Is there more insect folivory in warmer temperate climates? A latitudinal comparison of insect folivory in eastern North America

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Summary

1. It is generally believed that warmer climate forests suffer more herbivory, as a proportion of leaf area, than cooler climate forests. However, standardized studies using the same methodology have rarely been performed.

2. We carried out a study on scattered forest-edge populations of four widespread tree species (*Quercus alba*, *Acer rubrum*, *Fagus grandifolia* and *Liquidambar styraciflua*) spanning 17° of latitude in North America.

3. We sampled early summer sun leaves (12 weeks after bud break) at each latitude in 2 years. Total insect folivory damage was estimated from the percentage area damaged in fresh leaves on forest edges, using a scanner-linked software.

4. The percentage area damage per leaf of all four species in both years shows a significant latitudinal trend, with less damage in lower latitude areas of eastern North America. This is contrary to what would generally be expected according to current ecological thinking. Among the four studied species, only *A. rubrum* showed a significant difference between the 2 years.

5. *Synthesis.* The observation of an inverse latitudinal trend may have wider implications for the study of community functioning, suggesting that strength of 'biotic' interaction between plants and herbivores might actually be no less important, or in fact more important, in cool temperate climates compared with warm temperate climates.

Key-words: folivory, herbivore, insect, latitude, North America, temperate forest, temperature

Introduction

It is widely believed that herbivore–plant interactions and plant defences vary with latitude. Herbivory is suggested as being more intense and plant defences better developed at lower latitudes (Dobzhansky 1950; MacArthur 1969; Lowman 1985; Coley & Aide 1991; Coley & Barone 1996; Grime 2001; Pennings & Silliman 2005).

At predicted warmer temperatures, insect damage is projected to increase for northern European forests (Wolf *et al.* 2008). Despite the widespread interest in such patterns, evidence for latitudinal gradients in herbivory is in short supply. There are several reasons why the existence of a latitudinal pattern is contentious. In a literature review of 42 studies, Coley & Barone (1996) found evidence of higher leaf herbivory (folivory) in the tropics (11.1% of leaf area per year in tropical trees, as opposed to 7.1% in temperate trees). They caution, however, that there was a paucity of accurate studies. Conclusions such as those reached in their review tend to be based on literature reviews rather than on systematic studies. Moreover, studies that have estimated rates of folivory have often used quite different methods from one region to another, complicating the comparison (Pennings & Silliman 2005). Various studies have used standardized methods to test for the existence of a latitudinal trend of leaf folivory. Andrew & Hughes (2005) found no evidence of a gradient in folivory (in terms of chewing, mining and sap sucking damage) on a single species of shrub (*Acacia falcata*) along a gradient of 15° latitude in eastern Australia. Sinclair & Hughes (2008) failed to identify a latitudinal trend of the proportion of leaf-mined species in eastern Australia. A standardized study by Lowman (1984), also in eastern Australia, found that cooler climate forests had more leaf folivory per unit area of leaf cover. Hallam & Read (2006)

reported that tropical plant species invested more in anti-herbivore defence than their temperate counterparts. An increasing foliar damage trend on *Betula pubescens* and *Betula pendula* along decreasing latitude was detected in Fennoscandia, while no geographical or climatic pattern was detected on *Betula pendula* in its more southern distribution region (e.g. Central Europe) (Kozlov 2008).

The present study used a closely standardized methodology to compare folivory (not including sap suckers) in selected temperate forest species along a latitudinal gradient using an extensive network of sites.

Methods and materials

DATA COLLECTION

Species selection

This study was based on sampling of early summer leaves under wild tree populations at a range of different latitudes in eastern North America (Fig. 1) covering a wide latitudinal range in temperatures. The four species used in our study (*Fagus grandifolia*, *Acer rubrum*, *Quercus alba* and *Liquidambar styraciflua*) were chosen because they are common and very widespread species in eastern North America, occur along a wide latitudinal temperature gradient and are easy to recognize. *Acer rubrum* occurs between 24 and 48° N and was sampled here between 28 and 45° N. *Fagus grandifolia* extends between 30 and 48° N and was sampled between 30 and 45° N. *Quercus alba* extends between 30 and 46° N and was sampled between 30 and 45° N. *Liquidambar styraciflua* occurs between 27 and 41° N and was sampled between 28 and 41° N.

Use of live leaves from forest edges

Standardizing the sampling procedure as much as possible to enable meaningful comparison across sites and latitude, we sampled live
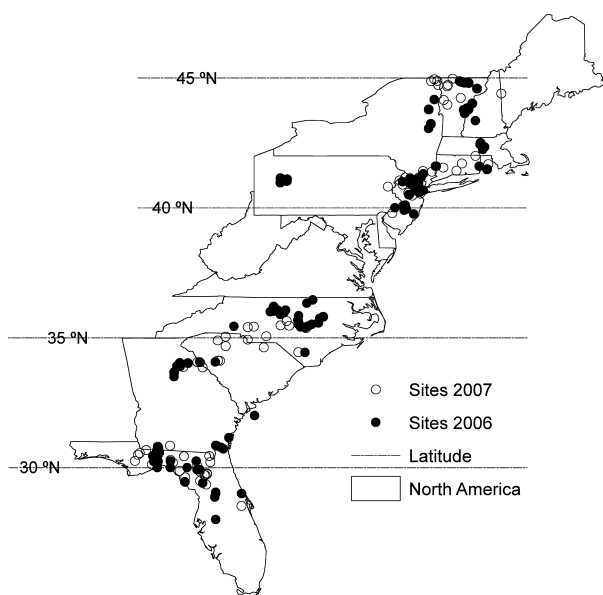

Fig. 1. Sites in North America along the east coast of the United States. Note that some individual dots mark multiple sites located close together.

leaves that were still attached to the tree, since this has advantages in terms of certainties about what exactly is being studied (Kozlov 2008). Sampling was carried out only using trees that grew along the edges of small roads or tracks 5–15 m in width and that were part of a contiguous forest of at least 10 ha on either side of the road.

Sites were located arbitrarily along pre-planned routes. Exact sample locations along back roads and in state parks and state forests were chosen by placing a finger with eyes closed on a road atlas page. We would then drive to the chosen area and sample the nearest populations that we could find to this chosen point, if it consisted of at least 10 individuals and was in an accessible location for sampling. Populations were located at distances of at least 5 km. The sampling sites represent a wide range of landscapes, from coastal plain to piedmont. Samples were mostly taken from areas below 330 m a.s.l., although in northern Vermont and New York States, some higher-altitude sites (up to 400 m) were sampled. So altitude effects can be excluded. A very wide range of landscapes and soil conditions were sampled within this scatter of sites (STATSGO 1994).

Along each forest edge population we located, we sampled 10 small branches of about 50 leaves, taking care that the branches consisted only of 'sun leaves', i.e. leaves observed to be in direct sunlight on the forest edge during the middle part of the day (10 AM–4:30 PM). We randomly selected one such branch per tree at around 4–5 m height. At this height, folivory damage cannot easily be seen from the ground, ensuring that branches were not chosen for the amount of damage. The branch was cut using a pole pruner and placed in a plastic bag. The next tree of the same species at least 10 m away along the forest edge was then sampled, until 10 trees in all had been sampled. All samples (one branch per tree) of the same species from the same site were placed together in a large plastic bag, labelled by site and taken for assessment of folivory damage. Branches were stored in their bags labelled by site in a cold room at 3 °C until they could be assessed for folivory damage.

Sampling from the bags was also carried out blindly. Water was sprayed into each bag to moisten the leaves and keep them supple and to make them stick together (which avoids size-sorting). All the leaves in the bag were then churned by hand to avoid any size or damage-level sorting. A handful of leaves was then grabbed blindly from the bag and assessed for damage. This was repeated until 75 leaves in total had been sampled. Each leaf was then scanned to assess herbivore damage. The SIGMASCAN software (v. 12.0; SPSS Inc., Chicago, IL, USA) allows the user to draw a shape around the likely extent of the intact leaf and then subtract areas identified as damaged, giving a rigorous estimate of folivory loss.

Both authors worked equally on temperate leaves from all latitudes to identify (i) chewed off areas, (ii) skeletonized areas, (iii) leafminers, and (iv) galls.

The folivory damage categories were as follows:

1 *Chewed off.* Areas missing from the leaf, either at the edge or as a hole in the interior of the leaf.
2 *Skeletonized.* Network of veins remaining, but the intervening tissue eaten (including epidermis).
3 *Leafminers.* Papery area, often as a curving surface, where the leaf tissue has been eaten, but the epidermis is left intact.
4 *Galls.* Lumps of many different forms, resulting from insects or mites laying eggs, which resulted in the leaf tissue growing to envelop the herbivore.

These categories were checked against the illustrations given in Cranshaw (2004), an authoritative source on insect damage types.

We assumed that only insects, not mammals, were the cause of the observed leaf area loss for two major reasons. First, the only arboreal folivorous mammal in eastern North America, the porcupine (*Erethizon dorsatum*), typically climbs and consumes trees that grow away from the forest edge. Secondly and most importantly, the leaf samples were taken at 4–5 m from the ground, far above the height that deer or other ground-dwelling herbivores in eastern North America can reach.

It is possible that some leaves were completely eaten by insect herbivores and thus may have gone unnoticed in the sampling. Visual inspection of harvested branches indicated that no leaves were completely eaten down to the petiole, suggesting that complete consumption was relatively uncommon. Since most leaves were only slightly damaged, it is reasonable to expect that an increase in overall damage levels would result in an increase in more heavily damaged leaves and a shift in the lognormal distribution, and thus a higher average folivory, even if completely eaten leaves go uncounted. Thus, we should expect that 'unseen' complete consumption of leaves would be detected by proxy, through an overall increase in average folivory on incompletely consumed leaves.

SAMPLING TIMES

Sampling at about the same time in all localities (north and south) would not only be logistically difficult but would also fail to take into account the major differences in phenology from north to south at a particular time. Such phenological differences could account for differences in folivory, which is most pronounced in the early stages of leaf growth, because toughness, nutrient content and phenolic concentrations change as leaves age (Coley & Barone 1996). The growing season in Florida begins months earlier than in northern New England and trees harvested in northern New England (*F. grandifolia*, *A. rubrum* and *Q. alba*, the three species in this study that extend this far north) would therefore have had less time for their leaves to mature and would have been exposed to several weeks less potential herbivory than those in Florida. Thus sampling took place in early summer (about 12 weeks after the mean bud break time as averaged across a range of deciduous species; Borchert *et al.* 2005) at phenologically analogous stages at different latitudes. Equivalent sampling times were estimated using two methods:

Method 1

Growing degree days (GDD) were calculated using the formula: $\{(T_{\max} + T_{\min})/2\} - B = \text{GDD}$, where B represents a base temperature value of 10 °C (McMaster & Wilhelm 1997). For the base 10∕30 method, the following adjustments were made: (i) temperatures below 10 °C were set at 10 °C and (ii) temperatures above 30 °C were set at 30 °C. The reasons for these 'cut-offs' in GDD calculations are that very little growth and biological activity takes place below 10 °C, whereas above 30 °C, there is no evident benefit to plant growth and other biological activity. However, these cut-off limits do vary among GDD indices. Climate data were obtained from the PRISM data (PRISM Group 2004).

Method 2

Phenological delay was calculated using the predictive formula of Borchert *et al.* (2005), which has a predictive R^2-value of 0.97 for bud break time throughout North America (week of bud break = 10.3 × 0.77 × mean temperature of the coldest month). This empirical formula was based on observations from the Southern

USA to Canada. While the formula characterizes the time of bud break, we used the relationship between seasonal delay and temperature (using climate data from PRISM) to determine equivalent delay in early summer sampling times 12 weeks after bud break, working northwards from Florida.

Averaging the two sources of phenological estimation, time intervals for sampling were as given below (1–4). Within each of these four 'bands', we started sampling at more southerly sites moving northwards over several days. Localities intermediate between these were sampled at correspondingly intermediate times.

1 Northern Florida and southern Georgia: 22–28 May.
2 Northern Georgia, northern parts of South Carolina and North Carolina: 10–17 June.
3 New Jersey, southern New York State: 6–13 July.
4 Northern Vermont and northern New York State: 20 July–25 July.

DATA ANALYSIS

To examine the relationship between folivory and the climatic factors which tend to vary with latitude, leaf folivory percentage area damage was regressed against climate variables for each year: mean temperature (e.g. mean 2006 temperature and mean 2007 temperature separately), hottest and coldest monthly mean temperature and annual precipitation. The climatic data for each site were derived from PRISM data (PRISM Group 2004), available online. Then stepwise regression (SAS 2008, version of 9.3) was utilized to detect variables correlated with leaf folivory loss. The entry threshold for adding each variable was set at the 90% confidence level.

To examine regional differences and annual variation in folivory, a nested ANOVA analysis was performed by designating region as a main factor and year as a factor nested within the region factor. The regions designated were 'the north' (including states north of Virginia) and 'the south' (states south of and including Virginia). Variables analysed included each of the four types of folivory damage (chewed off, skeletonized, leafminers and galls).

Overlapping sites that were sampled in both 2006 and 2007 were compared in terms of their folivory loss, using a paired sample *T*-test (SAS 2008, version of 9.3) to examine annual variation of each species.

Results

LEAF FOLIVORY LOSS IN COMPARISON WITH TEMPERATURE

Fagus grandifolia and *Q. alba* exhibited a significantly decreasing trend in folivory (at < 0.1 confidence level) against February temperature in eastern North America in 2006 and 2007 (Table 1). No significant correlation was detected with other climatic variables. *Acer rubrum* showed a significantly decreasing trend only along rising mean annual temperature in 2006 and 2007 (Table 1, Fig. 2). *Liquidambar styraciflua* exhibited an increasing trend along enhanced precipitation in 2006 and had a significantly negative correlation with increasing annual temperature in 2007. February is the coldest month in eastern North America. Considering the strong inter-dependence between the temperature in February and mean annual temperature ($R^2 = 0.94$), the folivory trend in relation to

Table 1. Statistical analysis results for total folivory trend of each species against temperature in 2006 and 2007

Species	Year	Correlated variable	Sample size	*r*	*P*-value
Fagus grandifolia	2006	February temperature	26	−0.378	0.057
	2007	February temperature	28	−0.638	0.0002
Acer rubrum	2006	Mean annual temperature	60	−0.243	0.06
	2007	Mean annual temperature	58	−0.695	0.0001
Quercus alba	2006	February temperature	36	−0.629	0.0001
	2007	February temperature	45	−0.676	0.0001
Liquidambar styraciflua	2006	Annual precipitation	47	0.246	0.096
	2007	Mean annual temperature	25	−0.558	0.0046
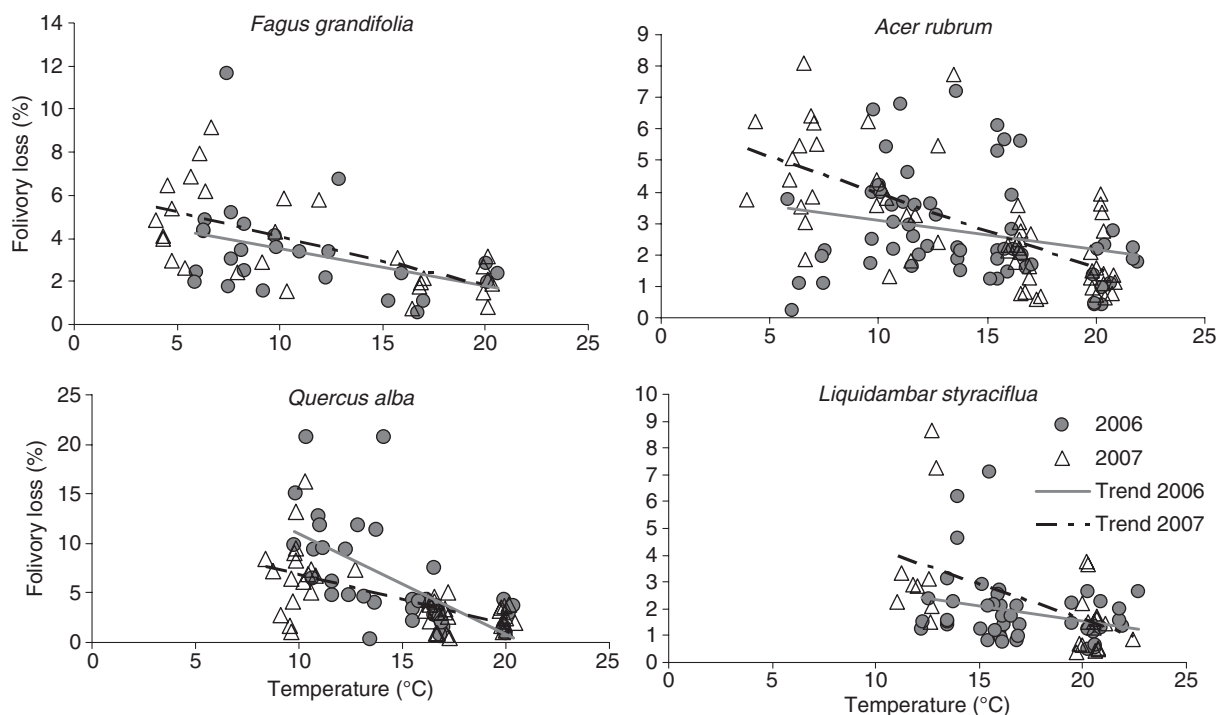
Fig. 2. Plots of folivory against mean annual temperature, for 2006 and 2007.

February temperature can be considered similar to that seen in relation to mean annual temperature.

REGIONAL DIFFERENCE AND VARIABILITY AMONG YEARS OF LEAF FOLIVORY

For *F. grandifolia*, *L. styraciflua* and *Q. alba*, there was no significant difference between years among the three folivory categories skeletonized, galls and leafminers. For folivory damage caused by chewed off, *L. styraciflua*, *F. grandifolia* and *Q. alba* showed a significant difference, while *A. rubrum* did not exhibit a significant difference (Table 2). For the folivory categories without a significant inter-annual difference, we combined the data of both years and examined their regional difference (Fig. 3).

All four species in the northern sites had a significantly higher level of folivory damage by chewed off than those in the southern sites (Table 2; Fig. 3). For the three other folivory categories, the four species in the northern sites had slightly higher

folivory loss than those in the southern sites (Fig. 3), but no significant differences were identified, possibly caused by high internal variation (Table 2).

LEAF FOLIVORY VARIABILITY BETWEEN YEARS FOR 2-YEAR OVERLAPPING SITES

There were 13 overlapping sites for *A. rubrum* and 11 sites for *F. grandifolia* between 2006 and 2007. For *L. styraciflua* and *Q. alba*, the overlapping site sample size was too small to be adequate for statistical analysis. The paired sample *T*-test demonstrated that there was no significant difference in folivory between 2006 and 2007 for *F. grandifolia* (*P* = 0.315) and for *Acer* (*P* = 0.518) as shown in Fig. 4.

RELATIVE FREQUENCY OF TYPES OF LEAF DAMAGE

Most leaf folivory in both the northern and southern sites was in the form of leaf material being chewed off (Fig. 3). For

Table 2. Nested ANOVAS on leaf folivory (annual variation nested within southern and northern region; the significance of each factor was indicated by *P*-value)

Folivory type	Species	Region (*P*)	Year (region) (*P*)
Chewed off	*Fagus grandifolia*	0.001	0.002
	Acer rubrum	0.001	0.199
	Liquidambar styraciflua	0.001	0.023
	Quercus alba	0.001	0.043
Skeletonized	*Fagus grandifolia*	0.242	0.284
	Acer rubrum	0.365	0.466
	Liquidambar styraciflua	0.194	0.064
	Quercus alba	0.492	0.539
Galls	*Fagus grandifolia*	0.291	0.336
	Acer rubrum	0.107	0.313
	Liquidambar styraciflua	0.152	0.993
	Quercus alba	0.396	0.050
Leafminers	*Fagus grandifolia*	0.199	0.289
	Acer rubrum	0.09	0.077
	Liquidambar styraciflua	0.342	0.22
	Quercus alba	0.024	0.128

F. grandifolia, the loss attributed to chewed off accounted for nearly 70% of the total leaf folivory loss. For *A. rubrum*, the loss attributed to chewed off accounted for nearly 98% of the total leaf folivory. For *L. styraciflua* and *Q. alba*, the chewed off accounted for nearly 85% of folivory damage. Skeletonized was the second most important form of leaf folivory after chewing damage. *Fagus grandifolia* had the highest skeleteton-ized leaf folivory which accounted for nearly 20% of the total leaf folivory loss. Leaf folivory in the form of leaf galls and leaf miners accounted for only a small proportion of the total leaf folivory. Leaf folivory area loss per leaf was typically smaller than 3%, with over 65% of leaves having lost <3% of their area. Only 7% of leaves lost more than 20% of their area to folivory damage (Fig. 5).

Discussion

The idea that there is more folivory damage to plants at lower latitudes appears to be a generally accepted paradigm in ecology (Coley & Barone 1996). This has implications for many aspects of community and ecosystem theory, including, for example, the strength of selection for co-evolution, and the maintenance of the far greater species diversity of the tropics (Janzen 1970). Given its potential importance in ecology, it is imperative that the paradigm is properly tested using similar methods in higher and lower latitudes. Our results do not appear to support the theory that there is more folivory in warm climates.

SPATIAL AND TEMPORAL VARIATION IN FOLIVORY ALONG THE LATITUDINAL GRADIENT

It seems that weather events such as a drought in the south-eastern USA in 2007 (NCDC 2008) were not sufficient to produce significantly lower folivory than in 2006. However, it is possible that a slight depression of folivory due to this drought (too small to exceed the formal statistical confidence limits) may have contributed to the highly statistically significant latitudinal trend seen in all four species in 2007.

It is important to note that folivory in temperate forests can occur through both a general and fairly consistent 'background' level of endemic folivory and 'outbreaks' of very intense folivory, which are far more intense, but variable in space and time (Turchin 1990). Our study could be measuring instances of both. However, few sites had folivory damage of more than 10% of leaf area.

Especially high folivory levels of >9% were found at some northerly sites, particularly in the latitudinal band between 40 and 45° N. These sites may play an important role in raising the average folivory level in the north for 2006 and 2007 (without them the latitudinal trend would certainly be weaker). None of the areas sampled was within 20 km of recorded gypsy moth (*Lymantria dispar*) outbreaks in that year, based on state forest agency reports in the states sampled (e.g. http://nj.gov/agriculture/divisions/pi/prog/gmhomeowners.html). As gypsy moth is a non-native addition to the ecosystem, present from southern Virginia northwards, it is important to remove from the data any sites likely to have been in outbreak areas. Our only site that was within several km of a known gypsy moth outbreak area was in Byrne State Forest, New Jersey in 2006, where average folivory of *Q. alba* was 23%. We eliminated this data point. It is likely that the high folivory (>8%) seen in several other sites was due to outbreaks of various native herbivores such as forest tent caterpillar (*Malacosoma disstria*) and other tent-forming caterpillars and remnants of tents were seen on the branches of trees sampled at several sites in New Jersey which showed particularly heavy folivory.

In this study, we only sampled once during the early part of the growing season at each locality. Although it is generally agreed that folivory occurs mainly during the earliest weeks of a leaf's lifetime (Coley & Barone 1996), it is possible that latitudinal differences in folivory or plant defences appear later in the season. Forests and parts of forest canopies can be sampled in a myriad of ways. Our method was chosen because it permitted sampling in a standardized way in different locations. Significantly, the present work represents one example of a closely standardized and consistent study. A parallel study by the same authors (work in progress) includes assessment of forest leaf litter folivory, which provides a whole-canopy and whole-community index of folivory damage.

EDGE EFFECTS

It is possible that the decision to sample on forest edges significantly altered the pattern of folivory found in this study. Various studies have found that trees on forest edges have either more or less folivory than those within the interior of the forest (Didham *et al*. 1996). However, there is no evident reason from previous studies why folivory on a forest edge should show a different latitudinal trend from that of the forest interior. However, one possibility is that the hotter temperatures and stronger sunlight that occur on forest edges at lower latitudes are
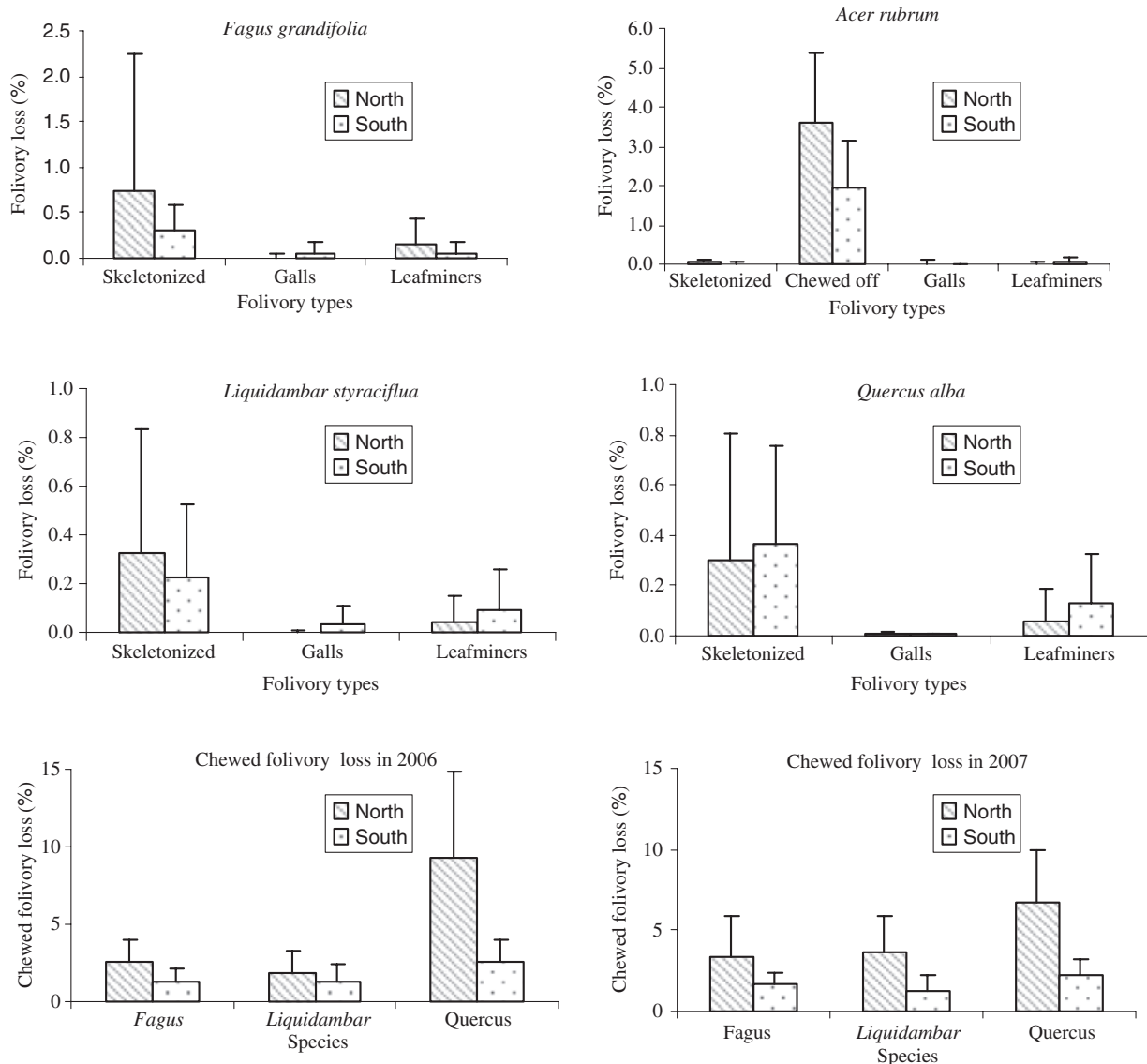
Fig. 3. Regional difference of folivory as classified by particular types (Skeletonized, area chewed off, area galls, leafminers). For the skeletonized, galls and leafminers of the four species and chewed off folivory from *Acer rubrum*, there was no significant annual difference and the data from both years were combined. For chewed off folivory alone in *Fagus grandifolia*, *Liquidambar styraciflua* and *Quercus alba*, there was significant annual difference and the 2 years of data were separated.

stronger suppressing agents on insect herbivore activity, allowing less herbivore damage to accumulate.

POSSIBLE IMPLICATIONS OF THE LACK OF THE 'EXPECTED' LATITUDINAL FOLIVORY GRADIENT

The concept that there is more folivory in the warmer parts of the temperate zone seems intuitively reasonable to many ecologists, since there is only a mild winter to control herbivorous insect populations. Without density-independent population crashes caused, for example, by harsh winters, herbivores may build up to levels at which density-dependent factors such as food limitation, disease and predation become important (Dobzhansky 1950). Although rarely mentioned explicitly in the literature, this viewpoint has permeated ecology, based on

our many conversations with other ecologists on this topic. A shift in relative importance of biotic and physical controls on populations is seen as a contrast between the tropics and temperate zone as a whole, and also within the temperate zone grading from warmer climates with mild winters to cooler climates with cold winters. If density-related controls are more intense in warmer climates, co-evolution may become more likely, possibly helping to generate the very high levels of diversity found in the tropics (Janzen 1970). Searching for a latitudinal difference in insect folivory becomes a means of testing one aspect of the important underlying hypothesis, that plant-herbivore biotic interactions are more intense in warmer climates. It also becomes an indirect test of the mechanisms that are thought to follow on from more biotic interaction in warm climates.
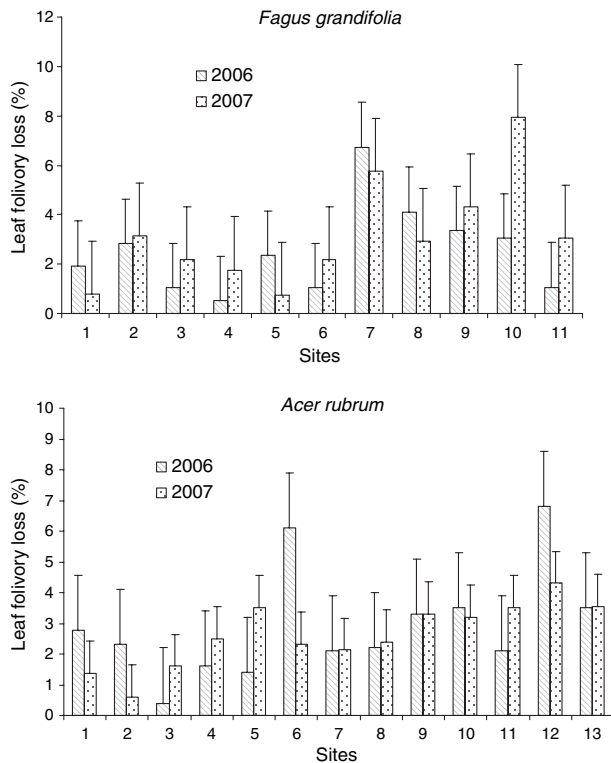
Fig. 4. Leaf folivory comparison between 2006 and 2007 for the same sites of *Fagus grandifolia* and *Acer rubrum*.
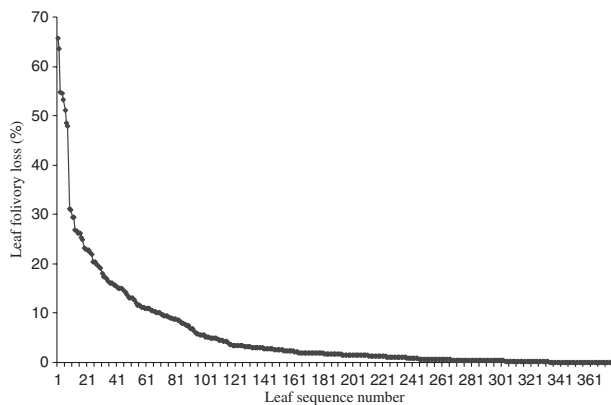

Fig. 5. Rank order of leaf damage per leaf (% area lost, with most heavily damaged leaves placed first). This curve represents the combined leaf samples of five randomly selected temperate eastern North American sites.

Various other studies have failed to show that lower latitude woody ecosystems have greater folivory than higher latitude ones (Andrew & Hughes 2005). The widely cited paper by Lowman (1984) also suggests less folivory at lower latitudes: cool temperate forests were found to have about 50% more folivory than subtropical forests whether steady-state or cohort studies were used. However, there are studies which have shown the 'expected' pattern (Kozlov 2008; Adams *et al.* 2009), with less folivory at higher latitudes.

A relevant observation is that the latitudinal difference in folivory in eastern North America that existed in all four

species in 2007, and in three species in 2006, is in absolute terms fairly small, mostly around 3–5% of leaf area (averaging 8% in one case, *Q. alba* in 2006) in the early summer leaves sampled. It is a moot point whether such a small latitudinal difference in folivory would be enough to affect community functioning significantly (Whittaker & Warrington 1985; Adams *et al.* 2009). Studies have, however, shown that low-to-moderate levels of insect folivory can impact trees in multiple ways. Whittaker & Warrington (1985) studied the impacts of different levels of insect folivory on *Acer pseudoplatanus* through experimental ant predation to lower herbivore populations. Mean radial growth of these mature trees with folivory levels of 6–10% leaf area was 35% lower than that of *A. pseudoplatanus* trees with folivory levels of 1–1.6% leaf area. Crawley (1983) found that oak trees with 12% defoliation had a more than 50% reduction in acorn production compared to controls. It is plausible therefore that the difference in folivory levels seen with latitude in this study could, over time, result in differences in both tree growth and seed output, although it is not certain that the trend is as strong in most years.

It is important to note that the longer overall growing season in lower latitudes could allow folivory in low latitudes to 'catch up' or exceed that at higher latitudes during the year as a whole. However, compared by the same criteria, folivory per unit time of growing season, we find no evidence here that the 'expected' pattern holds true.

Acknowledgements

References

Adams, J.M., Rehill, B., Zhang, Y. & Gower, J. (2009) A test of the latitudinal defense hypothesis: herbivory, tannins and total phenolics in four North American tree species. *Ecological Research*, **24**, 697–704.

Andrew, N.R. & Hughes, L. (2005) Herbivore damage along a latitudinal gradient: relative impacts of different feeding guilds. *Oikos*, **108**, 176–182.

Borchert, R., Robertson, K., Schwartz, M.D. & Linera, G.W. (2005) Phenology of temperate trees in tropical climates. *International Journal of Biometeorology*, **50**, 57–65.

Coley, P.D. & Aide, T.M. (1991) A comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. *Plant–Animal-Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (eds P.W. Price, T.M. Lewinsohn, G.W. Fernandes & W.W. Benson), pp. 25–49. Wiley & Sons, New York.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305–335.

Cranshaw, W. (2004) *Garden Insects of North America*. Princeton University Press, Princeton.

Crawley, M.J. (1983) *Herbivory, the Dynamics of Animal–Plant Interactions*. Blackwell, Oxford.

Didham, R.K., Ghazoul, J., Stork, N.E. & Davis, A.J. (1996) Insects in fragmented forests: a functional approach. *Trends in Ecology & Evolution*, **11**, 255–260.

Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, **38**, 209–221.

Grime, P. (2001) *Plant Strategies, Vegetation Processes and Ecosystem Properties*. Wiley, Chichester.

Hallam, A. & Read, J. (2006) Do tropical species invest more in anti-herbivore defence than temperate species? A test in Eucryphia (Cunoniaceae) in eastern Australia. *Journal of Tropical Ecology*, **22**, 41–51.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *The American Naturalist*, **104**, 501–528.

Kozlov, M.V. (2008) Losses of birch foliage due to insect folivory along geographical gradients in Europe: a climate-driven pattern? *Climatic Change*, **87**, 107–117.

Lowman, M.D. (1984) An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than we thought? *Biotropica*, **16**, 264–268.

Lowman, M.D. (1985) temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Australian Journal of Ecology*, **10**, 7–24.

MacArthur, R. (1969) Patterns of communities in the tropics. *Biological Journal of the Linnean Society*, **1**, 19–30.

McMaster, G.S. & Wilhelm, W.W. (1997) Growing degree-days: one equation, two interpretations. *Agricultural and Forest Meteorology*, **87**, 291–300.

NCDC (2008) *National Climate Data Center, NOAA Satellite and Information Center*. Available at: http://www.ncdc.noaa.gov/oa/ncdc.html (last accessed April 2009).

Pennings, S.C. & Silliman, B.R. (2005) Linking biogeography and community ecology: latitudinal variation in plant-herbivore interaction strength. *Ecology*, **86**, 2310–2319.

PRISM Group (2004) Oregon State University. Available at: http://www.prismclimate.org, created Feb 2004.

SAS (2008) *SAS User's Guide*. SAS institute Inc., Cary, NC, USA.

Sinclair, R.J. & Hughes, L. (2008) Incidence of leaf mining in different vegetation types across rainfall, canopy cover and latitudinal gradients. *Austral Ecology*, **33**, 353–360.

STATSGO (1994) *U.S. General Soil Map*. Available at: http://www.ncgc.nrcs.usda.gov/products/datasets/statsgo/description.html (accessed on ????).

Turchin, P. (1990) Rarity of density dependence or population regulation with lags? *Nature*, **344**, 660–663.

Whittaker, J.B. & Warrington, S. (1985) An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on Sycamore (*Acer pseudoplatanus*) III. Effects on tree growth. *Journal of Applied Ecology*, **22**, 797–811.

Wolf, A., Kozlov, M.V. & Callaghan, T.V. (2008) Impact of non-outbreak insect damage on vegetation in northern Europe will be greater than expected during a changing climate. *Climatic Change*, **87**, 91–106.