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Interaction patterns on populations of two clonal species in restoring succession series in a degraded meadow in Northeast China

Modelos de interacción interpoblacionales de dos especies de crecimiento clonal en restaurar la secuencia de sucesión de una pradera degradada en el Noroeste de China

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Abstract. Community succession is an orderly replacement process between dominant species of such community. The mutual populations changes of two clonal plant species, *Leymus chinensis* and *Kalimeris integrifolia*, were analyzed during a process of restoration succession in a degraded meadow in Northeast China. It was based on the methods of space-for-time substitution and continuous sampling in different mixed ratios of community sections. The results showed that the two species populations adjusted the size of ramets to ensure a relatively stable number in the mixed community. The fluctuation and instability were more obvious in the *K. integrifolia* than in the *L. chinensis* population. While density/biomass of *K. integrifolia* showed a linear decrease, there was a concomitant *L. chinensis* population increase from the middle to the end of the growing periods. The density and taproot biomass of the *K. integrifolia* population decreased logarithmically with increases in the biomass/cumulative rhizome length of the *L. chinensis* population during the late and end periods of the growing season. With the progress of succession, *K. integrifolia* will be eventually replaced by *L. chinensis*. However, *K. integrifolia* would be a companion species in the community for a long time.

Keywords: Biomass; Community; Density; Dominant species; *Kalimeris integrifolia*; *Leymus chinensis*; Rhizome.

Resumen. El proceso de sucesión en una comunidad es un proceso ordenado de reemplazo entre especies dominantes de dicha comunidad. Los cambios en las poblaciones de dos especies de plantas clonales, *Leymus chinensis* y *Kalimeris integrifolia*, se analizaron durante un proceso de sucesión de restauración en una pradera degradada en el Noreste de China. Se basó en los métodos de substitución del espacio con el tiempo, y muestreo continuo en diferentes relaciones de mezcla de secciones de la comunidad. Los resultados mostraron que las poblaciones de las dos especies ajustaron el tamaño de los ramets como para asegurar un número relativamente estable en la mezcla de individuos en la comunidad. La fluctuación e inestabilidad fueron más obvios en la población de *K. integrifolia* que en la de *L. chinensis*. Mientras la densidad/biomasa de *K. integrifolia* mostró una reducción lineal, hubo un incremento en la población de *L. chinensis* desde la mitad hasta el final del período de crecimiento. La densidad y biomasa de la raíz principal de la población de *K. integrifolia* disminuyó logarítmicamente con incrementos en la biomasa/longitud de rizomas acumulativa de la población de *L. chinensis* durante períodos tardíos o hacia el final de la estación de crecimiento. Con el progreso de la sucesión, *K. integrifolia* será eventualmente reemplazada por *L. chinensis*. Sin embargo, *K. integrifolia* sería una especie acompañante en la comunidad por un período de tiempo prolongado.

Palabras clave: Biomasa; Comunidad; Densidad; Especies dominantes; *Kalimeris integrifolia*; *Leymus chinensis*; Rizoma.

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INTRODUCTION

Community succession is a process where one dominant species replaces another. During the time period of succession, one of the species increases while the other declines at the same time. A lot of research has been carried out in community succession, and the classical theory and model of succession have been well determined (Whittaker, 1974; Miles, 1979; Shugart & West, 1980; Noy-Meir & van der Maarel, 1987; van de Maarel, 1988; Smith & Huston, 1989; McCook, 1994). However, the normal course of community succession has been often modified as a result of human activities, especially when natural vegetation resources have been frequently exploited or destabilized. Therefore, succession has always been a focus of study on community dynamics, and the breakpoint of community succession has been gradually transferred from the establishment of theory to the specific study on community composition because of anthropogenic environmental change (Schmidt, 1988; Farrell, 1991; Finegan, 1996; Vandvik, 2004; Kang et al., 2006).

Frequently, community succession has to go through a long-time period. However, it can be from the primary succession under natural conditions to the secondary succession as a result of various disturbances. There are always different sections for the spatial succession. Therefore, we can have a clear understanding of succession processes (Łaska, 2001) using the method of space-for-time substitution to analyze the spatial dynamics on characteristics of various community succession series. There are a large number of reports on the succession series, including population quantitative characteristics (Shan & Wang, 1998; Fan et al., 2006), production and distribution of material (Olff et al., 1990; Yang et al., 2003), biological diversity (Gao et al., 1997; Han et al., 1997; Liao et al., 2000; Xing et al., 2008), ecological niche of dominant species (Zhang et al., 2003; Bai et al., 2010), seed and bud bank (Xiong et al., 1992; Zhou et al., 2000; Yan and Yang, 2007; Li et al., 2012), accumulation and decomposition of litter (Zhang, 2000), physicochemical and stoichiometrical properties of soil (Shao et al., 2008; Yan et al., 2008; Lin et al., 2013), the fluctuant and dynamic law of the community importance value (Wang & Li, 1995) as well as the community distribution pattern (Wang, 2006; Wang et al., 2009). However, quantitative research on the interaction pattern between communities is still scarce (Li & Yang, 2004). Therefore, through exploring on community succession where the former and later dominant species grow and decline interactively, we can gain insight into the order and regularity of the community composition in the process of succession.

Both the dominant species and major companion species of the *L. chinensis* grassland are clonal plants. The degradation of the *L. chinensis* meadow steppe is caused mainly by overgrazing (Wang & Li, 1995). According to the biological properties of succession, the restoration of the degraded *L. chinensis* meadow steppe is secondary succession (Łaska, 2001). All clonal plants like *L. chinensis* are endowed with strong capability of vegetative propagation, which contributes to biological properties such as forming a community with a single dominant species in the appropriate environment (Li & Yang, 2004). As a result, once grazing disturbance is stopped, remaining clonal plants will quickly take up the space. Firstly, it is easy to form a complex mutually embedded community structure. Then, the dominant *L. chinensis* of the original community would gradually replace the various original companion or invasive species in the progressive succession series. Finally, it would form a new grassland (Li & Zheng, 1997).

We studied *L. chinensis* and *K. integrifolia* in a restoration succession series in a degraded meadow steppe in Northeast China. Using the method of space-for-time substitution, we studied the population characteristics of two clonal species in different mixed ratios of community sections. The results revealed the patterns of the mutual fluctuant changes of *L. chinensis* and *K. integrifolia* in this restoration succession process. This study contributes to the theories and methods of restoration succession, and also provides a theoretical guidance for the scientific management of grassland production.

MATERIALS AND METHODS

Natural conditions of the study area. The study was carried out in the Changling Horse Breeding Farm (44°45′N, 123°45′E), located at the southern area of Songnen Plain, Changling County, Jilin Province, China. The study area is in a temperate zone with semi-humid and semi-arid climate. The amount of annual precipitation ranges from 313 to 581mm, and over 70% occurs between June and September. The amount of annual potential evaporation is approximately 3 to 4 times that of the precipitation. Days with temperature ≥10 °C varied from 120 to 140. The maximum temperature is between 21.5 °C to 23.6 °C, and the absolute maximum temperature is 37.8 °C with an annual accumulated temperature of 2545 to 3374 °C (Li & Zheng, 1997).

The existing natural grassland in Songnen Plain is the major part of the Northeast grassland, and the climax vegetation type is a *L. chinensis* meadow steppe. Due to overgrazing, this area is very degraded, and there is an extensive soil alkalization in the bare surface resulting in a mutually embedded distribution of the soil and plant communities. *Kalimeris integrifolia* is widely distributed in the Northeast *L. chinensis* grassland. Because of its strong propagative capability of guerrilla-style root sprouting, *K. integrifolia* is often the subdominant or major companion species in different destabilized communities. It can also turn into a single dominant species of the community in a short time (Yang et al., 2003). In the area where natural restoration succession on degraded meadow is not salinized, there is a widespread spatial succession series of *K. integrifolia* and *L. chinensis* in a mixed ratio.

The choice of the experimental site and measuring methods. The experimental site was a degraded *L. chinensis* meadow steppe, which was enclosed 10 years for natural restoration in the Grassland Ecological Research Station of Northeast Normal University. The experimental site is 50 hm^2 in area, and it was in moderate to severe level of degradation before its enclosure in 2000. After 10 years of natural restoration, the plaque area of dominant *L. chinensis* species still accounts for a large proportion in spite of various mutually embedded distributions of the communities at the experimental site. Both *L. chinensis* and *K. integrifolia* are typical clonal plants with identical composition no matter if it is on either single dominant species or mixed community. They are the ideal object for the study of the former and later dominant species which grow and decline interactively in the process of succession.

Before sampling, we determined five relatively obvious population plaques in which *L. chinensis* and *K. integrifolia* were single dominant species. Besides, we numbered the plots in the ecotones between the two plaques in the continuous mixed succession communities. In addition, we dug up four plots according to the density of *L. chinensis*, from high to low as a four succession communities: 1) *L. chinensis* as the dominant species in the community with a small quantity of *K. integrifolia* as a companion species; 2) *L. chinensis* as the dominant species in the mixed community with *K. integrifolia* as the subdominant species; 3) *K. integrifolia* as the dominant species in the mixed community with *L. chine*nsis as the subdominant species; 4) *K. integrifolia* as the dominant species in the community with a small quantity of *L. chinensis* as a companion species.

From July to October 2010, we sampled the experimental site at the beginning of each month, and collected 20 plots every time. The size of the plot was 25 cm × 25 cm. When sampling, we dug up the plants from the rhizome/taproot to the ramet and took them back indoors. We counted the number of ramets of *L. chinensis* and *K. integrifolia*, and measured the cumulative length of the rhizome. We cut the ramets of *L. chinensis* and *K. integrifolia* from the nodes of root sprouts and collar, and oven-dried them at 80 °C until reaching constant weight. We used an electronic balance with a sensibility of 0.01 g to weigh the biomass of ramets and rhizome of *L. chinensis*, as well as the biomass of ramets and taproot of *K. integrifolia*.

Data processing. We converted all counting and weighing data of plots to a 1 m × 1 m scale. When making a statistical analysis of quantitative characters, we used mean values (M) to represent the overall level of the samples. The maximum (Max) and minimum (Min) values were used to indicate the range of samples, and standard deviation (SD) and coefficient of variation (CV) to reflect the absolute and relative data variation. For the analysis of correlation and equation, we employed the analytical model to analyze the law of orderly interaction and fluctuation of quantitative characters in *L. chinensis* and *K. integrifolia* populations. Besides, we used Excel and SPSS statistical analytical software for data processing, as well as for obtaining the variance and correlation analyses.

RESULTS

Quantitative characteristics of population modules. In the continuous spatial succession series of *K. integrifolia* and *L. chinensis*, the range and coefficient of variation in quantita-

Table 1. Quantitative characters of two population modules in restoring succession series in the degraded meadow steppe (n=20).
Tabla 1. Caracteres cuantitativos en poblaciones de dos especies clonales en la restauración de la sucesión en la estepa de pradera degradada (n=20).

Quantitative character	Month	*Kalimeris integrifolia*					*Leymus chinensis*				
		Max	Min	Mean	SD	CV%	Max	Min	Mean	SD	CV%
Density (ramets/m^2)	7	560	16	266.4	144.7	54.3	720	48	392.8	190.7	48.6
	8	960	32	385.6	294.0	76.2	752	32	419.2	202.9	48.4
	9	1280	32	416.8	302.9	72.7	720	48	379.2	213.7	56.4
	10	752	64	359.2	206.4	57.5	704	64	360.0	206.5	57.4
Biomass of ramets (g/m^2)	7	237.6	1.4	92.1	237.6	76.1	241.4	7.5	130.4	241.4	65.6
	8	266.4	5.8	113.2	266.4	85.9	283.4	9.0	160.6	283.4	79.1
	9	327.0	1.3	129.5	357.0	79.4	269.1	12.0	140.9	269.1	79.9
	10	145.0	12.2	73.9	145.0	43.5	273.0	9.4	135.2	273.0	77.7
Biomass of rhizomes/ taproots (g/m^2)	9	61.6	1.3	19.7	14.7	74.8	66.6	1.4	33.1	21.6	65.0
	10	52.5	2.4	22.8	14.3	62.8	86.9	3.0	40.0	24.0	60.0
Length of rhizomes (cm/m^2)	9	—	—	—	—	—	7701	246.4	3856	2151	55.8
	10	—	—	—	—	—	14821	596.8	5576	3720	66.7

tive characters between the two population module components were higher in the middle than in the late periods of the growing season (Table 1). Nevertheless, the average difference was not significant neither intra-species in each month nor inter-species in the same month (P>0.05). These results reflected that there was only a slight fluctuation in quantitative characters in the succession series between the two populations in the growing season. The coefficient of variation was lower for density than for biomass of ramets in the two population module components (Table 1). The density and biomass of ramets of *K. integrifolia* were most often lower than values in *L. chinensis*. These results showed that there were both consistency and difference in the succession between the two populations.

Variation in ramet number. In the continuous spatial succession series of *K. integrifolia* and *L. chinensis* communities, the density of *K. integrifolia* decreased in a linear manner as the density of *L. chinensis* increased (P<0.05; Fig. 1). These results revealed that during the succession from *K. integrifolia* to *L. chinensis*, the variation in the number between the two dominant species occurred in an orderly, linear replacement process.

Variation in ramet biomass. In the continuous spatial succession series of *K. integrifolia* and *L. chinensis* communities, the ramet biomass of *K. integrifolia* decreased linearly (Fig. 2) with increases in the *L. chinensis* biomass during the middle to the late periods in the growing season. These results showed that during the succession from *K. integrifolia* to *L. chinensis*, the changes in the ramet biomass between the two dominant species was also an orderly, linear replacement process.

Variation in underground modules. In the continuous spatial succession series of *K. integrifolia* and *L. chinensis* communities, the taproot biomass of *K. integrifolia* decreased logarithmically as the biomass/cumulative length of rhizomes increased in *L. chinensis* in September and October (Fig. 3). These results reflected that in the succession from *K. integrifolia* to *L. chinensis*, the replacement of the *K. integrifolia* underground modules by those *L. chinensis* was an orderly change which followed a logarithmic function.

Variation in aboveground (KI) and underground (LC) modules. After a further correlation analysis, it was found that the ramet density of the *K. integrifolia* population and the biomass/cumulative length of rhizomes of the *L. chinensis* population followed a negative logarithmic function in September and October (P<0.05; Fig. 4). These results show that during the succession from *K. integrifolia* to *L. chinensis*, the decrease of ramet density on *K. integrifolia* was also an orderly process of logarithmic function.

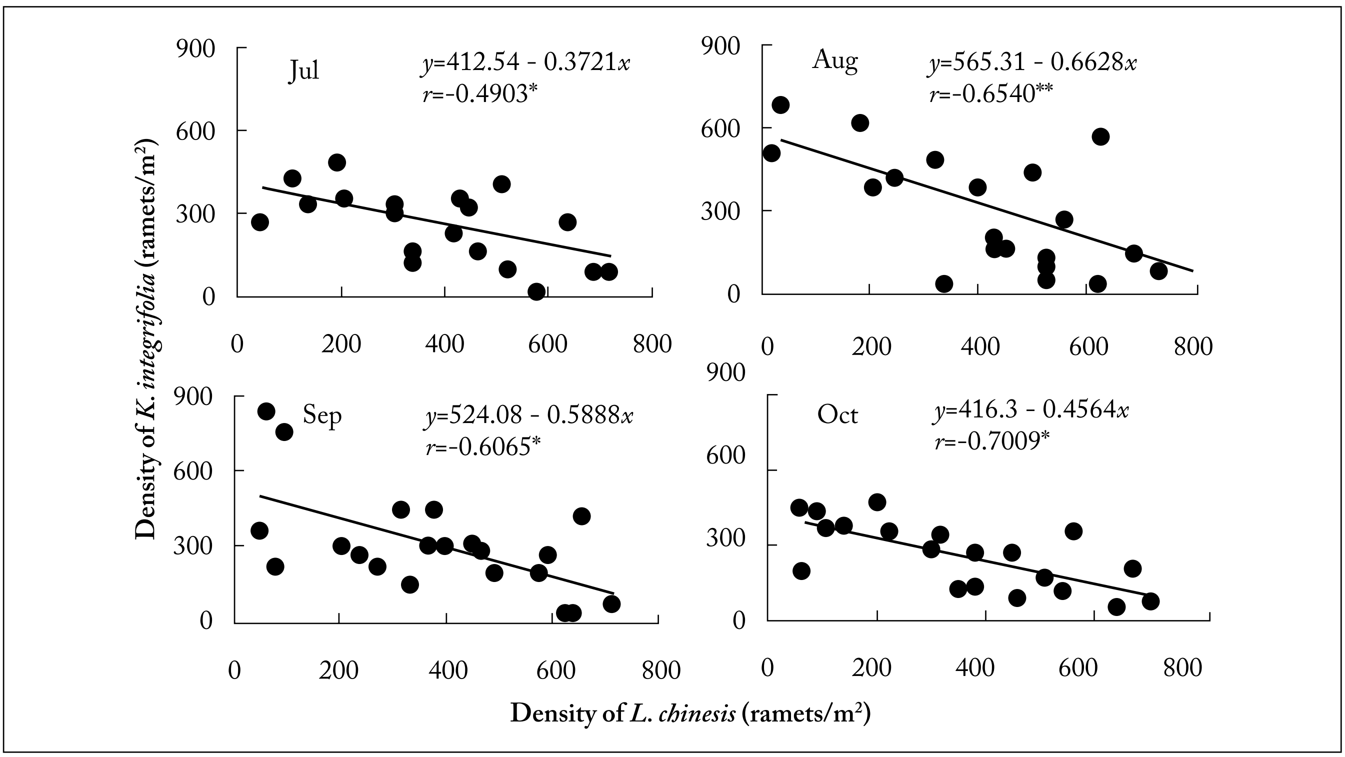

Fig. 1. Changes of ramet densities between two populations in restoring succession series in the degraded meadow (n=20).

Fig. 1. Cambios en la densidad de módulos entre las dos poblaciones de gramíneas perennes en la restauración del proceso de sucesión en la pradera degradada (n=20).

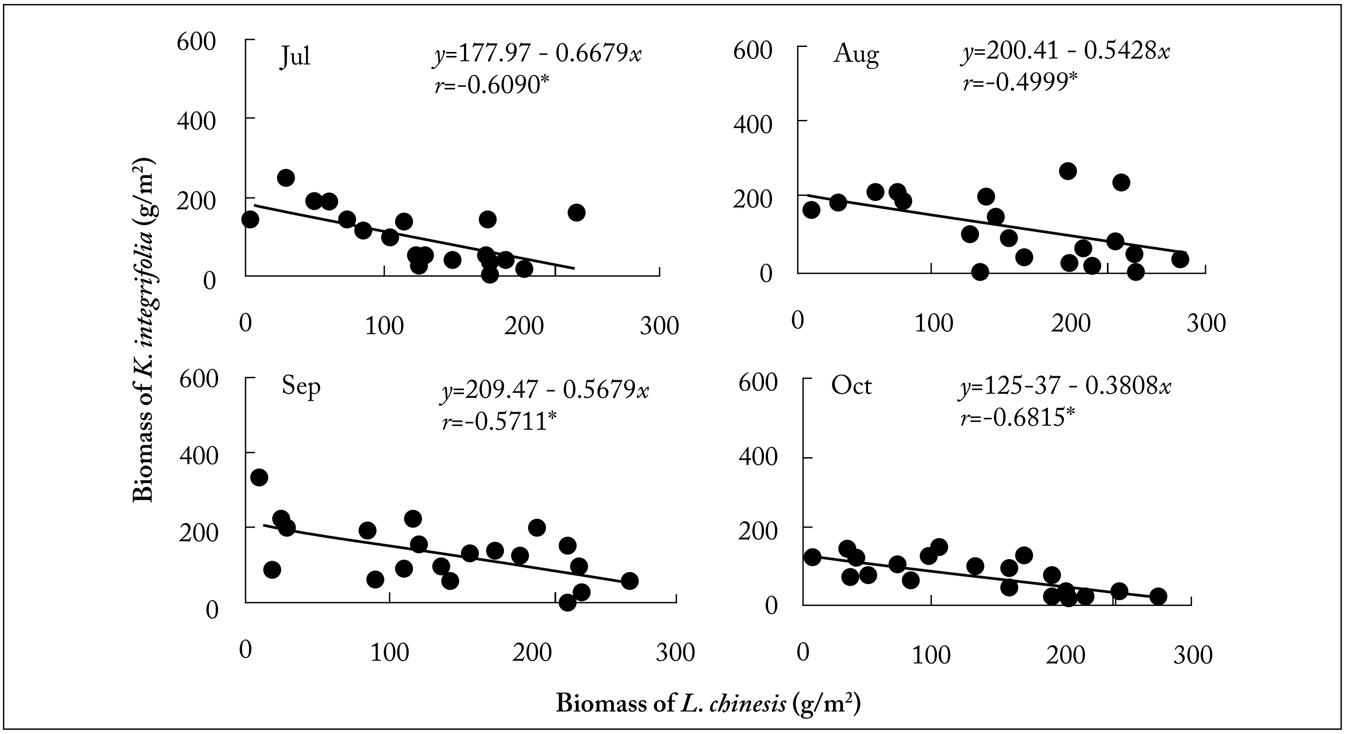

Fig. 2. Changes of ramet biomass between two population in restoring succession series in the degraded meadow steppe (n=20).
Fig. 2. Cambios en la biomasa de módulos entre las dos poblaciones en el proceso de restauración de la sucesión en la estepa de praderas degradadas (n=20).

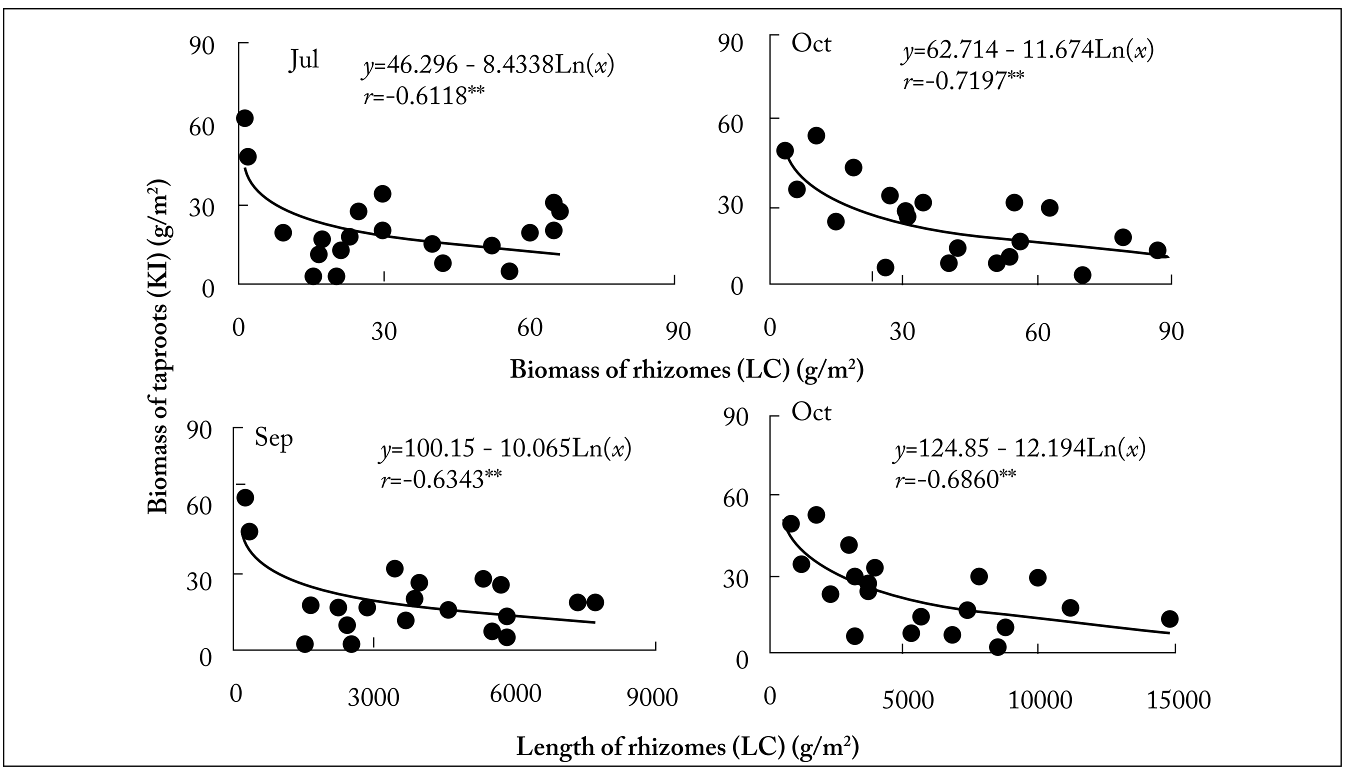

Fig. 3. Changes of underground modules between two populations in restoring succession series in the degraded meadow steppe (n=20).
Fig. 3. Cambios en los módulos subterráneos entre las dos poblaciones en la restauración del proceso de sucesión en la estepa de pradera degradada (n=20).

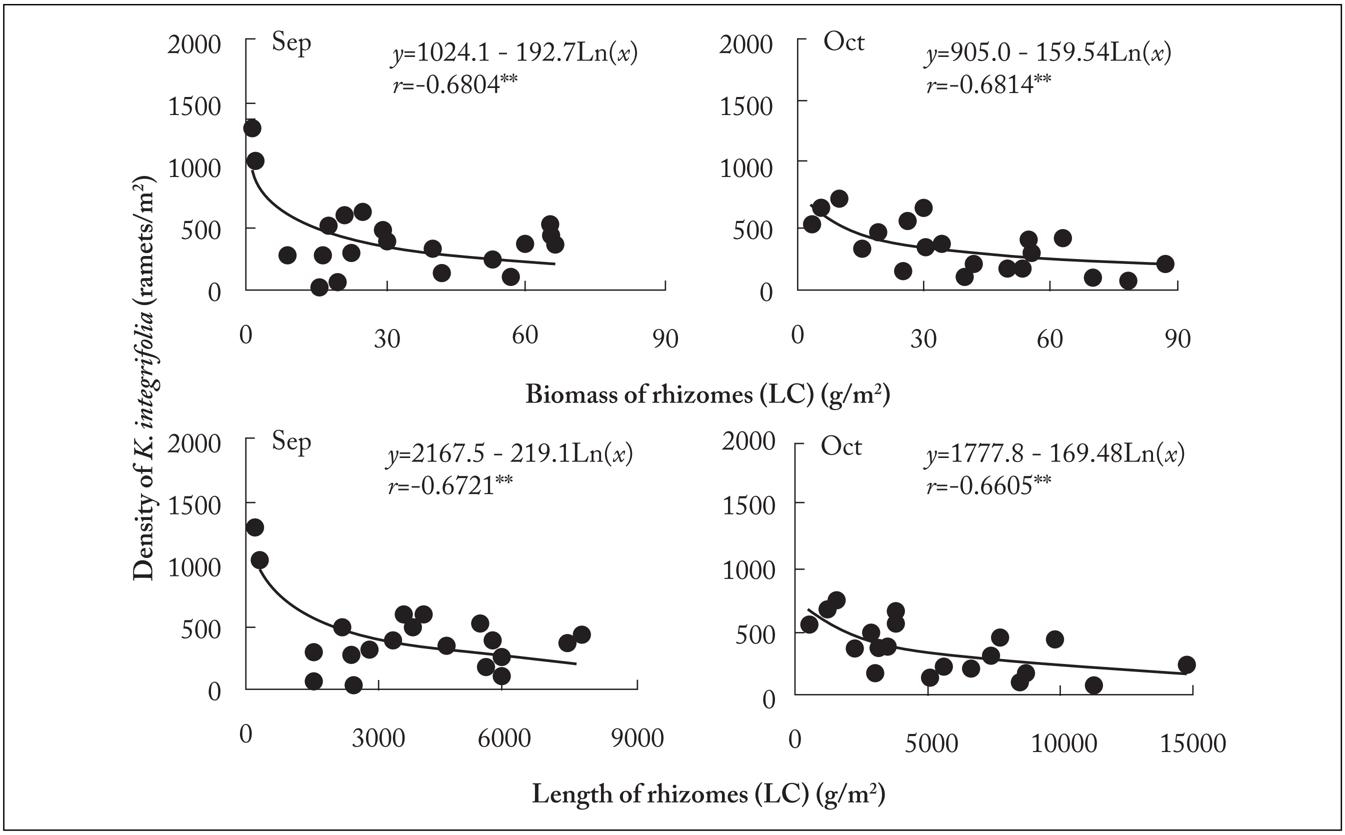

Fig. 4. Changes between the density on the population of *Kalimeris integrifolia* and the underground module length of the *Leymus chinensis* population in a restoring succession series in the degraded meadow steppe (n=20).

Fig. 4. Cambios entre la densidad en la población de *Kalimeris integrifolia* y los módulos subterráneos en la población de *L. chinensis* en la restauración del proceso de sucesión en la estepa de pradera degradada (n=20).

DISCUSSION

Although both *Leymus chinensis* (rhizome type of a grass family) and *Kalimeris integrifolia* (root sprouting type of a composite family) are typical clonal plants, there was an obvious variation concerning the overwintering characteristics of vegetative propagation. *Leymus chinensis* has over wintering ramets and sprouts, while *K. integrifolia* only has overwintering sprouts. The winter ramets refer to non-jointing ramets after the late vegetative period. Due to the underground growing points, they could overwinter safely and continue to grow in the next year. In accordance with the research, in the early period of the growing season, the winter ramets are of absolute advantage in the *L. chinensis* population, accounting for 83.9% to 98.4%, with spring ramets consisting of 1.6 % to 16.1% (Yang et al., 2000). Compared to *K. integrifolia*, a heliophile plant, which was formed all by sprouts and grew slowly in the seedling stage, winter ramets are of biological significance because they turn green early in the growing season and grow rapidly. As a result, winter ramets could take advantage of its spatial growth in the mixed community. Succession and replacement of dominant species during that process is an orderly process. Based on the method of space-for–time substitution, we obtained essential information about real succession on population dynamics, and the law of increase and decrease through the quantitative analysis of the natural succession series.

In the natural restoration succession from *K. integrifolia* to the original *L. chinensis* in the degraded meadow steppe in Northeast China, *L. chinensis* showed a growth advantage because of its rhizome propagation and growth of winter ramets early in the growing season. Finally, the *K. integrifolia* population was replaced by that of *L. chinensis* because of its advantages in biological properties. Therefore, the succession from *K .integrifolia* to *L. chinensis* was on the basis of abundant, appropriate biological properties.

The coefficient of variation is an important measure of the relative variation of quantitative characters, which can also measure the population regulation, and the relative fluctuation and stability between populations and quantitative characters to a certain extent. In general, the values of the coefficients of variation for the quantitative characters between population modules of *K. integrifolia* and *L. chinensis* were lower than those of biomass. At the same time, the values of the coefficients of variation for the quantitative characters were higher in *K. integrifolia* than in *L. chinensis*. The reason for the consistency of results in the two populations is due to strategies of survival and development by adjusting the size of ramets to ensure its relatively stable number during the succession process. The differences suggest that the fluctuations were higher on the *K. integrifolia* than that on the *L. chinensis* population. On the contrary, the stability was higher in the *L. chinensis* than in the *K. integrifolia* population. Therefore, our results revealed that the succession from *K. integrifolia* to *L. chinensis* was on the basis of population dynamics.

In the relative analysis of biological statistics, several functions showed the following common characteristics: when exchanging the position of independent and dependent variables, the relationships and coefficients of correlation between the linear and power functions were still the same; at the same time, only by exchanging the relationship of the exponential and logarithmic functions we obtained the same coefficient of correlation. The number and biomass of ramets between the two dominant species was an orderly linear replacement or changing process. The density and taproot biomass of the *K. integrifolia* population decreased logarithmically with increases of the biomass/cumulative rhizome length in the *L. chinensis* population during the late periods and at the end of the growing season. If the positions of the logarithmic correlations were exchanged, we could find that the taproot biomass and cumulative length of *L. chinensis* decreased logarithmically when increasing the density and taproot biomass of the *L. chinensis* population. In the natural restoration succession series from the *K. integrifolia* community to the original *L. chinensis* community in degraded meadow steppe in Northeast China, rhizomes of the *L. chinensis* population expanded exponentially into the *K. integrifolia* community. After replacement of the dominant species by *L. chinensis*, *K. integrifolia* would maintain its companion species status in the community for a long time. In other words, the taproot biomass and cumulative length of *L. chinensis* was a logarithmic function increase when density and taproot biomass decreased. *Leymus chinensis* constantly expanded its niche space by vegetative propagation of rhizomes. By analyzing the relationship of the exponential function with *L. chinensis* population as the independent variable, we could better explain the exponential expansion of *L. chinensis* rhizomes into the *K. integrifolia* community. But for the exponential function with the *K. integrifolia* population as the independent variable, we determined that as the dominant species was replaced by *L. chinensis*, *K. integrifolia* would maintain its companion species status in the community for a long time.

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