

Leaf phenology and herbivory along a temperature gradient: a spatial test of the phenological window hypothesis

Aizen, Marcelo A.^{1*} & Patterson III, William A.²

¹*Departamento de Ecología, Universidad Nacional del Comahue, CRUB, Unidad Postal Universidad 1336, 8400 Bariloche, Río Negro, Argentina;* ²*Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, MA 01003, USA;* *Corresponding author; Tel. + 54 944 26368; Fax +54 944 22111; E-mail: MARCITO@CAB.CNEA.EDU.AR

Abstract. In this study, we documented patterns of variation in leaf phenology and leaf herbivory in scrub oak (*Quercus ilicifolia* Wang) along the slope of a closed topographical depression, 15 m deep and 400 m wide, in the pine barrens of eastern Massachusetts. Minimum temperatures over the growing season averaged 6.5 °C lower at the bottom of the depression than at the top. Bud break at the bottom of the depression was 2-3 weeks delayed compared with the top. In both years of this study, 1988 and 1989, leaf damage by thrips increased down slope producing differences of about 10 % in the proportion of leaf area damaged between the top and the bottom of the depression. Because thrips fed exclusively on the youngest leaves, this pattern could be attributed to a closer synchrony between the timing of leaf flushing and the period of insect feeding activity towards the bottom of the depression. Average differences in leaf damage between years could also be accounted for by variation in leaf phenology. These patterns support the hypothesis that the degree of temporal overlap between availability of high quality foliage and the period of insect feeding activity may greatly determine spatial and temporal variation in leaf damage by insect herbivores.

Keywords: Insect herbivory; *Quercus ilicifolia*; Thrips; Topographical gradient.

Introduction

In temperate regions, the time at which plants come into leaf is related to a seasonal increase in temperature. The adaptive nature of this relation is apparent, as expanding leaves are highly susceptible to being damaged by frost. However, within a community different plant species flush their leaves according to a fixed sequence that extends over a relatively long period of time. Adaptation to past, rather than present climate conditions and phylogenetic constraints may, in part, explain disparate responses among species to a common environment (Lechowicz 1984). Less is known about the evolutionary role of biotic interactions in molding the time of phenological events (Murali & Sukumar 1993).

In plants, insect herbivory may account for a sizeable loss in leaf biomass (Landsberg & Ohmart 1989). Most folivorous insects, however, are restricted to foraging during the ephemeral, early stages of leaf development, as young, expanding leaves represent the only suitable source of food (Raupp & Denno 1983; Faeth 1985; Coley 1989). In temperate regions, this stage represents a 'phenological window' which, for a given plant species, may extend for a period of only a few weeks (Hunter & Lechowicz 1992). A consequence of these insect foraging constraints, which can be termed as 'the phenological window hypothesis', is that plants flushing their leaves before or after the peak period of feeding activity of a major folivore would exhibit lower leaf area losses than plants for which leaf flush coincides with peak periods of insect feeding. Temporal mismatches between insect feeding activity and food availability may occur because leafing phenology and the interruption of insect winter diapause may be triggered by different environmental cues or different thresholds of the same factor.

Although the typical time that a plant species comes into leaf may represent an evolutionary compromise among present climatic, biotic, and historical factors, the local temperature environment under which a given plant is growing is of overriding importance as the proximal determinant of bud burst and early leaf development. Thus, spatial and temporal variability in temperature during spring may strongly influence temporal and spatial patterns of food availability and therefore constitute an important determinant of insect population dynamics and community structure (Strong et al. 1984; Kareiva 1986). For a given level of insect activity, variability in leaf phenology of a particular plant species at a given site is likely to result in differences in the total cumulative amount of leaf-area damaged, because most herbivory can be attributed to one or a few species of spring-feeding insects (Barbosa & Wagner 1989).

In this study, we documented variation in leaf



Fig. 1. View across the depression looking north from near station 6 in the Myles Standish State Forest, Massachusetts, on June 5, 1988. *Quercus ilicifolia* at the top of the depression are fully leaved out whereas those at the mid elevation are just beginning to leaf out. Buds have not yet broken on those near the base.

phenology and leaf herbivory in scrub oak (*Quercus ilicifolia* Wang) along a topographically determined temperature gradient. We were specifically interested in testing a corollary of the 'phenological window hypothesis' which predicts that a local gradient in leaf phenology should result in differences in the extent of insect leaf damage.

Material and Methods

Quercus ilicifolia is a woody shrub species that grows on dry sandy barrens and rocky hillsides. It sprouts vigorously from the root crown after disturbances, such as fire, forming dense understory thickets reaching heights of 2 to 3 m. Scrub oak is a characteristic species of the pitch pine (*Pinus rigida* Mill.) barrens of eastern North America (Forman 1979). In eastern Massachusetts, where this study was conducted, scrub oak normally produces a single flush of leaves during a 7-10 day period in mid to late May. Severe defoliation or the occurrence of a killing frost induce the production of a second flush of leaves. However, light to moderate herbivory, like that reported in this study, does not induce the production of new leaves.

Scrub oak supports a diverse community of herbivores from the Coleoptera and Lepidoptera. However, in

our study area most observed damage may be attributed to only one insect species, *Heterothrips quercicola* (Thysanoptera: Heterothripidae) (T. Simmons pers. comm.). Leaf damage by thrips in scrub oak was observed to be restricted to the tender leaves exposed in opening buds. This damage is characterized by intervein, crescent-shaped necrotic areas, approximately 0.5 mm in length. These expand into more or less circular holes as leaves grow (pers. obs.). Fresh leaf damage by thrips was not observed after the first weeks of initial leaf development.

The study was conducted during 1988 and 1989 in one of several closed depressions in the Wareham Pitted Outwash Plain of Myles Standish State Forest, ca. 10 km southwest of Plymouth, Massachusetts. The area that we studied is an oval-shaped depression about 15 m deep and 400 m across (Fig. 1). Soils are coarse sands of the Carver Series with depths to bedrock > 30 m.

The local climate is seasonally influenced by the proximity of the cold waters of Cape Cod Bay, which is < 10 km to the east. Average monthly temperatures range from about 0 °C in January to 21 °C in July. Night temperatures decrease and the incidence of frost events increase towards the bottom of depressions because of the downward drainage of cold air. At least in the depressions, frosts can occur in any month (A. Mason pers. comm.). Annual precipitation ranges from 1050 to

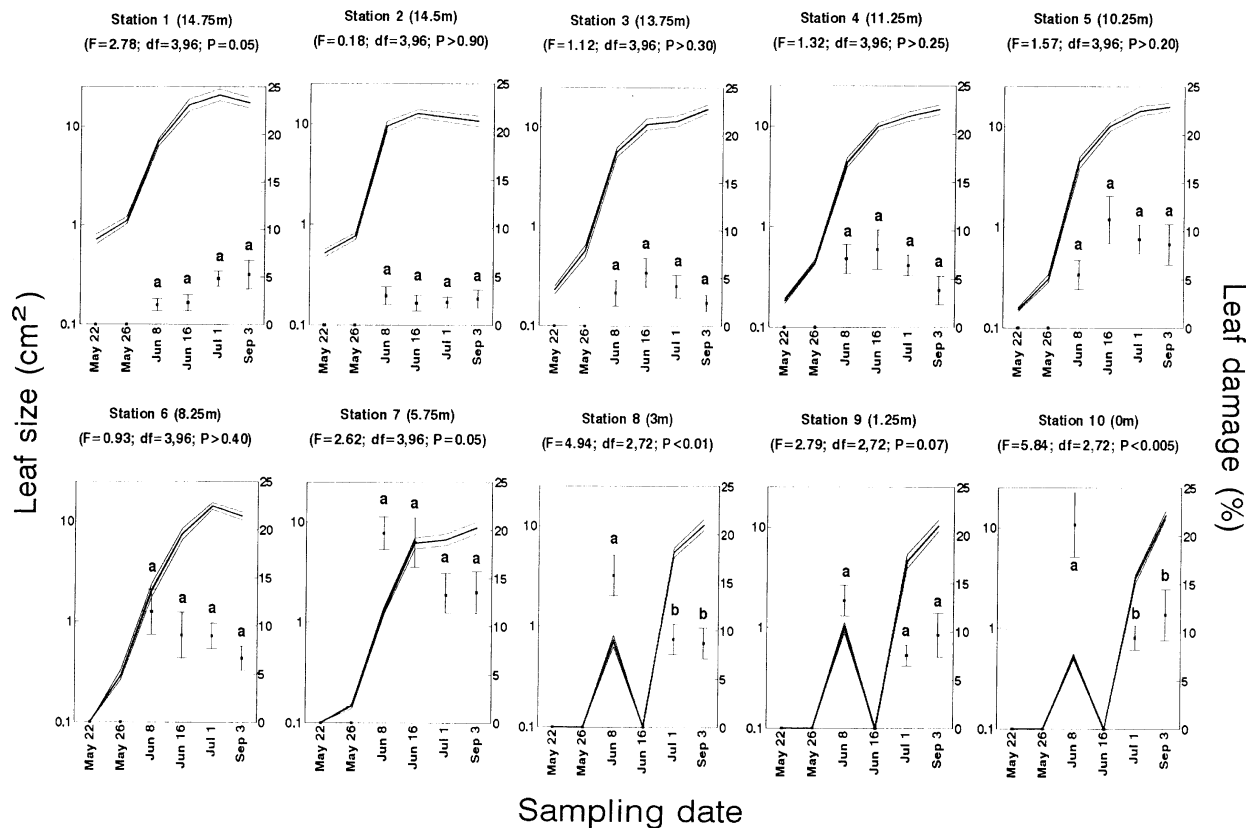


Fig. 2. Mean leaf size and leaf damage by insects for the 1988 growing season. Solid, dark lines connect mean log leaf size, and light lines ± 1 SE and ± 1 SE values respectively. Vertical bars represent mean leaf damage ± 1 SE. Information on the significance of one-way ANOVAs of the effect of time (sampling date) on mean leaf damage is reported for each sampled station. Means that do not differ significantly (Ryan's Q test, $P > 0.05$) within a station share a common letter.

1300 mm/yr and is evenly distributed across months.

Several fires have swept through the area in the twentieth century, with the most recent occurring in 1975. Most scrub oak stems were thus no older than 14 years in 1988. About 50 % of all scrub oak stems present in the depression in 1988 were recruited within a two-year period after the fire (unpubl. data).

During the spring of 1988, we established a permanent transect extending from the top to the bottom of the depression along its north-facing slope. Ten sampling stations were established at 25-m intervals along the slope. The relative elevation of each station with respect to the bottom of the depression (see Fig. 2) was determined from estimates of the slope angle measured with a clinometer.

Five maximum-minimum thermometers were set out on May 31, 1989, at 1 m high from ground level at stations 1, 5, 7, 9 and 10. Minimum and maximum temperatures were recorded at 1-2 week intervals through September 5.

On six dates in 1988 (May 22 and 26, June 8 and 16,

July 1, and September 3) we harvested several hundred scrub oak leaves at each of the 10 stations. 25 leaves per station and per collection date were randomly selected from the larger sample. For these leaves, we measured leaf length (from the base of the blade to the base of the terminal bristle), total leaf surface area, and the area damaged by grazing insects. Areas were estimated using a clear grid (62 squares / cm²) placed over individual leaves. Squares were recorded as undamaged or damaged, with the latter being those that overlapped holes, scraped surfaces, or areas of insect mining. Leaf damage was not categorized by type, but > 90 % of all observed damage was caused by thrips feeding. Total leaf area was used as an estimate of leaf size, whereas herbivory damage for each leaf was estimated as area damaged by insects expressed as a percent of total leaf area rather than as the absolute area damaged (see below).

On May 31 and June 12, 1989, leaves were harvested as in 1988 from stations 1 through 10, with leaf length measured in a random subsample of 25 leaves collected at each station on each date. In 1988 we found a strong

relationship between the square root of leaf area vs. leaf length for leaves collected and measured ($r^2 = 0.970$, $n = 1250$), so in 1989 we estimated individual total leaf area Y (cm²) from measurements of leaf length (cm) using the equation:

$$Y = (-0.256 + 0.576X)^2 \quad (1)$$

For 1989 leaves, leaf damage was visually estimated and assigned to the mid-point value of one of several consecutive categories incremented by 5 % (i.e. 0 % = no damage, 2.5 % = < 5 % but > 0 %, 7.5 % = between 5 and 10 %, 12.5 % = between 10 and 15 %, etc.). Calibration of this method by comparative trials confirmed that average damage values from visual estimates of 25 leaves differed by no more than ± 1 % from means obtained by counting squares.

By considering the percentage of leaf area damaged as a measure of herbivory, we assume that, although individual leaf size changes with time, a lack of change in the average percentage of leaf damage following leaf flush indicates that no new leaf damage has occurred. This implies that the relative rate of expansion of the damaged area equals the relative rate of leaf growth as a consequence of the process of leaf expansion (Lowman 1987). Because we were also interested in looking at the relationship between leaf size and herbivory on leaves already subjected to herbivory, we had to assume that herbivory did not affect the rate at which leaves expand. To test these two assumptions, we measured leaf lengths of 27 pairs of young leaves at station 4 on May 31, 1989.

Table 1. Linear regressions of mean log leaf size vs. sampling date (expressed as no. of days since May 22) between May 22 and June 16, 1988. The antilog of the slope is an estimate of the daily geometric rate of leaf expansion. Only two sample times were available for stations 8-10, because leaves were still concealed in the buds on May 22 and were frost-killed by June 16 (Fig. 2).

Station	<i>n</i>	slope	r^2	10 slope
1	4	0.057	0.987 **	1.141
2	4	0.062	0.933 *	1.154
3	4	0.070	0.977 *	1.175
4	4	0.072	0.986 **	1.181
5	4	0.078	0.976 *	1.196
6	4	0.075	0.999 ***	1.189
7	4	0.074	0.979 **	1.186
8	2	0.078	-	1.196
9	2	0.091	-	1.232
10	2	0.065	-	1.162

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Each pair included leaves of similar size attached to the same twig. A circular hole, 0.6 cm in diameter, was punched in one of the leaves of each pair, with a tag placed around the petiole of the undamaged leaf. Leaf lengths and hole diameters were remeasured on June 12. This two-week interval was chosen because it encompassed a period of very rapid leaf expansion. Individual total leaf area was estimated from leaf length – see Eq. (1) – and damaged surface was estimated as the area of a circle with the observed diameter. No natural damage was recorded on these leaves between the two sampling dates.

Leaf area was log-transformed for all the analyses in which this variable was involved. A logarithmic transformation not only increased homoscedasticity and normality, but also linearized differences in leaf size among sampling stations and periods during early spring. This is a consequence of the exponential nature of the leaf expansion process during the first weeks after bud burst (Maksymowych 1973). We used this property to test the assumption that growth rates after bud burst did not differ with position on the slope, and therefore leaf size may be used as a surrogate for leaf age early in the growing season. For this purpose, we used the more complete 1988 data set and fitted a separate regression line of mean log leaf size vs. sampling date between May 22 and June 16. Because the slopes of these regressions estimate the instantaneous rates of leaf expansion for each station, a test of homogeneity of slopes (Sokal & Rohlf 1981) was used to test the hypothesis of no difference in leaf expansion rate with elevation.

Results

Minimum temperature over the 1989 growing season averaged 7.7 °C at the top and 1.2 °C at the bottom of the depression. The relationship between mean minimum temperature (°C) and elevation (m) was well described by the linear regression

$$Y = 1.43 + 0.45X \quad (r^2 = 0.980, n = 5, P < 0.005). \quad (2)$$

Mean maximum temperature over the gradient averaged 33.6 °C and was not significantly related to elevation ($r^2 = 0.130$, $n = 5$, $P = 0.60$)

In both sample years, we found significant differences in leaf phenology associated with the strong minimum temperature gradient. In 1988, leaves at the highest station were relatively well expanded by May 22 while at the lowest station bud burst did not start until some time between May 26 and June 8 (Figs. 1, 2). A heavy frost occurring between June 8 and June 16, 1988 killed some scrub oak leaves at station 7 and all the

Table 2. Mean (± 1 SD) log leaf size and percent leaf area lost to herbivory by May 31 and June 12, 1989 at different elevations. Kruskal-Wallis tests were used to compare differences in the extent of leaf damage between sampling dates. $n = 25$.

Station	Leaf size [log (cm ²)]		Leaf damage (%)		X ²
	May 31	June 12	May 31	June 12	
1	1.063 \pm 0.223	1.406 \pm 0.215	0.60 \pm 1.65	1.00 \pm 1.77	1.57
2	0.978 \pm 0.165	1.289 \pm 0.184	0.90 \pm 1.75	0.80 \pm 1.73	0.09
3	0.886 \pm 0.176	1.165 \pm 0.157	1.00 \pm 1.25	1.20 \pm 2.90	0.91
4	0.569 \pm 0.243	1.199 \pm 0.187	1.80 \pm 3.92	1.00 \pm 2.16	0.44
5	0.624 \pm 0.183	1.264 \pm 0.155	1.30 \pm 2.18	1.50 \pm 3.75	0.27
6	0.607 \pm 0.253	1.111 \pm 0.249	1.40 \pm 2.70	1.00 \pm 1.76	0.41
7	-0.077 \pm 0.379	1.026 \pm 0.187	0.10 \pm 1.50	2.10 \pm 2.95	10.98 ***
8	-0.889 \pm 0.479	0.916 \pm 0.274	0.00 \pm 0.00	3.50 \pm 3.61	28.55 ****
9	-1.305 \pm 0.805	0.944 \pm 0.233	0.00 \pm 0.00	5.70 \pm 5.84	32.70 ****
10	-	0.667 \pm 0.203	-	8.50 \pm 4.08	-

*** = $P < 0.001$; **** = $P < 0.0001$.

leaves at and below station 8. This forced stems in the lower part of the gradient to produce a second flush of leaves (Fig. 2). Mean final leaf size measured in September, 1988 was not significantly correlated with elevation ($r = 0.450$, $n = 10$, $P = 0.18$), however.

Despite differences in the timing of bud burst, leaf expansion in 1988 occurred at a similar rate along the gradient (Table 1; test of homogeneity of slopes, $F_{9,14} = 0.82$, $P = 0.60$), so leaf size was strongly correlated with elevation during the first part of the growing season (Fig. 3). These findings support the assumption that during the first 4-5 weeks of the growing season, leaf size may be used as a surrogate for leaf age. During

these first weeks after bud burst, leaf expansion occurred at an average daily geometric rate of 1.18, or an equivalent daily arithmetic rate of 0.071 on a log scale (i.e. an average leaf increased its size by 18 % each day).

These leaf growth rates can be used to estimate phenological differences within and among years. Dividing the difference in mean log leaf size between stations 1 and 10 on June 8, 1988 (a date on which leaves were expanding along the entire gradient) by 0.071, results in an estimated phenological delay of ca. 17 days between the top and bottom of the depression. Because of this phenological gap and the exponential nature of leaf expansion, on June 8, 1988 leaves at the top of the

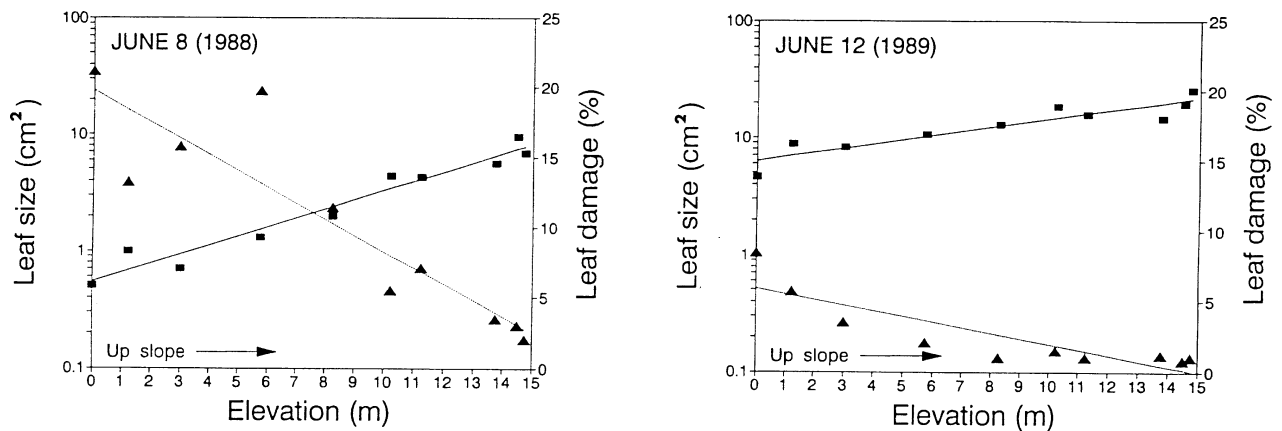


Fig. 3. Mean log leaf size (squares) and percent leaf area damaged by insects (triangles) on June 8, 1988, and June 12, 1989 vs. position in the gradient (X = elevation in meters). Regression equations are: $\log(\text{leaf size}) = -0.266 + 0.078X$ ($r^2 = 0.954$, $n = 10$, $P < 0.0001$), and $\text{leaf damage} = 19.808 - 1.155X$ ($r^2 = 0.822$, $n = 10$, $P = 0.0003$) for 1988; and $\log(\text{leaf size}) = 0.799 + 0.036X$ ($r^2 = 0.856$, $n = 10$, $P < 0.0001$) and $\text{leaf damage} = 5.941 - 0.400X$ ($r^2 = 0.740$, $n = 10$, $P = 0.001$) for 1989.

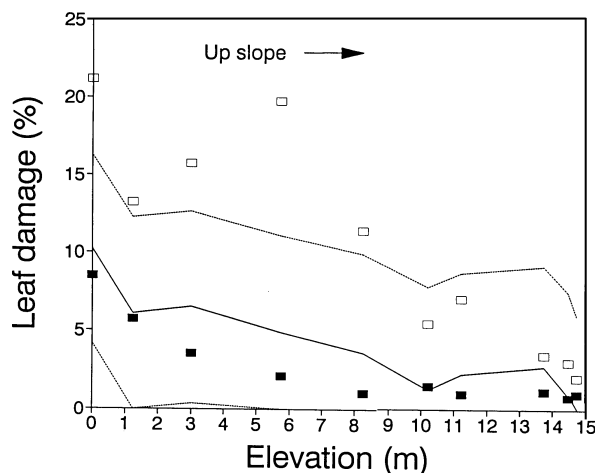


Fig. 4. Predicted leaf damage (continuous line) \pm 95% confidence interval (dotted lines) for 1989 based on the 1988 equation: leaf damage = $15.978 - 14.954 \log(\text{leaf size})$ ($r^2 = 0.888$, $n = 10$, $P < 0.0001$). Observed 1989 leaf damage values are represented by filled squares. Observed 1988 leaf damage values (open squares) are presented for comparison.

gradient (station 1) were on the average 13 times larger than those at the bottom of the depression (station 10).

We estimated the average leaf expansion rate for 1989 by dividing by 12 the difference between the grand means of log leaf size from stations 1-9 on May 31 and June 12 (Table 2; $X \pm \text{SE} = 0.275 \pm 0.059$ and 1.145 ± 0.017 , respectively). This resulted in an arithmetic expansion rate (on a log scale) of 0.072, remarkably similar to that estimated in 1988. By comparing the means in log leaf size at stations 1 and 10 on June 12, we estimated a phenological delay of ca. 11 days for 1989. This phenological delay was translated into a leaf-size difference of 5.5 times on this date between the top and the bottom of the depression.

We observed that bud burst in 1989 occurred 1-2 weeks earlier than in 1988. An eight day estimate was derived by dividing the difference between the grand means of log leaf size on June 8, 1988 and June 12, 1989 by either the 1988 or the 1989 growth rate (and discounting four days due to differences in the actual sampling dates). We similarly estimated that on June 8 leaves were, on average, $2.7 \times$ larger in 1989 than in 1988.

Paired comparisons showed that there were no significant differences between dates in the proportion of the total leaf area represented by the puncture hole ($X \pm \text{SE} = 3.85 \pm 0.19\%$ on May 31 vs. $4.33 \pm 0.22\%$ on June 12; $t_{26} = 1.67$, $P = 0.12$). Thus, it seems safe to assume that no change in the percentage of leaf area removed or damaged by herbivores between dates re-

lates to an absence of herbivory during that period. There were also no significant differences in growth (i.e. the difference in log leaf size between dates) between paired punctured and unpunctured leaves ($X \pm \text{SE} = 0.252 \pm 0.011$ vs. 0.257 ± 0.014 ; $t_{26} = 0.44$, $df = 26$, $P = 0.60$), supporting the assumption that past herbivory did not affect subsequent leaf growth.

All along the transect, insect herbivory first began sometime between May 26 and June 8, 1988, shortly after bud-burst in the lower part of the transect (Fig. 2). Because leaf flushing began in mid-May in the upper part of the gradient, there was a period of at least two weeks when leaves near the top of the slope grew free of herbivory (Fig. 2).

Between June 8 and September 3, 1988, few changes in the amount of leaf area damaged by herbivores occurred in the upper part of the gradient (Fig. 2). At station 1, a slight increase in leaf damage was apparent by the end of the summer (Fig. 2). However, for the growing season as a whole, estimates of mean leaf damage in the upper part of the gradient (stations 1-3) were in most cases $< 5\%$ (Fig. 2). This contrasts sharply with leaf damage levels $> 15\%$ recorded in the first flush of leaves in the lower part of the gradient (stations 7-10). Damage to the second flush of leaves in this portion of the gradient was still high (ca. 10%), but significantly less than for the first flush (Fig. 2). The reduction in leaf damage recorded at station 7 between June 16 and July 1 is attributed to the fact that the leaf samples collected after June 16 were composed of a mixture of highly damaged first-flush leaves and less-damaged second-flush leaves.

Similar results were found with the less intensive 1989 sampling. In general, we found very little damage along the gradient before May 31 (Table 2). Although no subsequent significant increases in leaf damage were found in the upper part of the gradient, significant increases in defoliation levels were found in the lower stations by June 12, 1989 (Table 2).

In both, 1988 and 1989, we observed a dramatic increase in the amount of herbivory damage during the first days of June (Fig. 2, Table 2). In both years, leaf damage increased significantly from the top to the bottom of the depression, although the slope of the linear regression fitted to the 1989 data was shallower (Fig. 3). This increase in the incidence of herbivory towards the bottom of the depression was negatively associated with the observed decrease in mean leaf size along the gradient (Fig. 3). The equation $Y = 15.98 - 14.95X$, with $Y = \text{leaf damage (\%)}$ and $X = \text{mean log leaf size (cm}^2\text{)}$, accounted for 89% of the variation in leaf herbivory on June 8, 1988 ($n = 10$, $P < 0.0001$); and the equation $Y = 14.21 - 10.54X$ accounted for 79% of the variation in herbivory on June 12, 1989 ($n = 10$, $P < 0.0001$).

Despite the similarities between years in these intraseasonal patterns, leaf damage on June 12, 1989 averaged only 2.60 ± 0.26 % ($X \pm SE$) over the gradient; much lower than the 10.25 ± 0.72 % overall leaf damage recorded on June 8, 1988. Because temporal and spatial variation in leaf phenology was the principal cause of differences in leaf size within and among years, we determined if phenological variation to the order of 1 week, as observed between 1988 and 1989, could cause the decrease in leaf damage observed in 1989 (Fig. 3). To do this, we used the June 8, 1988 equation relating leaf damage and mean log leaf size to predict the observed relationship between leaf herbivory and elevation in 1989. We used as inputs the mean log leaf size values from June 12, 1989 from which we discounted 4 days of growth. No observed leaf damage value differed by more than 3 % leaf area units from its correspondent predicted value, with all values falling within the expected 95 % confidence intervals (Fig. 4). Using the corrected grand mean in log leaf size, we predicted for 1989 an overall damage level of 3.9 %. This differed by only 1.3 % leaf area units from the observed value of 2.6 %.

Discussion

The results of this study show that, because of the exponential nature of the leaf expansion process, differences in bud burst of a few days between years or locations can produce dramatic differences in the size of leaves exposed to herbivory. Because the quality of leaves as an insect food resource decreases quickly with leaf size and age (e.g. Feeny 1970; Rockwood 1974; Schultz et al. 1982; Raupp & Denno 1983; Furuta 1987; Hunter & Lechowicz 1992), spatial and temporal phenological variation may strongly influence food availability and therefore the dynamics of resource-limited insect populations (Faeth 1987). By determining the timing of food availability, phenological variability may also constitute an important factor in the structuring of communities of folivorous insects (Niemelä & Haukioja 1982; Auerbach & Simberloff 1985; Crawley & Akhteruzzaman 1988). From a plant perspective, subtle differences in leaf phenology may determine spatial and temporal patterns in leaf defoliation, plant growth, survival, and reproduction, hence, affecting plant population dynamics (Crawley 1989). By determining patterns of defoliation and plant mortality, phenological variability may also have consequences at the community and ecosystem levels (e.g. influencing plant succession, patterns of biomass accumulation, and the frequency and intensity of fire events).

The strong spatial association between leaf phenology

and insect herbivory reported in this study fits the prediction of the 'phenological window hypothesis': leaf damage significantly increased from the top of the depression to the bottom, where bud burst coincided with the onset of feeding activity by thrips. Additionally, because of year-to-year constancy in the timing of feeding activity by thrips, variability in phenological events also appears to determine temporal patterns of insect herbivory. By the time thrips appeared in 1989, there was a smaller proportion of young, palatable leaves than in 1988, and a lower observed incidence of herbivory. Qualitative and quantitative differences in the amount of damage observed between 1988 and 1989 were consistent with differences in leaf phenology (Fig. 4). Observations in 1992, when bud burst was exceptionally late, further supported this model. On June 8, 1992, we found a much higher incidence of leaf damage by thrips than in both 1988 and 1989 (> 30 % in the lower part of the gradient; personal observation). Because leaf phenology was about 2 weeks later in 1992 than in 1988, there was, in 1992, a broader spatial and temporal 'window' of availability of small leaves.

Although our evidence strongly favors the 'phenological window hypothesis', we need to ask if there might be alternative explanations for the associations we found. White (1969, 1984) hypothesized that susceptibility of plants to insect attack is enhanced by environmental stress and that this can cause changes in host-plant nutritional value or chemical defence capabilities. Changes along this gradient in scrub oak growth and mortality (manuscript in preparation), and in flower and fruit production (Aizen & Kenigsten 1990) clearly indicate increased physiological plant stress towards the bottom of the depression. Rather than following an indirect pathway mediated by leaf size and triggered by temperature-related phenological differences, White's environmental stress hypothesis would explain the reported relationship between elevation and leaf damage (Fig. 3) as a direct consequence of low temperature stress on leaf nutritional quality. Although studies on leaf chemistry would be needed to evaluate this hypothesis, we believe that the 'environmental stress hypothesis' is a less likely general explanation for the herbivory gradients reported here, given the observed feeding habits of the thrip and the strong differences in leaf phenology existing along the gradient. Other studies, including several involving oak species, document dramatic changes in chemical and physical properties and overall palatability of leaves during the process of leaf expansion (Feeny 1970; Schultz et al. 1982; Faeth 1985; Mauffete & Oechel 1989; Hunter & Lechowicz 1992). Additionally, the overall evidence in support of the environmental stress hypothesis is controversial, and opposing arguments and evidence have been reported

(Mopper & Whitham 1992).

Early leaf-out increases the susceptibility of young leaves to frost events, but it also provides a mechanism for escaping damage by folivorous insects, which increase in diversity and abundance as spring progresses (Niemelä & Haukioja 1982). An optimal time for leaf flushing may result from the balance between these two opposing selective forces within certain limits imposed by phylogenetic constraints (Lechowicz 1984). According to this hypothesis, a delay in leaf flushing should be correlated with an increase in leaf damage. The opposing topographical clines in leaf phenology and herbivory report in this study support this proposition.

Acknowledgements. We thank C. Ezcurra, P. Feinsinger, T.G. Whitham, P.W. Price and two anonymous reviewers for suggestions and critical review. A. Kenigsten provided assistance in the field and in the lab. We also thank A. Mason for logistic support at Myles Standish State Forest and T. Simmons for thrip identification. This work was supported in part by the McIntire-Stennis Cooperative Forestry Research Program (grant no. MS-53 to WAP) and the National Scientific and Technical Research Council of Argentina (CONICET).

References

- Aizen, M.A. & Kenigsten, A. 1990. Floral sex ratios in scrub oak (*Quercus ilicifolia*) vary with microtopography and stem height. *Can. J. Bot.* 68: 1364-1368.
- Auerbach, M.J. & Simberloff, D. 1985. Responses of leaf miners to atypical leaf production patterns. *Ecol. Entomol.* 9: 361-367.
- Barbosa, P. & Wagner, M.R. 1989. *Introduction to forest tree and shade insects*. Academic Press, San Diego, CA.
- Coley, P.D. 1989. Effects of leaf age and plant life history patterns on herbivory. *Nature* 284: 545-546.
- Crawley, M.J. 1989. Insect herbivores and plant population dynamics. *Annu. Rev. Entomol.* 34: 531-564.
- Crawley, M.J. & Akhteruzzaman, M. 1988. Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Funct. Ecol.* 2: 409-415.
- Faeth, S.H. 1985. Quantitative defense theory and early feeding by insects on oaks. *Oecologia (Berl.)* 68: 34-40.
- Faeth, S.H. 1987. Community structure and folivorous insect outbreaks: the roles of vertical and horizontal interactions. In: Barbosa, P. & Schultz, J.C. (eds.) *Insect outbreaks*, pp. 135-171. Academic Press, San Diego, CA.
- Feeny, P.P. 1970. Seasonal changes in oak leaf tannins as a cause of spring feeding by winter moth caterpillar. *Ecology* 51: 565-581.
- Forman, R.T.T. 1979. *Pine barrens ecosystems and landscape*. Academic Press, New York, NY.
- Furuta, K. 1987. Amount of favourable feeding materials in spring for the maple aphid, *Periphyllus californiensis* Shinji, estimated from the phenological relations between the aphid and the host trees. *J. Appl. Entomol.* 104: 144-157.
- Hunter, A.F. & Lechowicz, M.J. 1992. Foliage quality changes during canopy development of some northern hardwood trees. *Oecologia (Berl.)* 89: 316-323.
- Kareiva, P. 1986. Patchiness, dispersal, and species interactions: consequences for communities of herbivorous insects. In: Diamond, J. & Case, T.J. (eds.) *Community Ecology*, pp. 192-206. Harper & Row, New York, NY.
- Landsberg, J. & Ohmart, C. 1989. Levels of insect defoliation in forests: patterns and concepts. *Trends Ecol. Evol.* 4: 96-100.
- Lechowicz, M.J. 1984. Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *Am. Nat.* 124: 821-842.
- Lowman, M.O. 1987. Relationships between leaf growth and holes caused by herbivores. *Aust. J. Ecol.* 132: 189-191.
- Maksymowych, R. 1973. *Analysis of leaf development*. Cambridge University Press, Cambridge.
- Mauffete, Y. & Oechel, W.C. 1989. Seasonal variation in leaf chemistry of the coast live oak *Quercus agrifolia* and implications for the California oak moth *Phryganidia californica*. *Oecologia (Berl.)* 79: 439-445.
- Mopper, S. & Whitham, T.G. 1992. The plant stress paradox: effects of pinyon sawfly sex ratios and fecundity. *Ecology* 73: 515-525.
- Murali, K.S. & Sukumar, R. 1993. Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. *Oecologia (Berl.)* 94: 114-119.
- Niemelä, P. & Haukioja, E. 1982. Seasonal patterns in species richness of herbivores: Macrolepidopteran larvae on Finnish deciduous trees. *Ecol. Entomol.* 7: 169-175.
- Raupp, M.J. & Denno, R.F. 1983. Leaf age as a predictor of herbivore distribution and abundance. In: Denno, R.F. & McClure, M.S. (eds.) *Variable plants and herbivores in natural and managed systems*, pp. 91-124. Academic Press, New York, NY.
- Rockwood, L.L. 1974. Seasonal changes in the susceptibility of *Crescentia alata* leaves to the flea beetle, *Oedynychus* sp. *Ecology* 55: 142-148.
- Schultz, J.C., Nothnagle, P.J. & Baldwin, I.T. 1982. Seasonal and individual variation in leaf quality of two northern hardwoods tree species. *Am. J. Bot.* 69: 753-759.
- Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. 2nd ed. W.H. Freeman, San Francisco, CA.
- Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984. *Insects on plants: community patterns and mechanisms*. Blackwell, Oxford.
- White, T.C.R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* 50: 905-909.
- White, T.C.R. 1984. The abundance of invertebrate herbivory in relation to the availability of nitrogen in stressed food plants. *Oecologia (Berl.)* 63: 90-105.

Received 21 September 1994;

Revision received 10 April 1995;

Accepted 10 May 1995.