

# Resource availability, species composition and sown density effects on productivity of experimental plant communities

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**Abstract** Productivity of artificial grassland communities was investigated in a 6-year field experiment on the Qinghai-Tibetan Plateau. In the experiment, assemblages varying in seven species compositions and four density gradients were grown in fertilized and non-fertilized subplots. We measured biomass of sown species as an indicator of community productivity. In general, 6-years of experiments indicated that: (i) species composition had a significant influence on community productivity. During the initial phase of the experiment, sown density significantly affected community productivity, but the effects disappear with the increase of grown years. This productivity increased with biodiversity increase and fertilization, while the biodiversity effects disappeared when the influence of composition was removed. (ii) The increase of commu-

nity productivity with biodiversity was resulted from joint effects of selection and complementarity. (iii) With an increase of growth time, the selection effects become weaker while complementarities become enhanced. Influence of density on both effects was significantly different in early stages, but ultimately this all became insignificant. Fertilization dramatically increased the complementarity effects in all experiment processes, but had different influences on selection effects during different experimental period.

**Keywords** Complementarity effect · Selection effect · Biodiversity · Fertilization · Tibetan plateau

## Introduction

The relationship between biodiversity and productivity has emerged as a major scientific issue during last three decades (Tilman 1982; Tilman and Downing 1994; Cadotte et al. 2008; Isbell et al. 2009; Marquard et al. 2009). There are many studies which address that community productivity is determined by both biotic [biodiversity (Bai et al. 2004), density (Marquard et al. 2009), species composition (Wardle 2002)] and abiotic (nutrient concentration and growth time) factors. However, previous studies are mainly focused on the role of a few factors determining community productivity, e.g. several studies observed the effect of species richness and fertilization on productivity in short-term experiments. These studies however, do not clarify the

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underlying mechanisms of the productivity-biodiversity relationship, especially the change of individual biotic factor along grown time increase.

Many experiments addressed how the increase of productivity resulted from species richness of communities (Tilman 1996, 1999; Hector et al. 1999; Lawton 2000; Hector et al. 2001; Mittelbach et al. 2001; Spehn et al. 2005). However, some studies discovered that productivity was mostly controlled by species composition rather than biodiversity or how their relationship was uncertain (Grime 1997; Huston 1997; Wardle 1998, 1999; Huston et al. 2000). Although many ecology theories believe that density is a key determinant of population productivity, e.g. the law of constant final yield (Kira et al. 1953; Harper 1977), community density has surprisingly received only little attention in regards to change of productivity; e.g. density was kept at only a certain level in previous biodiversity experiments. Several authors suggested that density should be considered when using the replacement series design (Connolly and Nolan 1976; Inouye and Schaer 1981; Taylor and Aarssen 1989; Jolliffe 2000). In recent studies, He et al. (2005) found that community biomass increased significantly with species richness and community density. It is well known that fertilization can rapidly increase the community aboveground biomass and further alter the biodiversity-productivity relationship (Tilman 1996; Reich et al. 2001; He et al. 2002; Fridley 2002, 2003). For example, Fridley (2002) found that biodiversity of sown species had little effect on productivity in low fertilized plots, but with high fertilized treatments, productivity was twice as high in species-rich plots as in monoculture plots.

In order to understand effects of these factors on ecosystem functions, we independently manipulated species composition, species richness, sown density and fertilization in field experiments to examine: (i) how they influenced community productivity, as well as what the biological mechanisms producing these results were; (ii) whether or not the relative importance of selection and complementarity effects changes through grown time.

## Material and methods

This field experiment was established in Hezuo branch of the Research Station of Alpine Meadow

and Wetland Ecosystems of Lanzhou University (N34°55', E102°53', and altitude 2900 m a.s.l). The yearly average temperature there is 2.0°C and precipitation is 557.8 mm (Ma et al. 2010).

We selected three perennial grasses with distinct and complementary characteristics, i.e., the tall-height *Elymus nutans* (En) with sparse-bush (80–120 cm), medium-height sparse-bush *Festuca sinensis* (Fs) (60–90 cm) and short-height dense-bush *Festuca ovina* (Fo) (30–60 cm)(Detailed in Zhang et al. 2010). These species are widely distributed over the alpine grassland of Qinghai-Tibetan Plateau (Zhou 2001).

We manipulated and contrasted herbaceous communities with different sown density and fertilization levels as treatment gradients to test the different effects of species composition, sown density and resource availability on community productivity. The species composition included seven assemblages of grass species, i.e., three monocultures for each of three species, three mixtures of two-species and one mixture of three-species. Four densities sown were selected, i.e., 400, 800, 1600 and 3200 grain·m<sup>-2</sup>. So we obtained 28 treatments. Furthermore, every plot (3×4 m) was averagely divided into two sub-plots to perform two different soil nutrient levels, i.e., fertilized and non-fertilized (the fertilizer used was (NH<sub>4</sub>)<sub>2</sub>HPO<sub>4</sub> and was fertilized about 60 gm<sup>-2</sup> every early spring), resulting in 56 sub-treatments. The plots were separated by 0.5 m buffer strips. All treatments were randomly ranged within a block, and replicated across four blocks, resulting in 224 subplots (7 species composition × 4 density levels × 2 fertilization levels × 4 replicates). Each quadrat (25×25 cm) was marked and fixed with pegs in each subplot.

Before sowing, the existing grassland vegetation was removed from the experimental field and a protective enclosure was built to isolate the area. The experiment used replacement design in mixture. For each species, the sowing-seed weight was calculated from sown density, seed mass and species germination rate. Seeds of all species were sown directly into the plots on 21–29 of June 2003. Weeds of non-target species were weeded weekly during July and August. We did not count the number of weed species and individuals seeding in the first year, but recorded them in the second year. We did not focus on the effect of weed growth in the presented study.

To remove the effect of sown growth in the first year, we harvested biomass and analyzed data from

the second year to sixth year (2004–2008). All individual plants in each of the quadrats were clipped 2 cm above-ground on 21–31 of August every year, sorted to species, dried to constant mass at 80°C for 24 h, and weighed to nearest tenth gram. Community productivity was the sum biomass of all sown species in each quadrat.

## Data analysis

We used a linear mixed model to analyze the effect of different factors on community productivity, selection effects and complementarity effects, all being dependent variables. The selection and complementarity effects were calculated quantitatively using the additive partitioning methods (Loreau and Hector 2001). All dependent variables were square-root transformed (preserving original positive and negative signs) to meet assumption of normality and homogeneity of variances (Fridley 2002; Caldeira et al. 2005; Zhang and Zhang 2006). The factors (independent variables) were species composition, species richness, density and fertilization. The plot was treated as a random effect. Being that species compositions do indeed determine species richness, e.g. species richness was two when the community was assembled by *Elymus nutans* and *Festuca ovina*, we excluded species richness in tests of composition, excluded composition when testing the effect of species richness, and also treated species composition as a random effect to remove the composition effect. The effect of density and fertilization were the same as in the above scenarios. The models were conducted in R (R

Development Core Team 2010) used nlme package (Pinheiro et al. 2010).

## Results

### Community productivity

Species composition significantly affected community productivity ( $P < 0.001$ , Table 1). Community productivity was lower in both *Festuca sinensis* and *Festuca ovina* monoculture communities, but was significantly higher in monoculture of *Elymus nutans* and mixtures of three species (Fig. 1a). In the second and third year of plant growth, productivity increased with the increase of sown densities, but the effects of sown densities disappeared in subsequent years (Fig. 1b). Community productivity significantly increased with fertilization ( $P < 0.001$ , Table 1, Fig. 1c) as well as species richness, e.g. productivity of three species mixtures being twice as high as monocultures ( $P < 0.05$ , Fig. 1d). However, the effects of species richness disappeared when composition was treated as a random factor in the mixed model ( $P > 0.05$ , Table 1).

### Selection effects

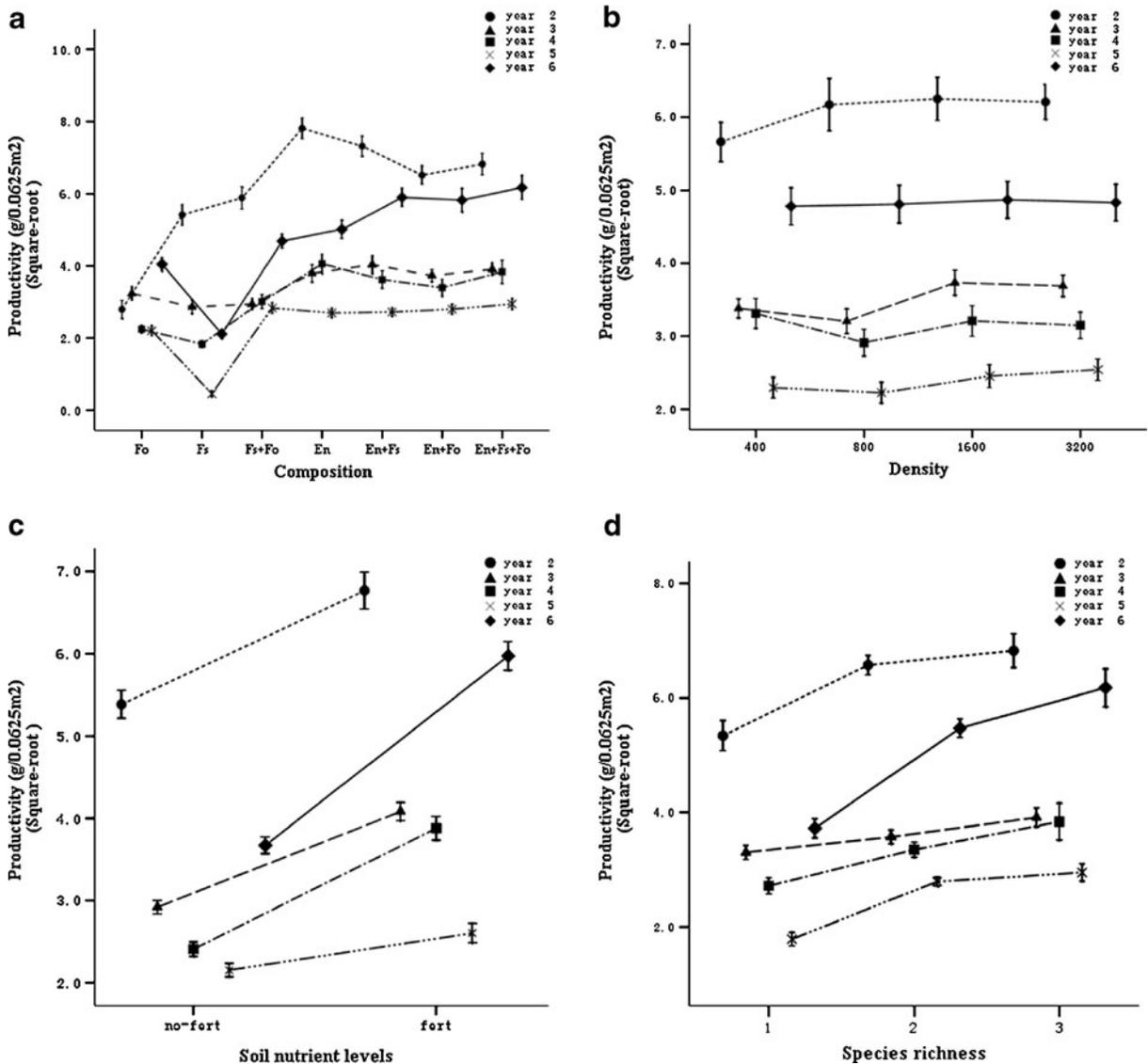
The selection effects were significantly influenced by species composition during the beginning stages, e.g. communities containing *Elymus nutans* had higher selection effects than those without *Elymus nutans* in the second and third year ( $P < 0.001$ , Table 2, Fig. 2a). However, the influence of composition disappeared in the subsequent years ( $P > 0.05$ , Table 2). Though the

**Table 1** Effect of composition, density, fertilization and richness on community biomass analyzed by linear mixed effects model, during five experimental years. The dependent variable (biomass) being square-root transformed, the factors

Source	df	2004	2005	2006	2007	2008
Composition	6	36.93***	8.50***	19.67***	41.77***	107.92***
Density	3	1.69	4.20**	1.42	1.95	0.13
Fertilization	1	66.19***	89.50***	133.40***	28.65***	498.99***
Species richness (1)	2	7.27**	4.10*	9.33**	21.34***	50.07***
Species richness (2)	2	0.43	0.56	0.77	1.36	2.54

The value indicated the  $F$ -ratios, and \* indicates the degree of significance test by  $F$ -test, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

were the species composition (excluding species richness), density, fertilization, species richness (one indicated species composition was excluded and two treated composition as a random factor), and the plot being treated as a random factor



**Fig. 1** Effects of composition, density, resource availability and species richness on the aboveground biomass of sown species from the second to the sixth year of the experiment.

Species abbreviations: En *Elymus nutans*, Fs *Festuca sinensis*, Fo *Festuca ovina*. Data were means  $\pm$  SEM

selection effects trends were more active at higher sown densities than that at lower densities in the second year, selection effects were generally uninfluenced by sown density (Table 2, Fig. 2b). With fertilization, the selection effects significantly increased during the beginning stage (04–05 years), did not significantly change during the middle stage (06–07 years), and decreased on the last year of the experiment (08 year) (Table 2, Fig. 2c). Although the selection effects of three species mixed communities trended

higher than that of two species mixed communities, the selection effects were not significantly influenced by the species richness as a whole (Table 2, Fig. 2d). The selection effects trended to decrease from the second year to the sixth year (Fig. 2).

#### Complementarity effects

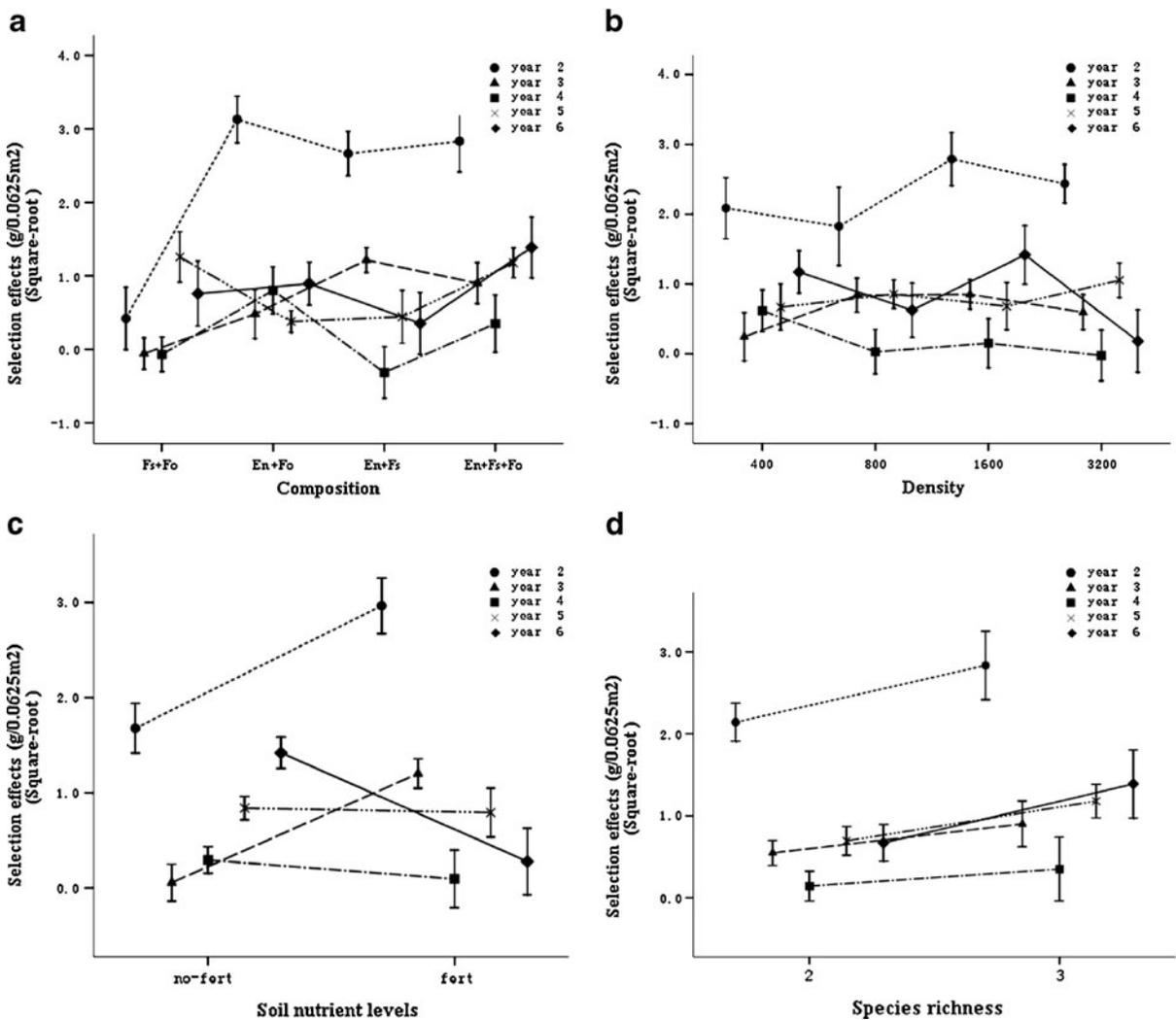
Complementarity effects were significantly influenced by species composition during the 04, 06 and 08 years

**Table 2** Effect of composition, density, fertilization and richness on selection effects analyzed by linear mixed effects model, during five experimental years. The dependent variable (selection effects) being square-root transformed, the factors

were the species composition (excluding species richness), density, fertilization, species richness (one indicated species composition was excluded and two treated composition as a random factor), and the plot being treated as a random factor

Source	df	2004	2005	2006	2007	2008
Composition	3	9.69***	5.56***	2.21	2.76	1.26
Density	3	1.79	1.47	0.78	0.41	2.13
Fertilization	1	19.06***	23.77***	0.36	0.03	9.02**
Species richness (1)	1	1.70	1.52	0.29	2.09	2.71
Species richness (2)	1	0.19	0.23	0.09	0.74	2.71

The value indicated the *F*-ratios, and \* indicates the degree of significance test by *F*-test, \**p*<0.05, \*\**p*<0.01, \*\*\**p*<0.001



**Fig. 2** Effects of composition, density, resource availability and species richness on the selection effects of communities in all experimental years. Data were means ± SEM

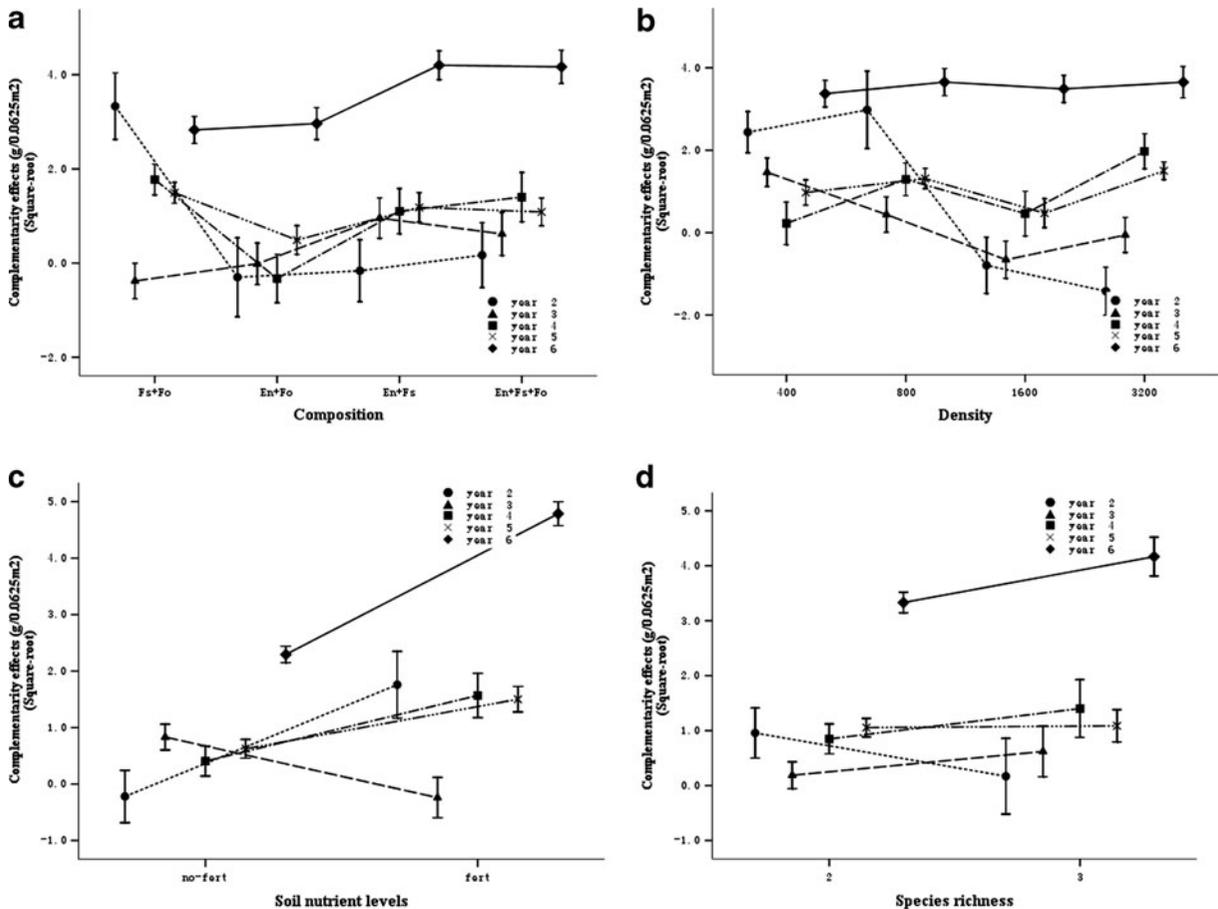
**Table 3** Effect of composition, density, fertilization and richness on complementarity effects analyzed by linear mixed effects model, during five experimental years. The dependent variable (complementarity effects) being square-root transformed, the

Source	df	2004	2005	2006	2007	2008
Composition	3	6.05**	2.13	3.45*	2.33	7.19***
Density	3	9.94***	4.72**	2.62	2.68	0.24
Fertilization	1	13.34***	7.78**	8.47**	10.83**	180.85***
Species richness (1)	1	0.63	0.77	0.83	0.01	5.56*
Species richness (2)	1	0.10	0.30	0.20	0.00	0.91

The value indicated the  $F$ -ratios, and \* indicates the degree of significance test by  $F$ -test, \* $p$ <0.05, \*\* $p$ <0.01, \*\*\* $p$ <0.001

( $P$ <0.05, Table 3, Fig. 3a). The complementarity effects significantly decreased while showing an increase of sown density in the initial stage (04 and 05 year), but did not differ significantly among density gradient in the subsequent three years (Table 3,

Fig. 3b). Except for the 05 year, fertilization significantly increased the complementarity effects in other years (Table 3, Fig. 3c). The complementarity effects did not differ significantly among contrasted communities of different species richness in all years except



**Fig. 3** Effects of composition, density, resource availability and species richness on the complementarity effects of communities from the second to the sixth year of the experiment. Data were means  $\pm$  SEM

for 08 year (this disappeared when composition was a random factor,  $P_{08}=0.44$ ) (Table 3, Fig. 3d). The complementarity effects trended to increase from the second year to the sixth year e.g. mean value was 0.59 and 12.53, respectively (Fig. 3).

## Discussion

The effects of species attribute, biodiversity, density and soil resource on productivity

In recent years, many studies found that species composition was a key determinant of ecosystem functions (Loreau 2000; Wardle et al. 2000). Fridley (2002) addressed that total species composition had the strongest effect on production, explaining 40% of the variation in biomass among plots, with biodiversity only accounting for 9%. Consistent with previous studies, our results indicated that species composition played a crucial role in the determination of community productivity whenever communities were assembled by single species, two species mixtures or three species mixtures. This was consistent with many previous studies that documented the contribution of species attributes to productivity (Reviewed in Balvanera et al. 2006; Hooper et al. 2005). We agreed that the relationship between productivity and species attribute was mainly because different species were characterized by specific functional traits, e.g. specific leaf area, leaf C/N and stem height. Those traits may conclude that species are different in nutritive utilization (Grime 2001; Violle et al. 2007), photosynthesis and biomass allocation (Bazzaz and Grace 1997), which may in turn conclude that a community with different species often has different levels of productivity (Isbell et al. 2009; Petermann et al. 2010).

It is well known that density is one of key determinants of population productivity, which mainly results from intra-specific competition (Harper 1977). Recently, some studies also suggested that community density significantly impacted the above-ground biomass as well as the total biomass (He et al. 2005; Weigelt et al. 2007), and density alone could drive a positive biodiversity-productivity relationship (Marquard et al. 2009). However, those results were often concluded from short-term experiments. Based on six years of studies, our results showed that sown density influenced community productivity in the

initial phase of experiment but did not influence productivity in subsequent years. We believed that this was mostly because of the fact that during the early stage of the experiment, the effect of competition among individuals was very weak because of the small size of the perennial plant. This resulted in higher productivity in high density communities. Through years of growth, ground surface was completely occupied by sown species with larger individual size, with competition becoming more and more intense, and the contribution of density to productivity becoming less important. This was consistent with previous studies that stated how productivity of mixed plant stands would maintain constancy when density exceeded the threshold value (He et al. 2005).

Obviously, the productivity of population or community showed a remarkable increase through the process of fertilization, this was documented continually by several studies (Reviewed in Rajaniemi 2003; Fridley 2002; He et al. 2002). Our studies indicated that fertilization increased the biomass of sown species during the experiment. Furthermore, the influence of fertilization on community productivity became more apparent in the later years of experiments. N or P limitation may result in this pattern for the present study (Chapin et al. 2002). The presented results were consistent with our previous studies which addressed how fertilization led to larger plant size and heightened leaf allocation. Also, these studies presented how fertilized communities were dominated by species with larger productivity (Niu et al. 2008; Niu et al. 2009).

For the effect of biodiversity, Elton (1958) assumed that more diverse communities were more productive. His assumption was supported by many studies both from theoretical models and field experiments (Tilman 1996; Hector et al. 1999, 2001; Spehn et al. 2005). Our results also supported how high biodiversity resulted in high productivity as many previous studies had also concluded (Joshi et al. 2000; Diemer and Shimid 2001; Hector et al. 2001). However, when we removed the effects of composition on productivity, there was no significant relationship between species richness and productivity (Table 1). This will support an opposite perspective that community productivity may not be related to biodiversity (Wardle 1999). Although it is very difficult to prove directly that more biodiversity results in higher productivity, some researchers found that biodiversity

accounted for very few variations in productivity (Fridley 2002). There were also very few long-term experiments which support positive biodiversity-productivity relations (Zhang and Zhang 2006).

#### Selection effect and complementarity effect

On the underlying mechanism of positive biodiversity-productivity, two viewpoints have been widely adopted for many years (Huston 1997; Wardle 1999; Tilman et al. 2001). The selection effects asserted that high biodiversity increases the probability that a community contains and becomes dominated by species with extreme traits such as high production. In the selection effect, low biodiversity assemblages are less productive than high biodiversity assemblages, only because they are missing the most productive species (Huston 1997; Fridley 2002). The complementarity effects assumed that diverse sets of species may be complementary in their ecological niches, which might allow for a more complete utilization of resources, resulting in more productivity (Tilman et al. 2001; Zhang and Zhang 2006).

Our study showed that communities containing more productive *Elymus.nutans* had higher productivity than communities without *Elymus.nutans* (Fig. 1). This exhibited how the selection effects were more prevalent in communities with *Elymus.nutans* (Fig. 2). However, we also noticed that the productivity of three-species mixed communities was still higher than the most productive single-species community in the last year (Fig. 1). This suggested that selection effects alone could not explain community productivity. Further analysis showed that the complementarity effect is stronger in communities with three species than with two species (Table 3), which supports that the complementarity effect also functions in the production of community biomass. Our results were consistent with previous studies which concluded that the increase of community productivity with biodiversity was through the joint effects of selection and complementarity (Joshi et al. 2000; Diemer and Shimid 2001; Hector et al. 2001).

Where before there were very few studies that discussed the effect of community composition, density, soil resource availability and species richness on distinguished selection effects and complementarity effects, our results addressed that density did not have an impact on selection effects, but did have an

influence on complementarity effects in beginning stages of growth. Opposite the effect of density, fertilization increased complementarity effects. Consistent with our results, Fridley (2002) found that plant mixtures of high fertility “overyielded,” or were more productive than expected based on single-species yields of component species. Fridley (2002) also found that the strength of selection effects was largely insensitive to fertility. Our results found that in the beginning stage, selection effects of communities were increased by fertilization; in middle stages, fertilization had no influence on the selection effects; and in last stage, fertilization unexpectedly decreased the selection effects. To determine if resource availability has a different influence on selection effects over time, further investigation would be needed.

Through survey, Zhang and Zhang (2006) found that positive selection effects were more likely to occur in the 1-year experiments (seven of eight experiments were positive); by contrast, for longer experiments (2 years and higher), only 50% of experiments exhibited the positive selection effects. Because our experiment lasted six years, we had the chance to find that selection effects were progressively weakened and complementarity effects strengthened. Our result was also in agreement with previous claims and provided a field-experiment proof for Pacala’s hypothesis that the complementarity effect strengthens though time and substitutes the role of the selection effect (Pacala and Tilman 2001; Tilman et al. 2001). However, Zhang and Zhang (2006) found that the complementarity effect showed no trend through time in experimental algal communities. Therefore, more experimental proofs were needed to prove whether the transition between the two mechanisms did exist.

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