ORIGINAL RESEARCH

Evidence of Phenotypic Plasticity in the Response of *Fagopyrum esculentum* to Population Density and Sowing Date

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Abstract Phenotypic plasticity is an important attribute that enables plants to survive across a range of environments. We conducted two experiments to investigate the plasticity of architectural traits and biomass ratios for *Fagopyrum esculentum* Moench in response to population density and sowing date. These included (1) inter-planting distances of 5, 10, 15, or 20 cm; and (2) sowing on 25 July, 1 August, 5 August, or 10 August. Many traits exhibited phenotypic plasticity that was coupled with changes in plant size. However, variations in leaf/mass ratio from either experiment, as well as leaf/root ratios in response to sowing date, were independent of size. When coefficients of variation were computed, some consistency was found in the magnitude of trait plasticity for both density and sowing date. For each experiment, leaf/root ratios, leaf/mass ratios, and stem/mass ratios were most plastic. Although this suggests that biomass ratios could be more responsive to environmental changes, a wide array of traits should be considered if we are to fully understand the mechanism for these phenomena.

Keywords Architectural traits · Biomass ratios · Plant size · Passive plasticity · Stem elongation · True plasticity

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Phenotypic plasticity is the ability of organisms to vary their morphology and physiology depending on their growth habitat (Bradshaw 1965; Schlichting 1986; West-Eberherd 2003). It is critical for plant species that live where environmental factors fluctuate both spatially and temporally (Schlichting 1986; Sultan and Bazzaz 1993). Although this attribute has been known since the beginning of the twentieth century, only in the last 15 years has it been recognized as an important source of diversity (Sultan 2000). Since then, many studies have demonstrated that plasticity is a major source of phenotypic variation, contrary to an earlier (neo-Darwinian) view of this variation as trivial "noise" (Sultan 2004).

Phenotypic variation can be due either solely because of differences in growth rates under environments with contrasting resource availability, i.e., "passive plasticity" (Coleman et al. 1994; Wright and McConnaughay 2002) or else as a result of "active plasticity" (Weiner 2004), in which fluctuations in growth trajectories are induced by changes in the environment that lead to ontogenetic or true plasticity (Wright and McConnaughay 2002). To distinguish between these two types, comparisons must be made as a function of plant size (allometrically). A plastic change that is independent of size is more likely to arise from an adaptive rather than a passive response to the environment (Moriuchi and Winn 2005).

Most phenotypic studies have been conducted under controlled conditions, where certain resources (e.g., light or nutrients) have been artificially supplied (Gedroc et al. 1996; Müller et al. 2000; Navas and Garnier 2002; Bonser and Aarssen 2003; Bell and Galloway 2007; Zhang et al. 2008). However, in nature, differences in population densities and seedling emergence dates are two selection pressures that can modify the amount of resources available to individuals within a population (Sadras et al. 1997;

Bouvet et al. 2005; Zhou et al. 2005; Wang et al. 2006). For example, the success of seeds sown at high densities is limited by light as a result of shading (Weiner and Fishman 1994; Bell and Galloway 2007). Seeds that germinate later in the growing season may receive insufficient radiation to complete their life cycle (Zhou et al. 2005; Wang et al. 2006). Little research has been focused on the effect of sowing date on phenotypic plasticity, but thus far has instead concentrated on reproductive allocation (Sadras et al. 1997; Zhou et al. 2005; Wang et al. 2006).

A logical corollary for modular organization is that the plasticity of the whole plant depends on both the component parts or traits that exhibit plasticity, and the nature of that plastic response. Moreover, traits may differ in the magnitude of their plastic responses to different resources, thus resulting in a "hierarchy" of responses (White 1979; Navas and Garnier 2002). This underscores the importance of considering a wider range of plant traits (Ryser and Eek 2000) rather than relying on very broad categories, such as root versus shoot biomass (Gedroc et al. 1996; Müller et al. 2000). In fact, Ryser and Eek (2000) and Navas and Garnier (2002) are part of the only research groups known to have evaluated the magnitude of plasticity for individual traits.

Here, our aim was to enhance our understanding of phenotypic plasticity in plants by manipulating the sowing date and population density of an annual species, *Fagopyrum esculentum* Moench. We examined the norms of reaction for some selected architectural traits and biomass ratios. Our hypotheses were that (1) the species would react significantly to changes in density and emergence date, (2) these responses would reflect "true" plasticity, and (3) such changes would be related to a hierarchy of plastic responses among traits.

Materials and Methods

Study Species

F. esculentum Moench is a broadleaf, herbaceous plant that grows rapidly and flowers prolifically over several weeks. Seedlings can emerge as soon as 4 days after sowing. Plants typically mature in 75 to 90 days and can be 0.6 to 1.2 m tall depending on environmental conditions. Growth form primarily shows sympodial branching. When the terminal bud ceases elongation (usually because a terminal flower has formed), an auxiliary bud or buds become the new main shoots, i.e., the renewal shoots.

Experimental Design and Treatments

Two experiments were conducted in 2006 at the Ecological Research Station of Northeast Normal University, Changling County, Jilin Province, China (123°44 E, 44°40 N). Experiment 1 for population density compared among plants that developed from seeds sown at spacings of 20, 15, 10, or 5 cm, which represented a low (L), medium (M), high (H), or very high (HH) density, respectively. All seeds for this evaluation were sown on 25 July. Experiment 2 analyzed the success of sowings (all at a 20-cm spacing) on 25 July, 1 August, 5 August, or 10 August. These experiments and treatments corresponded to the natural growing conditions for this species in our study location. One trial (treatment L sown on 25 July) was common to both experiments. A completely randomized design was implemented with three replicates, and individual plots were 3 m×3 m. All plots were irrigated, and N fertilization was supplied at the recommended rates to prevent water and nutrient stresses. Undesired weeds and insects were adequately controlled. At maturity (i.e., when about 80% of the plants in a treatment had fully produced seeds), ten plants per replicate (30 per treatment) were excavated and the number of branches per plant was recorded. Whole-plant biomass (hereafter referred to as total plant biomass) and leaf to root ratios were obtained after oven drying the samples at 65°C for 48 h. Stem/mass ratios or leaf/mass ratios were calculated as the ratio of stem or leaf biomass, respectively, to total biomass. Stem length, basal stem diameter, total branch length, and number of internodes also were measured. The dry masses of seeds and flowers were termed "reproductive biomass" (Table 1).

Data Analysis

All data were analyzed with a general linear model procedure (GLM) and SPSS statistical software (version 11.5). To reveal true plastic responses, we accounted for the effect of plant size (McConnaughay and Coleman 1999; Cheplick 2003). This was achieved by using total biomass as a covariate in the general linear model ANCOVA (Navas and Garnier 2002; Bell and Galloway 2007). When the effect of treatment was significant, differences in traits among treatments were assessed by a Bonferroni post hoc test. From ANCOVA, adjusted means corrected for the effect of total plant biomass were calculated for each experiment. Whenever total biomass explained significant variation in a trait response to either density or sowing date, this trait was said to exhibit passive plasticity (McConnaughay and Coleman 1999; Wright and McConnaughay 2002; Weiner 2004). By contrast, any variation in trait expression that was independent of total biomass (size) was considered an indication of true plasticity (Weiner 2004). Thus, we expressed the amount of plasticity for each trait as a coefficient of variation, calculated as: $CV=100\times$ standard deviation of individual treatment means / grand mean of treatment means (Schlichting and Levin 1986; Ryser and Eek 2000; Navas and Garnier 2002). Adjusted means were

Table 1 Field experiments at Changling

Experiment	Treatment code	Sowing date	Plant–plant distance (cm)	Plot size	Number of sampled plants
1	HH	25 July	5	3 m×3 m	30
	H	25 July	10	3 m×3 m	30
	M	25 July	15	3 m×3 m	30
	L	25 July	20	3 m×3 m	30
2	None	25 July	20	3 m×3 m	30
	None	1 August	20	3 m×3 m	30
	None	5 August	20	3 m×3 m	30
	None	10 August	20	3 m×3 m	30

used to represent the degree of plasticity for those traits that were partly influenced by differences in total plant biomass. For those traits that varied independently of total biomass, however, we used their true means to assess the level of plasticity. This value was computed separately for density and sowing date experiments. Because the variation in number of internodes from the density experiment was mainly a consequence of the change in total biomass, plasticity was not calculated for this trait.

Results

Almost all traits differed significantly among treatments (Table 2). Plants at the lowest density (L) were relatively large, with significantly higher total plant biomass and significantly longer and more branches compared with those at very high density (HH) (Figs. 1 and 2). The group of plants growing at HH or high density (H) had significantly longer stems than those at the two lowest densities (M and L; Fig. 2a). At HH, plants had a significantly higher stem/mass ratio (SMR), closely followed by plants at H, whereas those at M or L had the lowest SMR (Fig. 3a). Similarly, plants at HH had the highest leaf/mass ratio (LMR) and leaf/root ratio (L/R;

Fig. 3b, c). The differences in these two traits were, however, only significant for those at L.

Plants from seeds sown on 25 July had significantly greater total plant biomass compared with later sowings (Fig. 1b). They also had larger stems, longer branches, and more branches and internodes (Fig. 4). The total number of branches produced in plants from that date was significantly ($p<0.05$) different from that of plants established on 10 August (Fig. 4c). Plants from the first sowing also had a significantly higher SMR (Fig. 5a). Although plants from seeds sown on 10 August were relatively smaller, they had a significantly higher LMR and L/R than those started on 25 July (Fig. 5b, c).

Most of these responses were related to changes in total plant biomass (Table 2). Due to this size dependency, adjusted means varied substantially from true means for the number of internodes (Fig. 2d). Variations in L/R (density), stem length, stem diameter, number and length of branches, and the number of internodes (sowing) could be partially explained by changes in overall total biomass (Table 2). LMR varied independently of total plant biomass in both experiments, while the L/R varied independently of total biomass only in the sowing date experiment (Table 2, Figs. 3b and 5b, c).

Reproductive biomass was significantly reduced in plants at higher densities and with later sowing dates (Fig. 6).

Table 2 ANOVA/ANCOVA to examine variations in architectural traits and biomass ratios for changes in population density and sowing date

Total biomass was used as a covariate when ANCOVA was performed

ns not significant ($p>0.05$)

*$p<0.05$, significant effect

| Traits	Density		Sowing	Date
	Covariate F	Treatment F	Covariate F	Treatment F
Total biomass		34.514*		38.747*
Stem/mass ratio	30.949*	20.525*	39.447*	8.176*
Leaf/mass ratio	0.600 ns	3.055*	0.120 ns	5.188*
Leaf/root ratio	6.709*	4.563*	0.336 ns	3.770*
Stem length	28.287*	10.481*	27.696*	32.138*
Stem diameter	95.214*	5.264*	45.905*	2.814*
Branch length	77.744*	13.198*	65.431*	13.442*
Number of branches	9.451*	4.581*	14.115*	5.090*
Number of internodes	33.057*	0.196 ns	10.176*	11.353*
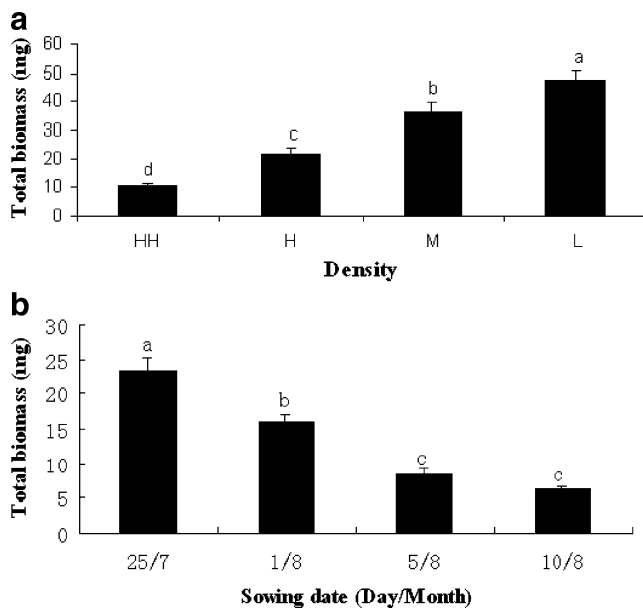
Fig. 1 Variations in total biomass in response to population density (a) and sowing date (b). *Means followed by the same letters* are not significantly different ($p < 0.05$)

Traits differed in their degree of plasticity for the two experiments (Fig. 7). Nevertheless, the pattern of plasticity was consistent for both density and sowing date. There, the L/R, LMR, and SMR were the most plastic, whereas stem length and stem diameter were the least plastic.

Discussion

Although plasticity is a major source of phenotypic diversity in plants, most studies of this have been conducted under controlled conditions (Dudley 2004; Bell and Galloway 2007). The effect of plant development on the expression of traits and investment toward different structures also is often overlooked when assessing environmentally induced plasticity (Coleman et al. 1994; McConnaughay and Coleman 1999). Our study focused on disentangling the effects of density and timing of germination on phenotypic variation due to altered developmental rates, with true plastic shifts of investment into architectural traits and biomass ratios so that we could identify the relationships between adaptive and passive plasticity.

We demonstrated both types of plasticity here (Table 2). Because the availability of resources fluctuated according to density and sowing date, our plants varied in the speed by which they passed through the ontogenetic trajectory (Weiner 2004). The apparent differences in true means for traits could have been a direct effect of developmental stage or plant size (Coleman et al. 1994; McConnaughay and Coleman 1999; Wright and McConnaughay 2002; Weiner
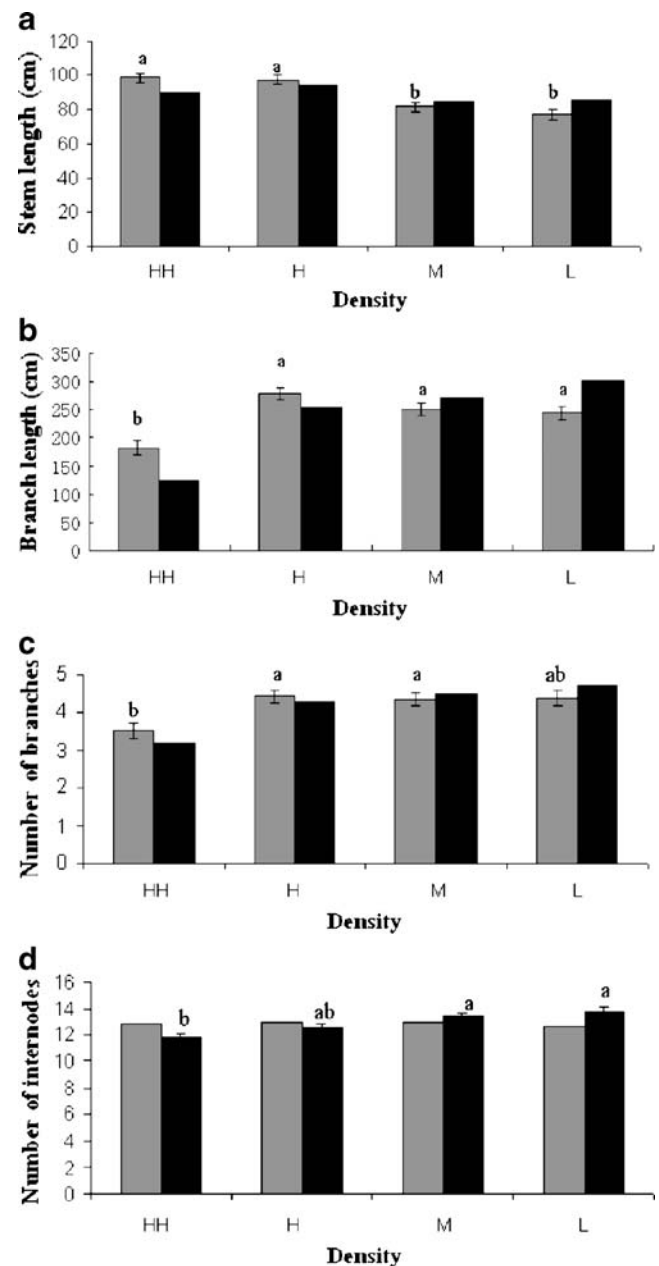
Fig. 2 Variations in stem length (a), branch length (b), number of branches (c), and number of internodes (d) in response to population density. True means are in *black* and adjusted means, corrected for effect of total biomass (see Table 2), are in *gray*. Post hoc test was performed only with adjusted means that showed significant treatment effect. *Means followed by the same letters* are not significantly different ($p < 0.05$)

2004). Often investment toward a range of structures during ontogeny increases exponentially, resulting in overall size differences among traits. Thus, we might conclude that the comparatively low trait values observed from higher densities and later sowing dates indicated that those groups of plants were in the early stages of growth when harvested. By contrast, higher values for the same traits from the low-density and earlier-sown treatments merely meant that those
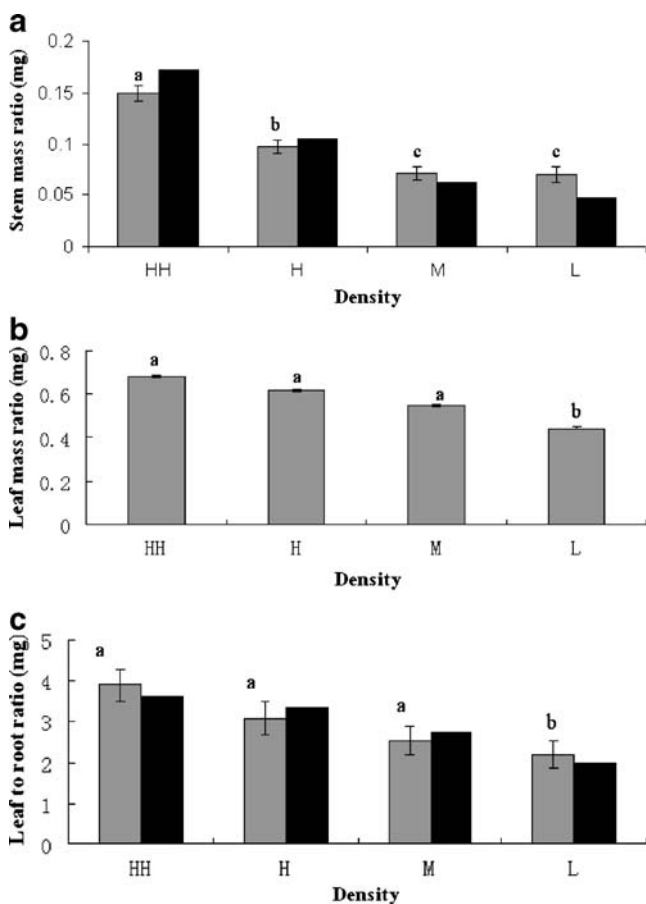
Fig. 3 Variations in stem mass ratio (**a**), leaf mass ratio (**b**), and leaf to root ratio (**c**) in response to population density. True means are in *black* and adjusted means, corrected for effect of total biomass (see Table 2), are in *gray*. Post hoc test was performed only with adjusted means that showed significant treatment effect. *Means followed by the same letters* are not significantly different ($p < 0.05$)

plants had reached later developmental stages. In this case, the differences observed did not necessarily translate into adaptive plastic responses but were due to differences in growth rates (Coleman et al. 1994; McConnaughay and Coleman 1999; Wright and McConnaughay 2002; Weiner 2004).

However, we did find some evidence of true or adaptive plasticity. For instance, when plants shade each other or are grown in environments with limited light, they tend to have a higher L/R (Tilman 1988; Thompson et al. 1992) and/or undergo a characteristic shade-avoidance response that is manifested in their elongation of stems and petioles (Ballaré and Scopel 1991; Schmitt 1993; de Kroon and Hutchings 1995; Sultan 1995; Dudley and Schmitt 1996; Huber and Wiggerman 1997; Gautier et al. 2001; Bell and Galloway 2008). This is precisely what we observed here (Figs. 2a and 3b, c). Even when the effect of total plant biomass was considered and removed, sowing at a high or very high density resulted in plants with significantly longer stems,
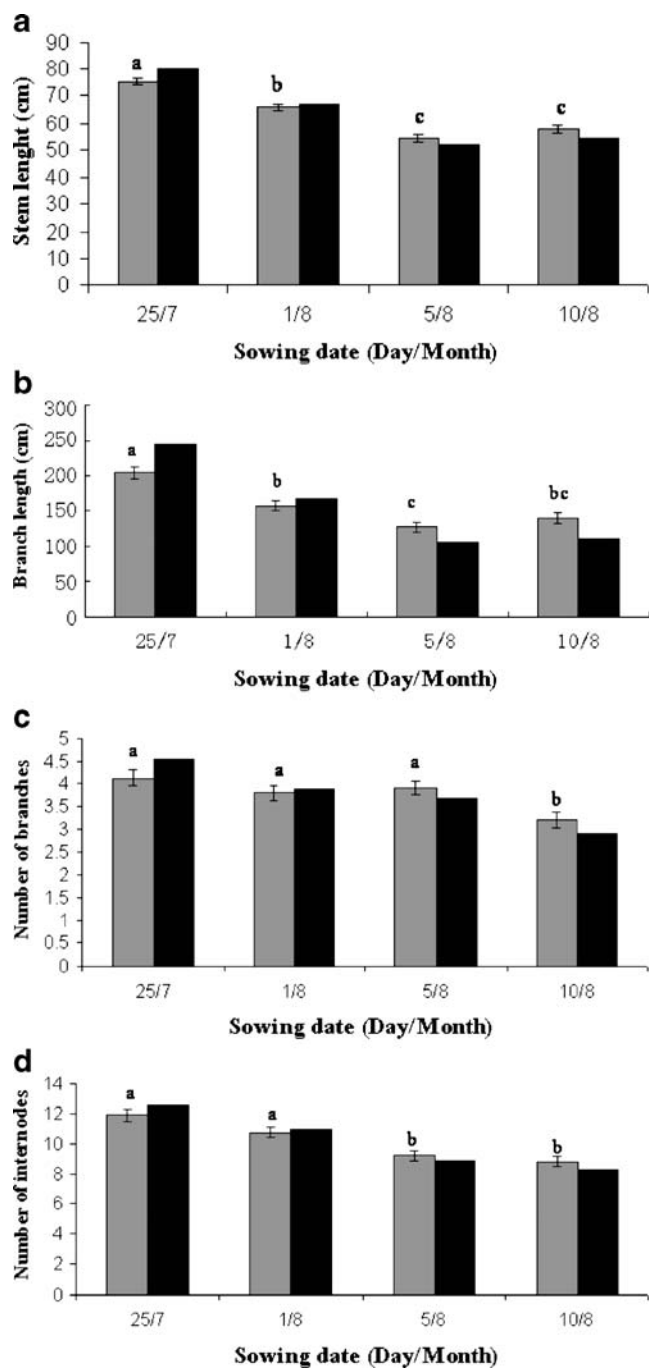
Fig. 4 Variations in stem length (**a**), branch length (**b**), number of branches (**c**), and number of internodes (**d**) in response to sowing date. True means are in *black* and adjusted means, corrected for effect of total biomass (see Table 2), are in *gray*. Post hoc test was performed only with adjusted means that showed significant treatment effect. *Means followed by the same letters* are not significantly different ($p < 0.05$)

higher LMR, and a greater L/R than those at the lowest density. When shading occurred, height could have been an important determinant of success because it enabled a plant to position its leaves above its neighbors for better light interception (Weiner and Fishman 1994; Bell and Galloway
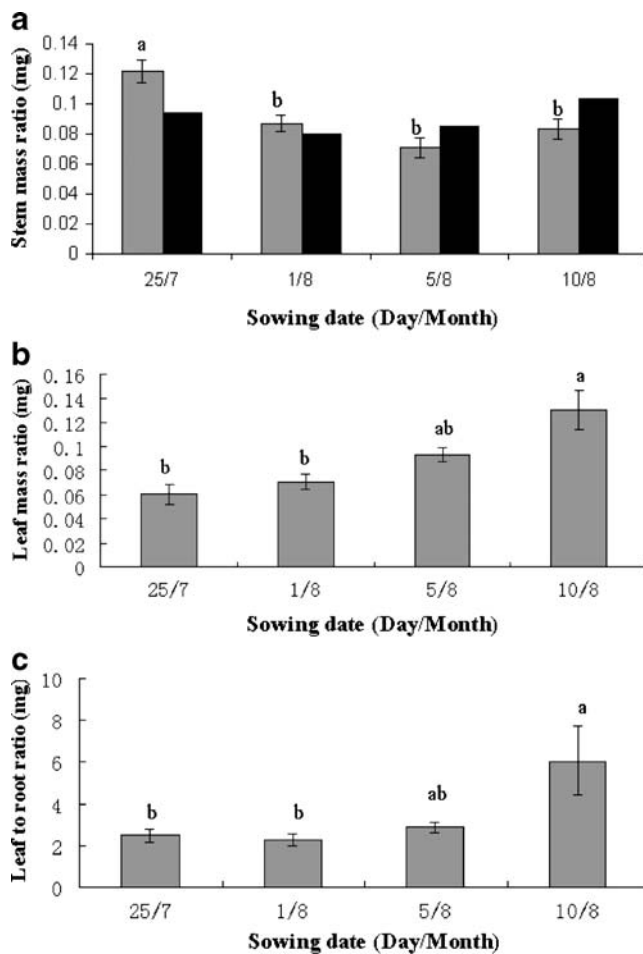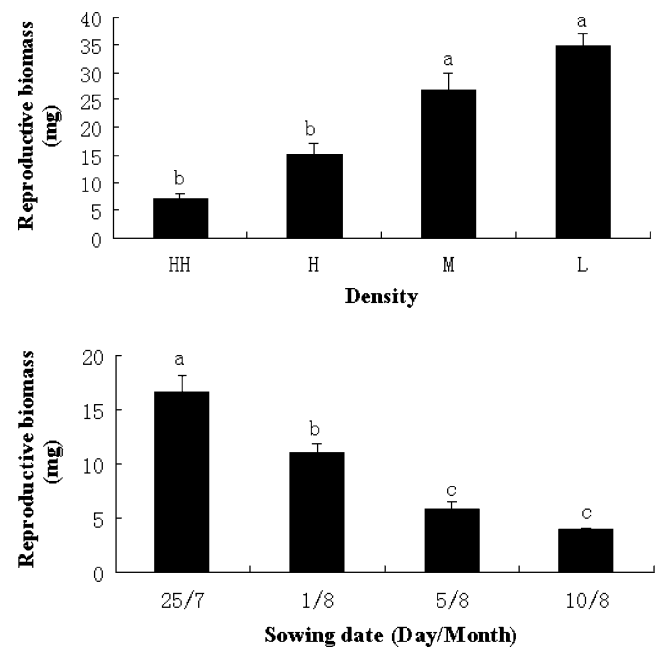
Fig. 5 Variations in stem mass ratio (**a**), leaf mass ratio (**b**), and leaf to root ratio (**c**) in response to sowing date. True means are in *black* and adjusted means, corrected for effect of total biomass (see Table 2), are in *gray*. Post hoc test was performed only with adjusted means that showed significant treatment effect. *Means followed by the same letters are not significantly different* ($p<0.05$)

Fig. 6 Variations in reproductive biomass in response to population density (**a**) and sowing date (**b**). Means followed by *the same letters* are not significantly different ($p<0.05$)

et al. 1985; Hirose 1987; Johnson and Thornley 1987; Dewar 1993).

Navas and Garnier (2002) reported no changes in LMR in response to reduced illumination. These conflicting observations could be partly due to the fact that their study was conducted in controlled environments, e.g., glass-houses. Indeed, contrasting results have been found for stem elongation from an oat variety sown at different densities in the field, as well as in a garden experiment where light was artificially supplied (Semchenko and Zobel 2005). This suggests that this group of plants might experience a different quality of light. Experiments with

2008), rather than because the taller plant had a more efficient photosynthetic mechanism (Schwinning and Weiner 1998). Thus, although the very high-density plants had significantly longer stems (Fig. 2a) and a significantly greater SMR (Fig. 3a), they also had significantly thinner stems (stem diameter) than those at the low density (data not shown). This clearly suggests that the most densely grown plants invested a significant proportion of their biomass toward the stems, to increase lengths, rather than toward the lateral expansion of stem diameter.
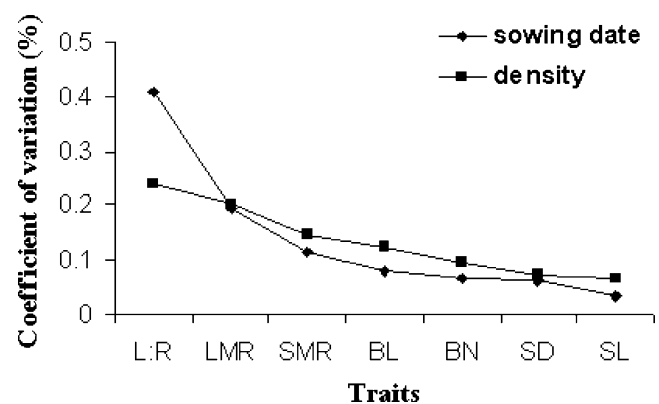
Although such a stem elongation response could improve fitness in dense populations, it could be maladaptive when light is not limiting (Dudley and Schmitt 1996; Pigliucci 2001). This further enhances the plausibility that elongation is adaptive and responsive to very high density (Bell and Galloway 2008). However, a high LMR and greater L/R might enable plants growing at high densities to optimize their capture of light (Bloom

Fig. 7 Coefficient of variation for traits in response to population density and sowing date. *L/R* leaf/root ratio, *LMR* leaf/mass ratio, *SMR* stem/mass ratio, *BL* branch length, *BN* number of branches, *SD* stem diameter, *SL* stem length

altered light availability have been performed under controlled conditions, for example, whole-plant shading versus natural growth in an open field, where only some parts of the plant might be shaded (Zhang et al. 2008).

Another response closely related to that seen with stem elongation was the decrease in length and total number of branches observed in plants grown at very high density (Fig. 2b, c). In fact, branching frequency can be reduced by increased population densities (Sultan and Bazzaz 1993; Callaway et al. 2003, van Kleunen and Fischer 2003). A greater branching intensity is generally associated with the potential for producing new plant modules (Watson and Casper 1984; Geber 1990; Fagerström 1992; Bonser and Aarssen 1996; Watson et al. 1997; Huber and During 2001), which may in turn maximize the final number of reproductive meristems (Duffy et al. 1999; Bonser and Aarssen 2003). Therefore, for an annual species such as *F. esculentum*, which can produce seeds along the length of its axes, a high branching intensity would maximize the number of seeds obtained at the end of the growing season. However, this decline in intensity might be adaptive under shaded conditions where strong apical dominance functions to induce vertical elongation rather than a lateral expansion of branches, thus further enhancing the ability of such individuals to "forage" for light (Schmitt and Wulff 1993; Bonser and Aarssen 2003).

Plants from seeds sown at different dates also showed some truly plastic responses, along with the direct effect of development (Table 2, Figs. 4 and 5). Delayed sowing is often coupled with shorter days, lower temperatures, and reduced radiation (Egli and Bruening 2000). Under these conditions, plants usually respond plastically—being smaller, having shorter and fewer stems and branches, and initiating flowering earlier (Zhou et al. 2005). Similar responses to limited light were suggested by our results. Compared with the first sowing, plants that arose from the last seeding had significantly shorter and thinner stems, fewer and shorter branches, and fewer internodes (Fig. 4). The diminished allocation of resources toward supporting structures, as well as early flowering, may be a strategy by which plants with a condensed, but complete, life cycle can still maintain population persistence, and are able to adapt to unpredictable year-to-year environmental variation (Zhou et al. 2005). Such an allocation strategy appears to benefit annual plants because they have shorter life cycles (Sultan 2000). Our plants from seeds sown on 10 August had a greater LMR and higher L/R compared with the other treatments, and this effect was entirely independent of total plant biomass (Fig. 5b, c). This suggests that a mechanism exists by which these plants retain a very small stature (compare total biomasses in Fig. 1) that is less costly in terms of carbon expenditure. Simultaneously, their investment in structures would improve their capture of limiting resources. Because delayed sowing is associated with decreased solar radiation (Egli and Bruening 2000), having a high L/R would optimize the ability of plants from later-sown seeds to exploit the available light (Bloom et al. 1985; Hirose 1987; Johnson and Thornley 1987; Dewar 1993).

Reproductive biomass was significantly reduced in plants at higher densities and with later sowing dates (Fig. 6). This suggests that, for these groups, investing more in competitive structures was preferred to reproduction. Indeed, researchers such as Waite and Hutchings (1982) have shown that, under unfavorable conditions, plants may invest more in resource-acquiring structures *in lieu of* reproduction.

Clearly the biomass ratios calculated here seemed to be more plastic than the other traits because all except SMR varied independently of total plant biomass (Table 2, Figs. 3b and 5b, c). This was confirmed by our computation for the coefficient of variation (Fig. 7), another index of plasticity (Schlichting and Levin 1986; Ryser and Eek 2000; Navas and Garnier 2002). For both experiments, the L/R, LMR, and SMR were most plastic, suggesting a consistent pattern of hierarchy for plasticity in response to density and sowing date. Biomass ratios can be more responsive than other traits to even slight changes in the environment (Poorter and Nagel 2000; Navas and Garnier 2002). Therefore, we might conclude that biomass ratios were more relevant for evaluating plasticity in response to density and sowing date in the species studied here.

A major limitation when applying biomass ratios, however, is that they do not reflect internal constraints that may control plant growth (Salomonson et al. 1994). Furthermore, the most limiting resources are not always correlated with biomass allocation (Weiner 2004). Plants may also utilize other strategies in response to resource availability—e.g., meristems that remain inactive or a re-allocation toward flowering or branching, depending on the nature of the limiting resource (Bonser and Aarssen 2003). Nevertheless, the responses of other traits that we observed emphasized how imperative it is to consider a wide range of traits to fully understand plant responses to the environment (Ryser and Eek 2000). The elongation of stems under high population density recorded here might be of adaptive value (Ballaré and Scopel 1991; Schmitt et al. 1995) because that trait enables a plant to display its leaves higher in the canopy, where it can capture more light.

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