

HOST-PLANT SPECIALIZATION IN NEEDLE-EATING INSECTS OF SWEDEN

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INTRODUCTION

It has been suggested that the enormous diversity of phytochemicals within the plant kingdom makes it impossible for one and the same insect species to exploit all plant species (Dethier 1954, Fraenkel 1959). Not surprisingly, the number and diversity of host plants utilized by different phytophagous insects are highly variable, and the specific selective pressures acting on them are still poorly understood (Bernays and Graham 1988, Strong 1988). Many hypotheses have been proposed to explain variations in host specificity among phytophagous insects. For example, there are those based on plant traits: plant defenses (Ehrlich and Raven 1964), plant apparency (Feeny 1976, Rhoades and Cates 1976), plant abundance (Root 1973), plant nutritional value (Mattson and Scriber 1987); those based on insect traits: degree of intimacy with the host plant (Mattson et al. 1988), neuronal capacity of the insect (Levins and MacArthur 1969) and finally those based on natural enemies' traits, e.g. the impact of generalist predators (Bernays and Graham 1988).

In this paper we examine the predictions resulting from hypotheses based on plant characteristics and insect intimacy. We have used the data available in the literature on host ranges of Swedish needle-eating insects reported to feed on the three major conifer species native to Sweden: Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and juniper (*Juniperus communis*). These species account for almost all of Sweden's coniferous flora.

HYPOTHESES EXPLAINING HOST-PLANT SPECIALIZATION

According to the plant apparency hypothesis, differences in tissue chemistry exist between long-lived perennial plants that are easily discovered by insects (apparent) and annual ephemerals that are more difficult to discover (unapparent) (Feeny 1976, Rhoades and Cates 1976). Supposedly, apparent plants contain relatively large amounts of unspecific allelochemicals of low toxicity, high in molecular weight (e.g. tannins), whereas unapparent plants contain small amounts of specific, highly toxic allelochemicals with a low molecular weight (e.g. glucosinolates). These groups of allelochemicals have been called quantitative and qualitative, respectively, by Feeny (1976). Owing to these differences, polyphagous insects are associated mainly with apparent plants and monophagous insects mainly with unapparent plants. Being long-lived and large, conifers meet all the criteria of apparent plants. Hence one can predict that a majority of insects feeding on conifers will be polyphagous. However the apparency hypothesis further predicts that the types of allelochemicals will vary among tissues within a plant depending on tissue apparency. Analogous to between-species variation, apparent tissue (usually perennial), containing unspecific allelochemicals, and unapparent tissue (usually short-lived), containing more specific allelochemicals, should favor polyphagy and monophagy, respectively.

According to the nutrition hypothesis, folivores that feed on nutrient-impooverished plants will have evolved special behavioral adaptations and digestive and metabolic systems that allow them to sequester nutrients from very dilute mediums (Mattson and Scriber 1987). Such adaptations should not in principle prevent them from also feeding on nutrient rich diets. Hence they have the capacity to be polyphagous if other factors are not limiting. Because the conifer species in this study tend to be adapted to nutrient poor sites, and characteristically have low concentrations of N in their needles (Tamm 1955), one might predict then that their phytophagous insects should tend to be polyphagous other things being equal. In fact, Holloway and Hebert (1979) reported that many species of macrolepidoptera feeding on conifers seem to be less specific in their choice of hosts than species feeding on Angiosperms.

According to the Host Intimacy Hypothesis, host specialization by insects will be proportional to the amount of time and body surface area which is spent in direct contact with living tissues of the host plant (Mattson et al. 1988). The rationale is that high intimacy requires highly elaborate behavioral, physiological, and temporal adaptations with a host plant and that increasing intimacy will therefore impose concomitant specialization. Hence the intimacy hypothesis predicts that intimate species such as leaf miners should tend toward monophagy whereas nonintimate species such as free feeding Lepidoptera should tend toward polyphagy.

METHOD AND DEFINITIONS

Information about food plants utilized by each insect species was obtained from Escherich (1931), Nordström et al. (1941), Schwenke (1974, 1978, 1982), Winter (1983), and Ehnström (pers. comm.) but the appendices provide further details. Only insects reported to occur on juniper (Cupressaceae), Scots pine (Pinaceae), and Norway spruce (Pinaceae) have been included. Most of the literature data concern insect occurrence at the plant species level, but in some cases information at the genus level has also been included.

Host-plant specialization is defined according to Cates (1980): insects are considered to be monophagous (Mono) if they utilize one or several plant species within a single genus, oligophagous (Olig) if they feed on two or more genera within one plant family or closely related families, or polyphagous (Poly) if they feed on plants from two or more families (i.e. at least one conifer and some angiosperm). Insect species feeding on one genus within the Pinaceae plus juniper, and insects feeding on two or more genera within the Pinaceae plus juniper, denoted MonoJ and OligJ respectively in the appendices, are included in the oligophagous group elsewhere. Chemistry and morphology are more similar between the two conifer families than between conifers and angiosperms (Thomas 1970), justifying our inclusion of insects denoted MonoJ and OligJ in the oligophagous group.

With respect to numbers of insect species associated with various host plants, a good correspondence has been found between faunal lists derived from the literature and data based on extensive field sampling (Southwood et al. 1982, Niemelä and Neuvonen 1983). Thus the coarse division of host range used in this study probably reflects actual conditions.

Needles were classified as either young or old. The young included buds and current-year needles; the old group included needles ≥ 1 year of age.

RESULTS

Detailed information concerning the host plants utilized by individual insect species as well as their host ranges, needle-age utilization, and feeding modes are presented in Appendices A-D.

No obvious trend in the degree of host-plant specialization is apparent when all insect species are considered (Table 1). However, the degree of specialization varies distinctly among feeding and taxonomic insect groups. Mining microlepidopterans are mainly monophagous ($X^2 = 13.38$, $p < 0.01$, $df = 2$). The absolute monophagy among the sawflies is notable. Chewing micro- and macrolepidopterans are predominantly polyphagous, the microlepidopterans, however, not significantly so ($X^2 = 5.76$, $p > 0.05$, $df = 2$, and $X^2 = 14.92$, $p < .001$, $df = 2$, respectively). Beetles are mainly oligophagous.

Table 1. Numbers of mono-, oligo-, and polyphagous species within different insect groups on Swedish conifers

Insect group	Monophagous	Oligophagous	Polyphagous
Microlepidoptera			
Chewing	2	5	10
Mining	13	6	0
Others	7	4	3
Macrolepidoptera	2	16	21
Hymenoptera			
Symphyta	28	0	0
Coleoptera			
Larvae	1	3	0
Adults	2	9	6
All chewing spp.	33	33	37
Total	55	43	40

Table 2. Degree of host-plant specialization among chewing insects as related to their needle-age (young vs. old) utilization on Swedish conifers (based on 14 Lepidoptera, one sawfly, and four Coleoptera species)

Host range	Young needles	Old needles
Monophagous	0	1
Oligophagous	5	5
Polyphagous	5	3

No association was found between the degree of host-plant specialization and needle-age utilization in chewing insect species (Table 2).

The oligophagous group predominates on all three conifers, comprising ca. 45 percent of the total number of insect species on each of them (Fig. 1). The relative proportions of monophagous and polyphagous insects differ between the tree species. Juniper, with its high proportion of monophages and low proportion of polyphages, differs significantly from both spruce and pine ($X^2 = 9.59$, $p < 0.01$, $df = 2$, and $X^2 = 6.15$, $p < 0.05$, $df = 2$, respectively). Although spruce and pine do not differ significantly, the proportion of monophages is slightly higher on pine.

DISCUSSION

All conifer species studied must be regarded as highly apparent to insects searching for ovipositional sites and low in nutritive value. According to the apparency and nutrition hypotheses, insects feeding on these tree species should tend toward polyphagy. Our data show no such trend when all insect species are considered. On the contrary, less than one third (29 percent) are polyphagous (Table 1). However, such a crude comparison might be too superficial. A more realistic assessment might be achieved by comparing our results with the proportion of monophagous and polyphagous insect species in studies including less apparent and more nutritious plants. This is possible only with specific insect groups (see below). Juniper differs from both spruce and pine, furthermore, in having relatively more monophagous insect species (Fig. 1). However, differences between the three conifer species with respect to apparency and nutritional value appear to be small. Ideally, any attempt to explain host-plant specialization based on plant characteristics should at least take variation in feeding habits among insect feeding guilds into account. The selection pressure on the insect varies depending on the plant traits encountered during feeding. Although this fact was earlier pointed out by Feeny (1976), among others, it has often been ignored. For example, insects feeding internally, such as mining insects, might be able to avoid some plant allelochemicals that are compartmentalized in the plant (Feeny 1970, 1976, Cornell 1989). On the other hand, they might expose themselves more to rapidly inducible defenses, such as phytoalexins. Although the nutrition

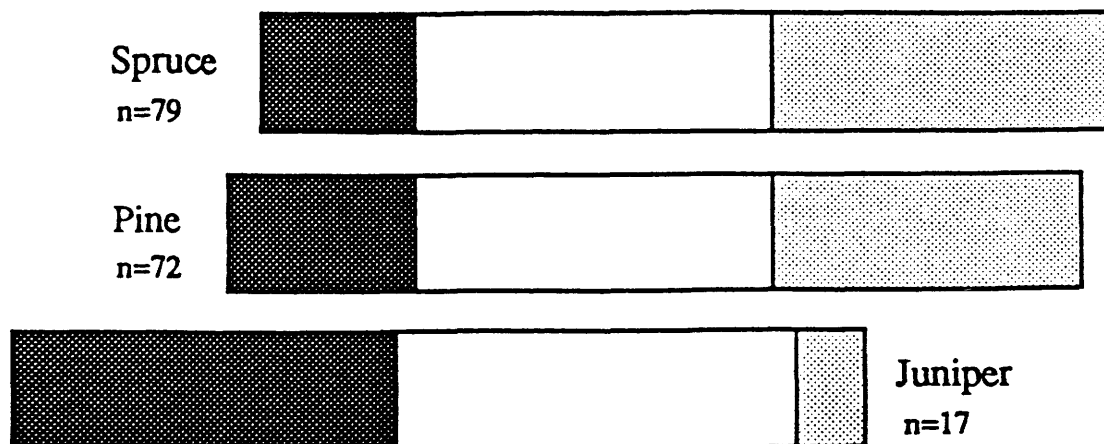


Figure 1. Relative proportions (%) of mono-■, oligo-□, and polyphagous ▨ insect species on each of the three conifer species. Each bar equals 100%. n = number of insect species.

hypothesis was developed based on free-living Lepidoptera, other groups might be more sensitive to variation in nutrient concentrations. In the following, therefore, we have broken down our data into feeding guilds.

Mining Microlepidopterans

The fact that the main defense compounds in conifers (terpenes) are concentrated in clearly defined resin ducts (Bennett 1954) may have important consequences for mining insects. For example, one needle-mining microlepidopteran (*Exoteleia pinifoliella*) utilizes only pine species whose needles have very few resin ducts, all of which are small. Thus this species appears to be avoiding the resinous defense of the host (Bennett 1954). Mining insects seem to be very specialized, irrespective of which food plants they utilize (Hering 1951, Claridge and Wilson 1982, Price 1983). This implies that the degree of host-plant specialization is determined by selective pressures other than those proposed by the apparency hypothesis. The intimate relationship between mining insects and their hosts can probably best explain the narrow host ranges of mining insects. For example, the need to adapt to the anatomy and phenology of the plant may determine the range of hosts that a miner can potentially exploit (Hering 1951). However, the high degree of specialization might actually be an artifact produced as a result of poor investigation of most mining insects (Connor et al. 1980, Powell 1980).

Chewing Insects

Generally, insects feeding externally on leaves and needles come into minimal contact with their host's chemical defense. Among the chewing insects in this study, however, the monophagous species constitute as large a proportion as the polyphagous species when compared over all conifer species (32 percent and 36 percent, respectively).

However, most of the monophagous species are sawflies (Table 1) and sawflies are predominantly monophagous, regardless of which type of plants they utilize (Hodkinson and Hughes 1982, Shaw 1984). Neither the apparency nor the nutrition hypothesis predicts this monophagy. In contrast, the intimacy hypothesis does because conifer-feeding sawflies insert their eggs into the needles of their host, and needle morphology is an important factor in determining oviposition success (Ghent 1959). The ability of females to find needles suitable for oviposition should therefore be strongly selected for. A behavioral adaptation of this kind could be a major reason for the prevalence of monophagy among needle-eating sawflies (Futuyma and Peterson 1985). Moreover, several conifer sawflies have evolved the ability to "detoxify" the defensive compounds produced by their hosts (Eisner et al. 1974, Larsson et al. 1986) and furthermore to use these substances in their own defense against natural enemies (Eisner et al. 1974, Morrow et al. 1976, Boevé and Pasteels 1985). This may be another reason why sawflies on conifers are so specialized. Thus the intimacy hypothesis is partially supported in the sawfly case.

The predominance of polyphagy among chewing Lepidoptera accords with the predictions of all three hypotheses. In two other studies including insects feeding on less apparent, more nutritious plants, the proportion of polyphagous species was reported to be 54 percent and 32 percent (Holloway and Hebert 1979, Hodkinson and Hughes 1982, respectively), whereas in this study it was 52 percent. According to both the apparency and the nutrition hypotheses, however, one would expect relatively more polyphagous insect species on conifers than on plants of lower apparency and higher nutritional value. Thus one out of two comparisons with other studies supports these hypotheses. In principal, a species may behave as a generalist either because every individual is generalistic or because the species consists of specialized individuals or subpopulations (Van Valen and Grant 1970, Jaenike 1978, Singer 1983). For herbivorous insects there are many examples of specialization among individuals and populations (Knerer and Atwood 1973, Fox and Morrow 1981, Singer 1983, Futuyma and Peterson 1985, Ng 1988). *Lasiocampa quercus* provides one such example in this study (Appendix B). Until

more data have been accumulated on the nature of polyphagy in herbivorous insects, any general conclusion would seem premature. Nevertheless, it is possible that "true polyphagy" (i.e. generalistic individuals) is a rare phenomenon. For example, the cost of multiple detoxification systems might be too great for individual insects (Karowe 1989).

Needle-Age and Degree of Specialization

According to the apparency hypothesis, young tissue should be protected by qualitative defenses and thus there should be selection for specialization among insects feeding on such tissue. However, there is no correlation between needle-age utilized and degree of host-plant specialization in our data (Table 2). Results from studies of insects on deciduous trees support the apparency hypothesis (Cates 1980, Niemelä 1983). This difference between conifers and deciduous trees with respect to degree of specialization and utilized tissue-age could be due to the fact that young needles develop more slowly than young deciduous leaves. Hence the absence of a correlation between needle-age and degree of specialization could be due to small differences in apparency between young and old needles. Still, there is evidence showing that young needles of jack pine (*Pinus banksiana*) and Scots pine contain a resin acid that repels sawflies normally feeding on old needles (Ikeda et al. 1977 and Niemelä et al. 1982, respectively). It has yet to be determined whether other needle-eating insects are repelled by the same substances (Buratti et al. 1990).

CONCLUSIONS

The applicability of the examined hypotheses to Swedish needle-eating insects can be summarized in the following way. 1) Polyphagy predominates among chewing lepidopterans, thereby supporting all three hypotheses. However, the many examples of specialized individuals among polyphagous insects and the comparison of our results with those obtained in studies of macrolepidopterans on other plant species weaken this support. 2) The absolute monophagy among sawflies supports the intimacy hypothesis and may be attributable to the oviposition behavior of the female and the detoxification ability of the larvae. 3) Although data on the mining insects also supports the intimacy hypothesis, the impact of generalistic predators cannot be ruled out. 4) No correlation was found between utilized needle-age and host-plant specialization, possibly because small differences in apparency exist between young and old needles.

The data presented here supply very little support for the apparency and nutrition hypotheses. In their defense, we readily acknowledge that they were never developed as explanations for host specialization by phytophagous insects. For this reason, then, they are too general as we have presented them. They treat herbivorous insects as a uniform group and do not distinguish between feeding guilds. It has become more and more apparent that insect feeding guilds must be treated separately if we are adequately to understand plant-insect interactions (Mattson et al. 1988, Cornell 1989, Larsson 1989). The intimacy hypothesis, which distinguishes between insect feeding guilds, is the hypothesis given most support by the data obtained in our survey of the literature.

SUMMARY

The degree of host-plant specialization in needle-eating butterflies and moths (Lepidoptera), sawflies (Hymenoptera, Symphyta), and beetles (Coleoptera) occurring in Sweden has been examined based on data in the literature.

No general trend was found when all insects were considered. However, a closer examination of certain feeding guilds revealed that 1) polyphagy is predominant among chewing Lepidoptera,

2) monophagy among the mining microlepidoptera and all sawfly species, and 3) oligophagy among beetles.

No correlation was found between utilized needle-age and degree of host-plant specialization.

A comparison of the relative numbers of monophagous, oligophagous, and polyphagous insect species on the three common conifers (i.e. Scots pine, Norway spruce, and juniper) in Sweden showed that the frequencies of oligophagy are similar for each of the conifer species. However, the proportion of monophagous species was found to be significantly greater in juniper than in pine and spruce.

These results are discussed with reference to hypotheses concerning patterns of host specificity in herbivorous insects based on plant characteristics.

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LITERATURE CITED

- BENNETT, W.H. 1954. The effect of needle structure upon the susceptibility of hosts to the pine needle miner (*Exoteleia pinifoliella* (Chamb.) Lepidoptera: Gelechiidae). Can. Entomol. 86: 49-54.
- BERNAYS, E. and GRAHAM, M. 1988. On the evolution of host specificity in phytophagous arthropods. Ecology 69: 886-892.
- BOEVÉ, J.L. and PASTEELS, J.M. 1985. Modes of defence in nematine sawfly larvae. Efficiency against ants and birds. J. Chem. Ecol. 11: 1019-1036.
- BROWNE, F.G. 1968. Pests and Diseases of Forest Plantation Trees. Clarendon Press, Oxford.
- BURATTI, L., ALLAIS, J.P., GERI, C., and BARBIER, M. 1990. Abietane and primarane diterpene acid evolution in scots pine, *Pinus sylvestris*, needles in relation to feeding of the pine sawfly, *Diprion pini* L. Ann. Sci. For. 47: 161-171.
- CATES, R.G. 1980. Feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores: the effect of resource abundance and plant chemistry. Oecologia 46: 22-31.
- CLARIDGE, M.F. and WILSON, M.R. 1982. Insect herbivore guilds and species-area relationships: leafminers on British trees. Ecol. Entomol. 7: 19-30.
- CONNOR, E.F., FAETH, S.H., SIMBERLOFF, D., AND OPLER, P.A. 1980. Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. Ecol. Entomol. 5: 205-211.
- CORNELL, H.V. 1989. Endophagous-ectophagous ratios and plant defence. Evol. Ecol. 3: 64-76.
- DETHIER, V.G. 1954. Evolution of feeding preferences in phytophagous insects. Evolution 8: 33-54.
- EHRlich, P.R. and RAVEN, P.H. 1964. Butterflies and plants: a study in coevolution. Evolution 18: 586-608.

- EIDMANN, H.H. and KLINGSTRÖM, A. 1976. Skadegörare i skogen. LTs förlag, Borås.
- EISNER, T., JOHNESSEE, J.S., CARREL, J., HENDRY, L.B., and MEINWALD, J. 1974. Defensive use by an insect of a plant resin. *Science* 184: 996-999.
- ENGEL, H. 1939. Beiträge zur Biologie des Kiefernspanners (*Bupalus piniarius* L.). *Mitt. Forstw. Forstwiss.* 10: 51-64.
- ESCHERICH, K. 1931. Die Forstinsekten Mitteleuropas. Bd. 3. Paul Parey, Hamburg-Berlin.
- ESCHERICH, K. 1942. Die Forstinsekten Mitteleuropas. Bd. 5. Paul Parey, Berlin.
- FEENY, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565-581.
- FEENY, P. 1976. Plant apparency and chemical defense. *Recent Adv. Phytochem.* 10: 1-40.
- FORSTER, W. and WOHLFAHRT, T.A. 1971. Die Schmetterlinge Mitteleuropas. Bd. IV. Eulen (Noctuidae). Franckh'sche Verlagshandlung, Stuttgart.
- FOX, L.R. and MORROW, P.A. 1981. Specialization: species property or local phenomenon? *Science* 211: 887-893.
- FRAENKEL, G.S. 1959. The raison d'être of secondary plant substances. *Science* 129: 1466-1470.
- FÜHRER, E. 1967. Untersuchungen über die Ursachen der Befallsdisposition der europäischen Fichte gegenüber *Epiblemma tedella* Cl. (Lep.: Tortricidae). *Z. ang. Ent.* 59: 292-318.
- FUTUYMA, D.J. and PETERSON, S.C. 1985. Genetic variation in the use of resources by insects. *Annu. Rev. Entomol.* 30: 217-238.
- GHENT, A.W. 1959. Row-type oviposition in *Neodiprion* sawflies as exemplified by the European pine sawfly *N. sertifer* (Geoff.). *Can. J. Zool.* 37: 267-281.
- GRÖNBERG, G. 1903. Tallspinnaren, *Lasicampa pini* (L.), dess naturhistoria och fiender, samt medel mot densamma. *Tidskr. Skogshushålln.* 31: 195-214.
- HANNEMANN, H.-J. 1961. Kleinschmetterlinge oder Microlepidoptera. I. Tierwelt Deutschlands. vol. 48. VEB Gustav Fischer Verlag, Jena.
- HANNEMANN, H.-J. 1964. Kleinschmetterlinge oder Microlepidoptera. II. Tierwelt Deutschlands. vol 50. VEB Gustav Fischer Verlag, Jena.
- HANNEMANN, H.-J. 1977. Kleinschmetterlinge oder Microlepidoptera. I. Tierwelt Deutschlands. vol 63. VEB Gustav Fischer Verlag, Jena.
- HEDQVIST, K.-J. 1972. Östliche Kiefern-Buschhornblattwespe (*Gilpinia verticalis* Guss.), ein für Schweden neuer Forstschädling. *Entomol. Scand.* 3: 244-248.
- HELLRIGL, K.G. 1971. Die Bionomie der Europäischen *Monochamus*-arten (Coleop., Cerambycid.) und ihre bedeutung für die Forst- und Holzwirtschaft. *Pubbl. N 154 del Centro di Entomol. alpina e forestale del Consiglio Nazionale delle Ricerche. Estratto da REDIA, Firenze* 52: 367-510.

- HERING, E.M. 1951. Biology of the leafminers. Dr. W. Junk, The Hague.
- HODKINSON, I.D. and HUGHES, M.K. 1982. Insect Herbivory. Chapman and Hall, London.
- HOFFMEYER, S. 1966. De danske målere. Univ. förl., Århus.
- HOFMANN, C. 1941. Beiträge zur Bionomie des veilgrauen Kiefernspanners *Semiothisa liturata* Cl. Z. ang. Ent. 28: 324-334.
- HOLLOWAY, J.D. and HEBERT, P.D.N. 1979. Ecological and taxonomic trends in macrolepidopteran host plant selection. Biol. J. Linn. Soc. 11: 229-251.
- IKEDA, T., MATSAMURA, F., and BENJAMIN, D.M. 1977. Mechanisms of feeding discrimination between matured and juvenile foliage by two species of pine sawflies. J. Chem. Ecol. 3: 677-694.
- JAENIKE, J. 1978. On optimal oviposition behavior in phytophagous insects. Theor. Popul. Biol. 14: 350-356.
- KAROWE, D.N. 1989. Facultative monophagy as a consequence of prior feeding experience: behavioral and physiological specialization in *Colias philodice* larvae. Oecologia 78: 106-111.
- KNERER, G. and ATWOOD, C.E. 1973. Diprionid sawflies: polymorphism and speciation. Science 179: 1090-1099.
- LARSSON, S. 1989. Stressful times for the plant stress - insect performance hypothesis. Oikos 56: 277-283.
- LARSSON, S. and TENOW, O. 1980. Needle-eating insects and grazing dynamics in a mature Scots pine forest in Central Sweden. In Persson, T., ed. Structure and function of northern coniferous forests: an ecosystem study. Ecol. Bull. (Stockholm) 32: 269-306.
- LARSSON, S., BJÖRKMAN, C., and GREF, R. 1986. Responses of *Neodiprion sertifer* (Hym., Diprionidae) larvae to variation in needle resin acid concentration in Scots pine. Oecologia 70: 77-84.
- LEVINS, R. and MACARTHUR, R. 1969. An hypothesis to explain the incidence of monophagy. Ecology 50: 910-911.
- MARTIN, I.L. 1959. The bionomics of the pine bud moth, *Exoteleia dodocella* L. (Lepidoptera: Gelechiidae), in Ontario. Can. Entomol. 91: 5-14.
- MATTSON, W.J. and SCRIBER, J.M. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral concentrations, p. 105-146. In Slansky, F. and Rodriguez, J.G., eds. Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. John Wiley & Sons, New York.
- MATTSON, W.J., LAWRENCE, R.K., HAACK, R.A., HERMS, D.A., and CHARLES, P.-J. 1988. Defensive strategies of woody plants against different insect-feeding guilds in relation to plant ecological strategies and intimacy of associations with insects, p. 1-38. In Mattson, W.J., Levieux, J., and Bernard-Dagan, C., eds. Mechanisms of Woody Plant Defenses against Insects: Search for Pattern. Springer-Verlag, New York.
- MONRO, H.A.U. 1935. The ecology of the pine sawfly *Diprion simile* Htg. Unpubl. thesis. McGill Univ.

- MORROW, P.A., BELLAS, T.E., and EISNER, T. 1976. Eucalyptus oils in the defensive oral discharge of Australian sawfly larvae (Hymenoptera: Pergidae). *Oecologia* 24: 193-206.
- NIEMELÄ, P. 1983. Seasonal patterns in the incidence of specialism: macrolepidopteran larvae on Finnish deciduous trees. *Ann. Zool. Fenn.* 20: 199-202.
- NIEMELÄ, P. and NEUVONEN, S. 1983. Species richness of herbivores on hosts: how robust are patterns revealed by analysing published host plant lists. *Ann. Entomol. Fenn.* 49: 95-99.
- NIEMELÄ, P., MANNILA, R., and MÄNTSÄLÄ, P. 1982. Deterrent in Scots pine, *Pinus sylvestris*, influencing feeding behavior of the larvae of *Neodiprion sertifer* (Hymenoptera, Diprionidae). *Ann. Entomol. Fenn.* 48: 57-59.
- NG, D. 1988. A novel level of interactions in plant-insect systems. *Nature (Lond.)* 334: 611-613.
- NORDSTRÖM, F., WAHLGREN, E., and TULLGREN, A. 1935-41. Svenska fjärilar. Systematisk bearbetning av Sveriges storfjärilar, Macrolepidoptera. Nordisk familjeboks förlags AB, Stockholm.
- NUNBERG, M. 1939. Das massenhafte Vorkommen des Kiefernswärmers *Sphinx pinastri* L. in Polen. *Verh. VII. Inter. Kongr. f. Ent. Bd. 3:* 2033-2051.
- PATOCKA, J. 1960. Die Tannenschmetterlinge der Slowakei. Verlag der Slowakischen Akademie der Wissenschaften, Bratislava.
- POINTING, P.J. 1963. The biology and behavior of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.), in southern Ontario. II. Egg, larva and pupa. *Can. Entomol.* 95: 844-873.
- POWELL, J.A. 1980. Evolution of larval food preferences in microlepidoptera. *Annu. Rev. Entomol.* 25: 133-159.
- PRICE, P.W. 1983. Hypothesis on organization and evolution in herbivorous insect communities, p. 559-596. In Denno, R.F. and McClure, M.S., eds. *Variable Plants and Herbivores in Natural and Managed Systems*. Academic Press, New York.
- RHOADES, D.F. and CATES, R.G. 1976. Toward a general theory of plant antiherbivore chemistry. *Recent Adv. Phytochem.* 10: 168-213.
- ROOT, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43: 94-124.
- SCHNAIDER, Z. 1976. Atlas uszkodzen drzew i krzewow. Panstwowe Wydawnictwo Naukowe, Warszawa.
- SCHWENKE, W. 1953. Beiträge zur Bionomie der Kiefernspanner *Bupalus piniarius* L. und *Semiothisa liturata* Cl. auf bionötischer Grundlage. *Beitr. Entomol.* 3: 168-206.
- SCHWENKE, W. 1974. Die Forstschädlinge Europas. Bd. 2. Käfer. Paul Parey, Hamburg-Berlin.
- SCHWENKE, W. 1978. Die Forstschädlinge Europas. Bd. 3. Schmetterlinge. Paul Parey, Hamburg-Berlin.
- SCHWENKE, W. 1982. Die Forstschädlinge Europas. Bd. 4. Hautflügler und Zweiflügler. Paul Parey, Hamburg-Berlin.

- SCHWERDTFEGGER, F. 1970. Waldkrankheiten. Aufl. 3. Paul Parey, Hamburg-Berlin.
- SHAW, M.R. 1984. Insects associated with birch. Proc. R. Soc. Edinb. Sect. B/Biol. Sci. 85: 169-181.
- SINGER, M.C. 1983. Determinants of multiple host use by a phytophagous insect population. Evolution 37: 389-403.
- SOUTHWOOD, T.R.E., MORAN, V.C., and KENNEDY, C.E.J. 1982. The assessment of arboreal insect fauna: comparison of knockdown sampling and faunal lists. Ecol. Entomol. 7: 331-340.
- SPULER, A. 1913. Die sogenannten Kleinschmetterlinge Europas. E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart.
- STRONG, D.R., ed. 1988. Insect host range. Ecology 69: 885-915.
- TAMM, C.O. 1955. Studies on forest nutrition. I. Seasonal variation in the nutrient contents of conifer needles. Medd. Statens Skogsforskningsinst. 45(5). 34 p.
- THOMAS, B.R. 1970. Modern and fossil plant resins, p. 59-79. In Harborne, J.B., ed. Phytochemical Phylogeny. Academic Press, London.
- TRÄGÅRDH, I. 1915. Bidrag till kännedomen om tallens och granens fiender bland småfjärilarna. Medd. Statens Skogsförsöksanst. 12: 71-132.
- TRÄGÅRDH, I. 1939. Sveriges skogsinsekter. Gebers förlag, Stockholm.
- VAN VALEN, L. and GRANT, P.R. 1970. Variation and niche width reexamined. Am. Nat. 104: 589-590.
- WINTER, T.G. 1983. A catalogue of phytophagous insects and mites on trees in Great Britain. For. Comm. Edinb.

APPENDIX A

Host-plant utilization, host range, utilized tissue-age, and feeding mode of microlepidoptera feeding on Swedish conifers. Information on the occurrence of individual species in Sweden was taken from Gustafsson (1979); reference not provided.

Family Species	Host plants ¹	Host range ²	Tissue age ³	Feeding mode ⁴	References
Yponomeutidae					
<i>Argyresthia abdominalis</i> Zell.	Jun	Mono	?	M	1,2
<i>A. arceuthina</i> Zell.	Jun	Mono	?	BM	1,2
<i>A. aurulentella</i> Stt.	Jun	Mono	?	M	1,2
<i>A. dilectella</i> Zell.	Jun	Mono	?	M	1,2
<i>A. fundella</i> F.v. Rösl.	Pic, (Abi)	Olig	Y+O	M	2,4,5
<i>A. glabratella</i> Zell.	Pic	Mono	Y	M	1,4
<i>Blastotere bergiella</i> Ratz.	Pic	Mono	Y	M	4
<i>Cedestis gysseleniella</i> Zell.	Pin, (Abi)	Olig	O	M	1,4,6
<i>C. subfasciella</i> Steph.	Pin	Mono	O	M	1,4,6,7
<i>Ocnerostoma friesei</i> Svensson	Pin	Mono	?	M	1,7
<i>O. pinariella</i> Zell.	PIN, Jun	OligJ	?	M	1,4,7,10
Gelechiidae					
<i>Dichomeris juniperella</i> L.	Jun	Mono	?	C	1
<i>D. marginella</i> F.	Jun	Mono	O?	C	1,3
<i>Exoteleia dodocella</i> L.	Pin	Mono	Y(O)	M	1,4,10,11
Momphidae					
<i>Batrachedra pinicolella</i> Zell.	Pic, Pin	Olig	?	M	1,3
Tortricidae					
<i>Acleris abietana</i> Hb.	PIN	Olig	Y+O	C	1,4,8,12
<i>A. hyemana</i> Haw.	PIN, D	Poly	?	C	1,8
<i>Aphelia paleana</i> Hb.	Pic, H	Poly	?	?	1,8
<i>A. viburnana</i> Den. & Schiff.	PIN, D, H	Poly	Y	C	1,4,8
<i>Archips oporana</i> L.	PIN, Jun	Olig	Y+O	C	1,4,6,12
<i>A. podana</i> Scop.	PIN, D	Poly	Y+O	C	1,4,12
<i>A. rosana</i> L.	Pic, D, H	Poly	?	C	1,4,5,10
<i>Blastesthia posticana</i> Zett.	Pin	Mono	Y	M	1,4,10
<i>B. turionella</i> L.	Pin, H	Poly	Y	M	1,4
<i>Clepsis senecionana</i> Hb.	PIN, H	Poly	?	M	1
<i>Cnephasia incertana</i> Treit.	PIN, H	Poly	?	M+C?	4,8
<i>Epinotia caprana</i> F.	Pin, D	Poly	?	C	1,8
<i>E. fraternana</i> Haw.	PIN	Olig	O	M	1,4,8
<i>E. nanana</i> Treit.	Pic	Mono	O	M	1,4,10
<i>E. nigricana</i> H.-S.	Abi, (Pic)	Olig	Y	BM	1,4
<i>E. pygmaeana</i> Hb.	Pic, (Abi)	Olig	Y(O)	M+C	1,4
<i>E. rubiginosana</i> H.-S.	Pin	Mono	?	M+C	1,8,10

APPENDIX A continued

Family Species	Host plants ¹	Host range ²	Tissue age ³	Feeding mode ⁴	References
<i>E. subsequana</i> Haw.	Abi, Pic	Olig	Y	M	1,4
<i>E. tedella</i> Cl.	Pic	Mono	(Y)O	M	1,4,13
<i>Olethreutus lacunana</i> Den. & Schiff.	Pic, D, H	Poly	?	C	1,4,8
<i>Pandemis cinnamomeana</i> Treit.	PIN, D, H	Poly	Y+O	C	1,3,4,12
<i>Philedone gerningana</i> Den. & Schiff.	Pic, D, H	Poly	?	C	1,3,8
<i>Philedomides lunana</i> Thnbg.	PIN, D, H	Poly	?	C	1,8
<i>Ptycholoma lecheana</i> L.	Pic, D	Poly	?	C	1,4
<i>Rhyacionia buoliana</i> Den. & Schiff.	Pin	Mono	Y(O)	M(BM)	1,4,14
<i>R. duplana</i> Hb.	Pin	Mono	Y	BM	1,4
<i>R. pinicolana</i> Doubl.	Pin	Mono	Y	BM	1,4
<i>R. pinivorana</i> Zell.	Pin	Mono	Y	BM	1,4
<i>Spilonota laricana</i> Hein.	Lar, (Pic)	Olig	Y	C→M	1,4
<i>Zeiraphera diniana</i> Guen.	Pic, Pin	Ol*	Y	C(BM)	1,4,10
<i>Z. ratzeburgiana</i> Ratz.	PIN	Olig	Y	C(BM)	1,4
Cochylidae					
<i>Aethes rutilana</i> Hb.	Jun	Mono	?	C	1,9
Pyralidae					
<i>Dioryctria abietella</i> Den. & Schiff.	PIN	Olig	Y	BM	4
<i>D. mutata</i> Fuchs	Pin	Mono	Y	BM	1,4
<i>D. schuetzella</i> Fuchs	Pic, Abi	Olig	Y	C	1,4

* The Picea-Pinus-race that might be a species (two other races exhibit other host plant preferences)

¹ Abi = *Abies*, Lar = *Larix*, Pic = *Picea*, Pin = *Pinus*, and Jun = Juniper; PIN = several spp. within Pinaceae; D indicates that the insect species utilizes one or several deciduous trees or bushes; H indicates that it utilizes one or several herbaceous plant species.

² Mono = monophagous, Olig = oligophagous, OligJ = feeding on some member of Pinaceae and Juniper, and Poly = polyphagous.

³ Y = young tissue (buds and current-year needles) and O = old tissue (1-year-old or older needles).

⁴ C = chewing, M = mining in needles, BM = mining in buds (and/or shoots). Arrows under Tissue-age and Feeding mode indicate that the insect shifts from x→y when it becomes older.

REFERENCES: 1) Winter (1983), 2) Escherich (1931), 3) Spuler (1913), 4) Schwenke (1978), 5) Schnaider (1976), 6) Trägårdh (1915), 7) Hannemann (1977), 8) Hannemann (1961), 9) Hannemann (1964), 10) Browne (1968), 11) Martin (1959), 12) Patocka (1960), 13) Führer (1967), and 14) Pointing (1963).

APPENDIX B

Host-plant utilization, host range, utilized tissue-age, and feeding mode of macrolepidoptera feeding on Swedish conifers. Information on the occurrence of individual species in Sweden was taken from Elmqvist et al. (1977); reference not provided.

Family Species	Host plants ¹	Host range ²	Tissue age ³	Feeding mode ⁴	References
Geometridae					
<i>Biston betularia</i> L.	Lar, Pic, D, H	Poly	?	C	1, 2
<i>Bupalus piniarius</i> L.	PIN	Olig	Y+O	C	1, 3, 4
<i>Deileptenia ribeata</i> Cl.	PIN, D	Poly	?	C	1, 3
<i>Ectropis bistortata</i> Goeze	PIN, D, H	Poly	Y?	C	1, 3
<i>Entephria caesiata</i> Den. & Schiff.	Pin, D, H	Poly	?	C	1, 2
<i>Eupithecia conterminata</i> Zell.	Pic	Mono	O?	C	2, 5
<i>E. indigata</i> Hb.	PIN	Olig	Y	C	1, 3
<i>E. intricata</i> Zett.	Jun	Mono	?	C	1, 2, 5
<i>E. lanceata</i> Hb.	PIN	Olig	Y	C	2, 3
<i>E. laricata</i> Fr.	Lar, Jun	MonoJ	Y?	C	1, 2, 3
<i>E. nanata</i> Hb.	PIN, H	Poly	?	C	1, 2, 6
<i>E. pusillata</i> Den. & Schiff.	PIN	Olig	Y+O	C	2, 3, 7
<i>Gymnoscelis rufifasciata</i> Haw.	Pic, Pin, D, H	Poly	?	C	1, 2
<i>Hydriomena furcata</i> Thnbg.	Pic, Pin, D, H	Poly	?	C	1, 3
<i>Hylaea fasciaria</i> L.	Pin, (Pic), D	Poly	O	C	1, 3, 8
<i>Odontopera bidentata</i> Cl.	Pin, Abi, H	Poly	O	C	1, 2, 3
<i>Operophtera brumata</i> L.	Pic, D	Poly	Y	C	1, 2, 3
<i>O. fagata</i> Scharf.	Pic, D	Poly	Y	C	1, 2, 3
<i>Peribatodes secundaria</i> Esp.	Pic, Pin	Olig	(Y)O	C	1, 3, 7
<i>Perizoma didymata</i> L.	Pic, Pin, H	Poly	?	C	1, 2
<i>Semiothisa liturata</i> Cl.	PIN, Jun	OligJ	O	C	1, 9, 10
<i>S. signaria</i> Hb.	PIN	Olig	O	C	1, 3
<i>Thera cognata</i> Thnbg.	Jun	Mono	?	C	1, 2
<i>T. firmata</i> Hb.	Pin, Jun	MonoJ	O	C	1, 3, 11
<i>T. juniperata</i> L.	Pic, Jun	MonoJ	?	C	1, 3
<i>T. obeliscata</i> Hb.	PIN, Jun	OligJ	?	C	1, 3
<i>T. variata</i> Den. & Schiff.	PIN, Jun	OligJ	Y+O	C	2, 3, 8
Lymantriidae					
<i>Lymantria dispar</i> L.	Lar, Pin, D, H	Pol*	Y	C	1, 3, 12
<i>L. monacha</i> L.	PIN, D	Poly	Y+O**	C	1, 3, 12
<i>Orgyia antiqua</i> L.	PIN, D, H	Poly	Y(O)	C	1, 2, 3
Noctuidae					
<i>Acronicta rumicis</i> L.	Pic, D, H	Poly	?	C	1, 2, 13

APPENDIX B continued

Family Species	Host plants ¹	Host range ²	Tissue age ³	Feeding mode ⁴	References
<i>Blepharita adusta</i> Esp.	Pic, Pin, H	Poly	0	C	1, 13
<i>Ceramica pisi</i> L.	Lar, Pic, D, H	Poly	?	C	1, 3, 13
<i>Panolis flammea</i> Den. & Schiff.	PIN, (Jun), D	Poly	Y+0	C	1, 3, 14
<i>Panthea coenobita</i> Esp.	PIN	Olig	0	C	2, 3, 7
Lasiocampidae					
<i>Dendrolimus pini</i> L.	PIN	Olig	Y+0	C	3, 15
<i>Lasiocampa quercus</i> L.	PIN, D, H	Pol*	?	C	1, 3
<i>Macrothylacia rubi</i> L.	Pic, D, H	Poly	?	C	1, 2
<i>Selenephra lunigera</i> Esp.	PIN	Olig	?	C	2, 3
Sphingidae					
<i>Hyloicus pinastri</i> L.	PIN	Olig	?	C	1, 3, 16

* Possibly ecological races with respect to host plant choice

** If on spruce, feeds as young larvae on young tissue and later as old larvae on old tissue; if on pine, vice versa

¹ Abi = *Abies*, Lar = *Larix*, Pic = *Picea*, Pin = *Pinus*, and Jun = Juniper; PIN = several spp. within Pinaceae; D indicates that the insect species utilizes one or several deciduous trees or bushes; H indicates that it utilizes one or several herbaceous plant species.

² Mono = monophagous, Olig = oligophagous, OligJ = feeding on some member of Pinaceae and Juniper, and Poly = polyphagous.

³ Y = young tissue (buds and current-year needles) and 0 = old tissue (one-year-old or older needles).

⁴ C = chewing, M = mining in needles, BM = mining in buds (and/or shoots). Arrows under Tissue-age and Feeding mode indicate that the insect shifts from x→y when it becomes older.

REFERENCES: 1) Winter (1983), 2) Nordström et al. (1941), 3) Schwenke (1978), 4) Engel (1939), 5) Hoffmeyer (1966), 6) Browne (1968), 7) Patocka (1960), 8) Escherich (1931), 9) Schwenke (1953), 10) Hofmann (1941), 11) Larsson and Tenow (1980), 12) Trägårdh (1939), 13) Forster and Wohlfahrt (1971), 14) Schwerdtfeger (1970), 15) Grönberg (1903), and 16) Nunberg (1939).

APPENDIX C

Host-plant utilization, host range, utilized tissue-age, and feeding mode of Hymenoptera, Symphyta feeding on Swedish conifers. Information on the occurrence of individual species in Sweden was taken from Hedqvist (pers. comm.).

Family Species	Host plants ¹	Host range ²	Tissue age ³	Feeding mode ⁴	References
Pamphiliidae					
<i>Acantholyda erythrocephala</i> L.	Pin	Mono	(Y)O	C	1,2
<i>A. flaviceps</i> Retz.	Pin	Mono	Y+O	C	2
<i>A. posticalis</i> Mats.	Pin	Mono	Y+O*	C	1,2
<i>Cephalcia abietis</i> L.	Pic	Mono	(Y)O	C	2
<i>C. arvensis</i> Panzer	Pic	Mono	Y+O	C	2
<i>C. erythrogastra</i> Htg.	Pic	Mono	Y+O	C	3
<i>C. falleni</i> Dalm.	Pic	Mono	Y+O	C	2
Diprionidae					
<i>Diprion butovitschi</i> Hedqv.	Pin	Mono	Y+O	C	2,3
<i>D. pini</i> L.	Pin	Mono	Y+O	C	1,2,4
<i>D. simile</i> Htg.	Pin	Mono	Y+O	C	1,2,5
<i>Gilpinia frutetorum</i> F.	Pin	Mono	Y+O	C	1,2,4
<i>G. hercyniae</i> Htg.	Pic	Mono	(Y)O	C	1,2
<i>G. pallida</i> Klug	Pin	Mono	Y+O	C	1,2
<i>G. verticalis</i> Guss.	Pin	Mono	Y+O	C	2,6
<i>G. virens</i> Klug	Pin	Mono	Y+O	C	1,2
<i>Microdiprion pallipes</i> Fall.	Pin	Mono	Y+O	C	1,2,7
<i>Monoctenus juniperi</i> L.	Jun	Mono	Y+O	C	1,2
<i>M. obscuratus</i> Htg.	Jun	Mono	Y+O	C	2
<i>M. subconstrictus</i> Thoms.	Jun	Mono	Y+O	C	2
<i>Neodiprion sertifer</i>	Pin	Mono	O	C	1,2,4
Tenthredinidae					
<i>Pachynematus montanus</i> Zadd.	Pic	Mono	Y+O	C	1,2
<i>P. scutellatus</i> Htg.	Pic	Mono	Y+O	C	1,2
<i>Pristiphora abietina</i> Christ.	Pic	Mono	Y+O	C	1,2
<i>P. ambigua</i> Fall.	Pic	Mono	Y+O	C	1,2
<i>P. amphibola</i> Först.	Pic	Mono	Y+O	C	1,2
<i>P. compressa</i> Htg.	Pic	Mono	Y+O	C	1,2
<i>P. saxesenii</i> Htg.	Pic	Mono	Y+O	C	1,2
<i>P. subarctica</i> Forssl.	Pic	Mono	Y+O	C	1,2

* Two forms, one feeding on young tissue and the other on old tissue

¹ Abi = *Abies*, Lar = *Larix*, Pic = *Picea*, Pin = *Pinus*, and Jun = Juniper; PIN = several spp. within Pinaceae; D indicates that the insect species utilizes one or several deciduous trees or bushes; H indicates that it utilizes one or several herbaceous plant species.

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⁴ C = chewing, M = mining in needles, BM = mining in buds (and/or shoots). Arrows under Tissue-age and Feeding mode indicate that the insect shifts from x→y when it becomes older.

REFERENCES: 1) Winter (1983), 2) Schwenke (1982), 3) Hedqvist (pers. comm.), 4) Escherich (1931, 1942) 5) Monro (1935), 6) Hedqvist (1972), and 7) Eidmann and Klingström (1976).

APPENDIX D

Host-plant utilization, host range, utilized tissue-age, and feeding mode of Coleoptera feeding on Swedish conifers. Information on the occurrence of individual species in Sweden was taken from Ehnström (pers. comm.).

Family Species	Host plants ¹	Host range ²	Tissue age ³	Feeding mode ⁴	References
SPECIES IN WHICH LARVAE FEED ON NEEDLES AND/OR BUDS					
Anobiidae					
<i>Dryophilus pusillus</i> Gyll.	PIN	Olig	Y	C	1,2
Curculionidae					
<i>Anthonomus phyllocola</i> Hrbst.	Pin, (Pic)	Olig	Y?	C	1,2
<i>A. pinivorax</i> Silfverb.	Pic, Pin	Olig	Y	C	1,2
<i>Brachonyx pineti</i> Payk.	Pin	Mono	?	C	1,2
SPECIES IN WHICH IMAGINES FEED ON NEEDLES AND/OR BUDS					
Scarabaeidae					
<i>Amphimallom solstitiale</i> L.	Pin, D	Poly	?	C	2
Cerambycidae					
<i>Monochamus galloprovincialis</i> Ol.	Pin, (Pic)	Olig	?	C	1,2,3
<i>M. sutor</i> L.	Pic, Pin	Olig	?	C	1,2
Chrysomelidae					
<i>Calomicrus pinicola</i> Duft.	Pin, (PIN)	Olig	O	C	1,2
<i>Cryptocephalus pini</i> L.	PIN, (Jun)	OligJ	Y?	C	1,2
<i>C. quadripustulatus</i> Gyll.	PIN	Olig	?	C	1,2
<i>Syneta betulae</i> F.	Pic, D	Poly	Y	C	1,2
Curculionidae					
<i>Anthonomus phyllocola</i> Hrbst.	Pin, (Pic)	Olig	?	C	1,2
<i>A. pinivorax</i> Silfverb.	Pic, Pin	Olig	Y?	C	1,2
<i>Brachonyx pineti</i> Payk.	Pin	Mono	?	C	1,2
<i>Brachyderes incanus</i> L.	Pin	Mono	?	C	1,2
<i>Otiorrhyncus leiodopterus</i> F.	PIN	Olig	?	C	1,2
<i>O. nodosus</i> Mull.	Pin	Mon?	?	C	1
<i>O. scaber</i> L.	PIN	Olig	?	C	2
<i>O. singularis</i> L.	PIN, D, H	Poly	Y(O?)	C	2,4
<i>Philopodon plagiatus</i> Schall.	Pin, Pic, D, H	Poly	?	C	1
<i>Strophosoma capitatum</i> de G.	Pin, Pic, D, H	Poly	?	C	1
<i>S. melanogrammum</i> Forst.	Pin, Pic, D, H	Poly	?	C	1

¹ Abi = *Abies*, Lar = *Larix*, Pic = *Picea*, Pin = *Pinus*, and Jun = Juniper; PIN = several spp. within Pinaceae; D indicates that the insect species utilizes one or several deciduous trees or bushes; H indicates that it utilizes one or several herbaceous plant species.

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³ Y = young tissue (buds and current-year needles) and O = old tissue (one-year-old or older needles).

⁴ C = chewing, M = mining in needles, BM = mining in buds (and/or shoots). Arrows under Tissue-age and Feeding mode indicate that the insect shifts from x→y when it becomes older.

REFERENCES: 1) Ehnström (pers. comm.), 2) Schwenke (1974), 3) Hellrigl (1971), and 4) Browne (1968).