Growing competitive or tolerant? Significance of apical dominance in the overcompensating herb *Gentianella campestris*

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Abstract: As a compensatory response to herbivory, plants may branch vigorously when the growth of dormant meristems is triggered by shoot damage. Undamaged plants, on the other hand, often restrain branching, and this limitation on growth can be considered a cost of tolerance to herbivory. Restrained branching is caused by apical dominance and may, alternatively, be associated with fitness benefits in competitive environments that favor fast vertical growth. To test these hypotheses regarding selection for restrained branching, we compared the performance of two subspecies of the biennial grassland herb *Gentianella campestris*; the tall, apically dominant ssp. *campestris* and the short, multi-stemmed ssp. *islandica*, which shows reduced apical dominance. For both subspecies, we manipulated the height of surrounding vegetation (competition) and damage intensity in grasslands of differing productivity (high, medium, low), and examined population growth rates using matrix population models combined with life table response experiments (LTREs). In the absence of damage, ssp. *campestris* exhibited a higher population growth rate than ssp. *islandica* in the tallest vegetation, however with the growth rate still being below one. In the medium and low productivity environments where the vegetation was shorter, the population growth rate of ssp. *islandica* was considerably higher than that of ssp. *campestris* as long as no more than about 50% of the plants were damaged. When plants were damaged, the apically dominant ssp. *campestris* showed a positive population growth rate ($\lambda > 1$) and often overcompensatory seed production in all productivity levels, while ssp. *islandica* showed no compensation and therefore the population was predicted to decline ($\lambda < 1$). We conclude that restrained branching in *Gentianella* cannot be selected for by competition alone, but that episodes of apical damage are required to maintain the trait. Furthermore, because of the costs of restrained branching, apical dominance should be selected against in grasslands where competition and disturbance are low.

Key words: apical damage, demographic model, herbivory, compensatory growth, population growth rate, grassland

INTRODUCTION

Thirty years ago, Paige and Whitham (1987) reported that browsed scarlet gilia (*Ipomopsis aggregata*) plants produced about 2.4 times more fruits than undamaged plants. Such overcompensation is now known to represent an extreme case in a continuum of plant compensatory responses (or tolerance) to herbivory or other shoot damage (Maschinski and Whitham 1989; Bergelson and Crawley 1992; Strauss and Agrawal 1999; Hawkes and Sullivan 2001; Wise and Abrahamson 2005). Overcompensatory seed production, i.e. when damaged plants produce more seeds than undamaged ones, has attracted particular attention when it occurs in short-lived species that reproduce only once during their lifetime, partly because it is counterintuitive that such plants do not seem to maximize reproduction in the absence of herbivory (Crawley 1987; Paige and Whitham 1987).

Plant tolerance is one of several adaptations by which plants can persist in environments with high risk of damage by herbivory. The anti-herbivore adaptations are usually classified into three main groups: (1) *escape* in time or space that reduces the risk of being found or reached by herbivores, and thus the risk of damage, (2) mechanical or chemical *defense* that reduces the degree of damage when the plant is found and attacked by herbivores; and (3) *tolerance* mechanisms including compensatory growth after damage that reduce the negative effects of damage of a given intensity once it occurs (cf. Belsky et al. 1993). Such adaptations have in particular been studied in grassland habitats in which biomass removal by wild or domesticated herbivores is a fundamental process (Frank et al. 1998) that promote high plant diversity. For example, reduced light competition favors small species, and reduced litter accumulation favors recruitment and short-lived species (Hayes and Holl 2003; Amatangelo et al. 2008). Such conditions, however, come with a high risk of herbivory damage and grassland plants exhibit a variety of anti-herbivore adaptations (Evju et al. 2009).

Tolerance and other adaptations to damage are based on combinations of several plant traits (Strauss and Agrawal 1999). The strongest compensatory responses to damage have been found in herbaceous species that have relatively unbranched shoot architecture when intact, but that produce multiple fruiting branches when the apically dominant shoot is damaged (Paige and Witham 1987; Huhta et al. 2000; Rautio et al. 2005). Two major hypotheses have been proposed for the evolution of restrained branching. According to the compensatory growth hypothesis, restrained branching conserves meristems and resources to be used for regrowth after damage (Crawley 1987; van der Meijden 1990; Vail 1992; Tuomi et al. 1994; Aarssen 1995). The limited branching and lower seed production of undamaged plants can be considered a cost of tolerance in the absence of damage, whereas overcompensation after damage represents the fully realized reproduction potential (Tuomi et al. 1994; Juenger et al. 2000). The evolution of overcompensation can be described in terms of a gambling strategy that is related to the relative probabilities of becoming grazed and avoiding damage (Nilsson et al**.** 1996). A certain frequency of predictable damage is required for the benefits of restrained branching to outweigh the costs (Crawley 1987; van der Meijden 1990; Vail 1992; Tuomi et al. 1994; Nilsson et al. 1996; Lehtilä 2000).

Another, not mutually exclusive, hypothesis for the selection of restrained branching suggests that it is linked to the fitness benefits of fast vertical growth (instead of branching) in competitive environments, such as in tall, dense vegetation. Aarssen and Irwin (1991) reasoned that vigorous branching following apical damage indicates the costs of apical damage for achieving the benefits of higher competition capacity. In the case of overcompensation, this hypothesis requires that plants do not branch until damage releases suppressed lateral meristems from the apical dominance (for discussion see Aarssen and Irwin 1991, Aarssen 1995, Järemo et al. 1996, Rautio et al. 2005).

The grassland biennial field gentian, *Gentianella campestris*, exhibits an extreme variation in apical dominance and branching patterns that has motivated the subdivision of the species into two subspecies: the tall, apically dominant ssp. *campestris* and the short, multi-stemmed ssp. *islandica* (Pritchard and Tutin 1972; Fig. S1 in Supporting information). These two subspecies sometimes co-occur, but usually grow in discrete populations. Subspecies *campestris* is known to overcompensate for experimental and natural damage, with some variation in the degree of tolerance between populations, depending on land-use history (Lennartsson et al. 1997; Lennartsson et al. 1998).

Here, we compare the performance of the two subspecies of *G. campestris* along environmental gradients of competition (different vegetation heights) and damage (clipping) at three levels of grassland productivity. Using a field experiment combined with population models, we aimed to test under which conditions restrained branching caused by apical dominance in ssp. *campestris* is advantageous over unrestrained branching in ssp. *islandica*. A competitive advantage of restrained branching in tall vegetation would support the competition hypothesis, and an increased capacity for compensatory growth after damage would support the compensatory growth hypothesis. We furthermore hypothesized that in the absence of damage and of strong competition, the vigorously branching ssp. *islandica* would have higher seed production and population growth rate than the apically dominant ssp. *campestris*, thus that restrained branching would be costly under certain environmental conditions.

MATERIALS AND METHODS

Study species

The field gentian, *Gentianella campestris*. (L) Börner (Gentianaceae), is an endemic European herb. Two biennial and one annual subspecies have been described, of which we study the two biennials here. The subspecies *campestris* has an erect growth form, about 15-25 cm high, whereas ssp. *islandica* has a multi-stemmed growth form about 5-10 cm high (Fig. S1 in Supporting information). At the flowering stage, intact individuals of ssp. *campestris* are relatively unbranched, but branching and overcompensatory seed production are common following grazing or mowing (Lennartsson et al. 1997; see Fig. S4 in Supporting information). Both subspecies lack vegetative propagation, and have blue or white flowers that are pollinated by bumblebees, although self-fertilization is frequent (Lennartsson 2002). The biennial life-cycle is obligate and all plants form a rosette in the first summer, overwinter as a tap root with a top meristem, and flower in the second summer, dying after that (Fig. 1).

Both subspecies occur in anthropogenic, semi-natural pastures and hay-meadows of unfertilized, semi-dry to mesic types. Such habitats are among the least productive grassland types in the agricultural landscape, but differences in soil moisture, soil type, and climate cause a certain variation in productivity between sites. The most low-productive habitats are usually found in high altitudes or latitudes, or in heathland habitats. Subspecies *campestris* is found over the entire distribution area and ecological range of the species, whereas subspecies *islandica* is confined to low-productive grasslands in a few montane, northern, and Atlantic parts of the species' distribution area. The intensity of grazing varies considerably between years, mainly depending on stocking density, but is on average lower in low-productive pastures compared to more productive habitats (T. Lennartsson, pers. obs.).

Experimental setup

We conducted the experiment in a 75 × 25 m area of a semi-natural grassland in central Sweden (59°44'41"N, 18°9'9" E), with dry-to-mesic species-rich herb-grass vegetation (Påhlsson1994). The grassland sloped slightly (about 4% incline) from a shallow valley to a low ridge. The soil on the ridge was slightly drier and coarser than in the valley, which created a productivity gradient that was reflected by decreasing vegetation height from the valley to the ridge. Apart from the height gradient the vegetation was homogenous. We used three 10 × 25 m sections of the productivity gradient for the experiment, with each section representing a productivity level: high (average vegetation height 15 cm, measured as 50% visual obstruction method under a 14˚ observation angle, Robel et al. 1970), medium (vegetation height about 10 cm), or low productivity (vegetation height about 5 cm). In August year one, the vegetation in each section was cut and removed together with old litter in order to create optimal conditions for establishment of *Gentianella*. We then established 18 plots of 2 × 2 m in the high productivity section, 12 plots in medium productivity, and six plots in low productivity, in which batches of 4000 seeds (2000 seeds per subspecies, randomly mixed) were sown in the 1.6 × 1.6 m center (to avoid edge effects). The sowing resulted in 17-31 plants per subspecies per plot (on average 20.6 plants of ssp. *campestris* and 19.0 of ssp. *islandica*, of which on average 15.1 and 13.6 plants were assigned to large plants (see section Data sampling). In years two and three, we used a grass shears with an adjustable distance runner to cut the vegetation in the plots to the three heights, representing different levels of competition (Fig. S2 in Supporting information). In the high productivity section, six plots were cut to a vegetation height of 12 cm, six to 8 cm, and six to 4 cm (Fig. S2). In the medium productivity section, six plots were cut to 8 cm and six to 4 cm (the vegetation was too short for 12 cm cutting), and in the low productivity section, six plots were cut to 4 cm (no 8 cm or 12 cm cutting was possible). In both years, the plots were cut three times during the summer (late June, mid-July, and mid-August), in order to keep each plot’s experimental vegetation height fairly constant. The cutting of years two and three determined the competition conditions for the rosette and adult stages, respectively. At the June and August cuttings of year three, all adult plants were left untouched, while at the cutting in mid-July, half of the *Gentianella* plants of each plot were clipped to the same height as plot’s vegetation height. We chose plants for clipping by sorting the individuals of each subspecies by size (number of buds) and then alternately assigning plants on the list to clipping or control. Small plants that were shorter than the assigned vegetation height of a given plot were not clipped. By this experimental setup we obtained subsamples of clipped plants subject to different levels of damage and competition, and unclipped plants subject to different levels of competition only.

Data sampling

At the August-cutting in year two, all rosettes that could be detected with a gentle search were marked using a 2.5cm grid, and their diameter and the number of leaves were recorded for each. As rosette survival was nearly 100%, it was possible to assign each rosette to a subspecies retroactively in the third year based on the position of the rosettes and adult plants. At the mid-July cutting in year three, all adult plants of *Gentianella* were recorded. Small adult plants emanating from small rosettes that had not been detected the previous year, were denoted as “small adults” and all other plants as “large adults” (Fig. 1). The numbers of flower buds, flowers, and fruits were counted in August, and the number of fruits again in late September. Seed production was estimated by multiplying the number of fruits per plant by the number of seeds of a randomly chosen fruit per plant. Seed weight was not considered here because previous studies (Lennartsson 1997; Lennartsson et al. 1997) have shown that seed weight does not differ between the subspecies or between clipped and unclipped plants.

Statistical analyses and tolerance

In the high productivity section that contained plots of all three experimental vegetation heights, we examined the effects of vegetation height and clipping on the fecundity (seed and bud production) and rosette size of the two subspecies with generalized linear mixed-effects models (function ‘glmer’ in the *lme4* package in R 3.2.2, R Core Team, 2016). In the model of seed production, we included subspecies, vegetation height (4, 8, 12 cm), clipping (yes, no), all two-way interactions, and a three-way interaction as fixed explanatory variables. Plot was included as a random effect to account for multiple observations per plot, and the model was fit with the negative binomial distribution and log link function. Since the three-way interaction (subspecies × vegetation height × clipping) was significant ($\chi^2 = 48.33$, df = 2, $P < 0.0001$), we constructed models for unclipped and clipped plants separately to examine seed production in more detail, with vegetation height, subspecies and their interaction as fixed explanatory variables. Moreover, to explore plant responses to clipping within subspecies, we ran models for each subspecies with vegetation height, clipping treatment, and their interaction as fixed explanatory variables. As the clipping treatment did not affect small adult plants, we excluded them from all analyses of the effect of clipping.

To investigate rosette size (number of rosette leaves × rosette diameter in cm) in relation to vegetation height, we conducted a glmer with subspecies, vegetation height (three levels), and their interaction as fixed explanatory variables, and with plot as a random effect. Rosette size was modelled using the Gaussian distribution and identity link function.

For the model of bud production, the fixed explanatory variables were subspecies, rosette size from previous year, vegetation height (3 levels), all two-way interactions, and a three-way interaction. Plot was again included as a random effect, and bud production was modelled using the Poisson distribution and log link function.

In all statistical models, the significance of the fixed explanatory variables was explored using the likelihood ratio test fit with maximum likelihood and by testing the model with a given variable against the model without that variable. The goodness of fit was confirmed by visual examination of the residual plots for each model. Moreover, the dispersion factor was examined for the models of seed and bud production (it was close to 1 in both cases, indicating a good fit of the models). Contrasts (function ‘glht’ in the *multcomp* package) were used for pairwise comparisons for significant explanatory factors, and least square means were calculated using the function ’lsmeans’ in the *lsmeans* package.

We quantified tolerance to clipping damage by comparing the mean seed production of the clipped large plants to that of the unclipped large ones separately for each productivity level, subspecies and vegetation height. A ratio less than 1 of clipped to unclipped plants indicates undercompensation, while a ratio greater than 1 indicates overcompensation (Belsky 1986).

Matrix population models

To examine the consequences of the competition and clipping treatments for the population growth rates of each subspecies, we used a stage-structured matrix population model that consisted of the following four life stages: a short-lived transient seed bank, rosettes, small adults and large adults (see Fig. 1). The matrix model describes the transitions of individual plants from life stages in year t to life stages in year $t+1$, and is appropriate for the studied *G. campestris* subspecies because they are strictly biennial (i.e. all plants flower in the second year irrespective of plant size; Lennartsson 1997). A transition matrix was constructed separately for each combination of subspecies, productivity level, and clipping treatment, resulting in a total of 12 autumn-autumn matrices per subspecies (Table 1). As the clipping treatments of the adult plants did not influence the rosette stage, we averaged the values of all rosettes per productivity level, subspecies, and vegetation height to calculate the life-cycle transitions related to recruitment and the fate of rosettes (g_{21}, g_{32}, g_{42}, Fig. 1).

Recruitment for the population matrices could not be properly estimated from the same experiment because the seeds had been sown under optimal recruitment conditions, thus overestimating the rosette/seed ratio. In order to form a litter layer related to each vegetation height, nine additional 2 × 2 m plots in the high productivity section were clipped to 12 cm, 8 cm, or 4 cm (three plots/height) annually in August over three consecutive years (Fig. S2). In late August of the second year, half of each plot was seeded with 2000 seeds of ssp. *campestris* and half with 2000 seeds of ssp. *islandica*. The number of rosettes of all sizes was recorded in mid-July in years three and four, which provided, respectively, estimates of recruitment from the previous year's seeds (f_{23} and f_{24}) and recruitment from the seed bank

(g_{21}, Fig. 1). We also examined potential recruitment from the seed bank in year five, but as it was very low (less than 0.01% for both subspecies), we did not consider a longer-term seed bank in the life-cycle. For each transition matrix, the deterministic population growth rate was calculated as the dominant eigenvalue (λ) that describes the rate at which population size is predicted to change in a constant environment (Caswell 2001).

Life table response experiments (LTREs)

We used a life table response experiment (LTRE; Caswell 2001) to determine the matrix elements (i.e. life-cycle transitions) that contributed to the observed differences in deterministic population growth rates between the clipped and unclipped matrices at each productivity level per subspecies. For details, see Supporting information.

Stochastic population growth rate relative to damage risk and productivity

To investigate the long-term stochastic population growth rate (λ_s) with respect to productivity and simulated grazing intensity, we conducted stochastic simulations for each productivity level (high, medium, low). For each subspecies, we used sets of the transition matrices constructed from a given productivity level (Table 1) and simulated population size for 10 000 years starting from 50 individuals in each life stage. The clipped matrices ("cl" in Table 1) in a given simulation were drawn at a probability of 0, 0.2, 0.4, 0.6, 0.8, or 1.0, and the unclipped matrices at the inverse probabilities. We assumed an equal likelihood for being grazed to 4 cm or 8 cm. For example, for the simulation of 40% damage risk of ssp. *campestris* in the high productivity environment, we drew the unclipped matrix no. 1 in Table 1 at a probability of 0.6 and the two clipped matrices no. 7 and 11 at a probability of 0.2 each. For each productivity level, we then calculated the average stochastic population growth rate with 95% confidence intervals across time steps based on population sizes; the first 1000 years were removed to omit transient dynamics. To facilitate comparison with the deterministic growth rates, we present all stochastic growth rates with the same scale, i.e., $\lambda_s>1$ indicates an increasing population and $\lambda_s<1$ indicates a declining population in a variable environment.

RESULTS

Effects of vegetation height on plant performance in the absence of damage

The effects of vegetation height on seed production differed between the two subspecies: seed production of the unclipped ssp. *islandica* plants was considerably higher than that of ssp. *campestris* plants in 4 cm and 8 cm vegetation, while the opposite was true in 12-cm-tall vegetation ($\chi^2 = 37.66$, df = 2, $P < 0.0001$ for the subspecies × vegetation height interaction; Fig. 2a).

For both subspecies, rosette size decreased with increasing vegetation height ($\chi^2 = 56.91$, df = 1, $P <0.0001$ for vegetation height and $\chi^2 = 2.23$, df = 2, $P = 0.329$ for the subspecies × vegetation height interaction; Fig. 3a). The rosette size in turn correlated strongly with the bud production of the following year’s adult plants, but this relationship differed between the subspecies across vegetation heights ($\chi^2 = 7.69$, df = 1, $P = 0.006$ for the subspecies × rosette size interaction and $\chi^2 = 116.54$, df = 2, $P < 0.0001$ for the subspecies × vegetation height interaction). In the two lowest vegetation heights, ssp. *islandica* produced more buds in relation to rosette size than ssp. *campestris*, but in the tallest vegetation, there was no such a difference (Fig. 3b). The negative LTRE contributions of rosette recruitment indicate recruitment limitation in tall vegetation (Fig. S3 in Supporting information).

For both subspecies, $\lambda > 1$ predicted unclipped populations to increase in 4 cm and 8 cm vegetation, while $\lambda < 1$ predicted unclipped populations to decline in the tallest (12 cm) vegetation (Table 1, compare matrices 5, 6, 9, 10 with matrices 1, 2). In 4 cm and 8 cm vegetation, ssp. *islandica* had a higher population growth rate than ssp. *campestris* in the absence of damage (Table 1, matrices 6 vs. 5 and 10 vs. 9) and this difference between subspecies was mostly due to ssp. *islandica*'s greater seed and rosette production, i.e. transitions f_{23} and f_{24} (Fig. 2, Fig. S3). Moreover, the population growth rate of both subspecies increased with increasing productivity level (Table 1, compare matrices 9, 17, 21 for ssp. *campestris* and matrices 10, 18, 22 for ssp. *islandica*).

Effects of clipping on plant performance

When the plants were clipped, the seed production of ssp. *campestris* was significantly higher than that of ssp. *islandica* in all vegetation heights, with the difference between the subspecies being most pronounced in 8-cm-tall vegetation ($\chi^2 = 18.97$, df = 2, $P < 0.0001$ for the subspecies × vegetation height interaction; Fig. 2b). Subspecies *campestris* overcompensated for clipping in the 4 cm and 8 cm vegetation (ratio of seed production of the clipped and unclipped plants = 1.06 for 4 cm; 1.45 for 8 cm), but undercompensated for clipping in 12-cm-tall vegetation (ratio = 0.81, $P < 0.05$ in all cases, contrasts; Fig 2). Subspecies *islandica* undercompensated for clipping in the 4 cm and 8 cm vegetation (ratio = 0.08 and 0.33, respectively, $P < 0.05$ in both cases based on contrasts), while clipping at 12 cm removed rather few buds in this low-growing subspecies and caused no difference from the unclipped plants ($P = 0.255$, contrasts; Fig. 2).

The compensatory growth of ssp. *campestris* after clipping led to a positive population growth rate ($\lambda > 1$) in the 4 cm and 8 cm vegetation, while clipping of ssp. *islandica* caused a negative growth rate ($\lambda < 1$; Table 1, compare *campestris* matrices 7 and 11 with *islandica* matrices 8 and 12). Clipping to 12 cm resulted in declining populations for both subspecies (Table 1, matrices 3 and 4). The LTRE analysis indicated that these population declines were due to dramatic reductions in rosette production, (Fig. S3). Overall, the LTRE analysis confirmed that the effect of clipping on population growth rate varied between subspecies and depended on the productivity level and clipping treatment in question, as indicated by large contributions for the subspecies × clipping interaction (Fig. S3).

Stochastic population growth rate in gradients of damage and productivity

In stochastic simulations ssp. *islandica* formed viable populations (λ_s>1) when the damage risk was low (<50% of plants being damaged) in the medium- and low-productivity environments (Fig. 4). In the most productive environment, λ_s of ssp. *islandica* increased with increasing frequency of grazed patches, but never reached growth rate >1 (Fig. 4). In contrast, ssp. *campestris* showed a positive population growth rate under conditions of high damage risk in the high-productivity (>80% damage risk) and medium-productivity (>40% damage risk) environments, and about stable population dynamics (λ_s=1) in the low productivity environment regardless of damage risk (Fig. 4).

DISCUSSION

Apical dominance and restrained growth for tolerance or competition?

Our comparison of the two *Gentianella campestris* subspecies showed that the apically dominant ssp. *campestris* was highly tolerant to shoot damage and less sensitive to tall vegetation. On average, damaged plants of this subspecies overcompensated for the damage in terms of seed production and had positive stochastic population growth rate in the productive grassland when >80% of the area was clipped to short vegetation, corresponding to 80% of the adult plants being damaged. The branchy ssp. *islandica* undercompensated for the damage and was predicted to decline in the high-productive grassland in spite of reduced vegetation height. When the plants were undamaged, ssp. *campestris* produced more seeds and exhibited a higher population growth rate than ssp. *islandica* only in the tallest (12 cm) vegetation, indicating an advantage of an erect growth form in shady environments. In the absence of damage and in lower vegetation, ssp. *islandica* had higher seed production and population growth rate, suggesting a cost of restrained branching under low damage risk and low light competition.

The differential compensatory responses of the two subspecies support the hypothesis that apical dominance and restrained branching are selected for as a tolerance mechanism in environments with a high risk of damage (Crawley 1987, Tuomi et al. 1994), such as grazed or mown grasslands (Lennartsson et al. 1997). On the other hand, the differential responses to tall vegetation support the alternative hypothesis, i.e., that apical dominance and fast vertical growth are selected for in productive habitats, in which tall plants may more efficiently compete for light and/or pollinators (Aarssen and Irwin 1991; Aarssen 1995). However, stochastic simulations indicate that this competitive advantage is not sufficient to maintain viable populations (having $\lambda_s > 1$) of ssp. *campestris* in grasslands that are constantly high-competitive. The reason is poor rosette growth, in turn reducing the size of adult plants, and poor recruitment, probably as a result of litter accumulation (e.g., Lennartsson and Oostermeijer 2001). In contrast, simulations indicate that tolerance to damage enables viable populations in grasslands that are constantly grazed and thus low-competitive. These results suggest that selection for tolerance is more important in this species than selection for competitive capacity, and that apical dominance and restrained growth may thus be predominantly a mechanism for tolerance.

The competition capacity of ssp. *campestris* may nevertheless contribute to the selection for apical dominance if grazing is patchy and spatially variable between years. Under such non-constant conditions, a proportion of adult plants will experience high-competitive vegetation, and vertical growth will then enhance the total seed production and growth rate of the population. Both theoretical and empirical studies have shown that spatial and temporal environmental variations enhance population persistence even in poor quality (sink) habitats (Jansen and Yoshimura 1998; Matthews and Gonzalez 2007).

Selection for apical dominance may also be mediated by pollination, as plant height influences pollen transfer (Donelly et al. 1998; Ehrlén et al. 2002) that, in turn, influences seed set and paternal fitness (Paige et al. 2001). Pollen limitation is, however, not likely in this highly self-pollinating species, which experiences little (if any) reduction of seed set when pollinators are excluded (Lennartsson 2002).

Tolerance and grassland habitats

The field gentian studied here has several traits in common with other grassland annuals and biennials, and our results therefore have implications for the interpretation of grassland plant traits in general. Specifically, similar to the field gentian, many short-lived grassland plants can rarely grow tall enough to overtop more competitive perennial neighbors, and can therefore be assumed to exhibit low seedling survival and poor growth and performance of other life stages in tall vegetation (Grime 1979; Mooney et al. 1986; Kelly 1989; Amatangelo et al. 2008). These plant species thus require low-competitive habitats for persistence. In grasslands maintained by grazing, such habitats come with a high risk of damage of adult plants, which usually affects seed production negatively (cf. Hayes and Koll 2003). Both seed limitation and recruitment limitation have been found in grasslands (Jacobsson and Eriksson 2000), and population viability of short-lived grassland plants can be expected to be strongly influenced by a trade-off between the positive effects of intense grazing on early life stages (due to improved recruitment) and negative effects on adults and fecundity (due to increased risk of being damaged). This trade-off should lead to strong selection for tolerance and other anti-herbivore adaptations to the disturbance in many short-lived species that inhabit grasslands maintained by grazing or mowing (cf. Rosentahl and Kotanen 1994). In such species, apical dominance may be more important as a tolerance mechanism than as a competitive advantage. Although compensatory seed production following apical damage has been observed in several grassland annuals and biennials (Huhta et al. 2003), the relative advantage of tolerance and competition capacity in most cases remains to be studied.

In grasslands where the turf height is limited by nutrient deficit or similar stress factors rather than by intense disturbance, selection for unrestrained branching should occur because of the cost of apical dominance under low competition and low risk of damage (Irwin and Aarssen 1996a; cf. Crawley 1987). For example, *G. campestris* ssp. *islandica* and a number of other grassland species including the *G. amarella* and *G. germanica* groups, *Rhinanthus*, and *Euphrasia*, are known to have branchy types at high altitudes (Prithchard and Tutin 1972; Westbury 2004). High-altitude ecotypes are usually interpreted as adaptations to harsh environments, but we propose that they in some cases represent selection for reduced apical dominance in short-vegetation grasslands that are maintained without intense summer disturbance. In the case of the field gentian, ssp. *islandica* occurs in Scandinavia only in pastures that are very low-productive due to poor soils and a short growing season. Low-productive grasslands support few grazers, and, as a consequence, gentians in such habitats experience rather little herbivory (usually less than 20% of the plants are damaged; T. Lennartsson, pers. obs.). In more productive pastures, where most populations of ssp. *campestris* occur, the frequency of damaged gentian plants is on average considerably higher, but often varies greatly between years from 20 to 100% depending on the farmer’s choice of a grazer, stocking density, timing of grazing, and duration of the grazing period (T. Lennartsson, pers. obs.). The difference in damage frequency between low-productive and more productive sites is probably consistent enough to cause different selection pressures on the branching pattern. Both subspecies studied in the present study originated from populations (one per subspecies) with a long history of grazing, although differing in intensity as described above. Previously, Lennartsson et al. (1997) found differences in tolerance between populations of ssp. *campestris* also in more productive grasslands; populations from pastures and hay meadows overcompensated for damage, whereas populations from unmanaged road verges and powerline corridors did not. Grazing-induced differentiation between ssp. *campestris* populations is, however, probably limited by the large between-year variation in damage frequency in productive pastures.

Compensatory growth in experiments and nature

In this study we used clipping and stochastic matrix modelling to imitate and simulate grassland disturbance, and the results need to be evaluated considering the similarities and differences between the experiment and natural conditions (Paige 1994). Clipping is the most commonly used experimental treatment to imitate herbivory, and has proven to give largely the same responses as shoot damage found in nature, provided that the degree and timing of damage are accurate (Paige and Whitham 1987; Strauss and Argrawal 1999). In pastures, grazing normally removes 40-80% of the shoot length of ssp. *campestris* and frequently trigs the same pattern of compensatory growth as our experimental clipping (T. Lennartsson, pers. obs., Fig. S4). We therefore consider that our experimental clipping represents a realistic type of damage. Moreover, grazing normally produces patchy vegetation in which the frequency of grazed patches increases with grazing intensity (Adler et al. 2001), i.e. similar to our stochastic simulations.

The degree of damage plays an important role in plant compensatory responses and, consequently, estimates of tolerance (McNaughton 1979; Belsky 1986; Huhta et al. 2003). In our study, the plants compensated best at intermediate damage levels (about half of the shoot removed). This is consistent with the theory that the damage on the one hand needs to leave enough resources and meristems for regrowth, but on the other hand needs to remove enough of the apical suppression of basal meristems (Huhta et al. 2000; cf. Sachs 1999; Klimešová et al. 2014.).

Also the timing of damage in relation to the species’ phenology influences compensation capacity. Paige (1994) showed that plants of *Ipomopsis aggregata* clipped early in the season compensated better than those clipped later, and related this result to the phenology of stem elongation and bud development (cf. Maschinski and Whitham 1989). *Gentianella campestris* partly shows the same pattern, i.e. damage closer to the date of flowering reduces the compensatory response. In this species, however, also very early clipping reduces compensation, probably because the below-ground resources become exhausted during the initial growth of the adult plant in the spring. Our clipping in mid-July corresponds to the time window of overcompensation identified in an earlier study (Lennartsson et al. 1998).

Tolerance and resources

Compensatory growth after damage is often fueled by carbon stored in roots (Strauss and Agrawal 1999). Although we have no data on taproot weight of adult plants of the two *Gentianella* types, ssp. *islandica* can be assumed to allocate most of the taproot resources to adult growth, whereas ssp. *campestris* should save some resources for regrowth, either by restraining the allocation to shoots in the spring or by re-storing resources in early summer. Both subspecies are probably maximizing resource storage during the rosette stage, and preliminary studies have shown that the tap root dry weight does not differ between subspecies when matched by rosette size (T. Lennartsson, unpublished data).

Based on the light competition hypothesis, Irwin and Aarssen (1996b) proposed that plants compensate best in environments with intermediate nutrient levels, and a meta-analysis by Hawkes and Sullivan (2001) showed that dicots compensate better in low than in high resource conditions. In our study, however, the average compensation of ssp. *campestris* (i.e. the ratio of clipped/unclipped seed production) decreased with decreasing nutrient status. This was due to a larger proportion of small, poorly compensating plants in low productivity(transition g_{32} in Table 1), whereas the compensation of large plants (f_{14}) was approximately even across productivity levels. Our study area probably represents only the intermediate to low end of a nutrient gradient, but it is also possible that our result reflects selection for tolerance rather than for competitive advantages. Under such selection, a certain proportion of the resources should be saved for regrowth irrespective of nutrient availability.

Benefits and costs of adaptations to herbivory

Even at maximum overcompensation, the population growth rate of ssp. *campestris* in this study was lower than that of undamaged ssp. *islandica* (only in 12 cm vegetation, damaged ssp. *campestris* plants had higher seed production than undamaged ssp. *islandica* plants, but in such tall vegetation, the population growth rate of both subspecies was far below one). This observation is consistent with theoretical models of the evolution of overcompensation, for example, resource and meristem allocation models (Vail 1992; Tuomi et al. 1994), which predict that the absolute fitness of a damaged and overcompensating grazing-adapted type will remain below that of an ungrazed non-compensating “ancestor” type that has evolved in the absence of herbivores (Mathews 1994; Tuomi et al. 1994). Subspecies *islandica* in this study represent such a non-compensating control and to our knowledge, provides the first empirical evidence of the predictions of the resource and meristem allocation models. In the models, the absolute fitness of overcompensators is reduced due to allocation costs of regrowth potential and because the damage that induces regrowth causes a certain loss of meristems and resources (Tuomi et al. 1994; see also Simons et al. 2007). In addition, the compensatory regrowth often leads to delayed flowering, which can reduce seed set in time-limited seasonal environments (Piippo et al. 2009).

Overcompensation is sometimes considered a case of plant-herbivore mutualism (Paige and Whitham 1987; Vail 1992, Agrawal 2000; but see Belsky et al. 1993), and our results can be discussed in a mutualism context. Overcompensation can be regarded an example of evolved dependence, i.e., that the plant through adaptation to a herbivore partner has compromised its ability to perform well in the absence of the partner (de Mazancourt et al. 2005). If ssp. *islandica* is viewed as an evolutionary ancestor of ssp. *campestris*, our study indicates that the overcompensation of ssp. *campestris* does not represent an ultimate benefit of herbivory in the sense of increased plant performance over evolutionary time (Järemo et al. 1999; de Mazancourt et al. 2005). The evolutionary benefits of grazing, however, also depend on indirect effects of grazing via changes in community structure and ecosystem processes (Crawley 1987; de Mazancourt and Loreau 2000; de Mazancourt et al. 2001), because the grazers function as niche constructors (Eriksson 2013). Just as the savanna grasses discussed by McNaughton (1979, 1986), *Gentianella campestris* ssp. *campestris* can be considered to be evolutionary dependent on, and favored by, herbivory since its habitat would not exist without grazing.

Concluding remarks

Similar to previous studies (cf. Ehrlén 2003, 2015), the present study emphasizes that the entire life-cycle of the study species must be taken into account when assessing the benefits of tolerance mechanisms and other plant adaptations in grassland habitats. When doing that, our results indicate that the grazing-tolerant ssp. *campestris* has evolved as an adaptation to grazing either in the presence or absence of episodes of competition, and that selection for apical dominance is a fundamental component of that evolution. We acknowledge that the evolution of apical dominance in most plant species represents an evolutionary response to competitive environments (Aarssen and Irwin 1991), but suggest that in grassland habitats that are shaped by intense grazing, apical dominance may be an important and overlooked mechanism for tolerance.

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Appendix Supporting information

Figure S1. A photo of the two studied subspecies of *Gentianella campestris.*

Figure S2. The experimental design.

Description of life-table response experiments (LTREs).

Figure S3. Results of the life table response experiment (LTRE) analysis on the effects of subspecies, clipping, and their interaction on λ relative to productivity.

Figure S4. Overcompensating *Gentianella campestris* ssp. *campestris* in the field.

Figure legends

Figure 1. The life-cycle graph of *Gentianella campestris* ssp. *campestris* and ssp. *islandica* used to construct a 4 × 4 matrix population model. The dotted lines indicate fecundity transitions between life stages and the solid lines show growth transitions.

Figure 2. Seed production for (a) unclipped and (b) clipped large plants of *Gentianella campestris* ssp. *campestris* and ssp. i*slandica* growing in three vegetation heights (least square mean ± SE). Sample sizes are shown on the bars and significant differences ($P < 0.05$ based on contrasts) between the subspecies are indicated with a star.

Figure 3. (a) Rosette size (number of leaves × diameter in cm; least square mean ± SE) and (b) Number of flower buds relative to rosette size in different vegetation heights for *Gentianella campestris* ssp. *campestris* and ssp. i*slandica*. In (a) *i-iii* indicate significant differences ($P < 0.05$ based on contrasts) between vegetation heights.

Figure 4. Stochastic population growth rates (mean ± 95% CI) for *Gentianella campestris* ssp. *campestris* and ssp. i*slandica* relative to damage risk at different productivity levels calculated over 10 000 time steps. The population is predicted to decline under the dotted line and increase above it. Note that CIs are small and therefore not visible at the current scale.

Table 1. Demographic transitions (see life-cycle in Fig. 1) and annual population growth rate (λ) for the unclipped (uc) and clipped (cl) populations of *Gentianella* ssp. *campestris* (cam) and *islandica* (isl) growing in environments that differed in productivity (high, H; medium, M; low, L) and competition (12 , 8 , 4 cm vegetation height). Growth transitions are g_{21} (seeds in the seed bank developing into rosettes), g_{32}, and g_{42} (rosettes developing into adults). Fecundity transitions are f_{14}, f_{13} (seed production to the seed bank), f_{23}, f_{24} (production of new rosettes).

Matrix no. and code	λ	Transitions						
		g_{21}	g_{32}	g_{42}	f_{13}	f_{23}	f_{14}	f_{24}
1 [H 12 cam uc]	0.567	0.00017	0.420	0.558	150.2	0.165	299.8	0.330
2 [H 12 isl uc]	0.440	0.00015	0.397	0.575	114.8	0.149	126.2	0.164
3 [H 12 cam cl]	0.530	0.00017	0.420	0.558	150.2	0.165	243.3	0.268
4. [H 12 isl cl]	0.446	0.00015	0.397	0.575	114.8	0.149	131.9	0.171
5 [H 8 cam uc]	1.031	0.00031	0.191	0.809	131.2	0.276	517.7	1.087
6 [H 8 isl uc]	1.338	0.00032	0.176	0.820	195.2	0.390	932.7	1.865
7 [H 8 cam cl]	1.220	0.00031	0.191	0.809	131.2	0.276	752.5	1.580
8 [H 8 isl cl]	0.832	0.00032	0.176	0.820	195.2	0.390	312.0	0.624
9 [H 4 cam uc]	1.188	0.00036	0.108	0.89	227.2	0.523	581.8	1.338
10 [H 4 isl uc]	1.800	0.00034	0.120	0.88	363.8	0.873	1373	3.296
11 [H 4 cam cl]	1.202	0.00036	0.108	0.89	49.10	0.112	617.4	1.420
12 [H 4 isl cl]	0.543	0.00034	0.120	0.88	40.90	0.098	105.2	0.252
13 [M 8 cam uc]	0.946	0.00031	0.230	0.770	105.8	0.223	448.0	0.941
14 [M 8 isl uc]	1.201	0.00032	0.241	0.759	148.3	0.311	755.1	1.586
15 [M 8 cam cl]	1.113	0.00031	0.230	0.770	105.8	0.223	542.1	1.382
16 [M 8 isl cl]	0.876	0.00032	0.241	0.759	148.3	0.311	363.4	0.762
17 [M 4 cam uc]	1.084	0.00036	0.160	0.844	184.6	0.426	497.4	1.143
18 [M 4 isl uc]	1.567	0.00034	0.180	0.820	317.2	0.729	1120	2.576
19 [M 4 cam cl]	1.082	0.00031	0.160	0.844	44.90	0.103	521.3	1.198
20 [M 4 isl cl]	0.750	0.00032	0.180	0.820	34.12	0.078	242.5	0.557
21 [L 4 cam uc]	0.992	0.00036	0.211	0.797	153.7	0.354	424.3	0.975
22 [L 4 isl uc]	1.445	0.00034	0.208	0.790	267.2	0.614	971.0	2.233
23 [L 4 cam cl]	1.016	0.00036	0.211	0.797	38.88	0.094	459.5	1.102
24 [L 4 isl cl]	0.712	0.00034	0.208	0.790	30.02	0.072	214.9	0.516

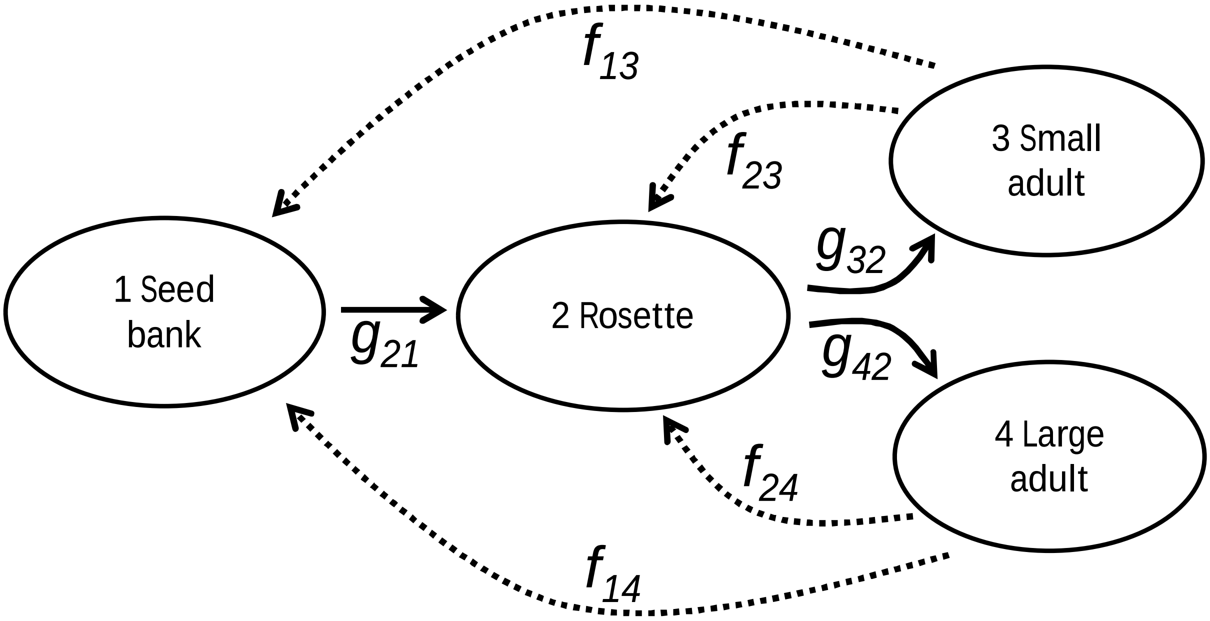
f_{13}
f_{23}
3 Small adult
g_{32}
1 Seed bank
g_{21}
2 Rosette
g_{42}
4 Large adult
f_{24}
f_{14}

Figure 1

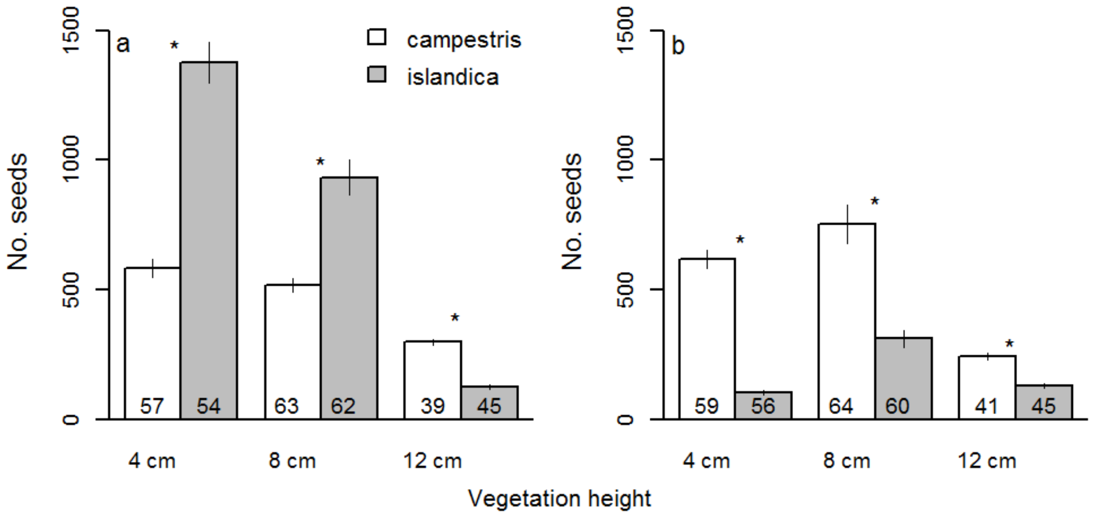
a
b
No. seeds
0
500
1000
1500
campestris
islandica
*
57
54
63
62
39
45
59
56
64
60
41
45
4 cm
8 cm
12 cm
Vegetation height

Figure 2

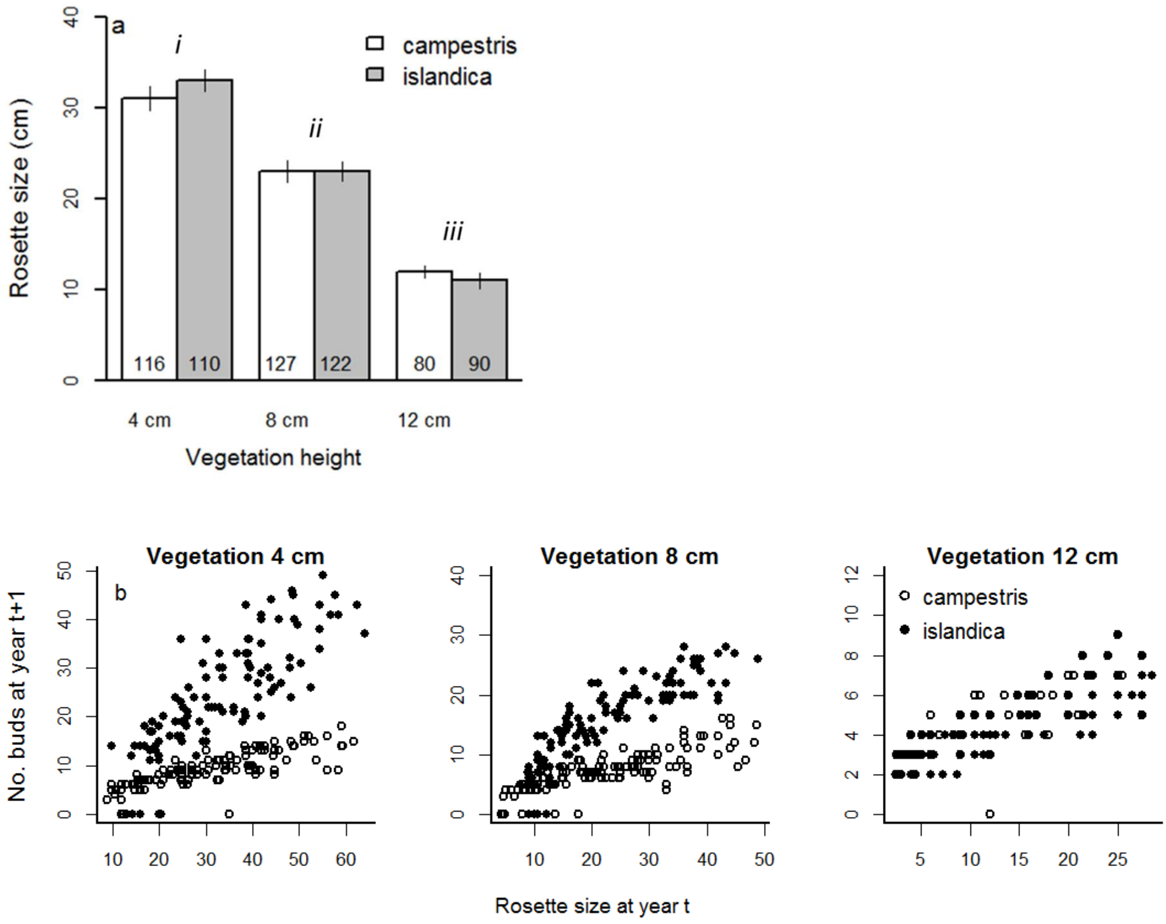
a
i
ii
iii
campestris
islandica
Rosette size (cm)
0
10
20
30
40
116
110
127
122
80
90
4 cm
8 cm
12 cm
Vegetation height
Vegetation 4 cm
Vegetation 8 cm
Vegetation 12 cm
b
No. buds at year t+1
0
10
20
30
40
50
10
20
30
40
50
60
0
10
20
30
40
10
20
30
40
50
0
2
4
6
8
10
12
5
10
15
20
25
campestris
islandica
Rosette size at year t

Figure 3

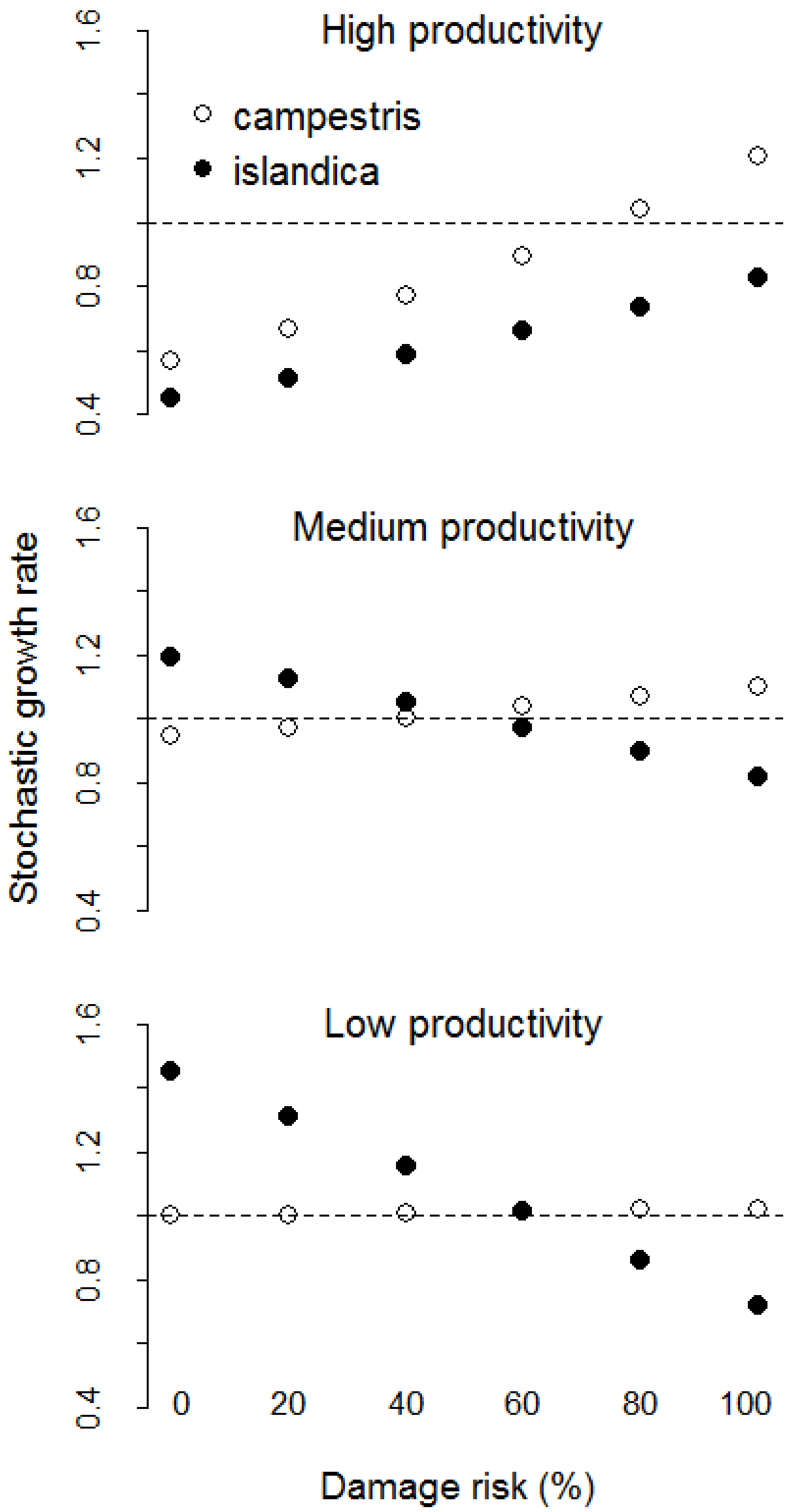
High productivity
campestris
islandica
Medium productivity
Low productivity
Stochastic growth rate
0.4
0.8
1.2
1.6
0
20
40
60
80
100
Damage risk (%)

Figure 4.