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RESEARCH ARTICLE

Responses of *Hedysarum Laeve*, a guerrilla clonal semi-shrub in the Mu Us Sandland, to local sand burial

LIU Fenghong[1,2], YE Xuehua[1,2], YU Feihai[1], DONG Ming (✉)[1]

1 Key Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
2 Graduate University of Chinese Academy of Sciences, Beijing 100039, China

Abstract In arid and semi-arid inland deserts, one of the environmental stresses for plants is recurrent sand burial, which can influence the physical and biotic microenvironments of the plants and soil. Previous studies have shown that different levels of sand burial have different effects on plants. Slight sand burial could increase the height increment, leaf biomass and the number of new ramets of the plants while heavy sand burial could impair the growth of the plants and even decrease their chances of survival. In other words, below a certain threshold level of burial, the growth of plants is stimulated probably because of multiple factors. However, as the level of burial increases, the positive response starts to decline until it becomes a negative value. Arid and semi-arid inland deserts are frequently colonized and stabilized by many rhizomatous clonal plants. Clonal physiological integration often helps clonal plants buffer local environmental stress encountered by ramets. A rhizomatous clonal semi-shrub, *Hedysarum laeve* (*H. laeve*), is the dominant plant species and important for vegetation restoration in the Mu Us sandland. To investigate whether clonal integration can increase the threshold of sand burial and help rhizomatous *H. laeve* tolerate heavy sand burial, we conducted a field experiment. The results showed that slight sand burial could accelerate ramet growth and enhance leaf biomass, stem biomass and shoot biomass, while heavy sand burial reducesed the biomass of the plant and impairs survival and growth of the ramets. Clonal integration increased the threshold of sand burial. Under heavy sand burial, ramets connected to other ramets not buried in sand were more in terms of height increment, stem biomass, leaf biomass and shoot biomass compared to the ramets encountering sand burial but disconnected from other ramets. It suggested that clonal physiological integration could help *H. laeve* ramets tolerate relatively heavy sand burial. We also discussed that clonal integration plays a role in *H. laeve* presence in the Mu Us sandland.

Keywords Clonal integration, *Hedysarum laeve*, Mu Su sandland, Sand burial

1 Introduction

One of the most obvious features on foredunes and inland dunes is recurrent burial (Maun and Lapierre, 1984; Maun, 1998). Sand burial can cause changes in the biotic and abiotic environments of plants such as photosynthetically active radiation (Sykes and Wilson, 1990; Brown, 1997), soil moisture (Baldwin and Maun, 1983), soil temperature (Baldwin and Maun, 1983; Zhang and Maun, 1990), rhizosphere oxygen content (Klimes et al., 1993), soil organics content (Baldwin and Maun, 1983) and activity of soil microorganisms (D'Hertefeldt and van der Putten, 1997). Burial levels vary due to differences in vegetation coverage and wind speed. Previous studies have shown that sand burial at different levels has different effects on plants (Zhang et al., 2002a; Yu et al., 2002, 2004). Slight sand burial may improve environmental conditions by eliminating susceptible species (Perumal and Maun, 1999) and enhancing soil moisture of the rhizosphere (Baldwin and Maun, 1983) and activity of soil microorganisms so that height, biomass and the number of new ramets of plants can increase (Eldred and Maun, 1982; Disraeli, 1984; Maun and Lapierre, 1984; Brown, 1997; Maun, 1998). However, with increasing intensity and/or depth of sand burial, environmental conditions become more severe (Sykes and Wilson, 1990). In other words, the positive effect of sand burial on plants declines until it becomes a negative factor. When it is over a certain threshold level, sand burial may impair growth and even survival of plants (Maun and Lapierre, 1984; Harris and Davy, 1986; Zhang and Maun,

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E-mail: dongming@ibcas.ac.cn

1990; Sykes and Wilson, 1990; Brown, 1997; Maun, 1998; Yu et al., 2002, 2004).

Different plants have different capabilities to withstand sand burial. Those that survive sand burial have developed various adaptive mechanisms during their long-term evolution (Yu et al., 2004). In habitats such as inland dunes in the Mu Us sandland of Inner Mongolia, there are many rhizomatous plants (Dong and Alaten, 1999) which are often the pioneer plant species in the community (Oosting and Billings, 1942; Maun, 1984; Maun and Lapierre, 1984; Sykes and Wilson, 1990; Dong et al., 1998; Dong and Alaten, 1999). Clonal plants have been proven to resist and/or buffer ecological stress by clonal physiological integration in a wide range of habitats (Jonsdottir and Watson, 1997; D'Hertefeldt and van der Putten, 1997; Alpert, 1999a, b; Amsberry et al., 2000). In the inland dunes of arid and semi-arid areas, desertification is becoming more serious and landscapes are becoming very fragmental. Meanwhile, for an individual of guerrilla rhizomatous plant in this area, some ramets subjected to sand burial often connect to the other ones without sand burial (Yu et al., 2002). With help of clonal integration, clonal plants, especially rhizomatous ones in the inland dunes, may have stronger capacity to withstand sand burial.

Hedysarum laeve (*H. Laeve*) Maxim. (Leguminosae), a rhizomatous clonal semi-shrub, is one of the major species used frequently in the revegetation of dune-fields in the sand lands of the northern part of China by means of aerial sowing. Vegetable (asexual) reproduction is very common in natural *H. laeve* population. Considering the species playing a vital role in combating desertification in the Mu Us sandland of China, it is very important to get basic knowledge about how it copes with the sandy environment. We also expect that the present study would provide some academic references for practical applications. The aim of this paper is to try to answer the following questions: how do different levels of sand burial affect survival, growth and aboveground biomass accumulation of *H. laeve* ramets; can clonal integration help *H. laeve* enhance its ability to resist sand burial?

2 Materials and methods

2.1 Species

Hedysarum laeve Maxim. (Leguminosae) is a rhizomatous semi-shrub, frequently dominating inland dunes in semi-arid regions of China (Fu, 1994). It propagates vegetatively by extension of belowground horizontal rhizomes bearing adventitious roots at their nodes (Zhang et al., 2001). The rhizomes extend linearly for a certain distance, and then turn upward to form aboveground shoots. Lateral buds on the basis of the shoot and/or on the rhizome nodes of the ramet(s) in the first ramet hierarchy may form, making up ramets in the second ramet hierarchy. Similarly, ramets in the third ramet hierarchy, in the fourth ramet hierarchy, etc., are developed. Commonly, the ramets persist for more than five years with shoots of 60–160 cm tall, and their rhizome connection is maintained (Chen and Dong, 2000). *Hedysarum laeve* is one of the major aerial species used frequently in revegetation of dune-fields in the sand lands of Mu Us Sandland of China (Shen, 1997).

2.2 Study site

The field investigation was carried out in the southeast Ordos Plateau in Inner Mongolia, China. This is a semiarid area with a mean annual precipitation of 260–450 mm and a mean annual temperature of 7.5–9.0°C (Zhang, 1994). Historically, this area was highly productive grassland (Zhang, 1994). However, due to human and natural disturbances, the land was seriously decertified, with mobile sand dunes and fixed dunes widely present. We selected a sand dune that was located about 0.5 km from Ordos Sandland Ecological Station (39.02′N, 109.51′E) Institute of Botany, Chinese Academy of Sciences in Inner Mongolia, China. On this inland dune *H. laeve* had a cover of about 60%, with other plant species, such as *Corispermum puberulum* and *Chenopodium aristatum*, covering less than 10%. The ramet population of *H. laeve* was roughly uniformly distributed on this dune, and there was no apparent large patch.

2.3 Experimental design

On July 13, 2004, 80 ramet pairs of *H. laeve* with similar size (ramet height and shoot width) and 80 ramets with similar size (ramet height and shoot width) were selected. Of these genets, the ramets pairs (clonal fragment) consisting of its two ramets with similar morphology and the single ramet were separated from the parent ramets by severing the rhizome to a certain depth by inserting a sharp blade perpendicular to the sand surface (Yu et al., 2004). After a week we checked the vitality of each *H. laeve* ramet and found that most ramets survived. We selected 56 connected clonal fragments and 56 disconnected ramets and measured their shoot height. One ramet from each of the connected clonal fragment did not experience burial, while the other connected ramet and the disconnected ramet were either unburied (0) or buried with 10%, 20%, 40%, 60%, 80% and 100% of its original shoot. Each buried ramet was fenced with a 70 cm high, sunlight-proof plastic belt, the lower 5 cm of which was buried in sand. Each belt was stabilized with four bamboo sticks bound together at the top with metal wire. Sand collected nearby was then filled into the belted quadrates to the special height. During this procedure care was taken to avoid bending the shoots within the quadrates. There were eight replicates for each of treatment.

2.4 Measurements and analysis

On September 11, 2004, the aboveground parts of all the experimental plants were harvested. Before harvesting, all the filled-in sand was carefully removed. The shoots had their height measured, were subdivided into leaves and stems, and dried to constant mass at 95°C.

The relative growth rate (RGR) of a shoot was calculated as the change in shoot length during the experiment divided by the original shoot length at the beginning of the experiment. Two-way ANOVAs were conducted for each measured character (the RGR, survivorship, biomass) to test the effects of burial, connection (whether the ramet was connected or not), and all interactions between these factors. All statistical tests were performed by using SPSS 11.5.

3 Results

3.1 Survivorship

When subjected to 100% sand burial treatment, half of the ramets connected to the ramets without sand burial died while none of the severed ramets survived (Figs. 1 and 2). Three of the eight severed ramets were incapable of survival when 80% of their original height was subjected to deep sand burial (Fig. 2).

3.2 Relative growth rate

Sand burial and rhizome connection or no connection as well as their interaction had significant effects on the RGR of ramets (Table 1). The connected ramet in 40% burial treatment grew the fastest, while the severed ones subjected to 10% sand burial grew during the experiment (Fig. 1A). When subjected to sand burial lower than 20%, there were no significant differences in RGR between the connected ramets and disconnected ones. When subjected to sand burial higher than 20%, connected ramets had more height increments than severed ones (Fig. 1A).

For the ramets without sand burial but connected to ramets subjected to sand burial, 20% burial treatment fueled faster growth than the control and had no differences from the other treatments (Fig. 2A).

3.3 Aboveground biomass and their allocation

Sand burial depth, rhizome connected or not and their interaction had significant effects on the stem biomass, leaf biomass and total aboveground biomass of *H. laeve* ramets (Table 1). Stem biomass and total aboveground biomass of connected ramets were enhanced by sand burial below and equal to 20% of their original shoot (10%, 20%) while leaf biomass was increased by sand burial less than 20% to their original shoot (10%, 20%). Those subjected to sand burial less than 20% to their original shoot (10%, 20%), the disconnected ramets had an increase in stem length and total aboveground biomass, while leaf biomass was also enhanced (Fig. 1). When subjected to above 20% sand burial, the connected ramets had more stem, leaf and total aboveground biomass than the disconnected ones. In the 0%, 10% and 20% burial treatments, no significant differences were found between

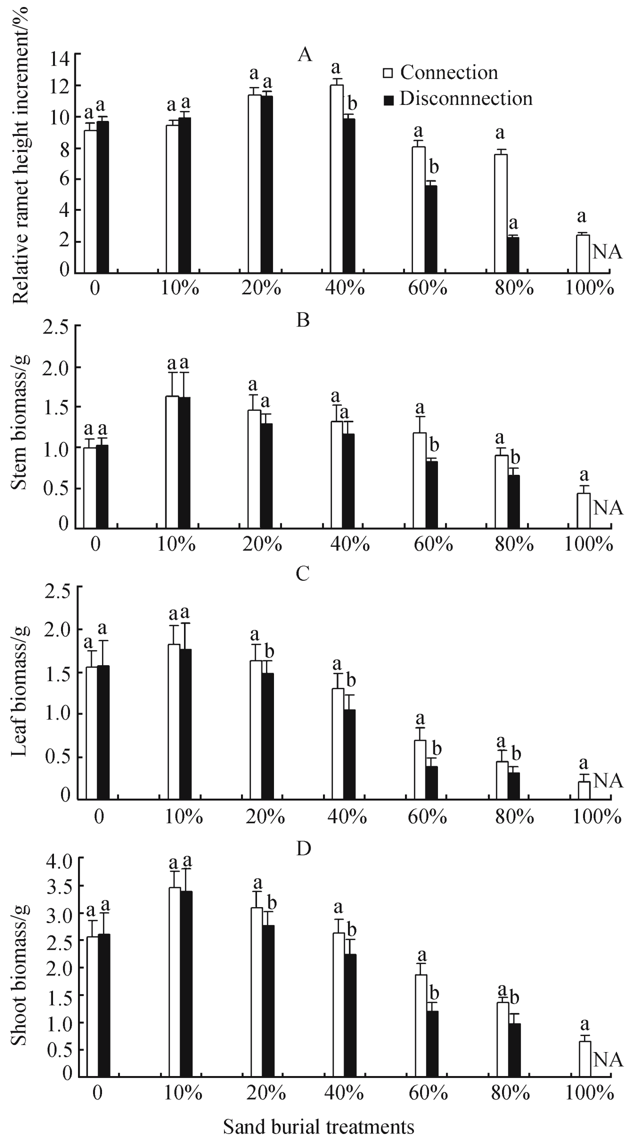

Fig. 1 Height increment (A), stem biomass (B), leaf biomass (C) and shoot biomass (D) of ramets which were subjected to sand burial connected to another ramet without sand burial or disconnected from another ramet. The vertical bars sharing the same letter are not different at $p = 0.05$ level between the two ramets; a different letter means significant difference

them (Fig. 2B). When subjected to less than 20% deep sand burial (0%, 10%, 20%), the leaf biomass of connected ramets varied with those of severed ones (Fig. 1B). Stem biomass and total aboveground biomass of the ramets without sand burial but connected to the ramets subjected to 100% sand burial were markedly lower than those in other treatments while leaf biomass did not vary among all the treatments (Fig. 2B).

4 Discussion

In the inland dunes of arid and semi-arid areas, sand burial is a recurrent event that plants are subjected to (Yu et al., 2002,

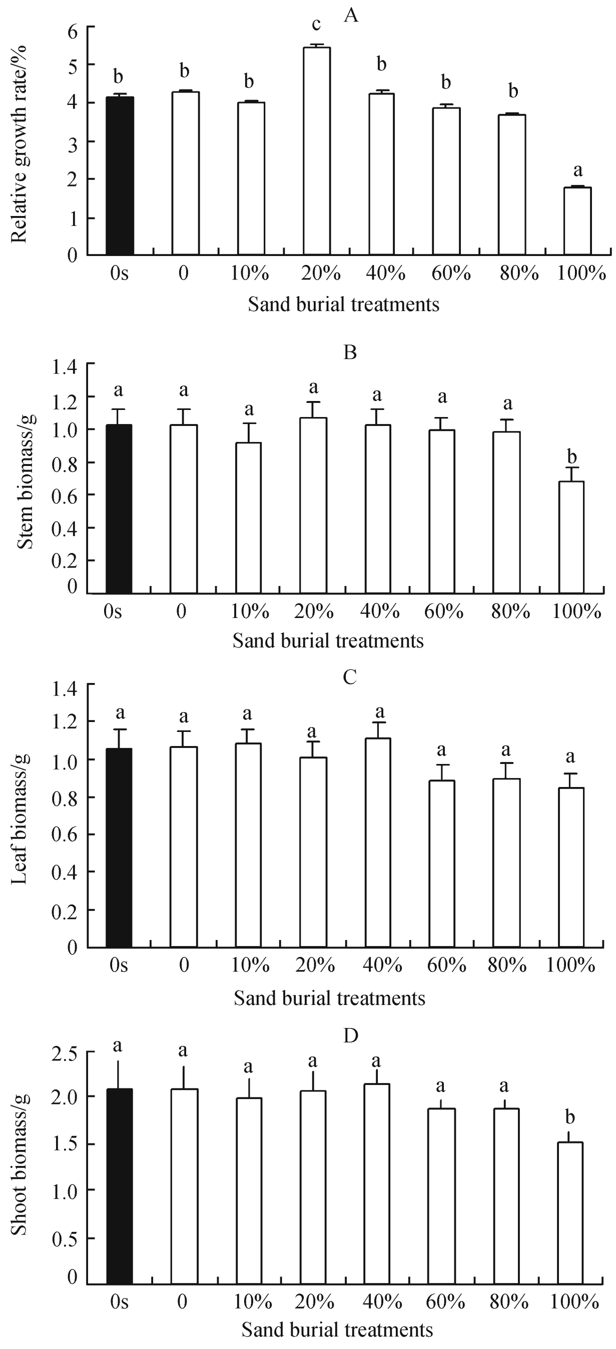

Fig. 2 Height increment (A), stem biomass (B), leaf biomass (C) and shoot biomass (D) of ramets which were not subjected to sand burial connected to another ramet subjected to sand burial. The filled histogram indicates the ramet not connected to any other ramet. The vertical bars sharing a different letter are different at $p = 0.05$ level or at $p = 0.01$ level between the two ramets. Significant level b, $p < 0.05$; c, $p < 0.01$

2004). Many rhizomatous plants in these areas play an important role in binding flowing sandy dunes (Dong, 1997; Dong et al., 1998; Dong and Alanten, 1999; Liu et al., 2004). In the field sand burial is often local and uneven. Some ramets of *H. laeve* may be covered by sand while others are not, i.e. the connected ramets are under different environmental conditions. Thus for *H. laeve*, the capacity to withstand sand burial may be enhanced through clonal integration.

Table 1 *F* values of two-way ANOVA for the effects of sand burial and rhizome connection as well as their interaction on the characters of the ramets subjected to sand burial

Characters	Sand burial		Rhizome connection		Interaction S × B	
	F	d*f*	*F*	d*f*	*F*	d*f*
Relative height increment (100%)	23.68[c]	6.84	15.69[c]	1.84	2.89[a]	5.84
Stem biomass (g)	5.87[c]	6.84	5.16[a]	1.84	2.53[a]	5.84
Leaf biomass (g)	10.32[c]	6.84	6.96[c]	1.84	5.01[c]	5.84
Shoot biomass (g)	8.62[c]	6.84	5.25[a]	1.84	4.81[b]	5.84

[a] $p < 0.05$; [b] $p < 0.01$; [c] $p < 0.001$.

This paper studied how sand burial affects growth and survival of *H. laeve*, a dominant semi-shrub in the Mu Us Sandland, and how clonal integration modifies its response. We conducted the field experiments in the dunes subjected to fire to keep all the experimental clonal fragments even. They had not reproduced sexually at the end of this experiment and it was possibly because they were newly recovered. The results showed that slight sand burial (10%–20%) could enhance the growth and biomass accumulation of *H. laeve* to some extent (Fig. 1). The greenhouse experiment also showed that the biomass and RGR of *H. laeve* seedlings were all higher than the control when depth of sand burial was up to 33% and 67% of their height (Zhang et al., 2002a). It is possible that slight sand burial has not touched the leaves of plants. On the other hand, it is beneficial to microenvironments by retaining soil moisture of rhizosphere and reducing soil temperature, leading to positive effects on plants. However, the leaves may be covered by the heavy sand burial and it reduced soil aeration. Thus, under this condition growth and survival of *H. laeve* was markedly reduced (Fig. 1). Meanwhile, the connected ramets had higher survival rates than the disconnected ones, height increments and biomass when they were in the same sand burial (Fig. 1). In addition, the connected ramets without sand burial were not depressed in terms of height increment, stem biomass, leaf biomass and aboveground biomass except those connected to ramets subjected to 100% sand burial (Fig. 2). These results suggested that clonal integration can help *H. laeve* resist heavy sand burial. The ramets without sand burial may transfer carbohydrates to the ones buried by sand (Zhang et al., 2001). Moreover, the rhizome of *H. laeve* has strong restored capacity (de Kroon and Knops, 1990; Dong and de Kroon, 1994) and its recovery from sand burial will depend on the release of restored resources and energy to a great extent (Maun, 1998). Since sand burial is actually slower and gradual in nature, *H. laeve* may have a stronger ability than that found in this experiment.

Globally, many important sand-binding plants, such as *Uniola paniculata*, *Ammophila breviligulata*, *Ammophila arenaria*, *Elymus farctus*, *Euphorbia glauca*, *Ipomoea stolonifera*, *Ipomoeapes caprae*, *Carex arenaria*, *Psammochloa villosa* and *Hedysarum laeve* are clonal plants

(Dong, 1997; Dong and Alaten, 1999; Chen and Dong, 2000; Roels et al., 2001; Zhang et al., 2002b, c). There have been experiments to demonstrate that clonal integration can help stolonifeous Potentilla anserine (Yu et al., 2002) and rhizomatous P. villosa (Yu et al., 2004) resist sand burial. As a typical ecotone between arid and semiarid areas, Mu Us sandland has high spatial heterogeneity even at a small scale (Dong et al., 1998; Chen et al., 2000). The sandy landscape consists of many patches with different types and sizes (Dong et al., 1998; Chen et al., 2000). Considering strong and frequent sand burial in the Mu US sandland, clonal integration may be one adaptive strategy in these sandy habitats with spatial-temporal heterogeneity (Pitelka and Ashmun, 1985).

For the rhizomatous plants, the seedlings developed from buds of rhizome have more capacities to restore resource and energy than those developed from seeds, so the former resist sand burial more than the latter (Harris and Davy, 1986). A rhizome not only reproduces as a bud pool (Maun, 1984) but also transports materials as the translocation channel (Marshall, 1990).

Hedysarum laeve, as one of the most common aerial sowing species in the Mu Us sandland of China, is a clonal, perennial plant with rhizome; the rapidly elongating rhizome contributes greatly to colonize sandy dunes and stabilize sand (Dong and Alaten, 1999). The field survey showed that clonal reproduction is becoming more important during the life history of *H. laeve* in the Mu Us sandland (Liu et al., 2004). The new seedlings are connected to the other ramets and carbohydrates, nutrients and water can be exchanged among them (Zhang et al., 2002b, c, 2003). Moreover, forms of multiple and dense layers of rhizomes of *H. laeve* belowground are very beneficial to stabilize sandy substrate to some extent and contribute to a reversion of the degradation process (Dong and Alanten, 1999).

In summary, *H. laeve* is suitable to heterogeneous environments as a clonal plant, in conjunction with the fact that it can provide forage for livestock, and it is feasible to aerial sowing *H. laeve* in the Mu US sandland of China.

References

Alpert P (1999a). Clonal integration in *Fragaria chiloensis* differs between populations: Ramets from grassland are selfish. Oecologia, 120: 69–76

Alpert P (1999b). Effects of clonal integration on plant plasticity in *Fragaria chiloensis*. Plant Ecology, 141: 99–106

Amsberry L, Baker M A, Ewanchuk P J, Bertness M D (2000). Clonal integration and the expansion of *Phragmites australis*. Ecological Applications, 10: 1110–1118

Baldwin K A, Maun M A (1983). Microenvironment of Lake Huron sand dunes. Canadian Journal of Botany, 61: 241–255

Brown J F (1997). Effects of experimental burial on survival, growth, and resource allocation of three species of dune plants. Journal of Ecology, 85: 151–158

Chen Y F, Dong M (2000). Genet characters of *Hedysarum leave* and its characters of ramet population in different habitats in Mu Us sandland. Acta Phytoecologica Sinica, 42(1): 40–45 (in Chinese)

Chen Y F, Yu F H, Dong M (2000). Spatial heterogeneity of the Psammophytic half-shrub community in Mu Us Sandland. Acta Ecologica Sinica, 20(4): 568–572 (in Chinese)

Chen Y F, Yu F H, Zhang C Y, Dong M (2001). Role of clonal growth of the rhizomatous grass *Psammochloa villosa* in patch dynamics of Mu Us Sandy land. Acta Ecologica Sinica, 21(11): 1745–1750 (in Chinese)

de Kroon H, Knops J (1990). Habitat exploration through morphological plasticity in two chalk grassland perennials. Oikos, 59: 39–49

D'Hertefeldt T, van der Putten W H (1997). Physiological integration of the clonal plant *Carex arenaria* and its response to soil-borne pathogens. Oikos, 81: 229–237

Disraeli D J (1984). The effect of sand deposits on the growth and morphology of *Ammophila breviligulata*. Journal of Ecology, 72: 145–154

Dong M (1997). Hierarchical structure and hierarchical selection in clonal plants. In: Zhang X, Gao Q, eds. Information Ecology. Beijing: Science Press, 136–141 (in Chinese)

Dong M, Alaten B (1999). Clonal plasticity in response to rhizome severing and heterogeneous resource supply in rhizomatous grass *Psammochloa villosa* in an Inner Mongolian dune, China. Plant Ecology, 141: 53–58

Dong M, Chen Y F, Yu F H, Zhang C Y (1998). Resource use of clonal plants in environmental improvement of ecotones. In: Dong M, Werger M, eds. A Spectrum of Ecological Studies, Chongqing: Southwest China Normal University Press, 14–19 (in Chinese)

Dong M, de Kroon H (1994). Plasticity in morphology and biomass allocation in *Cynodon dactylon*, a grass species forming stolons and rhizomes. Oikos, 70: 99–106

Eldred R A, Maun M A (1982). A multivariate approach to the problem of decline in vigour of Ammophila. Canadian Journal of Botany, 60: 1371–1380

Fu X Q (1994). Commission Editorial of Inner Mongolia Flora. Flora Intramogolica. Hohhot: Inner Mongolia People's Press, 339 (in Chinese)

Harris D, Davy A J (1986). The regenerative potential of *Elymus farctus* from rhizome fragments and seeds. Journal of Ecology, 74: 1057–1077

Jonsdottir I S, Watson M A (1997). Extensive physiological integration: An adaptive trait in resource-poor environments? In: de Kroon H, van Groenendael J, eds. The Ecology and Evolution of Clonal Plants. Leiden: Backbuys Publishers, 109–136

Klimes L, Klimesova J, Osbornova J (1993). Regeneration capacity and carbohydrate reserves in a clonal plant *Rumex alpinus*: Effect of burial. Vegetatio, 109: 153–160

Liu F H, Liu J, Dong M (2004). Spatial pattern of sandy vegetation and two dominant clonal semi-shrubs in the Ordos Plateau. Acta Ecologica Sinica, 24(11): 2374–2381 (in Chinese)

Marshall, C (1990). Source-sink relations of interconnected ramets. In: van Groenendael J, de Kroon H, eds. Clonal Growth in Plants: Regulation and Function. Hague: SPB Academic Publishing, 23–41

Maun M A (1984). Clonizing ability of *Ammophila breviligulata* through vegetative regeneration. Journal of Ecology, 72: 565–574

Maun M A (1998). Adaptations of plants to burial in coastal sand dune. Canadian Journal of Botany, 76: 713–738

Maun M A, Lapierre, J (1984). The effects of burial by sand on seed germination and seedling establishment of four dune species. American Journal of Botany, 73: 450–455

Oosting H J, Billings W D (1942). Factors effecting vegetational zonation on coastal dunes. Ecology, 23: 131–142

Perumal J V, Maun M A (1999). The role of mycorrhizal fungi in growth enhancement of dune plants following burial in sand. Functional Ecology, 13560–13566

Pitelka L F, Ashmun J W (1985). Physiology and integration of ramets in clonal plants. In: Jackson J, Buss L, Cook R, eds. Population Biology and Evolution of Clonal Organisms. New Haven: Yale University Press, 399–435

Roels B, Donders S, Werger M J A, Dong M (2001). Relation of wind-induced sand displacement to plant biomass and plant sand-binding capacity. Acta Botanica Sinica, 43: 979–982

Shen W S (1997). Population dynamics of main plant with which maowusu sandland was aerially. Acta Phytoecologia Sinica, 21(4): 328–334 (in Chinese)

Sykes M T, Wilson J B (1990). An experimental investigation into the response of New Zealand sand dune species to different depths of burial by sand. Acta Botanica Neerlandica, 39: 171–181

Yu F H, Chen Y F, Dong M (2002). Clonal integration benefits clonal fragment of *Potentilla anserina* suffering sand burial. Evolutionary Ecology, 15: 303–318

Yu F H, Dong M, Krusi B (2004). Clonal integration helps *Psammochloa villosa* survive sand burial in an inland dune. New Phytologist, 162: 697–704

Zhang C Y, Yang C, Dong M (2001). The clonal integration of photosynthates in the rhizometous half shrub *Hedysarum laeve*. Acta Botanica Sinica, 21: 1986–1993

Zhang C Y, Yu F H, Dong M (2002a). Effects of sand burial on the survival, growth and biomass allocation in semishrub *Hedysarum laeve* seedlings. Acta Botanica Sinica, 44: 337–343

Zhang C Y, Yang C, Dong M (2002b). The clonal integration and its ecological significance in *Hedysarum laeve*, a rhizomatous shrub in Mu Us sandland. Journal of Plant Research, 115: 113–118

Zhang C Y, Yang C, Dong M (2002c). The significance of rhizome connections of semi-shrub *Hedysarum laeve* in Inner Mongolia Dune, China. Acta Oecologica, 23: 109–114

Zhang C Y, Yang C, Dong M (2003). Interramet water translocation in natural clones of the rhizomatous shrub, *Hedysarum laeve*, in a semi-arid area of China. Trees, 17(2): 109–116

Zhang J, Maun M A (1990). Effects of sand burial on seed germination, seedling emergence, survival, and growth of *Agropyron psammophilum*. Canadian Journal of Botany, 68: 304–310

Zhang X S (1994). Principles and optimal for development of Maowusu grassland. Acta Phytoecologica Sinica, 18(1): 1–16 (in Chinese)