

RESPONSES OF AN INSECT FOLIVORE AND ITS PARASITOIDS TO MULTIYEAR EXPERIMENTAL DEFOLIATION OF ASPEN

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Abstract. Foliage quality may decline in deciduous trees following defoliation, thus affecting the insect generation responsible for the herbivory (rapid induced resistance, RIR), or future generations (delayed induced resistance, DIR). During outbreaks, trees often suffer partial or complete defoliation for two or more successive years, yet most studies have examined induced resistance following only one season of defoliation, which may not reveal its full impact on herbivores. In a field experiment, 40 trees from each of two clones of trembling aspen, *Populus tremuloides*, were severely defoliated for one, three, and four years in succession by experimentally manipulating densities of an outbreak folivore, the forest tent caterpillar, *Malacosoma disstria*. Treatments were applied such that the individual and combined effects of RIR and DIR on the fitness of the forest tent caterpillar could be assessed independently.

In field assays, defoliation treatments did not affect larval development time and only marginally affected survival. However, fecundity in both clones was significantly reduced by a single season of defoliation concurrent with the bioassay (effects of RIR), by three consecutive years of defoliation prior to the year of the bioassay (effects of DIR), and by four consecutive years of defoliation (combined effects of RIR and DIR). There were no differences among the three defoliation treatments, indicating that the effects of DIR and RIR combined were not greater than each acting alone. Reductions in fecundity were less than half those observed during natural outbreaks, suggesting that other factors also must contribute to declining fecundity during the collapse of outbreaks.

Short-term laboratory bioassays indicated that defoliation effects observed in long-term field assays were not due to changes in relative growth rate (RGR) of second instars or final-instar males, which were unaffected, possibly because of increased relative consumption rates (RCR). Defoliation treatments decreased RGR of final-instar females in laboratory bioassays, despite elevated RCR.

Both defoliation treatment and aspen clone influenced parasitism by tachinid flies that detect hosts through volatiles released from leaves damaged by caterpillars. Parasitism was highest on trees defoliated concurrently with the larval bioassay. However, there were no differences between trees defoliated prior to the bioassay and control trees, indicating that effects on parasitism were not due to defoliation-induced changes in host quality per se. Thus, there were no additive interactions between DIR and parasitism that would amplify delayed density-dependent effects on population dynamics. Spatial responses of these tachinids to host density or to current defoliation rather than the defoliation history of the trees may enhance the stabilizing effect of RIR on population dynamics. Conversely, differences in parasitism among clones could contribute to spatial variation in tent caterpillar population density. Neither defoliation effect on host quality nor parasitism was sufficient to slow reproductive rates to levels observed in declining outbreaks in nature, suggesting that single-factor explanations for tent caterpillar population dynamics are unlikely.

Key words: defoliation; induced resistance; *Malacosoma disstria*; parasitoids; plant–herbivore interactions; population dynamics; *Populus tremuloides*; tachinid flies; tent caterpillars; top-down and bottom-up; tritrophic.

INTRODUCTION

Defoliation-induced reduction in foliage quality is one of several mechanisms potentially responsible for

population cycles of outbreak forest Lepidoptera (Berryman et al. 1987, Haukioja 1991). In response to defoliation, two classes of induced resistance are recognized in deciduous trees, based on their effects on herbivore population dynamics (Haukioja 1991, Neuvonen and Haukioja 1991). Rapid-induced resistance (RIR) is expressed within hours or days of herbivory, affecting the herbivore generation responsible for the damage, and thus should exert a stabilizing influence

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on populations. In contrast, delayed-induced resistance (DIR) is not manifested until the following growing season(s), affecting only future generations of herbivores (Haukioja 1991). Reduction in foliage quality followed by a time lag in the recovery of defoliated trees may destabilize populations through delayed density-dependent effects on insect survival and fecundity, thus generating population cycles (e.g., Benz 1974, Rhoades 1983, Haukioja 1991). When modeled, cycles are generated if there is a sufficient time lag before maximum induction, or if relaxation of DIR is sufficiently protracted following induction (Underwood 1999).

Defoliation can decrease leaf quality for herbivores by inducing phytochemical changes, including elevated levels of secondary compounds such as hydrolyzable and condensed tannins, and/or reductions in primary nutrients such as nitrogen and water (Neuvonen and Haukioja 1984, Tuomi et al. 1984, 1990, Haukioja et al. 1985a, b, Rossiter et al. 1988, Clausen et al. 1989, 1991, Kaitaniemi et al. 1998). These changes in host quality can persist into subsequent growing season(s), and may not relax for several years (Tuomi et al. 1984, Haukioja and Neuvonen 1985, Neuvonen et al. 1987, Clausen et al. 1991, Bryant et al. 1993). Fecundity of insects feeding on previously defoliated trees may be reduced by 60–80%, although smaller effects have been more common (Haukioja and Neuvonen 1985, Rossiter et al. 1988, Ruohomäki et al. 1992, Kaitaniemi et al. 1999a, b).

During outbreaks of forest insects, trees are often defoliated for at least two successive years (see e.g., Mattson et al. 1991). However, most studies have quantified DIR after only a single year of defoliation, even though consecutive years of defoliation may have cumulative effects on host quality (Haukioja et al. 1988, Kaitaniemi et al. 1999a). In some multiyear studies, each successive year of defoliation had increasingly negative effects on insect performance (Werner 1979, Wallner and Walton 1979, Valentine et al. 1983, Clausen et al. 1991), whereas no cumulative effects were detected in others (Kaitaniemi et al. 1999a, Parry 2000). These disparities may reflect variation in experimental methods, study systems, and environmental factors, and underscore our limited understanding of the cumulative effects of defoliation on herbivores.

Trembling (quaking) aspen, *Populus tremuloides* Michx., the most widely distributed tree in North America, is a fast-growing, early-successional species (Perala 1990) prone to expansive insect outbreaks (Mattson et al. 1991). Although it does reproduce sexually, clonal propagation is common, with sprouts from parental rootstock generating large, even-aged stands with relatively low genetic diversity (Barnes 1969, Peterson and Peterson 1992). This life-history strategy, coupled with low probability of escaping defoliation during outbreaks, led Mattson et al. (1991) to suggest that aspen should deploy particularly effective induced responses

to herbivory, coupled with a high degree of tolerance to defoliation. *Populus* species are highly tolerant of defoliation (Duncan and Hodson 1958, Rose 1958, Kruger et al. 1988, Robison and Raffa 1994, Reichenbacher et al. 1996). However, the effectiveness of induced resistance, especially DIR, against its key herbivores remains an open question (Clausen et al. 1991, Roth et al. 1998, Osier and Lindroth 2001).

Large-scale outbreaks of several species of Lepidoptera occur in aspen. Of these, forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), a native species, defoliates more aspen annually than any other insect (Mattson et al. 1991). Outbreaks of this folivore occur at ~10-year intervals (range 6–16 years), often defoliating aspen stands for three or more years before subsiding (Hodson 1941, Hildahl and Reeks 1960, Sippell 1962, Ives 1971, Witter et al. 1975, Hodson 1977). Forest tent caterpillar fecundity can decline by $\geq 50\%$ over the duration of an outbreak (Ives 1971, Witter et al. 1975, Batzer et al. 1994). Sublethal levels of pathogens, especially nuclear polyhedrosis virus (NPV), have been postulated as the mechanism underlying fecundity declines (Rothman and Myers 1994, Myers and Kukan 1995, Rothman 1997), although evidence is equivocal. Alternative mechanisms that may reduce fecundity during outbreaks, such as changes in host quality elicited by repeated defoliation, have not been adequately investigated.

Plants damaged by feeding can emit chemical signals attractive to natural enemies of caterpillars (e.g., Eller et al. 1988, Turlings et al. 1993, Thaler 1997). Although research has focused on agricultural crops, similar tritrophic interactions have been identified in trees (e.g., Odell and Godwin 1984, Roland et al. 1995, Havill and Raffa 2000). Several species of parasitoids may be integral to both spatial and temporal variation in forest tent caterpillar population densities (Sippell 1957, Witter and Kulman 1979, Parry 1995, Parry et al. 1997, Roland and Taylor 1997). A number of these parasitoids utilize volatiles released from leaves damaged by larval feeding as kairomones for locating hosts (Bess 1936, Mondor and Roland 1997, 1998). Therefore, interactions between parasitoids and defoliation-induced responses may have significant effects on forest tent caterpillar population dynamics.

The objective of our study was to emulate interactions between forest tent caterpillar and aspen during outbreaks. Trees from two ontogenetically mature (flower-producing) clones were severely defoliated by forest tent caterpillars for one, three, or four consecutive years by manipulating larval densities. We used field assays to quantify effects of RIR, DIR, and RIR + DIR combined on forest tent caterpillar survival, fecundity, and development time. Additional insight into the effects of defoliation treatments on host quality was gained from measurement of larval growth rates and nutritional indices in short-term laboratory bioassays. To address potential interactions between in-

duced resistance and top-down factors, we assessed parasitism of forest tent caterpillar by two species of tachinid flies in each of the treatments.

MATERIALS AND METHODS

Experimental system

The study was conducted in an early-successional forest (~15 years old) dominated by sugar maple (*Acer saccharum*), red maple (*A. rubrum*), northern red oak (*Quercus rubra*), and aspen growing adjacent to a mature woodlot at Michigan State University (East Lansing, Michigan, USA). Two aspen clones were selected based on leaf morphology, phenology of budbreak, and autumnal senescence. Experimental trees were standardized with respect to height, aspect, exposure, and canopy volume. Budbreak differed between clones by 4–5 days each year. The clones were similar with respect to drainage, insolation, and proximity to mature forest.

In March 1997, 20 trees from each clone were selected for the experiment (mean diameter at 1 m = 3.4 cm, mean height = 3.7 m). To our knowledge, these trees experienced no significant defoliation prior to this study. The adjoining mature forest is heavily utilized for instruction, and any significant defoliation would have been reported. In 1996 (the year prior to the study), we noted typical background herbivory (~10%), indicating that control trees were free of significant defoliation for at least five years prior to our insect bioassays in 2000.

Implementation of treatments

In the initial year of the experiment (1997), 10 of 20 trees in each clone were randomly assigned to the defoliation treatment and subsequently were defoliated by tent caterpillars in 1997, 1998, and 1999, whereas the other 10 trees in each clone received no experimental defoliation during this period. In 2000, five of the 10 trees in each clone defoliated from 1997 to 1999 were not defoliated, whereas the other five were defoliated for a fourth consecutive year. Five additional trees in each clone were defoliated for the first time in 2000. This treatment structure allowed for simultaneous testing for RIR (DEF 00; trees defoliated for the first time in 2000 concurrent with insect bioassays), DIR (DEF 97-99; trees defoliated for three previous years but not defoliated in 2000, the year of the insect bioassays), and the combined effects of DIR + RIR (DEF 97-00; trees defoliated for four consecutive years, including defoliation concurrent with bioassays in 2000). Control trees (CONTROL) were kept free of tent caterpillar herbivory, with the exception of bioassay larvae reared on the trees in 2000.

To implement the defoliation treatments, we collected tent caterpillar eggs from aspen stands in Cochrane, Ontario, Canada (1997, 1998), Flin Flon, Manitoba, Canada (1999), and Ontonagon, Michigan, USA

(2000). Pathogens were eliminated from egg surfaces through removal of spumaline (an accessory gland secretion covering egg masses) with a razor blade, immersion and agitation in 4% bleach with a small amount of detergent for 3 min, followed by a 1-h rinse in distilled water (modified from Williams et al. 1996).

After surface sterilization, eggs were overwintered at 4°C in plastic bags at ~80% relative humidity. Concurrent with bud swell in spring, we placed 5–10 egg bands (~200 eggs/band) in cheesecloth packages at room temperature until shortly before hatch and then refrigerated them until budbreak. As bud scales separated, we attached 3–6 packets of eggs to branches on trees selected for defoliation treatments. These eggs hatched within two days, closely approximating natural synchrony between aspen and forest tent caterpillar (see Parry et al. 1998).

Treatment trees were 50–70% defoliated by instars 1–4, similar to levels found in natural outbreaks. Forest tent caterpillars wander extensively in the fifth (final) instar, and densities are high enough in natural outbreaks that all remaining aspen foliage is consumed. In our plots, final instars dispersed into the surrounding forest. To achieve uniform, high levels of defoliation (>70%) among replicate trees, two to four groups of 30–60 final instars were enclosed in mesh sleeve cages (70 × 30 cm) on branches where foliage remained. It is possible that the sleeves themselves may have enhanced induced responses in the trees, although we consider this unlikely, given the severity of the repeated defoliation treatments as well as natural disturbances such as wind, rain, and arboreal vertebrates. In addition, all trees received a sleeve cage containing bioassay larvae, as we will describe. These sleeves were moved frequently throughout the larval period, and all were moved on the same day. Thus, the extra sleeves associated with the defoliation treatments represented only a short-term increase in bagging over that experienced by control trees. Other studies have found no effect of sleeve cages, even when they are left in place much longer than in our experiment (Rossiter et al. 1988, Hanhimäki and Senn 1992). Larvae in the additional sleeves were not used in any bioassay. Wandering larvae were prevented from ascending the trunk of control trees by tree wrap coated with a band of Tanglefoot (Tangletrap, Grand Rapids, Michigan, USA).

In the defoliation treatments, herbivory was severe (70–100%) and was easily estimated visually using 10% increments. To more accurately estimate background herbivory on undefoliated trees in 2000, damage was quantified for two dominant lateral branches in the midcanopy. Beginning at the branch tip, the first 50 leaves were classified as undamaged if they were intact, suffered minor blemishes, and had <20% of the surface area removed. On undefoliated trees in 2000, 18% and 20% of leaves had some damage in Clone 1 and Clone 2, respectively. In contrast, 100% of the

leaves remaining on the defoliated trees were classified as damaged in each clone. Similar visual estimates were highly correlated with damage assessments of individual leaves on the same trees in another species of *Po-pulus* (Parry 2000).

Insect bioassays conducted in 2000

Field bioassay.—In 2000, we used field assays to estimate effects of previous and current-year defoliation on insect fitness by rearing forest tent caterpillar larvae from egg hatch through adult on each of the 40 experimental trees. Larvae for the bioassay were obtained from egg bands collected in the previous fall from aspen in Ontonagon County, Michigan, USA. The egg bands were large (150–200 eggs), indicating a growing population with little previous stress (the ratio of current-year to previous-year egg bands was 128:27 for three sampled trees).

Two days before budbreak (adjusted to synchronize caterpillars to the 5-day difference in phenology between the aspen clones), 45 egg bands were surface sterilized as previously described, and were held at room temperature until hatch. The progeny from all egg bands were allowed to mingle in a plastic container for 24 h, after which 30 neonates were randomly allocated to each experimental tree. Because neonates could escape through the mesh of the screen cages, they were reared in the laboratory (18°C, L:D photoperiod of 16:8 h) on foliage clipped from their assigned tree until the end of the first instar. Under these conditions, larvae grew at the same rate as those in the field. Twigs were cut under water and inserted into florist's aquapicks to maintain leaf turgor.

Following the first molt, each group of 30 larvae was confined to a branch on its assigned tree within a large mesh sleeve as previously described. While the larvae were small (second to third instar, L2–L3), sleeves were moved to new branches every 2–3 days to emulate the nomadic movement of natural feeding groups (Fitzgerald and Costa 1986). After the third molt, sleeves were moved more frequently, and nearly daily through the final instar. Frequent movement of sleeves ensured that caterpillars were feeding on foliage representative of the quality of the overall tree. Sleeve cages were always moved well before foliage was depleted.

At pupation, sleeve cages were returned to the laboratory, where pupae were promptly extracted from cocoons, weighed (to 0.1 mg), and held individually in vials (22°C and L:D photoperiod 16:8 h) until adult eclosion, when their sex and date of emergence were recorded.

To estimate treatment effects on fecundity, we reared caterpillars through pupation on nearby aspens. Pupae were weighed and held individually in vials until adults emerged. Using the methods of Parry et al. (2001), adult females were dissected, the egg complement was counted, and a regression equation relating fecundity

to pupal mass was derived ($y = 390.85x - 19.11$, $R^2 = 0.88$, $df = 24$, $P < 0.0001$).

Laboratory bioassay.—To gain insight as to how defoliation-induced changes in host quality may have affected larval performance in the field assay, we also conducted short-term laboratory bioassays with second and fifth instars. Neonates from 40 egg bands were mixed and several hundred were placed on neighboring non-experimental aspen trees as they were breaking bud. For the L2 bioassay, caterpillars were retrieved from the field when first instars congregated to molt. Foliage was clipped at the base of the petiole throughout the midcanopy of each experimental tree. Laboratory assays have been criticized because the quality of detached leaves may differ from that of intact foliage (Wolfson 1988). However, Osier et al. (2000) showed that the growth of laboratory-reared gypsy moth, *Lymantria dispar*, larvae on aspen foliage clipped at the petiole was highly correlated with the growth of caterpillars reared in bags on the same trees, indicating that clipping in this fashion did not substantively change host quality. Only leaves from determinate shoots (aspen produces both determinant and indeterminate shoots) were used in our short-term bioassays.

Foliage was placed in zip-lock bags on ice, returned to the laboratory, weighed, and placed in 125 × 50 mm plastic Petri dishes, which contained a plaster base saturated with water that maintained humidity and leaf turgor over the 2–3 day duration of the bioassays. Groups of second instars ($n = 12$) were randomly allocated to foliage from each of the 40 trees. The bioassay was conducted in an environmental chamber (23°C, 16:8 photoperiod) until the fastest growing groups ceased feeding prior to second molt (Clone 1, 51 h; Clone 2, 42 h). Remaining leaves and frass were collected, dried at 40°C for 5 d, and weighed. Relative growth and consumption rates of L2 larvae were calculated as we will describe for L5 larvae.

The L5 bioassays were conducted as described for the L2 bioassay. Fourth instars were collected from the field just prior to molting. Four newly molted L5's (two males and two females as identified from initial body mass; males 125–190 mg, females 190–250 mg) were reared individually for 72 h at 24°C on leaves collected from their assigned tree. After the bioassay, larval gender was confirmed as described in Stehr and Cook (1968). Caterpillars, frass, and uneaten foliage were collected, dried, and weighed.

Relative growth and consumption rates were calculated according to Gordon (1968). Fresh and dry mass values of 15 L5's from the same population were used to generate a regression equation for estimating initial dry mass of bioassay larvae. To estimate initial leaf dry mass for determining consumption rates, a portion of the leaves collected from each tree was dried before the experiment started and was used to obtain a fresh mass : dry mass conversion factor for each tree. Approximate digestibility of ingested food (AD) and ef-

efficiency of conversion of digested food to biomass (ECD) were measured gravimetrically following the methods of Waldbauer (1968). Caterpillars that died or did not feed were excluded from analyses.

Survival and parasitism.—Survival was assessed in the field bioassay as the proportion of larvae that pupated. To assess treatment effects independently of parasitism, we included all caterpillars that were parasitized and died as pupae. The effects of parasitism on survival were addressed separately (as we will describe).

Mortality was partitioned among parasitoids and unknown causes. Preliminary sampling showed the most abundant larval parasitoids of forest tent caterpillar to be the tachinids *Patelloa pachypya* and *Leschenaultia exul*, which is also true in other northern aspen forests (Sippell 1957, Witter and Kulman 1979, Parry 1995). Both flies oviposit microtype eggs on foliage, which are then ingested by larvae. Thus, sleeve cages need only enclose foliage where eggs have been deposited for parasitism to occur. Given the frequent and simultaneous rotation of sleeve cages in all our treatments, all bioassay larvae had equal probability of ingesting eggs. At pupation, sleeves were searched thoroughly for parasitoids that had emerged, which were then reared individually, as were those emerging from pupae. Parasitoids were identified using Sippell (1961) and Williams et al. (1996).

To address the relative effects of induced resistance and parasitism on population growth, approximate net reproductive rate (R_0) was estimated for each treatment. To simplify calculation, males were converted to female equivalents using the regression equation $y = 2.0798x - 0.1484$ ($R^2 = 0.67$, $df = 40$, $P < 0.001$), estimated from mean male and female pupal mass for each tree. Insects dying from causes other than parasitism (parasitized larvae were scored as survivors) were subtracted from the original 30 insects in each cohort to estimate survival, and were then multiplied by the mean fecundity in each treatment to determine R_0 (Southwood 1991). Fecundity was estimated using the pupal mass/fecundity regression previously calculated. Scoring parasitized larvae as survivors allowed us to separate the direct effects of defoliation-induced changes in host quality on R_0 from indirect effects of parasitoids by estimating R_0 with and without including parasitized individuals in the calculations.

Statistical analyses

A mixed-model ANOVA was used in all statistical analyses where $Y_{ijk} = \mu + C_i + D_j + T_k(C_i) + (C_i \times D_j) + \varepsilon_{ijk}$, where C_i is the aspen clone, D_j is the defoliation treatment, and T_k is the replicate tree. Aspen clone was considered a random effect and defoliation treatment a fixed effect in this model. F tests for defoliation treatment, clone $\times$ defoliation treatment, and tree(clone) were over the mean square error. Clone was tested over the $C_i \times D_j$ interaction. The PDIF option

following the LSMEANS statement (PROC GLM, SAS Institute 2000) was used to make preplanned, pairwise comparisons of treatment means within a clone and between the same treatments among clones. Individual trees were the experimental unit; thus all analyses were done using the tree-specific means for each measure of tent caterpillar performance. Prior to analysis, data were checked for normality (Shapiro-Wilk w statistic, $P < 0.05$) and homoscedasticity. Proportional and percentage data (nutritional indices, survival, and parasitism) were arcsine square-root transformed prior to analysis.

RESULTS

Effects of defoliation on larval growth

Field bioassay.—In bioassays encompassing the larval stage of forest tent caterpillars, pupal mass of females (and thus fecundity) and males was significantly lower in all three defoliation treatments than on undefoliated control trees (Fig. 1). However, pupal mass of either sex did not differ among the three defoliation treatments. Mean pupal mass of males and females was highly correlated among trees ($n = 40$, $r = 0.82$, $P < 0.001$). A single year of defoliation concurrent with the bioassay significantly reduced the pupal mass of females by 8% and 21% (reduction of 23 and 56 eggs) in Clones 1 and 2, respectively. Three consecutive years of defoliation prior to the bioassay, reduced female pupal mass by 13% and 18% (reduction of 34 and 49 eggs) in clones 1 and 2, respectively. Three years of previous defoliation, coupled with an additional year of defoliation concurrent with the bioassay, decreased female pupal mass by 20% (reduction of 51 and 55 eggs) on trees in both clones. Despite reductions in pupal mass, the duration of development from egg to adult was not affected by defoliation for either sex (Fig. 2). Host quality varied among clones. Female pupal mass was lower on Clone 2, although there was no effect on male pupal mass (Fig. 1). Development times of both males and females were longer on Clone 2 (Fig. 2).

Laboratory bioassays (second and fifth instars).—Defoliation treatments had no effect on relative growth (RGR) of second instars, and only a marginally significant effect on relative consumption rate, RCR (Fig. 3). RGR was higher and RCR was lower on Clone 2. There was no interaction between treatment and clone, or any effect of trees within clones on RGR of second instars.

Defoliation increased RCR and decreased RGR of L5 females (Table 1, Fig. 4), possibly due to the reduced ability of larvae to convert digested food to biomass (ECD), as defoliation had no effect on approximate digestibility (AD). Interestingly, aspen clone had an effect on RGR of L5 females opposite that of second instars, with Clone 1 supporting higher growth. There were no significant effects of clone on RCR, AD, and

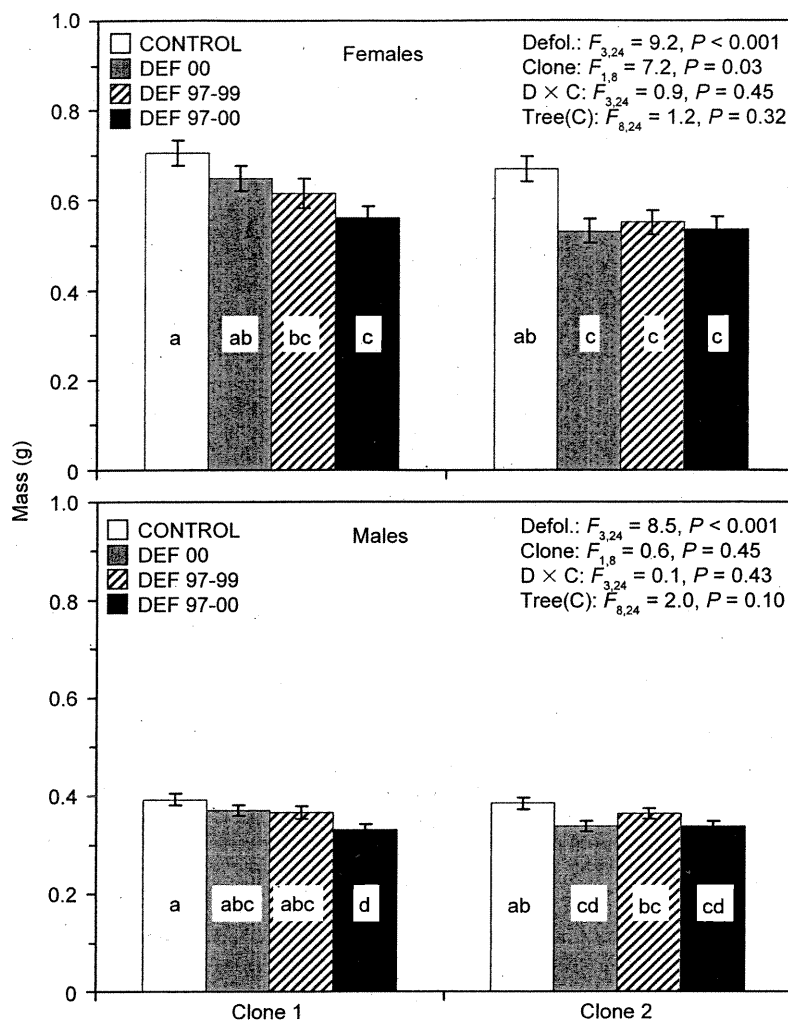


FIG. 1. Effect of defoliation treatments and aspen clone on pupal mass (mean $\pm$ 1 SE) of female and male forest tent caterpillars reared from egg hatch on aspen trees. Different letters indicate significant ($P < 0.05$) pairwise differences between means following a significant main effect of defoliation or clone. Preplanned comparisons were among treatments within a clone, and the same treatments among clones. Treatments are CONTROL, Control (undefoliated); DEF 00, one year of defoliation concurrent with the bioassay; DEF 97-99, defoliation for three consecutive years previous to the year of the bioassay; and DEF 97-00, four consecutive years of defoliation, including the year of the bioassay. F tests for the fixed effects Defoliation, Clone $\times$ Treatment, and Tree(Clone) were over mean square error. The F test for Clone, a random effect, was over mean square for Tree(Clone). Males and females were analyzed separately.

ECD. In contrast to females, there were no defoliation or clone effects on L5 males (Table 1, Fig. 4).

Effects of treatments on survival and parasitism

Survival of larvae from egg hatch to pupation was high (78%, $n_{\text{original}} = 1200$), and was affected only marginally by defoliation and clone (Fig. 5). Mortality in the sleeve cages was classified as unknown if parasitoids (hymenopteran cocoons or dipteran puparia) were not found, although predaceous bugs (Hemiptera: Pentatomidae) that attacked larvae through the mesh cages were likely to be the primary

cause. There was no obvious mortality from NPV or other pathogens.

Larvae were attacked by several species of parasitoids, with 78% of total parasitoid mortality being caused by the tachinids *L. exul* and *P. pachypyga*. Parasitism of the bioassay larvae by other species was low, partly because they were inaccessible to species that attack larvae directly. For example, the tachinid *Lespesia frenchii*, which oviposits on the integument, parasitized 2% of bioassay larvae, but $>30\%$ of late instars on trees near the plots. A small percentage ($<1\%$) of larvae were parasitized by *Meteorus* sp. and *Hyposoter*

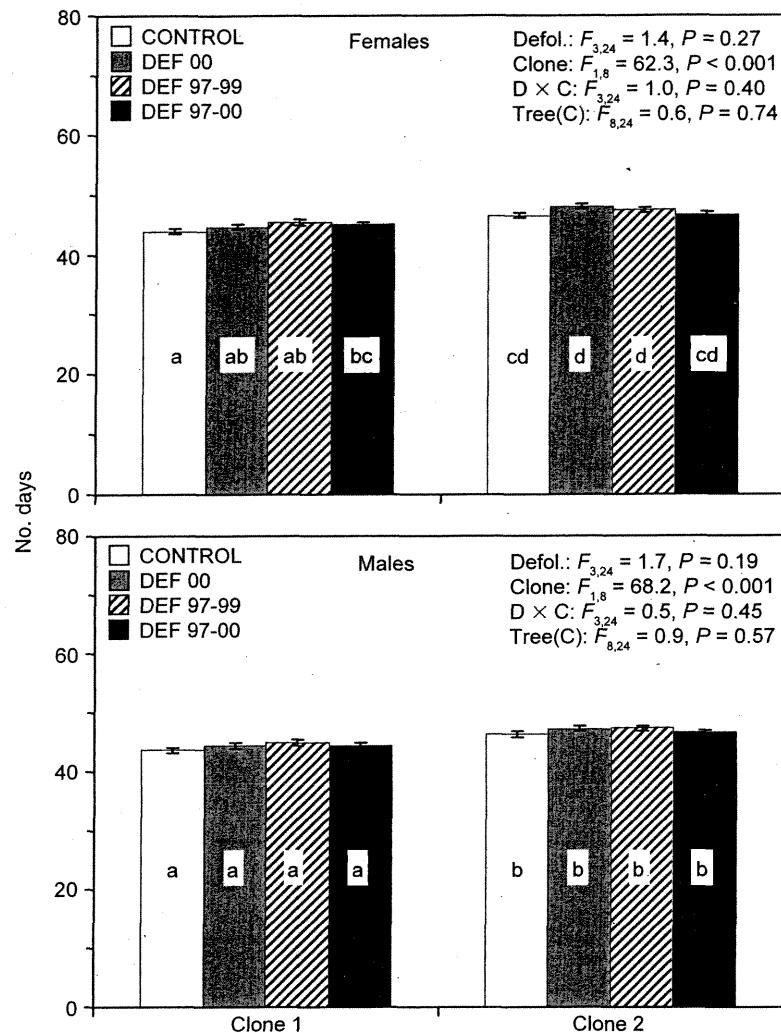


FIG. 2. Effect of defoliation treatments and aspen clone on development times (mean $\pm$ 1 SE) of female and male forest tent caterpillars reared from egg hatch on aspen trees. Different letters indicate significant ($P < 0.05$) pairwise differences between means following a significant main effect of defoliation or clone. Preplanned comparisons were among treatments within a clone, and the same treatments among clones. Treatments are as in Fig. 1. The F test for Clone, a random effect, was over mean square for Tree(Clone). Males and females were analyzed separately.

fugivitus (Hymenoptera: Braconidae) both inside and outside the sleeves.

Parasitism of bioassay larvae by *L. exul* and *P. pachypyga* varied with defoliation treatment, with the highest rates occurring on DEF 00 and DEF 97-00 trees, which were defoliated concurrently with the bioassay (Fig. 6). Trees in these treatments had high larval densities (>1000 larvae) in 2000, relative to the undefoliated DEF 97-99 and CONTROL treatment trees (≤ 30 larvae). Parasitism did not vary between the DEF 97-99 and CONTROL treatments. Parasitism was positively correlated with the percentage of defoliation for *L. exul* ($r = 0.54$, $df = 40$, $P < 0.001$) and *P. pachypyga* ($r = 0.52$, $df = 40$, $P < 0.001$). The effect of clone was significant only for *L. exul*.

Parasitism decreased the approximate reproductive rates (R_0) of forest tent caterpillar by as much as two-fold beyond the effects of defoliation alone (Table 2). On Clone 1, additional negative effects of parasitism on R_0 beyond those of defoliation effects on host quality ranged from 15% to 25%. In Clone 2, parasitism reduced R_0 by an additional 41% beyond the effects of current-year defoliation, and 30% beyond the combined effects of current and previous defoliation.

DISCUSSION

Severe defoliation elicited both rapid (RIR) and delayed induced resistance (DIR) in aspen. All three defoliation treatments reduced the growth and pupal mass (and thus the fecundity) of forest tent caterpillars rel-

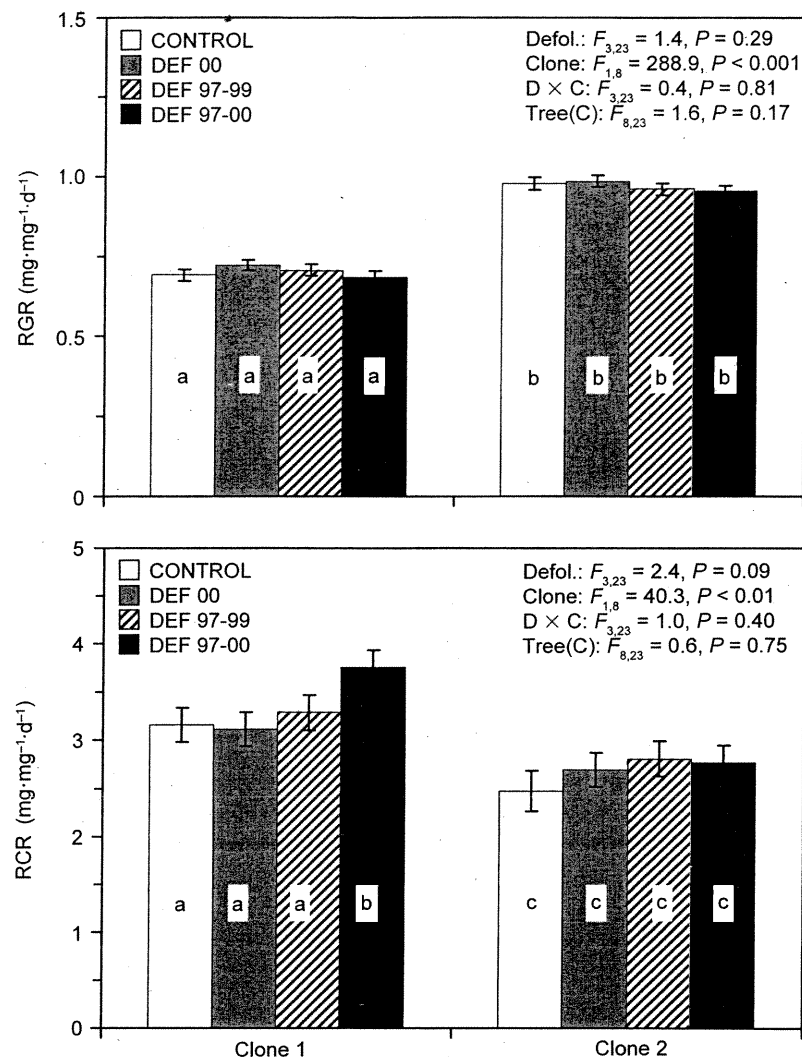


FIG. 3. Mean (± 1 SE) relative growth rates (RGR) and relative consumption rates (RCR) for second-instar forest tent caterpillars. Different letters indicate significant ($P < 0.05$) pairwise differences between means following a significant main effect of defoliation or clone. Preplanned comparisons were among treatments within a clone, and the same treatments among clones. Treatments are as Fig. 1. F tests for the fixed effects Defoliation, Clone $\times$ Treatment, and Tree (Clone) were over mean square error. The F test for Clone, a random effect, was over mean square for Tree(Clone). One control tree in Clone 2 was inadvertently excluded during setup, resulting in 38 total degrees of freedom.

ative to control trees. Contrary to expectation, the effects of a single year of defoliation (RIR) did not differ from treatments of three years of defoliation prior to the year of the bioassay (DIR), or four consecutive years of defoliation, including defoliation concurrent with the bioassay (DIR + RIR).

A single season of defoliation elicited RIR that had surprisingly strong effects on larval growth. In previous studies, the effects of RIR on forest tent caterpillars have been weak or nonexistent. For example, Roth et al. (1998) found no effect of defoliation, and Cappuccino et al. (1995) actually found a slight increase in pupal mass. Conversely, Robison and Raffa (1997) showed that prior feeding by forest tent caterpillars

reduced the growth rate of second instars, although the amount of defoliation and growth rate were not correlated. Defoliation of poplar by gypsy moths (*Lymantria dispar*) reduced pupal masses of forest tent caterpillars feeding on the same trees by 10% (Parry 2000).

Differences in the timing, severity, and type (manual vs. insect) of defoliation could explain variation among studies. Roth et al. (1998) observed that changes in aspen phytochemistry induced by forest tent caterpillars occurred primarily in response to feeding by final instars, which account for 80% of total leaf consumption (Hodson 1941). During their fourth-instar bioassay, differences in phytochemistry between control and

TABLE 1. ANOVA of relative growth rate (RGR), relative consumption rate (RCR), approximate digestibility (AD), and efficiency of conversion of digested food (ECD) for male and female fifth-instar forest tent caterpillar (*Malacosoma disstria*) larvae in a short-term bioassay.

Variable and source	df	Females			Males		
		MS	F	P	MS	F	P
RGR							
Defoliation (D)	3	0.011	5.1	0.007	0.007	2.3	0.25
Clone (C)	1	0.029	8.2	0.02	0.006		0.17
D × C	3	0.003	1.5	0.25	0.000	0.1	0.96
Tree(C)	8	0.004	1.7	0.16	0.003	0.8	0.63
Error	24	0.002			0.004		
RCR							
Defoliation (D)	3	0.045	6.4	0.003	0.069	1.4	0.26
Clone	1	0.021	0.5	0.51	0.001	0.0	0.88
D × C	3	0.009	1.3	0.28	0.044	0.9	0.45
Tree(C)	8	0.043	6.2	0.0002	0.057	1.1	0.35
Error	24	0.007			0.048		
AD							
Defoliation (D)	3	5.97	0.3	0.83	53.38	1.6	0.22
Clone (C)	1	118.89	3.2	0.11	46.09	2.5	0.15
D × C	3	16.39	0.8	0.50	1.26	0.0	0.99
Tree(C)	8	37.29	1.9	0.12	18.44	0.5	0.81
Error	24	20.19			34.02		
ECD							
Defoliation (D)	3	340.71	7.2	0.0001	121.69	1.6	0.23
Clone (C)	1	228.88	2.3	0.17	27.57	1.4	0.27
D × C	3	65.53	1.4	0.27	62.96	0.8	0.50
Tree(C)	8	101.85	2.1	0.07	19.24	0.3	0.97
Error	24	47.67			78.22		

Notes: *F* tests for fixed effects Defoliation, Defoliation × Treatment, and Tree(Clone) were over the mean-square error. The *F* test for Clone, a random effect, was over the mean square for Tree(Clone).

defoliated trees were minimal. Our results are consistent with this pattern: second instars were unaffected by defoliation treatments, whereas the growth of fifth instars declined. Furthermore, RGR of females was only modestly correlated with pupal mass, suggesting that aspen may require severe defoliation (70–90%) before RIR becomes apparent. The outcome of experiments may also be dependent on the type of bioassay. In our field bioassay, larvae could select leaves, whereas Roth et al. (1998) and Parry (2000) fed clipped foliage to larvae in laboratory bioassays. Robison and Raffa (1997) conducted their assays on potted trees in a glasshouse.

Few studies have investigated consecutive years of defoliation. Two consecutive years of defoliation of mountain birch, *Betula pubescens*, did not have greater effects on the growth and fecundity of the geometrid moths *Epirrita autumnata* and *Operophtera brumata* than did a single year of severe (75%) defoliation (Kaitaniemi et al. 1999a). In contrast, Valentine et al. (1983) found incremental decreases in gypsy moth performance with each successive year of defoliation on black oak, *Quercus velutina*. Similarly, survival of black-marked spear moth, *Rheumaptera hastata*, on Alaska paper birch, *Betula resinifera*, declined with each successive year of defoliation (Werner 1979), as did pupal mass of large aspen tortrix, *Choristoneura*

conflictana, on aspen (Clausen et al. 1991). We found that all treatments reduced forest tent caterpillar fecundity equally, suggesting that, in these aspen clones at least, there is an upper limit for induced resistance beyond which additional response is not physiologically possible, irrespective of the severity or duration of defoliation.

Forest tent caterpillars can compensate for reduced foliage quality through increased consumption rate (e.g., Williams et al. 1998). The RCR of second instars in our study increased on defoliated trees, compensating fully for reductions in host quality, as indicated by equal RGR across all treatments. This also suggests that induced resistance may not be fully expressed in the young, early-season foliage on which second instars feed. RCR of fifth instars also increased in all three defoliation treatments, although not enough to fully compensate for reduced host quality, as evidenced by decreased RGR and pupal mass. Furthermore, laboratory bioassays indicated that physiological effects of defoliation-induced reductions in foliage quality were post- rather than pre-digestive, as indicated by decreased ECD with no effects on AD.

Some aspects of our experimental design could have reduced the magnitude of induced effects relative to those of forest tent caterpillars in natural outbreaks. These include the lack of maternal effects that may

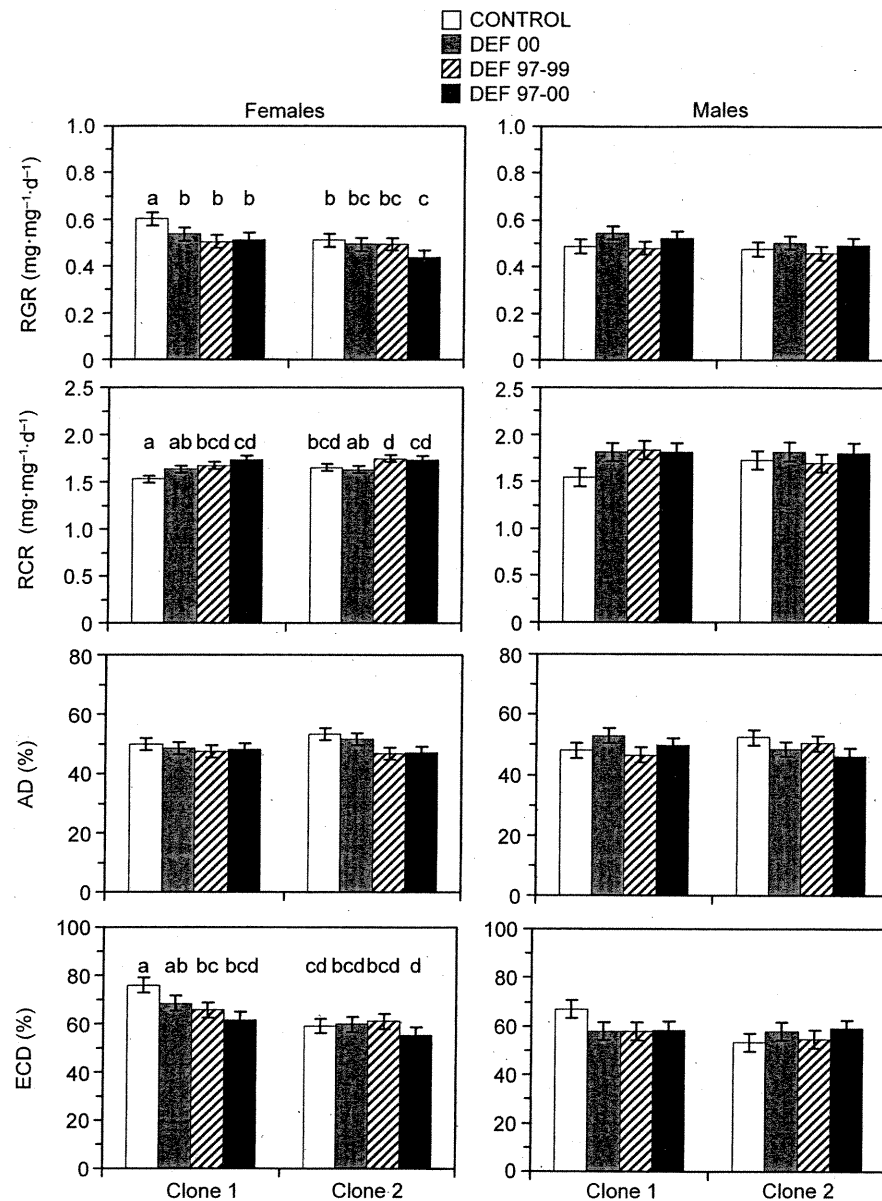


FIG. 4. Mean (± 1 SE) relative growth rate (RGR), relative consumption rate (RCR), approximate digestibility (AD), and efficiency of conversion of digested foliage to biomass (ECD) for final fifth-instar female and male forest tent caterpillars. Different letters indicate significant ($P < 0.05$) pairwise differences between means following a significant main effect of defoliation or clone (see Table 1). Preplanned comparisons were among treatments within a clone, and the same treatments among clones. Values for AD and ECD were arsine square-root transformed prior to analysis; actual values are shown in the figure. Treatments are as in Fig. 1.

occur in natural outbreaks and the potential existence of root connections between trees in our study. If insect quality also decreases with defoliation, then our experiment would underestimate reductions in fecundity relative to natural outbreaks because we did not incorporate maternal effects in our design. Environmentally based maternal effects occur in many organisms (Rossiter 1996), although in studies with insect folivores, defoliation experienced by females has had min-

imal effects on offspring (e.g., Harrison 1995, Rothman 1997, Myers et al. 1998, Erelli and Elkinton 2000a, b, Ruohomäki et al. 2000). Rossiter (1991) found that relatively low levels (10–50%) of defoliation experienced by females actually increased pupal masses of F_1 gypsy moths feeding on oak. To our knowledge, maternal effects in forest tent caterpillars driven by the stress of density or defoliation have not been investigated.

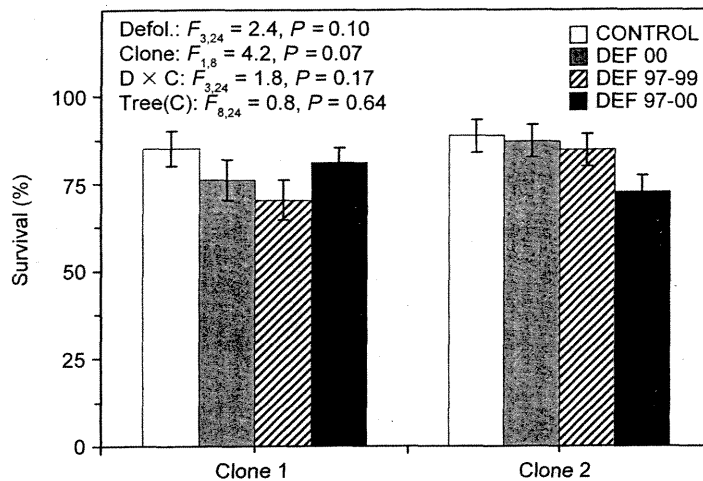


FIG. 5. Percentage survival (mean $\pm$ 1 SE) of forest tent caterpillars reared from egg hatch to pupation. Survival data include caterpillars that were parasitized. Different letters indicate significant ($P < 0.05$) pairwise differences between means following a significant defoliation or clone main effect in ANOVA. Analysis was performed on arcsine square-root transformed percentage survival; actual percentage survival values are shown. Preplanned comparisons were among treatments within a clone, and the same treatments among clones. Treatments are as in Fig. 1. F tests for the fixed effects Defoliation, Clone $\times$ Treatment, and Tree(Clone) were over mean-square error. The F test for Clone, a random effect, was over the mean square for Tree(Clone).

Although aspen ramets may sever root connections as they mature, this does not always occur (Barnes 1969, Peterson and Peterson 1992). The extent and nature of physiological interchange along common roots in aspens is not known. It is conceivable that signals transferred from defoliated to control trees via root connections could have elicited induced responses in our control trees, thereby decreasing their host quality and obscuring treatment effects. We are unable to propose any mechanism by which root connections would increase the differences in host quality between defoliated and control trees, resulting in an overestimation of induced resistance.

Variation in constitutive resistance to folivores among aspen clones is well documented (see Lindroth and Hwang [1996] and references therein). We also found significant differences in larval performance among clones, although the effect was less than the twofold difference in tent caterpillar pupal mass recorded previously (Hemming and Lindroth 1995, Hwang and Lindroth 1997). However, the overall effect of clone was at least as strong as that of defoliation, and was greater for some measures of larval performance (e.g., survival, development time, second-instar RGR and RCR). Thus, the genetic composition of an aspen stand may make greater contributions to population densities of the forest tent caterpillar than the defoliation history of the trees. However, unlike defoliation-induced effects, clonal variation in host quality would not generate the density-dependent reduction in fitness required to terminate outbreaks.

Several parasitoids of the forest tent caterpillar are attracted to volatiles released from damaged leaves (Bess 1936, Mondor and Roland 1997, 1998) and, hence, may magnify the effects of declining host quality. The tachinids *P. pachypyga* and *L. exul* parasitized more larvae on trees that were defoliated concurrently with the bioassay (DEF 00 and DEF 97-00 treatments) than in the DEF 97-99 and control treatments. However, differences in parasitism among treatments were not

driven by host quality per se, as predicted by the hypothesis that prolonged development through vulnerable larval stages increases exposure to natural enemies (Benrey and Denno 1997). Rather, larvae were equally susceptible to parasitism on lower quality DEF 97-99 trees and undefoliated trees. This suggests that although the effects of parasitoids and DIR are additive, they do not interact to enhance delayed density-dependent declines in forest tent caterpillar populations during late stages of outbreaks. Instead, because parasitism was positively correlated with defoliation, these tachinids were probably exhibiting spatial responses to host density and/or feeding damage, as has been shown previously (Parry et al. 1997). In the treatments in which parasitism was highest (DEF 00 and DEF 97-00), tent caterpillar density was also higher because of the presence of larvae used to defoliate the trees, whereas only larvae used in the bioassay were present on CONTROL and DEF 97-99 trees. High defoliation or density may provide stronger volatile cues about host location. Increases in parasitism in response to defoliation would enhance the stabilizing effects of RIR on population dynamics.

There were intriguing differences in parasitism rates between the two clones. Given that they were separated by only a short distance, shared similar environments, and had equivalent larval density, the markedly higher parasitism on Clone 2 may be related to properties of the trees themselves. For example, subtle clonal differences in the biochemical properties of the volatiles released from caterpillar-damaged leaves could alter the success of host detection by *L. exul* and *P. pachypyga*. Differences in parasitism among clones may contribute to spatial heterogeneity of tent caterpillar densities in aspen forests, which warrants further investigation.

The importance of defoliation-induced responses of plants in herbivore population dynamics remains a subject of debate. Fowler and Lawton (1985) argued that although they are statistically significant, the effects of

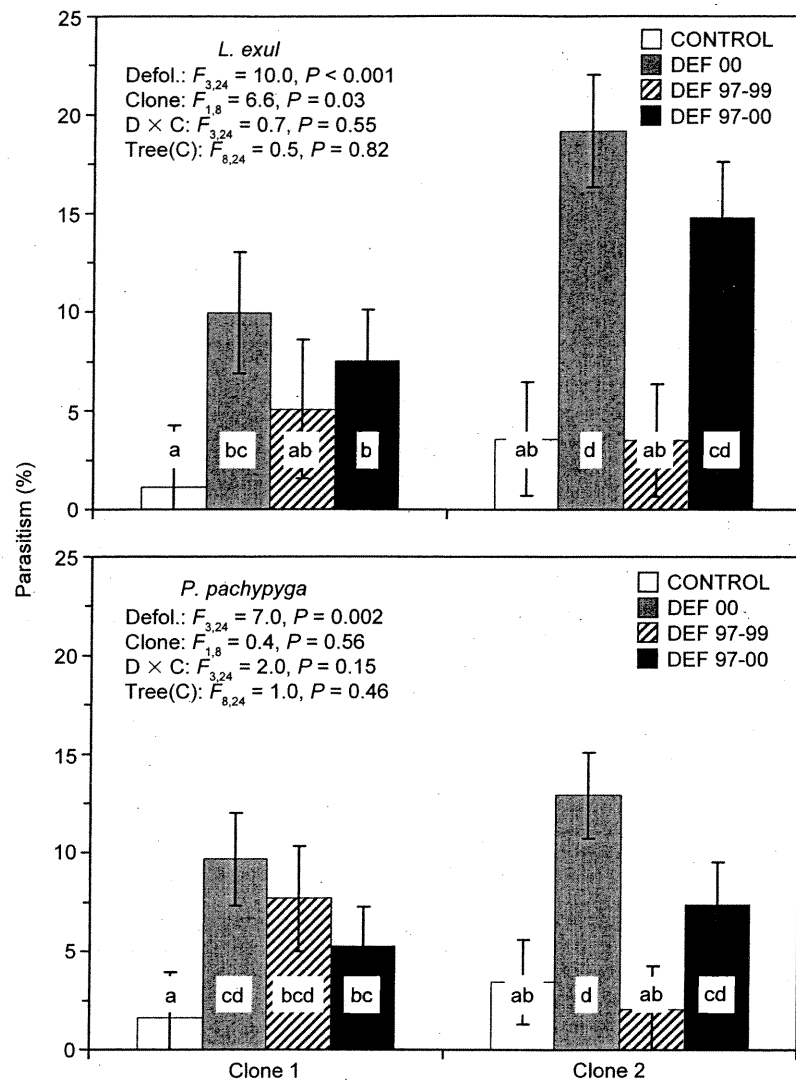


FIG. 6. Percentage of parasitism (mean $\pm$ 1 SE) of forest tent caterpillar larvae by the tachinids (a) *Leschenaultia exul* and (b) *Patelloa pachypyga*. Different letters indicate significant ($P < 0.05$) pairwise differences between means following a significant main effect of defoliation or clone. Preplanned comparisons were among treatments within a clone, and the same treatments among clones. Analysis was performed on arcsine square-root transformed percentage of parasitism. Actual percentages are shown. Treatments are as in Fig. 1. F tests for the fixed effects Defoliation, Clone $\times$ Treatment, and Tree(Clone) were over mean-square error. The F test for Clone, a random effect, was over the mean square for Tree(Clone).

induced resistance are often weak, as evidenced in mountain birch, where DIR reduced the performance of the autumnal moth (*Epirrita autumnata*) by $\leq 20\%$ in 16 of 21 studies (Ruohomäki et al. 2000). Furthermore, the effects of host plant quality on population dynamics were smaller than those of either weather or parasitism (Virtanen and Neuvonen 1999), although Bylund (1995) found the relative importance of these factors to vary in different outbreaks of the autumnal moth.

As with the autumnal moth, we found that DIR decreased the fecundity of the forest tent caterpillar by $\sim 20\%$. Furthermore, mortality of forest tent caterpil-

lars from parasitism and pathogens is much higher than for autumnal moths, suggesting that DIR is even less important for the population dynamics of forest tent caterpillars than for autumnal moths. However, larger reductions in fecundity ($\geq 50\%$) have been observed in natural populations of forest tent caterpillars following several years of defoliation (Ives 1971, Witter et al. 1975) suggesting that DIR may be stronger under some circumstances, or that other factors such as competition are equally or more important.

Female pupal mass and/or fecundity of the forest tent caterpillar is dramatically reduced in severely defoliated aspen stands (Hodson 1941, Witter et al. 1975,

TABLE 2. Approximate reproductive rates (R_0) for forest tent caterpillars from each of the defoliation (DEF) treatments and aspen clones. Reproductive rates were calculated for surviving females with and without parasitism.

Comparison, by clone	Control	DEF 00†	DEF 97-99†	DEF 97-00†
Clone 1				
No parasitism	115.3	91.5 (-20.6)	81.0 (-29.8)	84.1 (-27.0)
Parasitism included	113.3	68.4 (-39.6)	68.9 (-39.2)	71.6 (-36.8)
Clone 2				
No parasitism	110.2	84.3 (-23.5)	91.9 (-16.6)	75.6 (-31.4)
Parasitism included	100.0	49.6 (-50.3)	82.8 (-17.2)	53.1 (-46.8)
Clone 1				
Parasitism included, data from natural populations	113.3‡	63.1 (-44.3)	42.2 (-62.8)	42.9 (-62.1)
Clone 2				
Parasitism included, data from natural populations	100.0‡	57.4 (-42.6)	54.2 (-45.8)	34.4 (-65.6)

Notes: Initial cohorts had 30 female equivalents in which males were converted to females using a regression equation based on pupal mass (see *Methods*). Larval parasitism rates in natural outbreak populations corresponding to years 1, 3, and 4 in Parry (1995:863, Fig. 3 data) were used.

† Numbers in parentheses are percentage decreases from the undefoliated control treatment in each row.

‡ Data on parasitism rates in natural low-density populations are not available, so we substituted values from our experimental control plots.

Parry et al. 2001), suggesting that intraspecific competition may determine clutch size. However, fecundity may continue to decline in waning outbreaks even as population densities decrease (Ives 1971, Witter et al. 1975, Batzer et al. 1994). Sublethal levels of pathogens, especially nuclear polyhedrosis virus (NPV), have been postulated as the mechanism driving such declines in fecundity (Myers 1993). However, sublethal NPV infections only slightly reduced the fecundity (by < 10%) of the western tent caterpillar, *Malacosoma californicum* (Rothman and Myers 1994) in laboratory studies, and infected and uninfected females were not found to differ in high-density field populations (Rothman 1997). Thus, although mortality caused by NPV can contribute significantly to population decline, sublethal effects appear inadequate to explain the dramatic reduction in fecundity observed in natural populations.

To summarize our study, DIR and parasitism did not interact in a way that would amplify delayed density-dependent declines in forest tent caterpillar populations during late stages of outbreaks. Neither the effects of defoliation on host quality nor the stronger effects of tachinid parasitism were of sufficient magnitude to slow reproductive rates in our experimental populations to levels observed in declining outbreaks in nature, although total parasitism in natural outbreaks is generally much higher than in our study (Hodson 1941, Sippell 1957, Witter and Kulman 1979, Parry 1995). This suggests that single-factor explanations for tent caterpillar population dynamics are unlikely. We echo the call of other authors (e.g., Hunter and Price 1992, Hunter et al. 1997, Karban and Baldwin 1997) that bottom-up and top-down hypotheses should not be

viewed as mutually exclusive or considered in isolation.

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