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Alterations in canopy size and reproduction of *Caragana stenophylla* along a climate gradient on the Inner Mongolian Plateau

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ABSTRACT

In this study, we examined the alterations in canopy size and reproduction of *Caragana stenophylla* along the climatic drought gradient on the Inner Mongolia Plateau, China. We found that the canopy area and height of *C. stenophylla* increased gradually with increase of drought stress from the semi-arid zone to the strongly arid zone. The proportions of sexual reproduction decreased and the asexual reproduction increased with increase of the climatic drought stress. The majority of *C. stenophylla* offspring grew (separately) outside shrubs in the semi-arid (63.9%) and the arid zones (45.8%). But in the strongly arid zone, *C. stenophylla* offspring only grew inside shrubs. With the increase of climatic drought stress the ramet radius increased, while the spacer length decreased. In both the semi-arid and arid zones, the spacer length was more than 2 times of the ramet radius. Thus, some spaces were kept between the crowns of ramets. On the other hand, the spacer length was less than 2 times of the ramet radius in the strongly arid zone, so that the crowns were closely intertwined. Our results demonstrate that with the increase of climatic drought stress and associated desertification, the reproduction of *C. stenophylla* changes from more sexual reproduction to more clonal propagation; offspring establishment strategy changes from having more outside-shrub offspring to having only inside-shrub offspring; the clonal architecture changes from guerrilla type to phalanx type. Alterations in the reproduction of *C. stenophylla* along the climatic drought gradient result due to an increase of its canopy size from the northeast to the southwest on the Inner Mongolia Plateau.

Introduction

The reproductive strategy of clonal plants may change under different environmental conditions or due to disturbances (Bond and Midgley, 2001; Pluess and Stöcklin, 2005; Wesche et al., 2005). For example, sand accretion substantially reduces seed bank density and seedling density of the desert plant *Sophora moorcroftiana*, but it can also promote shoot sprouting and shoot growth of this plant (Zhao et al., 2007b). Studies showed that in a population of *Reaumuria soongorica* located in arid and sandy habitats, about 72.4% of the individuals propagated asexually; while in another population of *R. soongorica* located in relatively humid mountain grasslands, 53.5% of the individuals reproduced sexually (Zeng et al., 2002). The cactus *Opuntia rastrera* predominantly showed sexual reproduction in grasslands and clonal propagation in nopaleras (large areas of scrublands in North American deserts, dominated by Opuntia spp.) Mandujano et al. (1998). Under stressful conditions, populations of the herb *Paris quadrifolia* showed limited sexual reproduction (Jacquemyn et al., 2006). Wild rice (*Oryza rufipogon*) populations under seasonal drought tended to have more sexual reproduction, whereas populations with sufficient supply of water tended to have less sexual reproduction (Xie et al., 2001). In Brazilian rupestrian grasslands, the survival rate of *Leiothrix curvifolia* seedlings was low in the dry period; in contrast, the survival rate of ramets was 100% (Coelho et al., 2008).

Under severe drought conditions or in disturbed areas, the probability of seed development into seedlings may vary significantly inside versus outside shrubs. Inside shrubs, more nutrients (e.g., total carbon, organic matter and nitrogen) can be maintained, humidity is higher (Titus et al., 2002; Schade and Hobbie, 2005), and herbivores are better avoided than outside shrubs. Thus the conditions inside shrubs are favorable to seed germination and seedling establishment. Fertile island effects in shrubs of *Caragana* genus are common. For example, studies showed that not only organic matter, total N and P, available P and soil moisture, but also soil seed density, herbaceous species richness, densities, plant height, cover and aboveground biomass was higher in the shrub canopies of *Caragana microphylla* than in the open areas (Zhao et al., 2007a; Dong et al., 2009).

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Guerilla and phalanx are two extreme types of clonal architecture (Lovett, 1981). Guerrilla clonal plants show strong clone dispersive capacity, permitting the use of water and nutrient resources with a scattered distribution; phalanx clonal plants, with a weak dispersive capacity, easily use resources with a centralized distribution (de Kroon and Knops, 1990; de Kroon and Hutchings, 1995; Song and Dong, 2002). Clonal architecture of plants may be different not only among species, but also within the same species under different environmental conditions. The wetland sedge *Carex brevicuspis* changed its clonal growth form from phalanx type to guerrilla type in the response to sedimentation alteration (Chen et al., 2011). Another wetland perennial plant, *Scirpus olneyi* showed both types of clonal architecture (phalanx and guerrilla) within relatively small-scale environments (Ikegami et al., 2007). The mesophyte *Elymus repens* changed its colonizing strategy from guerilla type to phalanx type, when it was released from grazing pressure and subjected to competition (Amiaud et al., 2008). Another mesophyte *Prunella vulgaris* showed penetrating guerrilla type of growth in the presence of competitors, while in the absence of competitors plant growth was more condensed with shorter internodes (Macek and Lepš, 2003). The perennial herb, *Schoenoplectus americanus* produced more short-rhizome ramets in benign environments, but it produced more long-rhizome ramets in less favorable environments (Ikegami et al., 2009). Bamboo plants growing in soil with high water content produced longer spacers than in soil with low water content (Liu et al., 2004). The spacer length of a pasture grass *Leymus secalinus* under high level of nutrient supply was significantly shorter than when growing under medium level of nutrient supply (Ye et al., 2006). Less attention, however, has been paid to the alterations of clonal architecture of shrub species across environmental gradients.

Caragana stenophylla Pojark is a deciduous shrub distributed in steppe, desert steppe, semi-desert and desert areas in Inner Mongolia and northern Xinjiang of China (Wang and Ni, 2009), and in Dahuria, Chingan foothills, Eastern Gobi, and Gobi Altay of Mongolia. On the Inner Mongolia Plateau, *C. stenophylla* is distributed in the middle to the southwest (Wang and Ni, 2009). The climate on the Inner Mongolia Plateau is characterized by a gradual increase of solar radiation and air temperature, and gradual decrease of precipitation from the northeast to the southwest (Table 1). Precipitation decrease together with evaporation increase results in an evident climatic drought gradient from the northeast to the southwest. Vegetation coverage decreases gradually and desertification gradually became more severe from the northeast to the southwest (Table 1). The climatic drought gradient is suggested to be critical for plant growth, development and evolution in this region (Zhang and Fritsch, 2010).

We have previously reported the geographical distribution and adaptation of *C. stenophylla* to the semi-arid and intensively arid environments under aspects of morphology and physio-ecology (Ma et al., 2004a,b, 2006, 2008). We also observed that *C. stenophylla* shrubs had small canopy size in the semi-arid zone on the Inner Mongolia Plateau (Fig. 1), and its canopy size increases from the northeast to the southwest, as climatic drought stress and desertification become more severe. In the intensively arid zone of the southwest on the Inner Mongolia Plateau, *C. stenophylla* occurs as large shrubs, with diameters of 1–3 m, associated with sand dunes with heights of 40–60 cm (Fig. 1). Thereby it has a strong sand-fixing ability, which plays a very important role in maintaining the sustainability of the ecosystem in this zone.

Understanding the underlying reasons for the variation in the growth forms of *C. stenophylla* across the climatic drought gradient on the Inner Mongolia Plateau is critical for a better understanding

Table 1
Environmental data of the study sites.

Site	Longitude (°E)	Latitude (°N)	Altitude (m)	Annual precipitation (mm)	Annual average temperature (°C)	Sun time (h)	Moisture types	Vegetation type	Dominant plant species	Vegetation coverage
Xilinhaote	116.07	43.95	990	281	2.35	2932	Semi-arid	Steppe	*Leymus chinensis, Stipa grandis, Agropyron michnoi, Artemisia frigida, Cleistogenes squarrosa*	25–50%
Suniteyou	112.90	42.40	1151	211	4.93	3067	Arid	Desert steppe	*Stipa gobica, Caragana microphylla, Allium mongolicum*	10–35%
Alashanzuo	105.66	38.84	1561	110	7.80	3200	Intensively arid	Desert	*Caragana korshinskii, Caragana roborovskyi, Caragana tibetica, Atraphaxis frutescens*	1–20%

Note: Climate data are the mean values over 40 years (1968–2007).