

PLANT MORPHOLOGY AND ALLOMETRIC RELATIONSHIPS IN COMPETING AND NON-COMPETING PLANTS OF *TAGETES PATULA* L.

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ABSTRACT

Allometric relationships (defined as correlation coefficients between plant mass – stem diameter, plant mass – stem height and stem diameter – stem height) in plants of *Tagetes patula* L. (Brassicaceae) var. "Tangerine" were analyzed. Competing and non-competing plants were compared in a glasshouse experiment. Competing plants were grown in broad range of densities, from 200 to 6000 individuals · m⁻². For non-competing plants no allometric relationships were observed, while for competing plants they were strong, irrespective of density treatment used. Gradual changes of plant morphology (plant mass, stem diameter, stem height and height/mass ratio) with the increase of competition intensity were also analyzed.

The present study clearly showed, that the intraspecific competition influenced allometric relationships between height, mass and stem diameter of *Tagetes patula*.

KEY WORDS: intraspecific competition, competition intensity, plant morphology, allometric relationships, *Tagetes patula*.

INTRODUCTION

Competition alters not only the growth rate, survival and reproductive output of plants (Harper 1977) but also the allometry of growth, eg. relationships between biomass, height, leaf area, canopy projection area (Weiner and Thomas 1992; Weiner and Fishman 1994). In its most general sense the term "allometry" means any study of size and its consequences (Reiss 1989). Allometric equation represents relationship between two size measures (X and Y) of any individual as follows: $Y=aX^b$, where a and b are constants. Such relationship is caused by differential, as opposed to isometric, growth of parts or metrics of an organism (Gould 1966). Understanding the relationship between competition and allometry of growth is important because this relationship seems to be reciprocal i.e. plant morphology determines pattern of light interception during process of competition but, from the other side, allometric relationships may also be a result of competitive interactions between plants (Geber 1989; Weiner and Thomas 1992).

The allometry of growth was intensively studied in forestry (see Henry and Aarssen 1999 for review), while for herbaceous plants informations are scarce. The influence of competition on plant allometry in herbaceous plants was studied by Weiner and Thomas (1992). They found strong correlations between stem height, stem diameter and plant biomass for three species of annual plants: *Impatiens pallida*, *Tagetes patula* and *Polygonum pensyl-*

vanicum. Similar results were obtained by Weiner and Fishman (1994) for *Kochia scoparia*; strong relationships between measures occurred for non-competing as well as for competing plants. Moreover, Weiner and Thomas (1992) found that for non-competing plants relationships between stem diameter, height and plant mass were linear on log-log scale, while for competing plants these relationships were curvilinear. In the above cited studies Weiner and Thomas (1992), as well as Weiner and Fishman (1994), simply compared competing and non-competing plants i.e. they perform experiments with only one density level. In such experiments it was impossible to compare gradual changes of plant morphology and analyze possible changes of allometric relationships with the increase of density (and competition intensity).

In contrast to the above cited studies, I have applied a wide range of sowing density (i.e. competition intensity) for competing populations. The aim of the present study was:

- 1) to describe changes of plant morphology (above-ground plant mass, stem diameter, stem height and height/mass ratio) with the increase of plant density,
- 2) to describe changes of allometric relationships with the increase of plant density. Allometric relationships were defined as correlation coefficients between measures (mass, stem height and stem diameter).

To compare my results with the above cited studies (Weiner and Thomas 1992; Weiner and Fishman 1994) I have also analyzed linearity of the allometric relationships.

MATERIALS AND METHODS

A glasshouse experiment on annual species *Tagetes patula* L. (Brassicaceae) var. "Tangerine" was performed. *Tagetes* is a model species for study of density-dependent effects (Ford 1975; Ford and Diggle 1981; Weiner et al. 1990; Weiner and Thomas 1992).

In my experiment there was one group of 61 non-competing (isolated) plants and 14 groups (plant populations) grown in broad range of densities, from 200 to 6000 individuals \cdot m⁻². For each of all the 15 plant groups the following data were assessed: mean stem height, mean stem diameter, mean mass of above-ground part, value of height/mass ratio, index of competition intensity and correlation coefficients between height, diameter and mass. I have also tested the nonlinearity of allometric relationships between stem height, stem diameter and mass of above-ground plant part.

The number of individuals in each of the 15 plant groups ranged was from 14 to 214 individuals (after rejection of plants from the border zone). There were two replications in densities 500 and 1000 individuals \cdot m⁻² and four replications in density 3000 individuals \cdot m⁻². In other densities there were no replications (see details in Table 1). Non-competing individuals were grown in 7 \times 7 cm pots, and competing plants were grown in 42 \times 35 \times 7 cm containers. Pots and containers were filled with Grodan rock wool, tickled with Kemira medium. Concentrations of nutrients was as follows: 284 mg N, 230 mg P, 626 mg K, 190 mg Ca, 86 mg Mg \cdot dm⁻³ with 2 ml \cdot dm⁻³ HNO₃ added. Additional lighting 18 hours per day was applied, so that light intensity at the top of plants' level was about 150 μ Em⁻² s⁻¹.

Seeds were sown on 28-30 April and harvested on 24-26 June 1997. The above-ground parts of plants were harvested individually by cutting the stem approx. 2 mm above-ground level. Height of each plant was measured by a ruler from the cutting point to the base of the highest leaf. Stem

diameter was measured at the cutting point by means of stereoscopic microscope with micrometer. Plants were dried in temperature of 105°C and weighted to the nearest 0.1 mg. In a few, the most dense populations process of density-dependent mortality (self thinning) had started before the harvest. Dead plants were excluded from the subsequent analysis.

Intensity of intraspecific competition was measured within each population as the proportional reduction in mass per plant attributed to the presence of neighbours, i.e:

$$I = (M_{nc} - M_c) / M_{nc}$$

where:

I – index of competition intensity

M_{nc} – mean above-ground plant mass of non-competing plants (growing in isolation)

M_c – mean above-ground plant mass of competing plants (growing in population)

This competition index ranges from zero, for no effect, to one for complete competitive inhibition and is a commonly used measure of competition (Nicotra and Rodenhouse 1995).

Pearson's correlation coefficient (Sokal and Rohlf 1995) on log-transformed data was used to examine relationships between mass and diameter, mass and height, and height and diameter of plants. To fit allometric functions I used the linear regression model I or-polynomial regression where appropriate. Second-order polynomial regression was used to test for deviations from linearity in allometric relationships examined. A significant second-order polynomial term was considered as evidence that the relationship was curvilinear.

To compare the mean values of plant mass, stem diameter and stem height I used t-Student test of differences between two means (Sokal and Rohlf 1995).

TABLE 1. Allometric relationships between stem height (H), stem diameter (D) and mass (M) of above-ground part in non-competing and competing plants of *Tagetes patula* L. var. "Tangerine" at different densities. Correlation coefficients (on log-transformed data) significant at 0.01 significance level are marked in bold. Values of M, D and H are means \pm S.D. N – number of analyzed plants, I – index of competition intensity, H/M ratio – mean value of height/mass ratio.

density N*m ⁻²	N	M mg	D mm	H mm	I	H/M ratio	correlation coefficient		
							D-H	D-M	H-M
non- -competing	61	1374 \pm 173	4.3 \pm 0.3	105 \pm 17	-----	24.37	0.05	0.28	0.28
200	14	638 \pm 392	3.6 \pm 0.7	114 \pm 31	0.54	31.68	0.83	0.94	0.92
400	19	384 \pm 271	3.0 \pm 0.7	92 \pm 28	0.72	30.41	0.90	0.98	0.87
500	73	346 \pm 327	2.9 \pm 0.7	98 \pm 27	0.76	33.51	0.75	0.95	0.85
500	71	329 \pm 295	2.8 \pm 0.8	95 \pm 30	0.76	34.42	0.70	0.94	0.81
1000	37	229 \pm 167	2.6 \pm 0.3	101 \pm 25	0.84	38.48	0.68	0.83	0.88
2000	172	164 \pm 163	2.4 \pm 0.5	91 \pm 27	0.88	37.67	0.76	0.89	0.89
2000	153	179 \pm 164	2.4 \pm 0.5	90 \pm 25	0.88	37.03	0.60	0.83	0.82
2500	70	94 \pm 94	2.0 \pm 0.3	83 \pm 30	0.93	39.73	0.64	0.78	0.94
3000	214	112 \pm 128	2.2 \pm 0.5	86 \pm 29	0.92	38.98	0.64	0.84	0.87
3000	241	107 \pm 131	2.1 \pm 0.4	88 \pm 31	0.92	41.56	0.70	0.87	0.91
3000	198	130 \pm 155	2.2 \pm 0.5	90 \pm 30	0.91	40.14	0.61	0.85	0.86
3000	198	122 \pm 142	2.2 \pm 0.5	91 \pm 29	0.91	40.70	0.65	0.83	0.90
4000	65	70 \pm 74	1.9 \pm 0.2	87 \pm 27	0.95	44.58	0.58	0.75	0.91
6000	52	66 \pm 63	1.9 \pm 0.2	85 \pm 24	0.95	45.39	0.78	0.85	0.96

TABLE 2. Tests for nonlinearity of allometric relationships between stem height (H), stem diameter (D) and mass (M) of above-ground part in non-competing and competing plants of *Tagetes patula* L. var. "Tangerine". *p*: significance of second-order term (*b*) in regression: $y=ax+bx^2+c$ (on log-transformed data). Significance is evidence for curvilinearity; NS – relationship is linear, NO CORRELATION – lack of any relationship between measures; sign: sign of significant second-order term (*b*), sign and r^2 only for nonlinear relationships ($P<0.05$). N – number of analysed plants.

A

density N*m ⁻²	N	H-M allometry			D-M allometry			H-D allometry		
		<i>p</i>	sign	r^2	<i>p</i>	sign	r^2	<i>p</i>	sign	r^2
non- -competing	61		NO CORRELATION		NO CORRELATION		NO CORRELATION			
200	14	NS			NS			NS		
400	19	NS			NS			0.009	–	0.862
500	73	0.0025	–	0.753	NS			0.011	–	0.586
500	71	0.0001	–	0.716	NS			0.0014	–	0.552
1000	37	0.016	–	0.807	0.046	+	0.704	NS		
2000	172	0.015	–	0.802	NS			NS		
2000	153	NS			NS			0.0014	–	0.397
2500	70	NS			NS			NS		
3000	214	0.0004	–	0.764	NS			NS		
3000	241	0.00001	–	0.847	0.034	+	0.757	0.002	–	0.500
3000	198	0.00001	–	0.769	0.00018	+	0.738	NS		
3000	198	0.00001	–	0.838	0.0075	+	0.693	0.00001	–	0.525
4000	65	0.0004	–	0.926	NS			NS		
6000	52	0.00008	–	0.870	NS			NS		

RESULTS

Competition was more intense in more dense populations, starting from competition index (I) value of 0.54 in the least dense population (200 individuals · m⁻²) and reaching the maximum value of 0.95 in the two most dense populations (4000 and 6000 individuals · m⁻²) (Table 1).

Mean values of plant mass and stem diameter were significantly lower for competing than for non-competing plants (in almost all comparisons $P<0.0001$). The difference was greater when the competition was stronger. Mean stem height remained almost unchanged even in case of very intense competition. Mean height/mass ratios were higher for populations of higher density and competition intensity. In the most dense population the value of height/mass ratio was over 45, while for non-competing plants it was slightly more than 24. Moreover, at the harvest all non-competing plants were flowering, while for non-competing plants flowers or flower buds were observed very rarely.

The allometric relationship between above-ground plant mass and stem height (H-M allometry) was curvilinear in 10 of 14 plant populations. Allometric relationships between above-ground plant mass and stem diameter (D-M allometry), as well as between stem diameter and stem height (H-D allometry) were linear in most of plant populations. In all three cases for non-competing plants there were no allometric relationships at all (insignificant value of correlation coefficient between measures) (Table 2 and Fig. 1). For clarity of Fig. 1, I present there only two populations of competing plants (plants growing at weak competition with density 1000 individuals · m⁻² and at strong competition with density 6000 individuals · m⁻²).

For competing plants strong allometric relationships between above-ground plant mass, stem height and stem diameter were observed (Table 1). Values of correlation coefficients between log-diameter and log-height, log-

diameter and log-mass, log-height and log-mass were high for every plant population, irrespective of density treatment used. In group of 61 non-competing plants there were not such relationships at all.

DISCUSSION

The present study clearly showed, that the intraspecific competition caused not only a decrease in plant mass, but also influenced plant morphology in populations of *Tagetes patula*.

The collected data show (Table 1) that mean plant mass and mean stem diameter decreased with increase of competition intensity, while mean stem height remained almost the same. This result corresponds with many other papers (Lanner 1985; Weiner and Thomas 1992; Nagashima and Terashima 1995; Dudley and Schmitt 1996). Plant height plays an important role in the process of competition for light, which is in most cases asymmetric (larger plants obtain a disproportionate amount of light relatively to their smaller neighbours, Weiner 1990), because height determines the amount of light intercepted by an individual.

As a result of such reaction to competition, also the height/mass ratio increased with increase of competition intensity. It means that for a given height non-competing plants were much more huge than competing ones. Moreover if competition was stronger, competing plants were generally more thin and weak than in case of less intense competition.

Weiner and Thomas (1992) obtained similar results for populations of three species: *Tagetes patula*, *Impatiens pallida* and *Polygonum pensylvanicum*, but they had only one density level (i.e. competing in density of 1500 individuals · m⁻² and non-competing plants). In my study there was rather a large range of growing densities (from 200 to 6000 individuals · m⁻²), and as a result, competition inten-

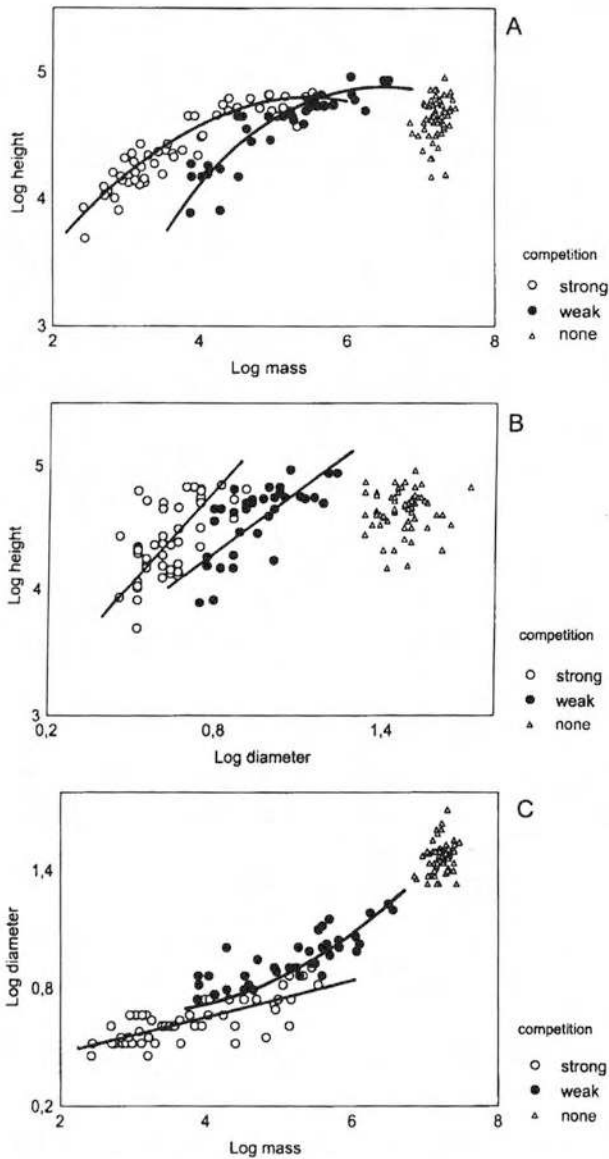


Fig. 1. Allometric relationships between above-ground plant mass (M), stem height (H) and stem diameter (D) for non-competing and competing plants of *Tagetes patula* L. var. "Tangerine", growing at two levels of competition intensity. Weak competition – density 1000 indiv. · m⁻², strong competition – density 6000 indiv. · m⁻², no competition – individually grown plants.

A – relationship between plant mass and stem height was curvilinear for plants growing so at weak ($\log M = 1.83 + 1.06 \log H - 0.09(\log H)^2$), as at strong ($\log M = 0.61 + 1.25 \log H - 0.10(\log H)^2$) competition intensity.

B – relationship between stem diameter and stem height was linear for plants growing so at weak ($\log H = 3.17 + 1.48 \log D$) as at strong ($\log H = 3.38 + 1.61 \log D$) competition intensity.

C – relationship between plant mass and stem diameter was linear for plants growing at strong competition ($\log D = -0.17 + 6.20 \log M$), and curvilinear ($\log D = 1.31 - 0.29 \log M + 0.04(\log M)^2$) for plants at weak competition intensity.

In all three cases for non-competing plants there were no allometric relationships at all (no correlation between measures).

sities. This enables to observe the gradual changes in plant morphology (plant mass, stem diameter, stem height and height/mass ratio) with increase of competition intensity.

My results also enabled to observe changes of allometric relationships between above-ground plant mass, stem height and stem diameter with the increase of competition intensity (Fig. 1), but it was impossible to compare regression lines because some of the relationships were linear, while other were not (Table 2). Moreover for non-competing plants there were no allometric relationships between measures at all.

As regards testing for nonlinearity of allometric relationships I have obtained curvilinearity in H-M allometry for 10 of 14 populations (Table 2), while Weiner and Thomas (1992) also for *Tagetes patula* populations found it to be curvilinear in all cases (they had 8 populations of the same density but for sequential harvests). In my study D-M allometry, as well as H-D allometry were linear in most of plant populations. Weiner and Fishman (1994) obtained similar results for *Kochia scoparia*, an upright annual herb with tree-like growth form, relationships $\log M$ - $\log H$ were changed by competition, while $\log M$ - $\log D$ were not. They discussed the possibility of different biomechanical constraints or different growth rules for height and diameter growth. Also Mandák and Pyšek (1999) reported difference between mass-height allometric relationship at low and high density for populations of *Atriplex sagittata*, while mass-diameter relationship was not different between high and low density treatment.

The collected data show that for group of 61 non-competing plants there was no relationship between mass, height and diameter (lack of correlation between measures), while for all 14 groups of competing plants, irrespective of competition intensity, these relationships were strong (high values of correlation coefficients with $P < 0.01$ in each case) (Table 1). This result is not in agreement with data obtained by Weiner and Thomas (1992) for *Tagetes patula* and two other species, and Weiner and Fishman (1994) for *Kochia scoparia*. They reported high correlations between height, mass and diameter for competing and non-competing plants.

It is difficult to explain these divergences, but my data do not seem to be obtained just by chance. I have compared allometric relationships between competing and non-competing plants four more times during other experiments (data not published). I have not included these results here because the above mentioned experiments were addressed to a somewhat different problem; there the possible changes in relationships between asymmetric competition and spatial effects in different light and nutrients regimes were studied. But I had also performed there the same measurements as during the described experiment (plant mass, stem height and stem diameter). In all four cases there was no correlation between measures (mass, height and diameter) for non-competing plants, while for competing plants these correlations were strong and highly significant.

One of the possible explanations of the results may be as follows. It is possible, that for individually growing plants, without any competition, stem height is not so important. Probably, a plant, growing without any neighbour interference allocates resources according to its own "growth program", written in its genotype, i.e. produces a bit higher but thinner stem, or just the opposite, lower stem but more thick. It may also, for example, produce more or less leaves or branches. Probably, a small difference in resource allocation does not matter for the reproductive output of an

individually growing plant. It may explain the lack of height-mass, height-diameter and mass-diameter correlations in non-competing plants. For plants competing for light, a fast stem growth determines the fate of an individual in the population.

For many plant species 'shade avoidance' response has been observed (Ballare et al. 1987, 1988, 1994; Smith 1995; Schmitt 1997). This response includes enhanced shoot elongation due to the decreased ratio of red to far-red light (R:FR), characteristic of foliage shade. It has been hypothesized to be a form of adaptive plasticity, which allows plants to detect neighbours and develop a morphology that enhances light interception in dense stands (Schmitt et al. 1999). It is possible, that *Tagetes* has also shown a similar response. Plant reaction to a density, which consist in maintaining at any cost the constant height, is an adaptation for life in competitive conditions (Schmitt 1997; Schmitt et al. 1999). Height growth is done at the cost of growth of other organs, e. g. instead of stem growing stouter.

This is one of the possible explanations of my results. The situation is more complicated if we include the possibility of differential response of individuals (genotypes?) to competition. Such possibility is suggested by some models of competition among individuals (Wyszomirski et al. 1999). The differential response consists in different patterns of matter allocation into different plant parts. However, it is impossible to evaluate the importance of such reaction.

It is obvious that allometric growth in plants is not a complete genetically determined characteristics of species, nor simple reflection of physical conditions of growth. Allometry plays an important role in determining the competition relationships between plants and, on the other side, allometric relationships are the result of dynamic interactions between competing plants.

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MORFOLOGIA ROŚLIN I ZWIĄZKI ALLOMETRYCZNE
U KONKURUJĄCYCH I NIE KONKURUJĄCYCH ROŚLIN *TAGETES PATULA* L.

STRESZCZENIE

Analizowano zależności allometryczne (określone jako współczynniki korelacji między masą osobnika – średnicą łodygi, masą osobnika – wysokością łodygi oraz średnicą łodygi – wysokością łodygi) u roślin z gatunku *Tagetes patula* L. (Brassicaceae) var. „Tangerine”. Porównywano rośliny nie konkurujące oraz konkurujące, rosnące w szerokim spektrum zagęszczeń, od 200 do 6000 osobników \cdot m⁻² w warunkach eksperymentu szklarniowego. Dla roślin nie konkurujących stwierdzono brak jakichkolwiek zależności allometrycznych, podczas gdy dla roślin konkurujących były one silne i niezależne od zastosowanego poziomu zagęszczenia.

Analizowano także stopniowe zmiany morfologii roślin rosnących w warunkach coraz silniejszej konkurencji. Stwierdzono, że w miarę wzrostu zagęszczenia maleje średnia masa osobnika i średnica łodygi, zaś wysokość pozostaje prawie nie zmieniona.

SŁOWA KLUCZOWE: konkurencja wewnątrzgatunkowa, intensywność konkurencji, morfologia roślin, związki allometryczne, *Tagetes patula*.