RESOURCE USE AND CLONAL DIFFERENCES IN ATTACK RATE BY THE DOUGLAS-FIR SEED CHALCID, *MEGASTIGMUS SPERMOTROPHUS* WACHTL (HYMENOPTERA: TORYMIDAE), IN FRANCE

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Abstract

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The within-cone distribution of *Megastigmus spermotrophus* Wachtl (Hymenoptera: Torymidae), the Douglas-fir seed chalcid, infesting Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] cones from north-central France was compared with that in samples from California. Results indicate that the mid-region of cones was more intensively utilized by seed chalcids in France than in California, whereas in the northwestern United States the mid-region is characteristically occupied by dipteran and lepidopteran species. This difference in distribution may explain the large discrepancy in infestation rates on the two continents. The potential impact of this finding on pest management strategies is discussed.

Cones were measured and dissected or X-rayed to determine seed chalcid infestation levels. Analysis of covariance performed on data from cones that were collected in 1986 and dissected showed cone diameter at maturity to be a highly significant factor in attack rate, although slopes were different among clones. Between-tree variation was also significant, but clonal source was not. Cone diameter, clonal source, and between-tree variation constituted 87.1% of the variation in rate of attack by the seed chalcid. Although clone was not a significant factor in data from dissected cones, X-rayed cones showed significant differences in attack rates for some clones.

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Résumé

La répartition des larves de *Megastigmus spermotrophus* Wachtl (Hymenoptère: Torymidae) aux cônes du sapin de Douglas [*Pseudotsuga menziesii* (Mirb.) Franco] du nord-central de la France fut comparée à celle des échantillons de la Californie. Les données montrent que la région centrale des cônes était utilisée plus intensivement par les chalcidiens en France qu'en Californie, tandis qu'au nord-ouest des Etats-Unis cette région des cônes est, en règle générale, occupée par les lépidoptères et les diptères. Il se peut que ces différences en ce qui concerne la répartition puissent expliquer la grande différence entre les taux d'attaque par le chalcidien sur les deux continents. On discute l'impact éventuel de ces renseignements sur la lutte contre cette espèce.

Des cônes furent mesurés et disséqués ou radiographiés afin de constater les taux d'attaque par le chalcidien. L'analyse de covariance conduite aux données des cônes cueillis et disséqués en 1986 a montré un rapport linéaire très significatif entre le taux d'attaque et le diamètre des cônes, bien que les pentes soient hétérogènes entre clones. La variation entre-arbres fut aussi significative, mais la souche clonale ne fut pas significative. Diamètre des cônes, souche clonale, et variation entre-arbre ont constitué 87,1% de la variation de taux d'attaque par le chalcidien. Bien que la souche clonale ne soit pas une variable significative pour les cônes disséqués, les données des cônes soumis aux rayons-X ont montré les différences significatives entre taux d'attaque pour quelques clones.

Introduction

The Douglas-fir seed chalcid, *Megastigmus spermotrophus* Wachtl (Hymenoptera: Torymidae), is a nearctic seed-infesting species that is specific to Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and big-cone Douglas-fir (*P. macrocarpa* Mayr) (Hussey 1955; Hedlin et al. 1980). Its range is coincident with that of its hosts throughout North America (Hedlin et al. 1980), and it has been accidentally introduced into Europe along with Douglas-fir (Roques 1983). This seed chalcid is now distributed throughout most of the region of introduced Douglas-fir in Europe, even where Douglas-fir is poorly represented in the flora (Roques 1981).

Clonal resistance to cone-feeding insects has promise in seed orchards because the crop is annual, seed orchards are small, and trees are planted at above optimum densities to allow for losses to graft-union failures and removal of undesirable clones. Thus, determination of the basis of clonal susceptibility has implications for pest management and may provide seed orchard managers with a criterion for selecting trees to be removed in normal thinning operations as orchard trees mature.

Clonal variation in susceptibility to the seed chalcid has been reported previously (Hedlin and Ruth 1978; Roques 1981). Evidence that this variation in susceptibility may be heritable has been presented (Jamblinne de Meux and Nanson 1969; Schowalter et al. 1986), although different mechanisms were postulated. Cone size may be a factor in this susceptibility (Lessman 1974), but Jamblinne de Meux and Nanson (1969) and Schneider (1985) found no relationship between cone size and rate of attack, at least within individual trees. Jamblinne de Meux and Nanson (1969) and Hussey (1955, 1956) speculated that phenological or terpene-mediated mechanisms were responsible for variations in attack.

No significant clonal variation in susceptibility was found in orchards where the entire cone crop was removed each year (Roques 1986); there the distribution of attacks appeared to be related to the size of the seed crop with respect to the number of immigrating insects, and among-tree variation was related to location of trees with respect to the prevailing winds during insect flight. When cone crops were heavy compared with the number of insects emerging, chalcid attacks were aggregated; when cone crops were small compared with the number of ovipositing chalcids, insect attacks were more evenly distributed throughout the orchard.

Competing species may also affect seed chalcid population densities. In its native range, the chalcid coexists with many other cone insect species. Although the seed chalcid has been implicated as the second most important seed-damaging species in the northwestern United States, it commonly destroys less than 20% of sound seed in that region (Hedlin et al. 1980; Schowalter et al. 1985). In European seed orchards, however, where the chalcid exists in the near absence of competing species, damage levels frequently approach 100% (Schnaider 1970; Kristek 1967; Roques 1981). Roques and Raimbault (1985) speculate that higher chalcid population densities in Europe are a consequence of competitive release, but this issue has not yet been resolved.

Our objectives were (1) to assess clonal susceptibility to the seed chalcid in Douglas-fir and the possible role of cone size; and (2) to examine the different patterns of resource use by the seed chalcid in its indigenous area, where other insects share the resource, and in its area of introduction, where it is the sole major pest in Douglas-fir cones (Roques 1983).

Materials and Methods

Site Selection. We collected cones from Ingrannes seed orchard, operated by the Institut National de la Recherche Agronomique (INRA), in the Department of Loiret in north-central France. This seed orchard, which showed a history of high levels of attack by the seed chalcid and a negligible incidence of competing pest species (Roques 1981), was chosen to minimize interactions among pest species that might obscure relationships

between the seed chalcid and its host. Ingrannes is unusual among French seed orchards because its trees have a rather extended flowering phenology (clones were not selected for synchrony of flowering) and annual sanitation of cones is not practiced (Roques 1981). It is maintained by INRA primarily for experimental purposes. Resource use by chalcids in Ingrannes was compared with that of chalcids in a coastal North American seed orchard (Little River seed orchard in Humboldt County, CA, operated by the Lousiana-Pacific Corporation), previously described by Rappaport and Volney (1986). The California site had a typical pest complex including *Contarinia oregonensis* Foote, *C. washingtonensis* Johnson, *Barbara colfaxiana* (Kearfott), *Dioryctria abietivorella* (Grote), and *M. spermotrophus*. Clonal and cone diameter effects were studied only in Ingrannes cones because of the difficulty in assessing these factors in North American cones, where other pest species might displace chalcids.

Clonal Variation in Attack Rate. Proportion of sound seed infested per cone was calculated by summing infested seeds and sound seeds per cone and dividing the number of infested seeds per cone by this sum, as described by Roques (1981). Cone length and diameter (average of two dimensions at the greatest diameter) were measured in a subset (two to seven cones per ramet) of the cones from Ingrannes seed orchard; the results were subjected to analysis of covariance (SAS Institute, Inc. 1982) with cone diameter as the predictor variable, clone number as the concomitant variable, and percentage of sound seeds infested by the chalcid as the response variable. Because the experiment was unbalanced and variances were unequal, the Games and Howell *T*-modification (Games and Howell 1976; Keselman and Rogan 1978) was used to assess the effect of clonal source on attack rate.

An additional 25 cones per tree were collected from all cone-bearing ramets of the five clones studied in Ingrannes orchard. Cones were dried and seeds extracted and X-rayed, according to techniques described previously (Roques 1981), to determine infestation levels. Similar surveys were conducted in 1983–1985 at Ingrannes, and these results also are reported here. Average percentage of sound seed was calculated as above; a nonparametric test, the Kruskall-Wallis procedure (Anonymous 1985), was performed to test for clonal variation in attack rate. Pairwise tests between mean attack rates per clone were performed using Bonferroni's inequality (Bailey 1977).

Resource Use. Mature cones were harvested from Ingrannes seed orchard in September 1986 from 12 trees representing five different clones. Two ramets were sampled from each of four clones and four ramets were sampled from the fifth. Seven cones were selected at random from each ramet and were dissected scale-by-scale; damaging agents were documented for each seed. Positions of damaged seeds, empty seeds, and sound seeds along the cone axis were noted. The total number of scales per cone was then divided by 10, with each 10th representing a consecutive stratum along the cone axis from the base to the tip. Numbers of insect-damaged, empty, and sound seeds per stratum were plotted as a function of position along the cone axis to show differences in patterns of resource use. Hotelling's T^2 (Dixon 1981) was used to test for differences between the distributions of chalcids in France and California by comparing the means of the cone axis vectors.

Results and Discussion

Cone diameter at maturity was a significant factor in rate of attack by the seed chalcid ($P = 0.0104$), although slopes were different among clones and the relationship between cone diameter and attack rate was not inversely proportional for all clones, as the work of Kozak (1963) and Lessman (1974) predicted. This phenomenon may have resulted at least in part from the fact that, except for clones 169 and 304, there was generally very little spread in mean cone diameter among ramets of a clone (Fig. 1). More intensive

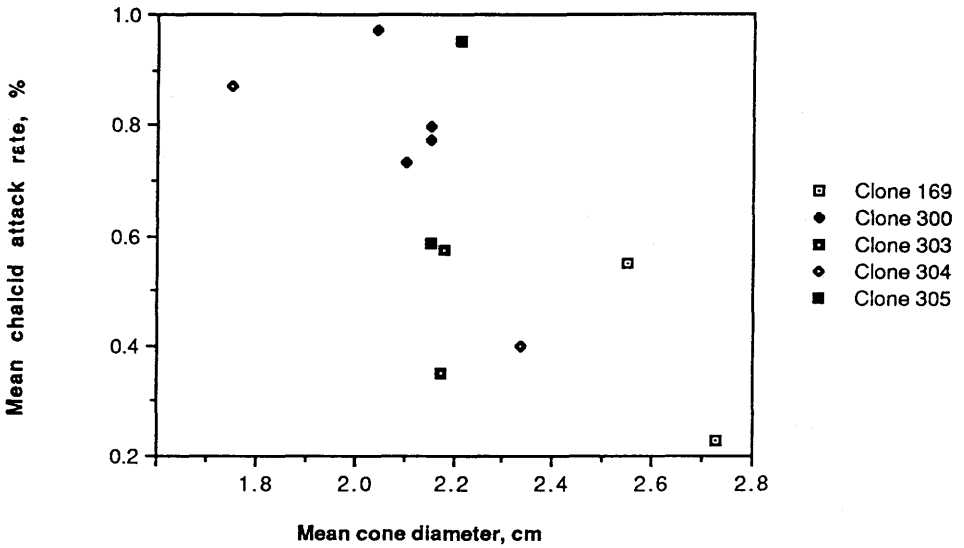

FIG. 1. Relationship between mean attack rate by the Douglas-fir seed chalcid and mean cone diameter per tree, Ingrannes seed orchard, 1986.

sampling using cones from broader size ranges would be required to establish whether there is a consistent relationship between diameter and attack rate for all clones.

There was also highly significant variation in attack rate among ramets of a clone ($P = 0.0082$), and cone diameters were heterogeneous among clones ($P = 0.0087$). However, attack rates were not significantly different among clones for cones that were analyzed by dissection ($P = 0.4357$). Among-tree variation, clonal variation, and cone diameter together accounted for 87.1% of the variation in rate of attack by the seed chalcid ($P \leq 0.0001$).

Results of seed X-rays and cone dissections from Ingrannes orchard are summarized in Tables 1 and 2, respectively. The orchard-wide mean loss of sound seed per cone to the seed chalcid in 1986 was 59.2% (Table 1); this rather low figure can most likely be attributed to the destruction of the 1985 cone crop by late frosts. The ranking of clones by rate of chalcid attack was not consistent from year to year, but results from the two assay methods (X-ray and cone dissection) were similar in 1986. The mean attack rates were consistently lower in X-rayed cones than in dissected cones. The difference was slight

Table 1. Summary of mean percentage of seeds (±SD) infested by seed chalcids in X-rayed cones for each clone and for the whole orchard, Ingrannes seed orchard, 1983–1986*

Clone No.	1983	1984	1985	1986
300	79.4(±10.5)a	72.8(± 4.3)a	—†	75.6(±15.9)a
305	73.3(± 2.8)a	20.8(± 2.5)b	—†	69.0(±29.3)a
304	80.3(± 9.2)a	—‡	—†	57.0(±43.8)ab
303	51.4(±18.1)b	18.0(±14.7)b	—†	37.7(±14.2)ab
169	47.4(±28.6)b	34.6(±18.4)b	—†	17.5(±11.8)b
Whole orchard	74.2	57.7	97.8%	59.2%

*For each year, attack rates followed by the same letter are not significantly different (experiment-wise error rate ≤0.05, using Bonferroni's inequality).
†Cones killed by late frost.
‡No cones produced that year.

Table 2. Summary of mean rate of attack by the seed chalcid (±SD) and mean cone diameter (±SD) per clone in dissected cones from Ingrannes seed orchard, 1986*

Clone No.	Mean % of seed attacked (±SD)†,‡	Mean cone diam. (±SD)§ (cm)
300	81.8±11a	2.11±0.051a
305	76.8±26a	2.18±0.424a
304	63.6±33a	2.04±0.414a
303	46.2±16a	2.18±0.003a
169	39.0±23a	2.64±0.124a

*Attack rates and cone diameters for clones followed by the same letter are not significantly different as determined by the Games and Howell *T*-modification (experiment-wise error rate = 0.05).
†Unadjusted sample means.
‡Least significant difference = 47.1%.
§Sample standard deviations.

except for clone 169, which showed a much lower rate of infestation in the X-rayed samples. This may indicate that infested seeds are not as readily extracted from cones as uninfested seeds, or that infestation is more accurately detected with dissection than with X-rays.

Although significant differences were not found among clones using data from dissected cones, pairwise testing of results from X-rayed cones did show significant clonal differences in attack rate [*t*-tests using Bonferroni's inequality and Games and Howell's *T*-modification ($\alpha = 0.05$), respectively]. We cannot explain this discrepancy because, although more cones were sampled per tree with X-ray analysis than with dissection, the variances using the two methods of analysis remained similar. Utilizing results from X-rays, both clone 300 and clone 305 had significantly different mean percentages of chalcid attack from clone 169 but not from the other clones. In X-rayed cones, the mean percentage of sound seeds destroyed per cone for the most susceptible clone, number 300, was 1.7- to 4.3-fold that of the least susceptible clone, number 169 (Table 2). As noted by Schowalter et al. (1986), a 2-fold difference in seed production between susceptible and resistant clones could have important consequences in terms of both the economics of reforestation and the genetic diversity of the resulting seedlings.

The results from the covariance analysis of dissected cones should be interpreted with caution because the results are from only 1 year which was characterized by a lower infestation rate than previously reported (Roques 1981). Data from previous years demonstrate the year-to-year variability in damage rate by clone (Table 1). Damage levels from clones 303, 304, and 305 are highly variable from year to year, but are related to overall infestation levels within the orchard. Clones 169 and 300 show consistently low and high levels of infestation, respectively, and are consistently significantly different from one another over time. A possible explanation for this is the large clonal variation in flowering times at the Ingrannes orchard. Clones 169 and 300 have been shown to have large phenological differences, the former showing very precocious development and the latter delayed development (Roques 1981). Kairomonal differences among clones, however, should not be rejected as a possible explanation for this phenomenon. The seed chalcid has recently been shown to locate cones through a combination of visual and terpene-mediated stimuli (Roques 1987).

These findings, although limited in scope, indicate more striking genetic variation in susceptibility to the seed chalcid than some previous reports (Hedlin and Ruth 1978; Roques 1986; Schowalter et al. 1986). However, Roques' (1986) study was conducted in a seed orchard that was subjected to removal of all cones each year, and was planted with clones that were deliberately selected for homogeneity of flowering phenology. Ingrannes, on the

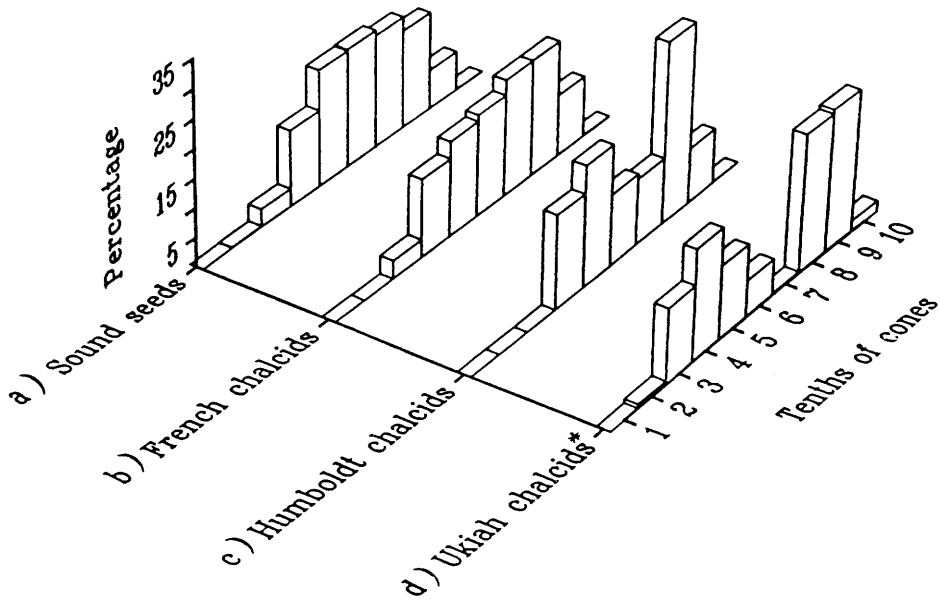

FIG. 2. Distributions of (*a*) sound seed and (*b*) seed chalcids in Ingrannes, France, Douglas-fir cones; and (*c*) and (*d*) seed chalcids in California cones. Vertical bars represent percentages of the total seeds/chalcids within each longitudinal stratum (10th) of the cone. [The data marked in the figure with an asterisk were redrawn with permission from Volney (1984).]

other hand, is an experimental seed orchard which is not subjected to annual sanitation regimes and which shows a much greater heterogeneity of flowering phenology than the newer, operational seed orchards. Furthermore, levels of chalcid attack are characteristically much higher throughout France than the level encountered at Ingrannes in 1986. It is possible that the clonal variation in chalcid damage seen in this seed orchard in 1986 occurs only in situations where levels of attack are low, flowering phenologies are protracted, and infestations result from residual rather than immigrant populations. These conditions would not be expected to hold for most seed orchards in most years under European conditions.

Because North American chalcid infestation levels are characteristically much lower than European levels and most older North American seed orchard clones were not selected for flowering synchrony (Michael A. Bordelon, Oregon Department of Forestry, Salem, OR, personal communication), it is surprising that studies on the North American continent failed to reveal such variation in susceptibility. However, it is possible that these studies were complicated by the presence of a multitude of pest species, interactions among which can obscure insect–host relationships that would be more apparent in single-pest systems. There are many examples of interactions among cone and seed insects (Annila 1973; Miller 1984; Volney 1984; Shea 1987) that could obscure clonal variations in host susceptibility.

Resource Use. Studies in North America show that, in areas where they are indigenous, the chalcids are more commonly found in the distal and proximal cone extremities than the mid-region of the cone axis, whereas the mid-region is most fully utilized by dipteran and lepidopteran cone-feeders (Kozak 1963; Volney 1984; Rappaport and Volney 1986). Potential explanations for this bimodal distribution of the seed chalcid in North America include cone morphology (centrally located seeds may be inaccessible to the ovipositor), scale hardness (scales may be more penetrable at the extremes), reduced larval survival in

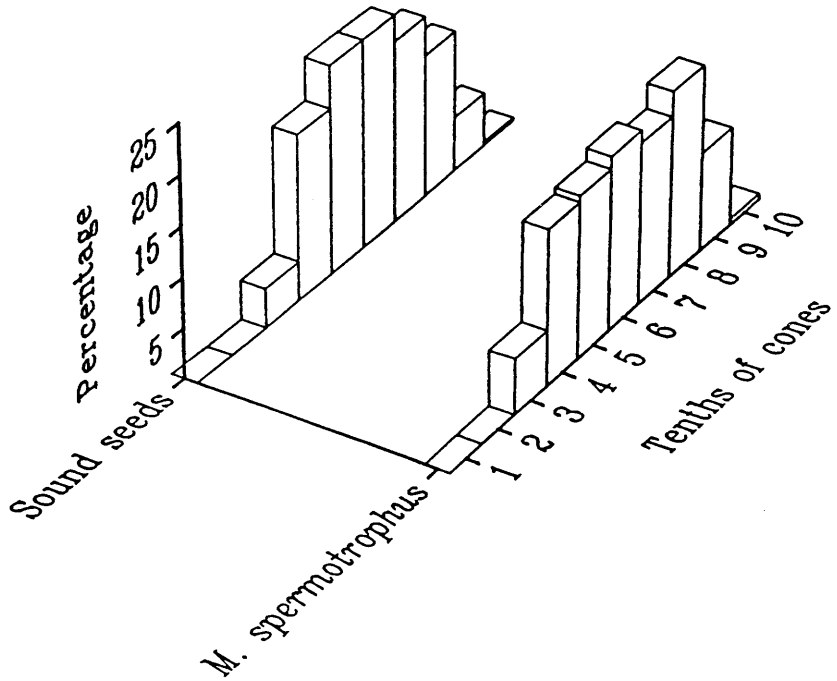

FIG. 3. Distributions of seed chalcids and sound seeds in European Douglas-fir cones with diameter >2.25 cm. Vertical bars represent percentage of seeds/chalcids occurring within each longitudinal stratum (10th) of the cone axis.

the mid-regions, enhanced attraction to seeds at the extremities, or competitive displacement. These alternatives were easily evaluated by a comparison of the frequency distributions of chalcid larvae and sound seeds along the cone axis in the indigenous and introduced regions of Douglas-fir.

The mid-region of the cone axis had a significantly greater percentage of infested seeds in the European than in the North American cones (Fig. 2) ($P<0.00001$, Hotelling's T^2) and the chalcid distribution in cones from the Ingrannes seed orchard clearly paralleled the distribution of sound seed, demonstrating that central seeds (which are presumed to be farthest from the surface) are quite accessible to the chalcid. These results do not agree with Lessman's (1974) observation that, although chalcids probe the mid-regions of cones most intensively during oviposition, greater numbers of larvae are actually produced in the distal third of the cone than in the mid-region. In Lessman's work, however, numbers of sound seed were nearly equal in the three cone regions, whereas in our study and that of Ho (1980), sound seeds were concentrated in the mid-region. Our data contradict the hypotheses that seed accessibility and cone durability limit chalcids to cone extremities in indigenous populations, and support the hypothesis that the chalcid has achieved higher population densities in Europe because of competitive release from other cone-inhabiting species.

The confirmation that the chalcid oviposits into the thickest diameter of the cones, coupled with the correlation between attack rate and cone size, led us to analyse the largest and smallest cones separately. We did so to determine whether patterns of resource use that might explain the correlation between chalcid densities and cone size had been obscured because we aggregated data from cones of all sizes. Frequency distributions were constructed separately for the largest subset (diameter >2.25 cm) and the smallest subset

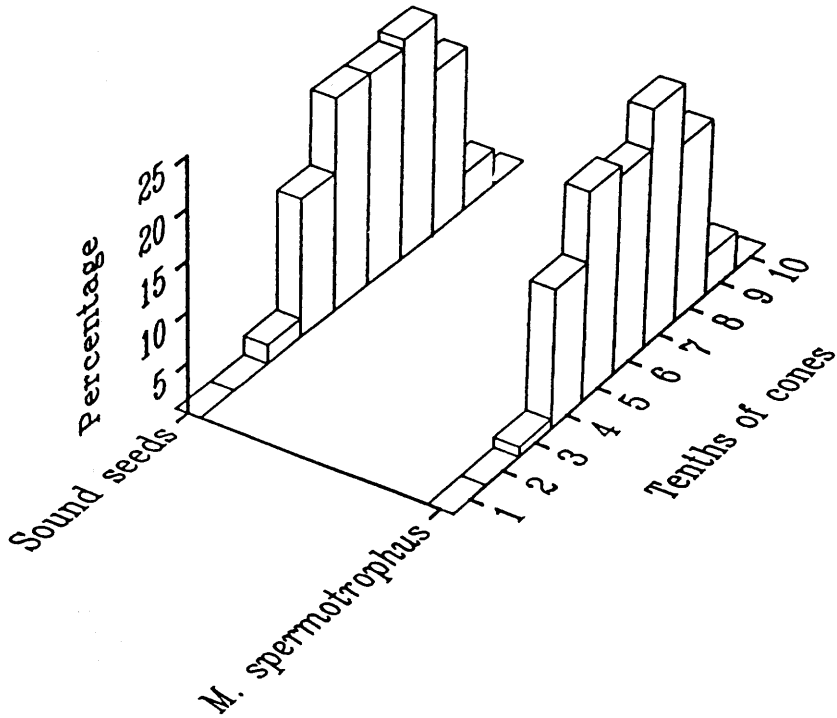

FIG. 4. Distributions of seed chalcids and sound seeds in European Douglas-fir cones with diameter <1.95 cm. Vertical bars represent percentage of seeds/chalcids occurring within each longitudinal stratum (10th) of the cone axis.

(diameter <1.95 cm) of cones. These subsets were derived by ranking cones by diameter, then dividing them into three classes of equal numbers. The resulting histograms (Figs. 3 and 4) reveal no discernible trend for chalcids to utilize cones differently according to cone size, other than the correlation with cone size noted previously for some clones. In both the largest and smallest subsets of cones, chalcids used seeds in proportion to their abundance rather than as a function of their distance from the cone surface (although it must be noted that cone diameter at maturity may not be an accurate indication of cone diameter at mid-season, when the chalcids are ovipositing). We conclude, therefore, that it is probably not seed accessibility that reduces chalcid abundance in large cones, but some other variable associated with cone diameter such as flowering phenology, cone permeability, visual cues, or volatile chemical composition.

If competitive release is indeed responsible for differences in population densities on the two continents, the consequences for pest management are two: first, we might infer that pest management methods aimed at the early arriving pest species (dipterans and lepidopterans) could, as predicted by Annila (1973) and Levins and Wilson (1980), simply free more of the niche for the chalcid without reducing crop damage [evidence from insecticide tests suggests that this may be the case (Annila 1973; Koerber and Markin 1984; Stein and Markin 1986; Summers and Miller 1986)]; second, the accidental introduction of other pest species from North America to Europe might not be the catastrophe predicted, if similar competitive interactions occurred in the region of introduction.

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