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Pearl Millet Developed Deep Roots and Changed Water Sources by Competition with Intercropped Cowpea in the Semiarid Environment of Northern Namibia

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Abstract : The practice of intercropping pearl millet with cowpea is widespread among subsistence farmers in northern Namibia. In this region, the scarce and erratic rainfall may enhance competition for the limited soil water between intercropped plants. Trials were conducted on a field of the University of Namibia (on-station) and on a farmer's field (off-station) to determine the effects of competition between pearl millet and cowpea on the water sources and plant growth of each crop. The deuterium analysis showed that pearl millet, intercropped with cowpea, significantly increased its dependence on the recently supplied labeled irrigation water. Intercropped cowpea also showed an increased trend of the dependence but it was not statistically significant. At the university field, intercropped pearl millet showed higher dependence on the irrigation water than monocropped pearl millet. At the farmer's field, the dependence of intercropped pearl millet on the irrigation water was low in the pearl millet-dominant zone. In contrast, the dependence on the irrigation water was high in the cowpea-dominant zone, indicating that the dependence on the irrigation water changes according to the size of the pearl millet canopy. The water sources of cowpea did not show a significant difference at either pearl millet-dominant or cowpea-dominant zone, indicating a stable water uptake trend under competitive conditions. Competition with cowpea significantly increased the root-weight density of intercropped pearl millet in the deep soil layers, but decreased that in the shallow layers. The root-weight density of intercropped cowpea, however, was reduced in most of the soil layers. In conclusion, cowpea has a higher ability to acquire existing soil water, forcing pearl millet to develop deep roots and shift to the surface irrigation water.

Key words : Heavy water, Leaf water potential, Rooting pattern, Stable isotope, Water stress, Water uptake.

In the local agriculture of northern Namibia, pearl millet is the major cereal crop commonly intercropped with cowpea. For subsistence farmers, the millet-based system aims to produce pearl millet as the staple grain food, while cowpea has secondary importance. To achieve this, farmers traditionally sow pearl millet with occasional rows of cowpea for the most part. In this region, precipitation deficits are associated with the great irregularity of rainfall, which are the major environmental factors limiting the productivity of pearl millet (Matanyaire, 1998). The shortage of water in these areas is also a consequence of the low water-holding capacity of the soils (Matanyaire, 1998). Payne et al. (1990) indicated that the proportion of soil water that remains in the root zone appears to be a more crucial limitation than the total rainfall in low-input millet fields in the Sahel, where the environment is almost identical with that of northern Namibia. Under such conditions, strong competition for limited soil water between intercropped pearl millet and cowpea may occur. Although the agronomy of the pearl millet-cowpea system has been extensively investigated (Stoop, 1986; Ntare, 1990; Reddy et al., 1992; Craufurd, 2000), only a few studies have dealt with water competition and the sources of water used. In pot and field experiments, we found that cowpea has higher ability to acquire existing soil water than pearl millet, forcing pearl millet to use recently supplied (irrigation) water (Zegada-Lizarazu et al., 2005, 2006). Under semiarid subsistence farming conditions, however, the higher competitive ability of cowpea to acquire existing soil water than that of pearl millet has not yet been evaluated. Furthermore, no field studies have compared the root development of neighboring species in the pearl millet-cowpea system under dry and wet conditions.

So far, several studies dealt with root development under mixed or intercropping conditions. For example, Whittington and O'Brien (1968) suggested that rye grass rooted more deeply when intercropped

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Abbreviations : ANOVA, analysis of variance; DAS, days after sowing.

with meadow fescue than when planted alone. Katayama et al. (1996), through minirhizotron measurements, found that the root density at the surface layers was reduced by intercropping in legume/legume (pigeonpea, groundnut, and cowpea) and legume/cereal (pigeonpea, sorghum, and pearl millet) combinations. Using the monolith method, they also demonstrated that the total root length of legumes was shorter under intercropping than in monocropping. However, there was no significant difference in the total root length of cereals between the monocropped and intercropped situations (Katayama et al., 1996). Furthermore, the root length density of intercropped cassava (Lose et al., 2003), the root weight of barley (Brenchley, 1919), and the degree of root branching and expansion of several cereals and weeds (Pavlychenko and Harrington, 1934, 1935) were reduced by competition. Under drought-stressed environments, intercropping may change the rooting patterns of neighboring species, and this interaction may also affect their competitive ability to capture the limited resources.

Water sources and root activity in competitive environments can be evaluated by measuring the variation in the relative abundance of deuterium in xylem sap water of plants. The comparison of the H isotope signatures from xylem sap with those of a simulated rainfall event (recently irrigated water) and existing (stored) soil water can be used to reveal the source of water used by intercropped plants. Recently, this technique has been used to reveal the water sources of tree/shrub communities (Dawson and Ehleringer, 1991; Ehleringer et al., 1991; Dawson, 1993) and annual crops (Zegada-Lizarazu and Iijima, 2004; Araki and Iijima, 2005; Iijima et al., 2005; Zegada-Lizarazu and Iijima, 2005; Zegada-Lizarazu et al., 2005, 2006). Tracing water sources is important to understand species interactions in competitive environments, particularly, where intercropped species vary greatly in functional characteristics (Burgess et al., 2000). The objective of the present study was to determine the effects of competition between the intercropped pearl millet and cowpea on the water sources and plant growth of each crop using deuterated water as a tracer together with measurements of leaf water status, shoot dry-matter production, and root development in a drought-prone environment in northern Namibia.

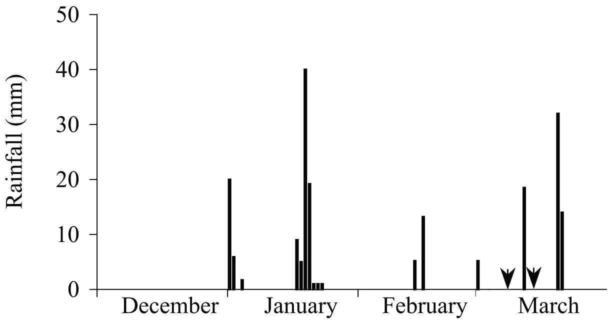

Fig. 1. Daily rainfall distribution between December 2004 and March 2005 at University of Namibia, Ogongo Campus. Arrows indicate the harvesting dates at the farmer's (8 March) and university fields (15 March). In December 2004 no rainfall was registered.

Materials and Methods

1. Study locations

Two field experiments were conducted to evaluate the plant growth and water sources of intercropped pearl millet with cowpea; one was at the University of Namibia, Ogongo Campus (latitude 17°43'S, longitude 15°15'E), referred to as the university field hereafter, and the other was at a private farmer's field in Omaandi, a village located at 3 km NE from the Ogongo Campus, referred to as the farmer's field hereafter. The owner of the farm field gave his consent to the research to be conducted on his field. At the Ogongo Campus, rainfall for the 2004-2005 cropping season was unevenly distributed, with a total of 192 mm (58 mm below the 5-year average). In December 2004 no rainfall was registered. Further information of the rainfall distribution during 2005 is presented in Fig. 1. The mean ambient temperature in the north central region of Namibia between December and

Table 1. Soil characteristics in the topsoil at the University of Namibia, Ogongo Campus (University field) and Omaandi (farmer's field). Values are means of three replications.

	N (mg Kg^{-1})	P (mg Kg^{-1})	K (mg Kg^{-1})	pH (H_2O)	OM[#] (%)	Sand (%)	Clay (%)	Silt (%)
University's field	0.01	9.98	70	6.8	0.35	90.6	5.5	3.9
Farmer's field	0.01	0.89	89	6.7	0.78	91.0	4.8	4.2

N - Kjeldahl acid digestion.
P - Olsen method.
K - Atomic absorption spectroscopy.
[#] Organic matter.
Soil analysis was done by the National Soil Science Laboratory, Namibia.

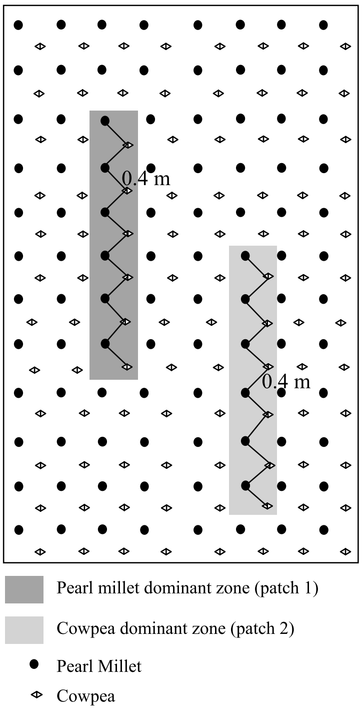

Fig. 2. Schematic representation of the zigzag planting pattern and dominant sampling zones at the farmer's field.

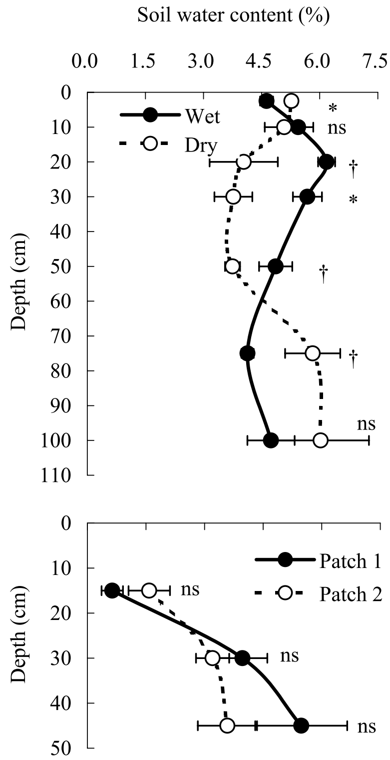

Fig. 3. Soil water content at the university field (upper) and farmer's field (lower). At the university field * and † indicates significant difference between wet and dry treatments at the 5 and 10 % levels, respectively. At the university field samples were collected at 66 DAS and at the farmer's field at 82 DAS. Values are means of three replications ± SE. Patches 1 and 2 are the pearl millet-dominant and cowpea-dominant zones, respectively.

February was 26.4°C. The temperature for March 2005 was not registered, but the historic average (1902-1985) for this month is 23.1°C (National Meteorological Center, Windhoek, Namibia). The topsoil (0-45 cm) in the field was sand at both the university and farmer's fields. Further information about the soil characteristics at both locations is presented in Table 1. The soil fertility at the different sampling positions was not measured in either experiment.

2. Treatments and field management

At the university field, one day before sowing, the land was prepared and leveled with a rotary plough to a depth of 15 - 20 cm. Before sowing 45 kg ha^{-1} each of N, P_2O_5, and K_2O was broadcasted and raked into the soil. No top dressing was applied. Pearl millet cv. Okashana-1 (*Pennisetum glaucum*) and cowpea cv. Nakale (*Vigna unguiculata*) were grown as monocrops and intercrops under wet and dry conditions, and replicated three times. A total of 18 plots were prepared in a randomized complete block design. Both monocropped and intercropped plots consisted of 4.5 m × 10 m, and the total planting area was 810 m^2. The crops were sown on 9 January. The inter-row and inter-hill spacing for monocropped pearl millet was 0.9 and 1.0 m, respectively, and that for monocropped cowpea was 0.9 m and 0.5 m, respectively. Intercrops were planted in an additive design, which is the most appropriate and widely used design to evaluate resource competition among plants (Snaydon, 1991; Gibson et al., 1999; Connolly et al., 2001a, b; Semere and Froud-Williams, 2001) and is commonly used by local farmers. In this design, the performance of a target crop (pearl millet) was evaluated in the presence of a secondary crop (cowpea). Pearl millet and cowpea were planted in additive series of alternating rows, with a planting density equal to that of each monocrop. Both monocropped and intercropped crops were thinned to one plant per hill at about two weeks after sowing. Weeding was carried out manually between 20 and 25 days after sowing (DAS). Watering for the wet treatment was carried out by a drip irrigation system at weekly intervals for up to 48 DAS. From 48 DAS up to harvest, at heading time (65 DAS), irrigation was done at three-day intervals. Watering for the dry treatment was done at approximately biweekly intervals up to 48 DAS; thereafter, irrigation was stopped completely. The total amount of applied irrigated water for the wet treatment was 138.5 mm (56.1 m^3), and that for the dry treatment was 37.8 mm (15.3 m^3). Neither pest nor disease management was conducted because no pests were observed.

At the farmer's field, only intercropped pearl

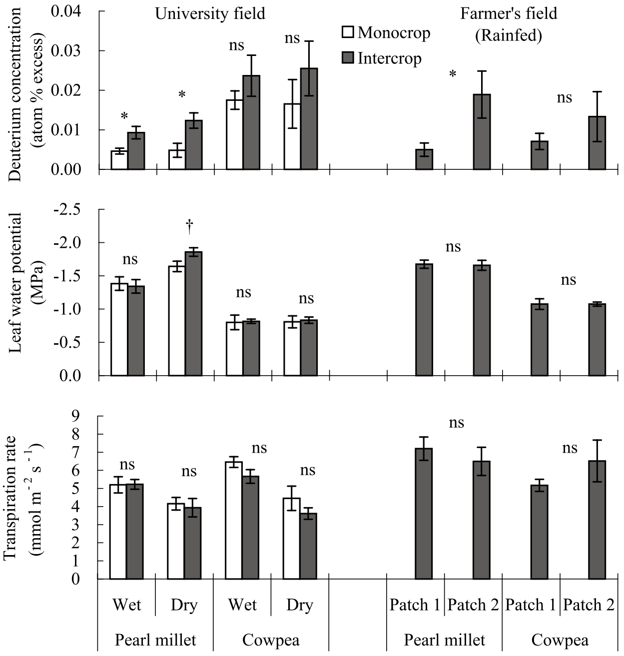

Fig. 4. Deuterium concentration in xylem sap (upper), leaf water potential (middle) and transpiration rate (lower) of monocropped and intercropped pearl millet and cowpea under semiarid conditions at two locations. At the university field * and † indicates significant difference between monocropped and intercropped plants at the 5 and 10 % levels, respectively. At the farmer's field * indicates significant difference within each species at the two sampling patches at the 5 % level. Values are means of six replications ± SE. Patches 1 and 2 are the pearl millet-dominant and cowpea-dominant zones, respectively.

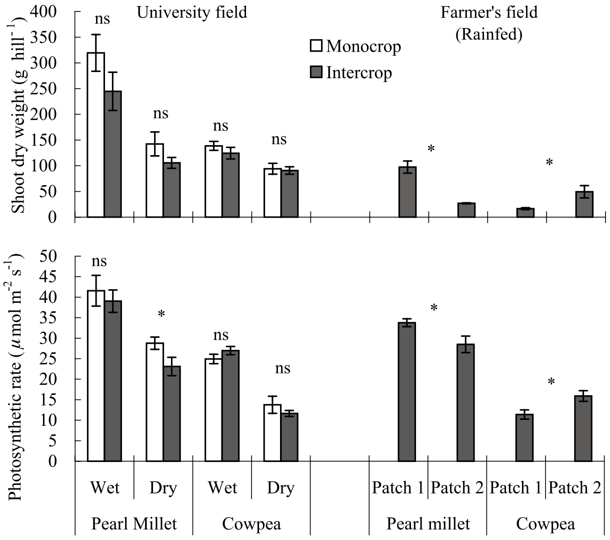

Fig. 5. Shoot dry weight (upper) and photosynthetic rate (lower) of monocropped and intercropped pearl millet and cowpea under semiarid conditions at two locations. At the university field * indicates significant difference between monocropped and intercropped plants at the 5% level. At the farmer's field * indicates significant difference within each species at the two sampling patches at the 5% level. Values are means of five to six replications ± SE. Patches 1 and 2 are the pearl millet-dominant and cowpea-dominant zones, respectively.

millet with cowpea was grown. All field management practices followed the local practices. The land was prepared by animal traction to an approximate depth of 10-15 cm. Neither chemical nor organic fertilizers were applied for this cropping season. The local landraces of pearl millet (cv. Kashana) and cowpea (cv. Ongori) used in the region were sown on 17 December. Sowing was done in small holes in a zigzag pattern with an approximate diagonal distance of 40 cm between pearl millet and cowpea holes (See Fig. 2). The inter-row and inter-hill spacing for pearl millet and cowpea was 0.7 and 0.5 m, respectively. Thinning was done to 2-3 and 1-2 plants hill^{-1} for pearl millet and cowpea, respectively, at about 20-25 DAS. Weeding was carried out only once between 20-25 DAS with a hoe. No pest management was conducted.

3. Crop measurements

At the university field, at 65 DAS, the monocropped and intercropped plants were harvested, and the shoot dry biomass was determined by oven drying at 80 °C for three days. One day prior to harvest, the photosynthetic and transpiration rates were measured with a portable photosynthesis analyzer (LC*i*, ADC BioScientific, Ltd., UK) using the first fully expanded leaf from the top. The midday leaf water potential was also determined one day before harvest with a pressure chamber device (SKPM 1405, Skye Instruments Ltd., UK) using the first fully developed leaf from the top. Leaf samples were taken between 12:00 and 13:00 h to obtain the values at the time of maximum plant water deficit.

Root samples were taken after shoot sampling. A trench measuring approximately 2 m in length, 0.8 m in width, and 1.1 m in depth was dug in each cropping pattern. Root samples were taken just below the plant canopy from the following depths: 2.5, 10, 20, 30, 50, 75, and 100 cm with a stainless core sampler (volume 100 cm^3). Roots in the cores were washed out with water over a sieve and separated from other organic debris. After removing all debris, the root fresh weight was measured, and the root-weight density (root weight soil volume^{-1}) was calculated. Soil cores for soil water content analysis (w/w) were taken from inter-row at the same depth intervals as the root sampling. One soil sample was taken from each sub plot of three cropping treatment, and then these three samples were regarded as the three replicates for the main plot of drought and wet treatments. Soil samples were oven dried for 24 hours at 105 °C to acquire the soil water content value (w/w).

At the farmer's field (70 × 50 m), the pearl

Table 2. Root weight density# (Kg m^{-3}) of monocropped and intercropped pearl millet and cowpea under semiarid conditions. * and † indicates 5 and 10 % level of significance for differences between monocropped and intercropped plants. Values are means of three to six replications.

		Depth (cm)						
		2.5	10	20	30	50	75	100
Pearl millet	**Wet**							
	Monocrop	127.25	17.33	2.32	0.20	0.13	0.44	0.04
	Intercrop	95.95 ns	17.49 ns	2.06 ns	0.55 †	0.82 ns	0.41 ns	0.77 *
	Dry							
	Monocrop	127.66	15.66	1.03	0.22	0.22	0.13	0.00 $
	Intercrop	77.49 *	14.03 ns	0.53 ns	0.28 ns	0.37 ns	0.19 ns	0.06 *
Cowpea	**Wet**							
	Monocrop	72.00	8.95	4.17	0.46	0.61	0.85	0.91
	Intercrop	44.88 †	4.99 †	0.95 ns	0.31 ns	0.68 ns	0.81 ns	0.14 †
	Dry							
	Monocrop	60.94	12.71	1.43	0.45	0.36	0.45	0.63
	Intercrop	55.01 ns	7.12 ns	0.96 ns	0.24 ns	0.39 ns	0.13 ns	0.01 †

Root fresh weight.
$ Roots were not detected.

millet-dominant zone (patch 1) and the cowpea-dominant zone (patch 2) were selected for sampling at 82 DAS (Fig. 2). These patches were originated by the differences in plant growth most probably due to different timing of germination and/or plant establishment. Both the pearl millet- and cowpea-dominant zones occupied the central part of the farmer's field and were 7 m apart. In the pearl millet-dominant zone (patch 1), intercropped pearl millet showed better plant performance than cowpea; on the other hand, in the cowpea-dominant zone (patch 2), the opposite was true. Planting densities at both patches were the same. In both dominant zones, the shoot dry weight, photosynthetic and transpiration rates, and leaf water potential were sampled and measured in the same way as at the university field. The soil water content (w/w) was determined from bulk soil samples taken from the top 45 cm of the soil profile at 15 cm-depth increments. Soil samples were collected from inter-row of each dominant zone, immediately after xylem sap collection. Three sub-samples from each dominant zone were measured in the same way as at the university field.

4. Deuterium labeling

In order to estimate the absolute value of plant water uptake from particular portion of the soil such as subsoil layer, the measurement of total water uptake is required (For example, Araki and Iijima, 2005). In this study, total water uptake was not estimated, therefore, only the water source changes were evaluated. At the university field and farmer's field, one day prior to plant harvest at the pearl millet heading (65 DAS; cowpea before flowering) and at the time of pearl millet flowering (82 DAS; cowpea flowering) 500 mL of deuterated water (1.0 and 0.5 atom % D_2O at the university and farmer's fields, respectively) was applied between two adjacent plants in the monocropped and intercropped situations. Deuterated water was applied at the same distance (approximately 22-23 cm) from the plant base in the monocropped and intercropped situations. The deuterated water was poured onto the soil surface using a measuring cylinder. About 15 h after the application of the deuterated water, xylem sap was collected from the labeled plants following the method of Zegada-Lizarazu and Iijima (2004). The deuterium abundance in xylem sap was measured by mass spectrometry (DELTA^{plus}, Finnigan Mat Instruments, Inc., Germany). Isotope ratios are presented in standard delta notation (δD) in parts per thousand (‰) relative to the Vienna Standard Mean Ocean Water (V-SMOW). The δD values were expressed as $\delta D = [(R_{sample}/R_{V\text{-}SMOW})-1]*1000$ ‰, where R is the molar ratio of heavy-to-light isotope (D/H), D being deuterium and H, hydrogen. These values were converted into the concentration of deuterated water (atom % excess) and used to determine the water sources of intercropped and monocropped plants. The application of heavy water was regarded as recent rainfall or recently irrigated water.

5. Statistical analysis

At the university field, a one-way analysis of variance (ANOVA) was used for the comparison of all the parameters measured between the monocropped and intercropped situations. Differences between wet and dry treatments with regard to the soil water content were also evaluated with a one-way ANOVA. At the farmer's field, the differences of all the parameters measured within each species at the two dominant zones were also evaluated with a one-way ANOVA. The number of replicates used for each analysis is indicated in the figures and tables.

Results

1. Soil water content

Fig. 3 shows the soil water content in the top 100 and 45 cm of the soil profile for the two experimental locations. At the university field, the average soil water content in the top 50 cm of the soil profile was slightly higher in the wet treatment than in the dry treatment (5.4 and 4.4 %, respectively). On the other hand, in deeper layers, the water content was lower in the wet treatment, probably due to the higher root-weight density and greater water uptake by plants in the wet treatment as will be discussed below. Three days before plant harvesting a rainfall of 18.5 mm was registered, which may contribute to the higher soil moisture content in the surface soil in the dry plot than in the wet (Figs. 1 and 3). Because the plant size in the dry treatment was relatively smaller as compared with wet treatment, the surface soil water in the dry treatment might not be fully consumed before harvesting. At the farmer's field, no significant differences in soil water content were found between the two dominant zones. In the top 15 cm of the soil profile, the average soil water content of both dominant zones was very low (1.1 %) and gradually increased up to 4.5 % at 45 cm depth. These low soil water content values are related to the rainfall pattern. A light rainfall (5.2 mm) was registered seven days before soil sampling (Fig. 1).

2. Source of water and leaf water relations

Figure 4 shows the water sources as indicated by the deuterium concentration in the xylem sap water and the effects of competition on the plant water status, as indicated by the leaf water potential and transpiration rate. At the university field, intercropped pearl millet had significantly higher deuterium concentrations in xylem sap compared to monocropped pearl millet in the wet and dry treatments (2.0 and 2.6 times, respectively). In contrast, intercropped cowpea did not significantly differ from monocropped cowpea in the deuterium concentration although the deuterium values increased by intercropping. The significant increase in deuterium value in intercropped pearl millet points to the higher dependence on recently supplied (irrigation/rainfall) labeled water. On the other hand, the water sources of cowpea were not significantly modified by the competition with pearl millet under any circumstances, indicating the higher ability of cowpea to extract existing soil water. At the farmer's field, the deuterium concentration of intercropped pearl millet in the pearl millet-dominant zone was low (0.005 atom %). By contrast, the deuterium values of pearl millet at the cowpea-dominant zone were significantly higher. In cowpea, no significant differences were found between the pearl millet-dominant and cowpea-dominant zones. These results indicate the strong dependence of pearl millet on the recently supplied irrigation water in the cowpea-dominant zone but not in the pearl millet-dominant zone, while cowpea did not change its water sources at either zone.

Intercropped pearl millet showed significantly lower midday leaf water potential than monocropped pearl millet under dry conditions. In contrast, cowpea did not show significant differences under both water treatments. At the farmer's field, no significant differences were found between the cowpea-dominant and pearl millet-dominant zones within each species. Regardless of the treatment or location, pearl millet always showed a lower midday leaf water potential than cowpea. At the university and farmer's fields, neither the water treatment nor the sampling zone modified the transpiration rate of the intercropped species. Overall, these results indicate that intercropping changed the water source of pearl millet; however, water competition was not observed in the midday leaf water potential and transpiration data, except for the drought treatment at the university field.

3. Shoot dry weight, photosynthetic rate, and root growth

Figure 5 shows the effects of water competition on the shoot dry weight and photosynthetic rate. At the university field, intercropped pearl millet showed lighter shoot dry weight than monocropped plants (23 and 26 % lower under wet and dry, respectively), but the differences were not significant due to the high variation among the replicate plants. On the other hand, the shoot dry weights of monocropped and intercropped cowpea were similar under both water treatments. At the farmer's field, pearl millet shoot dry weight was significantly heavier in the pearl millet-dominant zone than in the cowpea-dominant zone. The opposite was true in cowpea.

The photosynthetic rate, at the university field was significantly reduced by intercropping only in pearl millet under dry conditions. Under both water treatments, the photosynthetic rate of cowpea was not significantly influenced by intercropping. At the farmer's field, the photosynthetic rate of both species showed a pattern similar to that of shoot dry-matter production in both pearl millet-dominant and cowpea-dominant zones.

The effect of water competition on root system development (university field) is summarized in Table 2. Intercropping modified the root growth in the deep soil layers. The root growth of pearl millet at 30 to 100 cm depth was promoted by intercropping, although significant increments were found only at 30 and 100 cm depth in the wet treatment and at 100 cm depth in the dry treatment. In contrast, the root growth of cowpea in the deep layers was either reduced or not influenced by intercropping: a significant reduction was found at 100 cm depth in both water treatments. In the shallow soil layers (between 2.5 and 20 cm depth), the root-weight density of pearl millet was lower in intercropping than in monocropping under the dry treatment, but a significant difference was found only in the surface soil layers of 2.5 cm depth. In cowpea, a significant reduction of root-weight density by intercropping was found under wet conditions in the top 10 cm of the soil profile. Under dry conditions also the root-weight density tended to be reduced by intercropping, although the differences were not significant.

Discussion

1. Shoot growth, source of water, and leaf water relations

In this study, the effects of competition between intercropped pearl millet and cowpea on the growth, water source, and water relations of each crop were investigated. Deuterated water was applied as recently irrigated water between two adjacent plants to find out whether competition modifies the water sources of intercropped pearl millet. The results indicated that pearl millet, in the presence of cowpea, increased its dependence on the recently supplied water (irrigation/rainfall). Cowpea also tended to increase the dependence on the recently applied water, but the differences were not significantly (Fig. 4). Similar results were found by Zegada-Lizarazu et al. (2005, 2006) in pot and field experiments under Japanese summer conditions. This study also indicated that the dependence of pearl millet on recently supplied water is closely related to the plant size (Figs. 4 and 5). At the farmer's field in the patch where pearl millet had a well-developed canopy (the pearl millet-dominant zone), the deuterium concentration in xylem sap of pearl millet was relatively low. Well-established shoot canopy would most probably be related to a well-developed root system with a larger water-acquisition zone. Thus, the dependence on surface-applied easily accessible water would be relatively smaller due to its larger water-acquisition zone. On the other hand, in the pearl millet with poor shoot growth (cowpea-dominant zone), dependence on the recently supplied water was enhanced by severe competition with well-developed cowpea for existing soil water. In contrast, the deuterium concentration in the xylem sap of cowpea was not significantly influenced by the competition with pearl millet, even when cowpea plant growth was suppressed by competition (Figs. 4 and 5). These results confirm the higher ability of cowpea to extract existing soil water and demonstrate that its water sources were not significantly modified by competition with pearl millet.

In the present study, pearl millet intercropped with cowpea had lower leaf water potential than the cowpea (Fig. 4). This result is in agreement with the reports of Petrie and Hall (1992 a, b, c) and Zegada-Lizarazu et al. (2005, 2006). Under the dry treatment (university field), the midday leaf water potential of pearl millet was significantly reduced by intercropping, indicating the intensified water stress. This would be caused by the competitive advantage of cowpea in extracting existing soil water, as indicated by the deuterium analysis. At the farmer's field, the leaf water potential of intercropped pearl millet was low in both dominant zones. This indicates that, intercropped pearl millet reached a similar level of water stress regardless of the plant size. Since the midday leaf water potential is an approximate measure of soil water status at the time of maximum water deficit, the similar low leaf water potential values in both pearl millet-dominant and cowpea-dominant zones may be caused by the very low soil water content in the top 15 cm of the soil profile (Fig. 3). At the university and farmer's fields, the leaf water potential or deuterium concentration values of cowpea was not significantly influenced by competition with pearl millet (Fig. 4), indicating that cowpea had a higher capacity to withstand stressful conditions, most probably due to the high ability to extract existing soil water.

2. Root growth of intercropped species

Competition for water modified the root development patterns of both intercropped species, but not in a similar way. In pearl millet, the root-weight density was strongly reduced by intercropping in top layers, while it was increased in the deep layers (Table 2). Although competition has been suggested to promote the development of deep roots of intercropped grass species (Whittington and O'Brien, 1968), this is the first study, to our knowledge, to demonstrate the quantitative root biomass data in a pearl millet-based intercropping system. Even though the increased root-weight density in the deep layers may give access to wetter soil layers in intercropped pearl millet, the water supplied to the shoot seems to be insufficient to sustain the leaf water potential and dry matter production at same level as in the monocropped situation, especially under dry conditions. In contrast, intercropped cowpea had lower root-weight density in most of the soil layers than monocropped cowpea, whereas its water sources and shoot biomass were maintained at the same level under the two cropping systems. Katayama et al. (1996) indicated a similar pattern of growth of the roots and shoots in cowpea when intercropped with pigeon pea. Below-ground competition for the limited soil water is a possible reason for the modified root growth patterns, but the two species reacted differently to water stress. For example, in the shallow soil layers with densely distributed roots, water competition between the two species would be enhanced under dry treatment, causing lower soil moisture. This may cause the significantly reduced root growth in the surface layer in pearl millet but not in cowpea (Table 2). Due to the decreased root development in the surface layer by competition with cowpea, deep root growth would be enhanced in intercropped pearl millet. In cowpea, deep root development was not enhanced by intercropping, which implies the stronger ability to uptake the existing soil water. The different adaptation of the root systems of the two crops to competition is also reflected in their water uptake sources (Fig. 4), leading to the higher ability of cowpea roots to use or extract the limited existing (or stored) soil water. On the other hand, the higher dependence of pearl millet on the recently applied water (irrigation/rainfall) could be ascribed to its rooting pattern modified by intercropping.

In summary, the water sources and rooting patterns of intercropped pearl millet were modified by competition with cowpea. Cowpea has a higher ability to acquire existing soil water than pearl millet, forcing pearl millet to develop deeper roots and shift to recently supplied water. This may have important implications in the pearl millet production areas, where farmers seek to maximize pearl millet yields. Moreover, the source of water used by pearl millet seems to be highly correlated with its canopy biomass, but this requires further study.

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References

Araki, H. and Iijima, M. 2005. Stable isotope analysis of water extraction from subsoil in upland rice (*Oryza sativa* L.) as affected by drought and soil compaction. Plant Soil 270 : 147-157.

Brenchley, W. E. 1919. Some factors in plant competition. Ann. Appl. Biol. 6 : 142-170.

Burgess, S. S. O., Adams, M. A., Turner, N. C. and Ward, B. 2000. Characterisation of hydrogen isotope profiles in an agroforestry system : implications for tracing water sources of trees. Agric. Water Manage. 45 : 229-241.

Connolly, J., Goma, H. C. and Rahim, K. 2001a. The information content of indicators in intercropping research. Agric. Ecosys. Environ. 87 : 191-207.

Connolly, J., Wayne, P. and Bazzaz, F. A. 2001b. Interspecific competition in plants : how well do current methods answer fundamental questions? Am. Nat. 157 : 107-125.

Craufurd, P. Q. 2000. Effect of plant density on the yield of sorghum-cowpea and pearl millet-cowpea intercrops in northern Nigeria. Expl. Agric. 36 : 379-395.

Dawson, T. E. and Ehleringer, J. R. 1991. Streamside trees that do not use stream water. Nature 350 : 335-337.

Dawson, T. E. 1993. Hydraulic lift and water use by plants : implications for water balance, performance and plant-plant interactions. Oecologia 95 : 565-574.

Ehleringer, J. R., Phillips, S. L., Schuster, W.S.F. and Sandquist, D. R. 1991. Differential utilization of summer rains by desert plants. Oecologia 88 : 430-434.

Gibson, D. J., Connolly, J., Hartnett, D. C. and Weidenhamer, J. D. 1999. Designs for green house studies of interactions between plants. J. Ecol. 87 : 1-16.

Iijima, M., Asai, T., Zegada-Lizarazu, W., Nakajima, Y. and Hamada, Y. 2005. Productivity and water source of intercropped wheat and rice in a direct-sown sequential cropping system : The effects of no-tillage and drought. Plant Prod. Sci. 8 : 368-374.

Katayama, K., Adu-Gyamfi, J., Devi, G., Rao, T. P. and Ito, O. 1996. Root system development of component crops in intercropping. In Dynamics of roots and nitrogen in cropping systems of the semi-arid tropics. Proc. Int. workshop. 21-25 Nov. 1994. ICRISAT Asia Center, India. Patancheru, India. 199-209.

Lose, S. J., Hilger, T. H., Leinger, D. E. and Kroschel, J. 2003. Cassava, maize and tree root development as affected by various agroforestry and cropping systems in Benin, West Africa. Agric. Ecosyst. Eviron. 100 : 137-151.

Matanyaire, C. M. 1998. Sustainability of pearl millet (*Pennisetum glaucum*) productivity in northern Namibia : current situation and challenges. South African J. Sci. 94 : 157-167.

Ntare, B. R. 1990. Intercropping morphologically different cowpeas with pearl millet in a short season environment in the Sahel. Expl. Agric. 26 :41-47.

Pavlychenko, T. K. and Harrington, J. B. 1934. Competitive efficiency of weeds and cereal crops. Can. J. Agric. Res. 10 : 77-94.

Pavlychenko, T. K. and Harrington, J. B. 1935. Root development of weeds and crops in competition under dry farming. Sci. Agric. 16 : 151-160.

Payne, W. A., Wendt, C. W. and Lascano, R. J. 1990. Root zone water balances of three low-input millet fields in Niger, West Africa. Agron. J. 82 : 813-819.

Petrie, C. L. and Hall, A. E. 1992a. Water relations in cowpea and pearl millet under soil water deficits. I. Contrasting leaf water relations. Aust. J. Plant Physiol. 19 : 577-589.

Petrie, C. L. and Hall, A. E. 1992b. Water relations in cowpea and pearl millet under soil water deficits. II. Water use and root distribution. Aust. J. Plant Physiol. 19 : 591-600.

Petrie, C. L. and Hall, A. E. 1992c. Water relations in cowpea and pearl millet under soil water deficits. III. Extent of predawn equilibrium in leaf water potential. Aust. J. Plant Physiol. 19 : 601-609.

Reddy, K. C., Visser P. and Buckner P. 1992. Pearl millet and cowpea yields in sole and intercrop systems, and their after-effects on soil and crop productivity. Field Crops Res. 28 : 315-326.

Semere, T. and Froud-Williams, R. J. 2001. The effects of pea cultivar and water stress on root and shoot competition between vegetative plants of maize and pea. J. Appl. Ecol. 38 : 137-145.

Snaydon, R. W. 1991. Replacement or additive designs for competition studies? J. Appl. Ecol. 28 : 930-946.

Stoop, W. A. 1986. Agronomic management of cereal/cowpea cropping systems for major toposequence land types in the West African savanna. Field Crops Res. 14 : 301-319.

Whittington, W. J. and O'Brien, T. A. 1968. A comparison of yields from plots sown with a single species or mixture of grass species. J. Appl. Ecol. 5 : 209-213.

Zegada-Lizarazu, W. and Iijima, M. 2004. Hydrogen stable isotope analysis of deep root water acquisition abilities and hydraulic lift of sixteen food crop species. Plant Prod. Sci. 7 : 427-434.

Zegada-Lizarazu, W. and Iijima, M. 2005. Deep root water uptake ability and water use efficiency of pearl millet in comparison to other millet species. Plant Prod. Sci. 8 : 454-460.

Zegada-Lizarazu, W., Niitembu, S. and Iijima, M. 2005. Mixed planting with legumes modified the water source and water use of pearl millet. Plant Prod. Sci. 8 : 433-440.

Zegada-Lizarazu, W., Izumi, Y. and Iijima, M. 2006. Water competition of intercropped pearl millet with cowpea under drought and soil compaction stresses. Plant Prod. Sci. 9 : 123-132.