

WOODY PLANT GRAZING SYSTEMS: NORTH AMERICAN OUTBREAK FOLIVORES AND THEIR HOST PLANTS

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INTRODUCTION

In North America, about 85 species of free feeding and leafmining folivorous insects in the orders Lepidoptera and Hymenoptera periodically cause serious and widespread defoliation of forest trees (Appendix 1). We call these insects expansive outbreak folivores based on the following criteria: 1) population eruptions occur two or more times per 100 years, 2) severe host defoliation (> 50 percent) occurs for 2 or more years per eruption, and 3) the area of each individual outbreak exceeds 1,000 contiguous ha. There are about 20 other insects whose populations meet criteria one and two, but not criterion three. These we term local outbreak folivores and do not deal with them in this paper because they may operate on an entirely different scale than the expansive species.

CHARACTERISTICS OF EXPANSIVE FOLIVORE OUTBREAKS

Continent-Wide Infestation Area and Frequency

Between 1957 and 1987 in the United States, at least 60 species caused outbreaks exceeding 1,000 ha (USDA, Forest Service). The largest outbreak area (summed over many different geographic regions) caused by a single insect species (*Malacosoma disstria*) in a single year was 13.5 million ha (Appendix 2). At least 14 species had single-year infestation areas that covered 0.5 million ha. The four insects showing the most consistent outbreak frequency (> 25 yrs) as well as largest mean annual infestation areas (> 0.5 million ha) were the eastern and western spruce budworms, *Choristoneura fumiferana* and *C. occidentalis*, respectively, the forest tent caterpillar, *M. disstria*, and the gypsy moth, *Lymantria dispar* (Table 1). These insects are largely in a league by themselves because most other species had less frequent and less expansive outbreak areas. Although we did not examine similar data from Canada, the pattern is likely to be much the same but with a bias toward folivores of *Populus*, *Betula*, and boreal conifers. For example, in 1975 *C. fumiferana* was at a century-high defoliation peak on more than 55 million ha in eastern Canada (Kettella 1983). On the average, at least 7.6 million ha were under severe defoliation each year by all species combined between 1957 and 1987 in the United States (Appendix 2). These are conservative estimates because of the difficulty of exactly delimiting the beginning, ending, and area of each outbreak. Generally, only the most severe cases are observed.

Six Correlates of Defoliation Severity

The impact of outbreak defoliations on forest stands differs with the insect species and the characteristics of the forest. Nevertheless, some generalities seem to hold regardless of the particulars of individual cases: 1) defoliation severity increases directly with homogeneity of the forest composition, 2) defoliation severity increases with the average amount of exposure of the individual tree crowns, 3) defoliation severity increases, though not necessarily linearly, with tree age, 4) defoliation severity increases with warm, dry weather during the growing season, 5) defoliation severity increases with the folivore's predilection for polyphagy, and 6) the effects of defoliation on tree vigor are cumulative and not linear. These six factors may contribute to outbreaks for the following reasons: increasing the amount of available food per unit area (1,5) increases the insect's chances for survival and ultimate population growth; warmer, drier environments appear to favor folivorous insects (2,4) (Mattson and Haack 1987a, 1987b); and finally, as trees age, their crowns enlarge and they begin to flower, which can have both positive and negative effects on folivorous herbivores (see Herms and Mattson this volume). At the same time the trees become less suitable for sapfeeders (Schowalter 1989), which may have several important beneficial effects on free folivores (Mattson et al. 1989).

In North America, most cases of substantial tree mortality caused by outbreak folivores have occurred primarily in aging, "overmature" forests (Kingham 1954, Carroll 1956, McLeod 1970, Struble 1972, Turnock 1972, Drooz 1980, Lynch and Witter 1984). However, site quality and tree vigor status interact significantly with tree age--low vigor trees growing on poor sites are much more vulnerable to death after outbreak folivory than are vigorous trees on rich sites (Mason and Tigner 1972, Turnock 1972, Witter et al. 1975, Schultz and Allen 1977, Lynch and Witter 1984, Hix et al. 1987, Archambault et al. 1990). However, qualification is necessary here. Moderately poor sites may actually sustain less mortality per unit of defoliation than rich sites because the former tend to be under less intense plant-plant competition and have trees with higher relative root and storage investments that allow them to tolerate both abiotic and biotic stresses. Rich sites induce more severe competition for space and light which favors individuals that invest proportionally more in canopy (Clark 1990). Accordingly, they have intrinsically higher rates of natural mortality owing to larger numbers of trees that are under severe competition and that invariably succumb during defoliation episodes (Clark 1990, Crow and Hicks 1990).

Table 1. Numbers of folivore species in different outbreak frequency classes, and mean annual area size classes between 1957 and 1987 in the United States.

Outbreak frequency class (yrs)	Mean annual outbreak area class: (1000 ha)			
	1-5	6-50	51-500	501-5000
< 5	8	16	9	4
< 10	0	9	4	2
< 15	1	5	3	1
< 20	0	0	3	0
> 20	0	1	0	4

Data derived from Appendix 2.

High Grazing Tolerance: Woody Plant Grazing Systems

We hypothesize that many natural plant systems that regularly support expansive outbreak folivores have only nominal regulatory (damage inducible) defenses against those folivores. The same is probably not true for other folivore guilds that are more truly parasitic, such as phloem and xylem sappers (Mattson et al. 1988b). And, it is certainly not the case for the inner-bark feeding guilds (see Mattson et al. 1988a). In fact, the outbreak patterns observed for expansive folivores are an inevitable consequence of the plant's regulatory capacity. These plants have evolved only very weak capacities for regulating canopy herbivores because outbreak folivores generally have minimal impact on plant fitness. Note that this does not mean they have negligible impact on plant growth and reproduction. It means that when such impact occurs, it is nearly equally felt by all plants. For these reasons, we label them grazing systems as did McNaughton (1984, 1986) for certain grassland systems that are highly tolerant of and may be dependent on grazing by generalist mammalian herbivores.

We do not imply that forest and grassland systems are identical, only that they are similar because folivory may be a fundamental part of the overall adaptive syndrome of both. Both systems, by virtue of their large areal sizes of relatively uniform plant form, are predisposed to chronic and substantial folivores--albeit of different types. Both also support folivores that exhibit substantial mobility and little host plant specificity (i.e. grazers, sensu McNaughton 1984, Thompson 1988). Their level of adaptation to and interaction with host plants is more at the scale of the landscape and biome rather than the individual plant. The physiological constraints and the ecological consequences that accompany a perennial, woody plant life history strategy cause the two kinds of systems to differ on the basis of their time scales. Woody plant grazing systems are defined by 1) their expansive, dense, and usually mono-oligodominant community structure that predisposes them to severe canopy herbivory, 2) their capacity to physiologically tolerate consecutive seasons of high levels of grazing, 3) their capacity to ecologically tolerate grazing (maintain their competitive positions), 4) their generally low defenses against canopy herbivores, and 5) their commensalistic (indifference) or mutualistic dependence on folivory in fulfilling their life history strategy. That is, folivores have either a minor role or a very positive role in the plants' life history (Mattson and Addy 1975).

CONDITIONS SHAPING THE EVOLUTION OF PLANT DEFENSES

Physiological Capacity to Recover From Folivory

After experiencing herbivory, a plant must recover both physiologically and ecologically (Mattson et al. 1988b). Both recovery processes influence the eventual evolution of plant defenses. In physiological recovery, herbivore removal of tissues or fluids, for which the plant has little or no capacity to replace or compensate for should elicit strong selection pressure for the evolution of powerful and fast acting defenses (McKey 1979, Rhoades 1979). For example, herbivore consumption of phloem/sapwood tissue is far more serious than equivalent biomass removal from the leaf canopy because the plant's capacity to compensate for the former is negligible compared to the latter. Moreover, damage to vascular tissues has strong, immediate negative repercussions to all other plant organs (canopy, roots, etc.), whereas damage to the canopy has less effect. Accordingly, the defensive systems of trees against inner-bark feeders are among the most powerful known in woody plants (see Mattson et al. 1988a).

On the other hand, leaves are one of the tissues that plants are most capable of replacing. However, the total physiological cost of losing and replacing leaves differs substantially with the size, resources, and adaptive strategy of the plant (Givnish 1988). Plants may compensate for low to moderate (< 30 percent) levels of folivory by increased rates of photosynthesis in the other intact leaves due to 1) more light reaching lower and previously shaded leaves, 2) more water and nutrients available to the intact leaves, and 3) long-term acceleration of nutrient cycling (Mattson and Addy 1975, Ericsson et al. 1980a, 1980b, McNaughton 1984, Verkaar 1988, Maschinski and Whitham 1989, Prins et al. 1989, Williamson et al. 1989).

However, if folivory chronically exceeds a plant's capacity for tolerance, mortality can result directly from exhaustion of tree energy reserves or indirectly from secondary agents such as wood borers, bark beetles, and pathogens (Kinghorn 1954, Barbosa and Wagner 1989).

Ecological Capacity to Recover: Plant-Plant Competition

Although there is substantial evidence that severe defoliation can reduce tree growth and reproduction, and increase tree mortality, there is little substantive information about its impact on tree-tree competition. However, the important effects of folivory on non-woody plant competition and succession are much more widely appreciated (Cottam 1985, Cottam et al. 1986, Milchunas et al. 1988, Brown and Gange 1989, Crawley 1989a, 1989b, Jarosz et al. 1989, Polley and Detling 1989, Louda et al. 1990, Prins and Nell 1990a, 1990b). Competition is pervasive in all plant communities; it is one of the principal ecological variables affecting the evolution of carbon allocation patterns. Thus, an understanding of the effects of herbivory on competition is crucial to interpreting its effects on the evolution of woody plant defenses (Taylor et al. 1990, Tilman 1990, Herms and Mattson 1991).

CONDITIONS FAVORING PLANT GROWTH INSTEAD OF DEFENSE

In many systems prone to outbreaks, certain biological and ecological conditions interact to prevent the evolution of strong plant defenses against canopy folivory. For example, herbivory that occurs in overmature trees has little impact on fitness (except through effects on parent-progeny interactions) because such trees have already largely spent their reproductive capacity.

Oligospecies Plant Communities: Pioneer, Growth-Adapted Species

Folivory occurring in vast, monodominant communities of rapidly growing species (such as those typically created when pioneering tree species invade en masse following extensive disturbances) has little chance of selecting for the evolution of powerful, regulatory plant defenses. First of all, the suite of plant traits that are conducive to successful competition in such environments is not physiologically compatible with high defensive investments (Huston and Smith 1987, Loehle 1988, Taylor et al. 1990, Tilman 1990). Fast growth is of paramount importance for competitive success, and defense will come at its expense (Harper 1989, Herms and Mattson 1991). This requires that plants maintain large foliar surface areas having high levels of leaf nutrients and water, and low levels of secondary metabolites (Gower and Richards 1990, Hilbert 1990). Such species have high capacity to outgrow others but low capacity to tolerate resource depletion (Tilman 1990), because competition for light is largely asymmetric (Wiener 1990).

Second, in monodominated communities there is little evidence of consistent, long-term, differential herbivory among plants (although see Batzer 1969, Clancy this volume, Wagner this volume). Most outbreak folivores seem to exhibit little fine-tuned selectivity for individual host plants (Price et al. 1990). This is particularly true for macrolepidoptera on conifers, which seem to have broad host plant feeding capabilities (Holloway and Hebert 1979). Most often insect egg densities per tree increase directly with tree size or "target" area (Witter et al. 1975, Mattson et al. 1988c, Batzer et al. 1991) as would be expected if trees differ little in quality from the insect's perspective. Furthermore, larvae of these species exhibit little fidelity to their "mother" plant. In fact, in the case of *Malacosoma disstria*, the opposite is true: most larvae abandon their mother plant at about the third instar regardless of its current defoliation level (pers. observ.). For many other species, larvae regularly disperse by ballooning when very small or by dropping and crawling when large (Coulson and Witter 1984, Barbosa et al. 1989)--dispersal mechanisms with very high risk of mortality and low probability of finely tuned host selection.

Few studies have shown that inter-tree variation in folivory has a genetic basis (Mattson et al. 1988b, Ayres et al. this volume), except where differences in tree phenology are the explanation (Witter and Waisanen 1978, Du Merle 1988). The scant existing evidence suggests that all members of the host population within a forest are nearly equally susceptible to defoliation, although this does not imply that all the trees are equally suitable for insect performance (Harris et al. 1982, Mattson et al. 1988b, Schmid and Bennett 1988, Batzer et al. 1991). For example, during forest tent caterpillar outbreaks in trembling aspen forests (*Populus tremuloides*), virtually every member of the canopy community will be severely defoliated several times, including "nonhosts" that are never attacked when growing in isolation or in other communities. Defoliation also extends to most members of the small tree/shrub stratum, even into neighboring forest communities (Hodson 1941, Witter et al. 1975, pers. observ.).

Uniform Folivory Favors Evolution of Tolerance

Given that all members of the community receive equal levels of folivory during epidemics, can herbivory significantly alter the existing competition-derived fitness ranking of the member plants? We think not. Recovery is closely linked to size and growth capacity. Invariably, the suppressed, subdominant host trees quickly die, but they would probably not have survived thinning anyway. Severe defoliation shifts the competitive edge in favor of the larger and faster growing plants, selecting for tolerance traits, the capacity to quickly and strongly recover. We argue that tolerance capacity is the most likely evolutionary response by the plant population to folivory. Nonbiotic defoliation from hail, wind, and ice and snow storms may be more frequent (though not serially cumulative) than outbreak folivory and even more severe in some forests (Grier 1988), and it thus reinforces the evolution of general compensatory responses.

Physiological Cost of Leaves Increases with Plant Height

If the physiological cost of leaves (*sensu* Givnish 1988) to such plants is low enough, they may be able to cope forever with severe herbivory through compensatory mechanisms, as some grasses do (McNaughton 1984, 1986). However, this is unlikely for taller, woody plants because the physiological cost of a leaf increases directly with its height above ground due to the added construction costs of stem and roots for support and nutrient transport (Givnish 1988). Hence, we speculate that there is a vertical size threshold, above which plants need to use some kind of low cost defenses for curtailing the long-term, severe herbivory that seems inevitable in vast monodominant communities. We and others hypothesize that these should build with canopy injury, i.e. delayed inducible resistance (DIR, *sensu* Haukioja and Neuvonen 1987, Bryant et al. 1988, Haukioja 1991) and should interfere minimally with plant growth and other recovery processes, but at the same time erode the herbivore's continued capacity to grow and multiply (Haukioja 1991). One extreme solution might be to produce no leaves for one generation of the folivore, thereby forcing its starvation. Although effective for strictly univoltine insects, it is not viable because the cost is too high, and bivoltinism and extended diapause are easy counteradaptations. A less extreme but nevertheless efficacious variation of this tactic, is to produce less nutritious leaves for the next several growing seasons that directly debilitate the herbivore and concomitantly cause it to be more susceptible to natural enemies (Myers 1988b, Edelstein-Keshet and Rausher 1989, Haukioja 1991). This is apparently the case for *Betula resinifera* and *Populus tremuloides* in Alaska (Werner 1979, 1981). Most DIR traits appear to be amplifications of existing constitutive secondary metabolite pathways (Tuomi et al. 1988a, 1988b, 1990), coupled to diminished nutrient levels.

Can Natural Enemies Substitute for Delayed Inducible Resistance?

The evolution of DIR will be favored to the extent that it contributes to outbreak decline before folivory precipitates widespread mortality due to exhaustion of plant reserves (and concomitant attack by wood borers) or competitive exclusion by some other nonhost species. At this point, cost of defense is no longer important because death is the alternative. However, if there are abundant, efficacious natural enemies (pathogens, parasitoids, predators) that are consistently capable of numerical responses to mounting folivore populations, then they may obviate the plant's need for DIR. Instead, the plants may need only to evolve strong recovery capacity and perhaps traits that enhance their natural enemies: nectar secretions, domatia (leaf structures which shelter predaceous mites), etc. (Mattson et al. 1989, Herms and Mattson 1991).

Localized Rapid Inducible Resistance Complements Tolerance

In resource-rich, oligo-dominant communities, highly sensitive, systemic, rapid inducible resistance (RIR), and/or high levels of constitutive defenses are not viable tactics against free feeding folivores. Perpetual, whole-plant induction would chronically diminish the high growth rates that are fundamental to the basic life history strategy of such plants (Herms and Mattson 1991). However, very localized RIR may be a viable tactic if it serves only to disperse folivores among modules so as to reduce the average impact of folivory per plant (see Bogacheva this volume). In other words, RIR in this case functions primarily as a complement to physiologically based tolerance. However, RIR in these communities is not sufficient to prevent periodic, severe defoliation by "adapted" folivores because its proximate effects on behavior can be overwhelmed by starvation. Even biochemically very different, "nonhost" plants in and near the outbreak communities are stripped of their canopies.

We propose, therefore, that selection pressure by herbivores favors primarily 1) high levels of tolerance to injury, coupled to 2) some form of low cost, highly localized RIR, and finally 3) density-dependent DIR that increases the probability of folivore mortality from natural enemies that build in response to herbivore populations.

Grow and Then Reproduce: an Evolutionarily Stable Strategy?

Is it possible that herbivory in these communities could favor high levels of constitutive defenses, and/or a more powerful, regulatory defensive strategy? We think not. The underlying life history strategy of growth-dominated, shade-intolerant, pioneering plants provides strong physiological and ecological constraints to other evolutionary solutions (Huston and Smith 1987, van der Meijden et al. 1988, Taylor et al. 1990). Competition for light by juvenile plants is so intense that rapid growth coupled to minimal defense systems will always be favored. For example, Makela (1985) concluded that the maximum fitness strategy in a dense, monodominant system will result from first growing as fast as possible and then switching to reproduction when the cost of further height growth is more than the cost of subsequent shading from neighbors. Because all individual plants often establish simultaneously and play by the same fundamental physiological rules, they end up highly synchronized throughout life and even in death (Mueller-Dombois 1987). Their simultaneous, wave-like or cohort-like decline may be a consequence of the entire adaptive syndrome.

CONDITIONS FAVORING THE EVOLUTION OF STRONG DEFENSES

Oligospecies Plant Communities: Stress Adapted Species

Many of the preceding arguments apply also to oligospecies communities in low resource environments. However, the physiological capacity for tolerating and recovering from defoliation may now be substantially less than in high resource environments. This means that the physiological cost of leaf loss and replacement is much higher (*sensu* Givnish 1988). Hence, the adaptive strategy of stress-adapted plants requires a different mix of traits than those of growth-adapted plants (Huston and Smith 1987, Taylor et al. 1990). High rates of growth and leaf replacement are generally not sustainable due to shortages of critical resources (nutrients, water, etc). Therefore, plant emphasis is on the acquisition and efficient use of nutrients, low leaf turnover, and survival during critical drought and stress periods, etc.

Thus, environmentally induced slow growth and longer leaf longevity (in evergreen species) create a high risk of injury from herbivores. At the same time, however, they significantly reduce the opportunity costs of defensive investments (Herms and Mattson 1991). Therefore, it should be adaptive that such plants should protect well their foliage, at least in direct proportion to each foliage cohort's contribution to plant vitality (McKey 1979, Rhoades 1979, Mattson et al. 1988b). There is essentially a dichotomy between stress-adapted deciduous and evergreen species because of the different suites of adaptations that entail each kind of strategy (Bryant et al. 1988, Dickson 1989, 1991, Gower and Richards 1990). For example, the former tend to have higher rates of photosynthesis over a short photosynthetically active period and rely exclusively on storage for fueling each season's early growth. The latter have much lower rates of photosynthesis over a longer period and rely more on current photosynthates and leaf-stored nutrients to support early growth (Dickson 1989, 1991, Sprugel 1989). Foliage loss is more damaging to evergreen species because generally they do not refoliate in response to defoliation, and thus the losses must be integrated over the multi-year life span of such leaves.

Uniform Herbivory Favors Tolerance

A uniform plant community predisposes the plants to expansive outbreak herbivores and so does the wider tree spacing that often occurs on stressful sites. Under these circumstances, herbivore selection pressure still favors the evolution of tolerance to the degree that it is possible (in inverse relationship to the stress adaptation required). However, we hypothesize (Herms and Mattson 1991) that its complement, localized RIR, is not as adaptive in low as in high resource environments because of fundamental physiological and ecological constraints on its efficacious expression (especially in evergreen conifers). Furthermore, unlike the high resource case, folivory will favor additional, purely defensive traits that 1) reduce both the mean background level of herbivory and the likelihood of

herbivore population buildup, and 2) more swiftly stop herbivory once it has exceeded tolerance levels, i.e. a more powerful DIR. In the case of the first, higher levels of constitutive defenses and lower foliar nutritional quality will simultaneously reduce the overall herbivore species loading per plant (see Niemelä et al. 1982, Tahvanainen and Niemelä 1987) and lower the intrinsic rate of population increase of the many fewer adapted herbivore species. As for the second, there is good evidence in at least two deciduous tree-herbivore systems: *Larix decidua*/*Zeiraphera dineana*, and *Betula pubescens tortuosa*/*Epirrita autumnata* (Haukioja 1991). Likewise, the *B. resinifera*/*Rheumaptera hastata* and *P. tremuloides*/*Choristoneura conflictana* systems in Alaska may qualify (Haukioja and Neuvonen 1987.) However, there is yet little substantive evidence for significant DIR in evergreen conifers (see Neuvonen and Niemelä in this volume). If DIR does occur, it is most likely to be manifested in currently produced foliage, which is probably the only leaf tissue physiologically capable of DIR (Leather et al. 1987, Wagner 1988, Buratti et al. 1990, Geri et al. 1990) and in fast growing seedlings and saplings (Karban 1990a, 1990b).

Small Size and Slow Growth Preclude Tolerance Responses

Being very small predisposes young woody plants to the high probability of catastrophic, i.e. fatal, injury from herbivores merely because a small amount of herbivory is capable of devastating small plants. Normally, the risk of such injury would be small because it is spread widely among the vast number of individual seedlings that regenerate in cohort-like waves. However, slow growth compounds this risk significantly in direct relation to the time it takes to outgrow the risk of most such injury. Therefore small, slow growing, woody plants may die unless they use potent, deterrent constitutive defenses.

Polyspecies Plant Communities: Pioneer, Growth-Adapted Species

Selection pressure by herbivores for plant defenses is likely to be much more intense in polyspecies than in monospecies, pioneering communities. Consistent, differential herbivory among individual plants is more probable when the community is comprised of many species of plants. Each species, because of its inherent anatomical/morphological and biochemical uniqueness, tends to have its own suite of herbivores. Even polyphagous insects such as the gypsy moth show obvious host preferences. As a result, the preferred species are defoliated first and usually sustain the highest cumulative defoliation, and consequently, the highest mortality rates over an infestation episode (Crow and Hicks 1990).

In brief, then, the selective pressure from folivores in a polyspecies, pioneering community is likely to be higher and different than in an oligospecies community. This should be expected because interspecies plant competition for light and nutrients will generally lead to different evolutionary adaptations than will primarily intraspecies competition (Aarssen 1989, Keddy and Shipley 1989, Barnes et al. 1990, Connolly et al. 1990).

However, the high growth strategy of such plants entails a suite of correlated physiological and ecological traits that may constrain costly defensive investments. Therefore, we hypothesize that different, but ecologically equivalent, defensive tactics will evolve as a result of plants balancing investments in defenses against growth (including reproduction). The diversity of evolutionary solutions will depend on the number of competing plant species. One solution might be high growth and low constitutive defenses with concomitantly higher species loading per plant, while another might be medium growth with higher standing defense and lower herbivory per plant, and so on. For example, Prins and Nells (1990a, 1990b) and Prins et al. (1989) have elegantly shown that two competing herbaceous plant species can experience vastly different levels of herbivory, and can coexist because of different leaf tissue chemistries and specific elements of their life history strategies.

Defenses Vary in Relation to Intensity of Plant Competition

The strength of the DIR defensive response will vary with the time scale of plant-plant competition. Where interspecific competition is intense (e.g. rich sites) and debilitation over successive growing seasons can cause a serious loss in competitive status, we predict powerful, fast acting defenses that will impact the next generation of the herbivore. At the other end of the continuum, where competition is less intense and debilitation over two growing seasons does not seriously jeopardize an individual's competitive status, then "slower" defenses (within two to three growing seasons) are adequate.

Because competition is not constant over the course of plant ontogeny, constitutive and inducible defenses may also vary with the plant ontogeny in direct relation to competition. For example, per capita mortality rate curves for trees often are believed to be U-shaped, i.e. high mortality due to density independent factors and competition (other trees, shrubs, herbaceous matter, etc.) during the early period of establishment, followed by lower and relatively stable tree-tree competition-induced mortality up to old age, when mortality rates may rise again due to senescence (Harcombe 1987, Clark 1990). Hence, herbivore injury may be more critical in early life when plants are also more susceptible to competitive displacement. At this time, therefore, defenses would be desirable to prevent the compounding negative effects of herbivory. However, they should not come at the expense of competitive capacity (i.e. growth). One solution is escape as implied by Janzen (1970), who predicted that the success of such understory propagules will increase with their distance from parents or like conspecifics. Apparently, this is being borne out in tropical forests (Clark 1986). Other solutions would be low cost defenses such as bioassociations, or low concentrations of highly toxic, deterrent secondary chemicals (Herms and Mattson 1991).

Polyspecies Community: Shade-Tolerant Species

Shade tolerant species in polyspecies communities clearly require stronger defenses. Their strategy, at least in their early years, is often one of competition tolerance, the capacity to endure, to subsist on the meager amounts of light that reach the dimly lit forest understory (Givnish 1988, Taylor et al. 1990). One would expect, based on their unique suite of physiological and ecological traits, that they should also differ markedly from pioneering species in their evolutionary responses to herbivory (Loehle 1988, Taylor et al. 1990). Long periods of slow growth in low light (light stress) require strong defenses to survive prolonged exposure to mammalian and micro-herbivores. Because plant recovery capacity will be very limited, strong, highly effective constitutive defenses that drastically lower the herbivore loading per plant should be highly adaptive.

The capacity of such plants to tolerate herbivory may be so limited that neither localized RIR nor general DIR is a viable evolutionary option for understory plants, at least not until those plants are released from shade stress and growing substantially above their whole-plant, physiological compensation point (Givnish 1988). In fact, when occupying full light (e.g. full canopy position), they may exhibit some of the characteristics of pioneering species. In other words, some plants may have two suites of adaptive syndromes: one when subjected to very low light and the other when subjected to medium-full light and capable of faster growth. Such is apparently the case for sugar maple, *Acer saccharum*, a very shade tolerant tree species in eastern North America (Canham 1989).

Polyspecies Plant Communities: Conversion To Monodominance

Some polyspecies communities can eventually become oligospecies, monodominated communities (if left undisturbed) because of steadily increasing recruitment by species that have the least demand for light. This commonly happens in the Great Lakes Region where sugar maple and balsam fir often assume complete dominance in their respective mixed species forests (in the absence of fire) because of their superior shade tolerance and highly aggressive recruitment under their own canopies (Bourdo

1969, Tubbs 1969). This is also a well-established phenomenon in the world's tropical forests (Hart et al. 1989). Such single-species dominated, late successional forests can eventually become extensive over time. Hence, like the oligospecies, pioneer tree species forests, they may be highly prone to outbreak folivores. However, unlike the pioneer species, the late successional species have evolved in an environmental matrix consisting of polyspecies competition and shade tolerance. Some of the physiological traits needed for success there will likely carry over into those environments where the forest acquires monospecific dominance: stronger constitutive defenses, weaker DIR, lower tolerance capacity. On the other hand, such a plant species may be phenotypically plastic so that it acquires some of the traits of a pioneering tree species when growing monodominantly in full sunlight.

CHARACTERISTICS OF OUTBREAK FOREST SYSTEMS

Oligospecies Forests: Extremes of Shade Tolerance

There are about 85 species of expansive outbreak folivores in North America, but the number of plant systems supporting these insects is substantially smaller, between 30 and 40. Thus, some plant systems support more than one outbreak species: e.g. *A. balsamea*/*Picea* spp.: 4, *A. saccharum*/*Fagus grandifolia*: 5, *Pinus contorta*: 7, *P. tremuloides*: 8, *Pseudotsuga menziesii*: 8, etc. (Appendix 3).

Likewise, some insect species have several races that can reach outbreak proportions in more than one system: e.g. *Malacosoma disstria* in *A. saccharum*, *N. sylvatica*, *P. tremuloides*, and *Quercus* spp. forests.

Almost all these outbreak systems are oligospecies communities dominated by just one or two plant species (e.g. *P. tremuloides*, *Betula papyrifera*, *A. saccharum*/*F. grandifolia*, *Pinus banksiana*, *Pinus ponderosa*, *A. balsamea*, etc.). These species tend to fall largely into either one of two shade tolerance classifications: 1) highly light demanding, i.e. shade intolerant, or 2) highly shade tolerant, and capable of developing into monodominant communities (Appendix 3). This classification may also apply to outbreak forest systems in the tropics (Bruenig and Huang 1989). Some oak species exhibit medium shade tolerance and thus may be an exception.

Predictions of Insect Loading, Outbreak Frequency, Duration

The following predictions can be derived from the preceding discussions of plant life history strategies:

- 1) folivores species loading, and mean level of herbivory should rank as follows: pioneering, growth-adapted species (PGAS) > pioneering, stress-adapted, deciduous species (PSASd) > pioneering, stress-adapted, evergreen species (PSASe) > competition- and shade-tolerance adapted species (CSTS);
- 2) the frequency of outbreaks per unit life span should rank as follows: PGAS > PSASd > PSASe > CSTS;
- 3) the duration of outbreaks should rank as follows: PSASe > PGAS > PSASd > CSAS.

This ranking reflects the limited capacity of some stress-adapted plants, especially evergreen conifers, to exhibit substantive, efficacious inducible defenses of any kind (RIR, DIR) (Bryant et al. 1988, Neuvonen and Niemelä this volume, Herms and Mattson 1991). For example, severe defoliation of evergreen conifers can lead to an increase in adventitious sprouting and a general increase in foliar nitrogen (Batzler 1969, Goyer et al. 1990, Långström et al. 1990, Piene and Little 1990). The net result may ameliorate rather than deteriorate foliage quality for herbivores (Haukioja 1991, Haukioja et

al. 1990) at least until substantial rootlet mortality causes nutrient impoverishment to be more severe than plant carbon limitations.

Outbreak Patterns by Plant Growth and Shade Tolerance Classes

Outbreak Frequency

There is very little information regarding the number of outbreaks that occur during the life span of a given tree species under given site conditions. Instead, most information concerns insect dynamics over broad geographic regions (Myers 1988a). Thus, it is difficult to generate sound generalizations about differences in outbreak patterns among tree species. For most short-lived species (< 125 yrs), the data suggest that at least two outbreak episodes occur, invariably during the second half of the life span of these species. For some longer lived species, such as *P. menzeisii*, several outbreak episodes are likely during the second half of their life span (Swetnam and Lynch 1989). For other species, however, there is not enough information to make any conclusions.

In a few cases, obvious, regular patterns have been recognized in middle-aged to older trees: the apparent 5-year and 10- to 15-year-cycles of *M. disstria* on *Nyssa aquatica* (Goyer et al. 1990), and *P. tremuloides*, respectively (Hodson 1941, pers. observ.), the 10- to 15-year-cycles of *Acleris variaria* (Miller 1966), the 35-40 year cycles of *C. fumiferana* on *A. balsamea* (Royama 1984), and the apparent 10-year-cycles of *Orgyia pseudostugata* and 28-year-cycles of *C. occidentalis* on *P. menzeisii* in British Colombia (Myers 1988a, Shepherd et al. 1988).

Outbreak Duration

Only slightly more information is available about the average duration of outbreaks (Table 2). To look for trends in duration of defoliation by plant life history strategies, we classified insects on the basis of the shade tolerance and the growth rates of their primary host trees (Table 3). Few obvious patterns emerged. This is not altogether surprising, given the vagueness of the available data. Typically, most outbreaks lasted 2 to 3 years, regardless of the host plant's growth/shade classification (Tables 2, 3). However, some unusually chronic cases are associated with conifers and/or leaf miners: *Coleotechnites* spp. on *Pinus contorta* (> 10 yrs), *Pristiphora erichsonii* on *Larix laricina* (> 6 yrs), *Choristoneura* spp. on *Abies* spp. and *P. menzeisii* (> 6 yrs), *Archips argyrospila* on *Taxodium distichum* (> 5 yrs), and the maple leaf cutter, *Paraclemensia acerifoliella*, on *Acer saccharum* (> 4 yrs) (Ross 1962, Struble 1972, Turnock 1972, Swetnam and Lynch 1989, Goyer et al. 1990, see also Neuvonen and Niemelä in this volume).

Effects of Natural Enemies on Outbreak Patterns

Because host effects on folivore population dynamics are naturally confounded with natural enemy effects, it is difficult to tease apart the two (McNamee et al. 1981, Hanski 1987, Goyer et al. 1990). For example, it seems that most outbreak folivores are prone to bacterial, fungal, and viral epizootics that may limit their population outbreaks to about 3 years (Myers 1988a, Shepherd et al. 1988). If it is generally the case that natural enemies limit the duration of outbreaks, then one may have to seek enemy-free conditions to test the true host effects on folivore dynamics. For example, Shepherd et al. (1988) reported that where virus was not evident in *O. pseudotsugata* outbreaks, they either ended quickly by killing the host plants or they lasted for as long as 9-12 years on isolated *Picea* spp. Goyer et al. (1990) concluded that in permanently flooded *T. distichum* and *N. aquatica* wetlands where parasites and predators of folivores are scarce, *A. argyrospila* and *M. disstria* populations cycle continuously in response to foliage depletion. Other authors have also concluded that natural enemy-impoverished habitats are prone to more frequent and severe outbreaks of folivores (Turnock 1972, Hanski 1987, Mason 1987).

Table 2. Average duration (years) of outbreaks by different insects in North America.

Species	Years	Species	Years
<i>Acleris gloverana</i>	2-3	<i>Heterocampa manteo</i>	2
<i>Acleris variana</i>	2	<i>Lambdina fiscellaria lugubrosa</i>	3
<i>Archips argyrospila</i>	5	<i>Malacosoma americanum</i>	2-3
<i>Archips semiferranus</i>	2	<i>Malacosoma disstria</i> ¹	3
<i>Bucculatrix candensisella</i>	2-3	<i>Malacosoma californicum</i>	3-5
<i>Choristoneura conflictana</i>	2-3	<i>Melanolophia imitata</i>	2
<i>Choristoneura fumiferana</i>	5-8	<i>Neodiprion pratti banksianae</i>	2-3
<i>Choristoneura occidentalis</i>	3-6	<i>Neodiprion swaini</i>	3-4
<i>Choristoneura pinus</i>	2-4	<i>Nymphalis californicum</i>	1-2
<i>Coleotechnites milleri</i>	10-20	<i>Orgyia pseudotsugata</i>	1-3
<i>Coleotechnites starki</i>	10-20	<i>Paraclemensia acerifoliella</i>	3-6
<i>Coloradia pandora</i>	6-8	<i>Parorgyia griseifacta</i>	3
<i>Datana integerrima</i>	2	<i>Pristiphora erichsonii</i>	3-20
<i>Dryocampa rubicunda</i>	2	<i>Rheumaptera hastata</i>	2
<i>Heterocampa guttivita</i>	1-3		

Table 3. Comparing the duration of insect outbreaks by tree growth rates and shade tolerance classifications. Each number in the table represents an average outbreak period in years for an insect species that occurs on a host having that growth and shade classification.

Growth rate ²	Low shade tolerance ²	Medium shade tolerance	High shade tolerance
Low	2,3,7,15,15	2,5	2,2,2,4
Medium	2,3,3	2	3,3,3
High	2,2,2,3,3,3,3,3,4,6	n.a.	2,6
Very high	3,3,3	n.a.	n.a.

¹*M. disstria* in aspen forests.

²Data about tree classes derived from Appendix 3.

CLASSIFYING GRAZING SYSTEMS IN NORTH AMERICA

Although there may be only 85 species of outbreak folivores in North America, they annually chew their way through about 7.6 million ha of tree leaves across the United States (USDA, Forest Service). Most of the forests impacted by outbreaks support more than one species of outbreak folivore and sustain at least two severe defoliation episodes. Yet the forests survive, even though in some unique cases most overstory individuals die as a result of the defoliations (e.g. *Choristoneura* spp. on *Abies* spp.). Most vigorous trees, in fact, have the capacity to physiologically tolerate 2 successive years of near complete defoliation of current-year foliage. Moreover, those trees that grow in vast monodominant stands are not subject to the usual interspecies competitive encroachment that occurs during such outbreaks. The following is a partial description of three different types of grazing systems: chronic, coup-de-grâce, and limited systems.

Chronic Grazing Systems: Short-lived, Growth-Adapted Pioneers

In the case of most folivores that do not usually cause tree mortality, we argue that folivory is not so much a mutualistic as it is a commensalistic consequence of the plant's "life-style." Outbreak folivores are inevitable where plants grow in vast, monodominant, largely even-aged, pioneer communities. We label those as "chronic grazing systems," which by virtue of their short lifespan, high growth strategy, and low competition tolerance, cannot make substantive investments in defense. Chronic herbivory can be physiologically tolerated with little or no consequence to the competitive status of individuals--barring compounding stresses such as severe moisture deficits or excesses, and pollution. Such systems would be those dominated by *P. tremuloides*, *B. papyrifera*, *N. aquatica*, and perhaps some intolerant, fast-growing conifers such as *P. banksiana*, interior *P. menzeisii*, and *L. laricina*.

Coup-de-Grâce Grazing Systems: Short-lived, Shade-Tolerant Species--*Abies* spp.

True firs and tortricids appear to be a special case, i.e. a "coup-de-grâce grazing system." For example, the interaction between *C. fumiferana* and *A. balsamea*/*Picea* spp. forests in eastern North America may be highly coevolved because it apparently dates back at least 8,000-10,000 years (Anderson et al. 1986). Clearly, *A. balsamea* is not threatened by its association with *C. fumiferana* even though substantial mortality invariably results when outbreaks occur in mature stands (MacLean 1980). Such mortality increases nonlinearly with the age of the stand, the percentage basal area in balsam and spruce, and the severity of moisture stress (Batzer 1969, MacLean 1980, Hardy et al. 1983, Lynch and Witter 1984, Archambault et al. 1990). In fact, it is likely that the insect enhances balsam's ability to compete with other trees. Being shorter lived, faster growing, and more shade tolerant than its common associates (*P. glauca*, *P. rubens*, *P. mariana*), balsam competes by more rapidly turning over its populations, aided by wind, root, and stem herbivores, and *C. fumiferana* (Sprugel and Bormann 1981, Harcombe 1987, Loehle 1988). The spruces, on the other hand, are much less subject to wind-throw and defoliation-induced mortality (Archambault et al. 1990, MacLean 1980) and compete through their greater persistence (Gordon 1985). However, attaining larger size and older age is not always adaptive where the growing season is cold limited and where soils are shallow and nutrient poor. Givnish (1988) argued that because foliage costs increase substantially with tree height, the whole plant ecological compensation point dictates a smaller stature in resource limited environments.

Limited Grazing Systems: Long-lived, Shade- and Stress-tolerant Species

Shade-adapted species such as *A. saccharum*/*F. grandifolia*, and *Tsuga* spp., as well as the long-lived, stress-adapted species such as some *Quercus* spp., and *Pinus* spp. (e.g. *P. ponderosa*) may have very limited physiological capacity to tolerate severe, prolonged defoliation, especially as they reach

maturity. Hence, we classify systems dominated by these as "limited grazing systems." They are subject to extinction unless defoliation is in some sense limited, either quantitatively or qualitatively.

For example, the evergreen conifers may be able to cope much longer, if new growth is spared and folivory is strictly confined to older age classes of needles as is the case for sawflies (Diprionidae) and some lepidopterans such as the pandora moth, *Coloradia pandora*.

SUMMARY

High growth-adapted, short-lived plant species that form mono- and oligo-dominated systems are most susceptible to and most capable of tolerating chronic defoliation (Table 4). These plants tend to be shade intolerant and invest a very large fraction of their resources into enlargement of their canopies which have high nutrient and low allelochemical levels, i.e. high specific leaf areas.

High stress-adapted species that form mono- and oligo-dominant systems are also very susceptible to but not highly tolerant of chronic, severe defoliation (Table 4). Consequently they ought to have evolved defensive mechanisms to limit the frequency, duration, and the nature of folivory. They will have high levels of foliar allelochemicals, low levels of nutrients, and perhaps a significant delayed inducible defense--at least for deciduous species.

Table 4. Defensive responses³ evolved against folivores by plants that have different life history strategies.

	Monodominant-adapted life history		Polydominant-adapted life history	
	Deciduous	Evergreen	Deciduous	Evergreen
High growth adapted	Tol. high	Tol. med. ⁴	Tol. med.	Tol. low
	Con. low	Con. med.	Con. med.	Con. high
	RIR weak	RIR weak	RIR strong	RIR med.
	DIR weak	DIR weak	DIR strong	DIR med.
High stress adapted	Tol. low	Tol. low	Tol. v. low	Tol. v. low
	Con. high	Con. v. high	Con. v. high	Con. v. high
	RIR weak	RIR none	RIR weak	RIR none
	DIR med.	DIR none	DIR med.	DIR none

³Tol. = tolerance capacity, Con. = constitutive defense level, RIR and DIR = rapid inducible and delayed inducible resistance, respectively.

⁴Med. = medium

Growth-adapted, short-lived, shade tolerant plant species that form polydominant plant systems when young, but monodominant when older, may have the phenotypic plasticity to exhibit a blend of strategies for coping with outbreak folivores. When slow growing in heavy light competition with other species, they may be highly defended against folivores. On the other hand, when older and growing monodominantly they may rely more on tolerance and defenses similar to those of the shade intolerant group.

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APPENDIX 1

Outbreak folivores in North America and their primary host plants.

Genus	Species	Family	Primary host plant
<i>Acleris</i>	<i>gloverana</i>	Tortricidae	<i>Tsuga heterophylla</i>
	<i>variana</i>	Tortricidae	<i>Abies balsamea</i>
<i>Alsophila</i>	<i>pometaria</i>	Geometridae	<i>Quercus</i> spp.
<i>Anacamptodes</i>	<i>ephyraria</i>	Geometridae	<i>Taxodium distichum</i>
<i>Anisota</i>	<i>senatoria</i>	Saturniidae	<i>Quercus</i> spp.
<i>Archips</i>	<i>argyrospilus</i>	Tortricidae	<i>Quercus</i> spp.
	<i>argyrospilus</i>		<i>Taxodium distichum</i>
	<i>semiferanus</i>		<i>Quercus ellipsoidalis</i>
<i>Argyresthia</i>	<i>thuiella</i>	Argyresthiidae	<i>Thuja occidentalis</i>
<i>Argyrotaenia</i>	<i>tubulana</i>	Tortricidae	<i>Pinus contorta</i>
<i>Bucculatrix</i>	<i>canadensisella</i>	Lyonetiidae	<i>Betula papyrifera</i>
<i>Caliroa</i>	spp.	Tenthredinidae	<i>Quercus</i> spp.
<i>Choristoneura</i>	<i>biennis</i>	Tortricidae	<i>Abies lasiocarpa</i>
	<i>conflictana</i>		<i>Populus tremuloides</i>
	<i>fumiferana</i>		<i>Abies balsamea</i>
	<i>lambertiana</i>		<i>Pinus contorta</i>
	<i>occidentalis</i>		<i>Pseudotsuga menziesii</i>
	<i>orae</i>		<i>Abies amabilis</i>
	<i>pinus</i>		<i>Pinus banksiana</i>
	<i>retiniana</i>		<i>Abies concolor</i>
	<i>viridis</i>		<i>Abies concolor</i>
<i>Coleophora</i>	<i>laricella</i>	Coleophoridae	<i>Larix laricina</i>
	<i>serratella</i>		<i>Betula papyrifera</i>
<i>Coleotechnites</i>	<i>milleri</i>	Gelechiidae	<i>Pinus contorta</i>
	<i>starki</i>		<i>Pinus contorta</i>
<i>Coloradia</i>	<i>pandora</i>	Sphingidae	<i>Pinus contorta</i>
	<i>pandora</i>		<i>Pinus jeffreyi</i>
	<i>pandora</i>		<i>Pinus ponderosa</i>
<i>Dasychira</i>	<i>pinicola</i>	Lymantriidae	<i>Pinus banksiana</i>
<i>Datana</i>	<i>integerrima</i>	Notodontidae	<i>Carya illinoensis</i>
<i>Diapheromera</i>	<i>femorata</i>	Phasmatidae	<i>Quercus rubra</i>
<i>Diprion</i>	<i>similis</i>	Diprionidae	<i>Pinus strobus</i>
<i>Dryocampa</i>	<i>rubicunda</i>	Saturniidae	<i>Acer</i> spp.
<i>Ectropis</i>	<i>crepuscularia</i>	Geometridae	<i>Tsuga heterophylla</i>
<i>Ennomos</i>	<i>subsignarius</i>	Geometridae	<i>Carya</i> spp.
<i>Epinotia</i>	<i>meritana</i>	Olethreutidae	<i>Abies concolor</i>
	<i>solandriana</i>		<i>Betula papyrifera</i>
	<i>tsugana</i>		<i>Tsuga heterophylla</i>
<i>Epirrita</i>	<i>autumnata omissa</i>	Geometridae	<i>Tsuga heterophylla</i>
<i>Erannis</i>	<i>tiliaria</i>	Geometridae	<i>Acer saccharum</i>
<i>Fenusa</i>	<i>pusilla</i>	Tenthredinidae	<i>Betula papyrifera</i>
<i>Galenaria</i>	<i>consimilis</i>	Geometridae	<i>Pseudotsuga menziesii</i>
<i>Halisidota</i>	<i>argentata</i>	Arctiidae	<i>Tsuga heterophylla</i>

APPENDIX 1 continued

Genus	Species	Family	Primary host plant
<i>Heterocampa</i>	<i>argentata subalpina</i> <i>guttivita</i> <i>manteo</i>	Notodontidae	<i>Juniperus scopulorum</i> <i>Fagus grandifolia</i> <i>Quercus alba</i>
<i>Hydria</i>	<i>prunivorata</i>	Geometridae Gracillariidae	<i>Prunus serotina</i> <i>Populus tremuloides</i>
<i>Lithocolettis</i>	<i>ontario</i>		
<i>Lambdina</i>	<i>fiscellaria fiscellari</i> <i>fiscellaria lugubrosa</i> <i>fiscellaria somniaria</i> <i>punctata</i>	Geometridae	<i>Tsuga heterophylla</i> <i>Quercus garryana</i> <i>Quercus gambelii</i>
<i>Lymantria</i>	<i>dispar</i>	Lymantriidae	<i>Quercus</i> spp.
<i>Malacosoma</i>	<i>americanum</i> <i>californicum fragile</i> <i>constrictum</i> <i>disstria</i> <i>disstria</i> <i>disstria</i> <i>disstria</i>	Lasiocampidae Lasiocampidae	<i>Prunus serotina</i> <i>Populus tremuloides</i> <i>Quercus douglasii</i> <i>Acer saccharum</i> <i>Nyssa aquatica</i> <i>Populus tremuloides</i> <i>Quercus</i> spp.
<i>Melanolophia</i>	<i>imitata</i>	Geometridae	<i>Pseudotsuga menziesii</i>
<i>Neodiprion</i>	<i>abietis</i> <i>abietis</i> <i>burkei</i> <i>educolis</i> <i>excitans</i> <i>gillettei</i> <i>lecontei</i> <i>nanulus contortae</i> <i>pratti banksianae</i> <i>pratti pratti</i> <i>swaini</i> <i>taedae linearis</i> <i>tsugae</i>	Diprionidae	<i>Abies balsamea</i> <i>Abies concolor</i> <i>Pinus contorta</i> <i>Pinus edulis</i> <i>Pinus taedae</i> <i>Pinus ponderosa</i> <i>Pinus resinosa</i> <i>Pinus contorta</i> <i>Pinus banksiana</i> <i>Pinus virginiana</i> <i>Pinus banksiana</i> <i>Pinus taedae</i> <i>Tsuga heterophylla</i>
<i>Neophasia</i>	<i>menapia</i>	Pieridae	<i>Pinus ponderosa</i>
<i>Nepytia</i>	<i>freemani</i> <i>phantasmaria</i>	Geometridae	<i>Pseudotsuga menziesii</i> <i>Pseudotsuga menziesii</i>
<i>Odontota</i>	<i>dorsalis</i>	Chrysomelidae	<i>Robinia pseudoacacia</i>
<i>Operophtera</i>	<i>bruceata</i> <i>bruceata</i>	Geometridae	<i>Acer saccharum</i> <i>Populus tremuloides</i>
<i>Orgyia</i>	<i>pseudotsugata</i> <i>pseudotsugata</i>	Lymantriidae	<i>Abies grandis</i> <i>Pseudotsuga menziesii</i>
<i>Paraclemensia</i>	<i>acerifoliella</i>	Incurvariidae	<i>Acer saccharum</i>
<i>Parorgyia</i>	<i>griseifacta</i>	Lymantriidae	<i>Pinus ponderosa</i>
<i>Phaeoura</i>	<i>mexicanaria</i>	Geometridae	<i>Pinus ponderosa</i>
<i>Phryganidia</i>	<i>californica</i>	Dioptidae	<i>Quercus lobata</i>
<i>Phyllocnistis</i>	<i>populiella</i>	Gracillariidae	<i>Populus tremuloides</i>

APPENDIX 1 continued

Genus	Species	Family	Primary host plant
<i>Pristiphora</i>	<i>erichsonii</i>	Tenthredinidae	<i>Larix laricina</i>
<i>Rheumaptera</i>	<i>hastata</i>	Geometridae	<i>Betula papyrifera</i>
<i>Sciaphila</i>	<i>simplex</i>	Olethreutidae	<i>Populus tremuloides</i>
<i>Semiothisa</i>	<i>sexmaculata</i>	Geometridae	<i>Larix laricina</i>
<i>Symmerista</i>	<i>albifrons</i>	Notodontidae	<i>Acer saccharum</i>
	<i>canicosta</i>		<i>Quercus alba</i>
<i>Xylomyges</i>	<i>simplex</i>	Noctuidae	<i>Pseudotsuga menziesii</i>
<i>Zeiraphera</i>	<i>hesperiana</i>	Olethreutidae	<i>Pseudotsuga menziesii</i>
	<i>improbana</i>		<i>Larix occidentalis</i>
<i>Zelleria</i>	<i>haimbachi</i>	Yponomeutidae	<i>Pinus ponderosa</i>

Data derived from Furniss and Carolin 1977, Drooz 1985, and others.

APPENDIX 2

Size (ha) and frequency of outbreak areas by different folivore species in the United States during a 28-year period between 1957 and 1987. Derived from Annual Pest Reports by USDA, Forest Service.

Outbreak insect species	Average ⁵ area/episode	Maximum area	Frequency (yrs)	Average ⁶ area/year
<i>Acanthodyla circumcincta</i>	36,437	36,437	1	1,301
<i>Acleris gloverana</i>	3,980	27,530	12	1,706
<i>Acleris variana</i>	39,472	115,789	5	7,049
<i>Alsophila pometaria</i>	82,195	450,607	16	46,969
<i>Anacamptodes vellivolata</i>	20,243	20,243	1	723
<i>Anisota senatoria</i>	1,113	2,105	2	80
<i>Archips argyrospila</i>	19,555	47,773	10	6,984
<i>Archips semifuranus</i>	420,520	1,417,004	6	90,111
<i>Argyresthia thuiella</i>	52,632	52,632	1	1,880
<i>Bucculatrix candensisella</i>	6,073	8,097	2	434
<i>Argyrotaenia gogana</i>	41,970	80,972	3	4,497
<i>Caliroa</i> spp.	735,830	1,336,032	2	52,559
<i>Choristoneura carnana</i>	39,541	52,632	3	4,237
<i>Choristoneura conflictana</i>	362,295	2,631,579	19	245,843
<i>Choristoneura fumiferana</i>	1,384,858	3,103,644	26	1,285,940
<i>Choristoneura lambertiana</i>	26,846	109,717	8	7,670
<i>Choristoneura occidentalis</i>	2,290,445	5,353,610	28	2,290,445
<i>Choristoneura orae</i>	1,923	2,713	2	137
<i>Choristoneura pinus</i>	99,154	379,352	16	56,659
<i>Choristoneura retiniana</i>	152,591	224,049	4	21,799
<i>Choristoneura viridis</i>	43,015	143,320	5	7,681
<i>Coleophora laricella</i>	1,183,240	12,064,777	12	507,103
<i>Coleotechnites milleri</i>	105,457	242,915	13	48,962
<i>Coloradia pandora</i>	6,904	18,016	13	3,205
<i>Croesia albicomana</i>	140,663	323,887	4	20,095
<i>Daschyra pinicola</i>	7,535	25,709	9	2,422
<i>Diaphemorata femorata</i>	19,703	54,656	6	4,222
<i>Diprion similis</i>	974,176	1,943,320	2	69,584
<i>Dryocampa rubicunda</i>	12,551	24,291	2	896
<i>Ennomos subsignarius</i>	300,174	620,243	7	75,043
<i>Epinotia meritana</i>	8,967	47,368	11	3,523
<i>Epinotia solandriana</i>	14,650	59,166	6	3,139
<i>Erannis tiliaria</i>	1,754	4,049	3	188
<i>Galenaria consimilis</i>	1,518	2,429	2	108

⁵Infestation areas summed over the entire United States and divided by frequency (yrs).

⁶Average area x frequency ÷ 28.

APPENDIX 2 continued

Outbreak insect species	Average area/episode	Maximum area	Frequency (yrs)	Average area/year
<i>Halisodota argentata alpina</i>	2,699	4,049	3	289
<i>Heterocampa guttivita</i>	125,586	465,587	14	62,793
<i>Heterocampa manteo</i>	544,356	2,226,721	6	116,648
<i>Hydria prunivorata</i>	85,425	163,968	6	18,305
<i>Ichthyura inclusa</i>	6,680	6,680	1	239
<i>Lambdina anthasaria</i>	17,304	17,304	1	618
<i>Lambdina fiscellaria fiscellar</i>	207	405	2	15
<i>Lambdina fiscellaria somniaria</i>	826	842	2	59
<i>Lambdina fiscellaria lugubrosa</i>	8,085	28,340	8	2,310
<i>Lithocolletis ontario</i>	109,603	209,085	2	7,829
<i>Lithophane antennata</i>	42,510	80,972	2	3,036
<i>Lymantria dispar</i>	774,275	5,263,158	26	718,970
<i>Malacosoma disstria</i>	934,676	13,461,538	28	934,676
<i>Malcosoma californicum fragile</i>	30,476	121,943	16	17,415
<i>Nacophora mexicanara</i>	3,684	6,073	2	263
<i>Neodiprion pratti paradoxicus</i>	422,348	422,348	1	15,084
<i>Neodiprion abietis</i>	7,547	16,194	3	809
<i>Neodiprion educolis</i>	101,215	101,215	3	10,844
<i>Neodiprion excitans</i>	22,901	121,457	6	4,907
<i>Neodiprion gillettii</i>	810	810	1	29
<i>Neodiprion lecontei</i>	908	2,632	6	195
<i>Neodiprion nanulus contortae</i>	2,834	3,239	2	202
<i>Neodiprion pratti banksianae</i>	24,291	36,437	2	1,735
<i>Neodiprion pratti pratti</i>	633,907	1,113,360	4	90,558
<i>Neodiprion taeda linearis</i>	45,443	275,992	9	14,607
<i>Neodiprion tsugae</i>	11,985	28,664	8	3,424
<i>Neophasia menapia</i>	9,075	30,769	8	2,593
<i>Neptyia freemani</i>	904	1,417	3	97
<i>Opheropthera bruceata</i>	60,134	152,227	5	10,738
<i>Orgyia pseudotsugata</i>	36,433	323,887	21	27,325
<i>Paleacrita vernata</i>	5,465,775	10,931,174	2	390,413
<i>Paraclemensia acerifoliella</i>	9,399	24,291	3	1,007
<i>Phyllocnistis populiella</i>	202,429	202,429	3	21,689
<i>Pristiphora erichsonii</i>	85,701	202,429	11	33,668
<i>Rheumaptera hastata</i>	485,946	2,359,919	9	156,197
<i>Sciphila duplex</i>	37,454	68,826	4	5,351
<i>Semiothisa sexmaculata</i>	101,822	202,429	2	7,273
<i>Stilpnotia salicis</i>	3,644	3,644	1	130
<i>Symmerista albicosta</i>	13,360	18,219	2	954
<i>Symmerista canicosta</i>	220,951	526,316	4	31,564
<i>Xylomyges simplex</i>	3,239	3,239	1	116
<i>Zeiraphera griseana</i>	81,344	209,717	6	17,431
<i>Zeiraphera hesperiana</i>	45,142	49,798	2	3,224

APPENDIX 2 continued

Outbreak insect species	Average area/episode	Maximum area	Frequency (yrs)	Average area/year
<i>Zeiraphera improbana</i>	17,465	61,134	4	2,495
<i>Zeiraphera ratzeburgiana</i>	34,818	34,818	1	1,243
<i>Zelleria haimbachi</i>	15,083	69,636	11	5,926
Grand total area/year				7,618,488

APPENDIX 3

Outbreak host plant systems and their outbreak folivores in North America defined by the dominant plant species. Shade tolerance and growth rate classifications,⁷ typical age of mortality from Loehle (1988), and percent host domination of system from various sources, primarily Folwells (1965).

Species	Host plant parameters				Outbreak folivore species
	Shade tolerance	Growth rate	Average age at death	Percent system domination	
<i>Abies amabilis</i>	4	3	400	50	<i>Choristoneura orae</i>
<i>Abies balsamea</i>	5	4	125	50	<i>Acleris variana</i> <i>Choristoneura fumiferana</i> <i>Lambdina fiscellaria fiscella</i> <i>Neodiprion abietis</i>
<i>Abies concolor</i>	5	3	10	50	<i>Choristoneura retiniana</i> <i>Choristoneura viridis</i> <i>Epinotia meritana</i> <i>Neodiprion abietis</i>
<i>Abies grandis</i>	4	3	200	60	<i>Orgyia pseudotsugata</i>
<i>Abies lasiocarpa</i>	5	3	150	65	<i>Choristoneura biennis</i>
<i>Acer saccharum</i>	5	2	300	50	<i>Erannis tiliaria</i> <i>Malacosoma disstria</i> <i>Operophtera bruceata</i> <i>Paraclemensia acerifoliella</i> <i>Symmerista albifrons</i>
<i>Acer rubrum</i>	5	2	150	50	<i>Dryocampa rubicunda</i>
<i>Betula papyrifera</i>	2	4	100	75	<i>Bucculatrix canadensisella</i> <i>Coleophora serratella</i> <i>Epinotia solandriana</i> <i>Fenusa pusilla</i> <i>Rheumaptera hastata</i>
<i>Carya illinoensis</i>	2	3	300	50	<i>Datana integerrima</i>
<i>Carya</i> spp.	2	2	200	n.a.	<i>Ennomos subsignarius</i>

⁷Classes range from 1 to 5, low to high, respectively.

APPENDIX 3 continued

Species	Host plant parameters				Outbreak folivore species
	Shade tolerance	Growth rate	Average age at death	Percent system domination	
<i>Fagus grandifolia</i>	5	2	300	50	<i>Heterocampa guttivita</i>
<i>Juniperus scopulorum</i>	1	2	250	70	<i>Halisidota argentata subalpina</i>
<i>Larix laricina</i>	1	3	150	80	<i>Coleophora laricella</i> <i>Pristiphora erichsonii</i> <i>Semiothisa sexmaculata</i>
<i>Larix occidentalis</i>	1	2	700	70	<i>Zeiraphera improbana</i>
<i>Nyssa aquatica</i>	2	4	80	90	<i>Malacosoma disstria</i>
<i>Pinus banksiana</i>	1	4	80	80	<i>Choristoneura pinus</i> <i>Dasychira pinicola</i> <i>Neodiprion pratti banksianae</i> <i>Neodiprion swaini</i>
<i>Pinus contorta</i>	2	2	120	80	<i>Argyrotaenia tubulana</i> <i>Choristoneura lambertiana</i> <i>Coleotechnites milleri</i> <i>Coleotechnites starki</i> <i>Coloradia pandora</i> <i>Neodiprion burkei</i> <i>Neodiprion nanulus contortae</i>
<i>Pinus edulis</i>	1	1	350	50	<i>Neodiprion educolis</i>
<i>Pinus jeffreyi</i>	2	3	400	80	<i>Coloradia pandora</i>
<i>Pinus ponderosa</i>	2	3	600	70	<i>Coloradia pandora</i> <i>Neodiprion gillettei</i> <i>Neophasia menapia</i> <i>Parorgyia grisefacta</i> <i>Phaeoura mexicanaria</i> <i>Zelleria haimbachi</i>
<i>Pinus resinosa</i>	1	4	200	90	<i>Neodiprion lecontei</i>
<i>Pinus strobus</i>	2	2	200	50	<i>Diprion similis</i>

APPENDIX 3 continued

Species	Host plant parameters				Outbreak folivore species
	Shade tolerance	Growth rate	Average age at death	Percent system domination	
<i>Pinus taedae</i>	2	4	100	70	<i>Neodiprion excitans</i> <i>Neodiprion taedae linearis</i>
<i>Pinus virginiana</i>	2	3	100	80	<i>Neodiprion pratti pratti</i>
<i>Populus tremuloides</i>	1	5	70	80	<i>Choristoneura conflictana</i> <i>Malacosoma californicum fragile</i> <i>Malacosoma disstria</i> <i>Operophtera bruceata</i> <i>Phyllocnistis populiella</i> <i>Lithocolletis ontario</i> <i>Sciaphila simplex</i>
<i>Prunus serotina</i>	2	4	100	50	<i>Hydria prunivorata</i> <i>Malacosoma americanum</i>
<i>Pseudotsuga menziesii</i>	2	4	750	50	<i>Choristoneura occidentalis</i> <i>Galenaria consimilis</i> <i>Nepytia freemani</i> <i>Nepytia phantasmaria</i> <i>Orgyia pseudotsugata</i> <i>Xylomyges simplex</i> <i>Zeiraphera hesperiana</i> <i>Melanolophia imitata</i>
<i>Quercus alba</i>	2	3	300	50	<i>Heterocampa manteo</i> <i>Symmerista canicosta</i>
<i>Quercus douglasii</i>	2	2	100	70	<i>Malacosoma constrictum</i>
<i>Quercus ellipsoidalis</i>	2	2	80	50	<i>Archips semifervans</i>
<i>Quercus gambelii</i>	2	2	90	n.a.	<i>Lambdina punctata</i>
<i>Quercus garryana</i>	2	2	300	n.a.	<i>Lambdina fiscellaria somniaria</i>
<i>Quercus lobata</i>	2	4	200	70	<i>Phryganidia californica</i>
<i>Quercus rubra</i>	3	4	200	50	<i>Diapheromera femorata</i>

APPENDIX 3 continued

Species	Host plant parameters				Outbreak folivore species
	Shade tolerance	Growth rate	Average age at death	Percent system domination	
<i>Quercus</i> spp.	3	3	150	50	<i>Malacosoma disstria</i> <i>Alsophila pometaria</i> <i>Anisota senatoria</i> <i>Archips argyrospilus</i> <i>Caliroa</i> spp. <i>Lymantria dispar</i>
<i>Robinia pseudoacacia</i>	2	4	60	70	<i>Odontota dorsalis</i>
<i>Taxodium distichum</i>	3	2	600	50	<i>Anacamptodes ephyraria</i> <i>Archips argyrospilus</i>
<i>Thuja occidentalis</i>	4	2	300	50	<i>Argyresthia thuiella</i>
<i>Tsuga heterophylla</i>	5	3	400	50	<i>Acleris gloverana</i> <i>Ectropis crepuscularia</i> <i>Epinotia tsugana</i> <i>Epirrita autumnata omissa</i> <i>Halisidota argentata</i> <i>Lambdina fiscellaria lugubrosa</i> <i>Neodiprion tsugae</i>