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Sand-burial and wind erosion promote oriented-growth and patchy distribution of a clonal shrub in dune ecosystems

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ABSTRACT

Habitat selection by oriented-growth of plants has been investigated but field evidence for such growth is scarce, impeding efforts at sand stabilization and dune ecosystem restoration. Further, how clonal shrubs adapt to dune environments is unknown. In this study, we test the hypotheses that oriented-growth and patchiness are adaptive strategies of clonal shrubs to dune environments, while wind erosion and sand burial are the driving factors. We sampled 250 rhizomatous fragments to assess oriented-growth of *Calligonum arborescens*, and investigated the distribution (east, southeast, south, southwest, west, northwest, north and northeast) of *C. arborescens* in four different habitats of active dunes: inter-dune areas, windward slope, leeward slope, and the top of dune. We found that most of the fragments of *C. arborescens* grew in the northeastern and southwestern directions. Ramet number and biomass, and rhizome length and biomass in these two directions were significantly higher than those found in other directions. Interestingly, these directions were perpendicular to the direction of prevailing winds. Distribution of *C. arborescens* differed among habitats. Total number of individuals was significantly higher in inter-dune areas and on windward slopes than on top and leeward slopes of dunes; more clonal ramets were produced on top of dunes than elsewhere, and only 16.7% were found on leeward slopes. Both sand-burial and wind erosion affected the growth and regeneration of *C. arborescens*. Ramet number and biomass production decreased with increasing depth of burial and severity of erosion, but increased in moderate erosion treatments. We conclude that fragments of *C. arborescens* exhibited oriented-growth; most of the rhizomes grew in the direction perpendicular to the prevailing wind direction. Most of *C. arborescens* were found in inter-dune lands and on windward slopes. *C. arborescens* was well established in active dune fields through both vegetative propagation and sexual reproduction. Sand-burial and wind erosion were the key factors which led to the oriented-growth and patchiness of *C. arborescens*.

1. Introduction

Heterogeneity is a fundamental property of ecosystems and one of the most important factors which promotes patchy distribution of plants (Salzman, 1985; Fine et al., 2004; Roiloa and Retuerto, 2006; Yan et al., 2013). Because both abiotic and biotic environmental factors have non-uniform distributions in space and time (Slade and Hutchings, 1987; Hutchings and Wijesinghe, 1997; van Kleunen and Fischer, 2001; van Zandt et al., 2003), patchy distribution of plants is a very common phenomenon in most ecosystems. Plants favor habitats where resources such as light, nutrients, and water, are plentiful (Salzman, 1985; Hutchings and Wijesinghe, 1997; Kleijn and van Groenendael, 1999; van Kleunen and Fischer, 2001; Xiao et al., 2006), and where herbivores and other stress agents, such as soil pollution, are less common (Fine et al., 2004; Koivunen et al., 2004; Yan et al., 2013). Pressures of competition from neighbors may also lead to patchy distribution in some plants (Gersani et al., 1998; Leeflang, 1999; Morris, 2003; Sampaio et al., 2004).

Sand dunes often form after land degradation in arid, semi-arid, and dry sub-humid areas (Zhu and Chen, 1994; Kassas, 1995). The establishment and growth of vegetation in dune lands is of significant importance to restoration and land rehabilitation efforts (Guo et al., 1998; Lichter, 2000; Yan et al., 2007). Sand movement and wind erosion are frequent in dune systems, and they represent important stresses for plant growth (Brown, 1997; Yu et al., 2008). Plants growing on the leeward slopes of dunes often experience partial or complete burial, and those on the windward slopes may experience varying degrees of substrate erosion (Li et al., 2010; Maun, 1998; Yu et al., 2004, 2008). Sand-

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burial not only deprives plant leaves of sunlight, but it also increases soil moisture and decreases aeration (Perumal and Maun, 2006). The major deleterious effects of sand burial are suspension of photosynthesis and production of carbohydrates due to a decreased photosynthetic area created by the physical barrier of deep sand (Li et al., 2010; Maun, 1994; Perumal and Maun, 2006). Loss of soil constituents via wind erosion can lead to loss of soil productivity (Dong et al., 2000; Yu et al., 2008).

Clonal plants are widespread throughout the plant kingdom, and both productive and infertile habitats may be dominated by clonal species (Price and Marshall, 1999). Many mobile and semi-mobile dunes in drylands are colonized by rhizomatous plants that form large connected clones (Maun, 1984; D'Hertefeldt and Falkengren-Grerup, 2002; Yu et al., 2008). Inter-connected clones are potentially less susceptible than separate plants to physical damage caused by wind erosion, and this is important for vegetation restoration of dune lands (Yu et al., 2008). Some perennial dune plants endure sand mobility through special reproduction strategies (Yu et al., 2002; Yan et al., 2007). Vegetative propagation is believed to be more important than sexual reproduction in species establishment on active dunes (Yu et al., 2002; Li et al., 2005a,b). Therefore, a greater understanding of vegetation patterns on dunes will inform conservation and restoration measures in dune ecosystems (Zuo et al., 2008).

Directional growth of plants is an important basis for habitat selection, and much research focused on it in recent years (Leeflang, 1999; Hay et al., 2001; Sampaio et al., 2004; Runyon et al., 2006). Many clonal plants enter habitats via directional growth of rhizomes or stolons (Salzman, 1985; Kleijn and van Groenendael, 1999; Sampaio et al., 2004; Xiao et al., 2006). For example, the main growth of clonal fragments of *Aechmea nudicaulis* was preferentially directed toward bare sand environments where light was sufficient and competition was lower than elsewhere (Sampaio et al., 2004). One limitation of most studies on directional growth in habitat selection is that directional growth was demonstrated under controlled conditions or in greenhouse experiments (Salzman, 1985; Kleijn and van Groenendael, 1999; Gao et al., 2012), and only a few studies attempted to find field evidence for directional growth in natural habitats (Macek and Lepš, 2003; Sampaio et al., 2004). Therefore, field evidence for directional growth is still very limited.

Calligonum arborescens Litv. is a rhizomatous clonal shrub, and a popular sand-stabilizing plant in dune lands in the northern deserts of China (Zhuang et al., 2008). Plant growth in this area is limited by sand-burial and wind erosion (Zhao et al., 2007). Sand burial and severe erosion inhibited, and moderate wind erosion promoted ramet production of *C. arborescens* (Luo and Zhao, 2015b). Ramet density, expansion range, and average expansion rate of vegetative reproduction varied greatly depending on the location in the dune habitat (inter-dune lowland, windward- or leeward-slopes of dunes) (Zhuang et al., 2008). Clonal ramets were more frequently found on the top of dunes and on windward slopes than on leeward slopes (Luo and Zhao, 2015b). Most rhizomes grew in the direction perpendicular to the prevailing winds (personal observation). The main reason for this may be that wind erosion and sand-burial led to directional growth of rhizomes, and promoted patchy distribution of *C. arborescens*. Recent studies focused on the relationships among directional growth, patchiness of plants, and heterogeneity of soil nutrients, light, herbivores, and neighbors (Hutchings and Wijesinghe, 1997; van Kleunen and Fischer, 2001; Fine et al., 2004; Yan et al., 2013). However, little is known about the effects of wind erosion and sand-burial on directional growth and distribution of clonal shrubs in dune ecosystems. In this study, we selected a common clonal shrub to test the hypotheses that (1) fragments of *C. arborescens* exhibit oriented-growth. Rhizomes of *C. arborescens* may grow in different directions because the degree of sand burial and wind erosion vary among wind directions. (2) *C. arborescens* exhibits patchy distribution in dune lands. *C. arborescens* growing in different dunes habitats may experience varying degrees of burial or erosion, and that may lead to its patchy distribution. (3) Sand burial and wind erosion are key factors which lead to oriented-growth and patchy distribution.

2. Materials and methods

2.1. Study site

The study was conducted in a dune system near the Linze Inland River Basin Research Station of the Chinese Academy of Sciences (between 39° 22′N and 39° 23′N, and 100°07′E and 100°08′E), located in the Badain Jaran Desert in northwestern China. Mean annual precipitation is about 117 mm, with 65% falling between July and September (Zhao et al., 2007); potential evaporation is 2390 mm per year. Mean annual temperature is 7.6 °C, and lowest temperature is −27.3 °C in January (Zhang et al., 2015). Wind speed is greatest (21 $m \cdot s^{-1}$) 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*. Due to multiple stresses, such as low precipitation, high evaporation, and bare soil, vegetation cover in the desert area ranges from 5 to 7% (Zhang et al., 2015).

2.2. Study species

C. arborescens Litv. is a typical rhizomatous clonal shrub of dune lands (Mao and Pan, 1986; Ren, 2001). *C. arborescens* reproduces mainly by clonal reproduction, which helps maintain and extend its populations in dune lands (Zhuang et al., 2008). Average population density is 3.5 ramets/100 m^2 on dunes, and 5.8 ramets/100 m^2 in inter-dune lowlands, and an average rate of growth is 0.67 m per year on dunes, and 0.41 m per year in inter-dune lowlands (Zhuang et al., 2008). Most of the rhizomes are distributed at soils depths of 0–30 cm (personal observation). *C. arborescens* frequently experiences various levels of sand burial and erosion imposed by strong winds. Following a disturbance, such as wind damage, *C. arborescens* can be easily broken into segments of different sizes. The regeneration capacity of those fragments is affected by the depth of sand and diameter of fragments. Further, sand burial is one of the prerequisites for the survival of shrub fragments (Luo and Zhao, 2015a).

2.3. Experimental design and measurements

To assess oriented-growth of *C. arborescens*, we randomly sampled 250 rhizomatous fragments in the field. We used the base of each ortet ramet (ramet which developed from seed) as the plot center, and divided the circular area around plot center into eight parts corresponding to geographical directions (N, NE, E, SE, S, SW, N, and NW) (Fig. 1a). The eight parts represented eight possible growth directions. Then, we carefully excavated fragments from each direction. Fragments were severed when they crossed directions. We measured the total number and biomass of ramets, and the number, length, depth, and biomass of rhizomes of all fragments in each direction.

To investigate the patchiness of distribution of *C. arborescens* in dune lands, we established one, 2-km-long transect in every habitat: inter-dune land (IL), windward slope (WS), leeward slope (LS), and the top of dune (TD) (Fig. 1b). We selected 20 quadrats (20 m × 20 m) along each transect, with the distance between each quadrat of about 100 m. In each quadrat, all rhizomes were excavated; then seedling and ramet number, ramet biomass, and rhizome depth and biomass were measured. We also measured soil moisture in each quadrat. Three soil samples were collected from depths of 0 to 2.0 m in each quadrat, with every 0.2 m of depth defined as a different layer (20 layers total). Soil samples were oven-dried (105 °C) for 48 h prior to analysis.

To test whether the factors promoting patchiness of distribution of *C. arborescens* were sand burial and wind erosion, we designed another