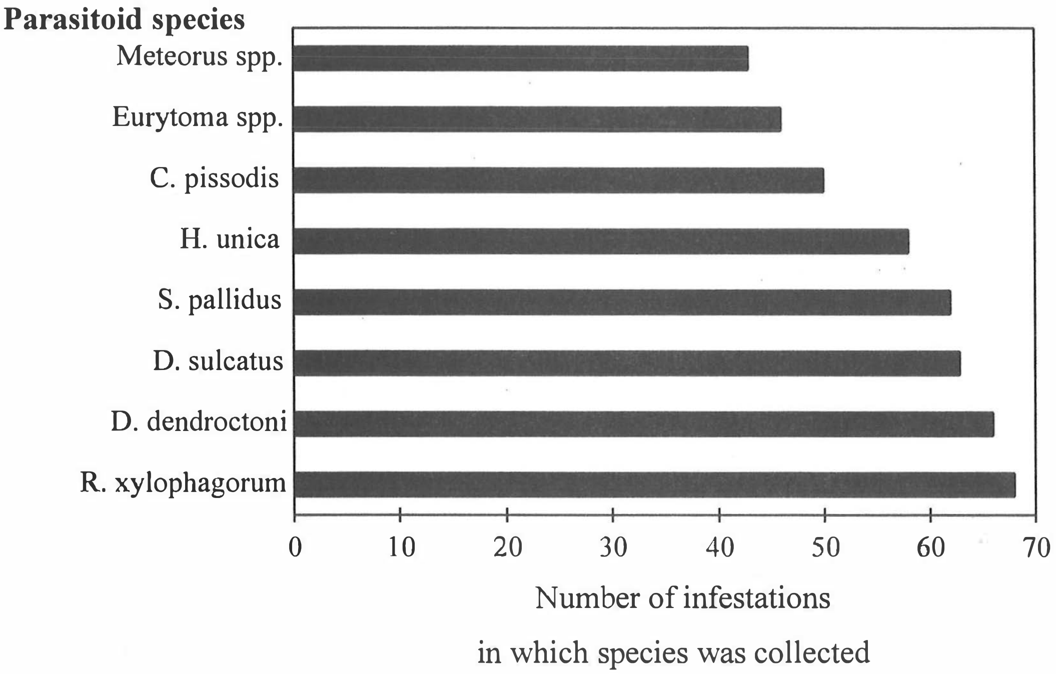

Figure 1. Number of times each of the eight common *D. frontalis* parasitoids was collected from a total of 72 infestations that were sampled between 1975 and 1992.

Research that provides estimates of parasitoid-caused mortality to *D. frontalis* populations is extremely limited. Those data that do exist support the conclusion that parasitoids do not cause high amounts of mortality, and despite many years of intensive research there are no published data that relate *D. frontalis* infestation growth over time and changes in parasitoid-caused mortality.

During 1991 and 1992 we intensively studied a large *D. frontalis* infestation by sampling infested trees and concurrently monitoring total infestation growth and size on the Indian Mounds Wilderness Area in east Texas (Fig. 2).

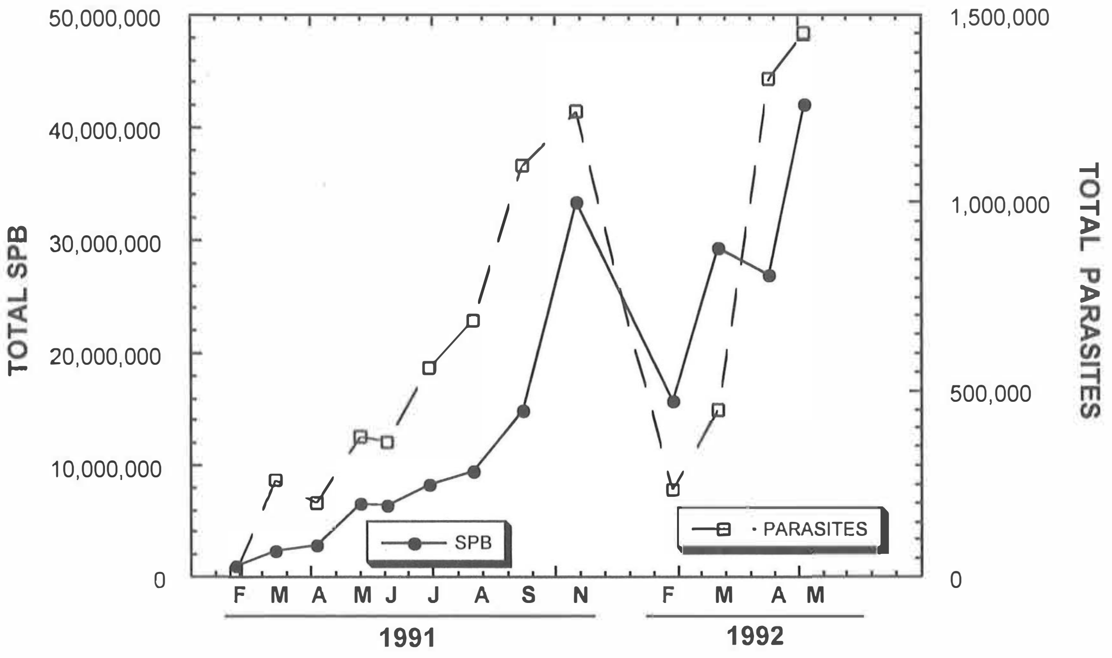

Figure 2. Numbers of adult *D. frontalis* (SPB) and adult parasitoids estimated in Spot 3, Indian Mounds Wilderness Area east Texas, over a series of sampling periods beginning in February 1991 and continuing to May 1992.

The infestation contained 74 currently infested trees in April 1991. It grew rapidly throughout the summer until by late September 1991 it consisted of 895 currently infested trees (and nearly 2600 cumulative dead trees). Beetle population levels declined over the winter, but the infestation began to grow again in the spring, and continued to grow until our final samples were taken in May 1992. In April 1991 we estimated approximately 2.8 million adult *D. frontalis*, and the rapid population growth that occurred from that period until November resulted in about 33.5 million beetles present at the start of the winter. Our sampling in February indicated about 15.8 million adults, but rapid increase in population led to nearly 42 million by May 1992. Total parasitoid numbers grew from less than 200,000 in April, 1991, to about 1.2 million in November, declined over the winter, then grew to about 1.45 million by May 1992. A visual comparison of increase and decrease in parasitoid numbers in relation to *D. frontalis* numbers indicates that patterns of change are closely related. Although parasitoid population abundance continually increased throughout spring and summer, percent parasitism was between 6 and 7% in both April and September (and fluctuated at about those levels in all intervening months) suggesting that although actual numbers of parasitoids increased in relation to changing beetle numbers, a numerical response probably did not occur (Fig. 3).

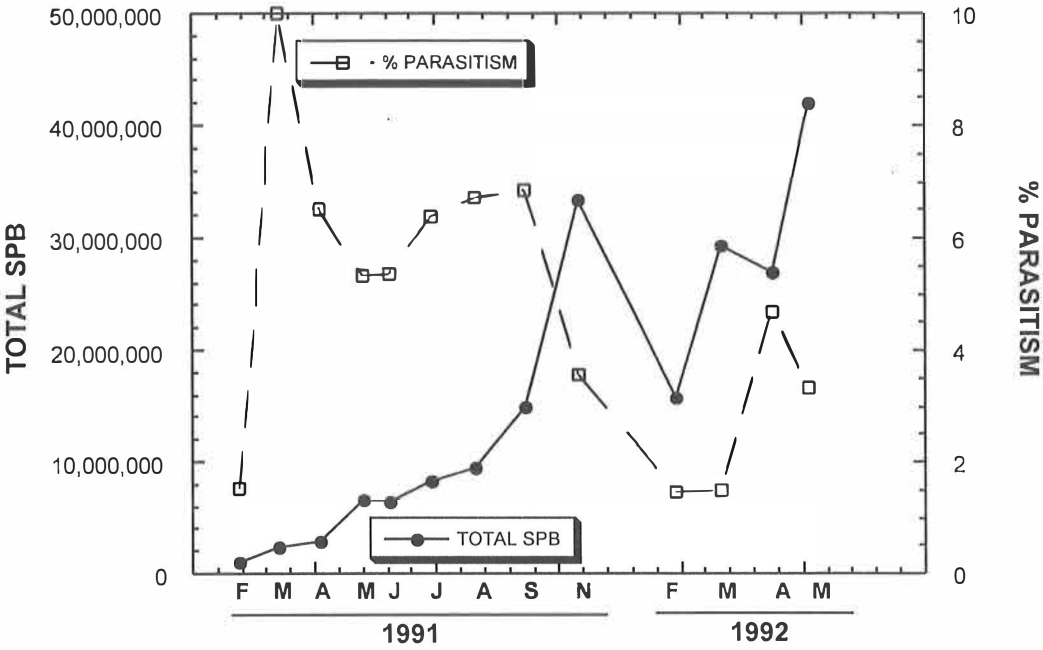

Figure 3. Numbers of adult *D. frontalis* (SPB) and percent parasitism estimated in Spot 3, Indian Mounds Wilderness Area, east Texas, over a series of sampling periods beginning in February 1991, and continuing to May 1992.

Our conclusion is that parasitoids inflicted variable, but relatively low mortality and did not exhibit a numerical response to increasing *D. frontalis* populations. When this conclusion is examined in relation to: (1) superabundance of continuously available *D. frontalis* host larvae; (2) parasitoid adults need only to traverse minimal distances within spots to locate these hosts; (3) observation of parasitoid aggregation at trees with suitable host larvae; and (4) parasitoid immature development rates that are nearly twice as rapid as their hosts (Table 1), it is perplexing that over several months of infestation growth a proportionally greater amount of parasitization did not occur.

Recently completed research designed to investigate egg load parameters in the complex of *D. frontalis* parasitoids (Hanano and Stephen, unpublished) indicates that among the different species the average number of eggs in newly emerged females ranged from about 5 to 17, with most species possessing less than a dozen eggs. Furthermore, these females rapidly resorb their eggs in the absence of nutrition (Table 3). In addition, Mathews et al. (unpublished) have determined that adult parasitoid survivorship is negatively influenced by lack of nutrition, and, in the absence of food, these adults are relatively short lived even under ideal lab conditions (Table 3).

Table 3. *D. frontalis* parasitoids are synovigenic.

Have a limited number of eggs when they emerge as adults.
Resorb their eggs to prolong their lives if food (or hosts?) are not available.
Require nutrition as adults to produce new eggs.
Are short lived without food or water.
Can produce more eggs with a nutrient rich diet.

These conclusions are in agreement with our hypothesis that lack of food for adult parasitoids may be the primary reason for the observed failure of parasitoids to adequately respond to increasing host densities. Carrying only the eggs at the time of emergence, adult females who do not receive additional nutrition cannot parasitize enough *D. frontalis* immatures to proportionally increase their abundance in relation to their hosts' density.

Entopath, Inc. has recently developed a nutritional supplement, Eliminade™, that specifically addresses the nutritional needs of adult hymenopterous parasitoids. We have used this product in our assessments of the role of nutrition for *D. frontalis* parasitoid egg production and longevity. Numerous authors have discussed the effects of forest management, or the lack of management, on the likelihood and severity of *D. frontalis* infestations. Silvicultural guidelines for reducing losses to *D. frontalis* are summarized by Belanger (1980). Pine stands that are highly susceptible to *D. frontalis* problems often are even-aged, single-species forests, that are overmature and over-stocked. Some of these conditions may be associated with poor forestry in the past and even some current intensive forest management practices (Table 4). Turchin et al. (1991) suggest that *D. frontalis* problems are becoming more severe. Perhaps pre-1900 forests, opened by fire, provided a more favorable environment for *D. frontalis* parasitoids because of greater diversity and structure that yielded an abundance of nectar-producing flowering plants encouraging parasitoid survival and reproduction when beetle infestations were initiated.

Table 4. Improperly managed southern pine forests may be....

Predominantly a single pine species.
Even-aged.
Densely stocked.
Closed in canopy structure.
Protected from fire.
Blanketed with a thick pine-straw litter layer.
Barren with respect to flowering annuals.

Our current research efforts are designed to field test the effectiveness of Eliminade™ as a nutritional supplement for *D. frontalis*. It is our intent to determine whether food supplements can enhance the effectiveness of the existing parasitoid complex of the bark beetle, and thus create an applied biological control tactic to reduce losses to *D. frontalis* that can be used alone or in combination with other IPM tactics. If Eliminade™ is effective, we anticipate that it will be a useful tool for forest pest managers as a method for direct control, as an aid in salvage operations, and useful in environmentally sensitive areas where salvage or cut-and-leave are not desirable alternatives.

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Spruce aphid population dynamics in relation to canopy character: scope for cultural regulation.

K.R. DAY AND H. ARMOUR

Environmental Research University of Ulster, Coleraine. N.Ireland BT52 1SA, U.K.

ABSTRACT The dynamic relationships between annual population densities of the spruce aphid in plantations of Sitka spruce are reviewed. The aphid is anholocyclic in western Europe and unlike many aphids on trees, it can be strongly affected by winter weather. In general, mild winters may be followed by higher aphid populations which are capable of causing widespread defoliation, but overcompensating density dependence between years is also indicated and among those processes responsible are behavioural responses of aphids to increased crowding in spring.

Alate aphids were found to accumulate on foliage bearing low initial aphid populations, but it was also significant that they preferentially accumulated on tree canopies which were more exposed (apparent) than those under normal plantation conditions (cryptic). From initially similar population densities of aphids, larger aphid populations were shown to develop on apparent trees than on cryptic trees of the same provenance. The redistribution of alate aphids can therefore be seen as a significant (although not the only) process responsible for generating differences in aphid numbers between trees. The process is density dependent but different canopy types could support different equilibrium densities of aphids.

The consequences of differences in canopy exposure in plantations (edges or spacing between trees) may be an increased risk of aphid damage, and this should be considered in silvicultural planning, particularly as better interactive models for the growth of Sitka spruce plantations become available and the economic effects of the aphid become better understood.

KEY WORDS *Elatobium abietinum,* dispersal, Sitka spruce, Picea sitchensis, plantations

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THE GREEN SPRUCE aphid *Elatobium abietinum* (Walker) is an important pest in Britain and in other maritime regions of western Europe. The insect is probably native to Norway spruce (*Picea abies* (L.) Karst.) on which it causes little damage, and problems are more or less confined to the exotic Sitka spruce *Picea sitchensis* (Bong.) Carr.. There is some irony in the fact that Sitka spruce is unlikely to be out-performed in the British Isles by other fast-growing timber trees (Low, 1987) but it is also one of the spruce species on which the aphid performs best (Nichols, 1987).

Damage to spruce foliage is caused during feeding when an injected toxin generates localised chlorosis (Fisher, 1987) and leads to premature needle abscission. The rate of needle loss corresponds closely to aphid population density (Day and McClean, 1991) and in turn results in a reduction in tree growth (see Straw, 1995 for a recent review). New foliage produced in the year of damage is not severely attacked (Jackson and Dixon, 1997) and trees are rarely killed, so the aphid remains a perrennial pest. Populations persist even on severely defoliated trees and fluctuate within a plantation from year to year.

Density related processes are commonplace in the population dynamics of tree-dwelling aphids (Dixon 1990) but the origins of such density dependence are often less well

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Pages 23-38 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

understood because of the complex age and morph structure in aphid populations. Spruce aphid population changes in maritime parts of western Europe are particularly difficult to interpret because, unlike other tree-dwelling species, the aphid here has no egg stage forming a convenient end-of-season point of reference. Growth and reproduction are possible year round. Nevertheless, it is becoming increasingly evident that population levels from year to year are, in part, a function of previous population densities. Some elements of the annual density dependent response of spruce aphid populations is thought to arise from differential aphid dispersal (Day, 1986).

Aphids undertake kinetic movements in response to the variable quality of the environment (Dixon, 1985) and these movements may involve aggregation or centrifugal dispersal in response to local resource status and the presence of other aphids. In this paper we look firstly at the patterns of alate production in a plantation forest and at the effect of population densities on the maintenance of alates on the tree at a time when damage is most likely to result. In addition we seek a relationship between the maintenance of alates and canopy exposure.

Natural boreal forest is characteristically even-aged (Peterken, 1987), and forests dominated by species such as Sitka spruce are less prone to disturbance, and hence local patchiness, than others, but it is also true that natural forest shows a greater diversity of canopy form and juxtaposition than its plantation counterpart. In plantations, trees are systematically spaced and re-spaced during a rotation to improve maximum mean annual increment (Lowe, 1987) and the physical relationships between adjacent canopies are often uniform. Sitka spruce thrives particularly well in closed stands and achieves high productivities through a foliar geometry which favours good light interception even in shaded positions (Cannell 1987). At present we have little idea how aphid pests respond to the silvicultural options open to plantation foresters. It is particularly important, for example, to explore the balance in economic gains achieved through respacing, and the losses which may arise from increased pest activity under different silvicultural conditions. As a first stage, this requires information on how pests respond to trees growing closer or further from one another.

Some accounts suggest that larger populations of the green spruce aphid, and consequently greater levels of foliar damage, develop on isolated trees, trees at the plantation edge and on trees prior to canopy closure at the so-called thicket stage of the rotation (Bevan 1966). This paper briefly reviews observations on the relationship of aphid populations to spruce canopies in a forest plantation where gaps between some trees have developed and given rise to different canopy types. Observations focus on the brief period in May when alate virginoparae are found in populations and when redistribution of aphids between trees is possible.

Methods

Populations of aphids were studied in field plantations of Sitka spruce in Clare Forest, Co. Antrim and in Springwell Forest, Co. Londonderry, Northern Ireland. The general field methods employed and forest sites have been described in Day (1984a & b). Samples of year n-1 age shoots were removed from the same trees at regular intervals through a season, or in the case of longer-term monitoring, once a year at the end of May when the population was known to be at its peak level. Aphids were removed from the foliage, counted in the laboratory and assigned to seven growth stages and morphs.

Recruitment rate was estimated from the ratio between adult aphids (virginoparae) present in the samples and the number of first instar aphids. The insects pass through the first instar in a day or so at this time of year so it is thought to be a good reflection of population fertility and anticipated population growth rate. The production of alates occurs during a relatively short period in May and is initiated by increasing daylength (Fisher, 1982). A comparison of the relative numbers of aphids entering the alate developmental pathway, and the numbers of alate aphids subsequently found in samples from the same trees, provided an index of net alate accumulation on a tree. Alate adults are capable of leaving shoots at almost any time, and are also capable of arriving from elsewhere. It was not possible to distinguish between immigrants and those which remained on their natal shoot, so net migration was the estimated function. This was termed the index of migration. The ratio of the integrated numbers of alate to apterous morphs was calculated from abundance curves of instar IV and adults throughout the season. The curves (eg. Fig 5) were plotted on a physiological time scale (accumulated day degrees above a developmental threshold of 4 ºC form January 1st) which adjusts the data for the temperature dependence of developmental rates. Areas under the abundance / physiological time curves were were designated as follows:

al	alate adults
al4	alatiform instar four nymphs
v	apterous adults
ins4	apteriform instar four nymphs

If the relative loss of alate adults by emigration was balanced by immigration, and there was therefore no net migration, the expected integrated abundance of alate adults would be given by:

$$al_{expected} = [(v) \times (al4)] / ins4$$

and an index of migration = $\log(al_{observed}) - \log(al_{expected})$

The index of migration actually indicates the outcome of migration and alate aphid survival for each tree studied.

The trees studied were of two main canopy types which reflected differences in their physical apparency (Fig 1). Where gaps had arisen in the forest plantation, or where trees were positioned at the edge of the forest, regardless of aspect, the canopies had developed with a third or more of their canopy perimeter at breast height without close proximity to other canopies ("apparent").

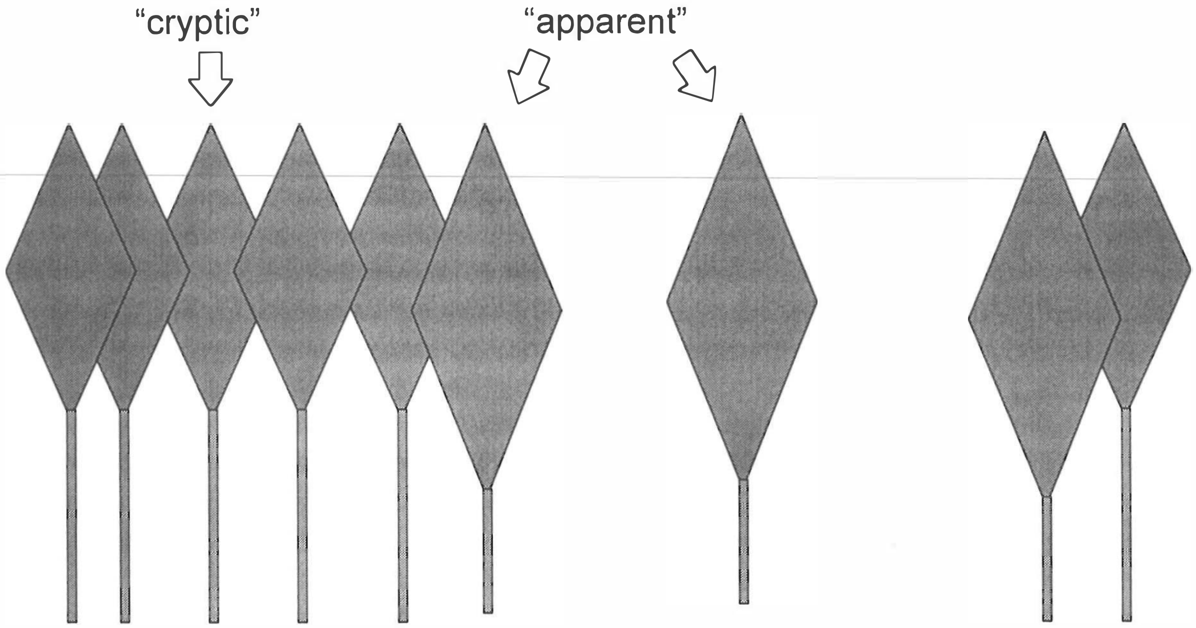

Fig. 1. Representation of canopy types based on differences in their physical apparency. Cryptic canopies formed part of the normal plantation pattern at 2m spacing of stems and canopies developed juxtaposed and in contact with those of adjacent trees. Apparent canopies developed with a third or more of their perimeter in gaps within the crop or at plantation edges.

Trees growing at normal 2m spacing from others had canopies at breast height which were completely surrounded by others ("cryptic"). A second series of observations was made on trees at Springwell forest in a collection of IUFRO Sitka spruce seed origins. Regular estimates of aphids were made on replicate trees of several provenances and we report here the monitored changes in population in six trees of a single Californian provenance. Here, three apparent and three cryptic trees started with rather similar aphid population densities before the aphid flight period in mid-May. The objective was to see if different population levels developed in the two canopy types where tree origin was better defined and where initial aphid densities were comparable.

Review of Population Dynamics

In the British Isles and most other parts of Europe where the aphid has become a pest, the seasonal patterns of aphid abundance are rather characteristic (Parry, 1974 and Fig.2). Aphid numbers start to increase in March when temperatures exceed a developmental threshold of 4°C (Crute and Day, 1990) and reach a peak towards the end of May (Day and Crute, 1990). A decline in sap nutrient quality following budburst results in the population falling to low levels by the beginning of July (Day, 1984a). Although translation of the population trajectory to a physiological time scale allows comparison of similar trends in different years (Fig. 2), it is the timing of budburst in any year which governs when the population is most likely to fall. In Northern Ireland this timing tends to be rather consistant (Day, 1984a).

The population peak is of particular interest since it determines the level of foliar damage in a forest. The amplitude of the peak varies from year to year, and is determined by factors and processes which can be broadly summarised as follows. Firstly, there is an inverse relationship between the rate of population change between years ($\log [N_{t+1} / N_t]$) and population density ($\log N_t$) (Fig. 3). This explains about 60% of the variation in population density and may comprise a number of processes acting on the population of aphids throughout the year, and whose joint effect is overcompensating density dependence (Day and Crute, 1990). The statistical validity of this relationship is dubious but there is some comfort in the knowledge that, although the axes are not strictly independent, more rigorous analyses of similar relationships in other aphids provide similarly significant results (Dixon, 1990; Wellings *et al.* 1985).

Secondly, the population of anholocyclic aphids which enters the winter will respond in a variety of ways to warmer or colder conditions (depending on the year or the locality) before population growth becomes exponential once more in the following April. In some cases the result will be a reduction in recruitment, and in others there will be mortality. Some of the critical conditions for a range of European forests are currently being analysed (Day, in prep.) and are summarised by Day and Crute (1990) and in Table 1.

Jointly, overcompensating density dependence and the three temperature conditions explain a very high proportion of the annual variation in peak aphid population density. A quite independent analysis of spruce aphid catches derived from the Rothamsted Insect Survey has revealed similar relationships with the previous year's catch and winter temperature conditions (Thacker, 1996). Stepwise regressions for 18 suction trap sites in Great Britain were significant for more than half the sites, although density dependence between years appeared to be undercompensating. Nevertheless, the similarity of the result is encouraging considering that the trap catches were quite coarse representations of actual population data.

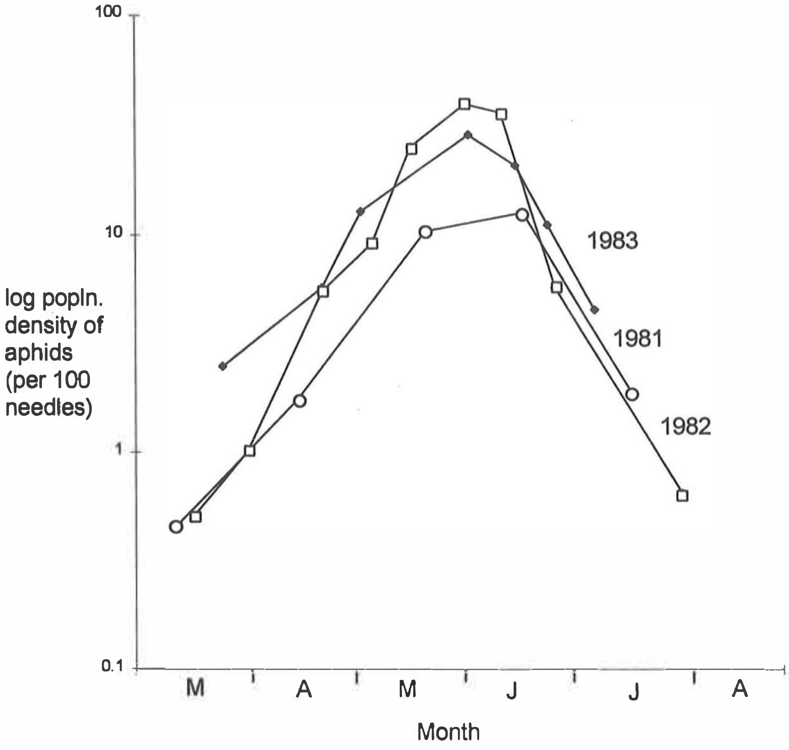

Fig. 2. Mean population densities of spruce aphids estimated from foliage samples.

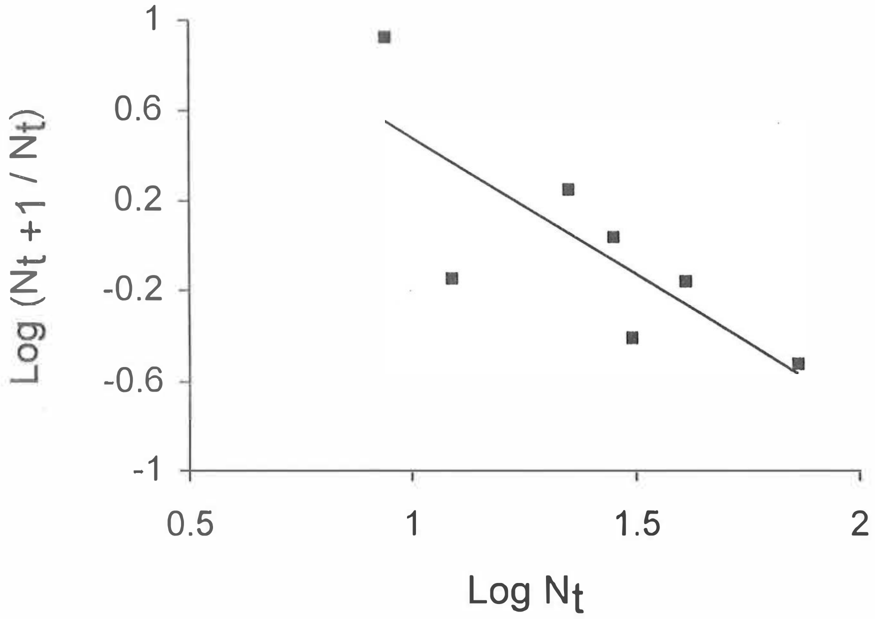

Fig. 3. **The relationship between the rate of population change and population density in consecutive years, based on estimates of maximum aphid population density in summer.**

Table 1 **Winter and spring temperature conditions which are associated with lower population densities of spruce aphids at the following summer peak**

condition	critical temperatures	seasonal prerequisite	r^2 for regression on residuals of dd relationship
PHYS	physiological time (see text) accumulated before budburst (low spring temperature means aphids fail to capitalise on high sap nutrient levels)	cool springs	0.77
CHILL	frequencies of periods of 14 consecutive days with a daily mean temperature ≤ 5°C (prolonged existence below the threshold for development causes chill coma)	cool winter	0.72
FREEZE	accumulated day degrees below -7°C (ice nucleation leads to freezing and death)	cold winter	0.70

Surprisingly, we know little about the processes which contribute to the overcompensating density dependent response of aphids to summer population densities. Plant effects and the actions of natural enemies, even at times of the year when aphids themselves are quite rare on the needlle leaves, cannot be ruled out. Here we explore the potential for density dependence at the level of individual trees and in terms of the relative losses or gains (net migration) of alate aphids, before looking at a further effect of canopy type on this relationship.

Results

Aphid populations are reported during the part of the season from March to July when they were conspicuously present on spruce foliage. At other times of the year aphid populations may be barely detectable by routine sampling. It was no surprise that recruitment rate increased prior to budburst and then gradually declined as the summer progressed (Fig 4, line b). Since the alates of many aphid species are thought to larviposit only after a migratory flight and the majority of alates are lost during migration, the recruitment rate was recalculated with the assumption that the alates present made no contribution to recruitment (Fig 4, line a). Comparison of the two lines strongly suggests that this assumption is wrong, and that a more likely interpretation is that alates contribute to reproduction at least as much as apterous virginoparae. Their relative loss from a tree would therefore be consequential to subsequent population growth (or decline).

A population which experiences almost equal recruitment of alate instar IV nymphs and alate adult aphids is illustrated in Fig. 5. These data represent the aphids sampled on one of the trees in the study. On a tree where the relative losses of alate adults was high, the shaded sector "al" on Fig. 5 for adults would have a smaller area than for the equivalent sector for instar IV above.

The converse would be the case for a tree on which relative gains of alate aphids were made. In this way the index of migration rate was calculated for each tree and plotted against initial aphid density in Fig 6.

Clearly the most important effect on net migration is initial population size, and the components of net migration rate appear to act in a density dependent manner. Alate aphids appear either to leave trees on which population density is increasing rapidly, or to settle preferentially on trees with lower aphid levels. Differential mortality is an unlikely explanation since the calculation of the migration index has taken any minor relative differences in survival of apterous morphs into account. Although alate morphs may have higher rates of mortality than those of apterae, it is hardly likely that, relative to one another, they will differ in respect of population density. Since alates have a much greater capacity to arrive on or leave trees by flight this is the probable explanation for the primary relationship in Fig. 6.

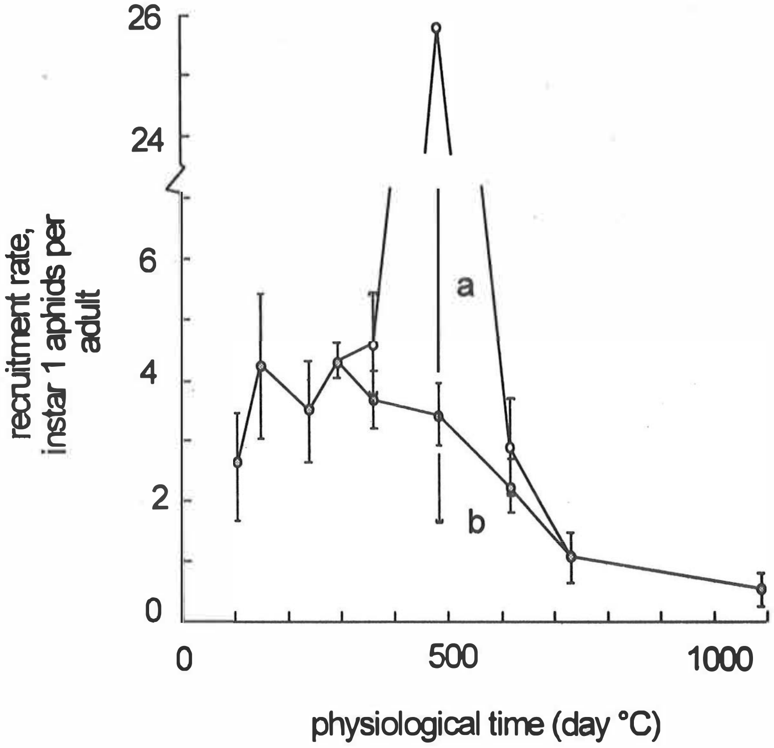

Fig. 4. The seasonal pattern of recruitment rate (ratio of first instar nymphs in samples to adult virginoparae), calculated a) on the assumption of no contribution from alatae and b) on the assumption that all virginoparae in samples contribute to recruitment.

A second influence on net migration is the apparency of the tree canopy . The slope of regressions through data representing the two canopy types are significantly different (P<0.005) and suggest that equilibrium densities of aphids will be higher on trees with apparent canopies. Of course, spruce aphid populations are rarely in equilibrium, rather they change quite rapidly during the early summer. Nevertheless, it is anticipated that cryptic canopies will support fewer aphids per foliage unit at the time of the population peak.

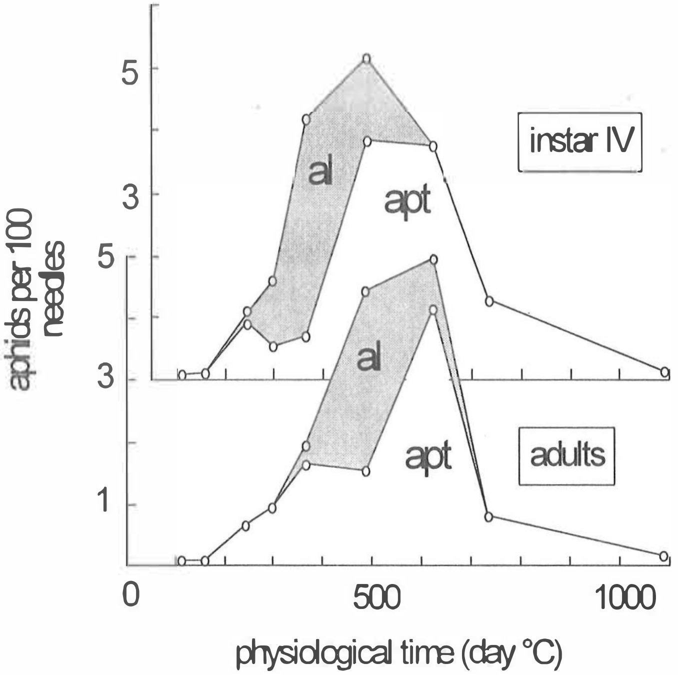

Fig. 5. The seasonal pattern of abundance of apterous and alate morphs in a population of spruce aphids estimated from the same tree. The shaded area represents alatoid or alate morphs in both cases.

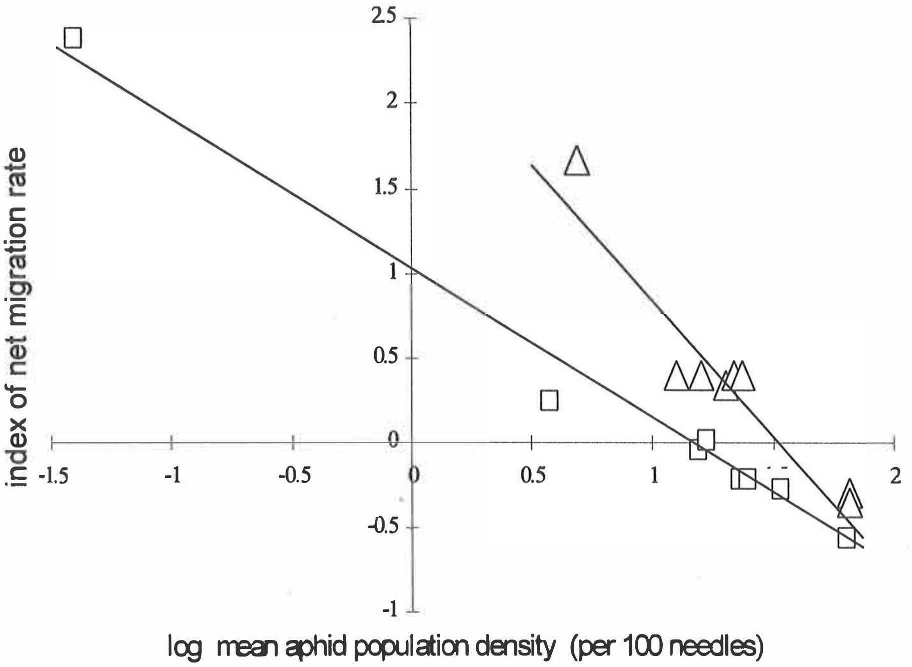

Fig. 6. Changes in net migration rate (based on the relative production of alatoid instar IV nymphs and the subsequent occurance on a tree of alate virginoparae) in relation to initial (April) population densities of aphids estimated for a tree.

A separate series of trees were selected for their canopy types and studied at Springwell forest. Trees were of the same provenance and initially (prior to alate production) supported similar population densities of aphids. The expectation was that trees with apparent canopies would support larger aphid numbers by the end of May. This was indeed the case for the six trees reported in Fig. 7.

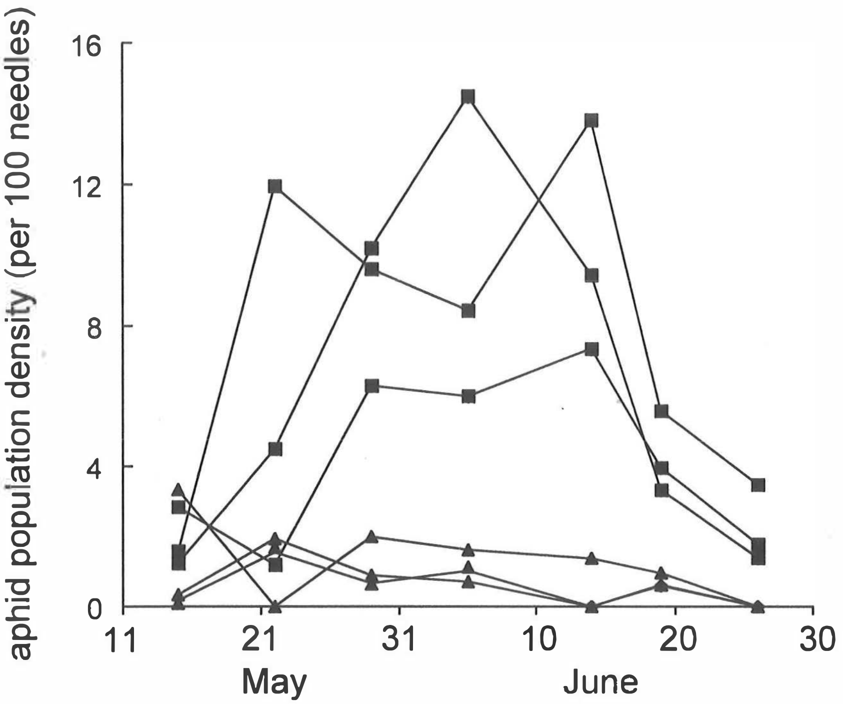

Fig. 7. The development of aphid populations on six trees of the same Californian provenance, where three trees were apparent (■) canopy types and three were cryptic (Δ) canopy types. Data represent mean population density based on shoot samples from each tree.

Discussion

Other aphids on deciduous trees also experience overcompensating density dependence (Barlow and Dixon, 1980; Wellings *et al.*, 1985) but this occurs within years, whereas between year dynamics are governed by strong density dependence. Intraspecific competition operating through changes in aphid quality appears to be the main process responsible for regulation, together with additional effects of natural enemies (Dixon, 1990). So far we have no knowledge of annual differences in spruce aphid quality, although when aphids were examined on trees supporting a range of population densities a crude measure of fecundity failed to show corresponding variation (Day, 1986). Loss of needle habitat may play a part, particularly since the rate of needle loss is proportional to aphid density (Day and McClean, 1991) and it appears that some needles are lost even at low aphid population density (Straw, in prep.). However, adult aphids are particularly vagile (Day, 1986) and may be expected to move from needles prior to abcission; the proximal cause of population change may therefore be losses of more mature aphids (with greater reproductive value) but the underlying process may be the response of the plant to aphid feeding. Results here suggest another contribution to density dependent regulation of aphid populations is at least possible when comparing dynamic responses between trees. Relative accumulation of alate aphids, known to play a major role in subsequent recruitment, was related to initial population density.

Canopy type or exposure was also important in appearing to determine different equilibrium aphid levels. It is a possibility that the clear differences in population development on trees of the same (Californian) provenance were simply the result of microclimate. Higher temperatures can cause quite large differences in mean relative growth rate at this time (Armour, in prep.). Trees growing close to edges experience differing exposure and edaphic factors altering insect survival as well as tree physiology and phenology. *Neodiprion sertifer*, for example, is frequently more abundant in unthinned stands (Pitman *et al.*, 1982). Temperature differences would only explain the canopy effect in the study at Clare forest if they affected aphid net migration.

It is interesting that isolated sycamore trees support fewer *Drepanosiphum platanoidis* because they sustain much higher losses from dispersal than do trees growing in clumps (Dixon, 1990). Here the effect is reversed compared with the spruce aphid, but then the migratory strategies of the two aphids are thought to be quite different, sycamore aphids undertaking only local flights between trees (Dixon, 1985) and spruce aphids capable of longer range dispersal which results in frequent interception by suction traps some distance from spruce forests (Thacker, 1995).

There are numerous examples in the literature of aphids selecting plants on the basis of background or of plant canopy spectral reflectivity (Berlandier and Cartwright, 1996). One of the changes that takes place in spruce canopies as aphid population density increases is that older foliage turns yellow before being lost entirely. Such changes may be profoundly important to immigrant aphids selecting new habitat, but would not explain different responses of alates to variations in canopy exposure. Perhaps aphids perceive and respond more favourably to canopies juxtaposed with habitats of contrasting physical character. As mentioned earlier, exposed canopies may provide a warmer microclimate than those which are closely juxtaposed and alate aphids may use this as a selection criterion. It is perhaps not surprising that aphids are capable of selecting new habitat on the basis of its current occupancy or its surface physical characteristics; the evolution of relationships between aphids and trees may have been strongly influenced by the aphids' perception of the relative surface area of specific plant parts (Dixon *et al.* 1995).

Spruce aphids undoubtedly affect the long-term growth of Sitka spruce crops (Day and McClean, 1991; Day and Cameron, 1997; Straw, 1995) and the results of periodic defoliation are currently being incorporated in plantation growth models (T. Randle and T.Ludlow, pers. comm.). Where thinning and respacing are components in Sitka spruce silviculture (Low, 1987), consideration might be given to the trade-off between potential gains in productivity through competitive release of trees and the effects of increased aphid loads on timber growth. Further work is needed on the development of aphid populations at several crop ages and under a range of thinning régimes in order to estimate costs and benefits of cultural management with greater precision.

Acknowledgements

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Integrating Tree Felling with Application of an Inhibitor Pheromone for Suppressing Southern Pine Beetle Infestations*

SCOTT M. SALOM[1], RONALD F. BILLINGS[2], C. WAYNE BERISFORD[3],
STEPHEN R. CLARKE[4], Q. C. MCCLELLAN[1], W. W. UPTON[2] , AND M. J. DALUSKY[3]

[1] Department of Entomology, Virginia Tech, Blacksburg, VA 24061-0319, USA
[2] Forest Pest Control Section, Texas Forest Service, Lufkin, TX 75902-0310, USA
[3] Department of Entomology, University of Georgia, Athens, GA 30602, USA
[4] Forest Health, USDA Forest Service, Lufkin, TX 75901, USA

ABSTRACT Recent efforts to develop a pheromone-based suppression tactic for southern pine beetle (SPB) are reported here. The suppression tactic relies on the use of the inhibitor pheromone verbenone to reduce or halt spread of southern pine beetle infestations. Verbenone-only and verbenone-plus-tree felling treatments were evaluated over a two-year period. In 1994, the verbenone-only treatment was effective in the eastern part of the SPB range, yet ineffective in Texas. Verbenone-plus-felling options were effective in all test areas. The ineffectiveness of verbenone-only treatment in Texas is attributed to a lower application rate of verbenone compared to rates used in the other test areas. This led to the development of a standardized protocol of verbenone application rates for 1995. Using the new protocol, the efficiency of all verbenone treatments increased in all test areas. Verbenone-only is recommended for infestations that are small in size and where felling or salvage of trees is not desired. Verbenone-plus-felling all active trees is more effective in larger infestations than verbenone-only, and does allow for salvaging of dead trees. In preparation for the release of these behavioral chemical tactics for operational use, we identify and discuss several issues that remain to be addressed.

KEY WORDS southern pine beetle, suppression, pheromones, verbenone, tree felling

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THE SOUTHERN PINE beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) continues to be the most serious insect pest of southern pines in the USA. In fact, 1995 was considered the most severe outbreak year in modern history, with regional losses estimated at $250 million (1996 Southern Forest Insect Work Conference Committee Report). Traditional direct control tactics such as 1. cut-and-remove (fell and remove attacked trees plus a buffer strip of unattacked trees); 2. cut-and-leave (fell infested trees plus a buffer strip of uninfested trees and leave them at the site); 3. cut-and-spray infested trees with insecticide; and 4. cut, pile, and burn infested trees, are used to treat infestations (Swain and Remion 1981). Yet during outbreak years, limited personnel and equipment make it very difficult to treat all infestations. In addition, forest managers would prefer an alternative that either doesn't include tree felling or reduces the amount of volume felled (Salom et al. 1997). This is especially true in pre-commercial stands and remote areas with limited access.

Pages 39-53 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

A new tactic employing the application of an inhibitor pheromone to SPB infestations will soon be available to forest land managers. It has been a long time coming, considering that the use of semiochemicals in pest management for SPB was first suggested 25 years ago (Vité 1971). Experimentally, pheromone-based techniques for suppressing SPB infestations have included: 1. treating trees with the aggregation pheromone frontalin and cacodylic acid (Vité 1971); 2. attempting to prevent aggregation and infestation growth by treating dead trees in the infestation with the SPB aggregation pheromone, frontalin (Payne et al. 1985) or by aerial application of frontalin (Vité et al. 1976); and 3. placing the inhibitor pheromone verbenone at the active head to prevent infestation spread (Payne et al. 1992, Billings et al. 1995). To date, the inhibitor-based suppression tactic has been the most effective and economical of the tactics utilizing pheromones.

Verbenone , the pheromone used in this tactic, is an oxygenated terpene derived from *trans*-verbenol, whose identity (Renwick 1967) and function (Renwick and Vité 1970) suggested that it may have potential use in managment of SPB. Successful tests of the compound in field trials by Payne et al. (1978) and Richerson and Payne (1979) led to the development of a verbenone-based suppression tactic (Payne and Billings 1989, Salom et al. 1992, Payne et al. 1992, Salom et al. 1995; Billings et al. 1995). This paper reports on the latest continued evaluation and comparison of verbenone-only and verbenone-plus-felling options of the suppression tactic. In addition, recent efforts to standardize infestation level release rates of verbenone and size of treatment buffer strips for all verbenone treatment options are discussed.

Protocol for Verbenone Suppression Tactics

Generalized procedures used in applying verbenone and evaluating success of two verbenone suppression tactics follow:

1. Identify active SPB infestations with < 120 currently infested trees.
2. Count the number of currently infested trees and verify the presence of fresh attacks.
3. Assess whether the infestation will continue to grow. Continued growth can be determined based in part on the number of fresh-attacked trees (trees where eggs have not yet been layed) and continued availability of susceptible trees in front of the active head (zone of most recent SPB attacks) (see Billings and Pase 1979).
4. Make decision whether or not to treat.
5. If the decision is to treat, apply one of the following available options:
    a. *Verbenone-only*: treat fresh-attacked trees and a buffer strip of unattacked trees with verbenone.
    b. *Verbenone-plus-tree felling all actively infested trees*: Fell all actively infested trees and treat buffer strip of unattacked trees with verbenone.
    c. *Verbenone-plus-felling fresh-attacked trees:* fell all fresh-attacked trees and treat buffer of unattacked trees with verbenone
6. Monitor infestation for 6 weeks to determine treatment effectiveness. Categories include:
    a. *Total suppression:* no new trees attacked beyond treated buffer strip during the 6-week post-treatment period.

b. *Partial suppression:* new trees attacked beyond treated buffer strip, yet infestation growth decreased by ≥ 50%.

c. *No suppression:* new trees attacked beyond treated buffer strip and infestation growth decreased by < 50%.

Verbenone Elution Device. Verbenone with the enantiomeric ratio of 34%(+): 66%(-) was used for all treatments (Salom et al. 1992). 5 ml of verbenone was place in white 1.2 mil polyethylene bags (8 x 13 cm) provided by Phero Tech, Inc., Delta B.C. The bag provided an elution rate of ca. 9.2 mg/h for 40 to 50 days during summer months (C.W. Berisford et al., unpublished data).

Comparisons Among Different Verbenone Treatment Options in 1994

The collaborators in this project were the Texas Forest Service (TFS), University of Georgia (UGA), and Virginia Tech (VT). The TFS evaluated sites in Texas, UGA in Alabama and Georgia, and VT in Virginia, North Carolina, and South Carolina. Three verbenone treatment options plus a check were evaluated as follows: verbenone-only (17 sites), verbenone-plus-felling all attractive trees (9 sites), verbenone-plus-felling all fresh attacked trees (8 sites), and no treatment checks (13 sites).

a. *Verbenone-Only-* In SPB infestations, all fresh-attacked trees plus a buffer strip (3 trees deep and 10 m surrounding the active head) were treated with verbenone. Bags were attached to trees at a height of 3 m. The number of bags attached to trees were based on tree diameter at breast height (d.b.h.). This relationship was applied differently between the TFS and the VT/UGA groups (Table 1). The TFS tended to apply fewer bags per tree d.b.h. than VT/UGA for trees with ≤ 28 cm d.b.h.

b. *Verbenone-Plus-Felling All Actively Infested Trees -* All actively infested trees were felled toward the older part of the infestation. A buffer strip of unattacked green trees, similar in size as used in the treatment above, was treated with verbenone. With the exception of the buffer, this treatment mimics a conventional cut-and-leave treatment that serves to open up the stand. The drastically different environmental conditions that result from opening the stand is believed to promote dispersal rather than aggregation. Brood in felled timber may be susceptible to increased radiant heat near the opened forest floor, resulting in a higher level of mortality. In addition, felling fresh-attacked trees reduces the production of secondary attractants.

c. *Verbenone-Plus-Felling Fresh-Attacked Trees-* In this option only freshly-attacked trees were felled. The same sized buffer strip of unattacked trees at the active head of the infestation was treated with verbenone. This treatment is aimed primarily at eliminating sustained production of beetle- and host-produced attractants within the treated infestation. The felling of freshly-attacked trees open up the stand, but to a lesser degree than when all infested trees are felled

d. *Check-* SPB infestations that met treatment criteria but could not be treated due to various constraints were left untreated and monitored for 6 weeks.

Table 1. Recommended number of verbenone bags placed on trees in southern pine beetle infestations by the Texas Forest Service and Virginia Tech/Univ. of Georgia during 1994 field season.

Texas Forest Service d.b.h. Range			Virginia Tech/Univ. of Georgia d.b.h. Range		
Inches	cm	# Bags/Tree	Inches	cm	# Bags/Tree
≤ 6	≤ 15	1	≤ 4	≤ 10	1
> 6 - 11	> 15 - 28	2	> 4 - 9	10 - 23	2
> 11 - 15	> 28 - 38	3	> 9 - 15	23 - 38	3
> 15 - 18	> 38 - 46	4	> 15 - 18	38 - 46	4
> 18 -20	> 46 - 51	5	> 18 - 20	46 - 51	5
> 20	> 51	6	> 20	> 51	6

Results *Verbenone-Only* - The efficacy of this treatment was quite variable in 1994. In the eastern portion of the range (NC, GA, and AL), infestation growth was reduced by an average of 62% in 5 infestations (Table 2). Four infestations were completely suppressed while one was unaffected by the treatment. In Texas, the verbenone-only treatment was essentially ineffective (Table 2). Complete suppression occurred in only 1 of the 12 treated infestations, and infestation growth was slowed by at least 50% in one other infestation.

We attribute the relative ineffectiveness of the 1994 verbenone-only treatment in Texas to a lower amount of verbenone used for each treatment (Table 1). In 7 randomly selected infestations from the 1994 field season (ranging in size from 23 - 129 actively infested trees), the number of bags recommended by the TFS was 23% less than the number of bags recommended by the VT/UGA group. These differences in application rates were addressed during the 1995 field season. The modified protocol and the ensuing results will be presented in a later section of this report.

Verbenone-Plus-Felling All Actively Infested Trees - Infestation growth over all 9 infestations was reduced 70% (Table 2). Although the percent reduction in spot growth was less than in previous years (Billings et al. 1995), the tactic was completely effective in 8 of the 9 infestations by the end of the post-treatment monitoring period.

Verbenone-Plus-Felling Fresh-Attacked Trees - This tactic was completely effective in 4 of 5 infestations in Texas and partially effective in the other (Table 2). In Alabama, the treatment was effective in one of two infestations.

Check - Thirteen infestations were used as controls to ensure that most untreated infestations would continue to expand. Nine infestations increased in size by > 1 tree/day, and 10 added more than 10 trees during the monitoring period (Table 2).

Relationship Between Verbenone Release Rate and Treatment Effectiveness - To help explain why treatment effectiveness differed between Texas and other areas in the SPB range, we looked at the relationship between the amount of verbenone applied to a treatment and the percent reduction in infestation growth from data collected in 1993 (Billings et al. 1995) and 1994. A significant relationship was observed for verbenone-only (Figure 1a), but

Table 2. Growth rates of southern pine beetle infestations before and after application of suppression treatments in 1994.

Treatment	Infestation No.	Mean DBH inches (cm)	Pre-treatment New Trees Attacked	No. of Days	Trees Killed/ Day	No. Active Trees at Treatment	Verb used ml/ft^2	New Trees Attacked[1]	Post-treatment No. of Days	Trees Killed/ Day	% Growth Reduction
Verbenone Only (East)	NC-1	13.3 (33.8)	9	8	1.1	46	21.2	19[a]	43	0.4	63.6
	NC-4	12.3 (31.2)	14	10	1.4	79	14.3	45[c]	40	1.1	21.5
	GA-2	4.5 (11.9)	4	6	0.7	37	25.0	8[a]	42	0.2	71.4
	GA-3	8.6 (22.6)	4	6	0.7	29	58.3	2[a]	45	0.04	94.3
	AL-4	5.0 (12.7)	6	5	1.2	47	50.0	17[a]	36	0.5	58.3
(West)	TX-26	7.9 (20.1)	39	7	5.3	140	27.5	171[c]	42	4.1	22.6
	TX-27	8.1 (20.6)	8	8	1.0	47	23.3	46[c]	42	1.1	-9.9
	TX-28	8.0 (20.3)	15	7	2.1	86	21.4	58[c]	42	1.4	33.3
	TX--37	15.7 (39.9)	17	8	2.1	53	10.0	52[c]	42	1.2	42.9
	TX-39	11.5 (29.2)	7	8	0.9	76	16.4	49[c]	42	1.2	-25
	TX-36	8.2 (20.8)	28	33	0.8	41	29.6	42[c]	45	0.9	-11.2
	TX-43	15.4 (39.1)	8	21	0.4	24	12.5	8[a]	30	0.3	25
	TX-30A	8.3 (20.3)	4	7	0.6	63	21.1	51[c]	41	1.2	-50
	TX-30	8.5 (21.6)	18	6	3.0	86	22.2	53[b]	42	1.3	56.7
	TX-27A	8.8 (22.4)	6	7	0.8	50	25.7	19[c]	41	0.5	37.5
	TX-26A	7.2 (18.3)	80	15	5.3	252	13.1	187[c]	41	4.6	13.2
	Mean	9.8 (25.0)	18.1	9.9	1.6	69.1	24.5	46.9	41.1	1.2	38.6[2]
Verbenone + Fell All Actively Infested Trees	VA-1	6.3 (16.0)	6	8	0.8	44	32.6	3[a]	43	0.07	91.3
	VA-2	7.5 (19.1)	8	6	1.3	24	36.5	2[a]	41	0.05	96.2
	NC-3	11.4 (29.0)	4	8	0.5	23	23.3	7[a]	40	0.2	60
	SC-1	7.2 (18.3)	52	9	5.8	115	32.2	5[a]	35	0.1	98.3
	SC-2	8.0 (20.3)	16	7	2.3	115	13.8	11[a]	36	0.3	87
	GA-1	6.6 (16.8)	16	25	0.6	129	9.8	32[c]	42	0.8	-25
	AL-3	6.4 (16.3)	7	14	0.5	96	19.2	17[a]	42	0.4	20
	TX-66	7.9 (20.0)	5	6	0.8	56	19.8	0[a]	42	0.0	100
	TX-68	7.4 (18.8)	17	7	2.4	107	25.8	0[a]	42	0.0	100
	Mean	7.6 (19.4)	14.5	10	1.7	78.8	23.7	8.6	40.3	0.2	69.8

Table 2.(Cont'd)

			Pre-treatment						Post-treatment	
Treatment	Infestation No.	Mean DBH inches (cm)	New Trees Attacked	No. of Days	Trees Killed/ Day	No. Active Trees at Treatment	Verb used ml/ft^2	New Trees Attacked[1]	No. of Days	Trees Killed/ Day	% Growth Reduction
Verbenone+Fell All Fresh Attacks	AL-1	5.5 (14.0)	8	8	1.0	24	116.2	14 [a]	49	0.3	70.0
	AL-2	7.8 (19.8)	11	14	0.8	87	--	42 [c]	36	1.2	-33.3
	TX-61	7.7 (19.6)	11	14	0.8	34	24.5	0 [a]	40	0.0	100
	TX-100	6.9 (17.5)	11	6	1.8	60	33.1	20 [a]	41	0.5	72.3
	TX - 14	8.5 (21.6)	31	14	2.2	86	22.1	11 [b]	29	0.4	82.8
	TX - 27	8.7 (22.1)	13	18	0.7	40	22.0	1 [a]	29	0.03	95.7
	TX - 29	6.2 (15.7)	31	14	2.2	60	31.3	1 [a]	29	0.03	99.6
	Mean	9.2 (18.6)	16.6	12.6	1.4	55.9		12.7	36.1	0.35	69.6
Untreated Check	NC-2	8.7 (22.1)	4	7	0.6	43		1	41	0.02	
	GA-4	5.6 (14.2)	20	7	2.9	250		99	41	2.4	
	TX-29C	7.7 (19.6)				51		46	42	1.1	
	TX -31C	7.5 (19.1)				189		144	36	4.0	
	TX -32C	13.1 (33.3)				35		6	21	0.3	
	TX -33C	17.0 (43.2)				33		51	22	2.3	
	TX -34C	15.5 (39.4)				37		39	35	1.1	
	TX -36C	8.2 (20.9)				24		28	33	0.8	
	TX -38C	12.6 (32.0)				77		177	54	3.3	
	TX -312	7.2 (18.3)				222		197	32	6.2	
	TX -332	17.0 (43.2)				81		118	38	3.1	
	TX -342	15.7 (39.9)				57		67	32	2.1	
	TX ---C	14.3 (36.3)				23		0	32	0.0	
	Mean	11.5 (29.3)				86.3		74.8	35.3	2.1	

[1] [a] Total suppression (no new trees attacked beyond treated buffer during 6-week post-treatment period).

[b] Partial suppression (new trees attacked beyond treated buffer, yet infestation growth decreased by ≥ 50%).

[c] No suppression (new trees attacked beyond treated buffer and infestation growth decreased by < 50%).

[2] Mean values were calculated by summing % reduction for each infestation and dividing by the number of infestations.

not for the verbenone-plus-felling all active trees treatment ($F_{1,6} = 1.767$; $p = 0.232$) (Figure 1b).

Comparisons Among Different Verbenone Treatment Options in 1995

Two treatments were evaluated in 1995 were verbenone-only and verbenone-plus-fell all active trees. Verbenone-plus-fell fresh-attacks was not evaluated due to time constraints from trying to carry out enough replicates of the other two treatments. We determined it was more important to focus on the verbenone-only and verbenone-plus-fell all active trees treatments, and thus have two field-tested and efficacious treatments to carry into a technology transfer program. We evaluated verbenone-only in 20 sites, verbenone-plus-fell all active trees in 19 sites, and 8 check sites.

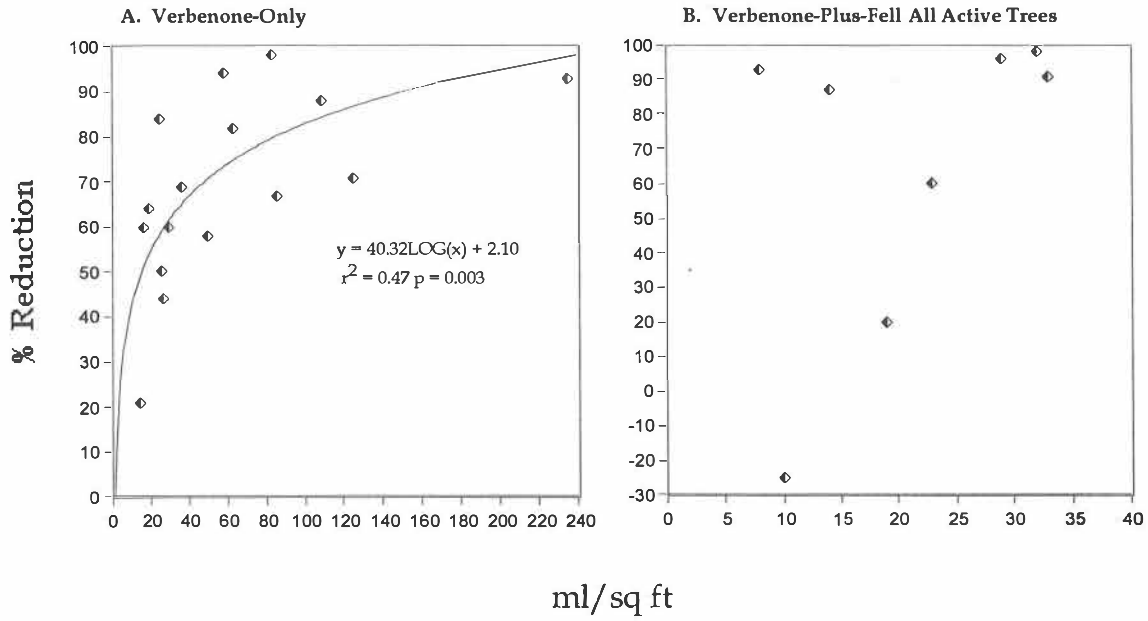

Figure 1. Relationship between verbenone application rate and percent reduction in infestation growth during the 6-week post-treatment monitoring period for treatments A. the verbenone-only and B. verbenone-plus-fell all active trees.

Standardized Verbenone Application Rates. Application rates of verbenone were increased for both verbenone-only and verbenone-plus-felling treatments for the 1995 season. The rates were modified from previous procedures (Billings et al. 1995) and based partially on data from Figure 1. Verbenone application rates were established to deliver 40 ml/ft^2 of basal area of actively infested trees for verbenone-only and 25 ml/ft^2 for verbenone-plus-felling all active trees (Table 3). Table 3 was designed to provide potential users with the number of bags required to treat infestations based on number of trees and mean tree diameter. Minimum buffer strip sizes of 12.2 m and three trees deep were used for verbenone-only and 7.6 m and two trees deep for verbenone-plus-felling all active trees. If the application rates listed above failed to meet the minimum buffer requirements, additional bags were added to treat all trees within the buffer. The number of bags attached to each tree ranged from 1 - 6, based on tree diameter size. The recommendations for bags/tree from VT/UGA section of Table 1 were used by all collaborators in 1995.

Results. *Verbenone-Only* - Infestation size averaged 42 trees, ranging from 15 - 88 trees at the time of treatment. Overall, infestation growth was reduced by 77% (Table 4). Not only was greater reduction (17%) observed in the eastern states when compared to data from 1994, was met in 14 of the infestations. In general, the data suggest the importance of a higher application rate.

Verbenone-Plus-Felling All Actively Infested Trees - Infestation growth rate was reduced 89% (Table 4). This was not significantly different from the verbenone-only treatment ($t_{0.05\,(2),\,37} = 1.99$; $p = 0.054$). Out of 19 infestations, 16 (84%) were completely

Check - Of the eight infestations used as controls, six expanded by > 1 tree/day (Table 4). Check infestations grew an average of 3.1 trees killed/day, versus 0.3 and 0.1 trees killed/day for verbenone-only and verbenone-plus-felling active trees treatments, respectively.

Table 3. Minimum number of verbenone bags recommended for treating southern pine beetle infestations for A. verbenone-only[1] and B. verbenone-plus-fell all active trees[2] in 1995.

A. Verbenone -Only (40 ml/ft^2)

Avg. d.b.h.	**Number of Actively Infested Trees**							
------------	**10**	**20**	**30**	**40**	**50**	**60**	**70**	**80**
6	50	50	50	63	79	95	110	126
8	50	56	84	112	140	168	196	224
10	50	88	131	175	218	262	306	349
12	63	126	189	252	315	377	440	503
14	86	171	257	342	428	513	599	684
16	112	224	335	447	559	670	782	894
18	142	283	424	566	707	848	990	1131
20	175	349	523	698	873	1047	1222	1396

[1] Number of bags = $(\text{mean d.b.h}/2)^2 * \text{no. active trees} * 0.1745$

B. Verbenone-Plus-Felling All Active Trees (25 ml/ft^2)

Avg. d.b.h.	**Number of Actively Infested Trees**											
------------	**10**	**20**	**30**	**40**	**50**	**60**	**70**	**80**	**90**	**100**	**110**	**120**
6	50	50	50	50	50	60	70	80	90	100	109	118
8	50	50	54	70	88	105	122	140	158	175	192	210
10	50	55	82	109	137	164	191	218	246	274	300	328
12	50	80	120	160	200	240	280	320	360	400	432	472
14	54	107	161	214	267	322	374	428	481	534	588	642
16	70	140	210	280	349	419	489	558	628	698	768	838
18	89	177	265	354	442	530	618	707	795	883	972	1061
20	109	218	327	436	545	654	763	872	981	1090	1200	1310

[2] Number of bags = $(\text{mean d.b.h}/2)^2 * \text{no. active trees} * 0.1091$

Table 4. Growth rates of southern pine beetle infestations before and after application of suppression treatments in 1995.

			Pre-treatment					Post-treatment			
Treatment	Infest. No.	Mean DBH inches (cm)	New Trees Attacked	No. of Days	Trees Killed/ Day	No. Active Trees at Treatment	Verb. used (ml/ft^2)	New Trees Attacked[1]	No. of Days	Trees Killed/ Day	% Growth Reduction
Verbenone Only	GA-1	5.2 (13.2)	27	14	1.9	35	86.2	29[a]	42	0.7	63
	GA-2	6.0 (15.2)	26	14	1.8	41	96.6	18[a]	42	0.4	78
	GA-5	7.6 (19.3)	8	7	1.1	27	58.9	19[c]	33	0.6	45
	AL-1	10.0 (25.4)	9	7	1.3	29	51.9	13[a]	42	0.3	77
	AL-2	6.0 (15.2)	18	7	2.6	64	48.6	27[a]	42	0.6	77
	AL-4	5.8 (14.7)	21	14	1.5	55	40.1	10[a]	42	0.2	87
	AL-5	8.6 (21.8)	19	7	2.7	63	25.6	13[a]	42	0.3	89
	MS-2	17.4 (44.2)	6	7	0.9	23	21.3	14[c]	29	0.5	44
	TX-1	9.6 (24.4)	8	11	0.7	41	54.9	7[a]	42	0.2	74
	TX-2	4.8 (12.2)	21	11	1.9	56	73.5	9[b]	42	0.2	87
	TX-3	6.9 (17.5)	20	6	3.3	71	42.3	9[a]	42	0.2	93
	TX-5	8.2 (20.8)	3	7	0.4	20	48.6	1[a]	42	0.02	95
	TX-6	8.2 (20.8)	4	7	0.6	17	48.2	3[a]	42	0.1	88
	TX-7	17.4 (44.2)	2	6	0.3	15	26.2	8[c]	22	0.4	25
	TX-8	18.3 (46.5)	7	11	0.6	29	33.5	12[a]	42	0.3	55
	TX-9	19.4 (49.3)	4	11	0.4	25	23.0	4[a]	42	0.1	72
	TX-10	8.0 (20.3)	12	8	1.5	48	43.2	2[a]	42	0.05	97
	TX-11	10.1 (25.7)	11	14	0.8	41	28.8	0[a]	42	0.0	100
	TX-12	6.8 (17.3)	12	7	1.7	27	67.4	0[a]	42	0.0	100
	TX-13	9.7 (24.6)	18	8	2.3	88	40.9	0[a]	42	0.0	100
	Mean	9.7 (24.6)	12.8	9.2	1.5	42.2	48.0	9.4	39.9	0.3	77.3[2]

Table 4 (Cont'd)

			Pre-treatment					Post-treatment			
Treatment	Infest. No.	Mean DBH inches (cm)	New Trees Attacked	No. of Days	Trees Killed/ Day	No. Active Trees at Treatment	Verb. used (ml/ft^2)	New Trees Attacked[1]	No. of Days	Trees Killed/ Day	% Growth Reduction
Verbenone + Fell All Actively Infested Trees	NC-1	8.1 (20.6)	11	7	1.6	35	25.6	0[a]	42	0.0	100
	NC-2	8.4 (21.3	23	7	3.3	122	22.3	21[a]	40	0.5	85
	NC-3	7.2 (18.3)	21	7	3.0	125	25.5	94[c]	40	2.4	20
	NC-4	8.5 (21.6)	32	7	4.6	122	23.6	38[b]	42	0.9	80
	NC-5	16.0 (40.6)	14	13	1.3	35	18.4	14[b]	42	0.3	77
	NC-8	8.9 (22.6)	6	5	1.2	52	23.1	0[a]	42	0.0	100
	NC-10	9.3 (23.6)	10	12	0.8	37	24	1[a]	42	0.02	98
	GA-3	6.3 (16.0)	17	14	1.2	48	27.4	0[a]	42	0.0	100
	GA-4	7.3 (18.5)	17	7	2.4	72	20.6	5[a]	42	0.1	95
	GA-6	7.2 (18.3)	12	7	1.7	58	49.1	0[a]	34	0.0	100
	AL-3	9.5 (24.1)	26	14	1.9	38	29.4	5[a]	42	0.1	95
	FL-1	9.4 (23.9)	18	7	2.6	81	24.4	24[a]	42	0.6	77
	FL-2	7.5 (19.1)	16	7	2.3	54	36.1	17[a]	41	0.4	83
	TX-14	11.1 (28.2)	2	8	0.3	30	29.4	0[a]	39	0.0	100
	TX-15	12.8 (32.5)	17	12	1.4	78	18.9	0[a]	42	0.0	100
	TX-16	11.0 (27.9)	20	18	1.1	46	26.4	0[a]	42	0.0	100
	TX-17	7.4 (18.8)	6	9	0.7	31	28.0	0[a]	41	0.0	100
	TX-18	7.4 (18.8)	6	9	0.7	41	28.5	0[a]	42	0.0	100
	TX-19	8.1 (20.6)	59	6	9.8	351	19.0	26[a]	42	0.6	94
	Mean	9.0 (22.9)	17.5	9.3	2.2	77	26.3	6	41	0.1	89.1

Table 4 (Cont'd)

			Pre-treatment					Post-treatment			
Treatment	Infest. No.	Mean DBH inches (cm)	New Trees Attacked	No. of Days	Trees Killed/ Day	No. Active Trees at Treatment	Verb. used (ml/ft^2)	New Trees Attacked[1]	No. of Days	Trees Killed/ Day	% Growth Reduction
Untreated Control	NC-6	13.0 (33.0)				73	-	179	42	4.3	-
	NC-7	10.0 (25.4)				158	-	230	42	4.3	-
	NC-9	10.8 (27.4)				85	-	306	40	7.7	-
	NC-12	10.8 (27.4)				88	-	78	48	1.5	-
	NC-13	12.3 (31.2)				38	-	19	42	0.5	-
	NC-14	9.6 (24.4)				79	-	31	14	2.2	-
	GA-8	11.5 (29.2)				27	-	85	42	2.0	-
	GA-10	6.4 (16.3)				18	-	24	28	0.9	-
	Mean	10.6 (26.9)				70.8		119	37.3	3.1	

[1] [a] Total suppression, no new trees attacked during the last two weeks of monitoring period.
[b] Partial suppression, infestation growth decreased by > 50%.
[c] No suppression

[2] Mean values were calculated by summing % reduction for each infestation and dividing by the number of infestations.

Conclusions and Future Needs

The inconsistency in the results observed between Texas and the eastern states in 1994, encouraged us to increase and standardize application rates of verbenone for both the verbenone-only and verbenone-plus-felling all active trees. These increased rates proved to be extremely effective for both treatments options in 1995. These revised rates in easy-to-use tables (Tables 3A & B) should enable forest land managers to treat SPB infestations without supervision. The verbenone-only treatment provides a control option in areas where felling timber is not permitted or desired (ie. precommercial stands, state parks or other protected areas). Where felling is a viable option, the verbenone-plus-felling treatment is an effective alternative to all felling treatments currently recommended and used. In general, it can be used in larger-sized infestations than the verbenone-only treatment, thus giving forest land managers more treatment options.

As these tactics approach operational status, there are still some technical issues that need to be addressed. One of the most important issues is the testing of a new verbenone bag. Currently the present bag elutes verbenone as soon as it is made and must be kept frozen prior to application. A new dispenser is being developed that will not release verbenone until it is attached to the tree. This will greatly ease shipping, storage, and handling of the bags.

Another issue we will consider is application height. Currently, verbenone is attached to trees 3-4m above ground on the tree bole. The rationale behind this is to position verbenone near the location on the bole where beetles first attack the tree (Dixon and Payne 1979). However, a special application tool, the Hundle Hammer, must be used to make this application. If the tactic can remain effective when attaching bags to the bole of the tree with a staple gun at arms reach, it will simplify the application procedure and reduce the application time. Promising results were obtained by the Texas Forest Service when they used this application approach for the verbenone-plus-felling treatment prior to 1994 (Billings unpublished data). Further tests of application height are planned.

The promising results obtained with the verbenone-plus-fell fresh-attacked trees in 1994 should merit further evaluation of this treatment. With standardized application rates of verbenone, there is no reason why this treatment could not be as effective and useful as the other two treatment options evaluated.

An issue currently being addressed is the registration of the verbenone bags with the U.S. Environmental Protection Agency (E.P.A.). The present status is that virtually all tests that have been requested have been conducted. Tests on immune response and an avian dietary study may still be requested. Once that issue is resolved, a registration package will be submitted for evaluation by E.P.A. (Steve Burke, Phero Tech, pers. commun.).

Lastly, the issue of technology transfer must be addressed. For the verbenone tactics to become accepted and used by foresters, efforts must be made to train foresters in their use and convince them that verbenone is a viable alternative to currently recommended SPB treatments. If the verbenone treatments are applied improperly, and as a result are ineffective, foresters may be reluctant to accept this new technology. Clark et al. (1997) address the issue of technology transfer for SPB in more detail.

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A user-friendly PC-based GIS for forest entomology: an attempt to combine existing software

MARIUS GILBERT

Laboratoire de Biologie animale et cellulaire, CP 160/12
Université Libre de Bruxelles, 50 av. F. D. Roosevelt, 1050 Brussels, Belgium

ABSTRACT We present a combination of existing software which should facilitate the use of GIS by forest entomologists. The use of existing GIS by ecologists who want to take advantage of the spatial component of their analyses is often hindered by the difficulty of use and cost of such tools. Moreover, it might be useful to have a system which can be carried to remote locations where access to a mainframe computer or powerful workstations is unavailable. It is now possible to have a good system running on a single personal computer due to the increasing power and the low cost of this type of hardware. We have gathered programs characterised by their simplicity, low cost, and performances. IDRISI is a simple and inexpensive GIS which has a simple file structure that allows the user to create his/her own analysis scripts with basic knowledge in computer science. VARIOWIN is a geostatistical package which performs exploratory variography and 2D modelling. SURFER is a surface mapping system able to create and to display grids using several methods of spatial interpolations including two dimensional anisotropic kriging. FRAGSTATS is a program which performs landscape analyses and finally, COREL DRAW is a vector-oriented package that can be used for output of both bitmap and vector output. These programs were not designed to work together and problems may occur due to the heterogeneous nature of the system. Conversion file difficulties were encountered and we were faced with the complexity of using different programs to perform one analysis sequence. An additional module is being developed to solve these problems and the whole system should be able to manage data, analyze their spatial component and display map output in a simple and user-friendly way.

KEY WORDS: GIS, Spatial analysis, geostatistics, software.

GEOGRAPHICAL INFORMATION SYSTEMS (GIS) are widely used in environmental management (Burrough 1993). In ecology and particularly in forest entomology they may be of considerable interest for the study of spatial pattern and insect spatial distribution (Liebhold et al. 1993, Coulson et al. 1993, Turner 1989). For example, the measurement of spatial dependence is essential in sampling methodology (Rossi et al. 1992, Legendre 1993, Fortin et al. 1989). Moreover, the interaction between insects and their environment always bears a spatial component (Borth and Hubert 1987, Hohn et al. 1993).

A GIS is a computer program designed to collect, retrieve, transform, display, and analyze spatial data. GIS can incorporate georeferenced data to produce maps or layers. Usually, a map layer or a theme is composed of only one type of data. GIS have the ability to import and manage data from different sources: mapped data, alphanumeric data, remotely sensed data. These types of data may then be combined to build a GIS database. Using this database, the user may create map outputs or display views relative to specific questions. These systems have recently improved their abilities to carry out spatial analyses integrating new built-in functions (spatial interpolation, spatial autocorrelation, overlay analysis, etc.). Furthermore, the user may create his own analysis functions with personal scripts.

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New GIS users often must choose between the performances of their system and the time that they will spend to be able to use it. Simple systems are easy to learn, but often lack integrated functions which obliges the user to write his/her own script to achieve specific goals.

Powerful systems are created for a diversity of purposes. They bear useful built-in functions, but users must become familiar with the whole GIS environment to use them properly. These powerful systems usually run on workstations. This type of hardware and associated software are expensive and demand knowledge of a new operating system environment. For example, the use of an important application software such ARC/INFO demands knowledge in the UNIX operating system, knowledge of the ARC/INFO file structure and topology, of the ARC/INFO high number of commands and of the AML (Arc Macro Language).

However, users who just want to take advantage of the spatial component of their data have different hardware and software requirements than users who are planning complete GIS research projects involving extensive data census. The first kind of users can not afford expensive systems to add a spatial analysis component to their ecological studies. This is why an inexpensive system working on a single PC might interest such users. Moreover, the increasing power of PCs makes GIS more and more efficient on this hardware. Finally, a system running on a single PC might be useful on the field or to remote locations where access to mainframe computer or powerful workstations is unavailable (Carver et al. 1995).

We present a combination of inexpensive and user-friendly PC-based software which should help potential users to integrate spatial components to their ecological studies.

System Presentation

First, information about existing software was collected, mostly on the Internet in Web pages. Additionally, user discussions available in newsgroups related to each software were followed.

The software applications were tested on a Pentium 90 MHz PC with 8 Mbytes of RAM, under the WINDOWS 95 operating system. ARC/INFO PC, MAPINFO and IDRISI have been tested for GIS functionality. VARIOWIN, Geostatistical Toolbox, Geo-EAS, FRAGSTATS and SURFER were tested as additional spatial analysis tools. These applications were first tested with external sample data and secondly with our own data. GIS were tested for their ability to create a new database, to manage it and especially to exchange data with other sources. Spatial analysis software were tested with the author's instructions.

The chosen combination of software is presented in figure 1. IDRISI for WINDOWS (Clark University, Eastman 1988, Cartwright 1991) is a raster GIS which includes vector-data management and display. It is highly user-friendly and bears a lot of built-in spatial analysis functions. Its very simple file structure facilitate the creation of new analysis scripts. IDRISI for Windows includes a database manager which allows users to relate geographic features to a database (DBase, Access, text files). We used it in our system because of its simple file structure in both vector and raster formats and its ability to import and export data in a large range of formats (raster or vector geographical data or database data). This software is very inexpensive and will be used as the central geographical data manager of our system.

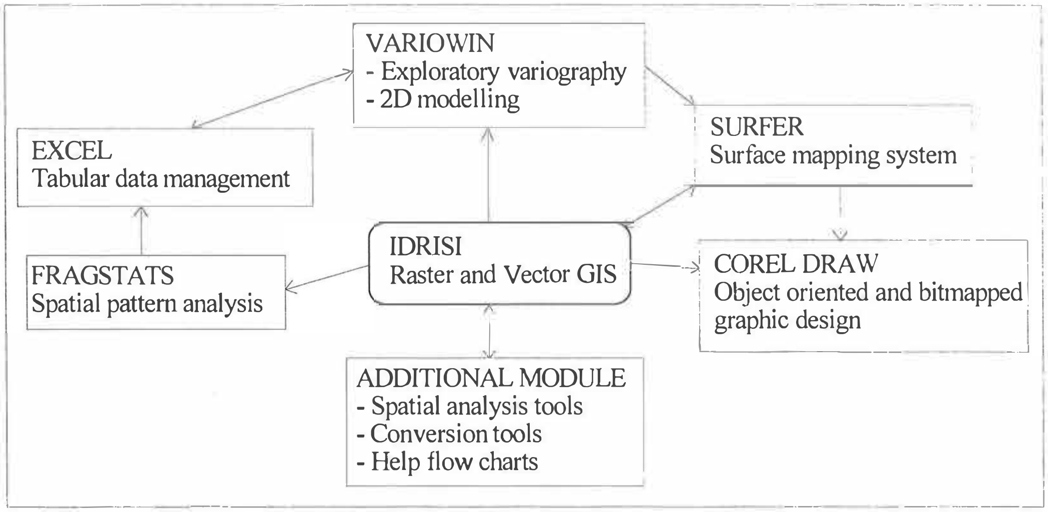

Figure 1: Structure of the system showing inputs and outputs between software.

VARIOWIN, written by Yvan Pannatier (University of Lausanne - Switzerland, Pannatier 1994) has been released with a manual (Pannatier 1996). Its aim is to compute geostatistical analyses and variogram modelling in 2D. There are three modules. The first creates a pair-comparison file on the basis of an ASCII file containing XY co-ordinates and attributes. The second module computes variogram surfaces, directional variograms, and a general variogram. It is also possible to estimate the semi-variogram with other estimators like the non-ergotic covariance or the non-ergotic correlogram which are often used in ecology (Sokal and Oden 1978(a), 1978(b), Johnson 1989). Moreover, the user may also create H-scaterplots and identify interactively potential outliers affecting the measure of spatial continuity. The last module offers an excellent tool to interactively model the semi-variogram.

SURFER (Golden Software, Inc.) is a surface mapping system designed to manage and display 3D raster-based data. Its first aim is to build surfaces by spatial interpolation on the basis of georeferenced data points. These interpolation methods include kriging but an input model created with another software has to be specified to perform it. The input and output files of VARIOWIN are fully compatible with the SURFER format and their combination has proved to be excellent to practice geostatistics. It is possible to export the interpolated grid in a format readable by IDRISI. The last version of SURFER has the capability to perform 2D anisotropic kriging with three nested structures.

FRAGSTATS is a DOS-based spatial analysis program for quantifying landscape structure written by K. McGarigal and B. J. Marks (Oregon State University). Landscape ecology involves the study of the landscape pattern which can be associated with other ecological characteristics, including vertebrate and invertebrate populations (Saunders *et al.* 1991, Turner 1989, Wiens *et al.* 1993). FRAGSTATS has been developed to quantify landscape structure by offering a comprehensive choice of landscape metrics. The PC version creates IDRISI raster-format files.

COREL DRAW (Corel Corporation) is a well known object-oriented vector and bitmapped graphic design software which is able to import and export in most of the graphic file formats. It is very flexible and can be efficiently used to manipulate and print map output.

EXCEL (Microsoft) is another well known software which is installed on many PCs. It may be used to manage input tabular data and output graphs and statistics.

Test With Our Own Data

This combination of software has been tested in two study cases. The aim of this test was to assess the system inadequacies in specific analyses and to list any problems encountered. These test studies concerned the spatial distribution of *Pulvinaria regalis* Canard in the city of Oxford (Speight et al. 1996) and *Dendroctonus micans* (Kug.) in the Massif central (unpublished). The use of the combined software in both cases is presented in Table 1. In both studies, IDRISI was used to manage the spatial data, VARIOWIN was used to calculate variograms, correlograms, correlogram surfaces, and for 2D isotropic and anisotropic modelling. SURFER was used to process kriging and to generate surfaces and map outputs. COREL DRAW was used to assemble the final map outputs. FRAGSTATS has not yet been tested with actual data.

Table 1: Use of the software for different stages of the study cases.

Software	***Pulvinaria regalis* in the city of Oxford**	***Dendroctonus micans* in the Massif Central**
EXCEL	Data encoding	Data encoding
	Exploratory Data Analysis	Exploratory Data Analysis
	Graph outputs	Print output of the correlogram
IDRISI	Database construction	Database construction
	Plotting of the samples on a map	Plotting of the samples on a map
	Quadrat analysis	Quadrat analysis
	Moving-Windows analysis	Moving-Windows analysis
SURFER	Print output of the correlogram surface	Isotropic 2D ordinary kriging
	Anisotropic 2D kriging	Creation of a Digital elevation model
	Map output of the density distribution	Map output of the density distribution
VARIOWIN	Creation of a Pair Comparison File	Creation of a Pair Comparison File
	Semi-variogram and semi-variogram surfaces	Semi-variogram and semi-variogram surfaces
	2D anisotropic semi-variogram modelling	2D isotropic semi-variogram modelling
COREL DRAW	Digitizing streets contour lines	Map output of the sample points
	Map output of the samples points	Digitizing forest stands contour lines
		Digitizing altitude contour lines

Results And Discussion

The use of this combination of software is very easy to learn and use. The interactivity of the exploratory variography performed with VARIOWIN is an excellent method for becoming familiar with the basics of geostatistics and is highly recommended to beginners. The kriging function of SURFER is elementary and other software must be used to perform other types of kriging (Varekamp *et. al.* 1996). Moreover, the user must take care not to use the kriging function of SURFER as a black-box tool; users should be aware of the hypotheses and assumptions involved in a kriging process (Isaaks and Srivastava 1989). The surface-management and the map-output abilities of SURFER are highly complementary to a

GIS such as IDRISI. FRAGSTATS has not been tested with our data but its use with data with the software provided is very easy. EXCEL and COREL DRAW are well known software and we do not need to comment on them. Taken as a whole, the system met all the requirements of these two case studies and we plan to carry on with almost the same configuration for further studies. The proposed combination of software allowed us to perform file input, data management, spatial analyses and map outputs.

However, considerable time was spent to solve computing problems. Basically, problems were caused by the fact that these applications were not designed to work together. First, some spatial analyses are not covered by this software combination. For example, a simple quadrat analysis might be used to determine whether sample spatial distribution is aggregative or not (Myers 1978). Second, the file formats used by the software are often different and conversion may involve a very detailed knowledge of the different software file structures. Fortunately, IDRISI allows the conversion of data from/to a wide range of formats. However we had problems even with the proper tools. For example, the missing data value used in the *.grd files used by VARIOWIN is not the same in the *.grd SURFER files (these files are described as having the same format). The grid files used by SURFER are binary files and must be first converted to ASCII files to be converted to IDRISI files. These problems are not serious if they can be easily identified, but they may otherwise cause important time losses. Sometimes, the automatic data transformations were not possible and we had to proceed manually within a text file. Third, due to the modular and heterogeneous structure of our system, we had to use different software to carry out an analysis sequence. For example, a basic geostatistical analysis involves exploratory data analysis (Tukey 1977) which can be computed with EXCEL, map output of the samples created with IDRISI, moving-windows analysis to detect sample-point aggregation and proportional effects calculated with separated programs (not included in the IDRISI analyses scripts), calculation of the estimated semi-variogram and its modeling carried out with VARIOWIN, and finally ordinary kriging processed with SURFER. This sequential analysis procedure was split into different small procedures within each software, with its own file input and output characteristics. Without an excellent knowledge of each software use and limitations, much time may be wasted.

To meet these problems, we plan to write scripts in Visual Basic gathered in one new additional module. First, they compute spatial analyses which are not covered by the other software (e.g. quadrat and moving-windows analyses). Second, to simplify the file conversions, we will write flow charts indicating steps to convert files. These flow charts should underline sensitive steps (e.g. replacement of one no-data value by another). If a file-conversion tool does not exist in the software combination, we plan to write it. Finally, we plan to write flow charts for typical spatial analysis procedures. These flow charts will be designed to help users to know how and where they can perform a given analysis. This additional module (figure 1) should complement the system in a user-friendly way: the additional tools will complement the existing software, conversion procedures and the flow charts should reduce the wasted time needed to become familiar with all the individual programs.

Varekamp et al. (1996) showed that it was possible to perform a wide range of geostatistical procedure with public-domain software available on the Internet (Englund and Sparks 1988, Pebesma 1993, Deutsch and Journel 1992). Their system is based on the use of

DOS executable programs or FORTRAN routines which provide more geostatistical analysis functions than our system. We have chosen to focus on user-friendly and basic software. The kriging abilities of SURFER are limited, but if a user wants to do more than two dimensional ordinary kriging, he can refer to other more powerful software (e.g. GSLIB) which is more complex and involves a better knowledge of spatial interpolation methods used in geostatistics. However, we insist on the fact that VARIOWIN is excellent for users to perform basic explorative and interactive variography and can be highly suggested for beginners users with geostatistics. Carver et. al. (1995) showed the advantages of having a GIS like IDRISI installed on a portable PC for expedition fieldwork (i.e. ability to develop sampling strategy as a result of immediate data visualisation). Additional spatial analysis modules enhance these advantages by a direct spatial analysis treatment of the data. For example, a strong spatial discontinuity in a species spatial distribution or a detection of data outliers might reveal interesting local environmental discontinuities. Such discontinuities detected afterwards are difficult to explain or interpret. Such fieldwork use of the GIS might then be of a considerable interest.

Our system is basically designed for beginners in GIS and geostatistics, but we believe that even experienced users will find interest in a portable and inexpensive system which allows small budget projects. Moreover, experienced users may use the same combination of software as a base which can be supplemented with additional software whenever they reach limitations. The flexible structure of the system and the simple file structure used should facilitate the integration of additional modules.

Conclusion

Taken as a whole, this system could be used as a reliable, portable, and inexpensive PC-based GIS and spatial analysis tool. Problems due to the heterogeneous nature of the system have been encountered but they can be solved easily by a good knowledge of each software characteristics. An additional module should facilitate the use of this system by beginners. The flexible and simple structure of the system will facilitate the integration of additional modules by experienced users interested in different aspects of spatial analysis.

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Tomicus piniperda in North America: An Integrated Response to a New Exotic Scolytid

ROBERT A. HAACK[1], ROBERT K. LAWRENCE[1], DEBORAH G. McCULLOUGH[2], AND CLIFFORD S. SADOF[3]

[1]US Department of Agriculture, Forest Service, North Central Forest Experiment Station,
East Lansing, Michigan 48823, USA.
[2]Michigan State University, Department of Entomology, Natural Science Building, East Lansing, Michigan 48824, USA.
[3]Purdue University, Department of Entomology, West Lafayette, Indiana, 47907, USA

ABSTRACT The pine shoot beetle [*Tomicus piniperda* (L.); Coleoptera: Scolytidae] was first discovered in North America in Ohio in 1992. As of 1 October 1996, it was found in 186 counties in 8 US states (Illinois, Indiana, Maryland, Michigan, New York, Ohio, Pennsylvania, and West Virginia) and in 17 counties in 1 Canadian province (Ontario). A federal quarantine imposed in November 1992 regulates movement of pine (*Pinus*) trees and logs from infested to uninfested areas. This paper summarizes information on the discovery of *T. piniperda* in North America, early survey efforts, recent interception history, development and changes in the federal quarantine, research efforts, development of a national compliance management program, and current efforts to evaluate the clerid *Thanasimus formicarius* (L.) for possible release as a classical biological control agent in the US.

KEY WORDS *Tomicus piniperda, Scolytidae, Thanasimus formicarius, Cleridae, Pinus,* exotic insect, biological control, regulatory entomology, quarantine.

THE PINE SHOOT beetle [*Tomicus piniperda* (L.); Coleoptera: Scolytidae] was discovered in Ohio in July 1992. As of October 1996, established populations of this beetle have been found in eight states in the United States and in one Canadian province (Table 1, Fig. 1). This exotic scolytid likely arrived in the Great Lakes region on one or more cargo ships that carried infested crating or dunnage (wood braces). DNA analyses suggest that there were at least two separate introductions: the first in Ohio and a more recent introduction in Illinois (Carter et al. 1996).

The Great Lakes region of North America is a highly suitable location for an insect such as *T. piniperda* (Niemela and Mattson 1996), given the region's temperate climate and widespread occurrence of pine (*Pinus* spp.) forests, Christmas tree plantations, and nurseries. Considering only the Christmas tree industry, over 10 million trees are cut and sold annually in the Great Lakes region, and of these about 75% are Scotch pine (*Pinus sylvestris* L.) (Dr. Melvin R. Koelling, Michigan State University, pers. comm.). Pine Christmas tree plantations are especially suitable for a univoltine, early spring-flying bark beetle like *T. piniperda*, because breeding material (e.g., pine stumps and slash) is created each autumn and there is ready supply of shoots for maturation feeding.

Considering the potential damage that this bark beetle could cause, the US Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) imposed a quarantine to regulate the movement of pine from regulated (infested) counties to unregulated (uninfested) counties within the US (USDA APHIS 1992). This paper discusses the history of *T. piniperda* in North America, including its discovery, survey, interception history, quarantine issues, research

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programs, development of a national compliance management program, and classical biological control efforts.

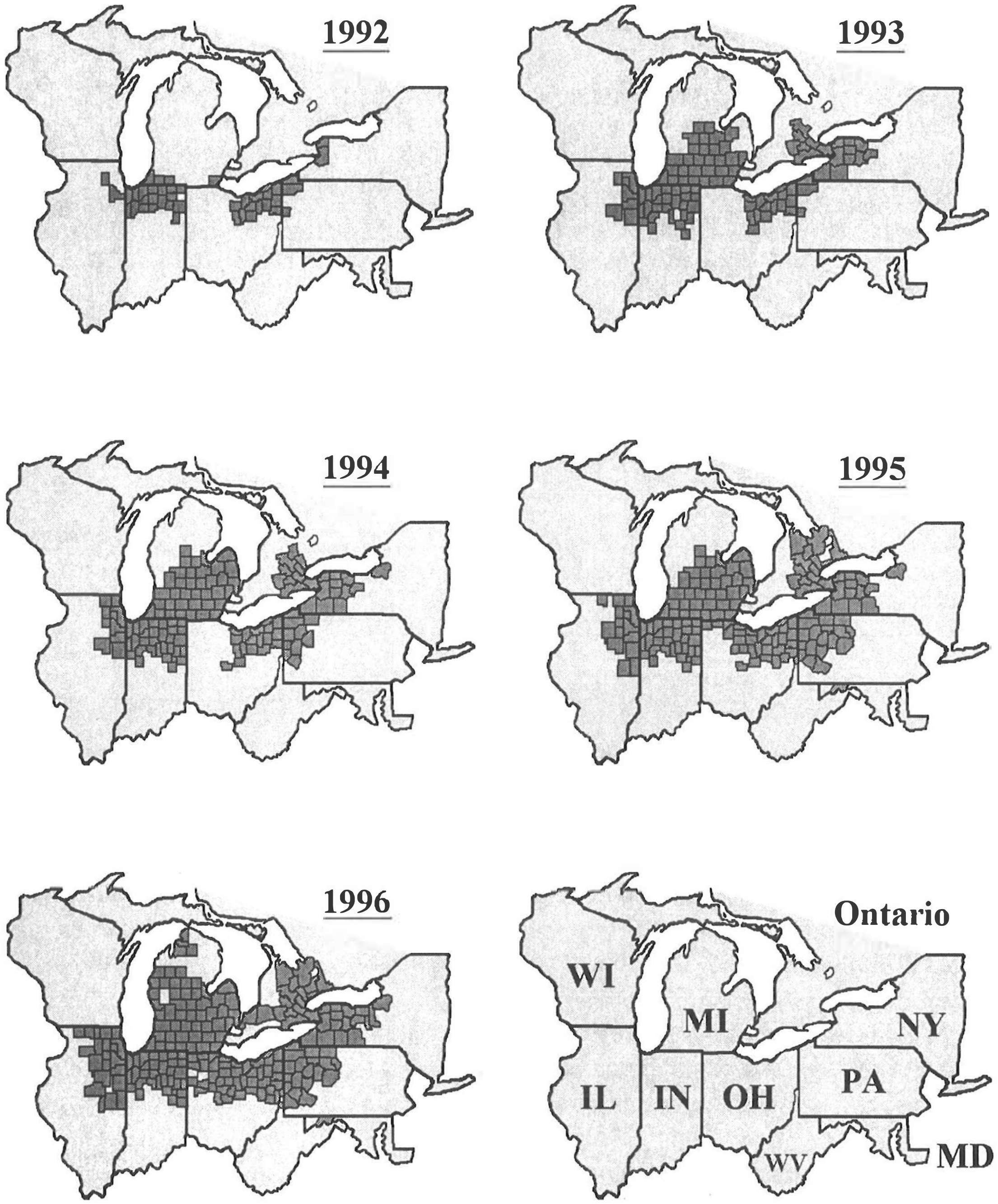

Fig. 1. Known distribution of *T. piniperda*-infested counties in North America from 1992 through 1 October 1996 (Source: USDA APHIS and Agriculture Canada). State abbreviations are: IL = Illinois, IN = Indiana, MD = Maryland, MI = Michigan, NY = New York, OH = Ohio, PA = Pennsylvania, WI = Wisconsin, and WV = West Virginia.

Table 1. Historical information for the discovery of *T. piniperda* in North America, including for each state or province the year when *T. piniperda* was first found, and the cumulative number of quarantined counties by year.

State or Province	Year of initial discovery	Cumulative number of positive counties by year 1992	1993	1994	1995	1996
Illinois	1992	2	7	10	15	21
Indiana	1992	18	26	31	31	32
Michigan	1992	4	30	37	37	52
Ohio	1992	14	16	18	31	43
New York	1992	2	10	12	13	16
Pennsylvania	1992	3	3	10	18	19
Maryland	1995	0	0	0	1	1
West Virginia	1995	0	0	0	1	2
US county totals		43	92	118	147	186
Ontario	1993		7	10	14	17

Initial Discovery and Survey Efforts

Specimens of an unknown scolytid were collected in a Christmas tree plantation in Lorain County, Ohio, near the port city of Cleveland on 1 July 1992. These beetles were delivered to Dr. David Nielsen for identification at Ohio State University. Not recognizing the beetles, he mailed the specimens to Dr. Stephen Wood, Brigham Young University, on 9 July 1992. Dr. Wood identified the beetles as *Tomicus piniperda* (L.) in a letter dated 16 July 1992. After receiving the letter, Dr. Nielsen informed the APHIS office in Ohio on 22 July 1992, which in turn notified its headquarters office near Washington, DC, that same day. Additional specimens of *T. piniperda* were collected from the original site and one additional site in Lorain County on 23 July 1992. Likewise, on 23 July 1992 in Washington, APHIS established a "New Pest Advisory Committee" to evaluate the potential pest status of this insect and options for quarantine and control. On 24 July 1992, USDA APHIS electronically notified regulatory and extension agencies throughout the US about the presence of *T. piniperda* in Ohio.

A great flurry of activity soon followed this announcement. Dozens of Ohio Christmas tree plantations and nurseries were inspected. Several training sessions were held in Ohio for APHIS inspectors and forest health specialists from nearby states to see the beetle and its associated damage. Regulatory personnel began to inspect Christmas trees and nurseries in surrounding states, and within one month of the initial USDA announcement, five new states reported finding *T. piniperda*: Indiana on 4 August, Pennsylvania on 13 August, Michigan on 14 August, New York on 20 August, and Illinois on 21 August 1992.

The fact that *T. piniperda* was found in six states during a 4-week period in 1992 strongly suggests that this scolytid had been in the US for several years before its discovery. One likely reason for the presumed delay in discovering *T. piniperda* is that it causes shoot damage that appears similar to that caused by several native insects and diseases, and thus the shoot damage associated with *T. piniperda* caused no special alarm. The current Great Lakes populations of *T. piniperda* probably became established in the 1980s given that scolytids surveys in Indiana (Deyrup 1981, Deyrup and Atkinson 1987) and Michigan (Dr. Lawrence R. Kirkendall, University of Bergen, pers. comm.) during the late 1970s and early 1980s did not detect *T. piniperda.* The earliest record of *T. piniperda* in a private insect collection from the Great Lakes region is a single adult collected in 1991 by Ronald Priest from a shoot on eastern white pine, *Pinus strobus* L., in Ingham County, Michigan; this beetle was first identified in 1993.

By the end of 1992, *T. piniperda* had been found in 43 counties in the 6 states of Illinois, Indiana, Michigan, Ohio, Pennsylvania, and New York (Table 1, Fig. 1). Surveys during 1993 and 1994 found several new infested counties but no new infested states. In April 1995, two new US states were added: Maryland and West Virginia. The first infested counties in Canada were found in the province of Ontario in 1993. As of 1 October 1996, *T. piniperda* was known to occur in 186 counties in 8 US states and in 17 counties in 1 Canadian province (Table 1, Fig. 1). When explaining the rapid increase in the number of infested US counties, it is important to consider both natural spread by dispersing adults as well as more intensive surveying by regulatory officials.

Most surveys for *T. piniperda* have been conducted in late summer or early fall (August-October) and have focused on locating damaged shoots. In more recent years, surveys have also been aimed at the initial spring flight of parent adults, using trap logs and traps baited with alpha-pinene. The largest survey effort that used trap logs was conducted by the state of Michigan during the years 1994-1996 in which all unregulated counties in Michigan's lower peninsula were trapped; over 300 trapping locations were monitored in 1994 (Haack and Lawrence 1994).

Table 2. Number of *T. piniperda* interceptions on wood products (e.g., dunnage, crates, and pallets) at US ports of entry during 1985-1995 by country of origin. (Source: USDA APHIS)

Interceptions		Interceptions		Interceptions	
No.	Country	No.	Country	No.	Country.
28	France	7	Europe*	1	Finland
19	United Kingdom	3	Netherlands	1	Greece
13	Italy	3	Russia	1	Hong Kong
12	Spain	2	Japan	1	Portugal
8	Belgium	2	Unknown	1	Sweden
8	Germany	1	China	1	Switzerland

*These seven interceptions were on cargo that originated in Europe, but no individual country could be identified.

Table 3. The 10 most commonly intercepted scolytids on wood products (e.g., dunnage, crates, and pallets) at US ports of entry during 1985-1995, including number of interceptions, number of countries of origin, and the five countries accountable for shipping the most infested material, in decreasing order (Source: USDA APHIS)

Insect species	No of interceptions	No. of countries of origin	Top five countries of origin
Pityogenes chalcographus	409	24	Germany, Italy, Belgium, Russia, Spain
Orthotomicus erosus	337	18	Spain, Italy, China, Portugal, France
Hylurgops palliatus	229	18	Germany Belgium United Kingdom Italy France
Ips typographus	182	19	Italy, Germany, Russia, Belgium, Francc
Hylurgus ligniperda	151	12	Italy, Portugal, Spain, Chile, France
Ips sexdentatus	125	10	Italy, Spain, France, Belgium, Portugal
Tomicus piniperda	112	16	France, United Kingdom, Italy, Spain, Belgium
Hylastes ater	40	8	Spain, Germany, United Kingdom, France, Italy
Polygraphus poligraphus	33	7	Italy, Germany, Belgium, Russia, France
Pityogenes bistridentatus	30	6	Spain, Italy, France, Israel, United Kingdom

Recent Interception History

It is not surprising that *T. piniperda* became established in North America, considering that it is commonly intercepted at US ports of entry on wood products such as dunnage, crates, and pallets. For example, during the 11-year period 1985-1995, *T. piniperda* was intercepted 112 times on cargo arriving from at least 16 different countries (Table 2). Overall, *T. piniperda* was the seventh most commonly intercepted scolytid on wood products at US ports during 1985-1995 (Table 3). *Tomicus piniperda* has been intercepted at ports throughout the US, from San Francisco, California, in the west to Brooklyn, New York, in the east, and from Miami, Florida, in the south to Duluth, Minnesota, in the north. The top five US ports for *T. piniperda* interceptions are, in decreasing order: Toledo, Ohio; New Orleans, Louisiana; Houston, Texas; Detroit, Michigan; and Miami, Florida. Overall, more than 40% of all *T. piniperda* interceptions in the US since 1985 have been at port cities on the Great Lakes. Hopefully the recent regulatory changes dealing with the import of logs, lumber, pallets, and other solid wood packing material will reduce the number of interceptions (USDA APHIS 1995a, 1995b).

Quarantine History

On 19 November 1992 a federal quarantine was imposed by APHIS on the movement of pine material from regulated (infested) counties to unregulated (uninfested) counties within the US (USDA APHIS 1992). The original quarantine affected movement of pine, spruce (*Picea*), fir (*Abies*), and larch (*Larix*) logs or lumber with bark attached, pine Christmas trees, and pine nursery stock. Regulated articles could be moved to areas outside the quarantine zone, but only after certain conditions were met (see below).

To many pine producers within the infested region of the US, especially within the Christmas tree industry, the federal quarantine came as a relief because it established one set of rules for the entire country. Up to that time, each state was able to declare its own separate quarantine, using its own set of conditions. For example, before the federal quarantine, seven individual US states had imposed their own state quarantines: Florida, Georgia, Kansas, Louisiana, North Carolina, Oregon, and West Virginia. The first state quarantine was imposed by North Carolina on 28 September 1992. The seven state quarantines ranged from being relatively flexible (e.g., Florida and North Carolina) in which regulated articles could be imported after passing a visual inspection and being declared free of *T. piniperda*, to relatively restrictive (e.g., Kansas) in which no regulated articles were allowed at all.

Since the original federal quarantine was imposed in November 1992, it has undergone several modifications (see below). These changes were based on new research findings from studies conducted in the US and on expert opinion from two European forest entomologists -- Dr. Alf Bakke of Norway and Dr. Bo Langstrom of Sweden -- who were consulted by USDA APHIS

Research Efforts

A large research effort on *T. piniperda* has been underway in the US since 1992. Research funding has come largely from APHIS and USDA Forest Service, but many other state, private, and professional organizations have contributed time and funding. These studies have involved various aspects of *T. piniperda* biology and management. Although most studies have not yet been formally published, early results have always been made available to APHIS so that the federal quarantine could be modified as needed. The bulk of the university research within the US has been conducted at Michigan State University, Ohio State University, Purdue University, State University of New York-Syracuse, University of Georgia, and University of Wisconsin-Madison. Some of the refereed publications on *T. piniperda* in the US have dealt with timing of initial spring flight (Haack and Lawrence 1995b), influence of pine felling date on colonization by *T. piniperda* and native *Ips* bark beetles (Haack and Lawrence 1995a), shoot feeding in native pines (Lawrence and Haack 1995, Sadof et al. 1994), foliar chemical control (McCullough and Smitley 1995), and DNA analysis of various *T. piniperda* populations (Carter et al. 1996). Many other papers have now been submitted or are in preparation.

Development of a National Compliance Program

After the 1992 federal quarantine was published, many state, federal, and industrial organizations began to seek changes in the quarantine that would ease the regulatory restrictions on the affected pine industries but still minimize the risk of accidental spread of *T. piniperda* to uninfested regions of the US. The three major industries affected by the quarantine include the forest, Christmas tree, and nursery industries.

The forest industry. As originally written in November 1992 (USDA APHIS 1992), the federal quarantine affected movement of logs and lumber with bark from all species of pine, spruce, fir, and larch. Moreover, the original ruling required that all regulated logs and lumber be either debarked or fumigated with methyl bromide before being transported to unregulated areas. Neither of these regulations were acceptable to the industry, so transport of logs from regulated to unregulated areas basically stopped. However, in 1993, two important changes were made to the federal quarantine. The first change exempted spruce, fir, and larch logs from regulation, because it was felt that these species were not primary hosts for *T. piniperda* reproduction and overwintering. The second change allowed for free movement of pine logs and lumber with bark if these trees were felled during July through October and if all branches and foliage were removed and left at the harvest site. This change was made because *T. piniperda* primarily feeds in shoots during these 4 months. Therefore, if all branches and foliage were left behind there would be relatively little risk of transporting *T. piniperda* to uninfested areas.

Although the forest industry favored the above changes, it requested additional easing of the regulations that affected log transport during November through June. As a result, meetings were held in both Michigan and Washington, DC, to explore possible modifications. Although much progress was made, no formal changes have yet been published in the Federal Register as of October 1996. Nevertheless, one possible scenario for moving logs with bark from regulated to unregulated areas within the US is as follows:

July 1 to September 30. Newly harvested pine logs (with no attached foliage) can be moved freely.

October 1 to February 14. Newly harvested pine logs can be moved to an approved facility (e.g., sawmill) if all slabs or bark from these logs are treated or destroyed before February 14 or within 4 weeks of felling.

February 15 to June 30. Newly harvested pine logs can be moved to an approved facility if all slabs or bark from these logs are treated or destroyed within 4 weeks of felling.

Record Keeping. Facility managers must keep records that pertain to the origin, date of felling, and date of milling for all pine logs that they receive from regulated areas. Similarly, managers must record the date on which all slabs or bark are treated or destroyed. Managers must allow regulatory officials to inspect their facilities and their records at any time.

The Christmas tree and nursery industries. In the original 1992 federal quarantine, Christmas tree managers were given the option either to have a certain number of trees inspected in each field scheduled for harvest or to subject the trees to an approved cold treatment or methyl bromide treatment before moving them to unregulated area. Under the inspection option for Christmas trees, evidence of a single *T. piniperda* beetle or a single attacked shoot was sufficient to cause rejection of all trees from that particular field. Because of the added costs of the cold or fumigation treatments and their potential harm to the foliage, almost all managers chose the inspection option. In both the Christmas tree and nursery industries, inspections were usually conducted a few weeks before shipping. Such timing was especially worrisome to Christmas tree managers. Many Christmas tree producers sign contracts with buyers during June and July, but their trees were not inspected usually until October. Therefore, even a single damaged shoot could result in serious economic losses for large wholesale Christmas tree producers. Overall, no major changes have been made to the original federal quarantine that pertain specifically to the Christmas tree industry.

As for the nursery industry, the original 1992 quarantine did not allow pine nursery stock to be moved to unregulated areas unless it was less than 24 inches (60 cm) tall (USDA APHIS 1992). However, in 1993, the quarantine was changed to allow pine nursery stock from regulated areas to move freely if it was either (1) less than 36 inches (90 cm) tall or less than 1 inch (2.5 cm) in stem diameter at the ground line, (2) subjected to 100% inspection and found free of *T. piniperda*, or (3) subjected to an approved cold treatment. Under the inspection option, infested trees could be rejected on an individual basis.

Given the above situation, it is understandable that the Christmas tree and nursery industries continued to request further modifications to the federal quarantine. In response to these requests, a research program to develop a national *T. piniperda* compliance management program was initiated in 1994. After a series of experiments, field trials, meetings, and approval by the National Plant Board this program was released for public comment in August 1996 (USDA APHIS 1996). This document is also available on the internet (http://www.ceris.purdue.edu:80/napis/pests/psb/index.html). Program guidelines will be modified as new information becomes available. Briefly, the major change made by this program is to allow growers in regulated areas to ship their trees to unregulated areas without inspection by regulatory agents if they agree to and follow a set of management guidelines. The rationale for this program is that if all pest management steps are followed, then the resulting *T. piniperda* population will be very low or undetectable. Therefore, shipping these trees will pose only a minimal risk of introducing *T. piniperda* into new areas.

Although there are several differences between the programs developed for the Christmas tree and nursery industries, they have many components in common (USDA APHIS 1996). For example, both programs will require (1) sanitation of all potential brood material by a specified date in spring, (2) monitoring of spring adult populations with the use of trap logs or traps baited with alpha-pinene, (3) chemical applications to foliage, trunks, or stumps when specified conditions are met, (4) monitoring trees for evidence of *T. piniperda* shoot feeding, and (5) record keeping of all pertinent information. The dates specified for field activities such as putting out traps or trap logs in spring will vary by state. In addition, managers must allow regulatory officials to inspect their trees and records at any time. To help this new program succeed, university extension specialists and state regulatory officials will (1) train growers in monitoring techniques and identifying beetles, (2) establish compliance agreements with producers and monitor their fields and records, and (3) establish a computerized master list of all cooperating producers that will be available on the internet. Educational materials and programs will be provided to producers, shippers, and buyers of these regulated products (McCullough and Sadof 1996). This program should be operational in 1997.

Biological Control Efforts

Classical biological control is being considered as part of the overall regional suppression program for *T. piniperda* in the US (USDA APHIS 1996). The main objective is to establish biocontrol agents that will reduce *T. piniperda* populations in forested areas of the US where active pest suppression using cultural and chemical controls is not practical or economical. In most years in the Great Lakes region, *T. piniperda* initiates host colonization 4-8 weeks before any competition from native pine-infesting bark beetles and their associated natural enemies (Haack and Lawrence 1995a, 1995b). As a result, entomologists looked to Europe and Asia for natural enemies that were better synchronized with the early spring flight of *T. piniperda*. After reading the literature and consulting with several European and Asian forest entomologists, there was general consensus that the clerid *Thanasimus formicarius* (L.) was the best candidate because (1) its spring flight closely matches that of *T. piniperda*, and (2) it causes high levels of *T. piniperda* mortality. In addition, species of rhizophagid beetles in the genus *Rhizophagus* were considered to be the next most important mortality agents of *T. piniperda*.

A cooperative effort was initiated in 1995 among three USDA agencies -- APHIS, Forest Service, and Agricultural Research Service (ARS) -- to evaluate *T. formicarius* for possible release in the US. Briefly, under the direction of Dr. Richard Dysart at the ARS European Biological Control Laboratory in Montpellier, France, several thousand *T. formicarius* adults were collected in 1995 and 1996 in France and shipped to Dr. Larry Ertle at the ARS quarantine facility in Newark, Delaware. These adults or their progeny were later shipped to Dr. David Prokrym at the APHIS biological control laboratory in Niles, Michigan, where various rearing techniques were developed. In 1996, several hundred *T. formicarius* eggs were shipped to the Forest Service laboratory on the Michigan State University campus to study potential non-target impacts of *T. formicarius* on the native clerid *Thanasimus dubius* (F.).

In September 1996, state officials from the *T. piniperda*-infested states who are responsible for approving the release of exotic natural enemies within their states' borders voted to postpone any release of *T. formicarius* until 1998 at the earliest. The main reasons for this vote were (1) *T. piniperda* has not yet caused significant levels of damage in the US to justify the release of an exotic predator, and (2) there is insufficient information available on the potential non-target impacts from such a release. Concern was raised that because *T. formicarius* is a "general predator" its release could destabilize the normal balance between native conifer-infesting bark beetles and their natural enemies, resulting in greater outbreak frequency of native bark beetles. In addition, some felt that *T. formicarius* could competitively displace certain native natural enemies and thereby upset native biodiversity. Perhaps in 1998, after more information has accumulated on the damage caused by *T. piniperda* in forested areas of the US and on the degree of non-target impacts to be expected, *T. formicarius* will be reconsidered for release.

Summary

The repercussions of a newly introduced exotic organism cannot be easily predicted. Their impact can range from no apparent change to dramatically altered forest ecosystems. In North America, although *T. piniperda* has not caused any widespread negative growth impact on native forests so far, federal quarantines have been implemented in both Canada and the US to slow the spread of this beetle. These quarantines have greatly altered normal trading relations and have had major economic impacts in the affected pine industries. Both national and international trade has been affected by the arrival of *T. piniperda*, especially among the countries of Canada, Mexico, and the US. The national *T. piniperda* compliance management program is a bold step towards reducing the regulatory burden on the affected pine industries while still minimizing the risk of spreading *T. piniperda* to uninfested areas. This program will serve as a model for dealing with future exotic pests that will undoubtedly arrive on our shores.

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Preliminary Investigations On The Relationships Between Phloem Phenolic Content Of Scots Pine And Maturation Feeding Of The Pine Weevil *Hylobius Abietis*

FRANÇOIS LIEUTIER, JACQUES GARCIA, ANNIE YART, LAETITIA GERAUD,
CLAUDE-BERNARD MALPHETTES[1] AND PAUL ROMARY

INRA, Station de Zoologie Forestière, Ardon, 45160 Olivet, France
[1]CEMAGREF, Domaine des Barres, 45290 Nogent-sur-Vernisson, France

ABSTRACT The phloem phenolic content of 5 Scots pine clones was analysed in the branches of 3 trees per clone. Five emerging beetles were encaged in one branch per tree and the damage were estimated 2 weeks later by measuring the area of removed bark. Phloem phenol content was analysed in another branch of the same trees. Clones were clearly separated from each other by their phenol content, but not by weevil damage. However, a significant negative correlation was found between the concentration of an acetophenone glycoside and weevil damage.

KEY WORDS *Hylobius abietis, Pinus sylvestris,* soluble phenols, maturation feeding, clonal variability

THE PINE WEEVIL *Hylobius abietis* L. causes heavy damage to young seedlings in coniferous plantations throughout Europe (Coutin 1984; Langstrom 1985; Ward 1988; Heritage et al. 1989; Sundkvist 1994). During adult maturation, it feeds on the bark of small branches and shoots, thus leading to the death of the attacked seedlings. All conifer species can be attacked, but almost nothing is known about the intra-specific variability of tree's susceptibility to attacks, especially in relation to host's secondary metabolites (Selander & Kalo 1979). The present paper reports a preliminary assay aiming at determining if phloem phenolic content of Scots pine branches can be related to resistance to pine weevil feeding.

Materials and Methods

The experiment was carried out with ramets of 5 Scots pine clones. The trees, which were grafted in 1982, originated from the natural provenance of Taborz (Poland) and were cultivated in the nursery of INRA (Cadouin, Dordogne, France). The beetles were obtained from Scots pine brood logs attacked in the field (Forest of Orléans, France) in May-June the year before the experiment and stored at 5°C from August until the beginning of the experiment. The logs were then placed at 25°C and emerging beetles were collected.

In early June 1996; 3 ramets per clone were submitted to weevil feeding. Five beetles were encaged with the distal 50 cm of one branch per ramet. Two weeks later, the encaged branches were cut from the trees, the weevils were removed, and the percentage area of consumed bark was measured on the main axis and the lateral axes. The same day, one 15 cm long sample of branch was cut from the main axis of a neighbouring branch in each

Pages 73-79 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

ramet, freezed in the field in liquid nitrogen, then freeze-dried in the lab, and stored until analysis.

For analyses, after removing the bark, the phloem was taken from each branch sample and ground. After washing the powder with pentane to remove resinous compounds (Alcubilla, 1970), soluble phenols were extracted at 4°C by 80% methanol containing 25 mg/l of gallic acid as internal standard, according to a method previously described (Lieutier et al., 1996). Analysis was performed by reverse-phase HPLC (Waters 600 E, photodiode array detector 991, column 250x4 mm with a C18 grafted silica phase). The detailed methods of analysis and the elution gradient have already been described (Lieutier et al., 1996). Results were read at 310 nm, except for (+)-catechin (280 nm), corrected using the internal standard, calibrated using pure compounds and expressed in nM/g of freeze-dried powder.

Phenolic compounds were characterized by UV spectra and by refering to the previous analyses carried out in the same tissue (Lieutier et al., 1996).

Multivariate analysis (principal component analysis = PCA) was used to check the existence of groups of variables (compound concentrations) explaining the phenolic between-clone variability. Beetle feeding parameters were added as supplementary variables, and trees were projected in the axes defined by the PCA.

ANOVA, followed by a Tukey's test, was used to compare between-clone concentrations of particular compounds. Correlations were calculated by linear and non linear regression.

Results

Between-clone variability of phloem phenolic content. The phenolic compounds observed were a paracoumaric acid ester, an acetophenone glycoside, taxifolin glucoside, taxifolin, catechin, and 5 other undetermined compounds. Their characteristics are presented in Table 1.

Table 1. Chromatographic and spectral characteristics of the phloem phenolic compounds.

Compounds	Retention time (min)	U.V. spectra		
		Maxima (nm)	Minima (nm)	Shoulder (nm)
Peak 1[a]	21	280	255	310
para-cou.	22	310	252	290
catechin	24	278	255-300	
Peak 2[a]	28	280	258	
acetophenone glycoside	30	277-306	252-297	
Peak 3[a]	37	280	260	310
Peak 4[a]	42	270	252	305
Peak 5[a]	56	280	260-300	
taxifolin glucoside	57	285	257	330
taxifolin	58	285	257	330

a = Unidentified compound. Retention times at 310 nm, except for catechin (280 nm). para-cou = paracoumaric acid ester.

Axes 1, 2 and 3 of the PCA explained 35 %, 26 % and 11 % of the variability, respectively (Fig. 1). Axis 1 was characterized by a group (group F1) of 6 closely and positively correlated variables, P2, P3, P5, taxifolin glucoside, taxifolin and catechin (Table 2). Axis 2 was characterized by P1, paracoumaric acid ester and P4. Axis 3 was correlated with acetophenone glycoside only.

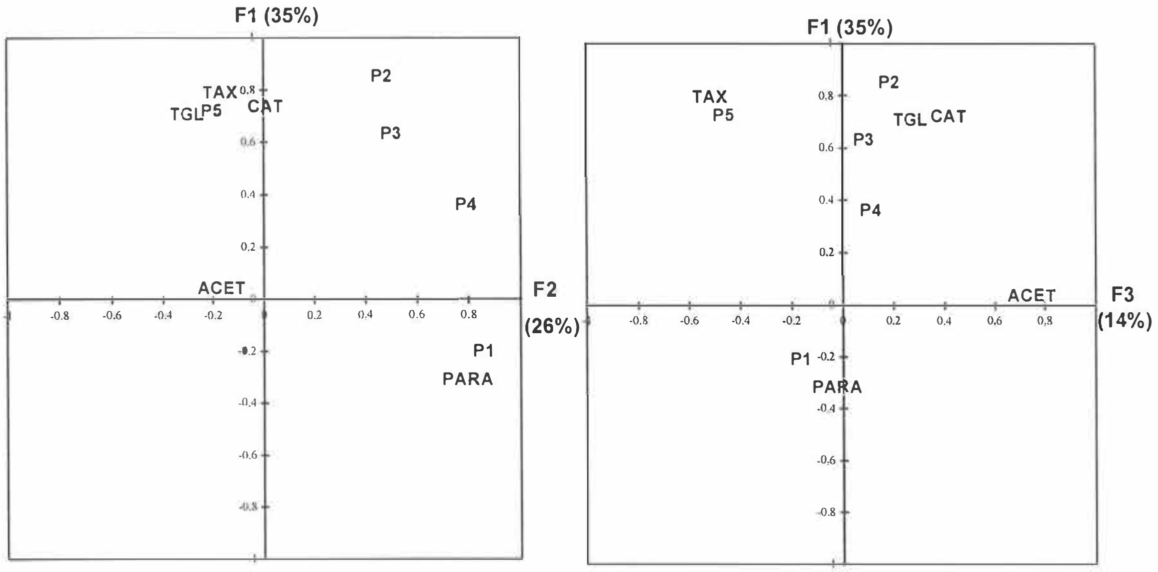

Fig. 1. Principal Component Analysis (PCA) between phenolic variables. P1 = peak 1; PARA = paracoumaric acid ester; P2 = peak 2; ACET = acetophenone glycoside; P3 = peak 3; P4 = peak 4; P5 = peak 5; TGL = taxifolin glucoside; TAX = taxifolin; CAT = catechin.

Table 2. Factor pattern of the Principal Component Analysis: correlations (r values) between variables and axes.

Compounds	Factor 1	Factor 2	Factor 3
Peak 1[a]	-0.20520	**0.86422**	-0.18041
para-cou.	-0.32333	**0.77642**	-0.02156
catechin	**0.70546**	-0.00985	0.40044
Peak 2[a]	**0.84197**	0.44966	0.17470
acetophenone glycoside	0.02383	-0.20167	**0.74410**
Peak 3[a]	**0.62727**	0.49451	0.06893
Peak 4[a]	0.36247	**0.78476**	0.10349
Peak 5[a]	**0.72351**	-0.22099	-0.47556
taxifolin glucoside	**0.69937**	-0.31251	0.26279
taxifolin	**0.76151**	-0.20312	-0.54072

a = Unidentified compound. Retention times at 310 nm, except for catechin (280 nm). Abbreviations: see Table 1.

Projection of the trees in these axes, according to their coordinates (Fig. 2), showed that clones were well separated with regards to axis 1 and axis 3. No real separation was observed along axis 2. Clones 278 and 306 were opposed to clones 312 and 316 along axis 1 and clone 278 to clone 312 along axis 3.

ANOVA and Tukey's test, for each phenolic compound tested individually, gave significant differences between clones for catechin, taxifolin glycoside, acetophenone glycoside, P2, P3 and P4 (Table 3).

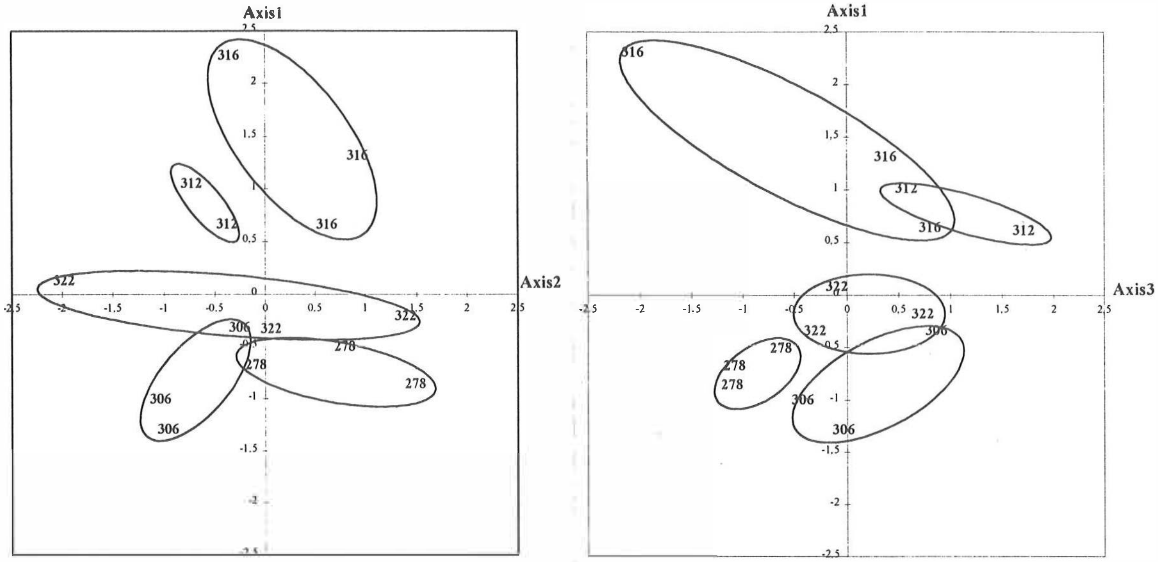

Fig. 2. Projection of trees in the axes defined by the multivariate analysis (PCA) between phenolic variables. Numbers refer to clones and trees.

Table 3. ANOVA between clones for different phenolic compounds tested individually.

Compounds	Clone separation					P values
correlated with Axis 1						
catechin	316(a)	322(a)	312(a)	306(b)	278(b)	0.0006
Peak 2	316(a)	312(a)	278(b)	322(b)	306(b)	0.0017
Peak 3	316(a)	278(ab)	312(ab)	306(b)	322(b)	0.1309
taxifolin glucoside	312(a)	316(b)	322(bc)	306(c)	278(c)	0.0001
correlated with Axis 2						
Peak 4	316(a)	322(ab)	278(ab)	312(ab)	306(b)	0.1252
correlated with axis 3						
acetophenone glycoside	312(a)	306(ab)	322(abc)	316(bc)	278(c)	0.0382

Only the significant results are presented. Abbreviations: see Table 1. Clones with the same letter did not significantly differ regarding compound concentration.

Between clone variability of weevil feeding. No differences among clones was observed concerning weevil feeding, in the main and the lateral axes (Fig. 3). Variability among trees inside a clone looked equal to or higher than clone variability.

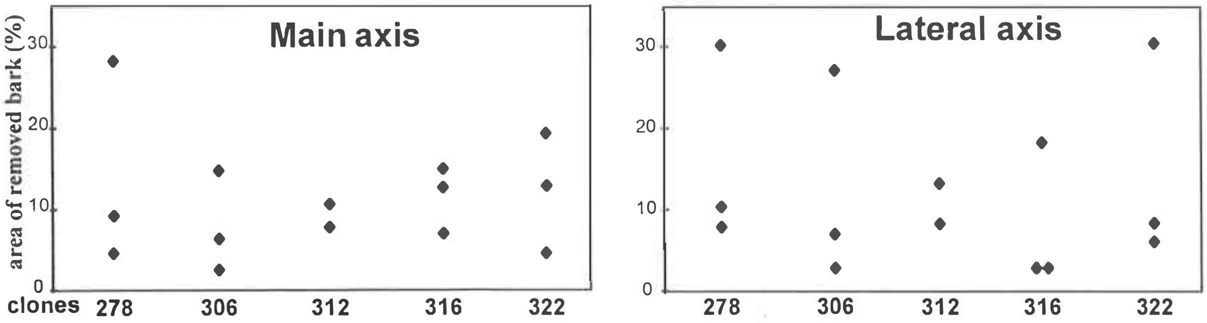

Fig. 3. **Percentage area of bark removed by the weevils in the main and lateral axes, for the different clones. Each point represents one tree.**

However, when weevil feeding parameters are added as supplementary variables in the axes defined by the above PCA, a slight opposition is observed between the feeding variables on the one hand and the phenolic variables correlated with axes 1 or 3 on the other (Fig. 4). Feeding parameters were not correlated with group F1 but weevil feeding in the main axis of the branches was significantly and negatively correlated with acetophenone glycoside in this axis when considering clones as elementary data (Table 4).

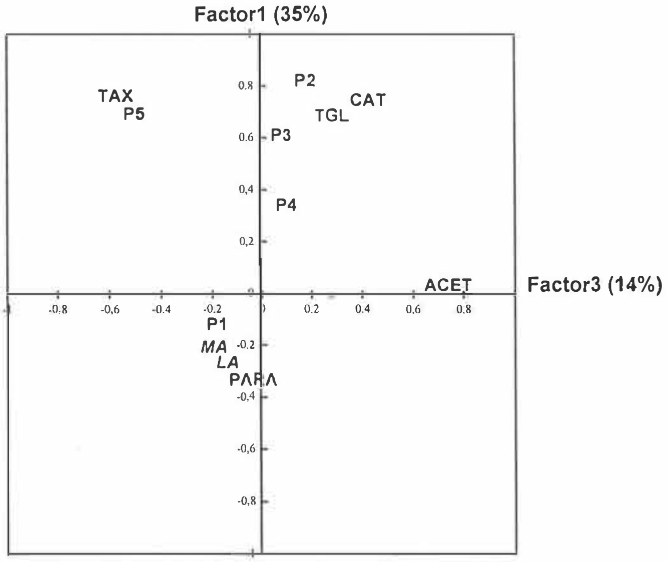

Fig. 4. **Position of the weevil feeding parameters in the axes defined by the multivariate analysis (PCA) between phenolic variables. MA = weevil feeding on the main axis of the branches; LA = weevil feeding on the lateral axes. Other abbreviations: see Fig. 1.**

Table 4. Correlations (r values) between, on the one hand, the feeding variables measured in the main and the lateral axes of the branches and, on the other hand, the groups of phenolic variables characterizing axes 1 and 3 of the PCA, when considering either trees or clones as elementary data.

	Group F1 (Axis 1) (P2, P3, P5, TGL., TAX., CAT.)		Axis 3 (Acetophenone glycoside.)	
	Trees	Clones	Trees	Clones
Main axis	-0.15 (P=0.60)	-0.77 (P=0.13)	-0.50 (P=0.07)	**-0.88*** (P=0.05)
Lateral axis	-0.26 (P=0.38)	-0.24 (P=0.69)	-0.42 (P=0.13)	-0.48 (P=0.41)

Abbreviations: see Fig. 1.

Discussion

Scots pine clones were well separated from each other by their phloem phenolic content in the main axis of the branches. Within clone variability was thus higher than within tree variability. In these conditions, the lack of within clone differences regarding weevil feeding does not allow us to conclude to a relationship between weevil feeding and constitutive phenolic content of the phloem. However, the existence of a significant negative correlation between acetophenone glycoside and weevil feeding in the main axis of the branches would lead to opposite conclusions.

The very small scale of the assay is probably responsible for these contradictory results. Before being allowed to conclude in one direction or another, an extended study with more trees and clones is necessary.

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Integrated bark beetle control: experiences and problems in Northern Germany

HANS NIEMEYER

Lower Saxonian Forest Research Center, Dpt. of Forest Protection, Graetzelstrasse 2, D-37079
Goettingen, RFA

ABSTRACT The integrated system of bark beetle control, including the use of traps since 1983 broadly practised mainly against *Ips typographus*, is described with particular reference to it's effective proper implementation. When correctly applied and under ordinary conditions (no competition by large windthrow or by an active attack simultaneously at hundreds of spruce next to a trap line) the complete control system is able to reduce infestation of living spruce by 70-100% compared to tree mortality where the system is runned without traps.

Recently, timber harvesting by the "Harvester" (a bark crushing harvesting machine) proved to be a good means to avoid successful breeding of *Ips typographus* and *Pityogenes chalcographus* in trunks stored undebarked in the forest. Thinning of younger stands - which leaves all material on the spot - should be conducted in plots separated from each other by a sufficient extent of space (>0.5 km) or of time (1 year) to prevent spreading of infestation by one bark beetle generation to the next throughout the whole of the forest.

Two problems remain unsolved: in very hot summers *Ips typographus* prefers the cool inner parts of stands for breeding instead of the stand margins. Inside the stands, it is very difficult to detect new attacks timely enough to stop spreading of infestation by sanitary felling.

Additionally, pheromone traps cannot be employed because the security distance of 10-12 m between trap and nearest spruce cannot be kept. To shorten the security distance, (s)-verbenon in different dosages has been tested: it was repellent only in traps but on living trees it was (slightly) attractive. To improve the efficiency of traps, monoterpenes ([-]-alpha-pinen and [+]-limonen) have been added to the commercial pheromone dispenser (Pheroprax^R), but with no difference to traps baited with Pheroprax^R alone. Poisoned heaps of thin spruce wood (tops, boughs etc.) containing one pheromone dispenser each proved to be very effective trapping devices, demanding only 6m of security distances, even with dry wood. No side effects of the alpha-cypermethrin contaminated beetles on nearby living birds could be proved.

KEY WORDS bark beetles, integrated control, pheromone traps, host volatiles, repellents, cultural tactics, trap wood heaps

IN GERMAN FORESTRY the spruce engraver *Ips typographus*, is the economically most important insect always found in all norway spruce forests. For hundreds of years, sanitary felling has been the basic control strategy. Trap trees were recommended first by H.J.v.Uslar at the end of the 18th century after a long lasting series of bark beetle outbreaks which devastated 30,000 ha of natural spruce forests in the Harz mountains in south-eastern Lower Saxony (Kremser 1982). In those times the biology of *Ips typographus* was widely unknown and scientists as well as practical foresters gave very contradictory recommendations how to deal with the "small black worm".

Pages 80-86 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

We now know much more about bark beetle biology but still the recommendations on control measures differ significantly not only throughout Europe but also throughout Germany.

The integrated system of bark beetle control in northern Germany

This system, broadly practised since 1983 but published only in german forestry-journals and leaflets, shall be briefly explained here; it consists of:

1. **Frequent searching for new infestations**, in order to allow a timely sanitary felling.
2. **Sanitary felling** of newly infested trees. The success of the entire control strategy depends mainly on whether the very first infested trees of a certain spot are felled soon enough to interrupt the initial pheromone mediated „chain reaction" of infestation from tree to tree - i.e. before the beetles can have an economically significant impact on resources.
3. **Additional mass trapping** of bark beetles either by trap trees (or trap wood heaps, see below) or by pheromone traps (black slot trap; Niemeyer et al.1983).

According to our experiences, pheromone traps should be employed only where bark beetle infestations occurred in the current or previous year - not in uninfested stands! To avoid trap induced infestations of nearby standing trees, traps baited for *Ips typographus* must maintain a safe distance from the next spruce of about 12 m, in no case more than 15m or less than 10m. Along the margin of a stand or of a big gap inside a stand, the traps must form a line with distances from trap to trap of about 30 m (less when the population level is high, more when it is low - but 50m at maximum).

I must emphasize that no bark beetle trapping system is able to reduce the population density of e.g. *Ips typographus* over a large area or a long time. Its mode of action is to lure at short range (maximum 50m) a sufficient portion of the beetles searching for material to breed in away from the endangered neighbouring trees and collecting them in the traps. The remaining population of the beetles at this spot is then not numerous enough to overcome the resistance of normal vigorous spruce by mass attack.

Field experiments clearly showed that the complete control system with traps (if well applied!) reduced the successful infestation of living spruce by 70-100% compared to tree mortality of systems without traps (Dimitri et al. 1992; Busch et al. 1992, Niemeyer et al. 1994, 1995).

There are also situations when employment of trap chains is not reasonable:

- where fresh windthrown stems in high numbers compete with the traps;
- when all man- and machine-power is needed to prevent the infestation of living trees from rapid spreading all over the forest. This was the case in the Harz National Park in early summer 1996 after 2 previous years with extremely hot summers and no sufficient countermeasures. In one area of about 60 ha thousands of spruce were infested within a few weeks. Positioning of trap lines was postponed to the end of the sanitary felling activities.

Thinning techniques supporting the integrated control system

During the last 2 years special thinning techniques have been integrated into the control system with good results:

1. Using a "Harvester": When thinning in spruce stands of medium diameter (up to 25 cm), the trunks normally are stored within that forest undebarked for some months, and constitute a steady source of *Ips typographus* and *Pityogenes chalcographus* to infest adjacent spruce stands. However, processsing the timber by means of that machine called "Harvester" proved to be a 100% effective prevention against successful breeding of both of these harmful insects. The reason is the crushing (squeezing) of the bark while the stem is pressed through the toothed conveying rolls; this procedure makes the bark of norway spruce unsuitable for the above mentioned harmful species but highly attractive for a competitor, the strictly secondary and therefore harmless bark beetle *Hylurgops palliatus*.

2. Separating subsequent thinnings: In stands of non-marketable spruce with small diameters, the thinned material remains after being felled on the spot. In practice, normally one thinned plot borders on the next and one thinning activity follows the next within a short time. Thus, each of the subsequent bark beetle generations gets ample breeding material and the infestation rate increases year by year throughout the district. It is simple to avoid this, but the practice obviously needs recommendations like the following: Separate each thinning plot from the next one by either space (0.5 km in minimum) or time (1 year).

Infestations inside stands: a problem unsolved

In very hot summers, the spruce engraver prefers the (cooler) inner parts of stands for breeding instead of the stand margins which are normally its habitat. Inside the stands, it is very difficult to detect bark beetle attacks early enough, and normally not possible to employ pheromone traps because safe distances between traps and neighboring spruce can seldom be kept.

Trap wood heaps: Although environmentally undesirable, when urgently needed, we construct small poisoned heaps of slash (e.g. tops and boughs), about 1m high and 1-2m wide, containing one pheromone dispenser each. This works very well in terms of reduction of nearby infestations, demanding only a 6m distance from uninfested trees. In 1995, field experiments with 106 trap wood heaps at different places revealed a 100% reduction of lethally infested trees.

Thus, such trap wood heaps can be used in small gaps of about 12m diameter which are not too rare in older spruce stands. However, so far we have not found a sufficient explanation as to why a safe distance between the traps and uninfested trees is so much shorter than with black slot traps. Even trap wood consisting of dry material (without bark, cut in the previous year) was able to reduce infestations of living spruce in their vicinity up to 100%, provided, the pyrethroid dosage was high enough (2g of Cypermethrin per liter spray liquid resp. 0.3 g alpha-Cypermethrin). However, an experiment with an alpha-cypermethrin dosage of only 0.15 g per liter spray liquid and the trap wood heaps underlaid with plastic sheets showed that fresh wood should be much better than dry:

Table 1: Numbers of dead *I. typographus* under trap wood heaps with fresh (TWF) or dry wood (TWD), both types in pairwise arrangement (pairs as columns)

TWF:	1319	520	914	847	1611	1986	total:	**7197**
TWD:	242	60	143	559	393	964	total:	**2361** (32.8%)

Wilcoxon matched pairs signed rank test: R^ = 0; R (6;0.05)=0; significance: 5%

This doesn't necessarily mean that fewer beetles are lured to the dry trap wood, for bark beetles on fresh wood spend a longer time there and try to bore into the bark; so they get more pesticide exposure and drop off earlier than bark beetles on dry wood. A much larger proportion of these latter fly away from the trap wood over a short distance but cannot start breeding anymore.

A remark on possible environmental impacts of contaminated bark beetles may be of interest: checks of 20 bird houses set at a distance of only 8-10 m to trap wood heaps did not reveal any influence on the development of the nestlings (tits, flycatchers, sparrows) compared with another set of 20 bird houses more than 0.5 km apart from poisoned trap wood.

Adding host volatiles to pheromones**:** Following findings of Reddemann (1993), we tested (-)-alpha-Pinen plus (+)-Limonen in PE-dispensers added to Pheroprax^R (identical with the natural aggregation pheromone of *Ips typographus*) resp. Chalcoprax^R (for *Pityogenes chalcographus*) in black slot traps to improve trapping efficiency and perhaps thereby to shorten the safe distance at which traps can be placed with reference to uninfested trees. Our results have been published recently in Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz (Niemeyer and Watzek 1996), remarks here are limited to some short conclusions: In 3 experiments, with 30 repetitions, no monoterpen-induced enhancement of *typographus*-catches was found; the same was true with *P. chalcographus* (2 experiments with 18 repetitions). The differences in catches between traps with and without the additional host volatiles, were extremely low: between 1 and 6%. These differences were not significant (Wilcoxon matched pairs signed rank test).

Repellents to protect spruce near traps**:** (S)-Verbenon seems to be a repellent, according to different authors (Ryker and Yandell 1983, Schlyter et al. 1987, Baader and Vité 1990, Kohnle et al. 1992, Kostyk et al. 1993). Indeed we also found a 98% reduction of *typographus*-catches when Pheroprax^R -traps were compared with those additionally baited with verbenone in polyethylene bags (Niemeyer et al. 1995). But since 1990 we have tried in vain to achieve a repellent effect of verbenone on living trees with release rates of 2.5g resp.57g /tree/day (Rumpf 1990, Greeb 1992).

In 1993 a higher release rate - namely 93mg/tree/day - and another type of dispenser were tested in the vicinity of an uncontrolled *Ips typographus*-outbreak area in the Harz mountains (Niemeyer et al. 1995): 6 test locations were set up, each with one Pheroprax^R-baited slot trap and with one verbenone-treated and one untreated living spruce, both of them at about 6m distance from the trap. At each of the 4 directions on the treated tree one PE-tube was suspended at a height of 3.8m. Each tube was 3.3m long, with 6 compartments holding

10ml of verbenone each, i.e. 240ml of verbenone per tree. The results were in direct opposition to what we expected, (Table 2.)

Verbenone-trees were attacked as soon as 2 days after treatment, untreated spruce not before 11 days after the beginning of the experiment. Verbenone-trees received 111 boring holes in total, untreated trees 3. The maximum height of attacks corresponds very well with the height of the verbenone-dispensers, and there was not even the slightest repellent effect next to the dispensers.

Table 2: *Ips typographus* - Starting date of boring and boring holes at verbenone-treated (V) and untreated control trees (C); number of caught *I.typographus* per trap (at 6m distance)

Rep.	Starting Date		Number		Max. height (V)	Mean distance from PE-disp.	Beetles caught
	V	C	V	C	m	cm	
1	5/2	-	16	0	2.88	3.28	756
2	5/2	-	4	0	3.10	2.25	1.101
3	5/2	-	7	0	2.85	5.43	737
4	5/2	5/11	22	2	3.80	4.16	1.615
5	5/2	-	38	0	3.50	3.47	1.143
6	5/9	5/11	24	1	3.30	6.90	1.747

This total lack of any repellent activity of verbenone on living spruce does not depend on photoisomerization of verbenone, converted to chrysanthenone, as described by Kostyk et al. (1993), as is shown by the following field test data (again obtained in the Harz mountains):

Table 3: Number of *I. typographus* caught in traps baited with Pheroprax^R (P) or P + verbenone after different durations of light exposure of verbenone

Exposure of verbenone	Duration of light-exposure to verbenone			
	1 hour	1 day	1 week	1 month
in full sun	35	39	31	61
sheltered in slot trap	67	40	45	44
not exposed	19	31	3	6
Pheroprax^R only (no verbenone)	1.635	1.639	1.492	1.239

Thus, verbenone released from a polyethylene-bag dispenser within a slot trap baited with Pheroprax^R reduced the response of *Ips typographus* at the (in trap trials) well known level of about 95-98%, regardless of the duration of the preceding light exposure within the scope of 1 hour to 1 month. That means, photoisomerization cannot be accepted as explanation for the failure of verbenone to repel *Ips typographus* from living spruce.

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A Molecular Method for Differentiating Sibling Species within the Genus *Ips*

CHRISTIAN STAUFFER

Institute of Forest Entomology, Forest Pathology and Forest Protection,
Universität für Bodenkultur, A-1190 Vienna, Austria

ABSTRACT Genetic analysis can facilitate identification of sibling species. For non-specialists, fast and cheap molecular techniques may help solve systematic problems in the future. The European genus *Ips* is comprised of seven species. In this genus *Ips typographus*, *I. amitinus* and *I. duplicatus* cause damage on spruce; *I. cembrae* on larch; and *I. acuminatus*, *I. mannsfeldi* and *I. sexdentatus* on pine. A host change from larch to spruce is often reported by the larch bark beetle whereas *I. typographus*, *I. amitinus* are rarely found on larch. *Ips typographus*, *I. amitinus* and *I. cembrae* are sibling species.

A molecular technique is reported that allows for differentiation among these *Ips* species. By polymerising a mitochondrial DNA region between the COI and tRNALEU genes, the species can be characterised on agarose gels. The polymerised DNA region is non-coding and the length varied among 10, 18, 23 and 57 for *I. amitinus*, *I. cembrae*, *I. typographus* and *I. mannsfeldi,* respectively. *Ips duplicatus* and the pine bark beetles *I. acuminatus* and *I. sexdentatus* did not have a non-coding region between these two genes.

This technique is suggested as a marker for identification of sibling species of American *Ips* group.

KEY WORDS Coleoptera, Scolytidae, *Ips*, mtDNA, phylogenetics

IN THE 1960's allozyme electrophoresis became an exciting molecular tool to study population genetics (Lewontin and Hubby 1966). In scolytid species many inter- and intra-specific questions were carried out (for review see Hayes and Robertson 1992). In the mid 1980's the detection that DNA can be polymerized with the help of a thermocycler (Mullis and Falloona 1987; Saiki et al. 1988) improved genetic methods. Since then genetic techniques like random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFLP) or sequencing methods have revolutionised population genetics and insect systematics (for review see e.g. Hoy 1994). Stouthamer et al. (1996) presented a study using the internal non-coding transcribed spacer region (ITS-2) of the ribosomal DNA for the identification of species of the hymenopteraen genus *Trichogramma* using the PCR technique. The PCR products were screened on an agarose gel and due to species characteristic length, this method proved to be an easy and cheap way to determine species within this genus.

The phloeophagous scolytid species within the genus *Ips* DeGeer (1775) are important pests of the European coniferous forests. Main characters of this genus are the structure of the antennal club sutures and the denticles spines on the lateral margin of the elytral declivity (Pfeffer 1995). The European genus *Ips* with 7 species (*Ips typographus*, *I. amitinus*, *I.cembrae*, *I. duplicatus*, *I. acuminatus*, *I. mannsfeldi* and *I. sexdentatus*) is less diverse than the North American genus with 25 species (Wood 1992). The *Ips* species are divided into

Pages 87-91 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

species groups. Sibling species exist in both the European and the American groups. In recent years Cane et al. (1990) and Cognato et al. (1995) have started to work on the phylogenetic relationship of the American *grandicollis* group which is comprised of seven species that have five pairs of spines on the elytral declivity. Allozymes and random amplified polymorphic DNA (RAPDs) revealed congruence in the parsimonious analysis and the grouping paralleled morphological and behavioural similarities. Stauffer et al. (1997) investigated the European *Ips* species by sequencing a region of the mitochondrial (mt) DNA and screening several isozymes. Extensive nucleotide divergence was found, suggesting a long divergence time for the species and the dendrogram suggested four speciation events regarding the host.

In this study a molecular technique to determine the species of the European genus *Ips* by using PCR and agarose gel electrophoresis is presented. A non-coding region showed variability in length among the species, suggesting this region to be a good marker for identification of *Ips* sibling species.

Methods

The parental generations of the seven *Ips* species were sampled from felled trees during the spring flight season in 1994. Only adult beetles were collected. Province and town for each site is given: *I. typographus* (Tyrol, Ehrwald), *I. amitinus* (Lower Austria, Gutenbrunn, Austria) and *I. duplicatus* (Morawia; Ostrau) were collected from *Picea abies*, *I. cembrae* (Styria, Kindberg) from *Larix decidua*, *I. mannsfeldi* (Lower Austria, Gänserndorf) from *Pinus nigra*, and *I. acuminatus* (Lower Austria, Retz) and *I. sexdentatus* (Lower Austria, Gänserndorf) from *Pinus sylvestris*.

Beetles were preserved in ethanol and DNA was extracted from head and thorax of individual specimens by using the protocol of Juan et al. (1995). A fragment was polymerised by using primers UEA 9 and UEA10 developed by Lunt et al. (1996). The PCR procedure is described in Stauffer et al. (1997). The products were screened on a high resolution agarose gel (2%). In order to distinguish between *I. typographus* and *I. cembrae*, a restriction enzyme (*Dra*I) was used. DNA purification and sequencing reaction of the single stranded DNA followed the procedures of Cooper and Hewitt (1993).

Results

The primers were used to polymerise a DNA product of about 300bp length. The PCR reaction was done for at least 6 individuals, for each species and the products were screened on agarose gels. *Ips mannsfeldi* showed a fragment of the size of 362bp. *Ips duplicatus* and *I. acuminatus* had a fragment of 307 bp and *I. sexdentatus* of 304bp. *Ips amitinus* had 319bp, *I. cembrae* 327bp and *I. typographus* 332bp. The restriction enzyme was used to differentiate between *I. typographus* and *I. cembrae. DraI* cut the fragment of *I. typographus* in a piece of 285bp and a fragment of 47bp. *Ips cembrae* had no restriction site for *Dra*I.

Table 1 presents the sequences responsible for this length variability. The region corresponds to a non-transcribed region between COI and the tRNA $_{\mathrm{LEU}}$ gene. Among four *Ips* species considerable difference in length was found. The length varied among 10, 18, 23 and 57 for *I. amitinus*, *I. cembrae*, *I. typographus* and *I. mannsfeldi* respectively. *Ips sexdentatus*, *I. acuminatus* and *I. duplicatus* had no intergenic region. Stauffer et al. (1997) reported that the stop codon of the COI gene varied between a single nucleotide (T for *I. duplicatus*, *I. acuminatus* and *I. sexdentatus*) and three nucleotides (TAA for *I. typographus* and *I. amitinus*, or TAG for *I. mannsfeldi)*. Further an insertion deletion (INDEL) before the stop codon in *I. mannsfeldi* and *I. sexdentatus* was found.

Table 1. Non transcribed region between COI and tRNA $_{\mathrm{LEU}}$ of four species of *Ips*

I. amitinus	AATAAAACCT
I. cembrae	CCATAAAAGA AAAAACCT
I. typographus	ATTTAAATAA AGAAATTTTC TTT
I. mannsfeldi	AAAATAAAAA TTAAGAATTA AGTTTAAATA AAGAATATTA TTATTCGTTA TATTCAT

Discussion

In recent years mt DNA sequence data have been used in coleopteran species to investigate problems in systematics (Funk et al. 1995; Emerson and Wallis 1996), conservation biology (Vogler et al. 1993) and colonisation (Juan et al. 1995). An important and often neglected feature in this science is the identification of appropriate markers which should be polymorphic, however should not be too polymorphic to intrigue the results.

Cytochrome oxidase (CO) provided useful information for inter- as well as intra-specific insect studies. The mt genome of honeybees is characterised by the presence of a long intergenic sequence located between the COI and COII genes. The length of this sequence varied between and within species and several length categories were characterised up to 650bp. High AT bias, stability profile, hairpin and coverleaf putative secondary structures suggest that this non-coding intergenic region might contain an origin of replication (Cornuet et al. 1991; Crozier et al. 1989).

Here a region between COI and tRNALEU in the genus *Ips* showed variability in length. The intra-specific variation was studied from the seven species (between 6 and 9 specimens) and no variation was found. In *I. typographus* about 124 specimens were screened during a phylogeographic study (Stauffer, Lakatos and Hewitt unpubl. data). No variation was found among these specimens.

The AT bias in the intergenic non-transcribed region was about 20% higher than in the COI gene in *I. mannsfeldi.* Also secondary structures of the putative ancestor sequence could be demonstrated in the black pine beetle.

The difference in length was long enough, to screen the differences on agarose gels, thus, avoiding the expensive and laborious procedure of sequencing. In the case of the two sibling species, *I. cembrae* and *I. typographus,* a blunt end restriction site (TTT/AAA) made the distinction easier.

Although in the scolytids the basic alpha taxonomy of the North American and European bark beetles is known, species groups, the phylogeny and other basic systematic questions are still unresolved (Bright, 1992). Bright (1992) mentions the lack of qualified future scolytid systematics. It would be helpful to have a genetic key book with which species can be determined. Such a key book would be absolute and applicable to all laboratories. The methods available for obtaining discrete markers, are the sequencing of mt DNA or also the genomic DNA (e.g. microsatellites). There are several groups attempting this approach. Therefore it is possible that in the near future more markers like the intergenic non-coding region between COI and COII will be available.

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Phenolic and Resistance of Scots Pine to Bark Beetles

EVELYNE BOIS, FRANCOIS LIEUTIER, DANIEL SAUVARD, AND ANNIE YART

INRA, station de Zoologie Forestière, Ardon,
45160 Olivet, France

ABSTRACT The response of Scots pine, *Pinus sylvestria,* via phenolic content to aggressions was investigated in clones susceptible and resistant to mass inoculation of *Leptographium wingfieldii*, a fungus associated with *Tomicus piniperda*. Modifications in phloem phenolic composition was studied during a period of 60 days after inoculation with fungi or sterile malt agar. In all resistant clones, pinosylvin, its monomethylether, pinocembrin and taxifolin were synthesized in the reaction zone after both fungal and sterile inoculations. In the susceptible clones, these compounds were neosynthesized only after fungal inoculation. Taxifolin glucoside was more abundant in the resistant than in the susceptible clones, both after inoculations and in unwounded phloem. Effects of these compounds on *L. wingfieldii* were assayed in liquid medium in microwells at different concentrations. All neosynthesized compounds except taxifolin inhibited fungal growth but they had no apparent effect on *T. piniperda*. These results are discussed regarding tree phenolic defense strategies to attacks by bark beetles.

KEY WORDS Scots Pine, phenolic compounds, resistance, markers, phloem induced reaction, *Tomicus piniperda*, *Leptographium wingfieldii.*

THE PHLOEM INDUCED reaction plays a basic role in conifer resistance to attacks by bark beetles and their associated fungi. It takes place around each point of attack, and important chemical modifications occur. In cases of limited numbers of attacks, it stops the attacking agents, but above a certain density of attacks, it becomes ineffective and the bark beetle population can successfully established. This threshold of attack density above which a tree is overcome is a measure of tree resistance and depends on the physiological status of the tree. Another relative estimation of the tree resistance can be obtained by replacing bark-beetles attacks with artificial mass inoculations of fungi isolated from beetles, thus leading to the determination of a threshold of inoculum density.

Previous experiments on Scots pine have showed that phenolic composition varies considerably after fungal inoculation. In the unwounded phloem of Scots pine, phenolics are mainly flavonoids [(+)-catechin and taxifolin glucoside], p-coumaric aci ester and acetophenone glycoside. In the wounded phloem (reaction zone), four compounds appear: two flavonoids (Taxifolin and Pinocembrin) and two stilbenes (Pinosylvin and its monomethylether).

This paper is a synthesis of several experiments on the interaction between Scots pine, *Tomicus piniperda* and its associated fungus *Leptographium wingfieldii.* The role of phloem phenolics in the efficiency of the induced reaction in stopping attacking agents (*T. piniperda* and *L. wingfieldii*) and in Scots pine resistance was investigated in two steps.

Temporal changes of phloem phenolic compounds during wound induced response. Six Scots pine clones were selected according to their different level of resistance to mass

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Pages 92-94 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

inoculation with *L. wingfieldii* : three were susceptible and three others were resistant. One tree of each clone was inoculated with *L. wingfieldii* and with sterile malt agar. Samples of inoculated phloem were taken 3, 7, 14, 30, 60 days later. At day 0 (the day of inoculation) and day 30, samples of unwounded phloem were also taken from each tree. Monophenols were analysed by HPLC.

Mechanism of the induced phenolic response. Changes in phenolic composition of the phloem after wounding and after wounding plus infection by *L. wingfieldii* showed that tree's reaction was not specific to the attacking agents. However, this reaction was modulated by the presence of the fungus. Two steps could be distinguished during reaction development:

1 - The first was an accumulation of compounds lacking in unwounded phloem (taxifolin, pinocembrin, pinosylvin and its monomethylether). 2 - The second, depended on the presence of the fungus, and was a stabilization of the concentration of these compounds after 7 to 14 days.

Because pinosylvin, its monomethylether, and pinocembrin and their precursors were completely absent in the unwounded phloem, the accumulation of these compounds, after both a sterile and a fungal attack, very likely resulted from neosynthesis by the tree. The stabilization of the concentration of the new compounds during the second step could result from the metabolization on the synthesized compounds by the fungus (pinocembrin, pinosylvin and its monomethylether). The appearance of these three compounds could thus result from the induction of a new metabolic pathway in Scots pine phloem. The cinnamate CoA ligase and stilbene synthase could be induced or activated during the induced reaction. The appearance of taxifolin after inoculation, could result from the activity of chalcone synthase, or could be due to the hydrolysis of taxifolin glucoside by the tree itself or by the fungus.

Differences between trees. The resistant and the susceptible trees were compared with respect to their phenolic composition. In both unwounded and wounded phloem, the resistant trees differed from the susceptible ones by higher concentrations of taxifolin glucoside. After fungal inoculation, four phenolic compounds appeared in all types of trees but later and/or more slowly in the susceptible trees than in the resistant ones. After wounding alone, the four compounds appeared but only in resistant trees. We thus hypothesize that susceptible trees differ from resistant ones by the inhibition of the cinnamate CoA ligase in a normal situation which can be removed in the presence of fungi and by a slower ability for neosynthesis after fungal attack.

In vitro bioassays

Fungal bioassays. Tests were performed in microwells. Phenolics and fungal spores were added in the liquid medium in sterile conditions. Fungal growth was measured with a spectrophotometer by measuring the difference between the absorbance of the fourth day of culture and day zero (beginning of the experiment). Effect of the fungus on phenolics was measured by extracting the compounds from the medium at the end of experiment and by analyzing the extracts with HPLC. *In vitro* bioassays showed that pinosylvin, its monomethylether, and pinocembrin inhibited fungal growth; that taxifolin had no effect; and (+)-catechin stimulated fungal growth. The fungus was able to metabolize pinosylvin, its monomethylether and pinocembrin, but it did not metabolize (+)-catechin and taxifolin.

Thus, corroborating the hypothesis concerning its role in the stabilization of these compounds during the second phase of the reaction.

Insect bioassays. Tests were performed in a rearing medium largely composed of ground phloem and agar. Phenolic compounds were added to the surfusion medium at 50°C. The effect of the phenolics on *T. piniperda* was measured by medium consumption and beetle mortality after 6 days. The phenolics present in rearing medium were re-extracted at the beginning of the experiment and at the end of the experiment, and were analyzed with HPLC.

The phenolic compounds tested in this experiment (catechin, taxifolin, pinosylvin, its monomethylether and pinocembrin) did not have a visible effect on the consumption of artificial medium by *T. piniperda*. However, analysis after re-extraction showed that the phenols were damaged in the medium.

Conclusions

The variations in the concentrations of phenolic compounds and their effect on the aggressors lead us to consider that phenolic compounds play an important role in Scots pine resistance to bark beetles and their associated fungi. The results of *in vitro* bioassays are in agreement with the tree's response mechanism by suggesting that the second step of this mechanism could effectively result from metabolization of the pinosylvin, its monomethylether and pinocembrin by the fungus. However, during their metabolization, these compounds would continue to be synthesized by the tree and they would thus be able to stop the growth of *L. wingfieldii*. Indicators of resistance can be proposed. They are pinosylvin, its monomethylther, pinocembrin, taxifolin glucoside and taxifolin.

Technology Transfer of Treatments using Verbenone for the Suppression of Southern Pine Beetle Infestations

STEPHEN R. CLARKE[2], RONALD F. BILLINGS[3], SCOTT M. SALOM[4], and C. WAYNE BERISFORD[5]

[2] Forest Health, USDA Forest Service, Lufkin, TX 75901
[3] Forest Pest Control Section, Texas Forest Service, Lufkin, TX 75902-0310
[4] Department of Entomology, Virginia Tech, Blacksburg, VA 24061-0319
[5] Department of Entomology, University of Georgia, Athens, GA 30602

ABSTRACT A three phase technology transfer program is currently underway to present potential users with the operational methods developed for suppressing southern pine beetle infestations with verbenone. The program is designed to ensure that the tactic is properly applied and to solicit feedback on the ease and viability of the methods. Three technology transfer sessions have been conducted to date, and the initial results indicate the application methods and directions for use are satisfactory. The major concerns voiced by foresters were treatment cost and efficacy. The results underscore the necessity of providing effective training in treatment application once verbenone is registered for use by the Environmental Protection Agency.

KEY WORDS southern pine beetle, verbenone, technology transfer, pheromones

THE SOUTHERN PINE beetle (SPB), *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), is the most destructive forest insect pest in the southern United States (Payne 1980). Methods for suppressing infestations have evolved over the past century. Early techniques involved salvage of infested trees, burning infested material, injection of chemicals into the sap of standing trees, and exposure of felled trees to solar radiation (St. George and Beal 1929, Craighead and St.George 1938). In the 1940s these tactics gave way to pesticide applications on felled trees, and the objective of control programs was the elimination of epidemics (Billings 1980). By 1970 it had become clear that pesticides were instead adversely affecting natural enemies of SPB (Williamson and Vité 1971), and epidemics continued to occur, so the emphasis shifted to integrated control. Forest managers utilized silvicultural practices to reduce SPB hazard, and implemented direct control measures to suppress infestations and reduce losses. Four suppression methods were commonly used and authorized by the Final Environmental Impact Statement for the Suppression of the Southern Pine Beetle: cut and remove, cut and leave, cut and hand spray, and pile and burn (USDA 1987).

While the approved direct control methods have proven efficacious for suppressing individual SPB infestations (Redmond and Nettleton 1990, Billings 1995), they all involve tree felling and therefore cannot be implemented in certain areas. Also, cut and remove and cut and leave include felling a buffer of uninfested trees. Researchers began searching for methods which did not require tree felling or sacrificing uninfested timber. Vité (1971) suggested the use of semiochemicals for the control of SPB, and techniques involving

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attractants and inhibitors have since been tested. The most promising tactic tested thus far has been deploying verbenone around the active front of an infestation (spot) to prevent continued spot expansion.

Verbenone is a pheromone produced primarily by male SPB. At high concentrations it inhibits aggregation of both male and female SPB and prevents overcolonization of individual hosts (Rudinsky 1973). In the summer, SPB are generally aggregated within infestations. Emerging and reemerging beetles are attracted by aggregation pheromones to trees currently under attack, and males release verbenone and other inhibitory pheromones. As concentrations of these inhibitory pheromones increase, beetles are deterred from these trees and instead attack nearby uninfested pines. By placing synthetic verbenone on uninfested trees at the head of a SPB infestation, it was theorized that spot expansion would be disrupted, emerging and reemerging SPB would disperse, and the spot would become inactive. After continued field testing and refinement of application methods (Payne and Billings 1989, Salom et al. 1992, Payne et al. 1992, Billings et al. 1995), standardized and effective operational techniques for two treatment techniques, verbenone plus felling and verbenone only, were developed (Salom et al. 1997a). These treatments will suppress SPB infestations within specified size categories.

Three steps are necessary to put operational techniques for suppressing SPB infestations using verbenone into practice:

1. Further refinement of the methods to potentially increase efficacy and ease of application while reducing costs
2. Final registration of verbenone from the U.S. Environmental Protection Agency (EPA)
3. Technology transfer to train potential users on the correct application of this tactic.

The focus of this paper is on the process of technology transfer.

Technology Transfer

The USDA Forest Service, Texas Forest Service, University of Georgia, and Virginia Tech have developed the operational methods and are working cooperatively to transfer this emerging SPB suppression tactic to southern foresters. The technology transfer program consists of three phases:

Phase 1. An initial survey of potential users

Phase 2. Preliminary, informal technology transfer sessions with small groups before final product registration

Phase 3. Formal technology transfer sessions with potential user groups or licensed applicators after product registration is complete.

The initial survey was designed to gauge the depth of knowledge of SPB among potential users and to help design the technology transfer protocol and materials necessary to effectively train foresters. The results from the survey (Salom et al.1997b) were used to plan phase 2.

Even though they precede EPA registration of verbenone, the phase 2 technology transfer sessions are important for several reasons. First, the operational methods of applying verbenone we developed may be effective, but they may not gain acceptance if foresters are hesitant to use them due to cost, complexity, time constraints, manpower required, or other considerations. These initial sessions will assess how users regard the tactic and suggest if and what refinements are necessary before EPA registration is complete. The feedback will help us identify problem areas and focus our future technology development . Second, the sessions will indicate the potential usage pattern of the product. This information will be beneficial to the company pursuing registration, Phero Tech Inc. (Delta, British Columbia), in developing marketing strategy, and to the EPA when considering exposure risks during the registration process. These sessions also serve to familiarize foresters with verbenone. The initial survey included questions on treating infestations with semiochemicals, but did not specifically mention verbenone, so these sessions will help ensure name recognition when verbenone becomes available for use. Finally, the feedback from these sessions will aid us in further developing the training materials and presentation techniques for phase 3.

After verbenone registration is obtained, the phase 3 technology transfer sessions will be designed to make foresters aware that verbenone is now available as a treatment option, and will teach them how and when to effectively apply the treatment. We want to insure that the product is properly applied so that treatment failures are minimized and foresters develop and maintain a high level of confidence in verbenone as a SPB suppression tactic.

Phase 2 Technology Transfer Sessions

Methods

The preliminary technology transfer sessions consisted of classroom instruction and a field demonstration, the preferred training methods indicated by foresters (Salom et al. 1997). The classroom instruction emphasized four areas: SPB biology, SPB population dynamics including the role of pheromones, history and results of verbenone technology development projects, and the current methods of verbenone application for SPB infestation suppression. When discussing SPB biology, we emphasized distinguishing SPB adults and infestations from those of *Ips* beetles, determining if fresh attacks are present and if the spot has the potential to expand, and how to determine if a tree has been vacated by SPB. These determinations are critical for effective application of the treatments, and all were areas where the survey indicated increased knowledge was needed.

The effects of verbenone on SPB behavior were stressed in the segment on SPB population dynamics. We explained how SPB uses semiochemicals to coordinate mass attacks on pines and initiate spot expansion. This discussion was designed to provide the logic for using verbenone to suppress SPB infestations. This led into a description of the history of technology development projects testing verbenone. We described the evolution of the elution device to the white pouch with sponge currently in use, and the development of standardized operational procedures detailed in Salom et al. (1997a).

Finally, we gave each participant a copy of the use directions we have written for inclusion on the verbenone label, and went through the treatment protocol step by step. We described how to use the tables to determine the number of pouches required to treat the infestation and the number of pouches per tree. We also prepared and distributed single page, simplified instruction sheets which are designed for field use.

In the field session, we first examined a spot we had previously treated with verbenone. This allowed us to illustrate how the tactic should be applied, and to demonstrate how to monitor treatment success. We then visited an untreated infestation and allowed the participants to analyze the spot, determine the number of verbenone pouches needed, designate the trees to be treated, and apply the treatment. The trainees practiced using the "Hundle" hammer, a verbenone application tool which allows the user to nail the pouch to the tree at a height of 4-5 meters. Questions were welcomed and addressed throughout the classroom and field sessions.

At the close of the field session, a training evaluation form was distributed to all attendees. The evaluation was designed to elicit how and to what extent the tactic might be used, and what factors were most important in determining its use pattern. We also included questions asking the participants to assess the practicality of the application methods and the effectiveness of the training session.

Results And Discussion

Three phase 2 sessions for USDA Forest Service personnel have been conducted to date. Ten people from the Sabine National Forest in Texas attended the first session, fourteen people from the Davy Crockett and Angelina National Forests in Texas were at the second session, and the third session was given to 37 people at the Ouachita National Forest in Arkansas. We had hoped to conduct sessions throughout the south in 1996, but the collapse of SPB populations did not allow us to schedule more training. The field sessions are vital to demonstrating the application procedures and allowing hands-on experience, so we plan to hold more training sessions when SPB infestations are available.

The attendees at the first three sessions all responded positively to the verbenone treatment procedures as described in Salom et al. (1997a). Every evaluation stated the elution devices were satisfactory, the tables designed for calculating number of pouches per tree and infestation were easy to use, and overall the application methods were practical. The comments we received during the field sessions indicated that verbenone applications would not be too time-consuming. Suggested refinements for applying the treatments included modifying the "Hundall" hammer so that it could accept nails on both ends, and producing pouches of various size so that only one pouch would be used per tree.

Comments from the first training session suggested that a more detailed explanation of treatment monitoring was needed, so we emphasized monitoring procedures in the subsequent sessions. We stressed that the full 6 week monitoring period is often necessary, and the treatment goal, particularly for the verbenone only treatment, is not to prevent attack on every treated tree, but rather to disrupt spot expansion and protect some of the green trees which would have been felled in other treatments. This point was particularly pertinent at the Arkansas demonstration session, where many of the treated trees had SPB attacks. Of the attacked trees, many only exhibited a few pitch tubes near the verbenone pouches, with no evidence of attack on the rest of the bole. We explained that these trees may not be successfully attacked, and the infestation might still go inactive, so two more weeks of monitoring (six weeks total) were needed. If the beetles had advanced beyond the treated buffer, or if fresh attacks were present at that time, then retreatment using verbenone or another suppression tactic should be considered. Monitoring two weeks later revealed that no new trees had been attacked.

A majority of the responses indicated that foresters would use both treatments on less than 25 percent of SPB infestations. They would usually recommend using verbenone in place of cut and leave or cut and hand spray. Foresters also responded that they favor using the treatments more in sensitive areas such as wilderness or streamside zones than in non-sensitive areas.

When asked to select factors which would be very important when deciding whether to use verbenone to treat a particular spot, and also to designate the most important factor, infestation size and preventing additional tree loss received the most mentions, and infestation size and treatment cost were rated as the most important factors. From their questions during the training, it was apparent that the most important concerns of the foresters about using verbenone in general were treatment efficacy and cost. Though we presented results from our field trials which demonstrate the treatments are effective when applied correctly, it appeared that positive results from personal applications or observations would be necessary to gain the foresters' complete confidence in the tactic. They also expressed reservations about the cost of the treatment, particularly when compared to costs of current suppression techniques.

The feedback from these initial sessions illustrate the importance of designing and providing effective technology transfer of this tactic. Foresters must be trained to use the tactic only within the infestation size parameters established for each treatment, and to apply the verbenone correctly. Comprehensive training should lead to acceptable treatment results, consumer confidence, and increased treatment usage. We may also need to develop and test methods which would allow larger infestations to be treated. The concerns over treatment costs indicate we need more data on benefit/costs of the tactic. We need to demonstrate that the value of the trees protected by verbenone which would have been felled in a buffer strip when using other treatments is greater than treatment costs. We should also search for ways to reduce product costs.

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Girdling of crownless Norway spruce snags: a measure against *Ips typographus* ?

BEAT FORSTER

Swiss Federal Institute for Forest, Snow and Landscape Research
CH-8903 Birmensdorf Switzerland

ABSTRACT In August 1992 a hailstorm destroyed 73 ha of forest on the north face of Rigi Mountain in Central Switzerland. Many spruces, though not thrown by the wind, had their crowns broken off. As the trees stood on steep slopes, the forest service decided to leave the snags standing as a protection against rockfalls and other natural hazards. This raised the question as to whether this procedure would enhance the propagation of bark beetles, in particular *Ips typographus.* An experiment was conducted to investigate whether girdling these fresh stumps would accelerate their dessication and thus more rapidly render them unattractive to bark beetles. Two measurements of wood moisture showed that neither girdling nor the height at which the crown broke off influenced the dessication of snags. The only significant factor was the diameter of the stem: thin stumps dried out more rapidly than thick ones. In this study, *Ips typographus* invaded only broken crowns lying on the ground, and it was possible to remove these in time to prevent the beetles from spreading. One year after the hailstorm all the snags had dried out without attack by *Ips typographus.*

KEY WORDS forest protection, storm damage, Norway spruce, girdling, bark beetles.

IN THE PAST few years forests in Switzerland have more frequently suffered storm damage as a result of extremely high winds. The storm "Vivian", which struck many parts of Europe on 27/28 February 1990 brought the worst gale ever recorded in Switzerland. It caused the loss of 4.9 million cubic meters of wood, about one year's regular cut for the whole country (Holenstein 1994).

Until now, it has been the usual practice to clear damaged areas of forest completely for regeneration or for reasons of forest protection, in particular to prevent secondary damage by bark beetles. These measures, however, do not cover their own costs and worsen the already difficult financial situation of forest owners.

On 21 August 1992 a hailstorm destroyed a large part of the forest on the north face of Rigi Mountain in Central Switzerland belonging to the Swiss Federal Railways. Over an area of 73 hectares, 28 000 cubic metres of wood, of which Norway spruce (*Picea abies*) comprised 25%, were broken off. As part of salvage operations, the upper parts of the stems which had been broken off were removed while the crownless stumps were left standing. The aim was to maintain protection against rockfalls, snow movement, mud slides and erosion. There was a simultaneous need to avoid the use of standing stumps as a haven for the reproduction and spread of harmful forest insects, in particular *Ips typographus* (Kläy and Mani 1993). This raised the question as to whether girdling these snags would accelerate their drying out and thus more rapidly render them unattractive to forest pests.

Pages 101-104 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

Over large parts of the areas damaged by the storm of February 1990 it was observed that spruce stems lying on sunny sites with total destruction frequently dried out before the population of *Ips typographus* had time to expand and consequently remained free from attack. On shady sites, in contrast, stems lying on the ground but still having a certain amount of contact with their roots were still being invaded one or even two years after the storm (Forster 1993). In order to accelerate their drying out, such stems were cut free of the stump.

The effects of girdling standing trees have been investigated in several studies, but these deal only with trees with intact crowns and are mostly concerned with finding economical methods of eliminating competitors.

Materials And Methods

As no reports on experiences with the girdling of standing crownless trees and the course of their drying out could be found, the forest service of the Swiss Federal Railways, in cooperation with the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, decided to conduct a case study to investigate the effects of girdling snags (Feiger et al. 1996).

In this study, conducted on three sites with total damage, 100 spruce snags were girdled and 100 were left ungirdled, and beetle attack and the course of dessication of the two groups were compared. The experiment was designedly focused on *Ips typographus* , because records from areas damaged by "Vivian" in 1990 showed that the most extensive secondary damage was caused by attacks by this bark beetle in damaged neighbouring stands (Forster 1993).

On three sites all the spruce snags, which totalled 200, were numbered and mapped after the storm. Diameter at breast height, height of the break in the stem and any particular features such as splits were recorded for each snag. At the beginning of May 1993 half of the snags were girdled three times above the base of the stem, cuts about 3 cm deep being made with a chain saw.

In May 1993 a lath sample was taken from every snag on the study sites and its moisture content determined in the laboratory (DIN 52'183. 1977). In September 1993 the process was repeated in order to determine the extent to which the stems had dried out.

During the summer of 1993 and in the spring of 1994 all snags were examined for insect attack. The adjacent area with damage was also checked. Further, the population of *Ips typographus* was monitored by means of pheromone traps.

Results

In May and June 1993, broken wood still lying on the ground displayed attack by *Ips typographus.* It was however possible to process and remove it before the new generation of beetles took wing. In contrast, none of the snags, whether girdled or not, evidenced attack.

In the autumn and winter of 1993/94 some standing but damaged trees outside the experimental plots still exhibited signs of attack, though all these trees still had some green branches.

Ips typographus did not appear on the stumps of the experimental plots. Both girdled and ungirdled spruce stumps were however frequently attacked by the following beetles causing secondary damage:

- *Hylurgops palliatus*	*(Scolytidae)*
- *Polygraphus poligraphus*	*(Scolytidae)*
- *Dryocoetes autographus*	*(Scolytidae)*
- *Trypodendron lineatum*	*(Scolytidae)*
- *Rhagium inquisitor*	*(Cerambycidae)*
- *Hylecoetus dermestoides*	*(Lymexylonidae)*

Free-standing snags were in general less heavily attacked by these beetles species than those scattered through the inner part of the remaining stands. The bark of heavily attacked snags began to peel off as early as July 1993. Such snags rapidly lost any attraction for *Ips typographus*.

Further checks in June 1994 , almost two years after the storm, showed that there were no longer any snags attractive to *Ips typographus*: the stems were already too dry.

The wood moisture measurements taken in spring 1993 showed a very wide range: minimum 30%, maximum 148%, scatter 16%. By autumn of that year the wood moisture of the snags had declined: minimum 16%, maximum 73%, scatter 12%.

Girdling did not influence the course of drying out of the snags. There were no differences between the wood moisture of girdled and that of ungirdled snags. Neither was there any evidence that the height of the breakage had any influence. On the other hand, in the spring of 1993 thick snags showed a higher wood moisture than thin ones. That was the only detectable difference. By the autumn of 1993, 15 months after the storm, this difference had disappeared. The thick snags must have dried out somewhat more slowly or later than the thin ones.

Because the snags were not attacked by *Ips typographus* at all and there was hardly any attack on the trees left standing within the stand, it is not possible to draw any definite conclusions as to the time frame of the insect's ability to breed or the probability of attack on the snags.

Discussion

In the case investigated, *Ips typographus* attacked only broken crowns lying on the ground, and it was possible to remove these in time to prevent the beetle from spreading. One year after the hailstorm all the snags left standing had dried out to such an extent that they were no longer attractive to dangerous forest pests, so that here it proved worthwhile to leave the snags standing: they maintained their protective function to a large degree, and there was enough manpower to remove wood already infested or any that might have attracted the pests.

The snags will continue to fulfil their function as a protection against rockfall, erosion and to a certain degree against snow movement until the forest has grown up again on the damaged areas. Further, the large amount of deadwood left undisturbed meets the needs of nature conservation. Even in protection forests, economics need not conflict with ecology.

Because attack by bark beetles and the development of their populations depend on numerous factors, such as the initial population, the weather and available breeding sites, it is not possible to make any generalized recommendations for the treatment of areas with storm damage.

Storm damage often poses complex problems for forest owners, involving work capacity, opening-up, marketing, forest protection, financing of operations, safety at work and many other factors, and therefore require in turn equally complex solutions tailored to meet each individual case. These may include leaving wood assortments likely only to show deficits standing or lying. Under today's conditions (state funding, nature conservation), indiscriminate processing and clearing at any price is becoming increasingly questionable. In every case of damage it is worthwhile first to analyse the situation in detail, then to estimate possible hazards, and finally to work out a refined concept of operations.

If it is decided to leave snags standing, it is unnecessary to girdle fresh stumps, as this does not accelerate their drying out. It is certainly possible that if *Ips typographus* undergoes a population outbreak even stumps may be invaded. Therefore it is essential to maintain observations for at least two years after storm damage occurs. Any infestation should be detected as early as possible and combative measures taken before a new generation is ready to take wing.

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Changes in the occurrence of bark beetles on Norway spruce in a forest decline area in the Sudety Mountains in Poland

WOJCIECH GRODZKI

Forest Research Institute in Warsaw, Forest Management in Mountain Regions Section,
ul. Fredry 39, PL-30-605 Kraków, Poland

ABSTRACT From 1988 to 1994 investigations on the occurrence of the bark beetles were carried out in the Western Sudety, Poland, where about 15 thousand hectares of Norway spruce stands died as a result of outbreaks of *Zeiraphera diniana* and bark beetles in 1977-86. During this period changes in the frequency and dominance of bark beetle species were found. *Pityogenes chalcographus* increased in dominance while the diversity of the total bark beetle complex on Norway spruce and their parasitoids declined. Possible causes of this phenomenon, such as the characteristic of trees and stands and their limited resistance, consequences of outbreaks of other insect species, and weakening of trees, are discussed.

KEY WORDS *Picea abies*, bark beetles, forest decline, Sudety Mts.

THE FORESTS IN the Sudety Mts. in Poland have exhibited a decline in vitality during the last 20 years. Composed mainly of Norway spruce, artificially planted at the beginning of the century from seedlings of foreign or unknown origin, these forests have been adversely affected over a long time by abiotic factors, such as snow, wind and air pollution. From 1977-83 Norway spruce in this area has been repeatedly defoliated by *Zeiraphera diniana* Gn. (Lepidoptera: Tortricidae). As a result of this defoliation and an outbreak of bark beetles in 1981-86, nearly 15 thousand hectares of trees died (Grodzki 1994). These outbreak conditions and mass trapping of bark beetle populations (Grodzki 1995), resulted in some changes in insect populations, described in this paper.

The aim of the study was the description of:

- qualitative and quantitative characteristics of the bark beetle populations in weakened stands,
- changes in characteristics compared with other Norway spruce stands in Polish mountains,
- role of selected factors influencing bark beetle populations.

Materials and Methods

Investigations were carried out in 1992-94 in Norway spruce stands when stand age varied from 45 to 124 years. In 12 experimental plots located at various altitudes and expositions, trees were numbered and defoliation levels were ranked using 5 classes. All trees infested by bark beetles in the late spring - early summer and in the late summer - early autumn, were felled and the infested bark was analysed in 4 half-meter sections: I - basal

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Pages 105-111 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

(0.5-1.0 m above the ground level), II - between the ground level and the crown base, III - in the crown base and IV - in the middle of the crown. The occurrence of all species infesting the bark was recorded and the infestation density, (i e. the mean number of the mating chambers [m.ch.] per dm^2), of the three most important species was estimated. Tree samples were also reared in the laboratory, to confirm the bark beetle composition and to determine the species of natural enemies. Comparative observations and analyses were carried out in Pieniny and Bieszczady National Parks, in the Carpathians. During the study period, 147 infested trees were analysed in the Sudety Mts.; additionally 68 samples were reared in the laboratory. For the comparative observations in the Pieniny and Bieszczady, 2 and 4 trees respectively were used together with 18 laboratory rearings.

Results

Species composition and frequency. During the study period, 71 species of insects were found. The most abundant were Coleoptera with 53 species from 15 families. There were 18 species from 6 families of Hymenoptera, and only 1 species of Diptera was found. Among Coleoptera, the most abundant were bark and wood boring families: Scolytidae with 21 species and Cerambycidae with 10 species. Species diversity of the group of bark and wood-boring insects, found in the Sudety Mts., was relatively low in comparison with other mountain regions in Poland. The presence of *Pissodes harcyniae* and the absence of Monochamus and Acanthocinus in the Sudety Mts. was an interesting phenomenon, indicating the differences in the quality of the breeding material between the Carpathian and Sudety's Norway spruce stands.

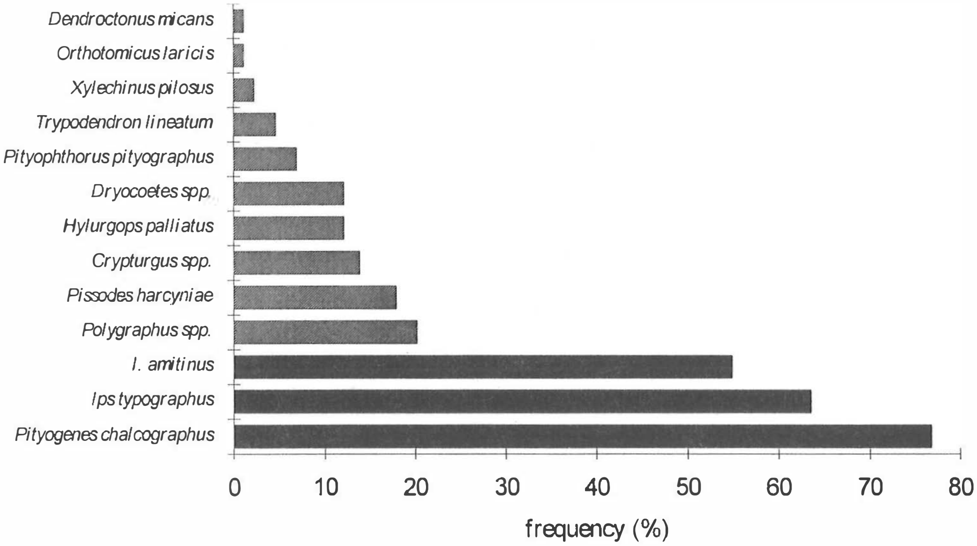

Fig. 1. Frequency of insect species on experimental plots in the Sudety Mts.

The most common species was *Pityogenes chalcographus*, found on 77% of sample trees; slightly less frequents were *Ips typographus* (64%) and *I. amitinus* (55%). In the most cases, infestation by these three species was the main cause of trees deaths. Insects belonging to the genus *Polygraphus* and the weevil *P. harcyniae* played a similar but less important role. Insects from the genera *Dryocoetes*, *Hylurgops* and *Trypodendron* were found on dying or dead trees. Other bark beetle species, like *Pityophthorus pityographus* or *Xylechinus pilosus* were rather scarce and played a negligible role (fig. 1).

The frequency of the most important species in tree sections was related to the different preferences of each insect (fig. 2). The frequency of *I. typographus* was the highest in the section I and decreased in higher tree sections; while in the case of *I. amitinus* the opposite tendency was observed. The frequency of *P. chalcographus* was less varied; the concentration of the species was the highest in sections II and III, but even in section I, this insect was found on 29% trees.

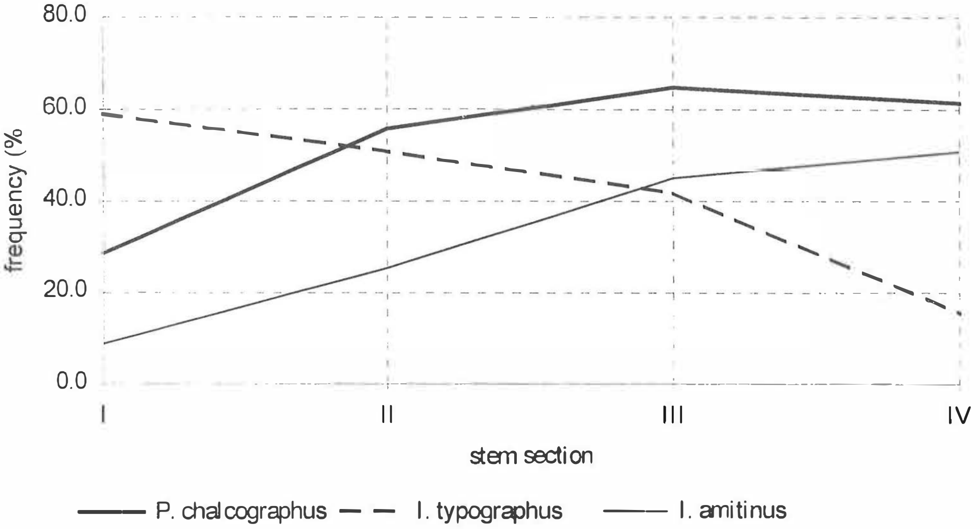

Fig. 2. Frequency of the most important bark beetle species in tree sections.

Infestation density of the most important species. The infestation density was analysed on 122 infested trees, for 3 insect species: *I. typographus*, *I. amitinus* and *P. chalcographus*. The highest mean density (1.78 m.ch./dm^2 with a range of 0.02-7.07) was reached by *P. chalcographus* : this density is much higher than reported by Ossowska (1990) from the Carpathians (1.0 m.ch./dm^2). The infestation density and its range for *I. typographus* and *I. amitinus* was much lower, reaching 0.54 (0.01-2.25) and 0.31 (0.02-0.97) respectively. The infestation density of the species in the tree sections was related to their frequency; for example, *P. chalcographus* was less abundant in the section I (max. 7.73 m.ch./dm^2) than in sections III and IV. (9.99 m.ch./dm^2).

Table 1. Infestation density of 3 bark beetle species related to its co-occurrence. (Tukey HSD test).

Factor (occurrence of):		Infestation density (m.ch./dm²) for:		
		I. typographus	*I. amitinus*	*P. chalcographus*
I. typographus	present	---	**0.80**	1.80
	absent	---	**0.26** ***	1.64
I. amitinus	present	**0.18**	---	**0.74**
	absent	**0.49** ***	---	**2.70** ***
P. chalcographus	present	0.38	**0.31**	---
	absent	0.30	**0.03** ***	---

***p<0.0001

The presence of each of the three species, significantly influenced the density of the other species except for the pair *I. typographus* - with *P. chalcographus* (Table 1). In most cases, the presence of one of the species inhibited the infestation density of the other species, except the species *P. chalcographus* and *I. amitinus.* This positive association was probably related to the similar bark thickness preferences of these two species.

Infestation density was related to elevation and aspect of the stand. Densities were higher at elevation > 800 m (ANOVA indicated significant effect of elevation on *I. typographus* [F=15.4***] and *P. chalcographus* [F=45.8***] densities. The highest densities of *I. typographus* were found on northern slopes (F=3.5*), and *P. chalcographus* was most abundant on western slopes (F=8.6***).

Insect communities and its role. Two main insect communities were present on living trees:
I. *P. chalcographus* + *I. typographus* + *I. amitinus* attacking living, weakened trees in groups, on stand edges and in forest gaps. This is the most important community from the phytosanitary point of view, but these species are difficult to control because of the dominance of *P. chalcographus*.
II. *Pissodes harcyniae* + *Polygraphus* sp. + (species from the community I), attacking individual trees inside more humid, dense parts of the stands. Local abundance of this community is related to favourable stand conditions.

The species composition of these communities is relatively poor in comparison with other parts of Polish mountains, even in the neighbourhood of the study area (Capecki 1978, Konca 1991).

Natural enemies. Among the natural enemies, the parasitoids from Chalcidoidea, and Braconidae were the most frequent and of major importance (Table 2). The three species, *Tomicobia seitneri*, *Dinotiscus eupterus* and *Rhopalicus tutela* (Pteromalidae) [polyphagous parasitoids attacking various bark beetle species (Balazy and Michalski 1962)] are important in the limitation of bark beetle populations composing community I. *Eubazus atricornis* (Braconidae) is a specific endoparasitoid of the genus *Pissodes* (Alauzet 1990), and its presence was related with local abundance of *P. harcyniae*. Generally the parasitoid complex found in the study area was not diverse in comparison with the material obtained from the Carpathians. Among the predators found in the Sudety Mts. the most frequent were *Medetera signaticornis* (Diptera, Dolichopodidae), *Thanasimus formicarius* (Col.: Cleridae) and *Corticeus linearis* (Col.: Tenebrionidae) being the non-specific predators of numerous bark beetle species, including *P. chalcographus* (Balazy and Michalski 1960, Kolomijec and Bogdanova 1980, Weslien 1992).

Table 2. Main species of parasitoids and predators obtained in 71 laboratory rearings

Insect species	number of rearings	frequency (%)
Tomicobia seitneri (Ruschka)	17	24
Dinotiscus eupterus Walk.	13	18
Rhopalicus tutela (Walk.)	12	17
Eubazus atricornis Ratz.	9	13
Roptrocerus sp.	6	8
Dendrosoter middendorffii Ratz.	3	4
Eurytoma sp	3	4
Dinotiscus sp.	2	3
Ibalia leucospoides (Hoch.)	2	3
Liotryphon sp.	2	3
Medetera signaticornis Lw.	13	18

Tree and stand characteristics. Defoliation levels, estimated during the study period on the experimental plots, was extremely high: in the sample of 878 described trees, 72% were classified in classes 2-4, (i.e. > 25% defoliation). The direct effect of air pollution was not found by chemical analysis; of samples taken at the observed stands. Observed damage on the crowns and reduced increment of trees is more likely the result of poor site conditions, especially altitude and aspect: on higher and western exposures defoliation levels were higher.

82.5% of the trees infested by bark beetles belonged to class 3 (defoliation >60%) in the period just before the infestation. Growth increment declined in all stands collapsed following defoliation by *Z. diniana*, but no differences were found in growth increment between the trees infested by both beetles and non infested ones.

Discussion

Results presented here indicate that the bark beetle populations in the Sudety Mts. significantly changed over the last years. The most important change has been an increase in the frequency and infestation density of *P. chalcographus*, related to the ecological plasticity and expansiveness of this species. These changes may be a partial consequence of the bark beetle control activities namely the mass application of selective, Pheroprax baited traps (Grodzki 1995). In stands with an abundance of fresh breeding material (downed logs, logging residues - branches, tree tops) *P. chalcographus* found extremely favourable conditions for population growth. Population growth was also stimulated by the disruption of competition patterns caused by pheromone suppression of *I. typographus*. In the study area, *P. chalcographus* was able to kill more trees and to succeed in competition with other species, mainly *I. typographus* and *I. amitinus*.

The bark beetle outbreak and later changes in insect populations are also related to the stand susceptibility and its reduced resistance (Christiansen et al. 1987). However the absence of a relation between infestation rate and tree increment was unexpected (Christiansen 1980, Nef 1994). Observations highlighted the effect of defoliation on susceptibility to bark beetle attacks (Althoff 1985, Oppermann 1985). The infestation density of *I. typographus,* and especially *P. chalcographus,* was significantly higher in stands localised on higher elevations and exposed to the west (defoliation level was also higher here). *P. chalcographus* was previously found in weakened stands (Chlodny et al. 1987), and this could explain its pattern of abundance in the study area. Generally, observed changes have rather temporary and local importance, related with the stand characteristics and favourable breeding conditions.

Conclusions

1. The major change in bark beetle populations in the study area was a reduction in diversity of bark beetle communities together with the increment of the population levels of *Pityogenes chalcographus*, dominating in the insect community and in spatial competition. Changes have temporary and local importance.
2. The reduced diversity of the natural enemies seemed to be related to the limited biodiversity of observed ecosystem, influencing its generally reduced resistance.
3. Factors causing the observed changes were both primary (origin and characteristics of stands) and secondary (insect outbreaks, breeding conditions).
4. The defoliation was a factor increasing the susceptibility of trees and stands to bark beetle attacks, but there was no relation to tree increment.
5. The main effects of the bark beetle outbreak from 1981-86 and a previously applied selective pest control strategy were mainly the disruption of competition patterns in insect communities, and the abundance of breeding material, favourable especially for *P. chalcographus*.

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Effects of integrating cultural tactics into the management of the balsam twig aphid *Mindarus abietinus* Koch (Aphididae: Homoptera) in balsam fir Christmas tree plantations.

PAULA K. KLEINTJES

Department of Biology University of Wisconsin-Eau Claire Eau Claire, WI 54702

ABSTRACT The balsam twig aphid *Mindarus abietinus* Koch causes needle distortion and/or loss on balsam fir Christmas trees. Insecticides, herbicides and fertilizers are used in the management of the trees with little monitoring of their effects upon the aphids. A complete randomized block split-plot design incorporating whole plot treatments (19-19-19 fertilizer/mowing, 19-19-19 fertilizer/Simazine herbicide, white Dutch clover intercrop and no treatment) with subplot treatments (Imidacloprid, Diazinon, Azadirachtin and no treatment) was used to determine treatment effects upon numbers of aphids and their natural enemies. Numbers of aphids and aphid-infested shoots were low on all treatments (<12 aphids/ subplot) although fertilized treated plots had slightly higher numbers of aphids. Diazinon treated subplots had significantly lower, albeit marginally, mean numbers of aphids/subplot. All treatments and their interactions had little effect upon proportions of infested shoots and resulting undamaged shoots (≥80% undamaged). Numbers of predators were too low too detect significant effects of treatments.

KEY WORDS *Mindarus abietinus*, balsam fir, twig aphid, Christmas trees, silvicultural controls

THE BALSAM TWIG aphid *Mindarus abietinus* Koch (Homoptera: Aphididae) is a pest of balsam fir *Abies balsamea* (L.) Mill. and Fraser fir *Abies fraseri* (Pursh) Poir. in nurseries and Christmas tree plantations (Saunders 1969, Nettleton and Hain 1982, Bradbury & Osgood 1986). Aggregations of aphids feed on new shoots causing them to twist and distort which can reduce the value and prevent the sale of the trees, one to three years after attack (Saunders 1969, Martineau 1984).

In a variety of plant crop-insect herbivore systems, applications of fertilizers, insecticides and/or herbicides are known to increase levels of nitrogen in plant tissues and increase numbers of insects, particularly aphids, feeding on those tissues (reviews by Mattson 1980, White 1984). Moreover, genetic provenances of balsam fir that contain high concentrations of the monoterpene ß-phelledrane are found to be most attractive to the balsam twig aphid and thus suffer greater feeding damage (DeHayes 1980). Previous observations indicate that Christmas tree growers use various combinations of these chemicals and nursery stock with little knowledge of their combined effects on aphid numbers. They are also concerned with the economic costs, environmental and health hazards associated with insecticides and are anxious for safer and more economical alternatives. Currently, Christmas tree growers control aphids by aerial applications of Diazinon, either prior to budbreak or after detection of aphid-infested shoots (Osgood 1977, 1979, Nettleton & Hain 1982, Bradbury & Osgood 1986, Kleintjes unpublished data).

In orchard and field crop systems, covercrops and herbaceous forb conservation have been used to enhance and conserve aphidophagous predator populations (Cowgill et al. 1993,

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Hodek 1993). In Christmas tree plantations, vegetation among trees is either mowed or treated with herbicide to reduce distortion or pathogenic infection of lower branches (growers, pers. comm.). Little is known about the effects of intercropping, mowing, or retaining vegetation among rows of trees upon insect pests or their natural enemies.

Despite the international success of utilizing cultural controls in integrated pest management, research and application for the balsam twig aphid in Christmas trees has been limited (Osgood 1977, 1979, Nettleton & Hain 1982, Bradbury & Osgood 1986). It is assumed that the competitive nature of the business, the historical reliance on chemical controls, and the variable acceptance rates of aesthetic damage have thwarted progress. As a result, the objective of this study was to examine the effect of current grower management practices (fertilizers, herbicides and insecticides) and potential cultural tactics (intercropping clover, mowing, selected use of fertilizer) upon numbers of aphids and their natural enemies.

Methods

The study was conducted on two balsam fir Christmas tree plantations, Pleasant Valley Tree Farm (PVTF)(Dunn Co.) and Swan's Balsam Tree Farm (SBTF)(Price Co.) in northwestern Wisconsin, from April to July 1996.

A complete, randomized block, split-plot design (Steel and Torrie 1980:377) incorporating whole plot treatments (fertilizer-mowing, fertilizer-herbicide, white Dutch clover intercrop, no treatment) with subplot treatments (©Provado, ©Neemix, Diazinon and no treatment) was used to determine their influence on numbers of the balsam twig aphid and their aphidophagous predators. The experimental areas consisted of four blocks (replicates) (0.21ha ea.) located within a 1km^2 area at each farm. Trees were 8-10 years old and planted at a density of 2500-2800 trees/ha. Mean (±SE) height and diameter-breast-height of trees at PVTF was 1.97±0.01m and 2.97±0.68cm and 3.47±0.17m and 2.16±0.05cm at SBTF. Blocks were located in areas that had both a history of annual balsam twig aphid infestations and previous aerial applications of Diazinon upon the appearance of aphid-infested needles. Each block was divided into four wholeplot strips (5 x 20 rows for a total of 100 trees), each randomly assigned one of four treatments with two rows of trees serving as buffers between each treatment. The whole plot treatment fertilizer-mowing consisted of a broadcast spread application of 19-19-19 fertilizer (Mixrite©, Keenan, WI.) applied at a rate of 222.3 kg/ha (late April-early May) followed by a late season mowing between rows of trees (PVTF: 15 July, SBTF: 24 June). The fertilizer-herbicide treatment included the same fertilizer application followed by a pre-budburst application of Simazine (Princep© 4L, Ciba-Geigy Inc., NC) at a rate of 3.33kg/ha in early May (PVTF, overhead sprayer; SBTF, base sprayer). The clover treatment consisted of planting white Dutch clover (*Trifolium repens*) (26.1 kg/ha) between rows of trees as soon as the ground thawed (late April-early May). Clover seed was sprinkled by hand on the soil surface and scratched 1 cm deep into the soil with a hand rake. The control plot received no treatment. Each whole plot was further subdivided into four subplots each receiving one of four treatments. Each subplot contained twenty-five trees in a 5 x 5 row grid with the central five trees receiving the treatment. Subplot treatments consisted of grower applications of: Imidacloprid, (Provado© 1.6 Flowable, Bayer Inc, Kansas City, MO.) at a rate of 0.16ml/l water, plus adjuvent Aquagene 90© (Universal Cooperatives, Inc.) at a rate of 0.31ml/l water; Diazinon AG 500 (Prentox©, Prentiss Inc., Sandersville, GA) at a rate of 1.27ml/l water, plus adjuvent Aquagene 90© at a rate of

0.31ml/l water; Azadirachtin (Neemix 4.5© botanical insecticide, W.R.Grace & Co.- Conn., MD.) at 6.3ml/l water and a no treatment control. These insecticides were used for testing because they were either commonly used by growers (Diazinon), were a new option for Christmas trees (Provado) or were a less toxic, botanical alternative (Neemix). Each treatment was applied to all sides of a treatment tree with a 15l Solo© backpack handpump fine mist sprayer. Spraying coincided with the dates aphid stem mothers reached the 3-4th instar and new growth was emerging (PVTF: 20 May and SBTF: 29 May).

Beating discs (53.4cm^2 plastic embroidary rings of black velvet) and visual counts of infested shoots (one 20cm branch/tree) were used to sample numbers of aphids and their predators on the outer midcrown of each treatment tree (5/subplot) (Kleintjes, unpublished data). Samples were taken once pre-treatment and 3 days, 1 and 3 weeks, post-treatment. Each period, beat samples were taken from a different but immediately adjacent side of the tree (clockwise rotation) with each midcrown of the tree beaten 5x to dislodge insects onto the disc. Mean numbers of aphids were calculated for each subplot each date. Visual counts were taken from permanently tagged midcrown branches to estimate the mean proportion of aphid-infested shoots, shoot size and extent of aphid damage to shoots. On the last sampling date, 3 weeks post the peak in aphid numbers, the numbers of shoots with no curling, slight curling (needles slightly twisted) and extensive curling (needles permanently curled around stem) were also counted. Preliminary sampling studies on balsam in Wisconsin and those of Bradbury and Osgood (1986) in Maine support the use of midcrown branches for sampling numbers of aphids, infested and damaged shoots.

Soil samples (15cm deep) were taken pre and post whole plot treatment with a soil core auger from each control subplot. Samples were analyzed for pH, % potassium, % phosphorus, % organic matter and total nitrogen (ppm). Leaf samples (six 5cm shoots per tree/5 trees) of new growth were collected from each control subplot and analyzed for percent total nitrogen. All analyses were conducted by the University of Wisconsin-Extension, Soil and Plant Analysis Laboratory, Madison, WI.

Split-plot analysis of variance tests were used to compare mean numbers of aphids, mean numbers of infested shoots and mean numbers of undamaged shoots among whole plot and subplot treatments (Steel and Torrie 1980). Mean numbers were log transformed and proportions received the arcsin sqrt. transformation in order to normalize data and obtain homogeneity of variances (Sokal and Rohlf 1981). Because of the block design at the whole plot level the interaction between (block *whole plot) effects was used as the correct error term to test whole plot effects (Steel and Torrie 1980:380). However, at the subplot level both the test of subplot effects and the interaction of (subplot *whole plot) effects used the error term that is the sum of the interaction of (block*subplot) effect plus the three-way interaction of (block*whole plot*subplot) (Steel and Torrie 1980:380). Numbers of aphids and infested shoots were from the sample date of highest infestation whereas data for undamaged shoots were collected post peak. An analysis of covariance(ANCOVA) was not used for post-treatment effects because numbers of aphids were too low pre-treatment, however, an ANCOVA was used to compare soil chemistry and post-treatment numbers (Sokal and Rohlf 1981). Systat©(1992) and Statistica©(1994) Software were used for analyses.

Results and Discussion

Results of the split-plot ANOVA's indicated that whole plot and subplot treatments had little effect upon numbers of aphids, aphid-infested shoots and aphid damage (Figs. 1, 2; Tables 1, 2). Treatments may have had little effect due to low numbers of aphids and aphid-infested shoots before and after treatment. At Pleasant Valley Tree Farm, less than 5 stem mothers were beaten from a total of 320 trees pre-treatment and over 90% of the shoots were undamaged. At Swan's Balsam tree Farm, less than 15 stem mothers were beaten from a total of 320 trees pre-treatment and over 78% of the shoots were undamaged. Moreover, peak numbers of aphids and aphid-infested shoots per subplot treatment at both farms were still too low (PVTF, <6 aphids; SBTF <11 aphids) to cause significant damage to shoots (over 78% shoots undamaged) (Figs. 3, 4). Cultural treatments at the whole plot level may have not proven significant due to several factors such as application methods, phenology of clover (blooming after aphid peak), variation in native vegetation among rows or timing of mowing.

Only mean number of aphids at Swan's Balsam Tree Farm significantly differed, albeit marginally, among subplot treatments with lower numbers of aphids on Diazinon treated subplots and greater numbers of aphids on the control subplots across whole plot treatments (ANOVA F=2.7, df=3, 36, p=0.059)(Fig. 2, Table 2). Both Nettleton and Hain (1982) and Bradbury and Osgood (1986) found insecticides (including Diazinon AG500) to cause signicant declines in numbers of aphids. Results of this study indicate that when aphid numbers are relatively low pre-budbreak, insecticides do not have a significant impact on aphids nor do they significantly reduce damage. Although application methods or timing could have been a factor for little treatment effect, the importance of monitoring can not be over-emphasized. Under non-experimental conditions these plots should not have been treated.

Of interest, particularly at Pleasant Valley Tree Farm, was that mean numbers of aphids were greater on the combination of fertilized whole plot and insecticide subplot treatments. However, numbers were neither significantly different from other whole plot treatments nor large enough to cause significant differences in damage among plots. The data suggest that higher levels of soil N influenced numbers of aphids feeding on balsam fir. Although soil chemistry differed little among treatments, it was observed that nitrogen levels increased after treatment (Tables 3,4). Most likely, fertilizer applications as well as natural biological processes associated with spring conditions increased total soil N. Since more aphids were found in fertilized areas it is suggested that growers evaluate whether annual applications of fertilizer are necessary and, if used, either avoid application in previous aphid-damaged areas or apply after the flush of new growth.

Numbers of aphidophagous predators were too low in all study areas to quantify any treatment effects or sampling methods (PVTF: 13 syrphids, 2 coccinellids on 320 sample trees; SBTF: 10 syrphids, 3 coccinellids and 3 chrysopids on 320 sample trees). Low numbers may have been a result of low prey availability or due to past use of insecticides in these areas. Studies on the use of resident vegetation or cover crops among rows of fruit trees to increase and conserve aphidophaga have produced variable results (Bugg and Waddington 1994). It is too early to conclude whether numbers of aphidophaga can be increased by either planting white clover or by mowing native vegetation after it has flowered among Christmas trees. Bugg and Waddington (1994) found that white clover was less attractive to beneficial arthropods than other annual clovers (*Trifolium* spp). On whole plot treatments of this study, white clover flowered after the aphid population had crashed although in all treatments a mix of flowering broad-leafed weeds, e.g. dandelion (*Taraxicum* sp.) was available. On many occasions, bumblebees (Apidae) and adult hoverflies (Syrphidae) were observed foraging on aphid-infested shoots, presumably for honeydew. The syrphids may also have been laying eggs. It is unknown whether flowering plants may detract predator species which feed on nectar, pollen or honeydew from the aphid-infested shoots.

In conclusion, pre-budbreak applications of fertilizer enhanced aphid numbers while mowing and herbicide effects were insignificant (although effects may not be detected until the next growing season). The three insecticide treatments did not cause any significant difference in the proportion of shoots that remained undamaged. Results suggest that if growers monitor aphid numbers early or take in account proportions of infested shoots on marketable trees, potential damage can be predicted and wise management decisions, rather than wasteful guesses, can be made. Once curling of needles begins, insecticides do not effectively reduce aphids and their subsequent damage. Moreover, many infested shoots straighten out with maturation and if not, can be removed by annual shearing.

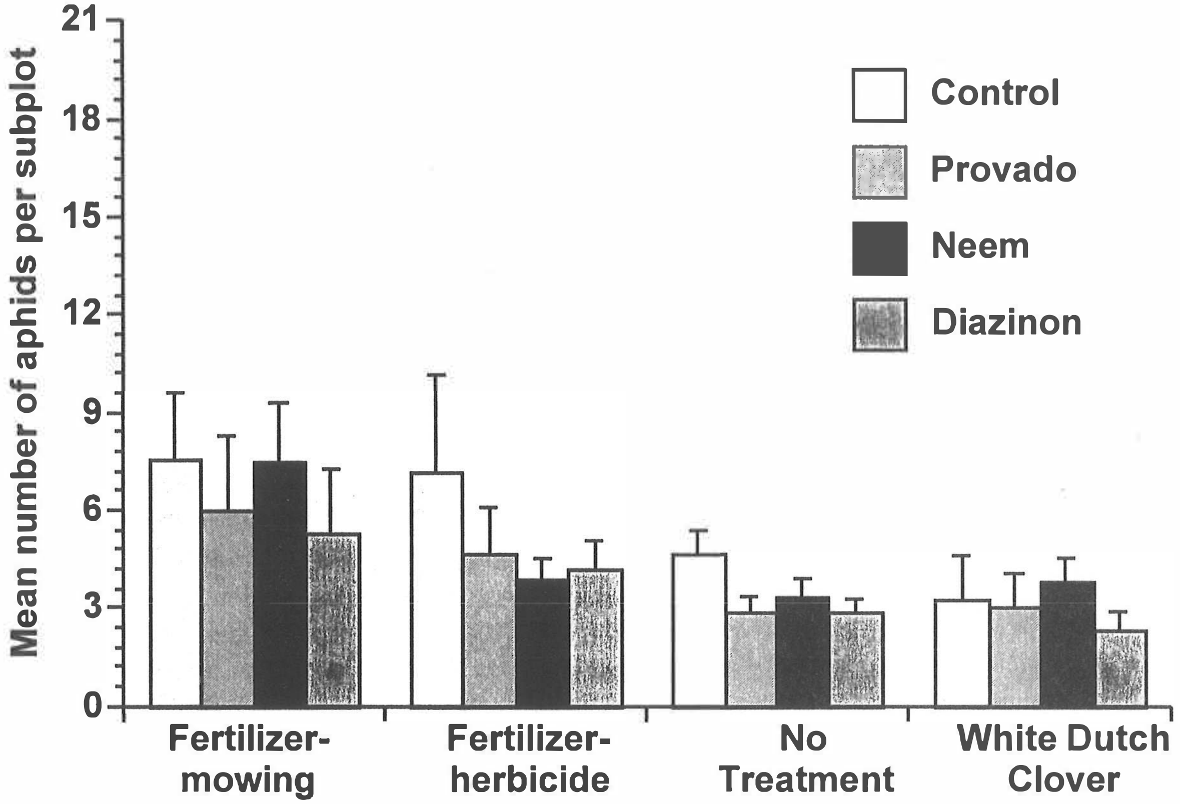

Fig. 1. Mean (+SE) number of aphids per subplot (n=16) at Pleasant Valley Tree Farm (ANOVA treatment effects; n.s. p>0.05).

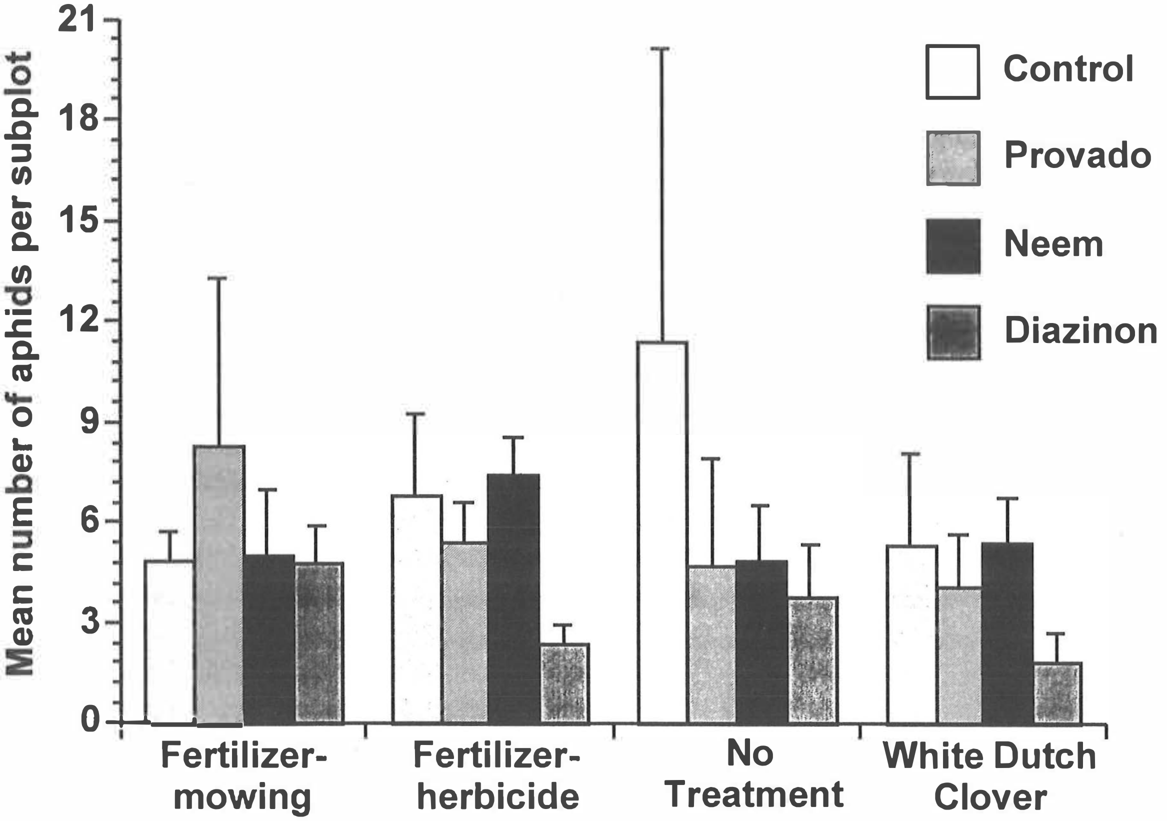

Fig. 2. Mean (+SE) number of aphids per subplot (n=16) at Swans Balsam Tree Farm (ANOVA subplot effect; F=2.71, df=3,36; p=0.059).

Table 1. Results of complete, randomized block split-plot ANOVA of whole plot and subplot effects and their interaction, Pleasant Valley Tree Farm, Dunn Co., WI.

Dependent Variable	Mean Sq. Effect	Mean Sq. Error	F	p - level
Wholeplot Effect (df=3)1				
Aphids	1.05019	0.56980	1.843093	0.2096312
Infested Shoots	0.04874	0.04121	1.182583	0.3697808
Undamaged Shoots	0.01273	0.04968	0.25616	0.8551214
Subplot Effect (df=3) 1				
Aphids	0.30001	0.18078	1.659538	0.1929587
Infested Shoots	0.02098	0.03260	0.643495	0.5920995
Undamaged Shoots	0.01162	0.01942	0.598659	0.6200449
Wholeplot * Subplot Effect (df=12) 2				
Aphids	0.113141	0.18078	0.625849	0.8061224
Infested Shoots	0.026552	0.032604	0.814357	0.6345344
Undamaged Shoots	0.022355	0.019415	1.151444	0.3526694

1 Block* wholeplot error term: df= 9

2 Sum of the interaction of (block* subplot) effect plus the three-way interaction of (block*whole plot*subplot: df=36

Table 2. Results of complete, randomized block split-plot ANOVA of whole plot and subplot effects and their interaction, Swans Balsam Tree Farm, Price Co., WI.

Dependent Variable	Mean Sq. Effect	Mean Sq. Error	F	p - level
Wholeplot Effect(df=3)1				
Aphids	0.34182	0.61477	0.5560141	0.6570467
Infested Shoots	0.01176	0.03054	0.3850351	0.7664896
Undamaged Shoots	0.01637	0.06080	0.2692756	0.8460211
Subplot Effect(df=3)1				
Aphids*	0.76226	0.28069	2.715645	0.0590342
Infested Shoots	0.03206	0.01833	1.749181	0.1743050
Undamaged Shoots	0.00700	0.02398	0.291725	0.8310814
Wholeplot * Subplot Effect(df=12)2				
Aphids	0.35108	0.28069	1.250758	0.2888916
Infested Shoots	0.02471	0.01833	1.348116	0.2356897
Undamaged Shoots	0.03662	0.02398	1.527213	0.1595603

1 Block* wholeplot error term: df= 9

2 Sum of the interaction of (block* subplot) effect plus the three-way interaction of (block*whole plot*subplot: df=36

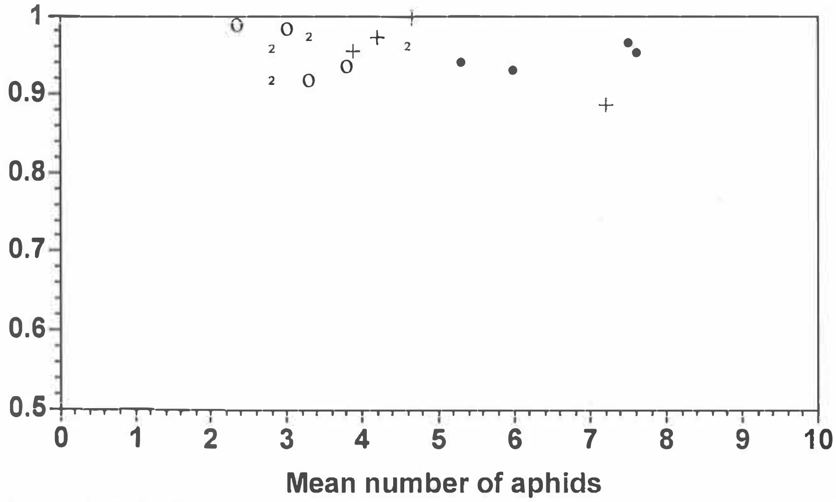

Fig. 3. Relationship between peak aphid infestation and resulting proportion of shoots undamaged within and among whole plot treatments, Pleasant Valley Tree Farm, Dunn Co. WI.

Table 3. Results of soil and leaf chemistry analyses, pre and post-treatment at Pleasant Valley Tree Farm, Dunn co., WI and Swans Balsam Tree Farm, Price Co., WI.

	pH		% O.M.		P (ppm)		K (ppm)		Total N (ppm)		% Leaf Nitrogen
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	
Pleasant Valley Tree Farm											
Fertilizer-Mowing	5.8a	5.9	1.7	1.8	50.0	59.0	58.8	47.5	782.8	838.8	2.9
	0.0b	*0.2*	*0.0*	*0.1*	*5.8*	*6.2*	*1.3*	*4.3*	*69.2*	*66.6*	
Fertilizer-Herbicide	5.8	5.6	1.7	1.9	80.0	79.5	62.5	51.3	731.4	864.3	3.0
	0.1	*0.2*	*0.2*	*0.2*	*13.5*	*9.0*	*2.5*	*3.1*	*111.3*	*98.2*	
Clover Intercrop	5.6	5.6	1.5	1.7	68.0	67.0	73.8	52.5	655.6	673.3	2.4
	0.1	*0.1*	*0.2*	*0.1*	*14.5*	*18.2*	*6.9*	*6.6*	*95.9*	*56.4*	
No Treatment	5.9	5.8	1.6	1.8	54.3	68.5	57.5	55.0	668.5	738.5	2.7
	0.1	*0.0*	*0.1*	*0.2*	*8.0*	*13.6*	*3.2*	*4.6*	*35.1*	*86.7*	
Swan's Balsam Tree Farm											
Fertilizer-Mowing	5.4	5.4	4.4	4.9	77.5	89.8	138.8	158.8	1684.2	1915.7	3.2
	0.1	*0.2*	*0.7*	*0.7*	*27.2*	*27.1*	*38.3*	*19.8*	*262.1*	*234.7*	
Fertilizer-Herbicide	5.4	5.4	4.9	4.8	61.5	64.3	145.0	136.3	1929.2	1938.7	3.4
	0.2	*0.2*	*0.6*	*0.3*	*13.6*	*12.8*	*31.8*	*20.3*	*211.2*	*124.2*	
Clover Intercrop	5.4	5.3	5.3	5.5	70.3	86.0	152.5	153.8	2063.6	2025.6	3.5
	0.1	*5.3*	*0.8*	*5.5*	*24.6*	*86.0*	*28.9*	*153.8*	*262.4*	*237.1*	
No Treatment	5.6	5.7	3.8	4.4	38.8	47.3	97.5	98.8	1487.0	1788.4	3.4
	0.2	*0.2*	*0.5*	*0.4*	*10.9*	*9.0*	*10.1*	*8.3*	*217.4*	*162.2*	

a=Mean of four subplots, b=SEM

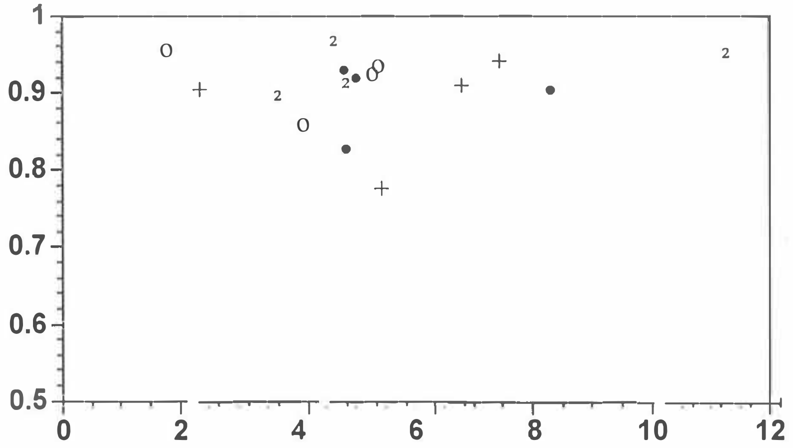

Fig.4. Relationship between peak aphid infestation and resulting proportion of shoots undamaged within and among whole plot treatments, Swans Balsam Tree Farm, Price Co.,WI.

Table 4. Results of complete, randomized block ANCOVA of treatment effects and their interaction upon soil nitrogen, Pleasant Valley Tree Farm, Dunn Co. and Swans Balsam Tree Farm, Price Co., WI.

	Pleasant Valley Tree Farm		Swan Balsam Tree Farm	
Wholeplot Effect	F	p - level	F	p - level
Block (df=3)	0.77	0.230	1.583	0.268
Treatment (df=3)	0.848	0.505	0.266	0.848
Pretreatment N (df=1)	11.41	0.010	12.139	0.008

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The natural role of spruce beetle and root pathogens in a sub-boreal spruce forest in central British Columbia: A retrospective study

B. STAFFAN LINDGREN AND KATHY J. LEWIS

Faculty of Natural Resources and Environmental Studies, University of Northern British Columbia
3333 University Way, Prince George, B.C., Canada V2N 4Z9

ABSTRACT The spruce beetle, *Dendroctonus rufipennis* (Kirby), is the most significant insect pest of spruce forests in North America. This bark beetle is responsible for intermittent, large scale outbreaks in mature stands, sometimes causing up to 90 % mortality. For that reason, spruce beetle outbreaks, along with stand replacing fires, have been considered driving forces in landscape level dynamics of these forests. In sub-boreal spruce stands in central British Columbia, we found that these stand replacement events are infrequent, and stand change generally gradual, largely due to root diseases and stem decays. Spruce beetle outbreaks act as species specific "high-grading" agents, removing mostly large, over-mature stems. Affected stands remain dominated by spruce, apparently due to this species' lower susceptibility or higher tolerance to stem and root decay than subalpine fir, *Abies lasiocarpa*.

KEY WORDS Spruce beetle, *Dendroctonus rufipennis*, root disease, decay, gap dynamics, *Picea, Abies lasiocarpa*, dendrochronology

THE SPRUCE BEETLE, *Dendroctonus rufipennis* Kirby (Coleoptera: Scolytidae) is the most significant insect pest of North American spruce forests. During the last century, extensive mortality of spruce due to sporadic spruce beetle outbreaks has occurred in eastern Canada and the New England states (U.S. Dept. Agric. 1991) and throughout western North America (Furniss and Carolin 1977). In three outbreaks between 1962 and 1982, spruce beetles killed an estimated 18 million m^3 of spruce in the Prince George Forest Region in northeastern British Columbia alone (Humphreys and Safranyik 1993). During such outbreaks up to 90 % of the spruce can be killed, sometimes over large areas. In British Columbia, spruce beetle mortality may account for as much as 10 % of the total volume of spruce harvested in any one year (Humphreys and Safranyik 1993).

Traditional methods of control include sanitation clear cutting, and the use of conventional trap trees, i.e., live trees felled into the shade (Humphreys and Safranyik 1993). The Bowron Valley clear cut in central British Columbia, a huge area stretching from the Bowron Lakes Provincial Park in the south to Purden Lake Provincial Park in the north, and subject to considerable controversy, was the result of sanitation and salvage logging in the wake of a devastating outbreak (Humphreys and Safranyik 1993). Other methods frequently used for spruce beetle management in northern B.C. include lethal trap trees and pheromone baiting.

Pages 122-130 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

Increased domestic and international public opinion against clear cutting as a generally acceptable forest harvesting method has led to forest management legislation in British Columbia restricting clear cut size. Partially in response to a public perception that traditional harvesting methods are unnatural, there is an increasing trend toward ecosystem management, central to which is the concept that we must learn from natural processes in order to effectively manage forest ecosystems in a sustainable fashion (Harvey 1994).

Schmid and Hinds (1974) made the first attempt at conceptualizing the successional dynamics of spruce-subalpine fir ecosystems in response to spruce beetle and other disturbances. They speculated that spruce and subalpine fir dominance in these ecosystems shift back and forth as the result of the influence by the spruce beetle and the western balsam bark beetle, *Dryocoetes confusus* Swaine. Because of its higher shade tolerance, subalpine fir dominates the understorey, but spruce maintains overstorey dominance due to a much lower mortality rate (Schmid and Frye 1977, Veblen 1986).

Using dendrochronological techniques and age structure analysis (Veblen et al. 1990), Veblen et al. (1991) found that the predominant effect by spruce beetle outbreaks in Engelmann spruce-subalpine fir stands in Colorado was the sustained growth release of previously suppressed understorey trees. This growth was sustained for more than 40 years, and was similar in magnitude for both spruce and subalpine fir. Both species continued to co-dominate stands following outbreaks. Veblen et al. (1994) calculated a mean return interval of spruce beetle outbreaks of 116.5 years, and a mean turnover time of 259 years. The return interval is the time between outbreaks in a particular stand, and the turnover time is the time interval during which all the stands in an area are affected by epidemics. Close to 39 % of the stands had been affected by spruce beetle epidemics, while 59 % had been affected by fire. Fire return interval in the same study was 202 years and turnover time 521 years (Veblen et al. 1994). Veblen et al. (1991) concluded that spruce beetle outbreaks may be as important as fire as a disturbance agent in some Colorado subalpine forests.

This study is a component of the research conducted within the context of the McGregor Model Forest. In response to increased national and international pressure, Canada implemented "Canada's Green Plan for a Healthy Environment" in December 1990. A component of the Green Plan was the "Partners in Sustainable Development of Forests" program, an element of which is the Model Forest Network (Oberle 1992). The Model Forest Network focuses on facilitating the implementation of sustainable forest management by developing innovative techniques, and by testing and demonstrating the best sustainable forestry practices available (Brand et al. 1996). The objective of our study is to assess historical natural impact of spruce beetle and other forest health agents on stand- and landscape-level ecological processes. The information will be integrated with other research and operational data, and used in the development of forest management strategies and tactics in spruce-subalpine fir ecosystems in central British Columbia. This paper presents some preliminary findings from this study.

Materials and Methods

The McGregor Model Forest consists of Northwood Pulp and Timber's Tree Farm License 30 (TFL 30), situated northeast of Prince George in the central interior of British Columbia. Its forests are dominated by white x Engelmann hybrid spruce and subalpine fir, with some lodgepole pine in the drier western areas, Douglas-fir mainly on well-drained ridges, and western hemlock and western red cedar in the wetter eastern part of the Model Forest. The majority of the Model Forest falls within the Sub-Boreal Spruce biogeoclimatic zone, (Pojar et al. 1987) which is characterized by a relatively cool and wet climate. The area has a history of harvesting, including selective harvesting of spruce conducted up until the 1950's, and clearcutting over the past 30-40 years. Spruce beetle infestations have had considerable impact on forestry activities in this area, and large areas of mature spruce forest have been clear cut in an attempt to control outbreaks.

Age class 8 and older (>140 years) spruce-leading stands were identified from Northwood Pulp and Timber inventory data. Eighteen stands were selected within TFL 30, and one stand outside the TFL. The stands were distributed across the central and western parts of the TFL to provide a reasonable coverage of the two major biogeoclimatic subzones within the sub-boreal spruce zone. In order to determine the kind of response resulting from overstorey removal in the study area, two sample stands were selected in areas where harvesting occurred in the 1940's and 1950's. One plot at site 10 was inadvertently placed outside the harvested area, and was not used for this assessment.

Increment cores were collected between September 11 and October 30, 1996. In each stand, cores were collected at 1.0-1.1 m from five or more dominant trees (mainly spruce, with some subalpine fir or Douglas-fir) in each of two plots. Thus, a minimum of 10 trees were cored in each of the stands. The diameter at breast height (dbh) and species were recorded. The cores were stored in a freezer until analyzed. Each core was mounted and sanded and ring width measurements were made using a WinDENDRO system at the Pacific Forestry Centre, Victoria, B.C. Ring widths were standardized using a horizontal line method, since this preserves early life growth characteristics, and provides better resolution for detecting growth releases (Veblen et al. 1990). Indices of all samples in each plot were averaged, to determine if there were consistent growth trends within and between plots, as well as within and between stands. The graphed data were visually assessed to detect long periods (30-40 years) of significantly increased growth occurring over a larger area. Such growth increases may signify a large scale disturbance, such as a spruce beetle outbreak (Veblen et al.1990).

Preliminary data on butt decay were collected from a clearcut near site 3. A 6 m wide line transect survey was conducted on July 12, 1996. Each stump along the line was visually examined for evidence of butt rot. The species of the stump was determined and its diameter measured. The incidence of butt rot was then calculated by tree species and 10 cm diameter class.

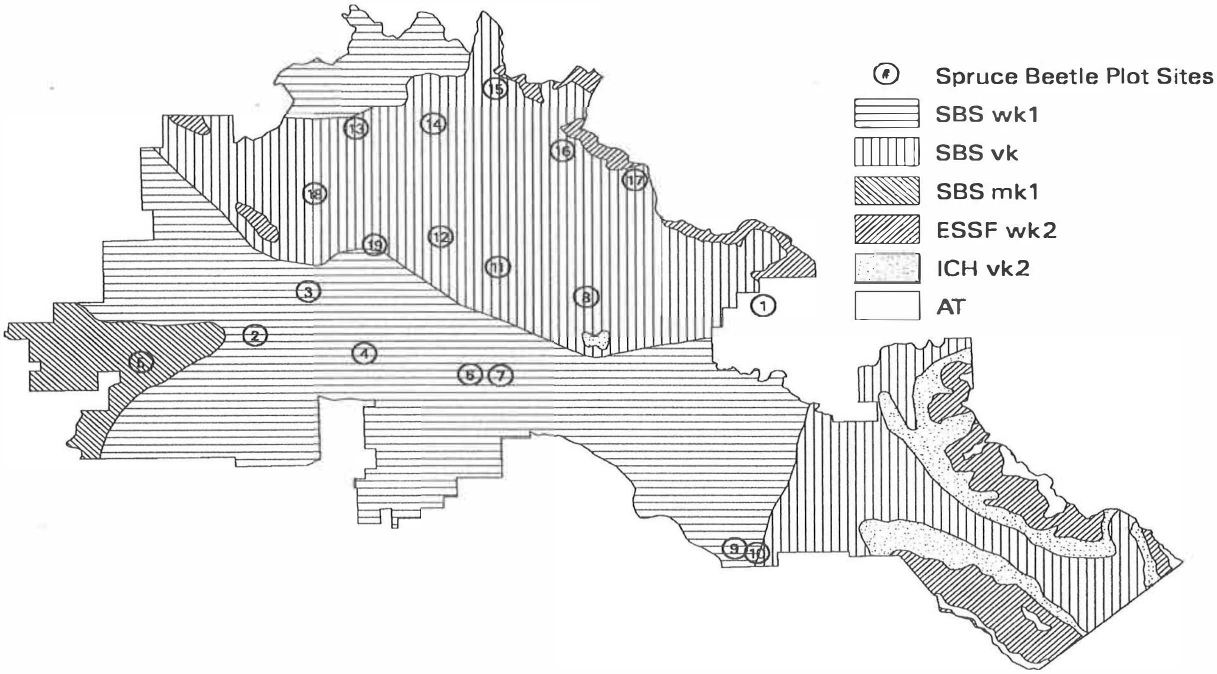

Figure 1. Map of Tree Farm Licence 30, northeast of Prince George, B.C., showing sample locations and biogeoclimatic zones and subzones. SBS = Sub-boreal spruce, wk = wet-cool, vk = very cool, mk = moist cool, ESSF = Engelmann spruce - Subalpine fir, ICH = Interior Cedar-Hemlock, AT = Alpine Tundra. See Pojar et al. 1987 for an explanation of the classification system.

Results and Discussion

Figure 1 shows the location of the sample sites in the TFL. Sites 9 and 10 were selected in areas which had experienced overstorey removal by selective harvesting in the 1940's and 1950's. At site 9, a significant release of tree growth is evident starting in the early 1940's and extending to the 1980's, after which growth rates are reduced (Fig. 2). Veblen et al. (1990) used a 250 % increase in growth to define a release. They argued that smaller increases could be due to widespread wind throw, or other events that affected surviving trees to a lesser extent than a widespread spruce beetle outbreak. The growth increase visible in site 9 is consistent with a release as defined by Veblen et al. (1990).

Stands in the eastern part of the TFL (sites 2, 3, and 5, and possibly 4) exhibited rapid initial growth in the mid- to late 1800's (Fig. 3). This indicates that the sample trees were established under open conditions, as would be the case following a stand replacing fire, or some other stand replacing disturbance event (Veblen et al. 1990). The oldest trees in these areas were about 130 - 140 years old.

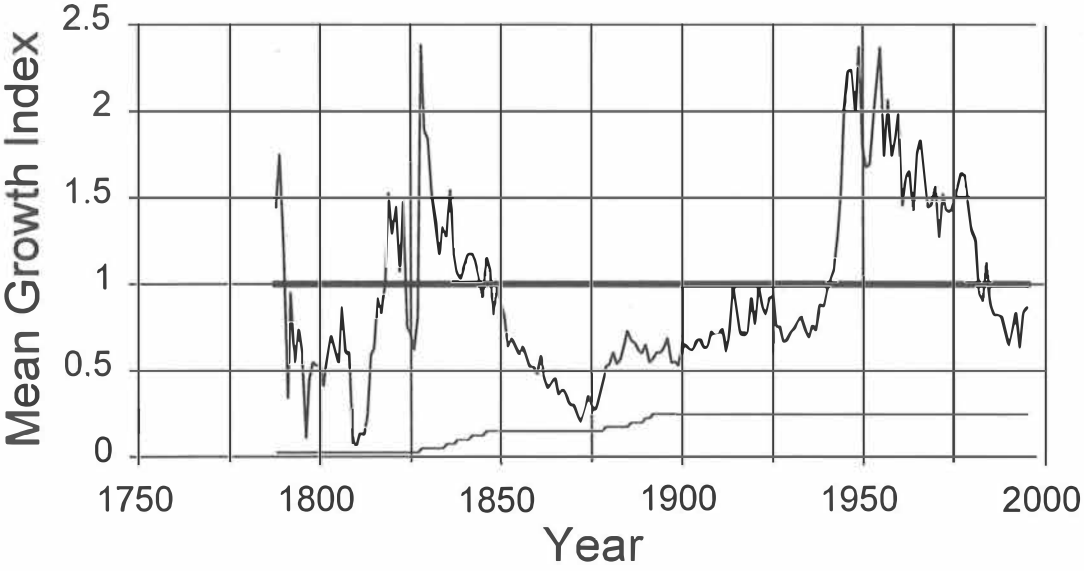

Fig. 2. Mean growth index of 10 trees at site 9, showing strong growth release following overstorey removal due to partial cutting in the 1940's. Note the increased growth in the early 1800's. The line at the bottom of the graph denotes sample size 1-10.

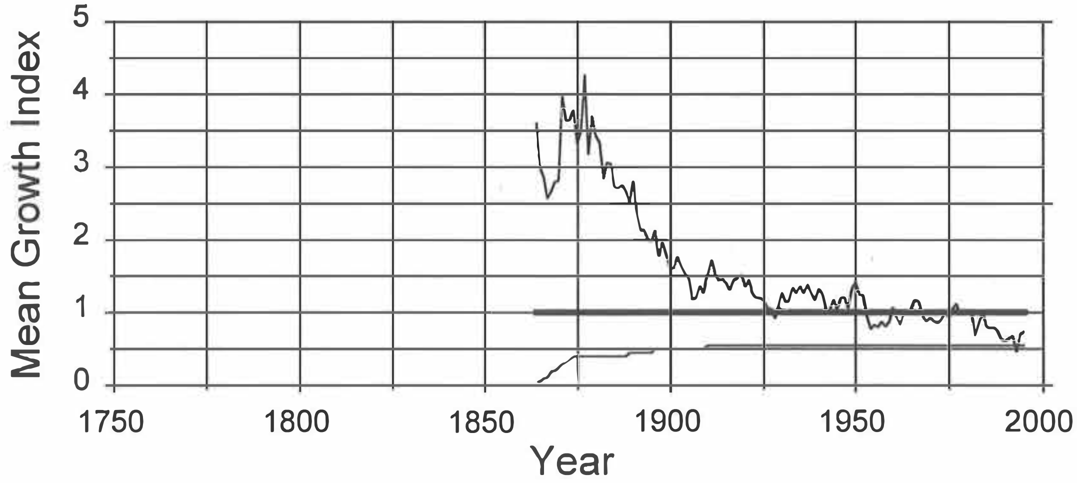

Fig. 3. Mean growth index of 10 trees at site 3, showing rapid initial growth indicating that the trees were established during open conditions. The line at the bottom of the graph denotes sample size 1-10.

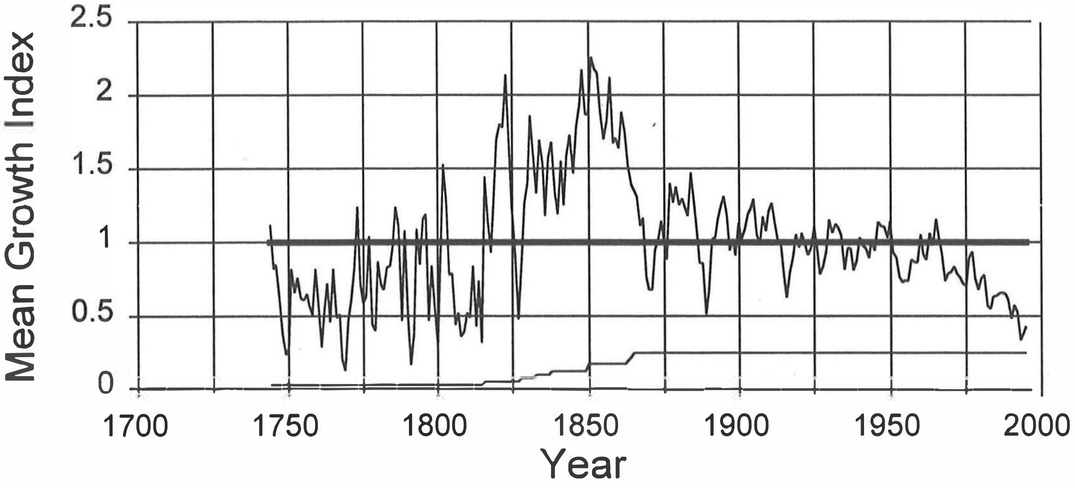

Figure 4. Mean growth index of 10 trees at site 11, showing increased growth from about 1820 to 1870, possibly indicating that this stand experienced a major disturbance, e.g., spruce beetle outbreak, at the beginning of this period. The line at the bottom of the graph denotes sample size 1-10.

In the rest of the TFL, the oldest trees sampled were 200 - 330 years old. In most of these stands there is a clear increase in growth rates starting in the early 1820's, and extending into the 1860's (Fig. 4).

The data prior to this period is highly variable, because only a low number of trees were found that were significantly older than 220 years. The level of increased growth is generally lower than defined by Veblen et al. (1990) as constituting a release, indicating that it could be the result of some influence other than spruce beetle. The increased growth occurs during a period which has been interpreted as cooler than normal, and it precedes a general warming trend which started around 1840, based on a climate reconstruction from tree ring indices of *Picea glauca* in Alaska and the Yukon (Jacoby et al. 1985). Climate reconstructed from *Pinus flexilis* in southwestern Alberta indicates a decrease in tree ring widths lasting from 1840 - about 1875 (Case and MacDonald 1995). Thus, it appears unlikely that climate is responsible for the observed increase in growth.

The most compelling support for the hypothesis that at least some of the growth increase is a result of spruce beetle-caused mortality comes from a fur trader by the name of John McLean. Describing the beautiful scenery of New Caledonia, as the area around Prince George was called, he noted in his diary in 1836 that "...unfortunately, however, the woods are decaying rapidly, particularly several varieties of fir, which are being destroyed by an insect that preys on the bark: when the country is denuded of this ornament, and its ridges have become bald, it will present a desolate appearance (McLean 1849). The "fir" he refers to would have been spruce. Thus, it is probable that significant mortality occurred some time before the mid 1830's, and that large scale spruce beetle outbreaks may in fact have occurred in the area as early as the 1920's.

Nevertheless, there are several potential explanations for the low rate of increased growth relative to Veblen et al.'s (1990) definition of a release. Firstly, the phenomenon may be due to widespread windthrow, as suggested by Veblen et al. (1990), and secondly, growing conditions may have become more favourable. However, John McLean's account (McLean 1849) indicates that significant bark beetle-caused mortality of spruce did occur in the area during this time. Thus, it is reasonable to assume that the growth increase is due at least in part to mortality of overstorey trees. The lower than expected response could then be explained by stand structure, at least if today's conditions are representative of what the stands looked like 180 years ago. The spruce stands in TFL 30 are relatively open to begin with, exhibiting many gaps and a very uneven canopy. Thus, moderate overstorey removal may not have affected stands as drastically as may be the case in Colorado. The growth release observed following partial cutting (Fig. 3) may be more similar to the release observed in Colorado since it is a sudden, very complete opening, while bark beetles kill the overstorey gradually, the killed trees remain standing for some time, and the distribution of mortality is frequently patchy.

Veblen et al. (1990) found that chronologies could be extended significantly by coring dead trees in areas with relatively recent mortality. Spruce trees killed by spruce beetle sometimes remain standing for up to 40 years in Colorado. In central British Columbia, however, dead trees appear to be rapidly colonized by decay fungi, and in most cases they become unsuitable for coring well within 10 years.

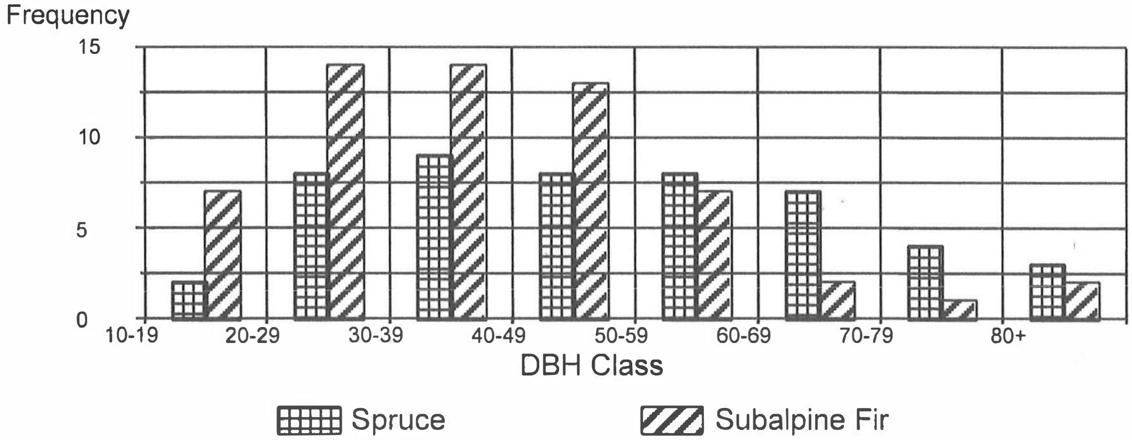

Figure 5. Diameter class distributions of spruce and subalpine fir, respectively, based on a stump survey of a clearcut near Site 11.

The preliminary survey of stumps revealed that small diameter classes were dominated by subalpine fir, i.e., subalpine fir dominated the understorey, whereas large diameter classes were dominated by spruce (Figure 5). If spruce beetle outbreaks periodically removed overstorey spruce, one should see a shift in stand composition to subalpine spruce, which obviously has higher recruitment rates in these mature stands. This is expected, since subalpine fir regenerates more readily than spruce under the canopy. However, similar to what Veblen (1986) observed in the Colorado front range, spruce continues to dominate the canopy trees in TFL 30. Veblen (1986) concluded that this was due to differential mortality of understorey trees. Our survey of stumps indicated that a similar phenomenon occurs in TFL 30, and that the mortality agents are pathogenic and decay fungi (Figure 6). In fact, it was extremely difficult to find large diameter subalpine firs for coring in these stands, since virtually all of these were more or less severely affected by butt rot. These trees would eventually die and fall, providing gaps and nurse logs, which act to increase recruitment of spruce in the stand.

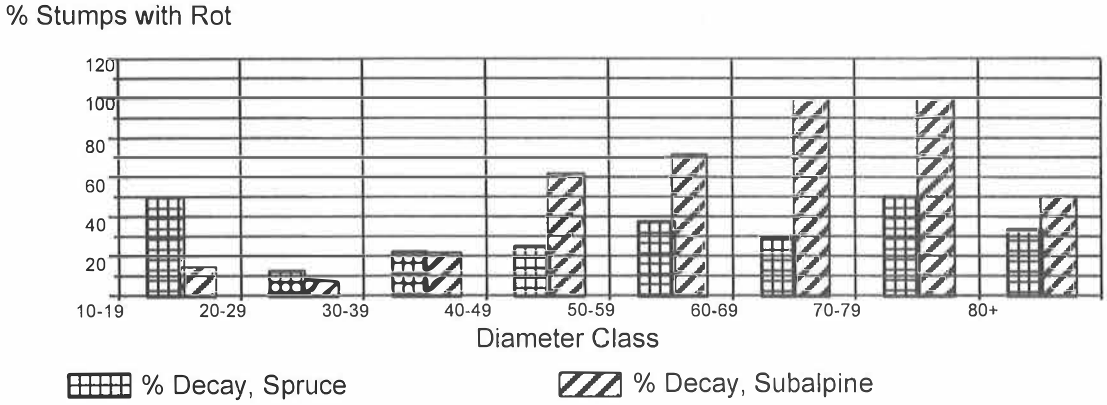

Figure 6. Percent of stumps with visible evidence of butt decay in a clear cut near Site 11.

CONCLUSION

Stand replacement fires in the area are very rare (B. Hawkes pers. comm.). For example, there is no evidence of fire in a stand of 350-400 year-old Douglas-fir even though the spruce component in the stand is only 200 - 250 years old. Based on this, and our preliminary data, we hypothesize that pathogenic and decay fungi are the primary agents of renewal in these ecosystems. These organisms accentuate the uneven stand structure by causing small gaps. They cause particularly high levels of mortality in subalpine fir, ensuring that stands remain spruce dominated even if spruce beetle outbreaks do occur.

The increased growth during the early part of the 19th Century could possibly be interpreted to be the result of a spruce beetle outbreak in TFL 30. However, the dendrochronological indication of this is unclear, possibly due to the open and uneven stand structure in the study area. The best support for the spruce beetle outbreak hypothesis is gained from the 1836 diary notation of a Hudson's Bay Company fur trader (McLean 1849), but his testimony does not reveal the exact geographical location of the bark beetle-caused mortality he observed. Thus, more extensive sampling is required to clarify how these stands have developed over the last centuries.

Acknowledgments

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Tomicus destruens (Wollaston): biology and behaviour in Central Italy

CATIA NANNI[1] AND RIZIERO TIBERI[2]

[1]Plant Protection Service - Emilia Romagna, Servicio fitosanitario regionale, via corticella 133,
I-40129 Bologna, Italy
[2]Forest and Agricultural Pathology and Zoology Institute, Florence, Italy

ABSTRACT The symptoms of decline that increase in Italian coastal pinewoods are caused by abiotic and biotic factors with the scolytid *Tomicus destruens* playing a leading role. Frequent and repeated physiological stresses, such as drought, climatic and ground water anomalies, phytophagous infestations (by sucking and defoliating insects) and fungal infections, have promoted the demographic increase of this endemic bark beetle. Like those of the others Tomicina, *T. destruens* infestations are very detrimental to the host because adults have to feed on the shoots of vigorous plants to enable their gonads to mature. Shoot death causes physiological anomalies and makes the plants vulnerable to subsequent attacks. In Central and Northern Italy, *T. destruens* develops two overlapping generations a year. The overlap in generations also occurs during hibernation, when adults, pupae, larvae and sometimes eggs have been observed at the same time. No significant difference has been observed concerning the biology of *T. destruens* in Central and Northern Italy, except that in the Northern Adriatic area mostly adults overwinter, in the shoots or in the stumps. These *T. destruens* biological characteristics greatly complicate pest management, which is already difficult in natural areas.

KEY WORDS *Tomicus destruens*, biology, behaviour, control

TOMICUS DESTRUENS (WOLLASTON), Coleoptera Scolytidae, which some authors still regard as a *Tomicus piniperda* L. termophile entity (Santini and Prestininzi 1991), is spread throughout the Mediterranean coastal area, and like the other *Tomicina* that are present in Italy, its preferred host are of the genus *Pinus*, especially, *P. halepensis* and *P. pinea.*

During the last few years, the coastal pinewoods of Central and Northern Italy have endured intense infestations from *T. destruens*. The high susceptibility of these biocoenoses to infestation appears to be connected with climatic and ground water unbalances that have caused physiological stress to the trees and have led to intense and repeated attacks by phytophagous insects and pathogenic agents (above all fungi) (Moriondo *et al.* 1995).

The purpose of the research was to study the role of *T. destruens* in the phenomena leading to the decline of pine stands and to define more precisely some aspects of their biology. The overall objective is to develop a programme for a rational and effective control.

Materials And Methods

The research was initiated in 1992, at two sites: in pine stands situated on the Tirrenic coast of Central Italy (Alberese, situated in Uccellina Park, and Feniglia on the Argentario

Pages 131-134 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

promontory); and in pine stands of the North Adriatic coast (Cervia and Classe, both situated in Po Delta Park).

The forests under examination consist of unevenaged *P. pinea*, with isolated plants or sporadic groups of *P. pinaster*, and broad-leaved trees. In the Tirrenic pine forests, the broad-leaved trees are present within relatively small groups of evergreen species, while in the Adriatic pine forests they are more frequent, represented by species such as *Quercus robur, Q. pubescens, Fraxinus* spp., *Populus* spp., *Salix* spp., *Alnus glutinosa, Carpinus orientalis.*

Biological and behavioural research of *T. destruens* has taken place previously in areas where its density was high, through systematic surveys in the field. Moreover, the life-cycle of this insect has been observed in detail on samples of infested trunks taken from different heights of the trees and reared in the laboratory.

Periodical monitoring has also been carried out throughout the entire pine forests in order to verify the extent and intensity of infestations.

Results

The data gathered in the Tirrenic and Adriatic pine stands did not show any significant differences between the two areas with regard to the development of the two generations that *T. destruens* completes each year, except that in the Northern Adriatic area primarily adults hibernate, and they do so in the shoots or in the stumps of the trees. In Tirrenic pinewoods pupae, larvae, adults and occasionally eggs can be observed at the same time. Adults remain in shoots or under bark from autumn to spring, and in some cases they were also observed reproducing.

In Central Italy, therefore, hibernation during different growth phases results in the oviposition of the first generation potentially spread over a long period of time (from February to May). However, most hibernating adults start their reproductive activity in April and May, attacking branches and boughs of vigorous plants which do not appear to be stressed. On pines broken off and on those that have just been cut down during normal silvicultural practices, we observed about 50 attacks for every metre of length on the entire trunk. In Northern Adriatic pinewoods, where adults hibernate, the oviposition of the first generation occurs over a much shorter period (between March and April). In spite of these differences, the adults of the first generation emerge at both sites at the beginning of the summer. This is indicated by the characteristic resin cones which appear on the shoots of vigorous plants. The resin cones demonstrate that adults have entered the shoots in order to attain reproductive maturity. This can be observed as early as July. In August, the infested shoots become reddish, an indication of both the presence and the intensity of the attack upon the crown of the plant by the adults of the first generation.

In August, the oviposition of the second generation also takes place. In the Adriatic pine stands oviposition is concluded before winter, while in the Tirrenic pinewoods it follows an irregular course. This is because the adults of the first generation remain in the shoots longer in order to reach sexual maturity. This delay is probably due to the high temperatures and the long drought periods which occur during the summer in Central Italy, and which influence the vegetative growth of the trees, thus slowing scolytid maturation.

In Adriatic pinewoods, *T. destruens* is more common in back dune areas, where ground water level is high and salt water enters. This weakens the plants, enabling primary attack by fungi, such as *Heterobasidion annosum* (Fr.) Bref. and *Phellinus (Fomes) pini* (Bref. ex Fr.) A. Ames (Nanni pers. obs., 1995). Similarly, the areas most attacked in Tirrenic pine stands are those where salt water infiltration occurs as a result of the lowering of the water-table, due to the intense drawing of fresh water which take place during the summer.

Discussion

The results that were obtained from the research have helped clarify several aspects of scolytid biology and the behaviour in Central and Northern Italian pinewoods.

This information is very important for pest management in these biocoenosis, the stability of which is very low from a silvicultural point of view (Tiberi 1995).

Generally, for the purpose of forest protection, it is impossible to use all the technical means available, not only in order to avoid undesirable collateral effects in the biocoenosis, but also because there is no economic imperative in the short term.

Moreover, many forests, which were planted for a range of different reasons now fulfill mainly environmental, protective and recreational roles. In pest management, therefore, it is necessary to consider the potential benefits from action, which depends on the use and the ecological importance of the forests concerned, the constraints of forestry politics, and the expectation of the public. To draw up a rational intervention programme it is necessary to have considerable knowledge of the interactions between the various ecosystem components as well as of the nature of the problem itself. This would guarantee a wide range of choice amongst the various defences that could be undertaken (Covassi 1989, Tiberi 1996). However, that choice is difficult when the forest concerned has been severely destabilized and subject to xylophagous attack, as is the case with the pine stands which have been the object of this research. In these situations, there are many obstacles in the way of creating an adequate control of *T. destruens*, primarily because of the behaviour of this insect. The long periods spent under the bark or within the shoots make it vulnerable to control methods for only a short period of time. Therefore, control efforts must rely upon preventive measures, such as the quick elimination and removal of stressed trees, which are more susceptible to scolytid infestation. Another course of preventive action, is to prepare several pieces of bait-trunk to attract the reproducing adults. Obviously, this practice is effective only if it is repeated over a period of many years.

Conclusions

During the last few years the Adriatic and Tirrenic coastal pine stands have been subject to various forms of stress as a result of a variety of interacting factors. The most important among these have been drought, ground water fluctuations, the attacks of primary pest-insects (sucking and defoliating insects) and fungal infection.

This phenomenon of extreme disturbance of the ecological balance of the forest stand has increased the activity of biotic factors, referred to as “weakness agents”, and amongst these, *T. destruens* is the most prevalent. Attacks of *T. destruens* is, therefore, a symptom of a greater problem.

In the areas under investigation *T. destruens* is endemic and has undergone dangerous and sometimes catastrophic increases. Intense attacks have taken place in limited but nevertheless wide areas, such as in the Alberese pine stands where, since 1988, some 200 mature trees have been felled each year, in addition to those young infested trees which are felled during the usual thinnings that are part of the standard working plan.

With regards to the coastal pinewoods of Central Italy, this investigation has confirmed that *T. destruens* develops two generations a year, with a considerable overlapping taking place of the different growth phases. This phenomenon also occurs during hibernation, when adults, pupae, larvae and sometimes eggs have all been observed at the same time. Clearly, this overlapping of different growth phases greatly complicates pest management.

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Integrating Pheromone and Silvicultural Methods for Managing the Douglas-fir Beetle

DARRELL W. ROSS[1] AND GARY E. DATERMAN[2]

[1]Department of Forest Science, Oregon State University, Corvallis, OR 97331-7501, USA
[2]USDA Forest Service, Pacific Northwest Research Station, 3200 Jefferson Way, Corvallis, OR 97331, USA

ABSTRACT Historically, approaches to reducing losses caused by the Douglas-fir beetle have focused on protecting the timber resource. Past recommendations included harvesting mature stands, treatment or removal of large diameter slash, prompt salvage of dead and dying trees, preventing tree stress and injury, thinning of young stands, and treatment or processing of infested material to destroy developing brood. Although some of these recommendations are still appropriate, there are limitations to implementing them in the context of ecosystem management. Recently, several new methods of using aggregation and antiaggregation pheromones of the Douglas-fir beetle have been shown to be effective for manipulating the distribution and possibly amount of tree mortality during outbreaks. These new methods along with existing silvicultural and pheromone-based treatments provide new opportunities to develop integrated programs for managing this important forest pest. The potency of these pheromone technologies suggest the potential for regulating beetle activity over wide areas, thus raising the need for field-testing at landscape scales.

KEYWORDS Scolytidae, *Dendroctonus pseudotsugae*, pheromones, 3-methylcyclohex-2-en-1-one, MCH, mass trapping

THE DOUGLAS-FIR beetle, *Dendroctonus pseudotsugae* Hopkins, is found throughout the range of Douglas-fir, *Pseudotsugae menziesii* (Mirb.) Franco, in western North America (Furniss and Carolin 1977). This beetle usually breeds in portions of tree boles that are greater than about 20 cm in diameter. At low population densities, most infestations occur in trees that have recently died or live trees with limited defenses resulting from stress or injury (McMullen and Atkins 1962, Furniss 1965, Rudinsky 1966, Furniss et al. 1981, Wright et al. 1984). When populations reach high densities, large numbers of healthy trees may be successfully attacked and killed (Johnson and Belluschi 1969, Furniss et al. 1979). Epidemics often develop following natural or human-caused disturbances that create abundant breeding sites. Tree mortality during epidemics can alter the structure, composition, and ecological processes of forests in ways that may conflict with resource management objectives (Cornelius 1955, Furniss and Orr 1978, Hadley and Veblen 1993).

The Douglas-fir beetle is similar to other aggressive bark beetle species in the genus *Dendroctonus*. This species has only one generation per year, although sister broods may be produced when the weather is favorable. Adults fly from early spring through mid-summer (Ross and Daterman 1996). Broods overwinter within the phloem in the adult, pupal, or late larval stages. The pheromone system of the Douglas-fir beetle has been well studied. Among the many compounds that have been found to be attractive to the Douglas-fir beetle, combinations of frontalin with seudenol, ethanol, and/or MCOL elicit the strongest responses (Pitman and Vité 1970, Vité et al. 1972, Rudinsky et al. 1974, Pitman et al. 1975, Libbey et al. 1983, Lindgren et al. 1992, Ross and Datermen 1995a). The antiaggregation pheromone, 3-methylcyclohex-2-en-1-one (MCH), significantly reduces beetle response to attractant

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odors (Kinzer et al. 1971, Furniss et al. 1972, Rudinsky et al. 1972, Furniss et al. 1974, McGregor et al. 1984, Lindgren et al. 1988).

History of Management Practices

Until recently, management of Douglas-fir in the U.S. was primarily directed toward timber production. Consequently, the earliest recommendations to prevent losses caused by the Douglas-fir beetle were developed to protect the timber resource. These recommendations emphasized silvicultural activities that either reduced the availability of breeding sites or directly reduced the beetle population (Bedard 1950, Furniss 1959, Lejeune et al. 1961, Williamson and Price 1971, Furniss and Orr 1978, Furniss et al. 1979). Recommendations for limiting potential breeding sites included harvesting mature stands, treatment or disposal of slash greater than 20 cm in diameter, prompt salvage of windthrown, fire-damaged, and otherwise dead and dying trees, fire prevention, and thinning of young stands. Harvesting or treatment of infested material to destroy developing broods was also encouraged to reduce beetle populations. During outbreaks, the use of felled trap-trees was recommended to concentrate beetle activity in accessible areas where the brood could be destroyed (Lejeune et al. 1961). The effectiveness of these practices was often limited because of an inability to treat the entire infested area in a timely manner.

New possibilities for managing the Douglas-fir beetle arose following the identification of its aggregation and antiaggregation pheromones. Because outbreaks often occur following disturbances, particularly windstorms, a considerable effort was devoted to developing ways to use MCH to prevent the infestation of windthrown trees. Although an effective treatment was developed and shown to be operationally feasible (McGregor et al. 1984), it has never been implemented because of continuing delays in the registration process. Aggregation pheromones have been used to bait trap-trees making them more competitive with natural sources of attraction (Knopf and Pitman 1972, Pitman 1973, Ringold et al. 1975, Thier and Weatherby 1991). Since this application of pheromones does not require registration in the U.S., baited trap-trees have been used in operational programs (Patterson 1992). However, the efficacy of baited trap-trees has never been fully evaluated.

Emerging Pheromone-Based Methods

Since 1992 we have been studying new pheromone-based management stategies for the Douglas-fir beetle. We have focused primarily on two treatments. First, using pheromones to protect live trees in relatively small, high-risk, high-value stands during outbreaks. And second, using pheromone-baited traps to affect the amount and distribution of beetle-caused tree mortality at the landscape scale during outbreaks.

Antiaggregation Peromone, MCH

A study conducted in northeastern Oregon in 1992 demonstrated the feasibility of using pheromones to protect live trees in small, high-value stands (Ross and Daterman 1994). A combination of pheromone-baited traps and MCH application significantly reduced the percentage of host trees that were infested compared with an untreated control (Fig. 1). Although this treatment was successful in reducing the infestation within the area designated for protection, there were some problems associated with using traps for this purpose including "spill-over" attacks on nearby trees. Consequently, a follow-up study was conducted in the same general area in 1993 to test the efficacy of MCH alone (Ross and Daterman 1995b). The results indicated that MCH alone was at least equal to and perhaps more effective than the combination of baited traps and MCH that was tested the previous year (Fig. 1). In both of these studies, MCH was applied as bubble capsules at a rate of 150 capsules per hectare (60 g/ha).

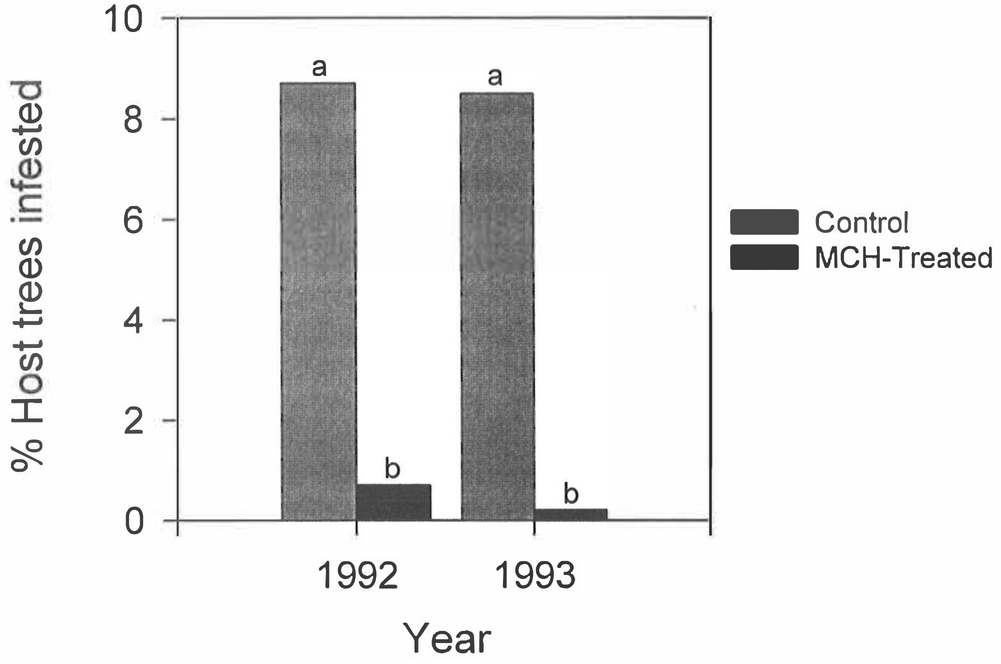

Fig. 1. Percentage of host trees infested on MCH-treated (60 g/ha) and control plots during studies conducted in northeastern Oregon in 1992 and 1993. In 1992, the treatment was a combination of MCH and pheromone-baited traps. In 1993, the treatment was MCH alone. Both years, differences between treated and control plots were significant ($\underline{P} < 0.05$).

Further studies were conducted in 1994 and 1995 to determine the lowest effective dose of MCH for protecting live trees (Ross et al. 1996). Each year, the tests were replicated in high-risk stands in Oregon, Idaho, Montana, and Utah. In 1994 and 1995, MCH was applied at rates of 0, 20, 40, and 60 g/ha and 0, 6, 12, and 20 g/ha, respectively. In 1994, all three doses of MCH were equally effective in reducing infestations compared to the untreated control (Fig. 2). In 1995, there were no significant differences in the percentage of host trees that were infested among the treatments, although the infestation rate at the highest dose was less than half that following any other treatment (Fig. 3). These results demonstrated that MCH applied at rates as low as 20 g/ha can reduce the probability that high-risk trees will become infested. However, for practical purposes slightly higher doses should be used to ensure treatment efficacy.

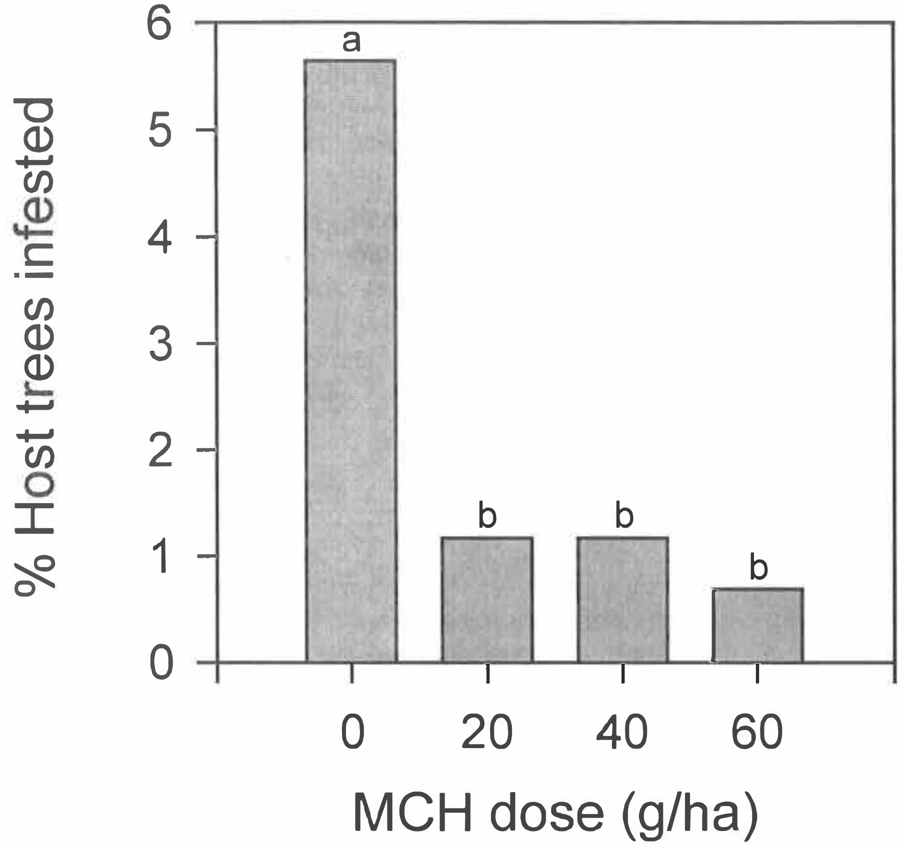

Fig. 2. Percentage of host trees infested following application of MCH at various doses on plots throughout the western U.S. in 1994. Letters indicate significant differences (P < 0.05).

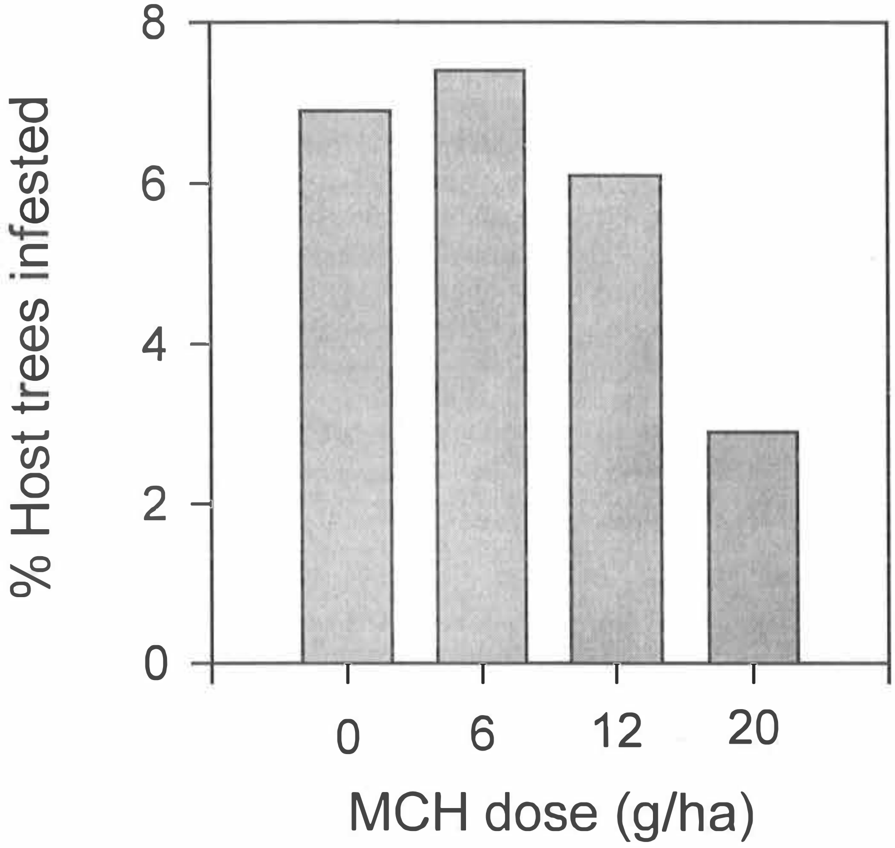

Fig. 3. Percentage of host trees infested following application of MCH at various doses on plots throughout the western U.S. in 1995. There were no significant differences among treatments ($\underline{P} > 0.05$).

In all four studies conducted between 1992 and 1995, pheromone-baited traps were placed at the center of MCH-treated and control plots to evaluate treatment effects. In every case, traps on MCH-treated plots caught significantly fewer Douglas-fir beetles compared with traps on untreated controls. In contrast, there were much smaller or, in most cases, no differences in catches of predators among MCH-treated and control plots (Fig. 4). Furthermore, there were no significant differences in abundance of natural enemies or brood production from the lower 7 m of mass-attacked trees on MCH-treated and control plots in 1995 (Table 1, unpublished data). This limited evidence suggests that MCH treatments have no negative impacts on natural enemies.

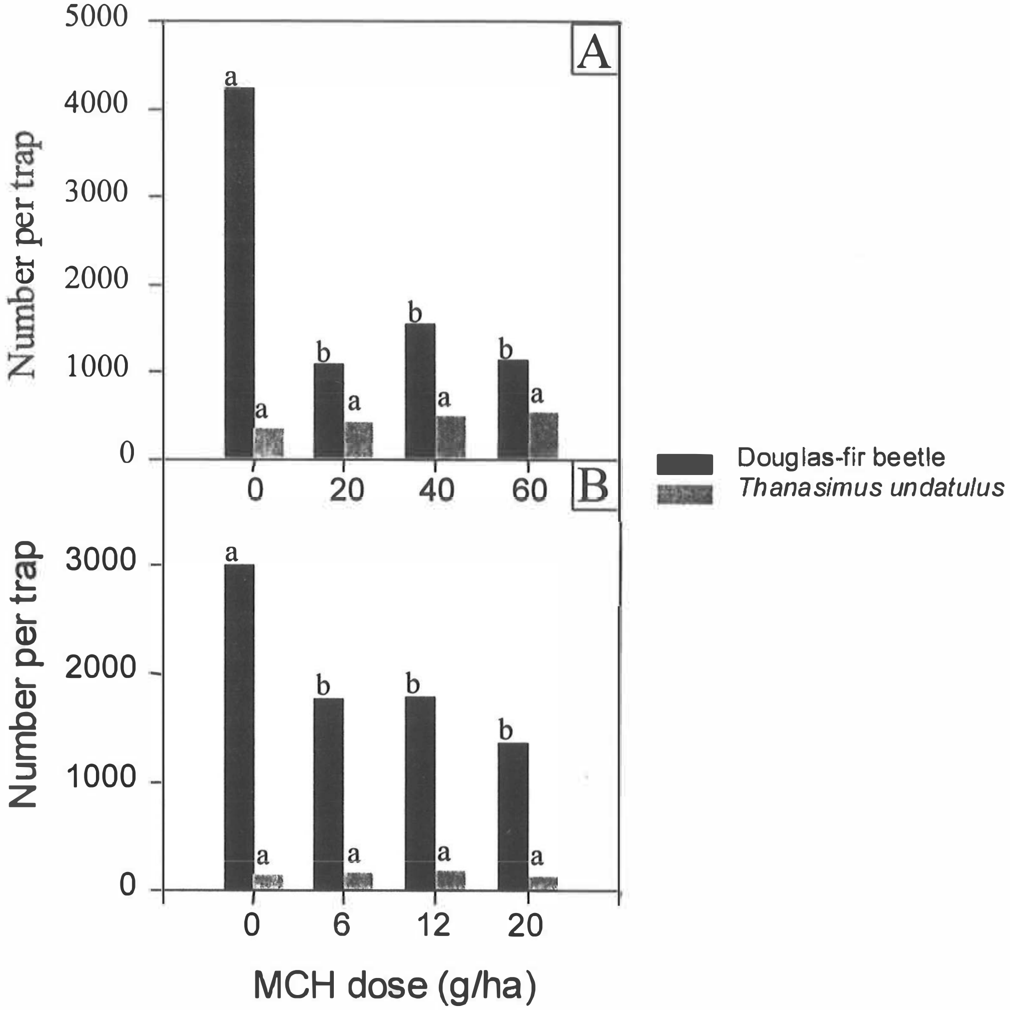

Fig. 4. Mean numbers of Douglas-fir beetles and *Thanasimus undatulus* collected in pheromone-baited traps at plot centers following application of MCH at various doses in (A) 1994 and (B) 1995. For each year and insect species, letters indicate significant differences ($\underline{P} < 0.05$).

Table 1. Brood production and brood adult and natural enemy densities (#/m²) in bark samples collected at 7 m height from Douglas-fir beetle infested trees on MCH-treated and control plots in northeastern Oregon, 1995.

	Control	MCH-treated
Brood production (brood adults/2(attacks))	0.58	0.59
Brood adults	138.2	162.3
Hymenopteran cocoons	129.2	144.9
Thanasimus undatulus	0	3.3
Enoclerus sphegeus	5.8	3.3

Data from four 120 cm² samples collected from 7 trees in each treatment. There were no significant differences between treatments ($\underline{P} > 0.05$).

At the present time, the use of MCH to protect live trees in high-value stands is an operational treatment. The only obstacle to full implementation of this technology in the U.S. is registration of MCH by the Environmental Protection Agency.

Aggregation Pheromones

Aggregation pheromones have been used in the trap-tree harvest method to concentrate Douglas-fir beetles. In this approach, pheromone-baited trees are harvested after they become infested to destroy the developing brood. Replacing the baited tree with an artificial trap could potentially increase the efficiency of a trapping program in a number of ways. Possible advantages of traps over trees include more flexibility in placement, unlimited trapping capacity, no reemergence, and less impact on some natural enemies.

A study conducted in northeastern Oregon in 1992 and 1993 demonstrated the potential for using pheromone-baited traps to manage the Douglas-fir beetle (Ross and Daterman 1997). Large numbers of beetles were collected in the traps and infested trees were concentrated near the trap sites. Although this study did not demonstrate conclusively that trapping reduced tree mortality in the outbreak area, it did show that mass-attacked trees were concentrated in the vicinity of traps even though traps were placed in openings 50-150 m from host trees. In British Columbia, pheromone-baited traps had a similar effect (Paulson 1995). Another potential problem with traps is the large numbers of predators that are collected. In the Oregon study, *Thanasimus undatulus* represented over 97% of the predators that were trapped and the ratio of Douglas-fir beetles to *T. undatulus* was about seven to one (Ross and Daterman 1996). The significance of catching such large numbers of *T. undatulus* is unknown. Under laboratory conditions, *T. undatulus* prefers smaller scolytids that are sometimes associated with the Douglas-fir beetle (Schmitz 1978). Additionally, over the last two years we have found approximately equal numbers of *T. undatulus* and *Enoclerus sphegeus* in bark samples from the lower 8 m of Douglas-fir beetle infested trees (unpublished data). The number of predators collected in multiple-funnel traps can be reduced by physical modifications that selectively exclude them or provide for their escape (unpublished data). Lure composition and pheromone release rates can affect trap selectivity also. There are still many questions that remain to be answered regarding the most efficient design of an operational trapping program. Other possible uses of Douglas-fir beetle pheromones include creating snags and canopy gaps to increase structural diversity in managed stands, monitoring population trends, and enhancing effectiveness of natural enemies.

Meeting Ecosystem Management Objectives Through IPM

Forest management in the U.S. has been undergoing dramatic changes in recent years, particularly on public lands. The emphasis on timber production that prevailed through the mid 1980's has been replaced by the concept of ecosystem management. Maintaining the ecological integrity and sustainability of forests while producing desired resources is the cornerstone of ecosystem management. Forestry has become much more complex as a result of this shift in policy. Forest managers are currently struggling to find the appropriate balance in producing a diverse array of resources and values.

Pest management has also become more complicated in the context of ecosystem management. There are now more constraints to implementing silvicultural controls for the Douglas-fir beetle than there were just a few years ago. However, silvicultural treatments remain the first line of defense for preventing undesirable tree mortality. Silvicultural strategies should be used wherever they are compatible with resource management objectives, especially on private lands managed primarily for timber. On most public lands, there are limited opportunities to prevent Douglas-fir beetle outbreaks through silviculture. For example, virtually all existing mature or old-growth stands on public lands are now reserved as habitat for species that depend upon late successional stage forests. The goal of management is to protect existing old-growth stands and facilitate successional processes in younger stands to increase the area of forests with similar characteristics. The short supply of old-growth forests makes them highly valued, but also places them at high risk to infestation by the Douglas-fir beetle which prefers to breed in large, old trees (Furniss et al. 1979).

A number of recent changes in silvicultural practices on public lands could potentially create favorable habitat for the Douglas-fir beetle. Rather than removing or treating large diameter slash following harvest operations as was common in the past, the current trend is to leave more of this material on the site. In some cases, trees are purposely topped or felled and left on the site to create standing and down woody debris for added structural diversity, wildlife habitat, and forage. There is also increasing opposition to removal of dead and dying trees such as those damaged by windstorms and wildfires. Much of this material is now being left in the forest for its ecological value rather than being removed for economic, pest management, or wildfire prevention considerations. There has been increasing interest in allowing wildfires to burn if they do not threaten life or property. If this trend continues, it may result in more fire-damaged trees some of which will not be salvaged. Although there is interest in thinning the abundance of overstocked stands on public lands, many areas will remain untreated to provide thermal and hiding cover for wildlife, to protect soil and water resources, and for other reasons. The combined effect of these changes in management practices will be to create more breeding sites for the Douglas-fir beetle.

Pheromone applications could help to prevent or alleviate some of the potential Douglas-fir beetle problems associated with changing silvicultural practices. MCH could be applied to high-value stands such as recreational, cultural, and administrative sites, highway corridors, old-growth reserves, and riparian areas to reduce the probability of tree mortality occurring in these locations during beetle outbreaks. At the same time, pheromone-baited traps could be located in general forest areas where tree mortality is less disruptive to management objectives. Sanitation or salvage logging might be prescribed in the vicinity of trap sites if it is consistent with management objectives. Where large volumes of fresh woody debris from natural or human-caused disturbances must be left in the forest, MCH could be applied to prevent the buildup of beetle populations that could threaten resource values. Other pheromone-based strategies that are yet to be developed could further compliment existing pheromone and silvicultural treatments. We plan to begin testing the application of pheromones at the landscape scale beginning in 1997.

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The attractiveness of pine branches infected with selected wood-colonising fungi to the Large Pine Weevil (*Hylobius abietis*)

IWONA SKRZECZ[1] AND ROGER MOORE[2]

[1]Forestry Research Institute, 00-973 Warsaw, Bitwy Warszawskiej 1920 r. No. 3
[2]Forestry Commission Research Division, Northern Research Station, Roslin, Midlothian, EH25, 9SY, UK

ABSTRACT This paper describes laboratory experiments designed to evaluate the attractiveness of pine branches overgrown by fungi to Large Pine Weevil (*Hylobius abietis)* females. These experiments attempt to explain differences observed in the field where *H. abietis* females have been shown to exhibit different colonisation rates of Scots Pine stumps infected with *Phlebia gigantea* (Fr.: Fr.) Donk and *Trichoderma harzianum* Rifai.

The results indicated, that in contrast to *T. harzianum*, the *Ph. gigantea* fungus inhibited the attractiveness of pine branches to this insect. The *Ph. gigantea* mycelium as well as the *T. harzianum* mycelium decreased the attractiveness of pine branches as food to the weevil.

KEY WORDS *Hylobius abietis*, *Phlebia gigantea*, *Trichoderma harzianum*, pine branches, pine stumps

WEEVILS OF THE genus *Hylobius* (*Coleoptera: Curculionidae*) are pests of young conifer plantations. The large pine weevil (*Hylobius abietis* L.) is perhaps the most important species commercially and is widely distributed throughout temperate parts of Europe and Asia. *H. abietis* is at its most damaging where reafforestation is attempted in clearfelled areas that previously supported a conifer crop. The beetles of *H. abietis* are attracted by the volatiles emanating from the resin of fresh conifer stumps left during clearfelling. These fresh conifer stumps then act as breeding material for the large pine weevil‘s development from egg to larvae and then pupae. Adults then emerge from the stumps causing serious economic seedling losses by feeding on the bark of these seedlings (mainly pine, spruce and larch). Heavy infestations caused by this pest may result in the widespread loss of young trees for several years after planting. *Hylobius pinastri* Gyll. is also a well known species, but of minor economic importance.

To estimate or to control the population density of those two species, pine billets or artificial traps with food attractant are commonly used in Poland (Kolk 1994). The most common method of protecting reforested areas against both species (Glowacka 1991) is to dip the seedlings in contact insecticides before planting and/or by spraying them with these chemicals after planting.

To protect forest plantations without the use of labour-consuming traps or insecticides, which may have a negative impact on the forest environment, experiments using a biological control agent were carried out in Poland. The main aim of these studies was to reduce pine weevil abundance within restocked areas, by disturbing the development of the *H. abietis* larvae in conifer stumps. The research estimated the impact of *Phlebia gigantea*

Pages 146-152 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

(Fr.: Fr.) Donk and *Trichoderma harzianum* Rifai fungi on the colonisation of Scots pine (*Pinus sylvestris L.*) stumps by the large pine weevil (Skrzecz 1996). *Ph. gigantea* as a competitor of *Heterobasidion annosum* (Fr.) Bref develops in pine stumps and their roots and causes a rapid decay of wood (Sierota 1981). The *Trichoderma* species are also wood-colonising fungi, which cause the suppression of the *H. annosum* mycelium (Sierota 1979).

The results of the field trials showed, that the infection of stumps with *Ph. gigantea* mycelium reduced their colonisation by *H. abietis* (Skrzecz 1996). Stumps infected with *T. harzianum* mycelium were colonised by the pest to the same degree as uninfected ones.

To find the causes of the differences between large pine weevil colonisation of stumps uninfected and infected with fungi, the laboratory tests were set up to evaluate the attractiveness of pine branches treated with the *Ph. gigantea* and *T. harzianum* mycelia. These experiments were carried out while the principal author was on research attachment at the Forestry Commission Research Division's, Northern Research Station in Scotland.

Materials and Methods

Beetles of *H. abietis* were collected in 1994 from a 1yr old clear-cut area felled in March 1993, in Tentsmuir forest on the eastern coast of Scotland. In the laboratory, the sex of the insects was determined with the use of a microscope and females were used in tests. Before the experiment, females were stored in plastic boxes without any food for 24 hours.

Fresh Scots pine branches were cut into fragments 10 cm in length and 2.5-3.0 cm in thickness. The fragments were divided into three groups. The first group consisted of fragments infected with *Ph. gigantea* mycelium, the second of fragments infected with *T. harzianum* mycelium, the third group were uninfected control fragments. The branch fragments were infected by placing an inoculated fungal disc of 0.5 cm diameter on each end of the stem section. These discs had been previously dissected from a maltose-agar medium overgrown for 8-days by pure strains of the fungi under study. Each group of fragments were placed in separate plastic containers with water-soaked filter paper in the bottom. All branch fragments were incubated for 4 weeks at a temperature of 20^0C. In the tests, the fragments of pine branches overgrown by a 4-week mycelium of *Ph. gigantea* or *T. harzianum* were used. After 4 weeks of branch incubation, about 50% of the surface area of each fragment infected with *Ph. gigantea* was covered by the mycelium, while the mycelium of *T. harzianum* overgrew about 30-40% of the surface area of each infected fragment. No mycelium were found on the control branch fragments.

The attractiveness of pine branches to large pine weevil females was tested using both a Time Lapse Video Arena and a 4-arm olfactometer.

The Time-Lapse Arena consisted of a glass box filled with dry forest litter. A video camera mounted over the arena was used to observe the beetles' behaviour over a long time period. Six fragments of pine branches were placed on the forest litter inside the glass box, these consisted of 2 replicate stem sections of uninfected material, 2 replicates of stem infected with *Ph. gigantea* and a further 2 infected with *T. harzianum*. The final position of branch fragments had the shape of a star, because the fragments infected with the same fungus and control ones were placed opposite to each other. Females of *H. abietis* were placed in the centre of this "star". To prevent beetles escaping from the Time Lapse Arena, the inner top border of the glass box was coated with fluon.

In a six-day experiment, 5 females marked with white paint were tested every day. Each test was started at 3 p.m. and the video camera placed above the glass box, recorded the insects' behaviour for 18 hours a day during the females most active feeding period. Prior to each test, the insects and fragments of pine branch were replaced.

After the tests, the video films were analysed and the attractiveness of pine branches to the insects was estimated on the basis of the number and duration of beetle visits to individual pine branches.

The statistical software programme STATGRAPHICS 5.0 was used for statistical analysis. The data related to the duration of insects visits to pine branches were analysed by one-way analysis of variance after applying Bartlett's transformation and Tukey's test.

The reaction of *H. abietis* females to the volatiles emanating from pine branches uninfected and infected with the fungi under study was determined using a 4-arm olfactometer. The main part of the olfactometer consisted of a flat square chamber joined in the corners with four glass containers, in which pine branches were placed. The air mixed with volatiles from branch fragments was driven to the main chamber, where individual beetles could choose to move towards an attractant odour or control. Each test was recorded by the video camera placed above the main chamber.

The fragments of pine branches infected with *Ph. gigantea* or *T. harzianum* and uninfected ones were placed separately in the 3-glass containers of the olfactometer while the fourth one was empty to test the responses of the beetles to the air without volatiles. Every two hours the pine branches were replaced.

One hundred females of the large pine weevil were studied and each insect was tested only once in the arena. The response of a beetle in this test was regarded as positive, when the insect went from the main chamber into the selected glass container and stayed there for at least 1 minute. The speed of the air flown from the containers with pine branches to the main chamber was 0.4 l/min. The experiments were conducted after 3 p.m. during the period of greatest weevil activity.

Results

The results obtained for the experiments in the Time Lapse Arena indicated that the beetles visited pine fragments infected with *Ph. gigantea* for the shortest time. The females remained slightly longer on the pine branches overgrown by *T. harzianum* but the longest visits were to control fragments. The average duration of each visit by *H. abietis* to pine branches are shown in Fig. 1.

The results of the one-way analysis of variance showed significant differences between the time of beetle visits on the pine fragments (Table 1).

Table 1. The duration of *H. abietis* visits to pine branches uninfected and infected with fungi *Ph. gigantea* or *T. harzianum.* One-way analysis of variance.

Source of variation	Sum of squares	d. f.	Mean square	F-ratio	Significance level
Between groups	2.469414	2	1.2347068	70.112	0.001
Within groups	15.215406	864	0.0176104		
Total	17.684820	866			

The Tukey's test revealed two homogenous groups (Fig. 1):

1. The time of beetles' visits to the pine branches infected with *Ph. gigantea* or *T. harzianum*,
2. The time of beetles' visits to the uninfected pine branches.

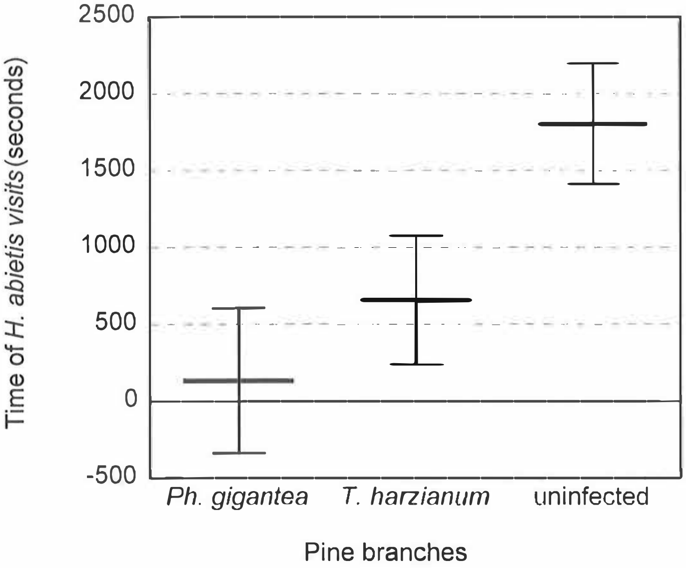

Fig. 1. The duration of *H. abietis* visits on pine branches uninfected and infected with the fungi *Ph. gigantea* or *T. harzianum.* The results of Tukey's test

Analysis of the frequency of pine weevil visits showed that a lower number of visits were made to the branches overgrown with *Ph. gigantea* mycelium (Table 2). A greater number of visits were made to branches infected with *T. harzianum* than *Ph. gigantea*, but uninfected branches were visited most frequently.

No evidence of beetle feeding was found on pine branches infected with these fungi but feeding was observed on uninfected pine branches.

Table 2. The number of *H. abietis* visits to pine branches uninfected and infected with the fungi *Ph. gigantea* or *T. harzianum*.

Pine branches	The number of visits
Ph. gigantea infected	233
T. harzianum infected	296
uninfected	338

The results of the olfactometer study indicated that the time to test each individual female of the large pine weevil was different and ranged from 5 to 45 min. Some of the beetles selected the attractant in a short time, while the others first chose one of the attractants and then they selected a different one.

It was found that pine branches overgrown by the *Ph. gigantea* mycelium attracted the lowest number of females (Table 3). Pine branches infected with the *T. harzianum* mycelium and volatile-free air attracted similar number of beetles, but the highest number of females was attracted by uninfected branches.

Table 3. Percentage of *H. abietis* females attracted by pine branches uninfected and infected with *Ph. gigantea* and *T. harzianum*.

Pine branches	Percentage of females
Ph. gigantea infected	6
T. harzianum infected	30
uninfected	37
air	27

Discussion

The beetles of the large pine weevil are attracted to clearfelled areas by the odours emanating from cut timber, stumps and slash. Experiments carried out in the 1970s in Finland (Selander 1979) and in the 1980s in Sweden (Tilles et al., 1986 a,b) indicated that monoterpenes such as alpha-pinene and 3-carene and the bio-degradation product ethanol were the most important attractants for the migrating pine weevils. As pine stumps treated with *Ph. gigantea* are not colonised by *H. abietis*, it raises the question of whether *Ph. gigantea* mycelium can inhibit the attractiveness of pine stumps to the pest. To answer this question laboratory tests of the attractiveness of fungi-infected and uninfected pine branches to *H. abietis* were performed.

In contrast to the more prevalent natural conditions, pine stem sections were used in the experiments rather than roots or stumps. This was because the experiments were logistically much easier to perform and also because pine branches and stems are also known to be used for weevil feeding and oviposition (Christiansen 1971, Skrzecz 1996).

The results revealed that *Ph. gigantea* mycelia inhibited the attractiveness of pine branches to *H. abietis* females. The lowest frequency, the shortest visits as well as the lowest number of female beetles were attracted to pine branches infected with *Ph. gigantea*. *T. harzianum*-infected branches showed intermediate attractiveness while the frequency and duration of beetle visits to control branches was found to be greatest for uninfected pine branches. These therefore appeared to be most attractive to *H. abietis* females.

Both fungi inhibited the attractiveness of branches as a food and probably would also decrease the value of stumps as an oviposition site for these insects.

The results obtained from early field tests and laboratory experiments suggest that *Ph. gigantea* grows rapidly in infected stumps, changes their wood structure and the quantity or composition of the volatiles emanated from the pine and that the infected stumps become less attractive to the *H. abietis* females.

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Spatial and Temporal Attack Dynamics of the Mountain Pine Beetle: Implications for Management

BARBARA J. BENTZ[1], JESSE A. LOGAN[1], AND JAMES A. POWELL[2]

[1]USDA Forest Service, Intermountain Research Station, Logan UT and Department of
Forest Resources, Utah Station University, Logan,UT, USA
[2]Department of Mathematics and Statistics, Utah State University, Logan, UT, USA

ABSTRACT Colonization of a host tree by the mountain pine beetle, MPB (*Dendroctonus ponderosae* Hopkins, Coleoptera: Scolytidae), involves a complex, synergistic interaction between host-produced chemicals and beetle-produced pheromones. This system of chemical communication enables a massive aggregation of beetles on a single resource, thereby ensuring host death and subsequent beetle population survival. Because a single host tree is a limited food and breeding resource, MPB populations have evolved mechanism(s) for termination of colonization on a tree at optimal beetle densities, with a concomitant shift of attacks to nearby trees. Several hypothesis attempt to explain this pheromone-mediated phenomena. In an effort to more fully understand the entire colonization process, including the switch of attacks among trees, we observed the daily spatial and temporal attack process of MPB (non-epidemic) attacking lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann). Our results from this preliminary study suggest that beetles switch attacks to a new host tree before the original focus tree is fully colonized, and that verbenone, an anti-aggregating pheromone, may be acting within a tree rather than between trees. Results from this and additional on-going studies are being used for parameterization of a spatially explicit model of MPB dispersal. Alternative hypotheses for MPB colonization and management implications are discussed.

KEY WORDS mountain pine beetle, verbenone, switching, spatial, lodgepole pine

MANY SPECIES OF bark beetles in the genus *Dendroctonus* (Coleoptera: Scolytidae) use kairomones and pheromones in the processes of host selection, attack, and colonization (Borden 1982, Wood 1972). Female *D. ponderosae* Hopkins (MPB), which in this species are usually responsible for initiating a new attack, bore into the bark and through a chemically mediated synergistic reaction with host chemicals, release *trans*-verbenol. *Trans*-verbenol is an aggregative pheromone attracting both sexes (Pitman et al. 1968, Hughes 1973, Pitman 1971). At higher concentrations of *trans*-verbenol, higher proportions of males are attracted (Renwick and Vite 1970). Males produce *exo*-brevicomin which at low concentrations primarily attracts females (Conn et al. 1983). Both inhibition (Borden et al. 1987, Rudinsky et al. 1974) and attraction (Shore et al. 1992) of beetles at higher concentrations of *exo*-brevicomin have been observed. This system of chemical communication enables a massive aggregation of individuals on a single "focus" tree which, for species such as MPB, is selectively advantageous in overcoming host defensive mechanisms. As with most herbivores, however, there is an optimal density range of individuals on an exhaustible food resource (Berryman et al. 1985). If beetle densities on a single tree are too high, mortality can result from within-tree competition for limited

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Pages 153-162 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

breeding and feeding space.

Several hypothesis attempt to explain the termination of colonization on a single tree at optimal beetle densities. The first assumes that anti-aggregative or inhibitory pheromones such as verbenone and *exo*-brevicomin deter incoming beetles, thereby terminating additional attacks and ensuring that beetle attack density does not exceed the threshold for optimum brood survival (Borden at al 1987). Verbenone is a semiochemical produced by MPB (Rudinsky et al. 1974), through autoxidation of host terpenes, and by enzymatic conversion by yeasts (Hunt and Borden 1989). Based on this hypothesis, as verbenone is released, the majority of beetles are dispersed at some distance, switching attacks from the focus tree to adjacent recipient trees (Gieszler et al. 1980).

A second hypothesis emphasizes the role of host resistance, citing cessation of resin exudation as the primary cause for termination of colonization on a particular tree (Renwick and Vite 1970, Raffa and Berryman 1983). As with the first hypothesis, attacks switch to adjacent trees once the focus tree becomes fully utilized--the difference lying in the roles of inhibitory pheromones and host-tree resins. In the second hypothesis, inhibitory pheromones are one component of a series of territorial behaviors which, in conjunction with a decrease in resin exudation, enable individual colonizers to maximize reproductive potential (Raffa and Berryman 1982, 1983). From this perspective, inhibitory pheromones are perceived and function at the local scale, while attacks switch to neighboring trees because the focus tree has become fully colonized and resin exudation ceases. A third hypothesis, labeled the "threshold model", assumes that as a tree is mass attacked, the high concentration of *trans*-verbenol being emitted in the local area causes incoming beetles to attack neighboring trees which are enveloped in the pheromone cloud (Coster and Gara 1968, Gara and Coster 1968, see Geisler et al. 1980). A threshold level of *trans*-verbenol is necessary to cause landing and attack on adjacent trees.

The presence of inhibitory pheromones in the genus *Dendroctonus* is known (Hunt et al. 1989, Libbey et al. 1985, Pitman et al. 1969, Ryker and Yandell 1983, Rudinsky et al. 1974). However, our lack of knowledge about the explicit function of these pheromones in MPB community ecology is exhibited by confounding results in past research endeavors (see Amman and Lindgren 1995 for a review). It is unclear whether inhibitory pheromones such as verbenone have a shielding effect around the tree under attack and are the main cause of switching, or if their function is to regulate attacks once beetles are on or very near the tree surface, playing a more localized role in the switching process. If indeed verbenone has a shielding effect, unknown parameters include the size of the shielding plume, and timing of its influence. The main objective of this study was to collect information on the spatial and temporal sequence of the MPB switching process. Original motivation for the study was to obtain quantitative information for parameterization of a mathematical model of MPB dispersal which includes chemical ecology and spatial interaction between beetles and host trees (Powell et al 1996). Data at the fine spatial and temporal resolution necessary for deriving model parameters was unavailable in published literature. In this study we did not measure pheromone emission, but rather the effect of these pheromones on beetle behavior.

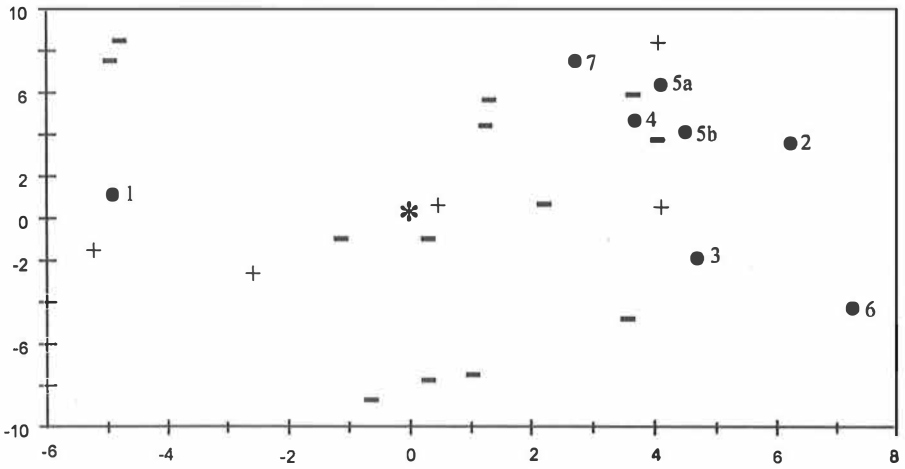

Figure 1. Spatial map (in meters) of all trees in Plot 1. ☆ is the baited tree at plot center, ① are successfully attacked trees, with the number representing the day in the attack sequence, ⊕ are strip-attacked trees, and ⊙ are live trees at the end of the attack period. Size of circle indicates relative dbh of each tree.

Methods

Three plots in lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) stands in the Gold Creek drainage of the Sawtooth National Recreation Area were selected. Species composition in the drainage is approximately 80% lodgepole pine and 20% Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). Currently there is a sub-epidemic MPB population which has been slowly building during the last 4-5 years. All plots were at an elevation of approximately 2073 meters, and at least 100 meters apart. On August 6, 1995, an MPB pheromone tree bait[1] was placed on the north side of a single tree in each plot. Based on emergence data from a nearby experiment (Bentz unpublished data), beetle flight in the area had just begun. The bait was left on each focus tree for 24 hours, then removed. All trees within a radial distance of 10 meters (20 meter diameter) from the focus tree were monitored for beetle attacks until August 18 at which time colonization of trees within the plots had, for the most part, stopped. Attacks were tallied twice per day (approximately 8:00 am and 5:00 pm), by height on the bole (0-1.2 meters, 1.2-1.8 meters, and 1.8-2.4 meters) and aspect of the bole (N, E, S, W) where the attack was located. An attack was counted once the nesting hole was initiated and resin or frass was noticed, and consequently landing rates were not included.

Each entry was marked with a colored push pin, and later tallied. Because our intent was to monitor the 'natural' attack process of MPB on lodgepole pine, those trees attacked while the bait was on the focus tree were removed from data analysis. A stem map was developed for each plot including diameter of each tree at 1.5 meters above the ground (dbh) (Fig. 1). Only results for plot 1 are included here.

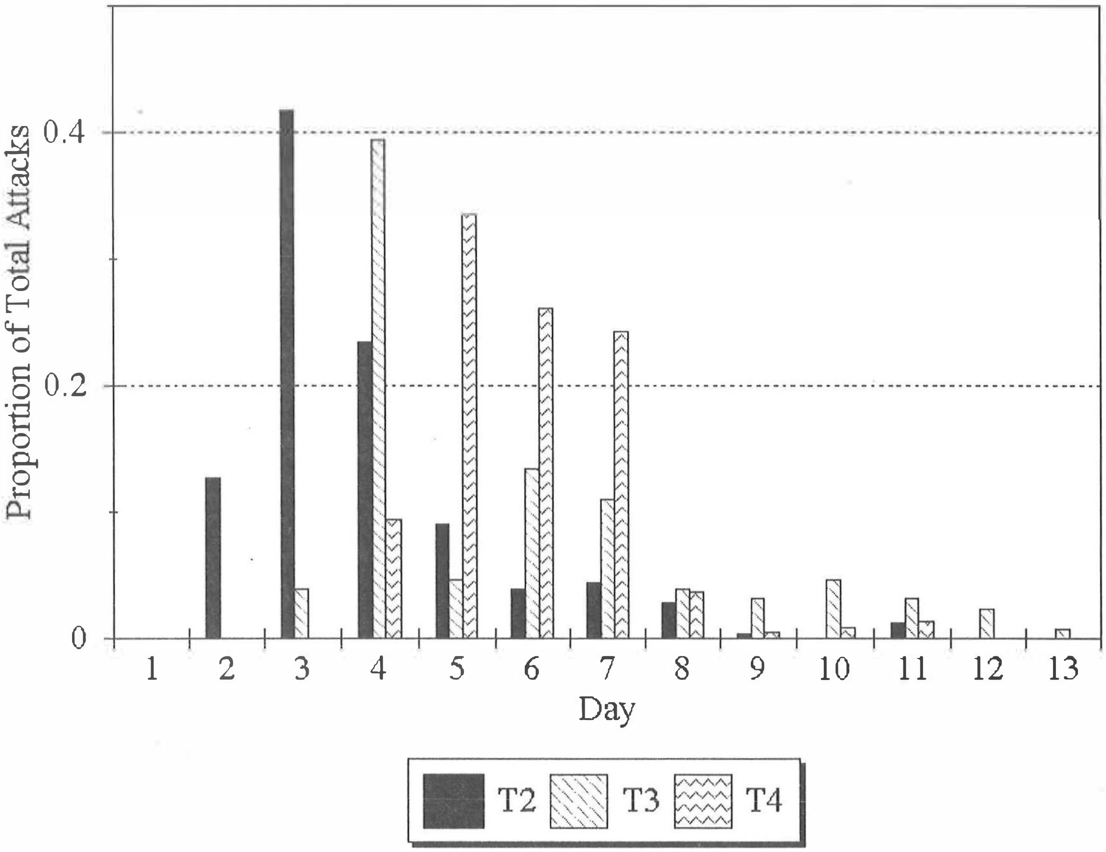

Figure 2. Proportion of total attacks on lower 2.4 meters of bole of 3 successfully attacked trees, by day of attack. Day 1 is August 6, 1995.

Results and Discussion

The first hypothesis for switching suggests that the production of inhibitory pheromones during the latter stages of colonization deter incoming beetles and therefore cause a switch to adjacent trees. If this is true, then inhibitory pheromones would be perceived prior to beetles landing on the focus tree, with a switch of attacks to adjacent trees once the original focus tree was fully colonized. At the point of full optimization of the focus tree, inhibitory pheromones would produce a shield, resulting in no additional attacks on that tree. Our results do not support this hypothesis. On the day of peak attack density on Tree 2, new attacks occurred on Tree 3. The following day, at peak attack density of Tree 3, Tree 4 was initially attacked (Fig. 2). The next day, at peak attack density on T4, T5a and T5b were attacked (Fig. 3). In all cases, on the day when attacks switched to another tree, the proportion of attacks on the current focus tree was less than 45% (Figs. 2, 3). These results suggest that attacks are redirected to a new tree prior to full utilization of the current tree under attack. McCambridge (1967) also observed that trees adjacent to the focus tree came under attack by MPB before the initial focus tree had been fully mass attacked. Anderbrandt et al. (1988) observed a similar pattern with *Ips typographus* Linnaeus. Others (Geiszler et al 1980), however, reported that the switch to a new tree occurred after the original focus tree had been fully mass attacked.

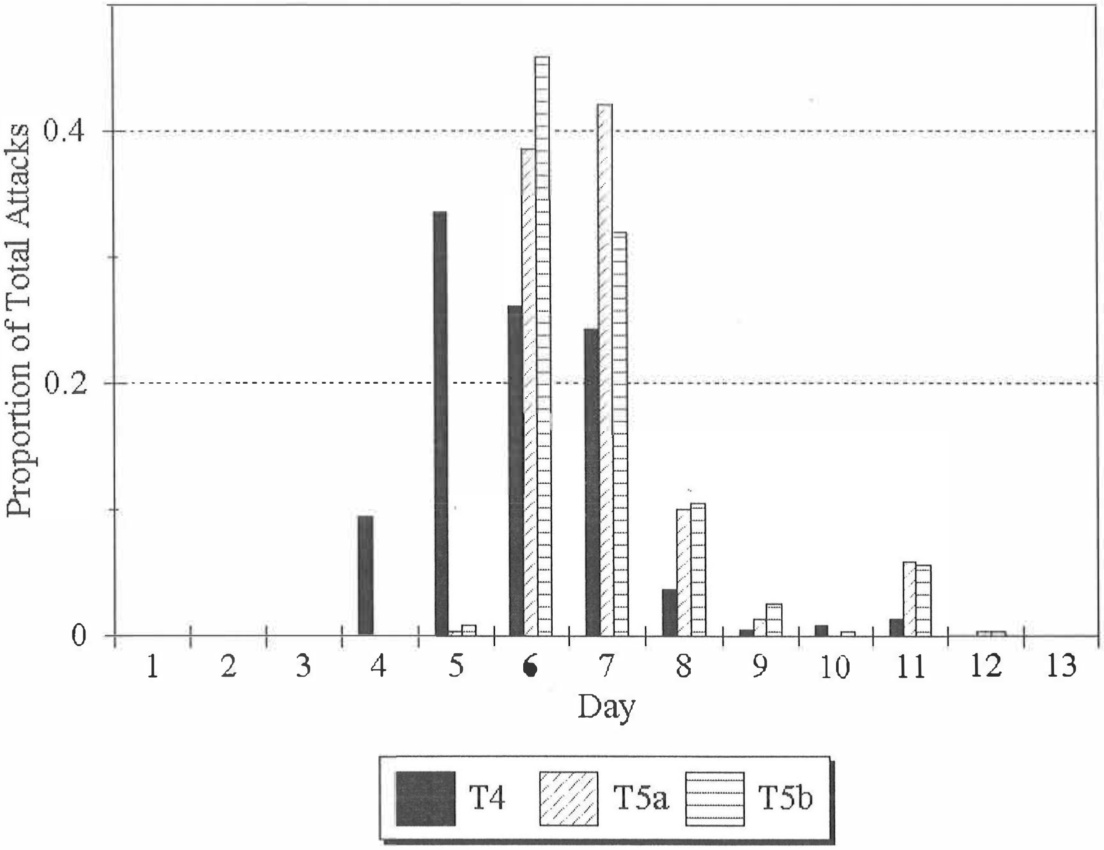

Figure 3. Proportion of total attacks on lower 2.4 meters of bole of 3 successfully attacked trees, by day of attack. Day 1 is August 6, 1995.

The basis of the second hypothesis is that resin exudation would cease when the original focus tree was fully colonized. At this time, attraction to that tree would be terminated due to an absence of the tree-produced precursor, α-pinene, necessary for beetle production of *trans*-verbenol. Without production of the aggregating pheromone *trans*-verbenol, additional attacks would not occur on the focus tree once the switch to adjacent trees begins. Again, our results do not support this hypothesis for switching of attacks. Beetles continued to attack the original focus tree after adjacent trees came under attack (Figs.2, 3).

The basis for the third hypothesis is that given a threshold number of attacking beetles on a focus tree, the level of *trans*-verbenol being produced would be great enough to envelope surrounding trees in the aggregating plume. All trees within the aggregation pheromone plume would be attractive and experience attacks. Therefore, additional landing and attacks could occur on the focus tree even after attacks were initiated on adjacent trees. The larger the focus tree the greater number of attacks, and hence the larger the size of the aggregating pheromone plume. Data from our preliminary study support this hypothesis for switching of attacks. We observed that attacks on nearby trees were initiated while the focus tree was also still being attacked.

We use the term "switch" to represent a shift in attacks on consecutive days between a focus tree and surrounding trees. In our study, switch in attacks from a focus tree to nearby trees typically occurred the second day of attack, and at time of peak daily attack density on the focus tree (Figs. 2, 3). This coincides with the time of maximum production of *trans*-verbenol which peaks for individual beetles at about 24 hours of feeding (Pitman and Vite 1969). However, female MPB which had fed in lodgepole pine bolts for 24 hours also contained significant amounts of verbenone (Hunt and Borden 1989). Therefore, the large concentrations of both aggregation and inhibitory pheromones in the first few days of attack on a tree may cause MPB to be attracted to the focus tree, and both space out on the bole and participate in the tree-switching mechanism (Bedard et al 1980, Birgersson and Bergstrom 1988). The function of inhibitory pheromones such as verbenone in this tree-switching mechanism is unclear, however.

Based on results in our study, shift in attacks to a new host occurred before the focus tree was fully colonized, although each tree continued to be attacked at a decreasing daily rate for 5-6 days. If beetles were responding to verbenone before landing on a tree as suggested by Bertram and Paine (1994), the range of perception in our study plot was smaller than the distance between the two closest trees attacked within a day (< 1 meter). If verbenone was providing an inhibitory plume around a tree, most attacks on that focus tree would cease, signaling a fully utilized resource, although additional attacks may occur due to variability in the response threshold of individual beetles. However, because attacks shifted to a new tree while less than 50% of total attacks had occurred on the focus tree, verbenone (and other inhibitory pheromones) could be functioning at a more local scale, perhaps around a particular entrance hole as was suggested previously (Raffa and Berryman 1983, Renwick and Vite 1970). While large amounts of aggregating pheromones are still being produced, verbenone may provide a means to reduce competition within a tree, while some other component of the pheromone system is the primary cause of attack switch to a new tree. Our results indicate that a shift in attacks to a new tree occurred on the day of greatest attack rate on a nearby tree. If we assume that time of greatest attack rate on a particular tree coincides with peak *trans*-verbenol emission from that tree, switch in attacks to a new tree could be explained by a spill-over effect. This would occur when the concentration of aggregation pheromone was large enough to envelope surrounding trees, resulting in random attacks on trees enveloped by the plume, setting up a new focus tree. The new focus tree then has an increase in number of attacks, while attacks on the old focus tree declines due to a reduction in attacks and concomitant *trans*-verbenol production (Pitman and Vite 1969). These results were seen in our data, whereby number of attacks on recipient trees the first day of switching was always less than number of attacks on the focus tree that same day, although the following day, attacks on recipient tree were greater than previous focus tree (Figs. 2, 3). Although we do not know the size of aggregation pheromone plumes, our data does suggest that the inhibitory, or anti-aggregation plume being released is smaller than the distance between two consecutively attacked trees spaced less than 1 meter apart.

Implications for Management

Techniques for identifying bark beetle semiochemicals were first developed in the 1960's (Silverstein et al. 1967). A plethora of field and laboratory trials for measuring the response of beetles to these semiochemicals have occurred since that time. Because opportunities for exploitation of beetle pheromones for forest management purposes are numerous, the temptation for researchers in this field to hastily launch into applied programs has been great. However, if the immense natural complexity of these semiochemicals is not fully understood, effectiveness of field applications may be inconsistent and often times unsuccessful (Borden 1995). This has been the case with attempts at applying synthetically produced verbenone for protecting stands of trees from attack by the mountain pine beetle (Amman et al. 1989, Amman et al. 1991, Amman and Lindgren 1995, Bentz et al. 1989, Gibson et al 1991, Lindgren and Borden 1993, Lindgren et al. 1989, Lister et al. 1990, Shore et al. 1992). The inconsistent results from year to year and between host types and geographic regions could be due to a number of reasons (Borden 1995) including: 1) technical problems with deployment of the pheromone, 2) effects of microclimate, 3) changes in behavior and/or genetic makeup with changes in the insect population phase (Amman 1993) and 4) inadequate knowledge of the functional role of inhibitory pheromones in MPB population dynamics.

Because verbenone is used by so many species of aggressive bark beetles, and a large portion is produced by microorganisms in decaying wood, it may be a signal to beetles that the immediate substrate, either an entire tree or a localized space on a tree, is no longer suitable for colonization (Borden et al. 1987, Leufven and Birgersson 1987). The question remains whether MPB are responding to verbenone prior to or after landing on the tree. Our results suggest that verbenone may be acting within a tree rather than between trees, and that it does not provide a very large inhibitory shield around the tree under attack. This is a different functional role for verbenone in MPB chemical ecology than the role researchers previously had in mind when applying synthetic capsules in field trials. To this date, synthetic verbenone has been applied either aerially or by stapling single capsules on trees spaced throughout an MPB infested stand. These experiments were aimed at deploying a certain dose of verbenone per hectare. Conversely, if the functional role of verbenone is to space beetles on a tree rather than between trees, alternative verbenone applications will need to be field tested.

Researchers have been tantalized by the hope that synthetically produced pheromones might be the answer to management of epidemic phase MPB populations. However, we need to step back and conduct additional research at the behavioral level to more fully understand the sequence of the colonization process, and the spatial and temporal influence of inhibitory pheromone(s) in MPB population dynamics. Inconsistent results in attempts to apply inhibitory pheromones in a management scenario attest to a current deficiency in our knowledge of their role in MPB chemical ecology.

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Does drought really enhance *Ips typographus* epidemics? -A Scandinavian perspective

ERIK CHRISTIANSEN & ALF BAKKE

Norwegian Forest Research Institute
N-1432 Ås

ABSTRACT Availability of defenceless or weakly defended breeding material, e.g. trees felled or damaged by major wind storms, is a necessary requirement for an outbreak of the spruce bark beetle, *Ips typographus*. Water stress is also hypothesised to be an important predisposing factor, although this idea is mostly based on circumstantial observation of a coincidence between dry weather and beetle outbreaks. Whereas a causal relationship may well exist for certain scolytid beetles, experimental evidence is often scarce and in some cases contradictory. We examine information pertaining to population dynamics of the spruce bark beetle *Ips typographus* in Norway. This includes (1) experiments to assess effect of drought stress on host tree susceptibility to the beetle's pathogenic fungal associate, *Ceratocystis polonica*, and (2) results from a population monitoring program which has been in operation since 1980. Because drought often coincides with hot weather, one can confuse a direct effect on beetle propagation by hot weather with an indirect effect on insect dynamics through predisposition of the host trees. We conclude that apart from extremely rare cases of severe droughts lasting for a long period of time, direct effects of spring weather on beetle propagation are more likely to affect *I. typographus* dynamics than are indirect physiological effects working through the host trees.

KEY WORDS Bark beetles, Scolytidae, *Ips typographus,* water stress, weather, population dynamics

BARK BEETLE OUTBREAKS are often associated with water stress on the host trees. This connection is largely based on circumstantial observation of a temporal coincidence between dry weather and beetle outbreaks, but very few experiments have been carried out to test this assumption.

Here we review some recent evidence pertaining to the spruce bark beetle, *Ips typographus* L., and stress conditions of its host Norway spruce, *Picea abies* (L.) Karst. Recurring outbreaks of this insect in Eurasia may encompass thousands of square kilometres and lead to the killing of millions of spruce trees (Christiansen & Bakke 1988, Führer 1996).

For an *I. typographus* epidemic to erupt, local populations must reach a certain density to exceed the "Threshold of Successful Attack" on living spruce trees (Thalenhorst 1958). Windstorms undoubtedly act as precursors by providing defenceless breeding substrate in the form of fallen trees. Moreover, trees left standing after a gale with part of their root system torn are probably an easier prey than are intact trees.

Epidemics often also coincide in time with extended periods of hot and dry weather (for discussion, see Christiansen & Bakke 1988). This weather situation could boost beetle populations in two different ways: (1) indirectly - by drought influencing the physiological state of the trees rendering them susceptible to attack , and (2) directly - by high temperatures promoting extensive flight and search for host trees and accelerating brood development.

Pages 163-171 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

Two Important Traits Of *Ips Typographus* Biology

A summary of our knowledge on the beetle's biology has been presented before (Christiansen & Bakke 1988), and we will only mention a few points that are relevant to our discussion here.

Very few of the world's ca 6000 bark beetle species are indeed "aggressive" or "primary" in the sense that they kill healthy trees. There is considerable evidence to support a general hypothesis that aggressive species have two crucial "assault weapons" in their arsenal: (1) effective aggregation pheromones, and (2) mutualistic fungi that help them in overcoming the tree's defences (Berryman 1972, Krokene 1996).

I. typographus possesses a highly efficient system of aggregation pheromones (Bakke et al. 1977, Schlyter 1985), the two main components being cis-verbenol and 2-methyl-3-buten-2-ol. Cis-verbenol is produced by oxidising α-pinene from host resin (Vité et al. 1972) and methylbutenol is synthesised *de novo* (Lanne et al. 1989, Ivarsson 1995).

I. typographus also vectors several blue-stain fungi, spores of which are carried both externally and internally (Furniss & al. 1990). The role of these fungi in tree-killing has been debated for a long time. Experimentally, the question could be addressed in two different ways; by inducing attacks of axenic beetles, or by artificially inoculating the fungi into trees. The first alternative is experimentally difficult and has not yet been tested, but in 1980 we took the other approach, and have since then carried out a series of inoculation experiments. An important result of these studies is that one particular species of blue-stain fungus, *Ceratocystis polonica* (Siem.) C. Moreau, (= *Ophiostoma polonicum* Siem.) is constantly at the advancing front of micro-organisms spreading into *I. typographus*-attacked trees (Solheim 1992). The experiments have also established that *C. polonica* is pathogenic enough to kill trees of various spruce species when artificially inoculated under the bark in adequate doses (e.g., Horntvedt & al. 1983, Christiansen 1985a). Douglas-fir may also get killed by artificial inoculation of this fungus (Christiansen & Solheim 1990).

Experiments To Assess Resistance Of Norway Spruce

Despite the assumed links between host tree condition and beetle attack, few experiments have been carried out to test this idea. A main reason is probably the logistic problems involved in such experimentation; both in manipulating water relations of large trees and in administering a controllable number of beetle attacks. Ideally, trees of the right size and age should be experimentally treated to alter their physiology and then exposed to a prescribed number of beetle attacks. However, a fixed "attack force" of beetles would, by means of their aggregation pheromones, summon an uncontrollable number of "wild" beetles from the surroundings and thus upset an experiment, unless it be carried out in a beetle-free area. One way to overcome this problem is to screen the trees with a fine mesh netting to deny access to newcomers. This can be done with beetles that mainly utilise the branch-free part of the stem (Raffa and Berryman 1983), but *I. typographus* attacks normally extend well into the green crown, making this approach impractical.

We have tried an indirect approach to the problem by substituting bark beetle attacks with artificial mass-inoculation of agar holding C. *polonica* mycelium. By administering a specific number of infections to a tree we can define its "Threshold of Successful Infection" above which the tree will succumb (Christiansen 1985a, b). This is parallel to Thalenhorst's (1958) "Threshold of Successful Attack", and although infection with mycelium is different from spore introduction by beetles, the number of *C. polonica* inoculations required to kill a given spruce tree appears to be roughly equivalent to the critical number of *I. typographus* attacks (Christiansen 1985b). Artificial mass-inoculation has also been used to estimate the relative resistance of Norway spruce trees subjected to various kinds of stress, such as drought and defoliation (Christiansen & Ericsson 1986, Christiansen 1992, Christiansen & Fjone 1993, Christiansen and Glosli 1996).

One experiment tested after-effects of water deficiencies (Christiansen 1992). Experimental trees (4-5 m tall) were deprived of precipitation for 3 consecutive growth seasons, during which they developed a significant but not extreme water stress, their pre-dawn xylem water potentials averaging ca -1.0 MPa (extremes down to -1.85), as compared to mean Ψ values of ca -0.5 MPa in unstressed controls. The experimental trees showed macro-nutrient deficiencies and lost a third of their foliage. In the fourth season they were not drought stressed but together with the controls they were mass-inoculated with a prescribed dose of C. *polonica,* high enough to cause fungal invasion of xylem and phloem. The hypothesis that stress would enhance the susceptibility to infection was refuted: on an average more cambium and phloem tissue was killed in control trees than in stressed ones (59% vs. 48%). This difference was, however, not statistically significant because of a high degree of variation between individual trees. Sapwood blue-staining did not differ between the two groups.

A later field experiment addressed the effect of current drought at the time of *C. polonica* infection (Christiansen & Glosli 1996). Clonal Norway spruce trees were used in this case, which significantly reduced the individual variation in host resistance. In autumn 1992 the ground below six ramets of each of two clones (#194 and #582) was covered with plastic tarpaulins to prevent winter precipitation from percolating into the ground, while six other ramets served as untreated controls. Next spring the tarpaulins were lifted from the ground and placed under the canopy of the (10-12 m tall) trees to lead precipitation away. By late June the experimental trees of clone #194 were significantly more stressed than controls, while clone #582 showed only slight differences. All trees were then mass inoculated with a standardised dose of *C. polonica.* When sapwood blue-staining was measured in autumn 1993 the stressed ramets of clone #194 proved to be much more resistant than the controls (Fig. 1). In clone #582 differences were small. Thus in clone #194 drought must have triggered some defence mechanism which enhanced the resistance to infection.

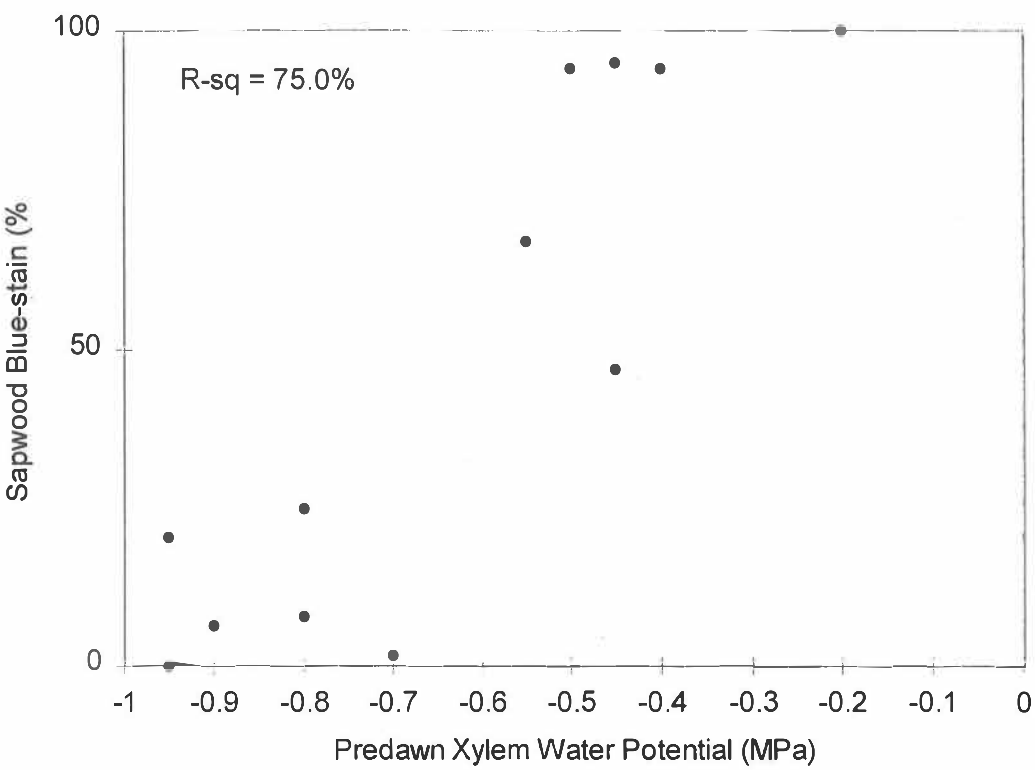

Figure 1. Percent of sapwood cross-sectional area discoloured in individual Norway spruce trees by 14 September after mass-inoculation with the blue-stain fungus *Ceratocystis polonica* on 25 June; in relation to pre-dawn xylem water potentials measured on 23 June. Clone #194.

The studies may shed some light on the drought - susceptibility issue. They provide no direct evidence since artificial inoculation of *C. polonica* was used instead of real bark beetle attacks, but, as stated earlier fatal threshold numbers for *I. typographus* attacks and *C. polonica* inoculations seem to be of the same magnitude (Christiansen 1985b). Another criticism of the results is that the trees used (particularly in the first experiment) were smaller than those normally attacked by *I. typographus.* Despite these problems, it seems fair to conclude that the experiments do not support the idea that drought promotes bark beetle outbreaks by rendering spruce trees more susceptible.

Population Dynamics And Weather

If drought does not promote *I. typographus* epidemics in South Norway by rendering trees more susceptible, we should consider the possibility that weather conditions act directly upon bark beetle propagation.

Since 1980 *I. typographus* populations in South Norway have been monitored annually with pheromone traps (Bakke & al. 1983). The captures, which show distinct annual fluctuations (Fig. 2), are analysed in relation to weather factors and a model is developed which applies for areas where *I. typographus* is univoltine (Bakke 1992, Bakke & al. 1995). According to this analysis the catch in a given summer is positively correlated to the mean monthly maximum temperature of the previous May ($R^2 = 0.40$). If the same temperature expression for the current May is included the correlation is improved ($R^2 = 0.64$). Autocorrelation with catches of the previous summer improves the fit slightly.

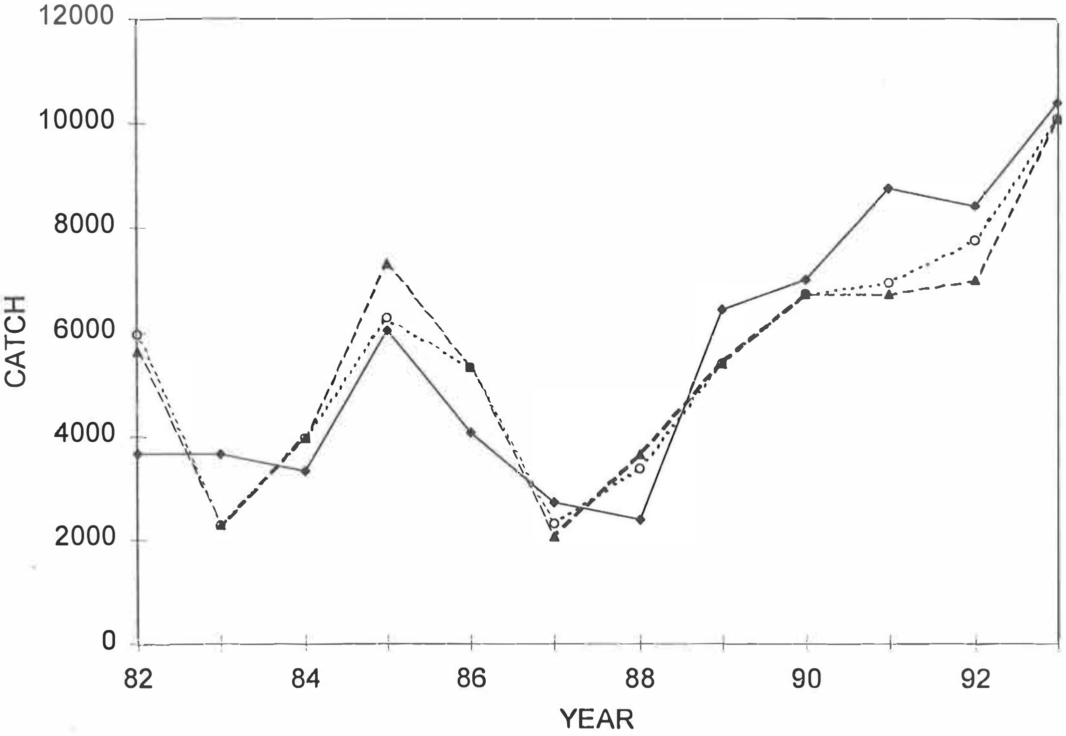

Figure 2. Catches of *Ips typographus* in drain-pipe pheromone traps (solid line) compared to predictions from a model based on mean maximum temperature for May of the previous and current year, without (dashed line) and with (stippled line) autocorrelation of the previous year's population.

The results are interpreted thus: May is normally the main flight period of *I. typographus*, which has a temperature threshold for flight at ca 20 ° C. When warm weather prevails in May, beetles emerge and fly within a short period of time; this results in concentrated and successful attacks on living trees. Consequently a large new generation ensues and a high number of beetles is caught the following summer; more so if warm spring weather increases attraction to the traps. Several consecutive warm days in May can, however, be rare in some years; these warm spells are often interspersed by periods of cool weather. This precludes mass flight and concentrated, successful attacks. Consequently, propagation is hampered and next year's flying population correspondingly smaller.

Discussion: Do We Confuse "Dry Summers" And "Hot Summers"?

As stated initially, bark beetle epidemics often coincide with hot and dry weather, and a causal relationship could be that drought stress reduces host tree resistance.

In South Norway severe drought on larger trees is probably a rather unusual condition at the time of *I. typographus'* main flight, i.e., only 1-2 months after snow melt and thawing of the ground. However, in extremely rare cases a drought may prevail for an extended period of time: during the years 1968-76 a water deficit developed corresponding to one whole year's precipitation and water tables dropped by several meters in deep gravel deposits of south-eastern Norway. From 1968 through 1973 a significant part of this deficit was recorded as a lack of autumn and winter precipitation; this was followed by three unusually dry summers and this sequence may have aggravated the bark beetle epidemics of the 1970s (Worrell 1983). A prolonged drought of the same magnitude also occurred during the 1840s, prior to an outbreak around 1850. This was the last major epidemic in South Norway before the 1970s; no comparable dry period is recorded over the 130 years that elapsed between the two events (see Worrell 1983 for discussion). Under such extreme conditions, and when summer droughts also coincide with snow-poor winters, spruce trees could conceivably suffer from drought even in spring and early summer.

Some work related to a major pest in the USA, the southern pine beetle *Dendroctonus frontalis* Zimm., may shed light on our problem. *D. frontalis* is multivoltine and its infestation levels exhibit a clear annual variation which appears to be related to water availability. However, beetle attacks are most severe in spring and early summer when water is abundant and trees are in good growth. According to the principles of plant growth-differentiation balance (see Lorio 1986), a physiological model has been suggested (Reeve & al. 1995). According to this idea moderate water stress (limiting growth but not photosynthesis) increases the production of carbon-based secondary metabolites (i.e. resin), thus reducing the suitability for the beetles. A more severe drought (limiting both growth and photosynthesis) reduces resin yield, and host susceptibility increases. Field experiments corroborate this idea (Dunn and Lorio 1993, Reeve & al. 1995).

The model is derived from a more generalised growth-differentiation balance model for plant defence (e.g., Herms and Mattson 1992, Lerdau et al. 1994), and also seems to be in accordance with the C/N balance - host suitability hypothesis (Bryant et al. 1983). It would also explain the results of the *P. abies* - *C. polonica* experiment described above, where resistance increased under mild water stress.

Coniferous trees also have other chemicals that play a part in the defence against invasion of their tissues, and it appears that phenolic and tannic substances play a role in the defence of Norway spruce against *C. polonica* infection (Brignolas et al. 1995). Tannins may, however, be differently affected by changes in the growth-differentiation balance than are terpenes (Lerdau et al. 1994).

In conclusion it appears that apart from extremely rare cases of severe droughts lasting for a long period of time, direct effects of spring weather on beetle propagation are more likely to affect *I. typographus* dynamics than are indirect physiological effects working through the host trees.

This conclusion applies for areas with univoltine *I. typographus* populations (viz. the Scandinavian peninsula), and may not at all hold true for southern areas where a second generation of beetles may encounter spruce trees suffering from much more severe late-season drought. Moreover, this reasoning may have no bearing on other bark beetle species, some of which seem adapted to exploiting their host trees during dry periods in late summer, e.g. *Polygraphus poligraphus* L. (Lekander 1959).

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Observations on the Transmission of *Ophiostoma ulmi* by the Smaller Elm Bark Beetles (*Scolytus spp.*)

M. FACCOLI & A. BATTISTI

Istituto di Entomologia agraria, I-35020 Legnaro PD, University of Padua - Italy

ABSTRACT The spreading of the Dutch elm disease caused by the fungus *Ophiostoma ulmi* by the smaller elm bark beetles belonging to the genus *Scolytus* has been studied in Northern Italy. The percentage of beetles (*Scolytus multistriatus* and *S. pygmaeus*) carrying spores of *O. ulmi* at emergence from infested logs is higher in the spring (May-June: 58%) than in the summer emergence (August: 10%). No significant differences between beetle species have been found. The effectiveness in the transmission of the fungus during the adult maturation feeding has been evaluated for the two most abundant species (*S. multistriatus* and *S. pygmaeus*) on different species/hybrids of *Ulmus spp.* A variable infection rate (3.3 - 22 %) has been recorded, using insects artificially loaded with different strains of *O. ulmi*. The results show that the smaller elm bark beetles can successfully transmit the fungus, and this may cause additional work in the usual sanitation programs.

KEY WORDS vector, bark beetles, fungus, transmission

THE TRANSMISSION OF *Ophiostoma ulmi* by the elm bark beetles via maturation feeding has always raised a great interest, in order to be able to intervene in a decisive way in the apparently perfect symbiosis existing between the insects and the fungus (Brasier 1990). The bark beetles of the genus *Scolytus* Geoffroy are known to act as vectors of the fungus since the 30's, immediately after the first description of the disease (Fransen 1931, in Webber and Brasier 1984). However, precise information on the relationships between the life cycle of both the fungus and the insects has been given rather recently (Webber and Brasier 1984). In another paper Webber (1990) compares the spore load of 3 species (*S. scolytus* (Fabricius), *S. multistriatus* (Marsham), and *S. kirschii* Skalitzky) emerging from infested logs collected in August-September in Spain. *S. scolytus*, characterized by the biggest size, is supposed to be the only species able to successfully transmit the fungus, and this fact is related to the pupation behavior. In fact, the pupal chambers of this species are located in the moist inner bark, whereas the smaller species pupate in the outer bark. Such material tends to dry out quickly during summer, and this may hinder the development of the fungus and then the contamination of the smaller species of bark beetles. Information on the real effectiveness in the successful transmission of the fungus to the trees by beetles is not given, neither it is available from other literature sources. However, there is evidence that a minimum of 10^3 spores/beetle are required for a successful transmission.

The research presented in this paper has been based on two smaller species of bark beetles, *S. multistriatus* and *S. pygmaeus* (Fabricius), a species vicariant of *S. kirschii* in Northern Italy. Bark beetles of larger size (*S. scolytus*, *S. sulcifrons* Rey) were not available because of the lack of big elms for breeding (Zanta and Battisti 1989). The work has been focused on 2 main aspects: 1. estimation of the percentage of beetles (*S. multistriatus* and *S. pygmaeus*) carrying spores of *O. ulmi* at both first (May-June) and second (August)

Pages 172-176 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

emergence, 2. evaluation of the effectiveness in the transmission of the fungus to the tree by adults of *S. multistriatus* and *S. pygmaeus* artificially loaded with spores of *O. ulmi*. Some preliminary results have been already published (Basset et al. 1992, Favaro and Battisti 1993).

Materials and Methods

Beetles carrying spores at emergence. Logs of *Ulmus minor* apparently infested by both the fungus and larvae of elm bark beetles were collected in various sites of North-Eastern Italy in the period 1991-1994. The logs were kept outdoor in boxes and adult emergence was recorded twice a day. Each beetle was put individually in sterile tubes, then identified, sexed, and inoculated in selective plates for *O. ulmi* (Gibbs and Brasier 1973) within 24 hours from the emergence. The plates were kept in the darkness at 20° C (Brasier, 1981) and the presence of *O. ulmi* mycelium was detected after one week.

Fungus transmission by bark beetles. Adults of *S. multistriatus* and *S. pygmaeus* coming from fungus-free logs were artificially loaded with spores of *O. ulmi* (aggressive strains North American (NAN 182), Eurasian (EAN H328 and H351)) by immersion and shaking for 60 seconds in a spore suspension (10^6 spores/ml). The final load of spores was determined with the dilution method (Webber and Brasier 1984). Adults were then forced to feed on 2 to 3-year-old branches of elm trees (*U. minor x U. pumila* and *U. glabra*). Bark beetles were introduced individually in dark plastic tubes with holes ensuring a correct air change. The tubes were then fastened to the branches with Parafilm. After 48 hours the bark beetles were removed and each tunnel was labelled. After one month the branches were collected and wood samples were taken at the tunnel level (0 cm), at 3 and 6 cm below. The wood samples were inoculated in selective plates for *O. ulmi*, kept in the darkness at 20° C and checked for the presence of the fungus after one week.

Results and Discussion

Beetles carrying spores at emergence. The proportion of *S. multistriatus* and *S. pygmaeus* carrying spores of *O. ulmi* at spring emergence from the logs is on the average 58% (Table 1). The infection was found on the 88% of the elm logs used for rearing beetles. A considerable amount of the beetles (65%) carried also other fungi, mostly belonging to the genus *Penicillium*. The sex-ratio of the adults was 0.94. No significant differences emerged between species and sexes (X^2 test).

The tests performed on beetles of summer emergence gave significantly inferior values in the percentage of insects carrying the fungus, around 8% on the average (X^2 test)(Tab. 1). The sex-ratio (0.55) is remarkably female-biased, suggesting the possible presence of re-emergence of adult females after the first egg-laying. No significant differences emerged between species and sexes (X^2 test).

Table 1. Proportion of smaller elm bark beetles carrying spores of *O. ulmi* at emergence.

Species	*O. ulmi* at spring emergence			*O. ulmi* at summer emergence		
	presence	absence	% of beetles	presence	absence	% of beetles
S. multistriatus	158	126	55.6	87	793	9.8
S. pygmaeus	28	19	59.6	23	363	5.9

The dramatic reduction in the percentage of beetles carrying *O. ulmi* in summer is likely due to the high temperature and to the consequent drying out of the outer bark where the beetles pupate, as it was observed by Webber (1990) in Spain. However, the same species are largely contaminated with spores in spring, when the conditions are more favourable to the development of the fungus and to a successful transmission of the spores in the large vessels of the early wood. In conclusion, *S. multistriatus*, *S. pygmaeus* and possibily its vicariant *S. kirschii* cannot be disregarded as potential vectors of *O. ulmi*, as suggested by Webber (1990). An indirect demonstration of this fact is given by the continuous spreading of the disease in Northern Italy, where the large species of bark beetles have been almost disappeared in the last decades.

Fungus transmission by bark beetles. The results concerning the transmission effectiveness are presented in Table 2. The artificial load of beetles as estimated with the dilution method was 130.1±14.7 colonies/beetle. It must be considered that one colony may be originated by more than one spore. In any experiment the transmission was successful, but with a rather low rate (min 3.3 - max 22.5 % at 3 cm from the feeding tunnel) considering that all the beetles were artificially loaded with the fungus.

The decrease in the trasmission of the fungus at 3 cm from the feeding tunnel is statistically significant (ANOVA) in all the cases with the exception of *Ulmus glabra*. This proves that the spreading of the fungus into the tree is related to the diameter of the vessels. They are in fact much larger in *U. glabra* than in *U. pumila x minor*, the latter being selected also for this feature (Mittempergher 1985). No significant differences in the spreading of the fungus have been observed between *S. multistriatus* and *S. pygmaeus* in 1991. The significant differences observed in 1994 between the fungus strains H328 and 182 seem to be probably linked to a different aggressiveness of the strains.

Table 2. Effectiveness in the transmission of *O. ulmi* by smaller elm bark beetles artificially loaded with spores.

Year	Species	Strain of *O. ulmi*	Tested trees (n)	Beetles/ tree	Transmission rate (%) at distance of cm 0	3	6
1991	*S. multistriatus*	H351	50	34	\	11.9	11.9
1991	*S. pygmaeus*	H351	50	22	\	9.1	9.1
1993	*S. multistriatus*	H328	20	40	20	12.5	\
1993	*S. multistriatus*	H328	20	40	22.5	22.5	\
1994	*S. multistriatus*	H328	15	20	20	6.7	\
1994	*S. multistriatus*	182	15	10	10	3.3	\

In conclusion, it seems evident that the fungus may be successfully transmitted by the smaller species of bark beetles also when the spore load is not as high as it could be expected (minimum of 10^3 spores/beetle according to Webber 1990). As a consequence, sanitation felling must include all parts of the tree because these species may breed in very thin twigs, and this may represent an additional problem in the control of the Dutch elm disease.

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Intensive sylvicultural practices increase the risk of infestation by *Dioryctria sylvestrella* Ratz (*Lepidoptera: Pyralidae*), the Maritime pine stem borer.

H. JACTEL and M. KLEINHENTZ

Laboratoire d'Entomologie, Station de Recherches Forestières, INRA
BP 45, 33611 Gazinet Cedex, France.

ABSTRACT The infestation dynamics of *Dioryctria sylvestrella* was studied in relation to fertilisation and pruning of the Maritime pine. The percentage of infested trees was recorded by comparing three levels of fertilisation doses and four levels of pruning severity. Fertilised trees exhibited significantly greater tree growth and higher infestation rates than controls. The removal of live branches resulted in an increase in *D. sylvestrella* infestation, demonstrating a significant positive correlation with the number of pruning wounds. A model of infestation behaviour was hypothesised which involved primary attraction mediated by oleoresin components exuding from the pruning wounds. Gas chromatographic analysis of volatile terpenes of the wood resin of Maritime pines showed that infested trees contained a significantly higher percentage of terpinolene. The rate of infestation of ten full-sib families showed a significant positive correlation with the mean percentage of terpinolene. In a cross-table analysis of the interaction between tree diameter and terpinolene richness, the distribution of infested trees frequencies indicated that both tree pruning, which creates bark wounds, and tree vigour, which increases bark cracking, could simultaneously increase wood resin flow, thus enhancing tree attractiveness. Modifications of forestry practices are proposed to reduce stem borer damage.

KEY WORDS *Dioryctria sylvestrella,* Maritime pine, fertilisation, pruning, tree selection, resin, terpene

THE MARITIME PINE, *Pinus pinaster* Ait, is the primary coniferous species in France (Merzeau, 1995) in terms of surface area (1.4 million ha) and harvest volume (5 millions m^3 per year). It is also one of the most intensively managed species: draining, fertilising, planting, thinning, and pruning are all commonly performed in Maritime pine stands. This intensive culture has yielded dramatic increases in profitability, by shortening rotations to 40 years, increasing annual productivity from 5 m^3/ha/year in the 1960s to 9 m^3/ha/year in the 1980s and increasing the proportion of clear lumber in the logs (Guyon, 1996).

In addition, there is a widespread belief among foresters that vigorous forest crops undergo outbreaks of insect pests more rarely than forests under stress. By improving the growth and the vigour of the trees, intensive management could increase overall "resistance" to forest pests. The evidence to support this theory are mainly provided by bark and shoot borer dynamics (Speight, 1986) since numerous bark beetles severely damage conifers during periods of water stress (Waring and Pitman, 1983; Worrell, 1983; Lieutier, 1990). A negative effect of fertilisation on chewing insects has also been reported (Smirnoff and Bernier, 1973). However, fertilisation of pine trees can increase forest pest populations, such as sap feeders (Heliovaara *et al.*, 1983), tip moths (Folz and Blakeslee, 1989; Ross and Berisford, 1990) and pine weevils (Selander and Immonen, 1991). In addition, vigorous coniferous trees are more

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prone to attack by some bark beetles, such as *Dendroctonus micans* (Vouland, 1991) and *Dendroctonus ponderosae* (Cole and Amman, 1980). The same relationship has been observed for *Dioryctria sylvestrella*, one of the major Maritime pine pests. Female moths attack fast growing pine trees more frequently (Guinaudeau, 1969) and fertilised or highly productive stands experience more severe damage (Ménassieu and Lévieux, 1990, Carisey *et al*., 1994). This variability in the response of insect infestation to tree vigour may result from the complexity of tree physiology. Tree growth improvement could increase the amount of photosynthate available for defense reactions and thus improve resistance to insect pests (Christiansen *et al.*, 1987). However, it could also increase the nutritive value of tree tissues and shift the process of carbohydrate allocation from the synthesis of secondary defensive chemicals to the development of organs and energy storage so that overall susceptibility to insect attack might increase (Speight and Wainhouse, 1989).

Recent studies have demonstrated that tree pruning also increases the level of *D. sylvestrella* attack (Jactel *et al*., 1994 and 1996a). Tree pruning, i.e. the removal of live branches, is used to reduce the occurence of knots and increase the proportion of clear lumber in the log. It was hypothesized that primary attraction, mediated by oleoresin terpenes exuding from bark wounds, might attract insects to host trees. The dynamics of the European stem borer, *D. sylvestrella,* could be closely related to the intensity of Maritime pine stand management. The aim of this study was to investigate the pattern of pine tree susceptibility as related to the intensity of growth and pruning. The information presented should help foresters to adjust their cultural tactics to reduce the risk of *D. sylvestrella* damage.

Materials and Methods

Effects of pruning on Maritime pine infestation by *D. sylvestrella.* The study was conducted in a pure stand of Maritime pine (13 ha), grown on mesophilous humid heaths in the Station de Recherches Forestières, Gazinet, France. Trees were 10 years old, with an average normal diameter of 10.3 cm. The experiment was a completely randomised block design with ten replications of four pruning treatments: removal of dead branches only (all live whorls retained), or removal of all branches except the four, three, or two upper whorls. Each replicate contained 32 trees, and every fourth tree was pruned in 1991 (8 pruned trees and 24 control trees). In 1991, all trees from all plots (1358 pine trees) were sampled for diameter at breast height and *D. sylvestrella* attack. For each pruned tree, the number of fresh wounds, resulting from the removal of live branches, was recorded as it varied according to the number of branches per pruned whorls and to tree polycyclism. For each attacked tree, the location of the attack on the trunk was recorded along with the age of the attacked stem internode.

Effects of fertilisation on Maritime pine infestation by *D. sylvestrella.* The study was conducted in two Maritime pine plantations, grown on a mesophilous humid heath at the Station de Recherches Forestières, Gazinet, France. Trees were 20 years old with an average normal diameter of 20.5 cm and 20.1 cm respectively. The experiment was a randomised block design with four replications of three fertilisation treatments: control, 63 and 126 kg.ha=^{1} P_2O_5. (natural phosphate). The fertiliser was mechanically broadcast over the rows. Each plot consisted of five rows of 4 to 60 trees separated by 4 m between the rows and 2 m between the plants in the row. The plots were separated by one row with no fertilisation treatment. In 1985 and 1995, all trees from all plots (2031 pine trees) were sampled for diameter at breast height. In 1995, all trees from the first plantation (793 trees) and the second plantation (1238) were sampled for *D. sylvestrella* attack.

Effects of terpene composition of wood resin on Maritime pine infestation by *D. sylvestrella*. The study was conducted in a Maritime pine clonal test comprising full-sib families, from a local provenance grown on a mesophilous humid heath at the Station de Recherches Forestières, Gazinet, France. Three to four trees per family were cloned 3 to 5 times by grafting. Trees were 10 years old with an average normal diameter of 14.7 cm. In 1995, 143 clones, of 10 families, were sampled for diameter at breast height, *D. sylvestrella* attack and wood resin composition. Constitutive oleoresin was collected at 2 m above the ground level and stored according to the method described by Jactel *et al.* (1996). For chromatographic analysis, 1 ml of oleoresin was solubilized in 1.5 ml of pentane and purified by column chromatography on SDS silica 70-230 mesh (10 ml). The terpenes were eluted by a pentane-ether solution (30ml; 98:2). The extract was concentrated by evaporation under moderate vacuum and analysed by FID-GC (Hewlett Packard® 5890; temperature program. 60°C to 90°C at $6°C.mn^{-1}$, 90°C to 102°C at $3°C.mn^{-1}$, 102°C to 280°C at $6°C.mn^{-1}$; splitless (injector 270°C, detector 290°C)) on a 30 -m x 0.25-mm-ID HP1 column (He 15 psi, 0.5 µl sample). The relative percentages of mono- and sesquiterpenes were calculated from the total of all recorded terpene peaks. Only 10 terpenes, with relative proportions higher than 0.1%, were used throughout the study. In order of increasing retention time, 6 monoterpenes (α-pinene, camphene, β-pinene, myrcene, limonene, terpinolene) and 4 sesquiterpenes (longipinene, longifolene, β-caryophyllene, α-humulene) were found.

Statistical analyses. All statistical analyses were performed using SAS Software (SAS Institute Inc., 1990). Analyses of variance (GLM, *t* test) of percentage variables were computed using the $\arcsin\sqrt{x}$ transformation (Dagnelie, 1973). A non-parametric analyses of variance (NPAR1WAY, Wilcoxon test) was used for oleoresin composition data which are proportions of *p* terpenes with the constraint $\sum_i p_i = 1$.

Results

Tree pruning. The percentage of attacked pruned trees increased significantly with the severity of pruning (F = 14.2, $P < 0.001$, N = 40) and the control trees were similarly damaged in the four pruning treatments (F = 2.3, $P > 0.05$, N = 40, Fig. 1).

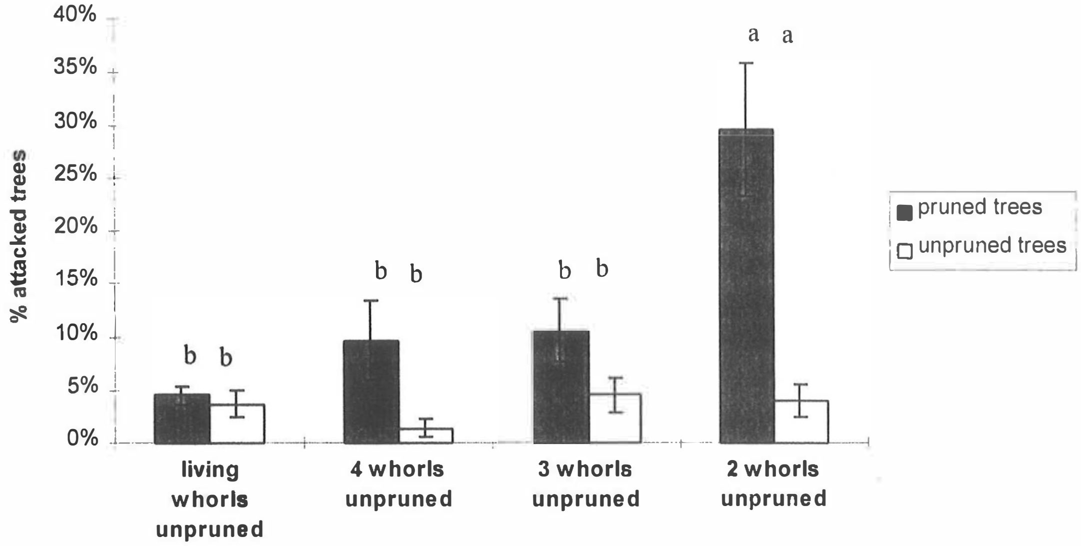

Fig. 1. Mean percentage of Maritime pine trees attacked by *D. sylvestrella* in relation to pruning severity. Means indicated by different lowercase letters are significantly different ($P < 0.05$) according to Duncan's multiple range test. Standard errors are indicated by vertical bars.

Attacked pruned trees exhibited significantly more fresh wounds than unattacked pruned trees (*t* test, $P < 0.05$) but did not differ significantly for normal diameter or for height of pruning (*t* test, $P > 0.05$). In contrast, attacked unpruned (control) trees had a significantly greater diameter than unattacked unpruned trees. The mean number of attacks per attacked tree did not differ significantly between pruned and control trees and averaged 1.4 ± 0.1. The mean height of *D. sylvestrella* attack did not differ significantly between pruned and control trees, or between pruning treatments. A Wilcoxon test demonstrated that the distribution of attacks among the internodes for pruned and control trees was similar ($Prob > Z = 0.56$). Their mode was observed for 2- to 3-year-old internodes (Fig. 2.). Ninety-five percent of the observed attacks were located less than 10 cm from the insertion point of the branch, left in place or removed by pruning.

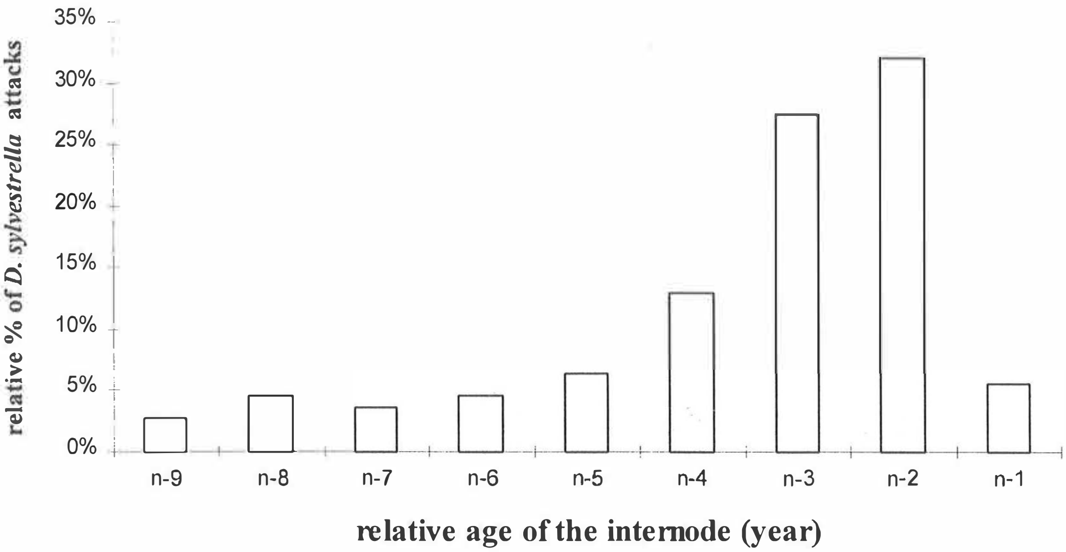

Fig. 2. Distribution of *D. sylvestrella* attacks among the internodes of 10-year-old pruned Maritime pine trees, expressed as the percentage of the total number observed. Internodes are identified by their relative age with respect to the year of study.

Tree vigour. The variance of the mean annual diameter increments, which characterised tree vigour, were analysed according to site (2 plantations, *df* = 1), fertilisation level (3 doses of phosphorus, *df* = 2) and their interaction (N = 2031). Tree growth, recorded between the tenth and the twentieth years, differed significantly between sites (F = 36.1, $P < 0.0001$) and significantly increased with fertilisation level (F = 12.9, $P < 0.0001$, Fig. 3); however these two factors interaction did not induce any significant differences (F = 2.2, $P > 0.05$). The variance of the infestation rate by *D. sylvestrella,* calculated as the percentage of attacked trees per row, was similarly analysed according to site, fertilisation level and their interaction (N = 24). The site and the two factors' interaction did not exhibit any significant differences (respectively, F = 1.33 and F = 0.07, $P > 0.05$). The level of attack was significantly higher in fertilised rows than in controls (F = 4.02, $P < 0.03$, Fig. 3).

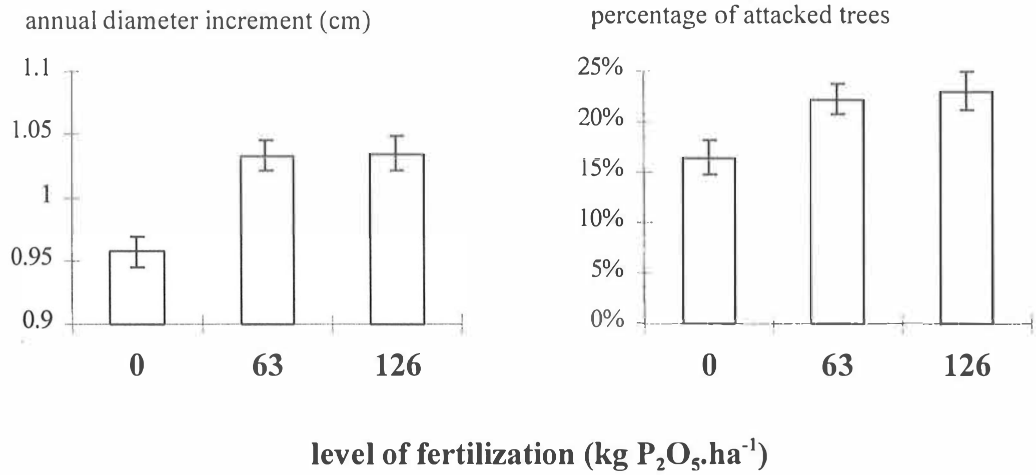

Fig. 3. Effects of fertilisation on Maritime pine radial growth and susceptibility to *D. sylvestrella.* Means indicated by different lowercase letters are significantly different ($P < 0.05$) according to SNK multiple range test. Standard errors are indicated by vertical bars.

The regression between the percentage of attacked trees per class of diameter increment and the median value of the class was significant (Fig. 4).

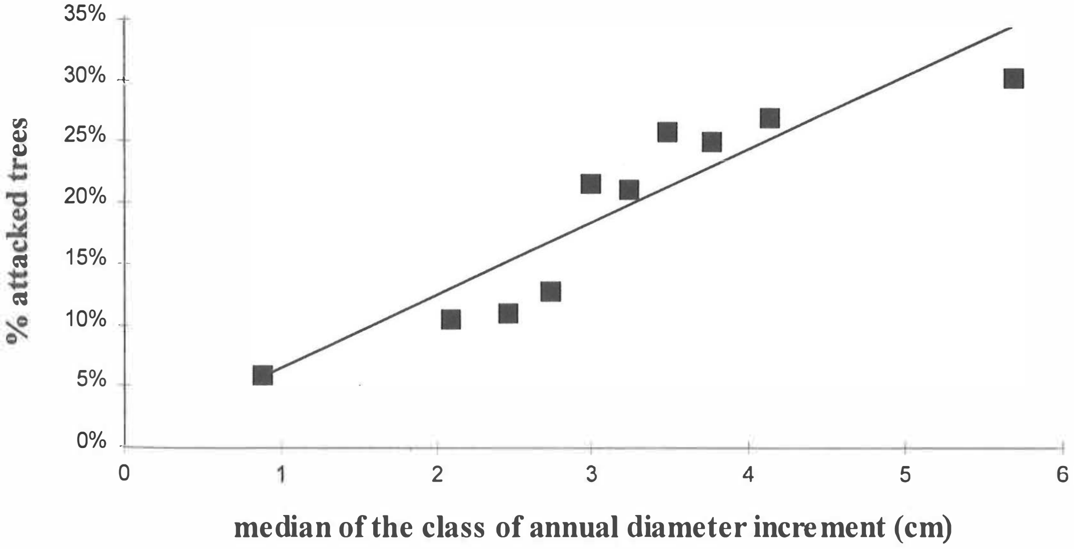

Fig. 4. Relationship between the class of tree growth and susceptibility to *D. sylvestrella.* Susceptibility to the moth is expressed as the percentage of attacked trees per class of annual diameter increment ($r^2 = 0.84$, $P < 0.001$, $n = 10$).

Terpene composition of the wood resin. Wood resin did not differ qualitatively between attacked (13.3 %) and unattacked trees, since both types of trees produced the same typical chromatogram of the same 10 terpenes. However, attacked trees exhibited significantly more terpinolene (Wilcoxon test, *Prob* > Z = 0.046, Fig. 5) and the regression between the percentage of attacked trees and the mean proportion of terpinolene per full-sib families (N = 10) was significant (Fig. 6).

In the same sample of 143 pine trees, the normal diameter was significantly higher for attacked trees than unattacked trees (respectively 14.8 cm and 13.7 cm, *t* test, $P < 0.05$).

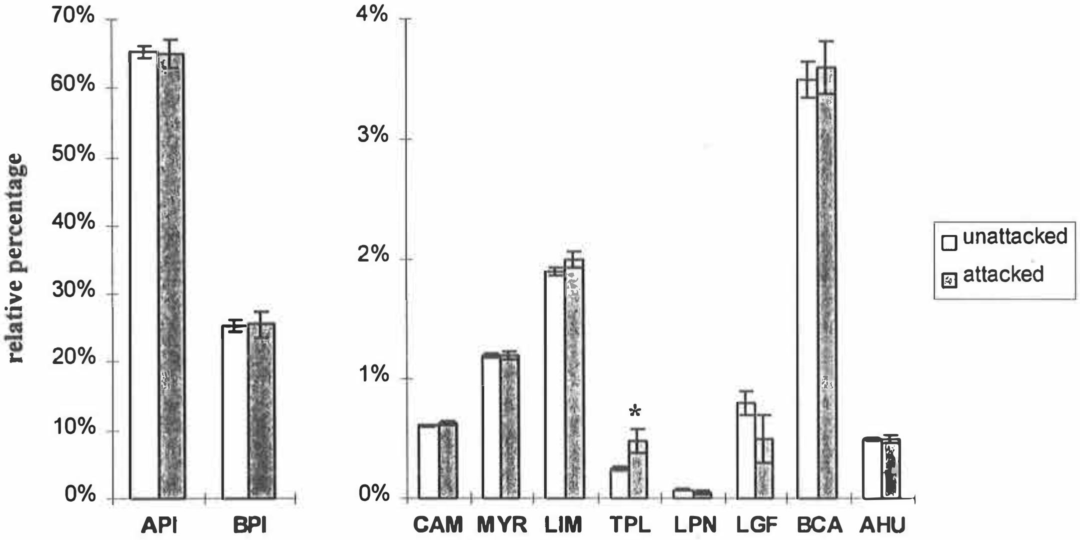

Fig. 5. Comparison of mean terpene profiles of wood resin in attacked and unattacked Maritime pine trees. Standard errors are indicated by vertical bars. One star above a pair of bars indicates a significant difference (*P* > 0.05). API: α-pinene, BPI: β-pinene, CAM: camphene, MYR: myrcene, LIM: limonene, TER: terpinolene, LPN: longipinene, LGF: longifolene, BCA: β-caryophyllene and AHU, α-humulene.

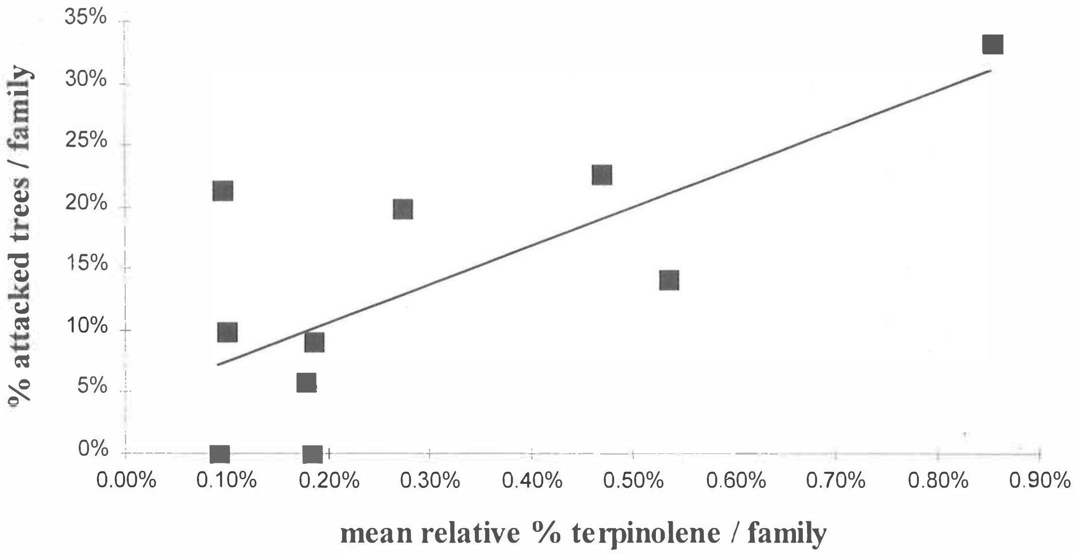

Fig.6. Relationship between the percentage of attacked trees and the mean relative percent of terpinolene in the wood resin per full sib family of Maritime pine. ($r^2 = 0.53$, $P < 0.05$, $n = 10$).

The interaction between vigour and oleoresin composition of the trees in relation to the risk of infestation by *D. sylvestrella* was investigated using two models of conditional probabilities. In the first model, it was assumed that attacked trees would exhibit both a large diameter *and* a high percentage of terpinolene in the oleoresin. Because the terpene composition of the resin was not correlated to tree vigour ($P > 0.05$), the theoretical frequencies of attacked trees in a cross table testing the interaction between those two factors could be calculated (Table 1, in italics) and compared with observed frequencies (in bold). The χ^2 test proved the observed and theoretical distribution frequencies to be different (df = 4, $\chi^2 = 123.9$). In the second model, it was assumed that attacked trees would exhibit either a large diameter *or* a high percentage of terpinolene in the oleoresin. The χ^2 test proved the observed and theoretical distribution frequencies (Table 1, in underlined characters) to be equal (df = 4, $\alpha = 0.01$, $\chi^2 = 11.2$).

Table 1. Observed and calculated* frequencies of Maritime pine trees attacked by *D. sylvestrella* in a cross table analysis of the interaction between the relative percentage of terpinolene in the wood resin and tree class diameter.

	class of terpinolene proportion (%)		
class of tree diameter (cm)	1 [0.07 ; 0.1] n = 35	2]0.1 ; 0.22] n = 63	3]0.22 ; 1.6] n = 45
1 [9.5 ; 13.4] n = 60	**0 (0 %)** 2.4 *0.1*	**2 (7.4 %)** 4.8 *0.2*	**3 (15.8 %)** 5.8 *0.4*
2]13.4 ; 15.3] n = 50	**2 (14.3 %)** 2.9 *0.1*	**1 (5 %)** 4.3 *0.2*	**3 (18.8 %)** 5.5 *0.4*
3]15.3 ; 18.8] n = 33	**1 (14.3 %)** 2.3 *0.2*	**3 (18.8 %)** 5.4 *0.4*	**4 (40.0 %)** 4.7 *0.5*

* The events are labelled as follows: A (attacked tree), A/D (attacked tree with known its diameter), A/T (attacked tree with known its terpinolene proportion).

in bold: observed frequencies and related percentage of attacked trees

underlined: theoretical frequencies calculated under the hypothesis that tree infestation depends on diameter *or* proportion of terpinolene in the wood resin

Proba (A) = Proba (A/(D or T)) = Proba (A/D) + Proba (A/T)

in italics: theoretical frequencies calculated under the hypothesis that tree infestation depends on diameter *and* proportion of terpinolene in the wood resin

Proba (A) = Proba (A/(D and T)) = Proba (A/D) x Proba (A/T)

Discussion

Effect of pruning on Maritime pine susceptibility to *D. sylvestrella* . Pruned Maritime pine trees were significantly more prone to attack by *D. sylvestrella* than control trees (Fig. 1.). It has already been shown that stem borers such as *Dioryctria zimmermani* Grote (Wrigth *et al.*, 1975) and *D. sylvestrella* (Jactel *et al.*, 1996) preferentially damage pruned trees, but this study demonstrated a significant positive correlation between the risk of *D. sylvestrella* infestation and the severity of pruning (number of live branches or whorls removed). Forestry policies recommend pruning Maritime pine up to 5.5 m above ground level to produce clear lumber in the two timber bolts. It can therefore be predicted that intensive sylviculture practices which increase the number of live branches in the lower part of young trees, such as fertilising and low density planting, may in turn increase stem borer damage after pruning.

The increase in infestation rate with pruning severity could result either from the increase in a survival brood or from the improvement of tree selection. There is a little information concerning the effect of pruning on forest pest insect abundance. Hard (1992) records that pruning live branches of spruce trees reduces successful *Dendroctonus rufinpennis* Kby attacks. The effect of pruning was related with micro-climatic changes near pruned boles, which reduced the survival rate of scolytids. But this hypothesis is unlikely to apply to *D. sylvestrella* infestation as it would assume that a significant correlation exists between the number of attacked trees and the volume freed by removal of branches, i.e. pruning height. It could also be assumed that removing live branches might induce physiological stress which would in turn modify the quantity or the quality of available food. However, if this were the case, the number of successful attacks per suitable tree and their location on the trunk, would also be changed. Moreover, due to the low number of attacks per tree (one or two), any food deficiency is unlikely to prevent the development of *D. sylvestrella* larvae. In contrast, only the removal of live branches appears to result in a higher infestation rate. Baer (1906) and Olmi *et al.* (1977) observed that injuries to the stem bark resulted in *D. sylvestrella* attacks. It is thus possible that pruning wounds release volatiles which act as a primary attractant for mature female moths. Since the removal of live branches created a resin flow outside the wounded bark area, one may assume that primary attractants are components of Maritime pine wood resin. Primary attraction to host odours has been suggested as a mechanism of host tree selection by numerous bark beetles (Raffa and Berryman, 1983; Vité *et al.*, 1986) and often involves monoterpenes, a family of volatile compounds naturally occurring in conifer resin. Hanula *et al.* (1985) have shown that a combination of α-pinene, myrcene and limonene is attractive to *Dioryctria amatella* (Hulst) and stimulates oviposition. The significant correlation between wound number and infestation level may also support the theory of a quantitative effect of this primary attraction. Olmi *et al.* (1977) link the susceptibility to *D. sylvestrella* of *Pinus excelsa* x *Pinus strobus* hybrids to the amount of resin exudate.

Effect of fertilising on Maritime pine susceptibility to *D. sylvestrella*. Fertilised trees, even at low doses, were more frequently attacked by *D. sylvestrella* than controls (Fig. 3.). While no nutrient analyses were made in the bark, the effects of fertilisation were studied in relation to tree growth. Fertilised trees exhibited significantly greater annual growth increments and were more heavily infested by *D. sylvestrella* (Fig. 4.). This result is consistent with data obtained in a previous study (Jactel *et al.*, 1996) as well as in numerous studies that investigated the relationship between tree vigour and sensitivity to the stem borer (Ménassieu et Lévieux, 1990; Carisey *et al.*, 1994). Wright *et al.* (1975) found that fast growing varieties of Scots pine are more susceptible to *D. zymmermani*. It is possible that vigorous trees present thicker phloem and thus improve the survival of *D. sylvestrella* brood by providing larger amounts of food to the larvae. However, due to the low number of attacks per tree, any variation in food availability is unlikely to affect the development of *D. sylvestrella* larvae. In contrast, Maugé (1987) observed that bark cracks were more common in fast growing pine trees. Therefore, Maritime pine trees with large annual diameter increments might release more attractive resin exudates. This hypothesis is consistent with the phenological concordance between the period of maximum radial growth in Maritime pine (Lemoine, 1975), which occurs from April to June, and period of female moth flight (Ménassieu *et al.*, 1989) which begins in June.

Effect of terpene composition of the resin on Maritime pine susceptibility to *D. sylvestrella*. In this study, the Maritime pine sensitivity to *D. sylvestrella* was significantly correlated with a high level of terpinolene proportion in the wood resin (Fig. 5.). In a previous study (Jactel *et al.*, 1996b), attacked and unattacked trees were discriminated by the relative proportion of six monoterpenes, including terpinolene, in the resin wood. Wright *et al.* (1975) also related the resistance of southern Scots pine varieties to *D. zimmermani* to low levels of terpinolene. Moreover, in an electroantennography test, terpinolene was the terpene which yielded the highest response in *D. sylvestrella* females (Jactel *et al.*, 1996b). Therefore, terpinolene could be a possible candidate for an effective host attractant. The action of terpinolene is also compatible with the quantitative effect of pruning wound attraction as the level of family infestation was significantly related to their mean terpinolene proportion (Fig. 6). Rappaport *et al.* (1995) consistently correlated the attack rate of *Megastigmus spermotrophus* Wachtl with the terpinolene levels in *Pseudotsuga menziesii* Mirb. cones.

If tree selection depended only on the presence of large amounts of attractants and tree colonisation depended only on the bark thickness, successful infestations should be recorded more frequently in trees with both a large diameter *and* a high percentage of terpinolene in the oleoresin. If this infestation process were correct, the frequencies of attacked trees which combine diameter and terpinolene proportion classes would have been significantly lower than those found (Table 1). In contrast, it appears that brood survival is slightly related to tree vigour and that female moth attraction requires the emission of a sufficient amount of terpinolene. Here, attacked trees should exhibit either a large diameter, *i.e.* a cracked bark from which large amounts of resin can flow, *or* a high percentage of terpinolene in the wood resin. In the sample of 143 trees, this model fitted the observed data (Table 1). Similarly Jactel *et al.* (1996 a) showed that both tree vigour, due to increased bark cracking, and tree pruning, due to bark wounding, effected tree attractiveness, and helped increase oleoresin flow.

Conclusions

In light of these results and data collected in our previous experiments, a model of host-infestation by *D. sylvestrella* can be proposed. Susceptible trees develop a primary attraction to the stem borer, mediated by some volatile attractants originating from the constitutive oleoresin. One of these compounds could be terpinolene. The attraction would not be effective unless the terpinolene, or a mixture of volatile attractants, is released in a sufficient concentration into the surrounding atmosphere. Factors that increase resin exudation may then be expected to increase tree attractiveness. It can be assumed, therefore, that forestry practices that favour tree wounding, such as pruning, or tree vigour (i.e. bark cracking), such as fertilising, intensive thinning and low density planting, may in turn increase stem borer damage.

In practice, foresters should be advised to reduce the severity of pruning or to delay its application to focus the attacks above the butt and second log, which is the stem region with the greatest timber value (Fig. 7).

Reduction of tree growth can hardly be recommended as a goal for wood production. Nevertheless, two strategies could be developed to reduce tree attractiveness, which have been proven to be the key step in tree infestation. Terpinolene proportion in the wood resin, provided that its heritability can be demonstrated, could be a suitable biochemical marker for selecting genetic resistance to *D. sylvestrella* (Jactel *et al.*, 1996b). Since bark thickness and cracking exhibit high infraspecific variability in *Pinus pinaster* (Shvester and Ughetto, 1986), the genetic improvement of bark permeability to resin exudates is also conceivable.

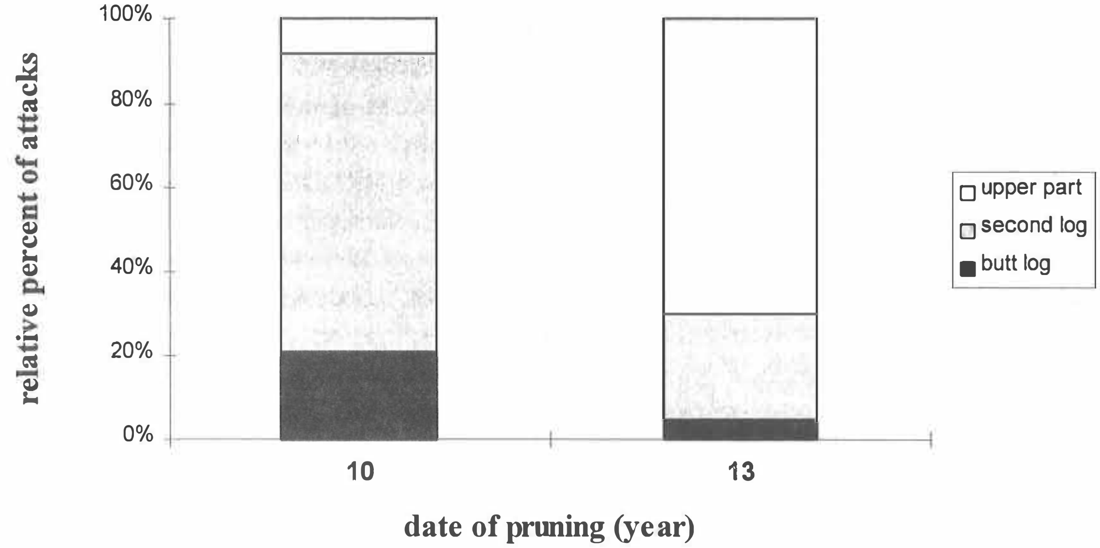

Fig. 7. Distribution of *D. sylvestrella* attacks in the butt log (0-3 m), the second log (3-5.5 m) and the upper part of the tree, as a percentage of the total number observed in 10-year-old trees and as a percentage of the total number calculated for 13-year-old trees according to the internode distribution model (Fig. 4.).

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Spatio-temporal geostatistical analysis of *Ips typographus* monitoring catches in two Romanian forest districts.

LAURENT RATY[1], CONSTANTIN CIORNEI[2] AND VASILE MIHALCIUC[3].

[1]Laboratoire de Biologie animale et cellulaire, Université Libre de Bruxelles, Bruxelles, Belgium
[2]Institute for Forest Research and Planning (ICAS), Station Bacau, Romania
[3]Institute for Forest Research and Planning (ICAS), Station Brasov, Romania

ABSTRACT Systematic trapping and monitoring of the spruce bark beetle *Ips typographus* has been carried out extensively in the Romanian Carpathians since 1984, using pheromone traps. We present here a geostatistical analysis of catches performed in two contiguous Romanian forest districts, Rastolita and Lunca Bradului. Numbers of insects caught per trap between 1987 and 1994 were aggregated over each year. These data presented very good spatial, and good temporal auto-correlation. Because of their strongly left skewed distribution, analyses were performed on logarithm of the catches. Data were spatially detrended by a median-polish., that produced spatially isotropic residuals. Isolated spatial outliers were Winsorized through robust krigings based on omni-directional variograms, and performed separately over each year. A global spatio-temporal (anisotropic) variogram was then fitted to Winsorized data, and kriging estimates were built. It was possible to estimate catch logarithm, using spatial kriging, with relative precision ranging around 10%, taking into account results of only the current year. More interestingly, spatio-temporal kriging also performed well to forecast logarithmic catch, using results from three previous years. In spatio-temporal kriging, auto-correlation between measurements spaced too closely introduced a loss of information. A theoretical analysis of the spatio-temporal variogram showed that, when kriging neighbourhood is limited in terms of number of data used to forecast next-year catches (thus when computation effort is limited), an optimal trap density may be calculated.

KEY WORDS *Ips typographus*, Romania, geostatistics, interpolation, forecast, monitoring

THE SPRUCE BARK BEETLE, *Ips typographus* (Coleoptera: Scolytidae), is a semi-aggressive bark beetle that can kill extensive areas of spruce by the burrowing activities of its larvae, particularly after natural, weather-linked, phenomena such as drought and windthrow. Loss of vigour due to stressing agents such as these is a very common precursor to serious pest outbreaks (Speight 1996). Control of this pest species is very difficult; sanitation management of forests can reduce the impact of *Ips typographus*, though the sheer magnitude of the outbreaks can render the operation unfeasible.

In the Romanian Carpathians (Moldavia and Transylvania), systematic trapping and monitoring program of the spruce bark beetle has been carried out very extensively since 1984. Pheromone-baited traps are now placed in virtually every forest likely to harbour insect populations. The results produced by this program have provided a valuable source of information concerning insect population fluctuations that might be related to climatic and biotic conditions (weather, soil conditions, geography etc.). Hence, after appropriate and exhaustive analysis, these data provide an unparalleled opportunity to study the outbreak dynamics and effects of potential pest management strategies of one of the most important insect pests in Europe.

In this paper, we present a spatio-temporal geostatistical analysis of the catches performed in two contiguous Romanian forest districts, Rastolita and Lunca Bradului,

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between 1987 and 1994. Our aims are to analyse the spatio-temporal variations of these catches (i.e. to see how catches vary spatially during each year, and how they vary from year to year at a given place), and to build estimates of the catches for places and years where no measure is available.

It is well known that damage due to semi-aggressive bark beetles are dependant on their population density. In particular, colonisation of a tree will be successful only if the number of beetles able to aggregate on that tree is high enough to overcome its defence reactions (i.e., Lieutier 1990). Assuming that trap efficiency does not vary too much from place to place or year to year, it seems logical to think to the number of insects caught in a trap is an indicator of the number of beetles crossing the trap neighbourhood and able to respond to their aggregative pheromone, e.g. able to aggregate on a host tree.

Building predictions of the catches for locations where no traps were set up might be useful to foresters, as it would give them a tool to know where they need to focus on and prepare for possible attacks and help them to locate colonised trees to destroy beetles. Forecasting the catches would be useful as well, as this might provide a tool to decide when and where preventive control methods might be usefully set up.

Data

Insect trapping data were produced by monitoring 300 permanent traps in the two Romanian forest districts of Rastolita and Lunca Bradului. This area covers a total of about 90,000 ha. Traps were black PVC drainpipe tubes 8 cm in diameter with numerous small holes and a Typolur (Cluj, Romania) pheromone dispenser hung inside the tube. Dispensers were set up at the beginning of the flight period and not renewed before next year. Attracted beetles land on the tube, enter one of the holes and fall into a collector (usually a glass jar half-filled with water). These traps have been visited roughly on a weekly basis, depending on accessibility of the location where the trap was set up, by Romanian forest employees.

Catches were combined for time each year to suppress temporal discontinuity inherent to insect catches made at short intervals (each catch is one discrete event). Summarizing data on a yearly basis also avoids problems that arise when comparing catches performed at different periods of the year, due to a decrease of pheromone-trap efficiency as the dispenser dries out (Raty et al. 1995).

Romanian forest are divided in planning units that are defined as homogenous in regard to slope, orientation, soil characteristics, type of station and type of forest. This results in a fairly large variation in the unit area, ranging from approximately 0.5 to 80 ha.

Our data initially associated traps to the planning units where they were set up. To convert these data into geographical co-ordinates, a Geographical Information System (GIS), Arc/Info, was used to digitise 1:20 000-scaled maps of the forest districts. Planning-unit boundaries were encoded in vectorial format, location of the centroids of the polygons delimited by these boundaries were computed, and each trap was associated to its planning-unit centroid. These results were used to produce an ASCII file associating aggregated yearly catches to trap location and the year considered.

Data analyses

We mostly used classical geostatistical tools, from which we will assume an elementary knowledge. Interested readers may find more complete and precise description of these tools in Isaaks and Srivastava (1989) and in Cressie (1993). We generally used the same notations as Cressie (1993). We think to our data as a partial realisation of a random process, noted $\{Z(\mathbf{s}) : \mathbf{s} \in D\}$ where **s**, the data location, varies continuously over D, which is a subset of the d-dimensional space $\Re^{d}$ ($d = 2$ when only space is considered and 3 when time is taken into account). Data are noted $\{Z(\mathbf{s}_1), ..., Z(\mathbf{s}_n)\}$. All analyses were performed on the basis of the ASCII file described above, using FORTRAN 77 routines that were, in most cases, written especially for this purpose.

Exploratory analyses

Exploratory Data Analysis (EDA) was introduced in spatial statistical analyses by Tukey (1977), and has since become a classical precursory stage to geostatistical studies (Cressie 1993, Rossi et al. 1992). Its main goals are visualising data set, analysing data distribution, investigating their stationarity and spatial (or spatio-temporal) continuity, and detecting possible outlying data. EDA mostly uses simple statistical methods, such as computing means, medians and histograms. According to Cressie (1993), EDA may be usefully completed by more spatial analysis techniques, including computation of directional variograms, computation of pocket plots and median polishing.

Data skewness - Our data exhibited a strongly left skewed distribution. Furthermore, when calculated over each year, catch mean was linearly correlated to catch standard deviation ($r = 0.77$; $p = 0.02$). These effects were corrected, as prescribed by Tukey (1977), with application of a logarithmic transformation ($Z' = \ln Z$).

Variograms and global non-stationarity - Observed directional spatial variograms were estimated for each year separately, following 4 directions (N-S, NE-SW, E-W and NW-SE), using the classical estimator (Matheron 1962) :

$$2\hat{\gamma}(\mathbf{h}) \equiv \frac{1}{|N(\mathbf{h})|} \sum_{N(\mathbf{h})} (Z(\mathbf{s}_i) - Z(\mathbf{s}_j))^2$$

A global pattern emerged from these computations. Variograms were fairly well shaped, exhibiting very small nugget-effects (close to 0), apparent sills ranging between 0.8 to 2 and apparent ranges between 4,000 and 8,000 m. At first glance, the data seem spatially continuous, and do not show evidence of strong measurement errors. However, zonal anisotropy was always clearly present. The E-W and SE-NW directions showed consistently higher sills than the two other directions. Furthermore, in these two directions, semi-variogram sills were typically larger than data variance. Combination of these two observations may be thought as evidence of global non-stationarity, and would indicate presence of a spatial trend in the data. Furthermore, this trend might have a permanent component, as patterns are comparable from year to year.

An observed temporal variogram was also estimated, with the whole data set. This variogram exhibited an apparent nugget effect of close to 0.4. This is much larger than spatial variograms, and may be due to significant variation in population density from year to year. After this abrupt vertical jump, the variogram increased slowly. At the scale of our study, it remained always smaller than twice the data variance (variance was 0.747; largest computed semi-variogram value, for a 4-years lag, was 0.408). This could be explained if we hypothesise a permanent spatial mean structure: in a purely temporal variogram, suppressed only data from the same spatial location are compared. Variation within these data, even when separated by large temporal lags, would be smaller than global variation.

Data detrending - From the above discussion, we will introduce the following model developed by Cressie (1993): assuming our data are partial realisation of a process that satisfies the following decomposition :

$$Z(\mathbf{s}) = \mu(\mathbf{s}) + R(\mathbf{s})$$

where $\mu(\mathbf{s})$ is a deterministic mean structure, called large-scale variation or trend and $R(\mathbf{s})$ is a stationary process, called small-scale variation. This kind of decomposition applied to a data set is called *detrending*. *Median polish* (Tukey 1977) is an EDA technique designed to identify large-scale and small-scale variation for gridded data, by analysing them as a 2- (or higher-) way table, and using the following additive model :

data = global effect + row effect + column effect + residual.

Decomposition follows an algorithm that alternatively sweeps medians out of rows and columns, and accumulates them in «row», «column», and «global» registers. A table of residuals results as well as preservation of additive decomposition relation at each step. If data are non-gridded, a low-resolution grid may be overlaid onto the data map. Each data point may be assigned to the nearest grid node (Cressie 1993), and median polish performed on this grid. A complete trend surface can be built by planar interpolation between the grid nodes.

A 2 km x 2 km grid was overlaid onto the data map. Each trap was assigned to the closest grid node and a spatial median polish was performed on this grid. To account for the apparently permanent character of the trend, we applied the algorithm only once, taking into account catches performed during the 8 years simultaneously. This produced a median-polish trend surface, showing obvious large-scale variation in both E-W and N-S directions.

Observed directional spatial variograms were estimated for each year, on the basis of the median-polish residuals. Most of the spatial anisotropy was captured by the median polish. Next steps of our analyses will be performed on the median-polish residuals, assuming they behave isotropically in space.

The temporal variogram remained clearly unchanged by the spatial median polish. However, as global variance of the median-polish residuals (0.437) was lower than variance of the original set of catch logarithms (0.747). The variogram values of the largest temporal lags were now much closer to twice the sample variance.

Local non-stationarity - The pocket plot technique (Cressie 1993) was used to detect pockets of local non-stationarity in median-polish residuals reassigned to the 2km^2 grid nodes that were used for the median polish. These analyses were performed separately for each year, and showed the presence of pockets of non-stationarity in each year.

Spatial geostatistical analyses

All analyses were performed on the basis of median-polish residuals, treated as a spatially isotropic data set. However, since we detected the presence of local pockets of non-stationarity in the last step of the exploratory analyses, we treat our data as a realisation of a Gaussian stationary process.

As with Hawkins and Cressie (1984), we will consider $R(\mathbf{s})$ as a mixture of a stationary Gaussian sub-process and some other sub-process with heavy-tailed distribution. This last sub-process will act only on measurement errors and micro-scale variations, for a small proportion of the global process (non-Gaussian contamination).

Robust estimation of the variogram - Because the classical variogram estimator presented above is very sensitive to outlying data. We used the robust estimator proposed by Cressie and Hawkins (1980) :

$$2\hat{\gamma}(\mathbf{h}) \equiv \frac{\left\{ \frac{1}{|N(\mathbf{h})|} \sum_{N(\mathbf{h})} |Z(\mathbf{s}_i) - Z(\mathbf{s}_j)|^{1/2} \right\}^4}{0.457 + 0.494/|N(\mathbf{h})|}$$

Robust omni-directional spatial variogram estimators were computed on median-polish residuals for each year.

Variogram model fitting - Choice of a model to be fitted to the observed variograms was made by eye, by comparison between observed-variogram shape of and model shape. We selected the spherical model :

$$2\gamma(\mathbf{h}) = \begin{cases} 0 & \mathbf{h} = \mathbf{0} \\ c_0 + c_s \left\{ \frac{3}{2} \frac{\|\mathbf{h}\|}{a_s} - \frac{1}{2} \left(\frac{\|\mathbf{h}\|}{a_s} \right)^3 \right\} & 0 < \|\mathbf{h}\| < a_s \\ c_0 + c_s & \|\mathbf{h}\| > a_s \end{cases}$$

A model was fitted to the observed robust variogram of each year, through the weighted-least-square method (Cressie 1993).

Robust Kriging - *Kriging* can be understood as optimal linear prediction (Cressie 1993). This leads to the classical kriging predictor :

$$p(Z;\mathbf{s}_0) = \sum_i \lambda_i \, Z(\mathbf{s}_i)$$

where the λ_i's are weights given to data values that minimise the mean-squared prediction error. However, optimality of *linear* spatial prediction relies on assumption that the expectation of $Z(\mathbf{s}_0)$ at a location $\mathbf{s}_0$ is linear in the data $Z(\mathbf{s}_i)$, which is the case when the random process Z is Gaussian.

Outliers due to non-Gaussian distribution can have a substantial effect on linear predictors. However, these data often support information and deleting them incorrect would be a loss of this information. It would be better to find some way to downweight them. This leads to *robust kriging* techniques, summarised by Cressie (1993). Turn back to our description of the process distribution, we now build a predictor :

$$p(Z;\mathbf{s}_0) = \sum_i \lambda_i \, Z(\mathbf{s}_i) \, w(Z(\mathbf{s}_i))$$

where $w(Z(\mathbf{s}_i))$ is a weight function, ranging from 0 to 1, which is close to 1 if datum $Z(\mathbf{s}_i)$ appears clean, but decreases to the extent that $Z(\mathbf{s}_i)$ appears to come from the contaminating distribution. Another way of writing this equation is :

$$p(Z;\mathbf{s}_0) = \sum_i \lambda_i \, Z^{(e)}(\mathbf{s}_i)$$

where $Z^{(e)}(\mathbf{s}_i)$ is an *edited* modification of $Z(\mathbf{s})$ that behaves as if there was no contamination.

The method we used is a geostatistical version of Huber's procedure for robust time-series analysis (1979, in Cressie 1993), but was performed with the robust variogram estimator proposed by Hawkins and Cressie (1984). Models fitted to robust variogram estimators were used to compute kriging weights for each $R(\mathbf{s}_j)$ from all the remaining $R(\mathbf{s}_i)$. A prediction:

$$\hat{R}_{-j}(\mathbf{s}_j)=\sum_{i\neq j}\lambda_i Z(\mathbf{s}_i)$$

was built on basis of these weights and the associated error was computed. Using these results, the $R(\mathbf{s}_j)$ were Winsorized. That is, they were replaced by an edited version such as:

$$R^{(e)}(\mathbf{s}_j)=\begin{cases}\hat{R}_{-j}(\mathbf{s}_j)+c\sigma_{-j}(\mathbf{s}_j) & \text{if } R(\mathbf{s}_j)-\hat{R}_{-j}(\mathbf{s}_j) > c\sigma_{-j}(\mathbf{s}_j)\\ R(\mathbf{s}_j) & \text{if } \left|R(\mathbf{s}_j)-\hat{R}_{-j}(\mathbf{s}_j)\right| \leq c\sigma_{-j}(\mathbf{s}_j)\\ \hat{R}_{-j}(\mathbf{s}_j)-c\sigma_{-j}(\mathbf{s}_j) & \text{if } R(\mathbf{s}_j)-\hat{R}_{-j}(\mathbf{s}_j) < -c\sigma_{-j}(\mathbf{s}_j)\end{cases}$$

Edited values were then used to compute a new robust observed variogram, to which a new model was fitted. This variogram served to perform a new Winsorization, and this procedure was repeated until convergence of the edited values.

Depending on the year, 5 to 8% of the data were edited. Edited data may be separated in two categories : real outliers (data with especially high or low values), and pairs of data spatially very close together, but with differing values. Part of these last data were probably not really outlying. Their outlying appearance may have been due to imprecision in the location associated to the data (the planning-unit centroids).

Winsorized data were used to build predictions and to estimate kriging error over the whole study area, on a 500m^2 grid. Summing these predictions to the median-polish trend surface, we obtained prediction maps for the catch logarithms. It has been showed by Cressie (1993), that error associated to these predictions is the kriging error associated to the residual kriging predictions. Within the area where traps were set up, the prediction relative precision (estimated by the ratio of half 95%-confidence interval to the prediction) rarely exceeded 10%. Maps of the predictions and the associated standard deviation for the years 1992 to 1993 are presented in Figure 1.

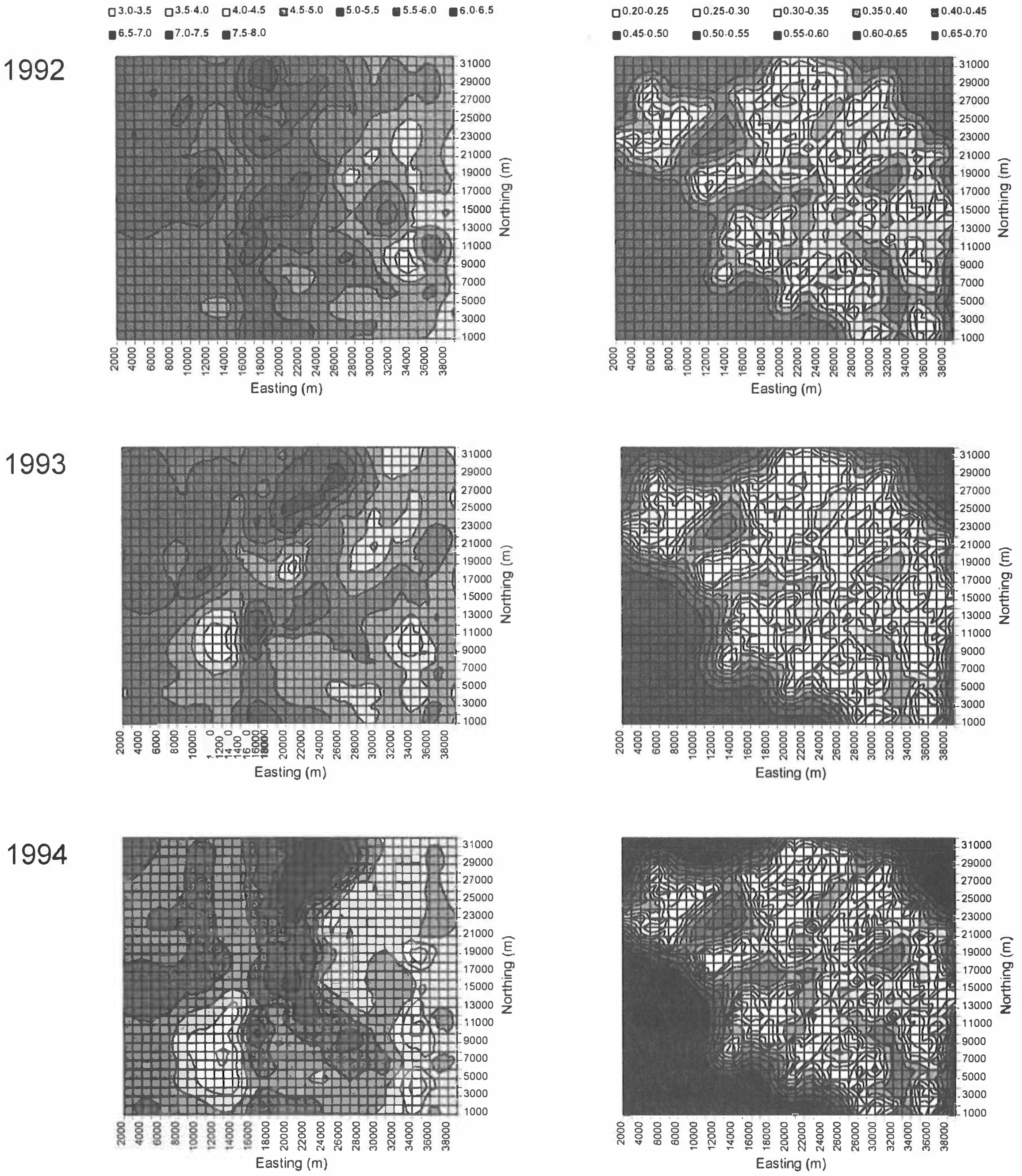


Figure 1. Predictions of the catch logarithms (left), and associated standard deviation (right), computed by spatial robust kriging on median-polish residuals.

Spatio-temporal analyses

Introduction of the time dimension was simply made by letting the location index **s** vary over an additional dimension. Spatio-temporal analyses were performed on the basis of the Winsorized median-polish residuals, produced by the robust spatial krigings.

Estimation of the spatio-temporal variogram - The robust variogram estimator developed by Cressie and Hawkins (1980) was used to compute an observed spatio-temporal variogram, for spatial lags from 0 to 10,000 m and temporal lags from 0 to 5 years (Figure 2a). In the spatial domain, variogram appeared very « clean », with nugget effect close to zero, and values growing slowly with the lag. An apparent sill was reached around 6,000 m, with a value between 0.7 and 0.8, slightly lower than twice the sample variance (0.437). In the temporal domain, nugget effect was clearly higher, and range was probably not reached within the temporal scale of our study. Given that, in the space-time domain, the variogram reached values that are higher than the apparent spatial sill, temporal sill was probably higher than this spatial sill.

Fitting of a spatio-temporal variogram model - Geometrical anisotropy is clearly inherent to any spatio-temporal variogram, as units are not the same along the space and time axes. Our data, however, showed clearly more complex behaviour than simple geometrical anisotropy : not only ranges differed between the axes, but also nugget effects and sills differed. For anisotropy, the usual way is to search for a linear transformation of the co-ordinate system that would produce a reduced isotropic variogram (Isaaks and Srivastava 1989, Cressie 1993).

To describe the spatio-temporal variogram of our data, we used a model with four additive structures : one pure nugget effect ($2\gamma_0$), one structure accounting for the anisotropy in the nugget effects ($2\gamma_1(\mathbf{h}_1)$), one accounting for geometrical anisotropy($2\gamma_2(\mathbf{h}_2)$), and the last one accounting for zonal anisotropy ($2\gamma_3(\mathbf{h}_3)$). These structures were all described by spherical variogram models :

$$2\gamma(\mathbf{h}) = 2\gamma_0 + 2\gamma_1(\mathbf{h}_1) + 2\gamma_2(\mathbf{h}_2) + 2\gamma_3(\mathbf{h}_3),$$

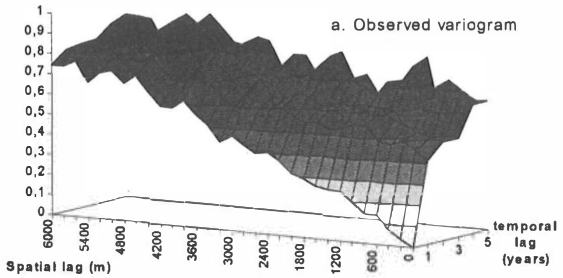
where :

$$2\gamma_i(\mathbf{h}_i) = \begin{cases} 0 & \mathbf{h}_i = \mathbf{0} \\ w_i \left\{ \frac{3}{2}\|\mathbf{h}_i\| - \frac{1}{2}(\|\mathbf{h}_i\|)^3 \right\} & 0 < \|\mathbf{h}_i\| < 1 \\ w_i & \|\mathbf{h}_i\| > 1 \end{cases}$$

$$\mathbf{h}_i = \begin{bmatrix} h_{i,x} \\ h_{i,t} \end{bmatrix} = \mathbf{T}_i\, \mathbf{h} = \begin{bmatrix} 1/a_{i,x} & 0 \\ 0 & 1/a_{i,t} \end{bmatrix} \begin{bmatrix} h_x \\ h_t \end{bmatrix}$$

This model has 9 parameters, namely w_0, w_1, w_2, w_3, $a_{x,1}$, $a_{t,1}$, $a_{x,2}$, $a_{t,2}$, and $a_{t,3}$ ($a_{x,3}$ is infinite, $a_{x,0}$ and $a_{t,0}$ are zero).

However, to simplify fitting, we assumed some relations between them. $\gamma_1(\mathbf{h}_1)$ accounted for additional nugget effect observed in the time domain. Nugget effect may be viewed as result of measurement error plus result of variations at smaller scale than smallest lag : as measurement errors occurred both in the spatial and temporal domain, additional nugget effect in the time domain had to be due to the other source. Within time domain, $\gamma_1(\mathbf{h}_1)$ needed therefore to have reached its range after one year, which was the shortest temporal lag that we considered. To account for that, $a_{t,1}$ was set to 1 year. Both the purely spatial and purely temporal variograms were well described by single spherical models (two additive models with different ranges did not improve significantly the fitting). Therefore, we set : $a_{x,1} = a_{x,2} = a_x$ and $a_{t,2} = a_{t,3} = a_t$. This left us with 6 parameters, that were estimated through weighted-least-square fitting. A three-dimensional plot of the fitted model is shown in Figure 2b.



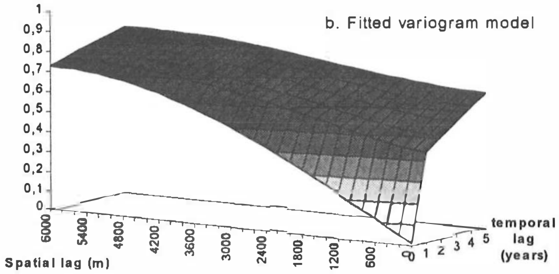


Figure 2. Spatio-temporal observed robust variogram computed on Winsorized median-polish residuals (a), and model fitted to this variogram (b).

Spatio-temporal kriging - Two practical situations may justify the use of spatio-temporal kriging, rather than (much more simple) spatial kriging : (1) to build *interpolation* predictions of the variable during one year where we have data, *if* it can improve the prevision precision, and (2) to *forecast* the variable for one year where no data are (yet) available. We will now take a look at these two situations.

Data values are not necessary to compute kriging weights and kriging error for the variogram if we assume a design with given data location. Let us assume a trapping design where permanent traps are located on a regular square grid. Within this design, locations where kriging error is largest are the square centres. Therefore, we will pay attention to these points. Kriging weights and error are functions of the location of the traps used to build the estimate that can let vary by changing the size of the grid squares. In this case, we vary the *trapping effort*. Furthermore, they are functions of the kriging neighbourhood, that may be expressed in terms of the number of traps used to build the estimate (spatial kriging neighbourhood), and of the number of years over which data are taken into account (temporal kriging neighbourhood). In this case, we vary the *computation effort*.

Taking only the symmetric spatial neighbourhoods into account, and restricting them to a reasonable number of data, a limited set of possibilities exists. The five smallest symmetric spatial neighbourhoods of our case study are illustrated in Figure 6. They respectively account of 4, 12, 16, 24 and 32 traps.

Spatio-temporal kriging used for interpolation - For the trapping device described above, kriging weights and error were computed, for distances between neighbouring traps varying from 500 m to 5,000 m, by steps of 500 m, and taking account of data from the 5 smallest symmetric spatial kriging neighbourhoods, first over the current year only, then over current and one previous year and, lastly, over current and two previous years.

Results showed that kriging error depended only on distance between traps, and increased, nearly linearly, with this parameter. On the other hand, increasing spatial or temporal kriging neighbourhood did not have any significant effect. When looking at the kriging weights, any data added to the 16-data neighbourhood of the current year was given a negligible weight. Trapping-prediction precision would therefore rely nearly entirely on the trapping effort. This was mainly due to the fast decrease of the spatial correlation between data when the distance separating them increased (this is sometimes referred as screen effect (Cressie 1993)), and to a much lower correlation between data from different years than between data from the same year.

Adding results from previous years has a high computational cost and did not increase the precision : it seemed useless to complicate kriging by adding the time dimension when the goal is only to make an interpolation for a year where data were available. Spatial kriging is much easier to apply and probably more correct as it does not requires hypotheses about temporal stationarity.

Spatio-temporal kriging used for forecasting - For the trapping device described above, kriging weights and error were also computed, for distances between neighbouring traps varying from 500 m to 5,000 m, by steps of 500 m, and taking into account data from the 5 smallest symmetric spatial kriging neighbourhoods, first over one previous year, then over two and, lastly, over three.

Results were obviously different from those obtained assuming current-year data were available. The relation between kriging error and distance separating traps was no longer monotone, but exhibited a minimum : there was a distance between traps that, for a given computation effort, was optimal (1,000 to 2,000 m). Also obvious was the fact that expanding the kriging neighbourhood, in space or in time, led now to increased precision. This last result was due to a slower decrease of the correlation between data when spatial lag increased, as soon as temporal lag was larger than zero (weaker screen effect than for interpolation).

The existence of an optimal trapping effort was probably the most anti-intuitive of these results. It was due to the spatial auto-correlation between data from the same previous year which, being higher than spatio-temporal auto-correlation between data from previous year and data from current year, introduced some redundancy in the information carried by spatially close data. A consequence was that it was not always best to use the spatially closest traps to forecast catches when the computation effort was limited.

In an effort to test the forecast method, it is clear that it cannot be done on the basis of the analyses that were performed up to now. the spatio-temporal variogram, as well as the median-polish trend surface, were computed with our whole data set. Instead, we tried to simulate a situation where forecast would be useful : taking only into account the data from a few first years, and trying to predict results from the next year. We selected a spatial kriging neighbourhood of 32 traps, and a temporal neighbourhood of 3 previous years. To compute a

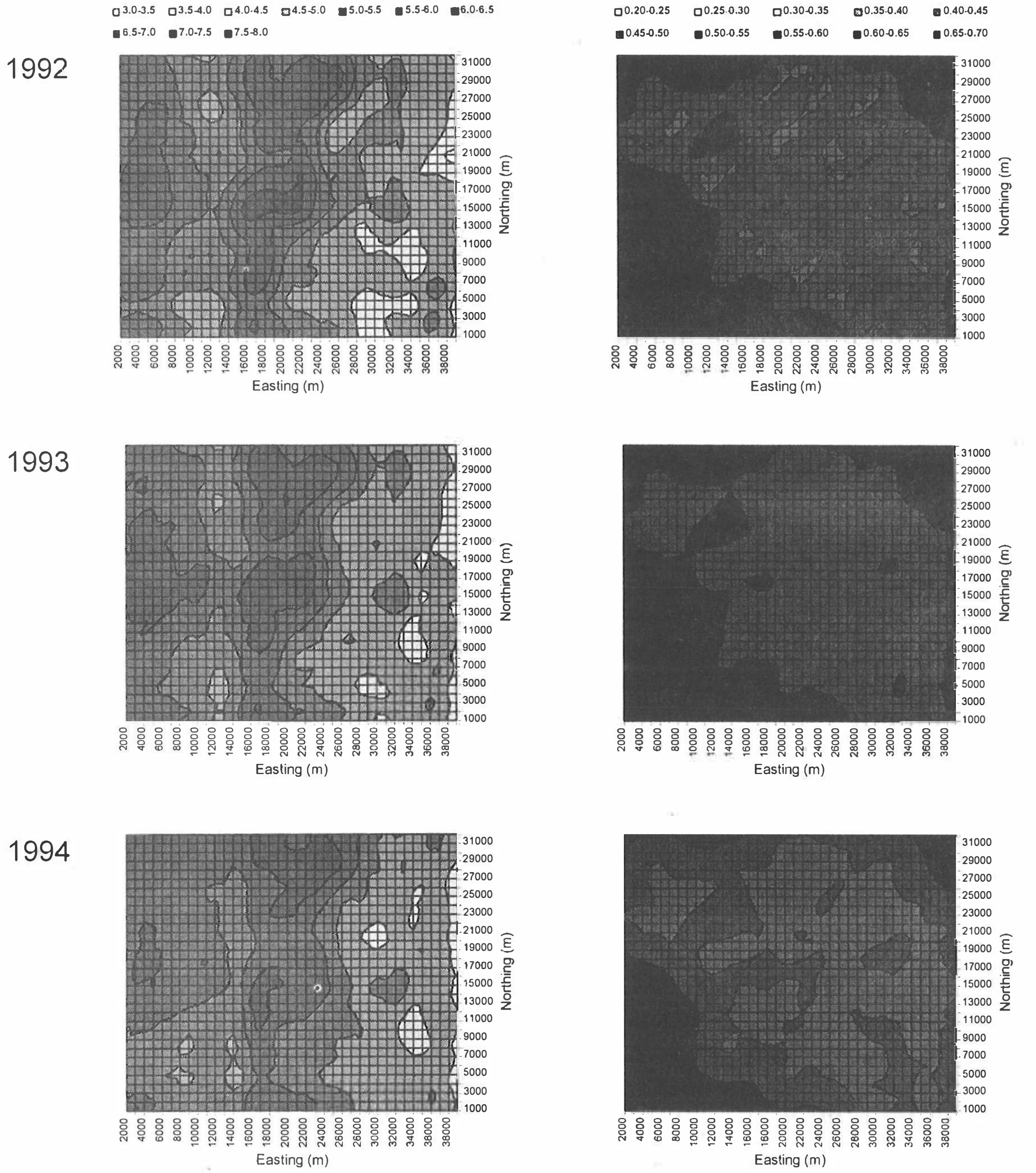


Figure 3. Predictions of the catch logarithms (left), and associated standard deviation (right), forecasted by a spatio-temporal robust kriging performed on median-polish residuals, using only data from previous years.

variogram with temporal lags up to 3 years, data from 5 years were a minimum. Forecasts were therefore computed only for years 1992 to 1994. For each of these three years, 5-previous-years data were used to compute a median-polish trend surface. Residuals of this median polish were Winsorized through robust spatial kriging. Winsorized residuals were then used to compute a spatio-temporal variogram to which a model was fitted. At last, this model was used to compute predictions and prediction errors for the considered year, with data from the 32 nearest traps and the 3 previous years. Results are mapped in Figure 3 and may be compared to results of the robust spatial kriging performed on the data of these years (Figure 1). There was a good correspondence between the forecast prediction and the robust spatial kriging prediction. For 1992, 1993 and 1994, respectively 100%, 95.89% and 93.67% of the spatial robust kriging predictions fell within the 95% confidence interval associated to the forecast prediction.

Conclusions

In conclusion, we think we showed that *Ips typographus*-monitoring trapping does not produce erratic results. On the contrary, results were highly structured, showing an apparently permanent mean structure and spatial as well as temporal continuity. Our analyses allowed us to build predictions of the logarithmic catch with an acceptable precision when using the current-year data, and to forecast this logarithm, with less precision yet still reliably.

It is important to stress that these analyses do not explain in any way the reasons of catch variations, they only describe them with mathematical tools. However, they might be a good beginning point to start other analyses. The median-polish trend surface, which remains constant in time, might be tentatively correlated to permanent ecological factors (such as forest or soil characteristics, elevation, slope orientation, etc...). Departures from forecast models might be correlated with more sudden events (such as windfall and snowbreak occurrences).

It must also be stressed that these whole analyses were performed on basis of results produced in an area where *Ips typographus* populations are endemic. In epidemic situation, results would have been probably much more erratic and less structured. Moreover, the transition between endemic and epidemic situation in a bark-beetle population is probably not a linear phenomenon. This transition might be described as departure from the linear model that we describe here.

Acknowledgements

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Impact of natural enemies on *Tomicus piniperda* offspring production

L.M. SCHROEDER

Swedish University of Agricultural Sciences Department of Entomology S - 750 07 Uppsala Sweden

ABSTRACT The occurrences of *Thanasimus formicarius* (L.) (Cleridae) and *Rhizophagus depressus* (F.) (Rhizophagidae) in cut Scots pines attacked by *Tomicus piniperda* (L.) (Col.: Scolytidae) were recorded in the field, and interactions between the species were studied in caged pine bolts attacked by *T. piniperda*. The relative population densities of *T. formicarius*, *R. depressus*, and *T. piniperda* in pine stands with or without attacks of *T. piniperda* the previous year were estimated with flight barrier traps.

T. piniperda offspring production per m^2 was reduced by 41 % when reared with *R. depressus*, by 81 % when reared with *T. formicarius*, and by 89 % when all three species were reared together, compared with *T. piniperda* alone. Both *T. piniperda* and *R.depressus* were caught in higher numbers in stands with attacks of *T. piniperda* the previous year than in stands without bark beetle attacks. In contrast, there was no difference in catch of *T. formicarius* between the two kinds of stand. The main flight period of *T. piniperda* only lasted for a few days. In contrast, the flight periods of the two predators *R. depressus* and *T. formicarius* were much more extended. The flight period of *R. depressus* lasted for about one and a half month until the beginning of June while the flight period of *T. formicarius* still not had ended after three months in the middle of July when the experiment was ended.

KEY WORDS *Tomicus piniperda, Rhizophagus depressus, Thanasimus formicarius*, bark beetle predators, biological control, dispersal

LARGE NUMBERS OF arthropod species are found in the subcortical environment of trees attacked by bark beetles (Dahlsten 1982, Weslien 1992, Stephen et al. 1993). Many of these may feed on the immature stages of bark beetles. Studies conducted on bark beetles of the genera *Ips*, *Dendroctonus* and *Tomicus* have shown that complexes of associated species may strongly reduce bark beetle productivity (Linit and Stephen 1983, Miller 1986, Weslien 1992, Schroeder and Weslien 1994a). Few studies have determined the impact of single antagonistic species on bark beetle offspring production (Weslien and Regnander 1992, Weslien 1994, Schroeder and Weslien 1994b, Nicolai 1995). The impact of most associated species on bark beetle productivity still remains to be clarified.

Bark beetle attacked trees are often widely scattered as a result of the spatial distribution of suitable breeding material. In accordance with this, several bark beetle species have been demonstrated to have a capacity to migrate long distances (Nilssen 1978, 1984, Forsse and Solbreck 1985, Weslien and Lindelöw 1989). Thus, the impact of natural enemies on bark beetles is not only determined by the interactions under bark but also by the capacity of the enemies to colonize bark beetle attacked trees in new places.

In the present study, interactions between the bark beetle *Tomicus piniperda* (L.), the clerid *Thanasimus formicarius* (L.) and the rhizophagid *Rhizophagus depressus* (F.) were

Pages 204-214 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

analysed both at tree level and stand level. In an earlier field experiment larvae of *Thanasimus* and *Rhizophagus* were the most frequent enemies emerging from bolts under natural attack by *T. piniperda* (Schroeder and Weslien 1994a). In Scandinavia *T. piniperda* is largely confined to Scots pine, *Pinus sylvestris* L. The beetles reproduce in logs, stumps and pines that are windbroken, windthrown or otherwise weakened. *T. piniperda* usually attacks areas with rough bark, which are found on the lower parts of the bole of Scots pine. The species is monogamous, and the female initiates the egg gallery. In Scandinavia the flight period occurs in early spring and may be essentially over within a few days if weather conditions are favourable (Eidmann 1965, 1974, Bakke 1968). *T. piniperda* lacks an aggregation pheromone, but is strongly attracted by host volatiles (Byers et al., 1985, Schroeder 1987, 1988, Schroeder and Lindelöw 1989). After emergence the adult bark beetles fly to the crowns of nearby standing pines where they bore into and feed in the shoots. In late autumn the beetles leave the shoots to hibernate in the bark at the base of the trees. At high population levels the shoot feeding can cause a considerable reduction in growth (Långström and Hellqvist, 1990, 1991). In southern China *T. piniperda* has been reported to cause high tree mortality following a long drought (Ye 1991). Recently, the species has also been discovered in the United States and in Canada where most native pine species seem to provide suitable habitat for breeding and maturation feeding (Haack and Lawrence 1995, McCullough and Smitley 1995).

R. depressus is strongly attracted to conifer host volatiles and may be caught in high numbers in flight barrier traps baited with α-pinene and ethanol (Schroeder and Lindelöw 1989). Adults have been found in the gallery systems of *T. piniperda* (Saalas 1923, Nuorteva 1956, Szujecki 1987). *R. depressus* has been reported to prey on bark beetle broods (Hanson 1937, Nuorteva 1956).

T. formicarius is one of the most abundant and voracious predators of bark beetles (Gauss 1954). The species is attracted to bark beetle pheromones and host tree volatiles (Bakke and Kvamme 1981, Schroeder 1988, Schroeder and Lindelöw 1989). The adults prey upon bark beetle adults, mate and lay eggs in bark crevices. The larvae feed on bark beetle brood and probably also on other insects present under the bark. One of the main prey species of *T. formicarius* in Scandinavia is *T. piniperda*. *T. formicarius* adults are often abundant on pine stems newly attacked by *T. piniperda*. *T. formicarius* has earlier been demonstrated to strongly reduce *T. piniperda* offspring production (Schroeder and Weslien 1994a).

The objectives of the present study were to determine: 1) the impact of the predator *R. depressus* alone on *T. piniperda* progeny production, 2) the impact of the two predators *R. depressus* and *T. formicarius* together on *T. piniperda* progeny production, and 3) the relative population densities of *T. piniperda*, *R. depressus* and *T. formicarius* in Scots pine stands with and without bark beetle attacks the previous year.

Materials and Methods

Impact of *R. depressus* and *T. formicarius* on *T. piniperda* offspring production

The experiment was conducted in the province of Uppland in central Sweden in 1994. Scots pines were felled in late March, and three to four bolts (diam. 12-16 cm, length 35 cm and mean surface area under bark 0.15 m^2) were taken from the basal part (with rough bark) of each tree. The bolts were placed under 1-mm screen mesh and held outdoors.

On 11 and 12 April, adult *T. piniperda* were collected in baited flight barrier traps (see Schroeder and Lindelöw 1989) placed in two Scots pine stands thinned one year earlier. *R. depressus* was collected in the flight barrier traps on 23 and 24 April. Copulating pairs of *T. formicarius* were collected on cut pine stems on 25 and 27 April. Collected insects were kept at +5° C in the laboratory until their release in the experimental cages.

The experiment had a randomized design with four treatments. It was conducted outdoors, at a distance of 300 m from the nearest forest in order to decrease the risk of uncontrolled insect colonization of the experimental bolts. Four bolts that had more than 500 egg galleries per m^2, which is exceptionally high (Nuorteva 1964, Saarenmaa 1983, Långström 1984), were excluded from the analysis. The treatments were:

T = *T. piniperda* alone, seven replicates (three bolts excluded).

TR = *T. piniperda* together with 30 *R. depressus* per caged bolt, ten replicates.

TF = *T. piniperda* together with two pairs of *T. formicarius* per caged bolt, eight replicates.

TRF = *T. piniperda* together with 30 *R. depressus* and two pairs of *T. formicarius* per caged bolt, seven replicates (one bolt excluded).

On 17 April, *T. piniperda* adults were released in each of two large cages containing all the bolts. Due to cold weather the release was conducted in the laboratory (+15° C). Two days later each bolt was placed separately in a cage (40 x 40 x 35 cm) with 0.5-mm screen mesh and held outdoors. On the same occasion the ends of all bolts were sealed with paraffin to prevent severe desiccation.

In a sample of 157 *R. depressus* beetles that were sexed alive, the proportion of males was 43 %. Sex determinations were made by examining the metasternum of *R. depressus*. Adult *R. depressus* were released in the cages on 27 April. *T. formicarius* adults may feed on *R. depressus* adults. Thus, the release of the *T. formicarius* adults was delayed for one week to give the *R. depressus* adults some time to settle in the bark beetle egg galleries. Every second week cages with *T. formicarius* were supplied with live-frozen *Ips* adults as food for the clerids. On days with hot weather the bolts were sprinkled with water.

The bolts were kept in the cages until 20 June, whereupon they were taken out and hung in emergence traps outdoors. Each emergence trap consisted of a white cotton bag (diam. 40 cm, length 110 cm) with a collecting funnel forming the bottom. The emergence bags were emptied about every third day until the emergence of *R. depressus* and *T. formicarius* larvae ended in October. The new generation adults of *T. piniperda* were easily recognized by their light brown colour. During the winter each bolt was debarked and the numbers and the lengths of *T. piniperda* egg galleries were recorded.

To study the developmental times, 87 larvae of *R. depressus* and 14 larvae of *T. formicarius* were sampled alive from the emergence traps on 8 July and put in 100-ml vials with moist sand and pieces of Scots pine outer bark on top of the sand. The vials were stored outdoors in the shade. Two of the sampled *T. formicarius* larvae were 14 mm long, while the rest were 6-12 mm long. The *R. depressus* larvae were distributed among seven vials while each *T. formicarius* larva was placed separately in a vial. The vials were inspected on 19 August.

Large scale spatial distribution of *T. piniperda*, *R. depressus* and *T. formicarius*

The experiment was conducted in the province of Uppland in central Sweden in 1995. The relative population densities *T. piniperda*, *R. depressus* and *T. formicarius* were compared in two kinds of Scots pine stands: A-stands which had been thinned during the winter of 93/94 and B-stands in which no logging operations had been conducted during the last five years. Apart from this difference the stands were similar. Nor had any logging operations been conducted recently in the stands adjoining the B-stands. In the A-stands *T. piniperda* and other insects, including natural enemies, reproduced in the stumps and slash during 1994. Inspections in early spring 1995 revealed large numbers of *T. piniperda*-bored pine shoots on the ground in the A-stands demonstrating the presence of local hibernating populations. No or only a few *T. piniperda*-bored pine shoots were present in the B-stands. In late autumn 1995 inspections of pine stumps in the A-stands revealed the presence of *T. formicarius* pupal chambers. The experiment was pair-wise arranged with one stand of each kind in each of four areas. Within the areas the distances between the stands were 3 to 5 km. The distances between the areas were 20 to 55 km.

Insects were caught in baited flight barrier traps (Schroeder 1988, type b). Under the barrier (a 40 x 40-cm transparent plastic sheet) a funnel ending into a water-filled jar was hung. In each stand five traps were arranged in a circle with a distance of 50 m between the traps.

The chemicals used were (–)-α-pinene (Fluka 97%, $[\alpha]^{20}_{D}$ –42 ± 3°) and 95% ethanol (5% water). The dispensers (one per trap) consisted of two test tubes, one of which (depth 150 mm, inner diam. 14 mm) was filled with ethanol and one (depth 100 mm, inner diam. 9.5 mm) with α-pinene. Each tube were supplied with a strip of filter paper (Munktell No. 3; ethanol: 145 x 13.5 mm, α-pinene: 96 x 9 mm) reaching from the bottom to about 1 mm from the rim. A plastic 35-mm film canister was fitted over the open ends of the tubes. In a earlier study (Schroeder & Weslien, 1994a) the field release rates were estimated by measuring the amounts of chemicals left before refilling. Based on these results the release rates in the present study should have been approximately 4 mg of α-pinene and 40 mg of ethanol per houre during warm weather. α-Pinene and ethanol were chosen as bait since the combination of these two substances strongly attract *T. piniperda*, *T. formicarius* and *R. depressus* (Schroeder 1988, Schroeder and Lindelöw 1989, Schroeder and Weslien 1994a).

Results

Impact of *R. depressus* and *T. formicarius* on *T. piniperda* offspring production

The new generation of *T. piniperda* beetles started to emerge at the beginning of July, and virtually all beetles had emerged within two weeks. Timing of F_1 emergence was similar for all treatments.

Table 1. *Tomicus piniperda* reproduction in pine bolts of different treatments: Offspring per m^2, breeding density, productivity and mean length of egg galleries*. T = *T. piniperda* alone, TR = *T. piniperda* + *R. depressus*, TF = *T. piniperda* + *T. formicarius*, TRF = *T. piniperda* + *R. depressus* + *T. formicarius*.

	T	TR	TF	TRF
Offspring per m^2	2867a^1 ± 535	1685b ± 1164	531c ± 296	312c ± 125
Egg galleries per m^2	285a ± 150	209a ± 122	149a ± 51	194a ± 39
Offspring per egg gallery	13.6a ± 8.6	11.1ab ± 9.7	4.6ab ± 4.5	1.7b ± 0.9
Mean egg gallery length (mm)	67.0ab ± 8.9	67.9a ± 9.7	80.5b ± 10.9	69.2ab ± 5.3

* Values are means of 5 replicates (bolts) in T, 8 replicates in TR and TF, and 7 replicates in TRF ± standard deviations.

(^{1}) Means followed by the same letter within rows are not significantly different at p = 0.05 level (ANOVA, Tukey multiple comparison test).

T. formicarius and *R. depressus* strongly reduced the number of *T. piniperda* offspring produced per m^2 (table 1). The two species together caused the greatest reduction (89 %), followed by *T. formicarius* alone (81 %) and *R. depressus* alone (41 %). All differences in *T. piniperda* offspring production per m^2 were statistically significant except for the difference between the treatments *T. formicarius* alone (TF) and *R. depressus* together with *T. formicarius* (TRF). Differences between treatments in the number of *T. piniperda* offspring produced per female showed the same pattern as the production per m^2 but they were much less pronounced. Only the difference between the treatments *T. piniperda* alone (T) and *T. piniperda* together with *R. depressus* and *T. formicarius* (TRF) was significant.

R. depressus and *T. formicarius* readily reproduced in all bolts offered to them. All *R. depressus* and *T. formicarius* offspring emerged from the bolts as larvae. The emergence of larvae of both species started at the end of June and continued for about two months.

Of the 87 larvae of *R. depressus* that were sampled alive from the emergence traps on 8 July, 57 were recovered as light brown teneral adults in the sand, at the inspection on 19 August. Of the 14 larvae of *T. formicarius* only the two fully grown individuals (14 mm long) had survived, one as a larva and the other as an adult. Both these individuals had hollowed out ovoid cells in pieces of bark. No cells had been formed by the other 12 *T. formicarius* larvae.

Large scale spatial distribution of *T. piniperda*, *R. depressus* and *T. formicarius*

T. piniperda, *R. depressus* and *T. formicarius* initiated flight on 13 April. 71 % (1981 of 2782) of all captured *T. piniperda* were collected during 13-19 April (Fig.1). In contrast, only about 5 % (108 of 2113) of all captured *R. depressus* and <1 % (3 of 531) of all captured *T. formicarius* were collected during the same period of time. Only a few *R. depressus* were collected after 6 June while *T. formicarius* continued to be captured until the end of the experiment on 12 July.

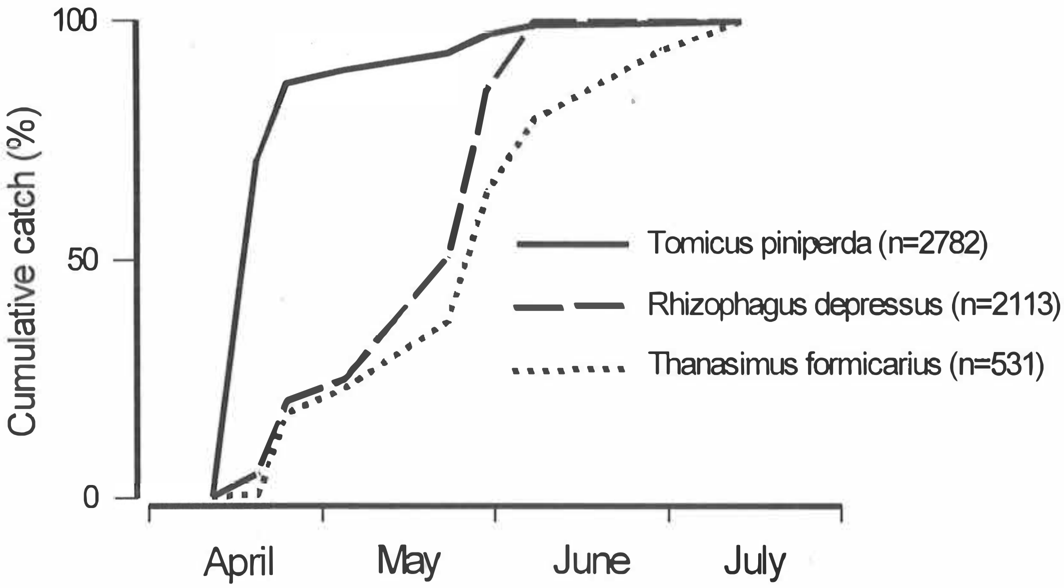

Fig. 1. Cumulative percent collections of *T. piniperda*, *R. depressus* and *T. formicarius* during April-July 1995 in baited traps.

The total catches of *T. piniperda* and *R. depressus* were 4-5 times higher in stands with attacks of *T. piniperda* the previous year (A-stands) than in stands without bark beetle attacks (B-stands) (Fig. 2). In contrast, there was no difference in total catch of *T. formicarius* between the two kinds of stands. The proportions of beetles caught in the two kinds of stands over time differed between the three species. The proportion of *T. piniperda* caught in A-stands was 91 % (N = 1981) during the early part of the flight period (13-19 April) and 55 % (N = 801) in the later part of the flight period (19 April to 12 July). This difference was statistically significant (chisquare test, $P < 0.05$). The proportion of *R. depressus* caught in A-stands was about the same in the early part of the flight period (83 %, N = 1071, 13 April to 22 May) as in the later part of the flight period (81%, N = 1042, 22 May to 28 June). The proportions of *T. formicarius* caught in the A-stands fluctuated strongly (33-88 %) between the different trapping periods and there was no trend over time.

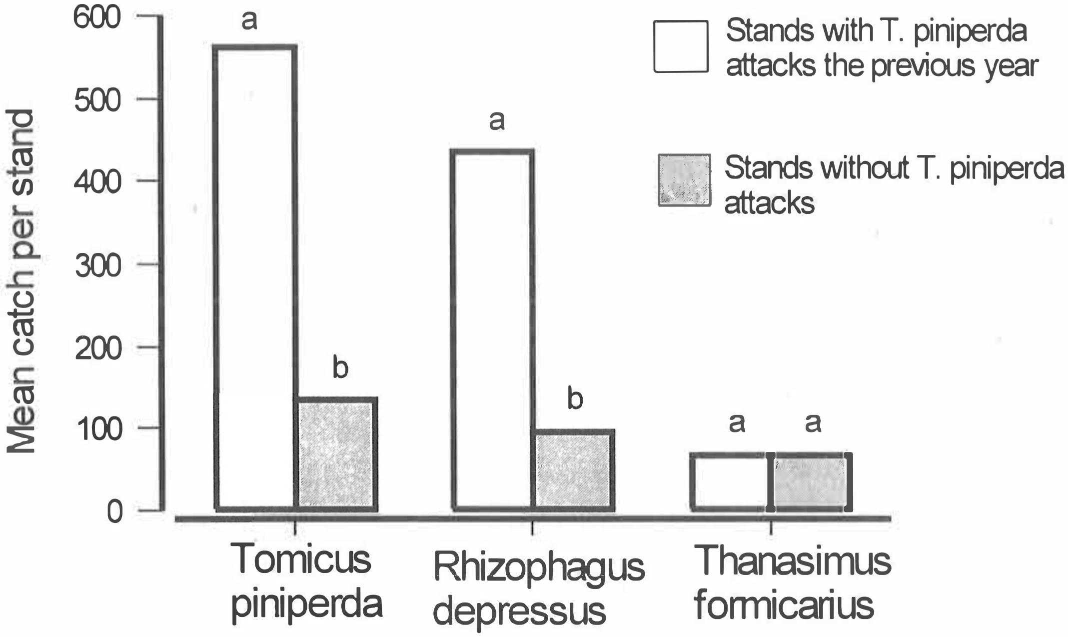

Fig. 2. Mean catches of *T. piniperda*, *R. depressus* and *T. formicarius* in Scots pine stands with and without previous attacks of *T. piniperda*. Five baited traps per stand. Columns with the same letter within the same species are not significantly different at p = 0.05 level. One-tailed paired-sample t-test.

Discussion

R. depressus and *T. formicarius* together reduced *T. piniperda* offspring production by 89 %. In a previous field experiment *T. piniperda* offspring production was reduced by natural enemies (including *R. depressus* and *T. formicarius*) by 90 % compared with the production in bolts protected from enemies by cages (Schroeder and Weslien 1994a). Thus, the result of the present study demonstrate that *R. depressus* and *T. formicarius* together are able to cause a reduction in *T. piniperda* progeny production of the same magnitude as that caused by the whole complex of associated species in the previous study.

The reduction in the production of *T. piniperda* offspring per m^2, caused by the release of 30 *R. depressus* per cage, was not as strong as that caused by the release of two pairs of *T. formicarius* per cage. The clerid larvae reduced *T. piniperda* offspring production by 81 %. In an earlier, similar study (four *T. formicarius* pairs released per cage) *T. piniperda* offspring production was reduced by 92 % (Schroeder and Weslien 1994b).

The percentage reduction caused by the predators was much lower in terms of bark beetle offspring produced per female than in terms of bark beetle offspring produced per m^2. This was a result of the attack densities being higher on the bolts of the T-treatment than on the bolts of the TR- and TF-treatments. Earlier studies have demonstrated that when reared alone in cages *T. piniperda* offspring production per m^2 is fairly constant at attack densities between 150 and 400 egg galleries per m^2 (Eidmann and Nuorteva 1968, Saarenmaa 1983). In contrast, the number of offspring produced per female decreases strongly with increasing attack density as a result of intraspecific competition. Thus, the reduction in *T. piniperda* offspring production per female, caused by the predators, was underestimated in the present study.

Both adults and larvae of *R. depressus* could have contributed to the reduction of *T. piniperda* offspring production. Nuorteva (1956) observed feeding by *R. depressus* larvae on bark beetle pupae. Adults of the rhizophagid *Rhizophagus grandis* Gyll. have been demonstrated to feed on both eggs and larvae of the bark beetle *Dendroctonus micans* (Kug.) (King et al. 1991).

The reduction in the production of *T. piniperda* offspring per m^2 caused by *T. formicarius* and *R. depressus* together was of similar magnitude to that caused by the former species alone. Thus, the absence of one predator species does not necessarily mean that bark beetle progeny production will increase.

T. piniperda, *R. depressus* and *T. formicarius* were all able to disperse to the B-stands (without bark beetle attacks the previous year) as demonstrated by the trap catches. But the proportions of beetles caught in the A- and B-stands differed between the three species. *T. piniperda* and *R. depressus* were both caught in much higher numbers in the A-stands (with bark beetle attacks the previous year) than in the B-stands while there was no difference in catch of *T. formicarius* between the two kinds of stands. Thus, despite the fact that *T. formicarius* reproduced in the A-stands the previous year (as demonstrated by the occurrence of pupal chambers in the stumps), the most important source for this species during the flight period in 1995 seem not to have been the stands themselves but the surroundings. The present study demonstrated that the new generation of *T. formicarius* can hibernate both as adults and fully grown larvae. Thus, one explanation for the lack of difference in catch between the A- and B-stands could be that the new adults disperse already in late summer of the first year and/or that the hibernating larvae do not develop into new adults until late in the second summer.

Obviously high numbers of *R. depressus* were produced in the A-stands in 1994 as demonstrated by the high numbers caught in 1995. The cage experiment demonstrated that the *R. depressus* larvae emerging from trees develop into new adults the same summer. But as late as 19 August the beetles were still callow and burrowed in the sand. This suggests that they do not leave the ground until the next summer which is in accordance with the high catches in the A-stands during 1995. The fact that the catches of *R. depressus* were continuously higher in the A- than in the B-stands could have been a result of (1) a low dispersal rate from the A-stands, and/or (2) the new generation adults leaving the ground during an extended period of time.

In the first days of *T. piniperda* flight almost all collected beetles were caught in the A-stands. The difference in flight activity of *T. piniperda* between the A- and B-stands levelled out at the end of the flight period as a result of beetle dispersal. But since the main flight period of *T. piniperda* only lasts for a few days most of the flight activity will take place in stands with hibernating populations.

The results of the present study demonstrate that the risk for attacks of the bark beetle

T. piniperda, estimated as density of flying population, is considerably higher in stands which experienced attacks the previous year, resulting in hibernating populations, than in stands without local populations. *T. piniperda* reproducing in stands with previous attacks of this bark beetle species will be exposed to higher population levels of the predator *R. depressus* than bark beetles reproducing in stands without previous bark beetle attacks.

The main flight period of *T. piniperda* only lasted for a few days which is in accordance with earlier studies (Eidmann 1965, 1974, Bakke 1968, Haack and Lawrence 1995). In contrast, the flight periods of the two predators *R. depressus* and *T. formicarius* were much more extended. A few individuals of the two predator species were caught during the main flight of *T. piniperda* but the main flight periods of the two predators took place subsequently to the main flight of *T. piniperda*. The flight period of *R. depressus* lasted for about one and a half month until the beginning of June while the flight period of *T. formicarius* still not had ended in the middle of July when the experiment was finished.

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Phenolic Compounds As Predictors Of Norway Spruce Resistance To Bark Beetles

FRANÇOIS LIEUTIER[1], FRANCK BRIGNOLAS[1], DANIEL SAUVARD[1], CHRISTOPHE GALET[1], ANNIE YART[1], MARTINE BRUNET[1], ERIK CHRISTIANSEN[2], HALVOR SOLHEIM[2], and ALAN BERRYMAN[3]

[1]INRA, Station de Zoologie Forestière, Ardon, 45160 Olivet, France
[2]NISK, Department of Forest Ecology, P.O.Box 1432, Ås-NLH, Norway
[3]Washington State University, Department of Entomology, Pullman, WA 99164, USA.

THE PHENOLIC COMPOSITION of Norway spruce phloem varies considerably after wounding, and several compounds have been suggested to play an important role in a tree's induced reaction to impede the development of *Ophiostoma polonicum*, a fungus associated with *Ips typographus* (Brignolas et al. 1995abc). This paper summarizes current research designed to identify phenolic predictors of Norway spruce resistance to bark beetles.

In 1993, the phenolic content of both the unwounded phloem and the phloem reaction zone induced by artificial wounding was compared in 2 clones previously defined as resistant or susceptible. It was suggested that resistance could correspond to a higher ability of the tree to stimulate the flavonoid pathway (Brignolas et al. 1995a). Based on that hypothesis, predictions were made in 1994 regarding resistance of 20 clones from 2 origins (Germany and Norway), according to their phenolic composition in the unwounded and the wounded phloem (Berryman and Christiansen 1995). These predictions were made for all compounds with multivariate analysis (principal component analysis) which defined a resistance axis (based upon the above hypothesis), as well as with some compounds highly correlated with that axis and considered individually. Resistance was evaluated in 1995 from mass inoculations of *O. polonicum* to those clones. High negative correlations were obtained between resistance prediction rankings and extension of sapwood blue stain after mass inoculation rankings. In 1996, 50 other clones belonging to 5 provenances and originating from the three natural geographic areas of Norway spruce in Eurasia (Baltic, Hercynian-Carpatic and alpine) were included in the study. The results confirmed those of the previous experiment. In addition, they clearly separated the Baltic provenances from the Hercynian-Carpatic and alpine ones. The clones from the first area were less resistant than those from the two other areas. Finally, an experiment taking into account 50 clones belonging to the same provenance gave the same separation between clones based upon phenolic content (multivariate analysis).

It is concluded that clone resistance is effectively related to the ability of that clone to favour the flavonoid pathway rather than the stilbene pathway. It is also concluded that phloem phenolic compounds in adult trees can effectively be used as predictors of resistance to bark beetle attacks. The best predictors are: 1) axis 1 from a multivariate analysis based upon all compounds in unwounded and wounded phloem; 2) a high concentration of (+)-catechin in the reaction zone 6 days after wounding; 3) a low concentration of isorhapontin in

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Pages 215-216 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

unwounded phloem. It is hypothesized that these conlusions are valid at the clone level, independently of origin, and for the whole Norway spruce species.

KEY WORDS *Picea abies, Ips typographus, Ceratocystis polonica,* Eurasia, phenolics, resistance predictors, induced reaction

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Cryphalus piceae and silver fir decline in Vallombrosa forest

FRANCO CERCHIARINI AND RIZIERO TIBERI

Forest and Agricultural Pathology and Zoology Institute, Florence, Italy

ABSTRACT Xylophagous insects play an important role amongst the numerous biotic and abiotic factors which have resulted in the serious decline of many silver fir, *Abies alba,* coenosis in Italy. Amongst these insects, *Cryphalus piceae* is the most damaging species in the fir-woods of Vallombrosa, as it attacks silver fir trees of all ages, including trees which had not previously been damaged by other adverse factors. *Cryphalus* infestations have always been damaging in this kind of biocoenosis, but they have reached record levels during the last few years. This is an event which has also coincided with the serious damage that this conifer has suffered as a result of the unusual climatic conditions during this period.

Observations have been carried out since 1992 on the biology and the behaviour of *Cryphalus piceae* in the Vallombrosa forest. The results show that this beetle always develops a first generation, with adults emerging in the middle of the summer; the second generation begins in August and September and is completed in the late autumn. However, in the second generation adults are often immature when they emerge. Moreover, during this period mature larvae and pupae can often be found under the bark of the host trees. Sometimes a sister generation can also be observed developing in parallel to the first. This is due to some of the females interrupting oviposition to feed themselves and then completing oviposition some days later. This phenomenon can sometimes become conspicuous, especially during the culminating phase of an infestation. The attack of *Cryphalus* begins on the most apical part of stressed but still standing trees, and then proceeds towards the base. The behaviour of *Cryphalus piceae* is different when it colonises trees or part of trees that are laying on the ground, for then the attack is massive and involves the whole trunk, resulting in a significant number of family units for every metre of length.

KEY WORDS *Cryphalus piceae*, biology, damage, Tuscany, Italy.

CRYPHALUS PICEAE (RATZ.), Coleoptera Scolytidae, is one of the most important bark beetles on silver fir, *Abies alba*. The activity of this insect in fir stands can become critical when trees are subject to recurrent physiological stresses from a variety of biotic and abiotic factors, as is the case of Vallombrosa Forest in Tuscany.

This bark beetle is found in many parts of Europe. In Italy it has long been known in silver-fir populations of the Alps belt and the Northern Apennines. Reports of *C. piceae* occurring on natural and artificial fir stands in the central and southern Apennine range are of more recent date (Pennacchio 1993).

C. piceae occurs not only on silver fir but also on *Abies pinsapo, Abies cephalonica* and *Abies nordmanniana*. In the forest of Vallombrosa there are also sporadic occurrences on Norway spruce and Douglas fir (Roversi *et al*. 1993; Battaglini unpublished data).

In areas where silver fir competes with other vegetation in mixed stands (these are more stable from an ecological point of view), beetle populations generally do not reach high densities, and damage is negligible. However, when conditions are favourable to *C. piceae*

Pages 217-219 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

development, population levels remain high and cause serious damage to silver fir which has serious repercussions for the rest of the biocoenosis.

Materials and Methods

In the spring of 1992, after many fir trees in Vallombrosa had been broken and uprooted by an exceptionally heavy snowfall in March of that year, observations were initiated to identify the most favourable conditions for increases in *C. piceae* populations.

In April, efforts were initiated to identify the areas most strongly affected by the adverse climatic conditions, and the biology and behaviour of the bark beetle could be better observed.

Observations were continued over the next years in order to determine whether trees that were not originally infested would later become infested. Various stations at altitudes ranging from 800-1200 m were established during the winter to examine the reproductive cycle of the insect. Bolts of about 1-1.5m in length were cut from infested trees and observed in the field, while other pieces were studied in the laboratory. Stem and branch sections of various diameters were also removed from trees that had been uprooted, broken, or felled during thinnings. All tree sections were placed in the forest in late winter/early spring each year, in shaded or open sites, in order to determine the time and intensity of bark beetle infestations at the onset of reproductive activity.

Results

The results showed that adults of *C. piceae* leave their overwintering sites between the end of winter (mid-March) and the beginning of spring, depending on climatic patterns and the location of the stands. During the last period, it was noted that overwintering adults initiated reproductive activity some two weeks earlier at lower altitudes, where climatic variations (temperature, precipitation) were less pronounced.

In Vallombrosa the bark beetle develops two generations per year, with an occasional sister generation produced by overwintering individuals emerging from the trees after an earlier infestation.

During the first phase of an infestation the most vulnerable trees are those which have been uprooted or broken, or which exhibit signs of stress due to adverse site conditions, or which have been weakened by low winter temperatures. Trees that did not receive enough water during the preceding autumn/winter period were also susceptible. Later, particularly with the arrival of the second generation of beetles, trees that became infested exhibited no sign of stress at the start of the insect growth cycle, even though they had certainly been previously affected by a predisposing cause of some kind.

On silver fir trees colonized by the first generation of bark beetles, up to 35 colonizations per 100 cm^2 bark area were observed, with the fecundity of the females ranging from 8-26 eggs per colonization. As regards the sister generation, fecundity ranged from three to 18 eggs, whereas in the second generation it ranged from 6 to 20 eggs per female.

Conclusions

Observations since spring 1992 on the biology and the behaviour of *C. piceae* at Vallombrosa confirmed the conclusion that the bark beetle is able to complete two generations per year, with the possibility of a sister generation produced by overwintering beetles.

Thus the Vallombrosa population was not limited to only one generation during the season, with in addition a possible sister generation, as reported by previous research (Pennacchio 1993).

The presence of overwintering populations on the branches of vigorous growing fir can seriously damage the trees, and this will predispose them for colonisation by the bark beetle during the successive reproductive phase.

Overwintering mainly occurs in the adult stage, but *C. piceae* also occasionally overwinters as mature larva or pupa under the bark; however, this mainly occurs in fir stands at higher altitudes.

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Japanese Phoretic Mites and Their Hyperphoretic Fungi Associated with Flying Adults of the Spruce Beetle (*Ips typographus japonicus Niijima)* (Col., Scolytidae).

JOHN C. MOSER[1], THELMA J. PERRY[1] AND KIMOTO FURUTA[2]

[1]USDA Forest Service, Southern Research Station, Pineville, LA, USA
[2]Department of Forestry, The University of Tokyo, Japan

THE SPRUCE BEETLE (SBB), *Ips typographus japonicus* (Niijima) is a transpalearctic species occurring mainly in spruce forests but rarely in pine, fir, and larch (Wood and Bright, 1992). In Hokkaido, Japan, it is the most destructive pest of *Picea jezoensis* (Siebold and Zucc). Carriere and *P. glehnii* (F. Schmidt) Masters. This insect is usually endemic, normally killing only over-matured or physiologically weakened trees. But when trees are harvested, SBB builds up in the slash and kills neighboring trees for about 3 years thereafter (Koizumi, 1977); yet their overall population level does not seem to increase greatly. Heavy winds usually precede SBB outbreaks, the largest of which was seen between 1956 and 1959 after a strong typhoon in 1954 (Yamaguchi, 1963; Yamaguchi et al., 1963).

Flying *Ips typographus japonicus* from Hokkaido (Japan) carried twelve species of phoretic mites, three of which were not previously recorded from Europe. The mite biologies were diverse, including specialists feeding on microorganisms, beetle eggs, and nematodes which were common under beetle elytra. Seven distinct species of fungal spores were found on these mites. In addition, an undetermined number were identifiable only as conidia. The spores stuck anywhere on the mite bodies with no special carrying structures evident. *Ophiostoma bicolor* was the most common species, with the pathogenic *Ceratocystis polonicum* present in small numbers.

This study iillustrates that a great deal of information can result from the survey of relatively few bark beetles when time and labor are important constraints to research. Twelve species of mites and at least 4 species of fungi are recorded here for the first time for Japan. The latter includes the virulent tree disease *Ceratocystis polonicum,* at least, which is apparently capable of being transmitted by SBB mites. Future studies should determine if a caucity of mite species really exists in Japan (compared to that of Europe), or if more sampling is needed. Emphasis here should be placed on two important European mite parasitoids, *Pyemotes dryas* (Vitzthum) and *Paracarophaenax ipidarius* (Redikortsev). If they are not native to Japan, then consideration should be given to introducing them as classic biocontrol agents for SBB. *P. dryas,* has been located as far east as Gansu Provence, China, phoretic on Polygraphus poligraphus ex. Picea asperata (Moser, unpublished). At least one mite, *Pleuronectocelaeno japonica,* may have evolved in Japan; another, *Trichouropoda hirsuta,* is a North American species not yet recorded for the rest of Eurasia.

Pages 220-221 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

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Current research on genetic resistance to white pine weevil in British Columbia

DR. RENE I. ALFARO

Pacific Forestry Centre, Canadian Forest Service, Victoria, BC. Canada. V8Z 1M5

THE WHITE PINE weevil, *Pissodes strobi* Peck (Coleoptera: Curculionidae) is the most serious native pest of spruce regeneration in British Columbia, attacking primarily Sitka (*Picea sitchensis* (Bong.) Carr), white (*P. glauca* (Moench) Voss), and Engelmann spruce (*P. engelmanni* Parry). The weevil has one generation a year. The eggs are laid from late April to June in punctures made by the female in the bark just below the buds of the terminal (year-old) shoot. The larvae burrow downward in the terminal beneath the bark, feeding on the phloem, which eventually kills the terminal. In many cases, the larvae mine past the year-old leader into the two- (and occasionally the three-) year-old shoot, causing even more dieback. By midsummer, they construct oval pupal cells in the wood and pitch, and pupation occurs within a "cocoon" of wood fibers. Depending on local climate, a portion of the larvae may remain to overwinter in the attacked leader. Most adults emerge from the leaders in late August and September; the newly emerged adults feed on terminals and branches and overwinter primarily in the duff. The following April or May, the adults move to young spruce terminals and resume feeding. They mate and lay eggs soon afterward. Occasionally, and specially in the interior, adults will re-attack below the previously attacked leader. Adults may live for up to four years (Alfaro 1994).

Current research results

Interior spruce family trials in British Columbia were surveyed for weevil resistance using an index which measured intensity of attack (number of attacks per tree), severity of each attack (how many internodes were destroyed) and tree tolerance to attack (i.e., if tree develops good form after an attack) (Alfaro *et al.* 1996a). The study demonstrated significant family variation in the attack index. Variation in resistance was related to ecoclimatic conditions of the place of origin of the parent trees. Analysis showed that parents from locations with high weevil hazard or high weevil populations yielded higher proportion of resistant trees. These sites are primarily low elevation, low latitude sites, especially on Moist-Warm habitats of the Sub-Boreal-Spruce (SBS) biogeoclimatic zone. Ying (1991) postulated that high selection pressures in high weevil hazard zones increased the proportion of resistant trees in stands located in these areas.

A study of the resin canal distribution on resistant and susceptible families at the Clearwater family trial extended the results obtained for Sitka spruce by Tomlin and Borden (1994): white spruce resistant families at Clearwater had significantly denser

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Pages 222-224 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

resin canal system in the bark than susceptible families (Alfaro *et al.* 1997). The study demonstrated significant family variation and potential for selection.

Another resistance mechanism was discovered. Dissection of interior and Sitka spruce leaders in which weevil attack had failed (eggs had been laid but no adult emergence occurred) demonstrated the existence of an induced defense reaction (Alfaro 1995). The response was initiated shortly after feeding and oviposition in the attacked shoot and consisted of the cambium switching from producing normal tracheids and parenchyma ray cells to the production of epithelium which differentiated into traumatic resin canals, arranged in a ring fashion in the developing xylem. In sectioned leaders, these traumatic resin canals could be seen emptying their contents into feeding and oviposition cavities dug by the adults, and into the larval galleries. This defense reaction killed eggs and larvae. When the leader survived the attack, the cambium reverted to producing normal xylem tissue leaving one or more rings of traumatic resin canals embedded in the xylem annual ring. Artificial wounding experiments have demonstrated that resistant trees are capable of a faster response and they are capable of repeated response whereas susceptible trees responded more slowly and generally produced a single ring of traumatic resin canals (Alfaro *et al.* 1996b).

Sahota *et al.* (1994) are investigating the existence of chemicals in the bark of resistant spruce which may have negative effects on the weevil reproductive physiology. The weevils utilize several strategies for overcoming the tree defenses. Hulme (1995) found that even the most resistant Sitka spruce clones could be successfully colonized if the attack occurred early in the season. Thus, it appears that the physiological processes that underlay the tree defenses may not be active the entire year, but they may be gradually activated in the spring.

Work in collaboration with University of British Columbia at Kalamalka Forestry Centre, in the interior of BC (McIntosh *et al.* 1996) is determining details of the weevil attack and dispersal behaviour on resistant and susceptible trees and will determine the occurrence of the induced defense mechanism in relation to insect behaviour.

We hope to integrate resistance as a component of an Integrated Pest Management System (Alfaro 1996a). An important consideration when utilizing resistant genotypes in reforestation programs is its deployment in mixtures with susceptible stock. Using cage experiments, Alfaro (1996b) found that, when confined to resistant trees, gravid females oviposited lower in the stem, below the leader, where resin canal density was reduced by the increase in stem diameter (a dilution effect). Therefore, there is a risk that, if large plantations of purely resistant genotypes are created, the weevil could adapt to attack older internodes, where resin canal density is lower. Therefore, deployment of these genotypes should, at all times, take into consideration the need for avoiding the risk of insect selection leading to biotypes capable of overcoming the resistance mechanisms.

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Mass Attack by *Tomicu piniperda* L. (Col., Scolytidae) on *Pinus yunnanensis* Tree in the Kunming Region, Southwestern China

HUI YE

Yunnan University, Institute of Ecology and Geobotany, Kunming, Yunnan, P.R. China.

ABSTRACT Patterns of attack by the pine shoot beetle, *Tomicus piniperda*, on Yunnan pine, *Pinus yunnanensis*, in the Kunming region of southwestern China are described. In some attacks, colinization is initiated by direct attacks on the upper or middle trunk. In other situations, attacks begin by beetles aggregating and boring on shoots. The latter pattern is thought to weaken the tree sufficiently and bettle attacks spread down the trunk. Attacks by *T. piniperda* are often associated with simultaneous colinization by *T. minor*.

MASS ATTACK IS an important phase of the life cycle of the pine shoot beetle, *Tomicus piniperda* (L.); beetles aggregate in and colonize host material for breeding (Bakke 1968; Ye 1991). In the Kunming region of southwestern China, mass attack occurrs on the trunk of living pines and causes considerable damage to the local forest (Ye 1991, 1992). Over the past 15 years, more than 1.5 million ha of Yunnan pine (*Pinus yunnanensis)* forests have been destroyed there (Ye 1992). The paper compiled here is an introduction of information about these beetle attacks in southwestern China.

Attack Initiation

Two basic attack patterns were proposed for trunk attack on the living Yunnan pine tree Kunming.

1) **Attack is initialed by 2 - 4 pairs of beetles**. These beetles are regarded as pioneer beetles (Ye 1995). The primary invader detects and locates the suitable host first; it is followed immediately by other beetles landing the same tree. The attack proceeds until most of the trunk surface is occupied. The location of the pioneer beetle on the host tree trunk is not fixed but it usually attacks the upper trunk, middle trunk, or the middle and upper trunk. The secondary beetles always land near to the pioneer beetles. The attacking population progressively disperes over the trunk surface as the attack population increases (Ye 1995). Under this attack patern, attacks do not always occur on the trunk inside the crown, and most shoots are not damaged as in attack pattern two.
2) **Attack commences from the attack of shoots**. In early spring or late winter just before trunk attack, many beetles fly to the crown and form shoot aggregations. On trees with shoot aggregations, more than 60% of the shoots are bored but only a few shoots are bored in nearby trees (Ye and Lieutier, unpublished manuscript). Shoot aggregation greatly weakens trees and causes subsequent trunk attacks.

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> Shoot attack is regarded as one of the critical phases of trunk attack, or the first step of mass attack. In attack pattern two, the attack is frequently started from the upper trunk, even from the trunk inside the crown. The attacking population disperses from the upper trunk down to the middle and base trunk.

Attack Distribution on Trunk

In Yunnan pine trees of 5-7 m height, the pine shoot beetle is capable of dispersal over the entire surface of the trunk, from the upper to the base. However, in most cases, the beetle is distributed on the trunk surface from the top to the base 1-2 m high above the ground (Ye 1995).

Attack Density

Attack populations rapidly increase in numbers during the primary attack phase. Attack rates reach their maximum about half way through the attack interval and attacks decline progressively (Ye 1995).

The highest attack densities are always concentrated on the middle-upper trunk, which contains more than 40% of the attacking population. Population densities decrease progressively above or below this position. The distribution of the attacking densities on the trunk appears to be normally distribution with a mean position in the upper and middle trunk (Ye and Ding, unpublished manuscript).

Attacks in the Consecutively Two Years

On Yunnan pine greater than 10 m height, trunk attacks are often observed in two consecutive years. In the first year, the attacks mostly occur the upper trunk, weakening the tree but not killing it, particularly in the case of attack pattern one. During the next spring, attacks are launched on the position of the trunk just below the attack from the previous year. The tree will be killed after two-years of attack (Ye 1992).

Attacks in Association with *Tomicus minor* (Hart.)

T. minor was always found to be associated with *T. piniperda* in the attacked tree in Kunming. This beetle is a secondary attacker that occurrs in the spring later than *T. piniperda*. *T. minor* is mainly distributed on the middle and base trunk. The attack position of *T. minor* on the trunk is exactly opposite that of *T. piniperda*, and opposite the distribution of *T. minor* in Scandinavia, where *T. minor* colonized on the upper trunk (Langstrom 1986). *T. minor* attacks benefit from *T. piniperda* , and *T. minor* also are helpful for *T. piniperda* colonization. (Ye 1992, Ye and Ding, unpublished manuscript).

Discussion

The attack of *T. piniperda* on Yunnan pine is apparently related to mild winters in Kunming. The beetle initiates mass attack once sexual maturity is complete and does not require a period of over-wintering as occurrs in European countries. The drought season from Oct. to May also often benefits the beetle to overcome tree resistance. Under these conditions the beetles damage not only weakened trees, but also some health trees (Ye 1991).

The attack density and distribution on the trunk is thought to be determined by the attack pattern and the locality of the beetle before attack commencement. When beetles attack the crown, it is likely that the pine shoot beetle will locate at upper and middle trunk.

The two different attack patterns explain why the beetle can attack and directly kill healthy trees. Beetles can weaken the tree through shoot aggregation as the first of attack which is then followed by trunk attack. This attack sequence makes the beetle more effective in overcoming the tree's resistance. This explains why shoot aggregation plays a critical role in tree killing.

Recent studies indicate that when *T. minor* joins attacks by *T. piniperda* this increases the speed by which the two populations overcome tree resistance. The mixed population adjusts their distribution efficiently, which, decreases inter-specific competition. The two pine shoot beetles working together strengthened their aggressions in population establishment in Yunnan pine tree.

There still exist some questions which we can not answer for the moment. For example, why does the beetle appear to have two varying attack patterns? Why does the beetle not colonize the base trunk in most cases? Why has this beetle developed shoot aggregation and is it a necessary phase for the beetle attack? All of these are being studied in current and future research.

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Uncommon Cases Of Damage To Young Coniferous Trees By Several Curculionoidea Species, And Possible Ecological Reasons

A. V. GOUROV[1,2], AND V. TAGLIAPIETRA[3]

[1]V. N. Sukachev Institute of Forest, Siberian Branch of the Russian Academy of Sciences, 660036
Krasnoyarsk, Russia
[2]Present address and correspondence: Dr. A.V.Gourov. Istituto di Entomologia Agraria, Università di Padova.
Via Romea, 16. 35020 LEGNARO (PD), Italy
[3]Istituto di Entomologia Agraria, Università di Padova, Padova, Italy

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ABSTRACT During the course of field observations and laboratory rearing, data on uncommon supplementary feeding on conifers was obtained for 5 specialized weevil species and for 8 species normally associated with herbaceous vegetation and deciduous trees and shrubs. In the case of specialized group, the uncommon feeding behaviour and change of food were registered on the conifers only, when the preferable food sources were present but sparse. Most unspecialized species demonstrated a change-over from the natural host plants to alternative ones but did not change their feeding manner under the conditions when their preferable food plants were absent. The wide food specialization was not taken as the only reason for uncommon feeding of polyphagous weevils on conifers. Probably, certain of the local conditions could be responsible for the facts described. Practically all the cases of uncommon curculionid damage to conifers were documented under the boundary or similar conditions, and the weevil species discussed were mostly registered on the border or separated trees. It is supposed that the change in insect behaviour and food preferences could be one of the "edge effects". Natural regeneration in openings and borders as well as young forest plantations, hedgerows and shelterbelts may be subjecte to damage by unspecialized weevils. Due to this, the study of the biology and ecology of phytophagous insects as related to forest borders has become important.

KEY WORDS Coleoptera, Curculionidae, uncommon behaviour, conifers, edge effects

IT IS WELL documented that the fragmentation of woodlands, and different kinds of silvicultural practices can cause changes in the behaviour, bionomical features and economic status of some phytophagous insect species (e.g. Arnoldi 1953, Graham and Knight 1965, Eidmann 1985). These are reflected by the broadening of the host plant ranges, changes in food preferences and level of specialization of species. As a consequence, formerly non-outbreak insect species have become economically important, and the list of potential forest pests increases. This could be illustrated with examples from the different taxonomic groups of dendrophagous insects in some regions: *Boarmia bistortata* Goeze (Lepidoptera: Geometridae), C*ephalcia lariciphila* Wachtl. (Hymenoptera: Pamphiliidae), and *Dendroctonus micans* (Kug.) (Coleoptera: Scolytidae) in Siberia, Russia (Prosorov 1934, Pleshanov 1982, Kolomiez 1990); *Zeiraphera diniana* Gn. (Lepidoptera: Tortricidae) in North England (Day 1994). Thus, the observation of "unusual behaviour" in some species could be useful from a preventional viewpoint.

Weevils (Coleoptera: Curculionoidea) constitute a complex insect superfamily, most species of which are phytophagous. Many species are known as dendrophagous although the

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Pages 228-243 in J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, editors. 1997. Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests. USDA Forest Service General Technical Report NE-236.

majority is associated with herbaceous plants (Arnoldi et al., 1965). Relatively small groups of species (especially from gg. *Hylobius*, *Pissodes*, *Magdalis*) are specialized to develop on conifers. Besides these, there are weevils characterized only by imaginal feeding on needles (gg. *Brachyderes*, *Philopedon*, *Strophosomus*, etc.), and the adults of some species can damage conifers although they prefer to feed on other host plants (e.g. *Otiorhynchus*, *Polydrosus*, *Phyllobius* sp. pl.). This knowledge is not adequate, since it often only refers to the location of damage and coniferous tree species. Moreover, there is little information on the feeding ecology and behaviour of many weevil species. When it is considered that the last more or less comprehensive reviews of the insect pests of Eurasian boreal forests (including weevils) were published before the mid seventies (Pavlovsky and Shtakelberg 1955, Schwenke 1974), even the data on well-known important species deserves further comment.

In this paper, the uncommon cases of damage to young coniferous trees by several specialized and nonspecialized weevil species is described. The supplementary feeding of *Rhynchaenus fagi* L., *Rhinomias forticornis* Boh., *Apion pisi* F. and some *Otiorhynchus* species on shoots and needles are recorded for the first time. A description of the biotope, the type and distribution patterns of damage are provided for every species observed.

Materials and Methods

Field observations were carried out in the forest-steppe, southern and mountain taiga subzones of Central Siberia and adjacent territories (Abansky, Bol'shemurtinsky, Ermakovsky, Nazarovsky, Suhobuzimsky districts of Krasnoyarsk Region, Bratsky and Ust'-Ilimsky districts of Irkutsk Region, Russia) in 1978-88, 1996, and in several mountain forest districts of the Italian Alps (Asiago, Auronzo di Cadore, Bosco del Cansiglio (Veneto), Monte Bondone (Trentino), Northern Italy) in 1993-1996.

Data on the accidental imaginal feeding of weevils on conifers was obtained during the course of visual examinations of the crowns of young trees. Most observations were organized along orthogonal transects crossing forest borders from the inner-stand positions to sparse young trees on adjacent openings or grassland. To reveal the structure of curculionid guilds, and the occurence and distribution patterns of species, the method of branch beating was used along the transects. For this, 3-5 sample trees were chosen randomly per every 5-10 m interval depending on the local situations, and from 3 to 5 randomly chosen branches per sample tree were beaten. Dropped insects were collected with an entomological net with the diameter of 40 cm. The distribution of curculionids crawling on the land surface was observed by pitfall trapping with the use of 200 ml plastic vessels with a neck diameter of 65 mm which were placed at 1 m intervals along the transects.

In order to describe the distribution of damage to needles caused by phyllophagous insects, 40 cm-long apical twigs were collected from 1 to 3 differently exposed branches of the sample trees along the transects mentioned above. The number of sample trees changed from 3 to 5 per every 5 m or 10 m interval as in the beating sampling. During the examination of needles, the deep holes gnawed through the needle body were recognized as the curculionid type of damage among other traces of grazing. The level of damage was measured as the percentage of holed needles from the total number of needles examined per sampling unit.

If some curculionid species were constantly collected on conifers, laboratory rearings were used to verify the possibility of feeding on shoots and needles. For this, single samples or small groups of weevils were reared in plastic cages where 1-year and current year shoots of coniferous trees were provided as food sources. Experiments were not aimed at revealing a food preference of species, that is why the weevils were allowed to feed on the conifers from which they were sampled.

In addition to observational data, appropriate information from the literature was used. Due to this, the paper is prepared partly as a short review especially in relation to curculionids which are not specialized in feeding on conifers. With one exception, the weevil species' names were used according to Abbazzi et al. (1994), and the names of the trees according to Kozlowski et al. (1991) and Vidakovic (1991).

Results

During the course of field observations and laboratory rearing, data on uncommon host associates on conifers was obtained for 5 specialized weevil species and for 8 species normally associated with herbaceous vegetation and deciduous trees and shrubs. Descriptions are given in order of decreasing weevil specialization regarding feeding on conifers.

***Pissodes validirostris* (Sahlberg)**, pine cone weevil. This is a wide-spread species in Scots pine stands, and the only *Pissodes* species adapted to development in cones. Besides *P. sylvestris*, it can colonize the cones of *P. sibirica* Du Tour (Florov 1951), *P. brutia* Ten., *P. contorta* Dougl. ex Loud., *P. halepensis* Mill., *P. nigra* Arnold, *P. pinaster* Ait., *P. pinea* L., and *P. uncinata* Ramond (Roques 1983). According to numerous studies, the supplementary feeding by adults occurs on young green cones.

In early summer (end of May - beginning of June) 1979-1986, we repeatedly observed the uncommon adult feeding of *P. validirostris* on the apical shoots of Scots pines in the forest-steppe pine stands of Central Siberia (Gourov 1987). Apparently, this supplementary feeding occurred during the mating period and before egg-laying, because it had not been documented later in the season. The feeding behavior was similar to that of other *Pissodes* species: round holes were chewed through the bark thereby damaging the phloem. Weevils occupied the upper crown of young pines on the borders of dense clumps in light pine stands, or sparsely growing pines under the canopy of secondary birch forests adjacent to mature pine stands. Perhaps, this feeding behavior could be responsible for the accidental development of *P. validirostris* in the pine leader shoots as mentioned by Bevan (1987).

***Hylobius albosparsus* Motschulsky**, larch root weevil. This is an endemic Siberian species. A short review of its distribution in the Siberian territory was made by Opanasenko (1976). According to published data, the species is polyphagous on conifers. The supplementary feeding of adults has been observed in young stands of Siberian larches, *Larix spp.* (Petrenko 1965, Rozhkov 1970, Galkin 1971), on the Siberian stone pine, *Pinus sibirica* (Zemkova 1963), and Scots pine, *P. sylvestris* L. (Rozhkov 1957). Spruces, *Picea spp.*, are also included in the list of food plants (Arnoldi et al. 1965). However, the latter authors noticed that serious damage by *H. albosparsus* occurred in larch stands, and Rozhkov (1970) proposed that larch is the preferred host tree of this species. All the authors agree that the adults normally feed on yong shoots and thin branches where they damage the bark and form feeding areas with roughly grazed borders.

The uncommon adult feeding of the larch root weevil was recorded for the first time during our observations on the Siberian fir, *Abies sibirica* Ledeb. It was noticed in June 1984 under the canopy of a dense, mixed Siberian pine/spruce/fir stand with the addition of *Betula verrucosa* Ehrh. and *Larix sibirica* Ledeb. in the basin of Upper Ket' river (Verhkazanskoe Forestry, Bol'shemurtinsky district of Krasnoyarsk Region, Central Siberia). The feeding occurred on 1-2 m-high firs along the borders of dense understory clumps. Individual weevils fed on apical shoots, grazing not only on soft tissues and green juvenile bark, but also on young short needles. As a consequence, the longitudal (up to 5-6 cm) shallow depression was usually organized on one side of the shoot. Later in the season, some curved apical shoots having this type of damage were repeatedly observed on young firs. This type of adult feeding, as well as its choice of fir as a host tree, had not previously been described for *H. albosparsus*.

***Hylobitelus (Hylobius) pinastri* (Gyllenhal)**, coniferous root weevil. This is a common but not abundant species widespread in Palearctic boreal forests. Supplementary feeding of adults on Scots pine (Florov 1950, Rozhkov 1957, Opanasenko 1976, Ozols 1985), Siberian larch (Rozhkov 1970) and, probably, on some other conifers (Arnoldi et al. 1965, Eidmann 1974) is known. Usually, adults damage the thin bark of young shoots in the proper "Hylobius manner".

In early July 1996, we collected several samples of *H. pinastri* on sparse young spruces, *Picea obovata* Ledeb., growing on the boundary between a mixed fir/pine stand and a wet meadow in the Buiba locality (Western Sayan mountain system, Ermakovsky district of Krasnoyarsk Region, Central Siberia). The branch-beating procedure along the transect crossing the forest border did not reveal the occurrence of this species under the canopy of the mature stand. It was also not noticed on young regenerations of *P. sibirica* and *A. sibirica.* Under laboratory conditions, the beetles were provided with apical shoots of spruce as host material. During the 1-week rearing, the bark of the shoots was not damaged by weevils, but a preference for the previous year's needles was markedly demonstrated. Deep and rough but "economic" grazing was oriented along the needle edges, and no remains (pieces, cut needles) were found at the bottom of cage. The replacement of shoots by the fragments of thicker branches (also having needles) did not change the weevil feeding behaviour. This type of supplementary feeding is uncommon for the *Hylobius* species, although needle damage by *H. abietis* L. has been previously noticed as very rare and accidental (Schwerdtfeger 1981).

***Magdalis phlegmatica* (Herbst)**, blue inert weevil. This species belongs to a group of poorly studied blue coniferous weevils (some species of the genus develop on deciduous trees and shrubs). The species is widespread but not abundant in the Scots pine stands. Besides *P. sylvestris*, other conifers may also be hosts of *M. phlegmatica* (Arnoldi et al. 1965), especially *Picea spp*., as was noticed for related *Magdalis* species (Maisner 1974). Usually, the supplementary feeding by adults occurs on the bark and phloem of shoots, thin stems and branches in young coniferous stands and plantations (Rozhkov 1957, 1970, Opanasenko 1976). In other species who use conifers as their primary hosts (e.g. *M. violacea* L.), supplementary feeding on deciduous trees has also been documented (Maisner 1974).

At the end of June 1984, we observed a single episode of uncommon supplementary feeding by an adult *M. phlegmatica* on the needles of a young Siberian spruce, *P. obovata*, under the canopy of a secondary birch stand adjacent to a mixed coniferous forest of dark taiga type (basin of Kem' river, Talovskoe Forestry, Bol'shemurtinsky district of Krasnoyarsk Region, Central Siberia). The type of damage was similar to the well-known imaginal feeding manner of *Brachonyx pineti* Payk. on the needles of Scots pine: the small hole is followed by a cavern in the needle body (Opanasenko 1976, Bevan 1987). Confirmation of the possible *Magdalis* maturation feeding on needles was obtained in early July 1996 in the Aradan locality (Western Sayan mountain system, Ermakovsky district of Krasnoyarsk Region, Central Siberia). Adults of *Magdalis sp.* were sampled on young spruces along the border of a pure *P. obovata* stand. In the laboratory, beetles were provided with apical shoots with 1-year and current-year needles. During the 1-week rearing, weevils demonstrated a marked feeding preference for young needles instead of shoot stems. The feeding manner was similar to that described above for *M. phlegmatica.*

Besides Siberian spruce, such type of needle damage was documented during our observations on several conifers in Europe: Swiss stone pine, *Pinus cembra* L. (Briançon, Franch Alps), European silver fir, *Abies alba* Mill. (Auronzo di Cadore, Northern Italy), Norway spruce, *Picea abies* (L.) Karst. (Bosco del Cansiglio, Northern Italy), and European larch, *Larix decidua* Mill. (Monte Bondone, Northern Italy). In the last two localities, the distribution of needles damaged in this manner was examined along the transects crossing forest borders. The results showed that such curculionid supplementary feeding, even if not intensive, occurs in plantations of different ages and in natural forests more or less constantly (Fig. 1). However, the low level of damage made it difficult to reveal any tendency in the distribution via an appropriate statistical treatment.

***Polydrusus* (*Metallites*) *pallidus* (Gyllenhal) (= *atomarius* Olivier).** Rather numerous members of the genus *Polydrusus* (*Polydrosus*) Germar, 1817 are mainly known as being polyphagous on deciduous trees and shrubs (Arnoldi et al. 1965). However, the more or less constant host associations with conifers were noticed for more than 10 Palearctic species (Pavlovsky and Shtakelberg 1955, Arnoldi et al. 1965, Rozhkov 1970, Schindler 1974, Joly 1975, Schwerdtfeger 1981). Among these, *P. pallidus* is one of the most important *Polydrusus* weevils to forestry. Adults of this species can damage buds, needles and young shoots of pines, spruces and firs, especially in young plantations (Schindler 1974, Schwerdtfeger 1981). Recently, a serious damage to P. cembra conelets by this weevil was observed in the French Alps (Dormont, Roques and Trosset, 1996). According to our knowledge, *Larix spp.* were not included in the list of food trees of *P. pallidus*, although for some related species (*P. impressifrons* Gyll., *P.marginatus* Steph., *P. sericeus* Schaller) associations with *L. decidua* have been noticed (Schindler 1974), and for *P. cervinus* L. the supplementary feeding on *L. sibirica* was documented (Rozhkov 1970).

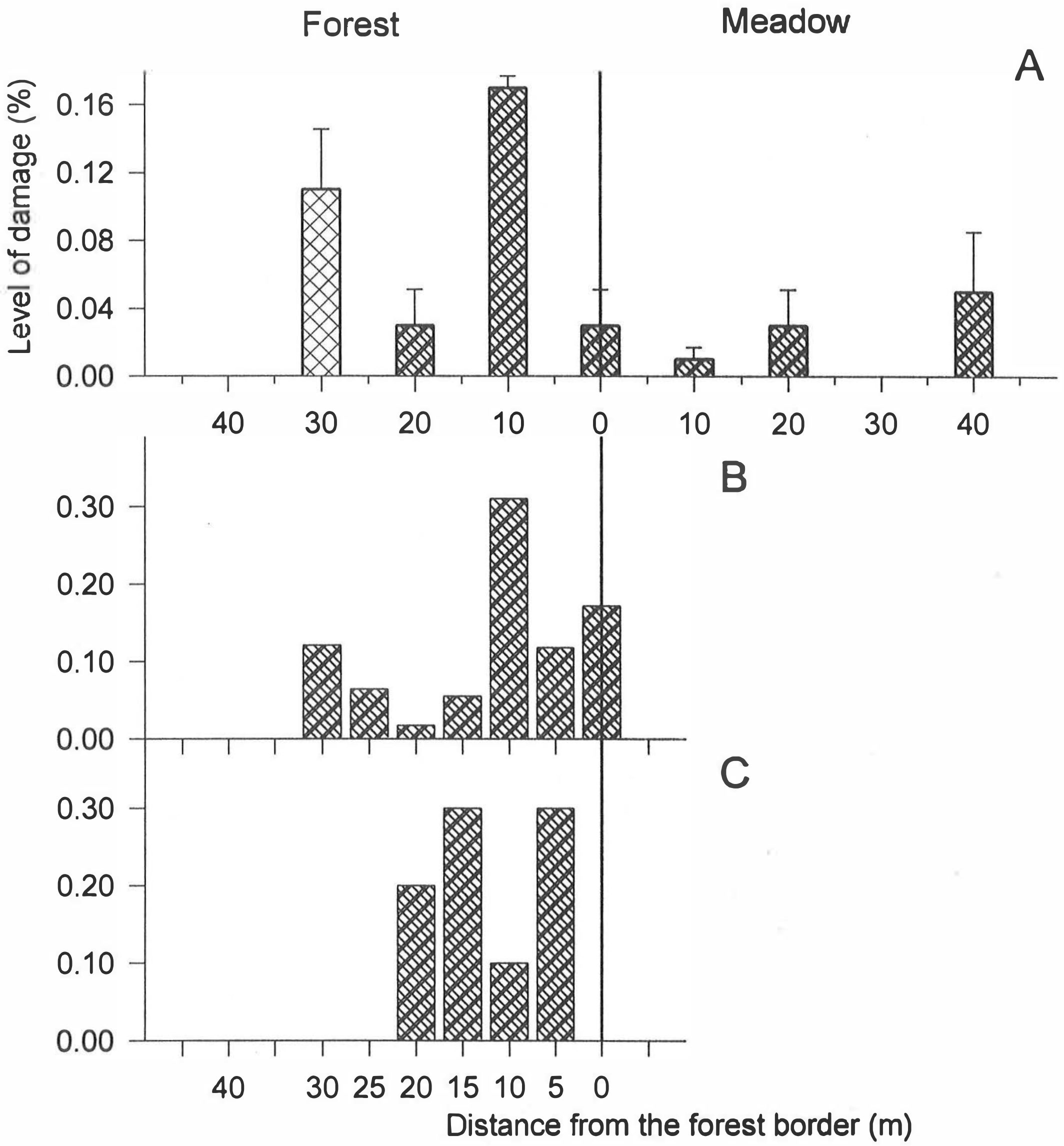

Figure 1. Distribution of needle damage by curculionids ("uncommon *Magdalis* type") along the transects crossing forest border: A - natural *Larix decidua* stand (August 1994) in Monte Bondone, Northern Italy; B - 50-year old Norway spruce plantation (May 1994, last year needles) and C - 20-year old Norway spruce plantation (July 1994, last year needles) in Bosco del Cansiglio, Northern Italy.

We observed the feeding by adult *P. pallidus* on the needles of *Picea abies* (Bosco del Cansiglio, 19.06.1994; Auronzo di Cadore, 5.06.1996, Veneto, Northern Italy) and *L. decidua* (Auronzo di Cadore, *idem*; Monte Bondone, 7.09.1996, Trentino, Northern Italy). In all localities, the weevils were collected from young trees planted artificially along the boundaries between woodlands and pastured meadows, using the branch-beating method. According to visual observations, weevils were most abundant in the low branches, just at the level of grass cover. In the mixed spruce/larch clumps, the beetles preferred to stay on spruce trees. For example, in Auronzo di Cadore, 15 spruces and 10 larches growing together were sampled (3-5 branches per tree). The density of weevils on spruce reached 2.96 ± 0.6 ex./sample, whereas only 3 specimens were caught on larch in total. But in the laboratory, weevils did not demonstrate any preference for a host tree: the needles of both tree species were damaged intensively, although on spruce the current year needles were preferred. Larch needles could be grazed along their full length, rather carefully, without numerous remains being lost, whereas some needles were cut just near the base. There were two types of damage to spruce needles: (1) the rough grazing similar to the feeding by *Brachyderes incanus* L. on pine needles (Schindler 1974), and (2) the grazing of small holes similar to those made by *Magdalis phlegmatica* mentioned above, but not so deep. Some examples of *P. pallidus* were reared in the laboratory for three weeks and they also fed on the needles of *Cedrus sp.* and decorative dwarf forms of spruce (the latter were preferred) showing the same type of grazing.

***Otiorhynchus* weevils**. The genus *Otiorhynchus* Germar, 1824 is the most rich and complex taxonomic group in the Curculionidae family (Arnoldi et al.1965). In Italy alone it is composed of 63 subgenera with 252 species and subspecies (Abbazzi et al. 1994). Besides this, a large number of species organize parthenogenetic forms and local ecological races. Most species are polyphagous on plants, and for some of them, feeding by adults on conifers is known (see a short review of Schindler (1974) on 10 Eurasian species). We observed uncommon feeding behaviour in *O. ovatus* L., and found a possibility of host associations with conifers for *O. vestitus* Gyll., *O. armadillo* Rossi, and *O. geniculatus* Germ.

***Otiorhynchus* (*Pendragon*) *ovatus* (Linné)**, the strawberry root weevil. This species damages Rosaceae, especially strawberry, and also the seedlings of conifers (e.g., Arnoldi et al. 1965). According to Western authors, it was noticed on young pines and spruces, when introduced in the USA with exotic conifers - on *Picea omorica* (Panc.) Purk., *Thuja occidentalis* L. and *Tsuga spp.* where the bases of needles were damaged during adult feeding (Schindler 1974). For Norway spruce, grazing on needles and buds, and also the debarking of 2-4-year seedlings were documented (Novák et al. 1976).

We repeatedly observed supplementary feeding of *O. ovatus* at the bases of young growing (green) shoots of Scots pine in the light forest-steppe pine stands of Central Siberia (Gourov 1987). Feeding occurred in May - June and contiued until the beginning of July when the period of full development of grass cover finished. Weevils preferred to feed on young pines, about 1 m in height growing along the forest roads or on the boundaries of small gaps. Often, the feeding occurred on curved shoots damaged by some other factors.

***Otiorhynchus* (*Dodecastichus*) *geniculatus* (Germar).** Five specimens were sampled on in June, 1996 during a branch-beating procedure on the borders of dense clumps of the Mugo pine, *Pinus mugo* Turra in the locality of Cima Larici (Asiago (VI), Veneto, Northern Italy). Pine clumps formed a patchy transition between the upper boundary of a fir stand and an alpine meadow, and thus, organized a local timberline (at about 2050 m asl). In the laboratory, beetles were provided with pine shoots but demonstrated a marked preference for the previous year's needles. Resulting damage was strong because of inefficient feeding when the needles were grazed roughly and many remains were dropped at the bottom of cage. According to our knowledge, this is a first report on the possible host association of *O. geniculatus* with conifers in general and particularly with *P. mugo* entomofauna of which has not been well-documented till now.

***Otiorhynchus (Elecranus) vestitus* Gyllenhal**. 27 specimens were sampled by the branch-beating method from the young trees of *Picea abies* (25) and *Abies alba* (2) in the mixed spruce/fir forest of Auronzo di Cadore (BL) (Veneto, Northern Italy) 5.06.1996. The dense (0.7-1.0) mature stand was dominated by the European silver fir and the Norway spruce (the latter was planted artificially) with the addition of *Fagus sylvatica* L. (particularly on slopes), *Acer platanoides* L., and *A. pseudoplatanus* L. in the gaps. In some areas, *Corylus avellana* L. and *Alnus sp.* organized the undergrowth but around the gaps and openings only. The under-canopy regeneration of conifers was intensive but concentrated (as well as the poor-developed grass cover) in lighter microhabitats.

O. vestitus constituted the majority of weevils found on young conifers (Table 1). Most samples were caught on spruce trees growing on the borders of small gaps.

Table 1. Structure of the Curculionidae community, sampled by the branch-beating method, from young coniferous regeneration in *Picea abies/Abies alba* forest 5 June 1996 (Auronzo di Cadore, BL, Veneto, Northern Italy, about 1000 m asl).

Species	Number of specimens caught			Total number caught
	Understory	Borders	Openings	
Otiorhynchus vestitus	2	25	-	27
O. armadillo f. obsitus	1	10	-	11
O. scaber	-	6	-	6
O. pupillatus	2	3	-	5
O. rhododendri	1	3	-	4
O. bisulcatus (n. f. ?)	-	1	-	1
Phyllobius calcaratus	-	3	-	3
Average number/sample*	0.12 ± 0.05	0.51 ± 0.07	0	0.29 ± 0.04

* Mean ± st. error from 50, 100, and 50 trees sampled in understory, border and open conditions correspondingly.

Under laboratory conditions, the weevils fed actively on the 1-year old and current year needles of *P. abies*. Feeding was not economic, and the grazing could start from any part of needle with a lot of remains dropping down as a consequence. There was no marked preference for old or young needles. Apparently, the frequent occurrence of *O. vestitus* in crowns and its active damage of needles presuppose the existance of the host associations of this species with conifers at least during the period of supplementary feeding.

***Otiorhynhus armadillo* (Rossi) *f. obsitus* (Gyllenhal).** Eleven samples were collected in the same biotope as *O. vestitus* described above. The only specimen was caught in an under-canopy position whereas others were collected on young spruce trees along the borders of gaps (Table 1). The species is polyphagous on different deciduous trees and shrubs, but can probably feed accidentally on conifers (M. Covassi - personal communication).

In the laboratory, weevils were provided with apical portions of the branches of *Picea abies* and showed a marked preference for current year needles and shoots. Beetles began to eat from the needle base and quickly grazed the lower part of the needles, so that numerous remains dropped down. Sometimes, the thin stems of shoots were also grazed or cut. The damaged shoots looked like those of *A. sibirica* grazed by *Hylobius albosparsus* described above, but without the longitudal depression along the shoot stem.

Other *Otiorhynchus* species caught were not so abundant as *O. vestitus* and *O. armadillo* (Table 1) and have not been examined in the laboratory. Among these, *O. scaber* L. is a well-known pest of conifers (Arnoldi et al. 1965, Schindler 1974, Schwerdtfeger 1981). As for *O. pupillatus* Gyll. noticed as a pest of *Salix spp.* (Schindler 1974), *O. rhododendri* St. and *O. bisulcatus* F., it is necessary to provide a repeat sampling on conifers following by laboratory examination.

The only member of other Curculionidae genera collected with *Otiorhynchus spp.* in Auronzo di Cadore was ***Phyllobius (Metaphyllobius) calcaratus* (Fabricius)**. Species of this genus are mainly connected with deciduous trees and shrubs (Arnoldi et al. 1965), but there ara also the accidental pests of conifers: *Ph. arborator* Hbst. on *Picea spp.* (Schindler 1974, Schwerdfeger 1981), *Ph. argentatus* L. on *Pinus sylvestris* (Arnoldi et al, 1955) and *Picea spp.* (Schindler 1974), *Ph. tournieri* Smirn. on *Larix sibirica* (Rozhkov 1970), *Ph. chloropus* L. (= *viridicollis* F.) on *Pinus spp.* (Schindler 1974, Joly 1975). As for *Ph. calcaratus*, it was documented that this species mainly damages *Corylus avellana* L. and *Alnus spp.* (Arnoldi et al. 1965) and in our case, all three specimens were caught on young spruces growing near hazel trees. In the laboratory, weevils refused to feed on spruce needles, and died.

***Holotrichapion* (*Apion*) *pisi* (Fabricius).** The constituents of the *Apion* curculionid complex are rather numerous and highly diversified (about 500 Palearctic species, according to Arnoldi et al. 1965) to be isolated in the Apionidae family (Abbazzi et al. 1994). These weevils are mainly associated with herbaceous vegetation but also with deciduous trees and shrubs. Examples of damage to conifers are very rare. For example, feeding by adults on the anthers of *Pinus sylvestris* and on young pine needles in nurseries and plantations was noticed for *Aspidapion* (*A.*) *aeneum* F., *Malvapion* (*A.*) *malvae* F. and *Oxystoma* (*A.*) *pomonae* F. (Pavlovsky and Shtakelberg 1955).

We observed serious damage to young developing shoots and needles by *Holotrichapion pisi* on a sapling of *Picea abies* planted in a small town park (Padova, Northern Italy) on 15 May 1996. The poorly developed sapling (0.5 m in height) was planted in a shady location surrounded by *Rosa sp.*, *Spiraea sp.* and *Nerium oleander* L. The nearest spruce trees were located at a distance of 25-30 m. Visual observation showed that 79 out of 82 developing shoots with needles were damaged by numerous "pin-holes" and small light spots originated from the grazing of the epidermis. In the laboratory cage, the weevils were provided with undamaged spruce shoots from the same sapling. All the shoots were damaged in a similar manner during the 1-week rearing. A mass occurrence of *H. pisi* was recorded on 20-23 May, when the specimens were collected both from coniferous (*P. abies*, *Cedrus sp.*) and deciduous trees and shrubs (mainly Rosaceae). The supplementary feeding of weevils on the needles of *Cedrus* was not noticed. Later (5 June), a single sample *H. pisi* was found on the needles of isolated spruce tree growing in the meadow in Auronzo di Cadore (Veneto). At the end of the season, all the damaged shoots of the sapling described above were dead or poorly-developed. According to our knowledge, this is the first report of feeding by adult *H. pisi* on conifers.

***Rhynchaenus* (*Euthoron*) *fagi* (Linné),** the beech leaf mining weevil. This is a well-known forest pest from a genus of highly specialized mining weevils associated with deciduous trees and shrubs. In many cases, the larvae are monophagous on the host plants mined, whereas adults may conduct supplementary feeding on different tree species (Maisner 1974). Previously, the occurrence of adult feeding on conifers (needles of *P. sylvestris*) was noticed for *R. jota* F. only (Pavlovsky and Shtakelberg 1955). Adults of *R. fagi* feed not only on different deciduous trees but also on herbaceous plants, and this feeding is of great importance in the seasonal activity of beetles (Bale and Luff 1978, Bale 1981).

We recorded uncommon adult feeding of *R. fagi* on the needles of *Larix decidua* in Monte Bondone (Trentino, Northern Italy) in late June 1994. Weevils were found on the low branches of larch trees growing along the boundary between the natural light *L. decidua* forest and an alpine meadow at about 1750 m asl. The density of beetles on trees was not measured numerically but, sometimes, it was possible to observe up to 4 individuals per brach. According to visual observations, the occurrence of weevils decreased sharply as the distance from the border increased: the only individuals were found on sparse larches at about 20 m from the border into the meadow, and none were noticed under the canopy of a mature stand. It was found that *R. fagi* came from the sparse shrubby foliage of *Fagus sylvatica* near the visual border line. All the beech leaves were strongly damaged by mines constructed during the development of larvae, and by phyllophagous grazing. The adults of *Phyllobius chloropus* L. (= *viridicollis* F.) were found together with *R. fagi* on beech leaves, herbaceous plants and the needles of *L. decidua*. It is known that this *Phyllobius* species feeds on deciduous trees and also on pines (Arnoldi et al. 1965, Joly 1975).

In the laboratory, both males and females of *R. fagi* fed actively on larch needles for about 10 days. Weevils formed light spots but not holes on the surface of the needles by grazing on the epidermis. In the field, the beetles disappeared from larch at the beginning of July.

***Rhinomias forticornis* (Boheman).** This is a rather rare species representing the depauperate genus *Rhinomias* Reitter, 1894 close to *Omias* Germar, 1817. The species is spread throughout Central Europe, Caucasus, and Asia Minor. The biology and ecology of this weevil has not been studied well. Probably, this is a meadow species occurring on low grassy vegetation (Hoffmann 1950).

In June and July 1994 we noticed samples of *R. forticornis* in pitfall traps along the transects crossing the boundary between a 50-year old Norway spruce plantation and a calcareous meadow in Bosco del Cansiglio (Veneto, Northern Italy). The pitfall-trapping did not permit evaluation of the real density of epigeic organisms but the catches at least showed that weevils were distributed both in the meadow and woodland (Fig. 2). Thus, the fact that this species belongs exclusively to the meadow weevil community is doubtful.

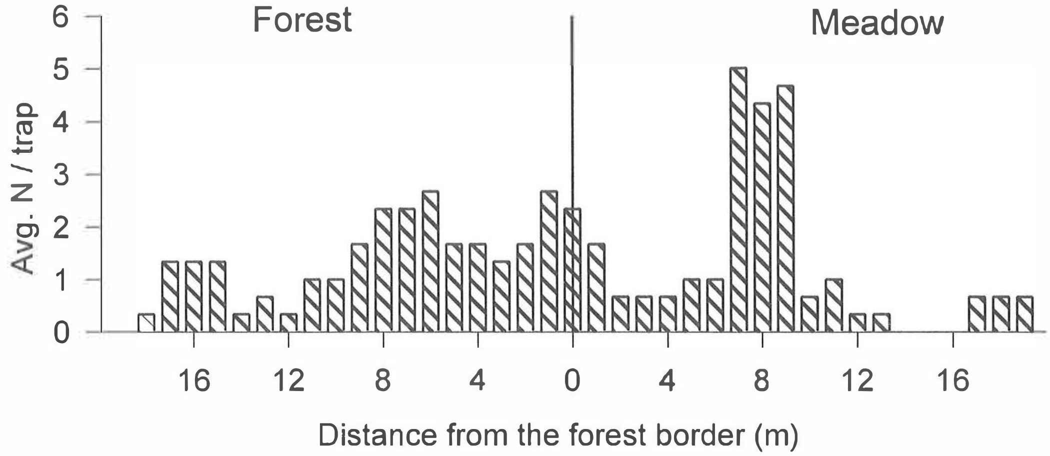

Figure 2. Distribution of *Rhinomias forticornis* across the boundary between a 50-year old Norway spruce plantation and a calcareous meadow (June - July 1994, Bosco del Cansiglio, Northern Italy).

The lower branches of the spruce trees growing along the forest margin were in contact with the ground. Living specimens of *R. forticornis* from the border traps (placed just near that branches) were reared in the laboratory where they fed on shoots and needles. Observations showed that the weevils were very bad climbers and thus fed on the needles at the bottom of cage. Feeding was not "specialized": the beetles gnawed through the needle rib in one place, and the needles were curved as a result. The needles of border spruces probably are only an accidental food source for *R. forticornis* which normally crawls on the ground, especially where a well-developed grass cover is absent under dense conifer plantations.

Discussion

The ability to switch from primary food sources to alternative ones is a well-known feature of phytophagous insects. It is closely related to the degree of dietary specialization of the insect species. Also, local conditions may influence insect feeding behaviour and food choice to a large extent (Fox and Morrow 1981, Futuyma and Moreno 1988, Jaenike 1990). In their review, these authors provided a description of some general sources of variation in food plant selection as affected by local conditions: herbivore behaviour, genetic variation among insects, competition among insects, changes in abundance of plants, changes in plant quality, and others. Probably, the cases of uncommon host associations in the curculionid species described above may be analysed both in the context of weevil specialization and from the viewpoint of the possible effect of local conditions.

First, when more attention was paid to the forestry needs, we examined the weevils from the viewpoint of their possibility to feed on conifers. That is why the species were ranged in decreasing order of this capability. *Pissodes*, *Hylobius* and *Magdalis* species could be combined into a highly specialized group as most of them are characterized by larval and adult feeding on conifers (Arnoldi et al. 1965, Eidmann 1974, Kudela 1974, Maisner 1974). The second group was composed of *Polydrusus*, *Otiorhynchus* and *Phyllobius* species, the larvae of which are probably super-polyphagous on roots. Most adults feed on herbaceous vegetation, deciduous trees and shrubs whereas a number of species are usually associated with conifers in the period of supplementary feeding (Arnoldi et al. 1965, Schindler 1974). The third group was rather mixed, including *Apion*, *Rhynchaenus* and *Rhinomias* species whose host associations with conifers are rare or accidental (Hoffmann 1950, Bale 1981). Of course, it is also possible to recognize the different levels of specialization on conifers within the limits of each group. Taking into account adult supplementary feeding only and basing ourselves on published material, it is necessary to conclude that most species under discussion are polyphagous or widely olygophagous herbivores. It could be one of the reasons why these weevils have demonstrated an uncommon feeding behaviour, change of food objects and host plants. But the individuals of polyphagous *Ph. calcaratus* mentioned above, when collected on spuce together with *Otiorhynchus spp*., refused to feed on spruce needles and died. Thus, wide food specialization is not the only reason for uncommon feeding of some polyphagous weevils on conifers. Probably, some of the local conditions, for example, the relative abundance and distribution patterns of host and nonhost plants, were responsible for the observations.

In the case of a specialized group, uncommon feeding behaviour and change of food objects were observed on conifers only. Thus, the more specialized *P. validirostris* was observed when provided leaders instead of green cones, but it did not change the host plant, *Pinus sylvestris*. Having been polyphagous on conifers, *H. albosparsus*, *H. pinastri* and *M. phlegmatica* demonstrated uncommon adult feeding on needles without leaving the host trees for some other vegetation. Even for *O. ovatus*, which belongs to a less specialized group but is known as a conifer pest, the change of host feeding location but not of the host tree was observed. The analysis of the local conditions showed that in cases of specialized weevils, the preferable food sources were present but sparse and thus, not "convenient energetically from the foraging point of view" (Vladyshevsky 1980) in comparison with other available coniferous food plants. The best example was demonstrated by *P.validirostris* in very light pine forests or in the secondary birch stands where mature pines with cones were distributed rather irregularly. However, under extreme conditions when the usual food trees are absent, the highly specialized coniferous weevils can also feed on absolutely uncommon plants as was noticed for *H. abietis* L. (Schwerdtfeger 1981, Eidmann 1985).

On the contrary, most unspecialized species demonstrated a change-over from their natural host plants (deciduous trees etc.) to alternate ones (conifers) but probably did not change their feeding manner. First of all, this concerned the rough grazing of needles by *Otiorhynchus spp*. For this group of polyphagous weevils, the local conditions were not characterized by irregular distribution but almost by an absence or very scarce growth of the prefered food plants. A dense, mixed coniferous stand in Auronzo di Cadore described above was distinguished by the absence of grass cover, poorly-developed undergrowth and the concentration of spruce/fir regeneration on the borders of the gaps. Apart from sparsely growing young deciduous trees, only conifers were constantly available for the supplementary feeding of weevils. That is why several unspecialized species were observed simultaneously on the young spruces on the borders of small gaps but not one individual was caught on the regenerating conifers in the opening covered by well-developed shrub and grass vegetation (Table 1).

Besides other reasons for a local food plant selection, Fox and Morrow (1981) noticed the effects of abiotic factors. Probably these could be partly responsible for the feeding of *R. fagi* on larch, and *O. geniculatus* on *Pinus mugo* under the conditions near the upper timberline in Italian Alps. For example, in the biotope observed, there was a well-developed undershrub and herbaceous layer where the adult feeding of *R. fagi* may occur (Bale 1981). The low ground-level temperatures at night could force some weevils to climb up the nearest larch trees.

The importance of changes in plant quality was carefully reviewed and discussed in Thorsteinson (1960), Futuyma and Moreno (1988), Jaenike (1990). It is possible to expect it on different forest borders exactly where the trees are subject to stronger effects of abiotic factors (e.g. Stevens and Fox 1991). The results of observations showed that practically all the cases of uncommon curculionid damage on conifers were documented under boundary or similar conditions, and the weevil species described above were mostly observed on the border or on separate trees. It was previously noticed that young Scots pine trees can be subject to serious damage by specialized weevils when they grow along the borders (Rozhkov 1955). Later, it was assumed that the forest borders and their analogues are preferable habitats for a great number of dendrophagous insects (Gourov 1991). The reasons for this preference could be discussed with the examples of weevil species in the situations described above.

Beetles could be attracted to the borders and its analogues due to: (1) a higher abundance of preferable food trees in comparison with under-canopy habitats (*H. pinastri* in Buiba, *Magdalis sp.* in Aradan, *R. fagi* in Monte Bondone); (2) the availability of alternative food sources when the preferable ones were scarce (*P. validirostris*, *H. albosparsus* in Kel'tom, *Otiorhynchus spp.* in Auronzo di Cadore). The change of food objects and feeding behaviour under border conditions could be explained by: (1) changes of nutritional quality of plants (*H. albosparsus* on *Abies sibirica*, *Apion pisi* on sapling of *Picea abies*); (2) microclimatic effects (*R. fagi*, *O. geniculatus*, *P. pallidus*); (3) accidental availability of the living low branches of border and separate trees for insects in comparison with the core forest habitats where the low branches are dead (*R. forticornis* in Bosco del Cansiglio, *P. pallidus* in Auronzo di Cadore). And of course, an element of chance must be taken into account because the boundary (ecotonal) zones are usually characterized by high biodiversity (Odum 1971), and there is a greater possibility of recording some accidental species (e.g., polyphagous *Otiorhynchus spp.*) feeding on uncommon food plants.

It is necessary to note that for several of the weevil species under study (*H. albosparsus*, *P. validirostris*, *M. phlegmatica*, *P. pallidus*, *O. ovatus*, and *A. pisi*), the uncommon feeding patterns were noticed by direct field observations. For all the rest (*H. pinastri*, *Magdalis sp.*, *R. fagi*, and *Otiorhynchus spp.*), the results of laboratory rearing were obtained. Some artificial conditions could be responsible for *H. pinastri* and *Magdalis sp.* refusing to feed on shoots, and for their uncommon feeding on needles. However, the bionomics and behaviour of many weevils such as *H. pinastri* and *Magdalis sp.pl.* have not been studied carefully yet

(Rozhkov 1970, Opanasenko 1976) because attention has been given to more important pests. That is why it is not unlikely to discover some new facts concerning the biology of groups and species of weevils, as exemplified by the more or less common occurrence of "Magdalis type" damage on the needles of spruce (Fig. 1) and the forest/meadow distribution of *R. forticornis* (Fig. 2). But of course, the capability of some species to damage conifers in the cage had to be confirmed by food-choice experiments because the food plant ranges are known to be wider under laboratory conditions (Bale and Luff 1978, Leather, Ahmed and Hogan 1994). During laboratory examinations we tried to recognize the potential possibility to feed on conifers for the weevils collected in the crowns of young coniferous trees only. The fact that not all the species managed to show such a capability (e.g., *Ph. calcaratus*) will make us take into account the cases of "positive response" as a basis for future investigations.

The main conclusion that uncommon adult feeding of many species is observed on the forest borders, suggests that the change in insect behaviour and food preferences is one of the "edge effects". Numerous borders which have originated during the course of forest fragmentation can be responsible for the spread of these phenomena. As a result, the natural regeneration in openings and borders as well as young forest plantations, hedgerows and shelterbelts may be subject to damage by unspecialized herbivores. Due to this, the study of the biology and ecology of phytophagous insects as related to forest borders has become important.

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