***Pak. J. Bot.*, 41(4): 1685-1694, 2009.**

REPRODUCTIVE ALLOCATION OF *CORISPERMUM ELONGATUM* IN TWO TYPICAL SANDY HABITATS

**YU-HUI HE[1*],□ HA-LIN ZHAO[1], XIN-PING LIU[1], XUE-YONG ZHAO[1],
TONG-HUI ZHANG[1] AND SAM DRAKE[2]**

[1]Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, 320 Donggang West Road, Lanzhou, 730000, PR China.
[2]Office of Arid Lands Studies, University of Arizona, 1955E. 6th Street, Tucson, AZ 85719, USA.
[*]E-mail: ahuihyh@126.com

Abstract

The annual plant *Corispermum elongatum* is endemic to the sandy soils in the Horqin Sandy Land of eastern Inner Mongolia, China. It plays an important role in sand stabilization and vegetation restoration in the Horqin region. However, studies about the difference of reproductive allocation in *C. elongatum* in different sandy habitats were limited. To detect this, a test was conducted on typical fixed and mobile sand dunes in the Horqin Sandy Land. The results showed that habitat type had a significant effect on the pattern of reproductive allocation in *C.elongatum*. The dry weight of reproductive structure, spike number, length of spike, dry weight of vegetative structure, dry weight of reproductive structure relative to total above-ground dry weight biomass, and the number of primary branches were all larger in *C. elongatum* plants in fixed sand dunes than in mobile sand dunes. The resources allocated to reproduction were size-dependent and also affected by the habitats sampled. *C.elongatum* plants inhabiting the better fixed-dune habitat seem to allocate more resources to reproduction to increase population size, while vegetative growth appears to be relatively more important for the survival of *C.elongatum* in the harsh mobile-dune habitat. This information is important for a better understanding of the adaptation strategy of *C.elongatum* in different habitats.

Introduction

Reproduction is the basic process of life. It concerns the completion of a plant's life cycle and the regeneration of plant populations (Silverton & Lovett-Doust, 1993; Pino *et al*., 2002), but there is a trade-off between resources allocated to reproduction and those allocated to growth, storage and defense etc., (Harper, 1977; Herms & Mattson, 1992; Konstadia *et al*., 2003). From an evolutionary ecology perspective, biomass distribution and the proportion of plant allocated resource to reproductive structures is important embodiment of plant fitness (Reekie & Bazzaz, 1987; Weiner, 1988; Hartnett, 1990; Vega *et al*., 2000). The reproduction allocation affects plant life-history strategies, plant community dynamics and plant evolution (Grime, 1979; Lehtilä & Sunds Larsson, 2005). Therefore study about reproduction allocation pattern is a still growing field of interest to ecologists (Reekie, 1998; Cruz & Moreno, 2001; Staffan Karlsson & Mendez, 2005).

The precipitation was less and highly unpredictable, the soil condition was poor, and other disturbances were frequently occurred in the arid and semi-arid sandy lands or desert ecosystems, all those harsh environmental conditions made plant growth face rigorous challenges (Zhang *et al*., 2002). So, knowledge of the resource allocation pattern of plants is beneficial to understanding their life history strategy in the sandy habitats, and helpful for informing the process of vegetation restoration.

Corispermum elongatum is an annual plant endemic to the Horqin Sandy Land of eastern Inner Mongolia, China (Zhang *et al*., 2004). The Horqin Sandy Land is located in the agro-pastoral transitional zone between the Inner Mongolian Plateau and the Northeast Plains of China (42°41′ to 45°15′ N, 118°35′ to 123°30′ E) and is one of the most seriously desertified regions of China (Wang, 2000). *C. elongatum* can occur in all kinds of sandy dunes, from mobile dunes to fixed dunes and is recognized as a pioneer sand-fixing plant for promoting restoration of vegetation. It plays an important role in sand stabilization and vegetation restoration in the Horqin region, where much researches have been carried out which provide valuable insight into environmental changes mechanisms and the ecological adaptation of some plants to the harsh environmental conditions (Su & Zhao, 2003; Li *et al*., 2005; Zhang *et al*., 2006). Li *et al*., (2005) had reported that the shrub *Artemisia halodendron* can propagate in this region through either sexual reproduction or vegetative propagation. However, it is not well known if there are differences in reproductive allocation in annual plants inhabiting this area, which can only persist through seeding recruitment. To determine this, *C. elongatum* was selected for study, and a test of field measurements was conducted on typical fixed and mobile sand dunes in the Horqin Sandy Land. The objectives of this study were to detect the differences in reproductive allocation in *C. elongatum* plants inhabiting two different dune habitats and the relationship between relative reproductive allocation and plant size of *C. elongatum* plants inhabiting these habitats.

Materials and Methods

The study area is located near the Naiman Desertification Research Station (42°58′N, 120°43′E, 345m above mean sea level) of the Chinese Ecosystem Research Network (CERN), in Naiman, Inner Mongolia, China, in a zone of continental semiarid monsoon climate. Landscape in this area is characterized by sand dunes (fixed or mobile) alternating with gently undulating lowland areas. The soils are sandy, with a loose structure and are particularly susceptible to wind erosion. The yearly average solar radiation is 5200 MJ/m^2. The mean annual temperature is 6.4°C and the frost free period is 137~150 days per year. Average annual precipitation is 362mm, nearly 70% of which falls from June through August. The yearly average evaporation is 1935 mm, more than five times the annual precipitation. Prevailing wind directions are northwest in winter and spring, and southwest to south in summer and autumn. The yearly average wind speed ranges from 3.4 to 4.1 m/s (Li *et al*., 2006).

The study habitats were fenced and no grazing was allowed. The vegetation included some shrubs (e.g., *Caragana microphylla*, *Lespedeza davurica*, *Salix gordejevii*), sub-shrubs (e.g., *A. halodendron*, *Hedysarum fruticosum* var. *ligosum*), forbs (e.g., *Agriophyllum squarrosum, Corispermum elongatum, Salsola collina*, *Artemisia scoparia*) and grasses (e.g., *Setaria viridis, Digitaria ciliaris, Aristida adscensionis, Cleistogenes squarrosa* and *Chloris virgata)*. Vegetative cover is less than 10% in the mobile dune habitat and 50 to 70% in the fixed dune habitat.

Sampling and measurements: To determine if there are influences of habitat type on the pattern of reproductive allocation in *C. elongatum,* a test of field measurements was conducted on typical fixed and mobile dune habitats which were about 1km apart. There were three replications of each habitat type and thirteen 1m×1m subplots in each habitat. In each subplot, three to six *C. elongatum* individuals were randomly sampled and cut off at ground level in August, when *C. elongatum* had set seeds but its above-ground parts still remained alive. For each plant, the number of spikes, the number of primary branches (branches from caulis) and the length of spikes were determined. Also, the biomass of vegetative structures, reproductive structures and the total above-ground structure were initially air-dried and later oven-dried at 75°C for 48 h and then weighed.

Soil environment conditions, including soil physical and chemical attributes, were also measured in these two habitats. The soil attributes included soil texture, soil bulk density, soil surface compaction, electrical conductivity, pH, soil organic carbon and total nitrogen. The soil samples were collected from six random locations to a depth of 30cm within each habitat. At each location, a composite soil sample was prepared from the soil collected from five sampling points using a soil auger. Soil cores were obtained with a stainless-steel cylinder (50cm^3 in volume) at each depth and location for the determination of soil bulk density. The soil samples were air-dried and then sieved to pass through a 2-mm screen for analyzing physical attributes and ground to pass through a 0.5-mm screen for analyzing soil organic carbon and total nitrogen. The organic C was determined using the Walkley-Black dichromate oxidation procedure (Nelson & Sommers, 1982). Total N was determined with the Kjeldahl procedure (ISSCAS, 1978).

Statistical analyses: The differences in total above-ground dry weight, dry weight of vegetative structures, dry weight of reproductive structures, number of primary branches, spike number, spike length, dry weight per spike and reproductive effort (RE = dry weight of reproductive structures/dry weight of vegetative biomass) between the two habitats were tested by One-way analysis of variance (ANOVA) and independent t-tests. To determine the effect of plant size (dry weight of vegetative biomass) on reproductive allocation, the form of the relationship between plant size and resources allocated to reproduction was examined by simple linear regressions using the random sampled individual plants in each habitat. The effect of dry weight of vegetative biomass on dry weight of reproductive structures between habitats was examined by comparing the slope (regression coefficient R) from the regressions. A greater slope indicated that for each additional unit of biomass allocated to growth the plants tended to allocate a larger proportion of biomass to reproduction.

Results

Soil properties in two sandy habitats: There were marked differences in soil properties between the mobile and fixed dune habitats (Table 1). Soil texture was finer in fixed habitat than in mobile habitat. The amount of organic carbon, total nitrogen, soil surface compaction, pH and the electrical conductivity of soil were significantly higher in fixed habitat than in mobile habitat ($p<0.05$). But no significant difference ($p>0.05$) was found in soil bulk density between the fixed habitat and mobile habitat.

Table 1. Soil properties in the mobile and fixed sand dunes studied. Means ± SE.

Soil texture (%)	MSD	FSD
Coarse sand (0.25-2.0mm)	53.27 ± 1.94^a	41.52 ± 1.24^b
Fine sand (0.05-0.25mm)	43.29 ± 1.14^a	55.01 ± 0.60^b
Silt and clay (<0.05mm)	3.44 ± 0.87^a	3.47 ± 0.75^a
Soil surface compaction (kg/cm^2)	0.087 ± 0.008^a	0.407 ± 0.030^b
Soil bulk density (g/cm^3)	1.63 ± 0.02^a	1.58 ± 0.02^a
Electrical conductivity (μs/cm)	15.00 ± 1.00^a	26.00 ± 5.51^b
pH	6.83 ± 0.01^a	7.50 ± 0.12^b
Organic C (g/kg)	0.490 ± 0.151^a	2.553 ± 0.691^b
Total N (g/kg)	0.072 ± 0.003^a	0.300 ± 0.048^b

Values with same letters within rows are not significantly different at $p<0.05$. MSD = mobile sand dune habitat and FSD = fixed sand dune habitat

Reproductive allocation in two typical habitats: There were striking differences in total above-ground dry weight biomass (F=40.392, $p<0.001$), dry weight of vegetative structures（F=38.938, $P<0.001$）and the number of primary branches (F=3.921, $p<0.05$) between the mobile and fixed habitats (Fig. 1 A-C). Even greater differences were found in dry weight of reproductive structures（F=41.152, $p<0.001$）, spike number（F=48.709, $p<0.001$）, length of spike（F=58.961, $p<0.001$）, dry weight per spike（F=13.428, $p<0.001$）and reproductive effort （F=122.616, $p<0.001$） (Fig. 1 D-H). The reproductive effort in fixed dunes was about eighteen times that in mobile dunes. The total above-ground dry weight biomass, dry weight of vegetative structures, number of primary branches, number of spikes, spike length, dry weight of reproductive structure and the proportion of biomass allocated to reproduction (RE) were consistently higher in *C. elongatum* plants in fixed sand dunes than in mobile sand dunes.

The relationship between reproductive allocation and plant size in two habitats: Regression results showed that total allocation of biomass to reproduction was size-dependent for plants from both habitats. As vegetative biomass increased, the reproductive biomass also increased in both habitats (Fig. 2). There were highly significant linear relationships between the dry weight of vegetative biomass and the dry weight of reproductive structure in the mobile and the fixed habitats. But plants in the fixed habitat showed a steeper slope from the regression of reproductive biomass on vegetative biomass than those in the mobile habitat. That is, for each additional unit of biomass allocated to vegetative structures the *C. elongatum* plants in the fixed habitat would allocate a greater proportion of biomass to reproductive structures than those in the mobile habitat. The relationship of spike number to vegetative biomass was similar to the relationship between dry weight of reproductive structures and dry weight of vegetative biomass in both habitats (Fig. 2).

The reproductive effort decreased with increased vegetative biomass in both habitats and there were significantly negative relationships both in mobile habitat and fixed habitat, but there were some differences between them (Fig. 3). However, no significant linear relationship between dry weight per spike and vegetative biomass was found in either habitat (Fig. 3).

Discussion

There was a highly significant linear relationship between the dry weight of vegetative biomass (plant size) and the dry weight of reproductive structure in the mobile and the fixed habitats in our study, reproductive biomass increased with increased vegetative biomass in both habitats (Fig. 2). Thus the reproductive structure size of *C. elongatum* was plant size-dependent in both habitats, in agreement with previous studies indicating that plant size is a key factor in determining the pattern of reproductive allocation (Weiner, 1988; Schmid *et al.*, 1995; Reekie, 1998). Similar relationships have been observed in other plants (Samson & Werk, 1986; Worley & Harder, 1996; Pickering & Arthur, 2003). But the present study also found that there was no significant linear relationship between dry weight per spike and the vegetative biomass in either habitat (Fig. 3). This suggests that reproductive effort is increased by production of more spikes rather than larger ones.

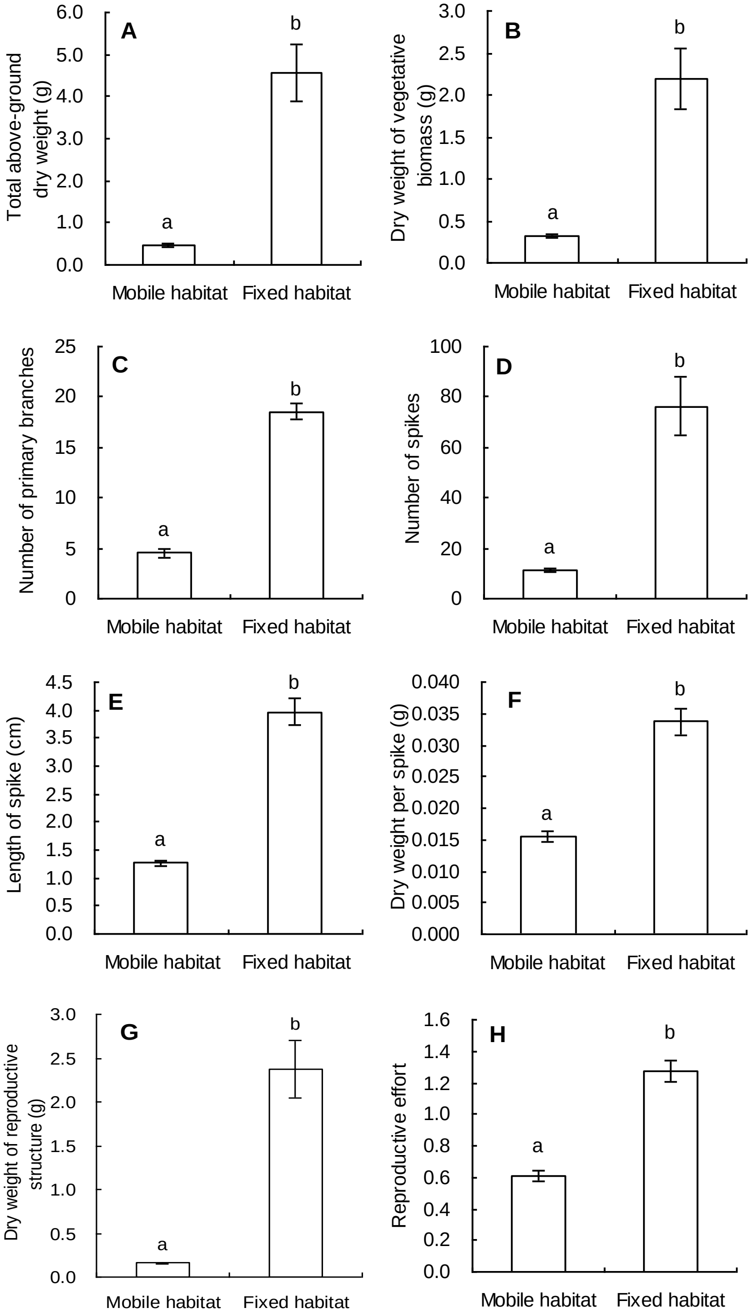

Fig. 1. The effects of habitat type on (A) total above-ground dry weight, (B) dry weight of vegetative biomass, (C) number of primary branches, (D) number of spikes, (E) length of spike, (F) dry weight per spike, (G) dry weight of reproductive structure, and (H) reproductive effort (dry weight of reproductive structure/dry weight of vegetative biomass). Means with different letters within each variable indicate significant differences at $p<0.01$ between the two habitats. Bars represent ±S.E.

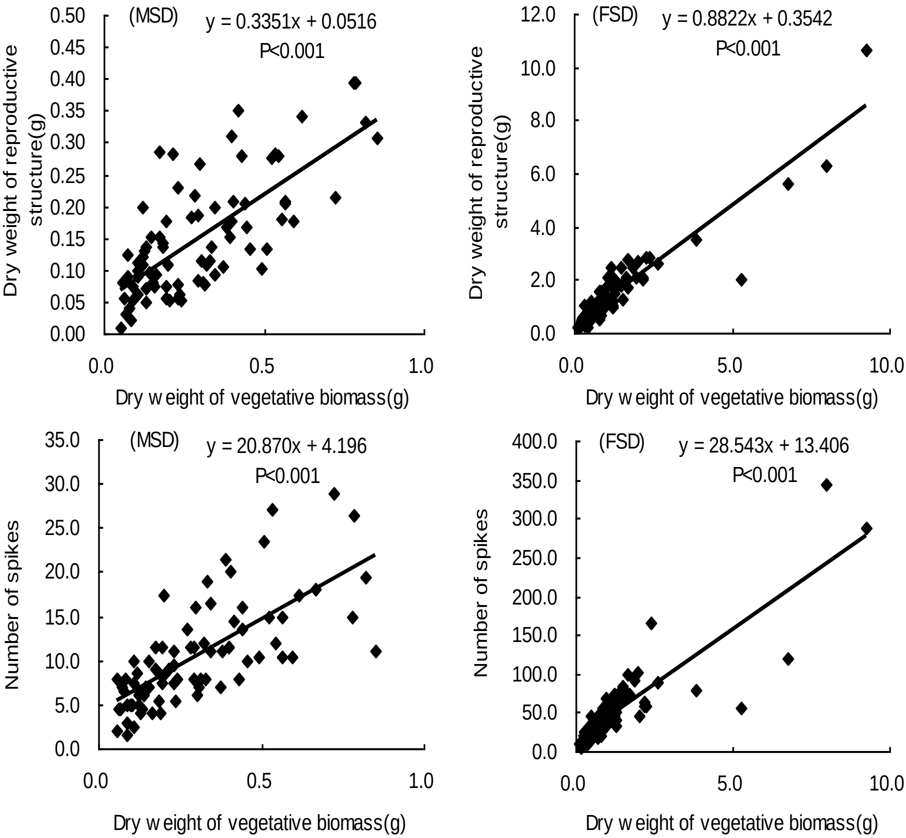

Fig. 2. Linear regressions for the relationships of dry weight of vegetative biomass vs. dry weight of reproduction structure (upper pair), and dry weight of vegetative biomass vs. the number of spikes (lower pair). MSD = mobile sand dune habitat and FSD = fixed sand dune habitat.

Results also showed that plant size (vegetative biomass), biomass allocated to reproductive structure, number of spikes and dry weight per spike were all significantly higher in the fixed dune habitat than in the mobile dune habitat, as was reproductive effort (Fig. 1). The reproductive effort in fixed habitat was about eighteen times that in the mobile habitat, indicating that plant size and size of reproductive structure were highly influenced by habitat type. Difference in resources allocated to reproduction could result from differences in spike length, number of spikes and dry weight of spikes. These results suggest that environmental selective forces could result in variation of reproductive strategies in this species (Silverton & Lovett-Doust, 1993). It has been documented that some species of plant would convert more resources and energy into reproduction, so as to increase the population size, when environmental conditions were improved with sand dune stabilization. In contrast, in poorly stabilized sand dunes, the plant would consume more resources and energy for vegetative development and maintenance in order to cope with the harsh environment (Zhang *et al*., 2005). Zhao *et al*., (2006) also found that plant biomass and seed production were significantly correlated to organic matter, total N and pH in a harsh soil environment. In the present study, we also found that the observed differences in resource allocation patterns of the

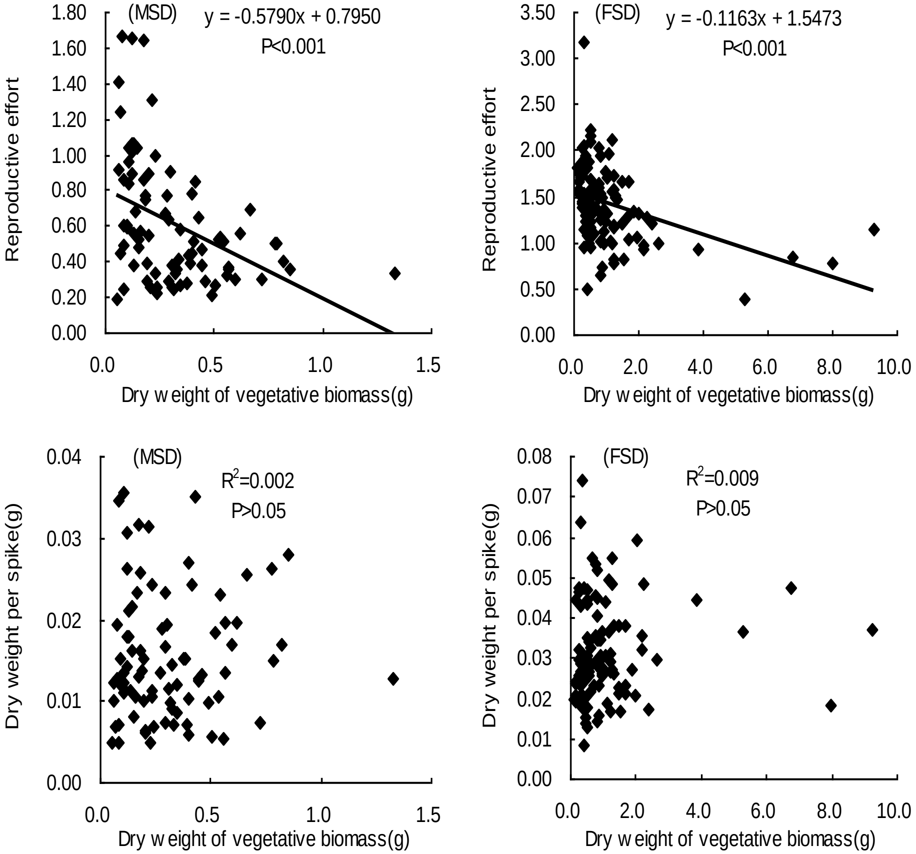

Fig. 3. Linear regressions for the relationships of dry weight of vegetative biomass vs. reproductive effort (upper pair), and dry weight of vegetative biomass vs. dry weight per spike (lower pair) MSD = mobile sand dune habitat and FSD = fixed sand dune habitat.

annual plant *C. elongatum* inhabiting two different habitats were associated in a similar way with the differences in environments and there was a relationship with stabilization of the sand dunes. In mobile habitat, there was more serious wind erosion, sand burial, poorer edaphic conditions (Table 1) and stronger selective pressures on plants (Zhang *et al*., 2002). In order to survive these conditions, the plant must allocate more resources to vegetative growth. However, when soil texture became finer and fertility increased in the fixed habitat, the plant would invest more resources in reproduction to maintain population continuity and increase population size (Konstadia *et al*., 2003). So, *C. elongatum* inhabiting the fixed sand dunes tended to allocate a greater proportion of biomass to reproductive structures, resulting in a significantly greater number of spikes and higher dry weight per spike.

Studies of other plant species have show that reproductive effort related to plant weight and decreased significantly with increasing plant size (Klinkhamer, *et al*., 1990; 1992). In our study, reproductive effort also decreased with increased vegetative biomass (plant size) in both habitats and had a significantly negative linear relationship, but some differences did exist between the two habitats. This indicated that the reproductive effort of *C. elongatum* was size-dependent, but was also influenced by environmental factors. This result is in agreement with the findings of other researchers (Silverton & Lovett-Doust, 1993; Pickering & Arthur, 2003; Liu *et al.*, 2002).

A better understanding of plant growth regulation and the interactions between plants and soils in fragile ecological environments has important implication for plant life-history strategy, population growth, species conservation and evolution and degraded vegetation re-establishment (Sun *et al*., 2001; Zhang *et al*., 2004; Li *et al*., 2005). From this point of view, the differences observed in reproductive allocation patterns of *C. elongatum* between the two habitats could be considered an important adaptation strategy to enhance the plant's fitness in rigorous environmental conditions. Moreover, this study provides helpful insight for ecosystem recovery in the study region and possibly other desertified areas. *C. elongatum* is one of the few plants which can disperse and spread naturally in all types of sand dunes. According to the above results showing that *C. elongatum* inhabiting the fixed sand dunes tended to allocate a greater proportion of biomass to reproductive structures and the reproductive effort was size dependent, if people could use those characteristics of *C. elongatum* to increase vegetative cover in mobile dunes by planting, sand dune fixation can be accelerated.

Conclusion

There are significant differences in reproductive allocation of *C. elongatum* in different sandy habitats. *C. elongatum* plants inhabiting the better environment of fixed dunes seem to allocate more resources to reproductive structures to increase population size, whereas vegetative growth appears to be relatively more important for the survival of *C. elongatum* in the harsher mobile-dune habitat. That is, with the sand land stabilization, the annual plant *C. elongatum* would allocate more resources to reproductive structures. Reproductive biomass was plant size-dependent and significantly affected by habitat type. Reproductive effort was not only influenced by plant size but also affected by environmental factors. The results are important for a better understanding of the adaptation strategy of *C. elongatum* in different sandy habitats and will be helpful for accelerating sand dune fixation by using plants resources.

Acknowledgements

Thanks are due to the anonymous referees for their critical review and valuable comments on this paper. The research was supported by China National Natural Science Foundation (40801036), Western Light PhD Project of the Chinese Academy of Sciences (O928641001), a Key project of the Chinese Academy of Sciences（KZCX2-YW-431）.

References

Cruz, A. and J.M. Moreno. 2001. No allocation trade-offs between flowering and sprouting in the lignotuberous, Mediterranean shrub *Erica australis*. *Acta Oecologica* 22: 121-127.

Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. Chichester: Wiley.

Harper, J.L. 1977. *Population Biology of Plants*. Academic Press, London.

Hartnett, D.C. 1990. Size dependent allocation to sexual and vegetative reproduction in four clonal composites. *Oecologia* 84: 254-259.

Herms, D.A. and W.J. Mattson. 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* 67: 283-325.

Institute of Soil Sciences, Chinese Academy of Sciences (ISSCAS). 1978. *Physical and Chemical Analysis Methods of Soils*. Shanghai Science Technology Press, Shanghai. 7-59.

Klinkhamer, P.G.L., E. Meelis, T.J. de Jong and J. Weiner. 1992. On the analysis of size dependent reproductive output in plants. *Functional Ecology,* 6: 308-316.

Klinkhamer, P.G.L., T.J. de Jong and E. Meelis. 1990. How to test for size dependent reproductive effort. *American Naturalist,* 135: 291-300.

Konstadia, L., A.L. Sebastiaan and M. Kooijman. 2003. Life history implications of allocation to growth versus reproduction in dynamic energy budgets. *Bulletin of Mathematical Biology* 65: 809-834.

Lehtilä, K. and A. Sunds Larsson. 2005. Meristem allocation as a means of assessing reproductive allocation. *Reproductive Allocation in Plants,* 51-75.

Li, F.R., A.S. Zhang, S.S. Duan and L.F. Kang. 2005. Patterns of reproductive allocation in *Artemisia halodendron* inhabiting two contrasting habitats. *Acta Oecologica,* 28: 57-64.

Li, Y.Q., H.L. Zhao, X.Y. Zhao and Y.P. Chen. 2006. Biomass energy, carbon and nitrogen stores in different habitats along a desertification gradient in the semiarid Horqin Sandy Land. *Arid Land Research and Management,* 20: 43-60.

Liu, Z.J., G.Z. Du and J.K. Chen. 2002. Size-dependent reproductive allocation of *Ligularia virgaurea* in different habitats. *Acta Phytoecologica Sinica,* 1: 44-50.

Nelson, D.W. and L.E. Sommers. 1982. Total carbon, organic carbon and organic matter, pp. 539-577, In: *Methods of Soil Analysis*, *Agronomy,* (Eds.): A.L. Page, R.H. Miller and D.R. Keeney. *Part 2, 2nd edition,* ASA, Madison, Wisconsin.

Pickering, C.M. and J.M. Arthur. 2003. Patterns of resource allocation in the dioecious alpine herb *Aciphylla simplicifolia* (Apiaceae). *Austral Ecology,* 28: 566-574.

Pino, J., X.F. Sans and R.M. Masalles. 2002. Size-dependent reproductive pattern and short-term reproductive cost in *Rumex obtusifolius* L. *Acta Oecologica,* 23: 321-328.

Reekie, E.G. 1998. An explanation for size-dependent reproductive allocation in *Plantago major*. *Canadian Journal of Botany,* 76: 43-50.

Reekie, E.G. and F.A. Bazzaz. 1987. Reproductive effort in plants. 1. Carbon allocation to reproduction. *American Naturalist,* 129: 876-896.

Samson, D.A. and K.S. Werk. 1986. Size-dependent effects in the analysis of reproductive effort in plants. *American Naturalist,* 127: 667-680.

Schmid, B., F.A. Bazzaz and J. Weiner. 1995. Size dependence of sexual reproduction and of clonal growth in two perennial plants. *Canadian Journal of Botany,* 73: 1813-1837.

Silverton, J.W. and J. Lovett-Doust. 1993. *Introduction to Plant Population Biology*. Blackwell Scientific Publications, Oxford. 141-157.

Staffan Karlsson, P. and M. Méndez. 2005. The resource economy of plant reproduction, pp. 1-49. In: *Reproductive Allocation in Plants*. (Eds.): E.G. Reekie and F.A. Bazzaz. Elsevier B.V., Amsterdam.

Su, Y.Z. and H.L. Zhao. 2003. Soil properties and plant species in an age sequence of *Caragana microphylla* plantations in the Horqin Sandy Land, north China. *Ecological Engineering,* 20: 223-235.

Sun, S.C., X.M. Gao and Y.L. Cai. 2001. Variations in sexual and asexual reproduction of *Scirpus mariqueter* along an elevational gradient. *Ecology Research,* 16: 263-274.

Vega, C.R.C., V.O. Sadras, F.H. Andrade and S.A. Uhart. 2000. Reproductive allometry in soybean, maize and sunflower. *Annals of Botany,* 85: 461-468.

Wang, T. 2000. Land use and sandy desertification in north China. *Chinese Journal of Desert Research,* 20(2): 103-107 (In Chinese with English abstract).

Weiner, J. 1988. The influence of competition on plant reproduction, pp. 228-245, In: *Plant Reproductive Ecology: Patterns and Strategies*. (Eds.): J. Lovett-Doust and L. Lovett-Doust. Oxford University Press, New York.

Worley, A. and L.D. Harder. 1996. Size-dependent resource allocation and costs of reproduction in *Pinguicula vulgaris* (Lentibulariaceae). *Journal of Ecology,* 84: 195-206.

Zhang, C.Y., C. Yang and M. Dong. 2002. The significance of rhizome connection of semi-shrub Hedysarum leave in an Inner Mongolian dune, China. *Acta Oecologica,* 23(2): 109-114.

Zhang, J.G., Z.S. Zhang, X.P. Wang and X.R. Li. 2005. Reproductive allocation of annual plant *Eragrostis poaeoides* in planted area for sand fixation in Shapotou Region. *China Journal of Desert Research,* 25(2): 202-206 (In Chinese with English abstract).

Zhang, J.Y., H.L. Zhao and T.H. Zhang. 2004. Dynamics of species diversity of communities in restoration processes in Horqin Sandy Land. *Acta Phytoecologica Sinica,* 28(1): 86-92.

Zhang, T.H., Y.Z. Su, J.Y. Cui, Z.H. Zhang and X.X. Chang. 2006. A leguminous shrub (*Caragana microphylla*) in semiarid sandy soils of north China. *Pedosphere,* 3: 319-325.

Zhao, H.L., R.L. Zhou, T.H. Zhang and X.Y. Zhao. 2006. Effects of desertification on soil and crop growth properties in Horqin sandy cropland of Inner Mongolia, north China. *Soil & Tillage Research,* 87: 175-185.

(Received for publication 16 May 2008)