

Water Competition of Intercropped Pearl Millet with Cowpea under Drought and Soil Compaction Stresses

Walter Zegada-Lizarazu¹, Yasuhiro Izumi² and Morio Iijima¹

¹Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya 464-8601, Japan;

²School of Environmental Science, The University of Shiga Prefecture, 2500 Hassaka, Hikone, Shiga 522-8533, Japan)

Abstract : Intercropping pearl millet with cowpea is a common practice in semiarid areas. Under limited water environments, competition for soil water between intercropped plants may be strong. Furthermore, the increasing soil compaction problems, due to the use of heavy machinery, may intensify competition for limited resources, particularly in the topsoil. Two field trials were conducted to evaluate the water competition ability of intercropped pearl millet when subjected to drought and soil compaction during the 2004 Japanese summer. For this purpose plant water sources were determined by the hydrogen stable isotope (deuterium) technique. Plant water relations and biomass production were also evaluated. According to the deuterium concentration values in xylem sap, pearl millet water sources were changed by the competition with cowpea. Pearl millet was forced to rely more on recently supplied (irrigation/rainfall) water. In contrast, the water sources of cowpea were unchanged by plant competition. When plants were subjected to drought, the transpiration rate of pearl millet was reduced by 40 % of its monocropped potential by competition, but that of cowpea was not. Moreover, intercropped pearl millet, under drought and soil compaction, showed lower leaf water potential and biomass than their respective monocropped counterparts. Cowpea had a higher competitive ratio under wet, dry, and compaction treatments, while pearl millet was more competitive under loose conditions. In conclusion, under drought and soil compaction, water competition restricted the water use of intercropped pearl millet, forcing pearl millet to shift to the recently supplied water. In contrast, cowpea did not show any significant changes under these stress conditions.

Key words : Deuterium, Heavy water, Leaf water potential, Mechanical stress, Stable isotope, Water source, Water uptake.

In the semiarid regions of Africa and India, pearl millet is cultivated extensively with intercropping systems. The most common crop companion used with pearl millet is cowpea. In this system, pearl millet is the primary or target crop, although cowpea often provides the benefit of an additional seed harvest for human consumption and fodder for animals (Ntare, 1990). In these areas, intercropping systems are often practiced in low-input farming systems as a means of stabilizing and improving agricultural production (Ntare, 1990; Singh and Joshi, 1994). However, in environments with such limited water supplies and increased plant density of intercropping systems, competition for the limited soil water may be enhanced. Although the agronomy of the pearl millet-based system has been extensively investigated (Ntare, 1990; Reddy et al., 1992; Craufurd, 2000), only a few studies have dealt with water competition. Most of them focus on pearl millet-tree/shrub interactions. Smith et al. (1997), for example, found that pearl millet and windbreak trees compete for soil water only at locations where ground water is inaccessible to the

tree roots. Other studies revealed more depressed yield of pearl millet near trees/shrubs than in more distant positions; they ascribed this depression to competition for limited soil water (Wezel, 2000; Bayala et al., 2002). The performance of companion crops in intercropping is determined by competitive use of the limited resources (Ofori and Stern, 1987; Morris and Garrity, 1993). For example, Nelson and Robichaux (1997) indicated that cowpea cultivars with a spreading habit have a higher suppressive effect on pearl millet yield than bush-type cultivars. The strong competitive pressure of cowpea over pearl millet could be ascribed to its higher drought tolerance, which may facilitate its access to available soil water. In pot experiments, we found that cowpea has a higher ability to acquire existing soil water than pearl millet, forcing pearl millet to shift to the recently supplied (irrigation) water (Zegada-Lizarazu et al., 2005). Under field conditions, however, the mechanism underlying the higher competitive ability of cowpea to acquire existing soil water than that of pearl millet has not yet been evaluated.

Received 19 July 2005. Accepted 12 September 2005. Corresponding author: Morio Iijima (mijima@agr.nagoya-u.ac.jp, fax +81-52-789-4020).

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

Due to the increasing population in many semiarid regions of the world, large areas of arable land have been cultivated with agricultural machinery. However, the improper use of agricultural machinery for field preparation often leads to soil compaction. The compacted soil layer shows higher penetration resistance, causing mechanical stress to root elongation (Iijima et al., 1991; Iijima and Kono, 1991). No-tillage practice also often causes an increase in mechanical stress in the top soil (Iijima et al., 2003; Izumi et al., 2004a and b; Iijima et al., 2005). Besides the negative effect on root elongation in the deep soil layer (Araki and Iijima, 1998, 2001, 2005), soil compaction hinders water movement and distribution in the soil, limiting the availability of water and nutrients to plants (Rosolem et al., 2002). The reports on the effects of soil compaction on water-uptake by the plants are inconsistent. The water uptake by Kentucky bluegrass (Agnew and Carrow, 1985), pigeon pea (Kirkegaard et al., 1992), and maize (Amato and Ritchie, 2002) was decreased by soil compaction. On the other hand, Lipiec et al. (1988) indicated that water uptake by maize was enhanced by higher soil bulk density. The effects of soil compaction on dry matter production are also contradictory. In a very dry season, pigeon pea yield was severely reduced by soil compaction (Kirkegaard et al., 1992). In contrast, pearl millet (Mamman and Ohu, 1997) and cowpea (Dauda and Samari, 2002) yields were increased when optimum levels of soil compaction were applied. Although there has been a broad range of studies and results reported on soil compaction and water uptake, the effects of intercropping on competition for soil water and water sources under soil compaction conditions have never been quantified.

In conjunction with the study of leaf water relations, the stable isotope method used for distinguishing plant water sources can be used to evaluate whether intercropped pearl millet and cowpea are competing for the same pool of water. Variations in the relative abundance of deuterium in plant xylem sap have been used as an indicator of water uptake from a simulated rainfall event (recently irrigated water) and existing soil water (Ehleringer et al., 1991; Dawson, 1993; Zegada-Lizarazu and Iijima, 2004; Araki and Iijima, 2005; Iijima et al., 2005). Water is the only source of hydrogen for plants, and no isotopic fractionation occurs during the movement of water from the roots to the shoot base. Therefore, the stable isotope ratio (deuterium/hydrogen) contained in xylem sap water at the shoot base should reflect the water sources of a plant (Dawson and Ehleringer, 1991; Thorburn and Ehleringer, 1995). Tracing water sources is an important method for understanding the interactions among species in intercropping systems, particularly when intercropped species vary greatly in functional characteristics (Burgess et al., 2000). Furthermore,

environmental stresses, such as drought and soil compaction, may modify the water sources and, hence, water competition patterns of intercropped plants. The objective of the present study was to evaluate the water competition between intercropped pearl millet and cowpea in field conditions by the use of the hydrogen stable isotope (deuterium) as a tracer together with measurements of leaf water status and dry matter production. The effects of drought and soil compaction on water competition were also evaluated in the field during the 2004 Japanese summer.

Materials and methods

1. Study sites

The effects of drought and soil compaction on water competition between intercropped species were evaluated at two locations with different soil and environmental conditions in the summer of 2004. The drought experiment (Exp. 1) was conducted at the experimental field of the University of Shiga Prefecture (latitude 35°15' N, longitude 136° 13' E, altitude 87 m.a.s.l.), and the soil compaction experiment (Exp. 2) at the Nagoya University Farm (latitude 35° 6' N, longitude 137° 5' E, altitude 67 m.a.s.l.). In Exp. 1, the rainfall for the 2004 summer (June – August) was 432 mm, and the mean temperature was 25.8°C (95 mm below and 1.4°C above the long-term average, respectively). In Exp. 2, the rainfall was 191 mm below (320 mm) the long-term average, and the temperature was 2.0°C above (26.2°C) the long-term average. In Exp. 1, the topsoil in the field was light clay with a pH of 7.02; total N, 1.75 g kg⁻¹; total C, 20.9 g kg⁻¹; CEC, 15.15 cmol kg⁻¹. In Exp. 2, the soil was characterized as clay loam with a pH of 6.4; total N, 1.90 g kg⁻¹; total C, 16.5 g kg⁻¹; CEC, 10.4 cmol kg⁻¹ (Yoshida et al., 2002 and 2003).

2. Treatments and field management

In Exp. 1, one day before sowing, the land was prepared and leveled with a rotary plough to a depth of 15-20 cm. Before sowing, 40 kg ha⁻¹ each of N, P, and K (slow-release type; CDU Kasei Hiryou) were broadcasted and incorporated 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 two soil moisture conditions (wet and dry), and replicated four times. A total of 24 plots were prepared in a randomized complete block design. Both monocropped and intercropped plots consisted of 1.8 m × 3 m, and the total planting area was 130 m². The crops were sown on 04 June. The between-row and within-row spacing for monocropped pearl millet was 0.6 × 0.6 m. Those for monocropped cowpea were 0.6 m between rows and 0.3 m within rows. 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 and b; Semere and Froud-Williams, 2001). 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 done manually between 30 and 35 days after sowing (DAS). The plants were grown with natural rainfall. The dry treatment was created by placing a vinyl shade of polyethylene transparent film (thickness 0.075 mm) over the plots, which prevented the plants from receiving rainfall. The prefabricated framework on which the vinyl shade was placed had a semicircular shape with a height at the center point of 2.5 m and high sidewall clearance for maximum vertical plant growth. The front and back were completely open when the sidewalls were open up to a 0.8 m height from the soil surface, allowing the air to flow freely inside the vinyl shade and minimize the effect of any other environmental factors, besides soil water content, affecting the dry treatment. The dry treatment was started 28 DAS and continued until harvest at 61 DAS. Watering was not done for the wet treatment. At 56 DAS, insecticide (Fenitrothion) was applied to control aphids. Pest management was not conducted.

In Exp. 2, soil compaction and loose soil treatments were applied. Pearl millet and cowpea were grown as monocrops and intercrops. The experiment was replicated three times. A total of 18 plots were prepared in a completely randomized block design. The size of each plot was 1.8 m × 1.8 m (total planting area was 58 m²). The field was cultivated using a two-wheel walking tractor (Honda FR615) with a weight of 160 Kg to a depth of 15 cm. The loose treatment was cultivated twice, and the compact treatment only once. For the compaction treatment, the soil was compacted with a roller (Star Nouki K type TKR 2000) with a length of 3.85 m, a diameter of 0.55 m, and a weight of 1,050 Kg. It was attached to an Iseki T7010 (F) tractor. The compaction treatment was done by three passes of the roller. Pearl millet and cowpea were sown on 09 June, and seeds that did not germinate (about 40 %, mainly, in the loose treatment) were replanted 7 ~10 days later. The same fertilization rate as in Exp. 1 was applied in Exp. 2, but a combination of urea, superphosphate, and potassium fertilizers was used. Insect management (Fenitrothion and Ortran) was conducted at 22, 29, 36, and 43 DAS in Exp. 2. Other field management practices, including planting density and planting design, were the same as those in Exp. 1.

3. Crop measurements

In both experiments, at 61 DAS, the monocropped and intercropped plants were harvested, and the shoot dry biomass was determined (by oven-drying at 80°C for three days). A competitive ratio (CR) for quantifying the yield advantage of a crop relative to the other was calculated following the method of Willey and Rao (1980): $CR_a = (Y_{ab}/Y_{aa}) / (Y_{ba}/Y_{bb}) * Z_{ba}/Z_{ab}$, where CR_a is the competitive ratio of crop "a" intercropped with crop "b," Y_{ab} is the yield per unit area of crop "a" intercropped with crop "b," Y_{aa} is the yield of the sole crop "a," Y_{ba} is the yield of crop "b" in intercrop, Y_{bb} is the yield of the sole crop "b," Z_{ab} is the proportion (number of plants) of crop "a" intercropped with "b," and Z_{ba} is the proportion of crop "b" intercropped with "a." One day prior to harvest, the photosynthetic and transpiration rates were measured with a portable photosynthesis analyzer (LI-6400, LI-COR, USA) using the first fully-expanded leaf from the top. The predawn and midday leaf water potential were also determined one and two days before harvest with a pressure chamber device (PMS-670, PMS Instrument Co., USA) using the first and second fully developed leaves from the top. Leaf samples were taken at predawn, between 0400 and 0500 hrs, and midday samples between 1200 and 1300 hrs to obtain values at the times of minimum and maximum plant water deficit. In Exp. 1, at the time of harvest, the leaf area was measured with a leaf area meter (LI-3100, LI-COR, USA). In Exp. 2, the leaf area was estimated according to the method proposed by Payne et al. (1991). Twenty-four leaves each of pearl millet and cowpea for each treatment were randomly selected regardless of the canopy level to obtain a wide range of leaf area and leaf mass. The selected leaves were cut and immediately placed into large plastic bags with moist cotton. The bags were then sealed and transported back to the laboratory, where the leaf area and dry weight were determined. The measured leaf area and leaf mass were used to develop regression equations, which were used to determine the total leaf area per crop and treatment based on their respective leaf mass.

Simultaneously, at harvest in both experiments, soil penetration resistance was measured with a cone penetrometer (DIK-5521, Daiki Rika Kogyo Co., Ltd., Japan) at 2.5 cm depth increments in the top 10 cm of the soil profile. In Exp. 1, the soil water content (v/v) was monitored by time domain reflectometry (TDR; Delta-T PR1, Delta-T devices Ltd., UK) up to a 40 cm depth. One access tube was installed at the center of each plot in two replications, which means that soil water content data presented in the monocropped and intercropped plots are mean values from two access tubes. In Exp. 2, soil cores in the upper 5 cm were sampled using a core sampler (volume of 100 cm³) to acquire the soil water content value (w/w).

4. Deuterium labeling

In both experiments, one day prior to harvest, 500 mL of deuterated water (0.5 atom % D₂O) was applied between two adjacent plants in the monocropped and intercropped situations. The deuterated water was poured to the soil surface with a measuring cylinder. About 15 h after the application of the deuterated water, xylem sap from the labeled plants was collected

following the method of Zegada-Lizarazu and Iijima (2004). The deuterium abundances in xylem sap were measured by mass spectrometry (DELTA^{plus}, Finnigan Mat Instruments, Inc., Germany). These values were converted into the concentration of deuterated water (atom % excess) and used to determine the water sources of intercropped and monocropped plants. Further details of the procedures for the determination of deuterium abundances are given in Zegada-Lizarazu and Iijima (2004). The application of heavy water was regarded as recent rainfall or recently irrigated water.

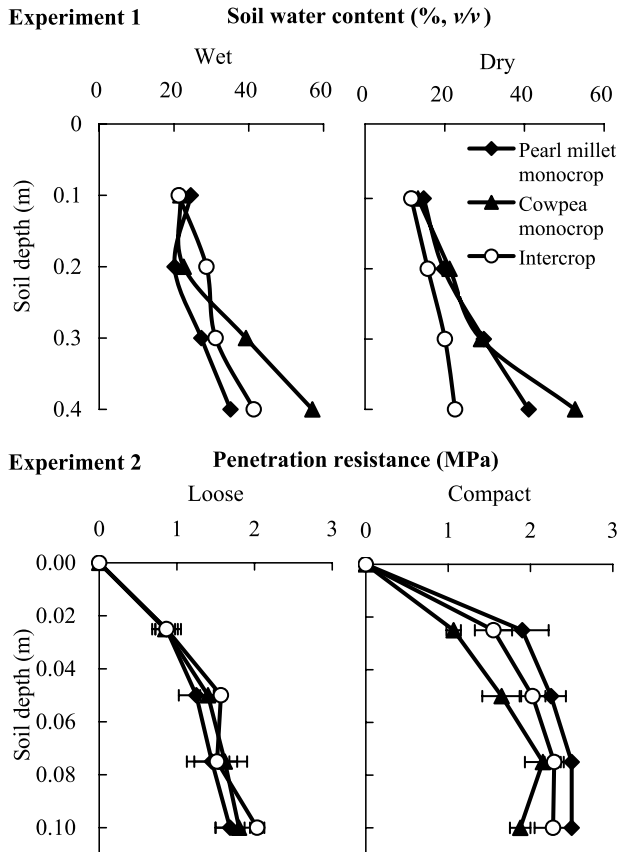


Fig. 1. Soil water content (upper) and soil penetration resistance (lower) in the top 40 and 10 cm from the soil surface in experiments 1 and 2, respectively.

5. Statistical analysis

In both experiments, 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 treatments with regard to the soil physical conditions and differences between species with regard to the competitive ratio were also evaluated with a one-way ANOVA.

Results

1. Soil physical conditions

Fig. 1 shows the soil water content in the top 40 cm of the soil profile for the monocropped and intercropped plots. In Exp. 1, the measurements by TDR indicated that the soil water content was higher under the wet treatment than under the dry treatment. In the top 10 cm of the soil profile, this difference was significant (22.5 ± 0.9 and 13.2 ± 1.9 % in the wet and dry treatments respectively), but, below 10 cm, no significant differences were observed between the water treatments (33.6 ± 4.8 and 28.0 ± 3.8 % in the wet and dry treatments, respectively). In the dry treatment, the monocropped plots had a higher soil water content than the intercropped plots, which implies the higher water consumption under intercropped situation. In Exp. 2, in the top 5 cm of the soil profile, the loose treatment showed slightly

Table 1. Deuterium concentration in xylem sap (atom % excess) of the plants after the application of deuterated water to the soil surface. * indicates significant differences between monocropped and intercropped plants at 5 % level by ANOVA.

	Experiment 1		Experiment 2	
	Wet	Dry	Loose	Compact
Pearl millet (PM)				
Monocrop (PM)	0.0051	0.0084	0.0091	0.0078
Intercrop (PM-CP)	0.0069 ns	0.0137 *	0.0156 ns	0.0191 *
Cowpea (CP)				
Monocrop (CP)	0.0072	0.0221	0.0309	0.0236
Intercrop (PM-CP)	0.0041 ns	0.0209 ns	0.0163 ns	0.0210 ns

Table 2. Effects of water competition on predawn and midday leaf water potential (MPa). * and † indicates 5 and 10 % level of significance for differences between monocropped and intercropped plants.

	Experiment 1		Experiment 2	
	Wet	Dry	Loose	Compact
Predawn leaf water potential				
Pearl millet (PM)				
Monocrop (PM)	-0.30	-0.63	-0.43	-0.42
Intercrop (PM-CP)	-0.33 ns	-0.84 *	-0.50 ns	-0.48 ns
Cowpea (CP)				
Monocrop (CP)	-0.32	-0.53	-0.40	-0.41
Intercrop (PM-CP)	-0.34 ns	-0.57 ns	-0.44 ns	-0.47 ns
Midday leaf water potential				
Pearl millet (PM)				
Monocrop (PM)	-1.34	-1.68	-1.44	-1.48
Intercrop (PM-CP)	-1.36 ns	-1.88 *	-1.78 *	-1.68 †
Cowpea (CP)				
Monocrop (CP)	-0.81	-1.21	-1.10	-1.15
Intercrop (PM-CP)	-0.81 ns	-1.16 ns	-1.06 ns	-1.12 ns

higher values than the compaction treatment (7.5 ± 0.3 and 6.7 ± 0.3 %, respectively; data not shown). In Exp. 1, the soil penetration resistance in the top 10 cm of the soil profile was higher under drought than under the wet treatment (average 1.1 ± 0.08 and 0.3 ± 0.03 MPa, respectively; data not shown) due to the lower soil water content. In Exp. 2, soil compaction caused 1.32 times higher soil penetration resistance than the loose treatment. No significant differences were found between the monocropped and intercropped plots at either loose or compaction treatments, but the monocropped pearl millet plot under compaction showed the highest values, probably due to the slightly lower soil water content in this plot (Fig. 1).

2. Water sources of intercropped plants

Table 1 shows the water sources of intercropped plants as indicated by the deuterium concentration in their xylem sap waters. Compared with monocropped pearl millet, intercropped pearl millet had significantly higher deuterium concentrations in xylem sap under drought and soil compaction (1.6 and 2.4 times, respectively). In contrast, cowpea did not show a significant difference between monocropping and intercropping in any of the four treatments. The enriched deuterium values of intercropped pearl millet show a higher dependence of pearl millet on recently supplied (irrigation/rainfall) water. On the other hand, the water sources of cowpea were not modified by the competition of pearl millet under any circumstances, indicating the higher ability to extract existing soil water in cowpea.

3. Leaf water relations

Table 2 shows the effects of competition on plant water status. In intercropped pearl millet, the effects of drought on the predawn leaf water potential and those of drought, loose, and soil compaction on the midday leaf water potential were significantly lower than in monocropped pearl millet. In contrast, monocropped and intercropped cowpea did not show significant differences in either predawn or midday potential in any of the four treatments. Regardless of the treatment or location, pearl millet always showed a lower midday leaf water potential than cowpea. These results indicated that competition for soil water by intercropping increased the water deficit of pearl millet, especially, under drought, when its predawn and midday leaf water potential values were significantly lower.

Table 3 shows the transpiration rate of the plants. In Exp. 1, competition significantly reduced the transpiration rate of pearl millet under the drought condition; intercropped pearl millet could transpire only about 60 % of its monocropped potential. On the other hand, under the wet condition, no significant differences were observed between the two cropping patterns. Cowpea did not show any significant differences in the transpiration rate between the two cropping patterns under either drought or wet conditions. In Exp. 2, intercropped pearl millet and cowpea under loose treatment showed lower transpiration rates than their respective monocropped counterparts. In contrast, soil compaction did not modify the transpiration rates in either species.

Table 3. Effects of water competition on the transpiration rate ($\text{mmol m}^{-2} \text{s}^{-1}$) of intercropped plants. * and † indicates 5 and 10 % level of significance for differences between monocropped and intercropped plants.

	Experiment 1		Experiment 2	
	Wet	Dry	Loose	Compact
Pearl millet (PM)				
Monocrop (PM)	4.02	1.47	5.63	4.42
Intercrop (PM-CP)	3.70 ns	0.89 *	4.49 †	4.43 ns
Cowpea (CP)				
Monocrop (CP)	4.75	1.91	5.37	5.25
Intercrop (PM-CP)	5.08 ns	2.62 ns	3.89 †	4.35 ns

4. Shoot dry weight, leaf area index, and photosynthetic rate

Fig. 2 shows the effects of water competition on the shoot dry weight. In Exp. 1, pearl millet showed a significant reduction in shoot dry weight under both water treatments by intercropping, but cowpea did not show any significant difference. The competitive ratio was always higher in cowpea, indicating that cowpea was more competitive than pearl millet. In Exp. 2, intercropped pearl millet plants also showed lower shoot dry weight than their respective monocropped plants (24 and 38% lower under loose and compaction, respectively), but the differences were not significant. Under loose conditions, intercropping significantly reduced the shoot dry weight in cowpea, which may have been caused by the replanting of the seeds that did not germinate about one week later. The competitive ratio indicated that intercropped pearl millet under loose was 1.9 times more competitive than cowpea, while the opposite trend was observed under compaction.

Fig. 3 shows the leaf area index and photosynthetic rate. In Exp. 1, the leaf area index was significantly reduced by intercropping only in pearl millet under wet conditions. Under both water treatments, the leaf area index of cowpea was higher than that of pearl millet. In Exp. 2, the leaf area index was reduced by intercropping in the loose treatment in both species. In pearl millet under soil compaction, the leaf area index was also reduced by intercropping, though not significantly. The photosynthetic rate was lowered by intercropping only in pearl millet under the dry treatment in Exp. 1. On the other hand, in Exp. 2, the photosynthetic rate was significantly lowered by intercropping only in cowpea under loose treatment.

Discussion

1. Water sources and plant water status

In this study, deuterated water was applied between two adjacent plants to examine the effects

of competition on the water sources between pearl millet and cowpea. According to the deuterium concentration values in xylem sap, water sources of pearl millet were changed by the intercropped competitor. Under the drought treatment, the presence of intercropped cowpea forced pearl millet to rely more on recently supplied (rainfall/irrigated) water, as indicated by the enriched deuterium values in xylem sap (Table 1). Similar results were found by Zegada-Lizarazu et al. (2005) in pot experiments. The present study also indicated that, under soil compaction, the water sources of intercropped pearl millet were changed by competition with cowpea. Soil compaction often increases the development and proliferation of branched roots near the soil surface (Iijima and Kono, 1991; Iijima et al., 1991) and reduces the water uptake ability of deep roots (Araki and Iijima, 2005; Zegada-Lizarazu and Iijima, 2005). The accumulated roots in the soil surface of pearl millet may absorb the recently supplied water more quickly than stored existing soil water. On the other hand, cowpea did not show any significant changes in the deuterium concentration values by competition (Table 1), indicating that cowpea has higher ability to extract existing soil water and that its water sources were not modified by competition with pearl millet. These results suggested that the drought and soil compaction treatments enhanced competition for existing soil water and that pearl millet was forced to rely more on the recently supplied (irrigation/rainfall) water.

In the present study, intercropped pearl millet had lower leaf water potential than cowpea (Table 2). This result is in agreement with those of Petrie and Hall (1992 a, b, and c) and Zegada-Lizarazu et al. (2005). The predawn leaf water potential is an approximate indicator of soil water status in the rhizosphere of whole root systems. Under the dry treatment, both the predawn and midday leaf water potentials of pearl millet were significantly reduced by intercropping, indicating continuous water stress, even at nighttime.

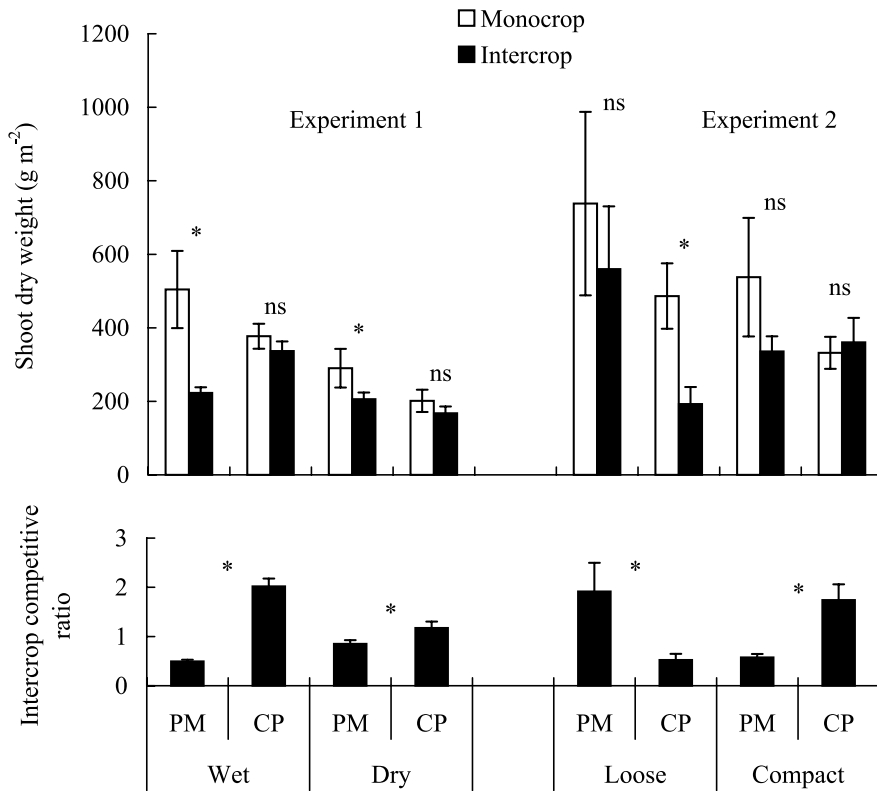


Fig. 2. Shoot dry weight (upper) and competitive ratio (lower). * indicates significant differences between cropping patterns (upper) and intercropped species (lower) at 5 % level. Pearl millet (PM) and cowpea (CP).

Intercrop competitive ratio (CR_a) = $(Y_{ab}/Y_{aa}) / (Y_{ba}/Y_{bb}) * Z_{ba}/Z_{ab}$, where CR_a is the competitive ratio of crop "a" intercropped with crop "b," Y_{ab} is the yield per unit area of crop "a" intercropped with crop "b," Y_{aa} is the yield of the sole crop "a," Y_{ba} is the yield of crop "b" in intercrop, Y_{bb} is the yield of the sole crop "b," Z_{ba} is the proportion of crop "a" intercropped with "b," and Z_{ab} is the proportion of crop "b" intercropped with "a."

This would be caused by the competitive advantage of cowpea to extract existing soil water, as indicated by the deuterium analysis. Under soil compaction, however, the predawn potential values (Table 2) and transpiration rates (measured early in the morning; Table 3) of intercropped pearl millet were similar to those of monocropped pearl millet, indicating that pearl millet water status recovered at night to nearly the monocropped predawn potentials, but, as the transpiration increased during the daytime, water competition with cowpea also increased. This would cause the significantly lower midday leaf water potential in the intercropped pearl millet.

In contrast, cowpea did not show any significant changes in leaf water potential or deuterium concentration values by competition (Tables 1 and 2), indicating the higher capacity of cowpea to withstand stressful conditions, most probably due to its high ability to extract existing soil water. These results suggest that, under drought and soil compaction, water competition restricted the water use of intercropped pearl millet, forcing pearl millet to shift to recently supplied water.

Under the dry treatment (Exp. 1), the higher plant density under the intercropped situation (because the additive design) resulted in higher water use than in the monocropped situation (Fig. 1). Morris and Garrity (1993) indicated that the water use of monocropped and intercropped plants is almost similar in arid environments due to the high soil evaporation under monocropped situations. The results contrasting with the present study may be caused by the different environmental condition (humid region) in which this experiment was conducted.

2. Dry matter production characteristics in relation to water competition

In Exp. 1, pearl millet biomass production was significantly lower when intercropped than when monocropped (Fig. 2). The same results were obtained by Nelson and Robichaux (1997) and Ntare (1990) in arid environments. Therefore, the suppressed dry matter production of pearl millet could be ascribed to the competition for soil water and/or vigorous leaf growth of cowpea (Fig. 3). In fact, in the wet treatment cowpea fully covered the soil surface, which may cause

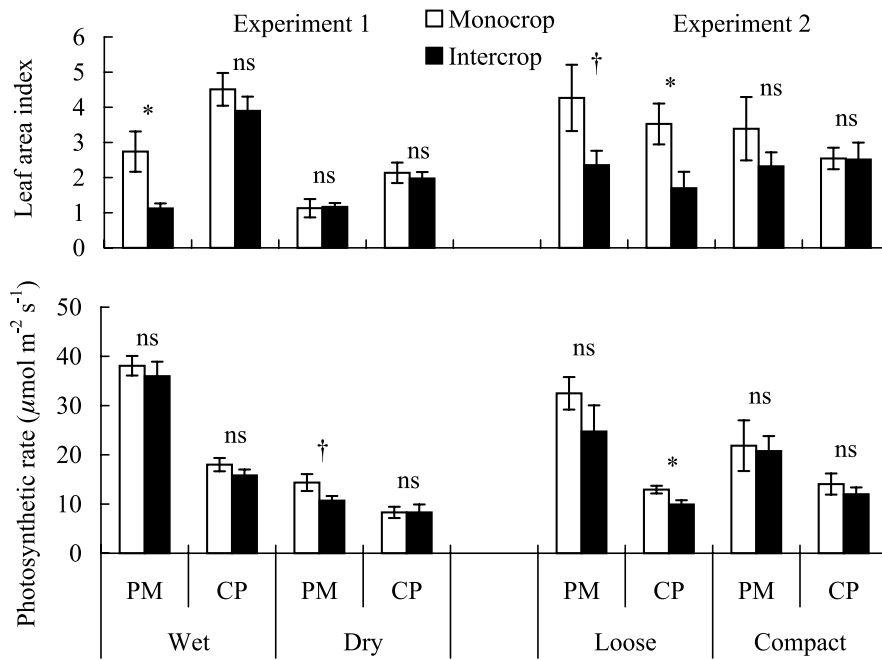


Fig. 3. Leaf area index (upper) and photosynthetic rate (lower). * and † indicates 5 and 10 % level of significance for differences between monocropped and intercropped plants.

the reduced tillering capacity of intercropped pearl millet (43 % less than monocropped pearl millet; data not shown) and consequent reduced biomass production. In Exp. 2, the same pattern was observed, but the differences between the monocropped and intercropped pearl millet biomasses were not significant due to the high variation among the replicate plants (Fig. 2). Under loose conditions, however, pearl millet showed greater competitive ability than cowpea. In this treatment, about 40 % of the total population of cowpea was replanted between 7 and 10 days later. This replanting may have contributed to some extent to the competitive advantage of pearl millet, as indicated by Reddy et al. (1992) and Zegada-Lizarazu et al. (2005). The late planting of cowpea would help pearl millet to overcome the water competition by cowpea.

Competition for soil water in terms of leaf area and photosynthetic rates is not as clear as that in the shoot dry matter production (Fig. 3). Competition for soil water and light would render in reduced biomass production and leaf area. In fact the leaf area index of intercropped pearl millet was significantly reduced under the wet and loose treatments. Under soil compaction, the leaf area index of intercropped pearl millet was also reduced, though not significantly. A reduced leaf area would result in a reduction of the amount of light (photosynthetically active radiation) intercepted and, thus, in a reduced conversion of intercepted light into dry matter. Sivakumar (1993), in a three-year experiment, also found that the leaf area of pearl millet, under improved and traditional-

management intercropping systems, was lower than that of the sole-relay cropping system.

In summary, under drought and soil compaction, cowpea has a higher ability to acquire existing soil water than pearl millet, forcing pearl millet to shift to recently supplied water. This may have important implications in pearl millet production areas, where farmers seek to maximize pearl millet yields. However, before extrapolating this result to those areas, further studies under semiarid conditions should be conducted. The performance of the pearl millet-based system may be different under semiarid environments, where soil fertility and scarcity of water are the major constraints for plant production.

Acknowledgement

We thank Mr. Yasuki Tahara, for technical assistance with the field management of Exp. 2 and Mr. Sutharsan Somasundaram for assistance during the sampling periods at both experiments.

References

- Agnew, M. L. and Carrow, R. N. 1985. Soil compaction and moisture stress preconditioning in Kentucky bluegrass. I. Soil aeration, water use and root responses. *Agron. J.* 77 : 872-878.
- Amato, M. and Ritchie, J. T. 2002. Spatial distribution of roots and water uptake of maize (*Zea mays* L.) as affected by soil structure. *Crop. Sci.* 42 : 773-780.
- Araki, H. and Iijima, M. 1998. Rooting nodes of deep roots in rice and maize grown in a long tube. *Plant Prod. Sci.* 1 : 242-247.
- Araki, H. and Iijima, M. 2001. Deep rooting in winter wheat :

- rooting nodes of deep roots in two cultivars with deep and shallow root systems. *Plant Prod. Sci.* 4 : 215-219.
- 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.
- Bayala, J., Teklehaimanot, Z. and Ouedraogo, S. J. 2002. Millet production under pruned tree crowns in a parkland system in Burkina Faso. *Agrofor. Syst.* 54 : 203-214.
- 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.
- Dauda, A. and Samari, A. 2002. Cowpea yield response to soil compaction under tractor traffic on a sandy loam soil in the semi-arid region of northern Nigeria. *Soil Tillage Res.* 68 : 17-22.
- 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. and Kono, Y. 1991. Interspecific differences of the root system structures of four cereal species as affected by soil compaction. *Jpn. J. Crop Sci.* 60 : 130-138.
- Iijima, M., Kono, Y., Yamauchi, A. and Pardales Jr., J.R. 1991. Effects of soil compaction on the development of rice and maize root systems. *Environ. Exp. Bot.* 31 : 333-342.
- Iijima, M., Izumi, Y., Yuliadi, E., Sunyoto, Afandi and Utomo, M. 2003. Erosion control on a steep sloped coffee field in Indonesia with alley cropping, intercropped vegetables, and no-tillage. *Plant Prod. Sci.* 6 : 224-229.
- 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.
- Izumi, Y., Uchida, K., and Iijima, M. 2004a. Crop production in the successive wheat-soybean rotation with no-tillage practice in relation to the root system development. *Plant Prod. Sci.* 7 : 329-336.
- Izumi, Y., Yuliadi, E., Sunyoto and Iijima, M. 2004b. Maize-soybean-cowpea sequential cropping as a sustainable crop production for acid-infertile clay soils in Indonesia. *Plant Prod. Sci.* 7 : 356-362.
- Kirkegaard, J. A., So, H. B., Troedson, R. J. and Wallis, E. S. 1992. The effect of compaction on the growth of pigeonpea on clay soil. I. Mechanisms of crop response and seasonal effects on a vertisol in a sub-humid environment. *Soil Tillage Res.* 24 : 107-127.
- Lipiec, J., Kubota, T., Iwama, H. and Hirose, J. 1988. Measurement of plant water use under controlled soil moisture conditions by the negative pressure water circulation technique. *Soil Sci. Plant Nutr.* 34 : 417-428.
- Mamman, E. and Ohu, J. O. 1997. Millet yield as affected by tractor traffic in a sandy loam soil in Borno State, Nigeria. *Soil Tillage Res.* 42 : 133-140.
- Morris, R. A. and Garrity, D. P. 1993. Resource capture and utilization in intercropping : water. *Field Crops Res.* 34 : 303-317.
- Nelson, S. C. and Robichaux, R. H. 1997. Identifying plant architectural traits associated with yield under intercropping : implications of genotype-cropping system interactions. *Plant Breed.* 116 : 163-170.
- Ntare, B. R. 1990. Intercropping morphologically different cowpeas with pearl millet in a short season environment in the Sahel. *Expl. Agric.* 26 : 41-47.
- Ofori, F. and Stern, W. R. 1987. Cereal-legume intercropping systems. *Adv. Agron.* 41 : 41-90.
- Payne, W. A., Wendt, C. W., Hossner, L.R. and Gates, C.E. 1991. Estimating pearl millet leaf area and specific leaf area. *Agron. J.* 83 : 937-941.
- 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.
- Rosolem, C. A., Foloni, J. S. S. and Tiritan, C. S. 2002. Root growth and nutrient accumulation in cover crops as affected by soil compaction. *Soil Tillage Res.* 65 : 109-115.
- 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.
- Singh, M. and Joshi, N. L. 1994. Performance of pearl millet-based intercropping systems under drought conditions. *Arid Soil Res. Rehabil.* 8 : 277-283.
- Sivakumar, M. V. K. 1993. Growth and yield of millet and cowpea in relay and intercrop systems in the sahelian zone in years when the onset of the rainy season is early. *Expl. Agric.* 29 : 417-427.
- Snaydon, R. W. 1991. Replacement or additive designs for competition studies? *J. Appl. Ecol.* 28 : 930-946.
- Smith, D. M., Jarvis, P. G. and Odongo, J. C. W. 1997. Sources of water used by trees and millet in Sahelian windbreaks systems. *J. Hydrol.* 198 : 140-153.

- Thorburn, P. J. and Ehleringer, J. R. 1995. Root water uptake of field-growing plants indicated by measurements of natural-abundance deuterium. *Plant Soil* 177 : 225-233.
- Wezel, A. 2000. Scattered shrubs in pearl millet fields in semiarid Niger : Effect on millet production. *Agrofor. Syst.* 48 : 219-228.
- Willey, R. W. and Rao, M. R. 1980. A competitive ratio for quantifying competition between intercrops. *Expl. Agric.* 16 : 117-125.
- Yoshida, S., Taguchi, H., Nomura, Y., Tashiro, T., Wada, T., Ezawa, T. and Tahara, Y. 2002. Evaluation of long term application of barnyard manure in the upland field of mineral soil. (1) Crop growth, yield, quality and disease tolerance. *Agric. Hortic.* 77 : 1310-1318*.
- Yoshida S., Katayama S., Kato T., Mizutani H., Ezawa T. 2003. Evaluation of long term application of barnyard manure in the upland field of mineral soil. (2) Soil chemical and physical characteristic and nutrient accumulation. *Agric. Hortic.* 78 : 407-413*.
- 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., Niitembu, S. and Iijima, M. 2005. Mixed planting modified the water source and water use of pearl millet. *Plant Prod. Sci.* 8 : 433-440.
- 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.

* In Japanese.