

Structural Dynamics of Survival and Competition of Clonal Plant Populations in *Stipa Baicalensis* Community

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Abstract: There are two hierarchically organized clonal populations: genetic individuals (genets) can consist of many physiological individuals (ramets). Each ramet takes up resources from its local environment, but the resource pattern can be reorganized within the clone by transport between ramets. According to observation measurement and surveillance of clones and their ramets of caespitose grass *Stipa baicalensis* population, we used architectural development and morphological observation, resource translocation, and competition coefficients to study caespitose clonal structure, reproductive function, and vegetative function ages of the clones, types of ramets, ramet competition for resources within clones in 1999-2002. We also discussed clonal longevity of *Stipa baicalensis*, ramet recruitment and mortality in *Stipa baicalensis* clones. [Nature and Science, 2004, 2(2):87-94]

Key words: Ramet competition, Resource translocation, Caespitose clone

1 Introduction

Caespitose grasses consist of the largest subgroups of clonal plants among terrestrial angiosperms (Tiffney & Niklas, 1985). Caespitose grasses represent a unique growth form which is different from rhizome and stolon growth forms. Caespitose grasses often occur on all continents from the high Arctic to the Subantarctic, and are distributed over a wide range of continental zones (Wang, 1992; Walter, 1979).

This growth form is particularly dominant in the grassland community that occurs on tropical and temperate grasslands, particularly including savannas and steppes. Caespitose grasses possess several attributes which could potentially limit their living success, including intense intraclonal competition for resources (Hartnett, 1993) and for photosynthetically active radiation (Ryel *et al.*, 1993, 1994), and a limited ability to access heterogeneously distributed resources in micro-patches of soil (Van Auken, *et al.*, 1992). This may pose the question, "What structural and functional contribute to the ecological success of caespitose grasses without the benefits conferred by rhizomes and stolons?". The adaptive value of caespitose grass clones must be sufficient to offset the benefits associated with rhizomes (Pedersen & Tuomi, 1995). Because they often possess minimal plasticity for ramet placement compared with rhizomatous and stoloniferous species (de Kroon &

van Groenendael, 1990), caespitose grasses may be an ideal growth form in which to evaluate ecological success conferred by clonality.

A greater understanding of the processes and mechanisms influencing and regulating ramet component within clones would increase insight into ecological success of caespitose grasses. For example, are ramets within clones interdependent or independent? What mechanism regulates ramet density, including recruitment and mortality, within clones? Do caespitose clones represent an alternative strategy to active foraging behavior of rhizomatous and stoloniferous species? How does the spatial arrangement of ramets within clones influence growth efficiency? Answers to these questions are essential for clearly understanding of the structure function, and competitive ability expressed by this important and widely distributed group of clonal plants. Unfortunately, plant population ecology on caespitose clones has received minimal attention compared with many aspects of study, for example resource translocation and foraging by rhizomatous and stoloniferous species. However, very little study of clonal plants has recently been broadened to incorporate the caespitose growth form (Wang, 2002).

Specific aims of this paper are: (1) to study reproductive and vegetative functions of clones of caespitose grass *Stipa baicalensis*, ages structure, clonal structure dynamics, competition for resource between ramets, (2) to assess competition and coexistence for resources among ramets of caespitose

clones of *Stipa baicalensis*. These two aims are related in that intraclonal regulation of ramet recruitment and mortality may optimize to growth efficiency of clones.

2 Study methods

2.1 Study site,vegetation and ecological environment

Stipa baicalensis population, one of the most representative meadow-steppe population, is not only widely distributed in the Sunliao Plain, and Northeastern Inner Mongolia Plateau(Zhu, 1983), but also in the northeast steppe zone of Mongolia and area of steppe of Outer-Bajkal of Russia (Zhu, 1983). *Stipa baicalensis* population is characteristic of the eastern area of the temperate zone steppe region in central Asia (Wang *et al.*, 1991). *Stipa baicalensis* formation distributed in Northeastern China is mainly composed of *Stipa baicalensis*-rhizomatic grasses subformation, *Stipa baicalensis*-forb subformation, *Stipa baicalensis*-caespitose grasses subformation, and *Stipa baicalensis* shrub subformation.

The study was conducted at the Green Grassland Pasture in the Taikang area of Heilongjiang Province in 1998~2001. The area, at an elevation of about 120~270 m, lies in the hinterland of the Song Nen Plain in northeastern China. Mean annual precipitation of the study area was 350~400 mm, with 70% typically falling during the growing season during July, August, and September. Mean annual temperature was 3.8~4.2 °C, and the frost-free period averages 140~145 days. The topography is flat to gently rolling, with occasional sand dunes. The soil of study area are sandy soil of chernozems type (Wang *et al.*, 1991).

The natural or climx steppe vegetation in the area was heavily dominated by *Stipa baicalensis*-caespitose grasses subformation. The subformation is rich in species composition.

According to the field investigation data of five typical sample areas, 89 plant species have been recorded in all. Depending upon the segregation of sample plots the species saturation of the community ranged from 20 to 39 species per m². Except that constructive species *Stipa baicalensis* strongly dominated in the community, there were different species that may attain to dominant status in various synusia. These species were as follows: *Cleistogenes squarrosa*, *Festuca ovina*, *Leymus chinensis*, *Arundinella hirta*, *Carex duriuscula*, *Lespedeza davurica*, *L. hedysaroides* and *Potentilla discolor*. Caespitose grasses synusia that consisted primarily of

Stipa baicalensis, *Cleistogenes squarrosa* and *Festuca ovina* played a constructive synusia role in the community, and then, rhizome grasses and meso-xerophyte forb synusia, as well as, half dwarf shrub synusia, which consisted of *Lespedeza* spp., sometimes also played an important role(Wang, 1992).

2.2 Observation of morphogenesis and developmental biology of clones and their ramets of Stipabaicalensis population

According to Welker and Briske (1992) and Vorontzova & Zaugolnova (1985), reproductive function, vegetative growth function, variation of clones, individual ramet hierarchies (individual ramet groups) and types of ramets within clone were observed using wang's method (2002) during growth season. Age structure of ramets, the number of various types of ramets and morphological structure of clone also were investigated per growth season.

2.3 The measurement of resource translocation among ramets within clone of Stipa baicalensis population

For different ramets within clone, translocation of ¹⁴C-photoassimilate between ramets within clones were measured using methods advanced by Wang (2002), Price, *et al.* (1992), Jonsdottir & Callaghan.(1989) during growth season.

2.4 Study of competition and coexistence among ramets within clone

These both problems were studied in terms of models of mechanism of resource competition (Putman & Wratten, 1984).

3 Results

3.1 Types, ages, architectural development, and reproductive function of clones of Stipa baicalensis population

According to our study, types of *Stipa baicalensis* population mainly consists of following clones: juvenile clone (*jc*), immature clone (*ic*), virginile clone (*vc*), young clone (*yc*), mature clone (*mc*), old clone (*oc*), sub-senile clone (*s-sc*), and senile clone (*sc*). *yc*, *mc*, and *oc* belong to reproductive genets (clones) while *s-sc*, *sc* and *ic*, *vc* belong to post-reproductive clones (genets) and pre-reproductive clones (genets), respectively (Fig.1).

As shown under our observation on morphogenesis and development of clones and ramets, ramet recruitment within clone of caespitose *Stipa baicalensis* mainly occurred in reproductive

clones mentioned in Figure 1 while their mortality mainly occurred in post-reproductive period, that is, at sub-senile and senile stages of clones. However, under conditions of vegetative (clonal) reproduction mature clone generally only consists of eight types of ramets, that is, *jc*'s ramet (*jcR*), *ic*'s ramet (*icR*), *vc*'s ramet (*vcR*), *yc*'s ramet (*ycR*), *mc*'s ramet (*mcR*), *oc*'s ramet (*ocR*), *s-sc*'s ramet (*s-scR*), and *sc*'s ramet (*scR*). Immature clone and old clone commonly only have about 3~6 types of ramets.

We must indicate that, clone essentially is identical with genet because a collection of genetical individual units (ramets) that may or may not be internected while collection of all ramets derived from a single zygote, or a genetic individual.

Our investigation indicated that clonal growth and size occupation in clone of *Stipa baicalensis* resulted from a condition termed meristem dependence. Active meristems are continually required to produce juvenileramets to offset mortality

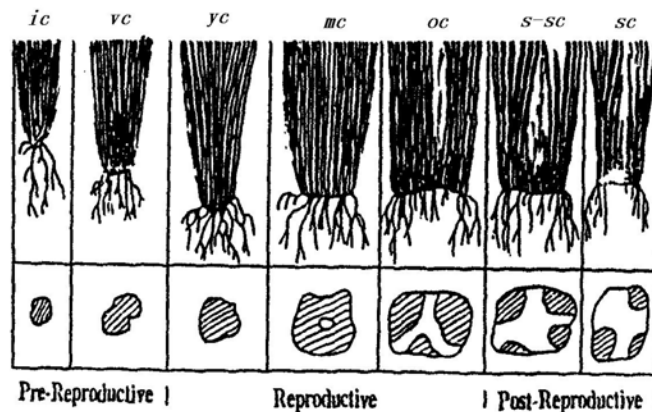


Fig.1 Diagram of estimates and architectural development of clone (genet) of *Stipa baicalensis* in the Song Nen steppe

(earlier 37~58 years is required for clones (genets) to proceed from seedlings to the senile clones.

Development of hollow crowns occurs in the reproductive earlier stage while clonal fragmentation occurs in reproductive later stage and the post-reproductive stage)

losses. Ramet recruitment of *Stipa baicalensis* can produce a number of connected generations. The number of ramet generation comprising ramet hierarchy, i.e. ramet system, is determined by the rate of ramet recruitment and ramet longevity as influenced by genetic and environmental constraints. Ramet systems are restricted to three generations because the older ramet generation dies and decomposes prior to development of the quaternary ramet generation. The numbers of ramets per system and ramet systems per clone define the size and architectural configuration of caespitose clones. With increasing clone size and age, ramet systems become separated as the initial ramet generations die and decompose. Disproportionate ramet recruitment at the clone periphery eventually reduces axillary bud availability within clone interior and limits ramet recruitment. The interior regions of clones may not be recolonized because of insufficient plasticity for ramet placement in this location.

Chronological estimates of the architectural development of *Stipa baicalensis* indicated that 37~58 years is required for clones to progress from

seedlings to senile clones (Figure 1).

The pre-reproductive, reproductive, and post-reproductive stages of *Stipa baicalensis* require about 6-11, 15-27, and 15-25 years, respectively. Clones develop hollow crowns at the reproductive stage and may fragment into about 3~6 units at the post-reproductive stage. We regard ring periphery of hollow crown as "bunch ramet ring". Clonal fragmentation is a common characteristic of perennial caespitose grasses in Song Nen steppe in northeastern China. All common species with caespitose clones here showed evidence of fragmentation into smaller units consisting of several ramets each. We refer to these units consisting of the ramets as "small senile clones".

Our observations (also see Wang, 2002) have proved that when rhizomatous or stoloniferous clones were fragmented into smaller clones there were no physical and physiological connections between these smaller fragmentation clones (Alpert, 1999; Price, et al., 1992) while although when caespitose clone of *Stipa baicalensis* was fragmented into smaller fragmentation clones there still were physical

and physiological connections between these smaller fragmentations of clones (that is, ramet hierarchies or ramet systems) due to mycorrhizal connection (Newman, 1988; Fischer Walter, et al., 1996).

3.2 Ramet competition and coexistence for resources within clones

As a rule, resource competition has a substantial influence on ramet recruitment, coexistence, and mortality in caespitose grass clones, and competition, presumably, influences resource availability. Although ramet recruitment is strongly influenced by both intraclonal and interclonal competition in clones of caespitose grasses (Cheplick & Salvadori, 1991), clone size and distribution also mediate competitive interactions and influence ramet initiation and clonal expansion. For example, a high density of small *Stipa baicalensis* clones exhibited greater relative increases in ramet density and basal area expansion than did a comparable number of ramets arranged in a low density of large clones. These responses clearly were mediated through a specific regulation mechanism, as opposed to increased efficiency of resource acquisition, because annual shoot biomass production was comparable for all various combinations of clones size and ramet distribution evaluated. Greater ramet recruitment from the high density of small clones was likely a function of the greater clonal periphery associated with a large number of small clones (Briske & Anderson, 1990). The mass of juvenile ramet recruitment occurs on the periphery, rather than the interior, of clones (Olson & Richards, 1988).

We have discovered that all the ramets share resources in caespitose clone through integration among ramets. We refer to this behavior as ‘sharing strategy of ramets’.

This sharing behavior for resource should result in competitive coexistence between ramets within clone. We would use following competition models of mechanism of resource competition (Putman & Wratten, 1984)

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - \alpha_{1,2} \frac{N_2}{K_1} \right) \quad (1)$$

and

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - \alpha_{2,1} \frac{N_1}{K_2} \right) \quad (2)$$

to describe ramet competition and coexistence of young and mature ramet types within caespitose grass clone due to resource competition and resource sharing, that is, to describe ramet resource competition and coexistence at low levels within clones, when resource translocation occurs among

various ramet types, N_1 and N_2 are the weights (resource) for ramets 1 and 2, K_1 and K_2 are maximal number of ramet 1 and maximal number of ramet 2 within clone (in correspondence with the carrying capacities), respectively. α mentioned in equations 1 and 2 is competition coefficient, α is likely to depend on the degree to which exploitation of resources by ramet 2 with that of ramet 1 (hence $\alpha_{1,2}$ is the effect of ramet 2 on 1).

The competition coefficient α may be calculated for real clonal population to quantify the degree of competition and competition experienced for some resource. In two equations mentioned above,

$$\alpha_{1,2} \frac{N_2}{K_1} \quad \text{and} \quad \alpha_{2,1} \frac{N_1}{K_2}$$

depend on the outcome of competition interaction for resources. We can see where there may be different outcomes in different circumstances: exclusion of one or other ramets, or coexistence. The actual conditions for exclusion or coexistence in each case can be derived by solution of the differential equation above. If ramet 1 is to outcompete ramet 2, then $\alpha_{1,2}$ must be relatively small, while $\alpha_{2,1}$ is correspondingly large; If ramet 2 is to exclude ramet 1, then $\alpha_{2,1} < \alpha_{1,2}$. For their coexistence both $\alpha_{2,1}$ and $\alpha_{1,2}$ must be very small.

If $\frac{dN_1}{dt} \geq 0$ and $\frac{dN_2}{dt} \geq 0$, then ramet 1 and ramet 2

coexist. For this to be the case

$$\frac{N_1}{K_1} + \alpha_{1,2} \frac{N_2}{K_1} \leq 1 \quad (3)$$

and

$$\frac{N_2}{K_2} + \alpha_{2,1} \frac{N_1}{K_2} \leq 1 \quad (4)$$

which means the ramets coexist if

$$\alpha_{1,2} \leq \frac{K_1 - N_1}{N_2} \quad \text{and} \quad \alpha_{2,1} \leq \frac{K_2 - N_2}{N_1}$$

Since there is resource translocation among ramets within clones of caespitose grasses *Stipa baicalensis* this caespitose clones have mechanisms of ramet regulation within clones due to resource translocation and resource sharing. Table 1 included 7 ramet types and 21 pairwise competition coefficient, $\alpha_{i,j}$. Of the 21 pairwise competition coefficients (pairwise $\alpha_{i,j}$) between pairs of the 7 ramet types, 18 pairwise competition coefficients are significant at the 0.1% level (Table 1). Only one of them was not significant. Table 1 further indicated that all the ramet types may coexist within a clone. Most of $\alpha_{i,j}$ are very small, they ranged from 0.103 to

0.315, except 0.740. This fact enough illustrated that these ramet types can coexist in the same ramet systems, that is to say, within the same clone. Ramet

coexistence rather than strong competition results from resource translocation and resource sharing among ramets within a clone.

Table 1 Pairwise competition coefficient ($\alpha_{i,j}$, lower left triangle of the matrix) among 7 types from juvenile ramet to sub-senile ramet within caespitose clone of *Stipa baicalensis* population

Ramet type	Ramet type						
	<i>jcR</i>	<i>icR</i>	<i>VcR</i>	<i>ycR</i>	<i>mcR</i>	<i>ocR</i>	<i>s-scR</i>
<i>jcR</i>		***	-	***	***	***	***
<i>icR</i>	0.149		***	***	***	***	***
<i>vcR</i>	0.171	0.223		***	***	**	***
<i>ycR</i>	0.148	0.184	0.234		***	***	***
<i>mcR</i>	0.130	0.297	0.204	0.211		***	**
<i>ocR</i>	0.740	0.214	0.301	0.315	0.214		***
<i>s-scR</i>	0.198	0.103	0.201	0.202	0.197	0.214	

Levels of significance are give in the upper right triangle of the matrix: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Translocation among and between ramets was proposed to function as a mechanism capable of ramet regulating within clones in this study. Resource translocation among and between ramets within clones may provide mechanisms (1) to distribute resource among ramets, (2) to minimize intraramet competition, and (3) to regulate ramet recruitment and ramet mortality.

3.3 Resource translocation of two ways among ramets within clones

Our experiments conducted with grass *Stipa baicalensis* in the heterogeneous micro-habitat demonstrated that resource translocation mainly was confined to ramet systems (hierarchies), rather than throughout all ramets within clones. However, radiotracer ^{14}C introduced into ramets within caespitose clone of *Stipa baicalensis* population did not remain completely within the labeled ramet systems. These findings confirmed that intracolon resource translocation was not complete in the grass. Complete resource translocation exists not only in ramet systems but also in whole clone, that is, individual clone of *Stipa baicalensis* because all ramets possess vascular connections with the seminal ramet produced from the embryo.

Resource translocation among only those ramets within ramet systems indicated ramet system function within clones, rather than as a sequence of completely integrated ramets (Figure 2). Thus, the

benefits of resource translocation mainly are restricted to these connected generations. Ramet systems, therefore, comprise physiologically integrated individual in this growth form. However, low levels of resource translocation observed between ramet systems may result from the occurrence of mycorrhizal connections among root systems between ramet systems.

According to these findings, we could conclude that there were both ways of resource translocation in caespitose clones of *Stipa baicalensis*: 1) partial resource translocation which was carried out by ramet systems; 2) complete (integrated) resource translocation that was carried out by all ramets of individual clone.

4 Discussion

For caespitose grass longevity, estimations of some plant ecologists (Harberd, 1961, 1962, 1976; Vorontzova & Zaugolonova, 1985; Zhukova & Ermakova, 1985; Steinger *et al.*, 1996; Wang, 2002) are different in longevity of individual genets. For example, Individual genets of *Festuca rubra*, *F. ovina* and *Holcus mollis* have been estimated to attain great longevities, perhaps exceeding 1000 years (Steinger *et al.*, 1996). However, the few grasses indicate that maximum clone longevity dose not exceed 50 years (Briske & Richards, 1995).

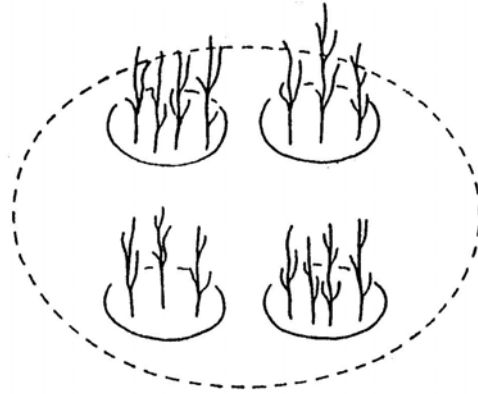


Fig. 2 Caespitose clones of *Stipa baicalensis* population are organized as assemblages of autonomous ramet systems, rather than as a sequence of completely integrated ramets

Comparable evaluations of caespitose grasses in Kazakhstan, including *Festuca*, *Koeleria*, and *Stipa* spp. suggest maximum clone longevitys of 30-80 years (Voronzova & Zaugolnova, 1985; Zhukova & Ermakova, 1985). Our age estimation for caespitose grasses *Stipa baicalensis* ranged from 37 to 58 years. This estimates for caespitose clone of *Stipa* conforms to age estimates mentioned above on the whole.

Clonal fragmentation is a common characteristic of clonal plants. Both perennial rhizomatous or stoloniferous clonal plants and caespitose clonal plants have clonal fragmentation phenomena. Caespitose perennial grass in Europe generally have clonal fragmentation habit (Wilhelm, 1995), and this fragmentation in Song Nen steppe of northeastern China also is the same as Euro. At present, plant population ecologists have paid a considerable attention to study clonal fragmentation of rhizomatous or stoloniferous clonal plants while few of plant population ecologists study caespitose clonal fragmentation. This paper initially studied caespitose clonal fragmentation in combination with age, reproductive function, architectural development of clone, and resource translocation among ramets within clones. This study firstly advanced a new hypothesis of resource translocation of caespitose clonal plants. This hypothesis include 1) small (partial) resource translocation among ramets within ramet systems (Fig. 2 in solid circles) at high level of the translocation; 2) large (or complete integrated) resource translocation among ramets within whole individual clones (Fig. 2 in dashed circle) at low level of the translocation.

Partial resource imigration can be explained on the basis of the developmental architecture of caespitose clones. Most investigations of intraracet

resource allocation in grasses have been conducted with young plants established from seed (Piteka & Ashmun, 1985). However, seminal ramet dies during the second or third growing season, disrupting complete vascular continuity within older clone (Briske & Butler, 1989), and thus this study is very difficult.

As above, documentation of partial resource translocation within caespitose clones requires that an alternative mechanism of intracolonial ramet regulation is identified and investigated further.

Up to now, ramet competition for resource has never been studied in the world while this paper studied both ramet competition and ramet coexistence within caespitose clones, as well as ramet regulation within clones of *Stipa baicalensis*.

Since 10 years, most of plant population ecologists have profoundly studied resource translocation, that is to say, physiological integration between ramet within rhizomatous or stoloniferous clones (Callaghan, 1984; Price, *et al.*, 1992; Wang, 2002; Alpert, 1999) while they have not studied this key problem of caespitose clones. Ways, types, ranges, and intensities of resource translocation within caespitose clones, that is, complexity of the translocation, therefore, have never been understood.

Although this study on resource translocation among ramets and ramet competition within caespitose clones are a preliminary groundwork it will create a new situation of studying resource translocation and ramet competition of caespitose clones.

In future, a greater understanding of the fate of clonal fragments should be required because it may

be the most relevant level at which to investigate the ecology of clonal plants (Cain,1990). Competition intensities of ramets and the effects of this competition on regulation of ramet recruitment and death within caespitose clones also should be studied in detail.

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