Plant Ecol (2009) 201:481–489
DOI 10.1007/s11258-008-9499-6

Reproductive allocation of *Carex flava* reacts differently to competition and resources in a designed plant mixture of five species

Matthias Suter

Received: 11 December 2007 / Accepted: 26 August 2008 / Published online: 21 September 2008

Abstract In natural plant communities, reproductive allocation can be affected by complex interactions among abiotic resources, species competition and plant size. This topic was addressed using a variety of designed mixed stands of five species (*Carex elata*, *Carex flava*, *Lycopus europaeus*, *Lysimachia vulgaris* and *Mentha aquatica)* under four abiotic conditions to investigate how competition and abiotic resources influence the reproductive allocation of one of the five species, *C. flava*. The plant mixtures varied systematically in both the relative abundance of the five species and the absolute density, and were each established with two levels of water and nutrients. In total, 176 mixtures were maintained for two growing seasons in large pots in an experimental garden. Reproductive allocation of *C. flava* increased from 6.8% to 9.7% under high nutrient application; however, for both nutrient levels, reproductive allocation was independent of shoot mass (size-independent allocation). Under low competition, reproductive allocation of *C. flava* decreased as its shoot mass increased, indicating a relatively high investment in vegetative structures under higher light availability. However, under strong competition, the allocation pattern changed and a constant reproductive allocation for different plant sizes was observed. Different water levels did not influence the shoot mass, seed mass or reproductive allocation of *C. flava*, indicating that the species was not stressed under dryer conditions. When under competitive pressure, however, the species responded with reduced shoot and seed production under more favourable water conditions. This behaviour indicates a trade-off between the ability to tolerate stress and the competitive and reproductive response of *C. flava*. In conclusion, *C. flava* was adversely affected by competition with some of the species, and competition, mediated by plant size, indirectly affected reproductive allocation. *C. flava* was able to modify its allocation pattern depending on the available resources and retained its reproductive allocation even under unfavourable conditions for varying plant sizes, which is interpreted as an advantageous reaction to greater competition pressure.

Keywords Fen meadow species · Nutrient water supply · Simplex design · Stress tolerance · Trade-off

Introduction

Plants allocate restricted proportions of resources to either vegetative or reproductive structures.

Electronic supplementary material The online version of this article (doi:10.1007/s11258-008-9499-6) contains supplementary material, which is available to authorized users.

M. Suter (✉)
Institute of Integrative Biology, ETH Zurich,
Universitaetstrasse 16, Zurich 8092, Switzerland
e-mail: matthias.suter@env.ethz.ch

According to environmental conditions, the species' allocation patterns may be adapted in ways that affect their fitness; therefore, resource allocation is expected to have important implications for plant life history and evolution (Reekie and Bazzaz 2005). Studying a plant species' reproductive allocation should thus highlight its survival strategy (Harper and Ogden 1970).

The mass of a plant's reproduction structures in relation to the total aboveground biomass has been defined as reproductive allocation (RA) (Karlsson and Méndez 2005). Within a species, the most important factor affecting RA is plant size (Weiner 1988; Sugiyama and Bazzaz 1998; Méndez and Karlsson 2004). In an analysis of 41 species, many perennials exhibited a decreasing RA with increasing plant biomass, whereas in the case of annuals, either the reverse was true or RA remained constant (Hara et al. 1988). Studies focussing on single species' RA have confirmed these patterns (Reekie 1998; Susko and Lovett 2000; Sletvold 2002).

Linking RA and plant size can be most effectively achieved by analysing a species' seed mass and shoot mass, which are often positively correlated and increase linearly on a log–log scale (Klinkhamer et al. 1994; Sadras et al. 1997; Sletvold 2002). This correlation becomes $Seed\ mass = \alpha\ shoot\ mass^{\beta}$ when expressed on a linear scale (Hendriks and Mulder 2008). Different allocation patterns, such as size-dependent or size-independent allocation, can be distinguished according to the relative change of seed mass and shoot mass (Weiner 1988; Sugiyama and Bazzaz 1998).

Intraspecific responses of RA to environmental stress have been thoroughly reviewed (Chiariello and Gulmon 1991; Reekie and Bazzaz 2005). Chiariello and Gulmon (1991) noted that many perennial species reduce RA in response to resource limitation (water, nutrients and light), but annual species often increase RA in response to shortage of water, decrease RA in response to light limitation and exhibit no response to nutrients. As shown by Karlsson and Méndez (2005), these trends are not consistent and vary greatly in response to environmental factors.

So far, the relationship between RA and resources has only been investigated with single species or in pairwise species comparisons (Sugiyama and Bazzaz 1998; Whitfield et al. 1998; Cheplick 2001; Arenas et al. 2002). Conclusions drawn from such experiments are not easily applied to plant communities, as species interactions in mixtures can be more complex than pairwise. The presence of a strong competitor could reduce the performance of a target species; however, the presence of additional species could considerably mitigate negative competition (Suter et al. 2007).

Interactions among several species can be investigated using experiments with numerous species and varying abiotic conditions. A specific design for the set-up and analysis of multi-component mixtures is the simplex design (Cornell 2002). The simplex design, originally developed for industrial trials, allows quantification of the effects of many species in a mixture on a target variable, including interactions between competition and resources (Ramseier et al. 2005). This design has recently been used to investigate the role of multiple species interactions in plant community development. In an experimental set-up, mixtures of five perennial species were established under two intensities of competition and four environmental conditions by combining two levels of water availability with two levels of nutrient supply (Suter et al. 2007). In the present article, the influence of the various treatments on RA and on shoot and seed production of one of the five species, *Carex flava* L., is analysed in detail.

Investigation of RA in *C. flava* under these semi-complex conditions should allow more accurate conclusions to be drawn on the species' reproductive behaviour in natural communities. *C. flava* is mainly observed in calcareous fens of low nutrient status (*Caricion davallianae*, Ellenberg 1996). In such habitats, nutrient enrichment can drastically influence community composition (Pauli et al. 2002). Because increased nutrient availability also changes the relative allocation to shoots and seeds (Karlsson and Méndez 2005), it is possible that *C. flava* adapts its RA when environmental conditions change. If, for example, *C. flava* is able to resist competition pressure from more productive species that profit from nutrient enrichment, its shoot and seed mass should only be marginally affected by increased density of neighbouring species, and RA should remain constant. In comparison, when strongly suffering from competition, shoot and seed mass should be reduced, but the relative allocation could be adapted so that RA is maintained or even increased (Chiariello and Gulmon 1991). In the latter case, *C.*

flava would act similarly to annual species that produce a high seed output under unfavourable conditions (Grime 2001; Karlsson and Méndez 2005). Specifically, this study examined (1) whether competition of different species and varying abiotic conditions interact in their effect on RA and shoot and seed mass production of *C. flava*, (2) whether species competition affects RA and shoot and seed mass of *C. flava* in the same way as varying nutrient levels and (3) whether a change in RA is an advantageous reaction for *C. flava* to maintain its occurrence under modified abiotic conditions.

Materials and methods

The experimental design is described in detail by Suter et al. (2007). An outline of the most important aspects relating to this study is presented here.

Plant material and experimental design

Plant mixtures consisted of five perennial species common to Swiss fens: *Carex elata* All., *Carex flava* L., *Lycopus europaeus* L. s.str., *Lysimachia vulgaris* L. and *Mentha aquatica* L. (Nomenclature following Aeschimann and Heitz 2005). Twenty-two different mixtures were established in accordance with the simplex design (Cornell 2002); all five species were present in each mixture. Mixtures were either equal stands (20% of each species), dominant stands (60% of one species, 10% of four others) or codominant stands (35% of each of two species, 10% of three others). Equal and dominant stands were planted in two overall densities of 20 (low density) and 50 (high density) seedlings per pot, whereas codominant stands were planted in an overall density of 20 seedlings per pot. Each mixture was established at two water and two nutrient levels and replicated twice.

The seedlings were planted on 7 and 8 May 2001 in pots of 75 l (50 cm diameter, 45 cm tall), containing quartz sand of 1 to 1.7 mm grain size. Within each pot, the interseedling distance was 6 cm for high density and 10 cm for low density mixtures. In total, 176 pots were randomly distributed at an experimental site of the Swiss Federal Institute of Technology, Zurich.

In the high water treatment, water level was maintained at sand surface (42 cm height in the pot), while in the low water treatment, the level was at half-pot height (21 cm), resulting in a dry zone above. Water levels were adjusted every other day with tap water during the growing season.

The pots with high nutrient levels received three times the amount of nutrients as those with low nutrient levels. Nutrients for the high level consisted of 6 g m^{-2} nitrogen in the 1st year and 9 g m^{-2} nitrogen in the second. The nitrogen/phosphorous (N/P) ratio was set to 4, and N and P were applied with a complete fertiliser that also included micronutrients (Wuxal, Maag, Switzerland).

Maintenance and measurements

Initial shoot biomass was estimated by drying and weighing 20 seedlings of each species, randomly selected from those remaining after planting. In the second growing season, when *C. flava* reached reproductive maturity, infructescences were carefully removed (18 and 19 June 2002), leaving the remaining plant biomass until the final harvest of all the species 2 months later. The seeds left within the utricles were cleaned from the bracts, and empty utricles were removed from the samples. Seed mass per pot was determined after drying the samples (75°C) to constant weight. All plants were harvested from 19 to 29 August 2002 by cutting aboveground living shoot mass. Again, biomass samples were dried (75°C) to constant weight, and dry mass per species and pot was determined.

The diaspore mass of *C. flava* was used for the analysis because it was not practical to separate the seed from the surrounding utricle. Nevertheless, the term “seed mass” rather than “diaspore mass” is used for convenience. Since the seed accounts for a large proportion of the diaspore mass, the inclusion of the utricle is unlikely to affect the conclusions drawn from the data.

Data analysis

The definition of mixtures with five species ($i = 1, \ldots, 5$) follows Suter et al. (2007). For *C. flava (cf)*, three response variables were calculated:

$$\text{Shoot mass} = \frac{(\textit{Final shoot mass})_{\text{cf}}\textit{per pot}}{d_{\text{cf}}},$$

$$\text{Seed mass} = \frac{(\textit{Total seed mass})_{\text{cf}}\textit{per pot}}{d_{\text{cf}}},$$

$$\text{Reproductive allocation} = \frac{\textit{Seed mass}}{\textit{Shoot} + \textit{seed mass}},$$

with d_{cf} being the number of planted *C. flava* individuals per pot. It follows that these variables refer to a mean value per pot and not to individuals within a pot. The effects of the initial biomass of the five species and of water and nutrients on these response variables were first assessed with

$$\text{Response} = \alpha + \sum_{i=1}^{5} \beta_i y_i + \gamma\, \textit{water} + \delta\, \textit{nutrient} + \varepsilon \qquad (1)$$

where y_i is the initial biomass of species i in a mixture at the start of the experiment. The effects of increasing species biomass (competition) are given by the β coefficients; γ and δ coefficients indicate the shift from the low to the high water and nutrient levels, respectively, and ε represents the error term. In order to meet the assumptions of linear regression (normal distribution and homogeneity of residual variance), the response variables shoot mass and seed mass were $\log_{10}$ transformed, and RA was arcsine-square root transformed. Quadratic effects of species biomass ($y_i * y_i$) and any two-way interactions between main effects ($y_i * \textit{water}, y_i * \textit{nutrient}$ *and* $\textit{water} * \textit{nutrient}$) were also tested (for further details on the analysis, see electronic appendix).

In order to evaluate the confounding effects of plant size on RA, the relationship between seed mass and shoot mass of *C. flava* was analysed in more detail with

$$\log_{10}(\textit{seed mass}) = \log_{10}(\alpha) + \beta \log_{10}(\textit{shoot mass}) + \gamma\, \textit{water} + \delta\, \textit{nutrient} + \lambda\, \textit{density} + \varepsilon \qquad (2)$$

where γ and δ estimates are as stated above. Density was included as a factor with two levels and served as a surrogate variable to assess the role of competition on seed mass and RA (Karlsson and Méndez 2005). Thus, the λ-coefficient indicates an overall competition effect due to the shift from low to high planting density.

Using the relationship $\log_{10}(\textit{seed mass}) = \log_{10}(\alpha) + \beta \log_{10}(\textit{shoot mass})$, the following considerations enable distinction of different allocation patterns. (1) Provided that β is 1, seed mass and shoot mass will increase proportionally, and RA will remain constant with increasing shoot mass. (2) If $\beta \neq 1$, then seeds will be allocated in a non-linear way and RA will increase ($\beta > 1$) or decrease ($\beta < 1$) with higher shoot mass. (3) An influence of abiotic or biotic factors (nutrients, water and competition) could either change the allocation pattern (change of β) or the α-coefficient. In the latter case, RA will change by a fixed amount, independent of vegetative biomass; thus, such effects are termed size-independent (Weiner 1988). All analyses were performed using the statistical software R (R Development Core Team 2007).

Results

Shoot mass and seed mass

After 2 years, mean shoot dry mass per individual of *C. flava* was 0.710 g and the mean seed mass was

Table 1 Regression coefficients for the effects of initial species biomass, water and nutrient levels on shoot mass, seed mass and reproductive allocation of *C. flava* in experimental plant mixtures with five species after 2 years

Effect	$\log_{10}$ (shoot mass)	$\log_{10}$ (seed mass)	Arcsin-sqrt (reproductive allocation)
Intercept	−0.155***	−1.304***	0.260***
Water	0.012	0.031	0.006
Nutrient	0.211***	0.386***	0.053***
C. elata	−0.837***	−0.351***	0.030
C. flava	−0.235***	−0.234***	−0.004
L. europaeus	−0.139	−0.056	−0.004
L. vulgaris	−0.151	−0.060	0.020
M. aquatica	−0.086	−0.561***	−0.128***
C. elata^2	0.379***	-	-
M. aquatica^2	-	0.257**	0.068**
Water × *L. europaeus*	−0.624**	−0.883**	-

Water and nutrient effects express the shift from the low to the high level

** $P \leq 0.01$; *** $P \leq 0.001$; - term has been omitted in the particular model

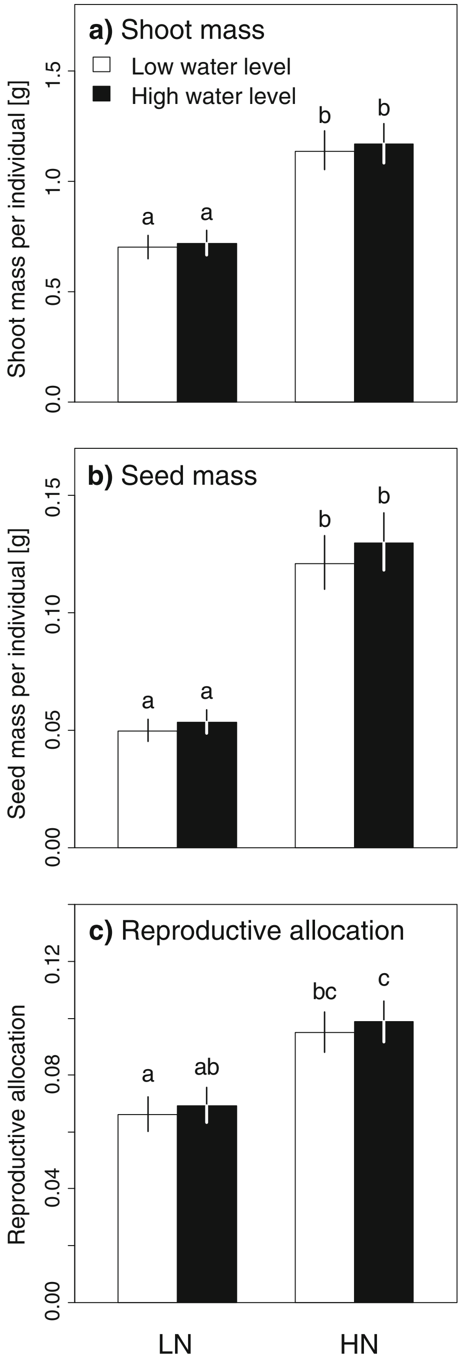

Fig. 1 Shoot and seed production and reproductive allocation of *C. flava* in experimental plant mixtures under four combinations of water and nutrient treatments. Means and standard errors are backtransformed predicted values from regression analysis (Table 1). LN: low nutrients, HN: high nutrients. Different letters indicate a difference at $P \leq 0.05$ (Tukey's multiple comparison test)

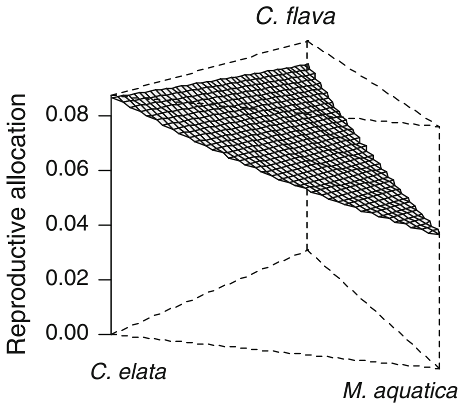

Fig. 2 Reproductive allocation of *C. flava* in experimental plant mixtures with five species after 2 years; the influence of the three most relevant species is displayed. The response surface refers to backtransformed values based on the regression of Table 1 and is for low water–low nutrients conditions. The corners of the surface refer to mixtures with one dominant species (see electronic appendix for further details)

0.052 g under low nutrient and low water conditions (Table 1; Fig. 1a, b). High nutrient application increased shoot mass by 62% and seed mass by 143%, whereas high water level did not affect either parameter (Table 1).

Competition effects depended strongly on the species. Greater initial biomass of *C. elata* (interspecific competition) and *C. flava* (intraspecific competition) caused a decrease in shoot and seed mass, with *C. elata* having a stronger influence than *C. flava* (Table 1). Competition from *M. aquatica* did affect seed mass of *C. flava* but not its shoot mass. *L. europaeus* only had a negative influence on shoot and seed mass with the high water level (water × *L. europaeus* interactions). The positive quadratic effects of *C. elata* and *M. aquatica* indicate that competition levelled off with a high initial biomass of these species.

Reproductive allocation

Reproductive allocation of *C. flava* was 6.8% under low nutrient conditions. Under high nutrient application, RA increased up to 9.7%, whereas water level had no influence (Table 1; Fig. 1c). Competition from four out of the five species did not change RA of *C. flava*; only *M. aquatica* had a significant negative

Table 2 Regression coefficients for the effects of shoot mass, water and nutrient levels as well as overall density (competition) on seed mass of *C. flava* in experimental plant mixtures after 2 years

Effect	Log_{10} (seed mass)
Intercept	−1.135***
Log_{10} (shoot mass)	0.509***
Water	0.040
Nutrient	0.246***
Density (competition)	−0.050
Density × Log_{10} (shoot mass)	0.594***

Water and nutrient effects express the shift from the low to the high level

*** $P \leq 0.001$

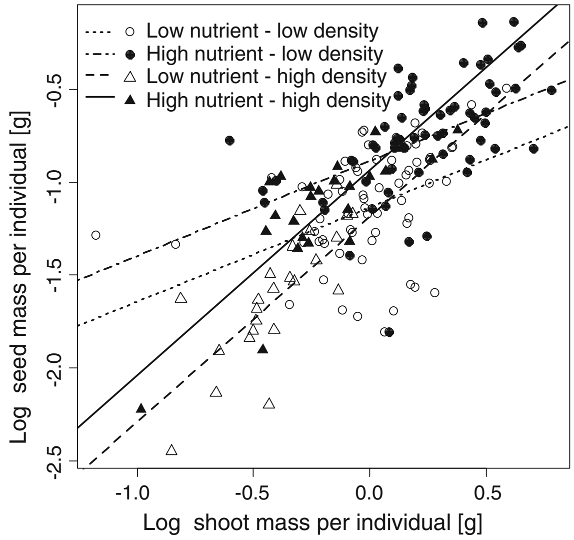

Fig. 3 Seed mass of *C. flava* as a function of its shoot mass, nutrients and density in experimental plant mixtures (log–log graph). Density has been used as a surrogate variable for overall competition. Both lines at low density conditions were significantly shallower than 1 ($P < 0.001$), whereas the lines at high density were not different from 1 ($P = 0.475$) (prediction based on regression of Table 2). Water had no significant effects

influence, which levelled off with an increasing abundance of this species (Table 1; Fig. 2).

Reproductive allocation of *C. flava* was further influenced by its own size, as demonstrated by the relationship between seed and shoot mass (Equ 2). Seed mass of *C. flava* was positively affected by its shoot mass (Table 2; Fig. 3). The shoot mass coefficient, however, was significantly smaller than 1 at low density conditions ($t_{170} = 6.159$, $P < 0.001$), indicating that RA decreased with plant size when competition from other species was low. Though higher overall density (high competition) did not further affect seed mass when the shoot mass of *C. flava* was taken into account, high competition did change the allocation pattern (Fig. 3; Table 2, density × shoot mass interaction). This interaction resulted in a shoot mass coefficient not significantly different from 1 with high density conditions (sum of coefficients: $0.509 + 0.594 = 1.103$, $t_{170} = 0.716$, $P = 0.475$ for difference from 1), indicating that RA became size-independent under increased overall competition. The positive effect of high nutrient application on seed mass represents a size-independent increase of RA (Fig. 3).

Discussion

Effects on shoot and seed mass

C. flava tussocks are perennial, but the species spreads both clonally and with seeds, and seed production of *C. flava* is usually high because of self-compatibility (Schmid 1984). These features could allow *C. flava* to alter its relative investment in shoots and seeds to optimise its survival under changing conditions. The natural habitats of *C. flava* provide high light availability even for smaller plants. Nutrient enrichment in these habitats will considerably impair the smaller plants through increased competition from species with rapid nutrient uptake and biomass production (Pauli et al. 2002; van der Hoek et al. 2004). Therefore, *C. flava,* as a relatively small species (mean size of 30 cm, Lauber and Wagner 2007), should decrease in its relative abundance with high nutrient levels. This is confirmed by the present experiment: though the vegetative growth of *C. flava* benefited from high nutrient levels (Table 1), its biomass proportion relative to the remaining species was significantly reduced (Suter et al. 2007).

C. flava was only partially resistant to adverse conditions and suffered considerably from competition. Under high competitive pressure from *C. elata*, shoot and seed mass of *C. flava* were adversely affected (Table 1). This strong impairment is explained by the large biomass production of *C. elata*, which was more than two times greater than each of the other four species (Suter et al. 2007). *C. elata* took-up most of the available resources and considerably affected not only *C. flava* but all the species in the plant mixtures. Though the level of RA in *C. flava* was not directly influenced by *C. elata*, this strong competitor reduced the shoot mass of *C. flava* more than its seed mass and changed the allocation pattern (Table 2).

Different water levels did not influence the shoot and seed mass of *C. flava*, indicating that *C. flava* was not stressed under dryer conditions. However, with the higher water level, i.e. more favourable water conditions, shoot and seed mass were reduced by competition with *L. europaeus*. The performance of *L. europaeus* was greatly enhanced by higher water conditions, and primarily affected *C. flava* in this experiment (Suter et al. 2007). The impairment of *C. flava* from competition under an increased water level thus indicates a trade-off between its ability to tolerate stress and its competitive response, a mechanism that is assumed to be of central importance for community dynamics (Campbell and Grime 1992; Suding et al. 2003; Liancourt et al. 2005). This could explain why *C. flava* also occurs under slightly dryer or disturbed conditions at the edges of fen meadows of low productivity (F. Klötzli, personal communication), but is absent in wetlands, where biomass production is high and light becomes a limiting factor for small species (e.g. *Magnocaricion elatae*, Ellenberg 1996).

While the adverse effect of *C. elata* was pervasive over all established resource levels, the competitiveness of *L. europaeus* was only pronounced under the higher water level conditions, and no significant effects could be found for *L. vulgaris* (Table 1). This shows that the interrelations between plants can be very species-specific and can also be modified by abiotic conditions (Ramseier et al. 2005; Emery and Gross 2007). Though the experimental time period may have been too short to detect further interactions between species and resources, the designed plant mixtures allowed quantification of some of these influences.

Effects on reproductive allocation

C. flava, as grown in the experimental plant mixtures, exhibited subtle reactions in RA to the manipulated parameters. The relative allocation of resources to shoots and seeds was influenced by nutrients and competition, but less so by water (Figs. 1 and 2). Under low planting density (low competition treatment), RA decreased with increasing plant size. Reekie (1998) explained a size-dependent decrease of RA with additional costs in support tissues. In larger individuals, such costs could be higher and, as a consequence, RA would diminish. In the present experiment, the low planting density with an inter-seedling distance of 10 cm allowed *C. flava* to produce larger individuals, and for these individuals, the relative investment in seeds was reduced.

Though vegetative growth of *C. flava* was impaired under the high planting density, competition had little or no direct effects on RA in *C. flava* (Table 1). However, the allocation pattern changed and RA became size-independent (Table 2; Fig. 3). *C. flava* reacts very sensitively to limited light (Edelkraut and Guesewell 2006), and growth of *C. flava* was restricted by the availability of light in the high density treatment. The two strongest competitors, *C. elata* and *L. europaeus*, prevented the growth of larger *C. flava* plants. Thus, the absence of large individuals with proportionally smaller seed mass could explain the relatively constant RA observed under high competition (Fig. 3). The change of the allocation pattern indicates that, under increased competition and shading, *C. flava* can ensure its survival by maintaining its RA and producing seeds even from the smallest individuals (Fig. 3). In fact, *C. flava* is able to produce seeds with less than 20 cm in size (Schmid 1984).

Regarding the change of RA, a similar behaviour has been observed in the annual species *Abutilon theophrasti* (Sugiyama and Bazzaz 1998). Free from competition, *A. theophrasti* has demonstrated decreasing RA with increasing plant size, but under competition and intermediate nutrient conditions, it maintained constant RA for different plant sizes. However, the competition effect on RA was an indirect effect mediated by plant size, rather than a direct effect. In *C. flava*, competition mainly affected shoot mass production, which, in turn, modified the pattern of RA. The present study thus confirms that competition predominantly affects the size of a plant, and that changed plant size affects other features such as RA (Weiner 1988).

With high nutrient levels, the absolute and relative resource allocation to seeds was enhanced (Tables 1 and 2). However, a shortage of nutrients did not have the same effect on RA as competition. With low nutrient application, total produced biomass was strongly reduced, and light availability was less limiting. Under these conditions, *C. flava* also produced individuals with large shoots in relation to seed mass, and the proportions of allocated resources were not affected by plant size.

C. flava was able to modify its allocation pattern and maintain seed output under increased competition. If a permanent nutrient enrichment followed by increased biomass production occurs in the natural habitats of *C. flava*, the species could maintain or increase its vegetative growth and RA for some time. However, in the long term, *C. flava* would be edged out by competition due to light limitation (Edelkraut and Guesewell 2006; Suter et al. 2007) and the species would survive only in the soil seed bank (Schmid 1986).

In summary, specific observation of the model plant communities allowed quantification of the effects of various abiotic conditions on the resource allocation of *C. flava. C. flava* modified its allocation pattern and retained its RA even under unfavourable conditions and in varying plant sizes. It is concluded that this modification is an advantageous reaction to higher competition pressure.

Acknowledgements I am grateful to T. Steffen for weighing the seed and biomass samples. I would also like to thank M. Fotsch, P. Borer and P. Kadelbach for assistance in practical work and K. Seipel for linguistic improvements. J. Connolly, P. Edwards, S. Guesewell, D. Ramseier and two anonymous reviewers provided helpful comments on an earlier version of the manuscript. The project was funded by the Swiss Federal Institute of Technology, Zurich (Grant No. 0-20891-01).

References

Aeschimann D, Heitz C (2005) Synonymie-Index der Schweizer Flora. Zentrum des Datenverbundnetzes der Schweizer Flora, Bern

Arenas F, Viejo RM, Fernandez C (2002) Density-dependent regulation in an invasive seaweed: responses at plant and modular levels. J Ecol 90:820–829. doi:10.1046/j.1365-2745.2002.00720.x

Campbell BD, Grime JP (1992) An experimental test of plant strategy theory. Ecology 73:15–29. doi:10.2307/1938717

Cheplick GP (2001) Quantitative genetics of mass allocation and the allometry of reproduction in *Amaranthus albus*: relation to soil nutrients. Int J Plant Sci 162:807–816. doi:10.1086/320778

Chiariello NR, Gulmon SL (1991) Stress effects on plant reproduction. In: Mooney HA, Winner WE, Pell EJ et al (eds) Response of plants to multiple stresses. Academic Press, San Diego, pp 161–188

Cornell JA (2002) Experiments with mixtures. Wiley, New York, USA

Edelkraut KA, Guesewell S (2006) Progressive effects of shading on experimental wetland communities over three years. Plant Ecol 183:315–327. doi:10.1007/s11258-005-9042-y

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart, Deutschland

Emery SM, Gross KL (2007) Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. Ecology 88:954–964. doi:10.1890/06-0568

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties. Wiley, Chichester, UK

Hara T, Kawano S, Nagai Y (1988) Optimum reproductive strategy of plants, with special reference to the modes of reproductive resource allocation. Plant Species Biol 3:43–59. doi:10.1111/j.1442-1984.1988.tb00170.x

Harper JL, Ogden J (1970) The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. J Ecol 58:681–698. doi:10.2307/2258529

Hendriks AJ, Mulder C (2008) Scaling of offspring number and mass to plant and animal size: model and meta-analysis. Oecologia 155:705–716. doi:10.1007/s00442-007-0952-3

Karlsson PS, Méndez M (2005) The resource economy in plant reproduction. In: Reekie EG, Bazzaz FA (eds) Reproductive allocation in plants. Elsevier, Amsterdam, pp 1–49

Klinkhamer PGL, de Jong TJ, Nell HW (1994) Limiting factors for seed production and phenotypic gender in the gynodioecious species *Echium vulgare* (Boraginaceae). Oikos 71:469–478. doi:10.2307/3545835

Lauber K, Wagner G (2007) Flora Helvetica. Paul Haupt, Bern, Schweiz

Liancourt P, Callaway RM, Michalet R (2005) Stress tolerance and competitive-response ability determine the outcome of biotic interactions. Ecology 86:1611–1618. doi:10.1890/04-1398

Méndez M, Karlsson PS (2004) Between-population variation in size-dependent reproduction and reproductive allocation in *Pinguicula vulgaris* (Lentibulariaceae) and its environmental correlates. Oikos 104:59–70. doi:10.1111/j.0030-1299.2004.12335.x

Pauli D, Peintinger M, Schmid B (2002) Nutrient enrichment in calcareous fens: effects on plant species and community structure. Basic Appl Ecol 3:255–266. doi:10.1078/1439-1791-00096

Ramseier D, Connolly J, Bazzaz FA (2005) Carbon dioxide regime, species identity and influence of species initial abundance as determinants of change in stand biomass composition in five-species communities: an investigation using a simplex design and RGRD analysis. J Ecol 93:502–511. doi:10.1111/j.1365-2745.2005.00999.x

R Development Core Team (2007) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org

Reekie EG (1998) An explanation for size-dependent reproductive allocation in *Plantago major*. Can J Bot 76:43–50. doi:10.1139/cjb-76-1-43

Reekie EG, Bazzaz FA (eds) (2005) Reproductive allocation in plants. Elsevier, Amsterdam, Netherlands

Sadras VO, Bange MP, Milroy SP (1997) Reproductive allocation of cotton in response to plant and environmental factors. Ann Bot (Lond) 80:75–81. doi:10.1006/anbo.1997.0402

Schmid B (1984) Life histories in clonal plants of the *Carex flava* group. J Ecol 72:93–114. doi:10.2307/2260008

Schmid B (1986) Colonizing plants with persistent seeds and persistent seedlings (*Carex flava* group). Bot Helv 96:19–26

Sletvold N (2002) Effects of plant size on reproductive output and offspring performance in the facultative biennial *Digitalis purpurea*. J Ecol 90:958–966. doi:10.1046/j.1365-2745.2002.00725.x

Suding KN, Goldberg DE, Hartman KM (2003) Relationships among species traits: separating levels of response and identifying linkages to abundance. Ecology 84:1–16. doi:10.1890/0012-9658(2003)084[0001:RASTSL]2.0.CO;2

Sugiyama S, Bazzaz FA (1998) Size dependence of reproductive allocation: the influence of resource availability, competition and genetic identity. Funct Ecol 12:280–288. doi:10.1046/j.1365-2435.1998.00187.x

Susko DJ, Lovett DL (2000) Plant-size and fruit-position effects on reproductive allocation in *Alliaria petiolata* (Brassicaceae). Can J Bot 78:1398–1407. doi:10.1139/cjb-78-11-1398

Suter M, Ramseier D, Guesewell S et al (2007) Convergence patterns and multiple species interactions in a designed plant mixture of five species. Oecologia 151:499–511. doi:10.1007/s00442-006-0594-x

van der Hoek D, van Mierlo AJE, van Groenendael J (2004) Nutrient limitation and nutrient-driven shifts in plant species composition in a species-rich fen meadow. J Veg Sci 15:389–396. doi:10.1658/1100-9233(2004)015[0389:NLANSI]2.0.CO;2

Weiner J (1988) The influence of competition on plant reproduction. In: Lovett Doust L (ed) Plant reproductive ecology. Oxford University Press, New York, pp 228–245

Whitfield CP, Davison AW, Ashenden TW (1998) The effects of nutrient limitation on the response of *Plantago major* to ozone. New Phytol 140:219–230. doi:10.1046/j.1469-8137.1998.00277.x