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

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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, Callaham 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.

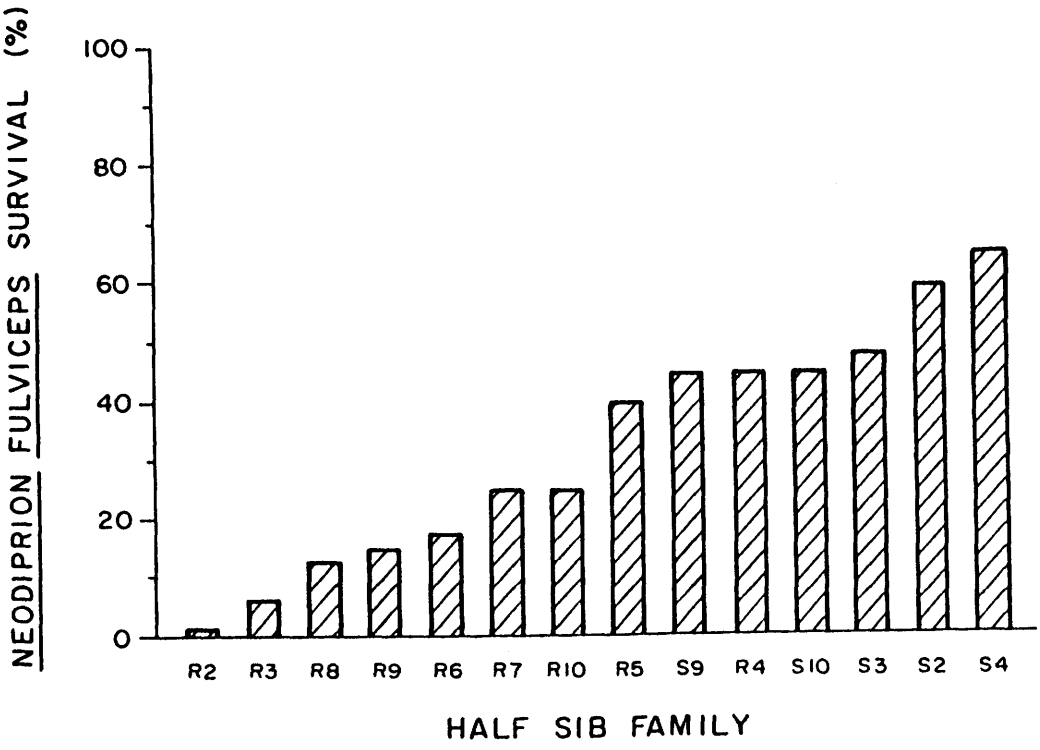

Figure 1. Total generational survival of *Neodiprion fulviceps* on maternal ponderosa pine trees from which 14 half-sib families have been established.

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 Heikkenen 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.

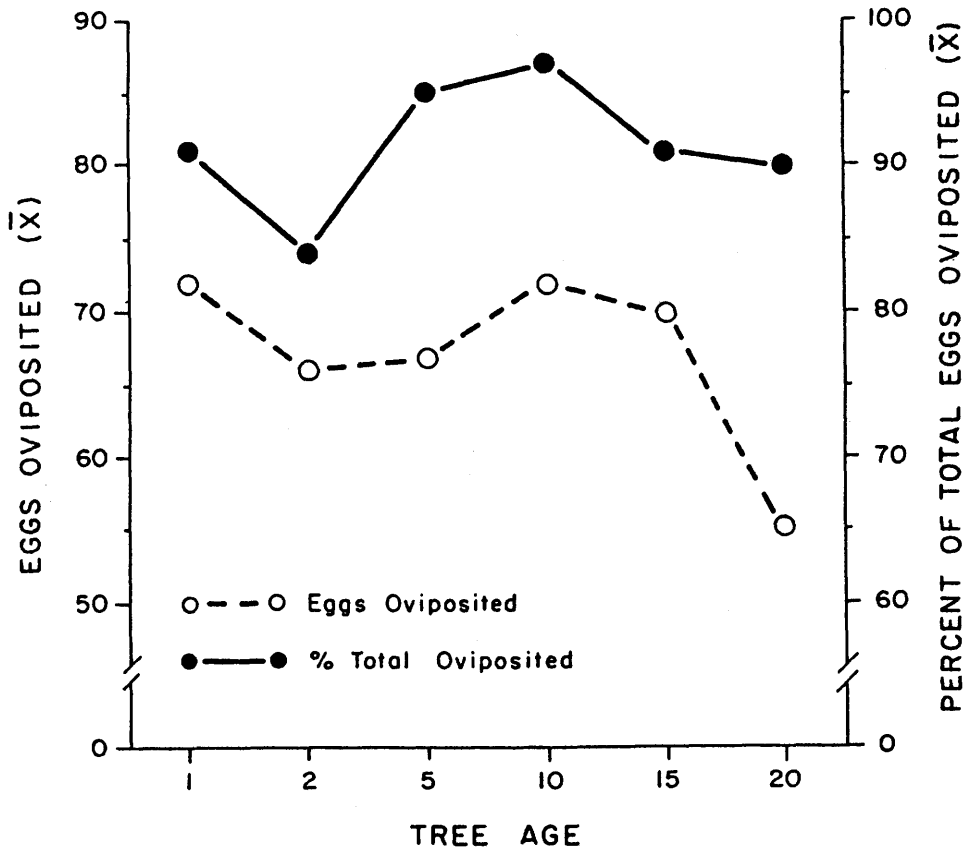

Figure 2. Influence of tree age on the number of eggs laid and the percent of total female fecundity oviposited for *Neodiprion fulviceps* on 1-year-old foliage of six different ages of ponderosa pine.

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.

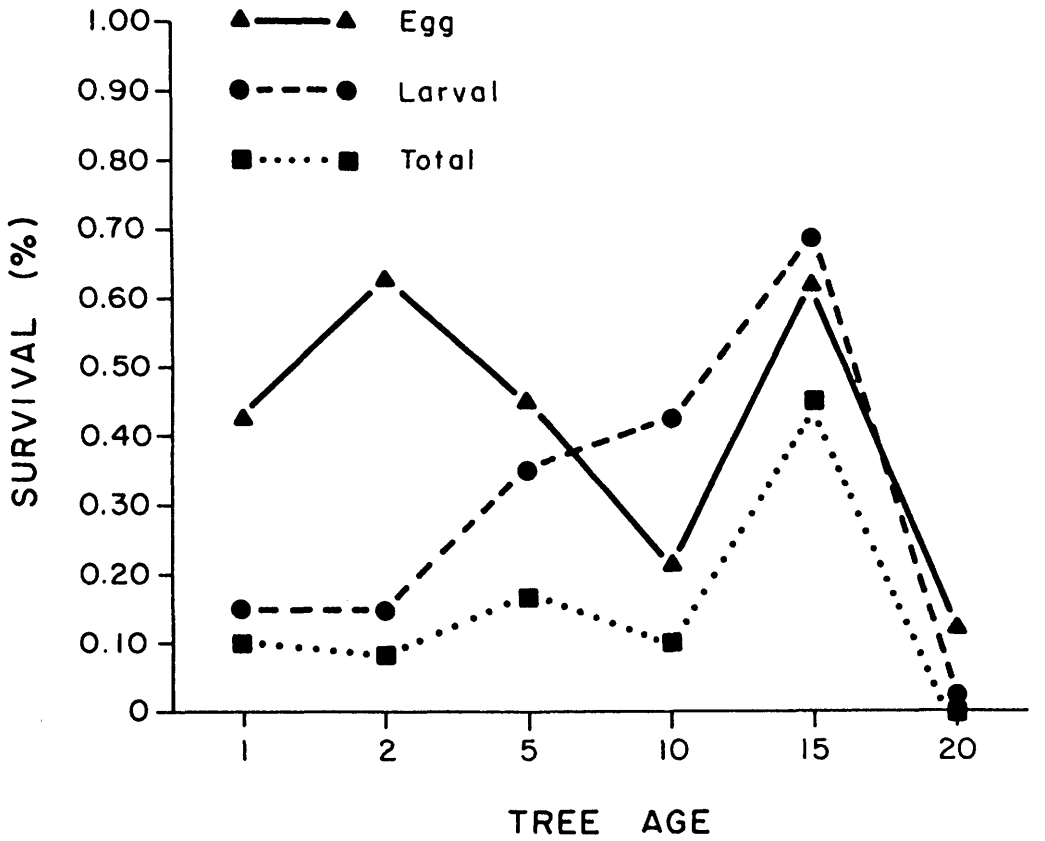

Figure 3. Influence of tree age on egg, larval, and total survival of *Neodiprion fulviceps*.

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

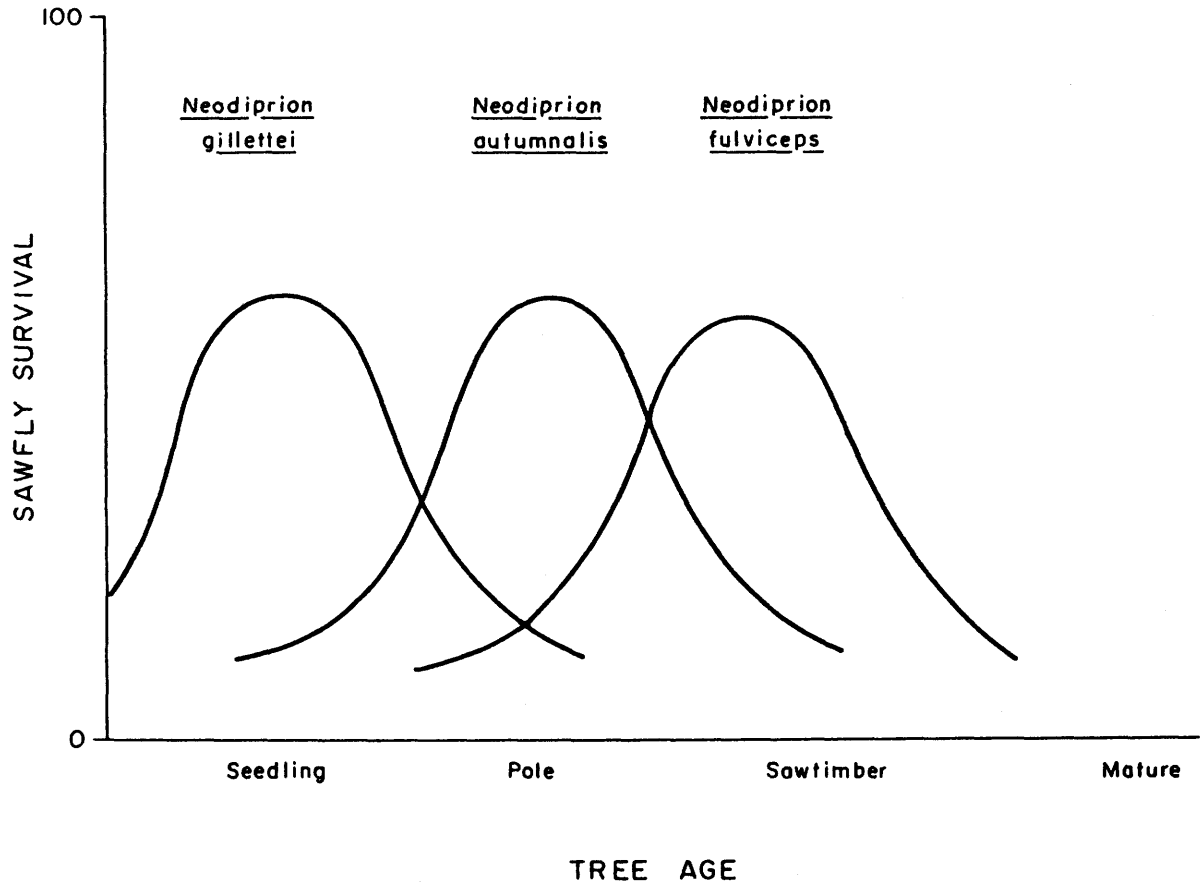

Figure 4. Hypothetical response functions for the effect of tree age on the survival of three species of pine sawflies that feed on ponderosa pine.

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.

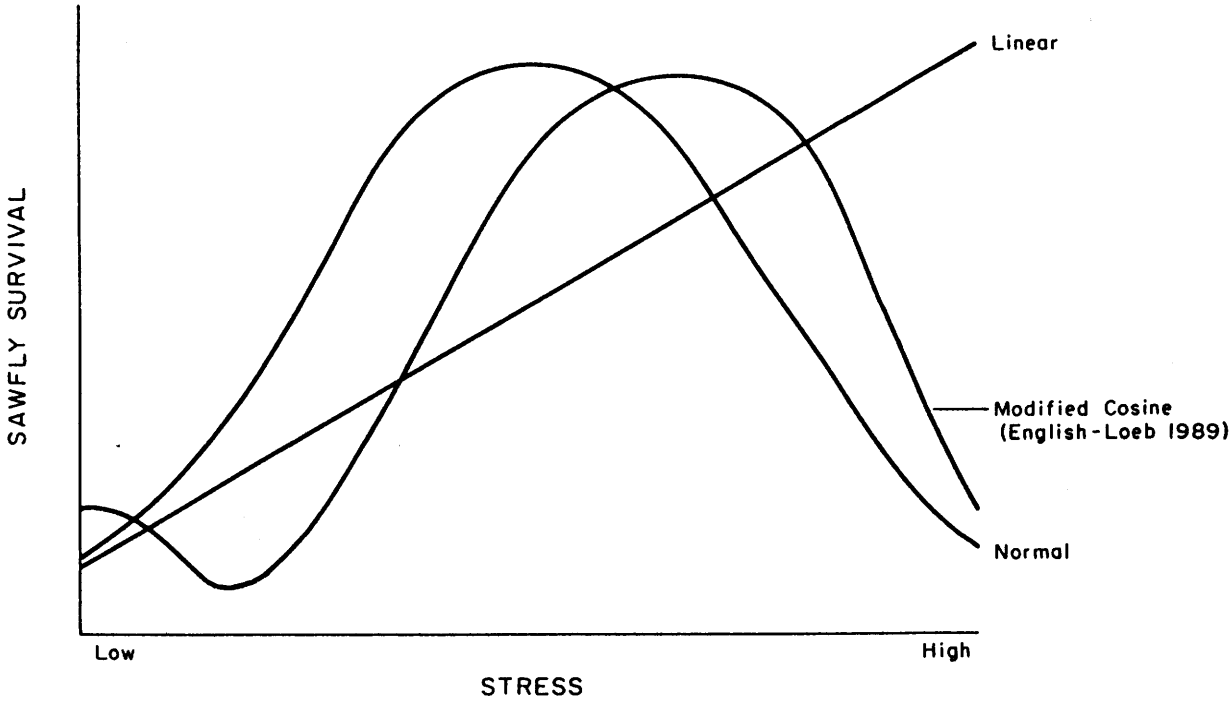

Figure 5. Three hypothetical response functions for the relationship between sawfly survival and the stress level of ponderosa pine.

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.

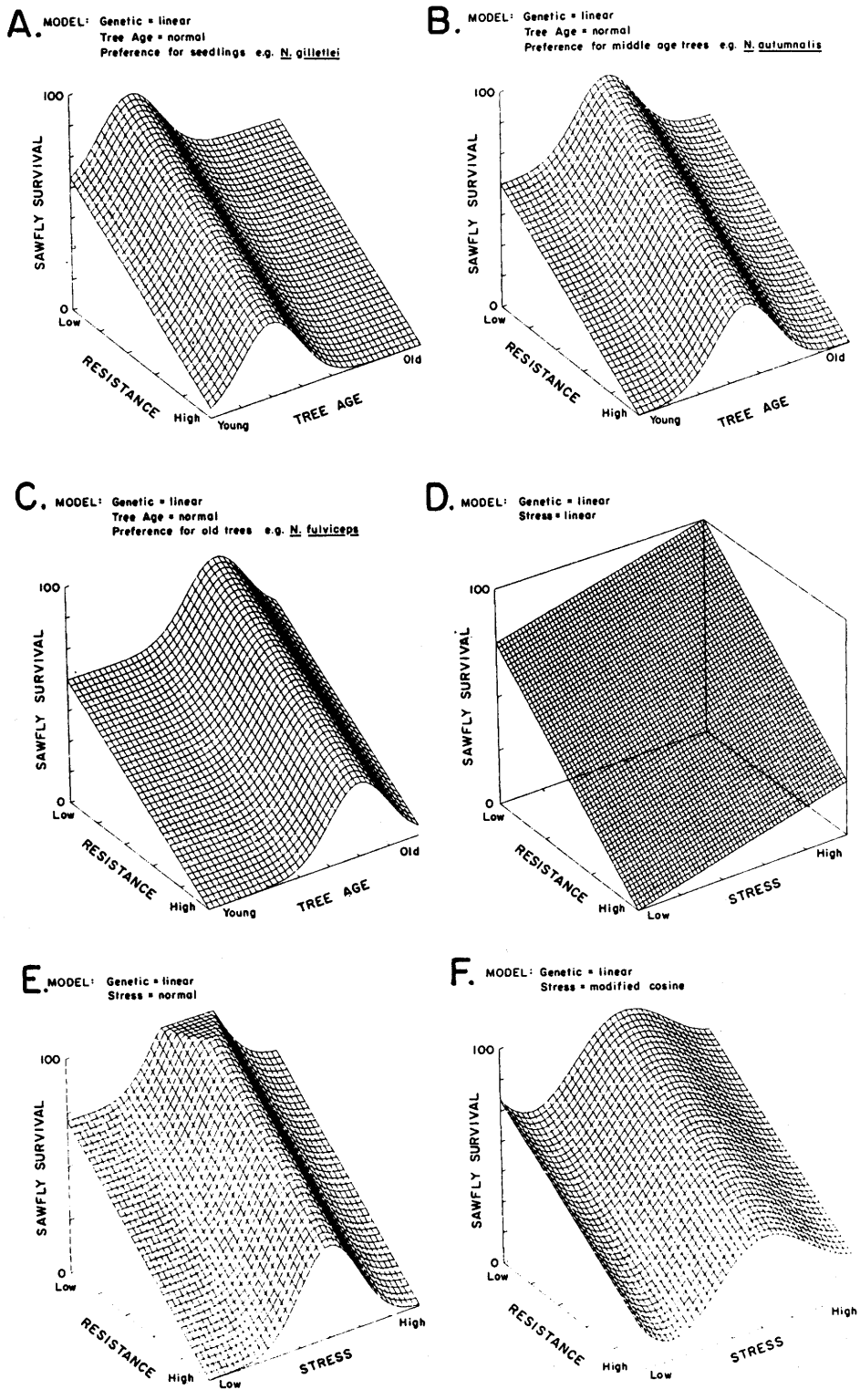

Figure 6. Hypothetical response surfaces for the effects of ponderosa pine genotype, tree age, and stress on the survival of pine sawflies. Response surfaces assume that the effects of tree age and stress are independent of genotype.

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 CONTRADICTORY 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

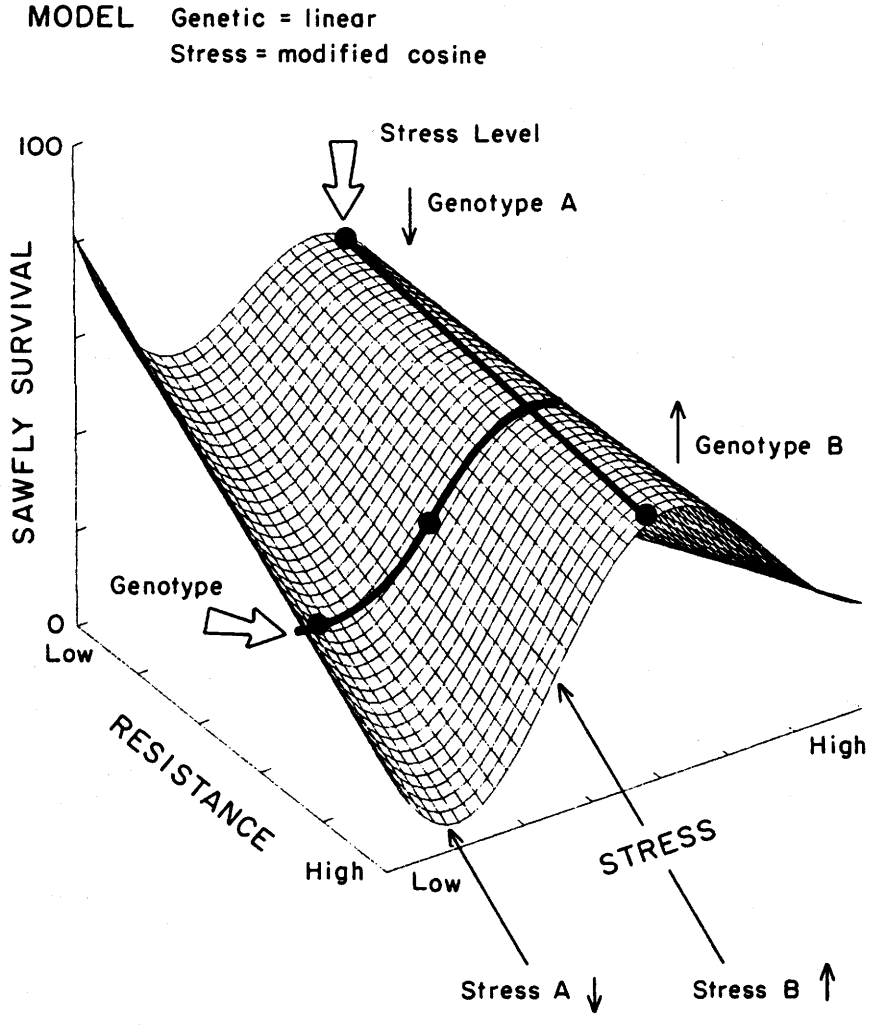

Figure 7. Hypothetical response function for the effects of genotype and stress on sawfly survival. Model assumes the stress response function is dependent on genotype.

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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.

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