VARIATION IN GROWTH RESPONSE OF COASTAL DUNE-BUILDING GRASS SPECIES *AMMOPHILA ARENARIA* AND *LEYMUS ARENARIUS* TO SAND BURIAL

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Abstract

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Ammophila arenaria and *Leymus arenarius* are dune-building grass species native to European seacoasts. The present study aimed to compare growth responses to the sand burial of *A. arenaria* and *L. arenarius* from coastal habitats of the Baltic Sea, when the intensity of sand accretion was relatively low under controlled conditions. Plants were grown from seeds collected from natural coastal habitats, transplanted into individual containers, buried in the sand at different depths in the rapid shoot elongation stage, and further cultivated (11 or 9 weeks) in an automated greenhouse. Burial in sand significantly stimulated the growth of shoots of *A. arenaria*, the effect was earlier at high burial intensities (46 and 60%) and was evident ten days after the start of treatment. Both shoot and root dry mass increased for plants buried at 13%; however, increased burial depth (37, 46 and 60%) resulted in a significant increase in root biomass. In comparison, shoot biomass decreased significantly at the highest burial intensity (60%). For *L. arenarius*, there was no direct dependence of shoot elongation rate on burial depth. There was a tendency for increased elongation growth and biomass allocation to leaf sheaths despite a decrease in total shoot mass. Most strikingly, root biomass decreased with sand burial in parallel with increased burial depth up to 21% intensity. In conclusion, although both grass species showed a positive shoot growth response to moderate sand burial intensity, differences in individual responses at the morphological and physiological level indicate the existence of different genetically based adaptation strategies.

Keywords: *Ammophila arenaria*, coastal dunes, grass species, growth response, *Leymus arenarius*, sand burial.

INTRODUCTION

Coastal dune habitats around the world are highly dynamic biogeographic and ecological systems maintaining substantial biological diversity (PROVOOST et al., 2011; KEIJSERS et al., 2015; CICCARELLI & BACARO, 2016). Sand accretion in coastal habitats, including beaches and dunes, is among environmental factors having a significant effect on plant species distribution as well as growth and reproduction of individual coastal plants (MAUN & PERUMAL, 1999; GILBERT et al., 2008; FIDALGO et al., 2014). Native sand dune species possess a high tolerance to burial by sand, being able to complete generative reproduction even after almost complete burial (IEVINSH, 2006).

Several coastal grass species represent dune-builders, having both excellent burial tolerance and the ability for stimulated growth under conditions of sand accretion. Two typical representatives of this group are *Ammophila arenaria* (L.) LINK and *Leymus arenarius* (L.) HOCHST., native to European seacoasts (BOND, 1952; HUISKES, 1979). Both species are specifically associated with coastal habitats, indicating the presence of specific adaptations giving an advantage in prevailing conditions of these habitats. Both plants represent umbrella species of the European protected habitat EUH 2120 "Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes)" (LAIME, 2013).

From the point of population biology, *A. arenaria*

has been characterised as a species with high phenotypic plasticity. Plants growing under optimal and unfavourable environmental conditions were compared; the measured difference in plant height was double, but the difference in total dry biomass exceeded 30 times (GRAY, 1985). In contrast, the existence of a mixed genetic polymorphism and plasticity can be proposed for *L. arenarius* based on differences in populations of coastal and inland Iceland (GREIPSSON & DAVY, 1996). However, in the case of the related species *Leymus mollis*, it has been shown that the differences among the different populations in subarctic dunes are caused by the environmental rather than genetic factors (IMBERT & HOULE, 2000). While both species exhibit clonal growth, their clonal strategy shows significant differences. *A. arenaria* plants can develop vertically expanding rhizomes, resulting in dense clonal expansion, but *L. arenarius* plants rely mostly on the horizontal spread of rhizomes, resulting in a relatively wider expansion of genets (PAVLIK, 1983; REIJERS et al., 2020).

Recent studies have shown renowned interest in the role of the biology of dune building grasses in ecology and coastal dune conservation (REIJERS et al., 2019, 2020). So far, no studies have directly compared burial responses of *A. arenaria* and *L. arenarius*. Therefore, the present study aimed to compare growth responses to the sand burial of *A. arenaria* and *L. arenarius* from coastal habitats of the Baltic Sea, where the intensity of sand accretion is relatively low. It was specifically intended to find out whether there are any differences in sand burial responses, possibly related to specific growth forms of the particular species.

MATERIALS AND METHODS

Seed source and plant establishment

Seeds of *A. arenaria* were collected in white dunes on the coast of the Baltic Sea near Ventspils, Latvia in August 2017. Seeds of *L. arenarius* were collected in white dunes on the coast of the Gulf of Riga near Jūrmala, Latvia in August 2018. Seeds were dried for one month under laboratory conditions and then stored at 4°C in paper bags. Before planting, seeds were surface sterilised in 50% commercial bleach (Ace, Procter & Gamble) for 10 min followed by an active rinse with deionised water (five

times for 5 min). After imbibition in deionised water for 4 h, seeds were planted in sterilised 200 mL plastic containers in a mixture of autoclaved commercial garden soil (Biolan, Finland) and quartz sand (1:1, v/v) mixed with sterile deionised water. Containers were placed in a growth cabinet with a thermoperiod 15/20°C (night/day) in conditions of 12 h photoperiod (photon flux density of photosynthetically active radiation 40 µmol m^{-2} s^{-1}). When seedlings formed second true leaf, they were individually transplanted to square plastic containers (11.3 × 11.3 × 21.5 cm, 2 L) filled with 1 L of garden soil and quartz sand mixture (1:1, v/v). Containers were placed in an experimental automated greenhouse (HortiMax, Netherlands) with supplemented light from Master SON-TPIA Green Power CG T 400 W (Philips, Netherlands) and Powerstar HQI-BT 400 W/D PRO (Osram, Germany) lamps (380 µmol m^{-2} s^{-1} at the plant level), 16 h photoperiod, day/night temperature 23/15°C, relative air humidity 60 to 70%. Position of individual plants was randomly changed every week.

Treatment and cultivation

Burial was performed two weeks after transplantation of seedlings in the active phase of shoot elongation to individual containers. The treatment was carried out as a single burial episode, using autoclaved pure quartz sand (Saulkalne S, Latvia). Five burial depths were used for *A. arenaria*: 13, 23, 37, 46 and 60%, respectively, to plant height (Fig. 1A). As it was initially expected that burial tolerance of *L. arenarius* would be relatively lower, seedlings were covered with sand up to 7, 13, 21 and 31% of plant height (Fig. 1B). To achieve deeper burial than the height of the individual container, containers of the same size without bottom were placed over the substrate and filled with sand to the indicated depth. Unburied plants (0%) were used as control. In the case of *A. arenaria*, two controls were used, one with plants in 2 L containers as for other treatments (shaded control, 0*), and another in smaller (1.2 L) containers. For *A. arenaria*, additional shaded treatment (25*) at 25% burial intensity was performed by placing empty 2 L container over the substrate (Fig. 1A). For each burial treatment, ten plants were used.

Soil moisture of control (unburied) plants was monitored with HH2 moisture meter, equipped with WET-2 sensor (Delta-T Devices, UK) daily not al-
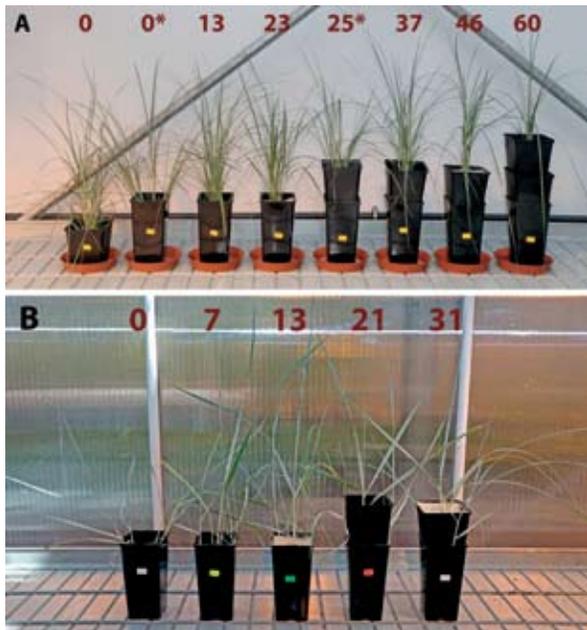
Fig. 1. Examples of *Ammophila arenaria* (A) and *Leymus arenarius* (B) plants in experimental sand burial treatments. Numbers indicate burial intensity in percentages from the height of the initial seedlings. The additional shaded treatments 0* and 25* were used for *Ammophila arenaria*

Measurements

Plant growth was periodically monitored as an increase in the height of the longest leaf within 11 and 9 weeks for *A. arenaria* and *L. arenarius*, respectively. At the end of the experiment, individual plants were separated from the substrate, and morphological parameters were measured. *A. arenaria* plants were measured for the number of tillers, the final shoot height, and the fresh and dry mass of shoot above the burial, the shoot below the burial, the roots within burial, and the roots in the initial soil volume. The number of leaves, the final shoot height, the length of the leaf sheaths, the fresh and dry root mass of the flag leaf, other leaf sheaths and other leaf blades of *L. arenaria* plants were estimated. The dry mass was determined by drying the tissues to constant mass in an oven at 60°C.

Data analysis

Data analysis was performed using KaleidaGraph (v. 4.1, Synergy Software). Growth data were analysed by one-way ANOVA, followed by Fisher's LSD test. Student *t*-test was used to estimate statistically significant differences for morphological data between individual treatments ($p < 0.5$).

RESULTS

lowing the decrease of substrate moisture lower than 60% water holding capacity. Plants were watered from the bottom using equal amounts of deionised water for all treatments. Once a week plants were fertilised from the bottom of the containers with a Kristalon Green Label fertiliser (NPK 18-18-18 with micronutrients; Yara International, Norway) solubilised in deionised water (150 g L^{-1}), with 5 mL of

Treatment of *A. arenaria* plants was performed during the active shoot elongation phase, which con-
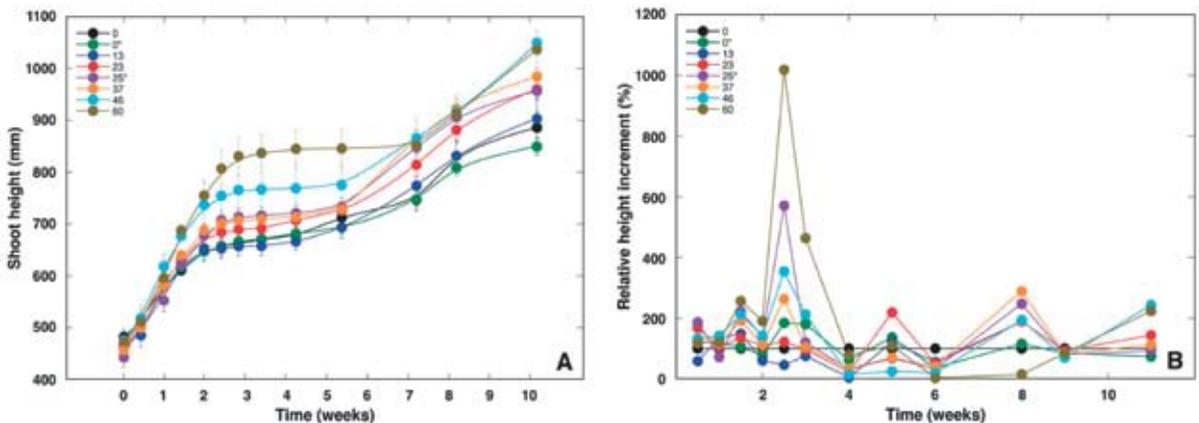

Fig. 2. Changes of shoot height in time as a response to sand burial at various depths of *Ammophila arenaria* plants (A). Data are means ± SE of ten individual plants. Changes in relative height increment of *Ammophila arenaria* shoots due to sand burial at various depths (B). Data are means of ten individual plants. 0* and 25* present the additional shaded treatments
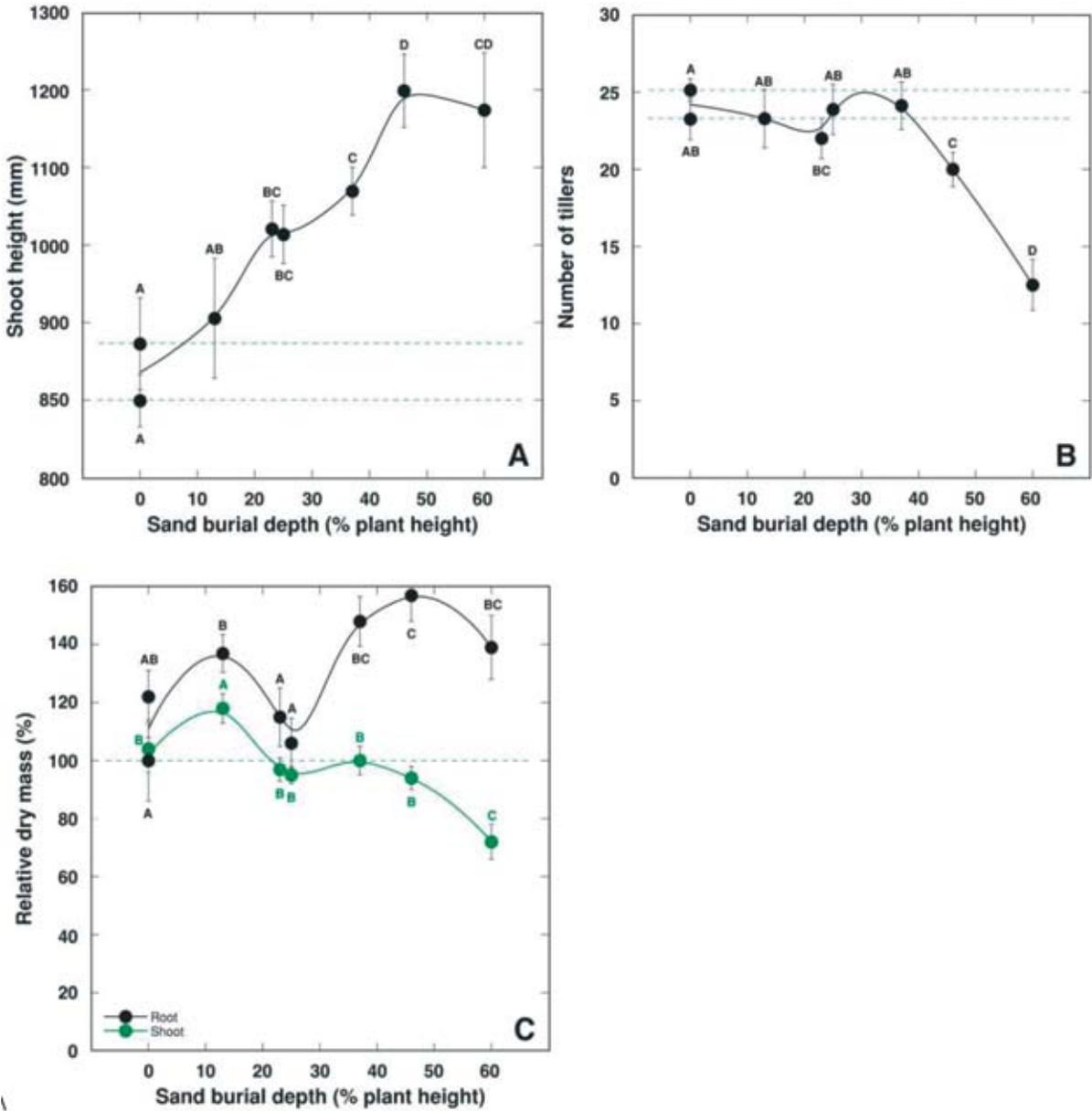
Fig. 3. Effect of sand burial depth on final shoot height (A), number of tillers (B), and relative dry mass of shoots and roots (C) of *Ammophila arenaria* plants. Data present the means ± SE of ten individual plants. Different letters indicate statistically significant differences

tinued for 15 days, followed by a minimal elongation phase of about 20 days and followed by a slower growth phase (Fig. 2A). The effect of burial depth on shoot elongation was highly statistically significant (F = 25.90, $p < 0.0001$). Positive growth response to sand burial in shoots of *A. arenaria* was pronounced more early at high burial depth (46 and 60%) and was evident ten days after the start of the treatment (Fig. 2A; $p < 0.05$). The growth rate of individual plants was extremely variable and mean shoot increment values did not follow the recognisable pattern (Fig. 2B), with no statistically significant effect of burial depth (F = 0.34, $p = 0.93$). During the minimum elongation phase, shoot length was relatively proportional to the degree of burial. Still, during the second elongation phase starting from six to seven weeks, initial differences between plants with moderate and high burial treatments partially levelled off.

At the end of the experiment, shoot height increased proportionally with an increase in burial depth up to 47% (Fig. 3A). There were no statistically significant differences between the two control treatments (with or without additional shading) as well as between the two identical treatments with or without additional shading (23 and 25%).

The number of shoots of *A. arenaria* plants initially did not change with burial, but significantly decreased from 47% burial depth (Fig. 3B). Both shoot and root dry mass increased for plants at 13% burial (Fig. 3C). Increased burial depth (37, 46, 60%) resulted in a significant increase in root biomass, but shoot biomass significantly decreased at the highest burial intensity (60%). Despite a substantial increase in shoot height with increased burial intensity, the proportion of biomass of unburied shoot part nearly linearly decreased (Fig. 4). Increase in total root biomass at high burial intensity was clearly due to adventitious root development in the buried part of the plant. Still, the biomass of roots in initial soil volume decreased.

Burial treatment of *L. arenarius* plants was also performed within a phase of active shoot elongation (Fig. 5A). However, there was no direct dependence of shoot growth on burial depth (F = 0.62, *p* = 0.65). Changes in relative height increment over time were affected by burial depth, but the effect was not sta-

tistically significant (F = 2.15, *p* = 0.10) (Fig. 5B). Increase in elongation rate during the 1st week was evident for all burial treatments (Fig. 5B). Further, the rate of shoot elongation decreased proportionally at a burial depth of 7–21%, but started to increase in treatment at 31% depth and, a week later, also for plants at other burial depths. After week four, the elongation rate for all burial intensities except the highest equilibrated and continued to decrease, but for 31% burial elongation was considerably higher until the end of the experiment. Statistically significant (*p* < 0.05) differences in shoot elongation dynamics were evident between control plants at 7, 13, and 31% burial depths. As a result, final shoot height was significantly higher than that in control plants only for 21 and 31% burial treatments, but no burial depth-dependent differences were found between all burial intensities (Fig. 6A). Besides, increased elongation and biomass allocation in the leaf sheaths were observed, despite the trend of decreasing total shoot mass (Fig. 6B). Most strikingly, the root biomass decreased with increased sand burial depth up to 21% intensity.

L. arenarius roots under non-buried conditions formed a larger part of plant biomass (> 80%; Fig. 7). The increased biomass allocation to leaves, especially leaf sheaths, was particularly pronounced when analysing the relative distribution of biomass between plant parts (Fig. 7). Due to the inhibition of root growth, the relative mass of leaf lamina and flag leaf also increased (Fig. 7).

DISCUSSION

It has been argued that *L. arenarius* is so-called obligate-buried species, with plant vigour declining under conditions of stabilised dunes (GREIPSSON & DAVY, 1994). Similarly, it has been shown that under conditions of stabilised dunes, *A. arenaria* stands deteriorate with time and eventually disappear completely (VAN DER PUTTEN & PETERS, 1995). Moreover, *Ammophila breviligulata*, a morphologically similar foredune plant from the Atlantic coast of North America, showed degeneration in the absence of sand accumulation (SELISKAR, 1994). One of the theories explaining the phenomenon is related to the increased availability of mineral nutrients as natural beach sand usually contains phosphorus and potassi-
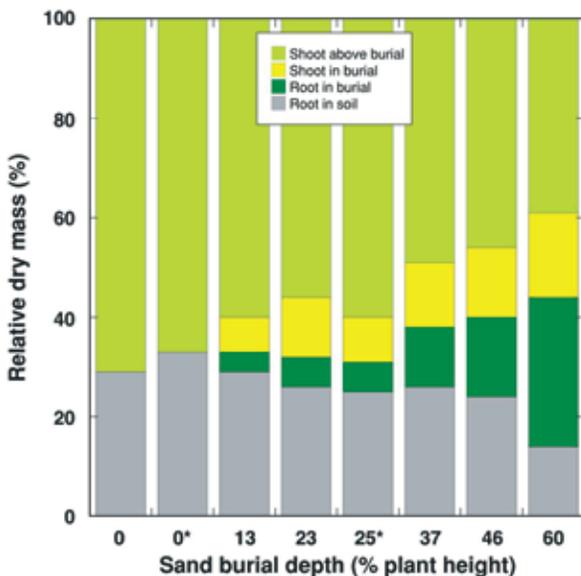

Fig. 4. Relative distribution of dry mass in different root and shoot parts of *Ammophila arenaria* buried in sand at different depths. 0* and 25* present the additional shaded treatments
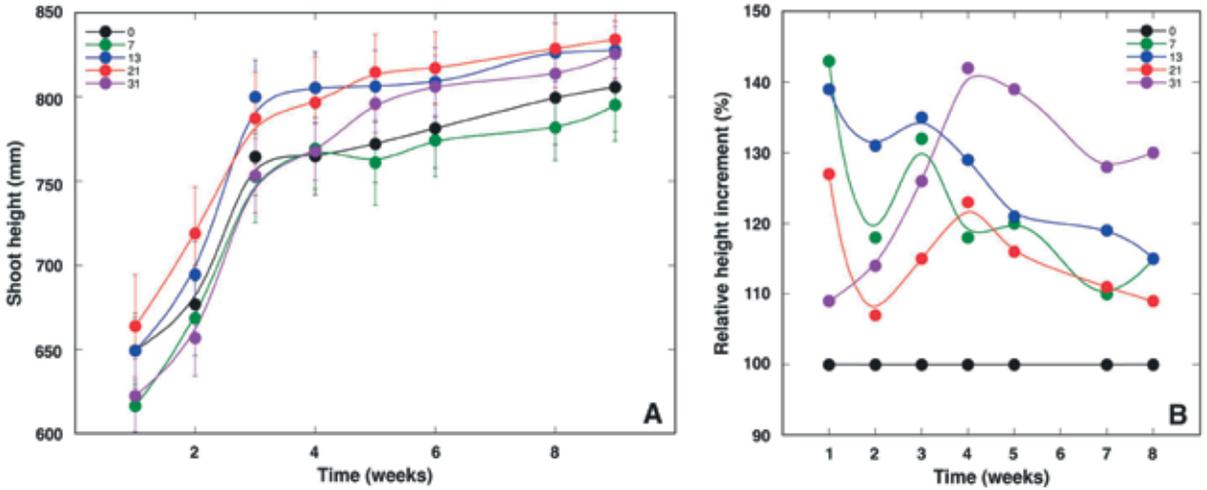
Fig. 5. Changes in shoot height in response to sand burial at various depths over time of *Leymus arenarius* plants (A). Data present the means ± SE of ten individual plants. Changes in relative height of *Leymus arenarius* shoots due to sand burial at different depths over time (B). Data present the means of ten individual plants
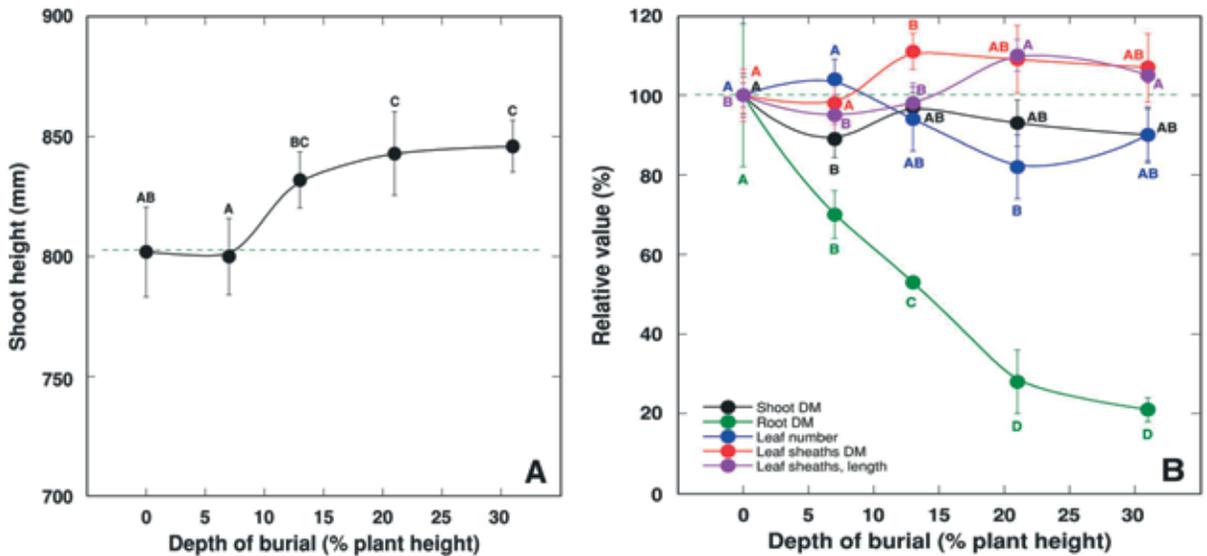

Fig. 6. Effect of sand burial depth on shoot height (A) and relative values of final morphological parameters (B) of *Leymus arenarius* plants. Data present the means ± SE of ten individual plants. Different letters indicate statistically significant differences

um (WILLIS, 1965). However, an alternative hypothesis has been raised that under stabilised dune conditions, burial-tolerant plants could not compete with newly appearing species with no sand burial tolerance (WATKINSON et al., 1979). The role of biotic factors in the decline of dune-stabilising grass species in the absence of sand accretion has also been proposed (VAN DER PUTTEN et al., 1988; SELISKAR & HUETTEL, 1993; BOUDREAU & HOULE, 2001). Irrespective of fate of dune-building plant species in stabilised dunes, it

has been indisputably established that the initial responses of sand dune-adapted species are significant growth stimulation (GILBERT & RIPLEY, 2010).

As tolerance to sand accretion is primarily associated with an ability of an individual plant to grow out of the deposited sand layer and maintain photosynthetic function, differences in short to middle term in growth responses could provide comparative evidence for their ability to withstand sand burial conditions. Surprisingly, there are no reports available on
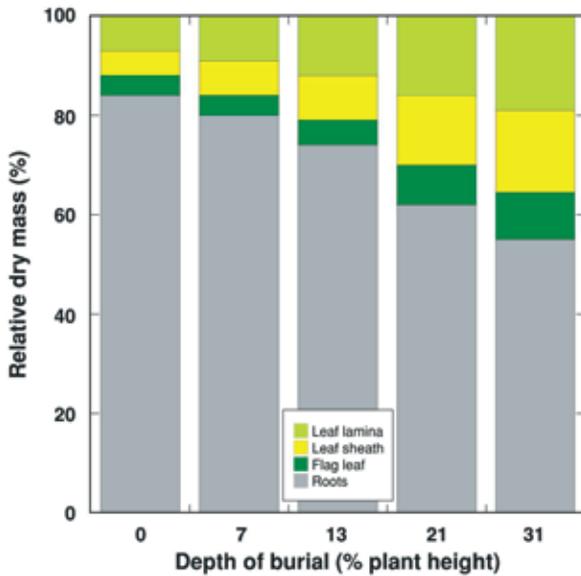
Fig. 7. Relative distribution of dry mass in different parts of *Leymus arenarius* buried in sand at different depths

experiments directly comparing these responses for *A. arenaria* and *L. arenarius* under controlled conditions. As pure quartz sand was used in the present investigation, any mineral nutrient effects through increased availability by sand burial could be ruled out.

In contrast to stress-like negative growth response of non-tolerant species to sand burial (SYKES & WILSON, 1990), growth response to the sand burial of well-adapted dune-building plant species usually exhibits three phases in dependence on burial depth: (i) growth stimulation at low to moderate sand accretion intensity, (ii) absence of any morphological effect with further increasing intensity, and (iii) growth inhibition above some threshold burial limit. However, even for dune builders, particular limits of burial intensity for each phase can vary significantly (MAUN, 1998).

The seedlings of 10-week-old *L. arenarius* showed increased resource allocation during glasshouse experiment to shoots without significant changes in total biomass, when subjected to gradual sand accretion 2 or 4 cm per week during seven weeks (GREIPSSON & DAVY, 1996). In the present study, with single burial episode, but identical total burial depth, total shoot biomass of *L. arenarius* did not increase, and the root biomass decreased significantly, indicating a distribution of resources to shoots, but with low

total carbon sequestration capacity in leaves, resulting in a lack of resources for shoot growth. In comparison, *A. arenaria* plants showed more pronounced resource acquisition capacity, with negative consequences for shoot development only at high burial intensities above 37% (Fig. 3B, C).

Differences in clonal underground architecture between the two species have been described, suggesting that low vertical growth of deeply buried rhizomes is responsible for generally lower burial tolerance of *L. arenarius* (HOBBS et al., 1983). In contrast, *A. arenaria* plants are capable of both horizontal and vertical rhizome growth, resulting in higher burial tolerance. Under buried conditions, *A. arenaria* plants initiate the development of new roots near freshly buried leaf bases (WILLIS, 1965). Also, purely physiological differences between the two species related to dry matter and nitrogen allocation could have affected the observed differences in burial responses. Thus, it was shown that the growth of *A. arenaria* is mostly shoot-oriented in comparison to primarily root-oriented growth of *Elymus mollis* (syn. of *Leymus mollis*; PAVLIK, 1983a). An opposite response was indicated for *A. breviligulata*, which maintained root biomass and decreased allocation to elongation as a result of sand burial, while remobilising nitrogen from buried parts to leaves (BROWN & ZINNERT, 2018). In a direct comparison between *A. arenaria* and *A. breviligulata* it has been shown that in contrast to the former, *A. breviligulata* is not able to develop vertically oriented rhizomes under conditions of sand burial (REIJERS et al., 2019).

Direct comparison of burial responses of the two species, *A. arenaria* and *L. arenarius*, in the present study, revealed somehow more complicated picture. First, shoot elongation response indeed showed a more pronounced positive effect for *A. arenaria* (up to 24% shoot height increase at 37% burial intensity, Fig. 3A) in comparison to that of *L. arenarius* (up to 6% shoot height increase at 31% burial intensity, Fig. 6A), and for the latter, the response did not depend on the depth of the accreted sand layer. Second, in contrast to what can be expected, *L. arenarius* plants showed an extreme degree of resource reallocation from roots to leaves in buried plants (Figs 6B, 7), but buried *A. arenaria* plants allocated resources to both shoots and buried roots at moderate burial intensity (up to 20%), but mostly to buried roots to sustain

clonal expansion at severe burial intensity (more than 30%) (Figs 3C, 4). It is notable that under control conditions, root biomass of *A. arenaria* plants was about 30% of the total biomass (Fig. 4), but that of *L. arenarius* plants more than 80% (Fig. 7).

It seems that the threshold value for single-dose burial intensity for *A. arenaria* can be 37%, but that for *L. arenarius* could not be easily established, due to low maximum limit of burial intensity used as well as clearly negative root growth response even at the lowest burial intensity. There is no doubt that gradual sand accretion as used in other studies (Greipsson & Davy, 1996) would result in a relatively higher burial intensity of the studied species, more resembling that under natural conditions. Moreover, a particular disparity between the results of the present experiments and these from other studies could be related to possible genetic differences of the plant material used as well as to variation in experimental conditions, mainly, when experimental manipulation by burial was performed under field conditions.

Consequently, with *A. arenaria* accumulating relatively more biomass in shoots and *L. arenarius* in roots under non-buried conditions, apparent differences found between *A. ammophila* and *L. arenarius* in sand burial responses (stimulation of growth of both parts for the first and translocation of resources from roots to shoots for the second species), are related to both morphological and physiological factors: spatial organisation of rhizome development and resource allocation towards leaf growth. From the other hand, dune building ability of the particular grass species is directly related to these differences in addition to simple burial tolerance. Due to differences in clonal architecture, *A. arenaria* plants can support the formation of relatively steep dunes, while dunes built by *L. arenarius* plants could be significantly wider, but lower.

It can be concluded that while both dune-building grass species *A. arenaria* and *L. arenari*us show positive shoot growth response to moderate sand burial, differences in individual responses at morphological and physiological level indicate the existence of different genetically-based adaptation strategies. This type of information could be useful for measures of practical dune conservation as well as habitat restoration needs.

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PAKRANČIŲ KOPAS FORMUOJANČIŲ ŽOLINIŲ RŪŠIŲ *AMMOPHILA ARENARIA* IR *LEYMUS ARENARIUS* AUGIMO ATSAKAS Į JŲ PANARDINIMĄ SMĖLYJE

Gederts Ievinsh, Una Andersone-Ozola

Santrauka

Ammophila arenaria ir *Leymus arenarius* yra būdingos Baltijos jūros pakrančių kopų buveines formuojančios žolinės rūšys. Tyrimo tikslas buvo kontroliuojamose sąlygose palyginti abiejų augalų rūšių augimo atsaką į jų panardinimą smėlyje. Tiriami augalai buvo išauginti iš sėklų, surinktų natūraliose pakrančių buveinėse. Augalai stiebėjimo stadijoje buvo persodinti į atskirus konteinerius, kuriuose buvo panardinti smėlyje skirtinguose gyliuose ir toliau auginti automatizuotame šiltnamyje 9–11 savaičių. *A. arenaria* panardinimas į smėlį paskatino augalų ūglių augimą. Poveikis buvo akivaizdus praėjus dešimčiai dienų nuo bandymo pradžios ir buvo reikšmingesnis, esant gilesniam panardinimui smėlyje (46 ir 60%). Ūglių ir šaknų masė padidėjo prie augalų panardinimo smėlyje 13%. Didesnis panardinimo smėlyje gylis (37,46 ir 60%) lėmė reikšmingą šaknų masės padidėjimą, tačiau ūglių biomasė žymiai sumažėjo, esant didžiausiam panardinimo intensyvumui (60%). Tačiau nenustatyta reikšmingos *L. arenarius* ūglių pailgėjimo priklausomybės nuo jų panardinimo smėlyje intensyvumo. Tuo tarpu šaknų biomasė sumažėjo didėjant panardinimo smėlyje gyliui. Apibendrinant galima teigti, kad nors abi tirtos augalų rūšys parodė teigiamą ūglių augimo atsaką į vidutinio intensyvumo panardinimą smėlyje, morfologiniai skirtumai parodė skirtingą jų prisitaikymo strategiją.