Tolerance to mechanical damage in ten herbaceous grassland plant species

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ABSTRACT

The establishment of plants with high damage tolerance may provide a means for soil protection on sites exposed to strong disturbance. In a pot experiment, we investigated the tolerance to mechanical strain of ten grassland plant species representing three growth form groups (cespitose: *Festuca arundinacea*, *Lolium perenne*, *Taraxacum officinale*; rhizomatous: *Achillea millefolium*, *Elymus repens*, *Poa pratensis*; stoloniferous: *Agrostis stolonifera*, *Festuca rubra rubra*, *Poa supina*, *Trifolium repens*). We hypothesised that growth form and pre-disturbance biomass allocation to the root serve as predictors of damage tolerance. With a tool imitating the action of cleated football boots or scratching chicken, we applied three standardized levels (moderate, medium, strong) of a torsional force which exceeded the shear strength of the sward and impacted on shoots and roots. Post-treatment shoot biomass in relation to shoot biomass of the non-treated control plants served as a measure of damage tolerance. Species, but not growth form groups, differed significantly in damage tolerance, with *F. arundinacea* and *P. pratensis* showing the best performance. Shoot re-growth was strongly correlated with relative post-treatment root biomass across all species and treatment levels (R^2 = 0.25, P < 0.001), but not with pre-treatment root biomass. We conclude that root resistance to mechanical damage is the prevalent determinant of tolerance to disturbance.

Keywords: *Festuca arundinacea*; physical disturbance; *Poa pratensis*; re-growth; root

Bare soil areas, which commonly arise as an unwanted consequence of overstraining of the vegetation cover at highly frequented sites, cause various environmental problems (Morgan 2005). In grassland sites which are subject to continuous mechanical disturbance, e.g. resulting from free-range chicken or horse husbandry or intensive leisure sports use, the maintenance of an intact vegetation cover remains a challenge to be tackled. The choice of plant species with strong tolerance to mechanical damage for the establishment of durable swards may be an answer to this issue.

Physical disturbance generally impacts on plants by tear-off or wounding of leaf, shoot or root tissue or by combinations of these. In agricultural contexts, studies on tolerance to disturbance in plants mainly focus on recovery from loss of biomass related to harvesting, e.g. mowing or grazing in grasslands (Ferraro and Oesterheld 2002), and on root or shoot herbivory by pest organisms (Maron 1998). In horse or chicken pasture or on sports grounds, however, different types of damaging impacts simultaneously and in an undirected way act upon the plant by wounding or tearing off leaves, parts of the shoot, and root tissue. So far, studies elucidating the tolerance of herbaceous plants to these combined damage regimes are rare.

Within the present study, we aim at filling this gap of knowledge. We investigated the response of ten grassland plant species to comprehensive mechanical strain by simulating disturbance arising e.g. from the action of scratching chicken or of soccer boots. Within a greenhouse experiment, we subjected potted plants to three standardized levels of mechanical damage (moderate, medium and strong) impacting on shoot and root simultaneously; non-treated plants served as a control. We used the ratio of post-treatment shoot biomass in relation to shoot biomass of the non-treated control as a measure of damage tolerance. We based species selection on high performance within intensive cutting and grazing systems. Despite their relative homogeneity in terms of tolerance towards the latter types of disturbance, we firstly hypothesized the species to differ markedly in tolerance to comprehensive mechanical disturbance exerted on both shoot and root. We expected post-treatment shoot re-growth to depend on traits related to pre-treatment biomass allocation to the roots, to storage organs and to the location of clonal growth organs (Iwasa and Kubo 1997, Klimešová and Klimeš 2007). We assumed tolerance to mechanical damage to be high in plants with strong biomass allocation to the root, with buds of clonal growth organs concentrated close to or underneath the soil surface and with storage primarily located in the tussock or root. Therefore, we chose the tested species in a way to represent three vegetative growth form groups differing in these traits: cespitose, rhizomatous, and stoloniferous plants. Based on this, we secondly hypothesized the overall damage tolerance to be high in cespitose and rhizomatous plants. The general aim of this study was to describe characteristics common to herbaceous plants with high tolerance to mechanical damage in order to facilitate the choice of species suitable for greening sites that are subject to heavy disturbance.

MATERIAL AND METHODS

Plant species. Ten species (cultivars, or wild seeds if no cultivar information is given) of herbaceous grassland plants were used for the experiment: three cespitose species (*Festuca arundinacea* Mustang; *Lolium perenne* Bargold; *Taraxacum officinale* agg.), three rhizomatous species (*Achillea millefolium*; *Elymus repens*; *Poa pratensis* Julius), and four stoloniferous species (*Agrostis stolonifera* Barifera; *Festuca rubra rubra* Rossinante; *Poa supina* Supreme; *Trifolium repens* Rivendel). Wild seeds were purchased from a domestic seed company. Species were selected based on their high tolerance to frequent and deep cutting, intensive grazing and cattle trampling according to indicator values given in Dierschke et al. (2002) and in the descriptive lists of turf grass cultivars (Bundessortenamt 2006).

Damage treatment. The plants were subjected to three levels of a damage treatment (moderate, medium, strong; control: no treatment) which simulated the action of disturbance inflicted on the sward e.g. by scratching chicken or by cleated soccer boots. In order to apply a standardized treatment, a special tool was constructed. It consisted of a wooden disc of 12 cm diameter attached to a handle with the disc being penetrated by 12 screws protruding the bottom by approx. 4 cm. The removable handle allowed loading the disc with weights of 10 kg. For treatment application, the tool was set onto the pot so that the screws would reach into the ground. The pot was fixed, and by means of rotation of the handle the spiked disc was moved within the sward. The level of treatment was produced by the degree of rotation: 90° for moderate, 180° for medium, and 270° for strong damage. By exerting a torsional force to the sward, the treatment simultaneously acted upon the plants by tearing off portions of varying extent of both the shoots and the roots.

The construction and operating mode of the damage tool combines some characteristics of instruments commonly used for testing shear resistance in turf (imitation of cleats reaching several cm into the ground, torsional force exerted to the sward). The treatment application in our setup, however, differs from the protocol used in shear strength measurement. In the latter, the measured target is the threshold value of force needed to break the shear resistance of the sward. In our experimental protocol, in contrast, the rotational force is set to values well above the threshold of shear resistance at all of the three treatment levels, with the intention of exerting a distinct disturbance to the whole plant. Therefore, we also chose the diameter of the tool to be larger than e.g. in a field vane tester, which, particularly in those parts of the sward located close to the edge of the spiked disk, further augmented the effectiveness of its application.

Setup and data sampling. The experiment was established in October 2008. It consisted of 10 (species) × 4 (treatment levels) × 3 (replications) = 120 pots placed in a randomized block setup. The plants were grown as monocultures in pots of 13 × 13 × 13 cm and with common potting soil from compost as substrate: P/K/Mg 44/119/26 mg/100 g dry matter (P and K extracted in 1:20 soil to calcium acetate lactate; Mg extracted in 1:10 soil to 0.0125 mol/L $CaCl_2$), C/N ratio 14.8, pH 7.3. 10 specimens in grasses and 2 specimens in herbs per pot were cultivated in the greenhouse with 16 h of light from sodium vapour lamps additional to daylight, and at temperatures of 11°C to 18°C at night and 18°C to 24°C at day time.

During the establishment phase, the plants were cut three times (92, 126 and 155 days after sowing) to 3 cm stubble height. Four days after the third time of clipping, the damage treatment was imposed. 14 days later, it was repeated with each pot receiving the same treatment level as in the first application, yet without a preceding harvest. Another 14 days later, a final harvest of the aboveground biomass was carried out by cutting to 3 cm stubble height. The complete belowground biomass was obtained by removing the stubbles and washing the roots clean of soil particles, and dry weights were determined. Throughout the course of the experiment, all pots were kept sufficiently watered and, to ensure a non-limiting nutrient status, they were supplied with six applications of 1.5 g of a 15/10/15 + 2 NPK + Mg fertilizer per pot.

Data analysis. All data were tested for normal distribution and transformed if necessary. Data on shoot biomass were square root transformed for analysis; data on root dry weights were log-transformed. Relative post-treatment shoot re-growth and relative post-treatment root biomass were calculated for each species and treatment level as percentage values of the post-treatment shoot or root biomass of the treated plants in relation to those of the respective control plants, and arcsine-square root transformed for analysis. A two-way ANOVA was performed to analyse treatment and species effects on shoot and root biomass. Intraspecific differences between biomass of treated and control plants were determined using the Tukey's HSD post-hoc test (95% confidence interval). Explanatory power of the factors growth form group and treatment on post-treatment shoot re-growth was also determined by means of a two-way ANOVA. We tested correlations of relative post-treatment shoot re-growth with both pre-treatment root biomass and relative post-treatment root biomass using linear models. For the former analysis, post-treatment root biomass of the control plant was used as an approximation for pre-treatment root biomass based on the assumption that root growth of the control plants would be minimal under the experimental conditions applied, i.e. at good water and nutrient supply, a long establishment phase pre-treatment, and a shoot biomass harvest immediately before the treatment (Caloin et al. 1990). For the latter analysis, relative biomass of the roots as determined at the final harvest date was utilized as an approximation of relative root biomass immediately after the treatment, as we assumed root growth to be minimal during the two weeks following treatment application (van der Meijden 2000). All statistical analyses were executed using of the R software (R Development Core Team 2011).

RESULTS AND DISCUSSION

Post-treatment shoot and root biomass in individual species. The factors plant species and treatment level were significantly explanatory for post-treatment shoot and root biomass ($P < 0.001$ for both factors). The interaction of the two factors was significant for shoot ($P < 0.001$), but not for root biomass ($P = 0.09$). In relation to the controls, we observed a reduction in shoot biomass which was paralleled by a reduction in root biomass in all plants having received the treatment. The species differed concerning the minimum treatment level at which significant reductions of shoot biomass relative to the control were determined. The decrease in root biomass relative to the control was significant only in *P. pratensis*, *T. officinale*, *T. repens* and *E. repens* (Table 1).

According to these data, *F. arundinacea*, which did not show statistically significant decreases neither in shoot nor in root biomass at any of the three treatment levels applied, and *P. pratensis*, with an average decrease in shoot biomass of only about 30% at the strong level of treatment, proved to have the highest damage tolerance of the examined species.

Damage tolerance of growth form groups. The factor treatment had a significant explanatory power for relative post-treatment shoot re-growth of the examined plants ($P < 0.001$). Growth form group (cespitose, stoloniferous, rhizomatous), however, had less explanatory power for this parameter ($P = 0.02$). Only at the moderate level of damage did relative shoot re-growth differ significantly between the three groups; rhizomatous plants displayed significantly higher values than stoloniferous plants; the values of cespitose plants were intermediate. The interaction of the factors treatment and growth form group in explaining relative shoot re-growth was not significant ($P = 0.3$).

Correlations between relative post-treatment shoot re-growth and root variables. Relative post-treatment root biomass, but not pre-treatment root biomass was a significant explanatory variable of relative post-treatment shoot re-growth at each of the three treatment levels applied (Table 2). The correlation of these two parameters also proved to be significant across the complete range of species and the three treatment levels (Figure 1).

Our data confirm our hypothesis that the species differ strongly in tolerance to mechanical damage. We chose to examine a range of plant species which have a strong tolerance to intensive grazing or frequent cutting in common and which are, thus, adapted to disturbance involving defoliation, shoot removal or soil compaction. The treatment applied in the present experiment, however, ex-

Table 1. Post-treatment shoot and root biomasses of the examined species representing three growth form groups at three levels of damage treatment and in non-treated control

Species	Shoot biomass (g dry mass/pot)				Root biomass (g dry mass/pot)			
	level of treatment							
	none (control)	moderate	medium	strong	none (control)	moderate	medium	strong
Cespitose								
F. arundinacea	6.4	5.9	4.6	3.1	12.1	12.9	10.6	8.4
L. perenne	7.3[b]	5.4[ab]	4.1[a]	3.6[a]	19.2	8.4	7.0	6.8
T. officinale	10.1[b]	9.5[b]	3.5[a]	4.7[a]	36.4[b]	29.6[ab]	18.5[a]	19.5[ab]
Rhizomatous								
A. millefolium	6.5[b]	5.0[ab]	1.8[a]	1.7[a]	4.8	4.1	1.6	1.2
E. repens	5.9[b]	5.0[b]	4.1[b]	1.0[a]	19.4[b]	10.9[ab]	13.1[ab]	6.9[a]
F. rubra rubra	7.1[b]	5.0[ab]	2.9[a]	3.0[a]	9.9	4.2	3.0	4.3
P. pratensis	5.0[c]	4.7[bc]	3.0[a]	3.4[ab]	6.3[b]	4.8[ab]	3.4[a]	3.1[a]
Stoloniferous								
A. stolonifera	7.2[b]	4.1[ab]	2.3[a]	2.1[a]	5.5	3.0	2.7	2.4
P. supina	5.9[b]	2.9[a]	2.1[a]	2.8[a]	2.6	1.6	1.9	1.8
T. repens	9.4[b]	5.6[ab]	3.3[a]	2.9[a]	2.5[b]	2.4[ab]	1.3[ab]	0.6[a]

Different letters indicate significant intra-specific differences

erted a more comprehensive kind of mechanical damage, i.e. a heavy strain upon both shoot and root, which the examined plants evidently tolerate to a widely varying extent.

Our hypothesis that pre-treatment allocation of biomass to the roots and the location of storage and clonal growth organs – as reflected in the three growth form groups considered here (cespitose, rhizomatous, stoloniferous) – serve as predictors of overall damage tolerance, however, was not supported. In comparison to stoloniferous plants, cespitose and rhizomatous plants exhibit stronger prevalence of the root and the tussock as storage organs, and their buds are concentrated closer to or underneath the soil surface. Therefore, we had expected these latter two groups to have a higher damage tolerance than stoloniferous plants. Yet, only at the moderate level of treatment did rhizomatous plant show significantly higher re-growth than stoloniferous plants. Obviously, other traits than those used to define the growth form groups are relevant for the explanation of post-treatment shoot re-growth. Our data indicated a significant correlation of relative post-treatment shoot re-growth and relative post-treatment root biomass across the whole range of examined species and the three treatment levels applied. Pre-treatment root biomass, however, did not serve as a predictor of shoot re-growth, which is in concordance with Chapin et al. (1990) who also point out that

Table 2. Results of regression analysis (R^2 and P values of linear models) with pre-treatment root biomass and relative post-treatment root biomass (proportion of the root biomass of the treated plant in relation to that of the non-treated control) as explanatory variables of relative post-treatment shoot re-growth (proportion of the harvested aboveground biomass of the treated plant in relation to that of the non-treated control) at three levels of damage treatment (moderate, medium, strong)

	Level of treatment							
	moderate		medium		strong		all data	
	P	R^2	P	R^2	P	R^2	P	R^2
Root biomass pre-treatment	0.08	0.086	0.08	0.073	0.8	–0.033	0.1	0.016
Rel. root biomass post-treatment	< 0.001	0.48	0.02	0.15	0.004	0.24	< 0.001	0.25

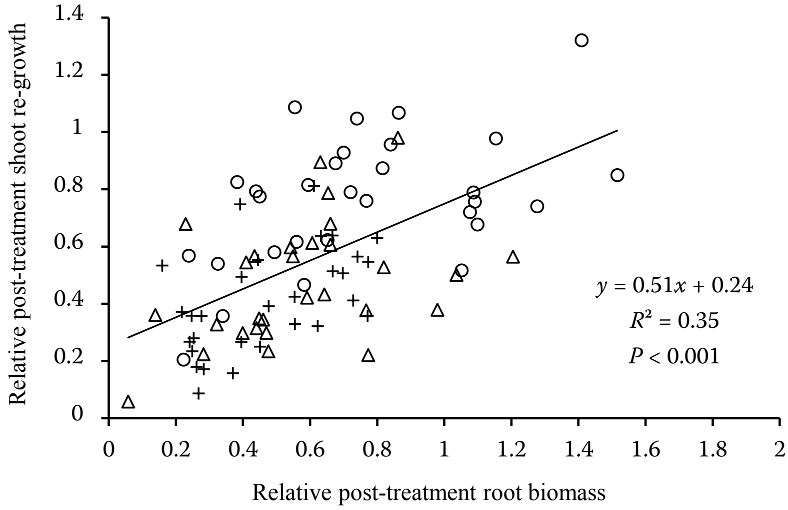

Figure 1. Correlation of relative post-treatment shoot re-growth (proportion of the harvested above-ground biomass of the treated plant in relation to that of the non-treated control) and relative post-treatment root biomass (proportion of the root biomass of the treated plant in relation to that of the non-treated control) across the whole range of species examined and for the three levels of treatment applied. Level of damage treatment: o – moderate; Δ – medium; + – strong

storage may not always be accessible for recovery after disturbance. Based on these findings, we conclude that the extent to which the root is reduced as a consequence of the damage event (by tear-off of root tissue) is an important predictor of post-treatment shoot re-growth. This is in concordance with previous studies which showed that the loss of root tissue has an over-proportionally more severe effect on plant fitness than the removal of aboveground biomass (Humphries 1958, Schmid et al. 1990, Reichman und Smith 1991).

A limitation of the applied experimental protocol is the fact that it only provided a measure of overall damage tolerance for the tested plants. As biomass of intact root and shoot tissue could not be assessed immediately after treatment, a differentiation between damage resistance on the one hand – resulting in high values of relative root and shoot biomass at the final harvest due to a limited impact of the treatment – and resilience on the other hand – resulting in high values of relative root and shoot biomass at the final harvest due to fast re-growth post-treatment – is not possible in the present approach. However, as explained above, under the applied experimental conditions we expect harvested root biomass to represent a fair approximation of biomass of intact roots immediately after treatment.

Another aspect deserving consideration is the fact that a number of species examined here display a significant intraspecific variation, and cultivars can, therefore, be expected to show high variation in damage tolerance. The species *L. perenne*, for instance, comprises forage cultivars as well as cultivars for sports turf, and even among the latter, damage tolerance varies notably (Bundessortenamt 2006). Still, we assume the strong correlation of relative post-treatment shoot re-growth and relative post-treatment root biomass which we discovered across the whole range of all the tested species also to be valid across different cultivars of one species. Intraspecific variation may, however, alter the ranking of overall damage tolerance among the tested species.

Altogether, the results of our experiment indicate that plants with high resistance to root damage (e.g. given by root architecture or lignification) may have a high overall tolerance to comprehensive mechanical damage. In order to evaluate the prospective practical application of the results shown, trials on the performance of the investigated species under field conditions as presented in Breitsameter et al. (2010) are of major importance.

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