

Overcompensation and adaptive plasticity of apical dominance in *Erysimum strictum* (Brassicaceae) in response to simulated browsing and resource availability

P. Rautio, A-P. Huhta, S. Piippo, J. Tuomi, T. Juenger, M. Saari and J. Aspi

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In the cases where overcompensation has been observed in monocarpic herbs, overcompensation is associated with an apically dominant shoot architecture of intact plants, increased lateral branching following herbivory, and increased reproductive success as a consequence of damage. The compensatory continuum hypothesis expects overcompensation to be more prevalent in resource rich environments compared to poor environments. This is paradoxical since in resource rich conditions the intact plants should branch most vigorously and hence any further increase in branch number should lead to lower seed yield. An explanation could be that apical dominance is rather insensitive to changes in resource availability, and that overcompensation is possible in conditions where plants experience meristem limitation (due to apical dominance) in relation to available resources.

We explored the branching patterns and fitness responses of tall wormseed mustard (*Erysimum strictum*) to simulated browsing, soil nutrients, and competition in common garden. Competition increased apical dominance and reduced plant fitness whereas fertilization had the reverse effects. Simulated browsing increased lateral branching and had little impact on plant fitness. Fitness overcompensation was observed only among plants grown in competition and in the absence of fertilization – the most resource poor treatment combination in the experiment. The results contradict both with the compensation continuum and the assumption that apical dominance shows no or very little plasticity in relation to growing conditions. Because directional selection gradients on branch number were invariantly positive irrespective of growing conditions, we propose that, in spite of phenotypic plasticity of apical dominance, the plants appear to be meristem rather than resource limited, and that meristem limitation is strongest in conditions where intact plants produce fewest lateral branches. Our results deviate from the compensation continuum because resource availability affected compensation ability more strongly through phenotypic plasticity of shoot architecture rather than via changes in resource availability per se.

P. Rautio, Finnish Forest Research Institute, Kaironientie 54, FIN-39700, Parkano, Finland (pasi.rautio@metla.fi). – A.-P. Huhta, S. Piippo, J. Tuomi, M. Saari and J. Aspi, Dept of Biology, Univ. of Oulu, P.O. Box 3000, FIN-90014, Oulu, Finland. T. Juenger, Section of Integrative Biology, Univ. of Texas, 1 University Station C0930, Austin, TX 78712, USA.

Many monocarpic herbs have relatively few branches. This feature is sometimes associated with their regrowth capacity following grazing or other disturbances that cause damage to the shoot or apical meristem. For instance, Paige and Whitham (1987) observed that ungrazed individuals of the scarlet gilia (*Ipomopsis*

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aggregata) had an unbranched architecture, whereas grazed plants showed vigorous branching from basal meristems. As a result, the grazed plants produced more fruits and seeds than the ungrazed ones (overcompensation, sensu Belsky 1986). It has been observed that other monocarpic plants sometimes behave in a similar way, e.g. *Thlaspi arvense* (Benner 1988), *Ipomopsis arizonica* (Maschinski and Whitham 1989), *Gentianella campestris* (Lennartsson et al. 1997, 1998, Huhta et al. 2000b, Juenger et al. 2000) and *E. strictum* (Huhta et al. 2000a, 2000c).

In these monocarpic species, overcompensation is associated with (1) a relatively unbranched shoot architecture in ungrazed condition, (2) increased lateral branching following damage to the primary inflorescence or apical meristem, and (3) increased flower and fruit production as a consequence of increased branching. Given physiological limitations to plant productivity, the occurrence of the second and third patterns would suggest that overcompensating plants are able to obtain adequate nutrients, water, and light in order to support increasing branching and fruit production. Therefore, overcompensation is expected to be the most probable in conditions where competition is weak and the plants are supplemented with additional nutrients and water, i.e. the compensatory continuum hypothesis (Maschinski and Whitham 1989). However, the first pattern (1) is somewhat contradictory with respect to high resource availability: if nutrients, water and light were abundant, why would ungrazed plants have an unbranched architecture in the first place and why would they produce only few flowers and fruits?

Crawley (1987) suggested that sufficiently frequent grazing may have favoured the evolution of restrained branching among ungrazed plants, provided that this improves their grazing tolerance when they experience herbivore attack. Vail (1992) modelled this situation by allowing plants to choose whether they use their limited resources for the growth and flowering of the primary shoot before herbivore damage or whether they leave the resources for regrowth following grazing damage. Analogously, plants may activate their meristems at the beginning of the growing season or they may leave most of them dormant so that they can be activated after herbivore attack (van der Meijden et al. 1988, Tuomi et al. 1994, Järemo et al. 1996, Nilsson et al. 1996a, 1996b, Lehtilä 1999, 2000). In these circumstances, the available resources could support greater plant growth and productivity but the plants have evolved mechanisms resulting in allocation to reserves instead. In a sense, this can be viewed as a bet-hedging strategy which on average provides an optimal compromise between the interests of both the damaged and undamaged plants (Vail 1992, Nilsson et al. 1996a, Juenger et al. 2000).

As an alternative, Aarssen and Irwin (1991) and Aarssen (1995) suggest that the unbranched architecture of ungrazed plants may be associated with competition for light and other selection pressures which favour fast vertical growth through apical dominance. In this case, quick vertical growth is obtained by funnelling resources through a single growing axis, rather than allocating limiting resources among multiple growing meristems. These authors argue that selection should favour fast vertical growth (and thus unbranched architecture) in dense vegetation, and this selection pressure will be relaxed in disturbed habitats when, for instance, herbivores reduce the height and density of surrounding vegetation. Consequently, branched architecture should be favoured in environments of weak competition for light and nutrients, i.e. in open, nutrient-rich habitats (Bonser and Aarsen 1996, Duffy et al. 1999).

If competition for light selects for apical dominance, one would expect directional selection for increased vertical growth among plants grown in competition. This selection pressure should be relaxed among plants grown free from competition. In contrast, selection for increased branch production should show the reverse pattern. Consequently, we expected (selection prediction 1, S1) a negative correlation between directional selection gradients on plant height and number of branches, and that (S2) directional selection gradients on plant height should be positive and larger as compared to selection gradient on the number branches among plants grown in competition and (S3) directional selection gradients on the number of branches should be positive and larger as compared to selection gradient on plant height among plants grown free from competition. Furthermore, if the number of branches is optimally adjusted to the prevailing growth conditions, (optimality prediction 1, O1) the number of branches should decrease in competitive growing conditions, (O2) increase as a result of supplemental fertilization, (O3) a further increase in branchiness should lead to a fitness cost and, hence, (O3a) the corresponding directional selection gradient should be close to zero or negative and quadratic selection gradient should indicate stabilizing selection and (O3b) seed production should decline as a consequence of increased allocation to branch production following apical damage (as a standard result of herbivory). The third prediction (O3) assumes that the optimal number of branches in the given growing conditions supports maximal seed production, and hence any further increase in branchiness above the optimum would lead to lower seed yield. In such a case, overcompensation would be impossible without introducing other selective forces in addition to competition (Aarssen 1995, Järemo et al. 1996).

In order to explain overcompensation, Aarssen and Irwin (1991) further assumed, following Harris (1974), that plants selected for apical dominance will remain

programmed for apical dominance even when growing without competition and with non-limiting resources. In such conditions, apical damage by herbivory will release the lateral buds from correlative inhibition and the plant will branch and more fully utilize the available nutrient and photosynthetic supply (Aarssen and Irwin 1991). This provides a potential explanation for overcompensation in situations where (1) the plants have previously evolved apical dominance in competitive or resource-deficient conditions, (2) the plants are moved to competition-free and nutrient-rich conditions, (3) in spite of these new environmental conditions, intact plants remain apically dominant, (4) apical damage removes correlative inhibition and induces vigorous branching and (5) increased branching leads to increased fruit and seed production relative to intact plants. This "competition hypothesis" implies that the intact, apically dominant plants behave suboptimally in relation to improved resources in competition-free conditions. Here removal of apical dominance through herbivory results in plants that are better able to utilize resources thus resulting in overcompensation.

Although these hypotheses (bet-hedging vs competition) differ in relation to the presumed selection forces that lead to the evolution of an apically dominant growth pattern, both of them seem to implicitly assume that, in conditions where overcompensation occurs, the unbranched architecture of undamaged plants is suboptimal in relation to the available resources. In such conditions, fruit and seed production of intact plants would appear to be meristem rather than resource limited (Watson 1986, Geber 1990), while vigorous branching following damage would create the reverse situation. A strong positive correlation between seed yield and branchiness or strong directional selection for increased branchiness may be an indication of limitation by the number of active meristems (meristem limitation prediction, M1). The bet-hedging hypothesis makes no prediction how resource availability as such may affect compensation. However, the bet-hedging models usually assume that damaged individuals compensate most strongly in the environment where unclipped individuals have the most restrained lateral branching. Thus overcompensation should be most probable in conditions where meristem limitation is strongest in relation to available resources. The competition hypothesis, on the other hand, agrees with the compensation continuum (Maschinski and Whitham 1989) provided that apical dominance shows no or very little phenotypic plasticity with regard to changing resource availability (Aarssen and Irwin 1991). If this were true, (competition prediction 1, C1) competition and fertilization should have little effect on shoot architecture of intact plants and (C2) compensation should be best in fertilized plants growing without competition. In contrast, if apical dominance is phenotypically plastic and the branchiness

of individual plants is optimally adjusted in relation to the available resources (Bonser and Aarssen 1996, Järemo et al. 1996), the predictions O1–O3 should hold.

We studied compensatory responses of the tall wormseed mustard (*Erysimum strictum*, Brassicaceae) in relation to resource availability. The intact plants of this biennial species are most frequently unbranched. When plants are subject to apical damage (e.g. 10–50% of the main stem removed by clipping), they produce more lateral branches and slightly overcompensate for the damage in terms of biomass as well as fruit and seed production (Huhta et al. 2000a, 2000c). The present study is based on a factorial experiment in which plants were grown with or without supplemental fertilizer and either with or without a tall competitor *Anthriscus sylvestris*. In all treatment groups, some plants were kept as intact undamaged controls and some plants received simulated browsing to the main inflorescence. We aimed to test whether the shoot architecture and seed production of *E. strictum* responds to changes in resource availability as expected by the compensatory continuum hypothesis and the competition hypothesis (C1 and C2) or by the optimal plasticity hypothesis (O1–O3). Moreover, we carried out selection gradient analysis to test the strength of directional selection on plant height and number of branches in different growing conditions (S1–S3), as well as possibility of relative meristem limitation (M1).

Material and methods

Study species

Tall wormseed mustard, *Erysimum strictum* P. Gaertn., B. Mey. and Scherb. (Brassicaceae) (syn. *E. hieracifolium* auct., *E. virgatum* Roth), is a 50–100 cm tall, biennial herb. Its seeds germinate in spring, develop into a rosette during the first summer, and flower during the second. Mature plants produce a single stalk, which is typically unbranched, but may sometimes be vigorously branched (Huhta et al. 2000a, 2000c). After reproduction, the plant dies and therefore estimates of seed production from a single season provide an excellent estimate of lifetime reproductive success. In Finland, *E. strictum* originally grows on sandy and gravelly sea- and riversides and, increasingly, in human-influenced habitats, such as dry meadows and railroad embankments (Ahti 1965).

Experimental design

The experiment was carried out during the summer 2000 in the Botanical Gardens of the University of Oulu, Finland. We transplanted one-year old rosette-stage plants from a natural habitat into a common garden in

mid-May. The transplants came from two natural habitats, including a gravelly roadside and a stony riverbank (Oulu, NW Finland, 65°00'N, 25°30'E). The plants were randomly planted 40 cm apart into 5 blocks (sandy beds containing small amounts of organic soil) each of which was further randomly divided into two parts. In half of every planting bed, seedlings of *Anthriscus sylvestris* were transplanted around every *E. strictum* individual. The presence of *A. sylvestris* resulted in intensive competition over light and nutrients. The remaining half of each planted bed was weeded weekly to reduce competition (Fig. 1). Transplanted seedlings of *Anthriscus sylvestris* grew quickly and approximately 20–30% larger than *E. strictum*. As a result, *E. strictum* growing in the competitive plot, on average, received 30% less sunlight than individuals growing free of competition (measurements done on a sunny day mid July: 69 135 lux vs 103 753 lux on average around individuals growing in competitive vs competition free environments respectively, $F_{1,4} = 70.67$, $p < 0.01$).

In both competition and competition-free plots, *E. strictum* individuals were further allocated into the following combinations of fertilization and clipping treatments: 1) neither fertilization nor clipping, 2) fertilization but no clipping, 3) no fertilization but clipping (25% of the shoot was removed), and 4) both fertilization and clipping (Fig. 1). Each treatment combination contained 20–21 plants, of which 65–100% survived to the final harvest. The survival of individuals was not dependent on the particular manipulative treatments (chi-square tests, $df = 1$): clipped vs un-clipped $\chi^2 = 0.823$, $p = 0.364$; competition vs non-competition $\chi^2 = 0.007$, $p = 0.934$ and fertilized vs non-fertilized $\chi^2 = 0.823$, $p = 0.364$. In general, mortality was

likely associated with early transplant shock of seedlings. The clipping manipulation was performed when both *E. strictum* and *A. sylvestris* had recovered transplant shock. At the time of clipping (early June) experimental plants were at the bud stage and their height was 18.2 ± 0.4 cm (mean \pm SE, statistical difference between the eight treatment combinations: $F_{7,135} = 0.99$, $p = 0.445$). Fertilization began three weeks after the clipping treatment was applied. The fertilized plants received 20 ml of liquid fertilizer four times during the growing season. One dose of fertilizer contained ca 19 mg of nitrogen (69% NH_4^- and 31% NO_3^- -nitrogen), 9 mg of phosphorus, 32 mg of potassium and smaller amounts of S, Mg, B, Cu, Fe, Mn, Mo and Zn. All experimental plants were watered (twice per week) during dry periods of the growing season.

The plants were harvested as soon as fruits were fully matured. We measured the following characteristics from each experimental plant: final height, shoot and root biomass, number of branches and fruits, seed weight (average of a sample of 100 seeds per plant), and the number of seeds per fruit. The number of seeds per fruit was measured as an average number of seed scars per silique (fruit) from three siliques taken from the lowermost, middle, and uppermost parts of each plant. The total seed number per plant was estimated by multiplying fruit number by the average number of seeds per fruit. Total seed mass (per plant) was computed by multiplying the total seed number by seed weight (estimated weight of an individual seed).

Statistical analysis

We analyzed the response variables from our study using a standard split-plot ANOVA approach. As all treatment combinations were repeated in each of the five planting beds, we considered planting bed a blocking factor. We considered competition (within each block) as the whole plot term, and each whole plot was further divided to subplot treatments (fertilization, clipping and their combination). The complete linear model included the following terms:

$$Y = \mu + B_{\text{lock}} + C_{\text{omp}} + B_{\text{lock}} \times C_{\text{omp}} + C_{\text{lip}} + F_{\text{ert}} + C_{\text{lip}} \times C_{\text{omp}} + F_{\text{ert}} \times C_{\text{omp}} + C_{\text{lip}} \times F_{\text{ert}} + C_{\text{omp}} \times F_{\text{ert}} \times C_{\text{lip}} + \varepsilon$$

Block (B_{lock}) and competition (C_{omp}) terms were tested against block \times competition ($B_{\text{lock}} \times C_{\text{omp}}$) interaction (whole plot error) and the other terms against the residual variation (ε), i.e. the subplot error (Montgomery 1984). We did not consider interaction terms of subplot treatments (fertilization and clipping intensity) and block essential and hence variation explained by these terms is included in the residual variation (ε). If the assumption of homogeneity of variances was not met for

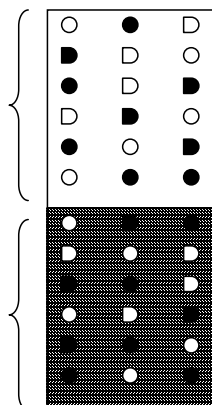


Fig. 1. Experimental set-up. Schematic figure of one of the five blocks representing three rows of six plants in both ends of the block (unshaded: competition free and shaded: competition with *Anthriscus*). Plants marked with black are fertilized and with white unfertilized. Plants marked with whole circles are intact whereas those with semicircle are clipped (25% of the shoot clipped away). Each of the three rows consisted of 4–7 plants (to which the fertilizer and cutting treatments were allotted) in both ends of each five block.

a particular response variable, we applied a Box-Cox transformation for that particular variable (Sokal and Rohlf 1995). Box-Cox transformations were performed by freeware program developed by Dr. Jouni Aspi. If the ANOVA results of the Box-Cox transformed data did not differ from that of original data, we report the results for the original (untransformed) data. We did not perform formal pairwise comparisons for the treatment means but we present 95% confidence interval in Fig. 2 and 3. Treatments having non-overlapping 95% confidence intervals are significantly different from each other at $\alpha < 0.05$. Note that our experimental design resulted in a low statistical power to test the main effect of competition because competition with *Anthriscus* was allotted to whole plots and not to individual plants. Nonetheless, for many performance parameters, we detected significant or marginally significant main effects of competition, and interactions involving competition and other treatments.

Estimating selection gradients

We explored the strength and pattern of selection on plant architectural traits using standard phenotypic selection analyses. Directional selection on the measured plant characters was examined with multiple linear regression:

$$i) \quad S = \alpha + \beta_H H + \beta_B B$$

Where (the fitness parameter) S was either total seed mass per plant or estimated weight of an individual seed, α is a constant, and β 's are slopes (i.e. selection gradients) for height (H) and branch number (B). Stabilizing/distructive/correlational selection on the seed production was evaluated by multiple quadratic regression:

$$ii) \quad S = \alpha + \beta_H H + \beta_B B + \gamma_H H^2 + \gamma_B B^2 + \gamma_{HB} H \times B$$

Where γ_H , γ_B and γ_{HB} are quadratic partial regression coefficients for height, branch number, and their interaction respectively. To make these independent variables (height and number of branches) comparable they were z standardized before the computation: $Y_z = (Y - \mu) / \sigma$, where Y_z is the new (standardized) value, Y is original value, μ is (treatment specific) mean and σ is (treatment specific) standard deviation. The dependent variable (number of seeds or seed weight) was divided by its (treatment specific) mean. This transformation is helpful as the comparison and interpretations of regression equations are simplified on this scale: when a particular trait (height or number of branches) increases (or decreases) by 1 SD, the fitness parameter (number of seeds or seed weight) increases (or decreases) by magnitude indicated by a coefficient (β or γ) of the trait. This two-step process, i.e. estimating β using an exclusively linear regression and γ using the full quadratic regression

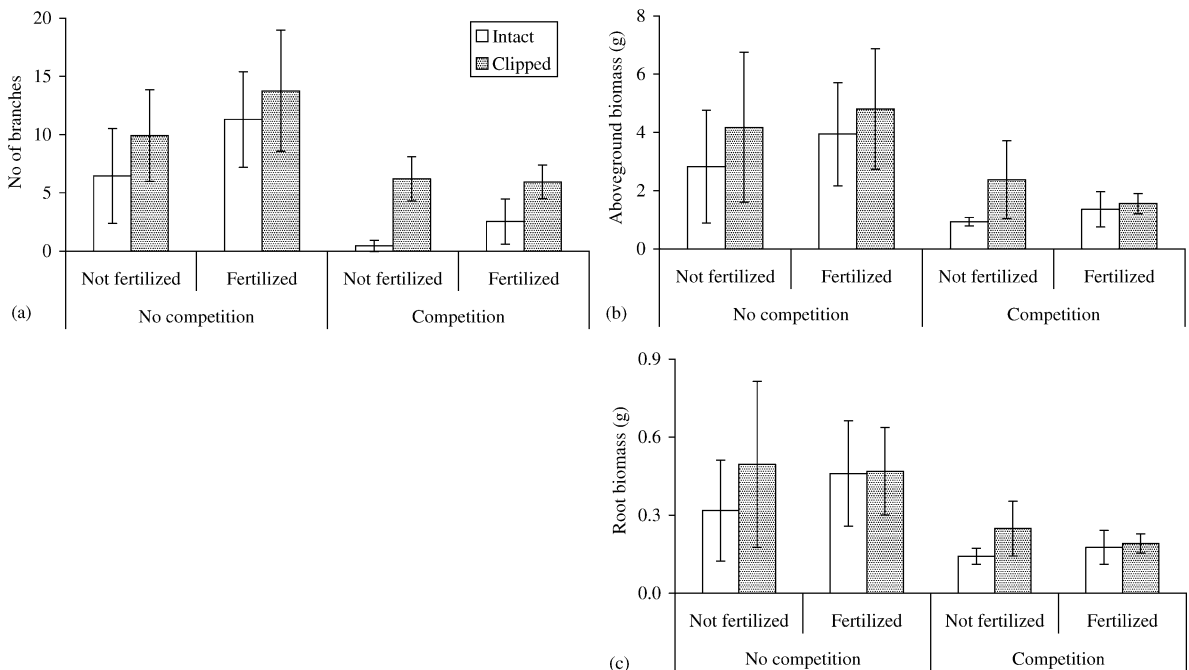


Fig. 2. Effects of competition, fertilization and apical damage (clipping) on the growth of *Erysimum strictum* (mean \pm 95% confidence intervals) in a factorial garden experiment: (a) number of branches, (b) aboveground and (c) root biomass (g dry weight). Open bars denote intact (unclipped) and shaded bars clipped (25% of the main stem removed) plants.

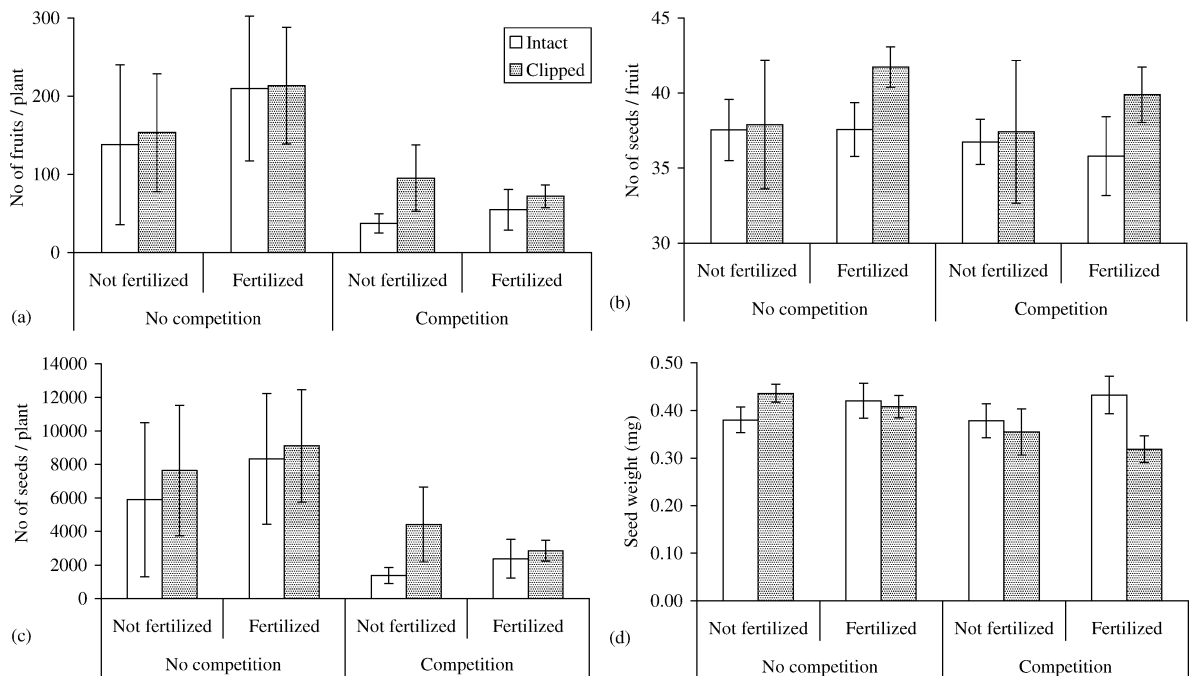


Fig. 3. Effects of competition, fertilization and apical damage on the reproductive performance of *Erysimum strictum* (mean \pm 95% confidence intervals) in a factorial garden experiment: (a) fruit number per plant, (b) seed number per fruit, (c) seed number per plant and (d) seed weight (mg dry weight). Open bars denote intact (unclipped) and shaded bars clipped (25% of the main stem removed) plants.

model is necessary because the covariance between linear and quadratic terms (in the same model) can lead to incorrect estimates of β and γ (Lande and Arnold 1983, Phillips and Arnold 1989). To evaluate the possible effect of seed production (number of seeds per plant) on seed weight (Swt) we included (standardized) number of seeds (S) to the model (i):

iii)
$$\text{Swt} = \alpha + \beta_H H + \beta_B B + \beta_S S$$

In above models (i–iii) directional selection (β) increases (positive β) or decreases (negative β) the trait mean (here the total seed mass or estimated weight of an individual seed). Stabilizing selection is indicated by a negative partial regression coefficient (γ) of squared terms (H^2 and B^2) and disruptive selection is indicated when these terms are positive. Correlational selection is indicated by the regression coefficient of the interaction terms: if, for example, γ for $H \times B$ is strongly positive these traits are being selected to become positively correlated (Phillips and Arnold 1989, Brodie et al. 1995). We compared directional selection gradients across particular treatment combinations using a t-test comparison of two slopes (Sokal and Rohlf 1995). Further relationship of these two gradients was explored with either Pearson correlation coefficient or sign-test.

Results

Resource availability and plant performance

Lateral branching in *E. strictum* is a phenotypically plastic trait in relation to resource availability. Plants that were grown in competition produced fewer branches than plants in the absence of competition, whereas fertilization increased branch number both in presence and absence of competition (Fig. 2a, Table 1). No significant treatment effects were detected on plant height (Table 1). Competition decreased and fertilization slightly increased above and belowground biomass (Fig. 2b, 2c, Table 1). Fertilization tended to increase above- and belowground biomass most strongly among plants grown without competition. Competition did not have a statistically significant main effect on fruit number per plant, seed number per fruit, seed number per plant, or seed weight, but again we detected several marginally significant interactions with fertilization (Table 2, Fig. 3). Namely fertilization increased fruit (Fig. 3a) and seed number (Fig. 3c) in competition-free environment, but not in competition.

Resource availability and grazing tolerance

Experimental clipping consistently resulted in enhanced branch production as well as increased aboveground

Table 1. Analysis of variance for growth parameters: number of branches (Branch no.), vertical height (Height), aboveground biomass (Abiom) and belowground biomass (Root). Box in prackets refers to Box-Cox transformation (see material and methods for details).

Source	df	Branch no. (Box)		Height		Abiom (Box)		Root (Box)	
		MS	F	MS	F	MS	F	MS	F
Block	4	4.55	0.25 ^{ns}	75.62	0.04 ^{ns}	0.09	0.01 ^{ns}	1.47	0.09 ^{ns}
Competition	1	78.95	4.37 ^{ns}	79.61	0.04 ^{ns}	8.7	1.3 ^{ns}	19.3	1.22 ^{ns}
Whole plot error	4	18.07		2009.4		6.57		15.8	
Clipping	1	142.05	56.09***	81.2	0.35 ^{ns}	1.87	4.2*	1.88	1.50 ^{ns}
Fertilization	1	32.32	12.76***	116.7	0.50 ^{ns}	3.28	7.4**	7.5	5.99*
Compet × Clip	1	15.36	6.06*	26.6	0.11 ^{ns}	0.17	0.39 ^{ns}	0.06	0.05 ^{ns}
Compet × Fertil	1	3.06	1.21 ^{ns}	103.5	0.45 ^{ns}	1.63	3.68 ^o	4.31	3.44 ^o
Clip × Fertil	1	8.24	3.25 ^o	148.9	0.64 ^{ns}	0.07	0.15 ^{ns}	0.002	0.001 ^{ns}
Compet × Clip × Fertil	1	0.002	0.001 ^{ns}	4.38	0.02 ^{ns}	0.03	0.07 ^{ns}	0.07	0.05 ^{ns}
Subplot error	131	2.53		232.4		0.442		1.25	

Significance symbols: ns = $p > 0.1$, ^o = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

biomass (Table 1). The enhancement was strongest among unfertilized plants grown in competition with *Anthriscus* (Fig. 2a, 2b). Clipping had no statistically significant effect on the final height of the plants (Table 1) or on root biomass (Table 1). In contrast, clipping increased fruit number per plant (Table 2) and this effect was most pronounced in plants grown in competition without fertilization (Fig. 3a). This pattern is consistent with the corresponding changes in shoot architecture (Fig. 2a). The positive effects of clipping were even more pronounced when considering seed production per plant (Fig. 3c, Table 2), due to the effect of clipping on the number of seeds per fruit (Fig. 3b). The increase in the number of seeds per fruit was most distinct when clipping was combined with fertilization (Fig. 3b) as seen also in a statistically significant clipping × fertilization interaction (Table 2). Even though clipping slightly reduced seed weight in plants grown in competition this reduction was significant only in nutrient rich competitive environment (Fig. 3d). This trend indicates that apical damage, which tends to enhance fruit and seed production, may lead to a fitness cost in terms of reduced seed weight and, hence,

possibly to lower seedling success in competitive environments.

Selection gradients on vertical growth and branch number

Directional and quadratic selection gradients on plant height and number of branches were estimated within each treatment group (Table 3–5). Both phenotypic traits correlated positively with seed production ($r = 0.16–0.94$) but inconsistently with each other ($r = -0.06–0.88$) within the different treatment groups. First, we used total seed mass per plant as a fitness measure for selection analyses on plant height and number of branches (columns H and B under β in Table 3). These traits explained a significant portion of the variation in seed yield (R^2 of the model varied between 0.47–0.94). Our experimental manipulations, however, did not seem to greatly influence these relationships since, for both traits, selection gradients were invariantly positive irrespective of growing conditions (Table 3). Among unclipped plants, the predictions (S2)

Table 2. Analysis of variance for reproductive parameters: number of fruits (fruit no.), number of seeds per fruit (seeds/fruit), average seed weight (seed wt) and total seed biomass per plant (tot seed biom). Box in prackets refers to Box-Cox transformation.

Source	df	Fruit no. (Box)		Seeds/fruit		Seed no (Box)		Seed wt		Tot seed biom (Box)	
		MS	F	MS	F	MS	F	MS	F	MS	F
Block	4	0.14	0.023 ^{ns}	18.27	3.21 ^{ns}	0.006	0.015 ^{ns}	0.007	0.37 ^{ns}	0.009	0.01 ^{ns}
Competition	1	13.5	2.2 ^{ns}	50.32	0.92 ^{ns}	1.04	2.67 ^{ns}	0.055	2.95 ^{ns}	2.51	3.1 ^{ns}
Whole plot error	4	6.14		54.88		0.39		0.019		0.81	
Clipping	1	4.41	12.45**	114.23	4.89*	0.48	14.01***	0.035	6.48*	0.46	8.37**
Fertilization	1	2.63	7.42**	59.99	2.57 ^{ns}	0.25	7.32**	0.008	1.4 ^{ns}	0.44	7.91**
Compet × clip	1	0.09	0.242 ^{ns}	0.257	0.011 ^{ns}	0.004	0.127 ^{ns}	0.05	9.34**	0.008	0.14 ^{ns}
Compet × fertil	1	2.21	6.23*	11.07	0.47 ^{ns}	0.13	3.64 ^o	0.003	0.54 ^{ns}	0.16	2.86 ^o
Clip × fertil	1	0.02	0.069 ^{ns}	142.42	6.1*	0.002	0.06 ^{ns}	0.01	2.62 ^{ns}	0.03	0.47 ^{ns}
Compet × clip × fertil	1	0.01	0.038 ^{ns}	2.13	0.09 ^{ns}	0.0003	0.009 ^{ns}	0.003	0.47 ^{ns}	0.02	0.27 ^{ns}
Subplot error	131	0.35		23.35 [§]		0.034 [§]		0.005 [#]		0.055 [✱]	

§ error df = 121, ✱ error df = 118, # error df = 123.

Significance symbols: ns = $p > 0.1$, ^o = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Table 3. Results for selection gradients β from the linear model ($S = \alpha + \beta_H H + \beta_B B$) and γ from the quadratic model ($S = \alpha + \beta_H H + \beta_B B + \gamma_H H^2 + \gamma_B B^2 + \gamma_{HB} H \times B$) and parameters for (unstandardized) original variables. In above models fitness parameter is total seed mass (S). N = number of plants used in computing selection gradients. Mean \pm 1 SE for: seed mass (grams), height (in centimetres) and number of branches. Equation-column present regression coefficients (slopes) for standardized H = height and B = number of branches. R^2 is the coefficient for determination. t-test gives the difference between H vs B in exclusively linear model. Coefficients in bold are significant at $\alpha < 0.05$.

Data	N	Seed mass	Height (cm)	Branch no.	β			γ		
					H	B	R^2	t-test	H	B
Intact: not fertil/no compet	17	2.5 \pm 1.1	60.6 \pm 5.5	7.1 \pm 2.4	0.67	0.94	1.78	2.59	0.77	0.99
Intact: not fertil/compet	20	0.5 \pm 0.1	57.4 \pm 2.1	0.5 \pm 0.3	0.70	0.89	-4.17	0.57	0.29	0.80
Intact: fertil/no compet	20	3.4 \pm 0.9	59.3 \pm 5.3	11.3 \pm 2.1	0.49	0.82	-0.9	-2.02	-0.12	1.66
Intact: fertil/compet	14	1.0 \pm 0.2	62.4 \pm 4.3	3.1 \pm 1.3	0.55	0.79	-0.21	-1.03	0.007	0.87
25% clipped: not fertil/no compet	10	3.3 \pm 0.9	62.3 \pm 4.7	11 \pm 2.4	0.43	0.93	0.14	-1.14	-0.53	0.95
25% clipped: not fertil/compet	13	1.6 \pm 0.4	59.7 \pm 4.4	6.4 \pm 1.1	0.76	0.82	1.83	-3.89	-1.45	0.97
25% clipped: fertil/no compet	20	3.7 \pm 0.7	61.5 \pm 2.5	13.8 \pm 2.7	0.31	0.90	-2.34	0.94	-0.20	0.95
25% clipped: fertil/compet	20	0.9 \pm 0.1	57.5 \pm 1.9	6.0 \pm 0.7	0.38	0.47	2.16	0.68	-0.78	0.64

and (S3) failed in three cases of the four and, hence, there was no indication that vertical growth is more important than branch number as determinant of seed mass in competitive conditions. Prediction (S1) was marginally supported as selection on these traits was negatively correlated, but only weakly so ($r = -0.14$). Among clipped plants, on the other hand, directional selection gradients on plant height were somewhat larger in the presence (0.76 and 0.38) than in the absence (0.43 and 0.31) of competition (Table 3). Selection gradients on plant height and number of branches correlated negatively with each other ($r = -0.39$), supporting prediction (S1). Directional selection on height was larger than that of branching in the presence of competition, supporting prediction (S2). On the other hand, in the absence of competition selection gradient on number of branches was equal or higher than gradient on height (S3). Consequently, in plants exposed to apical damage, allocation to vertical growth in competitive environment tended to yield more seeds than allocation to branch production, whereas this trend vanished or was reversed in competition-free environment (Table 3).

Second, we used seed weight (estimated weight of an individual seed) as the dependent fitness component and made corresponding analyses (columns H and B under β in Table 4). Unlike in the previous models, directional selection gradients for both height and branch number were rather weak and in most cases the gradient on branch number turned out to be negative and on plant height positive. Although in most cases the gradients as such were not significant (Table 4), and were significantly different only in half of the cases (Table 4) the overall difference between selection gradients on plant height (positive) and branch production (in most cases negative) was significant (sign-test, $P < 0.01$). Because seed number may affect seed weight, we made a further analysis where seed number per plant was used as an additional independent variable in the regression model with seed weight as the dependent fitness component (Table 5). This model indicated no clear tradeoff between seed weight and seed number; gradients on seed number (S, Table 5) varied from positive to negative without any consistent pattern. With respect to plant height and branch number, the results (Table 5) remained more or less the same as compared to the previous model (Table 4). Consequently, vertical growth and branch number affect seed weight most likely directly and not via their effects on seed number.

Third, using total seed mass as the fitness estimate and a quadratic model (columns H, B and $H \times B$ under γ in Table 3) revealed stabilizing selection (significant positive quadratic terms for H and B) only in one case, i.e. intact plants without fertilization and no competition. In other cases, the quadratic selection gradients varied from negative (disruptive selection) to weakly positive without

Table 4. Results for selection gradients β from the linear model ($Swt = \alpha + \beta_H H + \beta_B B$) and γ from the quadratic model ($Swt = \alpha + \beta_H H + \beta_B B + \gamma_H H^2 + \gamma_B B^2 + \gamma_{HB} H \times B$). Fitness parameter is seed weight (Sw), for other details see Table 3.

Data	N	Seed wt (mg)	β				γ			
			H	B	R ²	t-test	H	B	H × B	R ²
Intact: not fertil/no compet	17	0.38 ± 0.014	0.08	-0.05	0.19	1.60	0.21	-0.005	-0.45	0.32
Intact: not fertil/compet	20	0.38 ± 0.018	0.06	0.02	0.09	0.43	0.11	-0.02	-0.71	0.18
Intact: fertil/no compet	20	0.42 ± 0.019	0.09	-0.1	0.24	2.31	0.70	0.37	-0.26	0.64
Intact: fertil/compet	14	0.43 ± 0.020	0.03	-0.11	0.45	2.63	-0.18	0.06	0.20	0.50
25% clipped: not fertil/no compet	10	0.44 ± 0.009	0.13	-0.12	0.77	4.78	-0.44	-0.24	0.74	0.81
25% clipped: not fertil/compet	13	0.36 ± 0.025	0.08	-0.01	0.10	0.56	-1.06	-0.40	0.57	0.22
25% clipped: fertil/no compet	20	0.41 ± 0.012	0.07	-0.06	0.26	2.45	0.45	0.27	-0.75	0.43
25% clipped: fertil/compet	20	0.32 ± 0.014	0.02	-0.10	0.26	1.90	-0.18	-0.28	0.82	0.44

any consistent pattern. The tendency towards disruptive selection was strongest among unfertilized clipped plants growing in competitive environment. In most cases, there was some evidence for positive correlational selection ($H \times B$ under γ in Table 3), with only two nonsignificant negative $H \times B$ gradient. In this case, positive correlational selection would potentially lead to the evolution of tall and branchy plants.

Finally, quadratic models with respect to seed weight are also presented in Table 4. These models revealed stabilizing selection on branch production, but only for fertilized plants growing free from competition. Correlational selection (Table 4) was more variable than in the case of seed yield (Table 3). Negative interaction terms were mainly found among intact plants and positive terms among apically damaged plants, though none of these gradients were statistically significant (Table 4). As a whole, the quadratic models explained only a minor part of variation in the fitness components as compared to the linear models (cf. R^2 of the linear and quadratic models in Table 3 and 4).

Table 5. Results for selection gradients β from the linear model: ($Swt = \alpha + \beta_H H + \beta_B B + \beta_S S$). Fitness parameter is seed weight (Sw). Equation-column present regression coefficients (slopes) for standardized H = height, B = number of branches and S = number of seeds. R^2 is the coefficient for determination. Coefficients in bold are significant at $\alpha < 0.05$.

Treatment	N	β			
		H	B	S	R ²
Intact: not fertil/ no compet	17	0.2	0.06	-0.21	0.29
Intact: not fertil/compet	20	0.01	-0.13	0.17	0.12
Intact: fertil/no compet	20	0.09	-0.1	0.0001	0.24
Intact: fertil/compet	14	-0.06	-0.27	0.19	0.56
25% clipped: not fertil/ no compet	10	0.13	-0.11	-0.01	0.77
25% clipped: not fertil/ compet	13	0.26	0.04	-0.23	0.25
25% clipped: fertil/ no compet	20	0.07	-0.04	-0.03	0.27
25% clipped: fertil/ compet	20	-0.12	-0.17	0.19	0.52

Discussion

Contrasting proximate effects of resource availability on compensation

In most measures of performance, the tall wormseed mustard was able to completely compensate and even overcompensate for experimental clipping that removed 25% of the bolting inflorescence. The average seed yield of clipped relative to unclipped plants was 1.3 and 1.1 fold for unfertilized and fertilized plants in the absence of competition. The corresponding estimates in competition with *Anthriscus* were 3.2 and 1.2 fold, respectively. We thus found greater fitness overcompensation in the most unfavourable growth condition of our experiment, in the absence of fertilization and in the presence of competition. This is a surprising result given overcompensation is generally expected under favourable growth conditions with little competition (Maschinski and Whitham 1989, Mopper et al. 1991, Whitham et al. 1991, Bergelson and Crawley 1992a, 1992b, Juenger and Bergelson 1997, Huhta et al. 2000a). Our results agree with the meta-analysis of Hawkes and Sullivan (2001) suggesting that dicot herbs tend to overcompensate more frequently in resource-poor conditions.

The fact that overcompensation is associated with poor resource environments suggests that compensation to herbivory is primarily determined by some factor other than nutrient resources, such as meristem limitation. The competition hypothesis, as presented above in Introduction, may not explain overcompensation in this case because both predictions (C1 and C2) failed. Optimal adjustment of branch number in relation to available resources was partially supported (O1 and O2). When plants were grown in competition with *Anthriscus*, they produced fewer branches than plants grown without competition. Fertilization, on the other hand, had the opposite effect. Huhta et al. (2000a) also observed that fertilization increased lateral branching in *E. strictum*, while root competition with grasses reduced number of branches. We thus conclude that resource deficiency suppresses lateral branching in *E. strictum*.

However, the adjustment of branch number may not be perfect in relation to the amount of available resources because further increase in branching as a response to apical damage increased seed yield (cf. prediction O3b). Consequently, meristem limitation seems to be important for regrowth responses to simulated browsing. Because the treatments did not affect shoot height, this may be indicative that even our “low” resource treatments (no fertilization and competition) did not cause any severe resource limitation on plant growth and reproduction. The treatments affected above-ground as well as below-ground biomass, but these effects were highly parallel to changes in shoot architecture. Thus it is difficult to tear apart how much changes in biomass production actually reflect increasing or, alternatively, decreasing resource limitation as such and, on the other hand, phenotypic plasticity of shoot architecture in response to changes in growth conditions and hence the plant’s ability to utilize the available resources (light and mineral nutrients). From this perspective, our predictions C1 and C2 can be understood as specific outcomes of the competition hypothesis when apical dominance shows no phenotypic plasticity. If apical dominance shows some plasticity as predicted (O1 and O2) but these plastic responses are not perfectly matched in relation to available resources so that plants experience meristem limitation in relation to available resources (M1), our results could be interpreted in the favour of the competition hypothesis in this modified form (Aarssen and Irwin 1991, Irwin and Aarssen 1996).

In addition to positive correlations between branching and seed yield of intact plants, meristem limitation (M1) is indicated by the facts that plants responded to damage by increasing lateral branching and this response was strongest under growing conditions where undamaged plants had the lowest number of lateral branches. Unfertilized plants growing in competition produced on average only 0.5 branches when they were not clipped. Clipped plants in the same growth conditions produced over 6 branches, more than 13 times the number of branches produced by unclipped plants. As a comparison, clipping increased branch number from 6.5 to 10 among unfertilized plants growing free from competition (i.e. a 1.5 fold increase). Fertilization increased branch number and clipping caused a 1.2 and 2.4 fold increase in branching among fertilized plants growing without or with competition, respectively. Huhta et al. (2000a) observed 1.5–1.2 fold increase in branching of *E. strictum* following 10–50% clipping of the main stem in unfertilized plants growing in competition with grasses. In contrast, fertilization strongly increased branch number, and clipping decreased branching among fertilized plants (Huhta et al. 2000a). The consistent pattern

in both experiments is that simulated browsing most strongly increases lateral branching in growth conditions where undamaged plants have few branches. If undamaged plants already have many branches, simulated browsing increases branching less (present study) or may even reduce the number of branches produced (Huhta et al. 2000a). Simulated browsing has been shown to increase lateral branching also in natural growing conditions. In a field population studied by Huhta et al. (2000c), unclipped plants were strongly apically dominant (a single inflorescence), while plants with 10% of the main stem removed produced on average 4.2 branches.

It seems that resource availability may have contrasting effects on compensation ability of monocarpic herbs, such as *E. strictum*. First, if the effects of resource availability and browsing on fruit production are mainly mediated by phenotypically plastic changes in shoot architecture (number of branches), overcompensation will likely be most pronounced in conditions where the undamaged plants have few branches. In our case, this occurred in conditions with competition and no fertilization. Second, if the responses to apical damage are not mediated by shoot architecture but rather by available resources supporting fruit production and seed yield per fruit, the enhancement should be strongest in good growth conditions. In our case, this was observed in seed yield per fruit when the plants were fertilized and grown without competition. Thus both shoot architecture and resource availability may mediate the responses of *E. strictum* to apical damage, but the former effects were much stronger in the present experiment. However, the situation was the reverse in Huhta et al. (2000a). In this earlier experiment, overcompensation was found only among fertilized plants in the absence of competition where clipping improved fruit production but decreased branching.

The contrasting effects of resource availability may well explain why the prediction (C2) of the compensation continuum may sometimes fail, but unfortunately we are not able to exactly predict whether compensation should be best at low, moderate or high resource availability in different plant groups. Such predictions are likely to critically depend on the variation in the shapes of responses in phenotypic plasticity of shoot architecture as well as in utilization of resources in relation to their availability in the environment (Irwin and Aarssen 1996). In Fig. 4, we have outlined some possibilities of which some are consistent with the compensation continuum (curves B1 and B2) while others are not (B3 and B4). Here the branch production and compensation capacity are assumed to be correlated, that is the increased branch production will be eventually realized as enhanced seed production.

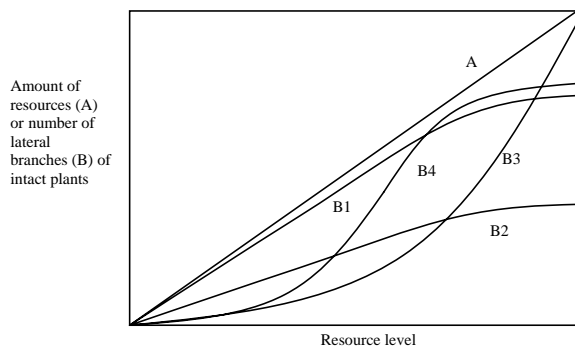


Fig. 4. Plasticity of lateral branching in relation to resource availability. (A) Plant resources are assumed to increase linearly with the amount of available resources. (B) Number of lateral branches (number of active meristems) of intact plants. The area between A-line and B-curve indicates the opportunity of apically damaged plants to increase reproductive output by increasing lateral branching when apical dominance is removed. B1 this plant produces many lateral branches when resources are at an adequate level. If resources increase above this level, the plant does not significantly increase branching. At these high resource levels, the plant may show weak overcompensation. When resource level decrease below the adequate level, lateral branching declines due to resource limitation. B2 as B1, but now the intact plant produces only few lateral branches at high resource levels. When apical dominance is interrupted, the plant increases lateral branching, and at high resource levels significant overcompensation is possible, as compensation continuum expects. B3 when there are plenty of resources, the plant produces very branched architecture. When resource level decreases, lateral branching is reduced more than expected by the decline in resources. When apical dominance is removed, lateral branching increases most at intermediate resource levels where also overcompensation is most probable, as Irwin and Aarssen (1996) suggest. B4 as B3, but at high resource levels, lateral branching of the intact plant does not respond to a further increase in resource levels. Tolerance is highest at low resource levels and intermediate.

Adaptive plasticity in shoot architecture and apical dominance

The evolution of growth and allocation patterns in response to herbivore damage can be considered the adaptive evolution of phenotypic plasticity (Juenger and Bergelson 2000, Juenger et al. 2000, Stowe et al. 2000). Theoretical models predict that plasticity should evolve such that individuals express appropriate phenotypes for specific environmental states in a way that increases the adaptation of populations to the variable environments they experience (Via and Lande 1985, Via 1987, van Tienderen 1997). The evolution of “appropriate” or adaptive responses depends on the strength and pattern of selection across environments, the frequency of environments experienced by a population, costs of plasticity, as well as the pattern of genetic variation underlying phenotypic responses. Importantly, strong skews in the frequencies of environments, high plasticity costs, or genetic tradeoffs in the production of phenotypes can lead to the evolution of “inappropriate” or maladaptive phenotypes in particular environments

(Via and Lande 1985, Via 1987, van Tienderen 1997, Juenger and Bergelson 2000, Juenger et al. 2000).

From this perspective, our assumption that the number of branches could be optimally adjusted to the prevailing growth conditions (O3) may not be justified in heterogeneous environments where phenotypic plasticity has evolved as a compromise of plant performance in divergent growing conditions. Alternatively, the assumption may fail in relation to seed production which we mainly used as fitness measure, but increasing branching leads to costs on some other fitness components (Irwin and Aarssen 1996). Indeed, our selection analysis indicated that, while the increased branch production is associated with a fitness benefit in terms of increased fruit and seed yield, it may have a fitness cost in terms of lower seed weight and, hence, possibly lower germination or seedling success (Huhta et al. 2000a, 2000c). The slight decline in seed weight in clipped plants grown in competition may further indicate that such a fitness cost is highest in competitive environments, and that the production of few branches might have been suboptimal in terms of seed yield, but not necessarily in terms of seed quality. Huhta et al. (2000a), however, found lower seed weight in fertilized, apically damaged plants irrespective of competition, and in the present data the decline of seed weight was most pronounced in fertilized, apically damaged plants growing in competition with *Anthriscus* (data not shown). It should also be noted that seed weight does not always reliably predict seedling success (Thomson and Grime 1979, Reader 1993), and, therefore, it is somewhat uncertain to what extent smaller seeds imply a fitness cost in nature.

Our data supports phenotypic plasticity with respect to lateral branching. In contrast, plant height was insensitive to our experimental manipulations. This may indicate that plants always prioritize investment in vertical growth irrespective of environmental conditions, or that the evolution of plasticity in height is further constrained by genetic or developmental mechanisms. Our data provide no evidence for a phenotypic tradeoffs between vertical growth and lateral branching in *E. strictum*, and no consistent evidence for stabilizing selection on branch number (cf. prediction O3a). Quadratic selection gradients revealed mainly weak positive correlational selection on plant height and lateral branching. Consequently, often in *E. strictum* the tallest and the most branched individuals have the highest relative fitness in terms of seed yield.

Plants were, however, more apically dominant under competitive environments as predicted by Aarssen and Irwin (1991). One way to interpret our results is to consider that (1) suppressed lateral branching at low availability of light and nutrients is an expression of plasticity induced by restricted availability of resources, and that (2) the suppression of branch production is greater than would be “appropriate” or adaptive, given

the physical level of resources available. *E. strictum* may developmentally respond to “low” resource levels with a more restrained lateral branching than the external resources could actually support. The observed overcompensation in terms of seed yield and the absence of negative selection gradients on branch number support this interpretation. If the plastic changes in shoot architecture really were adaptive responses to the resource conditions, we predicted a negative correlation between directional selection gradients on height and branch number and that in competitive environments the gradient on height should be higher than that of branch number and vice versa in a competition-free environment (S1–S3). In clipped plants our predictions held in most cases (in three treatments out of four), but in intact plants the predictions generally failed. Actually, in clipped plants the predictions held in all four cases when fitness was estimated in terms of seed number instead of seed mass, while the results were the same in unclipped plants with both fitness measures (data not shown). Consequently, among apically damaged plants growing in competition, selection for increased vertical growth was stronger than for increased branching, but in the absence of competition branching either prevailed or the two traits were nearly similar. A reason for these contrasting patterns may be that intact and apically damaged plants have made their investments in vertical growth and lateral branching at different phenological states, and the shading effect by *Anthriscus* may have been stronger during the regrowth period of apically damaged plants from the end of June onwards than during the undisturbed growth period of intact plants. Nonetheless, the strong directional selection for increased lateral branching among intact plants ($\beta = 0.58\text{--}0.70$) indicates that the fitness benefits or costs in terms of seed production do not fully explain the adaptive plasticity of the shoot architecture in *E. strictum* in the present garden conditions.

In conclusion, our experiments provide strong evidence for the role of meristem limitation in apically dominant plants as a primary mechanism leading to the occurrence of overcompensation. Furthermore, resource availability seems to be important for the compensatory responses of *E. strictum*, but in an unanticipated way. While increased resource availability may support higher photosynthesis and nutrient acquisition, the effects of resource availability on the plasticity of shoot architecture seems to be a major determinant of compensation responses in this species. In *E. strictum*, plants respond to “low” resource levels with a more restrained lateral branching than the external resources can actually support. We have not, however, found any conclusive explanation for why this is so. A cost of increased branching on other fitness components, such as seed quality or survival, might provide a potential explanation. Shoot architecture may also be subject to tempo-

rally variable selection pressures, e.g. due to fluctuating intensity of herbivory (Crawley 1987, van der Meijden 1990, Vail 1992, Nilsson et al. 1996a, Juenger et al. 2000, Gómez 2003) or variable climate (Lennartsson et al. 1998, Huhta et al. 2000a, Levine and Paige 2004) or variable resource availability (Aarssen and Irwin 1991, Bonser and Aarssen 1996, Irwin and Aarssen 1996, Järemo et al. 1996, Duffy et al. 1999), which operate on fitness effects integrated over generations and which may lead to suboptimal adaptation in the short-term (Seeger and Brockman 1987, Nilsson et al. 1996a). Whatever the ultimate causes, the present study suggests that overcompensation in monocarpic herbs occurs in conditions where the intact plants appear to be more meristem rather than resource limited. Further studies exploring selection on plastic responses in growth architecture, along with a better understanding of constraints on and costs of this plasticity, will provide additional insight into the evolution of tolerance to herbivory and the occurrence of overcompensation.

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