

A gall-inducing arthropod drives declines in canopy tree photosynthesis

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Abstract Mature forest canopies sustain an enormous diversity of herbivorous arthropods; however, with the exception of species that exhibit large-scale outbreaks, canopy arthropods are thought to have relatively little influence on overall forest productivity. Diminutive gall-inducing mites (Acari; Eriophyidae) are ubiquitous in forest canopies and are almost always highly host specific, but despite their pervasive occurrence, the impacts of these obligate parasites on canopy physiology have not been examined. We have documented large declines in photosynthetic capacity (approx. 60%) and stomatal conductance (approx. 50%) in canopy leaves of mature sugar maple (*Acer saccharum*) trees frequently galled by the maple spindle gall mite *Vasates aceriscrumena*. Remarkably, such large impacts occurred at very low levels of galling, with the presence of only a few galls (occupying approx. 1% of leaf area) compromising gas-exchange across the entire leaf. In contrast to these extreme impacts on the leaves of adult trees, galls had no detectible effect on the gas-exchange of maple saplings, implying large ontogenetic differences in host tolerance to mite galling. We also found a significant

negative correlation between canopy tree radial increment growth and levels of mite galling. Increased galling levels and higher physiological susceptibility in older canopy trees thus suggest that gall-inducing mites may be major drivers of “age-dependent” reductions in the physiological performance and growth of older trees.

Keywords *Acer saccharum* · Eriophyoid mite · Galls · Herbivory · Ontogeny · Gas-exchange

Introduction

Gall-inducing arthropods are herbivores that are intimately associated with their host plants, influencing these host plants in a number of ways. The initiation and maintenance of galls on plant organs (i.e., leaves, stems, fruits, and buds) have been shown to alter host traits, such as plant architecture (Larson and Whitham 1997), shoot growth (Vuorisalo et al. 1990), and nutrient allocation (McCrea et al. 1985), in addition to impacting whole-plant growth and survival (Hakkarainen et al. 2005). Similarly, gall formation has been found to significantly modify foliar gas-exchange processes (i.e., photosynthesis, stomatal water conductance, and water use efficiency), eliciting plant responses ranging from compensatory increases (Fay et al. 1993; Dorchin et al. 2006) to decreases (Larson 1998; Florentine et al. 2005). Thus, the limited information available suggests that the impacts of gall formation on gas-exchange processes are variable and likely determined by the type of gall inducer attacking the host plant (Welter 1989). Many fundamental questions concerning the influence of gall inducers on their hosts remain unaddressed: Are galling impacts (either positive or negative) on gas-exchange processes restricted to the vicinity of galls or extended across the

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entire leaf? Assuming that leaves respond to galling, at what level of galling do gas-exchange processes begin to respond? How do galling impacts vary with host age? Questions such as these are important not only for understanding the nature of impacts, but also when attempting to “scale up” effects to the whole-tree or plant level.

The role of gall inducers as drivers of host physiological functioning in forest ecosystems has received little attention from researchers in the past. Studies carried out to date on galling arthropod–plant interactions have largely examined the impacts of galling on crops, herbaceous plants, shrubs, or common species from agricultural systems; studies on galling impacts in forests have been limited to understory saplings (Aldea et al. 2006). Although leaf-galling arthropods are commonly found in forest canopies and are possibly ubiquitous in some forest canopies (Ribeiro and Basset 2007), little is known about their influence on the health and physiology of mature forest trees. Mature trees differ from seedlings and saplings in terms of physiology (Thomas and Winner 2002), growth requirements, and defence strategies; consequently, they can also differ in their response to herbivory. Among woody tree species, saplings are thought to be more vulnerable than mature trees to herbivory as they are constrained in their allocation of resources towards growth and development (Boege and Marquis 2005). In the case of gall inducers, hosts have been shown to exhibit differential responses in resistance to galling across their ontogeny, with increasing levels of hypersensitivity through host ontogeny (e.g., Santos and Fernandes 2010). However, the remote position of gall inducers in the canopy has thus far discouraged comparisons of physiological responses to galling between distinct developmental stages, such as juveniles (saplings) and mature trees.

In the study reported here, we addressed the following questions on the interaction between a gall-inducing mite and its host sugar maple (*Acer saccharum* Marsh): (1) What is the impact of mite-galling on gas-exchange processes in canopy leaves? (2) Are the impacts of gall formation restricted to the galled area or do they extend to ungalled portions of infected leaves? (3) How does photosynthetic rate respond to variation in galling intensity? (4) Does the response of gas-exchange processes to galling differ through the ontogeny of the host? (5) Are there detectable galling impacts beyond the leaf level, i.e., on shoot and whole-tree growth?

Methods

Study site and canopy access

This study was conducted within the limits of the Haliburton Forest and Wildlife Reserve in Ontario, Canada

(45°13'N, 78°35'W). Mean daily temperatures here range from 11 to 17°C during the growing months (May–August), with an average maximum daily temperature of approximately 25°C in July. The mean monthly precipitation during this period ranges from 76 to 94 mm. *Acer saccharum* is the dominant species in northern hardwood forests of eastern North America and accounts for approximately 60% of tree basal area in the study area. Leaves of sugar maple are galled by the highly host-specific eriophyoid gall mite, *Vasates aceriscrumena* (Riley) (maple spindle gall mite, hereafter SGM) (Jeppson et al. 1975). This mite is likely to be the single most common macroscopic animal present in sugar maple canopies in the study area: one typical canopy tree contains 10⁴–10⁵ SGM galls, each of which occupies <0.1% of the area of an individual leaf (see below) and houses 10–100 mites. Tree canopies were accessed using a mobile elevating work platform (Scanlift 240; Kesla Oyj, Kesälähti, Finland).

Foliar gas exchange

Gas-exchange parameters were measured in 2007 in situ in ten mature sugar maple trees and six saplings located in large canopy gaps using an infrared gas analyzer (Li-6400 portable photosynthesis system; LI-COR, Lincoln NE). A paired sampling design was used in which one galled leaf (with 20–50 galls/leaf) and one ungalled leaf (control) were selected on the same branch (but a different internode), thereby ensuring a similar canopy position and environmental conditions. Five to ten such pairs were measured per individual tree. For galled leaves, measurements were made in both galled areas and in a gall-free portion of the same leaf (>3 cm from the nearest gall) to observe if galling impacts extended to the entire leaf or were confined locally to areas surrounding the galls. Photosynthetic capacity (A_{\max}) is closely related to the integrated diurnal carbon gain at the leaf level (Zotz and Winter 1993) and is considered to be an integrator of general tree physiological performance (Field 1991). Gas-exchange measurements included A_{\max} , stomatal water conductance (g_s), transpiration (E), and instantaneous water use efficiency (WUE, ratio of A_{\max} to E). Gas-exchange measurements and leaf surveys were made at the upper (height 16–25 m) and lower (height 6–12 m) thirds of the tree canopies; saplings were located in large gaps in the same area (within 150 m of measured trees). Measurements were made during the months of June to August in 2007 and 2008 on fully expanded leaves, at temperatures of 20–25°C and 50–80% relative humidity (vapor pressure difference 0.5–1.6 kPa), between 0830 and 1100 hours to avoid possible midday photosynthetic depression effects. For both galled and gall-free groups, only leaves that were free from other forms of herbivory or pathogenic damage were selected for measurement.

To quantify the relationship between SGM infection and photosynthetic performance at the leaf level, we conducted similar gas-exchange measurements on an additional five canopy trees in 2008, with sampling in this case spanning a wide range of galling intensities. The total area occupied by a single gall (assuming that galls approximate a cylinder in geometry) was estimated using average height and width values measured from 294 galls [area of 1 gall = 4.48 mm^2 , ± 1 standard deviation (SD) = 2.38]. Average leaf area from approximately 80 canopy leaves was 43.52 cm^2 (± 1 SD = 8.81). Hence, the percentage of leaf area occupied by a single gall was 0.11%.

Leaf nutrient analyses

A subset of control ($n = 30$) and galled leaves ($n = 50$) from five trees were collected and dried for carbon (C) and nitrogen (N) analyses. For galled leaves, the galls were excised, and galls versus ungalled parts of leaves processed separately. Tissue samples were then crushed in liquid N, and leaf tissue samples were analyzed for C and N content using an ECS 4010 analyzer (Costech Analytical Technologies, Valencia, CA).

Galling frequency in relation to host ontogeny

To quantify size-dependent patterns of galling, we randomly collected leaves from 45 trees and 14 saplings (located in both understorey and gaps) using the canopy lift. Two hundred leaves per tree (100 each from the upper and lower canopy) and 100 leaves per sapling (where possible) were collected. Size (diameter at breast height, dbh) and height were also determined. A total of 9,337 leaves were scored. Data from the upper and lower canopy leaves were pooled for analysis as there was no significant difference in mean galling intensities between the two canopy positions.

Galling intensity in relation to shoot extension and tree growth

Shoot extension (length in millimeters) was measured from 46 terminal shoots collected from eight trees in 2008. Extension for the last 4 years was measured using callipers. Two-tailed unpaired Student *t* tests were used to test for differences in shoot extension between galled and gall-free shoots. To determine if whole-tree growth correlated with galling frequency (percentage of galled leaves/tree), partial increment cores, including at least ten of the most recent annual rings, were obtained from 30 of the 45 sampled trees. Mounted cores were finely sanded, and radial increments were measured with a table-mounted tree-ring increment measurement system (T.R.I.M #8505; OMNR, Toronto, ON, Canada) and dissecting scope (Wild M3; Wild Heerbrugg, Heerbrugg, Switzerland).

Statistical analysis

A one-way analysis of variance (ANOVA) was used to examine differences in A_{max} , g_s , WUE (separately) between control and infected leaves in (1) mature trees and (2) saplings. For mature trees, a post-hoc Tukey's multiple comparison test was then used to determine significant differences between groups (control, galled or ungalled). A model 1 linear regression was employed to examine the relationship between tree size (dbh) and photosynthesis in control and galled leaves. Analysis of the relationship between galling level and photosynthesis was based on log-transformed predictor (number of galls) and response (A_{max}) variables, with back-transformed slope and intercept parameters used to estimate the non-linear (allometric) relationship. The number of galls observed on individual leaves showed a frequency distribution with both a large number of zeros (many ungalled leaves) and a variance that was much greater than the mean. We therefore used a zero-inflated negative binomial regression model to test for the relationship between tree size and galling intensity, with the model also specifying individual leaf observations nested within trees. Following this, one-way ANOVAs were used to test for differences in the percentage of galled leaves and number of galls/galled leaf between saplings (<5 cm dbh) and three tree size classes chosen arbitrarily (10–20 cm dbh, 21–30 cm dbh, 31–55 cm dbh). A multivariate analysis of variance (MANOVA) was used to test for differences in C, N and C:N between control (gall-free) leaf tissue, galled leaf tissue and ungalled leaf tissue (from galled leaves). Where significant, univariate ANOVAs were then performed for each response variable separately; for significant ANOVAs, a post-hoc Tukey's multiple comparison test was used to determine differences in nutrients between treatments. The Pearson correlation coefficient was employed to examine the relationship between radial tree growth (millimeters), averaged over the two most recent 5-year periods, and galling frequency (percentage of galled leaves/tree). All statistical analyses were performed in R ® Development Core Team 2009).

Results

Foliar gas-exchange

Galled leaves in mature canopy trees (height >18 m) showed significant reductions in photosynthetic capacity (A_{max} ; $F_{2,154} = 63.5$, $P < 0.001$; Fig. 1a), stomatal conductance (g_s ; $F_{2,154} = 42.16$, $P < 0.001$; Fig. 1b), and instantaneous water use efficiency (WUE; $F_{2,154} = 8.57$, $P < 0.001$; Fig. 1c) compared to ungalled controls. Ungalled portions of galled leaves of mature canopy trees likewise showed reductions in A_{max} , g_s , and WUE compared to controls, with values similar to

those of galled parts of leaves ($P > 0.05$ in all cases; Fig. 1). Hence, the impact of SGM galling on gas-exchange processes was not restricted just to the vicinity of galls but extended to ungalled portions as well. There was no significant variation between trees in A_{\max} (control $F_{9,51} = 1.92$, $P = 0.09$; galled $F_{9,51} = 1.22$, $P = 0.31$; ungalled $F_{9,51} = 1.26$, $P = 0.29$), g_s (control $F_{9,51} = 2.00$, $P = 0.07$; galled $F_{9,51} = 1.27$, $P = 0.28$; ungalled $F_{9,51} = 0.99$, $P = 0.45$), or WUE (control $F_{9,51} = 1.60$, $P = 0.14$; galled $F_{9,51} = 1.54$, $P = 0.19$; ungalled $F_{9,51} = 0.92$, $P = 0.50$) within a given treatment class (i.e., control, galled, or ungalled). Sapling leaves exhibited A_{\max} and g_s values typical for this species (Ellsworth and Reich 1992; Sipe and Bazzaz 1994; Thomas 2010), but there were no detectable effects of galling on photosynthetic gas-exchange in saplings (A_{\max} : $t = 0.143$, $df = 40$, $P = 0.89$; g_s : $t = 0.3941$, $df = 40$, $P = 0.6956$; WUE: $t = 0.881$, $df = 40$, $P = 0.38$; Fig. 1), indicating clear ontogenetic differences in response. There was no significant variation between saplings for A_{\max} (control $F_{5,40} = 1.53$, $P = 0.24$; galled $F_{5,40} = 0.70$, $P = 0.59$), g_s (control $F_{5,40} = 2.03$, $P = 0.13$; galled $F_{5,40} = 1.14$, $P = 0.38$), and WUE (control $F_{5,40} = 0.58$, $P = 0.72$; galled $F_{4,40} = 0.88$, $P = 0.49$) within a given treatment class (control or galled).

Leaf nutrients

Leaf condition (gall-free, galled, or ungalled tissues from galled leaf) appeared to have an effect on leaf nutrients in trees (MANOVA, Pillai's trace = 0.18, $F_{6,150} = 2.45$, $P = 0.03$) but not saplings (MANOVA, Pillai's trace = 0.09, $F_{6,146} = 1.08$, $P = 0.38$). Univariate ANOVAs revealed that C (trees: $F_{2,78} = 2.52$, $P = 0.09$;) and the C:N ratio (trees: $F_{2,78} = 2.26$, $P = 0.11$) did not differ significantly between galls, surrounding ungalled tissue, or control leaves among trees, indicating that SGM galls do not act as strong sinks for photosynthetic assimilates. However, N level (% dry weight) was lower in galls [mean 1.75%, standard error of the mean (SEM) ± 0.036] than in surrounding ungalled tissue (mean 1.88%, SEM ± 0.038) or control leaves (mean 1.89%, SEM ± 0.034) within trees ($F_{2,78} = 3.44$, $P = 0.04$).

Galling–photosynthesis relationship

Photosynthesis was significantly reduced in leaves (from 6.7 to 3.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$) even at low levels of mite galling (<10 galls per leaf), but leaves continued to photosynthesize even at high levels of galling (>100 galls per leaf; Fig. 2). This finding indicates that SGM-induced galls had a considerable impact on the host even at very low intensities, but that they also did not completely eliminate net C uptake at high galling levels [non-linear regression of unbinned data: $\log_{10} A_{\max} = 0.779 - 0.263 \times \log_{10} (1 + \text{galls})$, $r^2 = 0.283$, $F = 37.25$, $P < 0.001$].

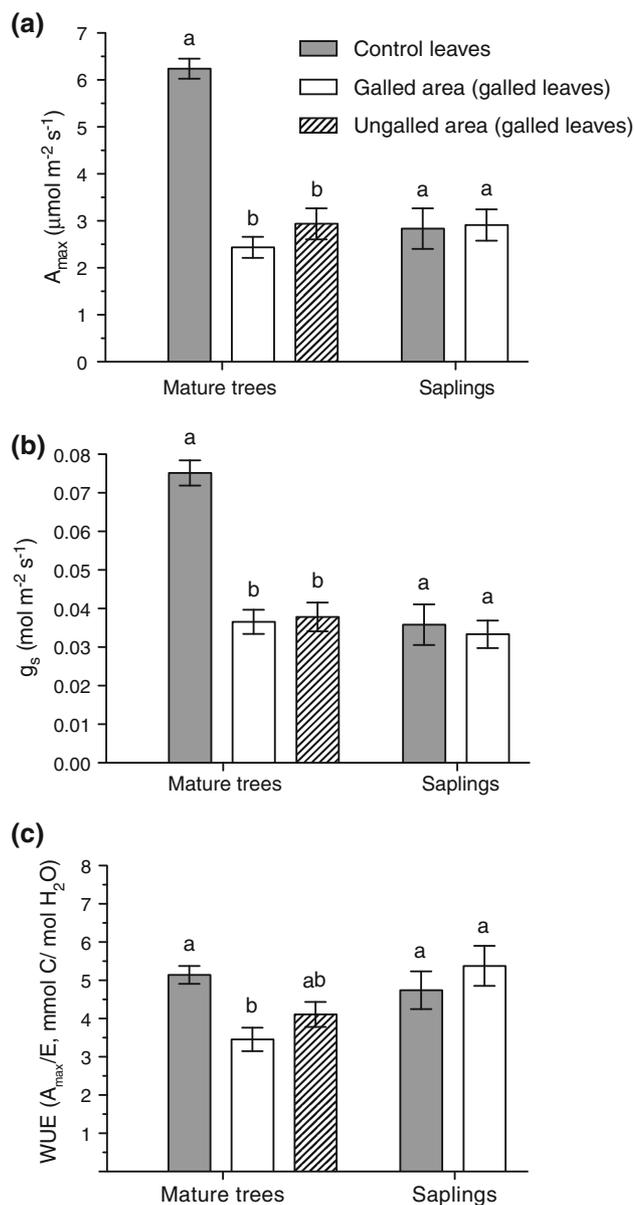


Fig. 1 Net photosynthetic capacity (A_{\max} ; **a**), net stomatal conductance (g_s ; **b**), and instantaneous water-use efficiency [WUE; ratio of A_{\max} to E (transpiration)] (**c**) of leaves or leaf portions in the crowns of sugar maple saplings and trees from Haliburton Forest, Ontario measured for gall-free (control) leaves, galled portions of leaves, and ungalled portions of galled leaves (canopy trees only) affected by the maple spindle gall mite. Different letters indicate a significant difference between groups within each category [$P < 0.05$; analysis of variance (ANOVA) followed by Tukey's multiple comparison test]

The dbh–photosynthesis relationship revealed that while the A_{\max} in control leaves decreased sharply (from 8 to 6 $\mu\text{mol m}^{-2} \text{s}^{-1}$; $r^2 = 0.64$, $P = 0.008$), the A_{\max} in galled leaves remained unaltered at significantly lower levels (<3.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$; $r^2 = 0.34$, $P = 0.13$) with increasing tree size (Fig. 5).

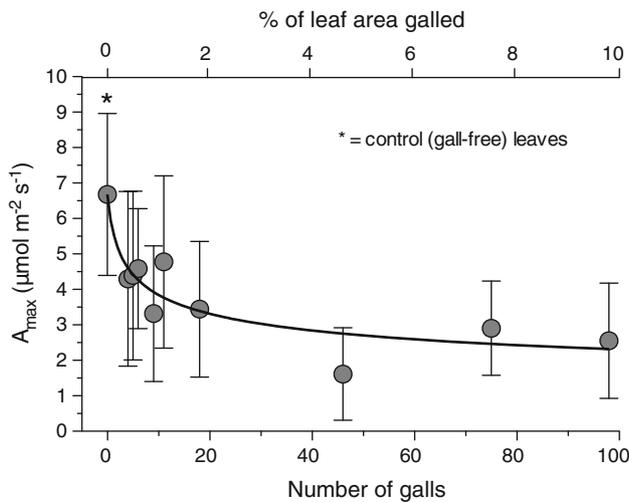


Fig. 2 Relationship between net photosynthetic capacity (A_{max}) and number of galls per leaf from a mature sugar maple canopy in Haliburton Forest, Ontario. Filled circles A_{max} averages (± 1 SD) of binned gall numbers (equal-sized bins of $N = 8$ replicates) expressed on a per-leaf basis, asterisk control (gall-free) leaves

Galling frequency in relation to host ontogeny

Galling frequency increased with host size (zero-inflated negative binomial regression, $P = 0.002$; Fig. 3; both the zero-inflation term and between-tree variation term in this model were also highly significant at $P < 0.001$). Of the 45 mature trees sampled, 41 (91%) were infected with SGM galls, with an average of 40.3% of leaves (across all tree sizes of trees > 20 cm dbh) infected. In contrast, among saplings, galling was found on an average of only 4.7% of the leaves sampled. Maple trees carried appreciably higher mite loads than saplings in terms of both the percentage of leaves galled ($F_{3,54} = 9.32$, $P < 0.001$; Fig. 3a) and number of galls per (galled) leaf ($F_{3,54} = 2.86$, $P = 0.04$; Fig. 3b). However, these mite loads did not differ significantly between adult tree size classes (% galled leaves: $F = 1.39$, $P = 0.26$; galls/galled leaf: $F = 0.61$, $P = 0.54$).

Galling intensity in relation to and shoot extension and tree growth

Shoot extension (length in millimeters) did not differ between galled and ungalled shoots when averaged over the last 4 years ($t = 0.3403$, $df = 44$, $P = 0.73$) or when measured for the present year's growth ($t = 1.099$, $df = 44$, $P = 0.28$).

Galling frequency was negatively related to tree radial increment when the last 5-year growth patterns were examined (Pearson's $r = 0.47$, $P = 0.008$; Fig. 4a). However, only a marginally significant correlation was detected when the previous 5-year (i.e., 6–10 years back) growth pattern

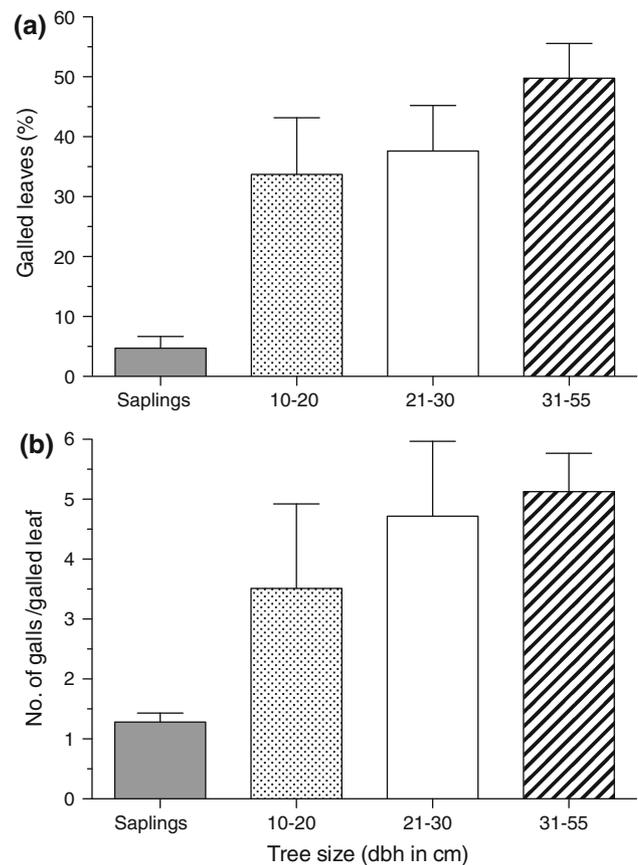


Fig. 3 Percentage of leaves galled (a) and number of galls per galled leaf (b) in four size categories: saplings (dbh < 5 cm) and trees with a diameter of breast height (dbh) of 10–20 cm, 21–30 cm, and 31–55 cm, respectively, from a survey of sugar maples in Haliburton Forest, Ontario. Error bars $+1.00$ SEM

was examined (Pearson's $r = 0.35$, $P = 0.06$; Fig. 4b). Radial increment did not correlate with tree size (range = 16.5–44.5 cm dbh) for the 30 trees that were examined (Pearson's $r = 0.20$, $P = 0.28$).

Quantifying galling effects on canopy-averaged photosynthesis

To estimate the effects of galling at the canopy-level of integration, we estimated a canopy-averaged A_{max} using leaf data from 33 canopy trees (size range 14.9–67.4 cm dbh, 100–200 leaves/tree were collected) that were surveyed for galls in 2007. For each tree, mean A_{max} was first calculated, assuming the tree was completely ungalled based on the A_{max} -dbh relationship from Fig. 5 ($A_{max} = 9.988 - 0.8759 \times dbh$, $r^2 = 0.64$, $P = 0.01$). Using this value, A_{max} was then calculated for every leaf (galled and ungalled) within each tree using the A_{max} -galling relationship from Fig. 2 $\{[\log A_{max} = a - 0.263 \times \log_{10}(1 + \text{galls})]$ where a = the y-intercept at $x = 0$ galls for a given dbh from Fig. 5}. We then calculated mean A_{max} per

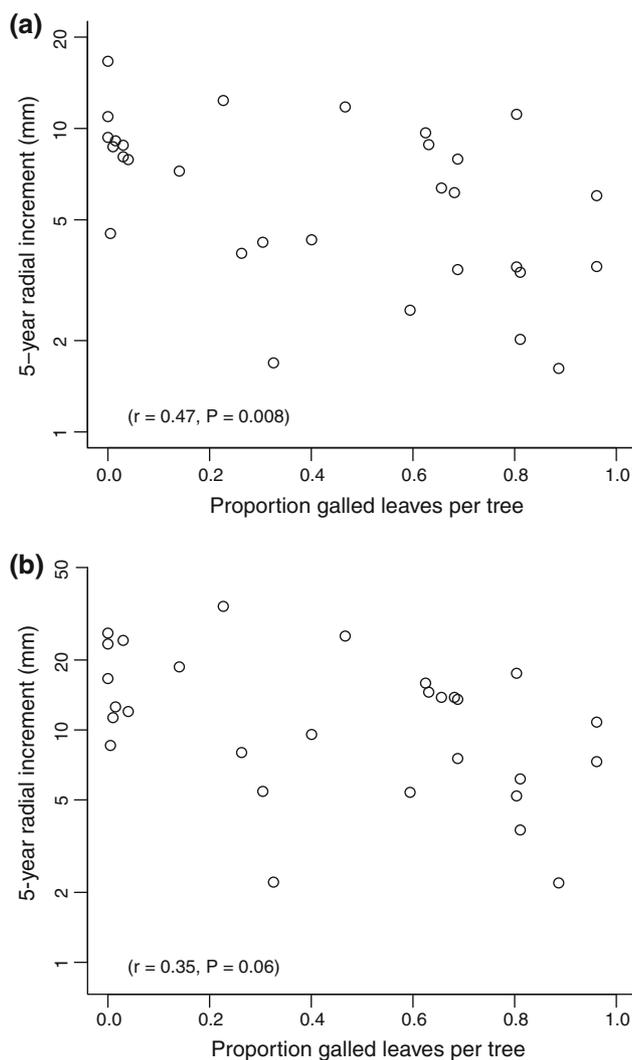


Fig. 4 Relationship between percentage of galled leaves per tree (expressed as arc-sine transformed proportions) and last 5-year **(a)** and previous 5-year (6–10 years back) **(b)** radial increment (in mm) from 30 sugar maple trees in Haliburton Forest, Ontario. Radial increment values are log-transformed. r = Pearson correlation coefficients

tree based on A_{\max} values from all leaves (galled and ungalled). The average reduction in A_{\max} across the entire stand of trees was approximately 15.6% (range 0.5–34%, ± 1 SD = 8.74).

Discussion

Gall formation by maple spindle gall mites caused large reductions in gas-exchange in mature canopy leaves of *A. saccharum*, but they had no such impact on saplings. Among leaves of mature trees, A_{\max} decreased by 57% in galled portions and 47% in ungalled portions of gall-infected leaves relative to gall-free leaves. Correspond-

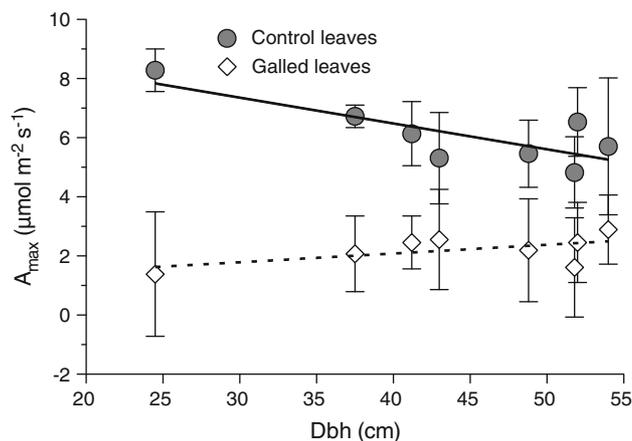


Fig. 5 Photosynthetic capacity (A_{\max}) in leaves from eight sugar maple trees in a mature forest canopy in Haliburton Forest, Ontario. Filled circles A_{\max} in control leaves, open diamonds A_{\max} in galled leaves, x -axis tree size (cm; dbh), error bars ± 1 SD

ingly, stomatal conductance (g_s) decreased by 48 and 47%, respectively, in the same regions. Instantaneous WUE also decreased with galling, but the difference was only significant between gall-free leaves and galled portions of infected leaves. Remarkably, the presence of even a few galls representing <0.5% of leaf area was enough to significantly reduce A_{\max} (Fig. 2). In contrast, galled sapling leaves exhibited levels of C uptake and stomatal conductance typical for *A. saccharum* within forest gaps (compare Ellsworth and Reich 1992; Sipe and Bazzaz 1994; Thomas 2010). Although there were no negative effects of galling on shoot extension growth, there was a significant negative correlation between recent tree radial increment and galling intensity (Fig. 4a) for canopy trees.

Galls had comparable levels of C to that of surrounding tissue and control leaves and therefore did not appear to act as strong sinks for photoassimilates, in contrast to certain insect galls (McCrea et al. 1985; Larson and Whitham 1991). This could be due to the fact that eriophyoid mites do not intercept vascular tissues directly during gall induction, and the region of mechanical gall initiation is restricted to cell walls of host epidermal cells (Westphal and Manson 1996; Kane et al. 1997). Leaf N was lower in galls of canopy leaves than in surrounding ungalled tissue and control leaves, a pattern that is consistent with results from other plants galled by eriophyoid mites (Hartley 1998).

Galling levels were much higher in mature trees than understory saplings. Relatively little is known about the distribution of gall-forming arthropods in forests; however, factors associated with the upper canopies of large trees, such as leaf sclerophylly, increased tannin levels, and decreased water and nutrient levels, often represent harsh environments for their natural enemies, such as predators,

parasitoids and fungi, but may be favorable habitats for gall-ing insects (Ribeiro and Basset 2007; Thomas et al. 2010). The patterns observed here are similar to prior observations of arthropod galling generally showing strong vertical gradients in forest ecosystems, with drier canopies carrying higher gall loads than moister sub-canopies and understorey environments (Fonseca et al. 2006). However, patterns of arthropod gall distribution appear to be highly varied (Ribeiro and Basset 2007), and an often-neglected stage along host ontogeny in these studies is old, senescent trees. In a broader survey of herbivory at the same study site, spindle gall mites were the single most common agent of herbivore damage in the canopies of old *A. saccharum* trees (i.e. >55 cm dbh), but much less abundant in the smallest trees. In contrast, the abundance of other galling arthropods did not vary across tree size classes (Thomas et al. 2010).

We detected a significant negative relationship between galling frequency (% leaves galled) and radial growth (Fig. 4a). Several alternative explanations exist for this pattern: (1) mites ‘choose’ to form galls on slow-growing trees; (2) slow-growing trees are more susceptible to mite infection and therefore show an accumulation of mite populations and galling levels; (3) high galling prevalence is responsible for declines in tree growth. The biology of galling mites argues strongly against the first explanation. Eriophyoid mites are poor dispersers and rely on local wind patterns to carry them to suitable habitats by passive dispersal; host choice is thus strongly inhibited (Sabelis and Bruin 1996). In temperate systems, eriophyoid mites are able to re-establish and maintain populations on hosts via the presence of a secondary female morph (known as “deuterogynes”). Deuterogynes exit galls in late summer and return to branches where they overwinter; they reemerge the following spring to induce galls on newly flushing leaves (Manson and Oldfield 1996). It thus seems likely that once a suitable tree is discovered and colonized, populations will continue to re-establish and grow in the same tree over time, resulting in “islands” of high gall density trees surrounded by relatively gall-free trees (Egan and Ott 2007). Long-term manipulative experiments would be necessary to rigorously distinguish the directionality of causation between slow growth and SGM galling levels. However, the inference that galling causes reduced growth is consistent with both the large observed photosynthetic impacts and the higher observed correlation with recent growth than with earlier growth (Fig. 4), suggesting likely cumulative impacts on growth with time. In contrast, galling by SGM appears to have no impact on growth at the shoot level. This result may be expected given that shoot growth in *A. saccharum* is completed rapidly following the spring flush and is thought to be entirely driven by carbohydrates mobilized from root stores (Kozłowski and Ward 1957; Wong et al. 2003).

Previous studies examining the impacts of galling on photosynthesis reported decreases in photosynthetic efficiency some distance away from the site of gall damage (up to 4 mm), but these differences were marginal (Aldea et al. 2006). One potential mechanism that may explain why infection by low numbers of minute SGM galls could alter leaf-level photosynthesis in *A. saccharum* is stomatal closure to compensate for non-stomatal water loss in and around elongated spindle-shaped galls that visibly disrupt the plant cuticle. Reductions in stomatal conductance indicate that canopy leaves respond to galling by closing stomata; WUE also decreased in response to galling, indicating either increased non-stomatal water loss in galled leaves and/or a shift in stomatal regulation. Leaves in the canopies of large forest trees are often under physiological water stress due to hydraulic limitations in water transport (Woodruff et al. 2004; Ryan et al. 2006), and they must also cope with high radiant heat loads in the upper canopy. Reduced stomatal conductance in galled leaves would result in decreased latent heat loss, which could further compromise photosynthesis in galled leaves in the upper canopy. In addition to effects mediated by leaf water and energy balance, eriophyoid mites have been found in some cases to transmit viruses (Jeppson et al. 1975), and disease transmission can not be excluded as a possible mechanism for the observed patterns. Finally, it is also possible that the physiological costs of induced defenses could play an important role (Zangerl et al. 2002). Further studies are required to distinguish among these mechanisms.

Declines in photosynthetic capacity and growth rates as trees age have largely been attributed to biophysical limitations on the physiological processes of large trees. A commonly cited explanation is that large trees experience increased hydraulic limitation with the increasing hydraulic pathlength, leading to stomatal closure (Ryan et al. 2006) and/or reduced leaf expansion (Woodruff et al. 2004) in upper canopies, resulting in decreased C uptake. Our study provides a specific example of a biotic mechanism that leads to a large age-related physiological decline in trees, analogous to biotic mechanisms of ageing common in other systems (e.g., Moller and De Lope 1999). More broadly, our results suggest large potential impacts of an endemic canopy arthropod on forest C processes. Studies of the global C cycle point to old-growth forests as important carbon dioxide sinks (Luyssaert et al. 2008; Lewis et al. 2009). In temperate forests, productivity periodically declines due to large-scale insect defoliations (Mattson and Addy 1975), and recent evidence indicates a shift from C sink to C source in these systems during outbreaks (Kurz et al. 2008). However, the impacts of “chronically associated” arthropod parasites, such as eriophyoid gall mites, have largely been neglected. We have shown that gall formation by eriophyoid mites can have large impacts on physiological

performance and that galling incidence is also associated with declines in whole-tree growth in mature temperate forest canopies. Gall formation is thus plausibly a major driver of large-scale forest processes, including both age-related declines in tree performance and patterns of forest growth and net primary productivity.

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