Écoscience

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/teco20

The responses of *Spinifex littoreus* to sand burial on the coastal area of Pingtan Island, Fujian Province, South China

Shuang Song, Jianhui Du, Qirui Wu, Mingyang Ni, Yijia Wang & Yingling Zhang

ÉCOSCIENCE
https://doi.org/10.1080/11956860.2021.1888523

The responses of *Spinifex littoreus* to sand burial on the coastal area of Pingtan Island, Fujian Province, South China

Shuang Song [a,b,c], Jianhui Du [a,d], Qirui Wu [a], Mingyang Ni [a], Yijia Wang [a,b,c] and Yingling Zhang [a]

[a]School of Geography and Planning, Sun Yat-Sen University, Guangzhou, China; [b]State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of Geographical Science, Beijing Normal University, Beijing, China; [c]Institute of Land Surface System and Sustainability, Faculty of Geographical Science, Beijing Normal University, Beijing, China; [d]Guangdong Key Laboratory for Urbanization and Geo-simulation, Sun Yat-Sen University, Guangzhou, China

ABSTRACT

The adaptive capacity of psammophytes to sand burial is crucial for the ecological restoration of coastal dune systems. The responses of *Spinifex littoreus* to different sand burial depths and levels were examined on the coast of Pingtan Island, Fujian Province, South China. The results indicated that, compared with the control group (CG), sand burial on the *S. littoreus* stolons had no significant impact on the vertical growth of its conjoint ramets. However, the horizontal growth of *S. littoreus* stolons was stimulated and significantly increased in half-intense (HI) and complete-intense (CI) sand burial treatments by 24.56% and 40.79%, respectively. Throughout the experiment, about 96% of adventitious roots were observed on the base section of stolons, while no roots in the control group (CG). After 20-day artificial sand burial treatments, the dry weight ratio between stem and leaf of *S. littoreus* was decreased in all three sections of stolons, especially for the top sections. Overall, *S. littoreus* can adapt to the complete and intense sand burial in growing season by rapid growth of stolons, abundant production of adventitious roots on the stolon base, and more germination of leaves on the stolon top.

RÉSUMÉ

La capacité adaptative des psammophytes à l'ensablement est cruciale pour la restauration écologique des systèmes dunaires. Les réponses de *Spinifex littoreus* à différentes profondeurs et différents niveaux d'ensablement ont été étudiées sur la côte de l'île de Pingtan (Fujian, Chine). Les résultats montrent que, comparativement au groupe contrôle, l'ensablement des stolons de *S. littoreus* n'a pas eu d'effet significatif sur la croissance des ramets. Toutefois, la croissance horizontale des stolons de *S. littoreus* a été stimulée et a augmenté significativement dans les traitements d'ensablement semi-intense et complètement intense, par 24,56% et 40,79%, respectivement. Durant l'expérience, environ 96% des racines adventives ont été observées à la base des stolons, tandis qu'aucune racine n'a été observée dans le groupe contrôle. Après un traitement d'ensablement artificiel de 20 jours, le rapport du poids sec entre les tiges et les feuilles de *S. littoreus* a diminué dans les trois sections des stolons, surtout celle du haut. En règle générale, *S. littoreus* peut s'adapter à un ensablement complet et intense durant la saison de croissance par la croissance rapide des stolons, la production abondante de racines adventives à la base des stolons et la production de plus de feuilles dans la partie supérieure des stolons.

ARTICLE HISTORY
Received 2 January 2021
Accepted 6 February 2021

KEYWORDS
Psammophytes; sand burial; *Spinifex littoreus*; responses; adventitious roots; Pingtan Island

MOTS CLÉS
Psammophytes; ensablement; *Spinifex littoreus*; réponses; racines adventives; île de Pingtan

Introduction

Coastal sand dunes can provide multiple ecological services and play an important role in the sustainable development of coastal areas with rising sea levels, surface subsidence and coastal hazards (Martínez et al. 2004; De Battisti and Griffin 2020). Recently, due to the influence from both climate change and anthropogenic activities, many coastal sand dunes have been modified or destroyed, and this can, or has potentially led to the retreat of coastlines, disappearance of habitats, loss of biodiversity, and severe degradation of ecosystem functions in coastal sand dunes (Feagin et al. 2005; Schlacher et al. 2011; Qu et al. 2017). With the rapid development of the economy in China, most coastal sand dunes were eradicated due to real estate and infrastructure development and tourism activities. Almost no well-preserved coastal sand dunes are left, which apart from the loss of ecological functions and habitats, may ultimately result in coastal erosion and loss of life, property and economy

CONTACT Jianhui Du dujh1982@hotmail.com School of Geography and Planning, Sun Yat-Sen University, No. 135, West Xingang Road, Haizhu District, Guangzhou City, Guangdong Province, Guangzhou, China 510275

(Yang et al. 2017). Hard engineering structures have been proven to be costly and detrimental for the protection of coastal regions, so it is important to select natural and environment-friendly methods for both the protection and restoration of the remaining coastal dune systems (Hanley et al. 2014).

Psammophytes can build and stabilize coastal sand dunes, which will favor the restoration of their ecological functions due to specific adaptive strategies (Yuan et al. 1993; Brown and Zinnert 2018; De Battisti and Griffin 2020). However, only a few species can survive in these ecosystems due to environmental stresses such as drought, salt spray, strong winds, and especially the frequent and intensive sand burial (Maun and Lapierre 1986; Hesp 1991; Maun 1994; Du and Hesp 2020). Sand burial is commonly considered as the selective force for coastal plant regeneration and survival (Moreno-Casasola 1986; Maun 1994), as it can decrease and even eliminate psammophytes if the level of sand burial exceeds their tolerance capacity, ultimately altering species composition in coastal dune systems (Maun and Perumal 1999; Miller 2015).

The tolerance capacity of species to different sand burial levels varies greatly, affecting initial and subsequent coastal dune development and morphology (Hesp 1989). Generally, psammophyte growth can be stimulated by low to moderate sand burial (Zhou et al. 2015b; Harris et al. 2017; Brown and Zinnert 2018; Wang et al. 2019), while intensive sand burial will decrease plant biomass and survival (Maun 1996; Franks and Peterson 2003). Wang and Wang (2005) demonstrated that both stem height in the vertical direction and leaf weight of *Messerschmidia sibirica* increased with light sand burial, while they decreased with moderate treatments. In addition, Zhou et al. (2015a) showed that the growth of *Artemisia desterorum* was enhanced by moderate sand burial, but inhibited by intense sand burial. Elongation of stolons, upward growth of ramets, and development of adventitious roots are the main adaptive strategies of plants to sand burial, potentially altering the biomass allocation of psammophytes in coastal sand dunes (Dech and Maun 2006; Frosini et al. 2012; Mendoza-González et al. 2014; Brown and Zinnert 2018).

Spinifex littoreus, a herbaceous plant, is the dominant species in coastal foredunes in South China. It often grows vigorously in the more dynamic foredune, while it declines in the more stabilized backdunes, similarly to its Australian and NZ cousins *S. hirsutus* and *S. sericeus* (Hesp 1989). Its peak growth occurs in summer, with two growth forms, including elongation of horizontal stolons and upward growth of vertical ramets, which sprout out from the same vegetative reproduction, and usually can be recognized as the same ramets (Jackson et al. 1985). The leaf apex of *S. littoreus* is very sharp and hard, which makes it difficult to be intruded, and is usually recognized as one of the good species for sand dune fixation in the region (Yang et al. 2017). Typhoons often occur in the growing season in South China, causing severe sand burial of *S. littoreus*, particularly its stolons on nebkhas (a sand dune that forms around vegetation) forming the foredune zone (Yang et al. 2017) (Figure 1). However, the tolerance capacity of this species to sand burial is still unclear, and so is the processes leading to its revitalization after sand burial caused by frequent typhoon events in the growing season. Furthermore, the local government has planted an invasive species (*Casuarinas equisetifolia*) to stabilize nebkhas originally formed by *S. littoreus*, which caused severe damage to the native species and will inevitably increase the fragility of coastal dune ecosystems in the region (Figure 1). Therefore, understanding the adaptive strategies of

Figure 1. Left: Intensive sand burial on the *Spinifex littoreus* nebkhas on Pingtan Island after typhoon Soudelor (1513) landed in Putian City, Fujian Province, China in August, 2015. Right: The nebkhas formed by *Spinifex littoreus* were stabilized by planting seedlings of an invasive species (*Casuarinas equisetifolia*) on Pingtan Island, Fujian Province, China.

S. littoreus to sand burial and its role in the stabilization of coastal sand dunes are crucial for effective coastal dune management and conservation in South China.

In this study, we assume that the growth of *S. littoreus* can be facilitated by increased sand burial, which is probably the key factor for this native plant to adapt to the intense sand burial caused by frequent typhoon events in the growing season. We measured the vertical height of ramets, horizontal length of stolons, and biomass allocation of adventitious roots, stems and leaves on stolons of *S. littoreus* under different simulated sand burial levels in a field experiment during a growing season on Pingtan Island, Fujian Province, South China.

Material and methods

Study area

Pingtan Island is located on the eastern coast of Fujian province, South China, with a sub-humid and oceanic monsoon climate. The study area is situated in the southeast of Pingtan Island (25° 26′ 36″ – 25° 26′ 48″ N, 119° 46′ 09″ – 119° 46′ 21″ E), and is usually regarded as the most well-preserved coastal sand dunes in China (Figure 2) (Yang et al. 2017). Annual average temperature is 19.5 °C, and precipitation is 1151 mm. Monsoons are the dominant wind in the area, SE in the summer and NE in the winter, with an annual average wind speed of 6.9 m/s. A total of 106 typhoons made landfall on Pingtan Island from 1981 to 2019, average 2.65 times per year, mainly from July to September. Maximum wind speed can be up to 32.7 m/s, ultimately leading to severe sand burial of psammophytes. Soil is mainly composed of medium to fine sand, with well-sorted grains. Sediments are transported by the wind and intercepted by the ramets and stolons of *S. littoreus*, and a discrete dune mound or hummock is usually formed by aeolian sand deposition within an isolated plant or group of plants (Hesp and Smyth 2019), ultimately developing into a 300 m wide nebkha dominated foredune zone (Figure 1). *S. littoreus* is the dominant species in the study area and auxiliary plants include *Oenothera drummondii, Cynodon dactylon, Pluchea pteropoda*, and *Sesuvium portulacastrum* (Yang et al. 2017).

Methods

Field experiments were carried out in July 2016, in Tannan bay, Pingtan Island (Figure 2). One study belt not affected by animals, pollutants or human activities

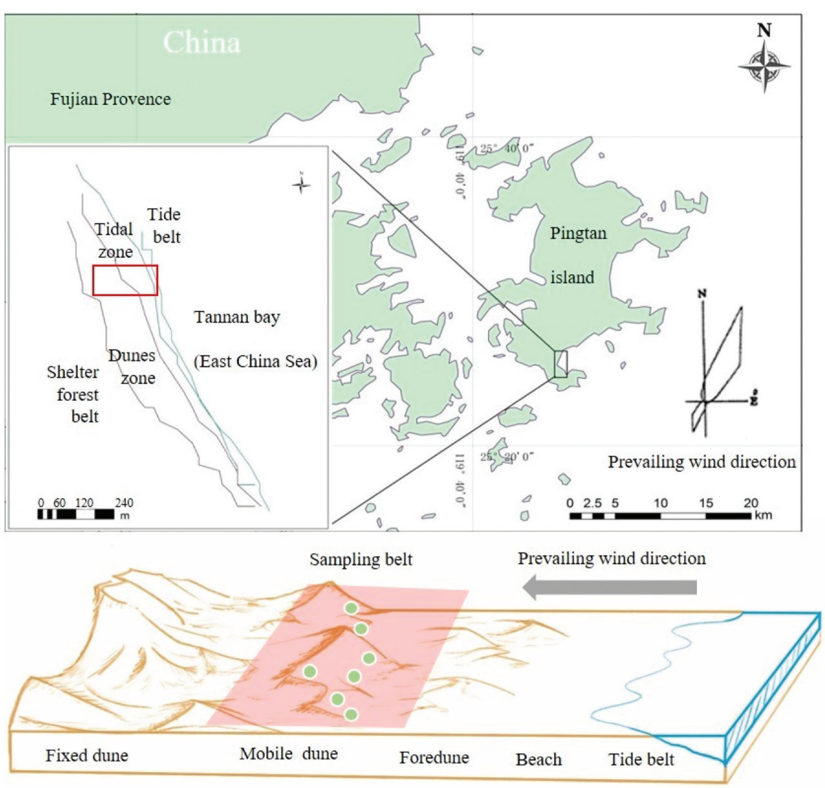

Figure 2. Schematic view of the field experiment.

was selected in the center of the coastal sand dunes. Considering most of the *S. littoreus* were distributed on the windward slope of nebkhas in mobile dunes belt, 35 healthy plants with uniform size were selected on this slope. All the observed plants could be well distinguished from surrounding plants, the height of vertical ramets and the length of stolons were all similar with each other before the burial treatments. Stolons of *S. littoreus* on the windward slopes were selected and labeled with a red cord at points 1/3 and 2/3 of the length from the stolon base to the stolon top. All plant species around the selected plants were manually cleared, and wooden frames 20 cm in height (similar to the height of stolons) were set around the selected plants. Later, all the observed plants were fixed with a label, and their serial numbers were recorded on the labels and wooden baffles to facilitate later, periodic measurements. The few adventitious roots present on the stolons of the observed plants were completely eliminated, the height of vertical ramets and length of stolons were measured separately before the experiment began. Later, all the plants were artificially buried with nearby sand (Figure 3, Table 1), while control groups (CG) were unburied throughout the experiment.

Since vertical ramets of *S. littoreus* are relatively high, it is unlikely for them to be completely buried in a single typhoon event (Figure 1). Thus, in the treated *S. littoreus*, only the stolons were buried at different depths and levels (Figure 3; Table 1). Moreover, some adventitious roots on the stolons of selected plants were observed only a few days after treatments, so the growth parameters of plants were dynamically investigated 5, 9, 13, 17, 20 days after the sand burial to investigate the response of *S. littoreus* to severe sand burial over a short time scale.

During the measurements, the sand burying the plants was carefully removed to one side in a wooden baffle, and the height of the vertical ramets, the length of the stolons and adventitious roots were all measured with a tape. Considering the uncovering and recovering of sand might affect the gravity signal of plants to sand burial, we finished our measurements in a very short time period (usually 3–5 minutes compared with days of interval) to minimize the potential disturbance, and recovered the plants to the previous sand burial level with the same sand. When the experiments were finished, both above- and belowground plant biomass were collected and separated according to the label on the stolons. Then, all the samples were taken back to the laboratory, and the roots, stems and leaves were separated from the stolons, dried in the oven at 65 °C for about 24 h until the weight was constant, and then weighed with an analytical balance (accuracy: 0.0001 g).

All the data were calculated as averages of all replications with standard error as a measurement of variability. The results were analysed with Python3 and package Pingouin (Vallat 2018). For each observed variable, we

Table 1. Sand burial treatments.

Treatment	Burial depth	Burial level
CG	No sand burial	No sand burial
HL	Half	Light
HM	Half	Moderate
HI	Half	Intense
CL	Complete	Light
CM	Complete	Moderate
CI	Complete	Intense

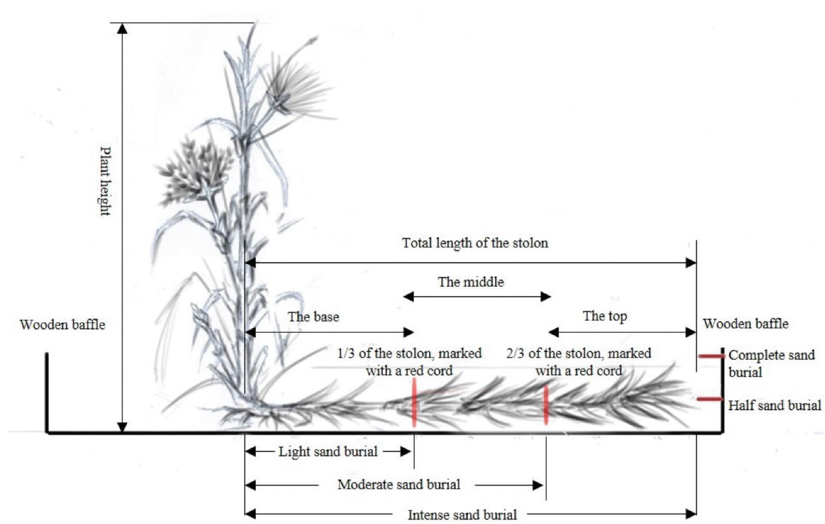

Figure 3. Schematic view of the sand burial treatments.

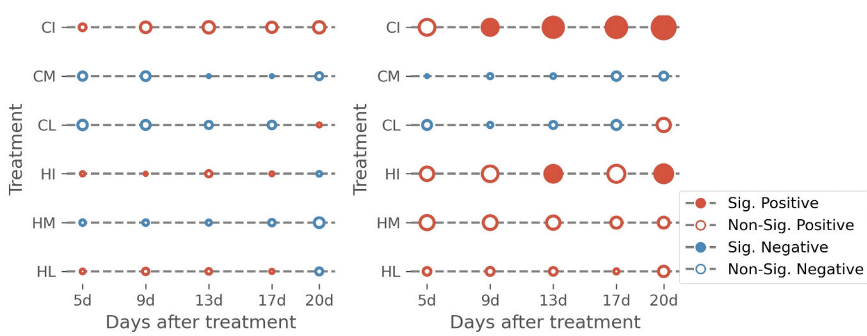

Figure 4. Difference in ramets height growth (left) and horizontal stolons (right) between control group (CG) and different sand burial treatments. The blue dots refer to negative differences (less than CG) while the red dots refer to positive differences (more than CG). The filled dots show statistically significant differences ($P < 0.05$) and the size of the dots denotes the size of the difference.

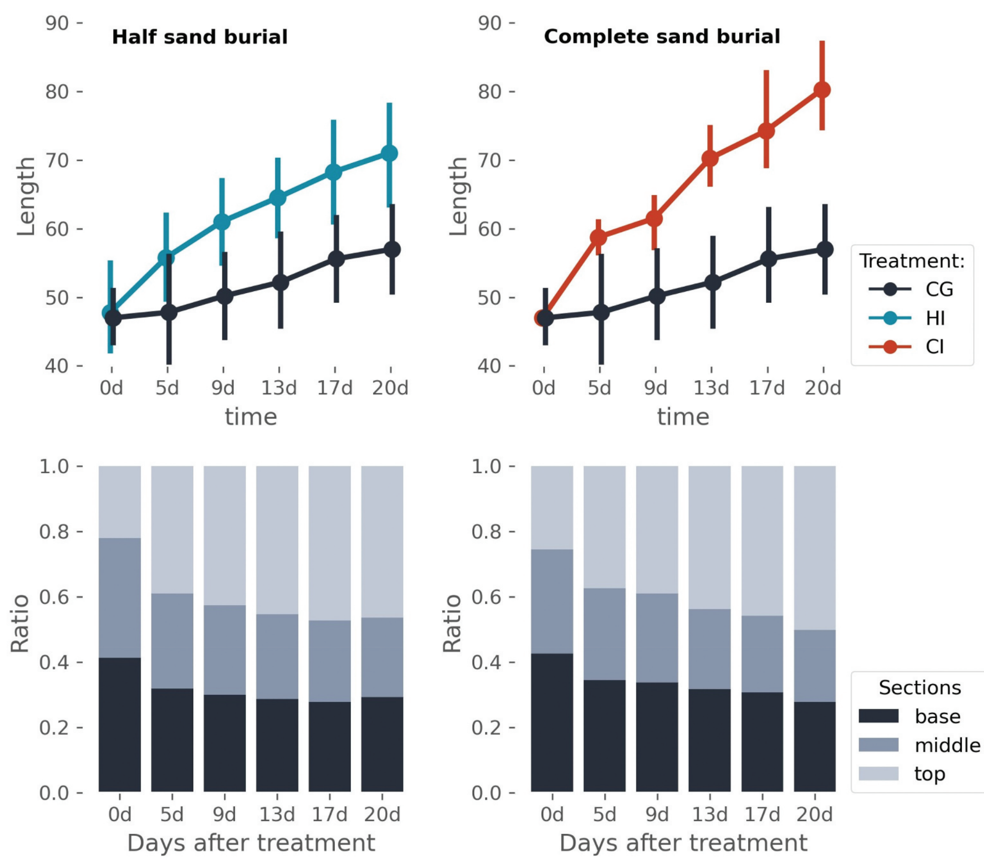

Figure 5. Growth process of horizontal stolons with half-intense (HI) group and complete-intense (CI) group plants. Upper left: Growth of horizontal stolons' length of the HI group, compared with the control group (CG). Upper right: Growth of horizontal stolons' length of the CI group, compared with the control group (CG). Lower left: growth of different sections of horizontal stolons' length of the HI group. Lower right: growth of different sections of horizontal stolons' length of the CI group.

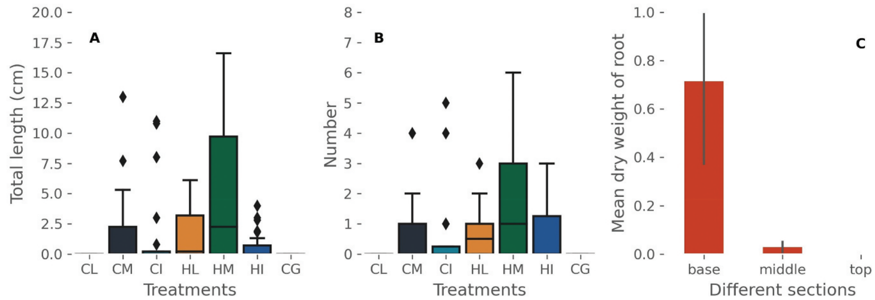

Figure 6. (a) Total length of adventitious roots under different sand burial treatments. (b) Number of adventitious roots under different sand burial treatments. (c) Mean dry weight in different sections of horizontal stolons.

used repeated measure ANOVA to test for significant effects of the experimental treatments ($P < 0.05$).

Results

Influence of sand burial on the growths of S. littoreus

After a 20-day sand burial experiment, ramet height of *S. littoreus* did not show any significant difference compared with the control group (CG). However, there were significant effects on the growth of horizontal stolons in both the half-intense sand burial (HI) and the complete-intense sand burial (CI) treatments, particularly the latter (Figure 4). Specifically, the significant effect of sand burial on stolon growth was first observed at 9 days in the CI treatments, while it was delayed at 13 days in the HI treatments ($P < 0.05$). Moreover, the growth of horizontal stolons was more enhanced by sand burial in the CI treatment than in the HI treatment, with stolon length increased by 40.79% in the CI treatment vs. 24.56% in the HI treatment after 20-day sand burial (Figure 5). Based on these results, stolon length in the top section increased continuously from 22.09% to 46.48% and from 25.53 to 50.20% in the HI and CI treatments, respectively.

Influence of sand burial on the biomass allocation of S. littoreus

The production of adventitious roots was promoted in most of the sand burial treatments, both in total length and number of roots. The highest increase was observed in the HM treatment where average root length was 5.1 cm and average root number was 2, while no adventitious roots were observed in the CG treatments (Figure 6). Adventitious roots were mainly found at the base section of stolons (96%), few (4%) were found in the middle section, and none were found in the top section (Figure 6). The dry weight ratio between stems and leaves of *S. littoreus* decreased under most sand burial treatments compared with the CG, and varied in different stolons sections. More biomass was allocated to leaves, particularly in the top section of the stolons (Figure 7).

Discussion

Responses of S. littoreus *to severe sand burial*

Sand burial can reduce the photosynthetic area of species, hence inhibiting plant performance in coastal sand dunes (Hesp 1991; Brown and Zinnert 2018). Species that withstand sand burial can recover rapidly by elongating internodes in vertical shoots to overcome this physical barrier (Frosini et al. 2012; Keijsers et al. 2016; Qu et al. 2017; Enríquez et al. 2019). However, this is inconsistent with our study, as we showed that none of the sand burial treatments had a significant effect on vertical growth of ramets on the nebkhas. This is probably due to the growth characteristics of *S. littoreus*, which displays both vertical and horizontal extension. The height of its ramets ranging from 40 to 60 cm, it is virtually impossible to bury the entire vertical ramets during a single typhoon event (Yang et al. 2017). For plants on the windward slopes, some unburied leaves are expected to provide photosynthetic substance to sustain the continuous growth of *S. littoreus* even when severe burial occurred (Figure 1).

Consequently, rapid ramet height growth in *S. littoreus* is not considered as the priority to escape sand burial, but it tends to increase stolon length due to its vulnerability to be buried in a typhoon event, which may contribute to the absence of a significant effect of artificial sand burial on ramet height in our experiment (Maun 1994). Our field investigation further showed that the maximum length of *S. littoreus* stolons could be up to 2–3 m, which was about to 4–6 times its ramet height (Figure 8). This is in agreement with Woodhouse et al. (1977), who reported that *Uniola*

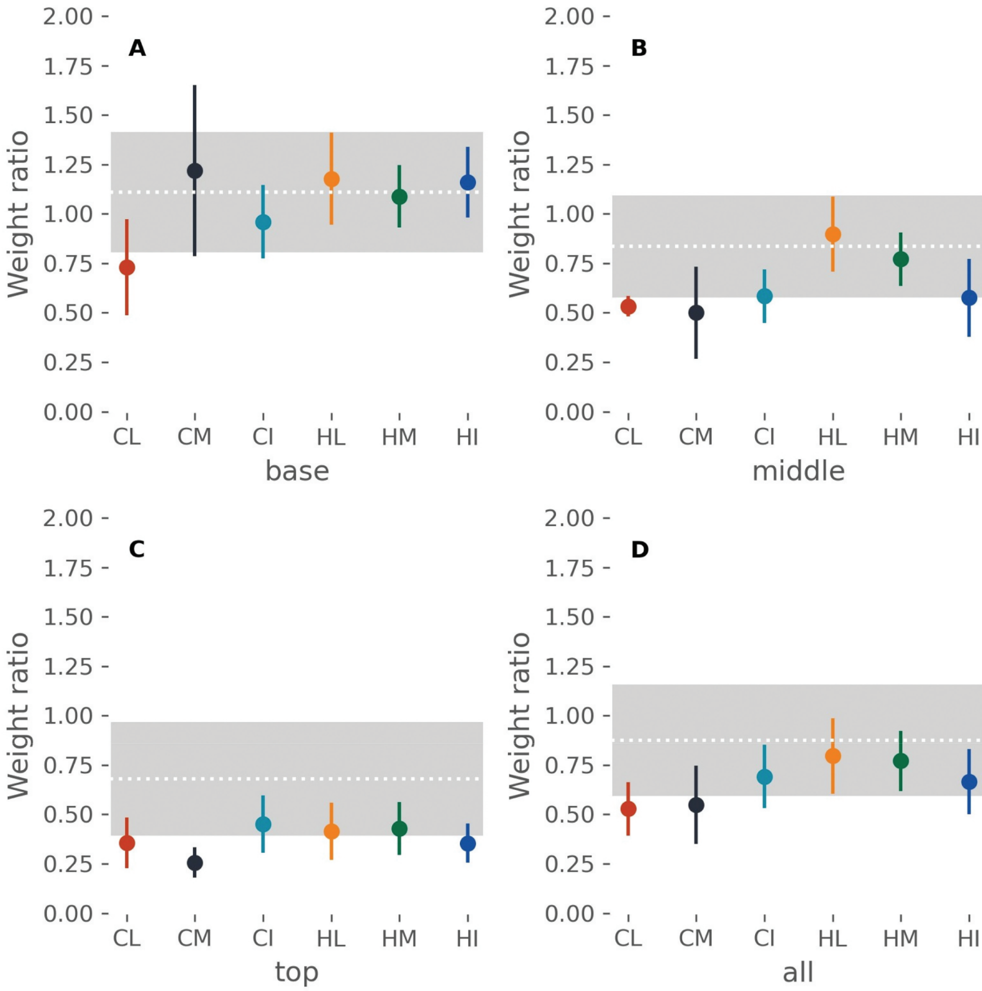

Figure 7. Weight ratio between stem and leaf after the end of experiments under different treatments. The white lines denote mean ratio of the control group (CG) while the grey areas denote the standard error of the control group. Weight ratios from different sections were compared one by one (a: base sections, b: middle sections, c: top sections, d: all sections).

paniculata tended to grow upward rather than seaward, while *Ammophila breviligulata* preferred to colonize seaward beach surfaces by rhizome growth, which may explain the wider distribution of the latter in intensive sand burial environments.

Extensive colonization of horizontal stolons after sand burial will increase the plants' capacity to access water and nutrients, which is especially critical for the establishment of plants in a resource-poor environment, such as coastal sand dunes, and further enhance their growth as the dominant species on coastal sand dunes (Mendoza-González et al. 2014; Divyasree and Raju 2019). Our results indicate that all sand burial treatments significantly promoted stolon growth, and complete sand burial had a more obvious influence than half sand burial. Species usually stimulate their growth

Figure 8. Stolon length of *S. littoreus* on nebkhas in the developmental period (left) and the stabilized period (right). Photo taken on Pingtan Island.

according to a gravity stress signal (Zhou et al. 2015b), and increase their node number and internode length to escape this physical barrier (Maun 1996). The gravity stress signal in complete sand burial was usually stronger than in half sand burial (Wang and Wang 2005). We found that the tall ramets of *S. littoreus* could intercept sand, while stolons were buried at different levels on nebkhas. The stolon length of *S. littoreus* on nebkhas in the developmental period was much longer than in the stabilized period, which can be attributed to more dynamic sand movement in the former (Figure 8).

Production of adventitious roots on the stolons will enhance the capacity of plants to use limited soil water and nutrition, and change the biomass and growth rhythms of plants (Martínez and Maun 1999; Dech and Maun 2006). Our results indicate that adventitious roots were produced on *S. littoreus* stolons in most of the sand burial treatments, both total length and number of roots were increased compared with the CG treatments, which will facilitate their revitalization from sand burial caused by typhoon events. More adventitious roots were allocated to the stolon base after sand burial. Generally, sand depth is higher at the stolon base than other stolon sections, which increases the capacity for root growth, thus improving access to soil water and nutrients (Yuan et al. 1993). Moreover, *S. littoreus* has a fibrous root system, and adventitious roots are initially produced from the primordium at the stolon node. However, only the primordium at the stolon base can develop well and finally break through the cuticular layer to produce adventitious roots (Hochholdinger et al. 2004).

The top section of stolons is usually the least buried, and more leaves emerging on stolon top will reduce the risk of further sand burial, increase light capture for photosynthesis and carbon gain (Yuan et al. 1993; Shi et al. 2004; Brown and Zinnert 2018), and ensure enough supply of carbohydrates for the plants to escape sand burial. We found that a larger percentage of leaves was observed on the top of stolons compared with other stolon sections. Gilbert et al. (2008) also demonstrated that sand burial could increase leaf area in mobile dune species, hence fully or partially replacing the lost photosynthetic leaf area, so the shoot must elongate its stem to keep newly produced leaves above the sand surface. Consequently, in order to reduce the cost of stem tissue production, stem tissue density is usually negative to the maximal stem elongation rate (Frosini et al. 2012). We also found that the extension rate was faster at stolon top than other stolon sections, and it grew even faster as the sand burial prolonged. Consequently, the dry biomass ratio of stem to leaves showed a decreasing trend from the stolon base to the stolon top of *S. littoreus* in all sand burial treatments.

Significance of S. littoreus*' adaptation to sand burial*

The response of plants to sand burial is usually species-specific, and plant growth will be enhanced under optimal sand burial rate (Nolet et al. 2018). We found that *S. littoreus* can adapt to the severe sand burial caused by frequent typhoons in our study area, and will revitalize later by increasing horizontal stolon length, producing abundant adventitious roots at the stolon base and allocating more biomass to leaves at the stolon apex (Yuan et al. 1993). However, if the sand burial rate exceeds some threshold, the growth of sand dune species will be inhibited (Maun 1996; Shi et al. 2004). Our field investigation showed that few *S. littoreus* can be found on the leeward slope of nebkhas (Figure 9), which can be attributed to excessive sand burial of both ramets and stolons. The absence of photosynthesis area, combined with continuous depletion of reserves stored in the plants (Frosini et al. 2012), finally lead to the failure of *S. littoreus* escape from excessive sand burial on the leeward slope of nebkhas (Figure 9). Similarly, if the sand burial rate is below the threshold, the species that cannot withstand severe sand burial will co-occur with those resistant to it. We found that low to moderate sand

Figure 9. Left: Leeward is the most severe sand-burial position where few plants can survive, including *S. littoreus*. Right: Swales are much better habitats for plants because of little sand burial. However, *S. littoreus* cannot be dominant in this area because of heavy competition. Photo taken on Pingtan Island.

burial treatments had no significant effect on stolon extension of *S. littoreus*, hence not favoring access to soil water and nutrients, and further weakening its position as dominant species. This is consistent with our field investigation, where *Oenothera drummondii*, an invasive species widely distributed on stabilized dunes in South China, more frequently co-occurred with *S. littoreus* on nebkhas stabilized by *C. equisetifolia* (Figures 8 and 9).

We consider that the capacity of *S. littoreus* to stabilize and build coastal sand dunes along the coastline of South China has been underestimated or neglected by the local government, and that coastal managers should allow the regular input of wind-blown sand towards this unique species (Nolet et al. 2018), which can mitigate the loss from coastal hazards in this region. The nebkhas formed by *S. littoreus* should be kept dynamic rather than stabilized by planting invasive species such as *C. equisetifolia*. Otherwise, the risk of species invasion (e.g., *O. drummondii*) will be higher on coastal sand dunes. Consequently, the native and highly adaptive *S. littoreus* will gradually be replaced and eradicated, and the degradation of coastal dune systems will be aggravated.

Conclusion

None of the sand burial treatments in our study had a significant impact on ramet height of *S. littoreus*. However, compared with the control group, sand burial significantly enhanced stolon extension of *S. littoreus* under half-intense and complete-intense treatments by 24.56% and 40.79%, respectively. Sand burial also stimulated the production of adventitious roots, mainly at stolon base, and enhanced the germination of leaves at the stolon top. *S. littoreus* can adapt to severe sand burial during the growing season; it can thus be considered one of the optimal species for stabilizing and building coastal sand dunes in South China.

Acknowledgments

Thanks to Patrick Hesp for his assistance with editing our paper. Thanks to Zhiqiang Ye, Jin Qin and Qi Zhang for their assistance with the field experiment.

Disclosure statement

The authors declare no competing interests.

Funding

This research was supported by the National Science Foundation [Grants # 41101011; 41801101].

ORCID

Shuang Song http://orcid.org/0000-0002-8112-8780

References

Brown JK, Zinnert JC. 2018. Mechanisms of surviving burial: dune grass interspecific differences drive resource allocation after sand deposition. Ecosphere. 9(3):e02162. doi:10.1002/ecs2.2162.

De Battisti D, Griffin JN. 2020. Below-ground biomass of plants, with a key contribution of buried shoots, increases foredune resistance to wave swash. Ann Bot. 125(2):325–334. doi:10.1093/aob/mcz125.

Dech JP, Maun MA. 2006. Adventitious root production and plastic resource allocation to biomass determine burial tolerance in woody plants from central Canadian coastal dunes. Ann Bot. 98(5):1095–1105. doi:10.1093/aob/mcl196.

Divyasree M, Raju AJS. 2019. An ecological study of reproduction in *Spinifex littoreus* (Burm.F.) Merr. (Poaceae), a dominant species of sand dune ecosystem along the Visakhapatnam coast, Andhra Pradesh. J Palynol. 55:35–54.

Du J, Hesp PA. 2020. Salt spray distribution and its impact on vegetation zonation on coastal dunes: a review. Estuar Coast. 43(8):1885–1907. doi:10.1007/s12237-020-00820-2.

Enríquez AR, Marcos M, Falqués A, Roelvink D. 2019. Assessing beach and dune erosion and vulnerability under sea level rise: a case study in the Mediterranean Sea. Front Marine Sci. 6:4. doi:10.3389/fmars.2019.00004.

Feagin RA, Sherman DJ, Grant WE. 2005. Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. Front Ecol Environ. 3(7):359–364. doi:10.1890/1540-9295(2005)003[0359:CEGSRA]2.0.CO;2.

Franks SJ, Peterson CJ. 2003. Burial disturbance leads to facilitation among coastal dune plants. Plant Ecol. 168(1):13–21. doi:10.1023/A:1024450623205.

Frosini S, Lardicci C, Balestri E. 2012. Global change and response of coastal dune plants to the combined effects of increased sand accretion (burial) and nutrient availability. PLoS One. 7(10):e47561. doi:10.1371/journal.pone.0047561.

Gilbert M, Pammenter N, Ripley B. 2008. The growth responses of coastal dune species are determined by nutrient limitation and sand burial. Oecologia. 156(1):169–178. doi:10.1007/s00442-008-0968-3.

Hanley ME, Hoggart SPG, Simmonds DJ, Bichot A, Colangelo MA, Bozzeda F, Heurtefeux H, Ondiviela B, Ostrowski R, Recio M, et al. 2014. Shifting sands? Coastal protection by sand banks, beaches and dunes. Coast Eng. 87:136–146. doi:10.1016/j.coastaleng.2013.10.020.

Harris AL, Zinnert JC, Young DR. 2017. Differential response of barrier island dune grasses to species interactions and burial. Plant Ecol. 218(5):609–619. doi:10.1007/s11258-017-0715-0.

Hesp PA. 1989. A review of biological and geomorphological processes involved in the initiation and development of incipient foredunes. Proc R Soc Edinb B. 96:181–201.

Hesp PA. 1991. Ecological processes and plant adaptations on coastal dunes. J Arid Environ. 21(2):165–191. doi:10.1016/S0140-1963(18)30681-5.

Hesp PA, Smyth TAG. 2019. CFD flow dynamics over model scarps and slopes. Phys Geogr. 42(1):1–24. doi:10.1080/02723646.2019.1706215.

Hochholdinger F, Park WJ, Sauer M, Woll K. 2004. From weeds to crops: genetic analysis of root development in cereals. Trends Plant Sci. 9(1):42–48. doi:10.1016/j.tplants.2003.11.003.

Jackson JB, Buss LW, Cook RE, editors. 1985. Population biology and evolution of clonal organisms. New Haven: Yale University Press.

Keijsers JGS, Groot AVD, Riksen MJPM. 2016. Modeling the biogeomorphic evolution of coastal dunes in response to climate change. J Geophys Res-Earth. 121(6):1161–1181. doi:10.1002/2015JF003815.

Martínez ML, Maun M. 1999. Responses of dune mosses to experimental burial by sand under natural and greenhouse conditions. Plant Ecol. 145(2):209–219. doi:10.1023/A:1009850304137.

Martínez ML, Maun MA, Psuty NP. 2004. The fragility and conservation of the world's coastal dunes: geomorphological, ecological and socioeconomic perspectives. In: Martínez ML, Psuty NP, editors. Coastal dunes: ecology and conservation. Berlin: Springer; p. 355–369.

Maun MA. 1994. Adaptations enhancing survival and establishment of seedlings on coastal dune systems. Vegetatio. 111 (1):59–70.

Maun MA. 1996. The effects of burial by sand on survival and growth of *Calamovilfa longifolia*. Écoscience. 3(1):93–100. doi:10.1080/11956860.1996.11682320.

Maun MA, Lapierre J. 1986. Effects of burial by sand on seed germination and seedling emergence of four dune species. Am J Bot. 73(3):450–455.

Maun MA, Perumal J. 1999. Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand. Ecol Lett. 2 (1):14–18. doi:10.1046/j.1461-0248.1999.21048.x.

Mendoza-González G, Martínez ML, Lithgow D. 2014. Biological flora of coastal dunes and wetlands: *Canavalia rosea* (Sw.) DC. J Coastal Res. 30(4):697–713. doi:10.2112/JCOASTRES-D-13-00106.1.

Miller TE. 2015. Effects of disturbance on vegetation by sand accretion and erosion across coastal dune habitats on a barrier island. AoB Plants. 7:plv003. doi:10.1093/aobpla/plv003.

Moreno-Casasola P. 1986. Sand movement as a factor in the distribution of plant communities in a coastal dune system. Vegetatio. 65(2):67–76. doi:10.1007/BF00044876.

Nolet C, van Puijenbroek M, Suomalainen J, Limpens J, Riksen M. 2018. UAV-imaging to model growth response of marram grass to sand burial: implications for coastal dune development. Aeolian Res. 31:50–61. doi:10.1016/j.aeolia.2017.08.006.

Qu H, Zhao HL, Zhao XY, Zuo XA, Wang SK, Chen M. 2017. Effects of sand burial on the survival and growth of two shrubs dominant in different habitats of northern China. Environ Monit Assess. 189(4):149. doi:10.1007/s10661-017-5866-x.

Schlacher TA, de Jager R, Nielsen T. 2011. Vegetation and ghost crabs in coastal dunes as indicators of putative stressors from tourism. Ecol Ind. 11(2):284–294. doi:10.1016/j.ecolind.2010.05.006.

Shi L, Zhang ZJ, Zhang CY, Zhang JZ. 2004. Effects of sand burial on survival, growth, gas exchange and biomass allocation of *Ulmus pumila* seedlings in the Hunshandak Sandland, China. Ann Bot. 94(4):553–560. doi:10.1093/aob/mch174.

Vallat R. 2018. Pingouin: statistics in Python. J Open Source Softw. 3(31):1026. doi:10.21105/joss.01026.

Wang G, Yu K, Gou Q. 2019. Effects of sand burial disturbance on establishment of three desert shrub species in the margin of oasis in northwestern China. Ecol Res. 34(1):127–135. doi:10.1111/1440-1703.1269.

Wang Y, Wang K. 2005. Advances of studies on the morphological plasticity, integration and foraging behavior of stoloniferous herbaceous plants. Chinese J Ecol. 24(1):70–74.

Woodhouse WW, Seneca ED, Broome SW. 1977. Effect of species on dune grass growth. Int J Biometeorol. 21(3):256–266. doi:10.1007/BF01552879.

Yang X, Du J, Qin J, Chen Z, Yang L, Song S. 2017. Diurnal variation characteristics of leaf water potential of *Spinifex littoreus* on the nebkhas in different succession periods on the coast of Pingtan Island, Fujian Province, China. Chinese J Appl Ecol. 28(10):3260-3266.

Yuan T, Maun MA, Hopkins WG. 1993. Effects of sand accretion on photosynthesis, leaf-water potential and morphology of two dune grasses. Funct Ecol. 7(6):676–682. doi:10.2307/2390188.

Zhou R, Hou Y, Wang Y, Zuo J. 2015a. The physiological adaptation mechanisms of four common desert species in response to desert environments. Acta Ecologica Sinica. 35(2):340–349.

Zhou R, Yang D, Zuo J, Wang Y, Li Q, Hu D. 2015b. Analysis on the growth strategy of creeping stem in *Vitex trifolia* var. *simplicifoliadapting* to sand burial. Acta Ecologica Sinica. 35(4):1165–1174.