

Herbivory patterns in mature sugar maple: variation with vertical canopy strata and tree ontogeny

SEAN C. THOMAS, AGNIESZKA J. SZTABA and SANDY M. SMITH Faculty of Forestry, University of Toronto, Toronto, Canada

Abstract. 1. Although leaf morphology and chemistry show profound changes as trees age, the consequences of such changes to herbivory have received little attention, particularly late in the ontogeny of canopy trees.

2. Using a mobile aerial lift for canopy access, patterns of leaf damage were evaluated in canopy-dominant mature sugar maple (*Acer saccharum* Marsh) trees ranging from ~20 to 70 cm in diameter, corresponding to an age range of ~40–180 years.

3. Herbivore damage patterns varied in relation to both vertical canopy position (among upper-, mid-, and lower-canopy positions) and with tree size. Damage types attributable to herbivores active on leaf surfaces, including leaf skeletonizers and leaf cutters (both principally Lepidoptera), and leaf stippling inducers (Hemiptera) showed decreases with tree size, and with increasing height in the canopy. In contrast, leaf damage from the most abundant gall-forming arthropod in the system, the eriophyid mite *Vasates aceriscrumena*, increased markedly with tree size.

4. The results indicate that herbivory patterns vary with both canopy stratum and with tree size in sugar maple, and that the relative strength of vertical stratification and tree ontogeny effects are similar in magnitude. The predominant patterns are of a decrease in herbivory with increasing height in the canopy and with tree size, but certain galling arthropods exhibit the reverse trends.

Key words. Forest canopy, galling, herbivory, ontogenetic succession, ontogeny, vertical stratification.

Introduction

Herbivores can play important roles in driving forest ecosystem processes by damaging photosynthetic tissue, by accelerating nutrient dynamics, and by altering the relative competitive balance among trees in the forest community (Schowalter *et al.*, 1986). Tree responses to herbivores, both evolved and phenotypic, also have profound effects at the ecosystem level. For example, production of plant secondary chemicals with an important defence function, such as phenolic compounds, can dramatically affect leaf decomposition and nutrient cycling (Hättenschwiler & Vitousek, 2000; Kraus *et al.*, 2003). Herbivory is highly heterogeneous in forest ecosystems, and in particular varies with canopy height and insolation. In tropical forests, the predominant pattern appears to be reduced herbivore abundance and tissue removal in the upper canopy as

compared with the lower canopy or understory strata (Lowman, 1985, 1992; Basset, 1991; Angulo-Sandoval & Aide, 2000). Vertical patterns of herbivory and/or herbivore abundance are less clear, but also less well studied in temperate forest canopies (Phillipson & Thompson, 1983; Holmes & Schultz, 1988; Le Corff & Marquis, 1999), and some authors have suggested that vertical *stratification* of herbivorous arthropod communities is generally weak in temperate forest canopies as compared with the tropics (Fowler, 1985; Lowman *et al.*, 1993; Basset *et al.*, 2003).

Tree age and developmental stage can also have important effects on herbivore communities and herbivory levels, but such effects have received less attention than vertical canopy gradients. Several studies examining herbivore impacts and susceptibility in relation to plant age have found a pattern of decreasing impacts and increasing investment in physical and chemical defences, and consequently reduced herbivory rates, with increasing plant age and size (Craig *et al.*, 1986; Price *et al.*, 1987; Boege & Marquis, 2005). However, studies to date examining ontogenetic changes in herbivore impacts

Correspondence: Sean C. Thomas, Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, M5S 3B3, Canada. E-mail: sc.thomas@utoronto.ca

and defence traits in trees have been restricted to comparisons of seedlings, or saplings versus mature trees (Reichardt *et al.*, 1984; Basey *et al.*, 1988; Macedo & Langenheim, 1989; Dominy *et al.*, 2003; Goodger *et al.*, 2004; Boege, 2005), or have focused on early ontogenetic stages alone (Bryant & Julkuntti, 1995; Fritz & Hochwender, 2001; Del Val & Dirzo, 2003; Webber & Woodrow, 2009). Potential changes in herbivory patterns and plant defences later in tree ontogeny have received little empirical attention. In a recent review it was hypothesised that there should be a decline in defence allocation, as well as a consequent increase in herbivore impacts after reproductive onset and during tree senescence (Boege & Marquis, 2005). This hypothesis follows on from the assumptions that increasing resource allocation to reproduction will compete with allocation to leaf defence functions (Bazzaz *et al.*, 1987), and that senescence will ultimately result in a decline in resources available for all leaf functions.

The hypothesis that herbivore impacts should increase late in tree ontogeny has not been directly addressed. However, empirical studies aimed at understanding ontogenetic changes in leaf functional traits appear to offer contradictory evidence, as continued increases in traits that may function in herbivore defence very late in tree ontogeny have been documented. For example, both conifers and angiosperms appear to show monotonically increasing leaf mass to area (LMA) with increasing tree size (Day *et al.*, 2001; Niinemets, 2002; Nabeshima & Hiura, 2004; England & Attiwill, 2006). Studies that have controlled for incident light (e.g. have compared open-grown saplings vs. upper leaves of canopy trees) indicate that ontogenetic changes in LMA and related traits do not simply involve sun/shade acclimation responses (Thomas & Winner, 2002; Thomas, 2009). It has also been suggested that exposure to herbivory may be one selective agent favouring increased LMA and leaf lignification in older trees (Thomas & Winner, 2002). In some conifers, very old trees even produce highly lignified cell types not found in earlier ontogenetic stages that have a putative defence function (Apple *et al.*, 2002). Physical properties of leaves, including LMA, are important determinants of palatability and plant defence (Coley, 1983; Agrawal & Fishbein, 2006; Hanley *et al.*, 2007); in fact leaf toughness has been suggested as the single most important correlate of herbivory in some comparative studies (Coley, 1983), and is generally closely correlated with LMA (Hanley *et al.*, 2007).

In addition to differences in defence allocation and realised herbivory levels, mature trees varying in age and size might be expected to differ in terms of herbivore community structure. Trees show increased structural complexity with age, in particular increased ramification of branching structure (Lawton, 1983) and an increased abundance and diversity of epiphytes (Lesica *et al.*, 1991; McGee & Kimmerer, 2002), both important structural habitat elements for canopy invertebrates. Very large, old trees also show reduced leaf size (Thomas & Ickes, 1995; Thomas, 2009) and reduced within-canopy leaf area index (Nock *et al.*, 2008) relative to younger canopy trees. Both patterns are likely to enhance desiccation-related stresses experienced by arthropods. Larger trees might

also be expected to show more pronounced vertical gradients in light levels and associated micro-environmental variables than smaller trees, although age-related declines in leaf area index (Nock *et al.*, 2008) might act to offset this pattern. In contrast to free-feeding arthropods, gall-formers are commonly positively associated with the degree of sclerophylly, and might be expected to increase in abundance with tree size and with height in the canopy (Ribiero & Basset, 2007).

In the present study, we examine age-dependent changes in standing herbivory levels and herbivore community composition in post-reproductive individuals of the winter-deciduous tree *Acer saccharum*. Trees were sampled using a mobile canopy lift in an area with heterogeneous canopy structure to enable selection of trees with fully exposed crowns across a wide range of tree size and age. We sampled branches from each individual along a vertical gradient to simultaneously examine vertical patterns of herbivory and related variables. We address the following questions: (1) Do overall levels of leaf removal by arthropod herbivores increase or decrease with increasing tree size after reproductive onset? (2) Are there systematic changes in herbivore community composition (as represented by herbivory type) with tree size, and if so, which species and/or damage types are most responsive? (3) Are vertical gradients in leaf damage and herbivore community composition more pronounced in older trees than in younger trees?

Material and methods

The study was conducted at the Haliburton Forest and Wildlife Reserve, a ~25 000-ha privately owned forest in Central Ontario's Haliburton Highlands (45° 15'N, 78° 35'W). The soils are of glacial origin (Sherborne till), predominantly silty sands derived from granitic deposits of the Precambrian Canadian Shield, and classified as brunisols or juvenile podzols, with a rooting zone pH of 4.6–5.4 (Gradowski & Thomas, 2006). Sampling was conducted on an upland site dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* L.), and yellow birch (*Betula alleghaniensis* L.).

An uneven-aged sugar maple stand was chosen for sampling, in conjunction with a study examining ontogenetic changes in within-crown leaf area index (Nock *et al.*, 2008). *Acer saccharum* at the site has an estimated reproductive size threshold of 14.2 cm diameter, at breast height, 1.3 m (dbh) (Thomas, 2009). A total of 30 reproductively mature sugar maple trees were sampled, with a dbh range of 17–67 cm. To select suitable trees, sampling progressed outward from the centre of each site, and included *A. saccharum* trees within 50 m of access trails. As sampling proceeded, the sample size was increased by adding a roughly equal number of small (<30 cm), medium (30–55 cm), and large (>55 cm) diameter trees, thus ensuring spatial interspersed and an equal representation of size classes. Mean tree age estimates corresponding to these size categories were 59 years (range: 37–79), 99 years (range: 57–148), and 151 years (range: 114–182), respectively, based on the tree ring counts of a

subset of cored trees for which complete ring series could be determined (for additional details see Nock *et al.*, 2008). All trees were canopy dominant or co-dominant and were accessed using an all-terrain 24-m working height mobile canopy lift (Scanlift SL240; Kesla Oyj, 2 Metsolantie, Kesälahti, Finland). We visually divided each crown into three equal strata (upper, middle, and lower) and harvested one representative branch from each stratum of each sampled tree. From each sampled branch, 20 randomly selected leaves were collected to quantify standing levels and type of herbivore damage; damage observations were thus made on a total of 1800 leaves (30 trees × 3 strata × 20 leaves/sample). All observations were conducted between 1 July and 31 August 2005.

Herbivore damage was quantified using visual assessment of nine arthropod feeding guilds clearly discernable by gross morphological features. In four cases these corresponded unambiguously to a single arthropod species (identification followed Rose & Lindquist, 1982). Damage types and associated species are listed in Table 1. A residual damage type *other chewing insects* was also recorded for damage not falling into any category that could be assigned to a known herbivore. Herbivory was quantified as the percentage of leaf damaged by each feeding guild. Visual estimates were made to the nearest 1% for levels <10%; otherwise to the nearest 5%. In the case of the galls made by the maple spindle gall mite, the number of galls was counted, and counts converted into a percentage of leaf damaged. The percentage herbivory values for all damage types were summed to estimate total herbivore damage for a given leaf. Visual estimations of standing herbivory rates have generally been found to be repeatable (Wint, 1983; Cooke *et al.*, 1984), but may underestimate total herbivore damage by omitting leaves entirely consumed or abscised after damage (Lowman, 1985). During herbivory surveys we did not detect either petioles lacking any leaf lamina, or leaf scars indicating premature abscission. Therefore, due to the omission of completely consumed leaves, bias is minimal in this system.

Trends in total and damage-class-specific herbivory as a function of tree size were assessed using a generalized linear model approach. Dependent variable distributions, particularly for less common damage types, included many zero values; accordingly a censored regression model with Gaussian error distribution (*tobit* model) was used, with herbivory estimates transformed by $\log(1 + \% \text{ herbivory})$ prior to analysis. Vertical gradients in herbivory were quantified as the slope of transformed herbivory values versus canopy stratum scored as an ordinal variable (lower-canopy = 1; mid-canopy = 2; upper-canopy = 3). In preliminary analyses, we examined trends in total and damage-type-specific herbivory with sampling date, and found no significant trend, so sampling date was not included as a covariate. Table-wide adjusted probability levels for damage-type-specific patterns of herbivory were calculated according to Hochberg (1988). Patterns of variation in community composition of damage type relative to tree size and canopy stratum were analysed using constrained correspondence analysis (CCA). Effects of independent variables were assessed using multi-response permutation

Table 1. Damage types and associated arthropod species used in herbivory assessments of sugar maple (*Acer saccharum*) at Haliburton Forest during the summer of 2005.

Damage type	Associated species
Leaf rollers	Maple leafroller [<i>Sparganothis acerivorana</i> MacKay: Tortricidae]* Maple basswood leafroller [<i>Sparganothis pettitana</i> (Robinson): Tortricidae]
Leaf skeletonisers	Maple trumpet skeletoniser [<i>Catagasta aceriella</i> : Tortricidae]*
Leaf miners	Maple leafcutter [<i>Paraclemensia acerifoliella</i> (Fitch): Incurvariidae]* Maple leafblotch miner [<i>Cameraria</i> (= <i>Lithocolletis</i>) <i>aceriella</i> (Clemens): Gracillariidae]*
Leaf cutters	Elm spanworm [<i>Ennomos subsignaria</i> (Hubner): Geometridae]* Forest tent caterpillar [<i>Malacosoma disstria</i> Hubner: Lasiocampidae]* Fall cankerworm [<i>Alsophila pometaria</i> (Harris): Geometridae]* Yellowlined caterpillar [<i>Nadata gibbosa</i> (J. E. Smith): Notodontidae]* Greenstriped mapleworm [<i>Dryocampa rubicunda</i> (Fabricius): Saturniidae] Cecropia moth [<i>Hyalophora cecropia</i> (Linnaeus): Saturniidae] Saddled prominent [<i>Heterocampa guttivitta</i> (Walker): Notodontidae] White marked tussock moth [<i>Orgyia leucostigma</i> (J. E. Smith): Lymantriidae] Polyphemus moth [<i>Antheraea polyphemus</i> (Cramer): Saturniidae] Pale tussock moth [<i>Halysidota tessellaris</i> (J. E. Smith): Arctiidae]
Leaf stippling	Hemiptera (not identified)
Spindle galls	Maple spindle gall mite [<i>Vasates aceriscrumena</i> (Riley): Eriophyidae]
Ocellate galls	Ocellate gall midge [<i>Acericecis ocellaris</i> (Osten Sacken): Cecidomyiidae]
Erineum galls	Crimson erineum gall mite [<i>Aceria elongatus</i> (Hodgkiss): Eriophyidae]
Vein galls	Gouty vein midge [<i>Dasineura communis</i> Felt: Cecidomyiidae]

In cases where >1 species was associated with a damage type, the most common associates (*) are listed first.

procedure tests (Legendre & Legendre, 1998), with 5000 randomisations per test. Data analyses were conducted in R v.1.13 (R Development Core Team, 2008).

Results

Across all samples the average tissue loss from total herbivory was 11.5%, of which 3.7% was galling damage, and 7.7% damage attributable to free-feeding arthropods. Total standing levels of herbivore damage decreased significantly with tree size ($P = 0.012$: Table 2), and also varied significantly among canopy strata, being highest in the lower canopy and lowest in the upper canopy ($P = 0.001$: Table 2; Fig. 1).

Table 2. Probability levels for generalized linear model tests (using a censored-dependent variable *tobit* model) for effects of tree diameter at breast height (dbh) and vertical stratum on standing levels of herbivore damage to leaves of *Acer saccharum* at Haliburton Forest during the summer of 2005.

Herbivory component	dbh	dir.	Stratum	dir.	Interaction
Total leaf loss	0.012	–	0.001	–	0.181
Total free-feeding loss	<0.001	–	<0.001	–	0.412
Total galling loss	0.126	–	0.858	–	0.634
<i>Free-feeding arthropods</i>					
Leaf skeletonisers	0.754	–	0.018	–	0.746
Leaf miners	0.019	–	0.042	–	0.771
Leaf stippling	0.007 (*)	–	0.001 **	–	0.121
Leaf rollers	0.662	–	0.740	–	0.262
Leaf cutters	0.005 *	–	0.027	–	0.199
Other chewing insects	0.275	–	0.524	–	0.140
<i>Galling arthropods</i>					
Spindle gall mite	0.001 **	+	0.940	–	0.720
Crimson erineum gall mite	0.478	–	0.955	–	0.902
Ocellate gall midge	0.357	–	0.608	–	0.780
Gouty vein midge	0.306	–	0.060	+	0.297

P-values < 0.10 are indicated in bold. Direction (dir.) of effects are indicated as follows: a “+” symbol indicates increasing rates of herbivore damage with increasing tree size or vertical stratum, and a “–” symbol indicates the opposite trend. In no case was the dbh × stratum interaction term (indicating size-dependence in the magnitude of the vertical gradient in herbivore damage) significant. Asterisks for damage-type-specific results indicate significance levels of P-values adjusted for multiple tests of a given factor (Hochberg, 1988):

(*) $P < 0.10$;

* $P < 0.05$;

** $P < 0.01$.

Patterns of variation in herbivory with tree size and vertical stratum varied strongly among damage types (Figs 2–3; Table 2). Relatively similar patterns were apparent for leaf

skeletonizer, leaf cutter, leaf miner, and leaf stippling damage types, with damage highest in the lower canopy, and reduced damage levels found with increasing tree size (the size trend being significant for the last three damage types). In contrast, two of the gall-forming damage types essentially showed the reverse pattern. Most dramatically, galling by the maple spindle gall mite (*Vasates aceriscrumena*) showed a strong trend of increasing damage with tree size ($P = 0.001$; Table 2), and was the most common damage type observed among the largest trees sampled (Fig. 3). Gouty vein midge (*Dasineura communis*) damage showed no strong pattern with tree size, but was more prevalent in the upper than lower canopy. This effect, although large in magnitude, was only marginally significant as a result of the rarity of this damage type ($P = 0.060$; Table 2). The other common gall-forming arthropods recorded (maple leaf ocellate gall midge and crimson erineum gall mite), as well as leaf roller damage, showed no significant pattern related to either tree size or vertical stratum (Figs 2 and 3).

The divergent patterns for individual damage types corresponded to highly significant changes in community composition of damage, as quantified by constrained correspondence analysis (CCA). Multi-response permutation procedure tests showed significant differences in the composition of herbivory types with respect to tree size ($P < 0.001$) and with vertical stratum ($P = 0.008$), but only a marginally significant size × stratum interaction ($P = 0.098$). The first CCA axis was most strongly positively associated with damage by gouty vein midge and maple spindle gall mite, and negatively associated with damage by leaf stippling and leaf cutters.

There was no evidence for any trend in the magnitude of the vertical gradient in herbivory patterns with tree size: no significant dbh × stratum effects were detected (Table 2). Likewise, no significant patterns were found using the slope of the relationship between herbivory rate and canopy position as a quantitative measure of the vertical gradient: this index (estimated for total herbivory and damage types considered separately) showed no significant relationship with tree size (analyses not shown).

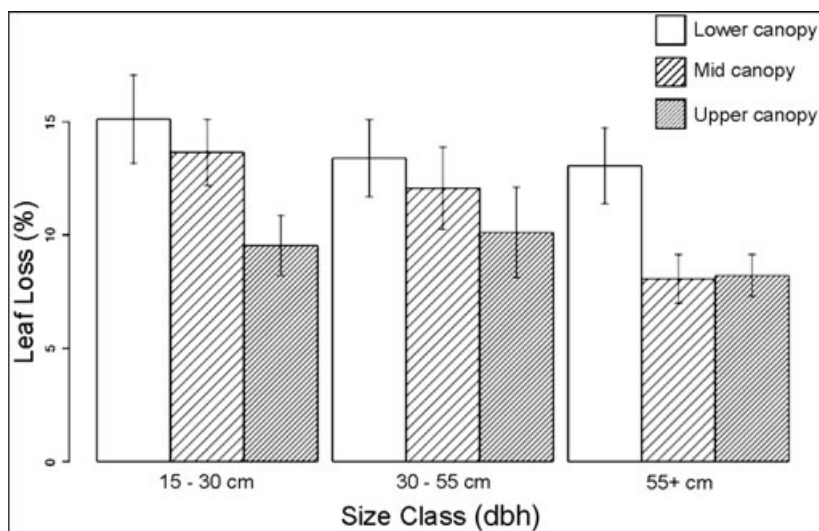


Fig. 1. Total leaf loss attributable to all herbivores in mature sugar maple (*Acer saccharum*) at Haliburton Forest during summer 2005, in relation to tree size and canopy stratum. Corresponding statistical tests, with diameter at breast height (dbh) treated as a continuous variable, are given in Table 2 (both dbh and stratum terms are significant at $P < 0.05$). Means are shown ± 1 SE.

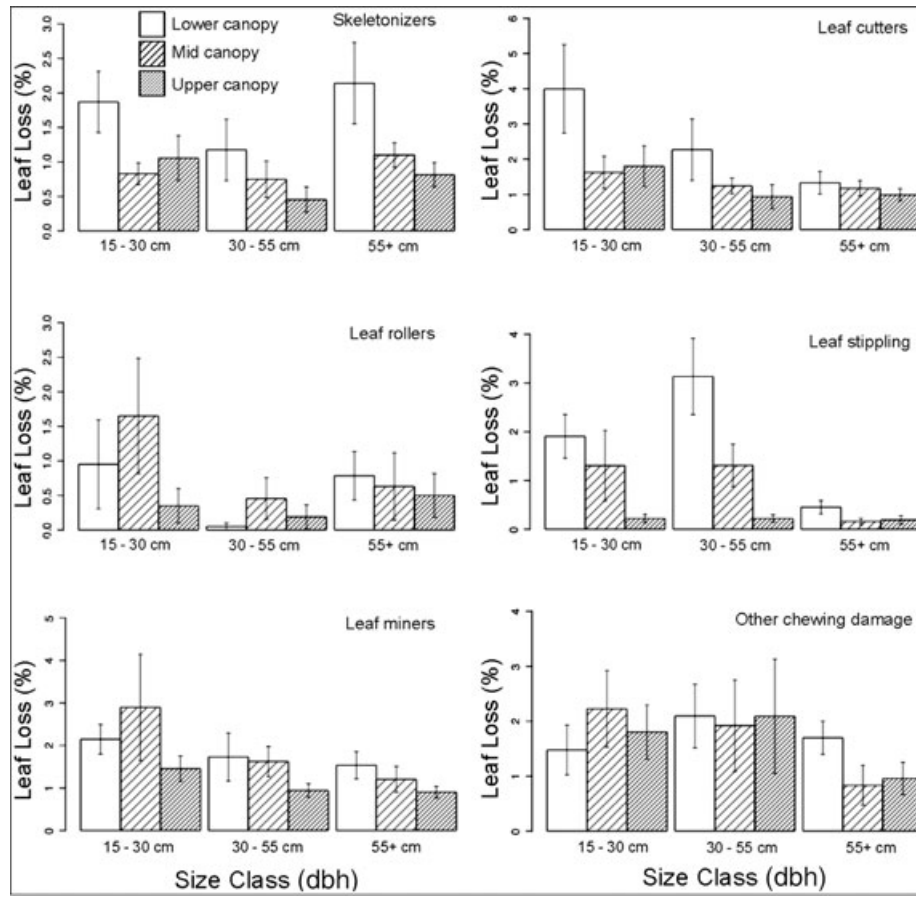


Fig. 2. Leaf loss attributable to free-feeding herbivores in mature sugar maple (*Acer saccharum*) at Haliburton Forest during summer 2005, in relation to tree size and canopy stratum. Corresponding statistical tests, with diameter at breast height (dbh) treated as a continuous variable, are given in Table 2 (leaf miners, leaf stippling, and leaf cutters show significant dbh terms; and leaf skeletonisers, leaf miners, leaf stippling, and leaf cutters show significant stratum terms at $P < 0.05$). Means are shown \pm 1 SE.

Discussion

The present study differs from prior efforts to assess effects of tree size and age on herbivory levels and herbivore communities in two important respects: first, we assessed changes occurring late in tree ontogeny after reproductive maturity and through senescence; second, all trees sampled had fully-exposed crowns and thus a similar light environment in the upper canopy. Prior studies examining changes in herbivore communities in relation to tree ontogeny have generally compared seedlings or saplings versus mature trees (e.g. Macedo & Langenheim, 1989; Boege, 2005). Such comparisons confound the effects of vertical micro-environmental gradients and ontogenetic state, as seedlings or saplings are sampled in the shaded understory, and compared with adult-statured canopy trees. Similar *understory* vs. *canopy* comparisons have also commonly been made for defence-related traits of trees (Reichardt *et al.*, 1984; Basey *et al.*, 1988; Macedo & Langenheim, 1989; Dominy *et al.*, 2003; Goodger *et al.*, 2004; Boege, 2005; Boege & Marquis, 2006). Here we document ontogenetic changes in herbivore damage level and

type independent of canopy position, thus elucidating effects of tree ontogeny per se rather than microenvironment. Overall levels of leaf removal by arthropod herbivores decreased with increasing tree size, and herbivory was reduced at higher levels in the canopy. These effects were similar in magnitude, with an average reduction of 23% in leaf loss when comparing trees 15–30 cm versus 55+ cm dbh, and an average 33% reduction when comparing foliage in the lower versus upper canopy (Fig. 1).

In a recent review, Boege and Marquis (2005), noting a lack of studies on herbivory patterns late in tree ontogeny, hypothesised that allocation to defence should decrease after reproductive onset and tree senescence. Such a pattern would be expected to result in increased herbivory levels with tree size and age. Our results contradict this prediction, in that post-reproductive trees show declines in overall standing levels of herbivore damage, specifically for damage types associated with free-feeding arthropods. Elsewhere, we report age-related increases in traits associated with reduced palatability (LMA, lamina tissue density and C/N ratio) across this same size range in *A. saccharum* and two co-occurring

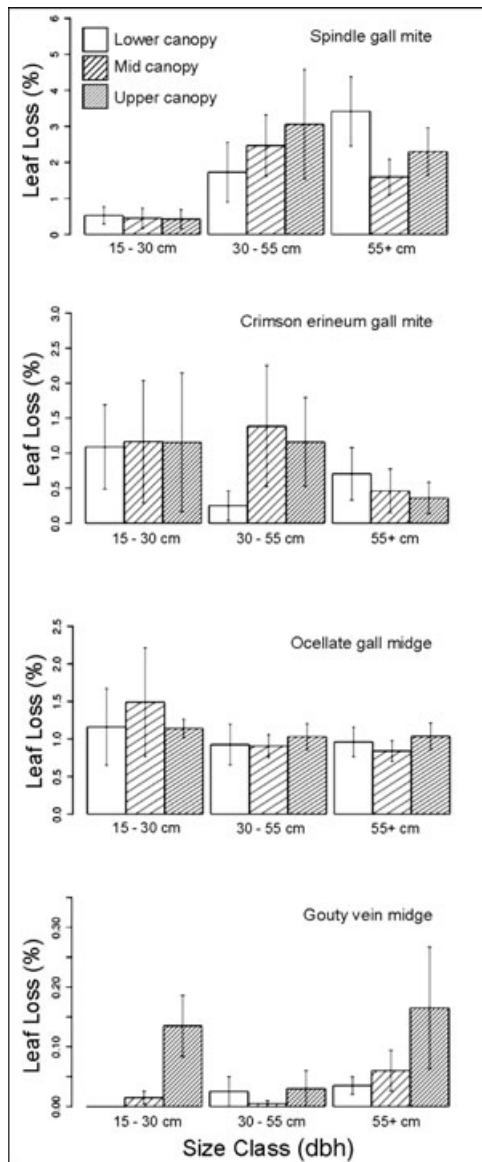


Fig. 3. Total leaf loss attributable to galling herbivores in mature sugar maple (*Acer saccharum*) at Haliburton Forest during summer 2005, in relation to tree size and canopy stratum. Corresponding statistical tests, with diameter at breast height (dbh) treated as a continuous variable, are given in Table 2 (spindle gall mite shows a significant dbh term, and gouty vein midge a marginally significant stratum term at $P < 0.05$). Means are shown ± 1 SE.

temperate deciduous species (Thomas, 2009). While not directly addressing herbivory, a large number of studies on age-related changes in leaf physiology and morphology have similarly noted increases in LMA and related characteristics, such as leaf tissue density and lignification late in tree ontogeny that are independent of *sun-shade* acclimation (Day *et al.*, 2001; Niinemets, 2002; Thomas & Winner, 2002; Nabeshima & Hiura, 2004; England & Attiwill, 2006).

Why would leaf palatability decrease late in tree ontogeny, in spite of the demands of increased allocation to reproduction, and possibly of resource limitations to all plant functions during senescence? A likely answer is that declining palatability of leaves late in tree ontogeny is actually a result of reduced resource availability in the canopies of older trees. In comparisons among species, low resource availability is generally associated with slow growth and a suite of leaf traits associated with reduced leaf palatability and herbivory rates (Coley, 1982; Coley *et al.*, 1989), likely reflecting selection for allocation to defence (Bazzaz *et al.*, 1987). Leaves in the upper canopy generally show *schlerophyllous* morphological features, particularly on very large, old trees (e.g. Koch *et al.*, 2004). Although a variety of physiological and developmental processes contribute to changes in leaf morphology and physiology with increasing tree size, limits to water transport, mediated either through reduced stomatal conductance (Bond, 2000) or reduced leaf turgor during expansion (Thomas & Winner, 2002; Woodruff *et al.*, 2004), are likely important. Leaf morphology also often shows changes associated with reproductive onset (e.g. Thomas & Ickes, 1995), and N allocation to reproductive structures would be expected to result directly in reductions in foliage quality to herbivores. Thus, we suggest that both selective pressures and the direct physiological consequences of increased tree size and reproductive effort are likely to reduce leaf palatability late in tree ontogeny.

The observed distribution pattern for the most common galling arthropod in the system differed from patterns found for free-feeding arthropods, a result that recalls a recent study reporting increased galling in the upper canopy of tropical forests (Ribiero & Basset, 2007). It has been widely observed that the abundance and diversity of galling arthropods tends to be greatest in vegetation characterized by *schlerophyllous* leaves, such as Mediterranean shrubland and savanna systems (Fernandes & Price, 1988; Price *et al.*, 1998). Comparative studies have suggested that the survivorship of galling arthropods is strongly enhanced under desiccating conditions, most likely as a result of decreased predation and disease risks under these conditions (Fernandes & Price, 1992). The upper portions of the canopies of older trees present a particularly harsh environment in terms of desiccation risks. Trees late in ontogeny typically show reduced leaf size (Thomas & Ickes, 1995; Thomas, 2009), and pronounced declines in intra-crown leaf area index with increasing tree size and age have also recently been documented (Nock *et al.*, 2008). Both of these patterns are likely to enhance desiccation risks to small-bodied arthropods by increasing exposure to solar radiation and by reducing the leaf and canopy boundary layer. It is of interest that the one damage type showing a pronounced increase related to tree age was galling by the minute eriophyid mite *Vasates aceriscrumena*, the likely predators of which are other mite species, some of which are closely associated with leaf domatia of *A. saccharum* (O'Dowd & Willson, 1997).

The observed changes in the community composition of herbivore damage types are indicative of a process of *ontogenetic succession*, or the directional change in dependent species composition triggered by the ontogeny of a focal organism (Fonseca & Fernandes, 2003). In the case of mature

A. saccharum, smaller trees near the onset of reproduction are predominantly host to lepidopteran larva (leaf skeletonizers and leaf cutters) and hemipteran phloem-feeders (resulting in leaf stippling), whereas a single species of the gall-forming mite, *V. aceriscrumena*, is predominant in the largest trees. Other well-documented cases of ontogenetic succession of tree-inhabiting arthropods have examined changes relatively early in tree ontogeny (Fonseca & Fernandes, 2003; Cuevas-Reyes *et al.*, 2004; Fonseca *et al.*, 2006). Our results suggest that important community changes also occur late in tree development. Such changes are of particular interest from a conservation and management perspective, as conventional forest harvesting operations result in the removal of most or all old trees in the system. Further documentation of changes in herbivore communities specific to the canopies of old and senescent trees, and of their associated predators and pathogens, thus represents an important priority from a conservation, as well as a pure science perspective.

Acknowledgements

We thank Haliburton Forest and Wildlife Reserve for their support of our research, and Charles Nock, and Ashley Wilson for their contributions in the field. This research was funded by grants from the National Science and Engineering Research Council of Canada, and the Sustainable Forest Management Network.

References

- Agrawal, A.A. & Fishbein, M. (2006) Plant defense syndromes. *Ecology*, **87**, 132–149.
- Angulo-Sandoval, P. & Aide, T.M. (2000) Effect of plant density and light availability on leaf damage in *Manilkara bidentata* (Sapotaceae). *Journal of Tropical Ecology*, **16**, 447–464.
- Apple, M., Tiekotter, K., Snow, M., Young, J., Soeldner, A., Tingey, D. *et al.* (2002) Needle anatomy changes with increasing tree age in Douglas-fir. *Tree Physiology*, **22**, 181–188.
- Basey, J.M., Jenkins, S.H. & Busher, P.E. (1988) Optimal central-place foraging by beavers: tree-size selection in relation to defensive chemicals of quaking aspen. *Oecologia*, **76**, 278–282.
- Basset, Y. (1991) The spatial distribution of herbivory, mines and galls within an Australian rain forest tree. *Biotropica*, **23**, 271–281.
- Basset, Y., Hammond, P.M., Barrios, H., Holloway, J.D. & Miller, S.E. (2003) Vertical stratification of arthropod assemblages. *Arthropods of Tropical Forests—Spatio-temporal Dynamics and Resource Use in the Canopy* (ed. by Y. Basset, V. Novotny, S.E. Miller and R.L. Kitching), pp. 17–28. Cambridge University Press, Cambridge, U.K.
- Bazzaz, F.A., Chiariello, N.R., Coley, P.D. & Pitelka, L.F. (1987) Allocating resources to reproduction and defense. *Bioscience*, **37**, 58–67.
- Boege, K. (2005) Herbivore attack in *Casearia nitida* influenced by plant ontogenetic variation in foliage quality and plant architecture. *Oecologia*, **143**, 117–125.
- Boege, K. & Marquis, R.J. (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology and Evolution*, **20**, 441–448.
- Boege, K. & Marquis, R.J. (2006) Plant quality and predation risk mediated by plant ontogeny: consequences for herbivores and plants. *Oikos*, **115**, 559–572.
- Bond, B.J. (2000) Age-related changes in photosynthesis of woody plants. *Trends in Plant Science*, **5**, 349–353.
- Bryant, J.P. & Julkunttiitto, R. (1995) Ontogenetic development of chemical defense by seedling resin birch: Energy-cost of defense production. *Journal of Chemical Ecology*, **21**, 883–896.
- Coley, P.D. (1982) Rates of herbivory on different tropical trees. *Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (ed. by E.G. Leigh, A.A. Rand and D.M. Windsor), pp. 123–132. Smithsonian Institution Press, Washington, DC.
- Coley, P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, **53**, 209–233.
- Coley, P.D., Bryant, J.P. & Chapin, F.S. (1989) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.
- Cooke, F.P., Brown, J.P. & Mole, S. (1984) Herbivory, foliar enzyme inhibitors, nitrogen and leaf structure of young and mature leaves in a tropical forest. *Biotropica*, **16**, 257–263.
- Craig, T.P., Price, P.W. & Itami, J.K. (1986) Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology*, **67**, 419–425.
- Cuevas-Reyes, P., Quesada, M., Hanson, P., Dirzo, R. & Oyama, K. (2004) Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life-forms, host plant age and plant density. *Journal of Ecology*, **92**, 707–716.
- Day, M.E., Greenwood, M.S. & White, A.S. (2001) Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiology*, **21**, 1195–1204.
- Del Val, E. & Dirzo, R. (2003) Does ontogeny cause changes in the defensive strategies of the myrmecophyte *Cecropia peltata*? *Plant Ecology*, **169**, 35–41.
- Dominy, N.J., Lucas, P.W. & Wright, S.J. (2003) Mechanics and chemistry of rain forest leaves: canopy and understory compared. *Journal of Experimental Botany*, **54**, 2007–2014.
- England, J.R. & Attiwill, P.M. (2006) Changes in leaf morphology and anatomy with tree age and height in the broadleaved evergreen species, *Eucalyptus regnans* F. Muell. *Trees*, **20**, 79–90.
- Fernandes, G.W. & Price, P.W. (1988) Biogeographical gradients in galling species richness: tests of hypotheses. *Oecologia*, **76**, 161–167.
- Fernandes, G.W. & Price, P.W. (1992) The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats. *Oecologia*, **90**, 14–20.
- Fonseca, C.R. & Fernandes, G.W. (2003) Ontogenetic succession in Amazonian ant trees. *Oikos*, **102**, 407–412.
- Fonseca, C.R., Fleck, T. & Fernandes, G.W. (2006) Processes driving ontogenetic succession of galls in a canopy. *Biotropica*, **38**, 514–521.
- Fowler, S.V. (1985) Differences in insect species richness and faunal composition of birch seedlings, saplings and trees: the importance of plant architecture. *Ecological Entomology*, **10**, 159–169.
- Fritz, R.S. & Hochwender, C.G. (2001) Seedling herbivory by slugs in a willow hybrid system: developmental changes in damage, chemical defense, and plant performance. *Oecologia*, **129**, 87–97.
- Goodger, J.Q.D., Ades, P.K. & Woodrow, I.E. (2004) Cyanogenesis in *Eucalyptus polyanthemus* seedlings: heritability, ontogeny and effect of soil nitrogen. *Tree Physiology*, **24**, 681–688.
- Gradowski, T. & Thomas, S.C. (2006) Phosphorus limitation of sugar maple growth in central Ontario. *Forest Ecology and Management*, **226**, 104–109.

- Hanley, M.E., Lamont, B.B., Fairbanks, M.M. & Rafferty, C.M. (2007) Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 157–178.
- Hättenschwiler, S. & Vitousek, P.M. (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology and Evolution*, **15**, 238–243.
- Hochberg, Y. (1988) A sharper Bonferroni procedure for multiple tests of significance. *Biometrika*, **75**, 800–802.
- Holmes, R.T. & Schultz, J.C. (1988) Food availability for forest birds: affects of prey distribution and abundance on bird foraging. *Canadian Journal of Zoology*, **66**, 720–728.
- Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D. (2004) The limits to tree height. *Nature*, **428**, 851–854.
- Kraus, T.E.C., Dahlgren, A. & Zasoski, R.J. (2003) Tannins in nutrient dynamics of forest ecosystems—a review. *Plant and Soil*, **256**, 41–66.
- Lawton, J.H. (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, **28**, 23–39.
- Le Corff, J. & Marquis, R.J. (1999) Differences between understory and canopy in herbivore community composition and leaf quality for two oak species in Missouri. *Ecological Entomology*, **24**, 46–58.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd English edn. Elsevier, Amsterdam, The Netherlands.
- Lesica, P., McCune, B., Cooper, S.V. & Hong, W.S. (1991) Differences in lichen and bryophyte communities between old-growth and managed 2nd growth forests in the Swan Valley, Montana. *Canadian Journal of Botany*, **69**, 1745–1755.
- 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.
- Lowman, M.D. (1992) Herbivory in Australian rain forests, with particular reference to the canopies of *Doryphora sassafras* (Monimiaceae). *Biotropica*, **24**, 263–272.
- Lowman, M.D., Taylor, P. & Block, N. (1993) Vertical stratification of small mammals and insects in the canopy of a temperate deciduous forest: a reversal of tropical forest distribution?. *Selbyana*, **14**, 25–26.
- Macedo, C.A. & Langenheim, J.H. (1989) Microlepidopteran herbivory in relation to leaf sesquiterpenes in *Copaifera langsdorfii* adult trees and their seedling progeny in a Brazilian woodland. *Biochemical Systematics and Ecology*, **17**, 217–224.
- McGee, G.G. & Kimmerer, R.W. (2002) Forest age and management effects on epiphytic bryophyte communities in Adirondack northern hardwood forests, New York, USA. *Canadian Journal of Forest Research*, **32**, 1562–1576.
- Nabeshima, E. & Hiura, T. (2004) Size dependency of photosynthetic water- and nitrogen-use efficiency and hydraulic limitation in *Acer mono*. *Tree Physiology*, **24**, 745–752.
- Niinemets, Ü. (2002) Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. *Tree Physiology*, **22**, 515–535.
- Nock, C.A., Caspersen, J.P., & Thomas, S.C. (2008) Large ontogenetic declines in intra-crown leaf area index in two temperate deciduous tree species. *Ecology*, **89**, 744–753.
- O'Dowd, D.J. & Willson, M.F. (1997) Leaf domatia and the distribution and abundance of foliar mites in broadleaf deciduous forest in Wisconsin. *American Midland Naturalist*, **137**, 337–348.
- Phillipson, J. & Thompson, D.J. (1983) Phenology and intensity of phyllophage attack on *Fagus sylvatica* in Wytham Woods, Oxford. *Ecological Entomology*, **8**, 315–330.
- Price, P.W., Fernandes, G.W., Lara, A.C.F., Brawn, J., Barrios, H., Wright, M.G. *et al.* (1998) Global patterns in local number of insect galling species. *Journal of Biogeography*, **25**, 581–591.
- Price, P.W., Roinen, H. & Tahvanainen, J. (1987) Plant age and attack by the bud galler, *Euura mucronata*. *Oecologia*, **73**, 334–337.
- R Development Core Team. 2008. *R: A Language and Environment for Statistical Computing*. Vienna, Austria.
- Reichardt, P.B., Bryant, J.P., Clausen, T.P. & Wieland, G.D. (1984) Defense of winter-dormant Alaska paper birch against snowshoe hares. *Oecologia*, **65**, 58–69.
- Ribiero, S.P. & Basset, Y. (2007) Gall-forming and free-feeding herbivory along vertical gradients in a lowland tropical rainforest: the importance of leaf sclerophylly. *Ecography*, **30**, 663–672.
- Rose, A.H. & Lindquist, O.H. (1982) *Insects of Eastern Hardwood Trees*. Canadian Forestry Service, Forestry Technical Report No 29. Canadian Government Publishing Centre, Hull, Quebec.
- Schowalter, T.D., Hargrave, W.W. & Crossley, D.A. (1986) Herbivory in forested ecosystems. *Annual Review of Ecology and Systematics*, **31**, 177–196.
- Thomas, S.C. (2009) Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. *Tree Physiology*, in press.
- Thomas, S.C. & Ickes, K. (1995) Ontogenetic changes in leaf size in Malaysian rain forest trees. *Biotropica*, **27**, 427–434.
- Thomas, S.C. & Winner, W.E. (2002) Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiology*, **22**, 117–127.
- Webber, B.L. & Woodrow, I.E. (2009) Chemical and physical plant defence across multiple ontogenetic stages in a tropical rain forest understory tree. *Journal of Ecology*, **97**, 761–771.
- Wint, G.R.W. (1983) Leaf damage in tropical rain forest canopies. *Tropical Rain Forest: Ecology and Management* (ed. by S.L. Sutton, T.C. Whitmore and A.C. Chadwick), pp. 229–240. Blackwell, Oxford, U.K.
- Woodruff, D.R., Bond, B.J. & Meinzer, F.C. (2004) Does turgor limit growth in tall trees?. *Plant Cell and Environment*, **27**, 229–236.

Accepted 7 September 2009

First published online 23 November 2009