Hydrogen Stable Isotope Analysis of Water Acquisition Ability of Deep Roots and Hydraulic Lift in Sixteen Food Crop Species

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Abstract : Deep root penetration, which allows access to deep soil water and hydraulic lift, may help plants to overcome drought stress. The aim of this study was to evaluate the ability of sixteen food crop species to take up water from deep soil layers and the extent of hydraulic lift by the use of deuterated water. Plants were grown in pots consisting of two loose soil layers separated by a hardpan and a Vaseline layer. The lower (deep) layers were always kept wet (32%; $\psi= -5$ kPa), while soil moisture in the upper (topsoil) ones was adjusted to 25% ($\psi= -7$ kPa) and 12% ($\psi= -120$ kPa) in the well-watered and drought treatments, respectively. The deuterium labeling of the deep soil water provided evidence that wheat, Job's tears, finger millet, soybean, barnyard millet, rice, and rye (in decreasing order of D_2O increments) extracted more water from the deep layers under drought than well-watered in topsoil. These species showed significantly greater hydraulic lift under drought, except for soybean. Most of these species also showed increased root length density in deep soil layers and sustained high photosynthetic rates under drought. In contrast, pigeon pea, cowpea, common millet, pearl millet, foxtail millet, maize, barley, and oat did not show a significant increment in either deep-water uptake or hydraulic lift under drought. In summary, increased extraction of deep soil water under drought was closely related with the magnitude of hydraulic lift.

Key words : Cereals, Deuterium, Drought, Legumes, Rooting ability, Transpiration, Water uptake, Water source.

In semi-arid areas, crop productivity is mainly determined by water use efficiency and root water extraction ability. In these regions, water supplied as light rain easily evaporates from surface soil layers. On the other hand, greater amounts of water are often available in deep soil, which the deep roots of some annual crop species may access. Deep rooting of annual food crop species has been extensively studied before (Araki and Iijima, 1998; 2001a and b; Araki et al., 2000). Vertical deep root penetration often helps plants to overcome drought stress (Sharp and Davies, 1985; Araki and Iijima, 2001b). For example, soybean (Reicosky et al., 1972), maize (Sharp and Davies, 1985), wheat (Proffitt et al., 1985), and upland rice (Araki and Iijima, 2001b; Araki and Iijima, 2004) show increased ability to take up water from deep wet soil when the topsoil dried out.

Water uptake in drought-stressed plants may be improved by hydraulic lift (Wan et al., 2000), which is the passive transport of water through the root axis from wetter soil layers to drier soil layers. It is driven by the water potential gradients between the plant roots and the soil (Richards and Caldwell, 1987). Generally speaking, the water in the deep soil layer is lifted up to the shallow, much drier soil through plant roots. This is usually evident at night, when transpiration ceases. When transpiration restarts, the uptake of stored water by the abundant shallow roots supplements the water uptake by the deep roots, resulting in higher rates of water supply to the shoot than would otherwise occur from the deep roots alone (Caldwell and Richards, 1989). The continuous operation of the deep roots under these circumstances could significantly increase their effectiveness (Yoder and Nowak, 1999). Furthermore, hydraulic lift has been proposed as a mechanism that can buffer plants against water stress during water deficit, serving as a drought-tolerance mechanism for some plants (Dawson, 1993; Yoder and Nowak, 1999; Wan et al., 2000).

Consequently, increased ability to take up water from deep soil layers and hydraulic lift may be desirable characteristics for food crop species cultivated in areas where substantial amounts of water are present in the subsoil and the topsoil is prone to drought. It is not clear, however, whether enhanced water uptake from wet deep soil is a common feature among food crop species. Furthermore, there is no information about the relationship between hydraulic lift and the ability of roots to take up water from deep soil. The objective of this study was to compare the deep root water uptake abilities of cereal and legume food crop species and their relationship with the hydraulic lift at the late stage of plant development.

Abbreviations : ANOVA, analysis of variance; δD, H isotope composition.

Material and Methods

1. Plant materials and growth conditions

The experiment was conducted in a greenhouse with average minimum and maximum temperatures of 24-35 °C in summer and 10-27 °C in winter. Three summer legumes [soybean (*Glycine max* L.; cv. Okuwarawase), pigeon pea (*Cajanus cajan*; cv. ICPV-87119), and cowpea (*Vigna unguiculata* L.; cv. Nakale)], nine summer cereals [rice (*Oryza sativa* L.; upland rice cv. IRAT 109), finger millet (*Eleusine coracana* G.; cv. Gifu, local), Job's tears (*Coix lacryma-jobi* L.; cv. Kyoto, local), barnyard millet (*Echinochloa utilis* O.; cv. Okayama, local), common millet (*Panicum miliaceum* L.; cv. Saitama, local), pearl millet (*Pennisetum glaucum* L.; cv. Okashana, local), foxtail millet (*Setaria italica* B.; cv. Saitama, local), sorghum (*Sorghum bicolor* M.; cv. Saitama, local), and maize (*Zea mays* L.; pop corn cv. Robust 30-71)], and four winter cereals [barley (*Hordeum vulgare* L.; cv. Syunrai), wheat (*Triticum aestivum* L.; cv. Norin 61), rye (*Secale cereale* L.; cv. Haruichiban), and oat (*Avena sativa* L.; cv. Hayate)] were grown in pots of 7.5 cm diameter and 50 cm height (Fig. 1) similar to those used by Araki and Iijima (2004). Summer crops were sown between 8 June and 28 July, and winter crops were sown between 25 November and 12 December in 2002. The split pots consisted of two compartments, each 25 cm high; the upper (topsoil) and lower (deep) compartments were separated by a Vaseline layer (2-3 mm thick), which prevented water movement between the two parts. The lower compartments were loosely filled with loamy sand soil with a bulk density of 1.33 Mg m^{-3}. In the upper compartments, a hardpan layer with a bulk density of 1.50 Mg m^{-3} was formed at a depth between 18 and 25 cm, and the rest of the compartment was loosely filled. Five seeds of each species were planted at the center of each pot. After one week, the number of seedlings was reduced to one per pot. The lower compartments were always kept wet (average 32%; $\psi = -5$ kPa), while soil moisture in the upper ones (shallow layer) was adjusted every day to 25% ($\psi = -7$ kPa) and 12% ($\psi = -120$ kPa) in the well-watered and drought treatments. Flowering and/or heading was initiated between 26 July and 16 September in 2002 for summer crops and 10 March and 11 April in 2003 for winter crops. Drought treatment was started between seven and ten days before flowering and/or heading. Until then, all plants were grown under well-watered conditions. Drought was continued for at least 15 days. Sampling was done between 10 August and 28 September for summer crops and between 1 April and 25 April for winter crops.

2. Deuterium labeling, xylem sap and soil sampling

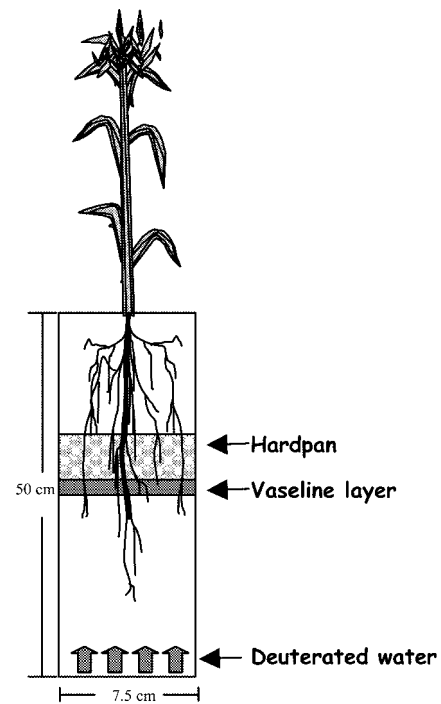Deuterated water that appears in xylem sap water

Fig. 1. Schematic representation of the two-compartment pot system. In the upper compartment, the well-watered and drought treatments were applied, while the lower compartment was always kept wet.

after enriched water has been applied to the deep layers could be considered as strong evidence of water uptake from the deep layers (Dawson, 1993; Caldwell et al., 1998). Heavy water (0.5 atom % D_2O), which was equivalent to the amount transpired the previous day, was applied to deep soil layers for three days before xylem sap collection. The deuterium concentration in the deep layer after three days of application was 0.12 ±0.02 atom %. Xylem sap samples were collected by cutting the stems, placing cotton puffs on the top of the stumps, and wrapping them with thin polyethylene film. Three hours after cutting the stems, cotton puffs containing xylem sap were gathered and placed in plastic bags and stored at −30 °C before analysis of δD (H isotope composition) of the extracted xylem sap. The xylem sap exudation rates were determined by weighting the xylem sap absorbed to the cotton puffs during three hours. Soil samples were collected from topsoil; care was taken to minimize evaporation and, therefore, isotopic fractionation. The visible root debris was carefully removed during soil harvesting so as to minimize the error factors due to the root contamination to the sampled soil. Soil samples were placed in double plastic bags and stored at −30 °C until centrifugation for δD analysis. Irrigation water (non-labeled water) applied to the upper compartments was also collected in Eppendorf tubes and stored in the same way as xylem sap and soil samples before deuterium analysis.
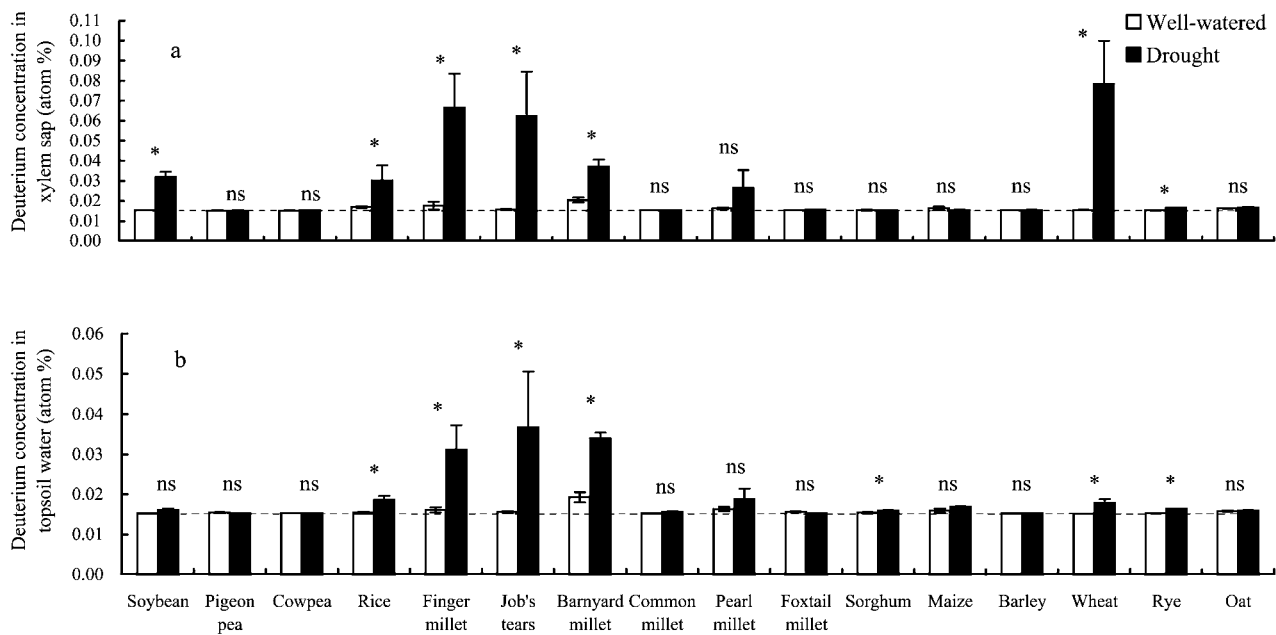
Fig. 2.   Water uptake from deep soil layers and hydraulic lift, expressed by deuterium enrichments in xylem sap (a) and topsoil water (b) of sixteen food crop species grown under different moisture conditions. Vertical error bars indicate the standard error of the mean. * indicates a significant difference at P<0.05. The dotted line indicates the average deuterium concentration in non-labeled irrigation water (tap water). A Vaseline layer prevented water movement between topsoil and deep soil layers. Deuterated water was applied only to deep soil layers.

δD values were determined by mass spectrometry (DELTA^{plus}, Finnigan Mat Instruments, Inc.) in water collected from plant xylem sap, soil water, and irrigation water. Isotope ratios are presented in standard delta notation (δD) in parts per thousand (‰) relative to Vienna Standard Mean Ocean Water (V-SMOW). The δD values were expressed as δ 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 %).

3.   Shoot and root sampling

Photosynthetic and transpiration rates were measured by a portable photosynthesis analyzer (LI-6200) between one and two days before plant sampling. Shoot samples were oven dried at 80 °C for three days for dry weight determination. Roots in all three layers were sampled immediately after xylem sap collection. Roots were carefully washed with tap water and preserved in FAA (formalin-acetic acid-alcohol) for further analysis. Roots of summer crops were digitally scanned into a personal computer for root length and diameter measurements using the NIH image program (a public-domain image analysis program) following the method developed by Kimura et al. (1999) and Kimura and Yamasaki (2001). In the case of winter cereals, only root length was measured, following the same procedure as for summer crops.

4.   Statistical analysis

Pots were arranged in a completely randomized design, with three and four replicates for summer and winter crops, respectively. One-way analysis of variance (ANOVA) was used to compare the effects of the drought treatments. The relationship between deep root water uptake and hydraulic lift was investigated by a simple linear regression analysis for summer and winter crops, respectively. The analysis was done separately due to the different evapotranspiration demand of these two seasons.

Results

1.   Water uptake from deep soil layers

Fig. 2a shows the ability of several crop species to take up water from deep soil layers, as expressed in the enriched deuterium values in xylem sap water. The dotted line shows the natural abundance of irrigated water, so the values beyond the dotted line are the atom % excess values. Wheat, Job's tears, finger millet, soybean, barnyard millet, rice, and rye (from the largest to the smallest increments, in that order) showed significant increments in the deuterium concentration in xylem sap water after they were subjected to drought in topsoil layers. The range of deuterium enrichment among these species was large. The deuterium concentration in wheat xylem sap rose up to 0.0631 atom % excess, while that in rye showed only 0.0013 atom % excess even though there was a significant difference. Soybean was the
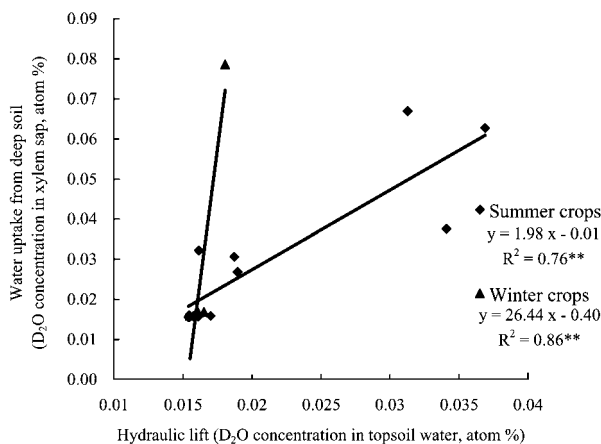
Fig. 3.   Relationship between the ability of deep roots to take up water (D_2O concentration in xylem sap) and the occurrence of hydraulic lift (D_2O concentration in topsoil layers) for summer and winter crops under drying topsoil layers. Each data point represents the average values of summer and winter crop species.

only legume that showed increased deuterium value (0.0167 atom % excess) under drought. Although pearl millet showed a higher deuterium concentration (0.0113 atom % excess) under drought, no significant difference was found due to the fluctuation among the replicate plants. On the other hand, the deuterium concentrations in xylem sap in the other two legumes and seven cereals were close to the deuterium values of irrigated tap water (non-labeled water). Furthermore, no statistical differences were found between the well-watered and drought treatments (Fig. 2a).

2.   Hydraulic lift

Increased deuterium values in topsoil water would be an indication that roots lifted water up from wet deep soil and released it into drier topsoil layers. Fig. 2b shows the deuterium values in topsoil water of the 16 species tested. In addition to marked increments in xylem sap water, significant deuterium enrichments of topsoil water were evident in wheat, Job's tears, finger millet, barnyard millet, rice, and rye but not in soybean (Fig. 2) when plants were subjected to drought. Sorghum also showed a statistically significant increment in deuterium concentration in topsoil although the difference between the treatments is not remarkable (only 0.0006 atom % excess). Results from the ANOVA demonstrated that the rest of the species did not exhibit significant increments in deuterium concentration in topsoil waters by drought. The deuterium values of topsoil water in these species were close to the deuterium values of irrigated tap water (0.0152 atom %).

The observations of hydraulic lift, expressed in deuterium enrichment in topsoil layers, were positively related (significant at P<0.01, R^2 = 0.76 and P<0.01, R^2

= 0.86 for summer and winter crops, respectively) to the ability of deep roots to take up water, expressed in increased deuterium values in xylem sap water by drought (Fig. 3). Wheat showed a remarked higher deuterium concentration in xylem sap although that in top soil water did not. Consequently, the value for wheat alone became far from those for other winter crops.

3.   Root length density in deep soil layers

In agreement with the increased deuterium values in xylem sap and/or in topsoil water, one legume and four cereals exhibited significant increments in root length density in deep soil layers by drought in topsoil layers (Table 1). For these species, the root length density was between 1.2 and 3.3 times higher than in the control plants. The highest root length density increment was found in soybean, followed by rice, finger millet, wheat, and barnyard millet. The rest of the species did not show significant differences with respect to their control plants (Table 1).

4.   Length of fine deep roots

The length of fine roots (diameter 0-0.1 mm) in the deep layers was significantly increased by surface-drying in soybean, rice, and barnyard millet (Table 1). Finger millet, common millet, and foxtail millet also showed increased trends although they were not statistically significant. In the rest of the species, the length of fine roots was not significantly altered by drought in topsoil layers.

5.   Photosynthetic rate

Drought stress in topsoil did not significantly reduce the photosynthetic rate of soybean, finger millet, Job's tears, barnyard millet, pearl millet, and wheat. This would be most probably attributed to the water supply from deep wet soil layers. Photosynthetic activity in the other nine species was significantly reduced by drought in topsoil layers (Table 1).

6.   Shoot dry weight, total root length, and xylem sap exudation rates

In this experiment drought was imposed to the plants for nearly two weeks around flowering time. The short-term drought did not significantly reduce the shoot biomass production except for pigeon pea and barley (Table 2). Total root length in a plant which was distributed to all three layers, i.e., shallow, compact, and deep soil layers were not significantly altered either, except for finger millet, barnyard millet, barley, and wheat. The reason for the interspecific difference observed in the biomass production and total root elongation might be related to the sensitivities to the short-term drought stress during flowering time and to the intensities of drought stress which differed depending on the relative root mass in a limited

Table 1.　Photosynthetic rate, root length density and length of fine roots in the deep soil layer (25-50 cm depth) of sixteen food crop species grown under different soil moisture conditions.

	Photosynthetic rate		Root length density		Length of fine root (diameter 0-0.1mm)[!]	
	Well-watered (μmol m^{-2} s^{-1})	Ratio [#]	Well-watered (cm cm^{-3})	Ratio [#]	Well-watered (m)	Ratio [#]
Soybean	7.01	1.02 [ns]	0.30	3.31 [*]	0.10	4.31 [*]
Pigeon pea	11.39	0.88 [*]	3.67	0.97 [ns]	0.87	0.87 [ns]
Cowpea	6.62	0.80 [*]	4.11	1.12 [ns]	1.22	0.69 [ns]
Rice	-	-	11.58	1.55 [*]	14.14	1.51 [*]
Finger millet	4.10	0.95 [ns]	23.64	1.52 [*]	10.04	1.42 [ns]
Job's tears	10.79	0.93 [ns]	5.01	1.44 [ns]	2.36	1.11 [ns]
Barnyard millet	8.54	0.93 [ns]	29.36	1.24 [*]	14.73	1.47 [*]
Common millet	8.52	0.68 [*]	8.94	1.18 [ns]	2.53	1.61 [ns]
Pearl millet	10.16	0.91 [ns]	13.94	1.08 [ns]	4.75	1.06 [ns]
Foxtail millet	9.43	0.84 [*]	6.44	1.70 [ns]	3.66	1.99 [ns]
Sorghum	11.92	0.91 [*]	14.21	0.73 [ns]	4.28	0.57 [ns]
Maize	9.44	0.92 [*]	9.35	0.89 [ns]	3.33	0.99 [ns]
Barley	4.21	0.72 [*]	5.06	0.86 [ns]		
Wheat	10.28	0.97 [ns]	6.44	1.34 [*]		
Rye	7.06	0.83 [*]	7.51	0.95 [ns]		
Oat	5.02	0.80 [*]	3.09	1.10 [ns]		

[#] indicates the ratio of drought to well-watered soil condition. * indicates a significant difference at $P<0.05$. [!] indicates that the fine root length of winter crops was not measured. – indicates no measurement.

volume of pot soil. In contrast, xylem sap exudation rates in most of the species showed significant reduction by the drought stress. The exudation rates would be related to the total root length, soil moisture availability in the rhizosphere soil, and the root activities under the drought condition imposed. The interspecific difference observed for shoot dry weight, total root length, and xylem sap exudation rates were not clearly related to the deuterium concentrations in either xylem sap or the top dry soil.

Discussion

Deep root water uptake and hydraulic lift during the flowering stage of sixteen food crop species were analyzed using a two-compartment pot system, emulating field conditions in which hardpan (compact soil layer) exists just above a water table and topsoil is prone to drought. Under these conditions, the extent of deep root water uptake and hydraulic lift differed among the food crop species.

1.　Water uptake from deep soil layers

The interspecific differences in deep root water uptake could probably be attributed to the development states of apoplastic barriers in deep roots

(Steudle, 2000), root penetration through compact soil layer, and root proliferation under wet soil conditions in the deep layers. Root elongation is usually reduced in compact soil layers, and the reduction rates differed significantly among crop species (Iijima and Kono, 1991; 1993; Iijima et al., 1991). In the present study, the root penetration abilities among species cannot be compared due to the lack of essential control for compact soil layers. This study mainly focused on the response of deep roots to drought in topsoil. Most of the species that showed higher deuterium values in xylem sap under drought showed increased root length density in the deep layers (Fig. 2 and Table 1). The soil water potential in the deep layers was around −5 kPa, which is a partly anaerobic condition for some of the species examined, such as common millet, pearl millet, foxtail millet, maize, barley, and oat, according to the criteria of Kono et al. (1987) and Yamauchi et al. (1988). Sinha (1980) and Umaharan et al. (1997) also observed the negative effects of waterlogging on the shoot and root development of pigeon pea and cowpea. Therefore, the wet soil condition in deep soil should be one of the main causes of species-specific responses in terms of water uptake from deep and wet soil under drought in the topsoil layer. In fact, deep

Table 2. Shoot dry matter production, total root length and xylem sap exudation rate of sixteen food crop species grown under different soil moisture conditions.

	Shoot dry weight		Total root length		Xylem sap exudation	
	Well-watered (g)	Ratio [#]	Well-watered (m)	Ratio [#]	Well-watered ($g\ h^{-1}$)	Ratio [#]
Soybean	7.07	0.80 [ns]	81	1.02 [ns]	0.10	0.48 [*]
Pigeon pea	9.60	0.73 [*]	164	1.06 [ns]	0.15	1.02 [ns]
Cowpea	9.20	1.01 [ns]	211	1.01 [ns]	0.71	0.66 [†]
Rice	9.63	1.08 [ns]	567	0.86 [ns]	1.21	0.95 [ns]
Finger millet	12.03	1.12 [ns]	619	1.35 [†]	0.24	0.42 [*]
Job's tears	6.87	1.12 [ns]	187	1.06 [ns]	0.63	0.51 [*]
Barnyard millet	14.67	1.04 [ns]	724	1.11 [†]	1.30	0.62 [†]
Common millet	7.97	1.06 [ns]	212	1.08 [ns]	0.21	1.08 [ns]
Pearl millet	17.97	0.95 [ns]	319	1.04 [ns]	0.33	0.85 [ns]
Foxtail millet	7.33	0.83 [ns]	292	1.15 [ns]	0.24	0.56 [*]
Sorghum	19.27	1.01 [ns]	613	0.79 [ns]	0.62	0.82 [ns]
Maize	19.47	0.94 [ns]	299	0.94 [ns]	0.71	1.07 [ns]
Barley	14.91	0.85 [*]	176	0.85 [*]	0.11	0.48 [*]
Wheat	11.28	0.95 [ns]	165	1.13 [*]	0.13	0.48 [*]
Rye	8.63	1.09 [ns]	323	0.87 [ns]	0.08	0.54 [†]
Oat	7.89	0.80 [ns]	113	0.92 [ns]	0.03	0.75 [†]

[#] indicates the ratio of drought to well-watered soil condition. [*] and [†] indicates a significant difference at $P<0.05$ and $P<0.1$ respectively.

roots are often exposed to the anaerobic condition due to the lesser circulation of air between soil and the atmosphere.

The proliferation of fine roots, most probably branched lateral roots, in deep soil layers will increase the water uptake efficiency per unit root mass from deep moist soil layers (Table 1). Fine roots are more efficient for water absorption because they have greater root surface area per unit root mass as compared with the thicker axile roots. Kono et al. (1988) found an increased number of nodal roots in rice, finger millet, Job's tears, barnyard millet, sorghum and maize under waterlogged conditions. In these nodal roots, lateral roots emerge, and the length of fine roots thus increases. The root length density of soybean in the deep soil layer also increased as a result of drought in surface soil, indicating that the small (see Table 1) but active deep roots of soybean played an important role in supplying water to the shoots; similar results in soybean have been reported in pot (Reicosky et al., 1972) and field (Stone et al., 1976) experiments.

2. Hydraulic lift

Evidence in the literature indicates that hydraulic lift is widespread and variable in magnitude and timing among plants. For example, Yoder and Nowak (1999) were able to detect hydraulic lift in only one of three *Lycium pallidum* plants tested. Wan et al. (2000) reported the linkage of hydraulic lift to genetic variations in drought tolerance and root characteristics of maize genotypes. Corak et al. (1987) showed evidence of hydraulic lift in alfalfa plants, but Dirksen and Raats (1985) were not able to detect it. We also found high variability among species, even among individuals of the same species. Seven of the sixteen species tested in the present study showed increased deuterium values in topsoil water (Fig. 2b), which indicated the occurrence of hydraulic lift. In agreement with our findings, Xu and Bland (1993) and Valizadeh et al. (2003) also reported the occurrence of hydraulic lift in sorghum and wheat, respectively. However, to our knowledge, this is the first experiment that describes it in rice, finger millet, Job's tears, barnyard millet, and rye. In contrast, the other nine species did not show significant deuterium enrichments in topsoil water by drought.

Hydraulic lift has been previously shown in pearl millet (Vetterlein and Marschner, 1993), maize (Wan et al., 2000), barley and oat (McCully, 1995), and pigeon pea (Sekiya and Yano, 2004), but we were not

able to detect it. The different results are probably the consequence of large discrepancies in the severity of water stress treatments (shallow soil drought and deep soil excess moisture). Galamay et al. (1992) proposed that the acropetal lignification of the protective tissues of nodal roots is one of the strategies of some millet species to overcome water stress, such as waterlogging. The waterlogged condition in the deep layer of the present study may have enhanced the lignification in the older root axis in the topsoil dry region. This may have prevented water leakage from the root axis, and, consequently, hydraulic lift could not be observed. The stage of root development at which hydraulic lift determinations were done should also have affected the development of protective tissue, such as suberization in older roots in the dry region (Glinski and Lipiec, 1990). Furthermore, in our experiment, the compact soil layer prevented root elongation before the roots could reach the deep moist soil layers. Therefore, these factors may affect the ability of the deep roots of some species to take up water from the wet deep soil and release it into the dry topsoil.

3. Photosynthetic rate and water uptake

Drought stress in topsoil did not significantly alter the photosynthetic rate of most of the crops, which showed enriched deuterium values in xylem sap, except for rye (Fig. 2; Table 1). The decreased rates in rye could be attributed to the extent of water uptake from deep wet soil layer; the deuterium enrichment in xylem sap under drought was relatively small as compared with other species which showed significant increment of the enrichment. In contrast, the photosynthetic rate of pearl millet was not altered by the drought, although its water uptake from deep soil did not significantly increase. Pearl millet may have absorbed some deep soil water as indicated with the higher average values of the deuterium concentration in drought. Another possibility is that the degree of drought stress imposed on the plants in the present study would not be too severe for this species, because pearl millet is one of the most drought-tolerant species among the cereals examined.

In summary, some cereal and legume species showed higher ability to increase their extraction of water from deep soil layers, and this ability was positively related with the magnitude of hydraulic lift and increased root length density. Further experiments under different soil water conditions would be necessary to confirm the ability of food crop species to withdraw water from deep wet subsoil layers and the occurrence of hydraulic lift.

Acknowledgment

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