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Seedling Biomass Partition and Water Use Efficiency of Switchgrass and Milkvetch in Monocultures and Mixtures in Response to Various Water Availabilities

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Abstract Seedling biomass and allocation, transpiration water use efficiency (TWUE), and species competition between switchgrass (*Panicum virgatum* L.) and milkvetch (*Astragalus adsurgens* Pall.) were investigated in a pot-cultivated experiment under different levels of water availability. The experiment was conducted using a simple replacement design in which switchgrass and milkvetch were grown in growth chamber with ten seedlings per pot, in three combinations of the two species (0:10, 5:5 and 10:0). Five water treatments included sufficient water supply (HW), gradual soil drying from HW (DHW), moderate water stress (LW), gradual soil drying from LW (DLW), and re-establishment of LW conditions after 12 days of drying from LW (RLW). Water treatments were applied over a 15-day period. Biomass production and its partitioning, and TWUE were determined at the end of the experiment. Species competitive indices (competitive ratio (CR), aggressivity (A) and relative yield total (RYT)) were calculated from the biomass dry weight data for shoots, roots and total biomass. Water stress significantly reduced seedling biomass production but increased root:shoot ratios in both monocultures and mixtures. In the RLW treatment, only switchgrass monocultures displayed compensatory biomass production and TWUE, while both species demonstrated compensatory growth in the mixture. Switchgrass was the dominant species and much more aggressive than milkvetch in the LW treatment, while in the other four treatments milkvetch was the dominant species as measured by the positive value of aggressivity and higher values of CR. The total biomass RYT values of the two species were higher than 1.0, indicating some degree of resource complimentarity. In the two-species mixture, although the biomass production was lower than that of milkvetch in the monoculture, there was better TWUE, especially under low and fluctuating water availability.

Keywords Milkvetch · Seedling stage · Species competition · Switchgrass · Water stress

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Introduction

Water availability is a major factor limiting plant growth and production in the semiarid Loess Plateau region of northwestern China. Annual precipitation is relatively low (300–500 mm) and seasonal distribution is highly variable (June–September accounts for about 60–80% of the total precipitation). The status of field soil water in the region can be collectively described as low and highly variable (Shan and others 2000a, 2000b). The establishment of introduced grassland species is difficult because of the adverse environmental conditions (Li and others 1999). Furthermore, introducing grass monocultures or simple species mixtures can cause problems because such homogenization of ecosystems across the landscape worsens the effects of ecosystem fragmentation and causes convergent ecosystem properties, not only in species assemblage but also in soil characteristics, nutrient and water cycles, and the dampening of random events and perturbations (Western 2001). Approaches to solve these problems include introducing appropriate grass varieties, selecting and breeding improved cultivars, and determining suitable combinations of grassland species that have greater adaptability to such harsh environments (Xu and others 2006b).

Switchgrass (*Panicum virgatum* L.) is a perennial warm-season grass native to Central and North America, and can be used as a forage or hay crop and/or for soil and water conservation (Sanderson and others 1999; Ichizen and others 2005). Much attention has been paid to switchgrass as a potential bioenergy crop because of its ability to produce high biomass yields under a range of different conditions and because of its economical and ecological advantages when compared with other bioenergy crops (Vogel and others 2009; Pimentel and Patzek 2005; Nelson and others 2006; Monti and others 2007; Varvela and others 2008; Monti and others 2008). As an introduced grass species, its ecological and biological characteristics are well-suited to the low and hilly land of the hilly-gully region on the Loess Plateau in China (Li and others 1999; Xu and others 2007). Milkvetch (*Astragalus adsurgens* Pall.) is a perennial legume that has been used in China as a palatable forage crop and it is widely cultivated in diverse environments in arid and semiarid areas of northern China. In addition to its use as a forage crop and for soil and water conservation, it is also used as an energy crop because of its high eco-adaptability and biomass production (Shan and Chen 1993).

The significance of water stress in plant physiology and growth has been recognized for decades, particularly for the growth and development of mature tissue, but much less attention has been paid to water stress during seedling development (Frank and Bauer 1991; Bi and Turvey 1994). Yet, seedling survival in water stressed conditions is one of the major limitations to crop establishment in many habitats, especially in rain-fed areas (Olssen and others 1996). In the semiarid hilly-gully region on the Loess Plateau, grassland species, especially the gramineous ones, are generally more difficult to establish and survival rates can be reduced by severe drought occurring during the vegetative stage (Shan and Chen 1993). This leads to subsequent serious yield reduction. Since switchgrass and milkvetch are often planted in marginal land with minimal fertilizer input and low rainfall, the early growth of these species should be evaluated under water stressed conditions. However, few studies on the growth and water use characteristics of these two species in the seedling stage have been reported. Therefore, the objectives of this study were: (1) to characterize the differences in root and shoot responses of the two grassland species in the seedling stage under different soil water regimes; and (2) to investigate competition between the seedlings of the two species when grown together. These characterizations will enrich our knowledge and should have applications when predicting their field performance in natural environments, and also improve the potential for seedling plantation in the region.

Materials and Methods

Plant Materials

Switchgrass (cultivar = Alamo) and milkvetch (cultivar = Super early) were used in a test of seedling growth and competition in response to drought. Seeds of the two species were obtained from the experimental fields at Ansai Research Station (ARS) of the Chinese Academy of Science (CAS). Seeds were stored in paper envelopes under ambient conditions for two years. For all seed batches, seed germination rates were >85% within 7 days as determined by using a Petri dish method at 25°C when the experiment was started.

Growing Conditions

The experiment was conducted in the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, CAS, which was about 300 km from ARS. A sandy loam soil was collected from the upper 20 cm of a cultivated field at ARS. The soil was air-dried, passed through a 2-mm mesh, and mixed with 0.1 g pure nitrogen as urea, and 0.1 g P_2O_5 as KH_2PO_4 per kg dry soil. The 2.5 kg air-dried soil was packed in plastic pots (16 cm × 17 cm × 10.6 cm; height × upper inner diameter × lower inner diameter) with a bulk density of 1.2 g cm^{-3} and 55% porosity. Soil gravimetric moisture content (SGMC) at field capacity and wilting point was 18.4 and 3.8%, respectively.

All seeds were soaked in deionized water for 24 h, and 20 seeds from each species to be planted as a monoculture and 10 seeds from both species to be planted in the mixtures were sown in the plastic pots. Each pot contained a plastic pipe adjacent to the inner wall to supply water to the base of the pot. The top of the soil in each pot was covered with 15 g perlite, about 1 cm thick, to reduce evaporation from the soil surface. The pots were placed in a growth chamber (PGV36, Cmp3244, Conviron8601, Canada) for germination. To ensure seedling emergence and avoid seedling death induced by high temperatures and low surface soil water contents due to evaporation, crop straw or shade netting are commonly used to ensure grass species seedling establishment in the region by reducing sunlight intensity and/or increasing relative humidity (RH) around the plants (Shan and Chen 1993). Thus, during the seedling establishment period we used a photosynthetic photon flux density (PPFD) of about 250 μmol m^{-2} s^{-1} 1 m above the grass canopy level and a temperature inside the chamber of 22°C (7:30–19:30 h) and 14°C (19:30–7:30 h). When the water treatment commenced, the light was adjusted to 375 μmol m^{-2} s^{-1} and the temperature to 26°C/18°C (day/night). RH inside the chamber was controlled at 75 ± 5% during the whole experiment.

Experimental Design

During the 40-day seedling establishment, the SGMC was maintained at about 80 ± 5% of FC in all pots by adding sufficient water at 18:00 h everyday through the plastic pipes. Plants were thinned twice to obtain ten similar healthy seedlings in each pot before water treatments were imposed. Three cultures were investigated, a switchgrass monoculture, a two-species mixture, and a milkvetch monoculture in which combinations of the two species were 0:10, 5:5 and 10:0, respectively, and were each grown in 50 pots. Switchgrass seedling growth stages were used as the reference point by which to begin the water treatments because the switchgrass seedlings grew more slowly than the milkvetch seedlings. Thus, when the switchgrass plants were at about the 3-leaf-stage, the SGMC of 30 pots of each culture was adjusted to establish a low water content treatment (LW) that was 50 ± 5% FC (i.e. SGMC of 9.2%). This was achieved by allowing them to dry to that moisture content and then maintaining it by daily watering as described above. The remaining 20 pots of each culture continued to be watered daily to maintain the standard high water treatment (HW), i.e. at 80 ± 5% FC. After 12 days, 10 pots from each culture in both the HW and the LW treatments were selected to dry gradually for 15 days without watering (the drought period, DHW and DLW, respectively). An additional 10 pots from each culture in the LW treatment were similarly dried for 12 days without watering and then the water treatment level (LW) was re-established for three days (RLW). The entire water-treatment experiment lasted 27 days, and is depicted in Fig. 1.

Transpiration

Evapo-transpiration was assessed by weighing the pots daily at 17:00 h and determining weight loss. For each watering treatment three pots without plants were used to estimate evaporation from the surface, and watered with the same frequency as the pots with plants.

Shoot and Root Biomass

Plant biomass was determined for each of the three cultures from all of the water treatments at the end of the experiment. Roots were separated from the soil by washing. For the mixture, the roots of switchgrass and milkvetch were carefully separated by hand in the water. Shoots and roots were then divided at the base of the stem, and the dry weights were determined after oven-drying at 70°C for 48 h. The root:shoot ratio was calculated as the ratio of root to shoot dry biomass.

Competition Indices

There are many indicators of species interaction used in intercropping research (Connolly and others 2001; Ghosh 2004). Weigelt and Jolliffe (2003) summarized and divided the indices into three categories by which to quantify the intensity of competition, the effect of competition and the outcome of competition. Here, two indices for studying the intensity of competition (i.e. competitive ratio and aggressivity) and two indices for analyzing competition effects (i.e.

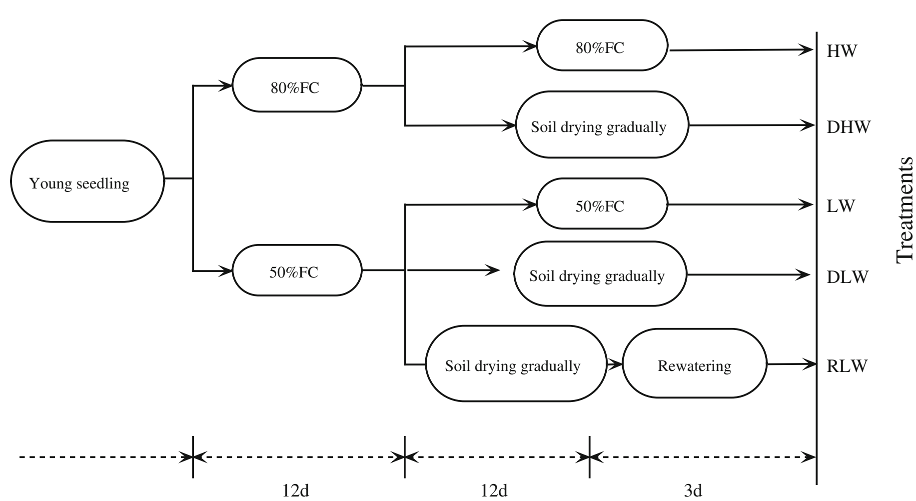

Fig. 1 Scheme of water treatments in the experiment

relative yield and relative yield total) were introduced and applied to the two-species mixture in this study.

The Competitive Ratio (CR) is proposed as a measure of intercrop competition and could be used to compare the competitive ability of different plants, to measure competitive changes within a given combination, and to identify which plant characteristics are associated with competitive ability (Willey and Rao 1980). In this study, CR was calculated as:

$$\mathrm{CRab} = \frac{Yab/Yaa}{Yba/Ybb} \tag{1}$$

where Yaa and Ybb denote the shoot, root or total biomass production of switchgrass and milkvetch per pot of the monocultures and Yab and Yba are their corresponding yields in a mixture of the two species, which were determined at the end of the experiment.

Aggressivity (A) is another index that represents how much the relative yield increase in crop 'a' is greater than that of crop 'b' in a mixture of crops 'a' and 'b' (Ghosh 2004). It measures the interspecies competition in intercropping by relating the yield changes of the two component plants (Willey and Rao 1980). In this article, we employed the aggressivity concept to evaluate the difference between the extent to which intercropped species 'a' (switchgrass) and 'b' (milkvetch) vary from their respective monocultures:

$$Aab = \frac{Yab}{Yaa} - \frac{Yba}{Ybb} \tag{2}$$

in which Yab, Yba, Yaa, and Ybb are as defined for Eq. 1. The aggressivity, Aab, is regarded as the difference between the relative change of yield of switchgrass in the mixture and the corresponding value for milkvetch. If $Aab = 0$, both species are equally competitive, and if Aab is positive then switchgrass is the dominant species while, if Aab is negative, switchgrass is dominated by milkvetch.

Relative Yield Total (RYT) gives an accurate assessment of the greater biological efficiency of the intercropping situation. A RYT value of 1.0 implies that the two species are making demands on the same limiting resources of the environment. Values of RYT >1.0 suggest that, although the species may still be competing for the same resources, they also make demands on different resources. Values of RYT <1.0 indicate a mutual antagonism (Bi and Turvey 1994; Keddy and others 1994). In this study, RYT was calculated as follows:

$$\mathrm{RYT} = (\mathrm{RYa} + \mathrm{RYb}) = \left\{\left(\frac{Yab}{Yaa}\right) + \left(\frac{Yba}{Ybb}\right)\right\} \tag{3}$$

in which RYa and RYb are the partial RYT values of switchgrass and milkvetch, respectively, and Yab, Yba, Yaa, and Ybb are as defined for Eq. 1. RYT values >1.0 also indicate that the mixtures are advantageous for biomass production compared to monocultures of the component species.

Statistical Analysis

Pots were arranged in five blocks according to water treatments and cultures were completely randomized in each block. There were ten replicates, each represented by an individual pot, for each culture and water treatment combination. The data obtained were analyzed by standard ANOVA using SPSS 11.0 and Excel 2003. Differences were considered significant if $P < 0.05$. Mean values are reported along with their standard errors (mean ± s.e.).

Results

Seedling Biomass

The total seedling biomass production per pot within a given culture was generally significantly greater in the HW treatment ($P < 0.05$) (Fig. 2). Seedling biomass of the milkvetch monoculture was significantly greater ($P < 0.05$) than that of either the mixture or the switchgrass monoculture in each of the five water treatments (Fig. 2). Moderate water stress (LW) reduced biomass production by about half for the three cultures (48.5, 49.7 and 46.2% for switchgrass, milkvetch and the mixture, respectively) compared with the HW treatment. Compared with HW treatments, DHW reduced the biomass of switchgrass, milkvetch and the mixture by 5.1, 62.1 and 39.5%, respectively. Compared with LW treatments, DLW reduced biomass yields by 2.1, 49.1 and 23.6%, respectively. After the 12 days of drying and three days of watering to re-establish the LW SGMC (RLW), the biomass of switchgrass seedlings and the mixture seedlings increased 2.1 and 7.5%, respectively, while the milkvetch seedlings biomass decreased 27.8% (Fig. 2). In the HW treatment, the biomass production ratio of switchgrass to milkvetch in the mixture was 0.11, and was significantly lower than in the other four treatments, where it ranged from 0.16 to 0.19 and averaged 0.18, and among which there were no significant differences ($P > 0.05$) (Fig. 3).

Root:Shoot Ratio

Switchgrass had a significantly higher ($P < 0.05$) root:shoot ratio than milkvetch in both the monoculture and the mixture under any water treatment (Fig. 4). Milkvetch had a higher ($P < 0.05$) root:shoot ratio in the monoculture than in the mixture, and water stress increased the values. Watering following the water stress conditions in the RLW

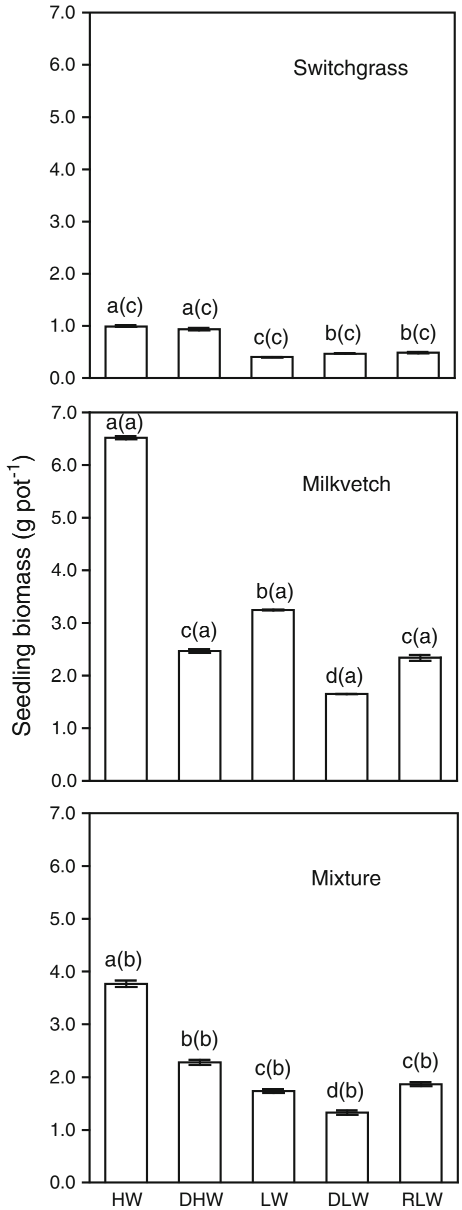

Fig. 2 Seedling biomass of switchgrass and milkvetch in monocultures and mixtures for each water treatment. Values are means with standard *error bars*. Different *small letters* indicate significant differences ($P < 0.05$) among water treatments in the same culture. Different *small letters* in brackets indicate significant differences ($P < 0.05$) among cultures for the same water treatment (Soil water content conditions: *HW* high water, *DHW* soil drying from high water, *LW* low water, *DLW* soil drying from low water, and *RLW* rewater to LW after drying from LW for 12 days)

treatment significantly decreased the root:shoot ratio of switchgrass and milkvetch in monocultures, while having the opposite effect on the mixtures (Fig. 4). Soil drying in the DHW treatment increased the root:shoot ratio for switchgrass and milkvetch. In contrast, the root:shoot ratio for switchgrass decreased significantly when soil dried in the DLW treatment. In the mixture, the root:shoot ratio of

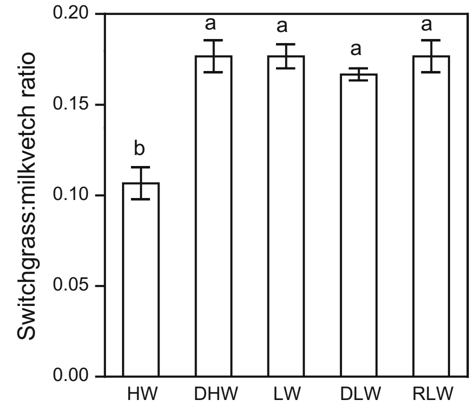

Fig. 3 Switchgrass:milkvetch ratio of the total seedling biomass for each water treatment. Values are means with standard *error bars*. Different *small letters* indicate significant differences ($P < 0.05$) among water treatments (Soil water content conditions: *HW* high water, *DHW* soil drying from high water, *LW* low water, *DLW* soil drying from low water; and *RLW* rewater to LW after drying from LW for 12 days)

milkvetch was significantly lower ($P < 0.05$) than in the monoculture, while switchgrass was significantly higher ($P < 0.05$) except in the HW treatment (Fig. 4).

Water Use Efficiency

Soil water evaporation was subtracted from total water consumption to give the amount of water used by the seedlings. From this, water use efficiency could be determined when taken to be the same as transpiration water use efficiency (TWUE) and defined as the amount of biomass produced per unit volume of water transpired by the plants. In the HW and DHW treatments, the switchgrass monoculture had the highest TWUE ($P < 0.05$) of the three cultures. The TWUE of the mixture was numerically, but not significantly, greater than that of the milkvetch monoculture (Fig. 5). In the LW, DLW and RLW treatments, the TWUEs of the switchgrass monocultures were significantly lower ($P < 0.05$) than the TWUEs of both the milkvetch monoculture and the mixture. Mixtures had the highest ($P < 0.05$) TWUE in the DLW and RLW treatments, while under LW conditions, the milkvetch monoculture had a similar TWUE to the mixture ($P > 0.05$) (Fig. 5). Soil drying from the HW moisture level (DHW treatment) reduced the TWUE significantly of the milkvetch monoculture and the mixture, while for switchgrass there was no significant change ($P > 0.05$). Soil drying from the LW moisture level (DLW treatment) significantly reduced the TWUE of milkvetch, but increased the TWUE for the other two cultures and notably for the switchgrass monoculture (Fig. 5). After re-establishing the LW moisture content in the RLW treatment, the TWUE values for switchgrass and the mixture increased by about 28 and

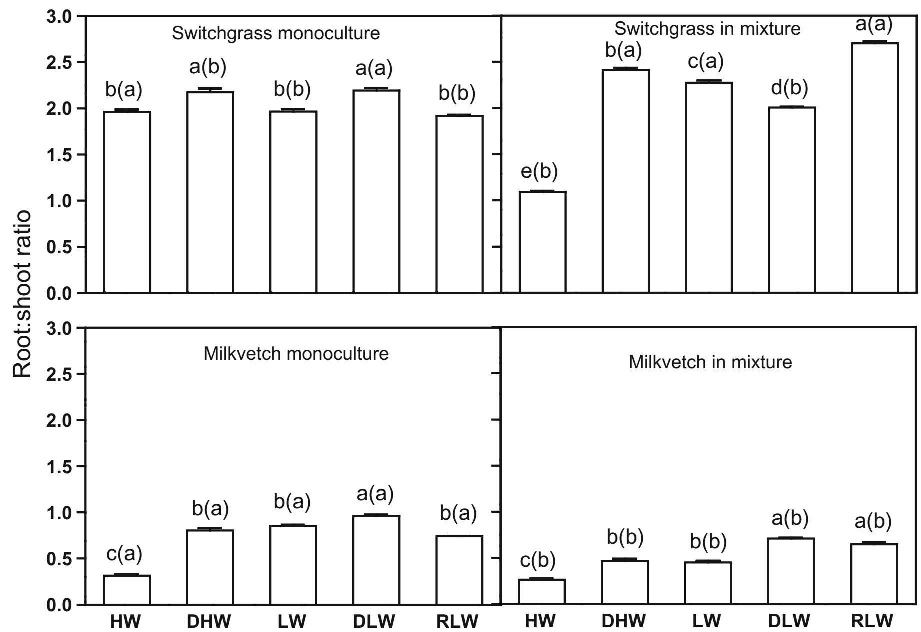

Fig. 4 Root:shoot ratio of switchgrass and milkvetch in monocultures and mixtures. Values are means with standard *error bars*. Different *small letters* indicate significant differences ($P < 0.05$) among water treatments in same culture. Different *small letters* in brackets indicate significant differences ($P < 0.05$) for each species for the same water treatment (Soil water content conditions: *HW* high water, *DHW* soil drying from high water, *LW* low water, *DLW* soil drying from low water, and *RLW* rewater to LW after drying from LW for 12 days)

14% relative to the LW treatment, respectively, but re-watering did not affect the TWUE of milkvetch in the RLW treatment (Fig. 5).

Competitive Indices

In the mixture in the LW treatment, switchgrass was the dominant species (A*ab* positive) but in the other four treatments it was the dominated species (A*ab* negative), especially under soil drying conditions (i.e. DHW and DLW, A*ab* was more negative) (Table 1). Switchgrass also had higher CR values in the LW treatment, while milkvetch in the mixture had higher CR values for the other four water treatments, indicating that milkvetch is generally more competitive than switchgrass (Table 1). While the CR values for switchgrass decreased when soil water declined, the CR values for milkvetch increased (Table 1). The partial RYa for switchgrass was higher than for milkvetch in the LW treatment, but lower in the other four water treatments. The partial RYb of milkvetch was higher than 0.5 in the mixture except when calculated for total biomass in the LW treatment, and for root biomass in both the HW and LW treatments. Most RYa values of switchgrass were lower than 0.5 except in the LW treatment (Table 2).

Discussion

Seedling Biomass and TWUE

Water stress was a very important limiting factor for plant seedling growth. Plant responses to water deficits are dynamic and varied, requiring coordination between the shoots and roots (Ranney and others 1990). The present study was consistent with those on other species in that water stress decreased total dry mass and altered biomass allocation to root systems resulting in higher root:shoot ratios in stressed seedlings (Figs. 2, 4) (Fotelli and others 2001; Li and others 2008). With the greater availability of soil water (i.e. HW and DHW treatments), the two-species mixture had a slightly higher ($P > 0.05$) TWUE than the milkvetch monoculture (Fig. 5). Under low (and especially changing) water conditions, the mixture had a higher ($P < 0.05$) TWUE than either of the two species alone (Fig. 5), implying that the mixture improved WUE under low and fluctuating soil water conditions.

Root growth is largely controlled by carbohydrate supply from the shoot, and is substantially influenced by soil environments such as soil water, nutrients, temperature and species interaction (Fotelli and others 2001; Weih and Karlsson 2001; Zobel and Zobel 2002). Higher root:shoot ratios in the mixture may have compensated for some of the negative effects of the drought conditions and may have enabled the plant to maintain much of its water uptake under moderate drought conditions (Susiluoto and Berninger 2007). Mixed cropping reduced the milkvetch root:-shoot ratios in each water treatment, but increased those of switchgrass except in the HW and DLW treatments (Fig. 4). Despite lower seedling biomasses, switchgrass had the highest root:shoot ratios under each water treatment when considering either the two monocultures or in the mixture. This would benefit the growth of the plant under dry conditions once the seedling was established (Xu and others 2006a, 2006b). In the LW treatment, the

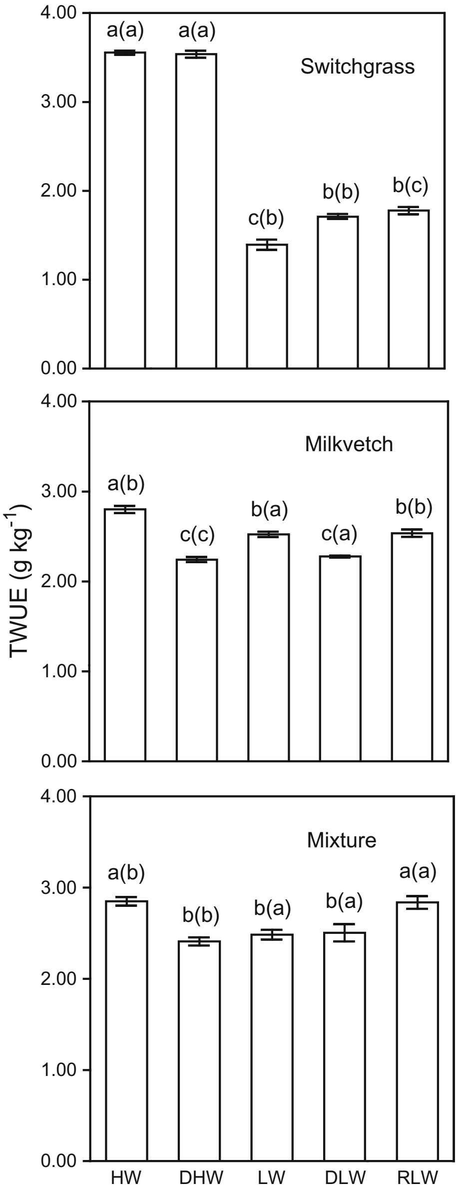

Fig. 5 Transpiration water use efficiency (TWUE) of switchgrass and milkvetch in monocultures and mixtures for each water treatment. Values are means with standard *error bars*. Different *small letters* indicate significant difference ($P < 0.05$) among water treatments in same culture. Different *small letters* in brackets indicate significant difference ($P < 0.05$) among cultures under same water treatment (Soil water content conditions: *HW* high water, *DHW* soil drying from high water, *LW* low water, *DLW* soil drying from low water, and *RLW* rewater to LW after drying from LW for 12 days)

root:shoot ratio of switchgrass in the mixture was about 1.2 times that in the monoculture, and that of milkvetch was about half that of the milkvetch monoculture, which may have enabled switchgrass to dominate the mixture resulting in the higher degree of competition between the two species. This may also induce the compensatory growth of milkvetch when rewatered after a short period of drought (i.e. RLW treatment) (Fig. 2). Although in the monocultures milkvetch had a higher biomass accumulation rate than switchgrass in all the water treatments (Fig. 2), the relative biomass contributions of switchgrass and milkvetch were nearly the same in the mixtures under the water stressed conditions (Fig. 3), indicating that the changes in the seedling biomass of both species were, for the most part, directly and similarly affected by the water treatment. However, the root:shoot ratio values of both species did not conform to the total biomass changes (Figs. 3, 4), because changes in root:shoot ratios depended on a number of factors, including the intensity of competition and the particular plant species (Zobel and Zobel 2002).

Compensatory Effect

Switchgrass alone and the two-species mixture performed better in terms of seedling biomass production and TWUE in the RLW treatment when compared with the LW treatment (Figs. 2, 5), which is normally called the compensatory effect (Huang 2000; Zhao and others 2004; Hu and Kang 2005). Compensation is a common phenomenon following environmental stresses such as drought, anoxia, salinity, or nutrient stresses, and also mechanical damage (Bai and others 2004; Zhao and others 2004). Greater biomass production and WUE following short periods of drought stress have been reported in several annual crop species such as winter wheat (*Triticum aestivum* L.) (Shan and others 2000a, 2000b; Zhao and Deng 2002), maize (*Zea mays* L.) (Guan and others 1997; Huang 2000), potato (*Solanum tuberosum* L.) (Shan and others 2000a, 2000b) and foxtail millet (*Setaria italica* L.) (Guo 1999; Xu and others 2007). Compensatory growth has also been found in some perennial species such as perennial ryegrass (*Lolium perenne* L.), tall fescue (*Festuca arundinacea* Schreb.), white clover (*Trifolium repens* L.), *Leymus chinensis* and *Stipa krylovii* when relieved from drought stress (Karsten and MacAdam 2001; Dong and Shen 2002; Staalduinen and Anten 2005; Zhao and others 2004). In this study, milkvetch did not exhibit compensatory biomass production and TWUE in the monocultures, but in the mixtures its biomass increased 8% relative to the LW treatment when rewatered (RLW). In contrast, switchgrass biomass only increased 5% in the mixture, and TWUE of the mixture increased by about 15% (Figs. 2, 5). Various mechanisms are attributed to explain the compensatory growth and water use efficiency in plants after recovering from drought (Wang and Huang 2004; Zhao and others 2004; Hu and Kang 2005), with the magnitude of the compensatory effects dependent on factors such as drought stress stage, degree and duration, and species-specificity (Zhao and others 2004; Hu and Kang 2005; Zewdie and others 2007). Plants with high osmotic adjustment ability during drought

Table 1 Competition indices of switchgrass (a) and milkvetch (b) in a mixture of equal seedling numbers

Water treatments	CRa			CRb			Aab		
	Total	Shoot	Root	Total	Shoot	Root	Total	Shoot	Root
HW	0.72 ± 0.10bc	0.98 ± 0.11a	0.67 ± 0.08c	1.38 ± 0.21bc	1.02 ± 0.12d	1.49 ± 0.23a	−0.16 ± 0.05d	−0.01 ± 0.06a	−0.15 ± 0.03c
DHW	0.47 ± 0.04d	0.36 ± 0.04d	0.68 ± 0.05c	2.11 ± 0.17a	2.79 ± 0.33a	1.46 ± 0.12a	−0.42 ± 0.02a	−0.62 ± 0.06d	−0.18 ± 0.03c
LW	1.48 ± 0.08a	1.06 ± 0.09a	2.30 ± 0.13a	0.67 ± 0.04d	0.95 ± 0.09d	0.43 ± 0.03c	0.19 ± 0.04c	0.01 ± 0.01a	0.40 ± 0.03a
DLW	0.61 ± 0.03c	0.57 ± 0.02c	0.70 ± 0.04c	1.64 ± 0.08b	1.77 ± 0.07b	1.43 ± 0.08a	−0.29 ± 0.02b	−0.34 ± 0.02c	−0.17 ± 0.02c
RLW	0.85 ± 0.08b	0.64 ± 0.04b	1.02 ± 0.13b	1.17 ± 0.12c	1.56 ± 0.11b	0.98 ± 0.14b	−0.11 ± 0.05d	−0.26 ± 0.02b	−0.01 ± 0.01b

Soil water content conditions: *HW* high water, *DHW* soil drying from high water, *LW* low water, *DLW* soil drying from low water, *RLW* rewater to LW after drying for 12 days from LW, *CR* competitive ratio, *Aab* aggressivity of switchgrass to milkvetch. Values are mean ± standard error. Values within a column followed by different *small letters* are significantly different ($P < 0.05$)

Table 2 Competition indices of switchgrass (a) and milkvetch (b) in a mixture of equal seedling numbers

Water treatments	RYa			RYb			RYT		
	Total	Shoot	Root	Total	Shoot	Root	Total	Shoot	Root
HW	0.38 ± 0.04b	0.53 ± 0.04ab	0.30 ± 0.04c	0.52 ± 0.02c	0.55 ± 0.02c	0.44 ± 0.01c	0.90 ± 0.04c	1.08 ± 0.03b	0.74 ± 0.06c
DHW	0.37 ± 0.04b	0.35 ± 0.05c	0.38 ± 0.04b	0.78 ± 0.03a	0.96 ± 0.06a	0.56 ± 0.02b	1.15 ± 0.07ab	1.31 ± 0.09a	0.94 ± 0.06b
LW	0.67 ± 0.05a	0.61 ± 0.06a	0.70 ± 0.05a	0.45 ± 0.01d	0.58 ± 0.02c	0.31 ± 0.02d	1.12 ± 0.06b	1.19 ± 0.08ab	1.01 ± 0.06b
DLW	0.42 ± 0.03b	0.45 ± 0.04bc	0.41 ± 0.03b	0.69 ± 0.04b	0.79 ± 0.05b	0.58 ± 0.03ab	1.11 ± 0.07b	1.24 ± 0.08a	1.00 ± 0.06b
RLW	0.58 ± 0.06a	0.46 ± 0.04b	0.64 ± 0.06a	0.68 ± 0.04b	0.71 ± 0.02b	0.63 ± 0.02a	1.26 ± 0.06a	1.17 ± 0.07ab	1.27 ± 0.05a

Soil water content conditions: *HW* high water, *DHW* soil drying from high water, *LW* low water, *DLW* soil drying from low water, *RLW* rewater to LW after drying for 12 days from LW, *RY* relative yield, *RYT* relative yield total. Values are mean ± standard error. Values within a column followed by different *small letters* are significantly different ($P < 0.05$)

stress, especially those with above average carbohydrate stored in stubble or root reserves, exhibited rapid growth when droughts were relieved in controlled experiments or when rain returned in natural environments (Staalduinen and Anten 2005). However, in this study, there was no direct evidence of a mechanism to explain the observed compensatory growth.

Competitive Effect

There was no obvious trend in competitive aggressivity for the two species under the various water treatments (Table 1). Switchgrass was the dominant species and much more aggressive than milkvetch at the seedling stage in the LW treatment, while in the other four treatments milkvetch was the dominant species as measured by the positive value of aggressivity (Dhima and others 2007). Results also showed that aggressivity scores were driven by the roots under relatively stable water conditions (i.e. HW and LW treatments), but driven by the shoots with changing soil water contents (Table 1).

Milkvetch had higher competitive ratios (CR) than switchgrass except in the LW treatment (Table 1). The CR and aggressivity values clearly show that milkvetch was more competitive in the mixtures (Dhima and others 2007). Soil drying decreased the CR of switchgrass but increased that of milkvetch. This indicated that milkvetch was more competitive because switchgrass was affected more as the water deficit increased (Table 1). The aggressiveness of one species towards another may depend on a number of genetic and physiological attributes that facilitate the capture of resources in competition (Bi and Turvey 1994). Greater competitive ability of milkvetch to exploit resources, especially soil water, has been reported (Shan and Chen 1993; Xu and others 2006a, 2006b). Root:shoot ratio values of switchgrass were greater than those of milkvetch in both the monocultures and the mixtures (Fig. 4). For the same amount of root mass, milkvetch was able to support more shoot growth (Figs. 2, 4). This may indicate that the milkvetch seedlings were more efficient in taking up water and nutrients than the seedlings of switchgrass, and the ability to fix atmospheric nitrogen may also have added to the competitive advantage of milkvetch (Bi and Turvey 1994). These differences in water uptake or competitive ability for water could also be attributed to differences in the root structures of the seedlings (i.e. taproot in milkvetch and fibrous roots in switchgrass).

Root RYT values lower than 1.0 in the HW and DHW treatments suggested that competition occurred underground in the mixtures (Bi and Turvey 1994; Jose and others 2006). The RYT values of the mixtures of the two species under low water availabilities were normally >1.00 indicating that, while the two species competed for resources, there was also some degree of resource complementarity between them (Bi and Turvey 1994; Fetene 2005). The aggressivity (Aab), CR and partial RY values were consistently greater for switchgrass than for milkvetch in the mixture in the LW treatment and indicated that switchgrass was the more competitive species (Table 1 and 2). The differences found between mixtures in our study may be attributed to the soil water conditions and also to other factors such as morphology, physiology and the different nutrient requirements as also reported by Dhima and others (2007).

On the semiarid Loess Plateau of China, finding sustainable and rational cropping patterns of various grass species is among the cardinal goals of research and extension systems (Shan and Chen 1993). Due to the low and highly variable annual rainfall patterns, it is essential to choose appropriate species or species combinations that have desirable performance traits such as superior biomass production and water use efficiency in response to fluctuating soil water conditions. Seedling growth, particularly of switchgrass, is often limited by moisture availability in the area. Results of this study show that soil water conditions have significant effects on biomass production of both species whether grown alone or in mixtures. The greater biomass production and TWUE with sufficient water supply suggests that planting should be carried out during the rainy season, which is from July to September. Although biomass production of the mixture was less than the milkvetch monoculture, the two species combination displayed an advantage in water use efficiency, especially under low and fluctuating water availability. Moreover, although switchgrass biomass was inhibited in the mixture, the presence of milkvetch can significantly increase the switchgrass root:shoot ratio in mixtures during the seedling stage. Thus, a possible strategy would be to plant both species in the first year and then harvest milkvetch while leaving switchgrass, which would be the better adapted perennial plant in latter stages. However, since our experiments were based on pot-grown seedlings using one planting density, extrapolation of the results to mature plants in the field may be limited, and the physiological mechanisms behind these results remain to be described. Further studies are needed to evaluate the performance of the two species in various mixture ratios under field situations throughout their entire growth periods.

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References

Bai YF, Han XG, Wu JG, Chen ZZ, Li LH (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431(9):181–184

Bi HQ, Turvey ND (1994) Inter-specific competition between seedlings of *Pinus radiata*, *Eucalyptus regnans* and *Acacia melanoxylon*. Australian Journal of Botany 42:61–70

Dhima KV, Lithourgidis AS, Vasilakoglou IB, Dordas CA (2007) Competition indices of common vetch and cereal intercrops in two seeding ratio. Field Crops Research 100:249–256

Dong ZX, Shen YX (2002) Compensatory growth of tall fescue following drought stress. Journal of Nanjing Agricultural University 25(1):15–18 (in Chinese with English Abstract)

Fetene M (2005) Intra- and inter-specific competition between seedlings of *Acacia etbaica* and a perennial grass (*Hyparrenia hirta*). Journal of Arid Environments 55:441–451

Fotelli MN, Geßler A, Peuke AD, Rennenberg H (2001) Drought affects the competitive interactions between *Fagus sylvatica* seedlings and an early successional species, *Rubus fruticosus*: responses of growth, water status and δ^{13} composition. New Phytologist 151:427–435

Frank AB, Bauer A (1991) Rooting activity and water use during vegetation development of crested and western wheatgrass. Crop Science 83:906–910

Ghosh PK (2004) Growth, yield, competition and economics of groundnut/cereal fodder intercropping systems in the semi-arid tropics of India. Field Crop Research 88:227–237

Guan YX, Dai JY, Xu SC, Huang CX (1997) Effects of soil drought during flowering and rewatering on plant compensative growth and yield of maize. Acta Agonomica Sinica 23(6):740–745 (in Chinese with English Abstract)

Guo XS (1999) Compensation effect of millet after drought. Chinese Journal of Applied Ecology 10(5):563–566 (in Chinese with English Abstract)

Hu TT, Kang SZ (2005) The compensatory effect in drought resistance of plants and its application in water-saving agriculture. Acta Ecologica Sinica 25(4):885–890 (in Chinese with English Abstract)

Huang ZB (2000) A study on drought-wet changing environment and compensative effect rules of crops. Eco-agriculture Research 8(1):30–33 (in Chinese with English Abstract)

Ichizen N, Takahashi H, Nishio T, Liu G, Li D, Huang J (2005) Impacts of switchgrass (*Panicum virgatum* L.) planting on soil erosion in the hills of the Loess Plateau in China. Weed Biology and Management 5:31–34

Jose S, Williams R, Zamora D (2006) Belowground ecological interactions in mixed-species forest plantations. Forest Ecology and Management 233:231–239

Karsten HD, MacAdam JW (2001) Effect of drought on growth, carbohydrates, and soil water use by perennial ryegrass, tall Fescue, and white clover. Crop Science 41:156–166

Keddy PA, Twolan-Strutt L, Wisheu I (1994) Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? Journal of Ecology 82:635–643

Li DQ, Liu GB, Huang J, Jiang J (1999) Study on introduction and bio-ecological characters of *Panicum virgatum* in Ansai loess hilly region. Journal of Soil Erosion and Soil and Water Conservation 5(Spe.):125–128 (in Chinese with English Abstract)

Li FL, Bao WK, Wu N, You C (2008) Growth, biomass partitioning, and water-use efficiency of a leguminous shrub (*Bauhinia faberi* var. *microphylla*) in response to various water availabilities. New Forests 36:53–65

Monti A, Fazio S, Lychnaras V, Soldatos P, Venturi G (2007) A full economic analysis of switchgrass under different scenarios in Italy estimated by BEE model. Biomass and Bioenergy 31:177–185

Monti A, Bezzi G, Pritoni G, Venturi G (2008) Long-term productivity of lowland and upland switchgrass cytotypes as affected by cutting frequency. Bioresource Technology 99:7425–7432

Nelson RG, Ascough JC II, Langemeier MR (2006) Environmental and economic analysis of switchgrass production for water quality improvement in northeast Kansas. Journal of Environmental Management 79:336–347

Olssen M, Nilsson K, Liljenberg C, Hendry GAF (1996) Drought stress in seedling: lipid metabolism and lipid peroxidation during recovery from drought in *Lotus corniculatus* and *Cerastium fontanum*. Physiologia Plantarum 96:577–584

Pimentel D, Patzek TW (2005) Ethanol production using corn, switchgrass, and wood: biodiesel production using soybean and sunflower. Natural Resources Research 14(1):256–261

Ranney TG, Whilow TH, Bassuk NL (1990) Response of five temperate deciduous tree species to water stress. Tree Physiology 6:439–448

Sanderson MA, Read JC, Read RL (1999) Harvest management of switchgrass for biomass feedback and forage productions. Agronomy Journal 91:5–10

Shan L, Chen GL (1993) Theory and practice of dryland farming on the Loess Plateau. Chinese Science Press, Beijing (in Chinese)

Shan L, Deng XP, Su P, Huang ZB, Zhang SQ, Zhang ZB (2000a) Excavating the potentiality of crop drought-resistance and water saving-the adaptability and adjustment of crop to highly variable and low water environment. Journal of Agricultural Science and Technology 2:66–70 (in Chinese with English Abstract)

Shan L, Su P, Guo LK, Liu WG (2000b) The response of different crops to drying wetting cycle in field. Acta Botanica Boreali-Occidentalia Sinica 20(2):164–170 (in Chinese with English Abstract)

Staalduinen MAV, Anten NPR (2005) Differences in the compensatory growth of two co-occurring grass species in relation to water availability. Oecologia 146:190–199

Susiluoto S, Berninger F (2007) Interactions between Morphological and Physiological Drought Responses in *Eucalyptus microtheca*. Silva Fennica 41(2):221–233

Varvela GE, Vogela KP, Mitchella RB, Follettb RF, Kimblec JM (2008) Comparison of corn and switchgrass on marginal soils for bioenergy. Biomass and Bioenergy 32:18–21

Vogel KP, Brejda JJ, Walters DT, Buxton DR (2009) Switchgrass biomass production in the Midwest USA: harvest and nitrogen management. Agronomy Journal 94:413–420

Wang ZL, Huang BR (2004) Physiological recovery of Kentucky bluegrass from simultaneous drought and heat stress. Crop Science 44:1729–1736

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

Weih M, Karlsson PS (2001) Growth response of Mountain birch to air and soil temperature: is increasing leaf nitrogen content an acclimation to lower air temperature? New Phytologist 150:147–155

Western D (2001) Human-modified ecosystems and future evolution. Proceedings of the National Academy of Sciences of the United States of America 98(10):5465–5485

Willey RW, Rao MR (1980) A Competitive ratio for quantifying competition between intercrops. Experimental Agriculture 16:117–125

Xu BC, Gichuki P, Shan L, Li FM (2006a) Aboveground biomass production and soil water dynamics of four leguminous forages in semiarid region, northwest China. South African Journal of Botany 72:507–516

Xu BC, Li FM, Shan L, Ma YQ, Ichizen N, Huang J (2006b) Gas exchange, biomass partition, and water relations of three grass

seedlings under water stress. Weed Biology and Management 6:79–88
Xu BC, Shan L, Li FM (2007) Water changes in soil and water use during seedling growth of three herbaceous grasses. Acta Botanica Boreali-Occidentalia Sinica 27(2):297–302 (in Chinese with English Abstract)
Zewdie S, Olsson M, Fetene M (2007) Growth, gas exchange, chlorophyll a fluorescence, biomass accumulation and partitioning in droughted and irrigated plants of two enset (*Ensete ventricosum* Welw. Cheesman) clones. Journal of Agronomy 6(4):499–508
Zhao LY, Deng XP (2002) Product effect of limited water supply before and after flowering of spring wheat. Chinese Journal of Applied & Environmental Biology 8(5):478–481 (in Chinese with English Abstract)
Zhao LY, Deng XP, Shan L (2004) A review on types and mechanisms of compensation effect of crops under water deficit. Chinese Journal of Applied Ecology 15(3):523–526 (in Chinese with English Abstract)
Zobel M, Zobel K (2002) Studying plant competition: from root biomass to general aims. Journal of Ecology 90:578–580