

# Initial density affects biomass–density and allometric relationships in self-thinning populations of *Fagopyrum esculentum*

Lei Li<sup>1</sup>, Jacob Weiner<sup>2</sup>, Daowei Zhou<sup>3\*</sup>, Yingxin Huang<sup>3</sup> and Lianxi Sheng<sup>1</sup>

<sup>1</sup>School of Urban and Environmental Sciences, Northeast Normal University, Changchun, 130024, China; <sup>2</sup>Department of Plant and Environmental Sciences, University of Copenhagen, Frederiksberg, DK-1958, Denmark; and <sup>3</sup>Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, 130012, China

## Summary

1. The form and generality of the biomass–density relationship, especially during self-thinning of crowded stands, have been intensively debated in recent years. All models of self-thinning assume that the trajectory is independent of the initial pre-thinning density, so populations differing in initial density can be analysed together. As plant allometry is a determinant of the self-thinning trajectory, and competition alters plants' allometric growth, initial density may have consequences for the self-thinning trajectory.

2. To ask whether initial density can influence allometric relationships and the biomass–density trajectory, we grew *Fagopyrum esculentum* populations at three high densities and measured shoot biomass, density and the height and diameter of individual plants at six harvests.

3. Initial density did not affect the slope of the log biomass–log density relationship, but there was a clear and significant effect on the intercept. Populations sown at higher densities had significantly more biomass at a given density of survivors.

4. If the data for all densities and harvests are analysed together, the log biomass–log density relationship is linear with a slope of  $-0.377$ , which is consistent with the predictions of Metabolic Scaling Theory. If the independent variable initial density is included as a factor, the estimated slope of the log B–log N relationship is much steeper and consistent with the classical 'Self-thinning Rule'.

5. The position of the self-thinning trajectory is determined in part by the biomass density: the relationship between mass and volume. Initial density could affect this by altering allometric growth in a way that influences architectural compactness. An alternative hypothesis is that competition at higher initial density is more size symmetric, which has been shown to reduce growth and mortality.

6. *Synthesis.* The self-thinning trajectory is not always independent of initial population density. Interpopulation scaling patterns, even within one species, do not reflect processes within populations, and this conflation lies behind much of the current debate about size–density relationships in plant populations and communities. Interactions among plants and allometry are more important than internal physiological scaling mechanisms in determining the self-thinning trajectory of crowded stands.

**Key-words:** biomass density, density-dependent mortality, growth form, height–diameter allometry, Metabolic Scaling Theory, plant–plant interactions, size-symmetric competition

## Introduction

Mass–density relationships are at the core of quantitative and theoretical ecology (Damuth 1981; Gaston & Blackburn

2000). When a crowded population of plants grows and develops, intense competition leads to mortality, in the process known as density-dependent mortality or 'self-thinning' (Yoda *et al.* 1963; Morris 1999). Early work in the area (Yoda *et al.* 1963) showed that the relationship could be described as a power law of the form  $M = K N^d$ , usually

\*Correspondence author. E-mail: zhoudaowei@neigae.ac.cn

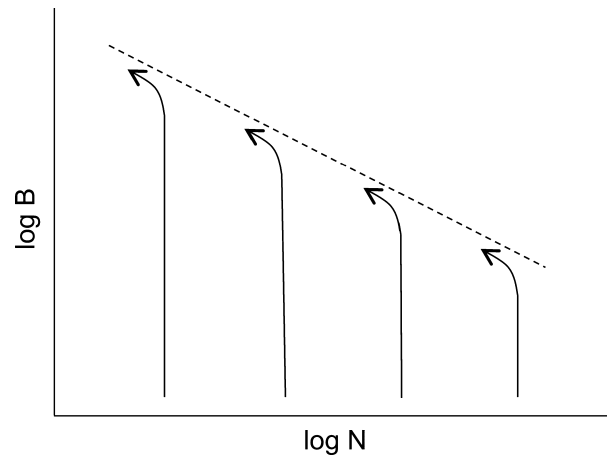
analysed as  $\log M = \log K + d \log N$ , where  $M$  is the mean mass of survivors,  $N$  is their density and  $K$  and  $d$  are parameters. For biological (Westoby 1984) and statistical (Weller 1987a) reasons, it is preferable to analyse the total biomass of survivors ( $B = N M$ ) rather than  $M$ , in which case  $B = K N^c$  or  $\log B = \log K + c \log N$ , where  $c = d + 1$ .

There has been much debate about whether the exponent of the mass–density relationship ( $d$ ) is a universal constant, and if so, what its value is (Weller 1987a; Lonsdale 1990; Enquist, Brown & West 1998). Early studies and simple geometric models of self-thinning predicted  $d = -3/2$  (Yoda *et al.* 1963; Miyanishi, Hoy & Cavers 1979), and this was called the ‘Self-thinning Rule’ (Westoby 1984). More recently, Metabolic Scaling Theory (West, Brown & Enquist 1997; Enquist, Brown & West 1998), based on the fractal nature of organisms’ internal transport mechanisms, predicts that  $d = -4/3$ . This hypothesis has received support from broad interpopulation and intertaxa comparisons (Franco & Kelly 1998; Enquist & Niklas 2001; Niklas, Midgley & Enquist 2003). Field data suggest that there may not be a single self-thinning power law with the same exponent for all stands, but rather that the value of the exponent can vary with species (Pretzsch 2006), environmental factors (Deng *et al.* 2006) and even biotic interactions (Zhang *et al.* 2010). Furthermore, plants’ allometric growth, specifically the change in plants’ shape as they grow, has been reported to have an important influence on the slope of the self-thinning line (Miyanishi, Hoy & Cavers 1979; Weller 1987b; Wang *et al.* 2004; Dai *et al.* 2009).

It has been difficult to test these alternative hypotheses definitively because (i) experimental data on self-thinning are resource demanding, as each harvested population yields only one data point, (ii) forest data on mass are rarely based on harvests but rather on estimates from static linear measurements, which are biased when applied to allometric growth (Weiner & Thomas 1992), and (iii) the large natural variation means that distinguishing between the slopes  $-1/2$  and  $-1/3$  statistically requires more data than are usually available.

All models assume that the self-thinning trajectory is independent of the initial density, that is, stands with different initial densities will converge on the same trajectory (Fig. 1), although we know of no studies that specifically tests this. If plant allometry influences self-thinning but is also altered by competition, it is reasonable to predict that crowded stands grown at different initial densities may thin along different lines. At higher initial densities, plants will interact earlier, when they are smaller, so changes in allometry due to competition will also begin when plants are smaller.

While many studies of self-thinning have focused on the value of and variability in the  $M$ – $N$  exponent (Weller 1987a,b; Lonsdale 1990; Deng *et al.* 2006; Dai *et al.* 2009), there has been much less discussion about variability in and the biological significance of the intercept  $\log K$  (White 1981; Lonsdale & Watkinson 1983). The parameter  $K$  has the unit  $\text{g m}^{-3}$ , reflecting biomass packing by plants (White 1981), which could be due to the density of plant tissues or growth form. If self-thinning is driven by interactions in three-dimensional



**Fig. 1.** Standard view of self-thinning trajectory as independent of initial density. All initial densities join the same trajectory when self-thinning becomes extensive.

space, such as physical space filling or competition for light,  $\log K$  will vary with the density of the material. If we imagine two species that are identical except for the density of their tissues or their architectural compactness, they will have the same thinning exponent but different coefficients.  $\log K$  has been shown to vary considerably among (Weller 1989) and within (Westoby & Howell 1986; Duarte & Kalff 1987) plant stands. It has a range of values restricted to one order of magnitude: for a wide variety of species,  $\log K$  lies between 3.5 and 4.4 (when  $M$  is measured in  $\text{g plant}^{-1}$  and  $N$  in  $\text{plants m}^{-2}$ ), with only a handful of examples transgressing a value of  $\log K = 4.4$  (White 1980). Some of this variability can be attributed to quantifiable differences in plants’ growth forms (Lonsdale & Watkinson 1983; Norberg 1988) or environmental conditions such as light intensity (Dunn & Sharitz 1990) and soil fertility (Morris 1999). For example, there is evidence that grasses tend to have higher  $\log K$  values than dicotyledons and that coniferous trees have higher  $\log K$  values than deciduous trees (Lonsdale & Watkinson 1983), which appears consistent with the hypothesized role of tissue density and architectural compactness.

We grew crowded experimental populations of *Fagopyrum esculentum* at three initial densities to ask the following questions:

- 1 Does initial density affect the self-thinning trajectory, or do all stands converge on the same trajectory?
- 2 Do biomass–density relationships among populations of one species reflect self-thinning trajectories within populations?
- 3 Are the self-thinning exponents more consistent with the Self-thinning Rule or the predictions of Metabolic Scaling Theory?
- 4 How does height–diameter allometry and the resultant plant shape change over density and time as stands develop?

Our specific hypotheses are as follows: (i) self-thinning trajectories differ among different initial densities, (ii)

interpopulation patterns are fundamentally different from self-thinning trajectories and (iii) the height–diameter allometric relationship is plastic in response to increasing intraspecific competition and changes during growth, influencing plant shape and the biomass–density relationship.

## Materials and methods

### STUDY SPECIES

*Fagopyrum esculentum* Moench (common buckwheat; Polygonaceae) is a widely cultivated, broad-leaved, erect annual with a single main stem, a sympodial branching form, a short taproot and fine lateral roots (Campbell 1997). It grows well on infertile soil and land that has recently been cleared for cultivation and requires a moist and cool temperate climate. Emergence can occur as early as 4 day after planting. The plant usually grows rapidly, reaching 0.6–1.3 m in height depending upon environmental conditions, and it flowers prolifically over a period of several weeks. Although *F. esculentum* can compensate for low density by increased branching, a high seeding rate is generally used to promote faster canopy cover.

### EXPERIMENTAL DESIGN

The experiment was conducted at the Ecological Research Station for Grassland Farming (ERGS), Chinese Academy of Sciences, Changling County, Jilin Province, China (123°44'E, 44°40'N), in 2009. Seeds of *F. esculentum* were purchased from the ChunYu Seed Co. and were stored in dark at room temperature (18–20 °C) before sowing.

The experiment was a completely randomized design with three initial densities and harvested on six occasions. A total of 72 plastic pots (28 cm diameter, 30 cm height) were filled with 'Pro-Mix' potting soil to a soil depth of 23 cm. The soil contained 2.0 g kg<sup>-1</sup> total N, 0.9 g kg<sup>-1</sup> extractable P and 1.5 g kg<sup>-1</sup> extractable K. Sowing occurred on 24 July 2009. Before sowing, a fine layer of soil was sieved over the pots to provide a surface as smooth as possible with minimal spatial heterogeneity. Seeds were sown at the rate of 500, 1500 or 3000 seeds per pot, equivalent to 8000, 24 000 or 48 000 seeds m<sup>-2</sup>. Populations were established by sowing seeds of *F. esculentum* at the surface of substrate, which was then covered with a thin layer of sandy soil. Seeds were scattered as evenly as possible onto the surface. Each density was replicated four times. The replicate pots for each density and harvest were then arranged in randomized blocks. Pots within a block were arranged in groups according to sowing densities and were packed closely together and then surrounded by a row of guard pots. As the plants grew *c.* 10 cm above the soil surface, a shade cloth collar was added around each pot and up to *c.* 2.5 cm below canopy height to minimize edge effects (Morris 1996). Successively higher collars were added as growth continued. Pots were watered as required and sprayed periodically against Lepidopteran pests (trichlorfon) and fungal pathogens (carbendazim). Regular manual weeding of non-target vegetation was performed, and no additional nutrients were supplied during the growing season.

### SAMPLING

Samples were harvested 12, 22, 32, 42, 54 and 64 day after sowing. At the final sampling, seeds of plants were nearing maturity, but there

was no sign of withering. At each harvest and for each density, four pots, one from each block, were randomly selected and sampled. To estimate the plant density and avoid edge effects, a circular steel ring with an internal diameter of 10.5 cm was positioned in the centre of each pot. Surviving plants within the ring were counted and cut at the soil surface; the total number within the quadrat was converted to density per m<sup>2</sup> (N). Dry mass determinations were made after oven-drying 48 h at 80 °C. Total above-ground biomass was converted to biomass m<sup>-2</sup> (B).

A random subsample of 9–13 individuals, excluding a few (< 10 individuals) distinctly different, extremely large and small individuals, was selected from each sampled population for height (h) and stem diameter (r) measurements. Height from the soil surface to the terminal shoot apex was measured to the nearest 1.0 mm. Diameter of the stem below the cotyledons was measured to the nearest 0.01 mm with electronic callipers.

As the two-dimensional area available to the plants within a pot remained constant, the volume of space occupied by the population (V) is directly related to the height of the canopy (Lonsdale & Watkinson 1983). Thus, the biomass density of the population (biomass per unit volume of space, B/V) was calculated as the ratio of plant biomass and mean height of the plants (units: g m<sup>-3</sup>) for each quadrat.

### DATA ANALYSIS

Self-thinning lines were fit to data points on the log biomass–log density plot, as the use of mean, rather than total, plant mass in the analysis of self-thinning has been criticized for statistical (Weller 1987a) and biological (Westoby 1984) reasons. The criteria of Morris (1996) were used to differentiate pre-thinning and thinning data points. Only the data from populations that showed the characteristics of self-thinning, that is, biomass accumulation with a substantial reduction from the initial density, were included in the analysis. This excluded the first harvest for all densities, but none of the later harvests, giving 60 plots. To compare effects of initial density on the biomass–density (B–N) relationship, each initial density was modelled separately, and we also analysed data for all densities and harvests together.

The slopes and the intercepts of biomass–density relationship, height–diameter relationship, biomass–canopy volume relationship and mean height–mean shoot mass relationship were estimated by the standardized major axis (SMA; SMATR version 2.0, <http://bio.mq.edu.au/ecology/SMATR/>) regression on log–log-transformed data, as there is not a dependent and an independent variable, and both variables have errors. For all lines, the 95% confidence intervals for the slopes and intercepts were calculated. Comparisons of slopes and intercepts of the self-thinning trajectories and each allometric relationship for populations among densities were performed in SMATR. First, a test of heterogeneity in slopes among the three density treatments was run (Warton *et al.* 2006). If *P* > critical value, we assume the slopes are not different, and we tested for differences in intercept. If there were significant differences in intercept of the data sets with a common slope, pairwise *post hoc* multiple comparisons (WALD test) among groups were used to identify which groups differ. Second-order polynomial regression on log-transformed data was used to test for signs of curvilinearity in the height–diameter allometric relationships (Weiner & Thomas 1992).

The effects of initial density and log density on log biomass were tested with general linear models. A multivariable analysis was used to test for interactions between initial density treatment and log

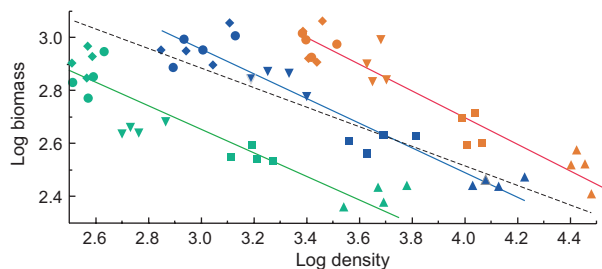
density. The effects of initial density on height-to-diameter ratio (H/D) and biomass density were compared by one-way analysis of variance (ANOVA) after testing for homogeneity of variance and log transforming the data if necessary to achieve homogeneity. The Duncan test at the 5% confidence level was used for comparisons.

## Results

### EFFECTS OF INITIAL DENSITY ON BIOMASS–DENSITY RELATIONSHIP

The log biomass–log density trajectory was significantly different among the three initial density treatments (Fig. 2). Initial density did not affect the allometric slope  $c$  (test statistic = 1.146,  $P = 0.570$ ), but there was a clear and significant effect on the coefficient  $\log K$  (test statistic = 295.24,  $P < 0.001$ ; Fig. 2 and Table 1): populations sown at higher densities had significantly more biomass at a given density of survivors. There is no evidence of an interaction between initial density and  $\log N$  ( $P = 0.421$ , Table 2). All three slopes are close to  $-1/2$  and significantly different from  $-1/3$  (Table 1).

If all the data for all 3 densities and 5 harvests are considered as a single data set, the distribution appears linear with an estimated slope close to  $-1/3$  and significantly different from  $-1/2$  (Fig. 2 and Table 3).



**Fig. 2.** Relationships between log shoot biomass and log density for *Fagopyrum esculentum* grown at 3 initial densities: 8000 (green), 24 000 (blue) and 48 000 (orange) ind.  $m^{-2}$  at harvest 2 (▲), 3 (■), 4 (▼), 5 (●) and 6 (◆). The dashed line represents the orthogonal (SMA) regression line where data for all densities and harvests were analysed together (Table 3). The three solid lines represent regression lines where data from self-thinning populations under different initial densities were analysed separately (Table 1).

**Table 1.** Estimated regression parameters of log shoot biomass–log density relationships in populations of *Fagopyrum esculentum* undergoing self-thinning grown at three initial densities, fitted by the SMA regression

Initial density (ind. $m^{-2}$ )	$n$	$r^2$	Slope	95% CI of slope	Intercept	95% CI of intercept
8000	20	0.829***	-0.445	-0.545, -0.363	3.988	3.717, 4.260
24 000	20	0.893***	-0.466	-0.547, -0.396	4.354	4.095, 4.613
48 000	20	0.906***	-0.504	-0.586, -0.433	4.715	4.423, 5.006

Data from self-thinning populations grown at different initial densities were fitted separately.

\*\*\* $P < 0.001$ .

**Table 2.** General linear model of the effects of initial density and log density on log biomass

Effect	df	SS	$P$
Log N	1	2.064	< 0.001
Initial density	2	1.220	< 0.001
Log N $\times$ density	2	0.009	0.421

**Table 3.** Regression parameters for log shoot biomass–log density relationship in populations of *Fagopyrum esculentum* undergoing self-thinning grown at three initial densities, estimated by the SMA regression

$n$	$r^2$	Slope	95% CI of slope	Intercept	95% CI of intercept
60	0.290***	-0.377	-0.470, -0.303	4.023	3.736, 4.311

Data for all densities and harvests were analysed together.

\*\*\* $P < 0.001$ .

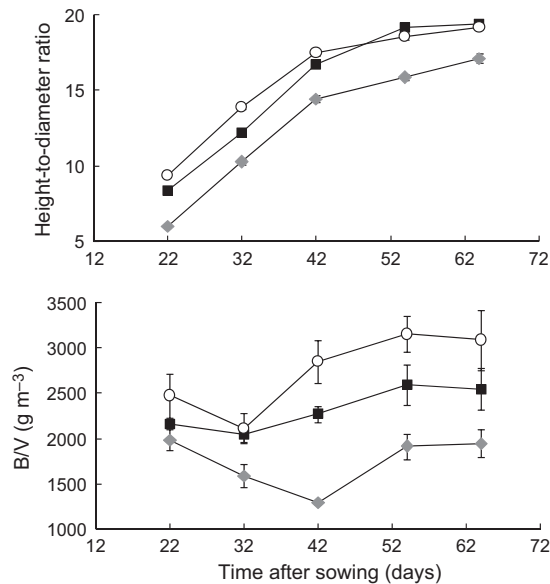
### EFFECTS OF INITIAL DENSITY ON METRICS OF PLANT GROWTH AND FORM

*Post hoc* tests for height-to-diameter ratio and biomass density were performed among densities at all harvests. Initial density had a strong effect on H/D of plants throughout the experiment ( $P < 0.001$ ). Plants grown at the lowest density had the lowest H/D (Fig. 3). The H/D did not differ between the two higher densities at the final harvest ( $P = 0.245$ ), although there were clear and significant differences prior to this period ( $P < 0.001$ ). As plants grew, the value of H/D increased at all densities (Fig. 3).

B/V significantly increased with initial density throughout the growing season (Fig. 3), even though values of B/V varied between successive harvests.

### ALLOMETRIC RELATIONSHIPS

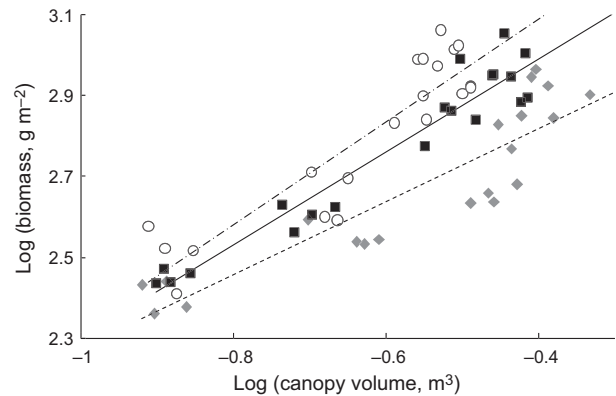
Initial density did not significantly affect the slope of the allometric relationship between biomass and canopy volume or height of population (test statistic = 5.016,  $P = 0.076$ ), whereas there was a strong effect on the intercept (test statistic = 44.950,  $P < 0.001$ ; Table 4). Populations sown at higher densities supported significantly more biomass per unit volume for a given canopy height (Fig. 4).



**Fig. 3.** Trajectories of height-to-diameter ratio (H/D) and biomass per unit volume of the population (B/V) for *Fagopyrum esculentum* grown at 3 initial densities: 8000 (◆), 24 000 (■) and 48 000 (○) ind. m<sup>-2</sup> over time (day 22 to day 64). Error bars represent one standard error.

The slope of allometric relationship between mean height and mean shoot mass was significantly different among the three initial density treatments (test statistic = 7.847,  $P = 0.021$ ; Table 5), and the position of this line was higher at higher densities. For a given shoot mass, plants grown at higher densities had greater height (Fig. 5).

For all three density treatments, populations undergoing self-thinning generally showed a linear relationship between log height and log diameter throughout the experiment (Fig. 6), but there were also signs of curvilinearity ('complex allometry', Jolicœur 1989; Weiner & Thomas 1992) in some harvests. For convenience in making comparisons, we used simple allometric equations to fit height-diameter relationships for all densities and harvests. There were significant differences in the log height-log diameter relationships among different density treatments over time. While the relationship between log height and log diameter clearly differed initially in intercept, it became less different with time at the two higher densities and eventually almost converged to a single relationship by day 64 (Fig. 6). Difference in slopes between the lowest density and the higher ones increased over time, while the two higher densities diverged a bit and then converged (Fig. 6). At 22 and 32 days, intercepts of



**Fig. 4.** Relationships between log biomass and log canopy volume for *Fagopyrum esculentum* grown at 3 initial densities: 8000 (◆), 24 000 (■) and 48 000 (○) ind. m<sup>-2</sup> at harvest 2–6. Parameters estimates are presented in Table 4.

log height-log diameter relationships differed significantly among densities ( $P < 0.001$ ), but there were no clear differences in slopes ( $P > 0.05$ ; Table 6). At 42 and 54 days, there was clear and significant difference in the slope of log height-log diameter relationships among densities ( $P < 0.001$ ; Table 6). On day 64, the log height-log diameter relationship differed significantly in slopes between the lowest density and the two higher ones ( $P < 0.001$ ), which did not differ significantly in slopes ( $P = 0.056$ ) or intercept ( $P = 0.082$ ; Table 6) between the two higher densities.

## Discussion

### EFFECTS OF PRE-THINNING DENSITY

Although all studies to date assume that the initial pre-thinning density does not alter the self-thinning trajectory (Fig. 1), our results show that this is not always the case. Although initial sowing density did not affect the self-thinning slope, there was a clear and highly significant effect of sowing density on the intercept. Populations sown at higher initial densities had greater biomass at all densities during the course of self-thinning. We present two possible explanations for this:

**1** Population density can alter the growth and form of plants (Weiner & Thomas 1992; Anten & Hirose 1998; Stamp *et al.* 2004) through modifying the amount of resources available to individuals within a population. Height-diameter allometry and the resultant height-to-diameter ratio of plants change

**Table 4.** Regression parameters of log shoot biomass-log canopy volume relationships in populations of *Fagopyrum esculentum* undergoing self-thinning grown at three initial densities, estimated by the SMA regression

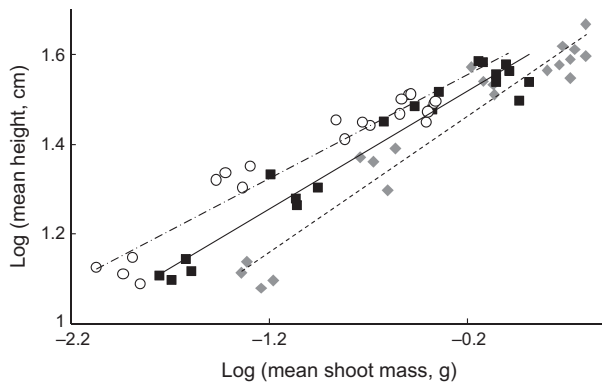
Initial density (ind. m <sup>-2</sup> )	<i>n</i>	<i>r</i> <sup>2</sup>	Slope	95% CI of slope	Intercept	95% CI of intercept
8000	20	0.812***	1.004	0.811, 1.242	3.237	3.109, 3.364
24 000	20	0.929***	1.194	1.047, 1.362	3.479	3.381, 3.577
48 000	20	0.821***	1.403	1.139, 1.727	3.681	3.492, 3.870

\*\*\* $P < 0.001$ .



**Table 5.** Regression parameters of log mean height–log mean shoot mass relationships in populations of *Fagopyrum esculentum* undergoing self-thinning grown at three initial densities, estimated by the SMA regression

Initial density (ind. m <sup>-2</sup> )	<i>n</i>	<i>r</i> <sup>2</sup>	Slope	95% CI of slope	Intercept	95% CI of intercept
8000	20	0.938***	0.313	0.276, 0.354	1.527	1.501, 1.553
24 000	20	0.949***	0.269	0.241, 0.301	1.576	1.549, 1.603
48 000	20	0.925***	0.242	0.211, 0.276	1.613	1.576, 1.651

\*\*\**P* < 0.001.**Fig. 5.** Relationships between log mean height and log mean shoot mass for *Fagopyrum esculentum* grown at 3 initial densities: 8000 (◆), 24 000 (■) and 48 000 (○) ind. m<sup>-2</sup> at harvest 2–6. Parameters estimates are presented in Table 5.

across densities and over time in our study, suggesting that initial density can alter plant allometry and cause major alterations in plant shape. At higher densities, interactions between plants will begin earlier, when plants are smaller. If competition affects plant allometry, it will affect it more and earlier at higher densities. If these changes affect self-thinning trajectories, then it is reasonable to expect that initial density has consequences for the thinning trajectory. If plants grown at higher densities have denser tissues, or a more compact growth form, the population will support more biomass at a given density.

2 Often, larger plants have a disproportionate advantage over small plants and suppress their growth, a phenomenon called ‘size-asymmetric competition’ (Stoll *et al.* 2002). Similarly, ‘size-symmetric competition’ implies that competitive effects of larger and smaller individuals are proportional to size (Weiner 1990). The size symmetry of competition alters the self-thinning intercept in simulation models, with size-symmetric competition allowing more biomass at a given density than size-asymmetric competition, and there is also experimental support for this (Stoll *et al.* 2002). This occurs because larger plants grow more slowly and smaller plants die more slowly under size-symmetric than size-asymmetric competition. If earlier, higher density competition tends to be more size symmetric, this could account for the increased biomass for a given density of survivors in initially higher density plots.

The two possible explanations are not exclusive and may be related. Earlier, higher density competition might be more size symmetric because of changes in allometric growth and

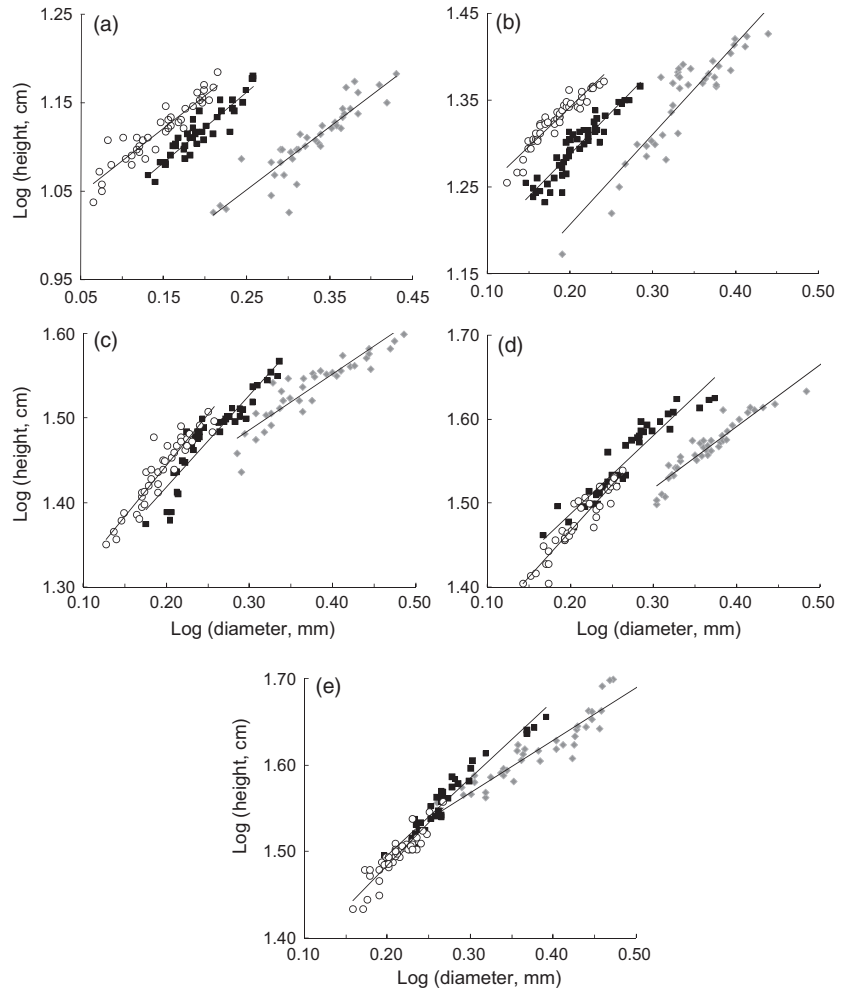
therefore plant shape during growth. The size asymmetry of competition is primarily if not solely due to shading. Density-induced changes in allometric growth and plant shape, especially canopy shape and extension, may reduce the advantage of being larger than neighbours.

It is of course possible that effects of initial density on the self-thinning trajectory are transient, and the different thinning trajectories would have eventually converged if growth had not ceased due to resource/space limitations, but there was no sign of this over the course of the experiment.

#### PLASTIC ALLOMETRY, BIOMASS PACKING AND THE MASS–DENSITY RELATIONSHIP

Allometric growth and density-dependent mortality occur simultaneously during self-thinning, and both the value of the intercept and slope of self-thinning trajectory reflect the change in an individual’s allometric pattern as the population density decreases (Wang *et al.* 2004). Field data collected across a moisture gradient showed that height–diameter allometric exponents vary with plant density, influencing biomass–density relationships (Deng *et al.* 2006). In our study, plants of a given height growing at higher densities are thinner and lighter than plants of the same height growing at lower initial densities. These results reflect the well-documented observation that plants allocate proportionately more biomass to height growth and less to diameter growth when growing at higher densities. These changes in above-ground plant form can be attributed in large part to changes in light quality (low-red : far-red ratios; Smith & Whitelam 1997) and quantity with increasing population density (Mitchell & Woodward 1988). The change in plant form during growth has been shown to alter the speed at which size hierarchies develop and therefore should affect self-thinning dynamics (Ellison 1987). As more height growth at the expense of radial extension means less contact with neighbours, more biomass can be added for a given amount of mortality (Weller 1987b).

These changes influence biomass packing, an important determinant of the self-thinning intercept (Lonsdale & Watkinson 1983; Morris 2003). As we argue above, if self-thinning is driven by interactions in three-dimensional space, such as physical space filling or competition for light, log *K* will vary with the biomass density of the plants. Initial density could affect the intercept by altering allometric growth in a way that influences architectural compactness, reflected in B/V and the B–V allometric relationship.



**Fig. 6.** Relationships between log height and log diameter for *Fagopyrum esculentum* grown at 3 initial densities: 8000 (◆), 24 000 (■) and 48 000 (○) ind. m<sup>-2</sup> at harvest 2 (a), 3 (b), 4 (c), 5 (d) and 6 (e). Parameters estimates are presented in Table 6.

**Table 6.** Regression parameter of log height–log diameter relationships in populations of *Fagopyrum esculentum* undergoing self-thinning grown at three initial densities for all five harvests (22, 32, 42, 54 and 64 day after sowing), as estimated by the SMA regression

Time (d)	Initial density (ind. m <sup>-2</sup> )	<i>n</i>	<i>r</i> <sup>2</sup>	Slope	95% CI of slope	Intercept	95% CI of Intercept
22	8000	40	0.814***	0.789	0.685, 0.908	0.848	0.811, 0.885
22	24 000	40	0.864***	0.858	0.760, 0.968	0.951	0.931, 0.972
22	48 000	40	0.858***	0.797	0.704, 0.901	1.002	0.987, 1.017
32	8000	40	0.838***	1.131	0.992, 1.291	0.968	0.916, 1.019
32	24 000	49	0.862***	1.044	0.936, 1.164	1.078	1.054, 1.102
32	48 000	48	0.898***	0.967	0.880, 1.063	1.150	1.132, 1.167
42	8000	38	0.848***	0.724	0.635, 0.826	1.264	1.227, 1.300
42	24 000	39	0.863***	1.177	1.041, 1.331	1.177	1.140, 1.215
42	48 000	40	0.874***	1.283	1.142, 1.441	1.188	1.158, 1.218
54	8000	40	0.906***	0.771	0.697, 0.852	1.284	1.256, 1.313
54	24 000	40	0.895***	0.987	0.888, 1.097	1.286	1.258, 1.315
54	48 000	37	0.891***	1.161	1.037, 1.300	1.235	1.207, 1.262
64	8000	40	0.906***	0.640	0.579, 0.708	1.373	1.348, 1.399
64	24 000	37	0.928***	0.928	0.847, 1.018	1.307	1.284, 1.331
64	48 000	40	0.825***	1.084	0.945, 1.244	1.266	1.234, 1.297

\*\*\**P* < 0.001.

#### MASS–DENSITY RELATIONSHIPS AMONG AND WITHIN POPULATIONS

If all the data for all three densities and five post-thinning harvests are considered as a single data set, the results are

consistent with the predictions of Metabolic Scaling Theory, but not the Self-thinning Rule. If the independent treatment variable is included in the analysis, a different picture emerges (Fig. 2 and Table 1): self-thinning trajectories are

consistent with the Self-thinning Rule but not Metabolic Scaling Theory. Thus, our results point towards a resolution of some of the debates concerning mass–density relationships in organisms. The search for generality in nature, modelled after physics, has encouraged researchers to look for general quantitative patterns that are independent of time and space, as well as species and environment (West, Brown & Enquist 1997; Enquist, Brown & West 1998). Indeed, broad patterns are an important starting point for macroecology and a source of theories and hypotheses. But in the biological world, much of the variation within the broad patterns is real, and it is not ‘noise’ but rather consists of many other ‘signals’, which do not parallel the overall trend but reflect processes occurring at different levels of biological organization (Price, Enquist & Savage 2007). The  $-1/3$  scaling of density applies generally among populations or species and encompasses much variation. This broad ‘envelope’ is made of lower-level relationships, many of which scale around  $-1/2$ . In this study, the only difference among the treatments is the initial density, yet both of the patterns hypothesized from two very different theories can be observed in the data. It has become clear that broad, static, interspecific allometric patterns are fundamentally different than dynamic self-thinning trajectories, although these have been conflated in much of the literature.

Species will vary in their tissue density, depending on factors such as lignin versus cellulose concentration, water content, etc., and in their architectural compactness due to differences in growth form. Even if the self-thinning exponents were universal, differences in the self-thinning coefficient among populations and species, combined with differences in the range of data in different studies, will create an overall pattern that has a different slope than the component populations (Weller 1989). The overall pattern is therefore more difficult to explain than some of the component patterns, such as self-thinning trajectories.

Our results suggest that biophysical and geometric constraints on how plants occupy space when crowded are more important than internal transport mechanisms and metabolism in determining the biomass–density trajectory of crowded stands. Our results emphasize the need for more comprehensive, reductionist theories that can explain higher-level phenomena in terms of lower-level mechanisms, rather than the search for single mechanisms that operate across all scales.

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