Flexible life history responses to flower and rosette bud removal in three perennial herbs

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Abstract

In a garden experiment we investigated the response to continuous removal of either flower buds or rosette buds in three perennial grassland species (*Hypochaeris radicata*, *Succisa pratensis* and *Centaurea jacea*), which differ in longevity and flowering type. We distinguished two possible responses: compensation for lost buds by making more buds of the same type, and switching towards development of other life history functions. Both responses were demonstrated in our experiment, but bud removal had significantly different effects in each of the three species. The degree of compensation and the expression of trade-offs between life history functions differed markedly between species and seem related to longevity and developmental constraints. With respect to switching, our results suggest costs of reproduction and a trade-off between life history functions, at least for *Hypochaeris* and *Succisa*. For these species weight of new rosettes increased when resource allocation to flowering was inhibited. In *Hypochaeris,* we see that both compensation for lost flower buds and switching from lost rosette buds increased production of flower buds, underscoring the pivotal role of sexual reproduction in this short-lived species. The most prominent response seen in *Centaurea* is compensation for lost rosette buds, indicating that this long-lived species with monocarpic rosettes relies on rosette formation. Although *Succisa* does respond to bud removal, time is an important constraint in this species with long-lived rosettes and preformed flowering stalks. Trade-offs in *Succisa* seem to operate at a larger time scale, requiring long-lasting experiments to reveal them. We conclude that the response of these species to inflicted damage is likely to be linked to their longevity and developmental constraints.

Keywords: bud removal, *Centaurea jacea*, compensatory effects, costs of reproduction, garden experiment, herbivory, *Hypochaeris radicata*, meristem allocation, phenology, resource allocation, *Succisa pratensis*, switching.

Introduction

Life history theory predicts that organisms optimise their life time fitness according to the trade-off between current sexual reproduction and growth, survival and future reproduction (Stearns 1989; Bazzaz and Grace 1997). In rosette-producing perennials this means that within each growing season the resources acquired are partitioned between flowering and seed set, production of new rosettes, and growth. Resource allocation towards the various life history functions may differ considerably between species (van Andel and Vera 1977; Bazzaz 1996), depending on environmental

variation, life span, competitive dominance, mode of vegetative spread and other factors (Harper 1967). Like in animal life history theory, traditional plant resource allocation theory stated that resources can be allocated towards one life history function only, and that trade-offs between these functions can therefore be expected.

However, this view may not accord with the modular character of plant parts or their ability to be self-sustaining. In plant ecology it has since long been recognised that photosynthesising plant parts do not only act as resource sinks but also as sources of carbon (Benner and Watson 1989; Vuorisalo and Mutikainen 1999). As a consequence trade-offs between functions are not necessarily apparent. Nowadays, also meristem allocation is regarded as an important feature in interpreting plant strategies (Olejniczak 2001), since it has been shown that, especially in nutrient-rich environments, meristems may be more limiting than resources (Geber 1990; Bonser and Aarssen 1996). Commitment of meristems to reproduction reduces the number of meristems available for vegetative growth. Conversely, dedicating meristems towards vegetative growth can increase the number of available meristems later in life (Watson 1984; Olejniczak 2001). Meristem allocation theory assumes that the costs of reproduction are paid in the currency of meristems rather than the amount of spent resources, e.g. Watson (1984) and Geber (1990). Although both processes are evidently important, still few studies have looked at biomass and meristem allocation concomitantly.

Prati and Schmid (2000) suggested that allocation in plants is essentially a two-step process. The first step involves the developmental decision to differentiate a particular meristem into a vegetative or a sexual structure or to remain dormant (Watson 1984; Duffy *et al*. 1999). The second step comprises the physiological control over resource flows that determine the sizes of structures, which often includes the abortion of fruits or seeds (Stöcklin 1997). In case it is unclear beforehand what the limiting factor is, both biomass and meristem allocation should be considered when investigating the importance of trade-offs between life-history functions.

Manipulating the effort a plant makes to a certain function can reveal the relative importance of life history functions (Stearns 1989; Ehrlén 1999; García and Ehrlén 2002). In bud removal experiments resources that cannot be used for the development of the removed plant parts become available for other purposes. In general, plants have two options of responding when plant parts are removed; they can either try to compensate for the loss by replacing the lost parts, or switch their resource investments towards other functions. This choice probably depends on developmental constraints, the expected life span, timing of damage, etc. In the various bud removal experiments performed so far, different responses were found for different species.

Compensatory fruit production after main stem clipping was found by Lennartsson *et al*. (1998) in *Gentianella campestris* and by Lehtilä and Syrjänen (1995) in two *Melampyrum* species. In the latter experiment flower removal also led to compensatory seed production later in the season. Examples of overcompensation are also known as a result of herbivory (Watson 1995). The release of apical dominance is assumed to be one of the mechanisms behind overcompensation. When the main apex has been removed, the apices behind it will become activated and start to develop and grow (Svensson and Callaghan 1988) and the overall effect can even be an increase in flowering.

Switches in resources allocation after manipulation have been found by Westley (1993) in the tuber-forming species *Helianthus tuberosus*, by Prati and

Schmid (2000) in the clonal *Ranunculus reptans*, and in the cantaloupe melon *Cucumis melo* by El-Keblawy and Lovett Doust (1996). A natural trade-off between life history functions in *Tipularia discolor* has been studied by Snow and Whigham (1989). They conclude that flowering and fruiting depleted stored resources that otherwise would have been allocated to growth, vegetative propagation or flowering in the following year. In some cases however, it is hard to make such a distinction, for instance if extra growth also implies more flower bud production (Avila-Sakar *et al*. 2001). There are several constraints to a plastic response of a plant to inflicted damage, such as meristem preformation (Geber *et al*. 1997), growth rate, timing of damage (Lennartsson *et al*. 1998) and plant architecture (Lehtilä and Syrjänen 1995). However, it remains unclear which of these underlying factors determine the choice between compensation and switching and the expression of trade-offs in herbaceous plant species.

In an attempt to increase our understanding of this topic, we performed a bud removal experiment with three perennial grassland herbs (*Hypochaeris radicata*, *Succisa pratensis* and *Centaurea jacea*). These three species all reproduce sexually as well as vegetatively by means of developing new rosettes, which eventually may become independent from the mother rosette. However, they differ in longevity (*Hypochaeris radicata* is short-lived, whereas the other two are long-lived) and flowering type (*Hypochaeris* and *Centaurea* flower apically, *Succisa* laterally). We addressed the following questions:

To what extent do these species compensate for lost plant parts and to what extent do they switch to other functions in response to flower bud removal and side rosette bud removal, respectively? Are changes in biomass and meristem allocation consistent with a trade-off between life history functions?

Material and methods
Species
We performed a garden experiment with three species: *Centaurea jacea* L. (Asteraceae), *Hypochaeris radicata* L. (Asteraceae) and *Succisa pratensis* Moench (Dipsacaceae) (Fig. 1). They are found in comparable habitats, rather nutrient-poor grasslands (Soons and Heil 2002), and have similar life history choices (clonal growth as well as sexual reproduction), but they differ in life span and flowering type.

Hypochaeris radicata is a relatively short-lived species (de Kroon *et al*. 1987; Fone 1989); its life span usually does not exceed two seasons. *Hypochaeris* flowering stalks and new rosettes are formed in the centre of the main rosette; the number of flowering stalks varies considerably (de Kroon *et al*. 1987). Flowering lasts from spring until late autumn (Fone 1989).

Centaurea jacea is a relatively long-lived perennial, although it has monocarpic shoots. Single individuals have been recorded to survive until at least the age of ten years (Tamm 1956). *Centaurea* rosettes have a single apical flowering stalk. During and after flowering, vegetative side-rosettes form on the rootstock and appear at the soil surface alongside the main stem (pers. obs.). Flowering lasts from June until the first frost (van der Meijden 1996).

Succisa pratensis, like *Centaurea*, can survive for many years (Adams 1955; Hooftman 2001). *Succisa* flowers laterally and usually produces more than one flowering stalk. New rosettes also emerge laterally. This species, which is rather rare in the Netherlands, flowers from late July until October (Vergeer *et al.* 2003).

Seeds were collected in a Cirsio-Molinietum vegetation in the nature reserve 'Bennekomse Meent' near Wageningen (52°01'N, 5°36'E). This remnant of a

formerly extensive communal hayfield is mown once a year in the beginning of August, it is not grazed by large herbivores. For a more detailed site description see van der Hoek and Braakhekke (1998). Plants of *Succisa* and *Centaurea* were grown from seed in a greenhouse one year before the start of the experiment. In May 2000 side rosettes were cut from these one-year-old plants and transplanted into the experimental garden. *Hypochaeris* plants were grown from seed, germinating in March 2000. Plants were put at an interval of approximately 0.5 m in nutrient poor soil in a hexagon of *Molinia caerulea* plantlets (5 shoots each) in order to mimic natural conditions.

Experimental design

The experiment was performed during the growing season of 2000. We used 15 plants per treatment and species. To minimise the effect of genetic variation and initial size, three new-born rosettes, descending from a single parent, with approximately the same weight and number of leaves and stems, were selected to form a "trio". Plants from each trio were randomly distributed over the three treatments. Trios of different size were used, as to be able to study the effect of initial size. For *Hypochaeris*, the "trios" consisted of seedlings that descended from one flower head. A randomised block design was used.

The plants were subjected to one of three treatments. The first was a flower bud removal treatment. We removed only the buds of capitula (hereafter called flower bud), since removing the whole flowering stalk would probably affect a plant's photosynthetic capacity (Fig. 1). Flower buds were removed when they were large enough to be removed without damaging the rest of the flowering stalk. Flower bud removal was applied approximately three times each month until the end of the experiment. The removed flower buds were counted per plant, dried at 70°C for two days and weighed. The second treatment was a rosette bud removal. For *Hypochaeris radicata* and *Succisa pratensis*, that produce new rosette buds above the soil surface, the buds were removed apically and laterally from the main rosette, respectively. For *Centaurea jacea*, that forms side-rosettes on the rootstock just beneath the surface, rosette buds were cut off after gently removing the soil around the rootstock. Rosette buds were counted, dried and weighed like the flower buds. The third treatment was a control, in which neither flower buds nor rosette buds were removed.

The number of flower buds, rosette buds, flowers and rosettes was recorded for each individual. For the removal treatments this was done partly during the experiment by counting and weighing the removed parts. Harvest took place just after most seeds had ripened; harvest date differed between the species (8th of August for *Centaurea* and *Succisa* and 3rd of October for *Hypochaeris*), since *Hypochaeris* has a more prolonged flowering season. At harvest plants were dug out, and above and below ground parts were weighed. To be able to determine the number and weight of the full-grown capitula with flowers and seeds that otherwise would have fallen from the plant during the experiment, small plastic wire-netting bags were placed over the capitula.

Data analysis

We used an analysis of variance model with species, treatment and trio (plants of identical genotype and same initial size) as factors for the dry weights. Number of flower buds and of rosette buds were analysed with a non-parametric Wilcoxon Signed Ranks Test, since the data were not normal or Poisson distributed, and their variances were significantly not homogeneous. This test was used to make pair-wise

comparisons between the plants in one trio. In order to compare all three treatments, the Bonferroni correction was applied: the significance level is lowered by division by the number of compared tests ($\alpha = 0.05 / 3 = 0.017$). There was no significant block effect. Four *Hypochaeris* plants died in the course of the experiment and were left out of the analyses.

Results
Timing and extent of flowering and rosette bud formation
Most plants flowered and produced new vegetative rosettes. Not all plants
(but at least 2/3 in every Species-Treatment combination) flowered or formed
new rosettes and therefore some plants could not receive the removal treatment that they were assigned to. The results are thus a conservative estimate of the real effects of the treatments.

The emergence of new rosettes occurred after the onset of flowering in all three species (Fig. 2). *Hypochaeris* produced several new ones for every removed flower bud. New rosettes were formed in August and September. *Hypochaeris* continued flowering and producing side rosettes until the plants were harvested. The *Succisa* plants produced flowers (about three flower heads per plant) in May and June, whereas the production of rosettes started in July. The *Centaurea* plants produced flower buds on their main stem in May and the beginning of June, but there was a second period of flowering in July, when the side rosettes started to flower.

Effect of bud removal on dry weights
The three species responded markedly different to flower bud removal (Table 1, Fig. 3). In *Hypochaeris* we see a strong trend (p=0.065) of an increase in total vegetative weight when flower buds were removed (Fig. 3c), but in *Centaurea* none of the biomass responses were significant (Fig. 3i). Only in *Succisa* flower bud removal led to a concomitant increase in total plant weight. The weights of the main and new rosettes increased (Fig. 3f). Since trio was an important explaining factor for dry weight in *Succisa* (Table 1), we tested for bivariate correlation between initial fresh weight and dry weight at harvest (n=45), resulting in a Pearson's correlation coefficient of 0.437 with a two-tailed significance of 0.003.

Rosette bud removal decreased total dry weight in *Hypochaeris* and *Centaurea* (Fig. 3c, i). Flower weight was not affected by the smaller biomass investment in side rosettes in these species. Main rosette weight was slightly lower for *Hypochaeris* and significantly lower for *Centaurea*, under rosette bud removal, but this treatment did not affect the weight of any part of the *Succisa* plants.

Effect of bud removal on numbers of flowers and rosettes
Flower bud removal caused an increase in the number of flower buds in all three species, although this was not significant for *Centaurea* (Fig. 3a, d, g). The most spectacular increase was seen in *Hypochaeris* that produced on average four times as many flower buds when flower buds were continuously removed. *Hypochaeris* plants in the flower bud removal group also produced more flowering stems (17.2 *versus* 10.7 for the control group, p=0.059) and showed more branching of stems. The number of side rosettes in *Succisa* increased when flower buds were removed.

Rosette bud removal induced an increase in the number of rosette buds (Fig. 3b, e, h). Especially in *Centaurea*, which produced four times more rosette buds if rosette buds were removed. Flower production declined for all three species when rosette buds were removed, and most clearly so in *Centaurea*, probably because for

these plants new rosettes could not contribute to flowering (Fig. 3g). For *Hypochaeris* compensation for lost rosette buds was not significant.

Plotting the effects of both treatments in the same graph (Fig. 4) can highlight the hypothesised effects of flower or rosette bud removal, compensation or switching. *Hypochaeris* shows the strongest compensation for lost flower buds, but the weakest for rosette buds, whereas *Centaurea* shows a strong compensation for rosette buds and the weakest for flower buds (Fig 4a). *Succisa* replaces flower buds and rosette buds at the same degree, it produces twice as many buds as it would have if buds had been allowed to develop (Fig 4.a). However, this compensatory effect was not seen in the dry weights (Fig 4.b), since flower buds were removed at a very small size.
A switch from rosette bud production towards flowering, in other words an increase in number of flowers or total flower weight when rosette buds were removed, did not occur in our experiment. All species and especially *Centaurea* showed a decrease in flower number and weight when rosette buds were removed (Fig. 4c and 4d). Switching from flowering to rosette production did occur in *Hypochaeris* and *Succisa*, but not in *Centaurea*.

Discussion

Our study revealed that inhibition of flowering or development of new rosettes had very different impacts on the three perennial herbs *Hypochaeris radicata*, *Succisa pratensis* and *Centaurea jacea*. The significant different responses of the three species with respect to meristem decisions and biomass allocation reflect differences between the species in life history traits and in constraints on allocation.

Compensation

All three species responded to flower bud removal by compensating for lost flower buds, but not all to the same extent. *Hypochaeris* showed a 3-4 fold increase in the number of flower buds formed. This, together with the fact that this species had the largest proportional reproductive effort in terms of biomass allocation to flower heads in the control treatment, indicates the great importance of seed production for this species. This may be related to its short life span, since the urge for sexual reproduction in a certain growing season is assumed to be larger for short-lived species (Ehrlén and van Groenendael 1998). De Kroon *et al.* (1987) showed that the growth of *Hypochaeris* populations is highly depending on the sexual pathway, unlike many other perennials.

Our results are consistent with compensatory effects shown in other experiments on short-lived species, such as the hemiparasitic annuals *Melampyrum pratense* and *M. sylvaticum* (Lehtilä and Syrjänen 1995), the biennial *Gentianella campestris* (Lennartsson *et al*. 1998) and the annual *Cucurbita pepo* ssp. *texana* (Avila-Sakar *et al*. 2001). Rosette bud removal led to a minor increase in number of rosette buds in *Hypochaeris*, probably because only few rosettes were removed. We conclude from the high branching rate, the flexible number of flowering stems and the strong and fast flower bud compensation that *Hypochaeris* is not noticeably limited by meristem availability. This, as well as the high growth rate, enables this perennial to respond quickly to damage to flower buds, for instance inflicted by herbivores. In the case of a yearly mown nature reserve like the place of origin of our plants, this adaptive response may also be beneficial, because the plant can start flowering again soon after having been mown. At the same time this short-lived species tends to increase its vegetative weight and the number of new rosettes, which has been shown

to contribute critically to plant fitness through enhanced seed production (de Kroon *et al*. 1987).

For *Centaurea*, compensation is shown, but only with respect to the new rosettes. This monocarpic species depends on new rosettes for survival since the main rosette dies after flowering. For *Centaurea* new rosettes may be more important than flowering, since due to the long life span of the genet it can wait until next year when circumstances may be more favourable.

Succisa shows some compensation, but to a lesser extent than the other two species. When buds are removed, it only produces twice as many buds compared to a control situation. This might be linked to a more strict developmental programme, indicated by the symmetric growth form as well as the strong correlation between initial size and dry weight at harvest that was shown by the results of the correlation test. However, since within each trio both initial size and genotype are more or less identical, we cannot conclude whether variation between trios is due to initial size or to genotypic effects.

Since the main rosette is polycarp, there is no necessity to immediately compensate for lost rosettes; the plant does not depend on new rosettes for survival like *Centaurea*. Unlike *Hypochaeris*, the long-lived rosette of *Succisa* can postpone sexual reproduction, what might explain the lower tendency to compensate for lost flowers.

Switching

Bud removal also caused shifts in allocation towards other life history functions in *Hypochaeris* and *Succisa*. In *Hypochaeris*, we see a tendency to shift from sexual reproduction towards vegetative growth and new rosettes when flower development is prevented. The number of new rosettes increased as a result of flower bud removal and the total weight of new rosettes also tended to increase, but there is no effect at total plant weight. A similar switch in allocation was demonstrated in an inflorescence bud removal experiment on the short-lived tuber forming species *Helianthus tuberosus* (Westley 1993). However, de Kroon *et al*. (1987) found that new rosettes are very important for current reproduction in *Hypochaeris*. New rosettes can therefore be seen as a way of switching and as a way of compensating indirectly for lost flowers. This means the plants switched to an increased resource allocation into the new rosettes, and at the same time compensated for lost flower buds.

 In *Succisa*, flower bud removal caused an increase in the number of side rosettes, even stronger than the switch in *Hypochaeris*. For this longer-lived species this investment will probably pay off in later years, whereas for the short-lived *Hypochaeris* the relative benefit of compensation for lost flower buds is more immediate. Flower bud removal also increased the weight of the whole plant as well as the weights of the separate parts in *Succisa*. Prati and Schmid (2000) found a similar increase in plant size as a result of flower bud removal for the clonal herb *Ranunculus reptans*, while proportional allocation towards the several functions did not change. Switches in biomass allocation towards vegetative size are an expression of costs of sexual reproduction, and have been described by Ehrlén and van Groenendael (2001) and El-Keblawy and Lovett Doust (1996), amongst others.

For *Centaurea*, flower bud removal did not cause a switch towards production of new rosettes. An explanation could be that only a small part of the plant's resources is used for the development of a small flower bud to a flower head with seeds, and thus only a relatively small amount of extra resources becomes available when flowering is prohibited. As is shown by the large response in the rosette removal

treatment, meristem preformation cannot explain the lack of response. The decrease in main rosette weight in response to rosette bud removal in *Centaurea* may be explained by assuming that the lower part of the main stem serves as a storage organ, which is depleted by the formation of compensatory rosette buds.

Timing has been recognised as an important factor determining the response of a plant to damage (Lehtilä and Syrjänen 1995). Response to damage may even be restricted to a certain period in the season (Lennartsson *et al.* 1998). In *Succisa*, most of the rosette formation took place after the flowering peak. Thus, it is hardly surprising that the impact of removal of new rosettes on flowering was very small, since decisions concerning allocation to flowering and meristem development were made before side rosettes were removed. This timing of allocation and of meristem activity might be a major constraint on the expression of trade-offs between allocation to either function.

In conclusion, we argue that both meristem and biomass allocation play an important role in determining the response to bud removal, in terms of the choice between compensating and switching. Our results suggest that the degree of compensation and the expression of life history trade-offs are related to longevity and developmental constraints.

Acknowledgements

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Table 1. ANOVAs on dry weight at harvest for all Species together and for each Species separate (*Hypochaeris radicata*, *Succisa pratensis* and *Centaurea jacea*). Species, Trio (plants of identical genotype and same initial size) within Species, Treatment (control, flower bud removal, and rosette bud removal) and Species x Treatment were used as explaining factors of the variation in dry weight (total, main rosette, new rosettes, and flower heads and buds).

Dry Weight of	Source of Variation	Total plant			Main Rosette			New Rosettes			Flower Heads&Buds		
		df	MS	F	df	MS	F	df	MS	F	df	MS	F
All plants	Species	2	1125.1	68.4 ***	2	728.1	87.5 ***	2	81.9	20.6 ***	2	103.7	93.3 ***
	Trio (within Species)	42	37.2	2.3 ***	42	18.1	2.2 **	42	5.7	1.4 (*)	42	2.4	2.2 ***
	Treatment	2	266.2	16.2 ***	2	107.2	12.9 ***	2	66.0	16.6 ***	2	28.4	25.6 ***
	Species x Treatment	4	62.6	3.8 **	4	43.9	5.3 ***	4	9.2	2.3 (*)	4	16.3	14.6 ***
	Error	74	16.5		77	8.3		77	4.0		79	1.1	
Hypochaeris radicata	Treatment	2	271.2	6.8 **	2	170.5	7.4 **	2	38.3	5.2 *	2	57.1	16.7 ***
	Trio	14	76.8	1.9 (*)	14	36.1	1.6	14	8.8	1.2	14	6.7	2.0 (*)
	Error	24	40.1		24	23.1		24	7.4		24	3.4	
Succisa pratensis	Treatment	2	16.6	4.7 *	2	11.5	5.4 *	2	3.3	6.3 **	2	0.9	11.0 ***
	Trio	14	21.5	6.1 ***	14	16.2	7.6 ***	14	0.9	1.6	14	0.4	4.6 ***
	Error	28	3.6		28	2.1		28	0.5		28	0.1	
Centaurea jacea	Treatment	2	76.9	10.9 **	2	5.6	5.4 *	2	39.2	8.6 **	2	0.4	3.2 (*)
	Trio	14	13.4	1.9 (*)	14	2	1.9 (*)	14	7.5	1.6	14	0.2	1.6
	Error	22	7.1		25	1		25	4.6		27	0.1	

Table 2. Wilcoxon Signed Rank Tests between Treatments (Control, Flower Bud removal, and Rosette Bud removal). Number of flower or rosette buds produced during the experiment were compared per Trio (plants of identical genotype and same initial size). Note that to determine significant differences between the three Treatments (as in Fig. 3) the Bonferroni correction is applied: the significance level is lowered by division by the number of compared tests ($\alpha = 0.05 / 3 = 0.017$).

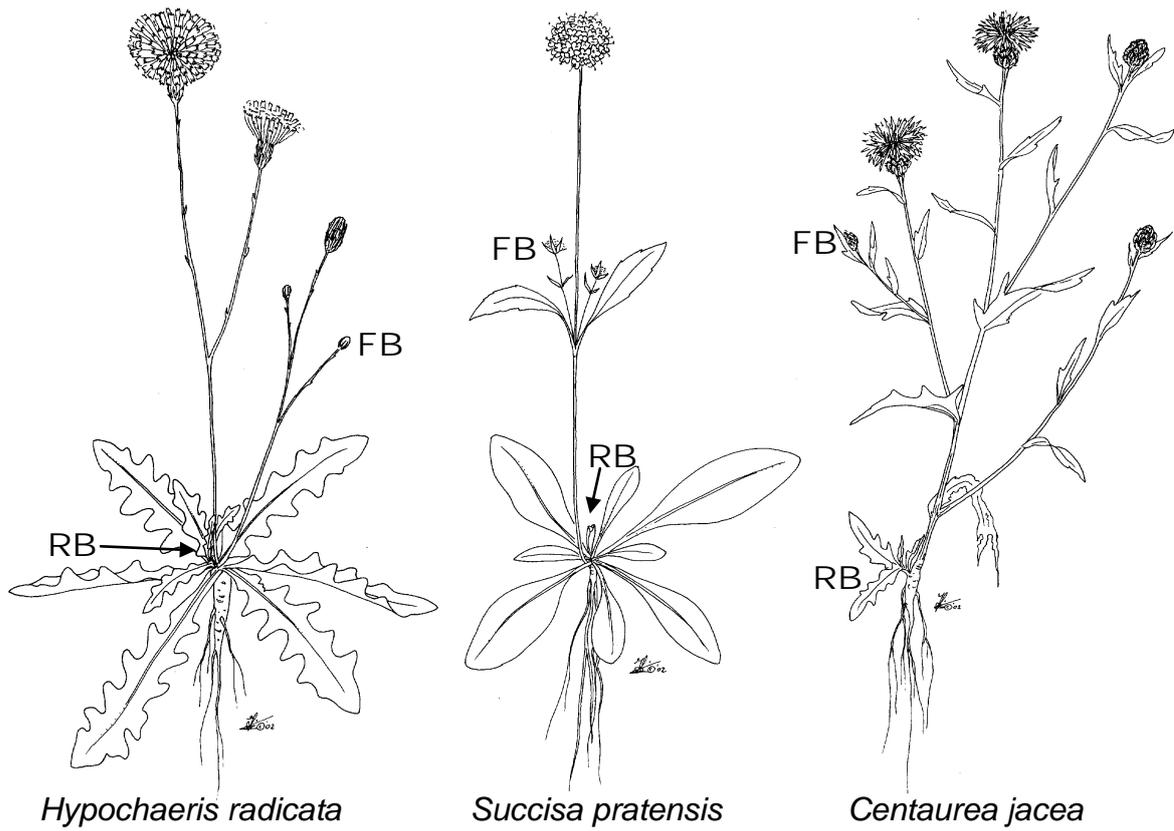| Number of	Comparison	*Hypochaeris radicata*		*Succisa pratensis*		*Centaurea jacea*	
		Z	p	Z	p	Z	p
Flower Heads&Buds	Control - FB removal	-2.900	0.004	-2.805	0.005	-1.848	0.065
	Control - RB removal	-2.001	0.045	-1.889	0.059	-2.397	0.017
	FB removal - RB removal	-3.180	0.001	-2.674	0.007	-3.415	0.001
Side Rosettes	Control - FB removal	-1.843	0.065	-2.559	0.011	-0.387	0.698
	Control - RB removal	-1.636	0.102	-1.299	0.194	-3.413	0.001
	FB removal - RB removal	-0.035	0.972	-0.916	0.360	-3.410	0.001

Figure 1. Drawings of *Hypochaeris radicata*, *Succisa pratensis* and *Centaurea jacea*. The flower buds (FB) and rosette buds (RB) that were removed in the experiment are indicated with arrows.
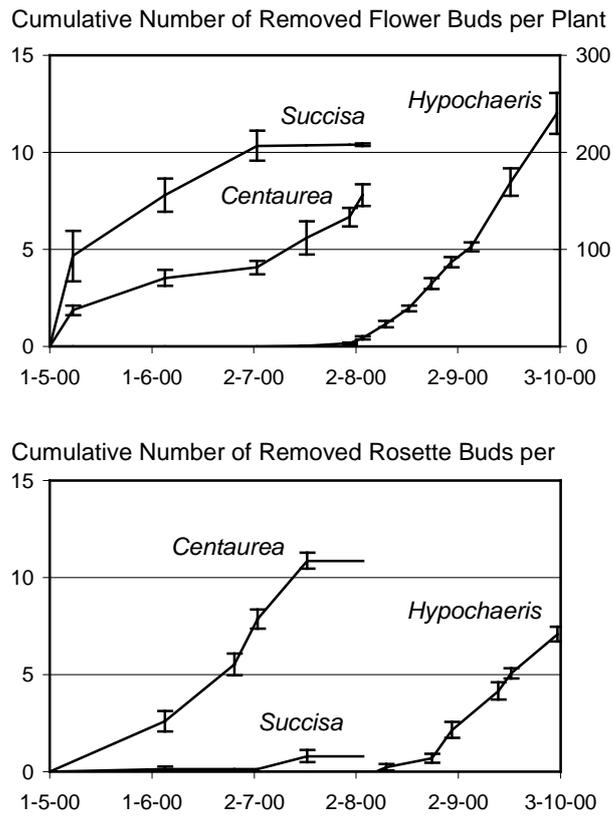
Cumulative Number of Removed Flower Buds per Plant

Cumulative Number of Removed Rosette Buds per

Figure 2. Cumulative number of removed flower buds and rosette buds per plant of *Centaurea jacea*, *Hypochaeris radicata* and *Succisa pratensis*. Note that the *Hypochaeris* flower buds are on the right-hand axis. Bars represent $\pm$ standard error of the number of removed buds per plant on that particular day. Small rosette and flower buds found at harvest are not depicted in this figure, but are included in Fig. 3.
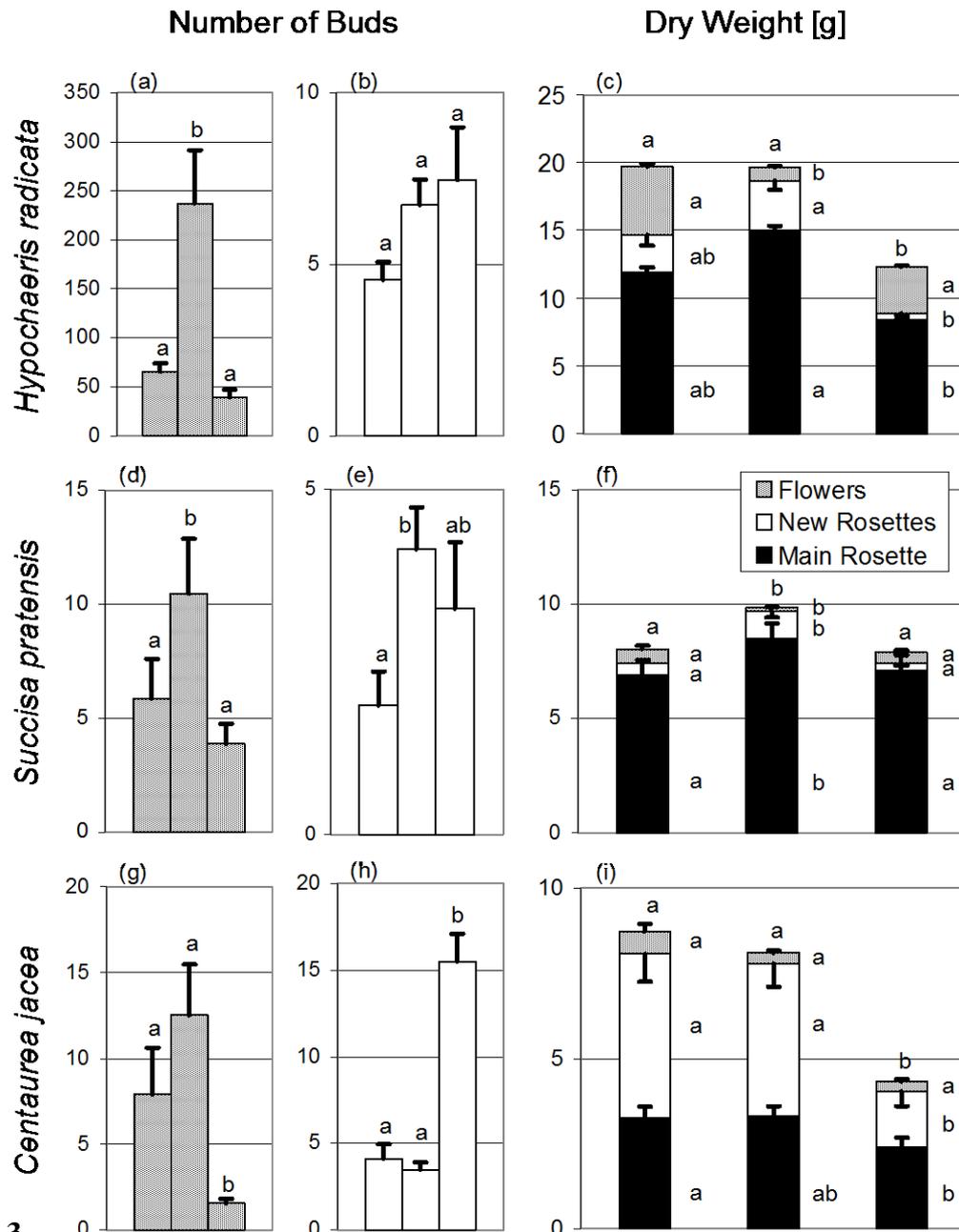
Figure 3.
Number and dry weight of rosettes and flowers per harvested plant, divided into main rosette (black), new rosettes (white) and flowers (dashed). The treatments (with n=15 plants) were control (Control), flower bud removal (FB removal) and rosette removal (RB removal).

Numbers of buds were analysed with a Wilcoxon Signed Ranks Test with Bonferroni correction (Fig. 3 a, b, d, e, g and h, see also Table 2). ANOVAs on the dry weight at harvest were performed with Treatment and Trio (plants of identical genotype or seed family and same initial size) as explaining factors (Fig. 3 c, f and I, see also Table 1). Note that the weight of the flowers for FB removal and the weight of the rosettes for RB removal should be interpreted as the weight of the removed plant parts. Within each graph a different letter with the same plant part denotes a significant treatment effect on that plant part.
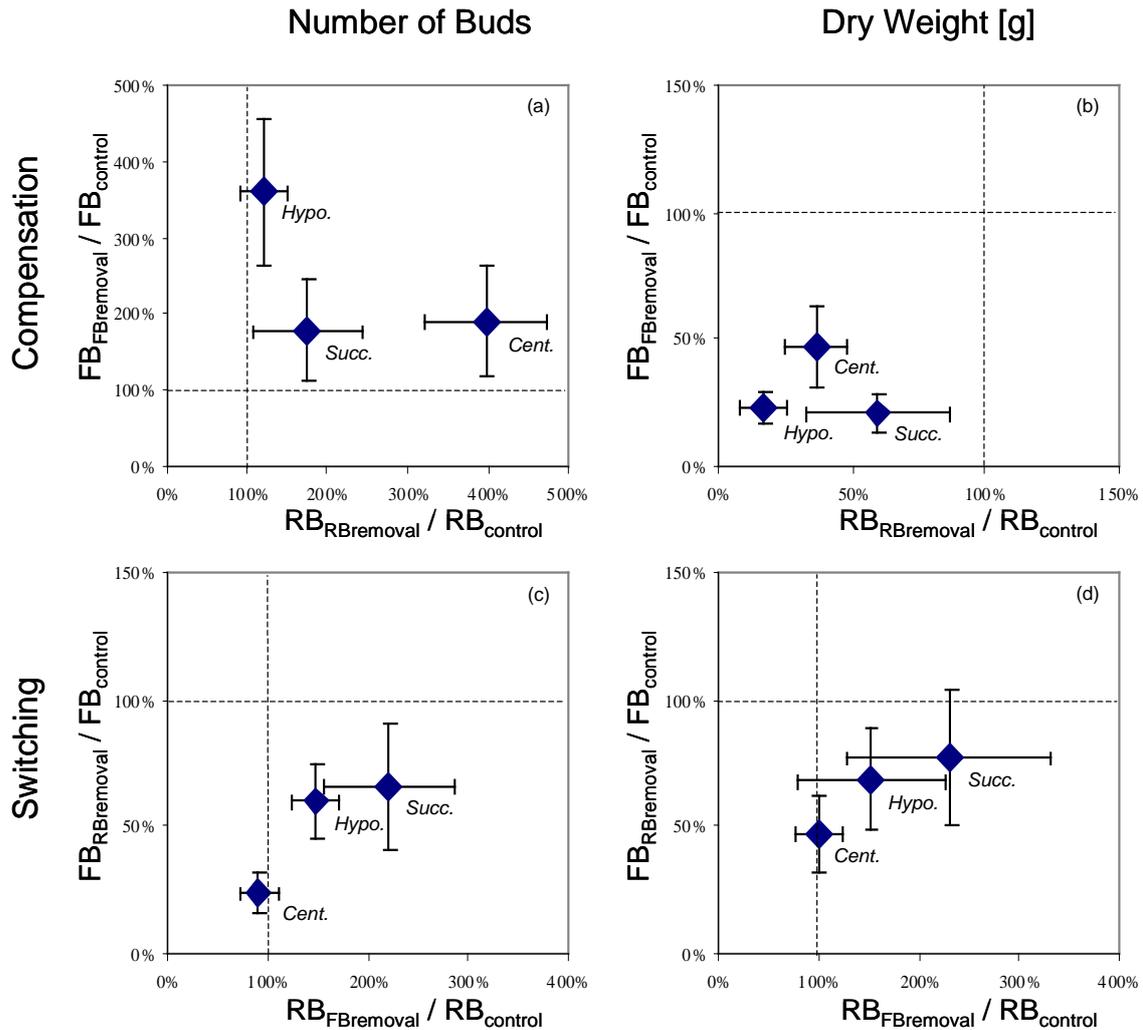
Number of Buds

Dry Weight [g]

Figure 4.

Summary of the effects of continuous removal of either flower or rosette buds on the number and dry weight of flowers and new rosettes of *(H) Hypochaeris radicata*, *(S) Succisa pratensis*, and *(C) Centaurea jacea*. In each diagram a treatment effect on flower allocation is plotted on the Y-axis, and a treatment effect on new rosette allocation on the X-axis. Compensation for continuously removed buds is calculated as the percentage change in the number (a) and dry weight (b) of that bud type, compared to the control group. Trade-offs are calculated as the percentage change in the number (c) and dry weight (d) of a certain bud type, when the other type of buds is removed. The 100%-lines indicate no effect of the treatments. Dots and bars represent species means and standard errors on basis of within trio comparisons.

$FB_{Control}$ = flower (buds) of the control group
$FB_{FBremoval}$ = flower (buds) of the flower bud removal group
$FB_{RBremoval}$ = flower (buds) of the rosette bud removal group
$RB_{Control}$ = new rosettes of the control group
$RB_{FBremoval}$ = new rosettes of the flower bud removal group
$RB_{RBremoval}$ = new rosettes of the rosette bud removal group