



United States
Department of
Agriculture

Forest Service

Northeastern Forest
Experiment Station

General Technical
Report NE-153



FOREST INSECT GUILDS: PATTERNS OF INTERACTION WITH HOST TREES

Edited by:

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Abakan, Siberia, U.S.S.R.
August 13-17, 1989



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COVER

The insects on the cover are all European dendrophilous species: *Nymphalis polychloros* (Nymphalidae), *Cimbex femorata* (Cimbicidae), and *Dasyneura rozkovi* (Cecidomyiidae). Mr. Victor Bakhtin (Krasnoyarsk, U.S.S.R.) was the artist.

**FOREST INSECT GUILDS:
PATTERNS OF INTERACTION WITH HOST TREES**

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Proceedings of a Joint IUFRO Working Party Symposium
Abakan, Siberia, U.S.S.R.
August 13-17, 1989

General Technical Report NE-153

U.S. Department of Agriculture, Forest Service
Northeastern Forest Experiment Station
100 Matsonford Rd., Suite 200
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PREFACE

This proceedings is the result of a symposium held in Abakan, Siberia, U.S.S.R., August 13-17, 1989. It was organized under the guidelines of the International Union of Forestry Research Organizations. Five IUFRO Working Parties convened to achieve this exchange: S2.07-01 (Seed and Cone Insects), S2.07-05 (Bark Beetles), S2.07-06 (Population Dynamics), S2.07-08 (Gall Midges), and S2.05-06 (Mechanisms of Tree Resistance to Insects).

The papers are arranged in three sections according to their subject matter: 1) general or theoretical papers, 2) highly mobile, external phytophages, and 3) poorly mobile, internal phytophages. The breakdown by external and internal feeding strategy was done to recognize that therein lies a fundamental dichotomy between the kinds of defenses employed by trees against these two broad classes of feeders. This is not to imply, however, that within each general class there are not still substantial guild-to-guild differences in plant defenses. There are. This was the subject of the symposium.

This publication is the result of a joint effort between the Northeastern Forest Experiment Station and the North Central Forest Experiment Station, USDA Forest Service. It is symbolic of their strong support for IUFRO goals of facilitating worldwide research on the significant problems facing forest resource managers.

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of the V.N. Sukachev Institute of Forest and Wood, Siberian Branch of the U.S.S.R. Academy of Science, and the U.S.S.R. State Committee for Forests. Without their unflagging commitment this symposium could not have materialized. In particular, Dr. A. Isaev, Minister of State Forests, provided crucial sponsorship.

We also thank Mrs. Svetlana Pusir for her very significant technical assistance.

Over the course of more than one year, many people helped to bring this printed volume to fruition. To them, we are especially indebted because they donated substantial time from their busy schedules. We recognize them in alphabetical order: Bruce A. Birr, Robert A. Haack, Robert K. Lawrence, and William A. Main. In addition, we thank Marilyn Brouwer and Robin Bolig for their exacting efforts in the technical editing and computer formatting of the entire volume.

Finally, we thank the INRA Station de Zoologie Forestiere, Ardon-45160 Olivet, France, for providing work space and support while editorial chores (of WJM) were being executed.

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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.

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

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 \geq 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

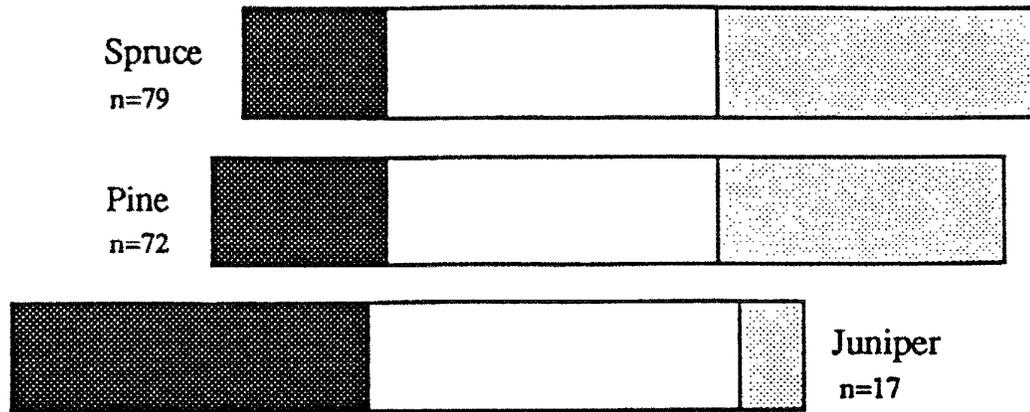


Figure 1. Relative proportions (%) of mono-█, oligo-□, and polyphagous █ insect species on each of the three conifer species. Each bar equals 100%. n = number of insect species.

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.

ACKNOWLEDGMENTS

We would like to thank Bengt Ehnström and Karl-Johan Hedqvist for providing information on the biology of the insects. We also thank Hubertus H. Eidmann, J. Mark Scriber, Donald Strong, and David Tilles for helpful comments on the manuscript.

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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. aurentella</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 gysselella</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. piniariella</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 histortata</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	O	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+O	C	1, 3, 14
<i>Panthea coenobita</i> Esp.	PIN	Olig	O	C	2, 3, 7
Lasiocampidae					
<i>Dendrolimus pini</i> L.	PIN	Olig	Y+O	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 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 to 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)0	C	1,2
<i>A. flaviceps</i> Retz.	Pin	Mono	Y+0	C	2
<i>A. posticalis</i> Mats.	Pin	Mono	Y+0*	C	1,2
<i>Cephalcia abietis</i> L.	Pic	Mono	(Y)0	C	2
<i>C. arvensis</i> Panzer	Pic	Mono	Y+0	C	2
<i>C. erythrogastra</i> Htg.	Pic	Mono	Y+0	C	3
<i>C. falleni</i> Dalm.	Pic	Mono	Y+0	C	2
Diprionidae					
<i>Diprion butovitschi</i> Hedqv.	Pin	Mono	Y+0	C	2,3
<i>D. pini</i> L.	Pin	Mono	Y+0	C	1,2,4
<i>D. simile</i> Htg.	Pin	Mono	Y+0	C	1,2,5
<i>Gilpinia frutetorum</i> F.	Pin	Mono	Y+0	C	1,2,4
<i>G. hercyniae</i> Htg.	Pic	Mono	(Y)0	C	1,2
<i>G. pallida</i> Klug	Pin	Mono	Y+0	C	1,2
<i>G. verticalis</i> Guss.	Pin	Mono	Y+0	C	2,6
<i>G. virens</i> Klug	Pin	Mono	Y+0	C	1,2
<i>Microdiprion pallipes</i> Fall.	Pin	Mono	Y+0	C	1,2,7
<i>Monoctenus juniperi</i> L.	Jun	Mono	Y+0	C	1,2
<i>M. obscuratus</i> Htg.	Jun	Mono	Y+0	C	2
<i>M. subconstrictus</i> Thoms.	Jun	Mono	Y+0	C	2
<i>Neodiprion sertifer</i>	Pin	Mono	0	C	1,2,4
Tenthredinidae					
<i>Pachynematus montanus</i> Zadd.	Pic	Mono	Y+0	C	1,2
<i>P. scutellatus</i> Htg.	Pic	Mono	Y+0	C	1,2
<i>Pristiphora abietina</i> Christ.	Pic	Mono	Y+0	C	1,2
<i>P. ambigua</i> Fall.	Pic	Mono	Y+0	C	1,2
<i>P. amphibola</i> Först.	Pic	Mono	Y+0	C	1,2
<i>P. compressa</i> Htg.	Pic	Mono	Y+0	C	1,2
<i>P. saxeseni</i> Htg.	Pic	Mono	Y+0	C	1,2
<i>P. subarctica</i> Forssl.	Pic	Mono	Y+0	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.

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 (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) 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	0	C	1,2
<i>Cryptocephalus pini</i> L.	PIN, (Jun)	Olig ^J	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 leoidopterus</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>Philopedon plagiatum</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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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).

SAWFLIES AND PONDEROSA PINE: HYPOTHETICAL RESPONSE SURFACES FOR PINE GENOTYPE, ONTOGENIC STAGE, AND STRESS LEVEL

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INTRODUCTION

Patterns that occur in nature are the result of a complex set of current and historical factors that interact with one another and the adaptive plasticity of plants. Scientists are forced to assess such processes on the basis of series of "snapshots" over a relatively short time that represent only part of the grand pattern. In the case of insects interacting with forest trees, there are dozens of environmental and host plant factors that could be the key factor responsible for the patterns we observe. Because of the high experimental standards of research and the many potentially important factors, scientists tend to construct models by which to test specific hypotheses about key factors. This methodology produces a body of knowledge about a particular factor (e.g. moisture stress) that does not necessarily integrate well with the body of knowledge about a second factor (e.g. genetic resistance). These disjoint sets of data encourage scientists to think in terms of components, and that leads them to draw conclusions about single factors, in isolation from many other important factors. Such conclusions can be misleading.

Given the single-factor focus of the scientific community, it is not surprising that inconsistencies and apparent contradictions are abundant. For example, despite considerable research effort, no clear pattern has emerged to determine the role of environmental stress in creating insect outbreaks (Larsson 1989). Drought or poor site conditions have been correlated with outbreaks of forest insects (Mattson and Haack 1987a, 1987b). In the specific case of sawflies (Hymenoptera: Diprionidae), many outbreaks have been correlated with drought conditions (Kapler and Benjamin 1960, McLeod 1970, Averill and Fowler 1973, Knerer and Atwood 1973, Larsson and Tenow 1984). One hypothesis explaining this phenomenon is that environmental stress changes the host plants and thereby increases herbivore performance in some way. Tests of this hypothesis for sawflies have not been consistently supportive (McCullough and Wagner 1987, Craig et al. 1991, Wagner and Frantz 1990). Meyers (1988) and Larsson (1989) have suggested that the general hypothesis that host plant stress causes outbreaks is "still very much open to debate." Careful reviews of the literature which stratify the evidence by insect feeding guilds clarify the question for some guilds such as bark beetles, but not for others such as defoliators (Larsson and Tenow 1984, Larsson 1989). The recent studies cited above might lead us to conclude that there is no relationship between stress and insect outbreaks, but what about all the previous correlative evidence and the anecdotal evidence that stress is related to insect outbreaks? It seems reasonable to hypothesize that stress is important under some circumstances and not others. The critical point is that several factors interact to create the particular insect/tree pattern we observe

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

at any given moment. When we consider multiple factors simultaneously, we can better define those instances in which a factor will or will not be influential.

In this paper I discuss the general evidence from the literature and my preliminary experimental evidence that at least three variables (genotype, ontogeny, and stress) influence the population parameters of *Neodiprion* spp. (Hymenoptera: Diprionidae), which feed on ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. I also present some hypothetical response functions for these single factors. Then I generate some three-dimensional figures that illustrate how two individual variables could interact to create a response surface. Finally, I illustrate how it is possible to generate from very realistic univariate response functions complex response surfaces which could explain otherwise apparently contradictory results.

ROLE OF GENOTYPE IN SAWFLY-PONDEROSA PINE INTERACTION

For most plants there is a range of natural suitability for insects that appears to be genetically controlled. Significant genotype variation in forest trees to insects has been identified for bark beetles (Stark 1965, Callahan 1966, Berryman 1972, Smith 1972, Smith 1975), scales and aphids (Hoff and McDonald 1977, Mattson et al. 1988), pitch midge (Hoff 1988), pine weevils (Hall 1959, King 1971, Wilkinson 1979, Harris et al. 1983, Brooks et al. 1987), shoot moths (Hertel and Benjamin 1975, Charles et al. 1982), cone insects (Askew et al. 1985), defoliators (Tigner and Mason 1973, Genys and Harman 1976, McDonald 1979, 1982, Fogal et al. 1982), and pine sawflies (Arend et al. 1961, Wilson 1966, Wright et al. 1967, Henson et al. 1970). Interestingly, Mattson et al. (1988) argue that there is relatively little evidence for genetic resistance to free-feeding defoliators. Part of their data is based on examination of the susceptibility of trees in range-wide provenance plantations. It may be that the procedures used for creating the provenances trials resulted in inadvertent selection of only susceptible genotypes. For example, it may be that the provenance collection sites were areas with relatively low defoliator pressure and hence a low selection for insect resistance. At any rate, the evidence suggests that there is some genotypic variation in insect susceptibility for most tree species.

For the past 3 years I have been attempting to identify individual trees that exhibit phenotypic resistance to pine sawflies. My basic procedure has been to identify unattacked trees within sawfly outbreak areas. These phenotypically resistant trees have then been paired with nearby phenotypically susceptible trees. To date 10 pairs of trees have been identified. I have bioassayed the trees by caging sawflies on them and measuring stage-specific survival. Following Hanover (1975), seed has been collected from 14 of the 20 trees and half-sib families have been established. The performance of sawflies on the maternal trees of the 14 half-sib families is presented in Fig. 1. Whether the traits that influence susceptibility to sawflies in the maternal trees are inherited by the progeny (half-sibs) has yet to be determined, but it is clear that there is considerable variation in sawfly resistance in the maternal phenotype (2 to 65 percent sawfly survival), and this is an indication of genetic resistance (Bingham 1966, McDonald 1979).

On the basis of the previously cited literature and my preliminary findings, I believe that there is substantive genetic variation in ponderosa pine resistance to herbivores. In other words, when all other factors are held constant, there can be considerable variation in insect performance based on plant genotype alone. For example, I observed a thirtyfold variation in sawfly survival among different ponderosa pine individuals (Fig. 1). As yet it cannot be established that all of this variation is the result of genetic factors, but it is highly probable that some of the variation is due to genetic factors. Greater knowledge about the genetic variation of ponderosa pine could greatly clarify our understanding of how host plants and herbivores interact.

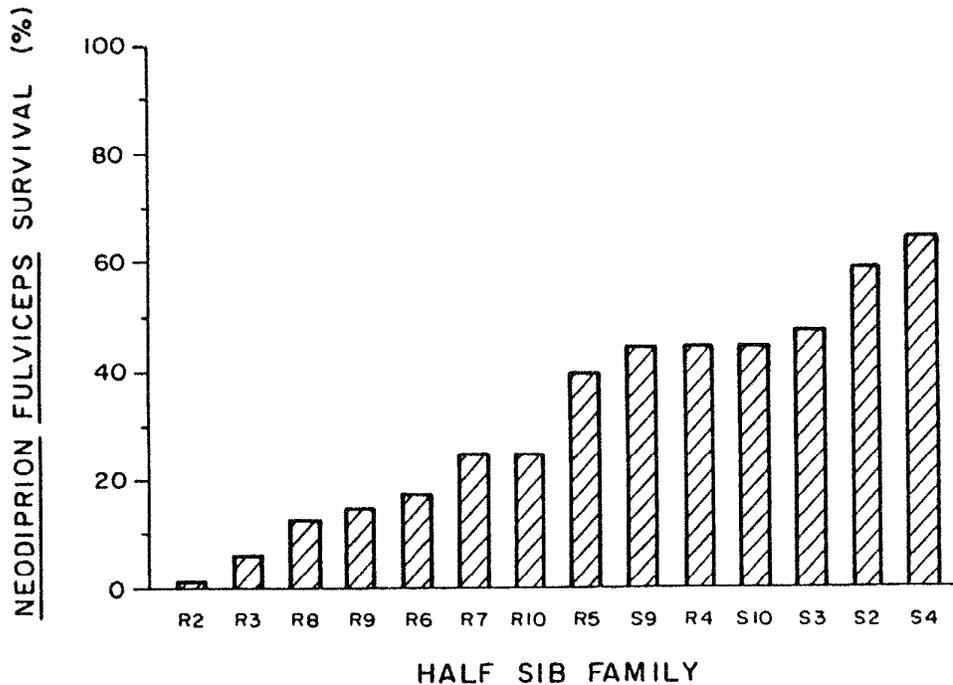


Figure 1. Total generational survival of *Neodiprion fulviceps* on maternal ponderosa pine trees from which 14 half-sib families have been established.

ROLE OF ONTOGENY IN SAWFLY-PONDEROSA PINE INTERACTIONS

Many plants show age-related changes in susceptibility to attack by specific insects. Some insect species attack juvenile trees, such as sawflies on willows (Craig et al. 1986), cynipid wasps on oaks (Washburn and Cornell 1981, Frankie and Morgan 1984), and a chrysomelid beetle on cottonwood (Kearsley and Whitham 1989). Other insects attack primarily mature trees: budworms (Blais 1958), spruce beetles (Schmidt and Frye 1977, Hard 1985), and *Pemphigus* aphids (Kearsley and Whitham 1989). Pine sawflies commonly show age-related preferences on their pine hosts (Knight and Heikkinen 1980, Coulson and Witter 1984, Wagner et al. 1986) and generally prefer pole-sized or smaller trees.

In 1987 we conducted some preliminary tests of the age-related suitability of ponderosa pine to *Neodiprion fulviceps* (Cresson). Branches were collected from five trees (similar vigor) of six different ages (1, 2, 5, 10, 15, and 20 years). One-year-old foliage was bioassayed under laboratory conditions. We observed patterns of oviposition (Fig. 2) and survival (Fig. 3) that suggested an effect of tree age. *Neodiprion fulviceps* had highest survival on 15-year-old trees which is within the usual range of tree ages where this sawfly species occurs. It is interesting to note that the optimal age for oviposition (< 10 years) was not the same as for survival. Because the trees used in this study were of unknown genotype and because the sample size was small, these data are tentative.

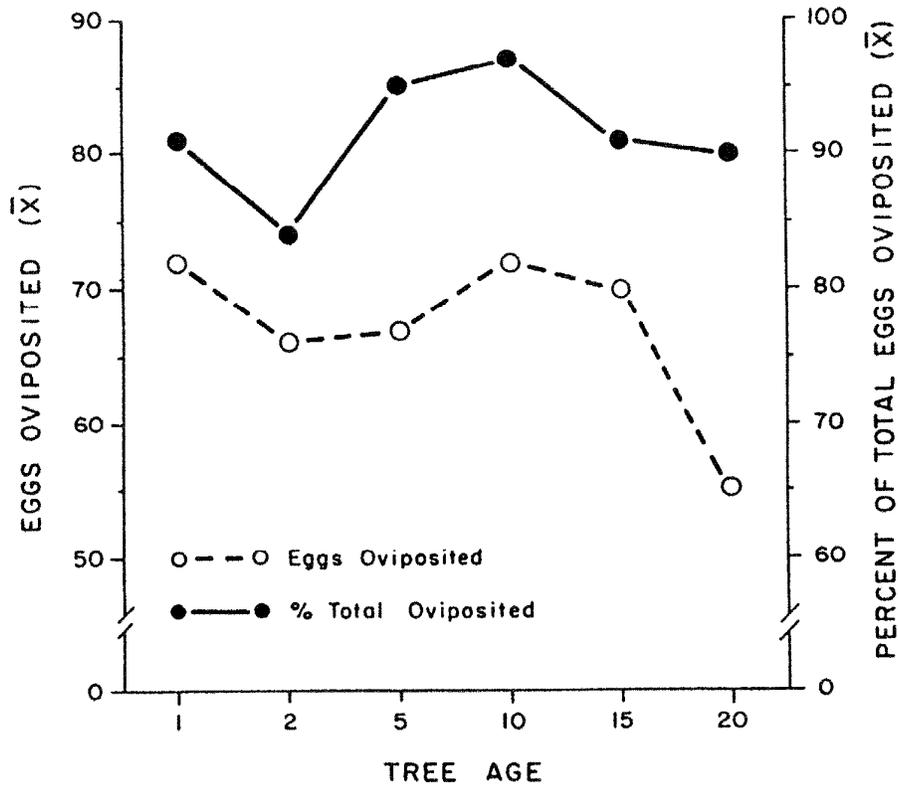


Figure 2. Influence of tree age on the number of eggs laid and the percent of total female fecundity oviposited for *Neodiprion fulviceps* on 1-year-old foliage of six different ages of ponderosa pine.

On the basis of the literature and the preliminary evidence collected, I hypothesize that for any given sawfly species there is a tree age at which sawfly survival would be optimal. The preferred tree age could vary among sawfly species on the same host. This could indicate a method by which sawfly species with similar life cycles partition their food resources to avoid competition. A hypothetical response function for the relationship between sawfly survival and tree age is presented for three ponderosa pine-feeding sawflies (Fig. 4). In this case *Neodiprion gillettei* (Rohwer), which occurs in nature on seedlings, would probably have optimal survival on young trees. In contrast, *Neodiprion fulviceps*, which occurs on much older trees in nature, would probably have optimal survival on older trees. I assume that both species' survival response to tree age approximates a normal curve.

The critical point here is that sawfly survival probably depends on tree age independent of other factors. It is possible that an experimental bioassay of a highly resistant and highly susceptible ponderosa pine genotype, above or below the acceptable age range for a particular sawfly species might indicate that there was no genetic effect, whereas the identical bioassay at the optimal age would indicate a clear difference in performance between genotypes. Any insect-plant interaction experiments conducted with plant material of an inappropriate age might produce very misleading results.

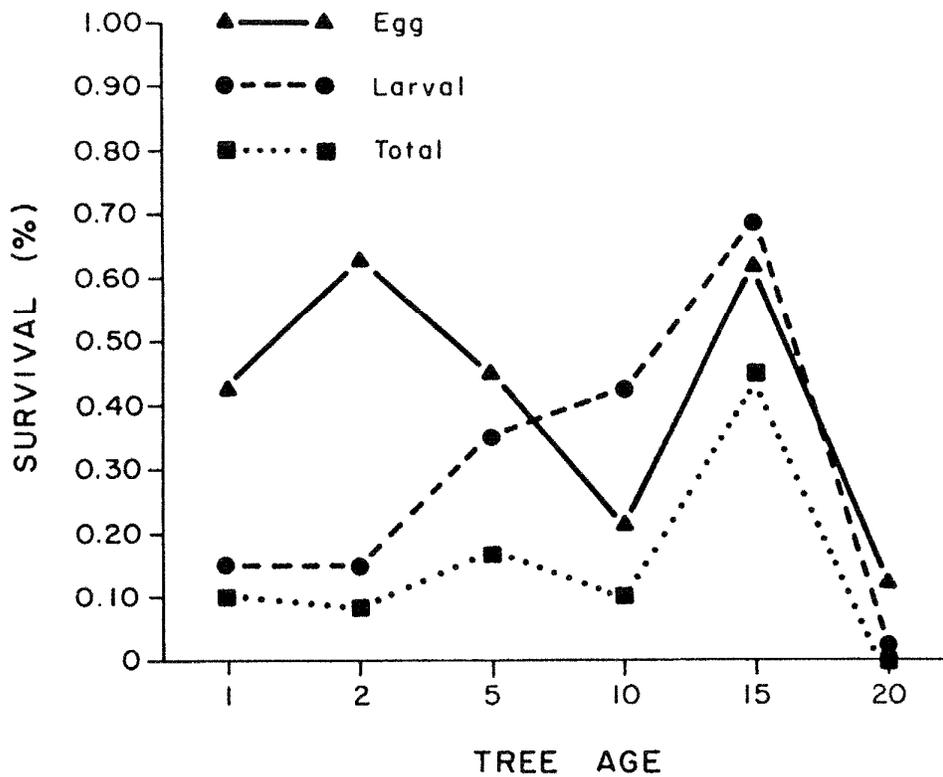


Figure 3. Influence of tree age on egg, larval, and total survival of *Neodiprion fulviceps*.

ROLE OF STRESS IN PINE SAWFLY-PONDEROSA PINE INTERACTIONS

There is yet no clear consensus on the role of environmental stress in provoking insect outbreaks even for a single-model system. After 5 years of experimentally stressing ponderosa pine under field conditions, we still have not established a clear pattern of stress effect (McCullough and Wagner 1987, Wagner and Frantz 1990, Craig et al. 1991). Larvae performed more poorly on stressed trees than on controls for most years. However, we have observed that increasing stress caused increased, then decreased sawfly performance at some period during the 5-year study. This suggests that there is some stress level for the plant at which insect performance is optimal and above or below which performance declines. Because our studies are on wild populations of unknown genotype and because the environmental conditions are not uniform between years, our data are inconclusive. Only rigorous, highly controlled experimental testing will reveal the true nature of the response function for sawfly survival as a result of ponderosa pine stress. In one of the most rigorous studies of water-stress effects on herbivores, English-Loeb (1989) measured a nonlinear population response by the

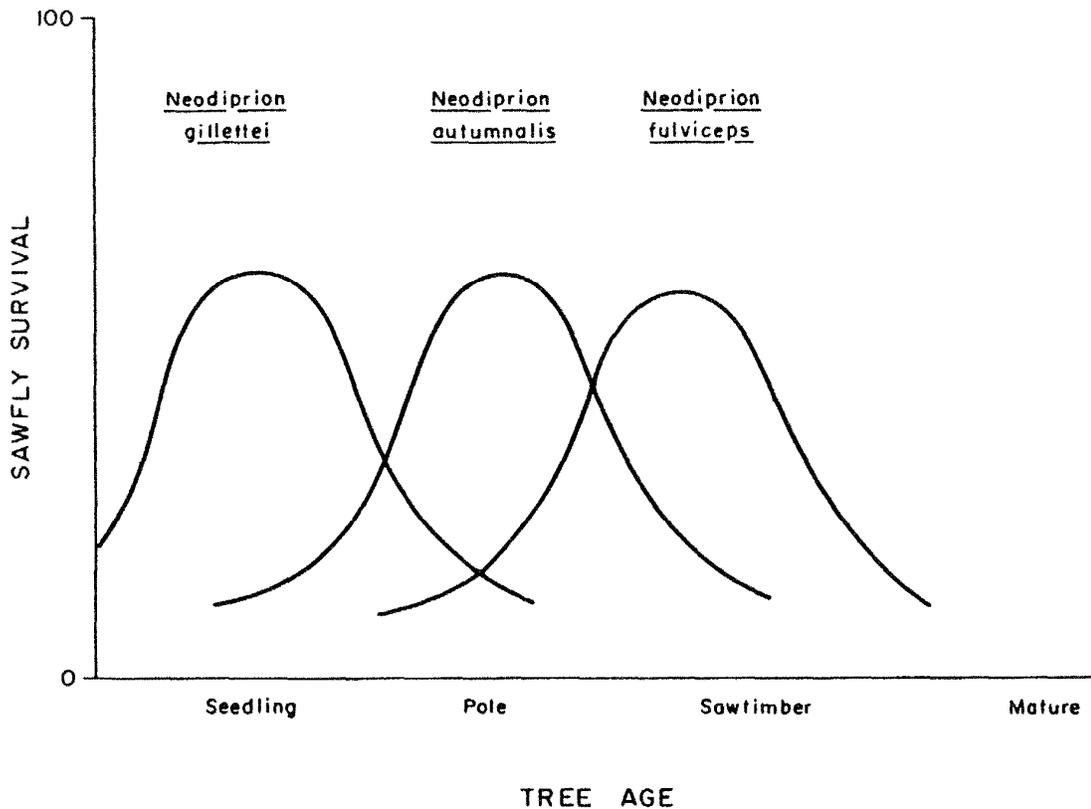


Figure 4. Hypothetical response functions for the effect of tree age on the survival of three species of pine sawflies that feed on ponderosa pine.

two-spotted spider mite, *Tetranychus urticae* Koch, to a range of water-stress levels of its host plant. The response was a modified cosine function in which, as stress increased, mite performance first declined, then increased to an optimum, and then declined again.

Considerably more data are required before a complete response function can be presented for the effect of ponderosa pine stress on pine sawfly performance. However, it is possible to suggest some shapes that response functions may take (Fig. 5). The three hypothetical response functions presented in Fig. 5 represent a range of relationships, any one of which might be the real one. The shape of that function can have profound effects on the interpretation of experimental results, as I will show in the next section.

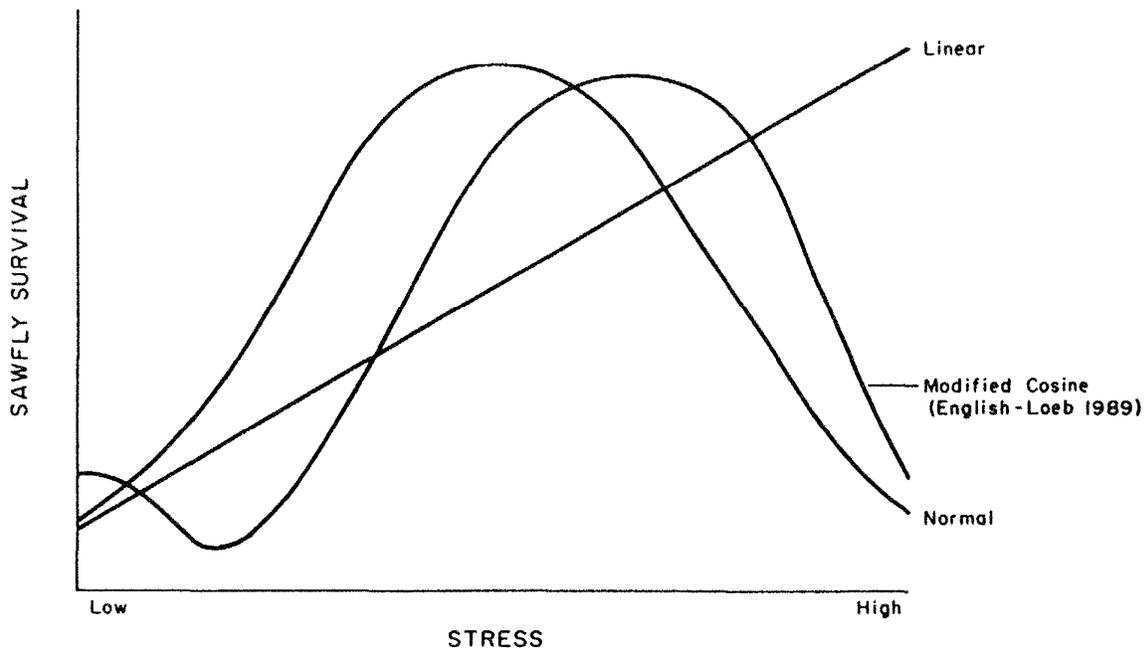


Figure 5. Three hypothetical response functions for the relationship between sawfly survival and the stress level of ponderosa pine.

RESPONSE SURFACES FOR HYPOTHETICAL RESPONSE FUNCTIONS

Up to this point, I have attempted to identify reasonable single-factor response functions for the effects of genotype, ontogeny, and drought stress on pine sawfly performance. In this section I present some reasonable response surfaces of two factors in combination and illustrate how they might influence sawfly survival.

Six hypothetical response surfaces are presented in Fig. 6. In each of the six cases, I have assumed that resistance is a linear function of genotype as approximated by the slope created by the bars in Fig. 1. While holding the genetic resistance factor constant, I have plotted the effect of tree age based on the hypothetical response functions presented in Fig. 4 (Fig. 6a, b, c) and the effect of stress based on the hypothetical response functions presented in Fig. 5 (Fig. 6d, e, f).

In examining the effect of tree age across a range of genotypes, one finds several interesting patterns emerging. First, sawfly survival can vary dramatically for a given tree age and sawfly species depending on the host genotype. The optimal age of ponderosa pine for *N. gillettei* on a resistant genotype would result in less than 50 percent survival, for example, whereas on a susceptible genotype, survival would be 100 percent (Fig. 6a). Likewise for a given genotype and sawfly species, sawfly survival can vary dramatically as a function of tree age. In the case of *N. autumnalis* Smith (Fig. 6b), survival on a susceptible genotype at the preferred age would be 100 percent, but survival on the same susceptible genotype at the least preferred age would be only about 50 percent. If an experimental system does not have control over both of these variables, it is possible to generate experimental data that demonstrate an infinite array of responses for sawfly performance as a function of tree age.

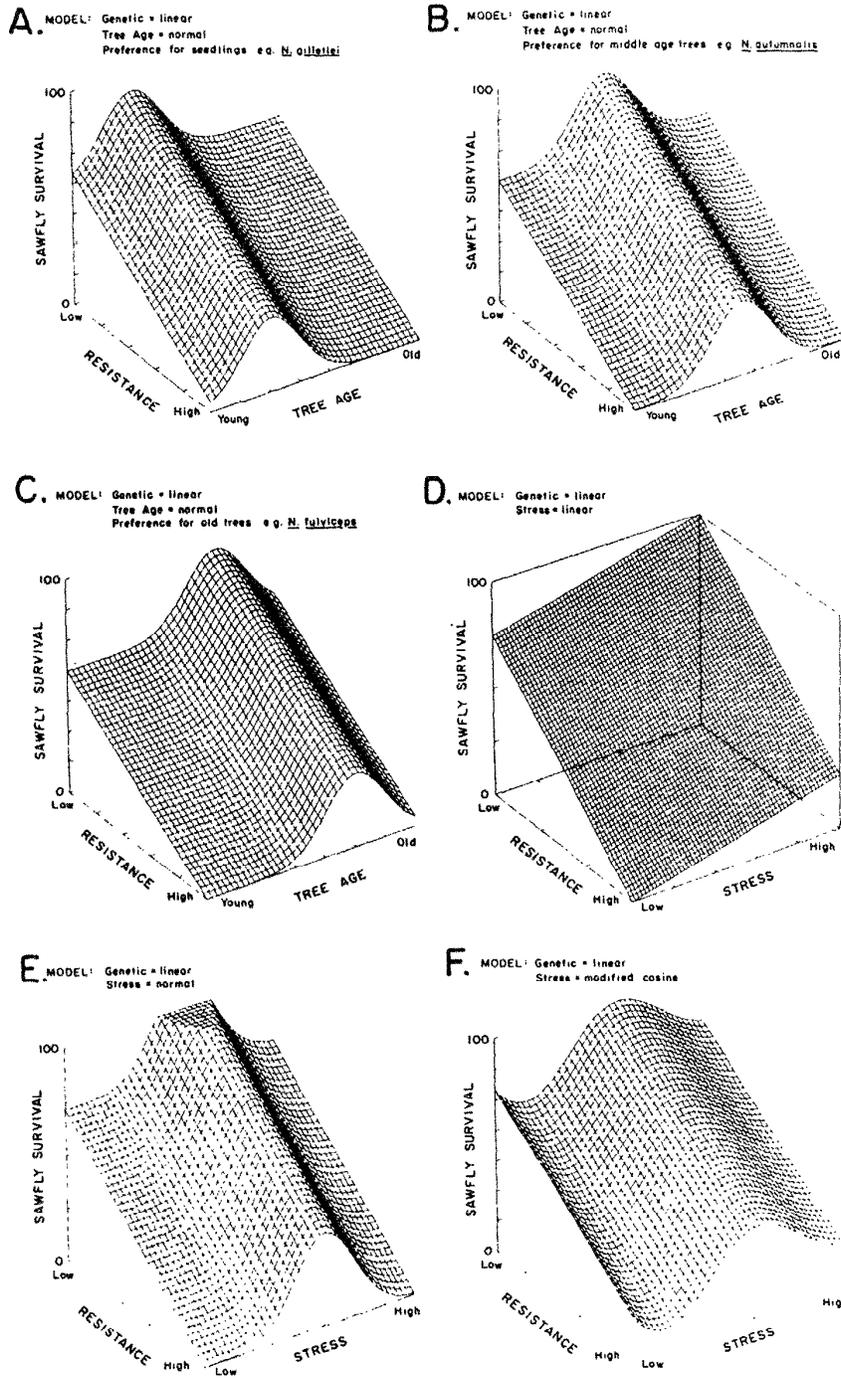


Figure 6. Hypothetical response surfaces for the effects of ponderosa pine genotype, tree age, and stress on the survival of pine sawflies. Response surfaces assume that the effects of tree age and stress are independent of genotype.

Similarly, tree stress can result in widely different effects depending on the tree genotype. Even in the simplest case, when the effects of stress and genotype are linear (Fig. 6d), it is still possible to obtain highly variable responses if either genotype or stress is not carefully controlled. In the most complicated case, when resistance is linear and stress is a modified cosine function (Fig. 6f), it is possible to observe an increase or decrease in sawfly survival with increasing stress depending on the initial level of stress. Finally, it is important to recognize that a wide variety of genotype, age, and stress levels could produce the same sawfly survival. A resistant genotype that was highly stressed could produce the same degree of sawfly survival as a susceptible genotype that was not stressed. Thus examination of response surfaces can greatly facilitate our understanding of these relationships.

RESPONSE SURFACES AS AN EXPLANATION OF CONTRADICTIONARY RESULTS

One of the assumptions I made in generalizing the hypothetical response surfaces in Fig. 6 was that the effects of tree age and stress were the same across all genotypes. In other words, I assumed that a resistant genotype would have the same response curve to tree age and stress as would a susceptible genotype. In fact there is no reason to assume that is so. For example, sawfly survival may not increase on a resistant genotype until that genotype is very heavily stressed. Conversely, sawfly survival might increase quickly with low-level stress on a susceptible genotype, but drop drastically at moderate to high levels of stress.

I have illustrated the potential effects of variable response functions across genotypes in Fig. 7. In this case I create slightly different response functions for susceptible and resistant genotypes. It is possible to observe (Fig. 7, large stress arrow) quite variable effects of an increase in stress at different specified stress levels. For genotype A, an increase in stress results in a decrease in sawfly survival, whereas for genotype B, an increase in stress results in an increase in survival. Likewise for a specific genotype (Fig. 7, large genotype arrow), sawfly survival will decrease with an increase in stress at stress level A and increase with an increase in stress at stress level B. It becomes obvious with examination of Fig. 7 that all of the hypothetical response functions presented for the effect of stress in Fig. 5 could be contained in a single complex response surface. The contradictory results reported in the literature and emerging from our own experimental data could be explained by a complex model such as that presented in Fig. 7.

UTILITY OF EXAMINING RESPONSE SURFACES

The purpose of the previous discussion on response surfaces was to demonstrate how reasonable, individual variable response functions could be combined to create very complex response surfaces. I have discussed only cases involving two factors interacting to influence sawfly survival. We know that in nature many more factors interact. I am led to conclude that much more carefully controlled experimental work is required before true response surfaces are likely to emerge for any insect-plant system and for any two sets of variables. Without a very disciplined approach to the analysis of individual factors and combinations of factors, we will probably wander for years generating points on a response surface without ever fully recognizing the shape of the overall surface.

To improve the probability of our discovering the true response surface of host plant variables influencing insect survival, I propose the following protocols. 1) Research should focus on single insect/host models. Only long-term attention to key host plant traits can identify true response surfaces. 2) Strongly experimental approaches are required which attempt to hold as many factors constant as possible while testing for the factor of interest. Common garden/field, greenhouse, or laboratory studies are more productive than natural field studies in which many variables are not controlled. 3) Experiments on single factors such as stress must test across the full range of that factor. As Figs. 6 and 7 demonstrate, an increase in stress could lead to quite variable effects on survival depending on the initial stress level. 4) Multifactor experiments are useful only when the

MODEL Genetic = linear
 Stress = modified cosine

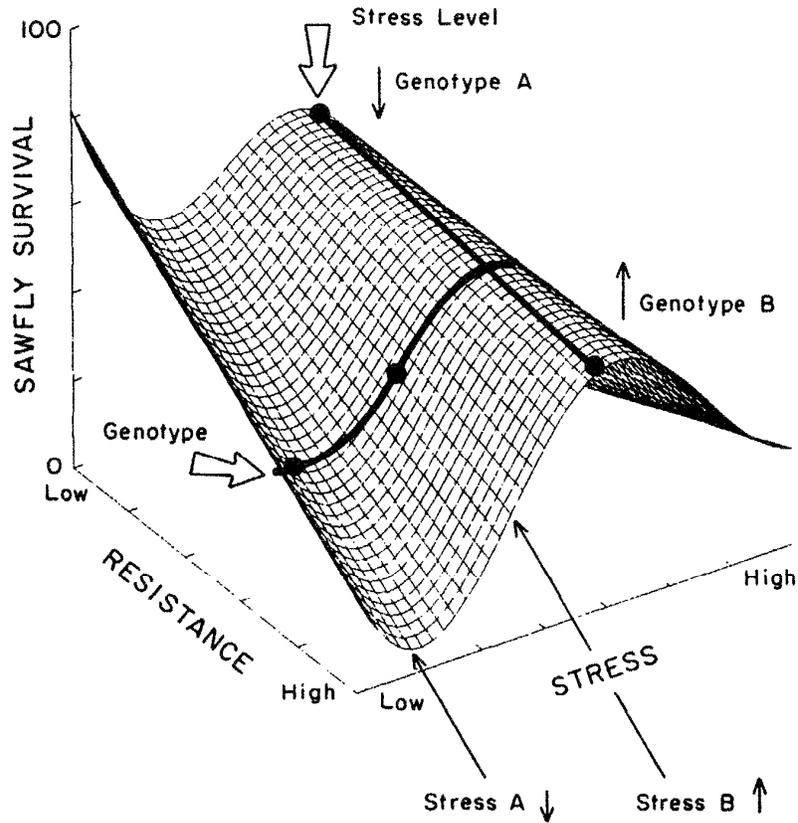


Figure 7. Hypothetical response function for the effects of genotype and stress on sawfly survival. Model assumes the stress response function is dependent on genotype.

individual factors are thoroughly understood. 5) Insect response variables need to be chosen carefully. The response variable chosen (e.g. total survival) should be one that can have a significant effect on insect population dynamics. Field data and population dynamics models can be helpful in identifying which population parameters are most important for a given insect/plant system. 6) We should be very careful about generalizing across insect and plant systems. What may be a key factor in one system may be unimportant in another. Observation of natural patterns will suggest which factors are most likely to be important for a given system and these should be explored first. 7) Finally, response surfaces must be carefully defined. As this paper has attempted to demonstrate, relatively simple single-factor response functions, when combined, can produce complicated response surfaces which must be understood before definitive conclusions can be drawn.

SUMMARY

In this paper I have reviewed the general literature and examined preliminary data that implicate genotype, ontogeny, and stress as host factors that influence survival of pine sawflies on ponderosa pine. Data and the literature have been used to generate hypothetical single-factor response functions. These response functions have been combined to create response surfaces illustrating the potentially complex nature of response surfaces derived from relatively simple response functions. Finally I propose some research protocols to ensure efficient methods of generating response surfaces in order to establish clear relationships between host plants and their insect herbivores.

ACKNOWLEDGMENTS

I would like to thank Zhao-Yi Zhang for assistance in collecting preliminary data on the effect of tree age on sawfly survival. I would also like to thank Karen M. Clancy, Clarence S. Dunbar, and Joel D. McMillin for reviewing the manuscript. D.P. Dykstra and T.E. Gross provided valuable assistance in generating the three-dimensional figures.

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DOES REPRODUCTION COMPROMISE DEFENSE IN WOODY PLANTS?

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PRINCIPLES OF RESOURCE ALLOCATION

A general principle of adaptive allocation was proposed by Cody (1966) who hypothesized that 1) all living organisms have finite resources to partition among growth and competing physiological processes such as reproduction and defense; and 2) natural selection results in the evolution of unique resource allocation patterns that maximize fitness in different environments. Today, it is well established that plants have limited resources to allocate among these processes (Bazzaz et al. 1987), and theories of life-history strategy rests on the assumption that there are fitness trade-offs associated with varying patterns of resource allocation (Stearns 1976, 1989, Reznick 1985, Bazzaz et al. 1987, Lovett Doust 1989). Trade-offs occur when an increase in resources allocated to one fitness component, such as growth, reduces the allocation to another, such as reproduction. Natural selection (acting within phylogenetic, physiological, and ecological constraints) should shape patterns of resource allocation, balancing the costs and benefits associated with these trade-offs, resulting in the evolution of life-history strategies maximizing fitness. There are direct and indirect costs associated with allocation to "nongrowth" processes such as reproduction. Direct costs are energy and assimilates invested in reproductive structures. Indirect costs are unrealized growth and future reproduction as a result of this investment (Bazzaz and Reekie 1985, Bloom et al. 1985, Bazzaz et al. 1987, Reekie and Bazzaz 1987c, Ronsheim 1988, Lovett Doust 1989).

The physiological cost of reproduction in the form of reduced vegetative growth has been documented in a number of cases (Gross 1972, Harper and White 1974, Gifford and Evans 1981, Willson 1983, Luken 1987, Clark and Clark 1988, Snow and Whigham 1989, Dick et al. 1990). However, this cost may not be universal (Tuomi et al. 1982, Reekie and Bazzaz 1987c, Reznick 1985). Genetic, ecological, and physiological trade-offs between growth and defensive secondary chemistry are also well documented (Bryant et al. 1983, Krischik and Denno 1983, Coley et al. 1985, Loehle 1988, Bazzaz et al. 1987, Pimentel 1988). Resource allocation patterns are the expression of source-sink

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

interactions within the plant and their control on assimilate partitioning. Complex physiological changes in patterns of assimilate partitioning are required to bring about the maturation of inflorescences, fruits, and seeds. Very likely, these changes will affect traits conferring plants with resistance to herbivores. Few studies, however, have examined the potential interactions between reproduction and defense.

In this paper we explore two hypotheses suggesting how plant reproduction may directly and indirectly affect herbivory and review the limited experimental evidence supporting each: 1) reproductive structures as carbon sinks reduce the allocation of resources to defense; 2) reproductive structures as nutrient sinks increase the carbon/nutrient ratio in nearby vegetative tissues, resulting in their increased secondary metabolism and consequent increased resistance to herbivores.

TRADE-OFFS BETWEEN REPRODUCTION AND DEFENSE

Plants have limited resources to support their physiological processes, hence all requirements can not be met simultaneously, and trade-offs occur among growth, maintenance, storage, reproduction, and defense processes. Consequently, there is sequential growth and maturation of tissues within organs and organs within plants and/or strong inverse relationships between the allocation of resources to growth and nongrowth processes, including reproduction and defense (Mooney 1972, Mooney and Chu 1974, Gifford et al. 1984, Bloom et al. 1985, Willson 1983, Krischik and Denno 1983, Coley et al. 1985, Alpert et al. 1985, Loehle 1988, McLaughlin and McConathy 1979, Bazzaz et al. 1987, Patrick 1988).

Though rarely documented, reproductive effort may come at the expense of defense, if resources are diverted from resistance mechanisms to reproductive structures. This may occur commonly in the case of nitrogen-based secondary metabolites such as alkaloids and cyanogens, the concentrations of which often decline in foliage as growth shifts from vegetative to reproductive processes (Mattson 1980, Krischik and Denno 1983, Harborne 1990).

Resistance of conifers to bark beetles is generally correlated with their growth efficiency, i.e. stemwood production per unit foliage (Waring et al. 1980, Waring 1983, Mitchell et al. 1983, Larsson et al. 1983, Waring and Pitman 1985). Susceptible individuals with low growth efficiencies are characterized by depleted levels of the stored energy necessary to support defensive reactions (Waring and Schlesinger 1986, Christiansen et al. 1987). Because heavy pollen and cone production can reduce growth efficiency, episodes of reproduction may increase susceptibility to bark beetles. For example, cone production has been shown to depress stem-wood growth and leaf area in several species of conifers (Eis et al. 1965, Owens 1969, Tappeiner 1969, Dick et al. 1990). Carbon allocated to reproduction at the expense of energy and substrate required for resin synthesis and wound-induced hypersensitive responses may contribute to increased bark beetle and pathogen susceptibility. Reproductive effort may interact with environmental stress to suppress conifer resistance to bark beetles and contribute synergistically to outbreaks.

Birch Reproduction and Resistance to Bronze Birch Borer

The pistillate catkins of *Betula* are known to be strong photosynthetic sinks, competing with and reducing resource allocation to vegetative growth (Gross 1972, Tuomi et al. 1982, Caesar and MacDonald 1983). Frequently trees producing especially heavy seed crops subsequently exhibit severe dieback symptoms (Gross 1972, Houston 1987).

Our studies into the physiology of birch resistance to bronze birch borer suggest there may be a direct trade-off between female reproductive effort and resistance to the bronze birch borer (*Agilus anxius*). Bronze birch borer larvae feed under the bark on the xylem-cambium-phloem interface and

are restricted to feeding upon living tissue. Feeding girdles the tree, disrupting the downward transport of photoassimilates. Dieback of roots occur as they are isolated from their energy source, thereby limiting nutrient and water uptake. As attack intensifies, dieback initiates and spreads within the canopy. Heavily infested trees are invariably killed (Anderson 1944, Barter 1957, Carlson and Knight 1969).

From 1986 to 1989, we conducted a controlled, factorial, field experiment investigating the effects of soil moisture, soil fertility, and defoliation on the expression of birch resistance to bronze birch borer. We found soil moisture to be the most important environmental variable affecting resistance. Water deficit reduced rates of photosynthesis, growth, and wound-callus formation, as well as resistance to bronze birch borer (Herms and Mattson, unpubl. data). We found that paper birch resistance to bronze birch may be based largely on generalized trunk responses to wounding, especially rapid wound-callus formation. Furthermore, we found that the strength of this response is dependent on an adequate supply of available current photosynthate (Herms and Mattson, unpubl. data). Feeding-wounds stimulate callus formation, which if rapid enough, may entirely encapsulate small larvae within suberized tissue containing high concentrations of secondary chemicals and low concentrations of nutrients. Normally xylem tissue is a poor source of nutrition (Haack and Slansky 1987); callus tissue may be even worse, preventing larvae from completing development. Larvae may also be physically crushed as they are overgrown by callus. In effect, larvae may be in a developmental race against the tree. Larvae move through the tree in essentially two-dimensional space as they feed, their rate of progress correlated with their rate of consumption. Lesion development characteristic of a hypersensitive response occurs in phloem and xylem tissue surrounding the wound. A rapid rate of callus formation, coupled with reduced rates of larval movement through the wood, may result in larval encapsulation. Implicit in this hypothesis is the prediction that the rate of callus formation necessary for resistance should be presented by a threshold value approximately equal to the maximum rate of larval movement through the plant. Our data suggest that birch trees with rates of callus formation falling below about 0.02 mm/day are highly susceptible to bronze birch borer.

Paper birch (*Betula papyrifera*) is monoecious, with pistillate (female) and staminate (male) catkins produced as separate structures. Male catkins are produced at the end of indeterminate long-shoots in mid- to late-summer following the termination of shoot elongation. They overwinter, elongating and releasing pollen as vegetative buds open in spring. Female inflorescences emerge from overwintering-buds on short shoots as buds break in spring. Female catkin maturation commences upon pollination, and continues throughout the growing season. Seeds mature in late summer and drop throughout the fall and winter.

The results of our experiments confirm previous reports showing a trade-off between vegetative growth and female catkin production (Gross 1972, Tuomi et al. 1982, Caesar and MacDonald 1983). Plants capable of altering the balance of resources allocated between male and female organs generally allocate proportionally more resources to female functions in high resource environments (Freeman et al. 1980). This occurs, presumably, because successful female reproduction requires, in general, a greater commitment of resources than does male reproduction. In our experiment, however, increased female reproductive output in 1 year was associated with resource-limited growth during the previous year. Slow growth may stimulate the initiation of female flowers. Female reproduction itself then further reduces vegetative growth through resource competition. A positive feedback loop may result. Female reproductive effort stimulated by slow growth further reduces growth, which further stimulates female reproduction. Because of reduced rates of callus formation associated with increased female reproductive effort, this positive feedback loop may result in ever-increasing susceptibility to bronze birch borer and eventual tree death. In fact, stress-triggered seed production may be an adaptation which maximizes the life-time reproduction of suppressed trees that are competitively doomed and are likely to be soon killed by bronze birch borer.

Another Look at Birch Dieback: Bronze Birch Borer is Central

Some students of forest decline in North America have been reluctant to assign the bronze birch borer a central role in the occurrence of widespread birch dieback (Anderson 1944, Hawboldt 1947, Carlson and Knight 1969, Houston 1987). At best, the bronze birch borer has been credited with a minor effect on over-all patterns of tree mortality, primarily killing trees already predisposed to death by other factors, such as disease. We argue that patterns of bronze birch borer outbreaks are in some ways analogous to those of the mountain pine beetle, *Dendroctonus ponderosae*, and are sufficient in themselves to contribute significantly to historical patterns of birch dieback in North America: 1) outbreaks of the bronze birch borer, like those of the mountain pine beetle, can be classified as "eruptive" (Berryman and Stark 1985), or more specifically "pulse eruptive" (Berryman 1987); 2) much like the mountain pine beetle (Raffa and Berryman 1983, 1987, Berryman and Stark 1985), we argue that bronze birch borer populations are usually regulated largely by the availability of host plants suitable for larval development and survival (e.g. Carlson and Knight 1969). Outbreaks occur at irregular intervals when biotic and/or abiotic stress factors increase the availability of suitable host trees. 3) Once populations reach epidemic proportions, the outbreak spreads to adjacent stands as large numbers of larvae are able to overwhelm the defenses of vigorous, normally resistant trees.

Paper birch frequently forms even-aged, monospecific stands throughout the boreal forest of North America. Under conditions favoring rapid tree growth, populations of bronze birch borer are constrained to endemic levels by lack of susceptible host material. In this situation, birch borer reproduction is primarily restricted to suppressed trees succumbing to density-dependent competition during the thinning phase of stand establishment. Intolerant of shade, suppressed trees are characterized by low net assimilation rates and lack the resources necessary to support a strong wound response.

Episodes of birch dieback, and associated out-breaks of bronze birch borer, have corresponded with periods of above-average temperatures and below-average precipitation (Hawboldt and Skolko 1948, Redmond 1955, Clark and Barter 1958). Combinations of severe stresses such as drought and defoliation may simultaneously weaken trees over wide geographic areas, resulting in rapid and substantial increases in host material suitable for the bronze birch borer, thereby releasing them from this constraint on population growth (Carlson and Knight 1969).

Female reproduction in birch may play a key role in sustaining bronze birch borer outbreaks. If stress-induced reductions in growth stimulates female reproduction, and female reproductive effort further compromises resistance to bronze birch borer, the result may be a positive feedback loop which rapidly increases the number of susceptible hosts, intensifying and sustaining an outbreak.

Under conditions of extremely high attack density, the defense mechanisms of otherwise resistant trees may be overwhelmed by simultaneous colonization by many larvae. Under these circumstances, larval-feeding behavior may act to subvert host defense mechanisms, facilitating the success of their own colonization as well as colonization by other larvae. When feeding in vigorous hosts, larvae display a zig-zag pattern of gallery formation as they continually double-back against the grain of the wood (Carlson and Knight 1969). This pattern of feeding may partially girdle the tree, causing localized reductions in the strength of wound-induced resistance mechanisms. On the other hand, in severely stressed host trees, galleries show no consistent pattern, as larvae apparently feed on the freshest phloem they encounter (Carlson and Knight 1969).

As borers kill susceptible trees, thereby removing them from the pool of suitable hosts, and as environmental conditions change favoring increased tree growth and stronger wound responses, the epidemic subsides. The borer population declines to an endemic level as the supply of suitable hosts dwindles.

Birch trees experiencing traumatic trunk and canopy death frequently maintain sufficient stored reserves to resprout from the roots. Substantial resprouting often follows above-ground mortality resulting from fire or snowshoe hare browsing. Higher levels of terpenoid surface resins of the bark of juvenile growth originating from root-sprouts are toxic to snowshoe hares and may contribute to the decline of hare population outbreaks (Bryant 1981, Fox and Bryant 1984). Trees killed by bronze birch borer can resprout, as well, and sprouts may be too small to permit bronze birch borer colonization for several years. Sprouting following trunk death is obviously an adaptation to catastrophic disturbances such as fire and herbivore outbreaks, contributing to the continued dominance by birch of seral sites.

Sexual Variation in Resistance and the Carbon/Nutrient Balance

Dioecious plants frequently exhibit sexual dimorphism in resources allocated to reproductive effort, with female effort generally greatest because of resources required for seed and fruit maturation (Lloyd and Webb 1977, Wallace and Rundel 1979, Hoffmann and Allende 1984, Bullock 1984, Clark and Clark 1988, Snow and Whigham 1989, Allen and Antos 1988). Several studies have documented intraspecific sexual variation in the degree of herbivory experienced by dioecious plants (Dannell et al. 1985, Lovett Doust and Lovett Doust 1985, Ågren 1987, Elmqvist et al. 1988, Allende 1989, Boecklen et al. 1990). The resource-competition hypothesis predicts increased herbivory on female plants because their typically greater reproductive effort competes for resources with defense mechanisms. However, data from the few existing studies suggest that the opposite is true. Male plants generally experience greater herbivory (Bawa and Opler 1978, Dannell et al. 1985, Ågren 1987, Allende 1989, Boecklen et al. 1990).

Male and female plants may often segregate along environmental gradients (Putwain and Harper 1972, Freeman et al. 1976, Bawa 1980, Cox 1981, Bierzychudek and Eckart 1988). Differential levels of herbivory, possibly resulting in skewed sex-ratios, may arise from 1) differential frequency of herbivore encounters in their respective environments, or 2) differential defensive allocations among male and female plants.

The nutrient capital required for the growth, maintenance, and maturation of flowers, fruits, and seeds can be substantial and is obtained in full from the rest of the plant (Bazzaz et al. 1979, Thompson and Stewart 1981). Limiting nutrients may be mobilized in relatively high proportions from vegetative tissue to reproductive sinks, thereby contributing to the reductions in vegetative growth associated with reproduction (Mooney 1972, Sinclair and de Wit 1975, 1976, Thompson and Stewart 1981, Bloom et al. 1985, Alpert et al. 1985). The high quantities of nutrients required for fruit and seed maturation may contribute to nutrient deficiencies and ensuing growth reductions in female relative to male plants (Bullock 1984, Allen and Antos 1988).

The reproductive structures of many species are photosynthetic, contributing in varying degrees to their own economy of energy and biomass (Dickmann and Kozlowski 1970, Bazzaz et al. 1979, Reekie and Bazzaz 1987a). Furthermore, enhanced sink strength associated with rapidly developing reproductive structures may stimulate increased photosynthesis in nearby source leaves, through feedback mediated effects (Neales and Incoll 1968, Watson and Casper 1984, Foyer 1988, Dick et al. 1990). As a result, the diversion of carbon from vegetative to reproductive structures may be proportionally less than that of nutrients, especially in female plants (Sinclair and de Wit 1975, 1976, van Andel and Vera 1977, Lovett Doust 1980, Williams and Bell 1981, Abrahamson and Caswell 1982, Mooney and Gulmon 1982, Bullock 1984, Allen and Antos 1988, Reekie and Bazzaz 1987b, Esler et al. 1989). Biomass alone may not always be a suitable measure of reproductive effort (Thompson and Stewart 1981, Abrahamson and Caswell 1982, Bazzaz and Reekie 1985, Reekie and Bazzaz 1987b).

Rapidly growing tissues are invariably strong photosynthetic sinks (Wareing and Patrick 1975, Patrick 1988). However, nutrient limitation slows their growth (Ågren 1988, Patrick 1988).

Photosynthesis, however, can be maintained in existing cells, at nutrient concentrations below those limiting to growth (Chapin 1980, Dietz 1989). Under sink-limiting conditions the carbon/nutrient ratio of the plant increases. Photosynthate assimilated in excess of growth requirements is frequently allocated to secondary metabolism, frequently increasing the plant's resistance to herbivores (Mattson 1980, Bryant et al. 1983, 1987a, 1987b, Mihaliak et al. 1985, 1987). Since "excess" photosynthates could be stored and contribute to future growth rather than be used in defense, enhanced secondary metabolism in response to sink limitation may represent a selected, adaptive use of resources minimizing herbivory (micro and macro) when the plant has limited ability to compensate (via growth) for it.

A nutrient deficiency in vegetative parts female plants relative to male plants resulting from a disproportionate allocation of nutrients from vegetative sources to reproductive sinks may limit vegetative growth (Allen and Antos 1988). Photosynthetic stimulation of source leaves by feedback control exerted by strong reproductive sinks, coupled with direct photosynthetic activity of reproductive tissues, may contribute to a favorable carbon economy within the plant. Together, these factors may interact to increase carbon/nutrient ratio in the foliage of female plants relative to males.

Female plants, because of reduced growth due to their greater reproductive effort, may have limited ability to compensate for herbivory relative to male plants (Ågren 1987, Elmqvist et al. 1987, 1988). Limited compensatory ability coupled with the need by female plants to protect their reproductive investment, may result in females being under stronger selection than males for powerful defense (Putwain and Harper 1972, Ågren 1987, Boecklen et al. 1990). Consequently, patterns of defense observed in female relative to male individuals of a species may mirror the phenotypic patterns of defense predicted by Bryant et al. (1983) in nutrient-deficient relative to nutrient-rich plants. Female plants, like nutrient-deficient plants, should display reduced growth, increased carbon/nutrient balance in vegetative structures, and higher concentrations of secondary metabolites. Very limited evidence supports this pattern. Male plants do seem to receive higher levels of herbivory (Putwain and Harper 1972, Dannell et al. 1985, Ågren 1987, Elmqvist et al. 1988, Alliende 1989, Boecklen et al. 1990, Krischik and Denno 1990, Jing and Coley 1990) and contain lower concentrations of secondary metabolites or have less tough foliage (Palo 1984, Boecklen et al. 1990).

Reproductive Effort in Monoecious Plants May Enhance Their Resistance to Folivores

The principles discussed above should also apply to monoecious plants if they translocate proportionally more nutrients than carbon from vegetative sources to reproductive sinks. This hypothesis predicts that the carbon/nutrient ratio of vegetative tissues will increase with increasing reproductive effort, resulting in increased concentrations of carbon-based secondary metabolites, and possibly enhanced resistance to folivores.

SUMMARY

The process of plant reproduction has pervasive effects on virtually all aspects of plant physiology and should have important effects on plant resistance to herbivores. We hypothesize that increased susceptibility to stem-invading herbivores could result as a consequence of the substantial cost of reproductive effort as resources are diverted from defensive structures and reactions to reproduction. On the other hand, we hypothesize that reproduction can increase plant resistance to folivores. Reproductive effort may result in an increased carbon/nutrient ratio in foliage, as nutrients are translocated to developing flowers, fruits, and seeds. Associated with this increased carbon/nutrient balance may be enhanced allocation to secondary metabolic pathways and increased resistance to some herbivores. Few data are available with which to test these hypotheses. The potential interactions between plant reproduction and herbivory are ripe for investigation.

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PLANT REPRODUCTIVE ORGANS AND THE ORIGIN OF TERRESTRIAL INSECTS

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INTRODUCTION

It is widely believed that plants facilitated the evolution of terrestrial insects (Southwood 1973). However, the mechanisms by which this evolution occurred are not yet fully understood. I therefore propose a hypothesis about one possible mode of formation of terrestrial insects and fauna. The soil, warm shallow lagoons, tidal zones, and accumulations of detritus are assumed by many authors to be the "bridges" for the transition of aquatic organisms to terrestrial existence.

The linkage of insects to plants has been offered as an explanation for the evolution of complete metamorphosis and the ability to fly. It has been suggested that holometabolism occurred in narrow cavities of the substrate, which might be represented by the cavities and ducts in the plant reproductive organs. It is assumed that wings and the ability to fly evolved owing to its advantages in finding food and escaping from enemies.

The Transit to Land

The aquatic fauna is known to be extremely diverse; ancestors of the present arthropods were highly differentiated in the aquatic environment. In the transient water-land zones, the proto-insect's migration onto the land seemed inevitable, although this transit took a long time. Thus it could not have been simultaneous for various insect groups, although some groups evolved concurrently. Each group probably had its own bridge. Let us imagine those conditions which contributed to an obligatory and inevitable transition of aquatic organisms to land. The earth at that time (the Lower Silurian-Upper Devonian) was represented mostly by rocky, dry desert with scanty vegetation, oxygen deficiency, and unlimited amounts of severe ultraviolet radiation.

Organisms living in water were shielded from UVR and from drying and over-heating. They could easily move in a water environment which provided them with necessary support. Those organisms which moved onto land faced formidable ecological difficulties, the most serious being the lower viscosity and density of the air as compared to those of the water. Their bodies actually lost support and their free movement became impaired. For such groups of ancestral arthropods, soil might have been the bridge to terrestrial life. The land was almost devoid of organic life, having drastic changes of temperature, humidity, and illumination. The chance to survive and have progeny was probably very small. The vegetation (the plant protocommunities) had not yet contributed to the process apart from accumulations of detritus and remnants of aquatic plants which served as screens.

Another, later evolutionary branch of aquatic arthropods was associated with the transition of plants to terrestrial existence. This happened as a result of differentiation of the plant life cycle into

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

sexual (gametophyte) and asexual (sporophyte) generations which was accompanied by the formation of a special reproductive organ "strobilus," which may be regarded as an analogue of modern cones.

Primary-terrestrial plant protocommunities were prostrate creeping plants partly yet connected with water, and served as optimal habitat for Arthropoda ancestors to be temporarily found outside the water. The reproductive organs rose above the water surface. If we take into account the fact that plants in a water environment could have been used as food and shelter by insects, then endophyte mode of life could be optimal. Plant fibers on land contained moisture and oxygen, and perhaps the reproductive structures provided for the best isolation from external hostile conditions. Moreover, they were food substrates rich in nutrients.

Within this hypothesis it is impossible to imagine other more ecologically optimal habitats for the insect's ancestors. Thus we can postulate the existence of two likely "bridges" for the transition onto the land of aquatic ancestors; they moved via the soil and via plant reproductive structures. This by no means excludes other ways and means. We should emphasize that these two bridges established the two further directions of evolution of terrestrial Arthropoda. The soil bridge Arthropoda actually "stopped" their evolution, e.g. the modern Apterygota, Myriapodes, and Arachnoides. Their environments excluded both the possibility and the necessity of complete metamorphosis and flying ability. The second group has undergone substantial evolution and has transformed into the modern Holometabola. We should postulate on the basis of the above that the aquatic ancestors of modern insects have not experienced any metamorphosis; this conclusion is recognized by many authors.

The Origin of Flight

We can suggest that flight and metamorphosis are inherent features of higher insects and have a common origin. They appeared because the association with plants predisposed their evolution. Peculiar features of plant reproductive organs, as habitats for endophytes, are their ephemeral, patchy existence in comparison with the constant character of the plant proper. They formed on the ends of the branches, being unevenly and irregularly distributed depending on dynamic weather and soil conditions. In other words, the habitats and food resources of this branch of terrestrial insects originally appeared to be discrete in space. Evolution in insects could have proceeded in the following way: a certain group of terrestrial insects under certain favorable conditions could make locally a morphological and physiological "jump" which can be regarded as aeromorphosis.

Living conditions in strobilus (or other reproductive organs) were such that an insect as a rule could not complete its ontogenesis in one strobilus, it had to move to another one situated nearby, on a neighboring branch, or a neighboring plant, the time for migration being extremely limited. Similar migrations were performed by adult insects to lay eggs and to provide the food for its progeny. Crawling would not have been optimal. A jump would be more advantageous, but jumping makes it necessary to overcome gravity and to move large distances. Insects with elongated bodies would be favored. The necessity for organs to appear, which would make the insects able to fly first in a passive mode and then in an active mode, would be accompanied by re-structuring of muscles and formation of a wing.

Let us now examine a hypothetical fate of an insect grown in the primary plant reproductive organ. Its life time was determined by the fulfillment of its own reproduction and was quite short, though this does not mean that the whole period of plant reproduction was so short: strobila (or other organs) could exist in the tree crowns quite long, new strobilae substituting for old ones. Those insects which could deposit their eggs faster had a higher probability to survive and have progeny, laying their eggs in the neighboring reproductive organs or in those which died later. Larvae hatched from these eggs, that is embryonization of post-embryonal development occurred as postulated by Iezhikov-Berleze theory. Under such conditions larvae had to live through unfavorable nutrition and development periods (cooling periods, droughts, absence of food and habitats). The development under these unfavorable conditions became retarded, but it should have been compensated for by faster rates

of physiological metabolism (hystolysis, histogenesis) in the period of transition from a wingless, sexless larva to the winged and sexually mature "imago."

The development within the living plant tissues did not require the development of morphological and physiological adaptation. Exactly the same advantages are available to primary wingless insects which occur (and still occur) in strongly moisturized soil cavities. (See Gilyarov 1970.) However, the temporal discreteness of plant organs and tissues forced the insect to exist outside plants during a certain period of their ontogenesis, which resulted in the forming of new adaptations. The development of an isolated pupa (where these processes take place), not affected by the environment, appeared to be an optimal evolutionary trend. In a number of cases the developed ability of retarding or stopping the development without morphological reconstructions was fixed, i.e. diapause.

On the other hand, those insects who primarily or secondarily were related to non-discrete plant organs (leaves, branches) and have created not only the chewing feeding mode but also a sucking one as well (Orthoptera, Heteroptera, Homoptera) did not develop the pupal stage, they are known as Hemimetabola.

The above presents the main concepts of a theory which is by no means complete. It should be considered as a preliminary assumption for a future hypothesis.

PREFERENCE OF DENDROPHAGOUS INSECTS FOR FOREST BORDERS

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INTRODUCTION

Numerous investigations have shown that forest insect outbreaks usually occur in specific habitats. Frequently these outbreaks do not generally extend to other territories occupied by these same host trees. Moreover, in every stand subjected to an outbreak, both slightly undamaged plots and heavily damaged plots are found. Perhaps some plots are initially more resistant to insect attack, and insect distribution within forest ecosystems may have a mosaic pattern. Therefore investigation of the relation between dendrophagous insect distributions and initial heterogeneity of ecosystems may help us to understand the nature of forest stand resistance. This question lends interest to the peculiarities of dendrophagous insect distribution in relation to forest borders because borders and different glades are important factors in forest ecosystem heterogeneity.

INSECT DISTRIBUTION WITHIN STANDS

There is no large body of information on this question in the literature. I have used the available information on different species from several natural zones and considered the distribution of 180 species belonging to 33 families of six insect orders. Insect distribution was analyzed only at the main feeding stages.

Table 1 shows the majority (73.3 percent) of the species considered to prefer the forest border and its analogues (single growing trees or low-density stands).

Distribution of insects within a forest stand may depend on two main factors: 1) the presence of available food; and 2) microclimatic conditions. It is known that availability of food is more important for xylophagous insects than for phyllophagous ones. On the other hand, microclimatic conditions are more important for phyllophagous free-living species than for xylophagous ones. Thus it is necessary to analyze the distribution of both these insect groups separately. My analysis showed the forest border and its analogues to be preferable for the majority of species from both groups: 59 percent of xylophages and 66 percent of phyllophages. Thus these stations may satisfy different requirements (food and climate, among others) of the majority of dendrophages.

Table 1. Preferred distribution of 180 phytophagous insect species over different forest parts

Habitats	Number of species	
	Total	%
Forest borders and their analogues		
Isolated trees (A)	3	1.7
A + B	5	2.8
Forest borders (B)	18	10.0
B + C	46	25.6
Open, low-density stands (C)	49	27.2
A + B + C	11	6.1
Forest thickets and their analogues		
Closed, high-density stands (D)	29	16.1
C + D	7	3.9
Uncertain distribution		
A + B + C + D	4	2.2
B + C + D	1	0.5
Uncertain	7	

Climatic conditions are different in every natural zone, however, and the insect species areas may occur over several bioclimatic zones. Therefore dendrophage distribution in relation to forest borders may be different. Dispersal from one natural zone to another provide ample evidence that insect species exchange one kind of habitat for another. We should take this principle into account in our strategies for controlling insect species epidemics, but for our present purposes it is more interesting to consider dendrophage distribution within different zones, such as forest and steppe regions.

My data analysis again showed the majority of species to prefer the forest border and its analogues: 84 percent the forest zone and 71 percent the steppe. So these "border" habitats are assumed to have an advantage over forest thickets and their analogue for insects.

There is data indicating some abundant species use the forest borders as a refuge between outbreaks. Moreover, the initial outbreak areas often coincide with these refugia. At the same time, my analysis showed both outbreak and nonoutbreak insect species (81 percent and 79 percent respectively) to prefer forest borders. We may say, then, forest borders not only function as refuges for abundant species, but are preferred habitats for the majority of nonoutbreak species as well. The question is why?

EXPLAINING HIGH BORDER PREFERENCE

Let us consider some possible reasons why forest insects prefer forest borders. Forest border habitats are characterized by a great variety of 1) microsites and 2) tree and shrub species. For these reasons, rich insect species communities occur in these habitats. The existence of species variety is impossible within narrow local microclimatic conditions. However, since the forest borders are characterized by maximal amplitudes of microclimatic parameter fluctuations, they allow for the coexistence of insect species with different microclimatic requirements.

It might be thought that all these factors relate only to phyllophages because xylophages depend on microclimatic conditions to a lesser degree and for them the availability of food is more important. Only the tree borders are subjected to strong winds and other unfavorable influences, however, and that circumstance makes for constant renewal of the food base by xylophagous insects.

It is necessary, finally, to account for the preference of forest borders by cone and seed insects. Unlike the trees in forest thickets, border trees such as conifers may produce cones between "yield years." As a rule, only border and single-growing trees produce cones every year. Consequently, border habitats become refugia for cone and seed insects. This may also be a factor in the preference for forest borders by dendrophages.

Thus we may conclude that: 1) forest borders and their analogues are preferable habitats for a great number of dendrophagous insects; 2) forest borders and their analogues are strategic sites for control of abundant forest insect species; and 3) forest borders may be used expressly for the analysis of fauna of dendrophagous species in certain forest ecosystems.