



Growth, root respiration and photosynthesis of a root-sprouting short-lived herb after severe biomass removal

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ABSTRACT

The predominance of short-lived species in disturbed habitats supports the view that generative regeneration is an advantageous strategy under these conditions. However, there are short-lived species that survive the destruction of aboveground biomass and resprout from roots. Yet, there is only limited knowledge on the effect of injury on the plant growth of individuals regrowing from roots, and nearly no research has been conducted on the physiological regulation of root-sprouting.

We experimentally tested the effect of total shoot biomass removal on the growth, root respiration and photosynthesis of the short-lived, root-sprouting herb *Barbarea vulgaris* (Brassicaceae) to assess the efficiency and importance of the root sprouting ability.

Regenerating plants compensated for the loss of photosynthetic area by producing a higher number of leaves with higher SLA, but we did not observe compensatory photosynthesis, which could potentially counterbalance the loss of photosynthetic area and allow accelerated growth. The root respiration rate significantly decreased immediately after injury and then slightly and consequentially increased. The belowground biomass of the injured plants decreased by more than four times a month after the injury comparing to the biomass measured immediately after the disturbance. This result suggests the intensive consumption of reserves located in roots, although the root respiration values did not indicate it.

Although we found physiological constraints that limited more vigorous resprouting, we conclude that the root-sprouting ability of short-lived species represents a useful strategy for population persistence in frequently disturbed habitats, in places lacking seed banks or when disturbances occur during less-than-suitable germination conditions.

Introduction

Disturbances are one of the strongest selective factors and are defined as mechanisms causing partial or total destruction of plant biomass (Silvertown and Lovett-Doust, 1993; Grime, 2001; Herben et al., 2017; McLauchan et al., 2020). The predominance of short-lived species in highly disturbed habitats supports the view that short life cycles, fast maturation rates, and high production of small seeds are advantageous strategies for plant populations under these conditions, whereas individual vegetative regeneration is not beneficial under the same conditions (Bellingham and Sparrow, 2000; Grime, 2001; Clarke et al., 2015). However, there are short-lived species that can survive the destruction of their aboveground biomass or even root fragmentation

(Klimešová et al., 2014; Sosnová et al., 2014; Martínková and Klimešová, 2016). These short-lived species do not rely only on seed banks, and vegetative regeneration after disturbance might play an important role in population persistence, similar to populations of perennial herbs.

The positioning and utilization of axillary buds define a plant's growth form and thus predetermine the extent of the tolerance of the plant to disturbance (Bellingham and Sparrow, 2000; Del Tredici, 2001; Huhta et al., 2003; Clarke et al. 2013; Clarke et al., 2015; Wigley et al., 2020). From this point of view, the most disturbance-tolerant species are clonal perennial herbs with belowground stem origin organs, such as rhizomes or perennial non-clonal herbs with buds located below the soil surface (Clarke et al. 2013; Ott et al., 2019), while the most sensitive

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herbs to disturbance are those lacking either belowground or basal axillary buds (e.g., erosulate annuals; Huhata et al., 2003). These plants tolerate only mild disturbances, such as the clipping of branches or apical meristem removal. Nevertheless, there are short-lived herbs that regenerate after severe disturbances in which all axillary buds are removed or even after root system fragmentation (Martínková et al., 2006, Martínková et al., 2016 a,b). This regenerative strategy is enabled by the resprouting of the plants from adventitious buds on the roots (Rauh, 1937; Bartušková et al., 2017). The extent of this ability varies among species and is influenced by several internal factors of the injured plant, e.g., its age, life-cycle phase, life-cycle mode, and stored reserves, as well as by external factors such as the severity and frequency of disturbance and the nutrient availability (Klímešová and Martínková, 2004; Malíková et al., 2010; Martínková et al., 2015; Martínková and Klímešová, 2016, Martínková et al., 2016). Root-sprouting (RS) species seem to have an evolutionary advantage over non-RS species in disturbed habitats where the benefits of root-sprouting abilities exceed the costs (Klímešová et al., 2017).

Even though competitive ability and related plant size are less important for short-lived species in ruderal habitats than, for example, for perennial plants in meadows (Grime, 2001; Semchenko et al., 2018; Liu et al. 2021), prompt biomass regrowth is a key prerequisite for the formation of sufficient carbohydrate storage with which to complete generative reproduction before the next disturbance event occurs (Iwasa and Kubo, 1997). Moreover, RS ability, i.e., vegetative regeneration from roots, might not be as limited by environmental conditions as the restoration of populations from seeds because germination is frequently driven by specific requirements (Baskin and Baskin, 2004; Sosnová et al., 2014). However, the regrowth of damaged aboveground biomass in RS species requires: first, the de novo formation of root buds or the initiation of existing buds, and the second, the mobilization of carbon reserves stored in intact roots allows the growth of new leaves that, consequentially, produce assimilates for the formation of the stores necessary for triggering seed production. The fast regrowth of leaves with higher specific leaf areas (SLAs) (McNaughton, 1985; Wright et al., 2004; Reich, 2014), increased root respiration rates (R_{root}) signalling the intensified usage of root reserves and a maximized leaf area-based rates of photosynthesis following an injury might thus confer the prompt and fast regrowth of biomass and minimize the loss of fitness caused by the injury (Aubrey et al., 2012; Salomón et al., 2015; Smith et al., 2016).

Although the RS strategy might be an adaptive and advantageous strategy in disturbed habitats, there is still only limited knowledge on the effect of total shoot biomass removal on the growth characteristics of individuals regrown from roots, and nearly no research has been conducted on the physiological regulation mechanisms behind it. In this study, we tested the effects of total shoot biomass removal on the growth characteristics, root respiration and photosynthetic parameters of the short-lived root-sprouting herb *Barbarea vulgaris* (Brassicaceae). Our goal was to assess the importance of RS for population persistence by comparing the growth characteristics of regenerating plants and seedlings and, thus, to identify the possible advantage of vegetative regeneration over germination from seeds after a disturbance. The next goal is to determine whether severe injury to a plant body leads to increased root respiration and leaf photosynthesis and how plant characteristics (e.g., the amount of biomass, SLA, root:shoot ratio (R:S ratio)) are influenced. We hypothesize that aboveground biomass removal will induce the mobilization of root energy reserves (detected by increased root respiration rates as a measure of the energy metabolism intensity), which will result in the faster development of new leaves with higher SLAs to maximize the photosynthetically active area. The leaves will then rapidly reach the maximum light-use efficiency and photosynthetic rate to compensate for the biomass and storage losses. The fast rebuilding of the photosynthetic area together with the utilization of root reserves will lead to a quick return to the values of the R:S ratio measured before shoot biomass removal.

Materials and methods

Growth experiment

For the experiment, we selected model biennial/short-lived perennial root-sprouting herb *Barbarea vulgaris* R.Br. (Brassicaceae) (MacDonald and Cavers, 1991; Dvořák, 1992; Klímešová et al., 2007). Seeds of *B. vulgaris* originating from a local natural population (GPS coordinates: 48.9737 N, 14.4561 E) and stored under dry laboratory conditions in paper bags over winter were germinated on wet sand in Petri dishes under controlled conditions in a growth chamber (light/dark: 15/9 h, 23/10 °C and 70/90% relative air humidity; PAR irradiance of fluorescence light: 184 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The seeds germinated 5–8 days after sowing. Seedlings of the same size and age were transplanted to plastic pots with volumes of 0.75 L filled with washed sand, and one seedling was planted per pot. The pots were transferred to the growth chamber, and all plants were grown under the same conditions. A standard NPK liquid solution (0.1/0.5/0.07 g N, P or K, respectively, per kg of wet sand) was used for nutrient supply every three weeks, and the plants were watered with tap water when necessary. After transplantation to the pots, in one-week steps, always five plants (five pots) were harvested and measured, and calculations of the following characteristics were assessed: the number of mature leaves, shoot and root dry biomass (dried at 50 °C), root to shoot ratio (R:S ratio), total leaf area, specific leaf area (SLA; Pérez-Harguindeguy et al., 2013), and root respiration rate and leaf photosynthetic parameters (for details on last two parameters see below).

At the age of six weeks, i.e. after six subsequent measurements at one-week steps, all aboveground biomass with all axillary buds was removed in half of the plants, so the injured plants could regenerate only from adventitious root buds. A six-week growth period was chosen considering the information that plants of *Rorippa palustris* (Brassicaceae, relative species with similar ecology) have 100% probability of successful root sprouting after injury at ages greater than six weeks (Martínková et al., 2004). The other half of the plants were not injured and served as controls. Each week after the injury, five injured plants (five pots) and five control plants were harvested and measured, and the same characteristics as those listed before were calculated. The measurements were repeated every week for six more weeks. Therefore, we obtained information on plant characteristics from one to twelve weeks of age for the control plants and from seven to twelve weeks of age for the injured plants, which were injured at the age of six weeks.

Root respiration

A criterion of root metabolic activity, the root aerobic respiration rate was measured in five experimental control plants and in five injured plants every week. For single measurements, the whole root systems were used for the smaller plants; for larger plants, halves of their root systems were measured in parallel (fresh mass, FM, 33–1750 mg). The oxygen-based respiration rates of the roots were measured using a Clark-type O_2 sensor and a chart pen recorder in a 10-fold diluted mineral nutrient solution (pH ca. 4.9) in an 8.6-mL or 40-mL stirred thermostatted chamber at 20.0 ± 0.1 °C in darkness (see, for details, Adamec, 2002 and 2005). Each measurement lasted 15–20 min, and the O_2 concentration was approx. 60–90% during the measurements. The FM and dry mass (DM, 80 °C) of the measured roots were estimated. The values of the aerobic respiration rates of the roots were expressed in $\text{nmol O}_2 \text{g}^{-1} \text{s}^{-1}$. The data collected for halved roots were averaged using weighted means.

Photosynthetic parameters

We constructed light response curves of the net photosynthetic rates (P_n) using LI-6400 portable gas exchange system (LI-COR, USA) equipped with a built-in red LED light source to evaluate the photosynthetic

parameters. The measurements were performed on the morning of every sampling day on a single leaf of each plant immediately after removing the plant from the growth chamber. We selected fully developed young leaves that were large enough to cover at least half the area of the standard 3 × 2-cm gas exchange chamber. The leaves were first acclimated at an irradiance of 1000 μmol m⁻² s⁻¹ for approximately 5 min until steady photosynthesis was achieved. Then, we gradually reduced the PAR irradiance in steps of 800, 600, 400, 200, 100, 50, and 25 μmol m⁻² s⁻¹ down to 0 μmol m⁻² s⁻¹, at which the leaf dark respiration (R_d) was recorded. Gas-exchange equilibration at each irradiance level took 60–120 s. The leaf temperature was maintained at 20 ± 1 °C, and the CO₂ concentration in the incoming air was 400 ppm.

Data analysis

CO₂ assimilation was expressed per unit of leaf area. We used the modified rectangular hyperbola equation to describe the light response of the net photosynthetic rate (P_n; μmol m⁻² s⁻¹) as follows:

$$P_n = \frac{\alpha \times I \times P_{max}}{\sqrt{\alpha^2 \times I^2 + P_{max}^2}} - R_d$$

where P_{max} is the maximum (asymptotic) rate of photosynthesis, R_d is the dark respiration rate, α is the maximum quantum yield (light-use efficiency) of photosynthesis (i.e., mols of assimilated CO₂ per mol of photosynthetically active radiation, PAR) and I is the irradiance in μmol (PAR) m⁻² s⁻¹.

Next, we applied Student's t-test to the independent samples to compare the means of the measured characteristics between the control and injured plants. We compared i) injured plants and controls of the same age (i.e., injured plants vs. controls at t₇₋₁₂) and also ii) injured plants and six-week-younger controls (i.e., injured plants vs. controls at t₁₋₆) (see Figs. 1, 2) to analyse whether growth characteristics of injured plants and trait trends in time correspond with i) those of controls of the same age or ii) those of six-week-younger controls.

A correlation table and Pearson's coefficient (Table 1) were used to highlight relationships among growth characteristics, root respiration and photosynthetic parameters.

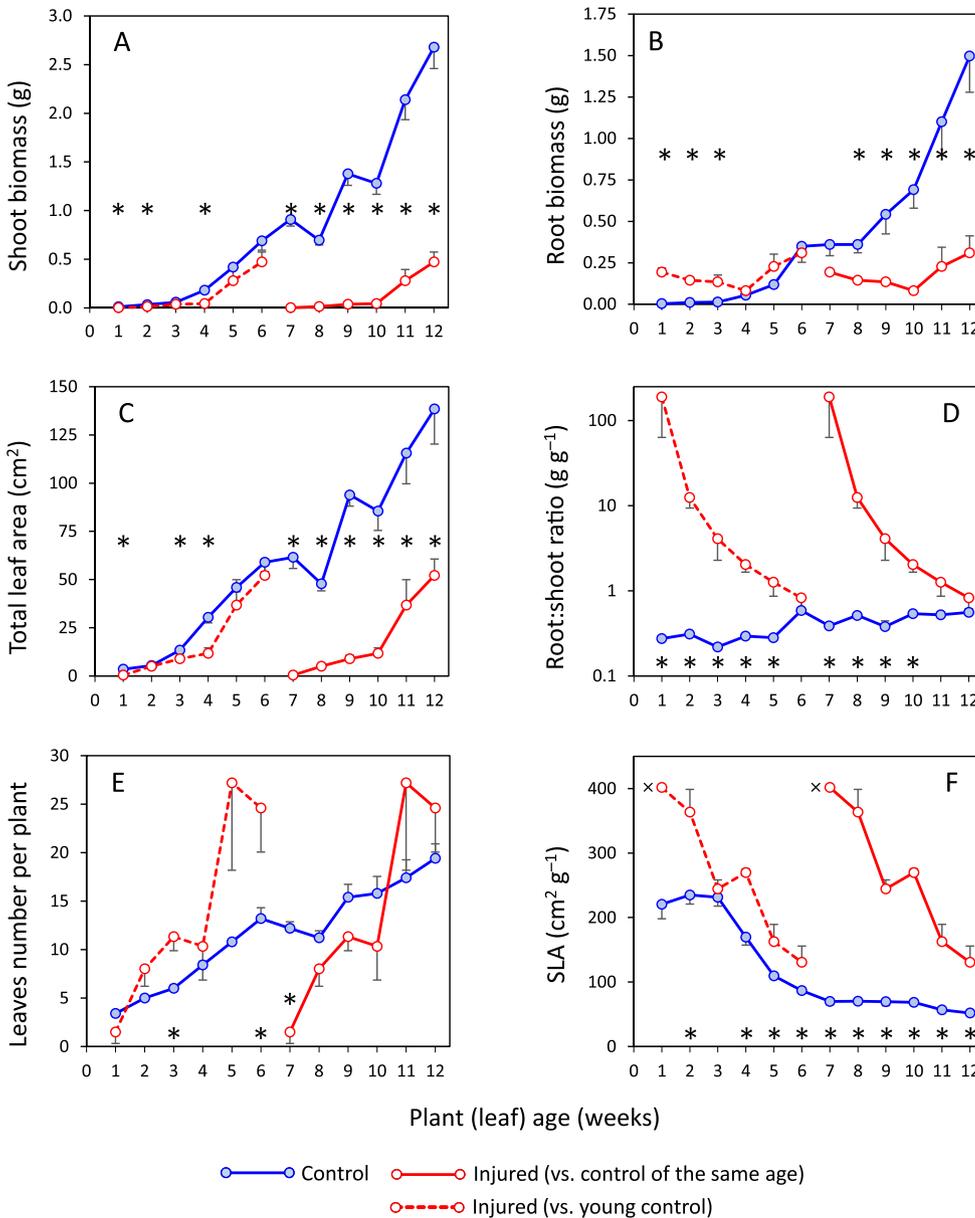


Fig. 1. Growth characteristics of *Barbarea vulgaris* plants measured for 12 weeks after the transplantation of three-day-old seedlings. Half of the plants acted as controls (blue full line), and the other half of the plants were injured (aboveground biomass was removed) at the age of six weeks (red full line). Each group was harvested every week for 12 weeks (control plants) or six weeks (injured plants). The courses of the injured plants are compared with i) same-aged cohorts (red full line) and ii) young, uninjured control plants (weeks 1 to 6, red dashed line). * – statistically significant difference between the control and injured plants (P < 0.05, t-test). Means ± s.e. are shown; × – indicates single observation.

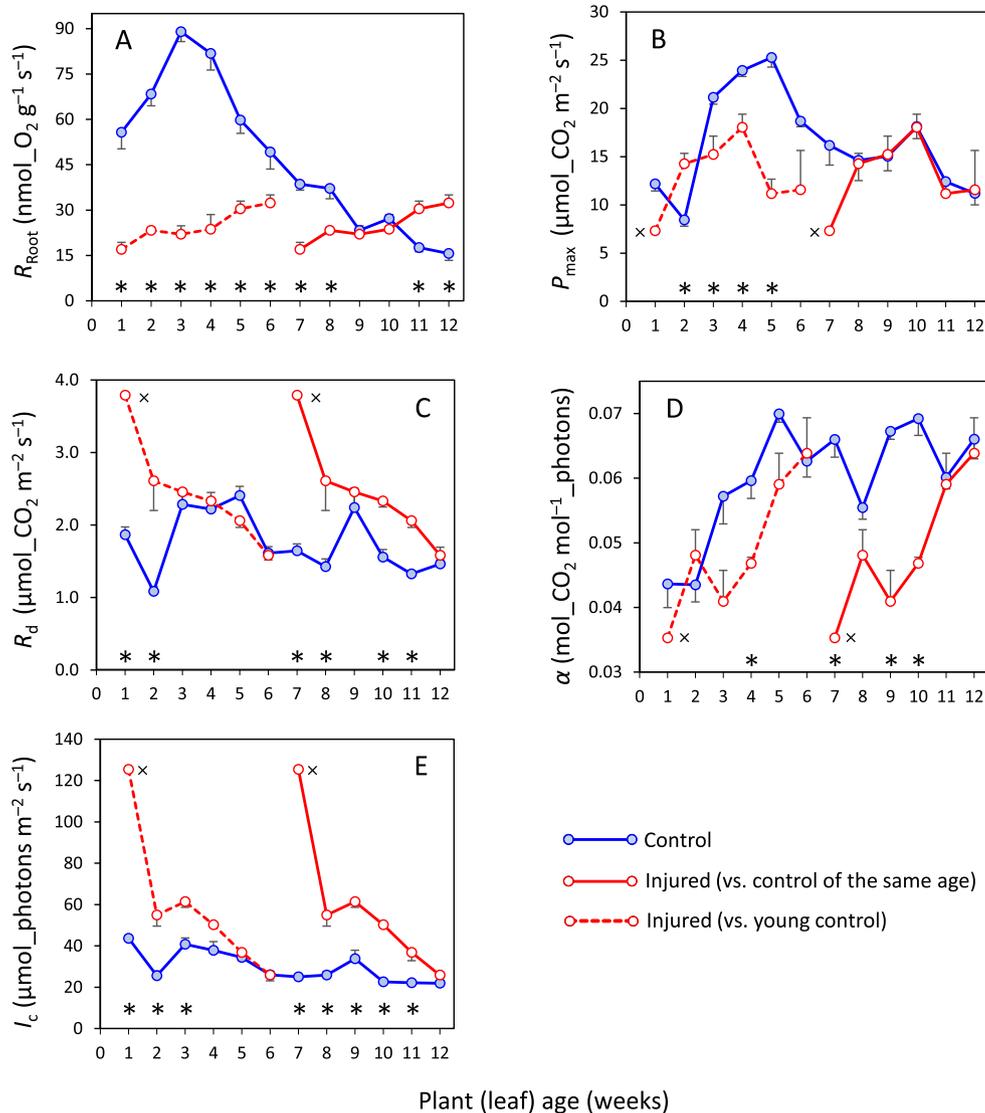


Fig. 2. Physiological characteristics of *Barbarea vulgaris* plants measured for 12 weeks after the transplantation of three-day-old seedlings. Half of the plants acted as controls (blue full line), and the other half of the plants were injured (aboveground biomass was removed) at the age of six weeks (red full line). Each group was harvested every week for 12 weeks (control plants) or six weeks (injured plants). The courses of the injured plants are compared with i) same-aged cohorts (red full line) and ii) young, uninjured control plants (weeks 1 to 6, red dashed line). * – statistically significant difference between the control and injured plants ($P < 0.05$, t-test). R_{Root} – dry-mass-based root respiration rate; P_{max} – maximum rate of photosynthesis; R_d – dark respiration; α – maximum quantum yield of photosynthesis; I_c – compensation irradiance. Means \pm s.e. are shown; x – indicates single observation.

All statistics were performed in software STATISTICA v. 13, TIBCO Software Inc.

Results

Growth characteristics

The observed changes in shoot biomass, root biomass and total leaf area showed similar patterns with regard to injury and time (Fig. 1A, B, C). Even though the values of these growth characteristics were significantly reduced due to the injury, the regenerated plants restored their shoot biomass within six weeks, thus reaching comparable biomass values with those of the six-week-old control plants. However, when these growth characteristics were compared with those of the control plants of the same age as the injured plants at the end of the experiment (twelve weeks old), the values of the regenerating plants were still very low, and the plants did not compensate for their biomass reductions. On the other hand, the increase in the R:S ratio that occurred due to shoot biomass removal was eliminated fully, and the R:S ratio values of the injured plants were restored and comparable to those of the twelve-week-old control plants (Fig. 1D). The leaf number was recovered within just three weeks after the injury, i.e., the injured plants reached the same leaf numbers as the controls and even exceeded those of the controls as early as five weeks after the injury (Fig. 1E). However, the

regenerated leaves were tiny and thin, which was reflected by the low shoot biomass and total leaf area and thus by a higher SLA (Fig. 1A, C, E).

Root respiration

The root respiration rates (R_{Root}) of the control plants rapidly increased from germination until the age of three weeks and then rapidly and constantly decreased until the end of the experiment at twelve weeks (Fig. 2A). In the regenerating plants, even though the R_{Root} values were very low immediately after the injury, the R_{Root} values constantly increased from the time of the injury on, reaching the same values as the control plants within three weeks (at the plant age of nine weeks) and exceeding those of the control plants of the same age at the end of the experiment (Fig. 2A).

Photosynthetic parameters

The maximum (light-saturated) gross photosynthesis rates (P_{max}) of the newly formed leaves were low immediately after the injury (Fig. 2B); however, only one plant developed leaves large enough for photosynthetic measurements to be conducted). Nevertheless, the P_{max} values of the regenerating plants increased to the levels of the control plants very quickly, within two weeks, and followed the patterns of the control

Table 1

Correlation coefficients of growth and physiological characteristics. A. control plants (n=60), B. injured plants (n=21). Positive or negative correlation coefficient values indicate positive (green) or negative (red) correlations, respectively. n.s. – non-significant relationship; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; R:S ratio – root to shoot ratio; SLA – specific leaf area; R_{Root} – root respiration rate; P_{max} – maximum rate of photosynthesis; R_d – dark respiration; α – maximum quantum yield of photosynthesis; I_c – compensation irradiance.

| A. Control | | | | | | | | | | | | | |
|-------------------|----------|---------------|--------------|-----------|-----------|-------------|---------|-------------------|------------------|--------|----------|-------|--|
| | Age | Shoot biomass | Root biomass | Leaf area | R:S ratio | Leaf number | SLA | R_{root} | P_{max} | R_d | α | I_c | |
| Age | — | | | | | | | | | | | | |
| Shoot biomass | 0.86*** | — | | | | | | | | | | | |
| Root biomass | 0.83*** | 0.97*** | — | | | | | | | | | | |
| Leaf area | 0.90*** | 0.97*** | 0.92*** | — | | | | | | | | | |
| R:S ratio | 0.50** | 0.40* | 0.56** | 0.39* | — | | | | | | | | |
| Leaf number | 0.89*** | 0.88*** | 0.83*** | 0.91*** | 0.40* | — | | | | | | | |
| SLA | -0.82*** | -0.64** | -0.58** | -0.70*** | -0.45* | -0.77*** | — | | | | | | |
| R_{root} | -0.83*** | -0.79*** | -0.74*** | -0.80*** | -0.38* | -0.77*** | 0.65** | — | | | | | |
| P_{max} | n.s. | -0.31* | -0.34* | n.s. | n.s. | n.s. | n.s. | 0.42** | — | | | | |
| R_d | n.s. | -0.25* | -0.31* | n.s. | -0.34* | n.s. | 0.26* | 0.36* | 0.69** | — | | | |
| α | 0.57** | 0.41** | 0.32* | 0.54** | n.s. | 0.54** | -0.59** | -0.38* | 0.45** | 0.36* | — | | |
| I_c | -0.61** | -0.51** | -0.51** | -0.48** | -0.40* | -0.61** | 0.70** | 0.59** | 0.40* | 0.77** | -0.29* | — | |

| B. Injured | | | | | | | | | | | | | |
|-------------------|----------|---------------|--------------|-----------|-----------|-------------|---------|-------------------|------------------|---------|----------|-------|--|
| | Age | Shoot biomass | Root biomass | Leaf area | R:S ratio | Leaf number | SLA | R_{root} | P_{max} | R_d | α | I_c | |
| Age | — | | | | | | | | | | | | |
| Shoot biomass | 0.69** | — | | | | | | | | | | | |
| Root biomass | n.s. | 0.88*** | — | | | | | | | | | | |
| Leaf area | 0.73** | 0.99*** | 0.85*** | — | | | | | | | | | |
| R:S ratio | -0.64** | n.s. | n.s. | n.s. | — | | | | | | | | |
| Leaf number | 0.63** | 0.89*** | 0.79*** | 0.94*** | n.s. | — | | | | | | | |
| SLA | -0.84*** | -0.75*** | -0.50* | -0.87*** | 0.64** | -0.70** | — | | | | | | |
| R_{root} | 0.63** | n.s. | n.s. | n.s. | n.s. | n.s. | -0.46* | — | | | | | |
| P_{max} | n.s. | -0.64** | -0.77*** | -0.59** | n.s. | -0.56** | n.s. | n.s. | — | | | | |
| R_d | -0.69** | -0.56** | n.s. | -0.60** | 0.71** | -0.52* | 0.72** | n.s. | n.s. | — | | | |
| α | 0.65** | 0.78*** | 0.55* | 0.75** | n.s. | 0.64** | -0.62** | 0.45* | -0.45* | n.s. | — | | |
| I_c | -0.77*** | -0.62** | n.s. | -0.65** | 0.87*** | -0.58** | 0.73** | -0.51* | n.s. | 0.84*** | -0.67** | — | |

plants thereafter (Fig. 2B). The leaf dark respiration rates (R_d) of the regenerating plants were first very high and then constantly decreased, reaching the values of the control plants at the end of the experiment at the age of twelve weeks (Fig. 2C). The newly formed leaves of the injured plants had reduced maximum quantum yields of photosynthesis (α), comparable to those of the young control leaves (of the one- and two-week-old control plants), and the dynamics of the α values of regenerating plants followed those of the young control plants, i.e., α increased with leaf age and reached a maximum in five-week-old leaves (Fig. 2D). The newly formed leaves of the injured plants had much higher compensation irradiance (light compensation point, I_c) values than those of the control plants (Fig. 2E), and similar to α , the optimum values were reached approximately five weeks after the injury (Fig. 2E).

Correlation of characteristics

The SLA area decreased with increasing growth characteristics (and thus age) in both the control and regenerating plants, except for the R:S ratio in the regenerating plants (Table 1A, B). The R_{Root} of the controls slowed down with increasing growth characteristics (and thus with age) (Table 1A). In the regenerating plants, R_{Root} was positively correlated with age and was independent of the growth characteristics (Table 1B). P_{max} was either negatively correlated with or independent of the growth characteristics and age in both the control and regenerating plants (Table 1A, B). R_d and I_c were negatively correlated with the R:S ratio in the control plants, while in regenerating plants, opposite relationships were found (Table 1). The α values were positively correlated with increasing growth characteristics and age in both the control and

regenerating plants (Table 1A, B).

Discussion

Regenerating *Barbarea* plants were not able to restore their shoot biomass to the same values as those of the control plants within six weeks following the injury. However, the trend in growth characteristics of the regenerating plants copied that of the control plants, and the parameter values of regenerating plants were similar to those of uninjured seedlings. Six weeks after injury, the sizes of the regenerating plants were similar to the sizes of seedlings of the same age (six weeks old). Under natural conditions, germination might not occur immediately after disturbance, as it usually requires special conditions. Therefore, plants regenerating from roots would have an advantage over seedlings because regeneration from roots might occur immediately after injury, as it is less condition-limited. Contrary to our expectations, the regenerating plants did not use compensation photosynthesis (Thorne and Frank, 2009) or intensified root respiration (Aubrey et al., 2012) to boost their growth after biomass removal.

Growth characteristics

In our experiment, the regenerating plants did not have an advantage over seedlings in their produced biomass, and their rate of aboveground biomass recovery was not greater than the biomass production of the control plants. This might indicate some developmental obstacles connected with the de novo formation of root buds or their initiation (Peterson, 1975; Saitou et al., 1993; Kerstetter and Hake, 1997; Guo

et al., 2017) or with the energy costs of root bud formation and growth (Vaz et al., 1998; Sosnová and Klimešová, 2013). These energy costs could be repaid by reserves stored in roots. Despite growth reduction, RS ability might provide a way to restore populations relatively quickly and efficiently without a seed bank (Martínková and Klimešová, 2016). Moreover, contrary to germination, RS ability might not depend on environmental triggers. While germination frequently occurs within a very narrow window of environmental conditions (Baskin and Baskin, 2004), RS is less limited and occurs during the whole vegetative season (Sosnová et al., 2014; Martínková et al., 2016).

In our experiment, we recorded, on average, 80% survival in six-week-old plants subjected to whole shoot biomass removal (Supplement 1). In other studies that similarly tested the survival of very young plants with the ability to produce adventitious buds after whole shoot biomass removal, very high survival rates were also reported. Approximately 80% of the two-week-old seedlings of the annual herbs *Euphorbia genicuata*, *E. peplus*, *Kickxia elatine* and *K. spuria* survived injury and successfully generatively reproduced (Latzel et al., 2010 and 2011; Malíková et al., 2012). This might confirm that populations of short-lived species forming adventitious buds on roots and hypocotyls are adapted to unpredictable disturbances occurring very early in their life cycles.

Root respiration

Stored carbohydrate reserves are mainly important for the growth and maintenance of individual plants (Salomón et al., 2015) and, in resprouting species, are directly related to both the resprouting ability and the magnitude of subsequent growth (Drake et al., 2009; Zhu et al., 2014). The rebuilding of photosynthetically active biomass after total aboveground removal is inevitably and entirely dependent, at least at the beginning of recovery, on the reserves stored in roots (Wyka, 1999). On the other hand, the dependence of the subsequent aboveground biomass regrowth on belowground stored reserves is ambiguous and differs greatly among species, from being negligible (Ryle and Powell, 1975; Richards and Caldwell, 1985) to crucial (Van der Heyden and Stock, 1996). Nevertheless, the initial regrowth of injured plants requires mobilization of the stored C reserves in roots and, thus, intensive root respiration (Volenc et al., 1996).

In our experiment, we found the highest mass-based R_{Root} values in the non-injured control plants at three weeks old. After that age, root respiration continuously decreased to only 10% of the highest respiration rate. These results imply a decreasing intensity of translocated photosynthetic assimilate utilization, e.g., for root growth, and probably imply their transformation into belowground reserves as well as increasing root lignification from the age of three weeks. Contrary to our expectation, in plants with removed shoots, the R_{Root} values slightly increased after the injury but were still only ca. 15–30% of the highest values measured in the control seedlings. However, the belowground biomass of the injured plants had decreased by more than four times when measured four weeks after disturbance. These results suggest the intensive consumption of reserves in roots, although the R_{Root} values themselves did not indicate this result. Nevertheless, although the R_{Root} values of injured plants in our experiment significantly decreased immediately after the injury and then slightly increased, the values were much lower than the respiration rates of the control plants of the same age or, later, much lower than the maximal root respiration of the control plants. There are two possible explanations for these results. First, regrowth after biomass removal might be limited by mineral nutrients, e.g., nitrogen, rather than by available carbon (Chapin and McNaughton, 1989; Mutikainen and Walls, 1995; Sadras, 1996) because the acquisitive capability (fine root growth) of the injured plant is reduced due to the preferential rebuilding of shoots (Fig. 1B, D). Second, our results might indicate either the partial or gradual usage of stored reserves whose (yet) non-utilized portions might serve as energy back-ups for possible repeated biomass destruction that occurs before

full recovery.

Photosynthesis

Photosynthetic studies of biomass removal have obtained ambivalent results, similar to studies on R_{Root} . While some studies found no evidence for higher photosynthetic rates in defoliated, clipped or grazed plants (Holland et al., 1996; Suwa and Maherli, 2008; Thorne and Frank, 2009), others concluded that compensatory photosynthesis was an important component of disturbance tolerance (Meyer, 2002; Peng et al., 2007; Meyer and Hull-Sanders, 2008; Zhao et al., 2008; Smith et al., 2016). Contradictory results were found even in studies of the same grass genus, *Agropyron* (Nowak and Caldwell, 1984; Smith et al., 2016).

In our study, we did not observe any signs of compensatory photosynthesis during compensatory growth. These results probably support the idea that newly formed leaves have the same photosynthetic activity as uninjured leaves of plants of the same age and that compensatory photosynthesis might be induced only in partially clipped leaves (Nowak and Caldwell, 1984; Meyer, 1997). The capacity for significantly increased photosynthetic activity in newly formed leaves might thus be limited by either ontogeny (leaf age) and related developmental and physiological reasons (Escuredo and Mediavilla, 2003; Nadal et al., 2020) or by the actual availability of resources in leaves, e.g., the availability of nitrogen or water (Fang et al., 2006; González et al., 2008; Gálvez and Tyree, 2009). In our study, during the process of root resprouting, nitrogen and water could be limiting factors because of the limited acquisitive abilities of roots due to the preferential building of aboveground structures. Alternatively, the photosynthetic rate has already reached its capacity before the injury occurred, which is indicated by the optimal values of the maximum quantum yield of photosynthesis (0.06–0.07); thus, the values of the photosynthetic rate measured after biomass removal could not be higher. The injured plants in our experiment thus compensated for biomass loss not by increasing the photosynthetic activity of new leaves but by increasing the number of leaves with higher SLAs (McNaughton, 1985; Meyer, 1997, 2002).

Conclusion

After shoot removal, young plants of the root-sprouting, short-lived herb *B. vulgaris* exhibited high survival (80%). However, neither an immediate increase in root respiration nor an immediate increase in compensatory photosynthesis were observed to compensate for the biomass reduction within six weeks of the injury. Although we found signs of physiological constraints limiting more vigorous resprouting, we conclude that RS ability in short-lived species represents a useful strategy for population establishment and persistence, especially in places lacking seed banks or when disturbances occur during unsuitable germination conditions.

Credit author statement

The authors confirm contribution to the paper as follows:

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All authors reviewed the results and approved the final version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

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