How does density and nutrient stress affect allometry and fruit production in the heterocarpic species *Atriplex sagittata* (Chenopodiaceae)?

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Abstract: Plants of *Atriplex sagittata* Borkh. were grown under different density and (or) nutrient conditions, and the effect of stress on plant allometry and variation in particular biometrical parameters was studied. Increasing density significantly reduced total weight, basal diameter, stem length, and number of branches. Nutrient deficiency had a negative effect on the total weight and basal diameter only, and the density × nutrients interactions were all nonsignificant. Basal diameter was the best predictor of the total weight, explaining 93.6% of the variation in the whole data set. The relationship between total plant weight and basal diameter was unaffected by growth conditions, indicating that competition determined the position of a plant along the line describing the allometric relationship between both variables but did not seem to alter the relationship. However, the allometric relationships between total weight and stem height and between total weight and number of branches found at low density were significantly different from those at high density, indicating a faster increase in total weight at low densities. Branching, and consequently plant form, were affected by competition. Branch length consistently increased with total plant weight in plants grown under high density, but for low density plants, such an increase was recorded only in branches of the middle section of the stem. In each fruit type, the total weight of fruits produced was more closely predicted by branch weight than by branch length. Allometric relationships between fruit production and branch weight differed among particular fruit types, with a faster increase in the production of type A than in that of types B or C. Competition had less effect on the mean size of type B fruits compared with that of types A or C. Fruits of types C and A had higher variation in mean weight, than type B fruit. Variation in total weight of fruits per plant was of a higher order of magnitude than that in the mean fruit weight. The results show that plants of *A. sagittata* grown under contrasting conditions change both their allometry and the number of particular fruit types produced. Nevertheless, the question of whether the shift in the fruit ratio is a function of allometric constraints or the result of a basic shift in allometry needs further study.

Key words: allometry, *Atriplex sagittata*, Chenopodiaceae, density stress, nutrient stress, heterocarpy.

Résumé : Les auteurs ont cultivé des plants de l'*Atriplex sagittata* Borkh. sous différentes conditions de densité et (ou) nutriments et ils ont étudié l'effet du stress sur l'allométrie de la plante et la variation de certains paramètres biométriques. Une augmentation de la densité réduit significativement le poids total, le diamètre basal, la longueur de la tige et le nombre de ramifications. Une déficience en nutriments exerce un effet négatif sur le poids total et le diamètre basal seulement, et les interactions densité × nutriments sont toutes non significatives. Le diamètre basal est le meilleur paramètre pour prédire le poids total, expliquant 93,6% de la variation dans l'ensemble des données. La relation entre le poids total de la plante et le diamètre basal n'est pas affecté par les conditions de croissance, ce qui indique que la compétition détermine la position d'une plante le long de la ligne décrivant la relation allométrique entre les deux variables, mais ne semble pas en altérer la relation. Cependant, à de faibles densités, les relations allométriques entre le poids total et la hauteur de la tige, et entre le poids total et le nombre de ramifications, sont significativement différentes de celles obtenues à fortes densités, ce qui indique que le poids total augmente plus rapidement aux faibles densités. La ramification, et conséquemment la forme de la plante sont influencées par la compétition. La longueur des branches augmente régulièrement avec l'augmentation du poids de la plante chez les plantes cultivées à fortes densités, mais aux densités plus faibles, on observe une telle augmentation seulement chez les branches de la partie médiane de la tige. Chez chaque type de fruit, le poids total des fruits produits est plus étroitement prévisible à partir du poids des branches qu'à partir de la longueur des branches. Les relations allométriques entre la production des fruits et le poids des branches différent entre les types de fruits, avec une augmentation plus rapide dans la production du type A, que des types B et C. La compétition a moins d'effet sur la grosseur moyenne des fruits de type B, comparativement aux types A ou C. Les fruits de types C et A montrent une plus forte variation de leur poids moyen que les fruits du type B. La variation du poids total de fruits par plant est

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supérieure d'un ordre de grandeur à celle des poids moyens des fruits. Les résultats montrent que les plants de l'*A. sagittata* cultivés sous des conditions contrastées modifient à la fois leur allométrie et le nombre de types particuliers de fruits produits. Tout de même, la question de savoir si le changement dans la proportion des fruits est fonction de contraintes allométriques ou s'il résulte d'un déplacement de base de l'allométrie nécessite d'autres études.

Mots clés : allométrie, *Atriplex sagittata*, Chenopodiaceae, stress densité/nutriments, hétérocarpie.

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Introduction

Biomass and (or) height allometry results from two contrasting forces, i.e., competition for light, which favours stem elongation, and gravity, which favours the development of a shorter and sturdier stem to support plant weight and increase its vertical stability (King 1990; Givnish 1995). Competition in annual plants and its effects on allometry have been intensively studied. It has been shown that interactions with neighbouring individuals alter the form, as well as the growth, survival, and reproductive output of plants. The significance of competition effects on static inter-individual allometric relationships has been clearly demonstrated (Weiner and Thomas 1992; Weiner and Fishman 1994).

Studies that focused on changes in biomass production under different density and (or) nutrient stress conditions are very rare for seed heteromorphic species (e.g., Cheplick and Quinn 1983); hence, the allometric pattern of changing biomass allocation to particular fruit types is unknown. Nonetheless, consideration of species producing two or more types of fruit or seed, each playing a different ecological role, adds an interesting aspect to the study of biomass allocation and variation in seed size.

Seed size may be affected by environmental conditions such as aridity, successional position, and habitat type (Werner and Platt 1976; Winn 1985). The adaptive significance of seed size variation has been intensively studied and it has been suggested that the effect of natural selection on seed size has been an important aspect of angiosperm evolution (Harper at al. 1970). Venable and Brown (1988) considered seed size, in combination with dispersal and dormancy, as a means of coping with environmental uncertainty. In their scenarios, seed dormancy and seed dispersal evolved in response to environmental predictability in time and space, respectively.

From studies of the relationship between seed size and growth rate of seedlings, it appears that (*i*) large seeds produce larger initial seedlings than small seeds and that this size advantage is maintained for the period after germination (Wulff 1986*a*; Jurado and Westoby 1992; Westoby et al. 1992); (*ii*) seedlings from larger seeds have larger root system (Jurado and Westoby 1992; Wulff 1986*a*), providing better access to soil moisture at deeper levels; (*iii*) large seeds facilitate establishment in soils with low moisture contents by allowing seeds to emerge from deeper soil layers where moisture levels are more favourable for germination and growth (Wulff 1986*a*); (*iv*) large seeds provide larger metabolic reserves for seedlings than small seeds; (*v*) large seeds have higher germination percentages and seedling survival than small seeds (Leishman and Westoby 1994). The advantage of seedlings from larger seeds over those from smaller seeds is demonstrated if both types are grown in competition (Wulff 1986*a*). However, in the wild seedlings from larger seeds have an advantage only under particular field conditions (Leishman and Westoby 1994).

The majority of plants produce only one fruit type. The size and ecological behaviour of this fruit is a consequence of the balance between genetic control and influence of the maternal environment. For example, the nutrient content of seeds can be influenced by the level of nutrients in the soil in which the maternal plant grew (Parrish and Bazzaz 1985). Heterodiasporic species (see Mandák 1997 for terminology), however, produce two or more types of fruit that differ from each other in size, form, and (or) color and exhibit different ecological behaviour. Seed polymorphism and its significance for survival under different ecological situations has been reported (Baar 1912; Beadle 1952; Koller 1957; Koller and Roth 1964; Flint and Palmblad 1978; Osmond et al. 1980; Baker and O'Dowd 1982; Khan and Ungar 1984; McEvoy 1984; Yamaguchi et al. 1990; Philipupillai and Ungar 1984; Venable and Levin 1985*a*, 1985*b*; Wertis and Ungar 1986; Venable et al. 1987, 1995; Imbert et al. 1996).

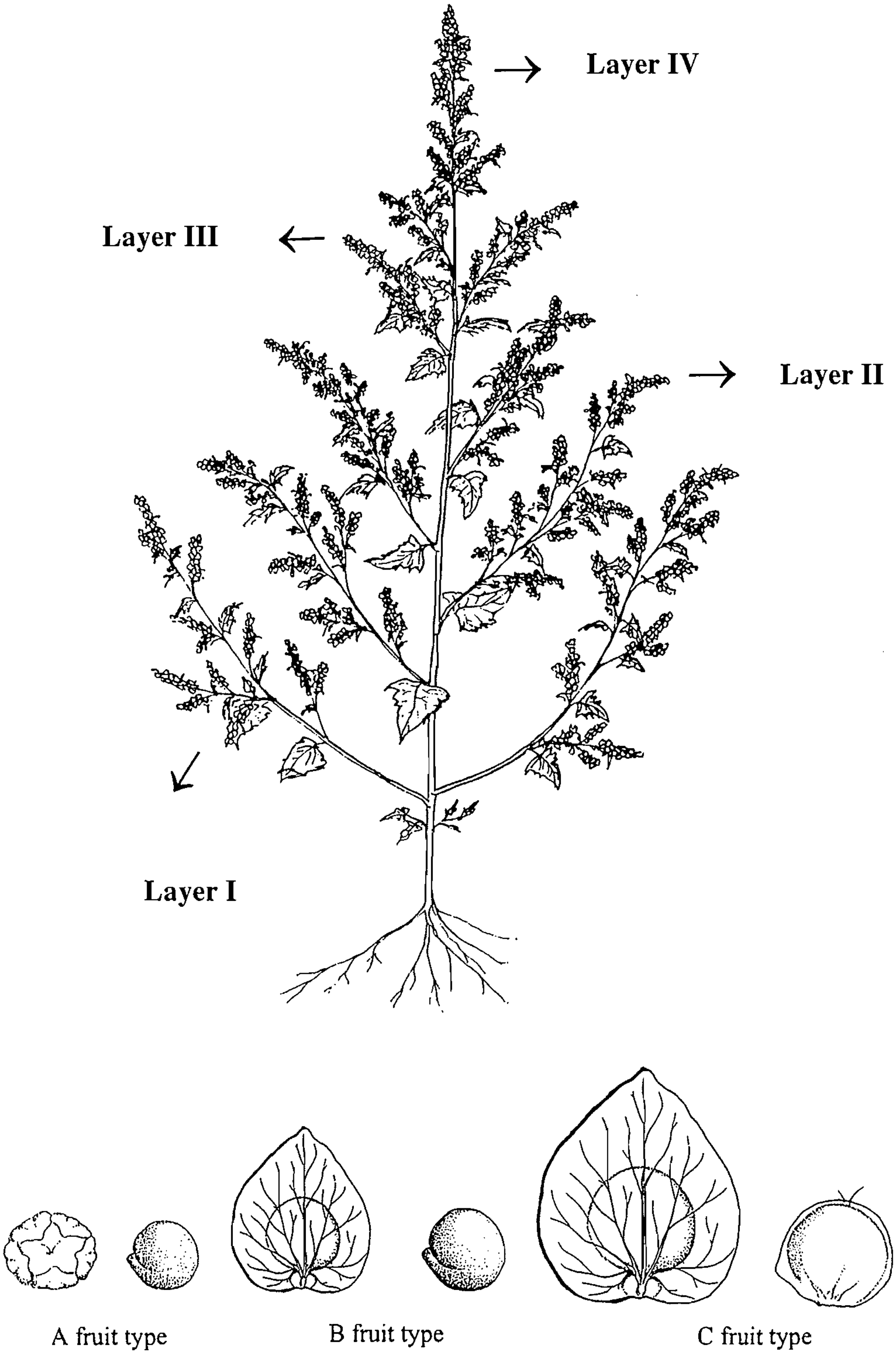
The present study was carried out on *Atriplex sagittata* Borkh. and focused on (*i*) evaluating the effect of density and nutrient stress on biomass production, biomass allocation, and fecundity, (*ii*) determining allometric relationships between particular biometrical parameters, and (*iii*) relating variation in production and size of particular fruit types to variation in biometrical parameters. The questions were addressed separately for particular fruit types; this makes it possible to discuss the different ecological roles played by these types in the life of the study species.

Materials and methods

Study species

Atriplex sagittata Borkh. [syn. *A. acuminata* W. et K., *A. hortensis* L. subsp. *nitens* (Schkuhr) Pons, *A. nitens* Schkuhr; see Kirschner (1984) for nomenclatural notes] (*Chenopodiaceae*), is an early successional annual species that prefers disturbed habitats such as urban areas, railway margins, and road ditches (Kirschner and Tomšovic 1990; Mandák and Pyšek 1998). It prefers nitrogen- and salt-rich soils (containing KCl and NaCl) along roads (Kopecký and Lhotská 1990). *Atriplex sagittata* is a sub-Irano-Turanian floristic element (Meusel et al. 1965; Hultén and Fries 1986). Its native distribution area covers Central Asia, Asia Minor, and eastern Europe. From there it has spread across southeastern and eastern Europe to western Europe (Meusel et al. 1965; Aellen 1960). The species is alien to Central Europe where it was introduced, probably as early as the Bronze Age, i.e., 2000–1500 B.C. (Khün 1981). Presence of bracteate and ebracteate flowers on one plant, non-Krantz anatomy, and a diploid chromosome number ($2n$ = 18) (Stutz et al. 1990) suggest an evolutionary position for *A. sagittata* close to the hypothetical ancestor of the genus *Atriplex*.

Fig. 1. Division of *A. sagittata* into the layers used (see Materials and methods for definitions of the layers) and the three types of fruit produced by the species.



Flowers are borne in terminal and axillary inflorescences. They are dimorphic and produce three types of fruits differing both morphologically (mainly in colour and the presence or absence of bracteoles; Fig. 1) and ecologically (Kopecký and Lhotská 1990; Mandák 1998; Mandák and Pyšek 1998, 1999).

The first fruit type (type A) originates from female or bisexual ebracteate flowers. It is small, black, and lens-shaped with a glossy, smooth testa and five-lobed perianth. This fruit type is undispersed, deeply dormant, with a low level of germinability. It forms a persistent seed bank (Type IV according to Thompson and Grime 1979).

The second fruit type (type B) is produced by female bracteate flowers. It is medium in size and has a similar appearance to the previous type, but it is covered by extended bracteoles. It is easily dispersed and is dormant, with a germinability intermediate between that of fruit types A and C. It forms a Type IV seed bank (following Thompson and Grime 1979).

The third fruit type (type C) is produced by female bracteate flowers and is rather large, brown, and covered by extended bracteoles, which are bigger than those of type B fruits. This type of fruit is easily dispersed, is nondormant, and forms a transient seed bank (Type II, following Thompson and Grime 1979).

In general, the development of type A fruit favours later germination and restricted dispersal with less survival risk, in contrast to the type C which favours earlier germination and a more efficient dispersal with associated survival risk. The type B has intermediate behaviour between types A and C, forming an ecological continuum between the two contrasting strategies. This conspicuous heterocarpy (sensu Voytenko 1968; see Mandák 1997 for terminology) is probably one of the reasons for the species expansion into man-made habitats in Central Europe (Mandák and Pyšek 1998).

Experimental design and plant measures

Fruits of *A. sagittata* were collected in autumn 1994 from a waste ground in Praha-Trója, Czech Republic, and stored in paper bags at room temperature. Bracts were removed from the fruits and fruits were sorted according to type (A, B, and C). Since type C has the highest germinability, usually up to 100% (Mandák 1998), it was used in the experiment. Seeds were germinated in plastic flats filled with commercial potting compost. After 10 days (6 June 1995), seedlings were transplanted into experimental pots 50 × 30 × 30 cm in size and filled with a mixture of equal amounts of potting soil and peat. To reduce the variation in initial seedling size, only those seedlings that germinated in the course of a single day (i.e., the day representing the peak of the population germination) were used for the experiment.

The experiment was carried out between June and October 1995 in an experimental garden at Kostelec nad Černými lesy, Central Bohemia, Czech Republic (50°00′N, 14°30′E). A randomized block design with 10 replicates was used. Each block consisted of six pots representing a combination of two densities and three fertilization levels. Density treatment consisted of (*i*) a single plant in the pot (low density) or (*ii*) one target plant surrounded by four border plants; plants in the pot had a regular spatial distribution, with the target plant located in the centre and border plants in the space between the centre and the pot corners (high density). For fertilization, a complete fertilizer, Herbasyn 5, was used (8.5% N, 8.5% P_2O_5, 12.0% K_2O, with the trace elements B, Co, Cu, Mg, Mn, Zn). The fertilization treatment included (*i*) watering with pure water (no fertilization), (*ii*) watering with Herbasyn solution alternated with pure water (moderate fertilization), (*iii*) watering only with Herbasyn solution (high fertilization). Fertilization started 20 days after the transplantation of the seedlings. Pots were watered every 3 days and the same amount of water or fertilizing solution was used for each pot (4 L).

Plants were harvested when all the fruits were ripe. Stem height and length of all branches were measured. Plants were then dried at 80°C for 48 h and weighed. Stem, branches, and leaves of each target plant were weighed separately (for technical reasons, those leaves that were lost prior to the harvest because of senescence processes were not considered). Border plants from high density pots were weighed without separation into parts.

To obtain information on the spatial distribution of particular fruit types within a plant, each plant was divided into four layers (Fig. 1) and one branch in each layer was sampled. The top 30 cm of the plant, bearing the inflorescence, was taken as Layer IV. Branches per plant were then counted (excluding the lowermost branches, which were poorly developed, seedless, and only 1–3 cm long), and the stem (excluding the terminal inflorescence) was divided into thirds, the division being based on the number of branches. Of each third, the lowermost branch was sampled and these branches were taken as representatives of Layers I–III.

For each sample branch, the total weight of fruits, bracteoles, and the rest of the branch was recorded (estimate of total plant fecundity was based on these data). Ten fruits of each type (A, B, and C) were randomly selected from each sample branch and weighed individually. Fruit and the bracteole weights were recorded separately. In total, 40 fruits of each type were sampled on each plant. A single plant of *A. sagittata* produces approximately 50 000 – 200 000 fruits. Consequently, fecundity was estimated based on sampling of particular branches. Weight of the stem, total weight of leaves, and the total weight of remaining branches (i.e., those not sampled in detail) was also recorded.

Data analysis

Data were analysed using linear regression and the differences between regression slope lines were tested with an *F* test (Snedecor and Cochran 1956). Because it is unclear what the proper criterion for showing an optimal functional relationship is (Sokal and Rohlf 1981), we used Model I regression. Since the layers belonged to the same plant and were not independent, the branch length at particular sections of the main axis was compared by ANCOVA with density, nutrient level, and layer as the factors and total weight as a covariate.

Two-way ANOVA was used for testing the differences between means. If a significant difference was found, Tukey's multiple range test was used to perform pairwise comparisons between individual treatments. The effect of border plants was considered by including their weight as a covariate in the ANCOVA, but it had no significant effect in any of the analyses.

Results

Allometric relationships of biomass production

Density, and fertilization both had highly significant effects on biomass production ($P < 0.001$, Table 1). Density also had significant effects on stem height, basal diameter, and number of branches. Fertilization significantly affected basal diameter but did not affect the other two biometric characteristics. The density × fertilization interaction did not significantly affect any of the plant measurements (Table 1). The values obtained for particular treatments increased from the high density – low fertilization to the low density – high fertilization treatment. The differences between particular fertilization levels, however, were all nonsignificant at high densities, while at low densities, fertilization contributed to further differentiation between treatments (Table 2).

Between-plant variation in total weight was linearly related to basal diameter, stem height, and number of branches (all variables log-transformed) (Fig. 2). Basal diameter was the best predictor of the total weight, explaining 93.6% of the variation in the whole data set. The basal diameters of plants grown under different densities did not overlap (Fig. 2). The allometric relationship between total weight and basal diameter was not different between high and low density treatments (Fig. 2). In contrast, the allometric relationships between total weight and stem height and between total weight and number of branches found at low density were significantly different from those at high density (Fig. 2).

Branch length was taken as an appropriate measure of the degree of branching and its relationship with total plant

Table 1. Summary of ANOVAs showing the effect of density (D), fertilization (F), and their interaction (F × D) on total weight and selected biometric characteristics of *A. sagittata*.

		Total weight		Basal diameter		Stem length		Number of branches	
Source of variation	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
D	1	300.29	***	398.74	***	66.46	***	63.80	***
F	2	7.45	***	4.36	*	1.52	NS	2.28	NS
F × D	2	1.43	NS	0.3	NS	0.9	NS	1.25	NS

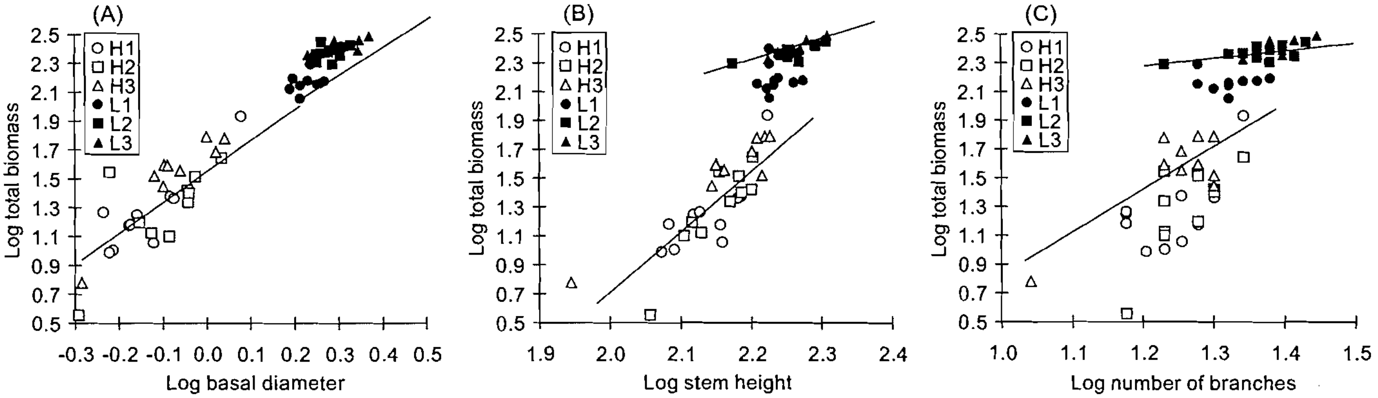
Note: Data were log-transformed to achieve homogenity of variances. The total number of sampled plants was 60. NS, nonsignificant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 2. Mean values of total weight and other biometric characteristics of *A. sagittata* as recorded under particular density and fertilization treatments.

Treatment	Total weight (g)	Basal diameter (cm)	Stem length (cm)	Number of branches
H1	23.04±7.14 a	0.74±0.06 a	138.71±5.06 a	17.50±0.75 a
H2	24.04±3.85 a	0.81±0.05 a	142.05±4.77 a	18.30±0.65 a
H3	41.24±5.52 a	0.87±0.05 a	147.50±7.51 a	17.90±0.85 a
L1	157.66±12.14 b	1.72±0.04 b	171.99±2.45 b	21.30±0.54 ab
L2	235.78±8.65 c	1.90±0.04 b	182.02±4.78 b	23.20±0.89 b
L3	262.27±11.24 c	2.00±0.06 c	184.38±3.73 b	24.40±0.54 b

Note: Means ± SE (n = 10) are shown. Values followed by the same letter within a column were not significantly different in pairwise comparisons at $P < 0.05$ (Tukey's test). Density treatments: H, high; L, low. Fertilization levels: 1, low; 2, moderate; 3, high.

Fig. 2. Allometric relationship (plotted on a log–log scale) between total weight and (A) basal diameter, (B) stem height, and (C) number of branches of *A. sagittata*. Density treatments: H, high; L, low. Fertilization levels: 1, low; 2, moderate; 3, high. Linear regressions for the pooled data are log total weight = 1.628 + 2.572 log basal diameter ($F_{[1,58]}$ = 851.9, R^2 = 93.6, $P < 0.0001$); log total weight = –13.213 + 6.839 log stem height ($F_{[1,58]}$ = 229.4, R^2 = 79.8, $P < 0.0001$); and log total weight = –5.684 + 5.774 log number of branches ($F_{[1,58]}$ = 128.5, R^2 = 68.9, $P < 0.0001$).



weight was investigated. This relationship changed remarkably with population density and the section of the main stem from which the branches derived (i.e., layer) (Fig. 3). Whereas branch length consistently increased with total plant weight in plants grown under high density, the pattern found for low density plants differed with respect to the position of branches on the plant (Fig. 3). For low density plants, branch length did not increase with the plant weight in either the upper or the lowermost section of the stem (i.e., the slope describing the relationship was not significantly different from zero; Table 3). In the middle section of the stem (Layer II), there was a significant increase in the length of branches with increasing total plant weight (Fig. 3, Table 3).

The differences between the slopes of regressions relating the branching at a particular section of the main axis to the total plant weight were significant as revealed by ANCOVA (density: $F = 0.151$, df = 1, $P = 0.7$; layer: $F = 9.533$, df = 3, $P < 0.0001$; interaction density × layer: $F = 5.627$, df = 7, $P < 0.0001$, $n = 10$). The allometric branch length – total weight relationship did not change between densities for the upper layer III (Table 3). For the middle and lowermost sections (Layers I and II), the relationship varied between densities (Table 3).

Total fruit production

Total weight of fruits was highly significantly correlated with other biometric parameters, the majority of which explained between 50 and 90% of the variation in fruit weight. In each fruit type, fruit weight was more closely predicted by branch weight than by branch length (Table A1, see Appendix). Allometric relationships between fruit production

Fig. 3. Relationship between the degree of branching (expressed as the sum of lengths of all branches recorded on the plant) and plant size (expressed as total weight) shown for particular densities (H, high; L, low) and layers on *A. sagittata* plants (I, bottom; II, middle; III, upper). The data were pooled with respect to fertilization treatments as these treatments had no effect on the production of branches (see Table 1). See Materials and methods for details of the sampling design and Table 3 for regression coefficients and testing of differences in the slopes.

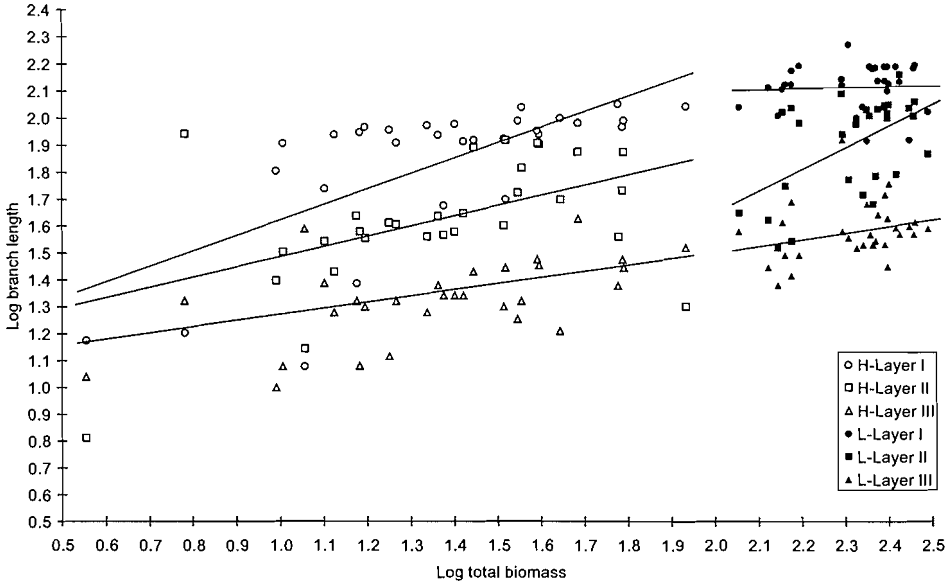


Table 3. Differences between slopes of regressions relating the branching at particular sections of the main axis of *A. sagittata* plants (dependent variable) to total plant weight (independent variable) (both variables log-transformed).

Density	Slope	SE of slope	Intercept	$F_{[1,58]}$	R^2	P
H-layer I	0.587 a	0.116	1.032	25.708	47.87	***
H-layer II	0.392 b	0.127	1.084	9.592	25.52	**
H-layer III	0.285 c	0.075	0.940	14.316	33.83	***
L-layer I	0.034 d	0.130	2.040	0.067	0.24	NS
L-layer II	0.808 e	0.232	0.032	12.105	30.18	**
L-layer III	0.238 c	0.160	1.025	2.225	7.36	NS

Note: Slopes followed by the same letter were not significantly different ($P < 0.05$) according to the F test (Snedecor and Cochran 1956). $n = 60$. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, nonsignificant. H, high density; L, low density; I, bottom layer; II, middler layer; III, upper layer (see Materials and methods for definitions of the layers).

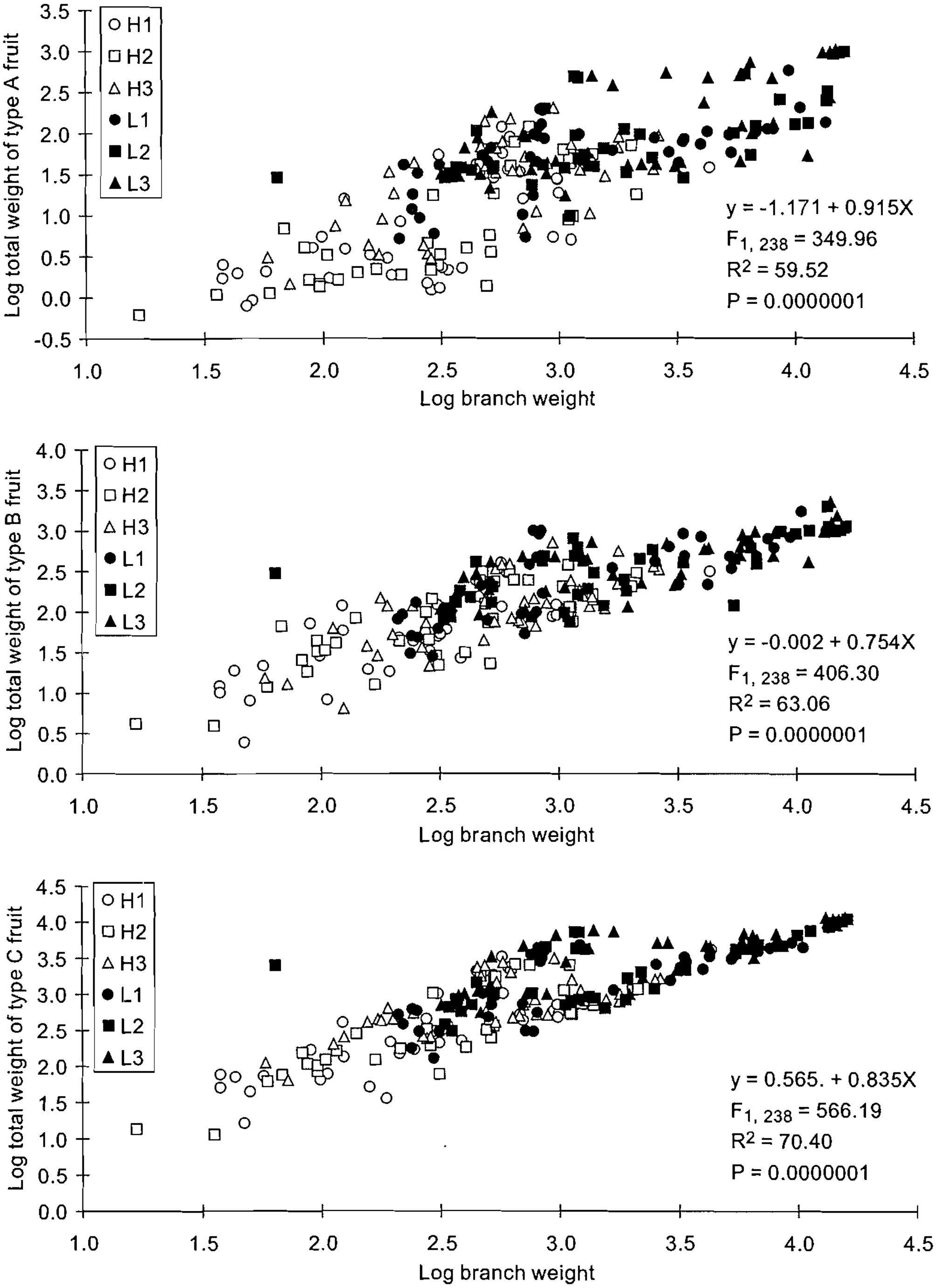
and branch weight differed among particular fruit types, which is indicated by the significantly different slopes of the regression lines (Fig. 4 and Table A1, see Appendix). There were also significant differences in regression line slopes among particular density–fertilization treatments within each type of fruit (Table A2, see Appendix).

Fruit size and bracteole area

Mean fruit weight differed significantly among fruit types (ANOVA: $F_{[2,7197]} = 8875.2$, $P < 0.001$), increasing from type A (0.83 ± 0.01 mg) to type B (1.52 ± 0.01 mg) to type C (3.76 ± 0.06). As in the case of total fruit weight, mean fruit weight was significantly related to various biometric parameters (Table A3, see Appendix). However, the percentage of variation explained by particular predictors was remarkably lower for mean fruit weight than for total weight of fruits, which is indicated by the R^2 values rarely exceeding 50% in the former (Table A3, see Appendix). The increase in mean weight with biometric parameters was slowest in the type B fruit and steepest in type A fruit and these trends were consistent for all the parameters considered. The results indicate that competition had less effect on the size of type B fruits compared with that of types A or C (Table A3, Appendix). To investigate the relationships between fruit characters and size of the bracteole, the area of the bracteole was estimated on the basis of its linear measures. For the type B fruit, the bracteole area was estimated using bracteole area = 0.011 + 0.713 (bracteole width × bracteole length), $F_{[1,48]} = 135.5$, $R^2 = 96.6$, $P < 10^{-6}$, and for type C fruit, the bracteole area was estimated using bracteole area = 0.009 + 0.713 (bracteole width × bracteole length), $F_{[1,48]} = 2918.7$, $R^2 = 98.4$, $P < 10^{-6}$.

Mean fruit weight was closely related to bracteole area ($R^2 = 49.9$ for type B and 71.1 for type C) and bracteole weight ($R^2 = 48.6$ for type B and 66.6 for type C) in both bracteate fruit types. The increase in weight of the type C fruit with bracteole area was twice as fast as that of the type B fruit (the value of the regression slope was 1.22 in type C as compared with 0.65 in type B and the slopes were significantly different; $F_{[2,478]} = 116.54$, $P < 0.001$).

Fig. 4. Allometric relationship between total weight of fruits and weight of branches, shown separately for particular fruit types of *A. sagittata*. Density treatments: H, high; L, low. Fertilization levels: 1, low; 2, moderate; 3, high. Note the log–log scale. See Table A1 in the Appendix for a summary of regression parameters and differences between slopes.



Variation in biometrical parameters

Particular biometrical parameters exhibited different degrees of variation, expressed by the coefficient of variation (Table 4). In general, low variation was found in stem height, number of branches, and bracteole area and weight; whereas, weight measures (with the exception of bracteole weight) and basal diameters exhibited remarkably higher variation. Considering fruit production, the highest variation was found in total weight of fruits, which ranged from 116.7 to 119.0% according to fruit type, while mean fruit weight exhibited comparably little variation, i.e., 19.7–35.1%.

Comparing particular fruit types, types C and A had higher variation in mean weight, than type B (Table 4, Fig. 5). Variation in mean weight of particular fruit types showed different patterns if plotted against total plant weight. In type A fruit, the coefficient of variation responded to the position on the density–nutrient gradient and was remarkably higher for plants growing in low nutrient condi-

Table 4. Summary of reproductive traits (means ± SE) in *A. sagittata*, for types A, B, and C, and their coefficients of variation (CV).

	Mean	SE	*n*	CV
Stem length (cm)	161.11	3.13	60	15.06
Basal diameter (cm)	1.34	0.07	60	42.54
Number of branches	20.43	0.44	60	17.03
Weight of stem (g)	0.02	0.001	60	50.00
Weight of branches (g)	123.82	1.34	60	84.10
Total plant weight (g)	123.84	13.44	60	84.09
Bracteole weight for type B (mg)	0.656	0.009	480	29.12
Bracteole area for type B (cm^2)	0.197	0.002	480	21.32
Bracteole weight for type C (mg)	1.21	0.019	480	36.20
Bracteole area for type C (cm^2)	0.33	0.004	480	26.97
Total weight (g) of fruit for type A	0.10	0.01	240	190.00
Total weight (g) of fruit for type B	0.30	0.02	240	116.67
Total weight (g) of fruit for type C	2.16	0.17	240	118.98
Total weight (g) of fruit for types A, B, and C	2.56	0.20	240	118.36
Total weight of bracteoles (g)	1.20	0.09	240	118.36
Mean weight (mg) of fruit for type A	0.83	0.005	2400	31.33
Mean weight (mg) of fruit for type B	1.52	0.006	2400	19.74
Mean weight (mg) of fruit for type C	3.76	0.027	2400	35.11

tions than for plants in high nutrient conditions whereas for types B and C, the variation in fruit weight was not affected by plant size (Fig. 5).

Discussion

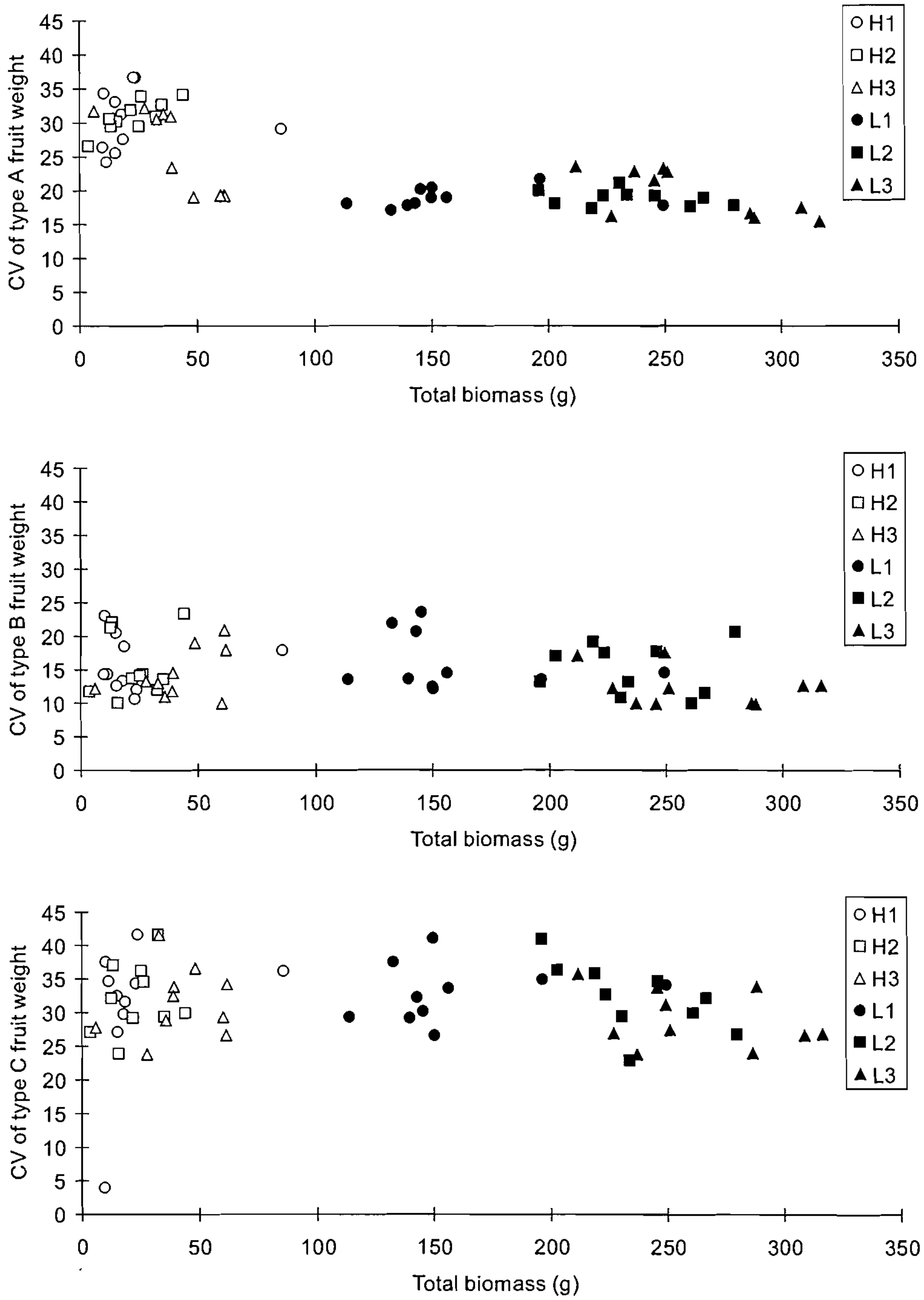
Competition can alter allometric relationships between different measures of plant size, as well as the distribution of these measures. Generally, uncrowded plants show linear relationships between log height, log diameter, and log weight (Weiner and Fishman 1994). In *A. sagittata*, competition and nutrient stress significantly reduced the weight of all measured plant parts, but the effect of increasing competition was stronger than that of nutrient deficiency. Whereas the relationship between total plant weight and basal diameter was unaffected by density (indicating that competition determined the position of a plant along the line describing the allometric relationship between both variables but did not seem to alter the relationship), the other allometries changed with increasing competition and also under nutrient stress. This could mean that (*i*) in our competition experiment, *A. sagittata* plants were not close to the limits of their biomechanical stability or (*ii*) no selective pressure was operating on stem height and number of branches to maintain specific relationships as they grew. On the other hand, Weiner and Fishman (1994) pointed out that an unalterable basal diameter – total plant weight relationship has little to do with biomechanical constraints.

The differences in branch development between plants growing under different conditions increased from lower to upper parts of the stem. The lower branches of plants that were not surrounded by neighbours were very long and vertical, hence shading and probably reducing the growth of other branches. In these plants, the upper section of the stem was located above the distal end of the lower branches, which is why no reduction in branching was observed in this part of the plant. On the other hand, the lower branches of plants exposed to competition from neighbours were reduced by the presence of surrounding plants. Hence competition, in the case of *A. sagittata*, has a profound effect not only on biomass production but also on plant structure and shape.

Variation in reproductive components of plants growing under density stress, lack of nutrients, or after defoliation has been reported. It has been shown that the patterns of regulation vary among reproductive components, depending on the stage of development at which a specific stress treatment is applied (Lee and Bazzaz 1982; Pyke 1989; Matthies 1990; Pyšek 1992). There is evidence that reproductive behaviour of many plants is determined primarily by the size they achieve (Weiner 1988; de Jong and Klinkhamer 1989).

Under stressful environmental conditions, reduction in weight of vegetative parts is usually greater than that of reproductive parts (Sultan 1990). Variation in fruit weight is commonly considered one of the least variable plant characteristics (Harper et al. 1970; Schmid and Dolt 1994). If the pooled data across the treatments applied in the present study are considered, the variation in total weight was much higher than that in fruit weight. Differences in seed weight within the inflorescence indicate that much of this variation may be of nongenetic origin, with environmental change during maturation being a probable cause (Pitelka et al. 1983; Cavers and Steel 1984). In contrast Harper et al. (1970) pointed out that fruit size is under tight genetic control and thus subject to evolutionary change. Seed size can affect germination, emergence of seedlings, and seedling growth rate (Harper et al. 1970; Roberts 1972; Khan 1977; Weiss 1982; Hendrix 1984; Stanton 1984; Schmid and Dolt 1994). If larger seeds produce larger seedlings, these may have a competitive advantage over those from smaller seeds, especially if the two types of seeds are grown in mixed stands (Black 1958; Gross 1984; Wulff 1986*a*, 1986*b*; Kromer and Gross 1987; Aarssen and Burton 1990). *Atriplex sagittata* can modify fruit weight (i.e., fruit size) under dif-

Fig. 5. Relationships between variation in fruit size (expressed as the coefficient of variation in mean fruit size) and total plant weight of *A. sagittata*. Particular density and fertilization treatments are distinguished by different symbols. Density treatments: H, high; L, low. Fertilization levels: 1, low; 2, moderate; 3, high.



ferent environmental conditions. It can be supposed that the observed reduction in allocation to fruits was caused by density and (or) nutrient stress (Harper 1977).

A close relationship between fruit weight and bracteole size was found in *A. sagitata*. This relationship can be supposed to principally affect the dispersal properties of the fruit. In type C fruit, compared with type B, the fruit weight is lower per unit of bracteole area. This explains the better floating ability of type B fruit as found in the previous study (Mandák 1998). The significance of bracteoles for dispersal of *Atriplex* species by water was described by Gustafsson (1970, 1973) who found a correlation between floating ability and distribution of coastal species. Dispersal of fruits by water flow or waves is crucial for heterocarpic plants inhabiting sea coast or lake shores. *Cakile edentula* var. *lacustris* (Brassicaceae) grows on beaches along Canadian lakes and produces a siliqua consisting of the upper and lower segments. Payne and Maun (1981) suggest that the upper fruit segment of this species disperses a long distance, while the lower one remains on the parent plant in the proven habitat. *Atriplex sagittata* is a typical inland species, but the dispersal by water is very important in riparian habitats, which are one of the main migration routes used by this species (Iljin 1936; Brandes 1982; Mandák and Pyšek 1998).

Branch weight was a better predictor of fruit production than branch length in *A. sagittata* because the former reflects not only the linear size of the branch but also its thickness and occupation of space by higher order branches. In our study, branch weight accounted for 59.5% (type A fruit), 63.1% (type B), and 70.4% (type C) of variation in fruit weight per branch. Subtle differences in the environment of microsites and genetic difference among individuals might account for the remaining variability in fruit production. The two types of flowers may be induced at different times during the growing season and each type therefore matures under different conditions in particular stages of development. Nobs and Hagar (1974) pointed out that in *Atriplex hortensis* L., a close relative of *A. sagittata*, black fruits are produced later (i.e., after main flush of flowering) than brown fruits. Winn (1991) discussed proximate and ultimate sources of variation in fruit mass in detail and concluded, on the basis of studies with *Prunella vulgaris*, that such within-plant variation in fruit weight is most likely due to constraints or physiological limitations that prevent seed parents from producing a uniform crop rather than being adaptive. However, a fitness advantage can be gained from variable fruit weight if parents possess a strategy to disperse fruits of different size selectively into different microhabitats (McGinley et al. 1987). This is a model of behaviour typical of heterocarpic plants in which the production of more than one fruit type makes it possible to place fruits in various microhabitats and at different distances from the mother plant (Venable 1985). Production of more than one fruit type should therefore decrease temporal variation in offspring success, hence increasing population fitness. The theory suggests that seed heteromorphism is favoured in temporally variable environments when variation in reproductive success is high for a single seed morph, while heteromorphism reduces this variation because morphs are successful under different conditions (Venable 1985). Seed heteromorphism is also favoured when there is a spatial heterogeneity in the microsites available to progeny (Lloyd 1984).

Variation in seed size, expressed by different values of the coefficient of variation found in particular fruit types, represents an additional level of variation (adding to that represented by the production of different types of fruit). Previous study has shown that whereas seed size did not affect the final percentage of germinated seeds, it affected how quickly the germination occurred: the largest fruits germinated most slowly (Mandák 1998). Variation in fruit size hence contributes to extending the time period in which the germination occurs. This is extremely important in type C where the highest variation in seed size was found. Seeds produced by this fruit type are nondormant and, under suitable conditions, germinate immediately. The risk that the whole cohort is killed by a catastrophic event is much higher compared with that of both dormant types and this risk can be reduced by spreading the germination over time by means of variation in size.

In its secondary distribution area, *A. sagittata* is an early successional species, commonly found in disturbed sites of human origin; in its native distribution area it inhabits deserts and semideserts (Mandák and Pyšek 1998). For such a species, high variability and plastic response to changing environmental conditions can be crucial factors in successful survival in environments with a high level ofs unpredictability and disturbance.

Variation in fruit number and size is a fascinating aspect of the life of heterocarpic plants. The effect of contrasting environments on this variation and its consequences for the life history of *A. sagitata* were described and discussed in a previous study (Mandák and Pyšek 1999). The present study demonstrated a pronounced effect of competition on plant allometry, as well as on the variation in biometrical parameters. However, it still remains to be answered whether the variation in the production of different types of seed among different environments is a function of allometric constraints or the result of a basic shift in allometry. The data used in the present study make it difficult to solve this issue because of a principal methodological problem. Under different conditions, plants of *A. sagittata* change both their allometry and the number of particular fruit types produced, but with the present data it is impossible to test if the shift in the fruit ratio is a consequence of changing allometry and plant structure or is caused by changes in the amount of available nutrients. To separate these effects, plants grown under different density and (or) nutrient conditions and having the same morphological structure, i.e., not differing in allometrical relationships, are needed. This represents a major challenge for further research.

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Appendix

Table A1. Summary of the relationships between the total weight of fruit produced (dependent variable) and selected biometric characteristics of *A. sagittata* plants (independent variable).

	Fruit type																	
	A						B						C					
	Intercept	Slope	SE of slope	$F_{[1,58]}$	R^2	P	Intercept	Slope	SE of slope	$F_{[1,58]}$	R^2	P	Intercept	Slope	SE of slope	$F_{1,58}$	R^2	P
Basal diameter	1.56	1.81 a	0.21	75.13	56.43	***	2.22	1.53 a	0.11	189.69	76.58	***	3.05	1.70 a	0.10	310.05	84.24	***
Stem height	−8.56	4.67 a	0.68	47.53	45.04	***	−6.25	3.91 a	0.41	88.91	60.52	***	−6.66	4.48 a	0.38	139.11	70.57	***
Stem weight	3.59	1.06 a	0.14	57.60	49.83	***	3.92	0.89 b	0.08	118.56	67.15	***	4.98	1.01 a	0.07	198.40	77.38	***
Number of branches	−3.01	3.63 a	0.68	28.59	33.01	***	−2.02	3.35 a	0.41	68.24	54.05	***	−1.88	3.89 a	0.38	106.01	64.64	***
Branch diameter	2.89	2.93 a	0.30	95.58	62.23	***	3.28	2.32 a	0.18	172.01	74.78	***	4.22	2.56 a	0.16	243.65	80.77	***
Branch length	−2.61	2.48 a	0.28	79.85	57.93	***	−1.14	2.00 a	0.16	151.05	72.26	***	−0.44	2.08 a	0.18	132.93	69.62	***
Branch weight	−1.16	0.92 a	0.07	170.47	74.61	***	0.12	0.71 b	0.04	355.94	85.99	***	0.76	0.78 b	0.03	585.27	90.98	***
Bracteole weight	−1.68	1.15 a	0.09	171.36	74.71	***	−0.32	0.91 bc	0.04	460.74	88.81	***	0.19	1.02 ac	0.01	7579.32	99.24	***

Note: Computations performed on pooled data ($n = 60$). ***, $P < 0.001$. Slopes bearing the same letter within a row were not significantly different ($P < 0.05$) according to the F test (Snedecor and Cochran 1956).

Table A2. Summary of regressions describing allometric relationships between the total weight of fruit (dependent variable) and the weight of branches (independent variable) (log–log scale). The results are shown for the three fruit types and the six treatment combinations.

	Fruit type																	
	A						B						C					
Treatment	Intercept	Slope	SE of slope	$F_{[1,38]}$	R^2	P	Intercept	Slope	SE of slope	$F_{[1,38]}$	R^2	P	Intercept	Slope	SE of slope	$F_{[1,38]}$	R^2	P
H1	−1.33	0.89 a	0.19	21.49	36.12	***	−0.44	0.88 a	0.18	24.42	39.13	***	−0.02	1.04 a	0.12	71.27	65.22	***
H2	−1.72	1.05 b	0.14	56.02	59.58	***	−0.16	0.80 a	0.10	63.63	62.61	***	0.09	0.97 a	0.10	86.25	69.42	***
H3	−0.91	0.85 a	0.16	29.49	43.69	***	−0.07	0.77 b	0.12	39.77	51.14	***	1.18	0.61 bc	0.11	33.18	46.61	***
L1	0.03	0.55 c	0.11	27.39	41.89	***	0.38	0.66 b	0.10	45.28	54.37	***	1.11	0.67 b	0.10	47.20	55.40	***
L2	0.20	0.53 c	0.10	26.64	41.22	***	1.02	0.46 c	0.08	33.68	46.98	***	1.56	0.55 c	0.09	37.08	49.39	***
L3	−0.19	0.67 d	0.12	30.17	44.26	***	0.83	0.52 c	0.06	66.11	63.50	***	1.53	0.59 bc	0.07	73.64	65.96	***
Pooled data	−1.17	0.92 A	0.05	349.96	59.52	***	−0.002	0.75 B	0.04	406.30	63.06	***	0.57	0.84 C	0.04	566.19	70.40	***

Note: $n = 40$ (see Materials and methods for details). ***, $P < 0.001$. Slopes followed by the same letter within a column were not significantly different ($P < 0.05$) according to the F test (Snedecor and Cochran 1956). For pooled data, the difference between slopes was across the row and indicated by uppercase letters. Density treatments: H, high; L, low. Fertilization levels: 1, low; 2, moderate; 3, high.

Table A3. Summary of relationships between mean fruit weight (dependent variable) and selected biometric characteristics of the plant (independent variable).

	Fruit type																	
	A						B						C					
	Intercept	Slope	SE of slope	$F_{[1,58]}$	R^2	*P*	Intercept	Slope	SE of slope	$F_{[1,58]}$	R^2	*P*	Intercept	Slope	SE of slope	$F_{[1,58]}$	R^2	*P*
Stem length	–1.84	0.79 a	0.13	37.36	39.18	***	–0.68	0.39 b	0.09	18.62	24.30	***	–0.70	0.58 c	0.10	33.81	36.83	***
Basal diameter	–0.12	0.31 a	0.42	54.32	48.36	***	0.17	0.14 b	0.03	19.82	25.47	***	0.55	0.22 c	0.03	45.71	44.08	***
Number of branches	–0.93	0.64 a	0.13	26.53	31.39	***	–0.30	0.37 b	0.08	20.54	26.15	***	–0.14	0.55 c	0.09	39.39	40.45	***
Stem weight	0.26	0.18 a	0.03	43.60	42.19	***	0.34	0.09 b	0.02	24.61	29.79	***	0.80	0.13 c	0.02	37.64	39.36	***
Branch diameter	0.09	0.46 a	0.07	48.86	45.73	***	0.28	0.25 b	0.04	30.68	34.59	***	0.70	0.32 c	0.05	39.83	40.72	***
Branch length	–0.76	0.83 a	0.06	41.59	41.76	***	–0.20	0.22 b	0.04	30.66	34.58	***	0.05	0.30 c	0.04	47.67	45.11	***
Branch weight	–0.52	0.14 a	0.02	56.03	49.13	***	–0.04	0.07 b	0.01	28.31	32.80	***	0.27	0.10 c	0.01	47.00	44.76	***
Bracteole weight	–0.60	0.17 a	0.02	59.16	50.50	***	–0.08	0.09 b	0.02	27.59	32.52	***	0.21	0.12 c	0.02	49.67	46.13	***
Total fruit weight	–0.67	0.17 a	0.02	56.96	49.55	***	–0.12	0.09 b	0.02	27.91	32.49	***	0.15	0.12 c	0.02	50.52	46.55	***
Dispersal unit weight[a]	–0.68	0.16 a	0.02	60.31	50.98	***	–0.12	0.08 b	0.02	28.93	33.28	***	0.15	0.12 c	0.02	52.12	47.33	***
Total plant weight	–0.31	0.12 a	0.01	65.94	53.20	***	0.07	0.06 b	0.01	27.82	32.42	***	0.41	0.09 c	0.01	58.77	50.33	***

Note: Computations were performed on pooled data ($n = 60$). ***, $P < 0.001$. Slopes followed by the same letter within a row were not significantly different ($P < 0.05$) according to the *F* test (Snedecor and Cochran 1956).

[a] Dispersal unit is understood to be fruit with bracteoles.