

A Trade-off Between Guerrilla and Phalanx Growth Forms in *Leymus secalinus* Under Different Nutrient Supplies

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• **Background and Aims** A phalanx growth form enables clonal plants to make better use of resource-rich patches, whereas a guerrilla growth form provides them with opportunities to escape from resource-poor sites. *Leymus secalinus* produces both spreading (guerrilla form) and clumping ramets (phalanx form). Here, the hypothesis that a trade-off between the two growth forms in *L. secalinus* exists under different resource levels is tested.

• **Methods** Ramets of *L. secalinus* were grown under three levels of nutrient supply.

• **Key Results** With increasing nutrient supply, the proportion of clumping ramets (in total number of ramets) increased, whereas that of spreading ramets decreased. With increasing nutrient supply, the number of buds increased, whereas biomass per bud decreased. A trade-off between bud number and size further supports the above hypothesis because larger buds were more likely to develop into spreading ramets, and smaller buds into clumping ramets. Mean spacer length between spreading ramets was significantly smaller under the high than under the medium nutrient supply.

• **Conclusions** The results suggest that a trade-off between the two growth forms in *L. secalinus* exists under different nutrient supplies. Such a trade-off together with plasticity in spacer morphology may enable *L. secalinus* to make better use of small-scale heterogeneity in resource supply.

Key words: Architectural plasticity, bud size–number trade-off, clumping ramets, growth form trade-off, *Leymus secalinus*, morphological plasticity, spreading ramets.

INTRODUCTION

Clonal plants are very common and diverse in the plant kingdom (Callaghan *et al.*, 1992; Klimeš *et al.*, 1997; Song *et al.*, 2001). Based on the spatial arrangement of ramets, clonal plants can be classified into different clonal growth forms (Lovett-Doust, 1981; White, 1984). Clegg (1978; cited by Oborny and Cain, 1997) and Lovett-Doust (1981) distinguished two classes of clonal growth form: phalanx and guerrilla. In the phalanx growth form, connections between ramets (i.e. spacers *sensu* Bell, 1984) have few and/or short internodes, resulting in closely packed ramets termed ‘clumping ramets’ (Shaver and Billings, 1975; Lovett-Doust, 1981; Bernard, 1990; Navas and Garnier, 1990). In the guerrilla growth form, by contrast, connections between ramets have many and/or long internodes, resulting in widely spaced ramets termed ‘spreading ramets’ (Shaver and Billings, 1975; Lovett-Doust, 1981; Bernard, 1990; Navas and Garnier, 1990).

The ecological significance of these two clonal growth forms has long been recognized. The guerrilla growth form is very common in early successional stages, as well as in resource-heterogeneous and/or disturbed habitats, whereas the phalanx form is more favoured in late successional stages and in relatively homogeneous and/or less disturbed habitats (Schmid and Bazzaz, 1987; Navas and Garnier, 1990; Krystyna, 1995; Scott, 1995; Adachi *et al.*, 1996). The guerrilla growth form enables clonal plants to spread

quickly in horizontal space so that, in a spatially heterogeneous habitat, clonal plants can more readily escape from stressful microsites and find favourable ones (Lovett-Doust, 1981, 1987; Sutherland and Stillman, 1988; de Kroon and Hutchings, 1995; Humphrey and Pyke, 1998; Oborny *et al.*, 2001). The phalanx growth form, by contrast, may enable clonal plants to tolerate more stressful conditions, make better use of locally abundant resources (monopolization strategy) and out-compete other species in a favourable microsite (Lovett-Doust, 1981, 1987; Schmid and Happer, 1985; Humphrey and Pyke, 1998).

The perennial grass *Leymus secalinus*, like many sedge species (Bernard, 1990), produces both spreading and clumping ramets, resulting in a combined growth form. In this growth form, spreading ramets are first produced at the end of long rhizomes and clumping ramets are then developed from the short rhizomes of the spreading ramets (Shaver and Billings, 1975; Bernard, 1990). A previous study has shown that severing rhizomes had little effect on the growth of the newly produced *L. secalinus* ramets in a spatially relatively homogeneous habitat (Dong, 1999), suggesting that the rhizomes of *L. secalinus* may be more important in foraging activities. Because spreading ramets have an advantage in exploiting open resources and clumping ramets may be more suited to monopolizing locally abundant resources, it is hypothesized here that a trade-off between the production of clumping and spreading ramets in *L. secalinus* exists under different resource supplies.

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To test this hypothesis *L. secalinus* were grown under three levels of nutrient supply. With increasing nutrient supply it is predicted that the proportion of clumping ramets in *L. secalinus* will increase, whereas that of spreading ramets will decrease.

MATERIALS AND METHODS

The species

Leymus secalinus (Georgi) Tzvel. is a perennial grass approx. 45–90 cm high, distributed in the Autonomous Regions of Inner Mongolia and Tibet, and the provinces of Hebei, Shaanxi, Gansu, Shanxi and Qinhai of China, as well as in Mongolia, Japan and the Far East (Yang, 1994). It occurs in grasslands, sandy grasslands, mountain slopes, farmlands and roadsides (Dong, 1999).

Experimental design

In May, 2004, ten clones of *L. secalinus* were randomly collected in a sandy grassland near Ordos Sandland Ecological Station (OSES; 39°02'N, 109°51'E; Institute of Botany, the Chinese Academy of Sciences), located in the south-east of the Mu Us sandy grassland of China. Three similar-sized ramets of each clone were selected and planted into 30 × 20 × 20-cm plastic containers at OSES. On 15 June, 2004, after 2 weeks of recovery, the three ramets of each clone were randomly subjected to three nutrient treatments. For nutrient treatments, a commonly available granular lawn fertilizer was used (Osmocote 301, Scotts, Marysville, OH, USA) with 15N : 11P : 13K : 2 Mg (elemental ratio) as the basic fertilizer and the commercial nutrient solution (Peters1, Scotts) with 20N : 20P : 20K (elemental ratio) as the supplemental fertilizer. Under the high-nutrient treatment each container received 13.6 g Osmocote 301 once and 100 mL Peters1 nutrient solution (0.417 g L⁻¹) once a week (Dong and Alaten, 1999). Both fertilizers (Osmocote 301 and Peters1) were reduced to 50% in the medium-nutrient treatment and to 10% in the low-nutrient treatment, respectively.

Measurement and analysis

The experiment was ended on 14 September, 2004. The number of clumping ramets, number of spreading ramets and number of buds (potential ramets) were counted. Spreading ramets are ramets produced by long rhizomes that eventually grow upright to form new ramets, whereas clumping ramets are ramets produced by tillering or very short rhizomes of spreading ramets. Each plant was then separated into roots, shoots, rhizomes and buds. Rhizome length and biomass of each plant part were measured after drying them at 80 °C for 48 h. Mean rhizome spacer length was calculated as the mean distance between two adjacent spreading ramets and specific spacer dry mass as the dry mass per unit spacer length. The data were analysed by using two-way ANOVA (without replication) followed by least-significant difference (LSD) tests to investigate the differences among the nutrient treatments.

TABLE 1. Effects of nutrient availability and clone on *Leymus secalinus*

Trait	Nutrient effect		Clone effect	
	<i>F</i> _{2,18}	<i>P</i>	<i>F</i> _{9,18}	<i>P</i>
(A) Biomass				
Plant dry mass	47.129	<0.001	2.640	0.038
Root dry mass	31.532	<0.001	2.730	0.033
Shoot dry mass	54.713	<0.001	2.420	0.053
Bud dry mass	23.583	<0.001	2.317	0.062
Rhizome dry mass	25.729	<0.001	0.792	0.628
(B) Ramet number and size				
Number of clumping ramets	34.875	<0.001	1.919	0.114
Number of spreading ramets	20.555	<0.001	0.422	0.906
Percentage of clumping ramets	17.513	<0.001	1.603	0.188
Percentage of spreading ramets	17.513	<0.001	1.603	0.188
Dry mass per ramet	0.371	0.695	2.768	0.032
Number of leaves per ramet	0.862	0.439	0.970	0.495
(C) Bud number and size				
Number of buds	35.717	<0.001	1.221	0.342
Dry mass per bud	8.382	0.003	0.997	0.476
(D) Spacer morphology				
Mean spacer length	6.553	0.007	1.305	0.300
Specific spacer dry mass	0.003	0.997	1.784	0.142

RESULTS

Biomass

With increasing nutrient availability, total plant dry mass and root, shoot, bud and rhizome dry mass all increased considerably (Table 1, Fig. 1A). With increasing nutrient availability, biomass allocation to root, bud and rhizome decreased greatly, whereas that to shoot increased (Table 1, Fig. 1B).

Ramet number and size

Both number of clumping ramets and number of spreading ramets were higher under higher nutrient supply (Table 1, Fig. 2A). The proportion of clumping ramets in total ramets increased significantly with increasing nutrient supply, whereas that of spreading ramets decreased (Table 1, Fig. 2B). Dry mass per ramet and number of leaves per ramet did not differ among the three nutrient treatments (Table 1).

Bud number and size

With increasing nutrient supply, the number of buds increased considerably (Table 1, Fig. 3A), whereas dry mass per bud decreased (Table 1, Fig. 3B).

Spacer morphology

Mean spacer length was the greatest under the medium level of nutrient supply and did not differ between the high- and low-nutrient treatments (Table 1, Fig. 4A). Specific spacer dry mass was statistically similar under the three nutrient treatments (Table 1, Fig. 4B).

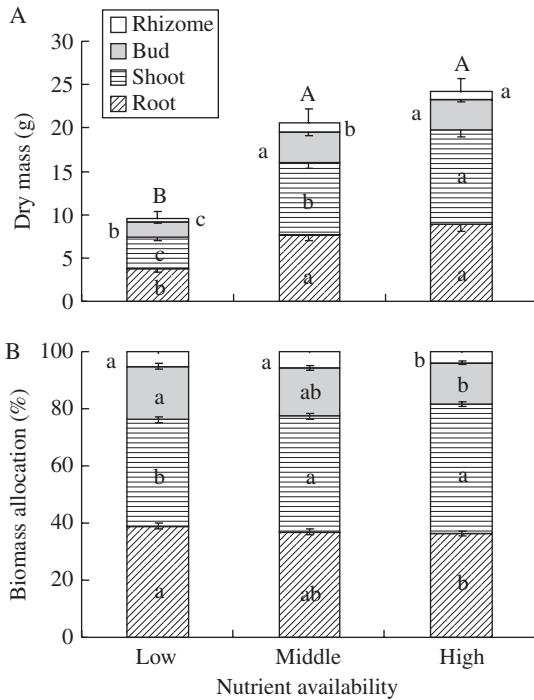


FIG. 1. (A) Dry mass and (B) percentage biomass allocation in *Leymus secalinus* under the three nutrient treatments. Horizontal bars and vertical lines indicate mean and s.e. For each compartment, bars sharing the same letters are not significantly different at $P = 0.05$.

DISCUSSION

Higher nutrient availability generally enhances biomass and module production, and decreases root to shoot ratio (Aung, 1974; Hunt and Nicholls, 1986; Sutherland and Stillman, 1988; Sakai, 1995; Stuefer *et al.*, 1996; Verburg *et al.*, 1996; Gardner and Mangel, 1999). This holds also for *L. secalinus* (Figs 1–3).

Trade-offs between growth forms

Within increasing nutrient supply, the proportion of clumping ramets in *L. secalinus* increased, whereas that of spreading ramets decreased (Fig. 2B). These results support our hypothesis that a trade-off between guerrilla and phalanx growth forms exists in the clonal grass *L. secalinus*, in response to resource availability.

Moreover, the number of buds of *L. secalinus* increased significantly with increasing nutrient supply (Fig. 3A), whereas dry mass per bud decreased (Fig. 3B), indicating a trade-off between bud number and size. The buds will develop into either spreading or clumping ramets. However, it is most likely that larger buds will develop into spreading ramets and smaller buds into clumping ramets, because developing into spreading ramets will involve more energy costs than developing into clumping ramets, and larger buds have a greater carbohydrate storage potential than smaller buds (McGinley *et al.*, 1987; Dong *et al.*, 1997). Producing more small buds under the high-nutrient supply enhanced production of clumping ramets. The number–size trade-off

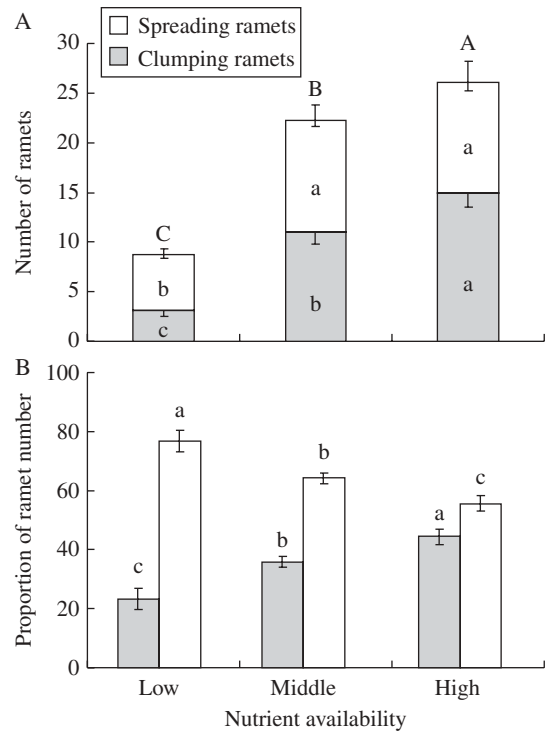


FIG. 2. (A) Number of spreading and clumping ramets and (B) the proportion of ramet number (number of spreading and clumping ramets, respectively, divided by total number of ramets) in *Leymus secalinus* under the three nutrient treatments. Horizontal bars and vertical lines indicate mean and s.e. For each compartment, bars sharing the same letters are not significantly different at $P = 0.05$.

of *L. secalinus* buds therefore further supports the above hypothesis.

Mean spacer length between two adjacent spreading ramets was lower under the high- than under the medium-nutrient supply (Fig. 4A), whereas mean spacer thickness and potentially also mechanical strength, as indicated by specific spacer dry mass (Fig. 4B), were not affected by nutrient supply. Therefore, the architecture of *L. secalinus* was more aggregated under high- than under medium-nutrient supply, suggesting a plastic modification from a guerrilla form towards a phalanx form (de Kroon and Knops, 1990; Evans, 1992; Dong and Pierdominici, 1995; de Kroon and Hutchings, 1995). However, mean spacer length was lower under the low- than under the medium-nutrient supply and did not differ between the low- and the high-nutrient supply (Fig. 4A). It is possible that under the low-nutrient supply there were insufficient resources available to be allocated to rhizomes. Therefore, plasticity in spacer length of *L. secalinus* in response to nutrient supply only partly supports the hypothesis.

Ecological significance in heterogeneous environments

In a spatially heterogeneous habitat, shortening spacers under resource-rich patches and elongating spacers in resource-poor patches may potentially position more newly produced ramets (feeding sites *sensu* Bell, 1984)

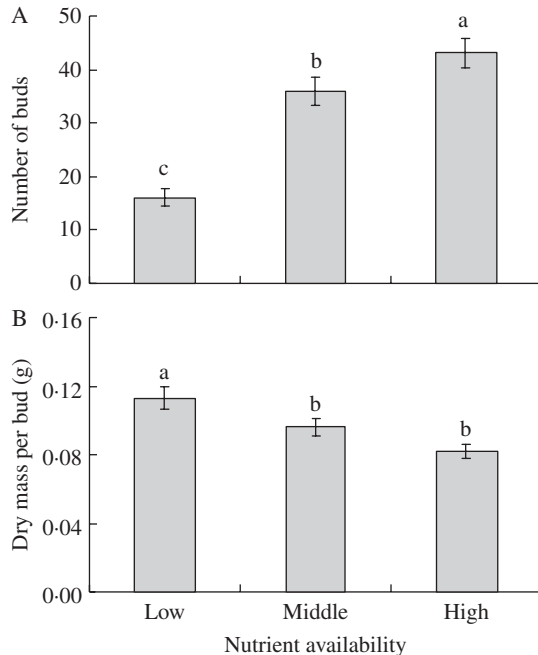


FIG. 3. (A) Number of buds and (B) dry mass per bud in *Leymus secalinus* under the three nutrient treatments. Mean \pm 1 s.e. is indicated. Bars sharing the same lower-case letters are not significantly different at $P = 0.05$.

in resource-rich patches to acquire resources efficiently, and thereby to increase survival (de Kroon and Knops, 1990; Evans, 1992; Hutchings and de Kroon, 1994; Dong and Pierdominici, 1995; de Kroon and Hutchings, 1995; de Kroon *et al.*, 2005). However, the extent of plasticity in spacer length is genetically determined and is also affected by the phylogeny of the species (de Kroon *et al.*, 1994). Therefore, if the resource-rich patches are too small (e.g. patch size close to the canopy size of an individual ramet or to spacer length), even shortening spacers may not guarantee that newly produced ramets are positioned in the same resource-rich patches, and thus may not enable clonal species to forage for resources efficiently and, consequently, will fail to increase the fitness of the whole genet (Briske and Derner, 1998).

In resource-poor nutrient patches, *L. secalinus* will not only increase spacer length between spreading ramets, but also increase allocation to buds and biomass to spreading ramets. These combined responses may enable *L. secalinus* to search for resource-rich patches more efficiently. Once a spreading ramet is positioned in a resource-rich patch, a decrease in spacer length together with an increase in the proportion of clumping ramets could enable *L. secalinus* to monopolize these locally abundant resources and to compete efficiently with other species (de Kroon and Schieving, 1990; Derner, 1999). Even when the favourable patches are very small, clumping ramets may still be readily positioned in the resource-rich patches, because there are either no spacers between the clumping ramets of *L. secalinus* or the spacer is very short (Shaver and Billings, 1975; Bernard, 1990). A previous study has shown that clonal integration was of little importance in *L. secalinus* in relatively homogeneous habitats (Dong, 1999). Therefore,

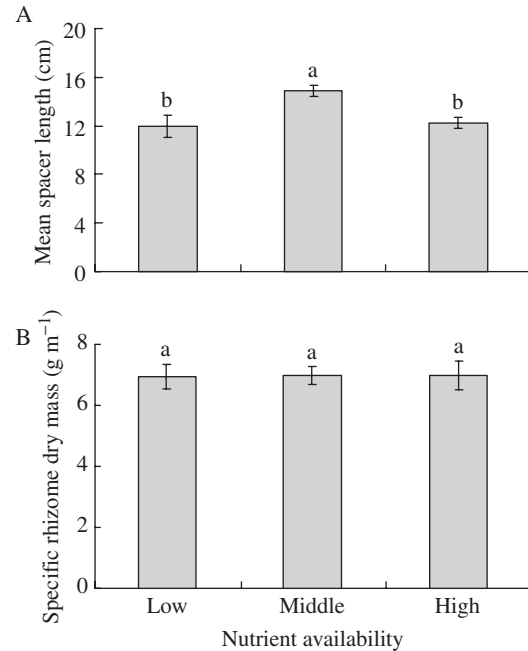


FIG. 4. (A) Mean spacer length and (B) specific rhizome dry mass (dry mass per unit length of rhizome) in *Leymus secalinus* under the three nutrient treatments. Mean \pm 1 s.e. is indicated. Bars sharing the same lower-case letters are not significantly different at $P = 0.05$.

trade-offs between the two growth forms together with plasticity in spacer length may have been selected for in *L. secalinus* to make good use of spatial heterogeneity in resource supply, even where this occurs at very small scales.

Although decreasing nutrient availability greatly reduced biomass and ramet production in *L. secalinus*, overall ramet size was not affected by nutrient supply (Table 1). Similar results were found by Stuefer *et al.* (2002), in which low-light treatment reduced plant biomass and number of ramets, but did not affect average ramet weight. This may be interpreted as a strategy that enables *L. secalinus* to cope with spatial and temporal heterogeneity in resource supply, and to ensure its survival in different habitats.

CONCLUSIONS

It was predicted that there would be greater architectural plasticity in clonal species with a mixture of phalanx and guerrilla forms (e.g. *L. secalinus*) than in those with either a distinctly phalanx or a distinctly guerrilla growth form. A trade-off between the two growth forms together with plasticity in spacer length enables *L. secalinus*, and possibly other species with a similar architecture, to make better use of spatial heterogeneity in resource supply, even where this occurs at very small scales.

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