Intra-crown variation in leaf herbivory and seed production in striped maple, Acer pensylvanicum L. (Aceraceae)

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Summary. Patterns of spatial variation in leaf herbivory and the effects of this variation on seed production and twig growth were studied in striped maple, Acer pensylvanicum (Aceraceae). Experimental removal of 25% of the leaf area from each of four leaves directly subtending a developing infructescence significantly reduced seed number in that infructescence. When leaf area was removed from leaves neighboring to, but not directly subtending developing infructescences, no reduction in seed production occurred. Together, these results suggest that only photosynthesize from leaves directly subtending infructescences contributes to seed production in nearby infructescences. Effects of the experimental removal of leaf area did not persist the second year, suggesting that mobilization of storage products from leaves directly subtending infructescences contributes to seed production in nearby infructescences. Because of limited resource movement, small amounts of leaf area loss (relative to a plant's total leaf area), but concentrated within a branch or branches, may result in a large reduction in reproduction by those branches. Depending on the relative contribution of the branch to the overall reproductive output of the plant, herbivores which remove relatively small portions of the leaf area, localized within branches, may have a selective impact on their hosts. It should be noted that the relative influence of various foliar damage patterns may vary with the degree to which developing fruits are photosynthetic (e.g., Bazzaz et al. 1979) and thus are able to provide their own assimilate for seed development.

Leaf herbivores influence plant growth and seed production by consuming leaf area, resulting in changes in the subsequent levels of carbon assimilation and nutrient uptake (Chapin and Slack 1979; Detling et al. 1979; Archer and Tieszen 1983). To quantify the relationship between the amount of leaf area removed and its effect on plant fitness, the traditional approach has been to consider plants as integrated organisms. The implicit assumption has been that resources throughout the plant body are equally available for mobilization and redistribution to sites of damage, allowing for the possibility of compensation following attack (e.g., McNaughton 1983). In this view, only the amount of leaf area removed and not the spatial distribution of damage would affect reproductive output.

Two lines of evidence suggest that the pattern of damage distribution must be considered if we are to understand clearly the potential for leaf herbivores to affect plant fitness (see also Janzen 1979; Watson and Casper 1984). First, the direction of assimilate movement from a given leaf greatly depends on the position of that leaf relative to sinks, i.e., growing meristems and reproductive structures (Gifford and Evans 1981). For example, leaves directly subtending developing fruits, in contrast to those farther away, are generally the primary energy sources for the development of those fruits (reviewed in Watson and Casper 1984). Thus, damage to leaves subtending reproductive structures is likely to have a greater effect on immediate reproductive output than damage to leaves farther away. Second, evidence suggests that carbon and nutrient movement are restricted between major morphological subunits (e.g., branches) within plants (Hansen 1967; Quinlan 1969; Khan and Akosu 1971; reviewed in Watson and Caspar 1984). Because of limited resource movement, small amounts of leaf area loss (relative to a plant's total leaf area), but concentrated within a branch or branches, may result in a large reduction in reproduction by those branches. Depending on the relative contribution of the branch to the overall reproductive output of the plant, herbivores which remove relatively small portions of the leaf area, localized within branches, may have a selective impact on their hosts. It should be noted that the relative influence of various foliar damage patterns may vary with the degree to which developing fruits are photosynthetic (e.g., Bazzaz et al. 1979) and thus are able to provide their own assimilate for seed development.

The importance of the intra-crown pattern of leaf area loss to herbivores for plant reproductive output has largely been ignored. Only three previous studies have considered the effects of single pattern, localized folivory in temperate woody species (Janzen 1976; Stephenson 1980; Bertin 1982). Other than studies with woody cultivars (e.g., Haller 1930; Quinlan 1969; Hansen 1969), there have been no reported studies of the effect of intra-crown variation in leaf damage on reproductive output in woody plants.

The first objective of this study was to determine, using experimental leaf area removal, how patterns of localized, small amounts of leaf damage differentially affect seed and flower production, and leaf and twig growth in striped maple, Acer pensylvanicum L. (Aceraceae). I then relate these results to observed within- and among-plant variation in natural patterns of leaf damage in this tree species. Finally, because timing of damage with respect to plant reproductive events can mitigate the effects of that damage (e.g., Hare 1980; Krischik and Denno 1983; Gregory and Wargo 1986), I describe seasonal variation in leaf damage levels with respect to the timing of seed maturation in striped maple.
Methods

Plant species and study site

The study site was the Mountain Lake Biological Station (approximately 1300 m elevation), Giles County, Virginia, owned and operated by the University of Virginia. The specific location was in closed canopy, secondary forest, dominated by Quercus alba, Acer pensylvanicum, Carya spp., Tsuga canadensis, Prunus virginiana, Ilex montana, and Amelanchier sp. The entire area surrounding the biological station was clearcut during the early part of the century.

Acer pensylvanicum is a subcanopy tree of closed canopy, eastern deciduous forest, occurring in moist woods from Nova Scotia to Minnesota south to Tennessee and North Carolina (Gleason and Cronquist 1963). Throughout its range, growth is greatest in temporary forest openings (Wilson and Fischer 1977; Hibbs et al. 1980). At Mountain Lake, striped maple rapidly colonizes treefall gaps and forest clearcuts, reaching a maximum height of 12 m in closed canopy forest. All individuals encountered at Mountain Lake were unisexual, but striped maple populations in Massachusetts consist of 4% monoecious individuals, with about 10% of the population switching sex from year to year (Hibbs and Fischer 1979). At Mountain Lake, plants flower at the time of leaf bud break (late April to early May) and final fruit maturation and dispersal occur in the September (personal observation).

Experimental leaf area removal

On June 7, 1986, six experimental branches were marked on each of 32 trees (mean diameter at breast height±SD = 20.6 cm±12.6). Each experimental branch consisted of a developing infructescence surrounded by four subtending leaves. The distance between these subtending leaves (measured from the most proximal leaf of the experimental unit) and the nearest non-subtending leaves ranged from 0.29 to 0.81 m (X±SD = 0.51±0.21 m). For a given tree, experimental branches were similar in height (1-3 m) and approximate insolation level. In striped maple, aborted flowers and samaras were in various stages of drying. All seeds from each infructescence were then scored for viability based on appearance. At this time seeds were either expanded with a fully developed, green embryo (viable) or one-quarter to three-quarters in size, flat, and either empty or with a thin, brown, undeveloped embryo (not viable). One seed was chosen haphazardly from each infructescence for fresh and dry mass determination. The remaining seeds were placed in mesh bags and kept in moist sand in the dark at 10°C until March 31, 1987, at which time germination was scored. The rate of increase in fresh fruit mass over the growing season was monitored by collecting haphazardly 10 fruits from each of 10 different marked, but non-experimental plants at five different sample dates during 1986.

The effects of the experimental treatment were followed into the second year, 1987. Experimental branches were censused for the number of flowers on May 2. On June 2, experiment branches were censused for leaf number and size, twig growth after full expansion, and presence of developing seeds both on the experimental branches themselves and on neighboring branches. None of the experimental trees switched sex between years. Leaf size was measured as leaf length in the field and then converted to area using a regression equation [(area) = 6.39(length) - 20.19] (r² = 0.82, P<0.0001) based on area of 100 leaves of known area and length. Sample size for the 1987 measurements was 29 trees, as one individual had become uprooted.

Natural leaf damage levels

Eighteen plants were censused three times during the study period for within-plant, spatial variation in damage levels to leaves. Censused trees were distinct from but were close to the experimental trees. On June 18–20, both area missing and original area (as if the leaves were undamaged) of 75-90°C leaves for each tree were estimated using a plastic grid (smallest squares=0.064 cm²). All leaves had fully expanded by this time. Leaves were located on one of four 1-2.5 m high branches for each census tree, 15-30 leaves not subtending the marked infructescence

The first five treatments were designed to determine the level at which localized damage affects seed production. The last treatment was included to determine whether photosynthetic leaves not directly subtending developing fruits is necessary for the maturation of those fruits. All treatments were begun on June 7. For each treatment, only one-quarter leaf was removed each day by clipping with scissors a section of the leaf between major secondary veins. Daily removal of small portions of each leaf and by quarter leaf sections simulated damage caused by a number of the lepidopteran caterpillar species which occur on Acer pensylvanicum at Mountain Lake. No leaf was damaged more than once (except in treatment 5 in which all four leaves were eventually removed). Natural leaf damage by herbivores subsequent to the experimental treatment was great enough in branches of two experimental trees to necessitate their exclusion from final analysis (final n = 30 trees).

Presence of developing fruits and seeds of infructescences from experimental branches was censused every two weeks subsequent to the experimental leaf area removal. On August 20, all infructescences were bagged with 1 mm square mesh to prevent seed removal by birds and rodents. On August 30, all infructescences were collected. At this time, embryos appeared fully mature although seed coats and samaras were in various stages of drying. All seeds from each infructescence were then scored for viability based on appearance. At this time seeds were either expanded with a fully developed, green embryo (viable) or one-quarter to three-quarters in size, flat, and either empty or with a thin, brown, undeveloped embryo (not viable). One seed was chosen haphazardly from each infructescence for fresh and dry mass determination. The remaining seeds were placed in mesh bags and kept in moist sand in the dark at 10°C until March 31, 1987, at which time germination was scored. The rate of increase in fresh fruit mass over the growing season was monitored by collecting haphazardly 10 fruits from each of 10 different marked, but non-experimental plants at five different sample dates during 1986.

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