

The leaf size/number trade-off in herbaceous angiosperms

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Abstract

Aims

In this study, we examined the extent to which between-species leaf size variation relates to variation in the intensity of leaf production in herbaceous angiosperms. Leaf size variation has been most commonly interpreted in terms of biomechanical constraints (e.g. affected by plant size limitations) or in terms of direct adaptation associated with leaf size effects in optimizing important physiological functions of individual leaves along environmental gradients (e.g. involving temperature and moisture). An additional interpretation is explored here, where adaptation may be more directly associated with the number of leaves produced and where relatively small leaf size then results as a trade-off of high 'leafing intensity'—i.e. number of leaves produced per unit plant body size.

Methods

The relationships between mean individual leaf mass, number of leaves and plant body size were examined for 127 species of herbaceous angiosperms collected from natural populations in southern Ontario, Canada.

Important Findings

In all, 88% of the variation in mean individual leaf mass across species, spanning four orders of magnitude, is accounted for by a negative isometric (proportional) trade-off relationship with leafing in-

tensity. These results parallel those reported in recent studies of woody species. Because each leaf is normally associated with an axillary bud or meristem, having a high leafing intensity is equivalent to having a greater number of meristems per unit body size—i.e. a larger 'bud bank'. According to the 'leafing intensity premium' hypothesis, because an axillary meristem represents the potential to produce either a new shoot or a reproductive structure, high leafing intensity should confer greater architectural and/or reproductive plasticity (with relatively small leaf size required as a trade-off). This greater plasticity, we suggest, should be especially important for smaller species since they are likely to suffer greater suppression of growth and reproduction from competition within multi-species vegetation. Accordingly, we tested and found support for the prediction that smaller species have not just smaller leaves generally but also higher leafing intensities, thus conferring larger bud banks, i.e. more meristems per unit plant body size.

Keywords: bud bank • leafing intensity • meristems • plant size • plasticity • reproductive economy

Received: 1 July 2009 Revised: 26 August 2009 Accepted: 10 September 2009

INTRODUCTION

Why are there so many different sizes of leaves in herbaceous angiosperms? From the giant leaf of *Arctium minus* Schk. to the tiny leaves of *Cerastium vulgatum* L., the range of leaf sizes within a single meadow can vary by more than four orders of magnitude (present study). One explanation relates to biophysical support constraints; a small species like *C. vulgatum* simply cannot support the large leaf size found in *A. minus*. Because bending movement of a cantilevered beam increases with the cube of its length as the mass becomes located further from the axis of bending, larger leaves would be expected to

require disproportionately more biomass for support structures (Niinemets *et al.* 2006, Niinemets *et al.* 2007a, Niinemets *et al.* 2007b). For the same reason, the relationship between leaf area and leaf mass is generally allometric; i.e. because of greater support requirements in larger leaves, light-capturing surface area increases less per unit of increase in leaf mass, which constrains maximum leaf size (Milla and Reich 2007, Niklas *et al.* 2007, Poorter and Rozendaal 2008).

Most previous interpretations of between-species leaf size variation have been based on adaptive interpretations of leaf size, i.e. the relative size of a species' leaf is considered to confer a direct fitness benefit, e.g. in terms of adaptation to herbivory

(Brown and Lawton 1991, Diaz *et al.* 2001, Moles and Westoby 2000), or as a product of optimizing selection for traits involved in photosynthesis, gas exchange, energy flux and/or water use efficiency that are affected by leaf size (e.g. Givnish and Vermeij 1976, Parkhurst and Loucks 1972, Zwieniecki *et al.* 2004). Numerous studies along environmental gradients have reported smaller leaved species in association with increased irradiance, decreased moisture, increased temperature and increased elevation (which affects aridity) (e.g. Cowling and Campbell 1980, Dale and Causton 1992, Gamperle and Schneller 2002, Geller and Smith 1982, Lambrecht and Dawson 2007, Lee *et al.* 1986, McDonald *et al.* 2003). Such correlations have been used in predictive models to infer past climatic conditions based on the fossil record (e.g. Glasspool *et al.* 2004, Jacobs 2002, Royer *et al.* 2005).

There is no reason to doubt these traditional interpretations, but there is also an additional and largely overlooked explanation for between-species leaf size variation: variation in leaf size may be a product of a trade-off with variation in the number of leaves produced—in other words, species that have high ‘leafing intensity’ (i.e. produce many leaves per unit of shoot growth) will necessarily have relatively small leaves (Kleiman and Aarssen 2007). The appeal of this interpretation lies in its simplistic inevitability—the same kind of inevitability (for interpreting life history) that characterizes the seed size/number trade-off in plants, i.e. species that produce relatively large seeds must necessarily produce relatively few seeds per unit plant body size (Aarssen and Jordan 2001). Recent studies on woody species have reported negative isometric relationships for leaf size, where most (90–99%) of the between-species variation in individual leaf size can be accounted for by variation in the number of leaves produced per unit growth of leaf-bearing shoots (Kleiman and Aarssen 2007, Milla 2009, Ogawa 2008, Yang *et al.* 2008). According to the ‘leafing intensity premium’ hypothesis (Kleiman and Aarssen 2007), relatively small leaf size need not be particularly adaptive *per se*; it may, to a significant extent, be a product of the trade-off associated with adaptive significance linked to high leafing intensity. Since each leaf is normally associated with an axillary meristem, a measure of leafing intensity is commensurate with a measure of meristem production intensity or a measure of ‘bud bank’ size per unit plant body size. Since each axillary meristem has potential to produce a new shoot or a flower, a large bud bank should provide the potential for high relative phenotypic and reproductive plasticity (Bonser and Aarssen 1996).

In the present study, we examine whether the leaf size/number trade-off reported previously for woody species applies also to herbaceous angiosperms. Further, we predict that a large bud bank (through high leaf/meristem production intensity) should be particularly advantageous for smaller species because of their general disadvantage in competition, especially for light within multi-species vegetation. In addition, many small species are opportunistic ruderals, where fitness is typically promoted by high reproductive effort that may in turn be promoted by a large bud bank available for deployment

of meristems as flowers. Accordingly, we tested the prediction that species with smaller plant body size should have higher leafing intensity.

MATERIALS AND METHODS

Species of herbaceous angiosperms ranging widely in leaf size were collected from natural populations in southern Ontario, Canada, in the vicinities of Queen’s University and the Queen’s University Biological Station near Kingston, Ontario (44°16′N, 76°30′W), the Royal Botanical Gardens in Hamilton, Ontario (43°16′N, 79°54′W) and the Agriculture and Agri-Food Canada Research Station in Harrow, Ontario (42°02′N, 82°54′W). A total of 127 species from 31 families were included (Appendix). Collection sites spanned a wide range of habitat types, including woodlands, meadows, farm fields, lakeshores, marshes, roadsides and other disturbed habitats. As many species were sampled as time permitted within the growing season. Since leaf size variation was of specific interest, care was taken to include species with the largest and smallest leaves that could be found. Sampling focussed on dicots because of their wide variation in leaf size and architecture and because of their more discrete leaf size at maturity; hence, grasses—where young leaves are often not visible and hence difficult to count—were specifically excluded from sampling. Cultivated species were not collected, and vines were avoided because of difficulty in collecting entire plants. Clonal species were generally avoided unless it was possible to easily distinguish individuals as distinct ‘rooted units’ (Aarssen 2008) based on minor soil excavation (this is another reason why grasses were impractical to collect). Aside from these criteria, species were sampled as they were encountered based on their availability and ease of access to local populations within the study region.

For each species, three to five replicate plants were collected, depending on local abundance and specimen quality. Only reproductive individuals (showing flower buds, flowers or fruits) were selected to ensure that the plants had attained typical adult size, as well as to aid in positive identification; otherwise, plants were selected randomly from within the local population of each species. Each plant’s height (maximum vertical extent) was measured and the entire above-ground biomass from the rooted unit was collected and transported to the laboratory. Samples were stored in a freezer until processing was possible.

For each sampled plant, the total number of leaves produced was determined by counting intact green leaves, dead (withered or brown) leaves and leaf scars (representing lost leaves) associated with the current year’s shoot growth. The intact green leaves (including petioles) were collected and dried at 60°C for at least 48 hours, after which their total mass was recorded and mean dry mass per leaf was calculated. Total per-plant leaf dry mass was adjusted to take account of lost leaves (indicated by leaf scars). Dry mass was also recorded for all remaining (non-leaf) above-ground tissue. The vast

majority of this was supporting shoot biomass but also included some reproductive biomass (the latter was not recorded separately because of the inordinate time required to separate it). Leafing intensity, analogous to Kleiman and Aarssen's (2007) measure, was calculated as the total number of leaves divided by the total biomass of supporting tissue—i.e. the total remaining (non-leaf) above-ground biomass.

To assess the effect of phylogeny on the leaf size/number trade-off, we constructed a phylogenetic tree based on the family-level phylogeny of Stevens (2001), developed from work of the Angiosperm Phylogeny Group. Published data on phylogenies were used to resolve the tree from the family level to genus level, and where these were not available for the species of interest, taxonomic groups were assumed to be monophyletic and used as a surrogate for phylogeny (Garland *et al.* 1992). Where more than one species shared a genus, mean trait values were assigned. The full tree is given in the supporting information (See online supplementary material). All tree branch lengths were set at 1.0. Unresolved nodes in the phylogeny were left as soft polytomies. Consequently, we opted for a conservative approach when testing hypotheses with independent contrasts, subtracting one degree of freedom for each unresolved branch (Garland and Diaz-Uriarte 1999, Purvis and Garland 1993). To test for the statistical adequacy of branch lengths, we performed the diagnostic analyses suggested by Garland *et al.* (1992). We computed standardized contrasts for log (leafing intensity) and log (mean leaf mass) across species using phylogenetically independent contrasts using the PDTREE module of the phenotypic diversity analysis programs (Midford *et al.* 2005) with Mesquite software (Maddison and Maddison 2006).

RESULTS

Smaller species produce both fewer leaves and smaller leaves, but the proportion of total above-ground biomass allocated to leaves is not related to variation in plant body size between species; i.e., total leaf biomass decreases significantly ($P < 0.001$) but proportionately with decreasing remaining (non-leaf) above-ground biomass (Fig. 1a). In addition, number of leaves decreases proportionately with decreasing remaining above-ground plant mass across species (Fig. 1b, $r^2 = 0.174$, $P < 0.001$; similar results were obtained with total above-ground plant mass (including leaves): $r^2 = 0.144$, $P < 0.001$). Individual leaf mass also decreases proportionately with decreasing remaining above-ground plant mass across species (Fig. 1c, $r^2 = 0.277$; similar results were obtained with total above-ground plant mass: $r^2 = 0.344$, $P < 0.001$).

However, much more of the between-species variation in individual leaf mass is explained by variation in leafing intensity—i.e. number of leaves divided by remaining above-ground plant mass (Fig. 2a, $r^2 = 0.879$; similar results were obtained with number of leaves divided by total above-ground plant mass: $r^2 = 0.95$, $P < 0.001$). Mean individual leaf mass decreases significantly ($P < 0.001$) and proportionately (slope,

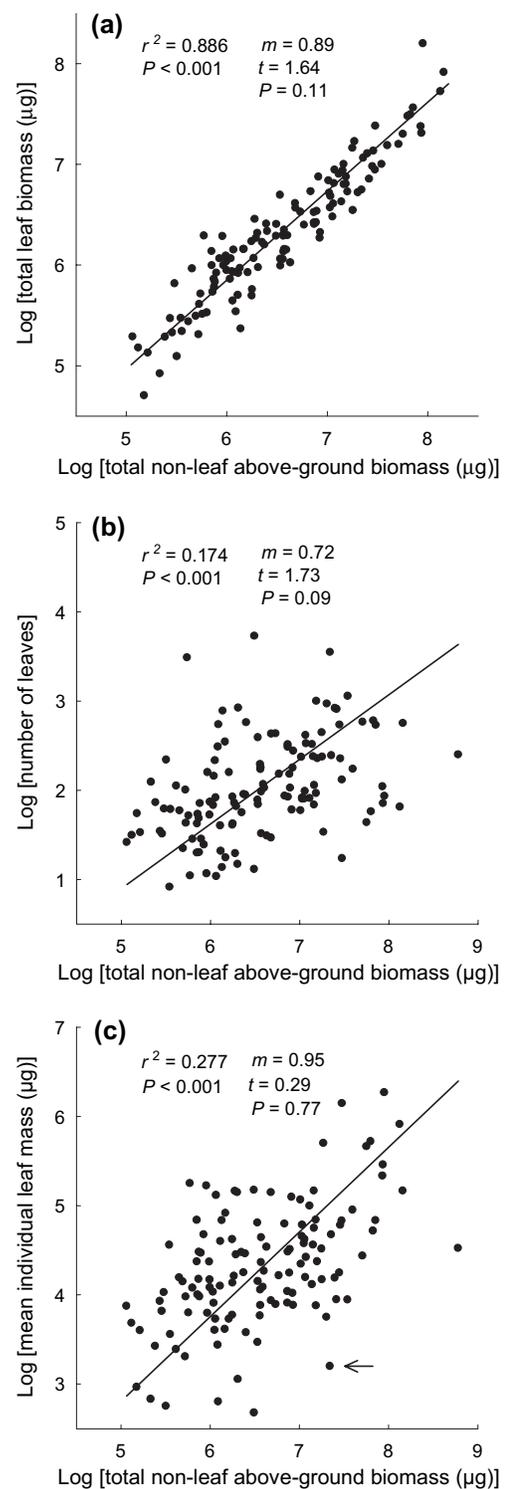


Figure 1: relationships between leaf traits and plant body size for 127 species of herbaceous angiosperms: (a) log (total leaf mass) versus log (total non-leaf above-ground biomass); (b) log (number of leaves) versus log (total non-leaf above-ground biomass); (c) log (mean individual leaf mass) versus log (total non-leaf above-ground biomass). Arrow in (c) points to *Aster ericoides* (see text). Lines are from reduced major axis (RMA) regression analyses; m = RMA slope; t and associated P values test for deviation from the null hypothesis of $m = 1.0$ (isometry).

$m = -1.02$) across species with increasing leafing intensity in an isometric trade-off relationship (t -test, m is not significantly different from -1.0 , $P = 0.81$) (Fig. 2a). This is also reflected in a least squares multiple regression analysis, where 89% of the

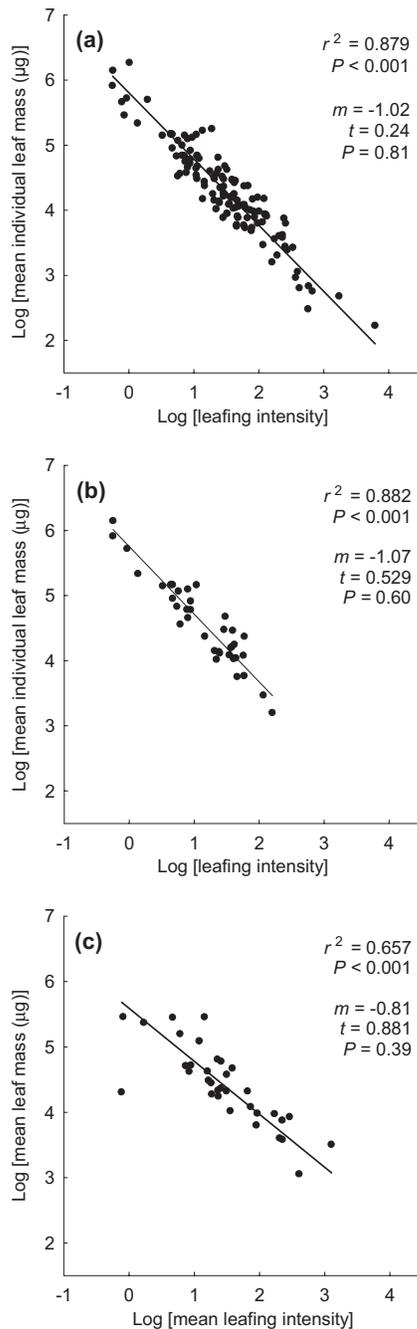


Figure 2: log (mean individual leaf mass) versus log (leafing intensity) for: (a) 127 species of herbaceous angiosperms; (b) 40 species belonging to the Asteraceae [a subsample of (a)] and (c) 31 families [based on averaged values for the species represented in (a)]. Leafing intensity was calculated as number of leaves divided by total remaining (non-leaf) above-ground biomass (g). Lines are from reduced major axis (RMA) regression analysis; m = RMA slope; t and associated P values test for deviation from the null hypothesis of $m = -1.0$ (isometry).

between-species variation in log (mean individual leaf mass) is explained by log (number of leaves) and log (remaining above-ground plant mass) used as predictor variables (Fig. 3).

The negative relationship between leaf mass and leafing intensity remained strongly negative after incorporating phylogenetic history among the plant species through the phylogenetically independent contrasts ($r^2 = 0.59$, $P < 0.0001$). Accordingly, the isometric leaf size/number trade-off detected for the full data set (Fig. 2a) is also evident for just the 40 species within the composite family (Fig. 2b, $r^2 = 0.882$) and also for the overall means for each of the 31 families (Fig. 2c, $r^2 = 0.657$) (where, for each family, the overall family mean of all the per-species leaf sizes was plotted against the overall family mean leafing intensity, calculated as the overall family mean of all the per-species number of leaves divided by the overall family mean of all the per-species remaining above-ground plant mass).

Smaller species had higher leafing intensity (Fig. 4, $r = -0.663$, $P < 0.001$). This is also reflected in the almost significant ($P = 0.09$) allometric relationship in the simple linear regression between number of leaves and remaining above-ground plant mass (Fig. 1b). Smaller species, therefore, produce more leaves, and hence more axillary meristems, than predicted by their above-ground (non-leaf) body size (Figs 1b and 4).

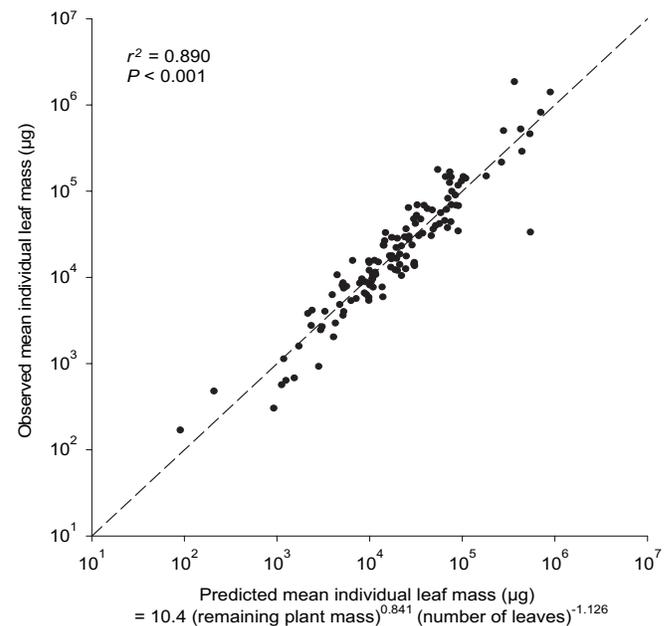


Figure 3: observed versus predicted (mean individual leaf mass) from a least squares multiple regression model for log-transformed data involving (number of leaves) and [remaining (non-leaf) above-ground plant mass] for 127 species of herbaceous angiosperms. The equation for predicted (mean individual leaf mass) is given below the x -axis. Note log scales. Dashed line is shown only to indicate where observed is equal to predicted. The scaling coefficient for remaining plant mass ($m = 0.841$) is not significantly different from 1.0 (t -test, $P = 0.0961$), but the scaling coefficient for number of leaves ($n = -1.126$) is significantly different from -1.0 (t -test, $P = 0.0112$).

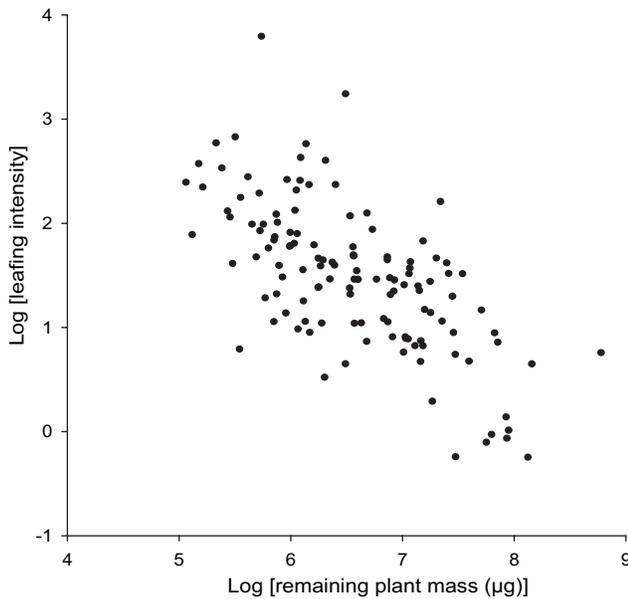


Figure 4: log (leafing intensity) versus log [remaining (non-leaf) above-ground plant mass] for 127 species of herbaceous angiosperms (Pearson product moment correlation, $r = -0.663$, $P < 0.001$).

DISCUSSION

The vast majority of plant species have relatively small leaves (e.g. Kleiman and Aarssen 2007, Ogawa 2008, Yang *et al.* 2008), including the herbaceous angiosperms sampled in the present study (Fig. 5a). This necessarily means that the vast majority of speciation events over evolutionary time have involved the origination of new species with small leaves. To a large extent, this can be accounted for by the fact that the vast majority of plant species are themselves relatively small (Aarssen *et al.* 2006); for biomechanical reasons, relatively small species must necessarily have relatively small leaves [and also relatively small seeds/fruits (Aarssen 2005)]. The preponderance of both small plants and small leaves may be in part a consequence of the ‘left-wall’ effect—i.e. the sizes of everything must be greater than zero (there can be no negative values) (Aarssen *et al.* 2006).

Importantly, however, only 28% of the between-species variation in leaf size in our data is accounted for by variation in plant body size, and so many relatively large species also have relatively small leaves; e.g. of the 127 study species, *Aster ericoides* L. (arrow in Fig. 1c) is the 20th largest in body size but the 7th smallest in leaf size. Relatively small leaf size, therefore, is also likely to be associated with particular fitness advantages (irrespective of plant body size), and most previous studies have interpreted these in terms of how a particular leaf size may optimize important physiological functions of individual leaves in particular environments (Whitfield 2006). Accordingly, the preponderance of small-leaved species might be accounted for by an ‘adaptive leaf size’ hypothesis—i.e. most

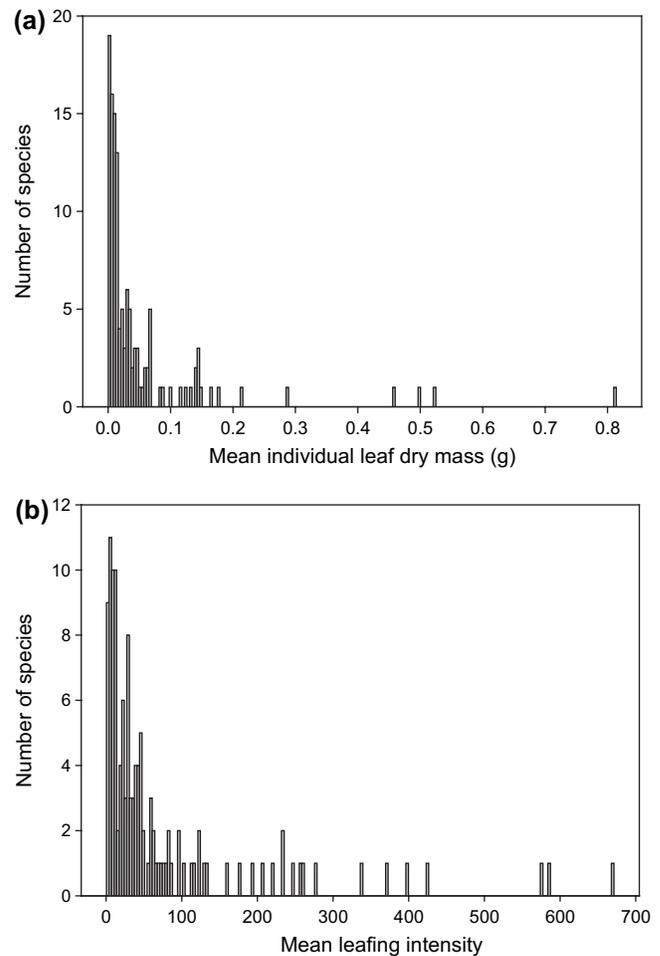


Figure 5: Frequency distributions of mean individual leaf mass (a) and leafing intensity (b) for the 127 study species. In order to facilitate greater resolution on the x-axis, the two species with the largest individual leaf mass were omitted from (a): *Inula helenium* (1.39 g) and *Verbascum thapsus* (1.84 g). Similarly, the two species with the highest leafing intensity were omitted from (b): *Euphorbia polygonifolia* (5325 leaves per gram of non-leaf above-ground biomass) and *Arenaria stricta* (6189 leaves per gram).

habitats for land plants (globally over evolutionary time) have/had environmental conditions for which adaptation is conferred through physiological optimization associated directly with relatively small leaf size (Kleiman and Aarssen 2007).

In the present study, however, we consider an additional possible explanation for the preponderance of species with relatively small leaf size—in terms of the proposed adaptive advantages associated with relatively high leafing intensity (the leafing intensity premium hypothesis)—i.e. most habitats (globally over evolutionary time) have/had environmental conditions for which adaptation is conferred through effects associated ‘indirectly’ with relatively small leaf size. According to this hypothesis, relatively small leaf size allows the production of many leaves per unit plant body size, which confers important fitness advantages associated with a large bud

bank—i.e. a large number of axillary meristems per unit plant body size (Kleiman and Aarssen 2007).

This last interpretation has been largely overlooked in traditional interpretations of between-species leaf size variation, and our results provide, to the best of our knowledge, the first reported empirical evidence for a leaf size/number trade-off in herbaceous angiosperms. As reported previously for woody species (Kleiman and Aarssen 2007), a very large percentage (88%) of the between-species variation in individual leaf mass in herbaceous angiosperms can be explained by a negative isometric relationship with leafing intensity (Fig. 2a).

Several potential adaptive advantages of high leafing intensity require further study. For example, by spreading out leaf tissue over a greater number of discrete units, higher leafing intensity may reduce leaf tissue loss from insect herbivory; having more (and hence smaller) leaves may increase the probability that some leaves will remain unoccupied, thus minimizing total herbivore damage (Brown and Lawton 1991). This could be particularly important in shorter lived herbaceous species compared with longer lived woody species since the latter will generally have more future growing seasons within which to recover from leaf tissue loss in any given season.

More generally, according to the leafing intensity premium hypothesis, because each leaf is normally associated with an axillary meristem/bud, the fitness advantage of relatively high leafing intensity is associated with a relatively large bank of available meristems (buds) per unit plant body size available for deployment as modules for growth (vegetative shoots) and/or reproduction (flowers). In some woody species, a large meristem/bud bank may be important for replacing shoots lost from physical damage, e.g. ice or snow loads (Vesk and Westoby 2004), or for producing a high density of shoots that may function as a 'windbreak', thus reducing the average wind force exerted on any given shoot.

We propose that a large meristem/bud bank provides a particularly important fitness advantage for relatively small species. Accordingly, we tested and found support for the prediction that species with smaller body size generally have higher leafing intensity (Fig. 4). Hence, smaller species generally make both smaller leaves (Fig. 1c) and fewer leaves (Fig. 1b), but importantly, they produce more leaves (and hence more meristems/buds) per unit plant body size (Fig. 4). This is a novel finding for herbaceous species. Yang *et al.* (2008) reported a parallel relationship for woody plants, where species with smaller individual (annually produced) twig mass had both smaller individual leaves and greater leafing intensity on these annual twigs. The latter can be predicted based on biomechanical constraints associated with large leaf size (Yang *et al.* 2008); i.e. a species that benefits from producing a relatively large leaf must also produce a relatively large twig in order to support it—Corner's rule (Corner 1949). A similar interpretation may apply to our herbaceous species; in other words, a selection premium may be linked to fitness benefits (e.g. through physiological

optimization) associated with large leaf size, which, in turn, requires a relatively large plant body size in order to physically support large leaves. Traditional theory also suggests that large plant size is essential for success in competition for light, and this is commonly facilitated by strong apical dominance, which need not necessarily require a large bud bank.

However, relatively few plant species are capable of growing to large/tall sizes; the vast majority of species (including resident species in crowded vegetation) are relatively small (Aarssen *et al.* 2006)—and moreover, even within a single population, the vast majority of resident plants (including reproductive ones) are forced to be suppressed weaklings (Chambers and Aarssen 2009). It is in this context where we speculate that the larger bud bank of smaller species may confer important fitness benefits. Specifically, we propose that the higher capacity for meristem production per unit plant size (i.e. the larger bud bank conferred by higher leafing intensity) in smaller herbaceous species may play an important role in promoting greater 'reproductive economy' in smaller species (Aarssen 2008)—i.e. their ability to leave at least some descendants in crowded vegetation despite their size disadvantage and/or in disturbed habitats despite limited time available for growth (e.g. in opportunistic ruderal species).

Accordingly, we suggest two main predictions for testing in future research: First, a larger meristem bank per unit plant size provides greater probability that, even when severely suppressed in size (e.g. because of competition with larger species or larger plants of the same species), a small species will still possess at least some axillary meristems that can be deployed for reproduction, thus maximizing 'fecundity allocation' for smaller species—i.e. a capacity to produce more offspring per unit plant size per unit time (Aarssen 2005, 2008). This could account for the results of recent research showing that, under the most crowded conditions in herbaceous vegetation, most of the total offspring production within a population that is available to form the next generation routinely comes from the collection of resident plants that belong to relatively small size classes (Chambers and Aarssen 2009).

Second, we also predict that a larger meristem/bud bank per unit plant size may allow greater architectural plasticity for smaller species in responding to variation in light availability, thus allowing optimal shoot and leaf placement for maximizing light interception when this is affected by competition from larger neighbouring species. If smaller species suffer disproportionately due to shading within multi-species vegetation, a relatively large meristem/bud bank may provide greater potential to produce shoots (and hence flowers) opportunistically in order to take advantage of light patches available through the canopy of larger neighbouring species, especially if these smaller species are also relatively shade tolerant (Kleiman and Aarssen 2007). These suggestions all represent testable predictions for future research.

Note that because most species have relatively small leaves (i.e. with a right-skewed leaf size distribution), this does not

mean that most species will also have relatively high leafing intensity (with a left-skewed leafing intensity distribution). Indeed both traits have a right-skewed frequency distribution (Fig. 5) (see also Milla 2009). This seems paradoxical given that the two traits have a highly significant negative relationship (Fig. 2). The two traits do indeed co-vary negatively, but in a 'proportional' fashion, where changes involve orders of magnitude—i.e. both traits have a log-normal distribution and so both traits (in Fig. 2) necessarily cluster relatively close to the origin on untransformed axes (not shown). Accordingly, it is mathematically inevitable that when a relatively 'small' quantity (e.g. of leaf mass or leafing intensity) is decreased (or increased) by an order of magnitude ($\times 10$), the absolute numerical difference will be much smaller than the absolute numerical difference that results when a relatively 'large' quantity (of leafing intensity or leaf mass, respectively) is increased (or decreased, respectively) by the same order of magnitude (i.e. $\times 10$).

Nevertheless, a critical question remains: if high leafing intensity confers important general fitness advantages, why then do most species not have relatively high leafing intensity (Fig. 5b)? We offer the following speculation: According to fossil evidence, the first leaves produced by early vascular plants were extremely small, beginning as outgrowths of the epidermis with eventual vascularization (Scagel *et al.* 1965). The conventional view is that leaf production was favoured by natural selection because of optimality benefits in terms of light interception and gas exchange associated with an increased ratio of photosynthetic surface area to tissue volume (Scagel *et al.* 1965). However, at some unknown point in this evolution, the leaf became intricately and predictably associated with a meristem—or vice versa—and so in the contemporary angiosperm flora, leaf production virtually always involves corresponding production of a bud bank of axillary meristems (Bell 1991). Consequently, as leaf size increased from zero over evolutionary time, eventually the plant-level gain from ever-larger leaves (associated with photosynthetic surface area/gas exchange benefits) would have been offset by plant-level limitation on bud bank size, resulting from concomitant reduction in leafing intensity. At the same time, natural selection could not be expected to maximize leafing intensity since extremely high leafing intensity (requiring extremely tiny leaves) would incur costly compromises in terms of photosynthetic surface area/gas exchange per unit plant body size.

The leafing intensity premium hypothesis predicts that this fundamental trade-off operating over evolutionary time has settled on a relatively small optimum leaf size for the vast majority of extant species because of the substantial leafing intensity (and hence bud bank size, with its attendant fitness advantages) that can be realized only when leaf size is relatively small. Importantly, however, because extremely few species would be expected to have extremely tiny leaves, it necessarily follows that very few species will have extremely high leafing intensity (because the latter is possible only with

extremely tiny leaves)—thus accounting for the right-skewed species frequency distribution for leafing intensity (Fig. 5b). Accordingly, the fact that most species do not have relatively high leafing intensity is just a consequence of the way in which leaf size and leafing intensity are scaled (i.e. proportionately) and does not invalidate the principal assumption of the leafing intensity premium hypothesis—that between-species leaf size distribution is, to a large extent, accounted for in terms of the trade-off resulting from natural selection associated with fitness benefits affected by leafing intensity/bud bank size (Kleiman and Aarssen 2007).

In conclusion, we propose that the leaf size/number trade-off and other fundamental trade-offs (e.g. Shipley *et al.* 2006) are likely to provide important new predictor variables for understanding between-species patterns of variation in leaf traits (Wright *et al.* 2004). Most interpretations of these relationships have involved the economics of the physical and biochemical properties of individual leaves (Whitfield 2006). Leafing intensity, however, is a whole-plant morphological trait that provides remarkable explanatory power in accounting for a fundamental pattern of leaf trait variation—it explains the vast majority ($\sim 90\%$ or more) of between-species leaf size variation in both woody species (Kleiman and Aarssen 2007, Ogawa 2008, Yang *et al.* 2008) and herbaceous angiosperms (this study). Leafing intensity represents the plant's level of investment in a bank of meristems that can be deployed for potentially flexible strategies of allocation to growth versus reproduction. Our data suggest that high leafing intensity is likely to be particularly important in defining the life history strategies of relatively small species, and future studies are required to quantify the fitness components associated with high leafing intensity.

FUNDING

Natural Sciences and Engineering Research Council of Canada Research Grant (14552 to L. W. A.); Undergraduate Student Research Award to T.W.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

ACKNOWLEDGEMENTS

Assistance with field work was provided by Laura Todd, Clare Tries, Catherine Gieysztor, Alexandra Howard, Amanda Mathys and Nicole Willie. Assistance in locating study populations was provided by Susan Weaver at the Agriculture and Agri-Food Canada Research Station (Harrow, Ontario, Canada) and by David Galbraith, Jim Pringle, Natalie Ivanicky, Sarah Baldwin and Kristi MacMillan at the Royal Botanical Gardens (Hamilton, Ontario, Canada). P. Grogan, R. Milla and B. Shipley provided helpful comments on earlier versions of the manuscript.

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Appendix

The study species; nomenclature follows Gleason and Cronquist (1991) and common names follow Newcomb (1977)

Family	Species
Amaranthaceae	<i>Amaranthus retroflexus</i> L. (redroot pigweed)
Apiaceae	<i>Cicuta maculata</i> L. (water hemlock)
Apiaceae	<i>Daucus carota</i> L. (Queen Anne's lace)
Apocynaceae	<i>Apocynum cannabinum</i> L. (Indian hemp)
Asclepiadaceae	<i>Asclepias incarnata</i> L. (swamp milkweed)
Asclepiadaceae	<i>Asclepias syriaca</i> L. (common milkweed)
Asteraceae	<i>Achillea millefolium</i> L. (yarrow)
Asteraceae	<i>Ambrosia artemisiifolia</i> L. (common ragweed)
Asteraceae	<i>A. trifida</i> L. (giant ragweed)
Asteraceae	<i>Anaphalis margaritacea</i> (L.) Benth. & Hook. (pearly everlasting)
Asteraceae	<i>Antennaria parlinii</i> (Fern.) Cronq. (smooth pussytoes)
Asteraceae	<i>Arctium minus</i> Schk. (burdock)
Asteraceae	<i>Aster laevis</i> L. (smooth aster)
Asteraceae	<i>Aster novae-angliae</i> L. (New-England aster)
Asteraceae	<i>Aster ericoides</i> L. (many-flowered aster)
Asteraceae	<i>Aster umbellatus</i> Miller. (flat-topped aster)
Asteraceae	<i>Bidens frondosa</i> L. (beggartick)
Asteraceae	<i>Centaurea nigra</i> L. (black knapweed)
Asteraceae	<i>Chrysanthemum leucanthemum</i> L. (oxeye daisy)
Asteraceae	<i>Cichorium intybus</i> L. (chicory)
Asteraceae	<i>Conyza canadensis</i> (L.) Cronq. (prostrate knotweed)
Asteraceae	<i>Erigeron annuus</i> (L.) Pers. (daisy fleabane)
Asteraceae	<i>E. philadelphicus</i> L. (common fleabane)
Asteraceae	<i>Eupatorium maculatum</i> L. (spotted Joe Pye weed)
Asteraceae	<i>E. rugosum</i> Houttuyn. (snakeroot)
Asteraceae	<i>Helianthus giganteus</i> L. (tall sunflower)
Asteraceae	<i>Helianthus microcephalus</i> L. (small wood sunflower)
Asteraceae	<i>H. aurantiacum</i> L. (orange hawkweed)
Asteraceae	<i>Hieracium lachenalii</i> C. Gmelin. (common hawkweed)
Asteraceae	<i>Inula helenium</i> L. (elecampane)
Asteraceae	<i>Lactuca biennis</i> (Moench) Fern. (tall blue lettuce)
Asteraceae	<i>L. serriola</i> L. (prickly lettuce)
Asteraceae	<i>Lapsana communis</i> L. (nipplewort)

Appendix Table (Continued)

Family	Species
Asteraceae	<i>Matricaria matricarioides</i> (Less.) Porter. (pineapple weed)
Asteraceae	<i>Rudbeckia laciniata</i> L. (tall coneflower)
Asteraceae	<i>R. hirta</i> L. var. <i>pulcherrima</i> Farw. (black-eyed Susan)
Asteraceae	<i>Silphium perfoliatum</i> L. (cup plant)
Asteraceae	<i>Solidago caesia</i> L. (blue goldenrod)
Asteraceae	<i>S. canadensis</i> L. (Canada goldenrod)
Asteraceae	<i>S. flexicaulis</i> L. (zigzag goldenrod)
Asteraceae	<i>Euthamia graminifolia</i> (L.) Nutt. (flat-topped goldenrod)
Asteraceae	<i>Sonchus oleraceus</i> L. (common sow thistle)
Asteraceae	<i>Tanacetum vulgare</i> L. (tansy)
Asteraceae	<i>Tragopogon pratensis</i> L. (yellow goatsbeard)
Asteraceae	<i>Vernonia noveboracensis</i> (L.) Michx. (New York ironweed)
Asteraceae	<i>Xanthium strumarium</i> L. var. <i>glabratum</i> (DC.) Cronq. (common cocklebur)
Balsaminaceae	<i>Impatiens capensis</i> Meerb. (spotted jewelweed)
Balsaminaceae	<i>I. glandulifera</i> Royle. (Himalayan balsam)
Balsaminaceae	<i>I. pallida</i> Nutt. (pale jewelweed)
Boraginaceae	<i>Echium vulgare</i> L. (viper's bugloss/blueweed)
Boraginaceae	<i>Myosotis laxa</i> Lehm. (forget-me-nots)
Brassicaceae	<i>Alliaria petiolata</i> (Bieb.) Cavara & Grande. (garlic mustard)
Brassicaceae	<i>Capsella bursa-pastoris</i> (L.) Medikus. (shepherd's purse)
Brassicaceae	<i>Erysimum cheiranthoides</i> L. (wormseed mustard)
Brassicaceae	<i>Hesperis matronalis</i> L. (dame's rocket)
Brassicaceae	<i>Lepidium campestre</i> (L.) R. Br. (field peppergrass)
Brassicaceae	<i>Rorippa palustris</i> (L.) Besser. (marsh cress)
Brassicaceae	<i>Sisymbrium officinale</i> (L.) Scop. (hedge mustard)
Campanulaceae	<i>Campanula rapunculoides</i> L. (creeping bellflower)
Campanulaceae	<i>C. rotundifolia</i> L. (harebell)
Caryophyllaceae	<i>Arenaria stricta</i> Michx. (rock sandwort)
Caryophyllaceae	<i>Cerastium vulgatum</i> L. (mouse-ear chickweed)
Caryophyllaceae	<i>Dianthus armeria</i> L. (Deptford pink)
Caryophyllaceae	<i>Silene latifolia</i> Poiret. (white campion)
Caryophyllaceae	<i>Saponaria officinalis</i> L. (bouncing bet)

Appendix Table (Continued)

Family	Species
Caryophyllaceae	<i>Silene vulgaris</i> (Moench) Garcke. (bladder campion)
Caryophyllaceae	<i>Stellaria graminea</i> L. (lesser stitchwort)
Caryophyllaceae	<i>S.media</i> (L.) Villars. (common chickweed)
Chenopodiaceae	<i>Chenopodium album</i> L. (lamb's quarters)
Dipsacaceae	<i>Dipsacus sylvestris</i> Hudson. (teasel)
Euphorbiaceae	<i>Acalypha rhomboidea</i> Raf. (three-seeded mercury)
Euphorbiaceae	<i>Euphorbia cyparissias</i> L. (Cypress spruce)
Euphorbiaceae	<i>E.polygonifolia</i> L. (seaside spurge)
Fabaceae	<i>Desmodium canadense</i> (L.) DC. (showy tick trefoil)
Fabaceae	<i>D.glutinosa</i> (Muhl.) A. Wood. (pointed-leaved tick trefoil)
Fabaceae	<i>Lotus corniculatus</i> L. (birdsfoot trefoil)
Fabaceae	<i>Medicago lupulina</i> L. (black medick)
Fabaceae	<i>Melilotus alba</i> Medikus. (white sweet clover)
Fabaceae	<i>M.officinalis</i> (L.) Pallas. (sweet yellow clover)
Fabaceae	<i>Trifolium aureum</i> Pollich. (yellow clover)
Fabaceae	<i>T.pratense</i> L. (red clover)
Geraniaceae	<i>Geranium robertianum</i> L. (herb Robert)
Clusiaceae	<i>Hypericum perforatum</i> L. (St. John's wort)
Lamiaceae	<i>Leonurus cardiaca</i> L. (motherwort)
Lamiaceae	<i>Lycopus uniflorus</i> Michx. (northern bugleweed)
Lamiaceae	<i>Monarda fistulosa</i> L. (wild bergamot)
Lamiaceae	<i>Nepeta cataria</i> L. (catnip)
Lamiaceae	<i>Prunella vulgaris</i> L. (self-heal)
Lamiaceae	<i>Satureja vulgaris</i> (L.) Fritsch. (wild basil)
Lamiaceae	<i>Scutellaria parvula</i> Michx. (marsh skullcap)
Liliaceae	<i>Smilacina racemosa</i> (L.) Desf. (false Solomon's seal)
Liliaceae	<i>S.stellata</i> (L.) Desf. (starry false Solomon's seal)
Malvaceae	<i>Abutilon theophrasti</i> Medikus. (velvet leaf)
Malvaceae	<i>Hibiscus trionum</i> L. (flower of an hour)
Malvaceae	<i>Malva sylvestris</i> L. (high mallow)
Onagraceae	<i>Circaea lutetiana</i> var. <i>canadensis</i> L. (enchanter's nightshade)

Appendix Table (Continued)

Family	Species
Onagraceae	<i>Oenothera biennis</i> L. (common evening primrose)
Onagraceae	<i>O.perennis</i> L. (small sundrop)
Oxalidaceae	<i>Oxalis stricta</i> L. (yellow wood sorrel)
Polygalaceae	<i>Polygala senega</i> L. (seneca snakeroot)
Polygonaceae	<i>Polygonum hydropiper</i> L. (marshpepper knotweed)
Polygonaceae	<i>P.lapathifolium</i> L. (smartweed)
Polygonaceae	<i>P.pensylvanicum</i> L. (Pennsylvania smartweed)
Polygonaceae	<i>P.persicaria</i> L. (lady's thumb)
Polygonaceae	<i>P.virginianum</i> L. (jumpseed)
Polygonaceae	<i>Rumex acetosella</i> L. (sheep sorrel)
Polygonaceae	<i>Rumex crispus</i> L. (curled dock)
Portulacaceae	<i>Portulaca oleracea</i> L. (common purslane)
Primulaceae	<i>Lysimachia quadrifolia</i> Sims. (whorled loosestrife)
Primulaceae	<i>L.terrestris</i> (L.) BSP. (swamp candle)
Ranunculaceae	<i>Anemone virginiana</i> L. (large white-flowered anemone)
Ranunculaceae	<i>Aquilegia canadensis</i> L. (wild columbine)
Ranunculaceae	<i>Ranunculus acris</i> L. (tall buttercup)
Rosaceae	<i>Agrimonia gryposepala</i> Wallr. (agrimony)
Rosaceae	<i>Potentilla argentea</i> L. (silvery cinquefoil)
Rosaceae	<i>Potentilla recta</i> L. (sulphur cinquefoil)
Scrophulariaceae	<i>Linaria vulgaris</i> Miller. (butter-and-eggs)
Scrophulariaceae	<i>Pedicularis canadensis</i> L. (wood betony)
Scrophulariaceae	<i>Penstemon hirsutus</i> (L.) Willd. (hairy beardtongue)
Scrophulariaceae	<i>Verbascum thapsus</i> L. (common mullein)
Scrophulariaceae	<i>Veronicastrum virginicum</i> Fabr. (Culver's root)
Scrophulariaceae	<i>Veronica arvensis</i> L. (corn speedwell)
Scrophulariaceae	<i>V.serpyllifolia</i> L. (thyme-leaved speedwell)
Solanaceae	<i>Solanum ptychanthum</i> Dunal. (eastern dark nightshade)
Solanaceae	<i>S.sarrachoides</i> Sendtner. (hairy nightshade)
Urticaceae	<i>Pilea pumila</i> (L.) A. Gray. (clearweed)
Verbenaceae	<i>Verbena hastata</i> L. (blue vervain)