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Soil nutrients influence the photosynthesis and biomass in invasive *Panicum virgatum* on the Loess Plateau in China

Zemin Ai · Jiaoyang Zhang · Hongfei Liu · Qi Xin · Sha Xue · Guobin Liu

Abstract

Background and aims The changes in the characteristics of *Panicum virgatum*, an exotic invasive species, after invading various plant communities on the Loess Plateau in China and the main soil nutrient factors in these communities closely associated with invasion remain unclear.

Methods A pot culture experiment was carried out to simulate the changes in photosynthesis, biomass, and biomass allocation in *P. virgatum* and to identify the main soil nutrient factors in various soils collected from local plant communities. *P. virgatum* was grown in soils collected from communities of *P. virgatum* (PS treatment), *Setaria viridis* (SS treatment), *Bothriochloa ischaemum* (BS treatment), and *Artemisia sacrorum* (AS treatment) and in a mixed soil from the communities of *S. viridis*, *B. ischaemum*, and *A. sacrorum* (MS treatment).

Results Photosynthesis in *P. virgatum* differed significantly among the soil treatments. Net photosynthetic rate, stomatal conductance, and photochemical efficiency (Fv/Fm) were highest in PS, whereas single-photon avalanche diode values were highest in PS and SS. The variation of biomass differed significantly in different tissues of *P. virgatum* in the treatments. Leaf and stem biomasses were highest in PS and SS, and root biomass was highest in PS and MS. Total biomass differed significantly among the treatments, except between BS and MS. Both the leaf to total and stem to total biomass ratios were highest in AS and SS, but the root to total biomass ratio was lowest in these two treatments. A constrained redundancy analysis and a path analysis suggested that the water-soluble nitrate-nitrogen (W-NN) concentration of the soil could significantly affect photosynthesis, biomass, and biomass allocation in *P. virgatum*.

Conclusions Photosynthesis, biomass, and biomass allocation in *P. virgatum* differed significantly when grown in soils from different local plant communities on the Loess Plateau. The soil W-NN concentration in these local plant communities likely has a large impact on the invasive success of *P. virgatum*.

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Introduction

Invasion by exotic species is a serious environmental threat and can cause the loss of biodiversity and decrease the stability and functioning of ecosystems (Sala et al. 2000; Vilà et al. 2010), which is attracting increasing attention from ecologists (Ehrenfeld 2003). Interactions between exotic invasive species and components of native ecosystems have been studied in recent decades, which have improved our understanding of the process of invasion (Vilà et al. 2010). Studies have mainly focused on determining the ecophysiological and ecological traits conducive to the growth of plants and their potential to invade new regions (Leffler et al. 2014; Pyšek and Richardson 2007) by comparing the characteristics of exotic and native species. The characteristics of exotic invasive plants, including high resource capture ability, efficiency, high phenotypic plasticity (Daehler 2003; Durand and Goldstein 2001; Pyšek and Richardson 2007), differences in resource acquisition (Funk and Vitousek 2007), and the suppression of the performance of competing native species and natural enemies (Zuppinger-Dingley et al. 2011), have been identified that facilitate their establishment and dominance in new regions. Most of these comparative studies have focused only on exotic invasive species, i.e., those spread rapidly and can displace native species and dominate in new regions. Studies of the characteristics of exotic invasive plants during the invasion of different plant communities in a new region, however, have been relatively limited. Understanding these characteristics will improve our ability to predict their impacts on natural plant communities in the predicted scenarios of global change.

High growth rates and photosynthetic capacities are conducive to the invasive success of exotic plants (Mcdowell 2002). Plant growth is an important index because it represents good fitness and survival (Shipley 2006). Successful exotic invasive species tend to have higher growth rates than native species (Pyšek and Richardson 2007; Reichmann et al. 2016). The ability of plants to use light is another important index of their competitive ability and fitness (Chazdon et al. 1996). Some exotic invasive species have patterns of biomass allocation that increase light capture by allocating more biomass to leaves and less to roots in response to light stress than native species (Ewe 2005) or by allocating more resources to the light-harvesting components of photosynthesis, such as chlorophyll (Durand and Goldstein 2001). Higher photosynthetic rates contribute to higher rates of invasive plant growth and biomass accumulation relative to native species, which may enable invasive species to acclimate to new environmental conditions (Anderson and Cipollini 2013). High photosynthetic rates should be adaptive attributes in productive environments with intense competition, because they promote rapid growth and enable plants to rapidly occupy space and capture resources (Verhoeven et al. 2004). Some invasive plants, however, have a lower photosynthetic capacity (Daehler 2003). Plant photosynthesis is sensitive to diverse environmental stresses, and changes in stomatal conductance (Gs) and chlorophyll fluorescence provide information on the responses of plants to environmental stresses (Panda et al. 2008). Furthermore, the factors that influence the selection of traits associated with growth, such as soil nutrients, likely vary in communities of different plant diversity (Verhoeven et al. 2004). If rapid growth provides plants with good access to soil nutrients, then selection for increased photosynthesis should be strong in newly invaded regions, where competition for these resources is intense (Sherrard et al. 2015).

Soil nutrients are an aspect of the environment that influence the characteristics of exotic plants (Kaokniffin and Balser 2008), so the success of exotic-plant invasion is correlated with changes in soil nutrients (Liao et al. 2008), and exotic plants may alter the cycles of soil nutrients differently than native species (Weidenhamer and Callaway 2010). Soils with different nutrient availabilities have different selective actions on exotic plant characteristics (Sherrard et al. 2015). Exotic species can alter various aspects of soil nutrients, including carbon (C), nitrogen (N), and phosphorus (P) concentrations, and can change the pH (Ehrenfeld 2003). Interestingly, nutrient concentrations can increase after an invasion, especially N and P, thereby making invasion easier for other exotic plants (Weidenhamer and Callaway 2010). A meta-analysis by Liao et al. found that the presence of exotic plants was correlated with increases in N mineralization and nitrification (Liao et al. 2008). Moreover, exotic species consume proportionally more nitrate N than ammonium N (Ehrenfeld et al. 2001). Conversely, reducing N availability decreased the performance advantage of the invader over its native congener (Bleier and Jackson 2007).

Panicum virgatum (L.) is a tall, erect C_4 perennial forage grass native to North American tall-grass prairie and oak savanna. *P. virgatum* has an extensive and

deep root system, tolerates drought, adapts to a wide range of habitats, and can grow in marginal land with high biomass productivity. *P. virgatum* has thus received much attention and has been well-studied (Ali and Fahej 2012; Casler et al. 2012). *P. virgatum* can adapt to harsh environments and prevent soil erosion, so it has been tested on the Loess Plateau in China as an herbaceous grass since the early 1990s (Ma et al. 2011). As an exotic species, *P. virgatum* has the potential to influence the growth of the native plant species and the ecological balance in this region. Many studies have reported the ecophysiological, ecological, and biochemical characteristics of *P. virgatum* on the Loess Plateau, including its growth, productivity, morphology, allelopathy, seed germination, water use characteristics, and soil requirements (An et al. 2014; Huang et al. 2016; Ma et al. 2011; Shui et al. 2010; Xu et al. 2008; Zhang et al. 2011). These studies, however, have concentrated on *P. virgatum* traits after its invasion of the plateau. The changes in the characteristics of *P. virgatum* when it invaded different local plant communities in the region, and the main soil nutrient factors in these communities that affected its invasion, remain unclear. Understanding the process of invasion will improve our predictions of the impact of *P. virgatum* on the natural plant communities in the region and help to resolve important questions in ecology and conservation.

We selected three plant species with different life forms typical in this region (*Setaria viridis*, an annual grass; *Bothriochloa ischaemum*, a perennial grass; and *Artemisia sacrorum*, a perennial forb) to investigate the effects of the soils collected from various local plant communities on the photosynthesis, biomass, and biomass allocation in *P. virgatum* and to study the main soil nutrient factors. A pot culture experiment was conducted with surface soil collected from pure *P. virgatum*, *S. viridis*, *B. ischaemum*, and *A. sacrorum* communities and with a mixed soil from the pure *S. viridis*, *B. ischaemum*, and *A. sacrorum* communities. We tested the hypotheses that (1) photosynthesis, biomass, and biomass allocation in *P. virgatum* would differ significantly in the plants grown in the different soils and that (2) N would be the main soil nutrient and the different nitrogenous components would have different effects (Ali and Fahej 2012; Bleier and Jackson 2007; Casler et al. 2012; Chapin et al. 1987; Ehrenfeld et al. 2001; Liao et al. 2008; Onoda et al. 2004; Weidenhamer and Callaway 2010).

Materials and methods

Plant materials

Seeds of *P. virgatum* were collected in late autumn 2014 from a pure *P. virgatum* community in the experimental fields at the Ansai Research Station (ARS) of the Chinese Academy of Sciences (36° 51′ 30″ N, 109° 19′ 23″ E; 1068–1309 m a.s.l.), which is in the center of the semiarid, hilly-gully region of the Loess Plateau in northwestern China. The seeds were sun-dried and then stored in sealed plastic bags at a laboratory in Yangling, Shaanxi Province, under natural dry conditions. The rates of seed germination on moist filter paper in Petri dishes at 25 °C were >90% before the experiment.

Growth conditions

The pot culture experiment was conducted at the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau in Yangling (34° 12′ N, 108° 7′ E; 530 m a.s.l.). The mean annual temperature was 12.9 °C with average temperatures of −2 and 26.7 °C in January and July, respectively. The average annual precipitation was 650 mm. This region has a seasonal semiarid climate with a frost-free period >200 days. The loessial soils for our experiment were collected from the 0–20-cm soil layers of a pure *P. virgatum* community (PS treatment), a pure *S. viridis* community (SS treatment), a pure *B. ischaemum* community (BS treatment), and a pure *A. sacrorum* community (AS treatment) at ARS. A fifth treatment used the soils from the pure *S. viridis*, *B. ischaemum*, and *A. sacrorum* communities mixed in a ratio of 1:1:1 (MS treatment). All soils were air-dried and passed through a 2-mm mesh. The gravimetric water contents of the soils at field capacity and the wilting point were 20.0 and 4.0%, respectively.

Pot experiment

The pot culture experiment began in late April 2015. Each of the five soil treatments, i.e., PS, SS, BS, AS, and MS, consisted of ten replicate plastic pots (20 cm high, 15 cm in diameter) with the same soil weight, for a total of 50 pots, all used to grow *P. virgatum*. The soil was well watered before sowing to ensure seedling establishment. Seeds of *P. virgatum* were sown into holes, and the soil-moisture content was maintained at >80% field capacity during seedling establishment. Excess

grass plants were manually removed to limit plants to one per pot of six plants, based on field studies at ARS of *P. virgatum* growth density. The pots were weighed daily to monitor and control the water status of the plants, and soil-moisture content was maintained at the desired level.

Measurements

Five pots with homogeneous and vigorous plants were selected in late July 2015 from each soil treatment for measurements on growing leaves, for a total of 25 pots. Three leaves from different plants in each pot were selected and marked for the measurements. Photosynthesis, single-photon avalanche diode (SPAD) readings, and chlorophyll fluorescence were measured on the same day in the morning, afternoon, and evening, respectively.

Photosynthesis

Net photosynthetic rate, Gs, transpiration rate (Tr), and intercellular CO_2 concentration (Ci) were measured with an open gas-exchange system (LI-6400XT, Li-Cor Inc., Lincoln, USA) between 08:30 and 11:30 in the morning. A saturating photon flux density was set at 1200 μmol m^{-2} s^{-1} during the measurements. The conditions in the leaf chamber approximated the growing conditions and were maintained at 25 °C, a relative humidity of approximately 30%, and an ambient CO_2 concentration of 380–400 μmol mol^{-1}. The leaves were placed in the leaf chamber for 5 min or more before the measurements to obtain a photosynthetic steady state. Measurements were recorded in triplicate from the three previously marked leaves.

SPAD readings

Single-photon avalanche diode (SPAD) values (SPAD-502, Konica Minolta Sensing Inc., Osaka, Japan) were recorded near the midpoints of the leaves of all marked plants after the measurements of photosynthesis.

Chlorophyll fluorescence

Chlorophyll fluorescence was measured using a leaf chamber fluorometer (LI-6400XT, Li-Cor Inc., Lincoln, USA) with the leaves previously used to measure photosynthesis (following a dark adaptation period of 2 h).

Various parameters of chlorophyll fluorescence were calculated using the fluorometer's software. Maximum F_m and minimum F_o fluorescences were obtained, and the yield of variable fluorescence F_v was calculated as $F_m - F_o$. Chlorophyll fluorescence was calculated as F_v/F_m (the maximum photochemical efficiency, which represents the ratio between variable and maximum fluorescences). Each measurement was recorded in triplicate, consistent with the measurements of photosynthesis.

Sampling

Each plant that had been selected for the measurements was harvested in early September 2015 and separated into leaves, roots, and stems; every part of the six plants was combined into one sample for each pot. All plant samples were dried at 65 °C to constant weights. The root to total biomass ratio (g root/g total plant), stem to total biomass ratio (g stem/g total plant), and leaf to total biomass ratio (g leaf/g total plant) were calculated. All soil samples were air-dried after removing the gravel, and coarse fragments were homogenized and sieved to 0.25 and 1 mm prior to analysis.

Laboratory analysis

Soil organic-C (SOC) concentration was determined using H_2SO_4–$K_2Cr_2O_7$ oxidation, soil total N (TN) concentration was measured using the Kjeldahl method (Bremner and Mulvaney 1982). Soil total P (TP) concentration was determined colorimetrically after digestion with H_2SO_4 and $HClO_4$, and available P concentration was measured by the Olsen method (Olsen et al. 1982). Soil ammonium N (AN) and nitrate N (NN) were extracted with 2 M KCl and quantified colorimetrically with an Alpkem autoanalyzer (OI Analytical, College Station, USA). Water-soluble organic C (W-SOC) and TN (W-TN) were extracted using deionized water. Soil water-soluble organic N (W-SON) concentration was calculated as W-TN concentration (soil water-soluble NN (W-NN) concentration + soil water-soluble AN (W-AN) concentration) (Jones and Willett 2006). Total water-soluble P was extracted using deionized water and quantified colorimetrically (Jarosch 2012). Soil pH was determined by an automatic acid-base titrator (Metrohm 702, Swiss) in 1:2.5 soil to water suspensions.

Statistical analysis

The data for all treatments were analyzed using analyses of variance (ANOVAs) followed by least significant difference tests. A redundancy analysis (RDA), a direct gradient analysis, was performed using CANOCO 5.0 (Biometris, Wageningen, The Netherlands). All ANOVAs were tested for significance at $P < 0.05$ using SPSS 20.0 (SPSS Inc., Chicago, USA), structural equation models (SEMs) were analyzed using the AMOS SPSS expansion pack, and graphical analyses were performed using SigmaPlot 12.5 (Systat Software, San Jose, CA).

Results

Photosynthesis

Pn, Gs, and Tr in *P. virgatum* differed significantly among the treatments, but Ci did not (Fig. 1a–d). Pn and Gs were highest in PS and were significantly higher in PS than AS and MS, respectively, and Pn and Gs were significantly higher in AS and MS than SS and BS (Fig. 1a, b). Tr was highest in AS and lowest in SS (Fig. 1c).

F_o, F_m, F_v/F_m, and the SPAD values clearly varied among the treatments (Fig. 2a–d). F_o and F_m were highest in SS where they were significantly higher than in AS and MS. F_o and F_m were significantly higher in MS than BS and PS (Fig. 2a, b). F_v/F_m was highest in PS and 4% higher ($P < 0.05$) in PS than BS (Fig. 2c). SPAD values were lowest in AS and BS, which were significantly lower (8–9%) than in SS and PS (Fig. 2d).

Biomasses and their allocation

Leaf, stem, root, and total biomasses varied considerably among the treatments and were highest in PS at 199.13, 196.25, 542.25, and 937.63 g m^{-2}, respectively, and were lower in BS than PS by 123, 214, 148, and 153%, respectively (Fig. 3a–d). Leaf biomass in SS did not differ significantly from those in PS and MS (Fig. 3a). Stem biomass had the same pattern of differences as leaf biomass; stem biomass was similar in SS and PS (Fig. 3b). In contrast, root biomass did not differ significantly between AS and BS (Fig. 3c). Total biomass did not differ significantly between SS and MS, consistent with leaf biomass (Fig. 3d).

The leaf to total biomass ratio was highest in AS and lowest in PS (Fig. 4a). The stem to total biomass ratio was highest in SS and lowest in BS (Fig. 4b). The root to total biomass ratio was highest in MS and lowest in SS, in contrast to the stem to total biomass ratio (Fig. 4c).

Effects of environmental factors on plant functional traits

The constrained RDA indicated that environmental factors affected the functional traits of *P. virgatum* (Fig. 5). The total variation was 19.22, and explanatory variables accounted for 85.6% of the variance. The first two axes explained 78.5% of the total variance, 68.2% for the first axis and 10.3% for the second axis. Of the 13 environmental factors, W-NN concentration was the most significant variable affecting the functional traits and accounted for 47.6% ($P = 0.002$) of the total variance. W-AN and TN concentrations were the next most significant environmental variables, accounting for 15.0% ($P = 0.002$) and 8.4% ($P = 0.004$) of the total variance, respectively. W-NN, W-AN, and TN concentrations were therefore important factors affecting the functional traits of *P. virgatum*.

Path analyses

The final SEM based on all indices adequately fitted the data describing the effects of soil nutrients on plant functional traits ($\chi^2 = 5.209$, $P = 0.517$; standardized path coefficients are shown in Fig. 6). The final model accounted for 43% of the variation in the SPAD values, 27% of the variation in Pn, 56% of the variation in leaf biomass, 69% of the variation in stem biomass, and 52% of the variation in root biomass. W-NN concentration was negatively correlated with the SPAD values ($P < 0.001$), Pn ($P < 0.01$), and leaf and stem biomasses ($P < 0.001$). The SPAD values ($P < 0.01$) and Pn ($P < 0.001$) were positively correlated with root biomass ($P < 0.001$). Leaf and stem biomasses ($r = 0.91$, $P < 0.001$), leaf and root biomasses ($r = 0.53$, $I < 0.05$), and stem and root biomasses ($r = 0.48$, $P < 0.05$) were strong positively correlated.
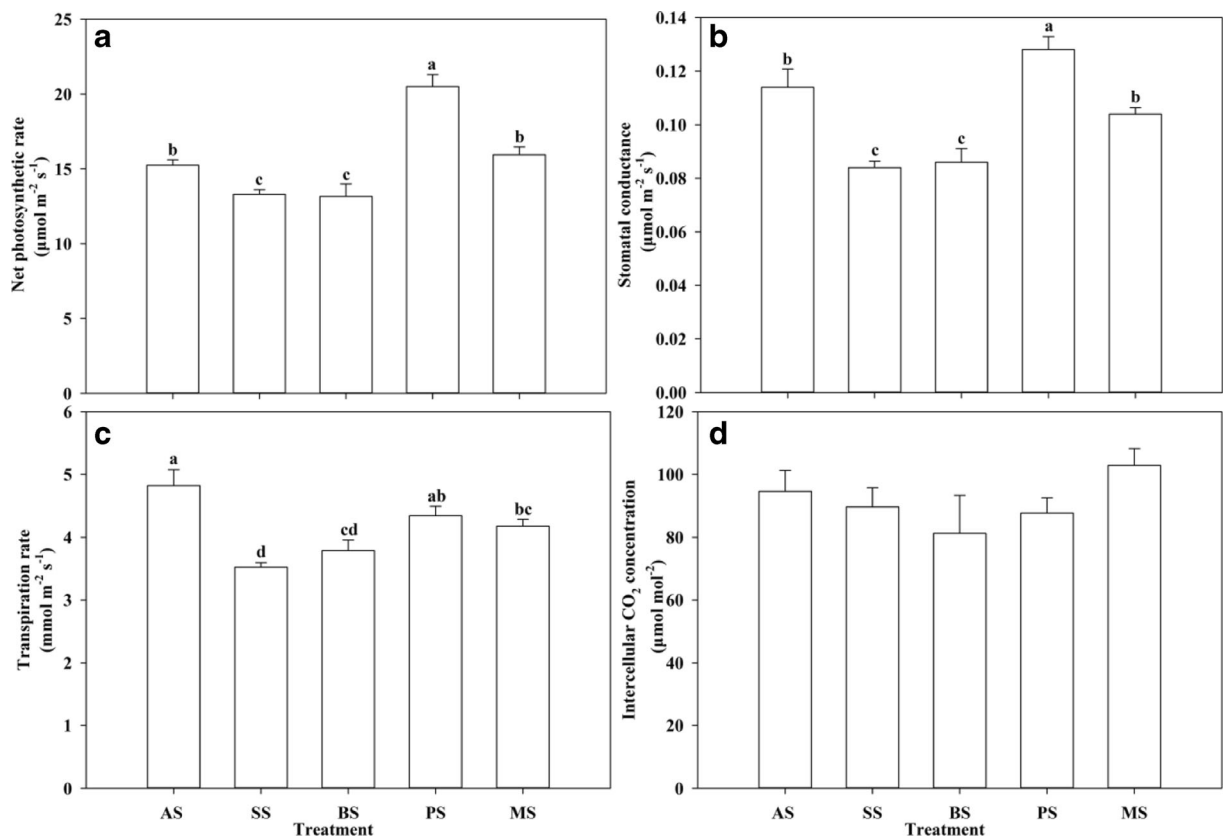
Fig. 1 Effects of soil treatments on net photosynthetic rate, stomatal conductance, transpiration rate, and intercellular CO_2 concentration in *P. virgatum*. *Error bars* are standard errors ($n = 5$). *Different letters above the bars* indicate significant differences at $P < 0.05$

Discussion

Effects of soil treatments on Pn and Gs

Photosynthesis is an important metabolic process in plants and is sensitive to changes in the external environment. The determination and analysis of plant photosynthetic indices can identify differences in the physiological characteristics of plants between habitats (Pierangelini et al. 2014). As an important indicator of plant photosynthesis, Gs indicates the degree of stomatal opening, which can affect photosynthesis, respiration, and transpiration for adapting to different environmental conditions (Niu et al. 2014). Pn, which is due to coordinated investments in the water-transport capacity needed to support a high rate of Gs, was highest in our study in PS, where it was significantly higher than in AS, SS, BS, and MS. The differences in Gs were consistent with those in Pn, which supported our hypothesis

that photosynthesis in *P. virgatum* would differ significantly among the treatments. Differences in Pn and Gs are often used as measures of responses to environmental stress and of plant resistance under duress by presenting low rates of growth and reproduction, respectively (Bussotti et al. 2015). Pn and Gs were lower in AS, SS, BS, and MS than PS, suggesting that *P. virgatum* growth would be suppressed in communities with these soil environments. Pn and Gs, however, were significantly higher in AS and MS than SS and BS, suggesting that the environmental stresses provided by the soil would differ among these plant communities, consistent with our first hypothesis.

Both the constrained RDA and the path analysis indicated that W-NN concentration was the main soil nutrient factor affecting Pn and Gs in *P. virgatum* (Figs. 5 and 6). N is an important limiting resource for plant growth in nature, so plants allocate more N to photosynthesis for faster growth, and small changes in
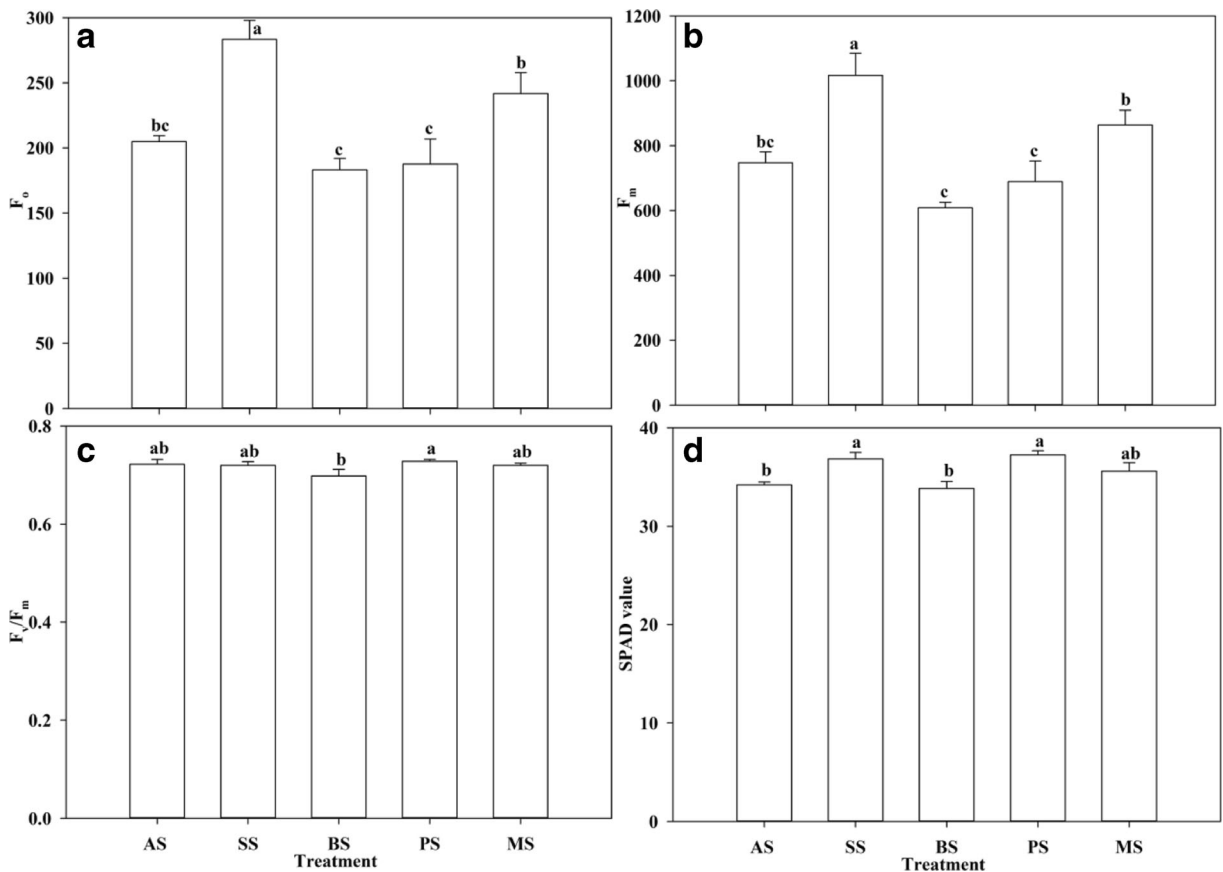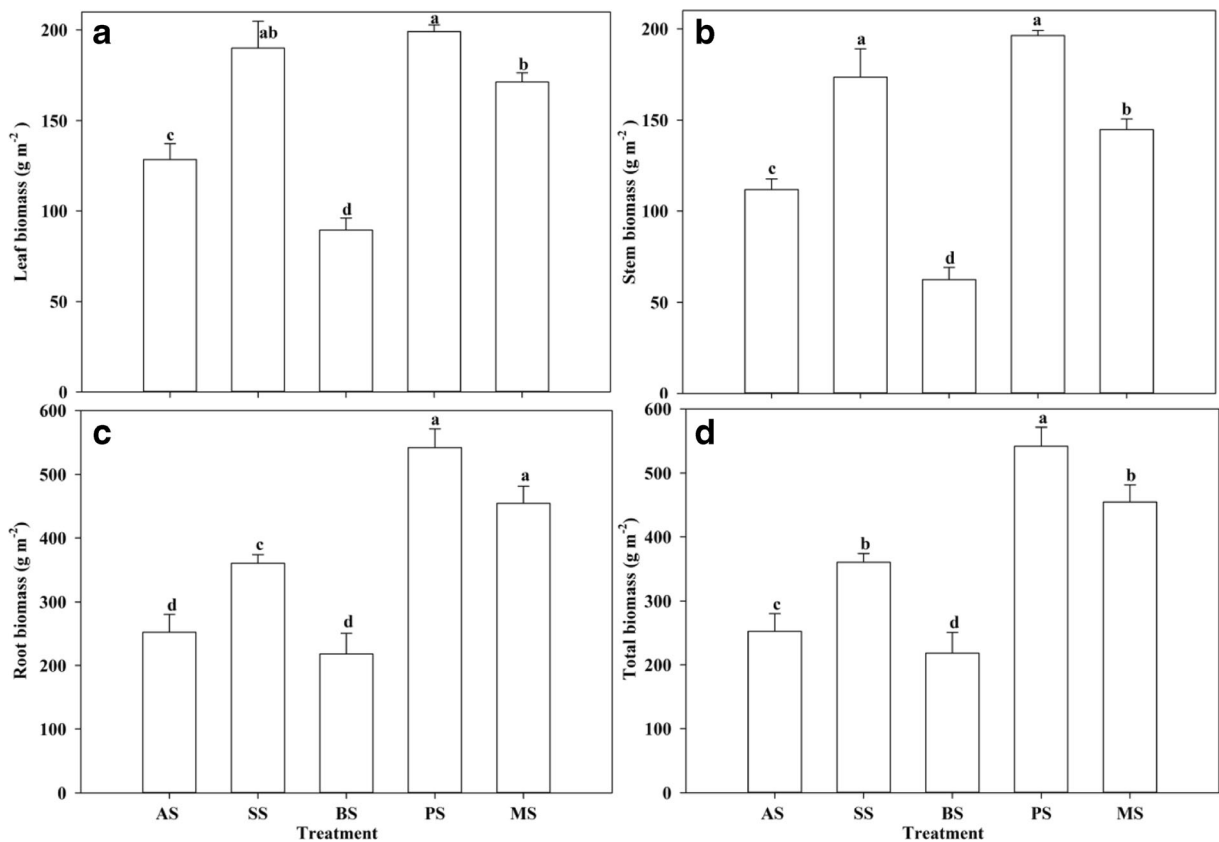
Fig. 2 Effects of soil treatments on F_o, F_m, F_v/F_m, and SPAD values in *P. virgatum*. *Error bars* are standard errors ($n = 5$). *Different letters above the bars* indicate significant differences at $P < 0.05$

N allocation can greatly influence Pn and therefore plant performance (Onoda et al. 2004). Pn and Gs are strongly correlated with soil nitrate N, and a deficiency of nitrate N can induce stomatal closure and decrease the rate of leaf growth; N deficiency can thus severely decrease root hydraulic conductivity, which may decrease Gs (Bouranis et al. 2014). Moreover, N deficiency depresses Pn by suppressing the activity of enzymes of the Calvin cycle, particularly ribulose-1,5-bisphate carboxylase/oxygenase (Seemann 1989). N is also mostly absorbed by plants as W-NN (Miller et al. 2008; Näsholm et al. 2009), so the differences in the W-NN concentrations of the test soils likely directly affected Pn and Gs in *P. virgatum*.

Effects of soil treatments on chlorophyll fluorescence and the SPAD value

Measurements of photosynthesis (chlorophyll fluorescence and/or SPAD values) can indicate plant stress,

because metabolism is affected under stress (Chai et al. 2016). Chlorophyll fluorescence measures the ability of plants to convert photosynthetic energy into biomass; it is an excellent indicator of environmental stress and a sensitive measure of stress-induced damage to the maximum quantum yield of photosystem II (Maxwell and Johnson 2000). F_o is an efficient tool for rapidly assessing the impairment of the photosynthetic apparatus (Percival and Sheriffs 2002), so F_o is a reliable index of photo-inhibition and structural damage to the photosystem II reaction center complex (Maxwell and Johnson 2000). F_o in our study was highest in SS, indicating that the photochemical efficiency was lower in this soil treatment than in BS and PS. The maximum quantum yield of F_v/F_m derived from the parameters of chlorophyll fluorescence is a sensitive indicator of plant photosynthetic performance; F_v/F_m usually decreases when plants are exposed to environmental stress (Björkman and Demmig 1987; Roiloa and Retuerto 2006). F_v/F_m for species under appropriate conditions

Fig. 3 Effects of soil treatments on plant biomass in *P. virgatum*. *Error bars* are standard errors (*n* = 5). *Different letters above the bars* indicate significant differences at *P* < 0.05

normally ranges between 0.75 and 0.85 (Björkman and Demmig 1987; Butler and Kitajima 1975), which is slightly higher than the range of 0.70 to 0.73 for *P. virgatum* in our study. Our F_v/F_m values suggested that the growth of *P. virgatum* in the three plant communities was suppressed by environmental stress provided by the soil. F_v/F_m was significantly higher in PS than BS, suggesting that the effect of stress for *P. virgatum* would be greater in a *B. ischaemum* community than in the other plant communities.

The differences in the SPAD values were consistent with those for F_v/F_m. The SPAD values of 33.8–37.2 were <40, which may have been due to the impairment of photosynthesis in *P. virgatum* (Netto et al. 2005) in the soils of the other three plant communities. Both F_v/F_m and the SPAD values suggest that the soil environment would inhibit the growth of *P. virgatum* during its invasion of these plant communities. The environmental stress provided by the soil was stronger for the soils from the *B. ischaemum* and *A. sacrorum* communities

than the *S. viridis* community and the mixed soil. F_v/F_m and the SPAD values also supported our hypothesis that the soil treatments would have significant but variable impacts on photosynthesis in *P. virgatum*.

The constrained RDA and the path analysis indicated that W-NN concentration was the main soil nutrient factor affecting F_v/F_m and the SPAD values (Figs. 5 and 6). The path analyses indicated that the SPAD value was significantly correlated with W-NN concentration (Fig. 6). The amount of N in the leaves was strongly correlated with F_v/F_m and the SPAD values. Leaf chlorophyll and N concentrations are likely closely associated, because the majority of leaf N is contained in chlorophyll molecules (Peterson et al. 1993). The N in the leaves of *P. virgatum* in our study likely came mainly from the soil, because soil N is mostly absorbed by plants as W-NN (Miller et al. 2008; Näsholm et al. 2009). The W-NN concentration of the soil would thus have a close relationship with leaf F_v/F_m and SPAD values.
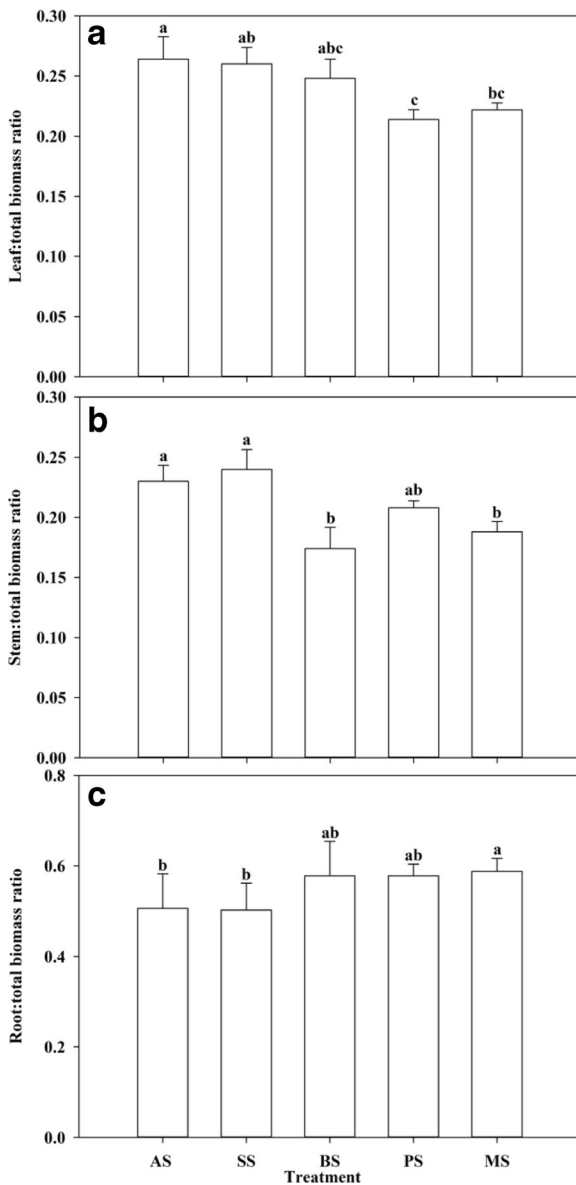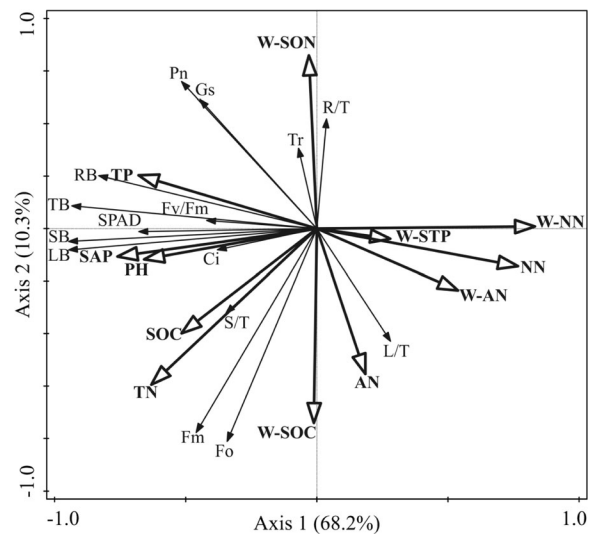
Fig. 4 Effects of soil treatments on plant biomass allocation in *P. virgatum*. *Error bars* are standard errors (*n* = 5). *Different letters above the bars* indicate significant differences at *P* < 0.05

Fig. 5 Bidimensional graph for the redundancy analysis indicating the relationships between plant functional traits and soil nutrient variables. *LB* leaf biomass, *SB* stem biomass, *RB* root biomass, *TB* total biomass, *L/T* leaf to total biomass, *S/T* stem to total biomass, *R/T* root to total biomass, *Pn* net photosynthetic rate, *Gs* stomatal conductance, *Tr* transpiration rate, *Ci* intercellular CO_2 concentration, *SOC* soil organic-carbon concentration, *TN* total-nitrogen concentration, *TP* soil total-phosphorus concentration, *SAP* soil available-phosphorus concentration, *NN* soil nitrate-nitrogen concentration, *AN* soil ammonium-nitrogen concentration, *W-SOC* soil water-soluble organic-carbon concentration, *W-NN* soil water-soluble nitrate-nitrogen concentration, *W-AN* soil water-soluble ammonium-nitrogen concentration, *W-SON* soil water-soluble organic-nitrogen concentration, *W-STP* soil water-soluble total-phosphorus concentration

Effects of soil treatments on biomasses and their allocation

Total biomass in *P. virgatum* was highest in PS and significantly higher in PS than SS (29.5%) and MS (21.7%). Total biomass, however, was significantly higher in SS and MS (47.0 and 56.5%, respectively) than AS and was significantly higher in AS (33.1%) than BS. These results indicated that the growth of *P. virgatum* in the AS, SS, BS, and MS soil treatments

was affected by environmental stress provided by the soil, and the amount of stress varied significantly among the soil treatments. These findings were consistent with our hypothesis that the soil treatments would have a variable influence on *P. virgatum* biomass. The results also suggested that *P. virgatum* would be more likely to invade *S. viridis* or mixed communities than *B. ischaemum* or *A. sacrorum* communities. This result was supported by the measurements of photosynthesis in *P. virgatum*.

Both the constrained RDA and the path analysis indicated that W-NN concentration was the main soil nutrient factor affecting the biomass in *P. virgatum* (Figs. 5 and 6). Plants require more N than the other nutrients (Chapin et al. 1987), which can often limit plant growth in natural ecosystems because of N's central function in the photosynthetic apparatus and high mobility in the soil (Bowman et al. 1993). The constrained RDA and the path analysis indicated that W-NN concentration had a large influence on

Fig. 6 Results of the structural equation models of W-NN concentration on plant Pn, SPAD value, and biomass. *Numbers on the arrows* are standardized path coefficients (equivalent to correlation coefficients). *Circles* indicate error terms (e1–e5). *Percentages near the endogenous variables* indicate the variance explained by the model
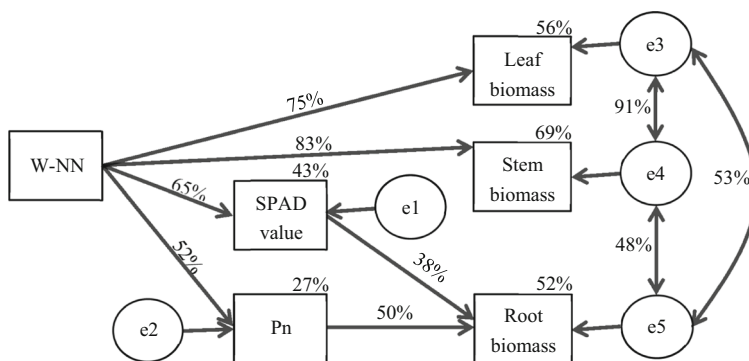
photosynthesis and root biomass in *P. virgatum* (Figs. 5 and 6). The uptake of N by plant roots requires pathways in these tissues to assimilate and transport this nutrient; plants can then assimilate the N in both photosynthetic and non-photosynthetic tissues (Mcallister et al. 2012). Kurai et al. found that plants under N-limiting conditions had high levels of N in their roots, with high root biomasses and high rates of photosynthesis (Kurai et al. 2011). Soil N could therefore likely influence root biomass in *P. virgatum* based on the effect on photosynthesis in leaves. *P. virgatum* biomass has been strongly correlated with the amount of N additives (Casler et al. 2012). Our path analyses found that W-NN concentration had a significant effect on leaf and stem biomasses in *P. virgatum*, and leaf, stem, and root biomasses were significantly positively correlated. The W-NN concentration of the soil thus had a significant effect on *P. virgatum* biomass (Figs. 5 and 6). Ehrenfeld et al. also reported that exotic plants had a higher demand for soil nitrate N (Ehrenfeld et al. 2001). W-NN would thus likely be the main nutrient for *P. virgatum* in invaded plant communities, in agreement with our hypothesis.

Biomass allocation is the distribution of dry matter accumulated within a period of time to each organ of the plant body and is usually used to calculate the proportion of biomass in each part of the plant (Glynn et al. 2003). The root to shoot ratio is used to characterize changes in the pattern of distribution of photosynthetic products and ignores the functions of leaves and stems in an ecosystem. We thus used root, stem, and leaf biomass ratios to indicate the distribution of the photosynthetic products to the various tissues, accounting for the proportion of total distribution (Werf and Nagel 1996). Strategies of biomass allocation by plants may directly affect the ability to adapt to the environment (Johnson et al. 2008). Both the leaf to total and stem to total biomass ratios in *P. virgatum* were significantly

higher in AS and SS than MS, but the root to total biomass ratio was significantly lower in AS and SS than MS. These differences in biomass allocation among the soil treatments suggested that biomass allocation in *P. virgatum* would differ in different invaded plant communities in a new region, supporting our hypothesis that biomass allocation would differ among the soil treatments.

Lower amounts of soil N would increase the allocation of photosynthetic products to the root system, a sufficient amount of soil N would increase the distribution of photosynthetic products to leaves, and the ability to change the pattern of distribution would depend on species and life habit (annual or perennial) (Glynn et al. 2003; Müller et al. 2000). The constrained RDAs indicated that TN concentration was correlated negatively with the root to total biomass ratio and positively with the leaf to total biomass ratio, and leaf to total biomass was positively correlated with W-NN concentration (Figs. 5 and 6). These results suggested that TN and W-NN concentrations would be the main soil nutrient factors influencing the allocation of biomass in *P. virgatum* in invaded native plant communities, consistent with our hypothesis that N would be the main soil nutrient and the different nitrogenous components had different effects.

Conclusions

Photosynthesis, biomass, and biomass allocation differed significantly but variably in *P. virgatum* among the soil treatments, suggesting that environmental stress provided by the soil would differentially affect the plant's invasive success in different plant communities on the Loess Plateau in China. The significant differences in photosynthesis and biomass among the soil

treatments suggested that *P. virgatum* would have different adaptive strategies in different plant communities in this region. *P. virgatum* is more likely to invade *S. viridis* and mixed communities than *B. ischaemum* or *A. sacrorum* communities. Soil N, especially W-NN concentration, would likely be the main soil nutrient factor affecting the invasive success of *P. virgatum* on the plateau. These findings will help us to understand the response of *P. virgatum* to the variations of soil nutrient factors in plant communities, thereby improving our ability to predict the impact of invasion on natural plant communities in this region. The findings will also help us to understand the ecological problems caused by exotic invasions. Such understanding would enable us to control the occurrence of invasion by regulating the local soil nutrients. The present study was a control experiment of *P. virgatum* growth only, although the findings could represent the changes to other *P. virgatum* characteristics to some extent. The interactions between *P. virgatum* and native plant communities invaded by *P. virgatum*, however, should be further investigated, especially in the field.

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