EFFECTS OF FERTILITY, WEED DENSITY AND CROP COMPETITION ON BIOMASS PARTITIONING IN *CENTAUREA CYANUS* L.

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(Received: October 21, 1997. Accepted: November 16, 1998)

ABSTRACT

The influence of environmental factors on biomass partitioning of annual arable weed *Centaurea cyanus* was analysed. We investigated the effect of fertilisation, density and competition with the winter rye crop on the reproductive investment. Three fertiliser treatments and three density levels were applied. In *Centaurea cyanus* differences in the pattern of biomass allocation to reproduction are related to plant size. The relationship between reproductive and vegetative mass is close to linear. It is consistent with the model of linear size-dependent reproductive output. In *Centaurea cyanus* this model worked well for size differences that have been generated by interspecific competition, nutrients supply and density. Our data support the hypothesis that plastic changes in relationship between vegetative and generative biomass are environmentally-induced. Significantly different relationship between vegetative and reproductive biomass were detected among populations growing at different density and fertility levels. The fertilisation with mineral fertiliser and manure resulted in an increase of generative biomass allocated to flowerheads and a decrease of reproductive effort. Generative dry weight increased more rapidly with plant size in higher densities of population and at lower fertility levels.

The experiment showed that the rate of weight allocated to reproductive structures was bigger under the pressure of competition with cereal crop. At low fertility level and high density, when the individuals were small, generative biomass increased faster with plant size.

The production of seeds was not directly dependent on biomass allocated into total reproductive structures. At low level of nutrient supply *C. cyanus* gave more offspring per gram of its biomass. We discuss the results in context of life-history theory. From the strategic point of view, size-dependent variation in reproductive effort and in efficiency of reproduction can be interpreted as good tactics to favour high reproductive investment in small individuals, thus ensuring some offspring. Such a strategy is due to developmental constraints like short vegetation, the small amount of resources available and strong competition with crop.

KEY WORDS: annual weeds, efficiency of reproduction, phenotypic plasticity, reproductive effort.

INTRODUCTION

Many recent manuscripts were aimed to highlight the adjustment of plant species to disturbed environments such as arable fields. The plasticity of several reproductive traits seems to be a unique feature of weedy arable and ruderal species. Their reaction can result in a phenotypic variation in response to a range of environmental conditions based on allocation of biomass within a plant (Turner and Rabinowitz 1983). Life-history theory has put special emphasis on the allocation of resources to generative reproduction. It predicts a trade-off between reproductive allocation and other activities that affect fitness, because resources invested in offspring are not available for future survivorship, growth, and reproduction (Dust 1989). Relative energy allocation to total reproductive organs has been studied and used as a significant measure for evaluation the adaptive strategy of plants (Harper and Ogden 1970; Harper 1977). A more frequent measure of resources allocated to reproduction is the reproductive effort (RE). It has been often defined as the share of biomass of or-

gans involved in reproduction in all above-ground plant parts (Reekie and Bazzaz 1992). Some authors argue that there is a stable level of RE (Harper and Ogden 1970; Fenner 1986), conditioned by genotype (Aarssen and Clauss 1992). Others have shown differences in RE depending upon environmental conditions (Hickman 1975). Samson and Werk (1986) show that while RE may depend on the biomass of an individual, it does not change due to external circumstances such as population density, fertilisation and competition. Weiner (1988) proposed a model in which reproductive output of plant is determined by its size. In this model, reproductive allocation increases lineary with size. In this context, the calculated reproductive effort will always be a function of size of the plants collected. In plants exhibiting a plastic biomass distribution when exposed to different environments we can expect a different reproductive effort. Many studies on reproductive strategies in annual and perennial weeds supported this theory. Size-dependent reproductive output was detected in *Setaria viridis* (Kawano and Miyake 1983), *Datura stramonium* (Weaver et al. 1985), *Panicum miliaceum* (Warwick

and Thompson 1986), *Diplotaxis erucoides* (Sans and Masalles 1994) and several species of agricultural weeds (Thompson et al. 1991). In most cases the relationship between reproductive output and vegetative biomass was linear.

To understand the role that the size-dependent reproductive allocation may play in natural selection, one must know how the relationship between reproductive output and plant size is influenced by genotype and environment. One of the possibilities pointed out by Schmid and Weiner (1993) is that a plastic relationship between reproduction and size is induced by environment. In this paper we investigate the influence of density and fertility on relationship between vegetative and generative biomass of *Centaurea cyanus*.

Centaurea cyanus L. (Asteraceae) is an annual arable weed, which produces seeds once during its life cycle. It develops one or more flowerheads which generate a large number of small seeds that colonise disturbed environments. The species does not exist in central Europe in natural or semi-natural environments. It can occur at various plant densities, ranging from several to hundred plants per square meter of area, in extremely varied soil habitats. *C. cyanus* germinates twice a year: during autumn (October and November) and during spring (March and April). Such a germination gives it an opportunity to colonise autumn seeded cereal crops, and effectively compete for resources, since farming activities on the field during this time are limited.

We investigated the effect of environmental conditions on the reproductive investment. The aim was to test the environmentally induced changes in reproductive output associated with environmentally induced changes in size of plants. We try to answer the question: May the phenotypic plasticity of resource allocation be understood as adaptation of *Centaurea cyanus* to the environmental conditions of arable field?

MATERIAL AND METHODS

Field studies

Studies have been conducted for two years, on the experimental field of Agriculture Chemistry Department of the Warsaw Agricultural University at Skierniewice.

Three fertilisation levels and three densities of *C. cyanus*, similar to those naturally occurring in fields, were investigated.

Three parallel transects, with different fertilisation levels were established in October 1989 in the winter rye crop (*Secale cereale*).

The soil was a typical hapludal developed from glacial loam. At the level 0-10 cm the pH value was 6.0-6.5, organic carbon = 0.63%, nitrogen = 60 mg, P = 5-6 mg and K = 9-11 mg per 100 g of soil. Fertilization with superfosphate, ammonium nitrate and potassium salt has been carried out at the beginning of the experiment.

The following fertilizer treatments were applied:

- 1) Ca calcium 1600 kg CaO/ha
- 2) CaNPK calcium 1600 kg CaO/ha
nitrogen 90 kg N /ha
phosphorus 60 kg P₂O₅/ha
potassium 110 kg K₂O/ha
- 3) CaNPK and manure
CaNPK as above
manure 20 000 kg/ha

The transects were 50 cm wide and 12 m long, with a distance of 25 cm between them. Each transect was divided into two plots with and without crop and the three density levels

randomly established within them. Plants germinated from seedbank occurring in the soil were thinned to final densities of 5, 20 and 50 plants per 0.5 m² in spring of 1990. During thinning, seedlings of uniform size, that had germinated in autumn, were selected, thereby eliminating any size differences due to seed size or germination time. Plants germinated in autumn were able to carry out photosynthesis and accumulate energy during the winter months and had greater biomass than the spring – germinated plants. They often allocate more resources to reproductive structures (Regehr and Bazzaz 1976; Benner and Bazzaz 1987). All other weeds were removed from within the plots and for a distance of 25 cm of adjacent ground. Thirty randomly chosen individuals were marked for each treatment before flowering. During the reproductive stage nylon bags were placed on the flower-heads to prevent blossom falling and seed loss. *C. cyanus* is self or bees pollinated. Bags were placed after flowering because the pollination affects seed production (Hainsworth et al. 1985; Klinkhamer and De Jong 1987). Plants were harvested, by cutting off at the ground level, after full completion of their development, in the third week of July. In total 560 plants were collected, thirty from each density x fertility x crop treatment.

The plant material was divided into shoot (stem and leaves), flower-head with blossom and seeds and air-dried (85°C) to a constant weight.

The field work was repeated, using the same protocol, in the 1991 growing season.

The dry weight of shoots and of generative organs was determined and the number of seeds per plant was counted. The reproductive effort (RE), defined as the proportion of dry weight of reproductive structures, i.e. flower-heads, flowers and seeds to total above-ground dry weight, was calculated (Reekie and Bazzaz 1987). Data on RE, on log-transformed vegetative dry mass (shoot) and on reproductive dry mass were subjected to three-way factorial ANOVA (Sokal and Rohlf 1969), using the SPSS/PC+ ANOVA program (SPSS 1992). The Kruskal – Wallis test was calculated to examine differences between distributions of not logarithmized values of generative dry weight (procedure NPAR) and for comparison of number of seeds/ generative weight ratio among treatments.

Effects of fertilising, density and crop on the relationship between vegetative and generative weight were assessed using the regression analysis (SPSS, procedure REGRESSION).

The relationship between defined in such way reproductive effort and plant size was not analysed because of their artefactual autocorrelation. An analysis of covariance (ANCOVA) was performed to compare the lines of regressions at different treatments (Oktaba 1971).

We tested the hypothesis that regression coefficient of groups compared are equal:

$$F_1 = \frac{\sum(Y_i - Y_e)^2}{c-1} / \frac{\sum(y - Y_i)^2}{n-2c}$$

and the hypothesis that we have one regression line that represents all groups:

$$F_2 = \frac{\sum(y-Y)^2 - \sum(y - Y_i)^2}{2c-2} / \frac{\sum(y - Y_i)^2}{n-2c}$$

where

n – number of observations

c – number of groups

Y_i – regression of group "i"

$(Y_i - Y_c)^2$ – sum of squared deviations of groups regression.

$(y - Y)^2$ – sum of squared deviations from the regression line that represent all groups.

$(y - Y_i)^2$ – sum of squared deviations from the regression line of group "i"

Greenhouse studies

To compare the germination of seed produced by plants from the mentioned combinations of fertilisers presented above, an experiment in a greenhouse was carried out. Soil from the field plots at Skierniewice was put into cuvettes 40 x 50 x 12 cm. A combination of peat and sand was used as a control soil. 108 seeds were put into each cuvette, 36 seeds from each fertiliser combination. The soil in the cuvettes was watered every day using the same amount of water per cuvette. Germinated seedlings were recorded every day for 6 weeks from beginning of the experiment. The median test was used to compare the number of germinated seeds.

RESULTS

Field studies

Mean dry weight of shoots and flower-heads was significantly greater in the plots without crop (Tables 1 and 2). ANOVA indicated significant effects of density, fertility and crop on the dry mass of shoots and generative structures (Table 2a, 2b). In the weed monoculture, plants with the highest average dry mass were in the CaNPK treatment, for all density levels. Lower values were recorded in the CaNPK + manure treatment and the lowest were found for Ca.

Smaller differences between dry weight of individuals of *C. Cyanus* were recorded in cereal crop. The lowest dry weights were in Ca treatment. Weight of shoots and generative structures decreased when density increased in all fertility treatments. Two-way interactions for fertility x density, fertility x

crop and density x crop treatment were observed. Density of population and fertility level affected the dry weight antagonistically. The results of ANOVA were similar for plants collected in 1990 and 1991.

The Kruskal – Wallis test indicated that the distribution of generative dry weight differs significantly between populations. In crop, when only the Ca fertiliser was applied, a vast majority of individuals had the generative weight ranging from 0.2 to 0.6 g. The distribution differed significantly between density levels. Within populations from CaNPK and CaNPK with manure about 10% of individuals achieved a biomass of 0.6-1.0g, whereas the weight of the rest was similar to that of Ca fertilised. When CaNPK with manure fertilisers were applied density did not significantly alter the biomass distribution. Classes of 0.4-0.6 g, 0.2-0.4 g and 0.0-0.2 g dominated in this populations.

In the weed monoculture the generative dry mass was higher. An increased mass of their generative organs was accompanied by more dispersed values. In CaNPK and CaNPK with manure treatment at density of 20 and 50 plants/0.5 m² the most represented class of generative dry weight distribution was that of 0.4-0.6 g. The biggest individuals attained 3.0-3.2 g. Plants with the highest dry weight of flowerheads occurred in CaNPK and CaNPK with manure treatments at density level of 5. The most numerous were classes: 0.8-1 g, 0.6-0.8 g and 0.0-0.2 g. The biggest individuals reached weights of 3.8-4.0 g. The number of specimens of which the weight was very high was the largest. Otherwise, the group showed a broad and regular distribution.

Reproductive effort (RE) differed considerably depending upon the site's condition. Three-way factorial ANOVA showed that RE was significantly affected by fertility, weed density and crop treatment (Table 2a, 2b). Of the above mentioned factors most significant was the fertilisation followed by density, while the weakest influence was of the field crop (see the mean squares, Table 2). The plants from transects fertilised only with Ca achieved, in opposite to the biomass, much higher RE values than those fertilised with CaNPK and CaNPK with manure (Table 1a, 1b). In most cases the highest RE was recorded when only Ca fertiliser was applied. In the

TABLE 1a. Effects of fertilizer, density and crop treatment on the vegetative dry weight (g), reproductive dry weight and reproductive effort in 1990. Data are means $\pm$ standard deviation, $n = 30$.

Fertility	Treatment Density	Crop	Vegetative dry weight	Generative dry weight	Rep. effort
Ca	5	+	0.457 $\pm$ 0.256	0.154 $\pm$ 0.075	0.257 $\pm$ 0.070
		–	2.503 $\pm$ 1.859	0.654 $\pm$ 0.460	0.213 $\pm$ 0.031
	20	+	0.377 $\pm$ 0.277	0.116 $\pm$ 0.089	0.222 $\pm$ 0.097
		–	1.741 $\pm$ 1.204	0.430 $\pm$ 0.273	0.201 $\pm$ 0.044
	50	+	0.368 $\pm$ 0.209	0.123 $\pm$ 0.069	0.267 $\pm$ 0.102
		–	0.864 $\pm$ 0.588	0.242 $\pm$ 0.160	0.227 $\pm$ 0.039
CaNPK	5	+	1.145 $\pm$ 0.974	0.276 $\pm$ 0.201	0.203 $\pm$ 0.069
		–	12.578 $\pm$ 8.134	3.411 $\pm$ 2.489	0.210 $\pm$ 0.057
	20	+	0.797 $\pm$ 0.818	0.188 $\pm$ 0.199	0.179 $\pm$ 0.072
		–	4.511 $\pm$ 3.108	0.986 $\pm$ 0.754	0.178 $\pm$ 0.041
	50	+	1.074 $\pm$ 0.637	0.227 $\pm$ 0.157	0.167 $\pm$ 0.056
		–	3.265 $\pm$ 3.514	0.566 $\pm$ 0.542	0.150 $\pm$ 0.060
CaNPK with manure	5	+	1.131 $\pm$ 0.684	0.251 $\pm$ 0.168	0.184 $\pm$ 0.058
		–	9.477 $\pm$ 5.031	2.668 $\pm$ 1.581	0.222 $\pm$ 0.053
	20	+	0.779 $\pm$ 0.614	0.174 $\pm$ 0.152	0.171 $\pm$ 0.068
		–	3.459 $\pm$ 2.319	0.872 $\pm$ 0.742	0.181 $\pm$ 0.085
	50	+	1.189 $\pm$ 0.766	0.263 $\pm$ 0.217	0.166 $\pm$ 0.058
		–	2.603 $\pm$ 1.629	0.544 $\pm$ 0.406	0.157 $\pm$ 0.070

TABLE 1b. Effects of fertilizer, density and crop treatment on the vegetative dry weight (g), reproductive dry weight and reproductive effort in 1991. Data are means $\pm$ standard deviation, n = 30

Fertility	Treatment Density	Crop	Vegetative dry weight	Generative dry weight	Rep. effort
Ca	5	+	0.594 $\pm$ 0.765	0.199 $\pm$ 0.274	0.245 $\pm$ 0.062
		—	1.858 $\pm$ 1.392	0.570 $\pm$ 0.412	0.243 $\pm$ 0.052
	20	+	0.469 $\pm$ 0.285	0.130 $\pm$ 0.085	0.211 $\pm$ 0.073
		—	1.447 $\pm$ 1.134	0.383 $\pm$ 0.251	0.213 $\pm$ 0.034
	50	+	0.394 $\pm$ 0.216	0.135 $\pm$ 0.083	0.258 $\pm$ 0.065
		—	0.912 $\pm$ 0.666	0.257 $\pm$ 0.184	0.230 $\pm$ 0.053
CaNPK	5	+	1.371 $\pm$ 1.093	0.330 $\pm$ 0.244	0.198 $\pm$ 0.047
		—	15.356 $\pm$ 10.017	4.422 $\pm$ 3.162	0.210 $\pm$ 0.056
	20	+	1.069 $\pm$ 0.766	0.270 $\pm$ 0.238	0.183 $\pm$ 0.067
		—	4.131 $\pm$ 3.030	0.908 $\pm$ 0.780	0.167 $\pm$ 0.061
	50	+	0.923 $\pm$ 0.609	0.212 $\pm$ 0.156	0.179 $\pm$ 0.058
		—	3.136 $\pm$ 3.232	604 $\pm$ 0.638	0.162 $\pm$ 0.061
CaNPK with manure	5	+	1.579 $\pm$ 0.798	0.393 $\pm$ 0.195	0.201 $\pm$ 0.053
		—	8.358 $\pm$ 5.675	2.379 $\pm$ 1.822	0.205 $\pm$ 0.072
	20	+	2.013 $\pm$ 2.399	0.488 $\pm$ 0.597	0.180 $\pm$ 0.054
		—	5.442 $\pm$ 4.588	1.184 $\pm$ 1.015	0.174 $\pm$ 0.050
	50	+	1.105 $\pm$ 0.797	0.231 $\pm$ 0.167	0.188 $\pm$ 0.139
		—	2.693 $\pm$ 1.842	0.649 $\pm$ 0.476	0.178 $\pm$ 0.079

presence of rye the reproductive effort of *C. cyanus* decreased with the addition of manure, but in the weed monoculture RE was higher in CaNPK + manure than in the CaNPK treatment. In transects, where CaNPK and CaNPK with manure was applied, RE tended to decrease when the population density increased. An opposite situation was found in the Ca treatment, where the highest RE was recorded at density of 50, medium at 5 and the lowest at 20 plants/0.5 m². Reproductive effort was higher when rye was present in the field.

The generative dry weight increased proportionally with dry weight of vegetative structures. Weight of organs responsible for reproduction was positively correlated with the weight of shoots in all fertility $\times$ density $\times$ crop treatments ($r^2 = 0.85 - 0.90$, p). The analysis of covariance showed that the regression of generative weight against vegetative weights had similar slopes (F1) but the y-intercepts differed significantly (F2) (Table 4). High variation in the intercepts among treatments was attributed to differences in proportion of reproduc-

tive dry weight between treatments. The ratio of vegetative/generative weight was significantly higher in the Ca treatment than in CaNPK and CaNPK with manure and decreased when plant density increased. In most populations compared, the slopes were parallel. Slopes differed significantly among populations of *C. cyanus* growing in crop and fertilised only with CaNPK and manure. At density of 5 plants/0.5m² the dry weight of flowerheads increased more slowly, than at 20 and 50 (Fig. 1). Similarly, different slopes affected by fertility level were observed in crop at density of 50 plants/0.5 m² (Fig. 2). The reproductive weight increased more rapidly with the plant size when fertilisers were applied. The between-year variations in the share of generative biomass were small and did not differentiate the regression significantly.

The average number of seeds produced by an individual in plots with a field crop was several times lower than in plots without a field crop (Table 3a, 3b). In most cases the number

TABLE 2a. Three-way analysis of variance for dry mass of shoots of *Centaurea cyanus* collected in 1990.

Source of variation	DF	Vegetative dry weight		Generative dry weight		Reproductive effort	
		Mean Square	F	Mean Square	F	Mean Square	F
Main effects	5	94.31	198.19**	51.01	83.28**	0.068	22.03*
Fertility	2	61.71	129.68**	22.90	37.39**	0.134	43.41**
Density	2	24.52	51.53**	41.17	67.22**	0.029	9.30*
Crop	1	299.08	628.51**	125.57	205.02**	0.018	5.98*
2-way interactions	8	4.96	10.43*	16.64	27.17*	0.019	6.27*
Fertility $\times$ density	4	1.57	3.29*	7.21	11.80*	0.011	3.62*
Fertility $\times$ crop	2	1.83	3.84*	15.33	25.03*	0.053	17.10*
Density $\times$ crop	2	14.89	31.28**	36.65	59.83**	0.001	0.43 [†]
3-way interactions							
Fertility $\times$ density $\times$ crop	4	0.77	1.62 [†]	6.67	10.90*	0.001	0.32 [†]
Explained	17	30.25	63.58	24.41	39.85	0.029	9.51

[†] — not significant; * — significant at $p < 0.05$; ** at $p < 0.001$

TABLE 2b. Three-way analysis of variance for dry mass of shoots of *Centaurea cyanus* collected in 1991.

Source of variation	DF	Vegetative dry weight		Generative dry weight		Reproductive effort	
		Mean Square	F	Mean Square	F	Mean Square	F
Main effects	5	86.98	143.63**	64.40	73.00**	0.061	17.86*
Fertility	2	78.73	130.00**	37.10	42.06**	0.115	33.74**
Density	2	27.24	44.97**	53.21	60.31**	0.036	10.64*
Crop	1	222.98	368.20**	141.75	160.68**	0.004	1.04*
2-way interactions	8	3.99	6.58*	26.11	29.60*	0.005	1.50*
Fertility x density	4	2.02	3.34*	16.08	18.27*	0.007	1.98*
Fertility x crop	2	3.29	5.43*	26.31	29.82*	0.003	0.93*
Density x crop	2	8.62	14.23*	46.38	52.58**	0.004	1.09
3-way interactions							
Fertility x density x crop	4	1.41	2.33 [†]	15.59	17.62*	0.002	0.47 [†]
Explained	17	27.79	45.89	34.89	39.55	0.021	6.07

[†] – not significant; * – significant at $p < 0.05$; ** at $p < 0.001$

Fig. 1. Relationship between generative and vegetative mass of plants at three density levels a) 5, b) 20, c) 50 plants/0.5 m².

Fig. 2. Relationship between generative and vegetative mass of plants at three fertility levels a) Ca, b) CaNPK, c) CaNPK and manure.

TABLE 3. Effect of fertility and density on number of seeds of *C. cyanus* per individual as a result of Kruskal-Wallis test. Values are means with standard error (n=30).

a) in crop; b) in monoculture.

a)	Density			Chi-Square
	5	20	50	
Fertility				
Ca	21.26 ± 3.35	11.20 ± 1.45	16.18 ± 1.44	12.15**
CaNPK	32.32 ± 3.90	30.26 ± 3.65	21.50 ± 2.43	3.97 ^{ns}
CaNPK with manure	30.78 ± 2.48	31.52 ± 5.34	27.73 ± 3.13	2.37 ^{ns}
Chi-Square	14.65***	18.66***	8.93*	
b)				
	5	20	50	Chi-Square
Fertility				
Ca	42.51 ± 4.36	33.76 ± 2.93	17.42 ± 1.56	32.85***
CaNPK	313.64 ± 37.63	75.28 ± 12.56	53.60 ± 7.37	56.35***
CaNPK with manure	209.29 ± 19.36	72.88 ± 10.20	55.95 ± 5.73	48.42***
Chi-Square	70.24***	12.17**	35.44***	

significant at: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant

TABLE 4. One-way ANCOVA tests for interaction between environmental factors and the relationship between generative and vegetative weight.

F₁ – tested hypothesis that regression coefficient of compared lines are equal;

F₂ – there is one regression line, representing all populations.

Factor	Source	Crop	F ₁	F ₂
Fertility	5	+	0.90 [†]	6.47**
		–	3.95 [†]	25.78**
	20	+	0.74 [†]	26.10**
		–	0.05 [†]	7.94**
	50	+	9.58**	23.65**
		–	0.82 [†]	11.58**
Density	Ca	+	0.56 [†]	19.73**
		–	1.21 [†]	6.08**
	CaNPK	+	2.97 [†]	16.26**
		–	0.72 [†]	10.44**
	CaNPK + manure	+	17.08**	22.12**
		–	2.64 [†]	26.01**

** significant at $p < 0.01$; [†] not significant

of seeds increased when the density of plants decreased (Table 3). In the weed monoculture and in the crop a considerably smaller number of seeds was detected for plants from the Ca treatment (11-21 seeds in the rye plots, and 17-42 of seeds in the plots without crop). There were small differences between plants from CaNPK and CaNPK with manure treatment. In the monoculture plants with the highest seed production originated from plots treated with CaNPK and in rye crop from CaNPK+manure. In the rye fields, plants fertilised by CaNPK+manure at the density of 20 generated the highest number of seeds.

In crop and in weed monoculture a significant difference of the seeds/generative weight ratio between populations occurred for three fertility levels (Table 5). When Ca fertiliser was applied, the number of seeds per unit of generative dry

weight was higher than in CaNPK and in CaNPK with manure treatment. In the weed monoculture differences between populations occurred for all density and fertility levels. Plants collected from transect fertilised only with Ca produced more seeds per unit of biomass. Similarly the level of plants density, except plants from the Ca treatment, significantly affected seeds/generative weight ratio.

Greenhouse studies

The experiment conducted in a greenhouse indicated that seeds originating from plots fertilised with Ca alone had the lowest germination rate – an average of 11%, whereas seeds from CaNPK plots had a 23% and seeds from CaNPK+manure field had a 34% germination (Table 6).

DISCUSSION

The generative weight and number of seeds of *C. cyanus* were dependent on the size of plants and affected by nutrient supply, density and interspecific competition. Our data support the hypothesis that the relationship between reproductive and vegetative mass is close to linear. There was a high, significant, positive correlation between these traits. In most studies, the data from agricultural weed species were consistent with the model of linear size-dependent reproductive output (Thompson et al. 1991). Weiner (1988) hypothesized that linear size-dependent reproductive output occurs when size differences are caused by competition rather than other environmental factors. In our experiment this model worked well for size differences that have been generated by nutrients supply and density (interspecific competition).

Some authors demonstrate the variability in the regression of plant size against reproductive output and suggest that this relationship is dependent on habitat conditions (Ohlson 1988; Clauss and Aarssen 1994). We could expect thus that environmental factors would influence the allocation of biomass to vegetative and reproductive structures. Significant variation of the regression equations indicates differences in biomass

TABLE 5. Effect of fertility and density treatments on number of seeds/generative dry mass ratio as a result of Kruskal – Wallis test. Values are the means with standard error (n=30); a) in crop, b) in weed monoculture.

a)	Density			Chi-Square
	5	20	50	
Fertility				
Ca	8.11 ± 0.55	9.25 ± 1.15	10.05 ± 0.97	1.7 ^{ns}
CaNPK	4.84 ± 0.46	8.81 ± 1.16	5.25 ± 0.58	10.5**
CaNPK with manure	6.02 ± 0.66	4.96 ± 0.75	5.08 ± 0.68	6.1*
Chi-Square	23.1***	19.2***	29.7***	
b)				
	5	20	50	Chi-Square
Fertility				
Ca	7.12 ± 0.77	6.29 ± 0.70	9.29 ± 0.83	9.1*
CaNPK	7.25 ± 1.44	1.66 ± 0.23	6.84 ± 0.89	30.8***
CaNPK with manure	1.29 ± 0.17	3.59 ± 0.65	4.06 ± 0.44	43.9***
Chi-Square	43.5***	54.3***	25.8***	

ns – not significant; significant at: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

TABLE 6. Germination of seeds collected from plants fertilised with Ca, CaNPK and CaNPK with manure. Data were compared using median test; (n=36).

Group	Mean	Standard Error	Median	Chi-Square
Ca	39.08	8.33		
CaNPK	97.83	14.64	93.5	16.67***
CaNPK with manure	144.16	36.47		

*** significant at $p < 0.001$

allocation among treatments. We showed that addition of fertilisers such as superfosfat and manure resulted in an increase of generative biomass allocated to flowerheads and decrease of reproductive effort. Our data support the hypothesis that plastic relationship between vegetative and generative biomass is environmentally-induced. On the other hand, this variation may have genetic background. On the basis of the comparison of generative weight distributions we may conclude that variability in biomass allocation is much higher in populations growing in more favourable habitats. Therefore, it should be noticed that plants from such a population (e.g. CaNPK with manure treatment) had a broad and regular distribution of generative dry weight ranging from 0.1 to 4 g. The ratio generative/vegetative dry weight tended to decrease when density of population increased. Significantly different slopes were detected among populations growing in crop at different density and fertility levels, but in two particular treatment combinations only. Generative dry weight increased more rapidly with plant size in higher population densities and at higher fertility levels. This comparison showed that differences in the pattern of biomass allocation to reproductive structures were related to plant size.

The life-history theory states that if early reproduction diverts resources from growth then survival and fertility may be lowered. Reduced growth rates associated with precocious reproduction may cause selection to favour vegetative growth

of juveniles and hence a higher reproductive effort at an older age and greater size (Doust 1989; Schmid and Weiner 1993). Our experiment showed that the rate of weight allocated to reproductive structures was bigger under the pressure of intraspecific competition with cereal crop. Differences in regression lines between reproductive and vegetative biomass were related to differences in plant-size distribution. In Ca treatment, especially at highest density, where the individuals were small, generative biomass increased faster with plant size. In monoculture higher RE was detected at CaNPK treatment but in the presence of cereal crop RE decreased when manure was applied. Differences of reproductive allocation between CaNPK and CaNPK with manure treatment were not evident.

Annual semelparous weeds do not have a threshold size for reproduction like perennial or biennial species. In the environment of arable field the length of the growing season is cut short by cultivation and fruiting should begin early to ensure seed production. The high reproductive effort and high efficiency of reproduction could compensate a small amount of resources available for reproductive investment. It was demonstrated that biomass allocation to reproductive structures was higher in small plants in several agricultural weeds such as *Datura stramonium*, *Sorghum halepense*, *Abutilon theophrasti*, *Panicum miliaceum*, *Diploaxis erucoides* (Sans and Masalles 1994). These results are consistent with the idea of Fox (1992), that the prediction of theoretical models of resources allocation should be considered in the context of developmental constraints within which plants life history must unfold.

One of the important conclusions is that efficiency of reproduction (Boggs 1992), defined as the proportion of accumulated resources (e.g. biomass) converted to reproductive output (e.g. number of offspring) may change across the gradient of fertility. The production of seeds was not directly dependent on biomass allocated into total reproductive structures. The fertility level significantly affected the relationship between number of seeds produced and biomass allocated to generative structures. Plants from Ca treatment generated more seeds per gram of dry generative weight than plants from CaNPK and CaNPK with manure treatment. At low

level of nutrient supply *C. cyanus* gave more offspring per gram of its biomass. On the other hand those seeds had lower germination power. The ability to maximize fecundity when resources are scarce would affect their fitness. Some other aspects of reproductive biology like pollination, breeding system, etc. are very significant while evaluating the reproductive strategy of plants (especially semelparous species) and their evolutionary status (Bierzychudek 1981; Klinkhamer 1987). Some researchers demonstrated that plasticity of the size-fecundity relationship had genotypic background (Aarssen and Clauss 1992; Schmid and Weiner 1993). The phenotypic plasticity can originate from many sources. It is very difficult to control all factors that may affect reproductive output under natural conditions.

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WPŁYW NAWOŻENIA, ZAGĘSZCZENIA I KONKURENCJI Z ROŚLINĄ UPRAWNĄ
NA ROZKŁAD BIOMASY CHABRA BŁAWATKA (*CENTAUREA CYANUS* L.)

STRESZCZENIE

Pracę poświęcono analizie wpływu czynników środowiskowych na rozkład biomasy chabra bławatka – rocznej rośliny segetalnej. Analizowano efekt poziomego nawożenia, zagęszczenia populacji i konkurencji z rośliną uprawną na wydatkowanie zasobów na reprodukcję. Zastosowano tu trzy poziomy nawożenia i zagęszczenia roślin. U *Centaurea cyanus* udział struktur związanych z rozmnażaniem w biomase rośliny jest zależny od jej wielkości. Zależność tę można opisać w przybliżeniu za pomocą funkcji liniowej. Jest to zgodne z modelem zależnego od wielkości rośliny wydatkowania zasobów na rozmnażanie. Model ten można zastosować do chabra bławatka, gdy różnice wielkości spowodowane są konkurencją międzygatunkową (jak w pracach Weinerja) oraz zmianą zagęszczenia roślin i poziomego nawożenia. Wyniki pracy potwierdzają hipotezę, że rozdział biomasy pomiędzy organy odpowiedzialne za wzrost i rozmnażanie ulega plastycznym zmianom pod wpływem czynników środowiskowych. Istotne statystycznie różnice w rozdziale biomasy stwierdzono porównując rośliny z powierzchni o różnym poziomie nawożenia i zagęszczenia. Nawożenie mineralne i obornikowe wywołało zwiększenie biomasy generatywnych części rośliny i zmniejszenie wysiłku reprodukcyjnego roślin. Jednocześnie stwierdzono, że wzrost masy generatywnej wraz z wielkością był intensywniejszy u roślin nienawożonych. Liczba nasion wytwarzanych przez chabra bławatka nie jest bezpośrednio zależna od biomasy kwiatostanów. Zaobserwowano, że przy niższym poziomie nawożenia liczba nasion przypadająca na 1 g suchej masy kwiatostanów jest istotnie większa.

Z punktu widzenia strategii życia rośliny zróżnicowanie rozdziału zasobów pomiędzy wzrost i rozmnażanie służy zwiększeniu wysiłku reprodukcyjnego i wydajności reprodukcji u osobników małych wzrastających na glebie uboższej w składniki pokarmowe. Poświęcanie większej części zasobów na rozmnażanie we wczesnym stadium wzrostu rośliny jest nieekonomiczne, ponieważ obniża prawdopodobieństwo przeżycia i zdolności rozrodcze w późniejszym wieku. Z drugiej strony w warunkach gdy sezon wegetacyjny jest krótki a ilość dostępnych zasobów ograniczona strategia taka zapewnia każdej roślinie wydanie nasion.

SŁOWA KLUCZOWE: plastyczność fenotypowa, wydajność reprodukcji, wysiłek reprodukcyjny.