Effects of water and nitrogen on growth and relative competitive ability of introduced versus native C4 grass species in the semi-arid Loess Plateau of China postprint

Authors: DING Wenli, XU Weizhou, GAO Zhijuan, XU Bingcheng, XU Bingcheng

Date: 2021-09-08T00:00:00+00:00

Abstract

Switchgrass is an introduced C4 grass in the semi-arid Loess Plateau of China, but there is a lack of information to assess its ecological invasive risk. In this study, Old World bluestems (native C4 grass) and switchgrass were sowed at five mixture ratios (8:0, 6:2, 4:4, 2:6 and 0:8) under two soil water levels (80% field capacity (FC) and 40% FC) and two nitrogen (N) treatments (0 and 100 mg N/kg dry soil, termed N0-unfertilized and N1-fertilized treatments, respectively) in a pot experiment in 2012. Biomass, root morphological traits and relative competitive abilities of these two species were analyzed. Results showed that biomass of both species was significantly greater under 80% FC or N fertilization, and switchgrass had a relatively larger root: shoot ratio (RSR). Total root length (TRL) and root surface area (RSA) of switchgrass were significantly higher under 80% FC irrespective of N treatment, while those of Old World bluestems were only significantly higher under N fertilization. N had no significant effect on TRL and RSA of switchgrass, while RSA of Old World bluestems significantly increased under 80% FC and N fertilization. Under 40% FC and N0-unfertilized treatment, the aggressivity of Old World bluestems was larger than zero at 2:6 and 4:4 mixture ratios of two species, whereas it was close to zero at 6:2 mixture ratio. Root competitive ability of switchgrass significantly increased under 80% FC or N fertilization. The aggressivity of Old World bluestems was negative at 6:2 mixture ratio under 80% FC and N fertilization, while it was positive at 2:6 mixture ratio. Switchgrass may become more aggressive when N deposition or rainfall increases, while a proper mixture ratio with appropriate water and N management could help with grassland management in the semi-arid Loess Plateau.

Full Text

Effects of Water and Nitrogen on Growth and Relative Competitive Ability of Introduced Versus Native C4 Grass Species in the Semi-Arid Loess Plateau of China

DING Wenli[1], **XU Weizhou**[2], **GAO Zhijuan**[1], **XU Bingcheng**[1,3*]

[1] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling 712100, China
[2] College of Life Science, Yulin University, Yulin 719000, China
[3] Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, China

---

Abstract

Switchgrass is an introduced C4 grass in the semi-arid Loess Plateau of China, yet there remains a lack of information to assess its ecological invasion risk. In this study, Old World bluestems (native C4 grass) and switchgrass were sown at five mixture ratios (8:0, 6:2, 4:4, 2:6, and 0:8) under two soil water levels (80% field capacity (FC) and 40% FC) and two nitrogen (N) treatments (0 and 100 mg N/kg dry soil, termed N0-unfertilized and N1-fertilized treatments, respectively) in a pot experiment conducted in 2012. Biomass, root morphological traits, and relative competitive abilities of these two species were analyzed. Results showed that biomass of both species was significantly greater under 80% FC or N fertilization, and switchgrass had a relatively larger root:shoot ratio (RSR). Total root length (TRL) and root surface area (RSA) of switchgrass were significantly higher under 80% FC irrespective of N treatment, while those of Old World bluestems were only significantly higher under N fertilization. N had no significant effect on TRL and RSA of switchgrass, while RSA of Old World bluestems significantly increased under 80% FC and N fertilization. Under 40% FC and N0-unfertilized treatment, the aggressivity of Old World bluestems was larger than zero at 2:6 and 4:4 mixture ratios of the two species, whereas it was close to zero at the 6:2 mixture ratio. Root competitive ability of switchgrass significantly increased under 80% FC or N fertilization. The aggressivity of Old World bluestems was negative at the 6:2 mixture ratio under 80% FC and N fertilization, while it was positive at the 2:6 mixture ratio. Switchgrass may become more aggressive when N deposition or rainfall increases, while a proper mixture ratio with appropriate water and N management could help with grassland management in the semi-arid Loess Plateau.

Keywords: aggressivity; nitrogen deposition; relative competitive ability; root trait; water stress

---

1 Introduction

Developing stable and high-yield artificial grassland is crucial for promoting ecological environment restoration in the semi-arid Loess Plateau of China [?]. However, precipitation is relatively low and unevenly distributed annually and seasonally in this area, and seasonal drought occurs frequently, threatening plant growth. Additionally, severe soil and water erosion combined with low plant productivity make it difficult for soil to accumulate organic matter. Water and nitrogen (N) are two limiting factors in the establishment of artificial grassland communities in the region [?].

The lack of distinct grass species in the Loess Plateau, especially herbaceous species, has led to problems of limited grass variety, low quality, and low quantity. Introducing excellent grass species represents a viable option to enrich the grass species pool. Switchgrass (*Panicum virgatum* L.), a perennial grass native to North America, was introduced to the Loess Plateau of China in the 1990s due to its high productivity, strong adaptability to drought and nutrient-poor soils, and benefits for water and soil conservation. It has enriched local herbaceous grass species and proven successful in the region [?]. However, introducing switchgrass as an exotic species to this area could cause biological invasion and threaten native biodiversity and local ecosystems, as it has been reported to have high invasive potential in California [?].

The invasion process of non-indigenous species includes transport, colonization, establishment, and landscape spread, with interspecific competition considered one of the most important processes in the establishment stage [?]. Competitive exclusion by native plant species appears to be a major filter in preventing invasive species establishment [?], either through single strongly competitive species or a suite of species that reduce limited resources. The high competitive ability of alien species could potentially facilitate invasion [?, ?]. Therefore, it is important to consider the competitive ability of both native and exotic species. Old World bluestems (*Bothriochloa ischaemum* Keng), one of the dominant species in natural communities in the semi-arid Loess Plateau of China, is a perennial C4 herbaceous grass species with high tolerance to drought and poor soils [?]. It represents an ideal native species for assessing the invasive potential of switchgrass [?].

As the resource hypothesis suggests, increased resource availability (light, water, and soil nutrients) tends to facilitate invasion by exotic plants [?, ?, ?]. This raises concerns about soil N availability, which is significantly enhanced by increased N deposition [?, ?]. Many studies have demonstrated that N deposition could facilitate the invasion of non-native species by increasing their growth and competitive ability more strongly than those of native species [?, ?, ?]. Water, another limiting factor in the semi-arid Loess Plateau of China, may also affect the invasion of alien species by influencing their growth and competition with native species [?, ?]. Therefore, it is necessary to include the effects of water and N when studying the competitive relationship between switchgrass and Old

World bluestems.

Plant root morphological traits, including root hair, root mass, root length, and root area, play important roles in resource acquisition (water and nutrients), which could contribute to plant growth and competitive ability [?, ?, ?, ?]. For example, N addition could increase the competitive ability of an invasive plant (*Solidago canadensis*) by enhancing its root biomass [?]. Semchenko et al. [?] also found that species with lower specific root length and less branched roots tended to be better at tolerating competition. Thus, it would be valuable to include root morphological traits in studies of competition between switchgrass and Old World bluestems under variable resource supplies.

Switchgrass can be used as a biofuel, and numerous studies have focused on increasing cellulosic ethanol production from switchgrass, either at the physiological or molecular level [?, ?, ?]. Switchgrass is also ideal forage due to its low requirements for agricultural inputs and positive environmental impacts [?]. Its resistance to drought, heat, cold, and alkaline stresses, as well as its benefits for soil and water conservation, nutrient recovery from runoff, and potential for carbon sequestration have also been studied [?, ?, ?, ?]. However, few studies have assessed the relative competitive abilities of switchgrass and local herbaceous grasses in the semi-arid Loess Plateau of China, and how this ability differs in response to changes in mixture ratio, water, and N supply.

Given that switchgrass was relatively poorly adapted to drought and its biomass was less responsive to N addition compared with Old World bluestems [?], and increased resources normally favor exotic plant reproduction [?], we hypothesized that: (1) increased water and/or N supply would improve the growth of both Old World bluestems and switchgrass; (2) the competitive ability of switchgrass would be weaker than that of Old World bluestems under low water and N conditions; and (3) increased water and/or N supply would increase the competitive ability of switchgrass relative to Old World bluestems.

---

2 Materials and Methods

2.1 Plant Materials

Old World bluestems and switchgrass were used in this experiment. Seeds of Old World bluestems were collected in October 2011 from the experimental fields at Ansai Research Station (ARS) of the Chinese Academy of Sciences (CAS) (36°51 N, 109°19 E; 530 m a.s.l.), located in the center of the semi-arid hilly gully region on the Loess Plateau, China. The seeds were stored in a sealed container in the laboratory under natural dry conditions. The switchgrass variety used was ‘Alamo’ , and the seeds were also collected from the same location in October 2005.

2.2 Experimental Design

2.2.1 Soil Properties The soil was collected from the upper 20 cm of a farm field at ARS, CAS. The soil moisture content at field capacity (FC) was 0.20 g/g. Soil pH (10 g dry soil in 25 mL water) was 8.77, and soil organic matter content, total N, total phosphorus (P), and total potassium (K) contents were 0.360%, 0.025%, 0.066%, and 1.900%, respectively. Soil available N, P, and K contents were 19.6, 50.8, and 101.6 mg/kg, respectively. After drying and sealing, 3.8 kg of soil was packed into each cylindrical pot (20 cm in diameter and 16 cm in depth), and a vertical plastic pipe was placed adjacent to the inner wall of each pot for water supply. The experiment was conducted under a rainfall shelter at ARS, CAS from April to November 2012. The annual mean temperature was 12.9°C, with a maximum mean temperature of 26.7°C in July and a minimum temperature of -1.0°C to -2.0°C in January. The mean annual precipitation was 638 mm.

2.2.2 Soil Field Capacity Determination Soil FC was determined as follows: (1) three 100-cm^3 core samples were filled with disturbed soil at a bulk density of 1.2 g/cm^3; (2) when core samples were saturated, they were placed on coarse sand soil to drain water freely, and the surface was covered to prevent evaporation; (3) soil wet mass (m_w) was determined until the weight of the soil core was constant (i.e., two measurements differed by <0.20 g). After that, core samples were dried in an oven at 105°C for 48 h and dry soil mass (m_d) was calculated; and (4) FC was calculated using the following equation: FC = (m_w -m_d)/m_d.

2.2.3 Species Mixture Ratios A replacement series design [?, ?] was used with a density of 8 plants per pot. Five mixture ratios of Old World bluestems (B) to switchgrass (P) (8:0, 6:2, 4:4, 2:6, and 0:8) were employed [Figure 1: see original paper]. The ratios of 8:0, 6:2, 4:4, 2:6, and 0:8 for these two species were abbreviated as B8P0, B6P2, B4P4, B2P6, and B0P8 in the following figures.

2.2.4 Nitrogen Treatments Two N fertilization rates (0 and 100 mg N/kg dry soil, termed N0-unfertilized and N1-fertilized treatments, respectively) were applied in this experiment. N was applied as $CO(NH_2)_2$ (urea) and mixed uniformly with soil during pot filling. There were three replicates for each treatment, and all pots were distributed in a completely random design inside the rainfall shelter.

2.2.5 Water Treatments Seeds were sown on April 3, and soil water content was maintained at 80% FC during seedling establishment. When seedlings of both species had three leaves and were approximately 0.10 m tall (25 days after sowing), seedlings were thinned to 8 plants per pot, and water treatments (40% FC and 80% FC) were initiated. Before the water treatment, a layer of perlite was spread on the soil surface of each pot (approximately 2.0 cm) to reduce soil evaporation. Daily evapotranspiration was assessed by weighing the pots at 18:00 (LST) daily, and water was added via the plastic pipes to maintain the desired level.

2.3 Biomass Measurements

Plants were harvested at the end of the growing season on October 5, 2012, for both species. Shoots were collected and separated into leaf and stem, and roots were collected and carefully washed free of soil. Weights of each part were determined after drying at 75°C for 72 h in an oven. Root:shoot ratio (RSR) was calculated.

2.4 Root Morphological Traits

Approximately one-third of total roots were subsampled for morphological trait measurements. The selected root samples were dyed with 0.5% methylene blue solution for 5 min, gently dried with paper tissue, and placed between two transparent plastic sheets. All samples were then scanned using a BENQ color scanner 5560 (BENQ Science and Technology Ltd., Shanghai, China) [?, ?] and analyzed using WinRHIZO 2009 (Regents Instruments Canada Inc., Quebec City, Quebec, Canada) to determine total root length (TRL), root surface area (RSA), and root average diameter (RAD).

2.5 Water Use Efficiency (WUE)

All pots were weighed and watered at 18:00, and the amount of water added was recorded. Pots filled with soil but without plants were used to estimate soil evaporation. Soil evaporation was subtracted from total water consumption. WUE was defined as the amount of total biomass produced per unit of water consumed by plants under each water and N treatment (WUE, g DW/kg H_2O). The formula is as follows:

$$\mathrm{WUE} = \frac{\text{total biomass}}{\text{total water consumption} - \text{soil evaporation}} \tag{1}$$

2.6 Competitive Indices

Competitive indices are useful tools for estimating the effect and intensity of competition [?], with two commonly used indices [?, ?]. Aggressivity (A) is considered an appropriate expression for the intensity of interspecific competition, while relative yield total (RYT) is commonly used to measure the effect of competition [?, ?, ?].

These two competitive indices are calculated as follows:

$$A = \frac{Y_{ab}}{Y_{aa} \times Z_{ab}} - \frac{Y_{ba}}{Y_{bb} \times Z_{ba}}, \quad \mathrm{RYT} = \frac{Y_{ab}}{Y_{aa}} + \frac{Y_{ba}}{Y_{bb}}$$

where Y_{ab} is the biomass of Old World bluestems in the mixture (g/pot); Y_{aa} is the biomass of Old World bluestems in monoculture (g/pot); Z_{ab} is the ratio of Old World bluestems to switchgrass in the mixture; Y_{ba} is the biomass of switchgrass in the mixture (g/pot); Y_{bb} is the biomass of switchgrass in monoculture (g/pot); and Z_{ba} is the ratio of switchgrass to Old World bluestems in the mixture.

For the index of A, A $<$ 0 indicates Old World bluestems is less competitive than switchgrass; A $=$ 0 indicates Old World bluestems is similarly competitive with switchgrass; and A $>$ 0 indicates Old World bluestems is more competitive than switchgrass.

For the index of RYT, RYT $=$ 1.0 indicates competition between two species; RYT $<$ 1.0 indicates mutual antagonism between two species; and RYT $>$ 1.0 indicates niche differentiation between two species [?].

2.7 Statistical Analysis

Generalized least square models were used to test differences in shoot biomass, root biomass, total biomass, WUE, TRL, RSA, RAD, A, and RYT among water levels, N treatments, mixture ratios, and their interactions. The residuals of each model were visually checked for heteroscedasticity, and in the presence of heteroscedasticity, appropriate variance structures were specified based on Akaike Information Criterion if they significantly improved the model [?]. Data and statistical analyses were performed using the R software platform [?]. The effect package was used to determine means, standard errors, and 95% confidence intervals [?]. The Multcomp package was used for Tukey' s post hoc comparisons to define differences at the P = 0.05 level.

---

3 Results

3.1 Biomass and Root:Shoot Ratio

Water, N, and mixture ratios significantly affected the growth and RSR of Old World bluestems and switchgrass . Regardless of water level, the biomass of both species under N fertilization was significantly higher than that under no N fertilization. The biomass of both species was also significantly higher under 80% FC than under 40% FC irrespective of N treatment. The shoot, root, and total biomass of each individual species decreased as its corresponding proportion decreased in the mixture (Figs. 2 and 3).

Total shoot biomass in the mixture was significantly lower than that of Old World bluestems in monoculture but higher than that of switchgrass in monoculture. Total root biomass in the mixture was significantly lower than those of both species in monoculture [Figure 2: see original paper]. Total biomass in the mixture was significantly lower than that of Old World bluestems in monoculture, while it was higher than that of switchgrass in monoculture only under N fertilization [Figure 3: see original paper].

RSR of Old World bluestems and switchgrass under N fertilization was generally significantly lower than those under no N fertilization irrespective of water supply. RSR of both species was also significantly lower under 80% FC than under 40% FC under N fertilization, while there was no significant difference between water levels under no N fertilization. RSR of switchgrass was significantly lower in the mixture than in monoculture, whereas RSR of Old World bluestems was significantly higher in the mixture than in monoculture under no N fertilization [Figure 3: see original paper].

3.2 Root Morphological Traits

The mixture of the two species did not have any significant effects on TRL and RSA of Old World bluestems and switchgrass . TRL and RSA of switchgrass were significantly higher under 80% FC than under 40% FC irrespective of N treatment, while those of Old World bluestems were only significantly higher under 80% FC than under 40% FC under no N fertilization [Figure 4: see original paper]. N showed no significant effect on TRL and RSA of switchgrass, and RSA of Old World bluestems was significantly higher under N fertilization for 80% FC. However, TRL and RSA of Old World bluestems were significantly lower under N fertilization for 40% FC [Figure 4: see original paper].

The mixture of two species had no significant effects on RAD of Old World bluestems. RAD of switchgrass varied among mixture ratios, with the largest value at B2P6 under 40% FC [Figure 5: see original paper]. In monoculture, RAD of Old World bluestems was significantly larger under 80% FC for no N fertilization, while it showed an opposite trend under N fertilization. Compared with 40% FC, RAD of switchgrass was always larger under 80% FC, except at B2P6. RAD of Old World bluestems in monoculture and B2P6 was significantly larger under N fertilization for 40% FC, whereas RAD of switchgrass from all mixture ratios was always larger under N fertilization [Figure 5: see original paper].

3.3 Competitive Indices

Mixture, water, and N significantly affected the aggressivity values (A) of Old World bluestems relative to switchgrass . The sequence of A values calculated from shoot, root, and total biomass followed the pattern B6P2 $\leq$ B4P4 $\leq$ B2P6. The A values from shoot, root, and total biomass were close to zero at B6P2 under 40% FC and no N fertilization, while they were negative under 80% FC and/or N fertilization .

The A value from shoot biomass under 80% FC was significantly lower than that under 40% FC within each mixture ratio under no N fertilization, while it was significantly higher at B4P4 and B2P6 under N fertilization. The A value from shoot biomass under N fertilization was lower for 40% FC, with the difference only significant at B6P2. Within 80% FC, the A values from shoot biomass at B4P4 and B2P6 were significantly higher under N fertilization than under no N fertilization, while the A value from shoot biomass at B6P2 showed an opposite trend .

The A value from root biomass at B6P2 was significantly lower under 80% FC than under 40% FC with no N fertilization, while water had no significant effect on those values at B4P4 and B2P6. The A values from root biomass at B6P2 and B4P4 were significantly lower under 80% FC than under 40% FC with N fertilization, whereas the A value from root biomass at B2P6 showed no significant difference between water levels. The A values from root biomass at B6P2 and B2P6 were significantly lower under N fertilization with 40% FC, while N had no significant effect at B4P4. The A values from root biomass at B6P2 and B4P4 were significantly lower under N fertilization with 80% FC, while N had no significant effect at B2P6 .

The A value from total biomass of each mixture ratio was significantly lower under 80% FC than under 40% FC with no N fertilization. The A value from total biomass at B6P2 was also significantly lower under 80% FC than under 40% FC with N fertilization, while it showed an opposite trend for B2P6. The A values from total biomass at B6P2 and B2P6 were significantly lower under N fertilization with 40% FC, while there was no significant difference at B4P4. The A value from total biomass at B2P6 was significantly higher under N fertilization with 80% FC, whereas it showed an opposite trend at B6P2 .

RYT values of Old World bluestems and switchgrass were significantly affected by mixture ratios , with RYT values from shoot biomass following the order B6P2 = B4P4 > B2P6 . RYT values under 80% FC or N fertilization were significantly higher than those under 40% FC and N0-unfertilized conditions, and RYT values under N fertilization and 40% FC were higher than those under N0-unfertilized and 80% FC. Under 40% FC and N0-unfertilized conditions, RYT values from shoot, root, and total biomass under each mixture ratio and water supply were all smaller than 1, while those values were all above 1 (the highest) under 80% FC and N fertilization. Additionally, RYT values from shoot biomass were greater than those from root and total biomass with N and water supply .

3.4 Water Use Efficiency

WUE values of Old World bluestems and switchgrass were significantly lower under 80% FC than under 40% FC. However, WUE values of Old World bluestems and switchgrass were significantly higher under N fertilization with 80% FC. Additionally, WUE values of Old World bluestems and switchgrass in the mixture were always lower than that of Old World bluestems in monoculture, while showing no significant difference with that of switchgrass in monoculture [Figure 6: see original paper].

4 Discussion

Water and N are the two most limiting factors in semi-arid ecosystems [?, ?]. Water deficit can restrict plant height, tillering number, and biomass, while N addition can alleviate these negative effects by preventing cell membrane damage and enhancing osmoregulation [?, ?, ?] or strengthen those negative effects [?]. Our results confirmed that water and N co-limited the growth of Old World bluestems and switchgrass, and N fertilization could alleviate the negative effects of water deficiency.

Water and N availability also affect plant competitive ability [?, ?, ?]. Aggressivity is an important index for determining the competitive abilities of different plant species, while RYT can be used to judge whether there are complementary effects between two species in mixture [?, ?]. Our study showed that under low water and N0-unfertilized conditions, aggressivity of Old World bluestems to switchgrass was greater than or close to zero, which agrees with our hypothesis that the competitive ability of switchgrass is weaker than that of Old World bluestems under low water and N0-unfertilized conditions.

Compared with switchgrass, Old World bluestems has relatively better adaptability to drought and nutrient-poor soils [?], and the competitive ability of switchgrass was restricted in this environment. Similarly, a meta-analysis showed that drought could potentially inhibit the growth of invasive species more than native species, thereby reducing plant invasion [?]. However, the competitive ability of Old World bluestems to switchgrass generally decreased as water or N supply improved individually. The higher competitive ability of Old World bluestems can be attributed to its adaptation to the local environment with low soil water and nutrients. When facing more available water, nutrients, or variable environments, Old World bluestems is recalcitrant to change [?]. These results agree with the resource hypothesis that invasive species outperform native species in high-resource environments [?, ?, ?, ?]. This may put Old World bluestems at risk under enhanced N deposition conditions [?].

The outperformance of switchgrass under 80% FC and N fertilization could be explained by its high resource-acquisition efficiency. Root morphology can reflect plant growth and resource exploitation strategy, and longer root length and larger RSA are always positively correlated with better water and nutrient uptake [?, ?]. A high or efficient resource uptake capacity of invasive plant species could confer a competitive advantage [?, ?]. It is also reported that invasive species could increase their competitive ability by allocating more biomass to roots (i.e., a higher RSR) [?, ?]. Thus, changing biomass allocation and modifying root morphology are widely recognized as effective strategies for plants to cope with competitive pressure [?, ?]. In our study, switchgrass generally allocated more biomass to roots than Old World bluestems, giving it advantages in acquiring limited soil resources. TRL and RSA of switchgrass increased under higher water supply alone, showing that the resource uptake capacity of switchgrass increased with more water supply. Interestingly, TRL and RSA of Old World bluestems decreased under N fertilization alone with 40% FC, indicating decreased resource uptake capacity of Old World bluestems with more N supply under drought conditions. The changes in TRL and RSA of switchgrass and Old World bluestems, together with the higher RSR of switchgrass, could partly explain the relatively increased competitive ability of switchgrass to Old World bluestems under higher water or N supply. It is noteworthy that although the shoot competitive ability of Old World bluestems to switchgrass was very strong, the root competitive ability of switchgrass was stronger, resulting in stronger overall (root and shoot) competitive ability of switchgrass to Old World bluestems. This also aligns with the general belief that belowground competition effects are greater than shoot competition and can determine which species or individuals dominate [**?**, **?**].

Mixture ratio or planting density can also affect competition outcomes. For example, low wood density is generally correlated with a low competitive effect on neighbors [**?**]. However, the competitive result in our study is opposite, i.e., the competitive ability of Old World bluestems to switchgrass was stronger with a lower proportion of Old World bluestems (B6P2 $\leq$ B4P4 $\leq$ B2P6). This suggests that plant density cannot simply be used to explain competitive outcomes. Interestingly, although individual water or N supply generally improved the relative competitive ability of switchgrass, the competitive ability of Old World bluestems at B2P6 was the highest under 80% FC and N fertilization, and there is niche differentiation between switchgrass and Old World bluestems. This is probably because niche differentiation varies among mixture ratios, and water and N supply could further enhance it.

We are experiencing global climate change, including spatiotemporal variation in extreme precipitation. General circulation model results showed that more frequent and intense precipitation will occur in the Loess Plateau, China [**?**], which could increase soil water content in the short term. Additionally, TRMM (the Tropical Rainfall Measuring Mission) multi-satellite precipitation data analysis showed that average precipitation in the Loess Plateau is increasing significantly at a rate of 4.46 mm/a [**?**]. N deposition is also increasing in China [**?**, **?**]. Based on our study results and the impacts of climate change on the Loess Plateau, we speculate that the invasion potential of switchgrass will increase in the future. Our recent study showed that increased water supply increased the aggressivity of Old World bluestems to *Lespedeza davurica* (Laxm.) Schindl. (a perennial C3 leguminous sub-shrub in the Loess Plateau; unpublished data). This also suggests that the aggressivity of switchgrass to *L. davurica* might be greater under increasing precipitation. Ecologists and farmers should be aware of the potential for switchgrass to increase its invasion potential in the Loess Plateau under increasing precipitation or N deposition.

5 Conclusions

Either increased water or N supply had positive effects on biomass production of Old World bluestems and switchgrass, and N fertilization could alleviate the negative effects of water stress on biomass production. Old World bluestems was relatively dominant under 40% FC and no N application; when water supply or N conditions improved, switchgrass became more aggressive. Root traits partly explain the change in relative competitive ability of switchgrass to Old World bluestems under increased water or N supply. However, a suitable mixture ratio with optimal water and N-fertilizer management could prevent switchgrass invasion. This means that when N deposition or precipitation increases in arid and semi-arid areas and the biological invasion potential of alien species increases, we can adopt suitable practices, such as changing species combination ratios, water, or nitrogen supply to reduce invasion risk. Although transferring results from a pot experiment on plant growth and competition to field conditions requires caution, the information from this study may help in predicting the risk of introduced invasive species.

Acknowledgements

This study was supported by the National Natural Science Foundation of China (41371509; 41771553) and the Intergovernmental International Cooperation on Science and Technology Innovation under the Ministry of Science and Technology of the People's Republic of China (2018YFE0112400). We thank Dr. PANG Jiayin, Dr. Patrick HAYES, two anonymous reviewers, and editors for their valuable comments on this manuscript.

References

Abid M, Tian Z, Ata-Ul-Karim S T, et al. 2016. Nitrogen nutrition improves the potential of wheat (*Triticum aestivum* L.) to alleviate the effects of drought stress during vegetative growth periods. *Frontiers in Plant Science*, 7: 981.

Aerts R, Boot R G A, van der Aart P J M. 1991. The relation between above- and belowground biomass allocation patterns and competitive ability. *Oecologia*, 87(4): 551–559.

Ashworth A J, Moore Jr P A, King R, et al. 2019. Switchgrass forage yield and compositional response to phosphorus and potassium. *Agrosystems, Geosciences & Environment*, 2(1): 1–8.

Barney J N, DiTomaso J M. 2008. Nonnative species and bioenergy: Are we cultivating the next invader? *Bioscience*, 58(1): 64–70.

Bennett J A, Riibak K, Tamme R, et al. 2016. The reciprocal relationship between competition and intraspecific trait variation. *Journal of Ecology*, 104(5): 1410–1420.

Blumenthal D. 2005. Interrelated causes of plant invasion. *Science*, 310(5746): 243–244.

Blumenthal D, Chimner R A, Welker J M, et al. 2008. Increased snow facilitates plant invasion in mixed grass prairie. *New Phytologist*, 179(2): 440–448.

Bobbink R, Hicks K, Galloway J, et al. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications*, 20(1): 30–59.

Collins H P, Kimura E, Polley W, et al. 2020. Intercropping switchgrass with hybrid poplar increased carbon sequestration on a sand soil. *Biomass and Bioenergy*, 138: 105558.

Cooney D, Kim H, Quinn L, et al. 2017. Switchgrass as a bioenergy crop in the Loess Plateau, China: potential lignocellulosic feedstock production and environmental conservation. *Journal of Integrative Agriculture*, 16(6): 1211–1226.

Daehler C C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, 34(1): 183–211.

Davis M A, Grime J P, Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, 88(3): 528–534.

de Wit C T. 1960. On competition. *Verslagen van Landbouwkundige Onderzoekingen*, 66: 1–82.

de Wit C T, van den Bergh J P. 1965. Competition between herbage plants. *Journal of Agricultural Science*, 13: 212–221.

Drenovsky R E, Martin C E, Falasco M R, et al. 2008. Variation in resource acquisition and utilization traits between native and invasive perennial forbs. *American Journal of Botany*, 95(6): 681–687.

Dziedek C, Härdtle W, von Oheimb G, et al. 2016. Nitrogen addition enhances drought sensitivity of young deciduous tree species. *Frontiers in Plant Science*, 7: 1100.

Fowler N. 1982. Competition and coexistence in a North Carolina grassland: III. mixtures of component species. *Journal of Ecology*, 70(1): 77–92.

Funk J L, Vitousek P M. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature*, 446(7139): 1079–1081.

Galloway J N, Townsend A R, Erisman J W, et al. 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science*, 320(5878): 889–892.

Goldberg D E, Rajaniemi T, Gurevitch J, et al. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, 80(4): 1118-1131.

Grace J B. 1995. On the measurement of plant competition intensity. *Ecology*, 76(1): 305-308.

Guo J Y, Yang Y, Wang G X, et al. 2010. Ecophysiological responses of *Abies fabri* seedlings to drought stress and nitrogen supply. *Physiologia Plantarum*, 139(4): 335-347.

He W M, Yu G L, Sun Z K. 2011. Nitrogen deposition enhances *Bromus tectorum* invasion: biogeographic differences in growth and competitive ability between China and North America. *Ecography*, 34(6): 1059-1066.

Hector A. 1998. The effect of diversity on productivity: detecting the role of species complementarity. *Oikos*, 82(3): 597-599.

Hooper D U, Johnson L. 1999. Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry*, 46(1): 247-293.

Jolliffe P A. 2000. The replacement series. *Journal of Ecology*, 88(3): 371-385.

Keane R M, Crawley M J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, 17(4): 164-170.

Keshwani D R, Cheng J J. 2009. Switchgrass for bioethanol and other value-added applications: A review. *Bioresource Technology*, 100(4): 1515-1523.

Kiær L P, Weisbach A N, Weiner J. 2013. Root and shoot competition: a meta-analysis. *Journal of Ecology*, 101(5): 1298-1312.

Kunstler G, Falster D, Coomes D A, et al. 2016. Plant functional traits have globally consistent effects on competition. *Nature*, 529(7585): 204-207.

Levine J M, Vilà M, Antonio C M D, et al. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 270(1517): 775-781.

Li S Q, Tian X H, Li S G. 2000. Physiological compensation effects of nutrient on winter wheat in dryland. *Acta Botanica Boreali-Occidentalia Sinica*, 20(1): 22-28. (in Chinese)

Li Z, Zheng F L, Liu W Z, et al. 2012. Spatially downscaling GCMs outputs to project changes in extreme precipitation and temperature events on the Loess Plateau of China during the 21st Century. *Global and Planetary Change*, 82-83: 65-73.

Liu X J, Zhang Y, Han W X, et al. 2013. Enhanced nitrogen deposition over China. *Nature*, 494: 459-462.

Liu Y J, Oduor A M O, Zhang Z, et al. 2017. Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biology*, 23(8): 3363-3370.

Lynch J P. 2013. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany*, 112(2): 347-357.

McGilchrist C A, Trenbath B R. 1971. A revised analysis of plant competition experiments. *Biometrics*, 27(3): 659-671.

Mitchell R, Vogel KP, Sarath G. 2008. Managing and enhancing switchgrass as a bioenergy feedstock. *Biofuels, Bioproducts and Biorefining*, 2(6): 530-539.

Muir J P, Sanderson M A, Ocumpaugh W R, et al. 2001. Biomass production of 'Alamo' switchgrass in response to nitrogen, phosphorus, and row spacing. *Agronomy Journal*, 93(4): 896-901.

R Core Team. 2019. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rajaniemi T K. 2002. Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. *Journal of Ecology*, 90(2): 316-324.

Rao L E, Allen E B. 2010. Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts. *Oecologia*, 162(4): 1035-1046.

Ravenek J M, Mommer L, Visser E J W, et al. 2016. Linking root traits and competitive success in grassland species. *Plant and Soil*, 407(1): 39-53.

Ren G Q, Li Q, Li Y, et al. 2019. The enhancement of root biomass increases the competitiveness of an invasive plant against a co-occurring native plant under elevated nitrogen deposition. *Flora*, 261: 151486.

Roy J. 1990. In search of the characteristics of plant invaders. In: di Castri, Hansen A J, Debussche M. *Biological Invasions in Europe and the Mediterranean Basin*. Dordrecht: Kluwer Academic Publishers, 335-336.

Sanderson M A, Adler P R, Boateng A A, et al. 2006. Switchgrass as a biofuels feedstock in the USA. *Canadian Journal of Plant Science*, 86(Special Issue): 1315-1325.

Semchenko M, Lepik A, Abakumova M, et al. 2018. Different sets of belowground traits predict the ability of plant species to suppress and tolerate their competitors. *Plant and Soil*, 424(1): 157-169.

Shan L, Xu B C. 2009. Discuss about establishing stable artificial grassland in semi-arid Loess Plateau of China. *Acta Prataculture Sinica*, 2(18): 1-2. (in Chinese)

Sheppard C S, Burns B R, Stanley M C. 2014. Predicting plant invasions under climate change: are species distribution models validated by field trials? *Global*

Change Biology, 20(9): 2800–2814.

Shui J, An Y, Ma Y, et al. 2010. Allelopathic potential of switchgrass (*Panicum virgatum* L.) on perennial ryegrass (*Lolium perenne* L.) and alfalfa (*Medicago sativa* L.). *Environmental Management*, 46(4): 590–598.

Theoharides K A, Dukes J S. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, 176(2): 256–273.

Wang Z, Xu W Z, Chen Z F, et al. 2018. Soil moisture availability at early growth stages strongly affected root growth of *Bothriochloa ischaemum* when mixed with *Lespedeza davurica*. *Frontiers in Plant Science*, 9: 1050.

Weigelt A, Jolliffe P. 2003. Indices of plant competition. *Journal of Ecology*, 91(5): 707–720.

White P, George T, Dupuy L, et al. 2013. Root traits for infertile soils. *Frontiers in Plant Science*, 4: 193.

Wilson J B. 1988. Shoot competition and root competition. *Journal of Applied Ecology*, 25(1): 279–296.

Xu B C, Shan L, Huang J, et al. 2003. Comparison of water use efficiency and root/shoot ratio in seedling stage of switchgrass (*Panicum vigarum*) and old world bluestems (*Bothriochloa ischaemum*). *Acta Prataculturae Sinica*, 12(4): 73–77. (in Chinese)

Xu B C, Niu F R, Duan D P, et al. 2012. Root morphological characteristics of *Lespedeza davurica* (L.) intercropped with *Bothriochloa ischaemum* (L.) Keng under water stress and P application conditions. *Pakistan Journal of Botany*, 44(6): 1875–1881.

Xu W Z, Deng X P, Xu B C. 2013. Effects of water stress and fertilization on leaf gas exchange and photosynthetic light-response curves of *Bothriochloa ischaemum* L. *Photosynthetica*, 51(4): 603–612.

Yang H, Li Y, Wu M Y, et al. 2011. Plant community responses to nitrogen addition and increased precipitation: the importance of water availability and species traits. *Global Change Biology*, 17(9): 2936–2944.

Yu G R, Jia Y L, He N P, et al. 2019. Stabilization of atmospheric nitrogen deposition in China over the past decade. *Nature Geoscience*, 12(6): 424–429.

Zhang X H, Xu B C, Li F M. 2007. Effect of planting density on the productivity and WUE of three legumes in highland of Loess Plateau. *Acta Agrestia Sinica*, 1(16): 593–598. (in Chinese)

Zhao Q, Chen Q Y, Jiao M Y, et al. 2018. The temporal-spatial characteristics of drought in the Loess Plateau using the remote-sensed TRMM precipitation data from 1998 to 2014. *Remote Sensing*, 10(6): 838.

Zuur A F, Leno E N, Walker N J, et al. 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer Science and Business Media, 71-100.

Note: Figure translations are in progress. See original paper for figures.