

Effect of plant architecture on colonization and damage by leafyiting caterpillars of *Quercus alba*

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Leafyiting caterpillars that attack white oak, *Quercus alba*, use silk to tie together two leaves to form a “leaf sandwich” or leafyite within which they feed. Because leafyiting caterpillars are small when they first eclose (< 1 mm in length), they apparently require touching leaves in order to construct their leafyites. We first show that saplings of *Q. alba* vary greatly in the degree to which leaves are spatially distributed throughout their canopies, i.e. percent leaves touching varies from 4% to 36% per plant. We then tested the hypothesis that this difference in plant architecture, in the form of the number of touching leaves, influences the abundance of leafyiting caterpillars and the amount of damage they cause. First, surveys of all leaves on a set of non-experimental saplings showed that trees that naturally had more touching leaves had a greater number of leafyites. Second, we increased the number of touching leaves by tying together bases of leaves around branches, and compared subsequent colonization by leafyiting caterpillars on these experimental branches with colonization on similar but unmanipulated control branches. Experimental manipulation increased the number of touching leaves, leafyiting caterpillars, and leafyites, and increased damage by this guild of insect herbivores. Together, these results suggest that architectural traits that minimize leaf-to-leaf contact in *Q. alba* may be defensive traits against leafyiting caterpillars.

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Of the potential plant traits that may influence intraspecific variation in herbivore attack, those comprising plant architecture are among the least examined (Marquis 1992, Alonso and Herrera 1996). A growing number of studies demonstrate, however, that plant architecture influences attack by both vertebrate and invertebrate herbivores. Specifically, overall plant shape and stature may influence the susceptibility of plants to vertebrate herbivores. For example, plants may grow tall enough to be no longer susceptible to vertebrate browsers in African savannah (Milewski et al. 1991, Palo et al. 1993). Alternatively, short stature has been hypothesized to have evolved in New Zealand plants to reduce feeding by moas (Greenwood and Atkinson

1977) and on the Aldabra Atoll in response to grazing by tortoises (Merton et al. 1976).

For invertebrate herbivores, both direct and indirect effects of plant architecture have been implicated as factors influencing intraspecific variation in attack. Leaf position and distribution within the crown of a plant (Alonso and Herrera 1996) and plant stature (Karban and Courtney 1997, Oghiakhe et al. 1993, Alonso and Herrera 1996, Haysom and Coulson 1998; see refs in Marquis 1992) appear to directly influence attack through their effect on oviposition choice by gravid females moths and searching behavior of their larvae.

In some cases, plant architecture may not directly affect herbivore abundance; only when a predator is

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added does herbivore abundance depend on architectural traits, as some architectural types provide hiding places while others do not (Clark and Messina 1998b). Some of the more detailed studies of the mechanisms behind the effects of architecture on herbivore distribution and feeding are those of the indirect effects on predator and parasitoid foraging (Kareiva and Sahakian 1990, Grevstad and Klepetka 1992, Clark and Messina 1998a, b, Cloyd and Sadof 2000). These studies demonstrate that contrasting leaf morphologies may provide differential hiding places (Clark and Messina 1998b), and that both vertebrate (Whelan 2001) and invertebrate predators (Kareiva and Sahakian 1990, Grevstad and Klepetka 1992, Davidson and McKey 1993) are less able to physically maneuver on some plant architectural types than on others.

The role of architecture as it directly affects herbivore feeding may be particularly important for shelter-building insect herbivores. For species that build shelters using more than one leaf, plants with more widely spaced leaves are likely to be less susceptible to attack. Shelter-building caterpillars are abundant components of many insect herbivore faunas, and this mode of feeding occurs in at least 12 families of Lepidoptera (Berenbaum 1999) including the Gelechiidae, Hesperidae, Noctuidae, Nymphalidae, Oecophoridae, Pieridae, Pyralidae, Stenomidae, and Tortricidae.

Quercus alba L., white oak, in Missouri, USA, is attacked by 15 species of shelter-building caterpillars (henceforth leaf-tying caterpillars) that tie together two or more leaves with silk. They then spend most or all of their larval stage within a single shelter, skeletonizing the leaves of the shelter. Because the majority of these caterpillars are Microlepidoptera, first-instar larvae (the stage that first makes the ties and which is typically 1 mm or less in length) probably require leaves that are actually touching or in very close proximity to initiate a leaf-tie. Thus, we hypothesized that plants with a greater number of leaves actually touching each other would be more susceptible to attack by leaf-tying caterpillars than plants with leaves more widely spaced.

We tested the above hypothesis in two ways. First, we quantified natural variation among plants in architecture, in terms of the number of touching leaves, and correlated that measure with the probability of natural leaf-tie formation in unmanipulated plants. We predicted a positive relationship between the two variables. We did so for a set of non-experimental saplings, in which we counted the total number of touching leaves throughout each plant's entire canopy. Second, we manipulated plant architecture to determine its impact on leaf-tie colonization, leaf-tie formation, and leaf damage. We did so by tying together the petioles and leaf bases of neighboring leaves on individual branches so that the number of leaves touching was increased compared to control branches. We predicted that manipulated branches, with their increased number of touching

leaves, should be colonized by more leaf-tying caterpillars, have higher leaf-tie formation, and suffer greater skeletonization damage than control branches. We further predicted that damage by free-feeding caterpillars (edge damage) would be greater in experimental branches than in control branches because many free-feeding caterpillar species use leaf-ties as temporary shelters (JTL and RJM, pers. obs.).

Methods

Study site

The study site was the Big Sugar Creek Wild Area of Cuivre River State Park (near Troy, Missouri). The area is covered by secondary forest, with the canopy dominated by oaks (*Quercus* spp.) and hickories (*Carya* spp.). The understory woody vegetation is a mixture of oak, hickory, and *Acer* saplings, *Cornus florida*, *Rhamnus carolinianus*, and *Rhus aromatica*.

Natural variation in architecture and leaf-tie colonization

In late May 2000 on a calm day with little wind and prior to any leaf-tie formation, we censused 29 saplings of *Quercus alba*, ranging in height from 1.5 to 4 m, and approximately 100–2000 leaves ($\bar{x} \pm \text{SE} = 319 \pm 31$). For each tree, we recorded the number of leaves touching one or more other leaves of the same sapling. We then censused these trees three times (mid-July, mid-August, and mid-September), recording the number of leaf-ties present.

Experimental protocol

On 28 June 2000, approximately three weeks after the first appearance of leaf-tying caterpillars, we marked two pairs of branches on each of 15 saplings or low hanging branches of canopy trees of *Quercus alba*, matching branches of a given pair for approximate canopy position and number of leaves. Mean number of leaves per branch ($\pm \text{SE}$) was 17.4 ± 1.2 (range 7–39). We then randomly assigned each member of a pair of branches to one of two treatments, control (no manipulation) or manipulated (tie petioles and bases of leaves together with 1–2 strands of nylon fishing line). We counted the number of touching leaves (any point of contact) on each branch following application of the treatment. We subsequently censused all branches three times (also mid-July, mid-August, and mid-September), recording the abundance and species of leaf-tying caterpillars and number of tied leaves. In mid-October, just before leaf fall, we collected leaves from both experi-

mental and control branches, measured their length and width, area lost to skeletonization, and area remaining. Area skeletonized by leaf-tiers was first marked on acetate paper, and then this area and the actual leaf area present were measured using Sigmascan Pro 5.0 (SPSS 1999). We estimated the initial undamaged area of each leaf using the regression equation, undamaged area = (length in cm × width in cm) × 0.539 + 2.56 ($R^2 = 0.93$, $P < 0.001$), and then calculated the percent damage resulting from skeletonization by leaf-tiers and non-leaf-tiers. Finally, at the last census in mid-September, we recorded the number of abscised leaves from experimental and control branches, as heavily skeletonized leaf-ties often abscise prematurely (JTL and RJM, pers. obs.).

Statistical analysis: natural variation in architecture

For control branches of experimental trees and the 29 non-experimental trees, we regressed the maximum number of leaf-ties recorded across the three censuses on the original number of touching leaves. We used the maximum number of caterpillars and leaf-ties recorded over the three censuses instead of total number because of the possibility that the same individual caterpillars and their ties could be encountered in successive censuses. Results were qualitatively similar for the total number of ties and caterpillars.

Analysis of the experiment

We analyzed the data for a treatment effect on percentage of touching leaves, density of leaf-tying caterpillars (maximum number recorded per leaf over the three censuses), percent of leaves in leaf-ties, percent total leaf area missing, and percent leaf area loss to skeletonizers as a split-plot ANOVA design (using SAS PROC GLM [SAS 1995]), with replicates within trees as the within-plots subject, and treatment as the between-plots subject. Tree was considered to be the plot in the analysis. All percent values were first arcsin-square root transformed to improve normality of the residuals.

Results

Natural variation in architecture

Both unmanipulated saplings and control branches of experimental plants varied greatly in their architecture related to proximity of leaves. In both cases, this natural variation was correlated with variation in natural tie formation. Unmanipulated oak saplings varied greatly in leaf proximity, ranging from a low of 4% of the

leaves touching to a high of 36% (Fig. 1). Non-experimental trees with more touching leaves had more ties than those with fewer touching leaves (Fig. 2a, $R^2 = 0.37$, $P = 0.0005$). Likewise, percent touching leaves varied from 0 to 57% on control branches of our experimental plants; those control branches with a greater number of touching leaves were colonized to a greater degree during the study period by leaf-tying caterpillars (Fig. 2b, $R^2 = 0.31$, $P = 0.0009$).

Experimental manipulation of architecture

Manipulation of architecture significantly increased the number of touching leaves within experimental branches ($\bar{x} \pm \text{SE} = 13.8 \pm 0.8$) compared to control branches (4.7 ± 0.5 ; $F_{1,14} = 113.0$, $P < 0.0001$). Similarly, the percentage of leaves on a branch that were touching at least one other leaf also increased significantly, from $28.2\% \pm 2.9$ to $80.0\% \pm 1.9$ ($F_{1,14} = 251.0$, $P < 0.001$). Manipulating plant architecture significantly increased leaf-tier colonization, leaf-tie formation, and damage caused by leaf-tiers, compared to controls. We encountered eight species of leaf-tiers on experimental and control branches over the course of the experiment (Table 1). The number of these leaf-tying caterpillars (maximum number encountered over the three censuses) was three times higher on manipulated than on control branches ($F_{1,28} = 10.3$, $P = 0.0033$; Fig. 3a). This higher leaf-tier abundance resulted in four times as many leaves tied on manipulated than on

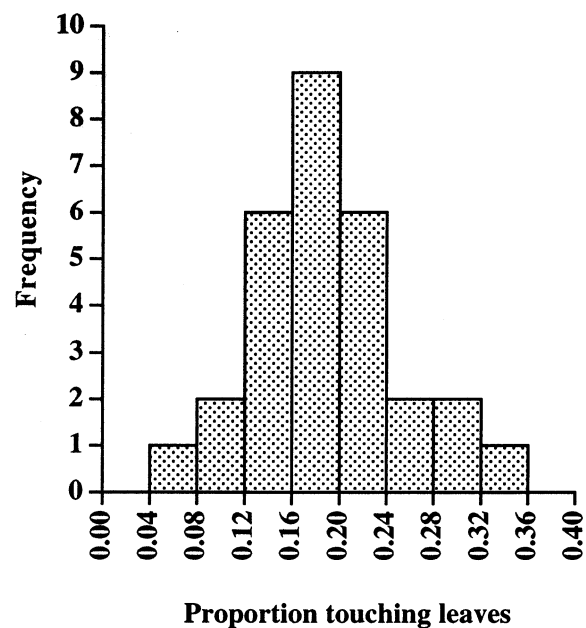


Fig. 1. Natural variation in the proportion of touching leaves per plant in early June, before leaf-tie formation, for 29 oak saplings of *Quercus alba*.

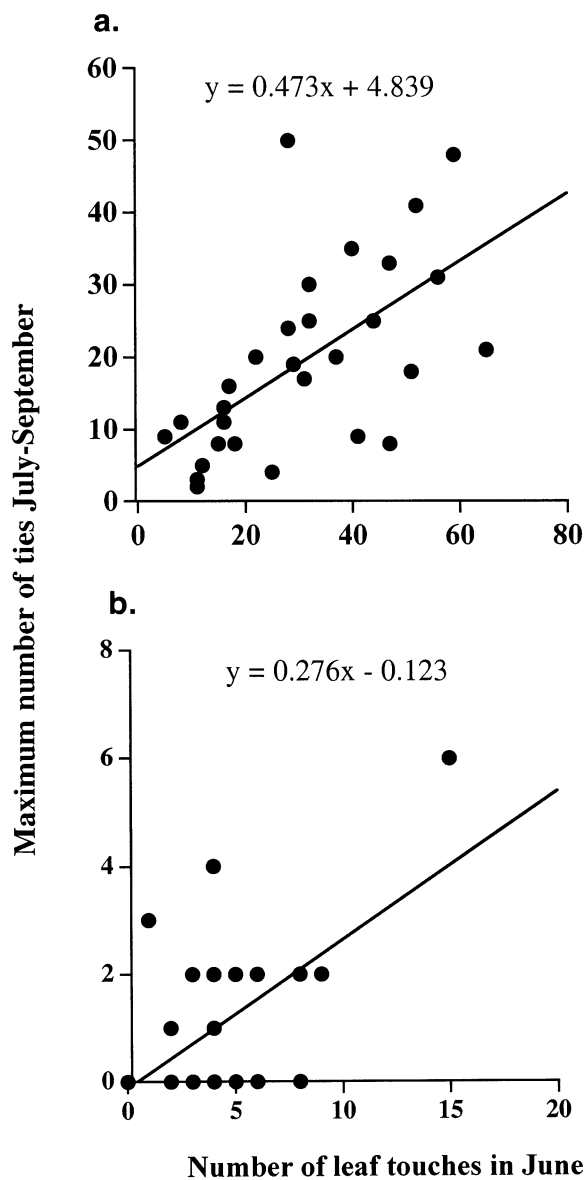


Fig. 2. Relationship between number of leaves found touching in June before leafy colonization and subsequent maximal number of leaf ties found in July–September for: **a** 29 non-experimental saplings of *Quercus alba*, and **b** control branches of experimental plants. There are 12 hidden points in **b**.

control branches (maximum number encountered, $F_{1,28} = 33.3$, $P = 0.0033$, Fig. 3b). As a result, damage directly attributable to leaf tiers (i.e. skeletonization) on manipulated branches was twice that on control branches ($F_{1,28} = 40.7$, $P = 0.0001$, Fig. 3c). Despite differences in amount of skeletonization, total damage (including skeletonization) measured at the end of the season, did not vary significantly among treatments ($F_{1,28} = 2.6$, $P = 0.10$, Fig. 3d). Although chewing damage was higher for leaves of control branches (21.2 ± 1.2 vs 18.7 ± 1.1), this difference was not significant

($F_{1,14} = 2.11$, $P = 0.15$). Finally, there was no treatment effect on early abscission of leaves ($F_{1,28} = 0.49$, $P = 0.0033$, $P = 0.49$), as measured by the number of leaves on marked branches that had abscised by mid-October. The tree effect (plot factor) was significant for percent total leaf area loss ($F_{1,13} = 6.3$, $P < 0.001$), percent skeletonization ($F_{1,13} = 4.6$, $P < 0.001$), and percent chewing damage ($F_{1,13} = 7.7$, $P < 0.001$), but not for the other variables.

Discussion

White oak saplings vary greatly in the spatial distribution of their leaves. Some plants have almost no touching leaves whereas others have as many as 36% of the leaves touching, as estimated for entire plants, and 57% as measured for single branches. On unmanipulated branches and on entire saplings, the number of new ties was positively correlated with the number of touching leaves prior to colonization. The degree of leaf overlap influences the probability that leafy caterpillars will colonize a given individual of white oak.

Our manipulation and comparison of branches within the same individuals suggests that the observed correlation between plant architecture and attack by leafy caterpillars was a causal one. Thus, our conclusion is that saplings of *Q. alba* with fewer touching leaves are less likely to be attacked than those with a greater percentage of their leaves touching, resulting in decreased damage by this guild of herbivores. Because increasing leaf area loss often results in decreased growth and reproduction in plants (Marquis 1992), we assert that traits that minimize leaf-to-leaf contact within oak canopies may be defensive traits against these leafy caterpillars on oaks. Here, we define defense traits as those that confer a fitness advantage in the presence of herbivores (Strauss and Agrawal 1999). A loss of 8–12% leaf area has been shown to affect acorn production in *Quercus robur* (Crawley 1985). The relevant traits in white oak might include twig length and angle of new twig production, number of leaves and twigs produced at each node, leaf dimensions, and the pattern of branch abscission, as it might influence

Table 1. Species of caterpillars encountered in leaf ties during the course of the experiment on *Quercus alba*. Nomenclature follows Hodges (1983).

Family	Species
Gelechiidae	<i>Arogalea cristifasciella</i> Cham.
Gelechiidae	<i>Chionodes fuscomaculella</i> Cham.
Gelechiidae	<i>Pseudotelphusa</i> sp. nov.
Oecophoridae	<i>Psilocorsis cryptolechiella</i> Cham.
Oecophoridae	<i>Psilocorsis quercicella</i> Clem.
Oecophoridae	<i>Psilocorsis reflexella</i> Cham.
Pyralidae	unidentified sp.
Stenomidae	<i>Setiostoma xanthobasis</i> Zell.

contact between leaves of neighboring branches. Inasmuch as architecture also influences preferences of ovipositing females, it can also be considered to be a resistance trait, i.e. it reduces preference or performance of herbivores (Strauss and Agrawal 1999).

This study adds to our understanding of the mechanisms by which plant architecture can influence insect herbivore attack and subsequent damage. In *Daphne lanceolata*, ovipositing females prefer larger plants, and larvae choose plants with shorter stems and more clustered leaves (Alonso and Herrera 1996) to reduce the energetic costs of locomotion (Alonso and Herrera 1996), or perhaps to reduce susceptibility to predators (Schultz 1983, Bernays 1997). Larger plants may be colonized preferentially simply because they are more apparent or because they represent a larger resource. Plant height is also important for escape against vertebrate herbivores (Milewski et al. 1991, Palo et al. 1993). In *Populus deltoides*, the success of gall-making *Pemphigus betae* aphids is influenced by the number of buds, which compete with galls as sinks for photosynthates. Gallmakers are more successful on plants with naturally lower numbers of buds and on branches with experimentally reduced numbers of buds compared to control branches on the same tree (Larson and Whitham 1997). Leaf surface characteristics (pubescence, slipperiness) (McAuslane et al. 1995, Grevstad and Klepetka 1992, and references therein), leaf morphology (Clark and Messina 1998a, b), and branching angle and petiole length (Whelan 2001) can influence mobility of predators and parasitoids, and the subsequent abundance of their prey on plants. Finally, in systems involving shelter-building caterpillars, larger leaf size may increase attack by *Anacamptis niveopulvella*, which makes rolls of individual leaves on cottonwood hybrids (Martinsen et al. 2000). In systems in which multiple leaves are incorporated into a leaftie, leaf stiffness plays a role but its contribution is complex. Mature leaves of *Asimina* hybrids make better shelters than do young leaves because the latter wilt with damage (Damman 1987). In contrast, *Eucalyptus risdonii* (with floppy leaves) is more susceptible to attack by four species of leaftiers than is *E. amygdalina* (with stiff leaves), apparently because leaves of the latter are too rigid to manipulate (Whitham et al. 1994). Distance between leaves may be important in *E. amygdalina* as it is in *Q. alba*, as ties are only made in *E. amygdalina* when leaves are touching (Whitham et al. 1994).

Whether natural selection imposed by leaftying caterpillars to decrease leaf overlap results in a realized change in architecture will depend in part on constraints imposed by the contribution of architecture to other plant functions. An overall decrease in the amount of leaf overlap would likely increase photosynthetic efficiency through decreased self-shading,

particularly in shaded environments (Pearcy and Yang 1996). Constraints may exist, however. Decreased overlap is less optimal for light gathering in high light environments (Pearcy and Yang 1996) and it reduces shading of plants underneath the oak canopy, resulting in increased competitive ability of nearby plants. The degree to which leaf overlap has a genetic basis in *Q. alba* is unknown.

There are two possible pathways by which plant architecture may influence attack by leaftying caterpillars in this system. First, architecture may influence colonization preferences of leaftying caterpillars or oviposition by female moths. Second, attack may be influenced indirectly through changes in susceptibility of the leaftying fauna to the third trophic level during colonization. There are three reasons to believe that the first mechanism is more likely. First, eggs are oviposited preferentially in artificial leafties made by clipping leaves together compared to non-tied leaves (JTL and RJM, in prep.), suggesting that leaf proximity is critical to colonization by leaftiers. Second, touching leaves likely provide little protection against predators prior to tying as a touching leaf usually touches only one other leaf and does so at a single contact point. In contrast, in a system in which architectural effects were mediated by the third trophic level, morphological features provided obvious hiding places: differential distribution of aphids on two species of grasses was due to differences in hiding place availability, and resulting differential predation by lacewing larvae, associated with flat open leaves vs naturally rolled leaves (Clark and Messina 1998a). Thirdly, the timing of the system is such that predators may not have the opportunity to affect leaftier distribution prior to leaftie formation. Upon colonizing a plant by oviposition, leaftying caterpillars immediately construct a leaftie, prior to feeding. It is rare to see larvae of any instar outside of ties, and never those of the first instar. Presumably this obviates the possibility of plant architecture mediating leaftier abundance via the third trophic level. Manipulation of predator abundance on trees of different architecture, however, is necessary to resolve the role of direct vs indirect effects.

We found differences in abundance of leafties based on architecture both among control branches of experimental trees and among entire saplings. Differences in leaftier abundance within trees related to canopy height (Carroll and Kearby 1978) might be due to differences in architecture depending on height within a canopy. Differences among individuals in architecture could result in natural selection for decreased leaf overlap if degree of overlap is related to damage level and subsequent survival and/or reproduction of the trees involved. Contrary to our prediction, we found no differences in total damage at the end of the season, despite an increase in the amount

of skeletonization damage suffered by manipulated branches. Non-leaftying herbivores preferentially damaged control branches with fewer tied leaves, but not significantly so. The overall defensive role of architecture in this system may depend on the interaction of architecture with the leaftying and non-leaftying caterpillars at the whole tree scale. Future experiments should attempt manipulations at the whole tree scale to clarify the defense role of architecture in this system. It is important to note that our experiment likely underestimates the impact of architecture on damage by leaftying caterpillars because we initiated the experiment after the first wave of leaftiers was completed.

The number of touching leaves did not explain all variation in abundance of leafties on control branches of experimental plants. In fact, a number of control branches were not colonized despite having substantial number of touching leaves (Fig. 3a,b). Because all experimental plants were colonized, lack of discovery is

not likely. Instead, other leaf quality factors also might have contributed to the level of attack. Lill and Marquis (2001) have shown that protein-binding capacity of white oak leaf extracts influences pupal weight of *Psilocorsis quercicella*, one of the members of this community. Perhaps ovipositing females actively avoid leaves of low quality, in addition to being attracted to those with large numbers of touching leaves.

Although we believe the underlying mechanism linking leaftier and leaf abundance to plant architecture is greater oviposition preference for plants with more touching leaves, protection gained against the third trophic level (generalist predators in particular) may be the ultimate selective factor for the evolution of the leaftying habit itself. This adaptive explanation is only one of a number of alternative or additional possibilities, including modification of the abiotic environment and modification of leaf quality (reviewed by Fukui 2001). We are currently investigating these alternatives.

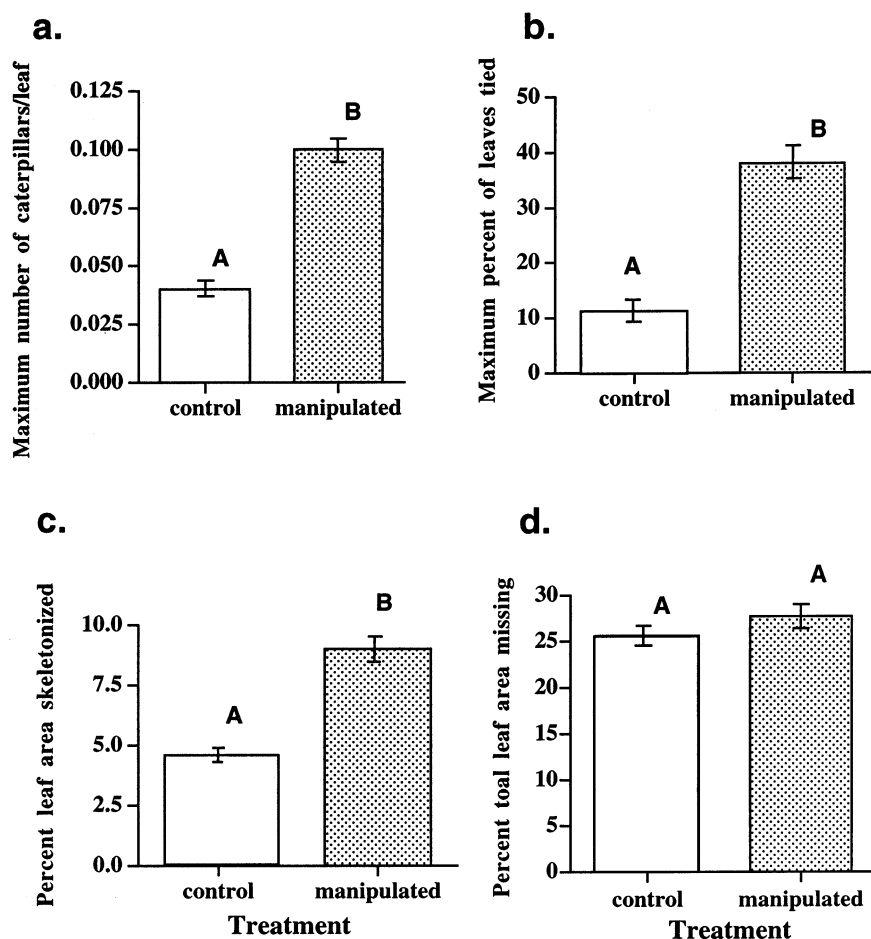


Fig. 3. Effect of experimental increase in the number of touching leaves (= manipulated treatment) on: **a** maximum number of leaftying caterpillars censused July–September, **b** maximum percent of leaves found in a leaftie, **c** leaf area loss to skeletonizers, and **d**, total leaf area loss to all leaf-chewing insects. Means (\pm SE) are presented on a per branch basis (N = 30) for each treatment.

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