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Response of millet and sorghum to a varying water supply around the primary and nodal roots

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- **Background and Aims** Cereals have two root systems. The primary system originates from the embryo when the seed germinates and can support the plant until it produces grain. The nodal system can emerge from stem nodes throughout the plant's life; its value for yield is unclear and depends on the environment. The aim of this study was to test the role of nodal roots of sorghum and millet in plant growth in response to variation in soil moisture. Sorghum and millet were chosen as both are adapted to dry conditions.
- **Methods** Sorghum and millet were grown in a split-pot system that allowed the primary and nodal roots to be watered separately.
- **Key Results** When primary and nodal roots were watered (12 % soil water content; SWC), millet nodal roots were seven times longer than those of sorghum and six times longer than millet plants in dry treatments, mainly from an 8-fold increase in branch root length. When soil was allowed to dry in both compartments, millet nodal roots responded and grew 20 % longer branch roots than in the well-watered control. Sorghum nodal roots were unchanged. When only primary roots received water, nodal roots of both species emerged and elongated into extremely dry soil (0.6–1.5 % SWC), possibly with phloem-delivered water from the primary roots in the moist inner pot. Nodal roots were thick, short, branchless and vertical, indicating a tropism that was more pronounced in millet. Total nodal root length increased in both species when the dry soil was covered with plastic, suggesting that stubble retention or leaf mulching could facilitate nodal roots reaching deeper moist layers in dry climates. Greater nodal root length in millet than in sorghum was associated with increased shoot biomass, water uptake and water use efficiency (shoot mass per water). Millet had a more plastic response than sorghum to moisture around the nodal roots due to (1) faster growth and progression through ontogeny for earlier nodal root branch length and (2) partitioning to nodal root length from primary roots, independent of shoot size.
- **Conclusions** Nodal and primary roots have distinct responses to soil moisture that depend on species. They can be selected independently in a breeding programme to shape root architecture. A rapid rate of plant development and enhanced responsiveness to local moisture may be traits that favour nodal roots and water use efficiency at no cost to shoot growth.

Key words: Millet, *Pennisetum glaucum*, plasticity, adventitious roots, crown roots, lateral roots, sorghum, *Sorghum bicolor*, split-root system, soil moisture.

INTRODUCTION

Cereals have primary roots that originate from the embryo within the seed, and nodal (also known as crown or adventitious) roots that originate from nodes along the stem (Esau, 1977; Hochholdinger *et al.*, 2004). Primary and nodal roots can be distinguished based on their location, timing of emergence and basal anatomy (Watt *et al.*, 2008). One can be selected over the other to change root architecture (Crush *et al.*, 2010; Singh *et al.*, 2010). This is valuable for targeting root architecture to a farming system if primary and nodal roots contribute differently to soil resource acquisition and yield.

Controlled environment and field experiments have been conducted to determine the contribution of primary and nodal root systems to cereal growth and yield. Krassovsky (1926) grew wheat, barley and rye in nutrient solution in jars to separate and excise the primary and nodal roots independently. She concluded that the primary roots absorbed 25 % of the water between

flowering and maturity; the nodal roots absorbed the remaining 75 %. Excision of the nodal roots stimulated the primary roots and did not alter yield. In a field experiment, Sallans (1942) amputated the primary and nodal roots of wheat differentially and transplanted the plants to estimate their contribution to yield. Primary roots contributed more to yield on an individual basis, but together the nodal roots were more important (contributing 62 % of the water for yield). Similarly, maize was grown to maturity in the field with their full complement of nodal roots plus the primary root, or with amputated nodal roots and only the primary root (Shane and McCully, 1999). The shoots looked similar, but plants with the single primary root wilted more at mid-day, suggesting that the nodal roots provide water to shoots in the control plants. Passioura (1972) grew wheat plants on one or three primary roots to maturity in 90 cm deep pots of soil that were moist at planting and not rewatered during the experiment. The nodal roots were restricted in a small volume of air-dry surface soil. Plants with one primary

root had produced 20 % more root length than plants with three primary roots by 2 weeks after germination, and yielded twice as much grain. This study did not compare plants with and without nodal roots, but shows that they are not essential for yield, and a single primary axile root compensates with additional branch length, and conserves water for grain filling by increasing the hydraulic resistance to the shoots. Volkmar (1997) developed an elegant split-pot system to avoid amputating or severely restricting the roots to determine their function and growth, and whether they sent signals to the shoot. Wheat primary roots were contained in an inner pot of soil that sat within a larger pot that accommodated the nodal roots with a water supply similar to or different from that in the primary root pot. He found that nodal root growth was stimulated when water supply was decreased. Shoot growth was sensitive to water supply to the primary and nodal roots; more so to primary roots. Together, the literature suggests that primary roots alone can support grain production in cereals. Nodal roots are not essential to yielding grain, but, when allowed to develop, they supply water, and possibly other resources such as nitrogen and phosphorus for grain.

The aim of this study was to understand further the growth of nodal roots when soil water content varies, and their relationship to shoot growth and water uptake. We hypothesized that nodal root length increased (1) with plant growth and (2) when moisture became more available. We investigated two drought-tolerant cereals, sorghum and pearl millet. Pearl millet tends to occupy drier parts of the semi-arid tropics than sorghum, and extends into the arid zone, where soils tend to be more sandy, the growing season shorter and drought stress more frequent (Rai *et al.*, 1999). We selected these cereals with the expectation that their nodal root growth responses to moisture would differ.

We used the split-pot experimental system developed by Volkmar (1997) to see how their nodal roots respond to soil water, and the effects on shoot growth, primary root growth and water use. The roots of both sorghum and millet are composed of a single primary root system, and a nodal root system which emerges from nodes along the stem (Hoshikawa, 1969). The Volkmar system was ideal to separate the responses and effects of the primary and nodal roots of these two cereals because they form a mesocotyl, an elongation of the stem between the seed and primary root and the first nodal roots at the soil surface.

MATERIALS AND METHODS

Soil conditions and plant growth

Pearl millet (*Pennisetum americanum* L. 'Nutrifeed'; synonym *Pennisetum glaucum*) and Sorghum (*Sorghum bicolor* 'Sugargraze') were sourced from Pacific Seeds, Toowoomba, Australia. Both are modern cultivars developed for biomass production and animal grazing. Experiments were conducted in a glasshouse at CSIRO Black Mountain Laboratories between the summer months of September and December in Canberra, Australia. The temperatures were maintained at 35 ± 5 °C and 20 ± 5 °C during the day and night, respectively. Daylength was approx. 14 h and light regularly exceeded $2000 \mu\text{mol m}^{-2} \text{s}^{-2}$. A split-pot system adapted from Volkmar (1997) was used to separate primary seminal roots from nodal or adventitious roots (see Fig. 1). An inner pot (25 cm long and 9 cm diameter)

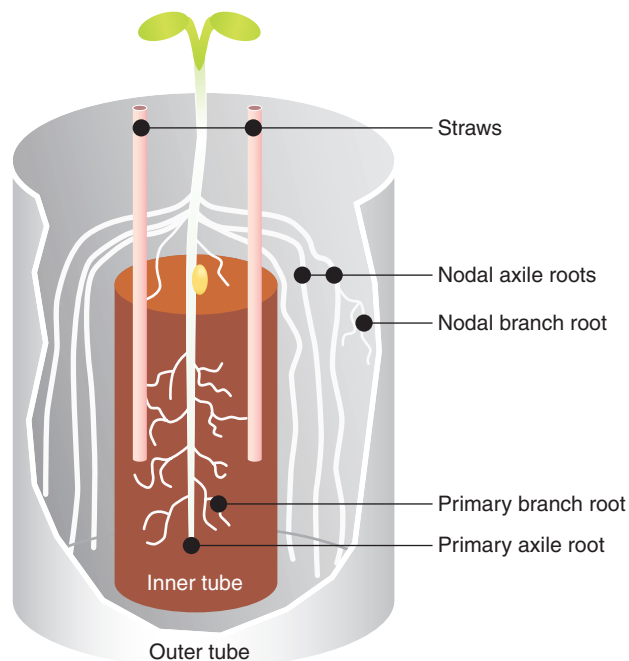


FIG. 1. Split-pot system used in experiments to separate seminal and nodal roots, adapted from Volkmar (1997). The inner pot (25 cm long \times 9 cm diameter) is within the outer pot (30 cm long \times 25 cm diameter) and is watered through straws that reach the soil surface of the outer pot. The seed is placed just inside the inner pot and the seminal roots are allowed to grow within the inner pot. The nodal roots are constrained within the soil of the outer pot and prevented from penetrating the inner pot by plastic.

that will contain the primary root was first filled with soil and covered with plastic with one hole in the middle for planting one or two seeds. Two plastic straws with several small holes were inserted through the inner plastic pot to irrigate the primary roots in this inner pot. The inner pot was contained within the outer pot (30 cm long and 25 cm diameter) in which only the nodal roots grew. A sandy soil mix (details in Boyer *et al.*, 2010) was used in both the inner and outer pots (see also moisture/potential curves typical of sandy soils in Brady, 1990). Eight days after sowing, seedlings were thinned to one plant per pot. Plants were harvested 21 d after sowing. In some pots, a plastic cover was placed over the soil surface to prevent evaporation from the soil surface.

The water contents of the inner and outer pots were varied. The treatments were: (1) moist primary root/moist nodal roots for the duration of the experiment (control); (2) moist primary root at sowing and watering withheld/moist nodal roots at sowing and watering withheld; (3) moist primary root/dry nodal roots at sowing without evaporation; and (4) moist primary root/dry nodal roots at sowing with evaporation. The moist water content was initially set to 12.52 % (g g^{-1}).

The soil water content was adjusted to its original level every 2 d by directly weighing the pots, except for treatment 2, where water was withheld from both compartments. The water was injected through the straws to the inner pot only in moist primary/dry nodal treatments, and to the inner and outer pots in the moist primary/moist nodal treatments. The soil water contents of the inner and outer pots before and at harvest in the second experiment are shown in Table 1.

Plant measurements

At harvest, shoots were separated into stem and leaf. Leaf area was recorded with a leaf area meter (Delta-T Devices, Burwell and Cambridge UK). Plant parts were oven-dried for 2 d at 75–80 °C and weighed.

Roots were carefully washed from the outer pot first and then the inner pot, maintaining the entire root systems intact. Roots were immediately preserved in 50 % ethanol until measured. Roots were first photographed intact in the region around the seed and crown with a digital camera. From the images, the angle between the two outer nodal roots of the crown was calculated using the freeware image analysis package ImageJ (<http://rsbweb.nih.gov/nih-image/>). Two lines were first drawn with the software along the length of the outer nodal roots, and the angle of their spread was determined with the software. Then the number of nodal roots was counted, and the lengths of the main axile roots of primary and nodal roots were measured by ruler. The total nodal and primary root length was measured after separation and staining with a root length scanner system (WINRhizo software and an Epson 1680 modified flatbed scanner, Regent Instrument Inc., Quebec, Canada) using the methods described in Watt *et al.* (2005). Branch root length was calculated by subtracting the axile length measured by a ruler from the total scanned length.

Statistical analyses

Experiments were designed as a factorial arrangement in a completely randomized design with four or five replicate pots per species per treatment. The first factor was plant species and the second was water treatment. Analyses of variance were carried out and comparisons between mean values were made using least significant differences (l.s.d.) between means at a significance level of $P = 0.05$.

RESULTS

Treatment 1: moist primary/moist nodal

Millet shoots grew almost twice the size of those of sorghum in the well-watered control (Table 2). The total shoot dry weight of millet was 86 % greater than that of sorghum; the leaf area was 70 % greater although the tiller number was similar for the two species. Millet used 37 % more water than sorghum and it also had a higher water use efficiency (WUE) for above-ground growth (Table 2).

As with the shoots, millet roots were twice as long as those of sorghum (Table 3). This was due entirely to millet having more nodal root length in the outer moist pot, which was six times greater than that of sorghum (Table 3, Fig. 2B). Primary root

TABLE 1. Soil water content (SWC) in the outer pots of the split-pot experimental set-up shown in Fig. 1 at the beginning (initial) and at harvest of pearl millet and sorghum

Species	Soil treatment	Initial SWC (outer pot, % g g ⁻¹)	Final SWC (outer pot, % g g ⁻¹)
Sorghum	1. Moist primary/moist nodal	12.5	11.5
	2. Moist primary watering withheld/ moist nodal watering withheld	12.5	5.14
	3. Moist primary/dry nodal without evaporation	2.5	1.25
	4. Moist primary/dry nodal with evaporation	2.5	0.74
Millet	1. Moist primary/moist nodal	12.5	11.3
	2. Moist primary watering withheld/moist nodal watering withheld	12.5	3.82
	3. Moist primary/dry nodal without evaporation	2.5	1.19
	4. Moist primary/dry nodal with evaporation	2.5	0.66

Inner pots were at 12.5 % SWC. Treatments describe the moisture conditions in the inner pot around the primary (seminal) roots and in the outer pot around the nodal roots.

TABLE 2. Shoot parameters of sorghum and pearl millet after growth in the experimental set-up shown in Fig. 1, with primary (seminal) and nodal roots growing in different soil moisture contents

Species	Soil treatment	Shoot dry weight (g) per plant	Tiller number per plant	Leaf area (cm ²) per plant	Total water used (g)	Water use efficiency (shoot dry weight per water, g L ⁻¹)
Sorghum	1. Moist primary/moist nodal	0.662	2.5	178	198 ± 15	3.289 ± 0.25
	2. Moist primary watering withheld/moist nodal watering withheld	0.600	1.0	106	164 ± 15	3.267 ± 0.203
	3. Moist primary/dry nodal without evaporation	0.640	1.6	151	178 ± 16	3.131 ± 0.271
	4. Moist primary/dry nodal with evaporation	0.44	0	82	111 ± 18	3.078 ± 0.463
Millet	1. Moist primary/moist nodal	1.234	2.8	261	272 ± 23	4.540 ± 0.07
	2. Moist primary watering withheld/moist nodal watering withheld	1.280	2.6	217	272 ± 26	4.331 ± 0.127
	3. Moist primary/dry nodal without evaporation	0.935	2.8	148	184 ± 38	3.730 ± 0.238
	4. Moist primary/dry nodal with evaporation	0.810	2	135	166 ± 9	3.943 ± 0.637
L.S.D.		0.22	0.7	61	NA	NA

Values are means of five replicate pots per species and treatment. Means followed by the same letter are not significantly different at $P = 0.05$. L.S.D., least significant difference at $P = 0.05$. Water-related means followed by standard deviation.

TABLE 3. Length of pearl millet and sorghum root systems and their percentage nodal components when grown in the split-pot system shown in Fig. 1 with varying moisture contents around primary (seminal) roots in the inner pots and nodal roots in the outer pots

Species	Soil treatment	Total length (cm)	% of total root length that is nodal root	% of total nodal root length that is branch root
Sorghum	1. Moist primary/moist nodal	5636	13	70
	2. Moist primary watering withheld/moist nodal watering withheld	3749	10.3	69
	3. Moist primary/dry nodal without evaporation	4051	10.5	70
	4. Moist primary/dry nodal with evaporation	3220	1.1	0
Millet	1. Moist primary/moist nodal	10010	58	93
	2. Moist primary watering withheld/moist nodal watering withheld	8996	80	95
	3. Moist primary/dry nodal without evaporation	5355	16	61
	4. Moist primary/dry nodal with evaporation	4851	0.6	0

Values are means of five replicate pots per species and treatment.

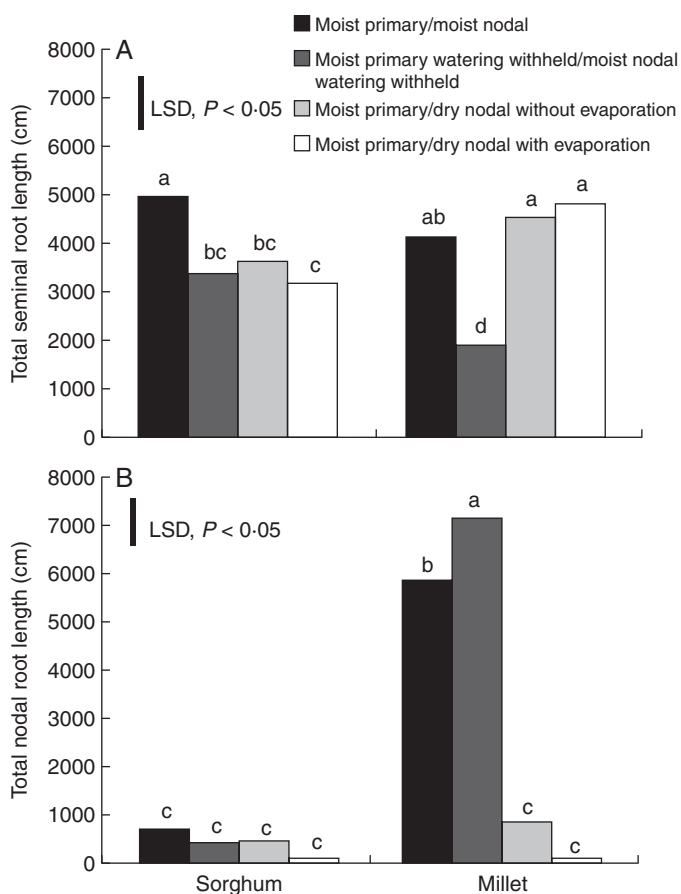


FIG. 2. Mean of (A) total seminal root length and (B) total nodal root length in the inner and outer pots, respectively, of the split-pot system shown in Fig. 1. Values with different letters are significantly different at $P < 0.05$.

lengths were similar (Fig. 2A). Millet nodal root number and nodal axile root length were approximately double those of sorghum, and nodal root branch length was approx. 10-fold greater (Fig. 3).

Treatment 2: moist primary watering withheld/moist nodal watering withheld

Withholding water from the inner and outer pots had no significant effect on the total shoot weight of sorghum and millet

compared with the well-watered control (Table 2). Leaf area and tiller number were significantly lower in sorghum but not millet. Compared with treatment 1, millet had the same water use and WUE for above-ground growth, whereas total water use in sorghum was less than in treatment 1 (Table 2).

The length of the primary roots declined in both species as a response to the soil drying in both compartments (Fig. 2A). In millet, the total nodal root length increased (Fig. 2B) due to a 20 % increase in the length of the branch roots (Fig. 3C). In sorghum the length of the nodal roots declined but the spread angle widened (Figs 3B and 4B).

Treatment 3: moist primary/dry nodal soil without evaporation

Total shoot weight, leaf area and water use were significantly lower in millet, relative to the watered control, but not in sorghum. The WUE also declined in millet but not in sorghum.

Millet nodal root length declined >6-fold in the outer dry soil, but primary root length was not changed compared with treatment 1 (Fig. 2). For sorghum, there was no significant decline in the total nodal root length compared with treatment 1. However, the primary root length declined 28 %, despite continuing to receive moisture (Table 3, Fig. 2). This large decline in millet nodal root length in the dry soil was due almost entirely to a large loss of branch root length (Fig. 3C). The millet nodal axile root number did not change between treatments 1 and 2 (Fig. 3A), and the axile root length only declined about 30 % (Fig. 3B). For both sorghum and millet, the mean diameter of the nodal roots increased in the dry outer soil (Fig. 4A). The nodal roots grew at a more vertical angle in the dry soil compared with the moist soil of treatment 1, but this was significant only for millet (40 % narrower spread angle, Figs 4B and 5).

Treatment 4: moist primary/dry nodal soil with evaporation

The removal of the plastic from the surface of the outer pot allowed evaporation from the soil surface and resulted in a very dry soil moisture content of approx. 0.7 % around the nodal roots at harvest (Table 1). Sorghum was more sensitive to surface soil evaporation than millet compared with treatment 3, with plastic. Shoot weight was not significantly reduced, but leaf area, tiller number and water used by sorghum were all significantly lower than in treatment 3; however, this was not so in millet. Millet used 50 % more water than sorghum, shoot

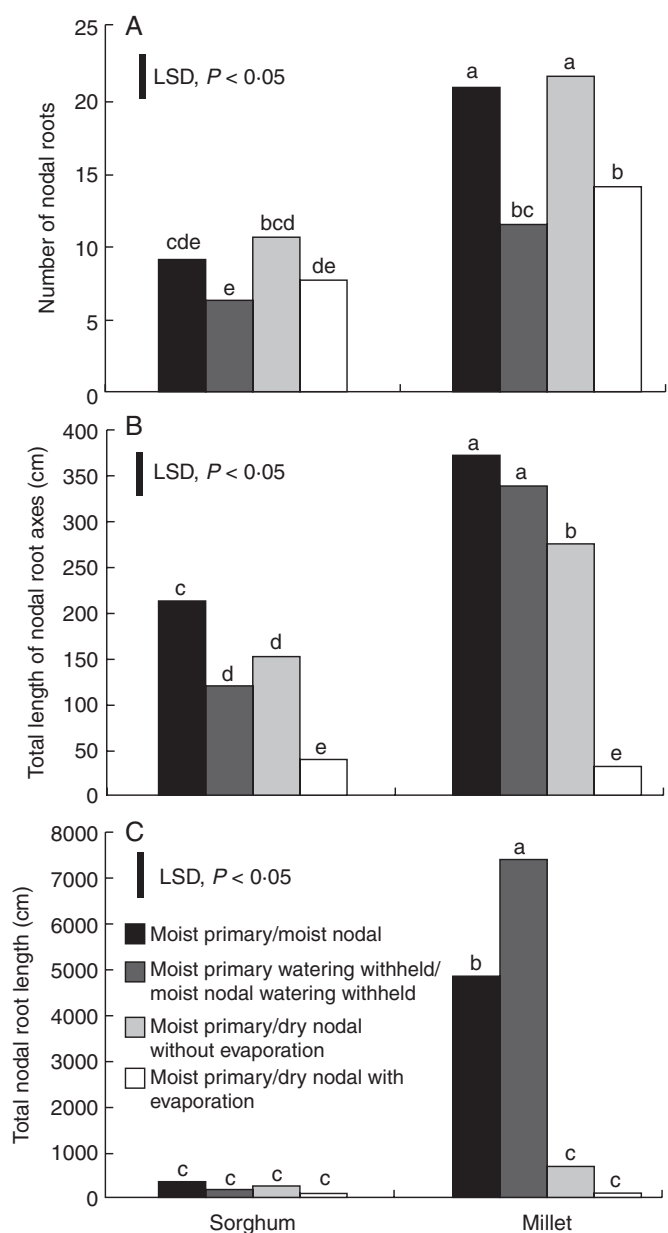


FIG. 3. (A) Nodal root number, (B) total axile length and (C) total branching of sorghum and millet measured after growing in the outer pot of the split-pot shown in Fig. 1. Values with different letters are significantly different at $P < 0.05$.

biomass was 86 % greater, and WUE was greater but not significantly different (Table 2).

The total length of the root system (primary and nodal roots) was similar between treatments 2 and 3 for both species (Fig. 2). Sorghum primary roots were shorter than in treatment 1, but millet primary roots were similar for treatments 1–3. Sorghum total nodal root length was similar for treatments 1–4. In contrast, the nodal axile root length declined >4-fold in both species between treatments 2 and 3 (Fig. 3B), while the nodal root diameter increased (Fig. 4A). In sorghum, the spread angle was narrower between treatments 1 and 3, but not significantly narrower between treatments 2 and 3 (Fig. 4B). In contrast, the spread angle of millet was more responsive to the

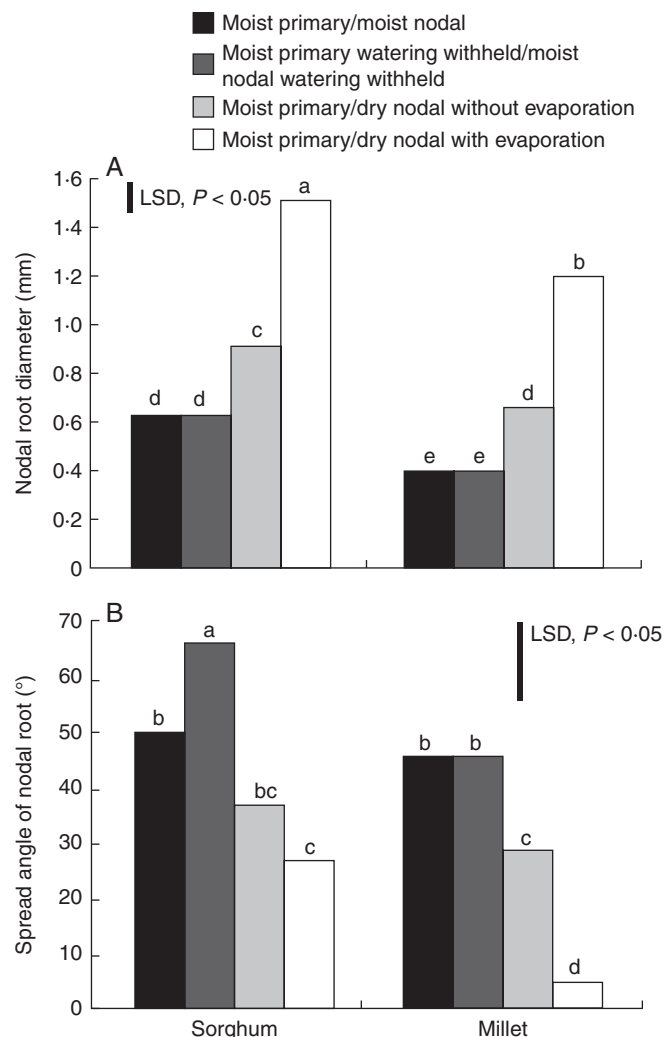


FIG. 4. (A) Nodal root diameter and (B) spread angle (shown in Fig. 5) of sorghum and millet measured after growing in the outer pot of the split-pot shown in Fig. 1. Values with different letters are significantly different at $P < 0.05$.

water content of the dry outer soil, being 10-fold narrower in treatment 3 than in treatment 1 (Figs 4B and 5B–F).

DISCUSSION

Millet and sorghum developed as expected. Millet was fast growing in all treatments and, despite its smaller seed, had the larger dry weight, leaf area, water use, WUE and total root length in almost every treatment. Despite both cereals being well adapted to dry environments, millet responded most favourably to the dry conditions. Millet had the smallest reduction in growth and water use in the treatment where water was withheld from both the primary and nodal root compartments. It also maintained a higher WUE, produced more tillers in the dry treatment than sorghum and its root system was more responsive.

The split-pot system allowed the following main observations to be made: (1) millet nodal roots showed greater phenotypic plasticity than those of sorghum, as length and angle responded more to water supply at no expense to shoot growth; and (2) nodal axile roots of millet and sorghum grew in very dry soil. However,

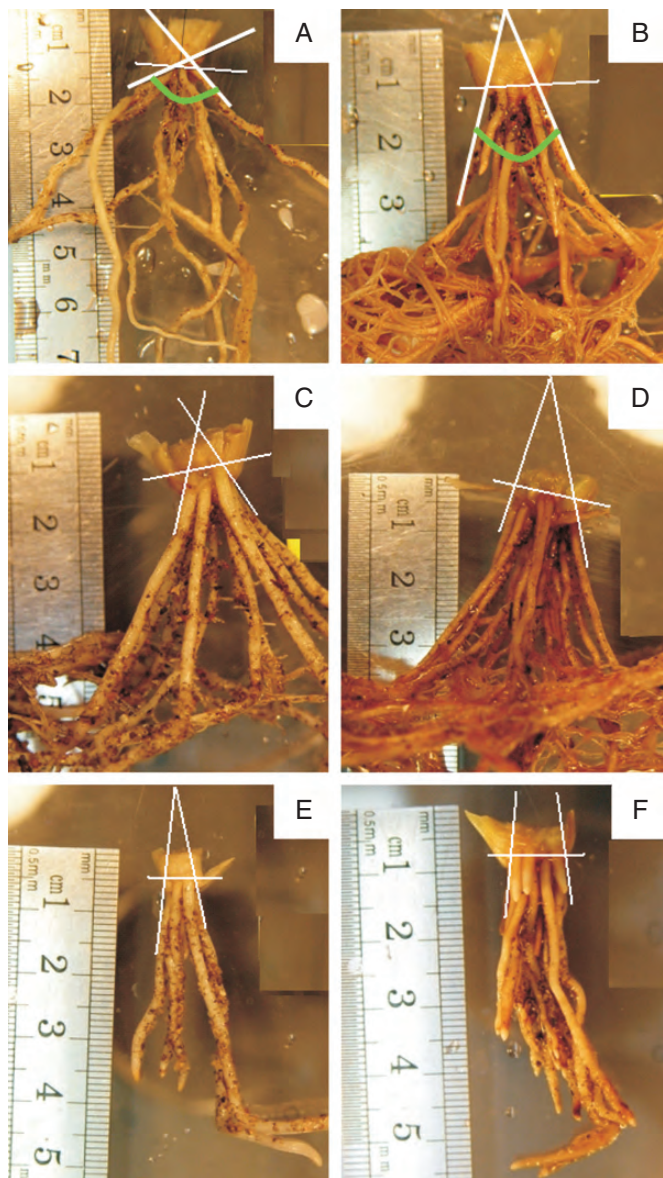


FIG. 5. The nodal roots for (A, C, E) sorghum and (B, D, F) pearl millet after growth in different soil moisture contents in the split-pot system in Fig. 1. Roots in (A) and (B) grew in moist soil, roots in (C) and (D) grew in dry soil covered in plastic, and roots in (E) and (F) grew in dry soil without plastic. The white lines drawn on the outside of the nodal roots were used to measure the angle of spread (indicated by green lines).

there were limitations to the system. First, in treatment 1, it was not possible to know from which compartment water was used because it was not possible to weigh the separate primary and nodal root compartments. This problem could be overcome by using moisture probes within the pots. The second limitation was that nodal axile roots could be impeded by the inner pot, especially when the outer soil was dry and they grew at a vertical angle (Fig. 5E). By modifying the shape of the inner pot into an inverted cone, impedance could be reduced. The third limitation was that occasionally roots found the hole at the top of the inner pot, presumably by hydrotropism. This could be minimized by making this hole as small as possible.

Millet showed greater phenotypic plasticity than sorghum and was more responsive to water supply around the nodal roots

Within the time of the experiment, millet grew 7-fold longer nodal roots than sorghum (mainly branch roots which were 10-fold longer) in all treatments where moisture was available to the nodal roots at sowing. One possible explanation for this responsiveness is its inherent shoot and root vigour, which was greater than that of sorghum in all four treatments (Table 2). We wondered if the onset of nodal axile roots and their branch roots was dependent on shoot size and developmental stage. Since millet was more vigorous (greater shoot biomass), nodal roots may have initiated earlier in millet and had more time to grow and respond to the outer pot conditions, especially their branch roots which contribute a large component of total length. We plotted root lengths against shoot biomass for millet and sorghum across treatments to test this relationship between fast shoot growth and earlier onset of nodal root growth (Fig. 6). Figure 6A shows that shoot mass and total root length (primary and nodal) are strongly positively correlated. When shoots were below approx. 1 g dry weight, primary root length is positively correlated with shoot mass (Fig. 6B). Shoots >1 g are strongly, positively correlated with nodal root length (Fig. 1C), and most of this nodal root length is branch roots (graph not shown). Larger shoots are not correlated with primary root length (Fig. 6B). Figure 6 also shows that only millet shoots grew larger than 1 g in these experiments. Thus an explanation for millet's nodal root response to soil moisture is that millet grows more quickly than sorghum. Sorghum could respond similarly if the experiment were allowed to run longer. The basis for rapid growth in millet compared with sorghum is unknown.

Other studies suggest that flowering time and vigour may be important for greater nodal root growth. Blum *et al.* (1977) compared two sorghum lines that differed only in their time of flowering, and followed their primary and nodal root development in hydroponics. The early-flowering line initiated nodal roots 2 d earlier than the late line and had 30 % more nodal axile roots by 35 d after emergence. These nodal roots maintained fast elongation rates and grew branch roots more readily than the later line if the primary root was excised. Time of flowering, however, may not explain the earliness of millet nodal root emergence in our study, as this cultivar is bred for long vegetative growth for animal grazing, and is at least as late flowering as the sorghum cultivar in the field (Rostamza, 2009). Uprety *et al.* (1979) compared four wheat varieties in the field, two more vigorous than the other two. The vigorous wheats had earlier emergence of nodal roots. If the early nodal roots emerged and managed to grow rapidly downwards through dry surface soil into moisture, they were more important to yield than the primary roots.

A different explanation for millet's response to soil moisture is that millet roots sense and grow in response to lower water contents than sorghum, independently of shoot size. Figure 6C shows that millet plants in treatment 2 grew more nodal root at 3–4 % SWC than those of similar shoot size in treatment 1, at 12 % SWC. Nodal root length appeared to be at the expense of seminal root length. Volkmar (1997) also observed that wheat nodal root length increased up to 2-fold when exposed to dry soil (approx. 2–3 % SWC) over the moist controls (approx.

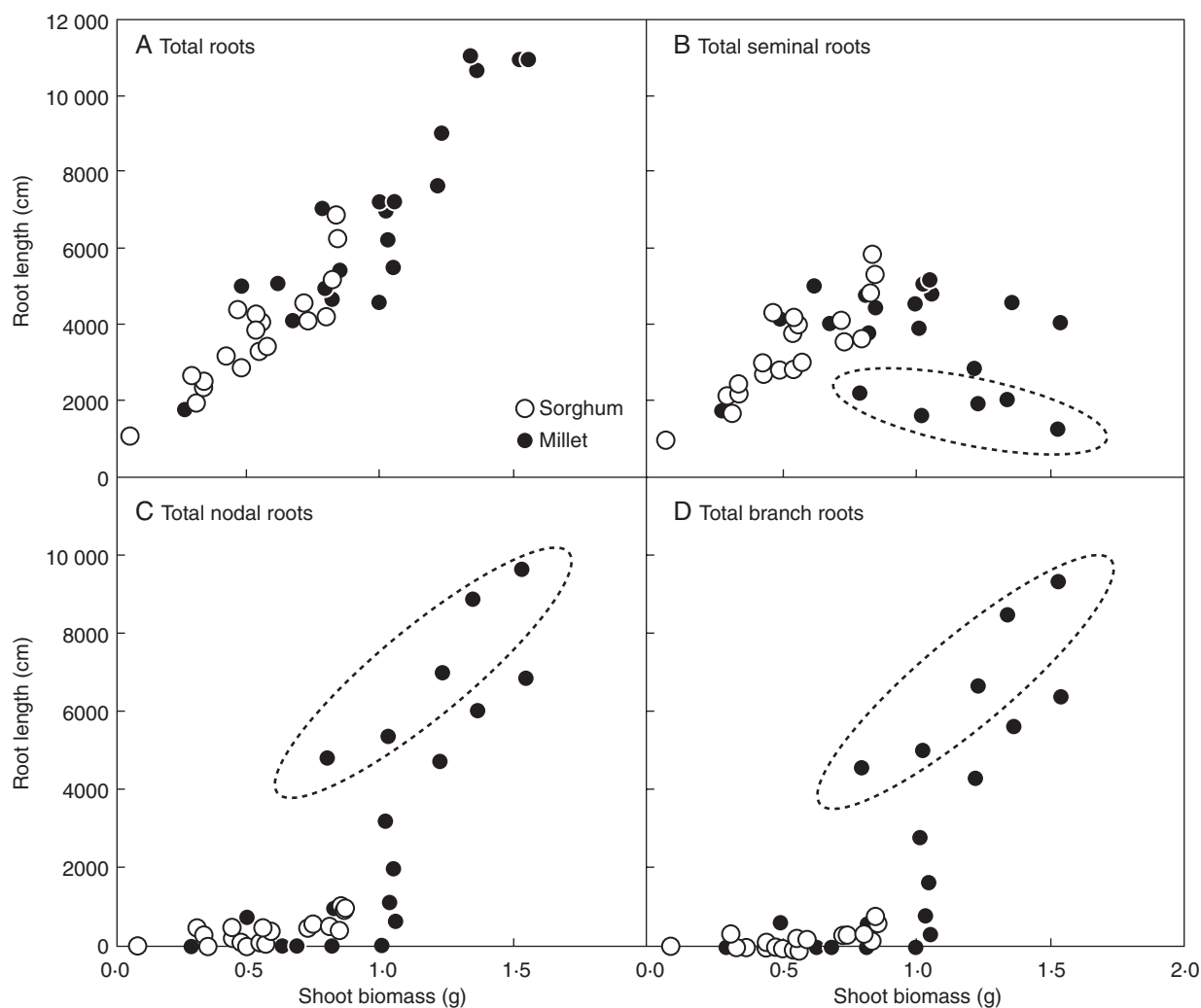


FIG. 6. Root length of millet and sorghum (as indicated in key) plotted against shoot total dry biomass (leaves and stems). All plants from the four treatments are presented to illustrate the relationships between shoot size and root length for the two species. The dashed ovals enclose millet plants in treatment 2, where water was withheld from the inner and outer pots.

9 % SWC). This was at the expense of shoot growth. The root length stimulation in millet was entirely in the branch roots. We can assume much of wheat's response was also in branch roots. Suralta *et al.* (2008) observed more branch roots under transient moisture stress in an aerobic, upland rice genotype than in a lowland, irrigated genotype. A number of studies report a greater root to shoot ratio as soil dries, indicating more root growth in drier soil (Sharp *et al.*, 2004). Comparing plants of similar shoot and total plant size such as in Fig. 6 is needed to see first if growth stage is important, and to identify the components of root systems responding most to water.

Nodal roots of millet and sorghum grew in extremely dry soil

Soil in the nodal root compartment of treatment 4 (no covering plastic) was air-dry (<1 % SWC), yet the nodal axile roots of millet and sorghum emerged and elongated about 3 or 4 cm. There would have been almost no water available for direct uptake for growth. We propose that water for elongation was taken up by the primary roots in the moist soil of the inner

pot and delivered to the nodal root tips via the phloem. This supports theoretical calculations of the amount of water maize root tips can receive from the phloem (Weigers *et al.*, 2009). Experimental studies with wheat primary axile roots showed that they grow in air, although more slowly than in moist soil, and that up to 45 % of the water for elongation at the root tips comes from the phloem (Boyer *et al.*, 2010). Interestingly, branch roots did not elongate in either species when the nodal compartment was dry, suggesting that phloem water was not used for their growth.

Covering the air-dry soil with plastic (treatment 3) raised the water content to just over 1 % – still an extremely dry environment. However, the nodal axile root length increased 6-fold in sorghum and 12-fold in millet (Fig. 3B). The reason for this large effect produced by a small increase in water content is unclear because the soil was still presumably too dry for direct uptake. We speculate that the main role of the plastic was to maintain 100 % humidity around the nodal roots, reducing root loss of water to the soil. Management or genetic factors that increase the humidity of surface soil are likely to increase nodal axile root

elongation and enable access to more soil water and nutrients. Management factors could include stubble retention or denser planting, and genetic factors include prostrate growth habit of lower leaves or leaf shedding to cover the soil surface. Interestingly, these cultivars became prostrate, shading the soil around the plant bases in field experiments when water was depleted below the wilting point (Rostamza, 2009).

Nodal roots of millet and sorghum grew more vertically in the dry soil, similar to maize nodal roots (Nakamoto, 1993). The downward direction of growth was in response to gravity and other signals to tropism. It may be moisture moving by capillary action from the primary root inner pot, which was not completely sealed from the outer pot to allow the stem to grow and expand. The mechanism of gravitropic response to extremely low soil water is a puzzle, since the root water potential would be expected to be higher than that of the soil, and water uptake not possible.

Conclusions, and root architecture components to select for breeding

Millet nodal roots had greater phenotypic plasticity in response to moist soil per unit time. This plasticity was associated with greater water capture, WUE and shoot growth. This plasticity may explain millet's adaptation to dry environments that receive some in season rainfall or irrigation (Zegada-Lizarazu and Iijima, 2005; Nicotra and Davidson, 2011). The results of this study indicate that in conditions where moisture is likely to be available to nodal roots, cereal genotypes could be selected for vigour and related ability to grow nodal roots early, and for greater root growth, especially branch roots, at lowish moisture contents. This should be tested in the field, as primary root depth may be compromised.

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LITERATURE CITED

- Blum A, Arkin GF, Jordan WR. 1977. Sorghum root morphogenesis and growth. I. Effect of maturity genes. *Crop Science* **17**: 149–153.
- Boyer JS, Silk WK, Watt M. 2010. Path of water for root growth. *Functional Plant Biology* **37**: 1105–1116.
- Brady NC. 1990. *The nature and properties of soils*, 10th edn. New York: MacMillan Publishing Company.
- Crush JR, Nichols SN, Ouyang L. 2010. Adventitious root mass distribution in progeny of four perennial ryegrass (*Lolium perenne* L.) groups selected for root shape. *New Zealand Journal of Agricultural Research* **53**: 193–200.
- Esau K. 1977. *Anatomy of seed plants*. New York: John Wiley and Sons.
- Hochholdinger F, Park WJ, Sauer M, Woll K. 2004. From weeds to crops: genetic analysis of root development in cereals. *Trends in Plant Science* **9**: 42–48.
- Hoshikawa K. 1969. Underground organs of the seedlings and the systematics of Gramineae. *Botanical Gazette* **130**: 192–203.
- Krassovsky I. 1926. Physiological activity of the seminal and nodal roots of crop plants. *Soil Science* **21**: 307–325.
- Nakamoto T. 1993. Effect of soil-water content on the gravitropic behavior of nodal roots in maize. *Plant and Soil* **152**: 261–267.
- Nicotra AB, Davidson A. 2010. Adaptive phenotypic plasticity and plant water use. *Functional Plant Biology* **37**: 117–127.
- Passioura JB. 1972. Effect of root geometry on yield of wheat growing on stored water. *Australian Journal of Agricultural Research* **23**: 745–752.
- Rai KN, Murty DS, Andrews DJ, Bramel-Cox PJ. 1999. Genetic enhancement of pearl millet and sorghum for the semi-arid tropics of Asia and Africa. *Genome* **42**: 617–628.
- Rostamza M. 1990. *Productivity and forage quality of pearl millet (Pennisetum americanum) as affected by water deficit and nitrogen fertilizer at different vegetative growth stages*. MSc Dissertation. Department of crop production and plant breeding, University of Tehran.
- Sallans BJ. 1942. The importance of various roots to the wheat plant. *Scientific Agriculture* **23**: 17–26.
- Shane MW, McCully ME. 1999. Root xylem embolisms: implications for water flow to the shoot in single-rooted maize plants. *Australian Journal of Plant Physiology* **26**: 107–114.
- Sharp RE, Poroyko V, Hejlek LG, et al. 2004. Root growth maintenance during water deficits: physiology to functional genomics. *Journal of Experimental Botany* **55**: 2343–2351.
- Singh V, van Oosterom EJ, Jordan DR, Messina CD, Cooper M, Hammer GL. 2010. Morphological and architectural development of root systems in sorghum and maize. *Plant and Soil* **333**: 287–299.
- Suralta RR, Inukai Y, Yamauchi A. 2008. Genotypic variations in responses of lateral root development to transient moisture stresses in rice cultivars. *Plant Production Science* **11**: 324–335.
- Upreti DC, Tomar OPS, Sirohi GS. 1980. Study on the contribution of nodal and seminal roots to the growth and yield of wheat varieties. *Indian Journal of Plant Physiology* **23**: 206–219.
- Volkmar KM. 1997. Water stressed nodal roots of wheat: effects on leaf growth. *Australian Journal of Plant Physiology* **24**: 49–56.
- Watt M, Kirkegaard JA, Rebetzke GJ. 2005. A wheat genotype developed for rapid leaf growth copes well with the physical and biological constraints of unploughed soil. *Functional Plant Biology* **32**: 695–706.
- Watt M, Magee LJ, McCully ME. 2008. Types, structure and potential for axial water flow in the deepest roots of field-grown cereals. *New Phytologist* **178**: 135–146.
- Wiegiers BS, Cheer AY, Silk KW. 2009. Modelling the hydraulics of root growth in three dimensions with phloem water sources. *Plant Physiology* **150**: 2092–2103.
- Zegada-Lizarazu W, Iijima M. 2005. Deep root water uptake ability and water use efficiency of pearl millet in comparison to other millet species. *Plant Production Science* **8**: 454–460.