



Young clonal and non-clonal herbs differ in growth strategy but not in aboveground biomass compensation after disturbance

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Abstract

Clonal plants have more traits enabling individual persistence (larger belowground storage of buds and assimilates), whereas non-clonal plants have more traits enabling population persistence (a higher reliance on regeneration from seeds). This difference presumably makes those groups respond differently to disturbance. We asked whether this difference is already expressed in the first year of the plant's life. In a pot experiment with 17 congeneric pairs of clonal and non-clonal herbs, we investigated response to a disturbance at the individual level. We were interested whether the leaf C/N ratio (a proxy reflecting active growth and photosynthetic efficiency), the R/S ratio (a proxy for belowground storage) and the amount of compensated biomass differ between clonal and non-clonal herbs. Moreover, we asked whether compensation for the loss of aboveground biomass after disturbance can be predicted by the R/S ratio or explained by the leaf C/N ratio. We found that clonal herbs have higher leaf C/N and R/S ratios than non-clonal herbs. Under disturbance, the leaf C/N and R/S ratios decreased in the clonal herbs and increased in the non-clonal herbs. However, the clonal and non-clonal plants did not differ in biomass compensation ability. Neither the R/S ratio nor the leaf C/N ratio explained the compensation abilities of the herbs. These results show that even though the growth strategies of clonal and non-clonal plants and their reactions to disturbance are different, the groups are similarly capable of compensating for the loss of aboveground biomass. Clonal plants do not have an advantage over non-clonal plants under disturbance during their first year of life.

Keywords Bud · C/N ratio · Growth · R/S ratio · Strategy

Introduction

Among perennial herbs, clonal and non-clonal species represent distinct reproductive strategies and body architectures (Harper 1977; Klimeš et al. 1997; Klimešová et al. 2018a, b). While clonal herbs invest more into vegetative than generative reproduction and their populations rely on genetically identical vegetative offspring rather than on seedlings, non-clonal herbs use the opposite strategy predominantly (Silvertown et al. 1993; Herben et al. 2015). Non-clonal

herbs invest in seeds and genetically variable progeny (Grime 1979). Vegetative multiplication of clonal herbs is allowed by the production of connected and repeated rooting units (ramets), which have the potential to become independent from their parent (van Groenendael and de Kroon 1990; Ottaviani et al. 2017). On the other hand, the body of non-clonal herbs consists of only one rooting unit (Ottaviani et al. 2017) because they have neither the ability to produce adventitious roots on shoots nor adventitious buds on roots (Groff and Kaplan 1988). Therefore, clonal plants might have more traits enabling individual persistence, and non-clonal plants might have more traits enabling population persistence. This presumably makes those two groups respond differently to disturbance both at the level of plant individuals as well as a population level (Eriksson and Jerling 1990; Eckert 2001; Fischer and van Kleunen 2002; He et al. 2011; Wilmking et al. 2017). Although the response to a disturbance at the individual level is easier to assess we lack comparative studies of damage effect on clonal versus non-clonal plants.

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Disturbance, e.g., cutting, flooding, fire, or frost damage, usually acts aboveground by removing or destroying biomass, and surviving plants rely on buds on belowground organs (Vesk and Westoby 2004; Klimešová and Klimeš 2007; Fidelis et al. 2014; Pausas et al. 2018). The deeper belowground buds are located, the higher the probability of successful resprouting is (Iwasa and Kubo 1997; Lehtila 2000; Vesk and Westoby 2004; Klimešová et al. 2018a). Belowground stems of clonal herbs, i.e., rhizomes, bear a high number of deep buds, while in non-clonal herbs, the number of buds is significantly lower and buds are shallower positioned (Suzuki and Stuefer 1999; Moore et al. 2018; Herben and Klimešová 2020). Nevertheless, even non-clonal herbs have buds suitable for resprouting after severe biomass destruction (Canadell and Zedler 1995; Bellingham and Sparrow 2000; Klimešová and Klimeš 2007; Higgins et al. 2008; Lawes and Clark 2011; Pausas and Keeley 2014). A disturbance that does not disrupt soil profile and does not fragment plant bodies belowground, i.e., only destroys aboveground biomass such as frost, grazing and mowing, might thus have a similar effect on both herb groups.

Not only bud bank characteristics but also the amount of belowground storage and adequate growth response to injury determine success and the outcome of regeneration after disturbance (Wise and Abrahamson 2007; Kobe et al. 2010; Klimešová et al. 2018a, b). Plants with more reserves have a higher chance of resprouting and compensating for biomass removal enough to stay competitively efficient (Clarke and Knox 2009; Paula and Ojeda 2009). Similarly, herbs with the ability to properly arrange storage versus growth investments after injury are more capable resprouters than those that are less flexible (Enquist and Niklas 2002; Knox and Clark 2005; Nzunda et al. 2014). The compensation ability of injured individuals represents, therefore, a good measure of immediate individual response to disturbance although it does not reflect all components of fitness, whose quantification is problematic in perennial plants (Younginger et al. 2017). Therefore, herbs that can compensate more for aboveground biomass loss can be considered better adapted to a disturbance at the individual level (Belsky 1986; Latzel et al. 2014).

Although clonal and non-clonal herbs show different reproductive and regenerative strategies, this only holds for adult plants. A young plant that starts to form belowground organs (e.g., rhizomes) might or might not respond to disturbance differently from an adult plant. Nevertheless, young plants are those founding a population on a new substrate created by human activities or natural forces or when species expand their area (Eriksson 1997). The response of young plants to disturbance might decide the success of the species/population. The motivation for our experimental study is to test which group of young clonal or non-clonal plants better copes with disturbance in terms of biomass compensation

in the first year of their life. Seventeen congeneric pairs of clonal and non-clonal dicotyledonous perennial herbs were subjected to four different disturbance types typical for temperate grasslands: flooding, early frost, cutting of whole aboveground biomass and cutting of 70% of aboveground biomass. We examined two plant traits that are potentially responsible for plant biomass compensation: belowground investments at the time of disturbance (i.e., root-to-shoot ratio) and actual investment in leaf acquisitive strategy (carbon to nitrogen ratio in leaves).

The root-to-shoot ratio (R/S ratio) is one of the most important characteristics reflecting plant strategy in response to nutrient availability and disturbance regimes (Mokany et al. 2006; Bessler et al. 2009). Plants with a higher R/S ratio invest relatively more into belowground structures than to aboveground biomass. In the case of perennial herbs and shrubs, a substantial part of belowground biomass represents storage organs such as taproots and rhizomes that enable resprouting after disturbance (Clarke et al. 2013; Klimešová et al. 2018b). At the intraspecific level, the R/S ratio reflects ontogenetic development, storage accumulation and response to limited resources (Janeček et al. 2014; Mašková and Herben 2018). The C to N element ratio in the leaves (C/N ratio) is a trait reflecting the leaf economic spectrum (Wright et al. 2004) at the interspecific level. Plants with leaves containing proportionally more N are considered to be more acquisitive and have a lower survival probability when facing biotic and abiotic hazards (Sardans et al. 2012; Diaz et al. 2016). On the other hand, plants with leaves containing proportionally more C are conservative, have lower photosynthetic effectivity and slower biomass turnover (Wright et al. 2004; Sardans et al. 2012). At the intraspecific level, ratio changes with ontogeny and increasing C content suggest structural and storage investments in older leaves, while proportionally higher N content points to young leaves where photosynthesis is enhanced by N remobilisation from other tissues or root acquisition (Latanzi et al. 2005; Grechi et al. 2007; Irving 2015; Guo et al. 2016). Knowledge of the R/S and leaf C/N ratio in the context of compensation ability would provide detailed insight into the strategies of resource allocation in clonal and non-clonal herbs as a response to disturbance.

In a pot experiment with 17 congeneric pairs of clonal and non-clonal herbs, we asked (1) whether the R/S ratio and leaf C/N ratio differ in clonal versus non-clonal herbs, (2) how disturbance changes R/S and leaf C/N ratios in clonal versus non-clonal herbs, (3) whether aboveground biomass compensation differs between clonal and non-clonal herbs, and (4) whether the R/S ratio at the time of disturbance (a proxy for belowground storage) and actual leaf C/N ratio (a proxy for photosynthetic efficiency) could explain the level of compensation for aboveground biomass damaged by disturbance.

Materials and methods

Selection of species and germination

To assess the growth and compensation for aboveground biomass damaged by a disturbance in clonal and non-clonal herbs, we conducted a greenhouse experiment in 2016. For the experiment, we used congeneric pairs of herbs, one clonal (rhizomatous) and one non-clonal species from the same genus, to minimize the effect of phylogeny on the plant behaviour under experimental conditions. Data on whether the herbs were clonal or not were obtained from the CloPla database (Klimešová and Klimeš 2008). According to seed availability at the commercial supplier Planta Naturalis (Markvartice u Sobotky, Czech Republic; 50.4286017° N, 15.1989097° E), we pre-selected 114 predominantly common Central European herbs representing a total of 28 genera.

Seeds of the pre-selected species were sown separately by species on sterilized wet sand in Petri dishes and were kept under wet-cold stratification in a refrigerator (dark, 3 °C) in March 2016. After 1 month of stratification, the Petri dishes were transferred to a growth chamber (day, 23 °C for 15 h; night, 16 °C for 9 h) where they germinated. One week after germination, we selected 17 congeneric pairs (Table 1) that exhibited sufficient germination so that one clonal and one non-clonal species from the same genus were available.

In the middle of April 2016, 5-day-old seedlings were transplanted from Petri dishes to 2.2-L pots filled with sand

and garden substrate in a 3:2 ratio. We planted one seedling per pot and had 49 pots per species. Immediately after transplantation, the 1666 pots were placed in an open-sided, unheated greenhouse without artificial light at the Institute of Botany, Třeboň, Czech Republic (49.0057336° N, 14.7724625° E).

Experimental setup

The pots in the greenhouse were randomly assigned to seven groups with seven replicates per species in each group. Four groups were subjected to one of the following disturbance treatments all of which damaged and reduced biomass of experimental plants: removal of aboveground biomass 2 cm above soil (Rem2cm, severe aboveground disturbance), 70% aboveground biomass removal (Rem70%, moderate aboveground disturbance), late-spring frost and whole-body flooding (for details on treatments, see Table 2). Disturbance treatments were selected to reflect disturbance events that may occur in temperate grasslands from which experimental species originated. Disturbance treatments were applied in the second half of May 2016. Three groups of pots represented non-disturbance controls and underwent subsequent harvests to record undisturbed plant development (for details on treatments, see Table 2). A standard NPK nutrition solution was regularly added, and plants were watered with tap water when necessary during the experiment. Control plants were harvested in May, June and September 2016 to follow plant ontogeny in undisturbed plants. Disturbed plants were harvested in September 2016 (for details on harvests, see Table 2). The September harvest required 22 days (from Sept 5 to Sept 27) because of the high number of plants, and the plants were randomly harvested with respect to species and treatment to minimize the effects of differences in age and development.

Table 1 The 17 pairs of clonal and non-clonal congeneric species in the experiment (one pair per row)

| Clonal | Non-clonal |
|----------------------------------|---|
| <i>Artemisia absinthium</i> L | <i>Artemisia campestris</i> L |
| <i>Campanula bononiensis</i> L | <i>Campanula glomerata</i> L |
| <i>Campanula trachelium</i> L | <i>Campanula rapunculoides</i> L |
| <i>Centaurea jacea</i> L. s.l | <i>Centaurea stoebe</i> L. s.l |
| <i>Cirsium canum</i> (L.) All | <i>Cirsium vulgare</i> (Savi) Ten |
| <i>Dianthus deltooides</i> L | <i>Dianthus carthusianorum</i> L |
| <i>Euphorbia esula</i> agg | <i>Euphorbia illirica</i> Lam |
| <i>Galium boreale</i> L | <i>Galium album</i> Mill. ssp. album |
| <i>Hypericum perforatum</i> L | <i>Hypericum montanum</i> L |
| <i>Lychnis chalconica</i> L | <i>Lychnis flos-cuculi</i> L |
| <i>Lythrum virgatum</i> L | <i>Lythrum salicaria</i> L |
| <i>Rumex aquaticus</i> L | <i>Rumex conglomeratus</i> Murray |
| <i>Sanguisorba officinalis</i> L | <i>Sanguisorba minor</i> Scop. s.l |
| <i>Senecio jacobaea</i> L | <i>Senecio erraticus</i> Bertol |
| <i>Stachys palustris</i> L | <i>Stachys germanica</i> L |
| <i>Tanacetum vulgare</i> L | <i>Tanacetum parthenium</i> (L.) Sch. Bip |
| <i>Trifolium pannonicum</i> Jacq | <i>Trifolium montanum</i> L |

Plant traits

During the harvests, the fresh biomass of each plant was sorted by aboveground (stems and leaves) and belowground organs. The biomass was dried at 80 °C for 48 h and weighed. The root-to-shoot ratio (R/S ratio) was calculated as a ratio of belowground biomass to aboveground biomass. In the analytical laboratory of the Institute of Botany, C and N element percentage contents in dry and ground leaf biomass (all alive leaves from one plant were put together and homogenized) were analysed using a Carlo Erba NC 2500 analyser for the majority of harvested plants. Some leaf samples were not able to be analysed because of a low amount of biomass (less than approximately 3 mg), which limited the C and N content analysis. The leaf C/N ratios were calculated afterwards.

Table 2 List of disturbance treatments in the experiment with their descriptions and abbreviations used in figures and tables

| Treatment name | Abbreviation | Disturbance/harvest date | Treatment description |
|----------------------------------|-------------------|--------------------------|---|
| Severe aboveground disturbance | Rem2cm | 18 May/2–27 Sept | All aboveground biomass 2 cm above the soil surface was removed to simulate severe cutting |
| Moderate aboveground disturbance | Rem70% | 18 May/5–27 Sept | Approximately 70% of the aboveground biomass was removed to simulate disturbance such as mowing or herbivory |
| Frost | Frost | 16–27 May/5–27 Sept | Plants were exposed to two frost events to simulate late-spring frosts ($-3\text{ }^{\circ}\text{C}/3\text{ h}$ and $-10\text{ }^{\circ}\text{C}/3\text{ h}$). One week passed between frost events. Pots were taken from the greenhouse very early in the morning and put into a refrigerator with precise temperature regulation. After treatment application, plants were immediately returned to the greenhouse |
| Flooding | Flood | 23–30 May/5–27 Sept | Plants were taken from the greenhouse and placed in water tanks of 50-cm depth for 8 days to simulate whole-body flooding. Tanks were filled with water. After treatment application, pots with plants were returned to the greenhouse without any biomass manipulation or removal |
| Control May | C _{May} | None/18–19 May | No disturbance applied |
| Control June | C _{June} | None/28–30 June | No disturbance applied |
| Control September | C _{Sept} | None/5–27 Sept | No disturbance applied |

Date of treatment application and harvest are shown, all dates are from 2016

Statistical analysis

Leaf C and N element content and leaf C/N and R/S ratios To test the effect of clonality and disturbance on C and N leaf element content and on the leaf C/N and R/S ratios, we conducted a set of random-effects models. Models were computed in a Bayesian framework as follows:

$$\text{Response} \sim \text{normal}(\text{pair} + \delta_0 + \delta_1 \times \text{clonal} + \delta_2 \times \text{disturbance} + \delta_3 \times \text{clonal} \times \text{disturbance}, \phi)$$

where δ and ϕ are parameters estimated by the models. Pair is the random effect of the genus, which is modelled as normally distributed with zero mean and estimated variance. Clonal is a binary variable for each species denoting whether it is clonal. Disturbance is a dummy-coded factor with six levels corresponding to disturbance treatments and May and June controls (September is the reference level).

Biomass compensation To evaluate the effects of clonality, leaf C/N at the time of harvest and R/S ratio at the time of disturbance on aboveground biomass compensation, we used a random-effects model (with an ‘error in variable’ component) in the Bayesian framework. Because the leaf C/N ratio is from a principle response variable measured at the end of the experiment, we modelled it with measurement error. The model was specified as follows:

$$\begin{aligned} \log(\text{Above}B_i) \sim & \text{normal}(\log(\text{Above}B_c) + \text{PairEff} + \beta_0 + \beta_1 \times \text{clonal} + \beta_2 \\ & \times \text{disturbance} + \beta_3 \times \text{clonal} \times \text{disturbance} + \beta_4 \times R/S + \beta_5 \times \text{clonal} \times R/S + \beta_6 \\ & \times \log(C/N_{\text{est}}) + \beta_7 \times \text{clonal} \times \log(C/N_{\text{est}}), \zeta) \end{aligned}$$

where β and ζ are parameters of the model. *Above* B_i is the mean aboveground biomass of each species under each type of disturbance. *Above* B_c is the mean aboveground biomass of control plants of each species. *PairEff* is a random effect of each congeneric pair that was modelled as normally distributed with zero mean and estimated variance. Clonal is a binary variable for each species denoting whether it is clonal. Disturbance is a dummy-coded factor with three levels corresponding to disturbance treatments (the fourth treatment is the reference level). R/S is the R/S ratio of control plants at the time of disturbance (in May). C/N_{est} is an estimation of the leaf C/N ratio for each species and treatment. C/N_{est} was estimated as the posterior distribution of the fitted mean for each species and was modelled under the same treatment as C and N in the previous section (see above). C/N_{est} was centred prior to the analysis to increase the efficiency of the parameter estimation.

For all slope parameters, we used Cauchy distributed priors with zero mean and scale parameter 5 in all analyses. For variance parameters, half-Cauchy distributed priors were used with zero mean and scale parameter 5. For intercepts, we used the default uniform (on \mathbb{R}) priors. All models were evaluated using a Hamiltonian Monte Carlo with the No-U-Turn sampler (Hoffman and Gelman 2014) with four chains with 10,000 iterations each, and half were used as a warmup phase. We

Table 3 Effect of clonality on traits of the control plants

| Trait | C _{May} | C _{June} | C _{Sept} |
|-----------|---------------------|-------------------------|-------------------------|
| C% | [− 1.41, 0.53] | [− 0.35, 0.87] | [− 0.03, 1.21] |
| N% | [− 0.05, 0.21] | [0.06, 0.22] | [− 0.28, − 0.11] |
| C/N ratio | [− 0.21, 0.04] | [− 0.19, − 0.05] | [0.09, 0.21] |
| R/S ratio | [0.08, 0.43] | [− 0.33, 0.05] | [0.43, 0.83] |

The tested traits were C% (C content in leaves), N% (N content in leaves), C/N ratio (ratio of C to N content in leaves), and R/S ratio (ratio of belowground to aboveground biomass). C_{May}, C_{June}, and C_{Sept} represent the control plants in May, June and September, respectively. The posterior distribution of the parameter (δ_1) of the model (for model description see “Materials and methods”) was inspected, and 95% credible intervals are shown. Intervals not overlapping zero (in bold) indicate the difference in trait values between the clonal and non-clonal herbs

inspected the posterior distribution of parameters or their sums to test our questions (for details, see Tables 3, 4 and 5). We interpreted 95% credible intervals as corroborating our hypotheses if they do not overlap with zero.

All analyses were performed in R (version 3.6.1; R Core Team 2016) using package *rstan* (version 2.19.2; Carpenter et al. 2017; Stan Development Team 2018).

Results

While in May, the leaf C/N ratio of clonal and non-clonal herbs did not differ, in June and September, the clonal herbs had a higher C/N ratio than the non-clonal herbs (Fig. 1c; Table 3). This difference was caused by a difference in N content (Fig. 1b; Table 3), while the amount of C was similar and stable over time in both groups (Fig. 1a; Table 3). The R/S ratio was different between the control clonal and non-clonal herbs sampled in May and in September and was higher in the clonal group (Fig. 1d; Table 3).

Similarly, under disturbance, the leaf C/N ratio differed between the clonal and non-clonal groups, and the difference was caused by changes in N only (Fig. 2a–c; Table 4a–c— δ_3). While the C/N ratio decreased in the disturbed clonal plants (Rem2cm and Rem70% treatments, Fig. 2c; Table 4c— δ_3), it increased in the disturbed non-clonal plants (Frost and flood treatment, Fig. 2c; Table 4c— δ_2). The disturbance decreased the leaf C/N ratio of clonal herbs to the level of the leaf C/N ratio of control non-clonal herbs (Fig. 2c) in all treatments, except frost. The R/S ratio was influenced by disturbance much less than the leaf C/N ratio in general (Fig. 2d; Table 4d— δ_3 , $\delta_2 + \delta_3$, δ_2). Nevertheless, while the R/S ratio of the clonal herbs decreased (Rem2cm treatment, Fig. 2d; Table 4d— $\delta_2 + \delta_3$), the R/S ratio of the non-clonal herbs increased under disturbance (Flood treatment, Fig. 2d; Table 4d— δ_2).

Table 4 Effect of individual disturbance treatments (for individual treatment descriptions, see Table 2) on species traits

| Treatment | δ_3 | $\delta_1 + \delta_3$ | $\delta_2 + \delta_3$ | δ_2 |
|--------------|-------------------------|-----------------------|-----------------------|-------------------------|
| a) C% | | | | |
| Rem2cm | [− 0.42, 1.3] | [0.40, 1.63] | CL | [− 0.34, 0.88] |
| | | | n-CL | [− 0.78, − 0.45] |
| Rem70% | [− 1.08, 0.68] | [− 0.23, 1.02] | CL | [− 0.81, 0.44] |
| | | | n-CL | [− 0.61, 0.64] |
| Frost | [− 1.53, 0.21] | [− 0.71, 0.53] | CL | [− 1.21, 0.04] |
| | | | n-CL | [− 0.53, 0.69] |
| Flood | [− 1.26, 0.66] | [− 0.46, 1.02] | CL | [− 0.42, 0.88] |
| | | | n-CL | [− 0.18, 1.26] |
| b) N% | | | | |
| Rem2cm | [0.04, 0.28] | [− 0.12, 0.05] | CL | [0.12, 0.29] |
| | | | n-CL | [− 0.03, 0.13] |
| Rem70% | [0.06, 0.29] | [− 0.10, 0.07] | CL | [0.06, 0.22] |
| | | | n-CL | [− 0.12, 0.05] |
| Frost | [0.03, 0.26] | [− 0.13, 0.03] | CL | [− 0.05, 0.12] |
| | | | n-CL | [− 0.20, − 0.03] |
| Flood | [0.15, 0.41] | [− 0.01, 0.19] | CL | [0.11, 0.29] |
| | | | n-CL | [− 0.18, 0.01] |
| c) C/N ratio | | | | |
| Rem2cm | [− 0.19, 0.01] | [− 0.02, 0.14] | CL | [− 0.20, − 0.06] |
| | | | n-CL | [− 0.11, 0.04] |
| Rem70% | [− 0.23, − 0.02] | [− 0.06, 0.11] | CL | [− 0.14, 0] |
| | | | n-CL | [− 0.02, 0.12] |
| Frost | [− 0.21, − 0.01] | [− 0.04, 0.13] | CL | [− 0.04, 0.10] |
| | | | n-CL | [0.06, 0.20] |
| Flood | [− 0.34, − 0.11] | [− 0.17, 0.02] | CL | [− 0.19, − 0.04] |
| | | | n-CL | [0.02, 0.20] |
| d) R/S ratio | | | | |
| Rem2cm | [− 0.51, 0.60] | [0.19, 0.61] | CL | [− 0.43, − 0.02] |
| | | | n-CL | [− 0.20, − 0.21] |
| Rem70% | [− 0.37, 0.20] | [0.34, 0.75] | CL | [− 0.02, 0.02] |
| | | | n-CL | [− 0.12, 0.28] |
| Frost | [− 0.35, 0.24] | [0.37, 0.78] | CL | [− 0.25, 0.16] |
| | | | n-CL | [− 0.19, 0.22] |
| Flood | [− 0.64, − 0.02] | [0.06, 0.53] | CL | [− 0.10, 0.35] |
| | | | n-CL | [− 0.42, 0] |

The effects of severe aboveground disturbance (Rem2cm), moderate aboveground disturbance (Rem70%), frost, and flood were tested on a) C content in leaves (C%) b) N content in leaves (N%) c) Ratio of C to N content (C/N ratio) d) Belowground to aboveground biomass ratio (R/S ratio) in CL—clonal and n-CL—non-clonal herbs. The posterior distribution of the parameters or the sum of the parameters (δ_3 , $\delta_1 + \delta_3$, $\delta_2 + \delta_3$, δ_2) of the model (see the text in “Materials and methods”) were inspected, and 95% credible intervals are shown. Biological questions each model tested were: δ_3 —Is the difference between the control and treatment plants the same in clonal versus non-clonal herbs? $\delta_1 + \delta_3$ —Do clonal and non-clonal plants differ in response to disturbance treatments? $\delta_2 + \delta_3$ —Do control and treated clonal plants differ? δ_2 —Do control and treated non-clonal plants differ? Intervals not overlapping zero (in bold) indicate differences

The clonal and non-clonal plants did not differ in terms of compensation for the loss of aboveground biomass after disturbance (Fig. 3; Table 5). Neither the R/S ratio at the time of disturbance nor the actual C/N ratio in leaves had an effect on the compensation ability of any of the studied herbs (Table 5), except for the C/N ratio in the non-clonal herbs.

Discussion

In the experiment, we found that the growth strategies of clonal and non-clonal herbs and their reactions to disturbance are different already during the first year of life, i.e. soon in their ontogeny. However, they are similarly capable of compensating for the loss of aboveground biomass. The R/S ratio and leaf C/N ratio are higher in clonal than in non-clonal herbs. Disturbance changes the leaf C/N ratio in the clonal herbs so that the ratios become more similar between groups. Compensation for the loss of aboveground biomass after disturbance, however, does not differ between clonal and non-clonal herbs. Neither the R/S ratio at the time of disturbance (a proxy for belowground storage) nor the actual leaf C/N ratio (a proxy for photosynthetic efficiency) explains the compensation for the loss of aboveground biomass. Clonal and non-clonal herbs have the same ability of aboveground biomass compensation when disturbed in the first year of their life but use different strategies to attain this goal.

The C/N ratio and R/S ratio of control plants

The C and N elements reflect different yet linked processes in a leaf (acquisition, storage and growth). We found that clonal and non-clonal herbs differed in leaf C/N ratio from

three months of plant age (Fig. 1c; Table 3) and, only N concentration was responsible for this difference (Fig. 1b; Table 3). Clonal plants that have a higher C/N ratio seems to possess more conservative leaf traits with lower photosynthetic efficiency than non-clonal plants in our dataset. A more pronounced decrease in leaf N during ontogeny might indicate a switch from aboveground to belowground investments, for example, the growth of new rhizomes. A higher R/S ratio in clonal than in non-clonal herbs supports this explanation. Alternatively, non-clonal herbs might be more capable of N acquisition than clonal herbs, due to better-developed root system early in ontogeny (Šmilauerová and Šmilauer 2007; Weiser et al. 2016). Nevertheless, different C/N ratio suggests that clonal and non-clonal plants have different strategies already at their early stages of life.

Greater belowground investments and thus larger storage (Chapin et al. 1990) in the clonal group support the idea that the clonal plants are better adapted to a severe disturbance that removes a significant proportion of assimilation organs, as was proposed by Eriksson and Jerling (1990), Eckert (2001), Fischer and van Kleunen (2002), He et al. (2011), and Wilmking et al. (2017). On the other hand, a higher percentage of N in leaves and a lower R/S ratio in the non-clonal group suggests higher aboveground investments and thus presumably an aboveground competitive advantage of non-clonal herbs over clonal ones (Iwasa and Kubo 1997; Kobe 1997; Funk and Wolf 2016).

The C/N ratio and R/S ratio under disturbance

Similar to the conditions without disturbance, in the treated plants, the element responsible for the changes in leaf C/N ratio was N as the leaf C percentage in biomass remained unchanged (Fig. 2a–c; Table 4a–c—S3). While the

Table 5 The effects of clonality and R/S ratio at the time of disturbance and the actual C/N ratio on aboveground biomass compensation

| Parameter | Question | 95% CI |
|---------------------|---|---------------------|
| β_1 | Do clonal and non-clonal herbs differ in biomass compensation in Rem2cm treatment? | [−0.58, 0.36] |
| $\beta_1 + \beta_3$ | Do clonal and non-clonal herbs differ in biomass compensation in Rem70% treatment? | [−0.60, 0.33] |
| $\beta_1 + \beta_3$ | Do clonal and non-clonal herbs differ in biomass compensation in Frost treatment? | [−0.49, 0.45] |
| $\beta_1 + \beta_3$ | Do clonal and non-clonal herbs differ in biomass compensation in Flood treatment? | [−0.06, 0.90] |
| β_7 | Is effect of C/N ratio on biomass compensation different between clonal and non-clonal herbs? | [−1.95, 0.25] |
| β_5 | Is effect of R/S ratio on biomass compensation different between clonal and non-clonal herbs? | [−1.5, 1.43] |
| $\beta_6 + \beta_7$ | Does C/N ratio affect biomass compensation in clonal herbs plants? | [−0.69, 1.11] |
| $\beta_4 + \beta_5$ | Does R/S ratio affect biomass compensation in clonal plants? | [−1.01, 1.23] |
| β_6 | Does C/N ratio affect biomass compensation in non-clonal plants? | [0.13, 2.00] |
| β_4 | Does R/S ratio affect biomass compensation in non-clonal plants? | [−0.98, 1.33] |

An effect of clonality was tested in the following disturbance treatments: severe aboveground disturbance treatment (Rem2cm), moderate aboveground disturbance (Rem70%), frost, and flood (for treatment descriptions, see Table 2). C/N ratio—ratio of C to N content at harvest. R/S ratio—belowground to aboveground biomass ratio at the time of disturbance. The posterior distribution of the model parameters (β_{1-7}) or their sums (see “Materials and methods”) were inspected. Presented are 95% credible intervals. The interval not overlapping zero (in bold) indicates a positive answer to the question

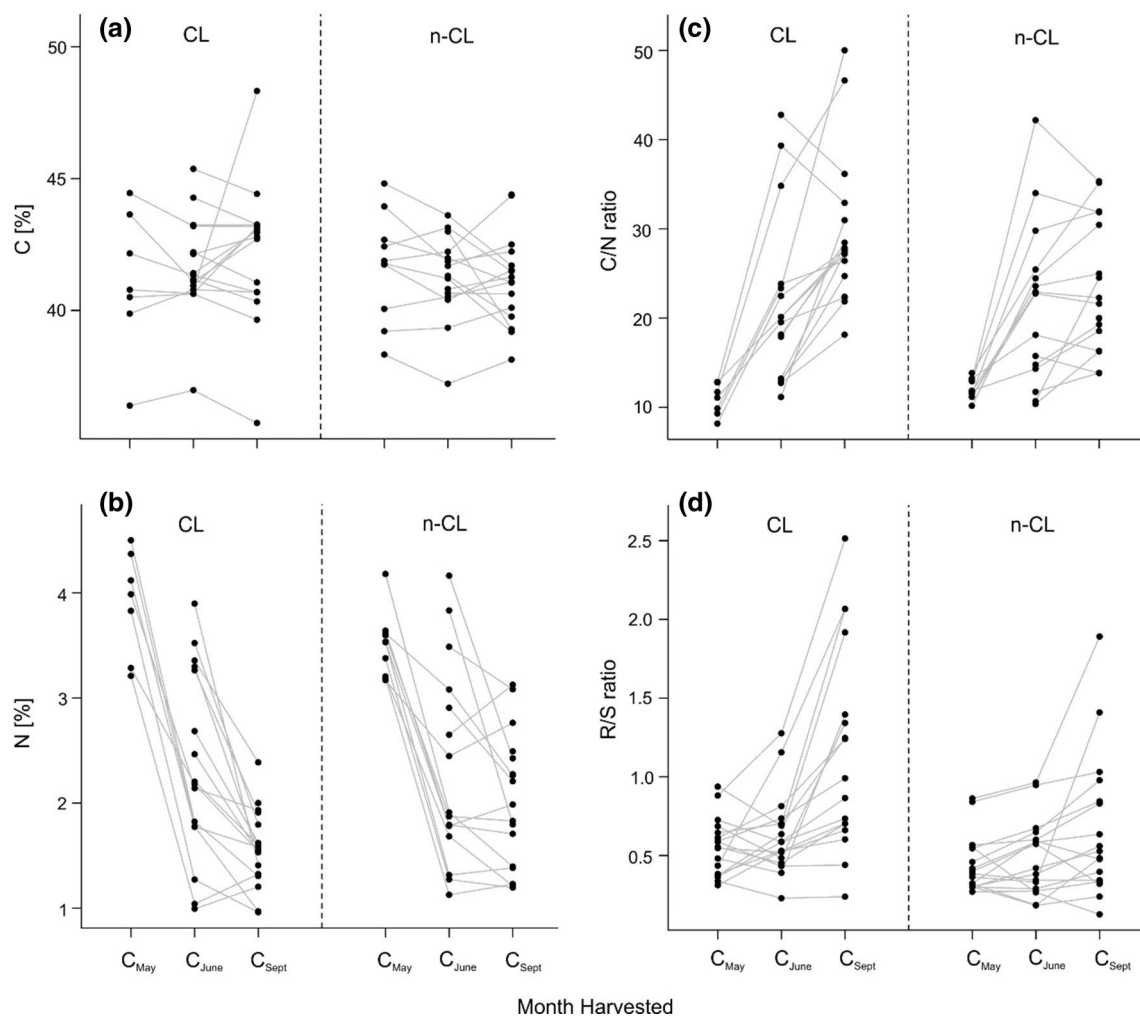


Fig. 1 Trait values in control plants: **a** C content in leaves (C%) **b** N content in leaves (N%) **c** ratio of C to N content (C/N ratio) **d** below-ground to aboveground biomass ratio (R/S ratio) in clonal plants (CL) and non-clonal plants (n-CL) harvested in May, June and September

(C_{May}, C_{June}, C_{Sept}). Black dots are mean values per species. Data for each species is connected by grey line. Some species are missing for some dates because of a low amount of biomass limiting the C and N content analysis. For statistical results, see Table 3

proportion of N markedly increased in the clonal herbs under disturbance, it did not change or decrease in non-clonal herbs (Fig. 2a–c; Table 4a–c— $\delta_2 + \delta_3$, δ_2). This result suggests that clonal and non-clonal plants have opposite strategies. While clonal herbs ‘switch’ from conservative to an acquisitive strategy under disturbance, non-clonal herbs keep the same leaf C/N ratio as before disturbance. The higher N allocation to leaves after disturbance in clonal plants could indicate an adaptation of clonal plants to quickly produce new leaves, restore assimilation capacity and continue with building belowground storage. Kleyer et al. (2012) found that with increasing grazing intensity, the leaf C/N ratio decreases in smaller perennial herbs in comparison with larger ones. Although there is, unfortunately, no distinction between clonal and non-clonal plants in the study of Kleyer et al. (2012), our findings and the results of Kleyer

et al. (2012) suggest that the leaf C/N ratio varies under disturbance among growth forms. The opposite strategies of clonal and non-clonal plants, which are not just present under disturbance, highlight the importance of clonality as a key functional trait in studies looking for general ecological patterns and processes (Herben et al. 2018; Klimešová et al. 2018a, b). Moreover, as is suggested by the economic leaf spectrum (Diaz et al. 2016), leaf N content seems to play a key role in the survival of disturbance, but the relationship deserves further research.

Similar to undisturbed conditions, the R/S ratio of clonal plants was higher than the R/S ratio of non-clonal plants, suggesting the stable belowground investment of clonal plants even after aboveground biomass removal (Fig. 2d). After the disturbance, clonal plants continued to preferentially grow belowground, although considerable investments

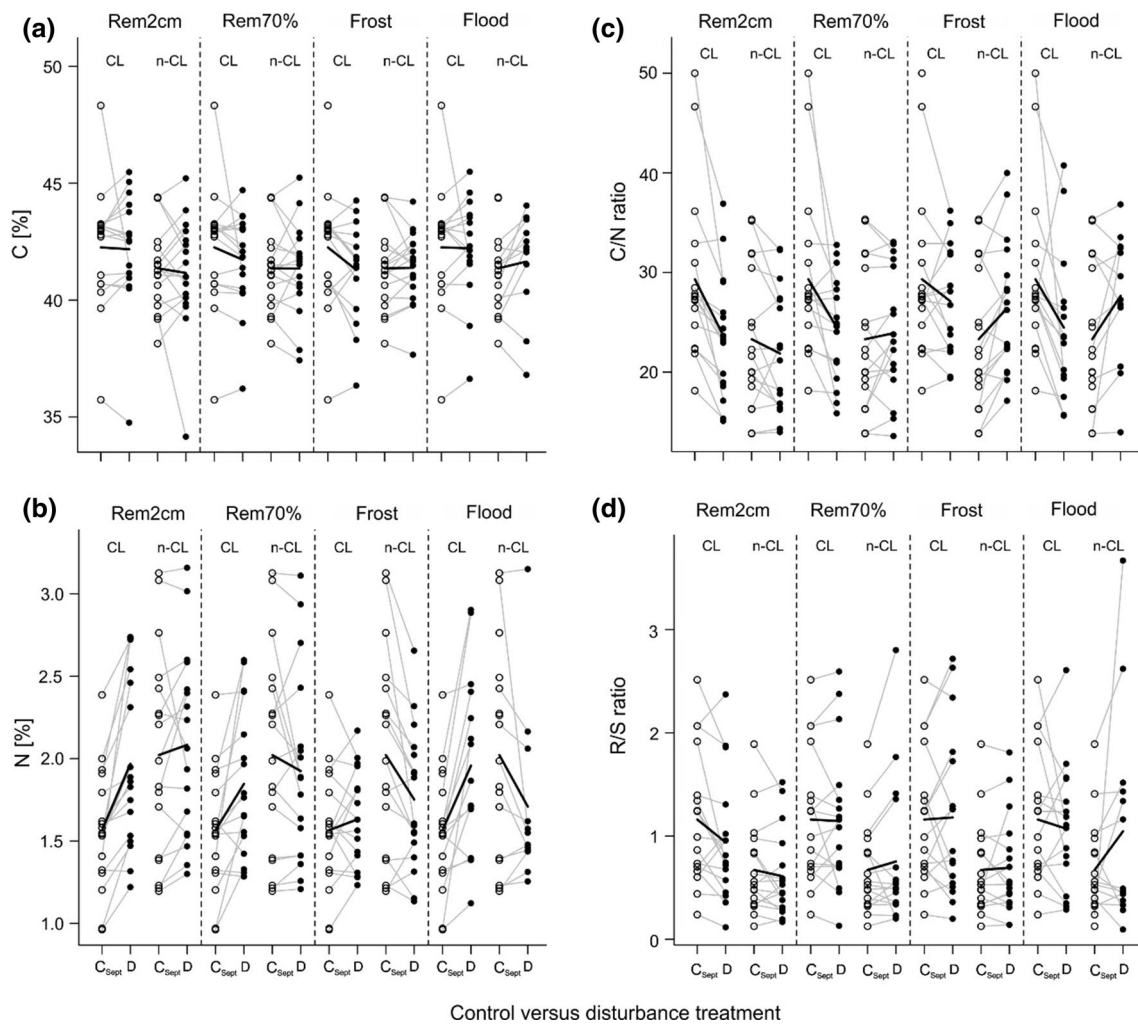


Fig. 2 Effects of disturbance treatments on species traits: **a** C content in leaves (C%) **b** N content in leaves (N%) **c** ratio of C and N content at the time of September harvest (C/N ratio) and **d** belowground to aboveground biomass ratio at the time of September harvest (R/S ratio). Rem2cm—severe aboveground disturbance, Rem70%—moderate aboveground disturbance, frost and flooding (for descriptions of the disturbance treatments, see Table 2). CL clonal plants, n-CL

non-clonal plants, C_{Sept} non-disturbed control plants harvested in September, D plants under disturbance treatment. White dots represent means for species in the control group, and black dots represent means for species under treatment. Data for each species is connected by grey line. Black lines connect the means for all species in each group (control and treatment). For statistical results, see Table 4

in the regrowth of aboveground organs were required. This fact supports not only the hypothesis that clonal plants are better adapted to disturbance but that they are also possibly better prepared for more frequent or repeated disturbances (Meijden et al. 2000).

Aboveground biomass compensation

Surprisingly, the clonal and non-clonal herbs compensated for the loss of aboveground biomass to the same extent, and neither the difference in the actual leaf C/N ratio nor in the R/S ratio at the time of disturbance had an effect on the compensation after disturbance (except for the non-clonal plants and the C/N ratio) (Table 5). Although clonal herbs seem to

have an advantage over non-clonal herbs in terms of larger belowground biomass, non-clonal herbs are similarly capable of compensating for the loss of aboveground biomass under disturbance, at least during their first year of life. The ability to regrow biomass is closely related to the plant's amount of reserves (Chapin et al. 1990; Klimešová and Klimeš 2007; Clarke et al. 2013). It seems that building belowground biomass has some cost that, even though the reserves of clonal herbs might be higher than those of non-clonal herbs, does not allow clonal herbs to regrow aboveground biomass to a higher extent than non-clonal herbs. Alternatively, the reason for the similar extent of compensation could be the readiness of clonal plants for repeated disturbances (Ivasa and Kubo 1997; Meijden et al. 2000; Herben et al. 2018). Clonal plants

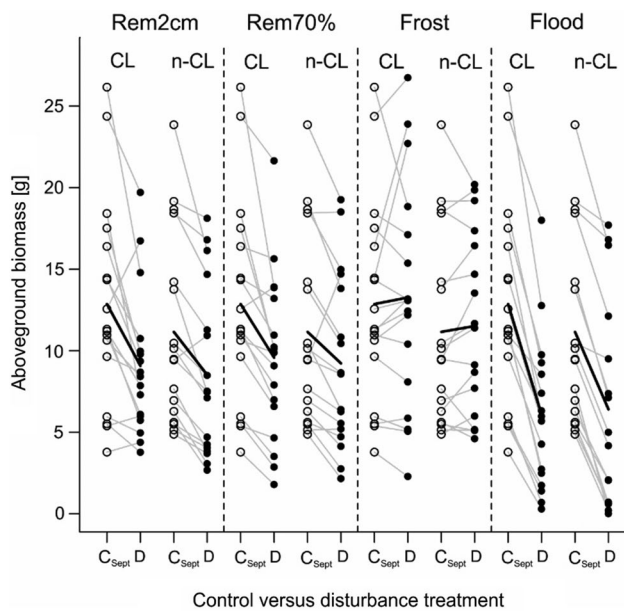


Fig. 3 Effects of disturbance treatments on aboveground biomass. *CL* clonal plants, *n-CL* non-clonal plants, *C_{Sept}* non-disturbed control plants harvested in September, *D* plants under disturbance treatment. White dots represent means for species in the control group, and black dots represent means for species under treatment. Data for each species is connected by grey line. Black lines connect the means for all species in each group (control and treatment). The aboveground biomass of treated plants after accounting for the biomass of control plants was interpreted as the compensation ability of plants, and the effects of clonality, R/S ratio at the time of disturbance and actual C/N ratio on compensation ability were inspected (for details of the model see “Materials and methods”; for statistical results see Table 5)

probably use only the amount of reserves required to restore aboveground biomass and remain competitively efficient, but they are still capable of easily overcoming another disturbance. Testing the effect of repeated disturbance with defined frequency on clonal and non-clonal herbs is necessary to support this idea.

Although our experiment was performed on young plants, some of them had already flowered and set seeds and, in the case of clonal ones, started to produce rhizomes. However, their belowground organs were not as developed as those of the plants in the field, which are usually older. The building of belowground organs, such as rhizomes or storage roots, is a process spanning months or years (Klimešová and Klimeš 2008). Nevertheless, when young and still unitary, the clonal plants are equally capable of coping with disturbance as non-clonal ones.

Conclusions

Our results suggest that even though growth/investment strategies of clonal and non-clonal plants are markedly different, both groups are similarly capable of compensating for

the loss of aboveground biomass under disturbance at their early stages of life. The ability of clonal plants to ‘switch’ from storage to growth when injured and generally large investment into the belowground system might suggest that they have the advantage under disturbance. On the other hand, the more intensive aboveground growth of non-clonal plants might reflect their potential aboveground competitive advantage over clonal plants. The different strategies of each group might lead to an equal probability of establishing clonal and non-clonal herbs in grasslands and pastures, which are typical habitats in the simultaneous action of competition and disturbance. However, this hypothesis needs to be tested.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* 89:409–416. <https://doi.org/10.1034/j.1600-0706.2000.890224.x>
- Belsky AJ (1986) Does herbivory benefit plants? A review of the evidence. *Am Nat* 127:870–892
- Bessler H, Temperton VM, Roscher C, Buchmann N, Schmid B, Schulze ED, Weisser WW, Engles C (2009) Aboveground overyielding in grassland mixtures is associated with reduced biomass partitioning to belowground organs. *Ecology* 90:1520–1530. <https://doi.org/10.1890/08-0867.1>
- Canadell J, Zedler PH (1995) Ecology and biogeography of Mediterranean ecosystems in Chile. Springer, New York
- Carpenter B, Gelman A, Hoffman MD, Lee D, Goodrich B, Betancourt M, Brubaker M, Guo J, Li P, Riddell A (2017) Stan: a probabilistic programming language. *J Stat Softw* 76:1–32. <https://doi.org/10.18637/jss.v076.i01>
- Chapin FS, Schulze E, Mooney HA (1990) The ecology and economics of storage in plants. *Annu Rev Ecol Syst* 21:423–447. <https://doi.org/10.1146/annurev.es.21.110190.0022>
- Clarke PJ, Knox KJE (2009) Trade-offs in resource allocation that favour resprouting affect the competitive ability of woody seedlings in grassy communities. *J Ecol* 97:1374–1382. <https://doi.org/10.1111/j.1365-2745.2009.01556.x>
- Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE (2013) Resprouting as a key functional

- trait: how buds, protection and resources drive persistence after fire. *New Phytol* 197:19–35. <https://doi.org/10.1111/nph.12001>
- Diaz S, Kattge J, Cornelissen HC, Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Gillison AN, Zanne AE, Chave J, Wright SJ, Sheremet'ev SN, Jactel H, Baraloto C, Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A, Falczuk V, Rüger N, Mahecha MD, Gorné L (2016) The global spectrum of plant form and function. *Nature* 529:167–171. <https://doi.org/10.1038/nature16489>
- Eckert CG (2001) The loss of sex in clonal plants. *Evol Ecol* 15:4–6. <https://doi.org/10.1023/A:1016005519651>
- Enquist BJ, Niklas KJ (2002) Global allocation rules for patterns of biomass partitioning in seed plant. *Science* 295:1517–1520. <https://doi.org/10.1126/science.1066360>
- Eriksson O (1997) Evolution of seed dispersal and recruitment in clonal plants. *Oikos* 63:439–448. <https://doi.org/10.2307/3544970>
- Eriksson O, Jerling L (1990) Hierarchical selection and risk spreading in clonal plants. In: van Groenendael J, de Kroon H (eds) *Clonal growth in plants: regulation and function*. SPB Academic Publishing, Hague, pp 79–94
- Fidelis A, Appezzato da Gloria B, Pillar VD, Pfadenhauer J (2014) Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands? *Flora* 209:110–116. <https://doi.org/10.1016/j.flora.2013.12.003>
- Fischer M, van Kleunen M (2002) On the evolution of clonal plant life histories. *Evol Ecol* 15:565–582. <https://doi.org/10.1023/A:1016013721469>
- Funk JL, Wolf AA (2016) Testing the trait-based community framework: do functional traits predict competitive outcomes? *Ecology* 97:2206–2211. <https://doi.org/10.1002/ecy.1484>
- Grechi I, Vivin P, Hilbert G, Milin S, Robert T, Gaudillere JP (2007) Effect of light and nitrogen supply on internal C:N balance and control of root-to-shoot biomass allocation in grapevine. *Environ Exp Bot* 59:139–149. <https://doi.org/10.1016/j.envexpbot.2005.11.002>
- Grime JP (1979) *Plant strategies and vegetation processes*. Wiley, Chichester
- Groff PA, Kaplan DR (1988) The relation of root systems to shoot systems in vascular plants. *Bot Rev* 54:387–422. <https://doi.org/10.1007/BF02858417>
- Guo H, Xu B, Wu Y, Shi F, Wu C, Wu N (2016) Allometric partitioning theory versus optimal partitioning theory: the adjustment of biomass allocation and internal C–N balance to shading and nitrogen addition in *Fritillaria unibracteata* (Liliaceae). *Pol J Ecol* 64:189–199. <https://doi.org/10.3161/15052249PJE2016.64.2.004>
- Harper JL (1977) *Population biology of plants*. Academic Press, New York, NY
- He T, Lamont BB, Downes KS (2011) *Banksia* born to burn. *New Phytol* 191:184–196. <https://doi.org/10.1111/j.1469-8137.2011.03663.x>
- Herben T, Klimešová J (2020) Evolution of clonal growth forms in angiosperms. *New Phytol* 225:999–1010. <https://doi.org/10.1111/nph.16188>
- Herben T, Šerá B, Klimešová J (2015) Clonal growth and sexual reproduction: tradeoffs and environmental constraints. *Oikos* 124:469–479. <https://doi.org/10.1111/oik.01692>
- Herben T, Klimešová J, Chytrý M (2018) Effects of disturbance frequency and severity on plant traits: an assessment across a temperate flora. *Funct Ecol* 32:799–808. <https://doi.org/10.1111/1365-2435.13011>
- Higgins SI, Flores O, Schurr FM (2008) Costs of persistence and the spread of competing seeders and sprouters. *J Ecol* 96:679–686. <https://doi.org/10.1111/j.1365-2745.2008.01391.x>
- Hoffman MD, Gelman A (2014) The No-U-Turn sampler: adaptively setting path lengths in Hamiltonian Monte Carlo. *J Mach Learn Res* 4:1–30
- Irving LJ (2015) Carbon assimilation, biomass partitioning and productivity in grasses. *Agriculture* 5:1116–1134. <https://doi.org/10.3390/agriculture5041116>
- Iwasa Y, Kubo T (1997) Optimal size of storage for recovery after unpredictable disturbances. *Evol Ecol* 11:45–65. <https://doi.org/10.1023/A:1018483429029>
- Janeček Š, Patáčková E, Klimešová J (2014) Effects of fertilization and competition on plant biomass allocation and internal resources: does *Plantago lanceolata* follow the rules of economic theory? *Folia Geobot* 46:49–64. <https://doi.org/10.1007/s12224-013-9161-5>
- Kleyer M, Dray S, de Bello F, Lepš J, Pakeman RJ, Strauss B, Thuiller W, Lavorel S (2012) Assessing species and community functional responses to environmental gradients: which multivariate methods? *J Veg Sci* 23:805–821. <https://doi.org/10.1111/j.1654-1103.2012.01402>
- Klimeš L, Klimešová J, Hendriks R, van Groenendael J (1997) Clonal plant architecture: a comparative analysis of form and function. In: de Kroon H, van Groenendael J (eds) *The ecology and evolution of clonal plants*. Backhuys Publishers, Leiden, pp 1–29
- Klimešová J, Klimeš L (2007) Bud banks and their role in vegetative regeneration—a literature review and proposal for simple classification and assessment. *Perspect Plant Ecol* 8:115–129. <https://doi.org/10.1016/j.ppees.2006.10.002>
- Klimešová J, Klimeš L (2008) Clonal growth diversity and bud banks of plants in the Czech flora: an evaluation using the CLO-PLA3 database. *Preslia* 80:255–275
- Klimešová J, Martínková J, Herben T (2018a) Horizontal growth: an overlooked dimension in plant trait space. *Perspect Plant Ecol* 323:18–21. <https://doi.org/10.1016/j.ppees.2018.02.002>
- Klimešová J, Martínková J, Ottaviani G (2018b) Belowground plant functional ecology: towards an integrated perspective. *Funct Ecol* 32:2115–2126. <https://doi.org/10.1111/1365-2435.13145>
- Knox KJE, Clark PJ (2005) Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. *Funct Ecol* 19:690–698. <https://doi.org/10.1111/j.1365-2435.2005.01006.x>
- Kobe RK (1997) Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos* 80:226–233. <https://doi.org/10.2307/3546590>
- Kobe RK, Iyer M, Walters MB (2010) Optimal partitioning theory revisited: non-structural carbohydrates dominate root mass responses to nitrogen. *Ecology* 91:166–179. <https://doi.org/10.1890/09-0027.1>
- Latanzi FA, Schnyder H, Thornton B (2005) The sources of carbon and nitrogen supplying leaf growth. Assessment of the role of stores with compartmental models. *Plant Physiol* 137:383–439. <https://doi.org/10.1104/pp.104.051375>
- Latzel V, Janeček Š, Hájek T, Klimešová J (2014) Biomass and stored carbohydrate compensation after above-ground biomass removal in a perennial herb: does environmental productivity play a role? *Folia Geobot* 49:17–29. <https://doi.org/10.1007/s12224-013-9162-4>
- Lawes MJ, Clark PJ (2011) Ecology of plant resprouting: populations to community responses in fire-prone ecosystems. *Plant Ecol* 212:1937–1943. <https://doi.org/10.1007/s11258-011-9994-z>
- Lehtila K (2000) Modelling compensatory regrowth with bud dormancy and gradual activation of buds. *Evol Ecol* 14:315–330. <https://doi.org/10.1023/A:1010869605855>
- Mašková T, Herben T (2018) Root:shoot ratio in developing seedlings: how seedlings change their allocation in response to seed mass and ambient nutrient supply. *Ecol Evol* 8:7143–7150. <https://doi.org/10.1002/ece3.42381>

- Meijden E, de Boer NJ, Van Der Veen-Van Wijk CAM (2000) Pattern of storage and regrowth in ragwort. *Evol Ecol* 14:439–455. <https://doi.org/10.1023/A:1010985028360>
- Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root:shoot ratios in terrestrial biomes. *Glob Change Biol* 12:84–96. <https://doi.org/10.1111/j.1365-2486.2005.001043.x>
- Moore NA, Camac JS, Morgan JW (2018) Effects of drought and fire on resprouting capacity of 52 temperate Australian perennial native grasses. *New Phytol* 221:1424–1433. <https://doi.org/10.1111/nph.15480>
- Nzunda EF, Griffiths ME, Lawes MJ (2014) Resource allocation and storage relative to resprouting ability in wind disturbed coastal forest trees. *Evol Ecol* 28:735–749. <https://doi.org/10.1007/s10682-014-9698-7>
- Ottaviani G, Martínková J, Herben T, Pausas JG, Klimešová J (2017) On plant modularity traits: functions and challenges. *Trends Plant Sci* 22:648–651. <https://doi.org/10.1016/j.tplants.2017.05.010>
- Paula S, Ojeda F (2009) Belowground starch consumption after recurrent severe disturbance in three resprouter species of the genus *Erica*. *Botany* 87:253–259. <https://doi.org/10.1139/B08-134>
- Pausas JG, Keeley JE (2014) Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytol* 204:55–65. <https://doi.org/10.1111/nph.12921>
- Pausas JG, Lamont BB, Paula S, da Gloria BA, Fidelis A (2018) Unearthing belowground bud banks in fire-prone ecosystems. *New Phytol* 217:1435–1448. <https://doi.org/10.1111/nph.14982>
- R Core Team (2016) R: a language and environment for statistical computing, R Foundation for Statistical Computing, Vienna. <https://www.r-project.org/>. Accessed 13 July 2019
- Sardans J, Rivas-Ubach A, Penuelas J (2012) The C:N: P stoichiometry of organisms and ecosystems in a changing world: a review and perspectives. *Perspect Plant Ecol* 14:33–47. <https://doi.org/10.1016/j.ppees.2011.08.002>
- Silvertown J, Franco M, Pisanty I, Mendoza A (1993) Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J Ecol* 81:465–476. <https://doi.org/10.2307/2261525>
- Šmilauerová M, Šmilauer P (2007) What youngsters say about adults: seedling roots reflect clonal traits of adult plants. *J Ecol* 95:406–413. <https://doi.org/10.1111/j.1365-2745.2007.01218.x>
- Suzuki JI, Stuefer JF (1999) On the ecological and evolutionary significance of storage in clonal plants. *Plant Spec Biol* 14:11–17. <https://doi.org/10.1046/j.1442-1984.1999.00002.x>
- Stan Development Team (2018) RStan: the R interface to Stan. R package. <https://mc-stan.org/>. Accessed 13 July 2019
- van Groenendael J, de Kroon H (1990) Clonal growth in plants: regulation and function. SPB Academic Publishing, Hague
- Vesk PA, Westoby M (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. *J Ecol* 92:310–320. <https://doi.org/10.1111/j.0022-0477.2004.00871.x>
- Weiser M, Koubek T, Herben T (2016) Root foraging performance and life-history traits. *Front Plant Sci* 7:779. <https://doi.org/10.3389/fpls.2016.00779>
- Wilmking M, Buras A, Eusemann P, Schnittler M, Trouillier M, Würth D, Lange J, van der Maaten-Theunissen M, Juday GP (2017) High frequency growth variability of White spruce clones does not differ from non-clonal trees at Alaskan treelines. *Dendrochronologia* 44:187–192. <https://doi.org/10.1016/j.dendro.2017.05.005>
- Wise MJ, Abrahamson WG (2007) Effects of resource availability on tolerance to herbivory: a review and assessment of three opposing models. *Am Nat* 169:443–454. <https://doi.org/10.1086/51204407>
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lus C, Midgley JJ, Nava ML, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economic spectrum. *Nature* 428:821–827. <https://doi.org/10.1038/nature02403>
- Yang Y, Luo Y (2011) Carbon: nitrogen stoichiometry in forest ecosystems during stand development. *Global Ecol Biogeogr* 20:354–361. <https://doi.org/10.1111/j.1466-8238.2010.00602.x>
- Younginger BS, Sirová D, Cruzan MB, Ballhorn DJ (2017) Is biomass a reliable estimate of plant fitness? *Appl Plant Sci* 5:1600094. <https://doi.org/10.3732/apps.1600094>