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Patterns of reproductive allocation in *Artemisia halodendron* inhabiting two contrasting habitats

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Abstract

The perennial chenopod sub-shrub *Artemisia halodendron* Turcz. ex Bess. is endemic to the semi-fixed and mobile sand dunes in Inner Mongolia of northern China and is an important sand-stabilizing plant. *A. halodendron* can persist through either sexual reproduction (seedling recruitment) or vegetative propagation. However, it is not known if there are differences in patterns of reproductive allocation in *A. halodendron* inhabiting semi-fixed and mobile habitats. To characterize this, a test of field measurements was conducted on two typical semi-fixed and mobile sand dune habitats. In each habitat, 120 individual *A. halodendron* plants were randomly sampled at the time of seed production to examine changes in some reproductive characters including the number of flowering shoots, dry weight of flowering shoots, dry weight per flowering shoot, dry weight of seed, and reproductive effort (RE = seed dry weight/total above-ground dry weight) between habitats. Although total above-ground dry weight and dry weight of vegetative biomass were similar between habitats, plants inhabiting the less eroded semi-fixed habitat produced more flowering shoots, greater dry weight of flowering shoots, dry weight of seed and RE than those inhabiting the more eroded mobile habitat. This suggests that sexual reproduction is relatively favored by plants from the semi-fixed habitat, whereas vegetative propagation is favored by plants from the mobile habitat. The allocation of resources to reproduction was size-dependent and specific to habitats sampled. Reproductive biomass and the number of flowering shoots per plant increased with increasing vegetative biomass, with plants in the semi-fixed habitat producing more flowering shoots and greater reproductive biomass than plants in the mobile habitat. Plant size did not influence RE, indicating that allocation of resources to reproduction appeared to be a constant proportion across all plant sizes sampled.

Keywords: Environmental heterogeneity; Mobile sand dune; Reproductive effort; Semi-fixed sand dune; Sexual reproduction; Vegetative propagation

1. Introduction

Artemisia halodendron Turcz. ex Bess. is a native sub-shrub that is endemic to the sandy steppes in the Horqin Sandy Land of eastern Inner Mongolia, China. In general, *A. halodendron* occurs primarily in moderately to severely degraded semi-fixed and mobile sand dunes and is often the dominant species in these grassland types (Li, 1991; Chao et al., 1999). Despite its dominance in semi-fixed and mobile grasslands, the value of *A. halodendron* as a pioneer sand-fixing plant for improving microhabitat conditions and promoting restorative succession of psammophytic vegetation through sand stabilization and accumulation of wind-blown dust, litter and seed has only recently been recognized (Chang et al., 1994; Li et al., 2002; Zhang et al., 2004). Due to its low nutrient requirements and superior capacity to produce offspring through vegetative propagation under the condition of sand burial, *A. halodendron* easily colonizes bare patches to establish populations in unstable, nutrient-poor sandy habitats (Li and Zhang, 1991; Chao et al., 1999). Therefore, *A. halodendron* is usually used as the species for re-vegetation of stabilizing mobile sand dunes. In general, twigs with roots taken from *A. halodendron* plants are transplanted directly into severely desertified land in the wet season (Chang et al., 1994). This technique of establishing artificial sand-stabilizing *A. halodendron* vegetation on mobile sand dunes has proved to be very successful in the Horqin region (Li et al., 2002; Zhang

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et al., 2004). Locally, once artificial *A. halodendron* vegetation has been established, the *A. halodendron* canopy will act as a seed accumulator (by physically trapping dispersing seed) (Aguiar and Sala, 1997; Pugnaire and Lázaro, 2000) and a sink for resources, either actively through root uptake of soil water and nutrients (Hook et al., 1991; Gutiérrez et al., 1993; Burke et al., 1995) or passively accumulating wind-blown dust and litter from nearby unprotected areas (i.e. development of 'fertile islands' around shrub plants; Barth and Klemmedson, 1982; Garner and Steinberger, 1989; Schlesinger et al., 1990; Wezel et al., 2000). Consequently, this will facilitate invasion and colonization of other plant species under or near its canopy and lead to an increase in species diversity and abundance of the degraded sandy land ecosystems (Pugnaire et al., 1996; Li et al., 2003a).

A number of studies have recently been carried out in the Horqin region. These studies have provided some valuable insight into the mechanism of ecological, morphological and physiological adaptation of *A. halodendron* to the harsh environmental conditions that are characterized by frequent drought, high temperatures, and sand burial in the sandy land ecosystems (Wang and Zhou, 1999; Zhou, 1999; Zhou et al., 1999a, 1999b). However, it is not known if there are differences in patterns of reproductive allocation in *A. halodendron* inhabiting mobile and semi-fixed sand dune habitats. To our knowledge, no studies have examined the variation patterns of reproductive allocation in *A. halodendron* plants inhabiting these two different habitats. To characterize this, a test of field measurements was conducted on two typical semi-fixed and mobile sand dunes in the Horqin Sandy Land of eastern Inner Mongolia. The objectives were to determine (1) if there are differences in patterns of reproductive allocation in individual *A. halodendron* plants inhabiting two heterogeneous habitats and (2) if individual *A. halodendron* plants inhabiting these habitats differ in their relative reproductive allocation with increasing size of plants.

2. Materials and methods

2.1. Study site

The study was conducted in Naiman county (42°55′N, 120°44′E; altitude ca. 360 m a.s.l.) in the eastern part of Inner Mongolia, China, about 500 km northeast of Beijing (Li et al., 2003a). Naiman is located in the southwestern part of the Horqin Sandy Land, which is roughly 400 × 400 km in size and represents the most desertification-threatened area in North China (Andrén et al., 1994). Landscape in this area is characterized by sand dunes alternating with gently undulating lowland areas. The soils are sandy, loose in texture, and particularly susceptible to wind erosion (Li et al., 2003b). The climate is temperate, semi-arid and continental, receiving 360 mm annual mean rainfall, with 75% of the annual rainfall falling in the June–September period. The annual mean potential evaporation is 1 935 mm, and the annual mean temperature is 6.5 °C (Li et al., 2003b).

The study site was originally a grass-dominated steppe community with sparsely distributed woody species (mainly elm *Ulmus* spp.). When the study was initiated, the original vegetation had been substantially degraded, primarily due to overgrazing by livestock (Li et al., 2000). Degraded grassland is generally classified into three main forms: fixed or stabilized (light degradation), semi-fixed or semi-stabilized (moderate degradation) and mobile or unstabilized (severe degradation), and these forms represent a realistic range of historically grazing activities and impacts. Although the vegetation in these three grassland types differs in species composition, abundance and diversity, a number of psammophilic species were dominant (Zhao et al., 2003). These included some shrubs (e.g. *Caragana microphylla*, *Lespedeza davurica* and *Salix gordejevii*), sub-shrubs (e.g. *A. halodendron* and *Hedysarum fruticosum* var. *ligosum*), forbs (e.g. *Agriophyllum squarrosum, Corispermum macrocarpum, Salsola collina* and *Artemisia scoparia*), and grasses (e.g. *Setaria viridis, Digitaria ciliaris, Aristida adscensionis, Cleistogenes squarrosa* and *Chloris virgata*).

2.2. Experimental species

A. halodendron (Asteraceae) is a deciduous sub-shrub, with well-developed rhizome system near the soil surface. There are many perennating buds on rhizomes from which give rise to above-ground shoots that possess axillary buds in spring. For a shoot, some of its axillary buds sprout to form new shoots and in a few years, a large cluster of branches develops. An adult individual consists of several generations of shoots, with current-year established shoots including two types: flowering shoot and non-flowering (vegetative) shoot. Flowering shoots flower in early July and set seed in early August, and seed matures in early October, and then they die off with the first ground frost at the end of October. Vegetative shoots can survive for some years, during which time the shoot diameter increases and shoots become woody and generate new flowering or vegetative shoots each year (Li and Zhang, 1991). *A. halodendron* can persist through either seedling recruitment (sexual reproduction) or vegetative spread by fragmentation (vegetative propagation).

2.3. Sampling and measurements

To determine if habitat type influences the pattern of reproductive allocation, a test of field measurements was conducted on two typical semi-fixed and mobile sand dunes. These two sites were about 1.5 km apart. In each site, 120 isolated individual *A. halodendron* plants were randomly sampled in the second week of September 2003, when *A. halodendron* had set seeds but its above-ground parts still remained alive. The sampled plants were at least 15 m apart from one another, to ensure that shoots from one plant were not connected to those of another plant. The plants were cut off at ground level. For each plant, the number and biomass production of current-year flowering shoots, current-year veg-