Plant genotype determines biomass response to flooding frequency in tidal wetlands

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10 **Abstract.** The persistence of tidal wetland ecosystems like salt marshes is threatened by human interventions and climate change. Particularly the threat of accelerated sea level rise (SLR) has recently gained increasing attention by the scientific community. However, studies investigating the effect of SLR on plants and vertical marsh accretion are usually restricted to the species or community level and do not consider phenotypic plasticity or genetic diversity. To investigate the response of genotypes within the same salt-marsh species to SLR, we used two known genotypes of *Elymus athericus* (Link) Kerguélen 15 (low-marsh and high-marsh genotypes). In a factorial marsh organ experiment we exposed both genotypes to different flooding frequencies and quantified plant growth parameters. With increasing flooding frequency, the low-marsh genotype showed a higher aboveground biomass production compared to the high-marsh genotype. Additionally, the low-marsh genotype generally formed longer rhizomes, shoots and leaves, regardless of flooding frequency. Belowground biomass of both genotypes decreased with flooding frequency. We conclude that the low-marsh genotype is better adapted to higher flooding 20 frequencies through its ability to allocate resources from below- to aboveground biomass. Given the strong control of plant biomass production on salt-marsh accretion, we argue that these findings yield important implications for our understanding of ecosystem resilience to SLR as well as plant-species distribution in salt marshes.

1 Introduction

Salt marshes are wetland ecosystems predominantly found along coastlines where they form a transition zone between the 25 marine and the terrestrial environment. Salt marshes provide important ecosystem services like protection of coastlines against storm surges by wave attenuation (Möller et al. 2014), supply of nursery grounds for commercially important fish (Bolle et al., 2009) and mitigation of climate change by long-term carbon sequestration (McLeod et al., 2011). However, human interventions such as land reclamation, eutrophication and climate change threaten the persistence of salt marshes, causing loss rates of 1-2 % of the global area per year (Duarte et al., 2008). Particularly the threat of accelerated sea level rise (SLR) 30 has recently gained increasing attention by the scientific community (Fitzgerald et al., 2008; Kirwan and Megonigal, 2013; Schuerch et al., 2018).

Generally, up to a certain locally varying threshold of SLR, salt marshes are able to keep up with rates of SLR through their ability to accrete vertically (Kirwan and Megonigal, 2013). During this process, salt-marsh plants act as 'ecosystem engineers' because their aboveground biomass reduces water flow velocity during flooding events and therefore increases sediment
35   settlement. Furthermore, a high belowground biomass production and decreased decomposition rates in oxygen-deficient soils lead to an accumulation of organic matter and thereby expansion of soil volume. Whether above- or belowground processes predominantly contribute to vertical accretion, depends on the marsh type (i.e. minerogenic vs. organogenic) and is often depending on local tidal amplitude (Allen, 2000; Kirwan and Megonigal, 2013; Nolte et al., 2013). Yet, in both cases, biomass production of the marsh vegetation is an important driver of accretion. When accretion rates are too low and threshold values
40   of SLR are exceeded, plant growth is negatively affected, leading to a negative feedback loop, which ensues marsh submergence and finally marsh loss (Chmura, 2013; Kirwan and Guntenspergen, 2012).

Recently, more studies have therefore been focusing on salt-marsh resilience to projected rates of SLR by studying the vegetation response. To examine how vegetation responds to changes in flooding regimes, so called 'marsh organ' experiments have been proven as convenient and insightful approaches. A marsh organ consists of several mesocosms arranged next to
45   each other and along an elevational gradient. Kirwan and Guntenspergen (2012), for example, placed a marsh organ in a brackish marsh to examine the effect of varying sea levels on plant growth of two marsh species and what possible implications this may have on accretion processes. They observed that marsh elevation within the tidal frame determines whether root biomass increases or decreases with SLR. In contrast to belowground productivity, aboveground biomass response was species depended. Numerous other studies confirmed that responses of marsh plants to sea level changes are highly species-specific
50   (Eleuterius and Eleuterius, 1979; Kirwan and Guntenspergen, 2015; Langley et al., 2013; Morris et al., 2013). Therefore, the effect of SLR on plant biomass production, and thus the ability of the ecosystem to accrete vertically, can only be understood if also SLR-induced shifts in plant species composition are taken into account.

However, such studies on the effect of SLR on plants are usually restricted to the species or community level. They usually do not consider the high degree of phenotypic plasticity and genetic diversity within many species, as for instance evident between
55   different locally adapted populations (Valladares et al., 2014). Yet, understanding a species' adaptive genetic plasticity can be crucial to evaluate its response to environmental change (Razgour et al., 2019). Indeed, in some cases environmental change can in fact induce larger variability in plant biomass production within than between species (Beierkuhnlein et al., 2011). We therefore argue, that intraspecific differences in the biomass response to SLR of salt-marsh plants are likely relevant and require more attention by the scientific community to understand ecosystem resilience.

60   To investigate the response of genotypes within the same salt-marsh species to SLR, we used two known genotypes of the grass *Elymus athericus* (Link) Kerguélen. This species is widely distributed in NW European salt marshes and usually grows in high-elevated and therefore less-frequently flooded zones of the salt marsh (= high marsh) (Nolte et al., 2019). In the high marsh, the tall grass forms dense, monospecific stands with a low local plant species diversity (Bakker et al., 2003). Recently, however, populations of *E. athericus* have been observed spreading into lower and thus more frequently flooded zones of the
65   marsh (= low marsh) (Olff et al., 1997; Veeneklaas et al., 2013). Low- and high-marsh genotypes are visually distinguishable,

as the low-marsh genotype develops a specific phenotype different from the high-marsh genotype (Bockelmann et al., 2003). If genotypes respond differently to increased flooding frequencies, for instance in biomass productivity, it might affect salt-marsh responses to SLR.

The aim of this study was to investigate potential adaptations of the low-marsh genotype to increased flooding frequencies, to
70   improve current evaluations of salt-marsh resilience to SLR. To test the hypothesis that the low-marsh genotype performs better (e.g. produces more biomass) at increased flooding frequencies than the high-marsh genotype, we conducted a factorial marsh organ experiment. We exposed both genotypes of *E. athericus* to three different flooding frequencies and quantified plant growth parameters to compare their performance and assess morphological adaptations of the low-marsh genotype.

2 Material and methods

75   ### 2.1 *Elymus athericus*

Plants were collected in April 2015 from a salt marsh on the Dutch Island Schiermonnikoog (53°30′N, 6°16′E) from stands that have previously been identified to be dominated by genetically distinct populations of *E. athericus*, i.e. high-marsh and low-marsh genotypes (Bockelmann et al., 2003). Individuals were propagated vegetatively (via rhizomes) and kept in trays under identical environmental conditions at the Institute of Plant Science and Microbiology in Hamburg, until July 2017 when
80   the experiment commenced. Plants of similar size were transferred into pots (15 cm diameter, 17 cm height), filled with salt marsh soil taken from the salt marsh at Sönke-Nissen-Koog, Germany (54°36'N, 8°49'E).

2.2 Experimental set-up

Plants were placed onto three steps within a tidal-tank facility (Hanke, Ludewig, & Jensen, 2015), to create three different flooding frequencies. The tidal tank is located outdoors at the Institute of Plant Science and Microbiology and has a total
85   volume of 6.75 m³ (dimensions: 3 x 1.5 x 1.5 m). A pump was used to fill and empty the tidal tank at regular intervals to mimic tides by alternating between three different maximum water levels. Flooding with the respective maximum water level lasted two hours and took place twice a day. The lowest step was flooded every day, which represented the highest frequency. The flooding of the middle step (moderate flooding frequency) happened weekly, while plants on the highest step were flooded only every two weeks (lowest flooding frequency). A CTD diver combined with a baro diver (Van Essen Instruments, Delft,
90   The Netherlands) was used to monitor flooding cycles. Artificial sea salt (AB Aqua Medic GmbH, Germany) was suspended in tap water to create a salinity of about 20-22 ppt. Eight replicates per genotype were placed on each step, so that a total number of 48 plants were used in this study. To minimize the impact of other effects than flooding frequency and genotype, the pots were circulated on each step, other seedlings and algae were removed once a week. Concurrently, water level and salinity were checked as well. The experiment ran for approx. 12 weeks from mid-July to early October 2017.

2.3 Measurements

2.3.1 Biomass

At the end of the experiment (2nd of October 2017), the plants were harvested, separated into above- and belowground biomass, dried for two days at 70°C and weighed. Additionally, rhizomes were separated from roots and weighed. Rhizome length was also recorded.

2.3.2 Plant growth

At the beginning and the end of the experiment, plant shoot and leaf length as well as number of shoots and leaves were measured. The difference between both measurements was calculated and designated as Δ. Only living plant material was taken into account and length measurements (leaf and shoot length) were carried out on the longest leaves or shoots.

2.4 Statistical analysis

Data were tested for normality by applying the Shapiro-Wilk-Test. Except count data (e.g. number of leaves), all parameters were normally distributed and therefore further analysed applying factorial ANOVAs. Due to the well-balanced study design, potential moderate deviations from homogeneity of variance between groups were considered unimportant for ANOVA testing (Box, 1954; McGuinness, 2002). Each analysis included genotype and flooding frequency as well as their interaction as explanatory variables. To detect significant differences between treatments (flooding frequency and genotype), post-hoc tests (Tukey's HSD) were conducted. To analyse count data, i.e. number of shoots and number of leaves, generalized linear models (GLM) were applied assuming a Poisson distribution and including the explanatory variables genotype and flooding frequency, as well as two-way interaction effects. Each GLM was checked for overdispersion (Pearson Chi2 dispersion parameter) and was refitted afterwards if necessary, using the standard procedure of the applied program. All statistical analyses were performed using STATISTICA 13 (StatSoft Inc., Tulsa, OK, USA).

3 Results

3.1 Biomass

Total biomass, defined as the sum of dry above- and belowground plant biomass, differed significantly between genotypes and flooding frequencies (Table 1). In addition, the interaction of both factors showed a significant effect on total biomass. Total biomass production of the high-marsh genotype decreased steadily with increasing flooding frequency, whereas the total biomass of the low-marsh genotype decreased less distinctly (Fig. 1). The difference between low-marsh and high-marsh genotypes was most pronounced at the highest flooding frequency. In fact, the low-marsh genotype produced almost twice as much total biomass at highest flooding frequency as the high-marsh genotype (LM: 4.61 ± 0.70 g and HM: 2.66 ± 0.52 g, mean ± standard deviation).

Genotype and flooding frequency as well as their interaction had a significant effect on the aboveground biomass production.
Aboveground biomass of the high-marsh genotype decreased with increasing flooding frequency from 3.31 ± 0.57 g to 2.03 ±
0.38 g (Fig. 2). However, aboveground biomass production of the low-marsh genotype maintained constant at about 3.46 ±
0.45 g on all flooding frequencies.

In contrast to the genotype-specific aboveground biomass response to flooding, belowground biomass of both genotypes
decreased with increasing flooding frequency (Fig. 2). Results indicate a more pronounced effect of flooding frequency on
belowground biomass production compared to the factor genotype (Table 1). Under all flooding frequencies, the low-marsh
genotype produced slightly more belowground biomass than the high-marsh genotype (LM: 1.63 ± 0.78 g, HM: 1.30 ± 0.76
g).

3.2 Δ Shoot and leaf length

The increase in shoot and leaf length significantly differed between genotypes (Table 1). Increase in shoot length of the low-
marsh genotype was twice as high as that of the high-marsh genotype (LM: 10.78 ± 6.18 cm, HM: 5.57 ± 6.58 cm). Regarding
leaf length, the high-marsh genotype showed approximately the same increase on all flooding frequencies (1.9 ± 4.45 cm).
The low-marsh genotype had similar increases of leaf lengths at the lowest flooding frequency but showed pronounced
increases of leaf length with flooding frequency (7.03 ± 2.17 cm) (Fig. 2).

3.2 Δ Number of shoots and leaves

Neither genotype nor flooding frequency had a significant effect on the increase in number of shoots (Table 1). However, for
the increase in number of leaves, a significant effect of flooding frequency was detected (Wald = 19.69, p < 0.001). With
highest flooding frequency, both genotypes produced the lowest number of new leaves (LM: 10.4 ± 4.0, HM: 8.9 ± 2.1).

3.3 Root and rhizome biomass

Root biomass production was significantly affected by flooding frequency (F = 10.69, p < 0.001), but did not differ between
genotypes. Root biomass decreased with increasing flooding frequency for both genotypes (Fig. 2). In contrast, biomass of
rhizomes was significantly affected by both genotype and flooding frequency (genotypes: F = 6.49, p < 0.05; flooding
frequency: F = 3.84, p < 0.05). Mean rhizome biomass of the low-marsh genotype was higher than of the high-marsh genotype
(LM: 0.55 ± 0.50 g, HM: 0.26 ± 0.28 g) with the most pronounced differences on lowest and highest flooding frequency (Fig.
2). In some cases, the low-marsh genotype formed very long rhizomes (up to 166 cm length, coiled around the soil). On
average, rhizomes of the low-marsh genotype were nearly twice as long as those of the high-marsh genotype (LM: 51.43 ±
41.11 cm, HM: 26.63 ± 27.23 cm). Genotypes significantly differed in the length of rhizomes (F = 6.102, p < 0.05).

4 Discussion

Assessments of plant responses to changed hydrological conditions (e.g. SLR) have thus far focused mainly on comparisons on species level. However, variability in plant responses within species can be considerably higher than between species
155   (Beierkuhnlein et al., 2011). In this study, we therefore investigated differences in plant response between genotypes of the same species (*Elymus athericus*) to better understand the importance of intraspecific variability for evaluations of future ecosystem functionality and resilience. We found, in line with our hypothesis on biomass production, that the low-marsh genotype performs better than the high-marsh genotype under increased flooding frequency. Additionally, the low-marsh genotype generally formed longer rhizomes, shoots and leaves, regardless of flooding frequency (Fig. 2). We argue that these
160   findings yield important implications for our understanding of ecosystem resilience to SLR as well as plant-species distribution in salt marshes.

We found a higher total biomass of the low-marsh genotype, which was particularly pronounced under high flooding frequency (Fig. 1). This result indicates a better adaptation of the low-marsh genotype to lower elevated, more frequently flooded conditions. When separating above- and belowground biomass, the high-marsh genotype showed a decrease of both biomass
165   parameters in response to increasing flooding frequency. Aboveground biomass is important for maintaining photosynthesis, so that its reduction can be interpreted as reduction in performance as well. In contrast, the low-marsh genotype was able to maintain a high aboveground biomass production independent of flooding frequency. We also found a decrease of belowground biomass with increasing flooding frequency in both genotypes. This can be interpreted as an adaptive trait, because a reduction of belowground biomass reduces the number of respiring roots and thereby improves the diffusion of
170   oxygen to the roots (Naidoo and Naidoo, 1992; Voesenek et al., 1988). In line with these results, an increased aboveground biomass production while belowground biomass decreased was found for other flooding adapted plant species such as Taxodium distichum, Danthonia montevidensis and Paspalum dilatatum (Day and Megonigal, 1992; Rubio et al., 1995).

The difference in aboveground biomass response between the two genotypes seems to be mainly explained by genotype-specific increases in leaf and shoot length, whereas the number of both remained similar (Fig. 2, Table 1). Likewise, Voesenek,
175   Blom, & Pouwels (1988) found marked increase in leaf length in the flooding adapted Rumex palustris under waterlogging, but no increase in number of leaves. The distinct increase in leaf and shoot length in addition to the simultaneous reduction of belowground biomass of the low-marsh genotype of *Elymus athericus* found in our study, indicate resource allocation as response to flooding. For other species it was found that reallocated resources fuel elongation of shoots and leaves to maintain gas exchange and avoid light dissipation through water (Blanch et al., 1999; Grace, 1989). Our results suggest that this response
180   may be also present in *E. athericus*, which increases the chances for the establishment of its low-marsh genotype in more frequently flooded low-marsh sites.

Compared to the root biomass of both genotypes, which responded quite similar and decreased with flooding frequency, rhizome length differed significantly between the genotypes (Table 1). The formation of longer rhizomes by the low-marsh genotype, especially under high flooding frequency, could serve as an escape strategy to expand into more favourable habitats

185 (Hartnett and Bazzaz, 1983; Lovett-Doust, 1981). In previous studies, it was reported that *E. athericus* usually expands via a 'phalanx' growth strategy, which means that parental plants invest in many but rather short rhizomes to utilize resources in a favourable habitat (Bockelmann and Neuhaus, 1999). Field observations of the same authors and results of our study, however, indicate that *E. athericus* is able to alter its strategy to the 'guerrilla' form, by producing longer rhizomes. The 'guerrilla' strategy is usually found in plants characteristic for early successional stages as it enables plants to spread quickly and exploit

190 new favourable areas (Lovett-Doust, 1981). However, overall rhizome length of our study should be interpreted with caution because of potential edge effects caused by the experimental mesocosms.

4.1 Methodological considerations

We suggest that the experimental setup including a tidal tank and steps proved suitable to investigate the effects of different flooding frequencies on salt-marsh vegetation. Nevertheless, we recommend repeating this experiment in situ, for example as

195 a transplant experiment, to estimate actual effect size under more natural conditions, as drainage and plant-soil interactions might have been different in the tidal tank and could have affected biomass production.

5 Conclusion

The present work revealed marked differences in the plant biomass response to changes in flooding frequency between two genotypes of the dominant European salt-marsh grass *Elymus athericus*. Given the strong control of plant biomass production

200 on salt-marsh accretion (Kirwan and Megonigal, 2013), our results highlight the importance to consider interactions of environmental change and intraspecific trait variability in plants to evaluate ecosystem resilience. Furthermore, we observed large differences in rhizome production between genotypes, which is interpreted as a change in growth strategy. The alteration of its growth strategy and the higher aboveground biomass productivity of the low-marsh genotype implies a larger potential of the low-marsh genotype to invade and establish at lower elevations of the tidal frame.

205 ### 6 Data availability

All data presented in this paper is available from the corresponding author upon request.

7 Author contribution

All authors contributed to the design of the experiments. SR and HT conducted the experiment and performed the measurements. SR analysed the data and wrote the manuscript. All authors contributed to the discussion of results and the final

210 manuscript.

7 Competing interests

The authors declare that they have no conflict of interest.

8 Acknowledgements

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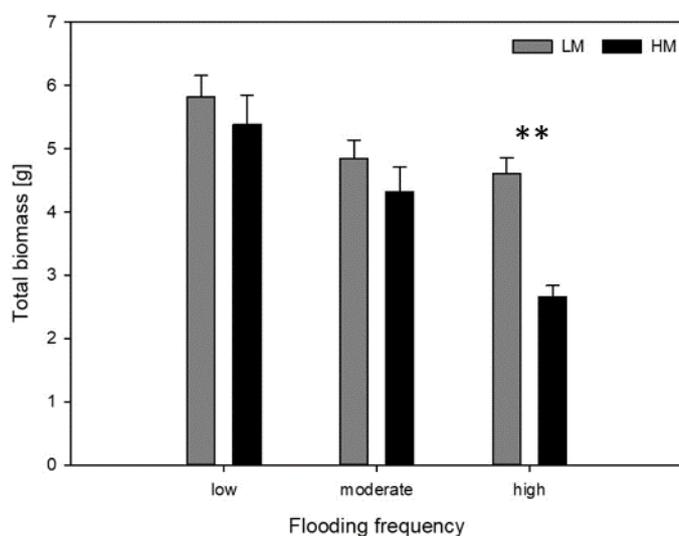
Figure 1: Total biomass [g] of both genotypes on three different flooding frequencies (mean + standard errors). Stars show significant
300 **differences between low-marsh (LM) and high-marsh (HM) genotypes within the same flooding treatment based on Tukey's HSD**
post-hoc test (* p < 0.05; **p < 0.01; *** p < 0.001).
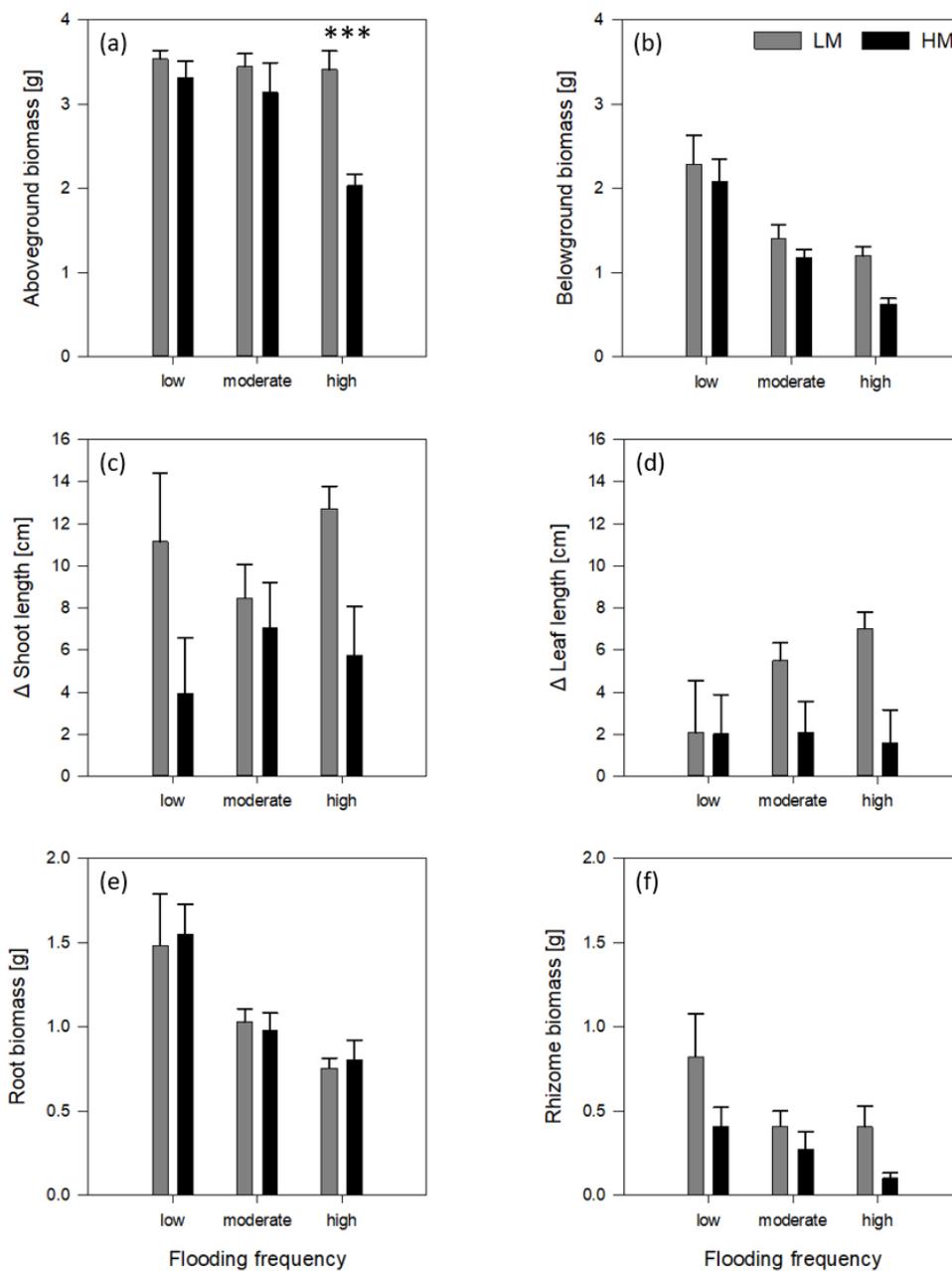
Figure 2: Aboveground biomass (a), belowground biomass (b), delta shoot length (c), delta leaf length (d), root biomass (e) and rhizome biomass (f) of both genotypes on three different flooding frequencies (mean + standard error). Stars show significant differences between low-marsh (LM) and high-marsh (HM) genotypes within the same flooding treatment based on Tukey's HSD post-hoc test (* p < 0.05; **p < 0.01; *** p < 0.001).

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310 **Table 1: Summary statistics of main response variables in the experiment testing for effects of flooding and genotype of *Elymus athericus* on its biomass and growth. Count variables (number of shoots, number of leaves) are analysed through GLM, all other variables by a two-way factorial ANOVA. Significant p-values are shown in bold letters.**

Response variable	statistical test	genotype (df =1) test statistic	p-value	flooding frequency (df = 2) test statistic	p-value	genotype * flooding frequency (df = 2) test statistic	p-value
Total biomass [g]	factorial ANOVA	F = 13.18	**0.001**	F = 18.24	**0.000**	F = 3.36	**0.044**
Aboveground biomass [g]	factorial ANOVA	F = 13.84	**0.001**	F = 6.38	**0.004**	F = 4.77	**0.014**
Belowground biomass [g]	factorial ANOVA	F = 4.31	**0.044**	F = 21.93	**0.000**	F = 0.53	0.594
Δ Shoot length [cm]	factorial ANOVA	F = 7.77	**0.008**	F = 0.32	0.725	F = 1.03	0.365
Δ Leaf length [cm]	factorial ANOVA	F = 5.09	**0.029**	F = 1.08	0.350	F = 1.42	0.252
Δ Number of shoots	GLM	Wald = 0.00	0.952	Wald = 5.87	0.053	Wald = 0.78	0.678
Δ Number of leaves	GLM	Wald = 0.44	0.507	Wald = 19.69	**0.000**	Wald = 1.60	0.449
Root biomass [g]	factorial ANOVA	F = 0.03	0.861	F = 10.69	**0.000**	F = 0.07	0.931
Rhizome biomass [g]	factorial ANOVA	F = 6.49	**0.015**	F = 3.84	**0.030**	F = 0.51	0.602
Rhizome length [cm]	factorial ANOVA	F = 6.10	**0.018**	F = 1.67	0.201	F = 0.45	0.640