Foliage quality changes during canopy development of some northern hardwood trees

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Summary. The ephemerality of high quality foliage in spring may act as a defense for trees against early season folivores, but only if the duration of high quality is so short that it is difficult for insects to synchronize their egression with the period of high quality foliage that follows budbreak. The rate of change in foliage quality on a day to day basis through the spring was determined for 9 species of hardwood trees in 2–3 years. Measurement of physical and chemical parameters and a bioassay with gypsy moth larvae both showed decreasing quality during the three to five weeks of canopy development in all species. Rates of decline differed among species but the patterns were similar from year to year on a degree-day scale. Growth rates of larvae raised through the first stadium on foliage of differing ages reflected these changes in foliage acceptability. Increasing toughness and declining nitrogen and water contents of leaves were correlated with changes in acceptability to larvae but explained only a small part of the variation in acceptability. The host-seeking period of gypsy moth larvae overlapped with the availability of highly acceptable foliage of the most preferred host species. Less preferred species had more rapid declines in foliage acceptability, and hence narrower overlaps with the host-seeking period, which may provide defense against use by this generalist forest pest.

Key words: Host quality – Leaf phenology – Synchrony – Insect-plant interactions – *Lymantria dispar*

Coley 1983, Lowman 1984), and only about 1% of folivorous insect species contribute significantly to this damage (Barbosa and Wagner 1989). In some cases predation and disease control herbivore numbers, but experiments to test these regulatory effects fail as often as they succeed (Price 1987). Another factor that may help limit defoliation to these low levels is the high heterogeneity in foliage quality (Denno and McClure 1983).

The quality of tree foliage for herbivores varies among species, among individuals of a species, among branches in individual trees, between sun and shade leaves within the forest canopy (Denno and McClure 1983), and also temporally at several time scales: inter-annual, seasonal, and diurnal (Raupp and Denno 1983). Nitrogen and water content decline during the growing season, toughness increases, and so, generally, do chemical and physical defenses (Mattson and Scriber 1987). Such spatial and temporal heterogeneity constrains insects by making high quality foliage difficult to find, and by forcing insects to move frequently in search of superior food, potentially attracting the attention of predators (Schultz 1983). Foliage heterogeneity may act as a component of tree defenses against high losses to leaf-feeding insects.

At least one group of folivorous insects sometimes evades tree defenses and causes serious levels of defoliation: species that feed on new leaves in spring (Hunter 1991). Spring-feeding insects synchronize egression from winter dormancy with the 3–5 week period of leaf development in temperate deciduous forests (Lechowicz 1984) when foliage quality is high. Variable synchrony with leaf emergence may contribute to the variability in population sizes of these species (Nothnagle and Schultz 1987, Hunter 1991). Early hatching is detrimental because larvae starve before leaves emerge, but later hatch will only be problematic if the temporal window in which foliage is of high quality is short, limiting opportunities for establishment. Conversely, if foliage quality stays high for a relatively long time, there is a greater opportunity for larval establishment and less likelihood of phenological mismatch between the insects and their hosts.

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Surprisingly little is known about the rapidity with which foliage quality deteriorates in the spring, nor about how the duration of high quality foliage varies among species and years. The seasonal trends referred to above are defined mostly by samples taken at monthly intervals (e.g. Feeny 1970, Haukojioa et al. 1978, Hough and Pimentel 1978, Ricklefs and Mathew 1982, Schultz et al. 1982, Lawson et al. 1984, Mauffette and Oechel 1989). Only a few studies have documented the changes in foliage quality in spring with finer temporal resolution (Feeny 1970, Schweitzer 1979, Wint 1983, Furuta 1987, Raupp et al. 1988). One of the best of these studies (Raupp et al. 1988) raised gypsy moth larvae on 4 tree species at intervals of 3 to 6 days during one spring and early summer. They demonstrated the adverse effects of older foliage on larval development, but did not explore the implications of changing foliage quality for host selection or early larval mortality. In the no-choice design of their trials, larvae may have fed on marginally acceptable leaves from which they would normally disperse by ballooning, with consequent risk of mortality (Bess 1961). Many other Lepidoptera foliivores also use this passive dispersal behaviour (Lance and Barbosa 1979, Barbosa et al. 1989). All of the facets of this complicated system require exploration to evaluate the role of variable synchrony in the plant-herbivore interaction.

We have quantified the day-to-day changes in foliage quality for the major deciduous tree species of northern forests and their acceptability to larvae of the gypsy moth (Lymantria dispar L.). This polyphagous, springfeeding species is a major forest pest both in North America and in Eurasia. Our immediate goal was to assess the temporal window of opportunity for establishment of gypsy moth larvae in northern forests over several years. This study is part of a larger analysis that relates long term gypsy moth population sizes to estimates of synchrony between eclosion and budburst of its favoured host species.

Methods

The study site and tree species

All field work was done at the McGill University Research Centre at Mont St. Hilaire, Quebec (45°3³ N, 73°0² W). Habitats include old-growth forests and successional stands on disturbed sites; for detailed stand description refer to Lechowicz (1983). Temperature records from an on-site datadep (Omnidata 212, Logan, Utah) were supplemented where necessary with Canadian Atmospheric Environment Service records from nearby St. Hubert Airport (45°3³ N, 73°2² W). Leaves were collected from natural forest within 200 m of the temperature recorder and the lab where experiments were performed. Foliage was clipped each morning from branch tips on 10–15 trees between 1 and 5 m from the ground and used immediately. Most trees were edge-growing, so that they had lower branches within reach.

Four tree species were used in 1988: red oak (Quercus rubra L.), trembling aspen (Populus tremuloides Michx.), sugar maple (Acer saccharum Marsh.) and white ash (Fraxinus americana L.). These species differ in their use as food by the gypsy moth: oak and aspen are highly preferred hosts, maple is intermediate, and ash is avoided (Mauffette et al. 1983). In 1989 and 1990, five more species of intermediate or high preference were added: white birch (Betula papyrifera Marsh.), gray birch (Betula populifolia Marsh.), ironwood (Ostrya virginiana (Mill.) K. Koch), beech (Fagus grandifolia Ehrh.) and basswood (Tilia americana L.). These are the principal deciduous trees of upland sites in the Great Lakes-St. Lawrence forest region (Rowe 1972). They differ substantially in the phenology of leaf emergence and the rate of canopy expansion (Lechowicz 1984).

Foliage quality parameters

Physical and chemical traits of leaves were measured at 2–3 day intervals from the end of April to early June. Leaf toughness and water content were measured on ten fresh leaves per sampling period for each species. Toughness was measured with a penetrometer (Feeny 1970). Kjeldahl nitrogen and pH were measured on two subsamples of frozen, bulked leaves from 10–15 trees as described in Lechowicz (1983). These parameters were correlated against foliage acceptability.

Foliage acceptability changes

Gypsy moth females deposit eggs in a single mass of up to 1200 eggs in midsummer, and the winter is passed as a fully embryonated egg (Leonard 1981). Since females do not fly, most dispersal is accomplished by ballooning first instars. On hatching in spring, neonates crawl up tree trunks to sample foliage. Larvae will either remain and feed, or spin down on silk and disperse. This behaviour can be used to gauge the acceptability of foliage of different ages and species (Caperera and Barbosa 1976).

Acceptability of foliage was measured at 2–3 day intervals in dispersal chambers (Caperera and Barbosa 1976). Water filled plastic vials containing leaves were placed in sections of maple logs surrounded by a net. Tanglefoot barriers prevented larvae from crawling off the log and net. Appropriate conditions for dispersal were maintained with overhead fans and temperature control (at 25°C). At the beginning of a trial, 30–50 one day old larvae were placed on the lower end of each log, with 4 replicate chambers/species. Each chamber contained foliage of one species, with 3–5 twigs per chamber. Six hours later the distribution of larvae (on foliage vs. in the net) was determined. The proportion remaining on the foliage is the acceptability. Controls were also run, in which waxed-paper leaf models or bare twigs were substituted for foliage. These controls consistently showed negligible numbers of non-dispersing larvae.

Eggs were collected in late winter from outbreak sites at Montebello, Quebec, Gatineau Provincial Park, Quebec, and Turkey Point Provincial Park, Ontario in 1988, 1989 and 1990 respectively. Egg masses were stored below 3°C until needed. Eggs were set out to hatch every other day in incubators at 25°C. All newly hatched larvae were removed from the egg masses daily and stored overnight at 18–20°C for use the next day. Eggs were taken from many masses at once, and since the masses hatched over 3–4 days, a mix of genotypes and early and late hatching larvae was used each day.

First instar growth and survival

Acceptability of foliage to larvae may be an analog for suitability to sustain larval growth, but this is not always a valid assumption (Thompson 1988). Martinat and Barbosa (1987) have shown that feeding responses of the gypsy moth match suitability, but we also examined the connection between acceptability and suitability by rearing larvae through the first stadium on foliage of different ages. One day old larvae were reared until the end of the first instar. This period is critical for establishment, and very young larvae have been found to be most sensitive to temporal changes in host suitability (Raupp et al. 1988). Five cohorts (N = 30/cohort/species) were
raised on each of four species (red oak, trembling aspen, sugar maple and white ash) in 1988. Since both the trees and the insects develop at a rate that depends on temperature more than on time, each cohort was reared beginning from fixed degree-day intervals (the sum of daily temperatures above a threshold temperature, in this case 5°C), rather than fixed time intervals. Cohorts were begun at 50 degree-day intervals from the emergence of the first 10% of leaves of a species (by visual estimate), except the final cohort, which was started on 6 June. The dates each cohort was begun are listed in Fig. 4. Larvae were reared individually in petri dishes with 24 hour photoperiod and at 18°C to keep foliage fresh. Foliage was sterilized in 0.5% sodium hypochlorite, then rinsed with tap water. Fresh foliage was provided every other day with supply in excess of requirements. Initial and final weights of individual larvae, time to molting and survivorship were recorded. The relative growth rate of individual larvae was calculated as:

\[ RGR = \frac{(w_f - w_i)}{(m_{DD_a})} \]

where \( w_f = \) mass of larva at final weighing, \( w_i = \) mass of larva at initial weighing, \( m = \frac{(w_f - w_i)}{\ln(w_f/w_i)} \) = mean exponential mass (Gordon 1968), and \( DD_a = \) degree-days (indoors, base 6.8°C) between times of weighing.

Gypsy moth hatch phenology

The phenology of gypsy moth egg hatch was assessed on egg masses found in situ at Mont St. Hilaire. Masses were encircled with tanglefoot to prevent neonates from leaving the egg mass. Larvae were counted and removed from within the circle every day. Sample sizes were 6666 larvae on 26 egg masses in 1988, 10 587 larvae on 49 masses in 1989, and 11 203 larvae on 60 masses in 1990.

Results

Foliation quality changes during canopy expansion

Leaf toughness increased in a roughly sigmoid fashion as shown by the lines fitted with locally weighted scatterplot smoothing (LOWESS, Fig. 1). This smoothing is used in all figures; LOWESS summarizes these trends better than arbitrary functions fitted by least squares regression, since no assumption is made about the shape of the function (Cleveland 1979, Efron and Tibshirani 1991). The long initial period of low toughness is partly due to variance in budburst dates among individual trees; while some individuals are beginning to toughen, others have only just broken bud, keeping average toughness low. Variances of 4–6 days among individuals in budburst dates are common for these tree species. Nitrogen levels (Fig. 1), and water content (not shown) decreased rapidly as leaves expanded. Patterns were fairly consistent from year to year when plotted on a degree-day scale (Fig. 1).

In general, acceptability of new foliage to gypsy moth larvae is relatively high and declines rapidly as the foliage ages (Fig. 2). This trend is seen even in a species that is generally avoided by gypsy moth larvae, white ash (Fig. 2i), although its maximum acceptability is low. Short durations (up to 15 days) of acceptability above 60% are seen for species of intermediate preference (maple, beech, basswood, Figs. 2, 3). The two most preferred species, oak and aspen, are highly acceptable for longer: 3–4 weeks. However ironwood, also a preferred species, is only accepted by more than 60% of larvae for 3–4 days (Fig. 2c, 3). The two birch species show an initial period of low acceptability but then briefly become more acceptable to larvae (Fig. 2e, f). These curves represent the mean quality of the local population of trees. Individuals break bud at different times, so the window when an individual tree is vulnerable to larvae may be more brief than for the whole population.

Windows of high acceptability

To quantify the opportunity for establishment on different hosts, we calculated the host-seeking period of the gypsy moth and compared it with the period of high acceptability of hosts. Periods of high (>60%) acceptability of host species (from our experimental data in Fig. 2) are shown as lines at the top of each graph in Fig. 3. To calculate the phenology of host-seeking, we assume that larvae can survive 5 days after hatching; this is the survival time reported for starved larvae at room temperature (Capanera and Barbosa 1976). The size of the potential host-seeking population on each day is thus the sum of the number of larvae that hatched in the previous 5 days (Fig. 3). However, larvae do not seek hosts when it is cool (<8°C) or raining (Leonard 1971); these dates are also indicated in Fig. 3. The overlap between the windows of highly acceptable foliage of each species and the host-seeking period of larvae can be read from Fig. 3.

Gypsy moth egg hatch coincides with the appearance of highly acceptable new leaves of oak, the primary host (Fig. 3). Although hatch appears late in 1990 with respect to oak budburst, cool temperatures after budburst maintained the leaves at an early ontogenetic stage until hatch time. There is some overlap between the host-seeking period of the gypsy moth and the acceptable period of most tree species (Fig. 3). Foliage acceptability of all species except red oak and trembling aspen declines before the end of larval dispersal. Sugar maple, ironwood and basswood leaf out early enough and develop quickly enough that few larvae are likely to use these as hosts (Figs. 2 and 3).

Differences among years

Four species were tested in three of the years, and five more in two years. In general the progression of events was faster in 1989 than in 1988 or 1990 due to higher temperatures during the canopy expansion period (Fig. 3). In 1990 a week-long heat wave in late April brought on budburst very early for many species but temperatures returned to normal in May, and consequently canopy expansion was prolonged. In spite of these differences patterns of change were similar on a degree-day scale within species from year to year (Figs. 1 and 2). Sugar maple and beech, species that had very rapid declines in acceptability, retained this pattern among years. Ironwood and basswood had fluctuating acceptabilities in both 1989 and 1990 (Fig. 2c, h). With the exception of the warm period in April 1990, the temperature patterns were within the normal range. The
degree-day accumulation for the last week of April 1990 was beyond the 90th percentile based on 53 years of data from St. Hubert Airport.

First instar performance
Larval survival through the first stadium was high (above 90%) except for the final cohorts on white ash and sugar maple. No larvae survived on sugar maple from the 6 June cohort. Patterns in the relative growth rates mirrored those for acceptability: oak and aspen supported the highest larval growth rates and the longest durations of high rates (Fig. 4). Sugar maple supported intermediate larval growth rates that steadily declined with increasing foliage age, and growth on ash was slow and decreased after the second cohort (Fig. 4).
Fig. 2A–I. Acceptability of foliage to gypsy moth neonates during canopy expansion in 1988 (○), 1989 (△) and 1990 (□) as a function of degree-days above 5°C. Means of four replicates per sampling date with lines fitted by LOWESS (f=0.5)
Table 1. Pearson correlations coefficients between mean acceptability to gypsy moth larvae and mean leaf toughness, Kjeldahl nitrogen, water content and pH during the canopy expansion period. N= number of days

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Toughness</th>
<th>Nitrogen</th>
<th>Water Content</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red oak</td>
<td>38</td>
<td>-0.72***</td>
<td>0.41*</td>
<td>0.62***</td>
<td>0.58***</td>
</tr>
<tr>
<td>Trembling</td>
<td>46</td>
<td>-0.70***</td>
<td>0.26</td>
<td>0.46***</td>
<td>-0.18</td>
</tr>
<tr>
<td>aspen</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grey birch</td>
<td>28</td>
<td>-0.32</td>
<td>-0.03</td>
<td>0.30</td>
<td>-0.33</td>
</tr>
<tr>
<td>White birch</td>
<td>32</td>
<td>-0.51**</td>
<td>0.39*</td>
<td>0.30</td>
<td>0.15</td>
</tr>
<tr>
<td>Sugar maple</td>
<td>39</td>
<td>-0.77***</td>
<td>0.67***</td>
<td>0.29</td>
<td>0.71***</td>
</tr>
<tr>
<td>Beech</td>
<td>27</td>
<td>-0.94***</td>
<td>0.60**</td>
<td>0.83***</td>
<td>-0.13</td>
</tr>
<tr>
<td>Ironwood</td>
<td>29</td>
<td>-0.40*</td>
<td>0.14</td>
<td>-0.35</td>
<td>0.20</td>
</tr>
<tr>
<td>Basswood</td>
<td>27</td>
<td>-0.70***</td>
<td>0.60**</td>
<td>0.55**</td>
<td>0.54**</td>
</tr>
<tr>
<td>White ash</td>
<td>30</td>
<td>-0.56**</td>
<td>0.35</td>
<td>0.39*</td>
<td>-0.01</td>
</tr>
<tr>
<td>All species</td>
<td>296</td>
<td>-0.31***</td>
<td>0.30***</td>
<td>0.10</td>
<td>-0.05</td>
</tr>
</tbody>
</table>

* P<0.05, ** P<0.01, *** P<0.001

Note: sample sizes for nitrogen analyses of oak, aspen, maple, ash, and all species together are 27, 31, 27, 21, and 245 respectively

Foliage quality and acceptability

Some foliage quality parameters were correlated with acceptability for individual host species or for all species together (Table 1), but no one factor we measured has an over-riding influence on acceptability. The parameter most strongly and consistently correlated with acceptability was toughness. However even toughness explains relatively little of the variation in acceptability when all species are considered together \( R^2=0.096 \), Table 1, Fig. 1). Gypsy moth neonates will feed on very tough leaves of trembling aspen and red oak (400–500 g required to pierce leaves), but did not survive on foliage of sugar maple which was not as tough (300 g) (first instar performance on leaves from 6 June, Figs. 1 and 4). Leaves of ash are relatively unacceptable and growth rates on them are low even when they are soft and high in water and nitrogen (Fig. 1, 2i, 4). Resin on very young leaves of the two birch species prevented measurement of their toughness, but they were relatively soft and the resin
ally decline as foliage ages, and more rapidly on species with more rapid decreases in acceptability. These results concur with those of Raupp et al. (1988) for gypsy moth larvae on beech and three other species not studied here. They found foliage age effects on a similar short time scale, that resulted in different development times and pupal weights of cohorts.

Opportunities for host-seeking are variable from year-to-year and limited because of inclement weather and the rapid rate of foliar development of some tree species. The bulk of the gypsy moth population is seeking hosts in only a short period, and opportunities are further reduced by poor weather. In the three years 16, 53, and 31% of the population were alive on days suitable for host-seeking. This proportion depends strongly on when cool or wet days occur with respect to the peak in host-seeking population size. Unpredictable weather combines with rapid changes in acceptability to make host selection opportunities more ephemeral.

The combined impacts on population dynamics of weather limitations on host-seeking, mortality during dispersal and slow growth due to asynchrony with hosts are potentially substantial. Miller et al. (1988) found that changes in the area defoliated in New England by gypsy moth larvae are correlated with weather at the time of gypsy moth hatch and leaf emergence, perhaps because of variable synchrony. Emergence of winter moth (Operophthera brumata) before host budburst has been observed in some years and asynchrony is a major contributor to numerical variability of this species (Embree 1965; Gradwell 1973). The fall cankerworm (Alsophila pometaria) is also susceptible to asynchrony with host budburst (Schneider 1980). Host plant heterogeneity, in this case on a short-term temporal scale, can help to constrain the success of spring-feeding foliviore in temperate deciduous forests.

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