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Size symmetry of competition alters biomass–density relationships

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As crowded populations of plants develop, the growth of some plants is accompanied by the death of others, a process called density-dependent mortality or 'self-thinning'. During the course of density-dependent mortality, the relationship between total population biomass (B) and surviving plant density (N) is allometric: $B = aN^b$. Essentially, increasing population biomass can be achieved only through decreasing population density. Variation in the allometric coefficient a among species has been recognized for many years and is important for management, assessment of productivity and carbon budgets, but the causes of this variation have not been elucidated. Individual-based models predict that size-dependent competition causes variation in the allometric coefficient. Using transgenic *Arabidopsis* with decreased plasticity, we provide experimental evidence that morphological plasticity of wild-type populations decreases the size asymmetry of competition for light and thereby decreases density-dependent mortality. This decrease in density-dependent mortality results in more biomass at a given density under size-symmetric compared with size-asymmetric competition.

Keywords: asymmetric competition; morphological plasticity; self-thinning; shade avoidance

1. INTRODUCTION

Size is fundamental in competitive interactions among plants. Often, larger individuals have a disproportionate advantage in competition with smaller individuals and suppress their growth, a phenomenon called 'size-asymmetric competition' (Begon 1984; Schwinning & Weiner 1998; Weiner 1990). Size asymmetry appears to be caused by competition for light, which is 'one-sided', in that larger plants shade smaller plants, whereas smaller plants have almost no effect on the light available to their larger neighbours. However, plants have evolved sensory mechanisms (Smith 2000) and morphological plasticity to avoid being suppressed by their neighbours (Ballaré 1999). The phytochrome system of plants perceives changes in red to far-red light ratios caused by shade and proximity to their neighbours (Ballaré *et al.* 1990; Novoplansky *et al.* 1990) and plants respond with increased height growth and decreased branching (Hutchings & de Kroon 1994; Whitelam *et al.* 1998). This 'shade avoidance' can counteract the inherent size asymmetry of competition for light (Ballaré *et al.* 1994; Schwinning & Weiner 1998).

Individual-based competition models (Huston *et al.* 1988) that include size-dependent competition have been developed, and predict testable effects on biomass–density relationships (e.g. self-thinning trajectories). In a 'zone of influence' model (Weiner *et al.* 2001), plants grow and compete for two-dimensional space in areas in which they overlap (see Appendix A). Under asymmetric competition, the largest individual obtains all the contested resources, whereas under symmetric competition, contested areas are divided equally among all contestants. Because asymmetric and symmetric are extremes of a continuum, we use the term 'size dependent' to refer to the entire range. Effects of the size dependence of competition on biomass–density relationships are conspicuous (figure 1). Under asymmetric competition, mortality starts immediately even at low densities, proceeds very rapidly at higher densities, and the log$B$–log$N$ slope b quickly approaches -0.5. Under symmetric competition, the growth rate of all plants is reduced by competition, and self-thinning occurs much more slowly (Yastrebov 1996), and only at very high densities. An intermediate biomass–density trajectory is produced if contested resources are divided in proportion to size. While the log$B$–log$N$ slope eventually converges to -0.5 in all competitive scenarios the allometric coefficient, and therefore the biomass of living plants at a given density, is lower under asymmetric than symmetric competition. Other models predict a lower thinning slope with more asymmetric competition and therefore a more rapid development of size hierarchies (e.g. Adler 1996). However, the intercept and slope of allometric equations are inevitably correlated (White & Gould 1965). Thus, the predictions are similar, but neither has been tested. We used far-red radiation 'blinded' and wild-type *Arabidopsis thaliana* (L.) Heynh. to experimentally test the prediction that reduced asymmetry of competition due to morphological plasticity slows the rate of density-dependent mortality and increases the allometric coefficient a.

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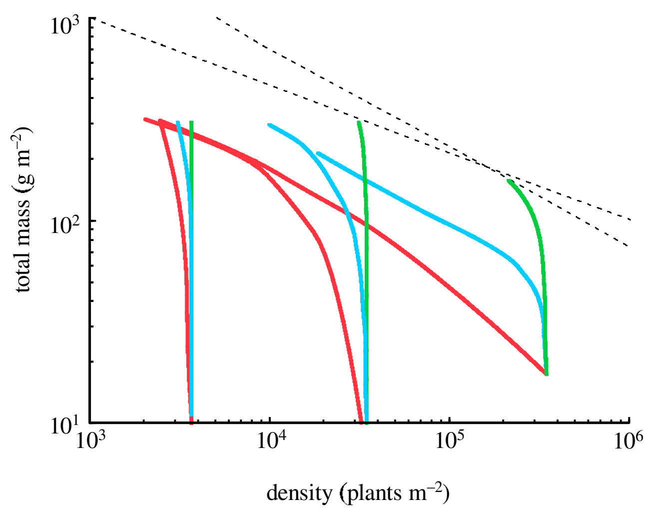

Figure 1. Simulated biomass–density relationships from the zone of influence model (Weiner *et al.* 2001) with size-dependent competition, i.e. asymmetric (red), symmetric (green) and proportional (cyan). The steeper dotted line has a slope of −1/2 and the shallow dotted line has a slope of −1/3. The three different sets of lines match the three densities used in the experimental test with transgenic and wild-type *Arabidopsis*.

2. MATERIAL AND METHODS

We grew two wild-type (WT 1 and 2, WTs to refer to both) and one transgenic (phy A) genotypes of *A. thaliana* at different densities and harvested replicate plots to count the number of surviving individuals and determine their dry mass. The transgenics over-expressed an introduced oat phytochrome A gene such that constantly high levels of phytochrome A effectively disable shade avoidance and morphological plasticity (Boylan & Quail 1991; Whitelam *et al.* 1992). Seeds of ecotype Nossen (WT 1) and *Lansberg erecta* (WT 2), and of a homozygous, isogenic phytochrome A over-expressor (phy A, line 13k7 with ecotype Nossen background) were provided by Professor G. C. Whitelam (Leicester, UK) and stored at 4 °C in the dark for one week prior to sowing on 7 May 1998. Plastic pots (7 cm × 7 cm × 7.5 cm) were filled with a 4 : 1 mixture of commercial soil (TKS1, Floragard Vertrieb GmbH, Oldenburg, Germany) and perlite. A fine layer was sieved over the pots to level the surface and avoid spatial heterogeneity. Seeds were mixed with sand (0.7 mg) and sieved to achieve a random spatial pattern. We used a randomized-block design including three densities (20, 200 and 2000 seeds per pot yielding *ca.* 3000, 30 000 and 300 000 seedlings per square metre) and three replicates per genotype, density and harvest combination. For the lower densities the seeds were counted, whereas for the highest density they were weighed based on $n = 10$ counted samples (mean ± s.e. = 1.47 ± 0.23, 0.67 ± 0.23 and 2.60 ± 0.60 mg for WT 1, WT 2 and phy A, respectively). The plants were watered twice daily and natural sunlight in the greenhouse (20 °C and 60% humidity) was supplemented by 16 h of artificial light (minimum of 170 mE m^{-2} s^{-1}; maximum of 230 mE m^{-2} s^{-1}). Three harvests were made at intervals of 15, 7 and 11 days from sowing. At the lower densities, harvested plants could easily be counted. At the highest density, plants were counted at first and second harvest within five 1 cm × 1 cm squares and the density estimates averaged. At the third harvest, the plants were substantially bigger and a central square (2 cm × 2 cm) was used to estimate density and avoid edge effects. Harvested plants were oven dried at 80 °C for 48 h. None of the plants flowered before the second harvest (day 22) after which flowering started without any obvious differences among genotypes. At the third harvest (day 33) some individuals had set seeds in all three genotypes.

We tested for a difference in the allometric coefficient *a* of the thinning lines by one-way analysis of variance of the residuals from a common slope. Regression lines were fitted to the highest density by reduced major axis regression, and expected slope regression (Rayner 1985) was used to test against −1/2. Because more recent work suggests values of −1/3 (Enquist *et al.* 1998; Franco & Kelly 1998), we also tested against this less negative value.

3. RESULTS AND DISCUSSION

The lack of morphological plasticity is clearly reflected in the differences in hypocotyl elongation response to density (figure 2*a*). In the blinded genotype there is only a small elongation response to density. By contrast, WTs more than doubled their hypocotyl length in response to density. In terms of average dry mass, WT 1 grew best and reached over 30 mg dry mass at the lowest density (figure 2*b*) where differences were significant between WT 1 and WT 2 ($F_{1,16} = 13.6$, $p < 0.01$) and WT 1 and phy A ($F_{1,16} = 18.6$, $p < 0.001$) but not between WT 2 and phy A ($F_{1,16} = 0.4$, $p = 0.55$). However, at the highest density and harvest 3, mortality in phy A was so much higher (see below), that average dry mass (mean ± standard deviation, *n*) was higher in phy A (2.63 ± 4.02 mg, 180) than in both WTs (1.32 ± 1.32, 180 and 1.41 ± 1.50 mg, 177, respectively). At first harvest, variability in hypocotyl length (not shown) was higher at all densities in phy A than in WTs but variability in mass was similar in all genotypes and generally increased with density (figure 2*c*). As expected, for the two higher densities and by the third harvest, variability in dry mass was much higher in phy A than in either of the WTs. These results agree with the results from tobacco plants, in which height (as opposed to mass) variability even decreased in wild-type but increased in transgenics in response to an increased canopy leaf-area index (a surrogate for density) (Ballaré *et al.* 1994). Thus, we conclude that compared with WTs competition among over-expressors is more asymmetric.

Both total dry mass and mortality differed significantly among genotypes (table 1). Specifically, total dry mass differed significantly between WT 1 and 2 ($F_{1,52} = 30.6$, $p < 0.001$) and WTs and phy A. However, there was no such difference in number of individuals between WT 1 and 2 ($F_{1,52} = 0.8$, n.s.). Thus, the significant genotype effect in number of individuals ($F_{2,52} = 13.3$, $p < 0.001$) does not result from differences between WTs but from differences between WTs and phy A ($F_{1,52} = 25.8$, $p < 0.001$). Similarly, significant harvest × genotype and density × genotype interactions in a number of individuals were caused by differences between WTs and over-expressors. At low density (not shown), there was no mortality in any of the three genotypes. At medium density, WTs showed almost no mortality, whereas mortality among over-expressors had already started at the second harvest (figure 3) and their density dropped by more than

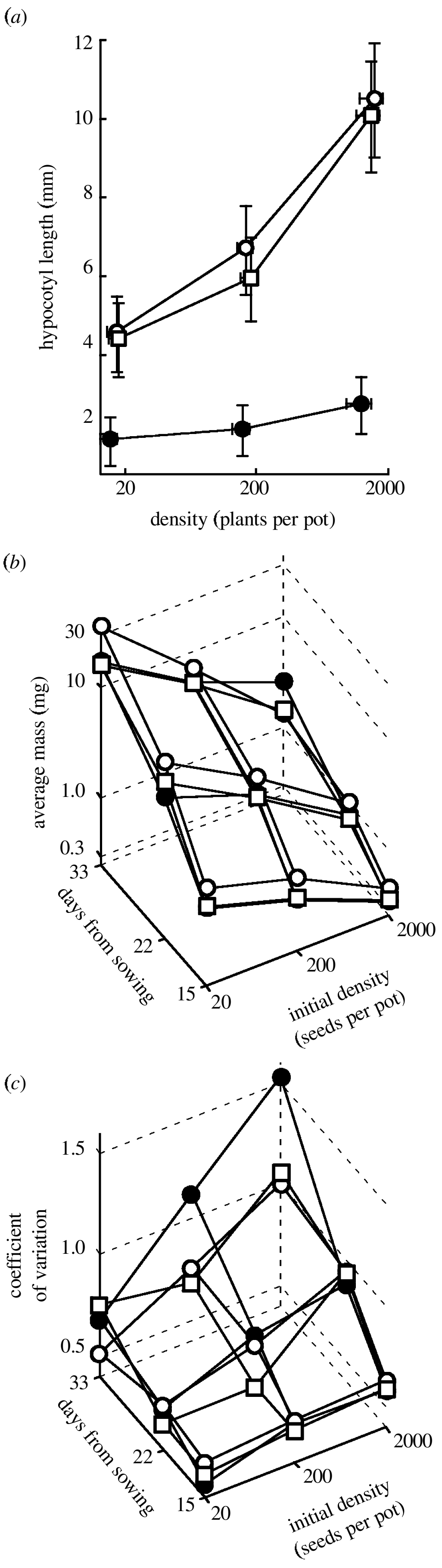

Figure 2. (*a*) Response of hypocotyl length in WT 1 (open circles), WT 2 (open squares) and phytochrome A over-expressing (filled circles) *Arabidopsis thaliana* to density after 15 days from sowing. Data points give means (± s.e., $n = 3$). Variance ratios for genotype and density genotype interaction effects from the analysis of variance are $F_{2,16} = 209.3$ and $F_{4.16} = 8.97$, respectively ($p < 0.001$). Contrasts between WT 1 and WT 2 were not significant and the effects were entirely due to differences between WTs and over-expressors (contrasts between WTs pooled and phy A: $F_{1.16} = 415.9$ and $F_{2,16} = 17.7$, respectively, $p < 0.001$). (*b*) Average dry mass of surviving WT 1 (open circles), WT 2 (open squares) and phytochrome A over-expressing (filled circles) *A. thaliana* at three densities and harvests. At the lowest density, all individuals were individually weighed and pooled across the blocks, at the two higher densities, 60 individuals per block were individually weighed and pooled across the blocks. (*c*) Coefficient of variation in dry mass between the individuals used in (*b*).

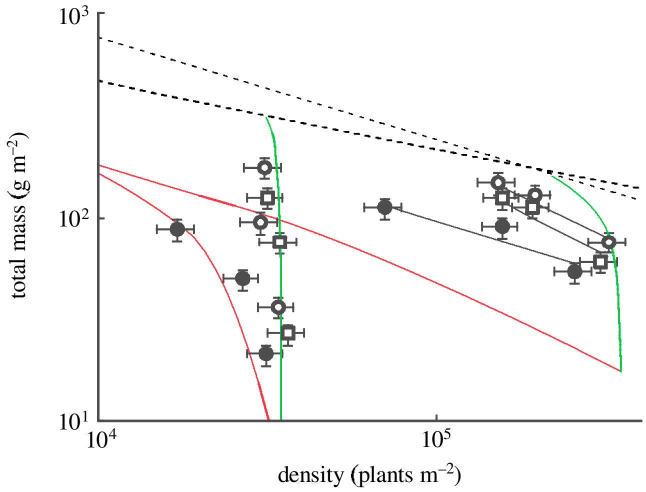

Figure 3. Relationship between total mass and density in WT 1 (open circles), WT 2 (open squares) and phytochrome A over-expressing (filled circles) *Arabidopsis thaliana* after 15, 22 and 33 days (bottom to top) from sowing. Data points give means (± 1 s.e., $n = 3$) from the analysis of variance (table 1). Solid lines for the highest density give the reduced major axes (RMA) regression lines with slopes as in table 2. The steeper dotted line has a slope of $-1/2$ and the shallow dotted line has a slope of $-1/3$. The model trajectories for asymmetric (red) and symmetric (green) competition from figure 1 are overlaid and the *x*-axis is rescaled (size-proportional competition is omitted).

33% by the third harvest. At the highest density, mortality was similar in all three genotypes between harvest 1 and 2 (figure 3). However, by the third harvest, mortality was substantially higher for the over-expressor compared with WTs. Because there was no difference in mortality at low density, the higher mortality at higher densities of crowded over-expressors compared with WTs can be interpreted as strong evidence for more asymmetric competition among overexpressors.

Although the thinning line of WT 1 was consistently higher than WT 2 (figure 3), the difference between them was only marginally significant ($F_{1,16} = 3.9$, $p = 0.06$). By contrast, the line for over-expressors was significantly

Table 1. Analysis of variance of the effects of harvest, density and genotype (WT 1 versus WT 2, and both WTs pooled versus phy A) on total dry mass ($g\,m^{-2}$) and number of individuals (m^{-2}) in *Arabidopsis thaliana*.
(Abbreviations: d.f., degree of freedom; *F*, variance ratio. No three-way interactions (not shown) were significant.)

		total dry mass		number of individuals	
source of variation	d.f.	*F*	*p*	*F*	*p*
harvest	2	459.5	***	25.0	***
density	2	443.5	***	2421.2	***
genotype	2	46.2	***	13.3	***
WT 1 versus WT 2[a]	1	30.6	***	0.8	—
WTs versus phy A[b]	1	61.8	***	25.8	***
harvest × density	4	55.8	***	11.8	***
harvest × genotype	4	1.2	—	2.8	*
WT 1 versus WT 2	2	2.0	—	0.5	—
WTs versus phy A	2	0.4	—	5.1	**
density × genotype	4	2.1	—	3.0	*
WT 1 versus WT 2	2	1.9	—	0.4	—
WTs versus phy A	2	2.3	—	5.5	**
residual	52	—	—	—	—
total	80	—	—	—	—

[a] Contrast between WT 1 and 2.
[b] Contrast between pooled wild-types (WTs) and over-expressor (phy A).
$^{*}\,p < 0.05$, $^{**}\,p < 0.01$, $^{***}\,p < 0.001$.

Table 2. Regression slopes for the relationship between density (individuals m^{-2}) and total dry mass ($g\,m^{-2}$) in wild type (WT 1 and 2), pooled WTs and phytochrome A over-expressing (phy A) *Arabidopsis thaliana*.
(Regressions were performed on block-adjusted values for total dry mass, because block effects for total dry mass (but not mortality) contributed significantly to variation ($F_{2,16} = 8.41$, $p < 0.01$). *n*, number of observations; r^2, variance explained by the correlation of density and total dry mass; RMA, reduced major axis; CI, confidence interval; $F_{\mathrm{e.s.r.}}$, variance ratio (with 1 and $n - 2$ degrees of freedom) in expected slope regression against $-1/3$ and $-1/2$, respectively.)

genotype	*n*	r^2	RMA	95% CI	$F_{\mathrm{e.s.r.}}\ -1/3$	*p*	$F_{\mathrm{e.s.r.}}\ -1/2$	*p*
WT 1	9	0.77	−0.802	−0.470, −1.368	9.84	*	3.69	—
WT 2	9	0.67	−0.899	−0.432, −1.873	7.47	*	3.52	—
WTs	18	0.65	−0.884	−0.586, −1.334	14.87	**	6.75	*
phy A	9	0.68	−0.519	−0.252, −1.071	1.21	—	0.10	—

$^{*}\,p < 0.05$, $^{**}\,p < 0.01$.

lower than for the pooled WTs ($F_{1,24} = 38.6$, $p < 0.001$). This difference in elevation of the experimental data may be partly due to the fact that WT 1 grew better than the over-expressor. However, WT 2 and the over-expressor did not differ in growth but still differed significantly in the allometric exponent ($F_{1,16} = 15.3$, $p = 0.001$). WT 1 and 2 had thinning slopes (*b*) considerably steeper than $-1/3$ and both wild-types pooled were significantly steeper than $-1/2$ (table 2). By contrast, over-expressors had thinning slopes that were not significantly different from either $-1/3$ or 1/2.

The predictions from the simulations and our experimental results support earlier theories that plant form in general and the change in form during growth in particular, do alter the speed at which size hierarchies develop and therefore should have profound consequences for self-thinning dynamics (Ellison 1987; Geber 1989; Harper 1967; Schmitt & Wulff 1993). More height growth at the expense of radial extension means less conflict with neighbours, so a given amount of biomass can be added with less attendant mortality (Weller 1987). Compared with broad-leaved trees, conifers or needle-leaved trees have higher thinning coefficients (Westoby 1984). There is empirical (Kikuzawa & Umeki 1996; Stoll *et al.* 1994) and theoretical (Yokozawa & Hara 1995) evidence that competition in conifers is less asymmetric than in broad-leaved trees. We propose that size dependence of competition in general and size symmetry of competition in particular, can explain such variation in biomass–density relationships.

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APPENDIX A

The zone of influence of each plant (*Z*) is modelled as a circle, growing in two dimensions, and is allometrically related to plant biomass (*W*):

$Z = kW^{2/3}$.

The area of the circle (Z) represents resources potentially available to the plant, and plants compete for resources in areas in which they overlap. The potential growth rate of a plant, i.e. its growth if there are no neighbours, is sigmoidal:

$$\frac{\Delta W}{\Delta t} = r\left[W^{2/3} - \frac{W^2}{W_{\max}^{4/3}}\right],$$

where W is the mass of the plant, $W^{2/3}$ is its area (Z), $W_{\max}$ is the maximum plant size, r is the initial (maximum) growth rate in mass per unit area occupied (in units of mass area^{-1} time^{-1}). When plants overlap, they compete for the resources in areas of overlap. The effective area of a plant (Z_e): the area it covers minus that part of the area lost to its neighbours, determines the realized growth rate of the plant during the next time interval:

$$\frac{\Delta W}{\Delta t} = r\left[Z_e - \frac{W^2}{W_{\max}^{4/3}}\right].$$

A plant dies if its growth rate over a time-interval falls below a threshold of 2% of its mass. The size dependency of competition is reflected in the rules for dividing up the overlapping areas (cf. main text).

REFERENCES

Adler, F. R. 1996 A model of self-thinning through local competition. *Proc. Natl Acad. Sci. USA* **93**, 9980–9984.

Ballaré, C. L. 1999 Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms. *Trends Plant Sci.* **4**, 97–102.

Ballaré, C. L., Scopel, A. L. & Sánchez, R. A. 1990 Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science* **247**, 329–332.

Ballaré, C. L., Scopel, A. L., Jordan, E. T. & Vierstra, R. D. 1994 Signaling among neighboring plants and development of size inequalities in plant populations. *Proc. Natl Acad. Sci. USA* **91**, 10 094–10 098.

Begon, M. 1984 Density and individual fitness: asymmetric competition. In *Evolutionary ecology* (ed. B. Shorrocks), pp. 175–194. Oxford: Blackwell Scientific.

Boylan, M. T. & Quail, P. H. 1991 Phytochrome A overexpression inhibits hypocotyl elongation in transgenic *Arabidopsis*. *Proc. Natl Acad. Sci. USA* **88**, 10 806–10 810.

Ellison, A. M. 1987 Density-dependent dynamics of *Salicornia europaea* monocultures. *Ecology* **68**, 737–741.

Enquist, B. J., Brown, J. H. & West, G. B. 1998 Allometric scaling of plant energetics and population density. *Nature* **395**, 163–165.

Franco, M. & Kelly, C. K. 1998 The interspecific mass–density relationship and plant geometry. *Proc. Natl Acad. Sci. USA* **95**, 7830–7835.

Geber, M. 1989 Interplay of morphology and development on size inequality: a *Polygonum* greenhouse study. *Ecol. Monogr.* **59**, 267–288.

Harper, J. L. 1967 A Darwinian approach to plant ecology. *J. Ecol.* **55**, 247–270.

Huston, M., DeAngelis, D. & Post, W. 1988 New computer models unify ecological theory. *BioScience* **38**, 682–691.

Hutchings, M. J. & de Kroon, H. 1994 Foraging in plants: the role of morphological plasticity in resource acquisition. In *Advances in ecological research*, vol. 25 (ed. M. Begon & A. H. Fitter), pp. 159–238. London: Academic Press.

Kikuzawa, K. & Umeki, K. 1996 Effect of canopy structure on degree of asymmetry of competition in two forest stands in Northern Japan. *Ann. Bot.* **77**, 565–571.

Novoplansky, A., Cohen, D. & Sachs, T. 1990 How *Portulaca* seedlings avoid their neighbours. *Oecologia* **82**, 490–493.

Rayner, J. M. V. 1985 Linear relations in biomechanics: the statistics of scaling functions. *J. Zool. Lond.* A **206**, 415–439.

Schmitt, J. & Wulff, R. D. 1993 Light spectral quality, phytochrome and plant competition. *Trends Ecol. Evol.* **8**, 47–51.

Schwinning, S. & Weiner, J. 1998 Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* **113**, 447–455.

Smith, H. 2000 Phytochromes and light signal perception by plants—an emerging synthesis. *Nature* **407**, 585–591.

Stoll, P., Weiner, J. & Schmid, B. 1994 Growth variation in a naturally established population of *Pinus sylvestris*. *Ecology* **75**, 660–670.

Weiner, J. 1990 Asymmetric competition in plant populations. *Trends Ecol. Evol.* **5**, 360–364.

Weiner, J., Stoll, P., Muller-Landau, H. & Jasentuliyana, A. 2001 Spatial pattern, competitive symmetry and size variability in a spatially-explicit, individual-based plant competition model. *Am. Nat.* **158**, 438–450.

Weller, D. E. 1987 Self-thinning exponent correlated with allometric measures of plant geometry. *Ecology* **68**, 813–821.

Westoby, M. 1984 The self-thinning rule. In *Advances in ecological research*, vol. 14 (ed. A. McFadyen & E. D. Ford), pp. 167–225. London: Academic Press.

White, J. F. & Gould, S. J. 1965 Interpretation of the coefficient in the allometric equation. *Am. Nat.* **99**, 5–18.

Whitelam, G. C., McCormac, A. C., Boylan, M. T. & Quail, P. H. 1992 Photoresponses of *Arabidopsis* seedlings expressing an introduced oat *phy*A cDNA: persistence of etiolated plant type responses in light-grown plants. *Photochem. Photobiol.* **56**, 617–621.

Whitelam, G. C., Patel, S. & Devlin, P. F. 1998 Phytochromes and photomorphogenesis in *Arabidopsis*. *Phil. Trans. R. Soc. Lond.* B **353**, 1445–1453. (DOI 10.1098/rstb.1998.0300.)

Yastrebov, A. B. 1996 Different types of heterogeneity and plant competition in monospecific stands. *Oikos* **75**, 89–97.

Yokozawa, M. & Hara, T. 1995 Foliage profile, size structure and stem diameter-plant height relationship in crowded plant populations. *Ann. Bot.* **76**, 271–285.