The leaf size/number trade-off within species and within plants for woody angiosperms

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Background and aims – The leaf size/number trade-off has been recently established as a wide-spread and highly predictable relationship associated with between-species leaf size variation. In this study, we examine whether this trade-off relationship also applies at the between-plant (within-species), and at the between-shoot (within-plant) levels associated with spatial variation in incident light availability within tree canopies.

Methods – Replicate current-year shoots were sampled from north-facing (shaded) and south-facing (sun-exposed) canopy sides of sixteen broadleaf tree species in eastern Ontario, Canada. For each shoot, measurements were recorded for mean individual leaf dry mass, number of leaves, number of side branches, and stem length, girth, and tissue dry mass. Leafing intensity was calculated as the number of leaves produced per unit of supporting stem tissue dry mass.

Key results – All of the direct trait measurements had generally larger values for shoots collected from south-facing canopy sides (as expected). However, negative isometric relationships between leaf size and leafing intensity were found at the between-plant level (for *Acer saccharum*) and the between-shoot (within-tree) level for at least some individuals of most species. The predominant trend at the within-tree level, however, was allometric – i.e. north-facing (light-limited) shoots generally had lower individual leaf dry mass but disproportionately higher leafing intensity compared with south-facing shoots.

Conclusions – The results confirm that there is a fundamental leaf size/number trade-off at the between-plant (within-species) level and also at the between-shoot (within-plant) level, as previously reported at the between-species level. But more specifically, the results reveal distinctly different leaf deployment strategies in response to spatial light variability within tree canopies: Under high light exposure, larger leaves are favoured (with lower leafing intensity imposed as a trade-off), but in deeply shaded portions of the canopy, smaller leaves result, we suggest, for two reasons: (i) they are favoured directly (because they minimize overlap of closely spaced adjacent leaves); (ii) they are imposed as a trade-off of selection favouring high leafing intensity, which in turn maximizes the size of the reserve bud bank (number of axillary meristems per unit of supporting stem tissue) available for initiating continued growth or reproduction in the following year.

Key words – allometry, bud bank, leafing intensity, leaf size, light availability, meristems, strategy, trade-off, tree canopy, twig size.

INTRODUCTION

Species that produce leaves with greater mass necessarily have smaller leafing intensity, i.e. they produce fewer leaves per unit of supporting shoot tissue production (Kleiman & Aarssen 2007). Several recent studies have now confirmed – for species associated with a wide range of habitat types and growth forms, including those coexisting within the same community, as well as those ranging differently across broad environmental gradients – that this is a general and highly predictable (and usually isometric) trade-off relationship in plants. As much as 90% or more of the between-species co-variation in these traits is commonly explained by linear regression of log-transformed data (Kleiman & Aarssen 2007, Ogawa 2008, Yang et al. 2008, Li et al. 2009, Milla 2009, Xiang et al. 2009, Whitman & Aarssen 2010, Xiang et al. 2010, Milla & Reich 2011). Analogous to the equally fundamental seed size/number trade-off, adaptive interpretations of the leaf size/number trade-off can be classified under two general types. In the first case – the 'leaf size premium' hy-

pothesis – leaf size variation is regarded as the principal target of selection, accompanied by co-variation in leafing intensity as a required, yet incidental (para-adaptive) trade-off. Particular sizes of leaves, for example, may confer adaptation to herbivory (e.g. Moles & Westoby 2000), or effects of wind (Niklas 1996), or they may be associated directly with optimization of certain physiological functions of individual leaves along environmental gradients (e.g. Wright et al. 2005). Leaf size may also be constrained by twig size which may in turn be affected by branching intensity (i.e. very large leaves cannot be physically supported on very small/thin twigs) (e.g. White 1983).

Alternatively, there may be a general selection premium instead on high leafing intensity, with the attendant small leaf phenotype representing merely a trade-off, i.e. with no direct adaptive value per se associated with relatively small size (Kleiman & Aarssen 2007, Whitman & Aarssen 2010). According to this 'leafing intensity premium' hypothesis, selection – by favouring high leafing intensity – is actually associated with maximizing 'bud bank' size, i.e. the density of axillary meristems, and thus the availability of meristems for optimal and flexible allocation strategies for dormancy reserve (e.g. connected with release from apical dominance, e.g. following browsing), or through deployment as modules for biomass accumulation (shoot and associated leaf production), architectural growth form plasticity (optimal shoot/leaf placement), or reproduction. The 'leafing intensity premium' hypothesis, although still largely unstudied, provides a particularly compelling explanation for why the vast majority of species – at every scale from local communities to regional floras to congeneric lineages – have relatively small leaves, i.e. leaf size distributions are generally strongly right-skewed (Kleiman & Aarssen 2007, Ogawa 2008, Yang et al. 2008, Dombroskie & Aarssen 2010, Whitman & Aarssen 2010).

To date, the leaf size/number trade-off has been examined only at the between-species level. Here we explore whether this trade-off can also be detected at the between-plant (within-species) level, and also at the between-shoot (within-plant) level. Specifically, using sixteen common tree species from eastern Ontario Canada, we tested whether the range of variation in leaf sizes within a species, and also within a single tree, exhibits a negative isometric trade-off relationship with leafing intensity. At the within-plant level, variation in leaf size – and hence any associated trade-off with leafing intensity, if it exists – is likely to be associated primarily with variable environment, especially light availability, affected by position within the plant canopy. Accordingly, drawing on predictions derived from both the 'leaf size premium' hypothesis and the 'leafing intensity premium' hypothesis, we investigate whether patterns of leaf size/number deployment can be interpreted in terms of variation in light harvesting strategies along gradients of incident light availability within tree canopies.

MATERIALS AND METHODS

Deciduous angiosperm trees were sampled from natural populations near Kingston, Ontario (7º25'N 39º17'W), Whitney, Ontario (10º27'N 29º11'W), and the Queen's University Biological Station, near Elgin, Ontario (44º33'N 76º21'W).

Table 1 – The sixteen study species from nine families.
Nomenclature follows Gleason & Cronquist (1991).

Family	Species	Common name
Aceraceae	*Acer negundo* L.	Manitoba maple
Aceraceae	*Acer rubrum* L.	red maple
Aceraceae	*Acer saccharum* Marsh	sugar maple
Betulaceae	*Betula papyrifera* Britton	white birch
Betulaceae	*Carpinus caroliniana* Walter	blue-beech
Betulaceae	*Ostrya virginiana* (Mill.) K.Koch	hop-hornbeam
Fagaceae	*Fagus grandifolia* Ehrh.	American beech
Fagaceae	*Quercus rubra* L.	red oak
Juglandaceae	*Carya cordiformis* (Wang.) K.Koch	bitternut hickory
Juglandaceae	*Carya ovata* (Mill.) K.Koch	shagbark hickory
Juglandaceae	*Juglans nigra* L.	black walnut
Oleaceae	*Fraxinus americana* L.	white ash
Rosaceae	*Prunus serotina* Ehrh.	black cherry
Salicaceae	*Populus grandidentata* Michx.	largetooth aspen
Salicaceae	*Populus tremuloides* Michx.	trembling aspen
Ulmaceae	*Ulmus americana* L.	white elm

Species with very large leaves (e.g. *Juglans nigra*, *Carya cordiformis*) and very small leaves (e.g. *Populus tremuloides*, *Prunus serotina*) were deliberately sampled, ensuring that a wide range of species leaf sizes were included. The remaining species (table 1) were sampled based on ease of availability at the study sites, but were otherwise selected without bias.

Sample sites consisted of south-facing woodland edges opening into old-field vegetation. This ensured that the canopies of sampled trees were exposed to a sharp gradient of light intensity, with one side (facing south into the open field) exposed to direct open sky for most of the day, while the opposite side (facing north) would be intensely and permanently shaded by the contiguous woodland. Three replicate reproductively mature trees (i.e. not saplings) were sampled for each of fifteen study species, while twenty replicate trees were sampled for *Acer saccharum* (all from the same population). All samples were collected during the summer, beginning in July, after shoot and leaf growth for the season were complete.

Following Kleiman & Aarssen (2007), a shoot sample was defined as all of the current year's 'leaf-bearing' growth emerging from all meristems (buds) produced on a single leader ('twig') that had been produced in the previous year – see Fig. 2 in Kleiman & Aarssen (2007). This includes the new terminal leader emerging from the terminal (apical)

meristem, plus any new lateral branches emerging from the subtending axillary meristems on the previous year's leader.

From each tree, ten shoots with minimal herbivore damage were sampled: the five highest (most sun-exposed) shoots on the south-facing side of the canopy (to the maximum limit of the tree pruner - 24 ft), and the five lowest (most shaded) shoots on the north-facing side. For each sampled tree, the height of attachment was recorded for the highest collected shoot on the south-facing side, and for the lowest collected shoot on the north-facing side. Incident light intensity was also measured from the north-facing collection point, using a Licor L1-250, while simultaneously measuring light intensity with a similar light meter positioned at 3 m above the ground within the adjacent open field (an approximation of the incident light intensity at the highest, south-facing sample point). In total, thirty shoots were sampled for each of fifteen study species, while two hundred shoots were sampled for *A. saccharum*. After being clipped from the trees, sampled shoots were returned to the lab and placed in cold storage (1°C) until processing.

For each sampled shoot, length and girth at the base were recorded for the terminal leader and for each associated lateral branch. The number of leaves and leaf scars (indicating lost leaves) were recorded from the terminal leader and associated lateral branches. After one week in a drying oven at 55°C, dry mass was recorded separately for the terminal leader, the collection of lateral branches, the collection of leaves from the leader, and the collection of leaves from all lateral branches. Leaves damaged by herbivores were counted but were omitted from dry mass measurement.

Using the dry mass values of each sampled shoot, mean individual leaf dry mass was calculated as the total mass of all leaves on the shoot (leader plus lateral branches) divided by the total number of these leaves. Leafing intensity was calculated as the total number of leaves produced per shoot divided by the total non-leaf shoot mass (terminal plus lateral branches). Branching intensity was calculated as the total non-leaf shoot mass (terminal plus branches) divided by the non-leaf mass of the terminal leader.

Standard tests for isometric/allometric relationships were applied using Type II regression analyses of log-transformed data, following all previous studies of leaf size / number tradeoffs (e.g. Kleiman & Aarssen 2007). Regressions were carried out using Sigma Plot 10.0, and Type II scaling coefficients were computed based on Zar (1999). Two-tailed *t*-tests were used to test the null hypothesis that the Type II regression slopes did not differ significantly from -1.0 (isometry, or proportionality). Slopes significantly different ($P < 0.05$) from -1.0 were considered allometric, i.e. where a ten-fold increase in one trait is accompanied by a greater or less than ten-fold decrease in the other trait.

RESULTS

On average, incident light availability on north-facing canopy sides (26.7 umol/m²/s) was only 1.9% of that on south-facing canopy sides (1316.4 umol//m²/s) (paired *t*-test, $t = -19.582$, $P < 0.001$). These differences were associated with striking patterns of biomass allocation and leaf deployment

(table 2, electronic appendix). Total shoot mass was significantly greater for south-facing shoots in all species (paired *t*-test, $t = 4.198$, $P = 0.0004$). All species, except *J. nigra* ($P > 0.05$) and *P. serotina* ($P > 0.05$), had significantly longer

Table 2 – Summary of general differences in shoot traits recorded from the south-facing (exposed) canopy side versus the north-facing (shaded) canopy sides.
Results were recorded for sixteen study species sampled along a south-facing woodland edge (see electronic appendix for details). Mean incident light intensity – south (exposed) side: 1316.4 umol/s/m²; north (shaded) side: 26.7 umol/s/m².

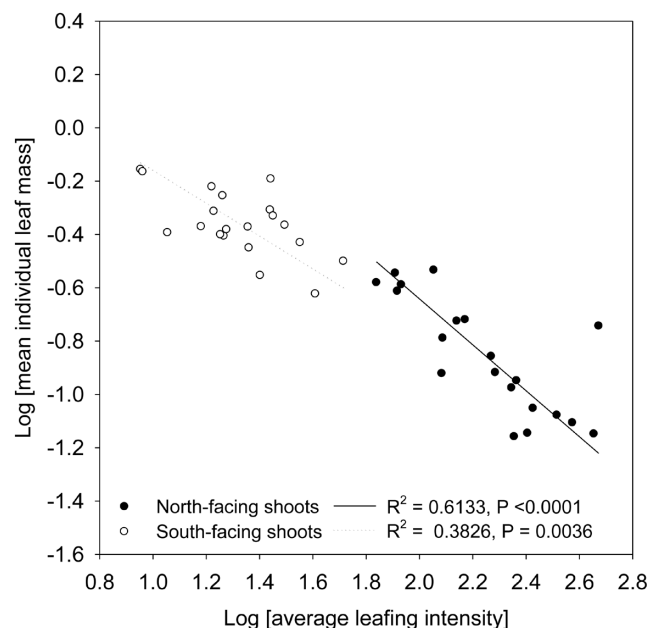| South-facing canopy side	North-facing canopy side
greater individual leaf dry mass	higher leafing intensity
greater number of leaves	greater total leaf:shoot biomass ratio
greater total shoot dry mass	greater terminal leader girth:length ratio
greater terminal leader girth	
greater terminal leader length	
greater branching intensity	

Figure 1 – Relationship between Log [mean individual leaf mass (g)] versus Log [average leafing intensity] for south-facing shoots (open symbols, $n = 20$) and north-facing shoots (closed symbols, $n = 20$) from the canopies of 20 trees of *Acer saccharum* (five south- and five north-facing shoots sampled per tree). Leafing intensity is the number of leaves per unit shoot dry mass (g). Lines and associated R^2 and P-values are from Type II (reduced major axis regression). Both slopes indicate isometric relationships (not significantly different from -1.0): for north facing shoots, $m = -0.861$, $t = -5.343$, $P = 0.664$); for south facing shoots, $m = -0.616$, $t = -3.340$, $P = 0.272$).
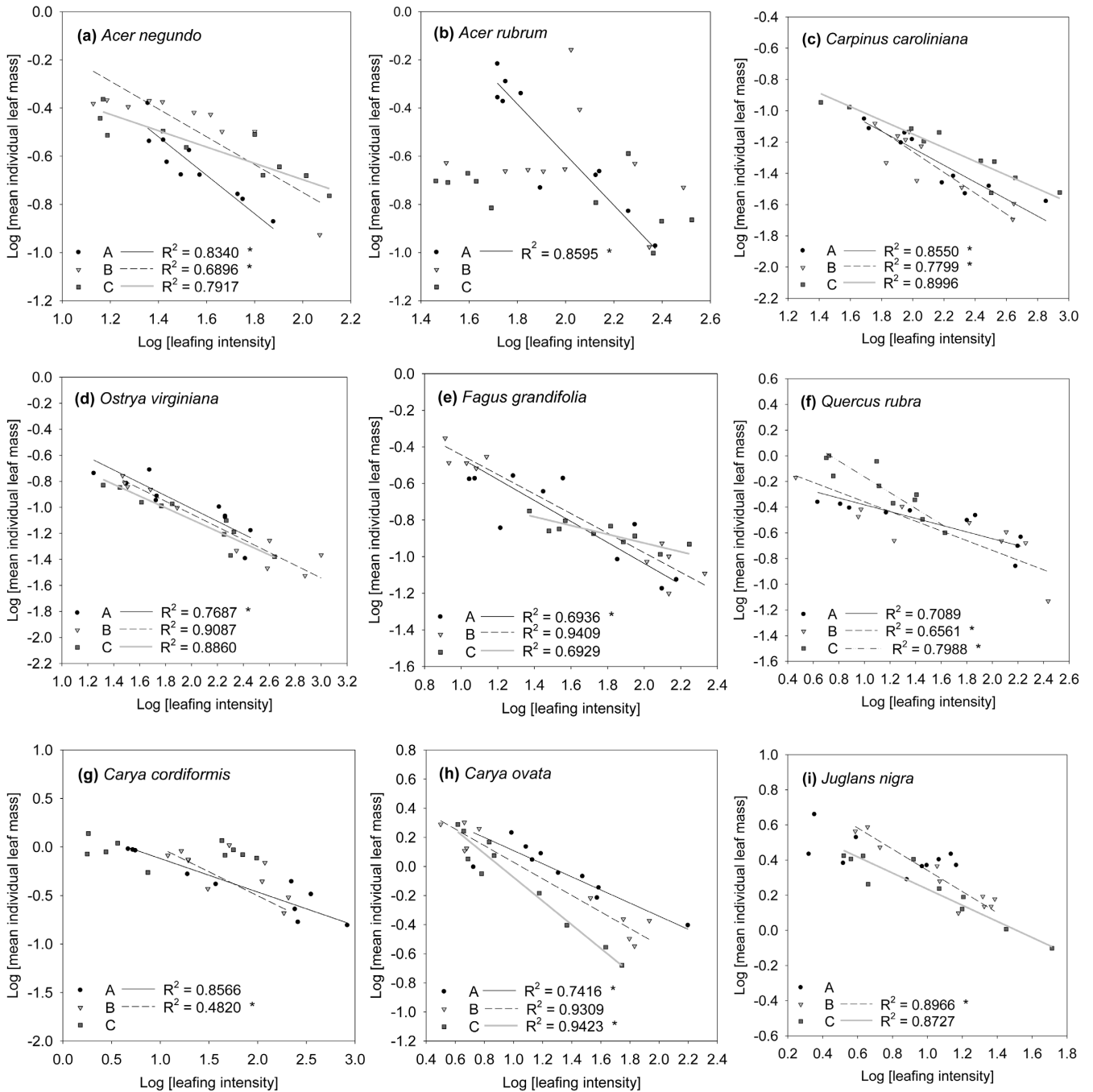
Figure 2 – Relationships between Log [mean individual leaf dry mass (g)] versus Log [leafing intensity] for individual trees from fourteen species (a–n) sampled from Southern Ontario. Leafing intensity is the number of leaves per unit shoot dry mass (g). For each species, results are shown for each of three individual trees (A, B, C) distinguished by separate symbols (n = 10 shoots per tree). Trees with significant negative relationships ($P < 0.05$) are indicated by separate regression lines (and associated R^2 values) derived from Type II (reduced major axis) regression. Asterisks refer to regressions that are isometric [with slope not significantly different from -1.0 (t-test, $P > 0.05$)].

south-facing terminal leaders (paired t-test, t = 3.755, P = 0.001). Mean individual leaf mass was significantly greater for south-facing shoots in all species (paired t-test, t = 2.996, P = 0.005) except *Acer rubrum* ($P > 0.05$) and *Betula papyrifera* (the latter having significantly larger leaves on north-facing shoots). South-facing shoots also had higher branching intensities in all species (paired t-test, t = 3.324,

P = 0.0002) (although this is not statistically significant ($P > 0.05$) for seven of the sixteen species). North-facing shoots however had greater leafing intensities in all species (paired t-test, t = -5.472, P <0.0001), and larger leaf / stem (non-leaf) biomass ratio in all species (paired t-test, t = -5.131, P <0.0001) (although this is not statistically significant ($P > 0.05$) for *P. serotina*). Leader girth/length ratio was also
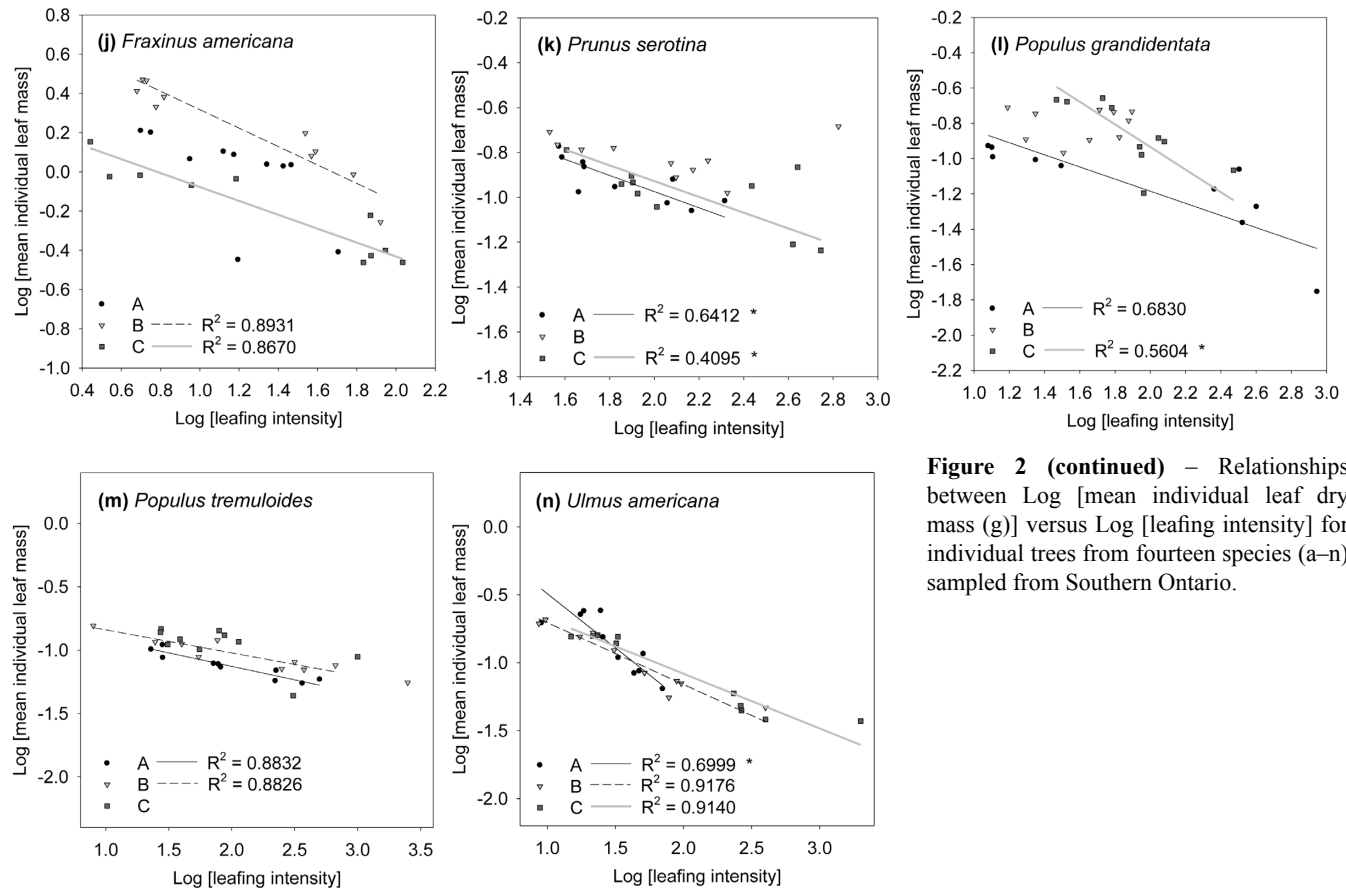
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Figure 2 (continued) – Relationships between Log [mean individual leaf dry mass (g)] versus Log [leafing intensity] for individual trees from fourteen species (a–n) sampled from Southern Ontario.

larger in north-facing shoots for all species (paired *t*-test, *t* = -3.708, *P* = 0.001) – although this is not statistically significant (P > 0.05) for *A. rubrum*, *J. nigra*, *Populus grandidentata*, and *P. serotina* – except one species; *Ulmus americana* had a significantly larger leader girth/length ratio in south-facing shoots (electronic appendix).

Between-tree trade-off – within a species (*Acer saccharum*)

Across all twenty individuals of *A. saccharum*, including shoots sampled from both north- and south-facing sides of the canopies, average leafing intensity and mean individual leaf dry mass co-vary over about one order of magnitude, with generally higher leafing intensity but smaller leaves on north-facing shoots, and with generally larger leaves but smaller leafing intensity on south-facing shoots (fig. 1). For each canopy side analyzed separately, the between-tree relationship was significantly negative and isometric (with Type II regression slope not significantly (*P* > 0.05) different from -1.0); i.e. trees that had higher leafing intensity generally had proportionately smaller mean individual leaf mass, on both north- and south-facing canopy sides (fig. 1).

Between-shoot trade-off – within a tree

At the within-tree level, the goodness-of-fit and slopes of the leaf size/number regressions vary between species and between trees within a species, but the relationship was numer-ically negative for all but one of the 45 sampled trees, and 34 of these were statistically significant (*P* < 0.05) (fig. 2). A significant within-tree trade-off relationship was recorded for at least one individual from each species (except *B. papyrifera*), and for all three individuals sampled from seven species, (*U. americana*, *Fagus granifolia*, *Carpinus caroliniana*, *Ostrya virginiana*, *Acer negundo*, *Quercus rubra*, and *Carya ovata*) (fig. 2).

Of the 34 individuals with significant regressions, all of them had regression slopes numerically less negative (more 'shallow') than -1.0, but half (seventeen) of these were not significantly different from -1.0 (*t*-test; *P* > 0.05), thus indicating an isometric within-tree trade-off relationship between leafing intensity per shoot and mean individual leaf dry mass per shoot. However, none of the species demonstrated isometry for all three individuals; at most, two individuals of the species *C. caroliniana*, *P. serotina*, *O. virginiana*, *Q. rubra*, and *C. ovata* displayed significant isometric relationships.

In the other half of the individuals (involving seventeen trees) showing significant (*P* < 0.05) regressions, the relationships were allometric (with slope significantly less negative than -1.0). In other words, shoots within these trees that had larger mean individual leaf dry mass generally had *greater than* proportionately lower leafing intensity; or stated another way, shoots within these trees that had smaller mean individual leaf dry mass had generally *greater than* proportionately higher leafing intensity.
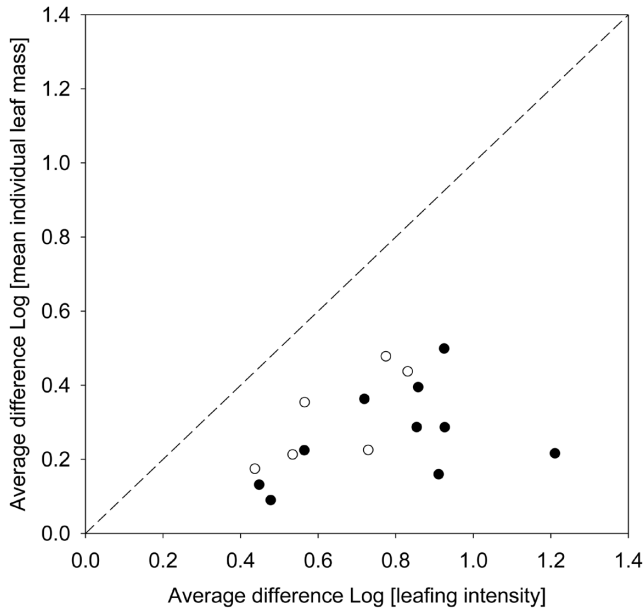
Figure 3 – Scatter-plot showing, for each of sixteen study species, average within-tree difference – comparing north-versus south-facing canopy sides – in Log [mean individual leaf dry mass (g)] per shoot versus Log [average leafing intensity] per shoot (see table 2). The dashed line is the 1:1 line, shown for reference only; all points are below the line indicating that, for all species, the difference (comparing north- versus south-facing canopy sides) is greater for Log [average leafing intensity] than for Log [mean individual leaf dry mass], with closed symbols indicating species for which this difference is statistically significantly ($P < 0.05$) – based on results from paired t-tests ($n = 3$ sampled trees per species, or twenty for *Acer saccharum*) comparing within-tree difference in mean values ($n = 5$ shoots from each canopy side).

The within-tree leaf size/number trade-off illustrated in figure 2 is obviously linked to smaller leaves (with higher leafing intensity) on the shaded, north-facing canopy side versus larger leaves (with lower leafing intensity) on the south-facing canopy side (electronic appendix). Strictly speaking, the regressions in figure 2 violate the assumption of equal independence between all possible pairs of data points (because five shoots were intentionally selected from the north facing canopy side and five were selected from the south-facing side). Accordingly, we can illustrate the allometry of this within-tree relationship also by comparing the average within-tree difference – for north- versus south-facing canopy sides – in Log (individual leaf dry mass) versus Log (leafing intensity) (fig. 3). For all sixteen species, the within-tree difference – comparing north- versus south-facing canopy sides – is greater for Log (leafing intensity) than for Log (individual leaf dry mass), and for ten of these species the greater difference for leafing intensity is statistically significant ($P < 0.05$) (fig. 3).

DISCUSSION

A negative, isometric relationship between leafing intensity and mean individual leaf dry mass has been reported at the between-species level in several previous studies. The

same relationship was also detected in the present study at the between-plant (within-species) level (fig. 1) and, for several sampled trees, also at the between-shoot (within-tree) level (fig. 2). The latter was detected for study species varying in leaf size by more than 10-fold. The between-tree trade-off could be associated with effects of (unmeasured) genotypic variation. Interestingly, however, the correlation for mean leaf mass from north- versus south-facing canopy sides across the twenty sugar maple trees was not significant ($r = 0.270$, $P = 0.249$); i.e. trees that had a relatively large leaf on the south-facing canopy side did not also generally have a relatively large leaf on the north-facing canopy side. Between-tree variation in mean leaf mass was also not correlated with sampling height from either the south-facing ($r = 0.212$, $P = 0.370$) or north-facing ($r = 0.084$, $P = 0.725$) canopy sides – nor was it correlated on the north-facing side with relative incident light intensity there (relative to open sky) ($r = -0.342$, $P = 0.140$).

The within-tree trade-off relationships (fig. 2), however, are obviously linked (substantially if not entirely) to environmental effects associated with intentional sampling from the
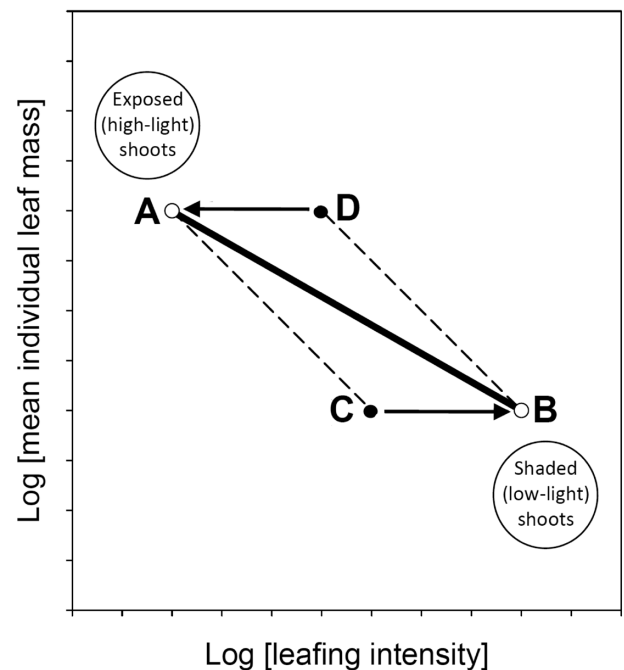

Figure 4 – Possible interpretations of deviation from an isometric within-tree trade-off relationship between Log [leafing intensity] and Log [mean individual leaf mass] – where south-facing (exposed) shoots have larger leaves but lower leafing intensity, and north-facing (shaded) shoots have higher leafing intensity but smaller leaves. The dashed lines (A--C, B--D) represent hypothetical 'null' (predicted) isometric relationships (slope = -1.0), and the solid line (A—B) represents a hypothetical allometric relationship (slope = less negative than -1.0), as observed for several trees in the present study (fig. 2). Arrows designate two hypothetical mechanisms (see text) for generating the allometric (rather than isometric) trade-off relationship, where leafing intensity varies disproportionately with variation in leaf size – i.e. leafing intensity is smaller (A instead of D) or larger (B instead of E) than predicted by isometry (see text).

most- and least-shaded extremes within the canopy. Importantly, the prominent trend is allometric (not isometric) at the within-tree level; i.e. the within-tree difference – comparing north- versus south-facing canopy sides – is generally greater for Log (leafing intensity) than for Log (individual leaf dry mass) (fig. 3). This is reflected schematically in the hypothetical regression A—B in figure 4, with slope less negative than -1.0. With high light availability – i.e. for south-facing shoots – growth produces more of everything (table 2). The larger individual leaf mass is accompanied by more stem tissue and more leaves, but importantly, the increase in stem mass is greater than the increase in number of leaves; thus leafing intensity – as well as leaf to stem (non-leaf) biomass ratio – are lower for south-facing shoots. Presumably this reflects a premium on two things: a larger stem girth for supporting heavier leaves, and a longer stem length for maximizing the likelihood that – through continued southward shoot elongation – leaves produced in both the current and subsequent year will continue to be displayed in full sun (as neighbouring shoots also continue to grow in the same direction). Moreover, this effect could be driving the allometric relationship, where leafing intensity for more sun-exposed shoots is lower than predicted by isometry, e.g. giving point A instead of point D in the schematic in figure 4.

In contrast, with decreasing light availability – i.e. for north-facing shoots, which receive on average only about 2% of the light intensity available to south-facing shoots – growth produces less of everything. The smaller individual leaf mass is accompanied by less stem tissue and fewer leaves, but importantly, the decrease in number of leaves is not as great as the decrease in stem mass; thus leafing intensity – as well as leaf to stem (non-leaf) biomass ratio – are greater for north-facing shoots. Stem length also decreases more than stem girth giving a greater girth:length ratio for north-facing shoots (table 2). We offer two interpretations here: (i) At the bottom of north-facing canopy sides, where light is severely (and essentially uniformly) limiting, investment in stem elongation would serve only to project leaves into a similarly (or even more) shaded environment, and the persistently low light there exacerbates the cost of non-photosynthetic tissue involved in stem construction; higher relative investment in leaf tissue, therefore, maximizes interception of what little light is available (while minimizing the cost of stem construction) – and the smaller leaves there also minimize overlap between adjacent closely spaced leaves. (ii) The higher leafing intensity in north-facing shoots also maximizes the size of the reserve bud bank (number of axillary meristems per unit of supporting stem tissue), thus maximizing the likelihood (under these severely light-limited conditions) that at least one viable, undamaged, and uneaten bud will be available for initiating continued growth or reproduction in the following year. Accordingly, this effect could also contribute in producing the allometric relationship, where leafing intensity for shaded, low light shoots is higher than predicted by isometry, e.g. giving point B instead of point C in the schematic in figure 4.

In conclusion, our results show that the leaf/size number trade-off – now a widely established generalization at the between-species level (Kleiman & Aarssen 2007, Ogawa 2008, Yang et al. 2008, Li et al. 2009, Milla 2009, Xiang et al. 2009, Whitman & Aarssen 2010, Xiang et al. 2010, Milla & Reich 2011) – is also evident at the between-tree (within-species), and even the between-shoot (within-tree) level. Future studies are required to explore the generality of these finer-scale patterns with broader phylogenetic representation. Importantly however, our data illustrate that the relationship at these finer scales is not always isometric (as in previous between-species analyses); the prevailing trend – particularly at the within-tree level – is in fact allometric (fig. 4). This can be interpreted in terms of flexible, optimizing leaf deployment strategies for harvesting the widely variable light supply distributed throughout a typical tree canopy. Further studies are required to test whether this allometry is a product of optimizing leaf size (the 'leaf size premium' hypothesis), or optimizing leafing intensity (the 'leafing intensity premium' hypothesis) – or both – across this light gradient. Central to these investigations is the recognition that the leaf (and its size) as well as the subtending axillary meristem (and its numbers) represent equally important products of leaf production – each playing a distinct role in presenting opportunities for maximizing fitness in a heterogeneous environment.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of the results from average shoot trait differences for nine traits (a – i) measured on south- versus north-facing shoots in the sixteen study species (pdf format).

ACKNOWLEDGEMENTS

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