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Effects of wind erosion and sand burial on growth and reproduction of a clonal shrub

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ABSTRACT

Sand burial and wind erosion are two of the most severe stresses for plants in arid areas. Performance of herbaceous plants after burial has been extensively studied in inland and coastal dune ecosystems. However, studies of how clonal shrubs withstand these disturbances remain relatively scarce. Here, we tested the hypothesis that sand burial has negative effects and moderate erosion has positive effects on a clonal shrub, and maintaining rhizome connections helps plants tolerate both burial and erosion. One hundred eight 2 m × 2 m plots of *Calligonum arborescens* were established on an inland dune in the Badain Jaran Desert in northwestern China. Rhizomes at the edges of 54 (half) plots were severed to mimic the loss of rhizome connections. The top 15 or 30 cm of sand was removed for 2.5 or 5 months to simulate short- and long-term moderate and severe erosion, respectively. Addition of 5, 10, 20, or 40 cm layers of sand simulated sand burial. Untreated plots were used as controls. Both sand burial and wind erosion had significant effects on the growth and regeneration of *C. arborescens.* The number of ramets and biomass production decreased with increased burial depth and with severe erosion, but increased in moderate erosion treatments. Rhizome connections greatly increased ramet number and biomass production under both sand burial and severe erosion treatments. We concluded that both sand burial and severe erosion had negative effects on the clonal growth of *C. arborescens*, but that moderate wind erosion had positive effects. Rhizome connections alleviated the negative effects of sand burial and of severe erosion on the growth and performance of *C. arborescens*.

1. Introduction

Sand burial and wind erosion represent important stresses for plant growth in areas of coastal and inland dune ecosystems worldwide (Brown, 1997; Danin, 1996; Li et al., 2010a; Maun, 1994; Yu et al., 2008). Plants growing on the windward slopes of dunes may experience varying degrees of substrate erosion, those on the leeward slopes often experience partial or complete burial, and those on the dune crests may experience both erosion and burial (Li et al., 2010b; Maun, 1998; Yu et al., 2004, 2008). Deep sand burial creates a physical barrier for vertical growth, reduces the photosynthetic area of plants, and limits the amount of oxygen available for roots; these effects can significantly suppress plant growth (Harris and Davy, 1987; Li et al., 2010b; Maun, 1994). However, relatively shallow sand burial can promote plant growth in terms of vertical elongation, and the number of leaves and biomass (Dech and Maun, 2006; Liu et al., 2008; Shi et al., 2004; Zhao et al., 2007a). Wind erosion can impoverish soils and lead to a reduction of soil productivity due to the loss of soil constituents (leading to water loss and reduced nutrition) (Dong et al., 2000; Lyles, 1975; Yu et al., 2008; Zhao et al., 2006). In many ways, sand burial and wind erosion are both selective forces driving plant succession in dry lands (Yu et al., 2008).

The degree and duration of sand burial and wind erosion vary greatly over spatial and temporal scales (Maun, 1998; Moreno-Casasola, 1986); the effects of burial and erosion on plants depend on the burial depth and period, the extent of erosion and its timing, and therefore vary among species and habitats (Li et al., 2010b; Liu et al., 2008; Zhang et al., 2002). Shallow, short-term, partial burial increases biomass production of some species, especially of those species in habitats with intensive burial (Cheplick and Demetri, 1999; Colling and Matthies, 2006; Li et al., 2010b; Zhang and Maun, 1990; Zhang et al., 2002; Zhao et al., 2007b). Long-term and severe

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burial, however, significantly reduces growth (Li et al., 2010b; Liu et al., 2008; Yu et al., 2008). Similarly, moderate erosion (i.e., exposure of a small proportion of the roots or rhizome systems) can have significant negative effects on both survival and growth of ramets (Li et al., 2010a,b; Yu et al., 2008), although such effects can be mitigated by clonal integration via rhizome connections (Evans, 1988; Yu et al., 2008). Severe erosion (i.e., exposure of most roots and/or rhizomes), however, always kills plants because plants loose the capacity for water and nutrient uptake, and for photosynthesis (Grace, 1977; Yu et al., 2008).

Clonal plants, often the dominant species in dune environments, develop diverse adaptive strategies in response to sand burial and wind erosion (Brown, 1997; Maun, 1996; Yu et al., 2002; Zhang et al., 2002). Clonal integration is one of the most important strategies of clonal plants for the survival of environmental stresses such as burial, erosion, shading, and drought (Alpert, 1999; Amsberry et al., 2000; D'Hertefeldt and Falkengren-Grerup, 2002; Stuefer et al., 1996). Clonal integration could provide the buried ramets with carbohydrates directly imported from the non-buried ones to ensure a certain amount of energy for morphological and growth responses (Maun, 1998; Yu et al., 2002). This allows buried ramets to resist darkness and mechanical pressure caused by sand cover (Yu et al., 2002). Division of labor and ramet-specialization are important benefits of clonal integration. Spatial division of labor between interconnected ramets occurs in various clonal species, and that specialization in resource uptake results in benefits for plant biomass and clonal ramet production (Stuefer, 1998; Roiloa et al., 2007). Connected ramets have the ability to share resources, such as water, carbon, and nitrogen, reciprocally (Alpert and Mooney, 1986; Stuefer et al., 1994). Therefore, intra-clonal specialization and cooperation is beneficial in native environments of certain species. Changes in adaptive values of clonal integration vary across environmental gradients. Clones in populations from uniform habitats are selected for lower resource sharing rates between ramets than clones in populations from patchier habitats (Alpert, 1999). When a ramet's growth increases with its resource level and size, the value of a future physiological integration is influenced (Caraco and Kelly, 1991).

Calligonum arborescens Litv. is a dominant perennial shrub in active sand dunes and in stabilized sand fields in the northern deserts of China; it is a rhizomatous clonal shrub and a popular sand-fixing plant (Zhuang et al., 2008). Wind erosion and sand burial are two of the most common and significant stresses for plants growing in these areas. Seedlings can easily be buried by sand or eroded by wind, and only a few of them survive. Thus, the selection of artificial sand-fixing vegetation is both difficult and important (Zhao et al., 2007a). Interestingly, based on our field observations, clonal plants such as *C. arborescens* survive even after severe sand burial or wind erosion. *C. arborescens* growing in moderately eroded patches can generate more clonal ramets than non-eroded specimens. Clonal ramets were found on the windward and not on the leeward side, perhaps because sand burial had negative effects on ramet growth and regeneration (personal observation). Thus, moderate wind erosion helped plants counteract the negative effects of heavy sand burial, facilitating plant growth. Some rhizomes of *C. arborescens* were under the soil surface because of wind erosion, but ramets from those rhizomes were still alive because other connected ramets were not buried by sand. Thus, clonal integration may play important roles in plant survival.

Recent studies focused on the performance of herbaceous plants after sand burial and wind erosion (D'Hertefeldt and Falkengren-Grerup, 2002; Liu et al., 2007; Yu et al., 2004, 2008). However, data regarding how clonal shrubs withstand sand burial and wind erosion remain relatively scarce. In this study, we selected a common clonal shrub *C. arborescens* to illuminate how clonal shrubs withstand erosion and burial. We tested the hypotheses that (1) sand burial has negative effects on the growth and regeneration of *C. arborescens*, (2) moderate erosion has positive effects on the clonal growth of *C. arborescens*, and (3) rhizome connections can help *C. arborescens* cope with severe wind erosion and sand burial, i.e., the growth and survival of ramets subject to erosion and burial would be greater in connected than in disconnected plants.

2. Materials and methods

2.1. The species

C. arborescens Litv. is a clonal shrub found in the sand dunes in the arid and semi-arid desert regions of northern China (Mao and Pan, 1986; Ren, 2001). The shrub propagates by producing horizontal rhizomes, and appears to be suitable for revegetating deserts because of its high tolerance to water deficits (Zhuang et al., 2008). Ramet density, expansion range, and average expansion rate of vegetative reproduction vary greatly depending on location (fixed-dune lowland, windward- or leeward-side of semi-mobile dunes). A population of *C. arborescens* invades a new habitat at the seedling stage with sexual reproduction, and then rapidly expands over a large area through vegetative reproduction, which continues to drive population expansion (Zhuang et al., 2008). *C. arborescens* also reproduces sexually during high-precipitation months or in wet years, and seedlings are occasionally found in the field; however, most of them die when precipitation level drops (personal observation). On mobile and semi-mobile dunes in northwestern China, *C. arborescens* populations frequently experience various levels of sand burial and erosion imposed by strong winds.

2.2. Study site

The study was conducted in a dune system near the Linze Inland River Basin Research Station (39°21′N, 100°07′E) of the Chinese Academy of Sciences, located in the Badain Jaran Desert in northwestern China. The mean annual temperature is 7.6 °C, and mean annual precipitation is 117 mm, with 65% falling between July and September (Zhao et al., 2007a). In this area, the wind is predominantly from the northwest, and is frequently high. Wind speed is greatest (21 $m\,s^{-1}$) in spring, but wind erosion occurs frequently throughout the year (Zhuang and Zhao, 2014). Dominant plant species include shrubs such as *C. arborescens*, *Nitraria sphaerocarpa*, and *Hedysarum scoparium*, and annuals such as *Bassia dasyphylla* and *Agriophyllum squarrosum*. The landscape has been acutely desertified, and consists of fixed, semi-mobile, and mobile dunes dominated by the shrub *C. arborescens* (Zhuang and Zhao, 2014).

2.3. Experimental design and measurements

On 1 May 2014, 108 plots (each 2 m × 2 m) were established on semi-mobile dunes. Each plot contained 5–7 ramets of *C. arborescens*. Fifty-four of the plots were randomly selected for rhizome-severing treatments (here after referred to as 'disconnected' plots) and the remaining 54 plots were used as controls (here after referred to as 'connected' plots). Along the edges of the disconnected plots the rhizomes of *C. arborescens* were severed by inserting a sharp blade perpendicular to the sand surface to a depth of 50 cm (Yu et al., 2004, 2008).

Twenty-four connected (C) and 24 disconnected (D) plots were randomly selected for one of four experimental wind-erosion treatments. Then, six plots of each C and D were randomly assigned to (1) short-term moderate erosion (CSM and DSM); (2) short-term severe erosion (CSS and DSS); (3) long-term moderate erosion (CLM and DLM); (4) and long-term severe erosion (CLS and DLS). Moderate and severe erosion levels were simulated by artificially