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Neighbour effects on tree architecture: functional trade-offs balancing crown competitiveness with wind resistance

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Summary

1. The architecture of trees is the result of constrained, morphologically plastic growth – constrained by an underlying architectural model embedded in their genome, the structure of which can be significantly altered during growth to match the changing environmental conditions to which the tree is exposed. Here, we examined the hypothesis that crowding from neighbours should cause trees to optimize traits for light competition at the expense of wind resistance, with the reverse being true for trees lacking neighbours. Previous studies have examined the influence of light competition or wind resistance on shaping tree architecture, but few, if any, have simultaneously addressed trade-offs for optimizing these traits in response to crowding from neighbouring trees in forests, as compared to open-grown conditions.

2. We studied the response of tree- and branch-level architectural traits of temperate, broadleaved, deciduous tree species of differing shade tolerance and wood strength from multiple locations across the north-eastern United States. Trees ranged in size (4–83 cm diameter at 1·3 m) and crowding conditions (open- and forest-grown) and occupied different canopy positions. The open-grown trees represented a null condition, where the lack of neighbouring trees to shape architectural traits could be contrasted with the influence of different levels of crowding in forests.

3. Our results show strong evidence for a tree neighbourhood-induced convergence of architectural traits across species and conditions, even when trees are growing in urban rather than natural forest conditions. After accounting for crowding, the effects of species and sample location contributed very little to explaining variation in architectural traits. One exception was crown dimensions, for which species-specific differences explained about 15% of the residual variation.

4. Under open-grown conditions, alleviation of light competition caused trees to develop relatively large crowns and branches and a squat growth form suitable to resist greater wind exposure. By contrast, increasing shading from neighbouring trees caused forest-grown trees to become increasingly more spindly in the main stem, with slender branches sparsely distributed over a disproportionately large crown volume – presumably to maximize light capture. Although the latter is an intrinsically less wind-stable form, it can be adopted to increase light capture because neighbouring trees reduce exposure to the wind, which should greatly reduce the likelihood of stem breakage or uprooting under critical wind pressures.

Key-words: allometry, biomechanics, branches, morphological plasticity, open-grown trees

Introduction

Exploring underlying mechanisms that control variation in tree architecture has long been a focal point for studying tree form and function (e.g. McMahon & Kronauer 1976; Halle 1978; King 1996; Archibald & Bond 2003; Iida *et al.* 2011). Tree architecture is the relative arrangement of different parts of the tree in a hierarchy of growth units (Barthélémy & Caraglio 2007). It can be described by measurable architectural traits, such as tree

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height, crown width, height of first branch and allometric ratios between them, e.g. the height-to-stem diameter ratio (Archibald & Bond 2003; Iida *et al.* 2011). Trees of different species have evolved to build a diverse array of architectures to enable survival and reproduction across large portions of the globe, under a variety of ecological conditions (Lines *et al.* 2012; Fournier *et al.* 2013). Tree architecture can provide fundamental insights critical for understanding life-history traits of tree species and the dynamics that give rise to various forest structures and functions (Valladares & Niinemets 2008). A better understanding of tree architecture can also aid ecologically driven approaches to manage trees (e.g. pruning to affect wind resistance, Pavlis *et al.* 2008) and forest ecosystems (e.g. optimizing canopy packing and biodiversity, Jucker, Bouriaud & Coomes 2015).

Studies of tree architecture show that it is partially determined by genetic constraints (e.g. Dardick *et al.* 2013), but is also plastic and varies ontogenetically (Niklas 1995; Poorter, Bongers & Bongers 2006; Iida *et al.* 2011). Trees must be sufficiently plastic to adapt to local ecological conditions, such that intraspecific variation can be quite large within the broad global niche of a species (Lines *et al.* 2012). For example, the realized crown architecture of any tree at any point in its lifetime is the result of accumulated stem and branch growth and losses (McMahon & Kronauer 1976; Mäkelä & Valentine 2006). Fundamentally, trees must build a scaffolding of stems and branches that positions their leaves to capture sufficient light energy – often in competition with other trees or plants – to maintain a positive carbon balance under light stress (Miyashita & Tateno 2014). Ultimately, the net carbon balance of a tree must be significantly positive in key components (leaves, branches and roots), and the whole tree, to survive and reproduce (Givnish 1988). However, optimizing tree architecture for light energy capture must be balanced against the need to respond to other factors that affect fitness. Perhaps the most important is mechanical stability in the face of environmental disturbances, like ice storms (Bragg, Shelton & Zeide 2003) and wind (Gardiner, Berry & Moulia 2016), which can damage parts of trees or induce whole-tree failure.

Studies of the mechanical stability of trees have historically focused primarily on height–diameter relationships as key functional traits, based on assumptions derived from dynamic beam theory (Niklas 1992). However, branch architecture also influences the magnitude of both static (e.g. snow or ice and self-weight) and dynamic (wind) loads, as well as the tree's ability to bear such loads. Although studies have explored the mechanics of branch breakage (Kane 2007; Evans *et al.* 2008; Kane *et al.* 2008a; Miesbauer *et al.* 2014), very little work has examined branch morphology of open-grown trees as it relates to the likelihood of trunk failure. Similarly, few studies (e.g. Sterck, Van Gelder & Poorter 2006) have examined the contribution of mechanical constraints on the branch traits of forest-grown trees as determinants of fitness or life-history variation.

Branch architecture can influence sway frequency (James, Haritos & Ades 2006; Sellier, Fourcaud & Lac 2006; Sellier & Fourcaud 2009; Kane *et al.* 2014), damping ratio (Sellier, Fourcaud & Lac 2006; Sellier & Fourcaud 2009; Kane *et al.* 2014) and dynamic amplification factor (the ratio of dynamic-to-static displacements of an excited structure) (Ciftci *et al.* 2013). Drag (Mayhead 1973; Rudnicki, Mitchell & Novak 2004; Vollsinger *et al.* 2005) and drag-induced bending moments (Kane & Smiley 2006; Kane *et al.* 2008b) are positively correlated with tree size, as is the critical static-bending moment to break stems or uproot trees (Nicoll *et al.* 2006; Peltola 2006; Peterson & Claassen 2013). For conifers of excurrent form, the fundamental sway frequency is proportional to the ratio of DBH to the square of tree height (Moore & Maguire 2004). But this is not true of open-grown trees of decurrent form (Baker 1997; Kane & James 2011; Kane *et al.* 2014), presumably because of the greater importance of branches on sway motion (Ciftci *et al.* 2013; James 2014).

We expect that crowding from neighbouring trees in forests, or the lack of neighbours for open-grown trees, should have a major influence on traits affecting both wind stability and light capture. However, few, if any, studies have simultaneously addressed trade-offs for wind stability and light capture, including both open-grown and forest-grown trees. Most studies of forest-grown tree architecture focus on saplings and small trees because of the desire to test hypotheses regarding shade tolerance and morphological plasticity on tree performance under shaded conditions (e.g. Coomes & Grubb 1998; Sterck, Van Gelder & Poorter 2006). Measuring the architecture of larger trees is also very time consuming and difficult without destructive sampling (MacFarlane *et al.* 2014). Of the many studies of allometry and architecture of trees and branches, very few have considered open-grown trees (Dahle & Grabosky 2010), especially larger individuals. Open-grown trees are primarily free of shading, but experience greater wind exposure.

Here, we analyse data from studies of open- and forest-grown trees in different canopy positions, covering multiple species and a wide range of tree sizes. This novel dataset provided an opportunity to explore functional variation in traits that define tree architecture as they respond to both competitive stress and wind exposure. As part of this study, we specifically examined the importance of branch- as well as tree-level traits for understanding tree architecture. We hypothesize that, along a gradient from heavy competition to open-grown conditions, architectural traits that promote wind stability will become increasingly dominant relative to traits that promote light capture, and vice versa; and that different species will converge on similar trait suites as a result of plasticity in tree form.

Materials and methods

FOREST-GROWN TREE STUDY

Forest-grown trees were destructively sampled from six forested locations in the southern Lower Peninsula of Michigan (Fig. 1), which has an annual average temperature of 8·9 °C, 750–900 mm of rainfall per year and a growing season ranging from 140 to 160 days (Dickmann 2004). Three tree species were included in this study to match data available for open-grown trees (see below): red maple (*Acer rubrum* L.), northern red oak (*Quercus rubra* L.) and American basswood (*Tilia americana* L.). Only live, healthy trees without obvious crown damage were selected for this analysis. For each species, individuals were selected to represent a wide range of tree sizes, as indicated by stem diameters (*D*, cm) at 1·3 m above-ground and canopy positions: Each tree was assigned to a canopy class (CC) to capture the effect of crowding and light competition from its neighbours. The CC were as follows: overtopped, intermediate, co-dominant and dominant. Before felling for destructive sampling, we measured *D*, total height (*H*, m) and average crown width (*W*, m) – the average of maximum crown width and crown width measured 90° from maximum – of each tree. The *D* of all neighbouring trees within a 7·3-m radius of the sample tree was recorded to assess crowding around the focal tree. The radius corresponds to the size of a standard Forest Inventory and Analysis plot of the United States Department of Agriculture (Bechtold & Patterson 2005).

After standing measurements were completed, trees were cut at a stump height of 15 cm above-ground level. Taking care not to damage crowns, trees were felled into a clearing where debris from other trees had been removed. All branches ≥2·5 cm, live or dead, were measured for basal diameter and branch length, and the position along the stem (i.e. height above-ground) was recorded. The length of the crown (*L*, m) was computed as the distance from the top of the tree to the lowest live branch, excluding any very small branches (<2·5 cm) that were discontinuous from the crown of the tree (e.g. epicormics branches).

We followed procedures described by MacFarlane (2015) to obtain the dry mass of tree components from fresh (green) masses obtained in the field. After measuring, each branch was cut from the stem and weighed green. A disk was removed from the mid-section of each branch, to obtain the dry weight to green weight ratio for the branch. After branches were removed, the main stems of trees were cut into sections, which were weighed green using a tractor-mounted crane scale, or an electronic balance for smaller pieces. Disks c. 5-cm thick were cut from the top of each cut stem section and weighed green with attached bark. Dry masses were computed for all tree parts using green weight–dry weight ratios computed from samples removed from each part and multiplied by its green weight. We followed procedures outlined by Williamson & Wiemann (2010) to measure the specific gravity of disks removed from the stem of each tree and then computed the average specific gravity (*g*) for the whole stem based on a weighted average of all the disks in the tree's stem. We also measured any areas of decayed wood in each main stem disk and then determined the 'soundness' of each disk as the ratio of sound wood to total cross-sectional area of each disk. A soundness index for the stem of each tree was the weighted average of the soundness of all disks in the tree's stem.

Fig. 1. Study area including forested and urban locations in the north-eastern United States.

URBAN TREE STUDY

Healthy, open-grown individuals of three species growing on the campus of the University of Massachusetts (U. Mass) in Amherst, MA, USA (average annual temperature and rainfall of 8·8 °C and 1168 mm, respectively) were selected at random, from strata defined by *D*. Individuals were selected from the first, third, fifth, seventh and ninth deciles of the campus-wide range of *D* for the species. Five individuals of *A. rubrum* and *Q. rubra* were available to compare to forest-grown trees of those species and five individuals of littleleaf linden (*Tilia cordata* Mill.) were available to compare to the forest-grown *T. americana*; these species are very similar in many of their traits, except for the size of the leaves of *T. cordata* (De Jaegere, Hein & Claessens 2016), and we did not incorporate leaves into comparisons of forest- and open-grown trees. We selected only structurally sound individuals that had not been recently pruned or otherwise lost branches. Although we did not know the pruning history of individual trees, the U. Mass engages in very little proactive pruning, which reduced the odds of past pruning events influencing architectural traits. We also did not know the seed origin of the trees, but they were sampled from a variety of locations on campus, reducing the odds that individuals were from the same seed source.

We measured *D*, *H* and *L* of open-grown trees as described above for the forest-grown trees. Trees were not sampled destructively, as in the forest study, but each tree was climbed to measure branch attributes. All live primary branches (attached at their base to the main stem) ≥2 cm in diameter were measured for basal diameter and length, and the height above-ground to the attachment point was recorded. Detailed measurements of branch angle and azimuth from the tree centre were also taken and used to compute *W* equivalent to the forest study.

Because the sample sizes for urban, open-grown trees were smaller than that of the forest study and the urban trees were only drawn from one location (See Fig. 1), additional urban, open-grown trees of the four species of interest were drawn from a large database of urban tree measurements from around the United States (McPherson, van Doorn & Peper 2016). We included only trees from the two climatologically consistent regions within the contiguous United States [derived from climate analyses (Karl & Koss 1984)] from the forest and U. Mass studies. For the forest study, the climatologically consistent region was the East North Central region: average annual temperature and rainfall of 9·7 °C and 722 mm, respectively. For the urban study, it was the Northeast region: average annual temperature and rainfall of 8·8 °C and 983 mm, respectively. The database included measurements of *D*, *H*, *L* and *W* for each tree. We excluded trees from the McPherson, van Doorn & Peper (2016) data growing over parking lots or where the crowns were conflicting with utility lines, to minimize the confounding effect of anthropogenic influences on the architecture of urban open-grown trees, when comparing them to forest-grown trees. We also excluded urban trees growing within 8 m of a structure to assure that no structures were within the plot radius (7·3 m) used for measuring neighbours of forest-grown trees. Finally, we selected only open-grown trees of the same size range as the forest-grown trees (from 4 to 85 cm stem diameter at 1·3 m). Our search added an additional 116 open-grown trees from two US cities (New York and Minneapolis), including individuals of all four species: *A. rubrum*, *Q. rubra*, *T. cordata* and *T. americana* (Table 1, Fig. 1).

METHODOLOGICAL APPROACH

Our objective was to understand the effect of crowding from neighbouring trees on tree architecture. Specifically, we examined the hypothesis that crowding from neighbours should cause trees to optimize traits for light competition at the expense of wind resistance, with the reverse being true for trees lacking neighbours. The open-grown trees in our study represented a null condition, where the lack of neighbouring trees shaping architecture could be contrasted with the influence of different levels of crowding in forests.

ASSESSING CROWDING AND SHADING

We examined crowding effects on focal trees in two ways: (i) using the assigned CC to reflect crown crowding and shading relative to neighbours (e.g. overtopped, open-grown, etc.) and (ii) using a quantitative variable to indicate the general crowding experienced by the tree. Cole & Lorimer (1994) demonstrated that trees compete primarily with trees immediately surrounding them, so we employed a basic crowding index (CI) reported by them, derived from the relative size of neighbouring trees:

$$\mathrm{CI} = \sum_{i=1}^{n} \frac{D_i}{D} \qquad \text{eqn 1}$$

where CI is the sum of the relative size (D_i/D) of (n) trees surrounding the focal tree (within 7·3 m). This formulation specifies that a small tree surrounded by multiple larger trees is highly crowded, which implies greater competition for light and reduced wind exposure (Gardiner, Berry & Moulia 2016). Thus, we expected CI to be negatively correlated with wind resistance and positively correlated with architectural traits that promote light capture. All the open-grown trees were assigned a CI of 0.

ARCHITECTURAL TRAITS RELATED TO CROWN COMPETITIVENESS

In competition with other trees, the principal ways trees increase their light harvesting capacity is to increase tree height, crown length, crown width or all three. As stem growth near the base indicates overall tree growth and successful light capture (King *et al.* 2005), the ratio of height growth or crown expansion to stem thickening can be used as an expression of a tree's need to harvest more light. So, using the full dataset, we examined the effect of crowding on four allometric relationships: stem slenderness, which is the ratio of height to diameter ($H : D$); relative crown length, the ratio of crown length to diameter ($L : D$), relative crown width, the ratio of crown width to diameter ($W : D$); and crown slenderness, the ratio of crown length to width ($L : W$). The effect of crowding on the first three allometric relationships should reflect the relative allocation of growth resources between light capture and cumulative secondary growth of the main stem. The fourth ($L : W$) captures narrowing vs. flattening of the crown. We expected that trees would become more slender, with shorter and narrower crowns, when crowded by neighbours, and shorter and fatter, with more flattened crowns, when growing without them.

ARCHITECTURAL TRAITS RELATED TO WIND RESISTANCE

Recent studies describe how tree architecture can affect the likelihood of wind damage (Peltola 2006; Fournier *et al.* 2013; Gardiner, Berry & Moulia 2016), including branch and stem breakage as well as uprooting. We did not have sufficient information on rooting conditions to consider the likelihood of uprooting, but we did have sufficient data to model stem breakage. Studies suggest that stem breakage can be modelled from basic tree attributes (Gardiner, Peltola & Kellomaki 2000; Fournier *et al.* 2013; Gardiner, Berry & Moulia 2016); as stem diameter increases, stem breakage is less likely as its load-bearing capacity increases as the cube of diameter. However, a taller tree with a longer and wider crown experiences greater drag and drag-induced bending. Based

Table 1. Basic attributes and sample sizes for study trees

Species	# Trees (# locations)		D (cm) [SD, min, max]	Modulus of rupture* (MPa) [SD, min, max]
	Forest	Open		
Acer rubrum	22 (2)	36 (3)	29·8 [19·9; 4·3, 77·0]	53·0 [2·8; 46·1, 67·3]
Quercus rubra	15 (3)	38 (3)	33·5 [23·1; 4·8, 83·3]	58·6 [5·0; 50·4, 82·9]
Tilia americana	15 (2)	21 (1)	34·9 [25·4; 5·3, 80·5]	34·1 [1·8; 28·3, 38·3]
Tilia cordata	0 (0)	35 (3)	29·9 [20·1; 4·8, 81·3]	34·0 [0·0; 34·0, 34·0]
Total	52 (6)	130 (3)	31·9 [22·0; 4·3, 83·3]	47·2 [11·3; 28·3, 82·9]

*For forest-grown trees, modulus of rupture was computed from measurements of specific gravity; for open-grown trees, values are from Kretschmann (2010).

on this, we specified wind resistance to stem breakage (ω, Nm^{-2}) as:

$$\omega = \frac{f\theta D^3}{AH} \qquad \text{eqn 2}$$

where A is the surface area of the crown = $(\pi/6)((W/2)/L^2)[((W/2)^2 + 4L^2)^{3/2} - (W/2)^3]$, assuming a generalized parabolic shape (Baral *et al.* 2017). θ is the modulus of rupture (MPa) of green wood in the stem at 1·3 m, f is a dimensionless coefficient (bounded between 0 and 1) that captures any reduction in wood strength, due to decay, for example

For the forest-grown trees θ was calculated from the measured specific gravity (g): $\theta = 121\ g^{1\cdot25}$ (Bragg, Shelton & Zeide 2003) of the tree. The open-grown trees were assigned a species-specific value of θ derived from the literature (Kretschmann 2010). The trees we selected from both the forest and urban studies were healthy trees without obvious signs of wood decay, so we assumed $f = 1$ for simplicity. Supporting this assumption, the mean soundness index (see above) of forest-grown tree stems was 0·996.

BRANCH ARCHITECTURE

For trees with detailed branch measurements, we computed branch architectural traits that should be important for both light capture and wind resistance. Studies have suggested that branch architecture should change under different levels of light stress (Valladares & Niinemets 2008) and positions the leaves in the crown, which fundamentally defines light capture potential (Pearcy, Muraoka & Valladares 2005). Branches also play a complex role in how trees respond to wind loads (Ciftci *et al.* 2013). Branches oscillate independently from the main stem, dissipating wind energy at the branch level rather than transferring it to the main stem, which reduces the likelihood of stem breakage or uprooting (James, Haritos & Ades 2006).

We expected crowding to change a tree's relative allocation of mass between branches and the main stem, which would affect both light capture and wind resistance. For the forest-grown trees, the dry mass of both the branches and main stem was known, but for the urban trees it was not. However, analyses of forest-grown trees showed that the mass of any branch of a given species was proportional to a proxy volume computed from the cross-sectional area of the branch at the base times its length (d^2l) (see Fig. S1a, Supporting Information). Similarly, the mass of the main stem was generally proportional to the cross-sectional area of the stem at 1·3 m times the total height of the tree (D^2H) (Fig. S1b). So, the ratio of branch to stem mass was estimated for both urban and forest-grown trees as:

$$\frac{M_\mathrm{b}}{M_\mathrm{s}} \propto \frac{\sum_{i=1}^{z} d_i^2 l_i}{D^2 H} \qquad \text{eqn 3}$$

where M_b is the proxy mass of z branches in the tree and M_s is the proxy mass of the main stem of the tree.

Both the vertical position of large branches (Ciftci *et al.* 2013) and the tree's centre of mass (which is affected by tree height and crown size) (Fournier *et al.* 2013) have been noted as important factors related to wind-induced sway motion. So, the mass-weighted average height of all branches above-ground (weighted by the proxy branch mass) was divided by the total height of the tree to get the relative average height of branch mass (R_b):

$$R_\mathrm{b} = \frac{\sum_{i=1}^{z} d_i^2 l_i \bullet h_i}{\sum_{i=1}^{z} d_i^2 l_i} \bullet \frac{1}{H} \qquad \text{eqn 4}$$

As R_b increases, the centre of branch mass is shifted relatively higher up in the tree. We expected light competition to increase R_b and wind exposure to decrease it.

Recent research by Ciftci *et al.* (2013) also suggests a greater influence of larger branches on the dynamic amplification factor of open-grown trees because of their greater proportion of the overall mass of the tree. So, branch mass inequality was computed for each tree as the Gini coefficient (Damgaard & Weiner 2000) of branch mass (G_b): the mean of the difference between all possible pairs of branches, divided by the mean branch mass:

$$G_\mathrm{b} = \frac{\sum_{i=1}^{z}\sum_{j=1}^{z} |x_i - x_j|}{2z^2\bar{x}} \qquad \text{eqn 5}$$

where x is the proxy mass (d^2l) for each branch in the tree and z is the number of branches in the tree. As $\mathrm{G_b}$ increases from zero to one, branch mass goes from being equally distributed between branches to concentrated in one large branch.

Finally, Ciftci *et al.*'s (2013) finite element model of an open-grown tree suggested that the slenderness of branches ($l : d$ *ratio*) might affect dynamic amplification factor. So, the average branch slenderness for each tree (S_b) was computed as:

$$S_\mathrm{b} = \frac{\sum_{i=1}^{z} \frac{l_i}{d_i}}{z} \qquad \text{eqn 6}$$

STATISTICAL MODELLING

We first examined if both CC and CI should be used together to represent crowding effects. CC explained about 96% of the variation in CI (see Fig. S2), so we used them separately in different models of crowding effects.

We modelled tree allometric relationships as linear functions of log-transformed variables H, W, L and D [e.g. log(H) vs. log(D)] using linear mixed effects modelling. We tested for significant effects of crowding and shading from neighbours (CC), as well as location and species, on model coefficients, treating them as random variables (MacFarlane & Weiskettel 2016). The general model was $\log(Y) = (\beta_0 + \mu_k + \mu_{jk} + \mu_{ijk}) + [(\beta_1 + \lambda_k + \lambda_{jk} + \lambda_{ijk}) \times \log(X)]$, where μ and λ are random effects coefficients for the intercept (β_0) and slope (β_1), respectively, and subscripts *i*, *j* and *k* represent location, species and CC, respectively. The relative contribution of these variables to explaining variation in tree allometric relationships was determined with the varcomp function within the APE R package (Paradis, Claude & Strimmer 2004).

We also examined how tree (*H*, *W*, *L*, *D*) and branch (R_b, M_b/M_s, S_b, G_b) architectural traits and ω varied as functions of CI. Data were fit to a range of functions, including linear, first-, second- and third-order polynomial, exponential and several asymptotic functions. These models were fit with linear and nonlinear least-squares regression (Chambers & Bates 1990). Bivariate (95%) confidence intervals were computed to assess the plasticity of traits within each CC.

For all analyses, we selected a final, 'best' model for each relationship as the one that had the smallest AIC with all statistically significant ($\alpha = 0{\cdot}05$) coefficients. We performed all statistical analyses using custom code and packages in R (R Core Team 2015).

Results

Allometric models fit to the data showed significant effects of crowding and shading from neighbouring crowns on tree architecture, for all relationships examined (full statistical details are shown in Table S1). The most notable effects were on stem slenderness (slope of the *H* : *D* relationship) and crown slenderness (slope of the *L* : *W* relationship) (Fig. 2), with CC explaining 85% of variation in *H* : *D* relationships and 72% of *L* : *W* relationships, across tree species. Open-grown trees were much shorter than forest-grown trees of the same species and stem diameter and had relatively flattened crowns (shorter and wider) across the full range of tree sizes examined (Fig. 2). Forest-grown trees showed distinctive allometric relationships within CCs, with stem slenderness being greatest for overtopped trees and decreasing for trees with increasing canopy dominance; the same pattern was found for crown slenderness (Fig. 2). Crowding also had a significant effect on the relative length (*L* : *D*) and width (*W* : *D*) of crowns, but CC explained only about 14% and 4% of variation in *L* : *D* and *W* : *D*, respectively.

After accounting for crowding, species and sample location explained very little of the variation in tree allometry (either non-significant or explaining less than 10% of residual variation, see Table S1), with one notable exception; species explained almost 15% of the residual variation in crown slenderness within CCs. For forest-grown trees, the crowns of *A. rubrum* were relatively wider than those of *Q. rubra* and *Tilia* spp., but that was not true for open-grown trees.

Examining how specific architectural traits responded to crowding from neighbouring trees, we found a range of responses, with CI explaining between 28 and 81% of the variation in these traits (Table 2). Consistent with the strong effects of crowding from neighbouring crowns on tree allometry, the ratios *H* : *D*, *L* : *D* and *W* : *D* were all strongly positively correlated with CI. The ratios *H* : *D* and *L* : *D* increased in a nonlinear fashion with CI, with the rate of increase levelling off at higher CI, whereas *W* : *D* ratios increased linearly (Table 2).

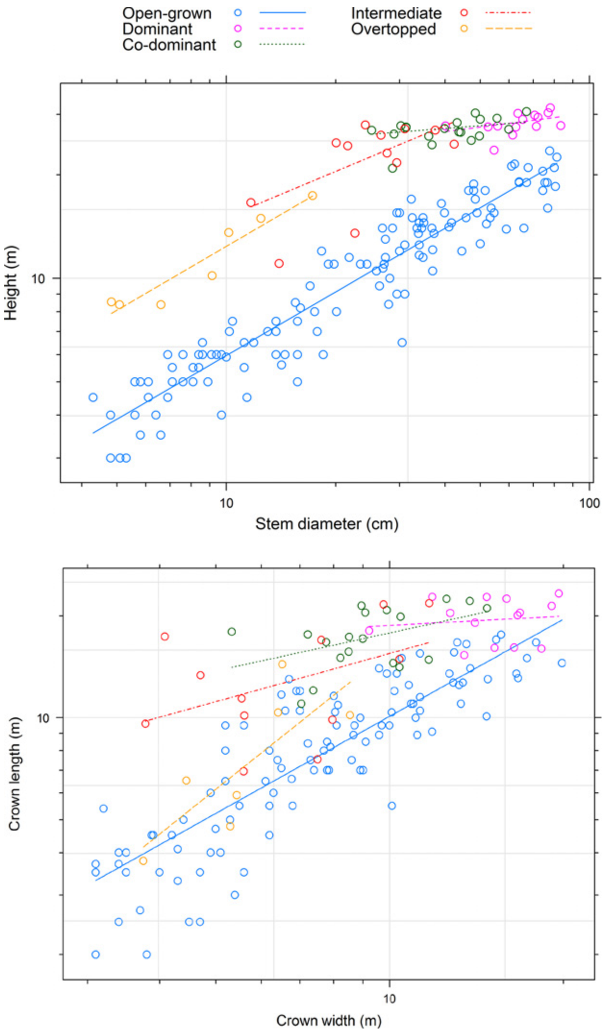

Fig. 2. Tree allometric relationships between height and diameter and crown length and crown width grouped by canopy class (CC). Dashed lines are regression functions fitted separately for each CC. Model coefficients are listed in Table S1.

Wind resistance declined as a negative exponential function of CI, which explained more than 50% of the variation in ω (Fig. 3, Table 2). Bivariate plots (Fig. 3) showed that overtopped trees exhibited the highest variation in crowding, but a fairly narrow range of wind resistance, whereas the opposite was true for open-grown and dominant trees.

The four branch architectural traits were also significantly correlated with CI (Table 2). CI explained almost 50% of the variation in the branch to stem mass ratio (M_b/M_s), with the highest ratio for open-grown trees and a steeply declining ratio with greater crowding from neighbouring trees (Fig. 4 and Table 2). Branch mass inequality (G_b) decreased linearly with CI (Table 2), with overtopped trees having the greatest equality in branch size, but also

Table 2. Functional relationships between crowding index (CI) and (i) wind resistance (ω) and (ii) tree and branch architectural traits

Function	β_0	β_1	β_2	R^2
$\frac{H}{D} = \beta_0 + \frac{\beta_1(\mathrm{CI})}{(\mathrm{CI}+\beta_2)} + \mathrm{CI}$	33·991 [3·478]***	96·886 [12·457]***	9·372 [3·069]**	0·813
$\frac{L}{D} = \beta_0 + \frac{\beta_1(\mathrm{CI})}{(\mathrm{CI}+1)} + \mathrm{CI}$	25·431 [2·976]***	20·448 [4·255]***	–	0·633
$\frac{W}{D} = \beta_0 + \beta_1(\mathrm{CI})$	21·477 [1·505]***	1·375 [0·133]***	–	0·621
$\omega = e^{(\beta_0+\beta_1(\mathrm{CI}))}$	6·913 [0·071]***	−0·271 [0·037]***	–	0·544
$\frac{M_b}{M_s} = \frac{\beta_1}{(\mathrm{CI}+\beta_2)}$	–	1·361 [0·291]***	2·00 [0·487]***	0·494
$G_b = \beta_0 + \beta_1(\mathrm{CI})$	0·705 [0·022]***	−0·016 [0·002]***	–	0·448
$S_b = \beta_0 + \frac{\beta_1(\mathrm{CI})}{(\mathrm{CI}+1)} + \mathrm{CI}$	59·161 [4·533]***	22·319 [6·628]**	–	0·365
$R_b = \beta_0 + \beta_1(\mathrm{CI}) + \beta_2(\mathrm{CI})^2$	−0·414 [0·019]***	0·021 [0·004]***	0·0006 [0·0001]***	0·281

Standard errors in [] follow coefficients (β_0, β_1, β_2), and significance levels are as follows: $^{**}P \leq 0{\cdot}01$, $^{***}P \leq 0{\cdot}001$.
$\frac{H}{D}$, stem slenderness; $\frac{L}{D}$, relative crown length; $\frac{W}{D}$, relative crown width; $\frac{M_b}{M_s}$, branch:stem mass ratio; G_b, branch mass inequality; S_b, branch slenderness; R_b, average relative height of branch mass.

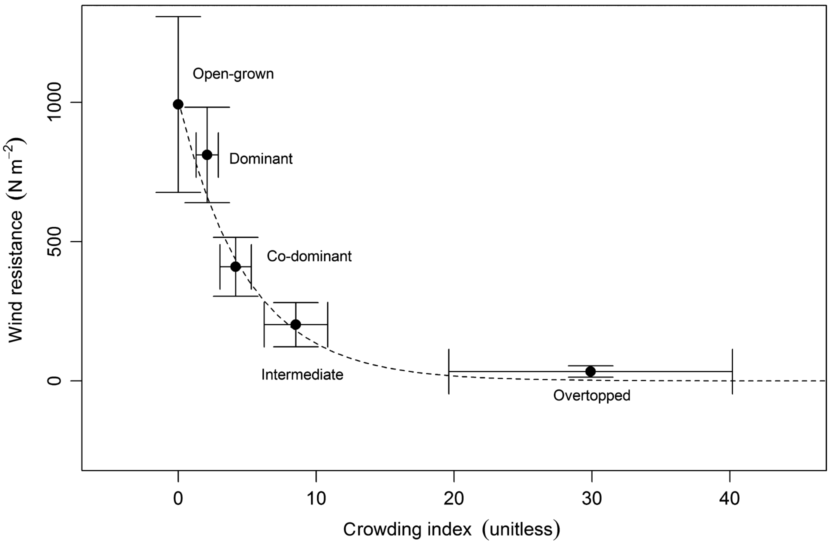

Fig. 3. Wind resistance (ω) as a function of crowding (CI) for trees of multiple species (Table 1) grouped by canopy class (CC). Dashed line is the regression function described in Table 2.

showing the greatest variability. The G_b of open-grown trees was significantly less than the average trend (Fig. 4). Average branch slenderness (S_b) increased in a non-linear fashion as CI increased (Table 2, Fig. 4). Open-grown and overtopped trees had the least and most slender branches, respectively, but within each CC, variation in S_b increased with increasing CI (Fig. 4). The average relative height of branch mass (R_b) showed a convex trend, initially increasing, but ultimately decreasing, as CI increased (Fig. 4, Table 2). Open-grown trees had their branch mass centred relatively closer to the ground (about 35 to 40% of tree height), whereas most forest-grown trees had their branch mass centred in a fairly narrow range between 45 and 65% of tree height, regardless of canopy position, with considerable overlap in the confidence intervals for the CCs (Fig. 4).

Discussion

NEIGHBOURHOOD-INDUCED CONVERGENCE OF TREE ARCHITECTURE

We studied the response of architectural traits of four tree species over a range of sites and crowding conditions, from open-grown urban to forest-grown and fully shaded by other trees. This enabled us to quantify simultaneous trade-offs between optimizing tree architecture for light capture and developing a wind-resistant growth form. While trees showed plasticity in growth form, there was strong evidence for a tree neighbourhood-induced convergence of tree traits across species and conditions. In general, an increase in tree height and crown dimensions relative to stem thickening, when crowded and shaded by

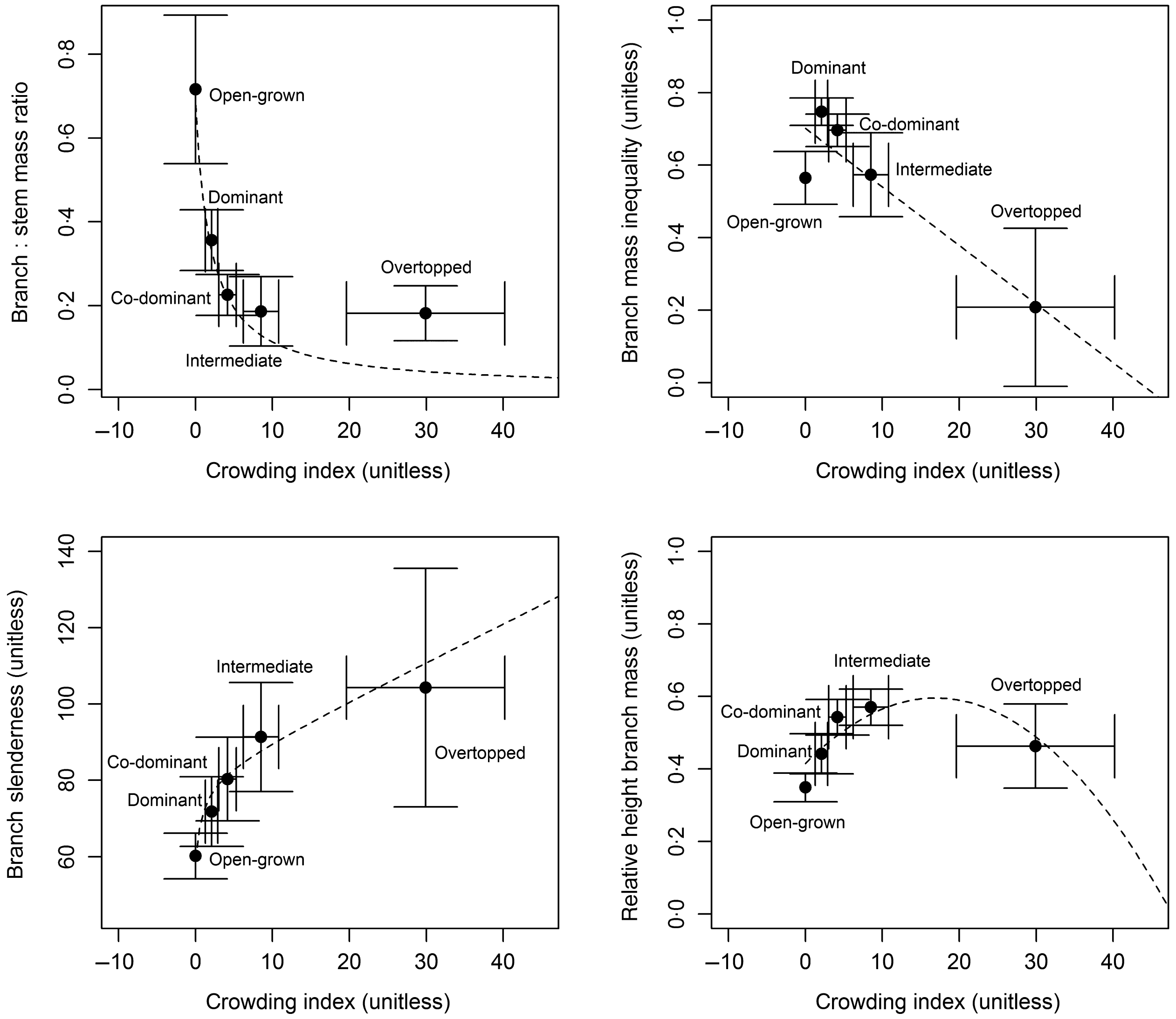

Fig. 4. Wind resistance (ω) as a function of branch architectural traits for trees of multiple species (Table 1) grouped by canopy class (CC). Dashed lines are regression functions described in Table 2.

neighbours, with a corresponding decrease in wind resistance.

Iida *et al.* (2011) also noted a convergence of tree architecture across 200 co-occurring tropical tree species and Jucker, Bouriaud & Coomes (2015) demonstrated that intraspecific plasticity in crown form was a dominant force in shaping tree architecture. Our study demonstrates a specific mechanism: that species have similar functional architecture because of convergent responses to light competition and the destructive force of wind, which likely masks otherwise tangible, genetically-mediated differences between species. Here, tree architecture varied predictably with a crowding index and within functional groups (CC) defining the trees' competitive position for light capture relative to neighbouring trees.

Trait convergence for the four species we studied is not surprising. They were all broad-leaved, deciduous trees adapted to similar cool climates, occurring over a moderate range of tolerance to shade [shade tolerance values from Valladares & Niinemets (2008): *Q. rubra* = 2·75; *A. rubrum* = 3·44; *T. americana* 3·98; *T. cordata* = 4·18], which somewhat restricted differences in trait responses to shading due to species. Intrinsically, broadleaf species tend to have weak apical control, which promotes branching (Wilson 2000; Dardick *et al.* 2013) at the expense of terminal growth of the main stem. While we did find an increase in the relative size of the crown ($L : D$ and $W : D$ ratios) with increased crowding, competition also drove these species to adopt a more slender stem form (higher $H : D$ ratios) with a lesser allocation of mass to branches than the main stem. This means that crowding caused trees to 'stretch' limited available light energy to try to obtain more light at the expense of secondary growth of the stem.

Poorter, Bongers & Bongers (2006) noted that understorey species adopt a strategy of developing a longer, wider crown, similar to the overtopped trees we studied. However, all of the overtopped trees in our study are species that can reach canopy dominance at maturity, so their life history also dictates a genetically-coded plan to grow much taller. The latter highlights the importance of ontogenetic as well as species-specific differences in height–diameter relationships. Niklas (1995) found such ontogenetic effects on height–diameter relationships, even when studying a single species grown in the open. In our study, ontogenetic effects should be largely accounted for by size and canopy position at the time allometric ratios were measured. Although species effects contributed very little to explaining allometry in this study, after location and crowding was accounted for (Table S1), *Q. rubra* exhibited the highest $H : D$ ratios, which followed the expectation for a species with an intrinsically lower shade tolerance.

Fundamentally, increasing tree height growth relative to diameter growth is a natural response to carbohydrate starvation caused by light deprivation, which explains why apical dominance of the terminal shoot is a fundamental attribute of trees that constrains tree form (Barthélémy & Caraglio 2007). Clearly this response can adversely affect the wind resistance of trees. So, the strong positive relationship we found between $H : D$ ratios and CI and the converse negative relationship between ω and CI is logical, given that it relates directly to the theoretical mechanical buckling limit, or critical height, that has been widely employed to understand the likelihood of stem failure at a given height–diameter ratio (McMahon & Kronauer 1976; King 1986; Niklas 1995; King 1996; King *et al.* 2009; Iida *et al.* 2011; Lines *et al.* 2012). While trees rarely actually reach this critical height, they may approach this limit where there is a high level of light competition (Lines *et al.* 2012) or where trees are sheltered from the wind (King *et al.* 2009). As such, responding to light competition represents a constant stress for forest-grown trees to respond to, whereas wind-induced mortality or damage represents a more uncertain one that, from an evolutionary perspective, may never occur or occurs only after the tree has matured and reproduced.

Archibald & Bond (2003) conducted one of the few other studies that looked at tree architecture over a wide range of light environments – including trees growing outside of forests, noting that open-grown trees may have greater plasticity in form because light competition does not impose a strong selective pressure on performance. Their study was conducted in the very different climates of South Africa, but their results suggest that crowding might reduce the plasticity of wind resistance. In support of this, we observed greater plasticity in ω and less variation in CI under more open conditions and the opposite trend when trees were heavily shaded (as indicated by bivariate confidence intervals in Fig. 3). On the other hand, some architectural traits like stem slenderness and relative crown length and width appeared to be more plastic among trees in light-stressed functional groups. However, the latter variation could reflect a greater heterogeneity in the below-canopy light environment experienced by overtopped or partially suppressed (i.e. 'intermediate') trees (Fig. S2).

FUNCTIONAL ASPECTS OF BRANCH ARCHITECTURE IN RESPONSE TO CROWDING

Overall, our findings indicate that crowding, particularly light deprivation from shading from neighbouring trees, resulted in longer, thinner branches that were fairly similar in size for overtopped trees, whereas open-grown and canopy dominant trees had thicker branches with more of the mass concentrated in large branches (Table 2 and Fig. 4).

Our detailed examination of branch architecture revealed greater variability in response to crowding than what we observed in whole-tree allometry (Table 2). This may in part reflect that our method of measuring crowding (CI) was anisotropic because we lacked a clear way to capture directional asymmetry in crowding with our data. In reality, light is not equally available from all directions and branches are typically clustered to maximize light gain and minimize exposure to or counteract gravitational forces or reduce crown collisions (Muth & Bazzaz 2003; Getzin & Wiegand 2007). This crown heterogeneity may help explain why branch mass inequality (G_b) was highest for dominant/co-dominant trees, but lower for both open-grown and overtopped trees, instead of following the general increasing or decreasing trends the other architectural traits followed along a crowding gradient (see Fig. 4). Muth & Bazzaz (2003) showed that crown asymmetry was largely the result of differential growth of branches into gaps and reduced growth to avoid competing crowns. Dominant and co-dominant trees should have the greatest amount of direct canopy competition, but can also produce sizeable branches and branch mass inequality is influenced by the maximum branch size as well as the branch size distribution within the tree. Overtopped trees are essentially shaded all around, but have little energetic capacity for growing large branches. The crowns of open-grown trees have no light competition to respond to (although there is some self-shading of branches), but they typically have large spreading crowns with multiple large branches (i.e. larger maximum branch and moderate branch-to-branch variation).

In terms of wind resistance, branch architecture should presumably be more important for open-grown trees. In a forest, only the canopy trees (dominant and co-dominant) might experience noticeable wind load, and their branches may grow mostly independently of mechanical constraints related to wind loading. Recent studies of both large (James, Haritos & Ades 2006; James 2014; Kane *et al.* 2014) and small (Miesbauer, Gilman & Giurcanu 2014) open-grown trees have demonstrated the relationship between branches and important sway characteristics of trees – frequency and damping ratio – that influence the likelihood of tree failure. Branch size is also correlated with leaf area (Cummings 1941; Rothacher, Blow & Potts 1954; Weiskittel *et al.* 2009), which influences drag (Kane & Smiley 2006), and the accretion of ice and snow (Petty & Worrell 1981; Cannell & Morgan 1989; Peltola *et al.*

1999). The negative exponential decline that we observed in M_b/M_s with increasing CI paralleled the functional relationship between ω and CI (compare Figs 3 and 4), supporting the idea that mass damping of branches influences tree sway in the wind (James, Haritos & Ades 2006). Open-grown trees had the lowest value for R_b, which should be beneficial for reducing wind-induced bending on a tree of any size. Forest-grown trees seem to equilibrate with respect to R_b, showing a similar relative centre of branch mass to match their position in the canopy. The latter seems to align with theories that suggest that trees are compensating for gravitational effects of branch loads as they grow (Fournier *et al.* 2013).

It has been theorized that slender branches might serve to diffuse drag by either increasing the fractal dimension of the crown (Eloy 2011) or by bending or breaking (Ciftci *et al.* 2013; Fournier *et al.* 2013). Beam theory shows that branch slenderness can affect the axial distribution of mechanical stress as well as the deflection and sway frequency of branches (Niklas 1992). However, open-grown trees showed the lowest branch slenderness and highest wind resistance, while crowding forced forest-grown trees to develop more slender branches. This seems to suggest an energetic, rather than wind-driven, response of branch slenderness to crowding and shading. As branch slenderness is a complex function of both species and canopy position, and it likely influences many aspects of tree function, more work is needed to study this important branch parameter.

CHALLENGES FOR MEASURING WIND RESISTANCE

A recent review by Gardiner, Berry & Moulia (2016) emphasized the complexity of wind–tree interactions and how broadly wind shapes the form and function of trees globally. One of the challenges in this study was choosing a way to measure wind resistance. Here, we used a morphologically based measure of the likelihood of wind-induced stem breakage (ω) that does not reflect the complexities of the actual wind (e.g. its velocity and frequency) that trees experience. However, it is reasonable to assume that ω captures a signature of the interaction in the growth form and wood density of the trees (Gardiner, Berry & Moulia 2016) and ω provided a clear and understandable pattern of response to crowding from neighbouring trees.

We did not consider resistance to uprooting, an alternative mode of wind-induced failure that is also referred to as 'toppling' (Schaetzl *et al.* 1989; Gardiner, Berry & Moulia 2016). Toppling is more complex to model than stem breakage because resistance to it depends on strength of the root system, the soil itself and their interaction. In general, a tree that fails under wind load tree will either uproot or its stem will break, but not both (Schaetzl *et al.* 1989; Kane & Clouston 2008). Snapped trees are often smaller, have a more slender form and have lower wood densities than those that are uprooted by wind (Schaetzl *et al.* 1989). If we consider that M is a function of $D^2H \times g$ (MacFarlane 2015), then resistance to uprooting is proportional to the square of stem diameter and resistance to breakage proportional to its cube (see eqn 2), for a given stem wood density. However, if a tree has substantial stem decay (captured in coefficient f in eqn 2) relative to the strength of its roots and the soil, it may break before uprooting, and vice versa.

Toppling (T) is generally proportional to the mass of the tree (M) (Gardiner, Peltola & Kellomaki 2000; Gardiner, Berry & Moulia 2016): $T = cM$, where c (Nm kg^{-1}) is a coefficient derived from tree pulling experiments [in the range 100–200 Nm kg^{-1} (Hale *et al.* 2015)]. Hale *et al.* (2015) showed that, e.g. holding other factors constant, shallow soils have a lower c than deeper ones. In general, there is very little data on tree pulling experiments to estimate c, and most of it is for coniferous rather than broadleaved, deciduous species, such as those studied here. However, we can expect that trees in windy environments are less likely to uproot (Gardiner, Berry & Moulia 2016) and that open-grown trees are also much less likely to uproot than forest-grown ones, unless the roots have been damaged, e.g. in urban areas, during some sort of excavation or where roots are spatially limited by infrastructure. Kane & Clouston (2008) conducted tree pulling experiments with 24 healthy shade trees of three species in the genus *Acer* at a suburban property in MA, USA: none of the trees uprooted; all the failures were stem or lateral branch breakage at the point of attachment of co-dominant stems. Our models did not include the possibility of branch breakage at all, which has been theorized to act as a 'safety fuse' to relieve pressure on the whole tree (Fournier *et al.* 2013).

COMPARABILITY OF URBAN- VS. FOREST-GROWN TREES

Broad questions about how trees differ in form along a continuum of crowding were an important focus of this paper. Part of the novelty of this work is that it may be one of the first attempts to compare both form and function of trees along a gradient from forest- to open-grown conditions. However, it is important to consider that all of our 'open-grown' trees were growing in urban areas. Studies of urban tree growing environments (e.g. McHale *et al.* 2009) emphasize that the benefit of being released from competition with other trees is only one aspect to consider, when compared to trees in forests; urban trees tend to experience less favourable conditions in terms of soil moisture, humidity and air and leaf temperatures.

We observed that the urban trees were shorter at same diameter across all diameters (Fig. 2), highlighting the possibility of at least some environmental–physiological constraints on height growth for urban trees. It is well understood that tree height growth is at least partially limited by water availability (Ryan, Phillips & Bond 2006) and the soil rooting environment and associated water availability is often more limited for urban trees (Close *et al.* 1996). However, our results showed that after accounting for CC, there was only a very small effect of location on height–diameter ratios, with no clear pattern in random-effect sizes between the forested and urban locations (Table S1). So, the relatively shorter height and shorter, more flattened crowns found in open-grown trees, likely reflected the need to better resist wind exposure, rather than an 'urban' environmental effect. Thus, the general convergence in tree architecture across the gradient of crowding that we observed shows that competition from other trees and increased exposure to wind without neighbours are likely major drivers in shaping tree architecture. While it would be challenging to devise an experiment that made forest- and urban-grown trees strictly comparable, more studies of this type are needed to separate the effects of urban vs. rural environments from the effects of neighboring trees.

Conclusion

Our study shows strong effects of crowding from neighbouring trees, or lack thereof, on tree architecture, via a mechanism related to functional trade-offs balancing crown competitiveness with wind resistance. Individuals of broad-leaved deciduous species exhibited a convergence in tree and branch architecture along a gradient of crowding and shading, from forest conditions to open-grown conditions without tree neighbours. Although not perfect models for all open-grown trees, urban open-grown trees exhibited this trait convergence despite clear differences in urban vs. natural forest conditions. Alleviation of light competition stress in the absence of neighbours allows trees to develop relatively large branches, and a squat, branchy growth form, which is intrinsically relatively wind stable. By contrast, increasing crowding and shading from neighbours causes trees to become increasingly more spindly in the main stem, with slender branches stretched thin over a disproportionally large crown area to try to increase light capture. The latter, intrinsically less wind stable form can be adopted by a tree to increase performance at low light levels because competing trees in the surrounding forest reduce wind exposure, and, in turn, the likelihood of stem breakage or uprooting. However, even if light-stressed, trees have adequate stability in a closed canopy stand, this may contribute to the mortality of competitively inferior trees if there is an opening that allows wind to penetrate into the stand.

Authors' contributions

D.M. and B.K. conceived the idea for the study; D.M. designed the analyses and analysed the data; D.M. and B.K. designed data collection protocols and collected the data; D.M. led the writing of the manuscript. Both D.M. and B.K. contributed to writing and editing the drafts and gave final approval for publication.

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Data accessibility

Data used for the forest-grown tree study in Michigan and the urban-grown tree study at the University of Massachusetts has been archived at the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.c15d8, MacFarlane & Kane 2017. The additional allometric data from urban trees used in this study (from McPherson, van Doorn & Peper 2016, see References) were already publicly available prior to this study and can be accessed freely at: https://doi.org/10.2737/RDS-2016-0005.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Tree branch (a) and stem (b) mass (dry weight basis) vs. branch (a) and stem (b) proxy volume.

Fig. S2. Box plots depicting variation in the tree crowding index (CI) within canopy classes (CC).

Table S1. Allometric scaling relationships between height (H, m), crown length (L, m), crown width (W, m) and stem diameter at 1·3 m (D, cm).