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Effects of nitrogen, phosphorus and potassium addition on the productivity of a karst grassland: Plant functional group and community perspectives

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ABSTRACT

Rocky desertification is currently the most serious ecological and environmental problem in karst region of southwestern China. Its negative consequences for both natural ecosystems and the human inhabitants of the karst region have created a need for effective ecosystem restoration strategies, but success in these efforts has been limited. We hypothesized that scarcity of mineral nutrients could be a crucial factor in vegetation recovery, but relatively little information is available about the limiting roles of various mineral elements. We investigated responses of aboveground biomass and nutrient concentrations of a degraded karst grassland to nitrogen (N), Phosphorus (P) and Potassium (K) additions over a period of three years. Nutrient additions significantly increased aboveground biomass and nutrient concentrations for both the plant community and individual plant functional groups. Total aboveground biomass was significantly increased by N (by 35.6%), P (by 35.3%) and K (by 11.7%) fertilization over three years of nutrient additions. The interaction effects of year × N and year × P on total biomass were significant. Additions of N and P increased the biomass of grasses by 39.2% and 15.0%, respectively, and additions of P increased the biomass of forbs by 69.3%. The biomass of shrubs was significantly increased by P (by 111.3%), K (by 45.3%) and N (by 38.5%), and there were strong interaction effects of N, P and K on shrub biomass. P and K additions significantly increased the relative biomass of shrubs but decreased that of grasses, especially under the NPK treatment. Our results suggest that the productivity of degraded grassland in the karst region of China is co-limited by N, P and K, with N and P being the primary limiting factors. Among functional groups, grasses are mainly limited by N and P, forbs by P, and shrubs by all 3 elements, with P being the most limiting factor overall. Mineral fertilization stimulates plant growth and may be a useful tool in efforts to restore woody vegetation in degraded grasslands, thus counteracting the process of rock desertification in the karst region of southwestern China.

1. Introduction

The subtropical karst region of southwestern China, occupying about 0.51 million km^2, is one of the largest regions developed on carbonate bedrock in the world (Jiang et al., 2014). The region is characterized by extremely slow soil formation from the underlying limestone, very shallow and patchy soils with a low water retention capacity, and high porosity of the underlying limestone rock (Zhu, 1997; Liu, 2009). Typical undisturbed karst vegetation is a mixed evergreen and deciduous broad-leaved forest (Guo et al., 2011). In past decades, many karst forests have experienced varying degrees of degradation caused by human disturbances, such as deforestation, agricultural expansion, livestock overgrazing and fire (Liu, 2009). Rocky desertification, referring to the processes that transform a karst area covered by vegetation and soil into a rocky landscape, is the most serious ecological and environmental problem in this region (Jiang et al., 2014). A large number of restoration projects have been carried out to counteract this trend. Many of these projects, involving planting of either indigenous or exotic species, have not been successful because of a lack of knowledge about the ecophysiological responses of the

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plants to the main stresses they face in the harsh karst habitats. For a long time, drought stress has been considered to be the most important factor limiting plant growth and vegetation restoration in the karst region (Zhu, 1997; Liu, 2009), and a number of studies have focused on ecophysiological adaptations of karst plants to drought stress (Wei et al., 2007; Liu et al., 2010, 2011). However, recent studies have suggested that shortage of mineral nutrients resulting from the limited total soil mass could be a crucial factor restricting plant growth and ecosystem productivity in this region (Zhang and Wang, 2009; Guo et al., 2011). Indeed, several researchers have reported that the mean depth of topsoil on the karst hills is only about 2–9 cm (Zhang and Wang, 2009; Liu et al., 2013).

The deficiency of plant-available phosphorus (P), resulting from lowered mobility of P bound to calcium phosphates, may be one of the most important factors limiting plant productivity in calcareous soils (Niinemets and Kull, 2005; Piao et al., 2005), and this was found to be the case for limestone grassland in the UK (Wilson et al., 1995). However, the overall productivity of calcareous grassland in northwest Switzerland was limited by nitrogen (N), and legume growth was limited by P (Niklaus et al., 1998; Stöcklin and Körner, 1999). The wooded meadows on calcareous soils in Estonia (Niinemets and Kull, 2003, 2005) and calcareous grasslands in the Peak District of the UK (Morecroft et al., 1994), northern Switzerland (Köhler et al., 2001) and Germany (Storm and Süss, 2008) were found to be co-limited by N and P.

To date, a few studies on plant nutrient stoichiometry have indicated that plant growth in the karst region of southwestern China is limited by P or co-limited by N and P (Du et al., 2011; Liu et al., 2014). The availability of soil N, P and potassium (K) were reported to be the most important nutrient factors determining woody species distribution in this region (Zhang et al., 2011; Du et al., 2015). However, previous studies based on the critical N:P ratios (Koerselman and Meuleman, 1996; Güsewell, 2004) have not drawn consistent conclusions. For example, according to Du et al. (2011), P mainly limits vegetation growth during secondary succession, whereas Zhang et al. (2015) found that there was a shift from N-limitation in grassland to P-limitation in secondary and primary forests during vegetation succession. Thus, there is no direct evidence indicating which nutrient indeed limits vegetation productivity and recovery in this karst region.

Although the criterion of Koerselman and Meuleman (1996) has been applied to various ecosystems, the critical N:P ratios may vary among species and ecosystems (Tessier and Raynal, 2003; Drenovsky and Richards, 2004; Güsewell, 2004; Reich and Oleksyn, 2004). Published N:P ratio thresholds for N limitation range from 6.7 to 16, while those for P limitation range from 12.5 to 26.3 (Tessier and Raynal, 2003). For example, the N:P ratios of a wooded meadow on calcareous soils in Estonia, which was N and P co-limited, ranged from 5.6 to 7.5 (Niinemets and Kull, 2005). Further fertilization experiments are needed to evaluate the application of published criteria to the karst ecosystems of southwestern China and to elucidate how nutrients limit vegetation recovery in this region (Zhang and Wang, 2009; Du et al., 2011; Liu et al., 2014). This is crucial for understanding plant-soil interactions and successional mechanisms of native karst vegetation (Zhang et al., 2015) as well as providing fundamental knowledge for revegetation programs (Guo et al., 2011).

We hypothesized that scarcity of mineral nutrients could be a crucial factor limiting vegetation recovery of degraded karst ecosystems in southwestern China. In this study, we conducted a 3-year fertilization experiment to investigate the responses of a degraded karst grassland to N, P and K addition in order to determine their relative importance in limiting the productivity of grassland in this region. We also expected that different plant functional groups would respond differently to nutrient additions.

2. Materials and methods

2.1. Study site

This study was carried out at Puding Karst Ecosystem Research Station, Chinese Academy of Sciences, in Guizhou Province, China (26°22′25″N, 105°45′30″E; 1214 m asl). This region is a representative landscape for karst plateau in southwestern China (Wang et al., 2013). Long-term mean annual precipitation and temperature of this region are 1390 mm and 15.1 °C, respectively. The study was located on a karst hill with a slope of 25°. The original karst forest, mixed evergreen and deciduous broad-leaved forest, was destroyed in the late 1950 s and gradually degraded to a grassland due to continual human disturbances. This site has been protected from livestock grazing since 1991, but secondary succession from grassland to forest is very slow. The mean height of vegetation is 1 m and coverage is 80%. This community usually has three layers. The dominant layer of bunchgrass is dominated by *Themeda japonica* (Willd.) Tanaka and *Heteropogon contortus* (Linn.) Beauv. and contains *Bothriochloa bladhii* (Retz.) S. T. Blake, *Carex lanceolata* Boott and *Capillipedium parviflorum* (R. Br.) Stapf. The lower herbaceous layer consists of many forbs, such as *Potentilla chinensis* Ser., *Lotus corniculatus* Linn., *Micromeria biflora* (Buch.-Ham. ex D. Don) Benth., *Rostellularia procumbens* (L.) Nees, *Gerbera anandria* (L.) Sch.-Bip., *Senecio scandens* Buch.-Ham. ex D. Don, *Aster ageratoides* Turcz., *Viola verecunda* A. Gray and *Polygala tatarinowii* Regel. The scattered shrub layer contains *Rubus parvifolius* L., *Indigofera pseudotinctoria* Matsum., *Campylotropis macrocarpa* (Bge.) Rehd., *Lespedeza bicolor* Turcz., *Rosa cymosa* Tratt. and *Elsholtzia rugulosa* Hemsl.. The soil type is limestone soil, according to the Chinese soil genetic classification, similar to Rendolls in the USDA Soil Taxonomy (Soil Survey Staff, 1999). Soil pH is 7.7 and organic carbon content is 53.5 g kg^{-1}. Soil nutrient properties are described in Table 1. Due to the

Table 1

Community and soil properties of karst grassland from four replicates of the control plots over three years (Means ± SE; n = 12). Different lowercase letters indicate significant differences among plant functional groups.

Community property	Grasses	Forbs	Shrubs	Community
Aboveground biomass (g m^{-2})	197.49 ± 9.24 a	36.65 ± 5.98 b	33.20 ± 5.50 b	267.34 ± 12.76
Proportion of biomass (%)	74.25 ± 1.89 a	13.78 ± 2.19 b	11.98 ± 1.71 b	
N (g kg^{-1})	11.24 ± 0.29 a	14.05 ± 0.88 b	13.51 ± 0.93 ab	11.88 ± 0.21
P (g kg^{-1})	0.88 ± 0.05 a	0.94 ± 0.06 a	0.93 ± 0.08 a	0.89 ± 0.04
K (g kg^{-1})	7.37 ± 0.39 a	8.74 ± 0.53 a	7.48 ± 0.57 a	7.49 ± 0.32
N:P	13.17 ± 0.74 a	15.08 ± 1.06 a	14.98 ± 0.91 a	13.67 ± 0.56
N:K	1.58 ± 0.10 a	1.64 ± 0.14 a	1.93 ± 0.19 a	1.64 ± 0.08
K:P	8.61 ± 0.57 a	9.63 ± 0.80 a	8.39 ± 0.70 a	8.67 ± 0.46
Soil property		**Soil property**		
Total N (g kg^{-1})	3.99 ± 0.21	Available N (mg kg^{-1})		373.33 ± 18.79
Total P (g kg^{-1})	0.90 ± 0.04	Available P (mg kg^{-1})		6.32 ± 0.51
Total K (g kg^{-1})	1.85 ± 0.13	Available K (mg kg^{-1})		86.41 ± 5.77