Differences between Water Extraction Patterns of Three Wheat (*Triticum aestivum* L.) Cultivars at Different Soil Depths under Gradually Downward Soil Drying Conditions

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ABSTRACT

In drought prone environments wheat crop growth and production depends strongly on the water stored in the soil before anthesis and, although some water remains in the soil after harvest, plants experience water deficit. In order to investigate whether water extraction patterns, as a plant feature, have a regulating effect on the amount of water used by them at different soil depths, three wheat cultivars (Asakaze, BR9, BR10) differing in origin and drought resistance in terms of grain yield were grown in pots under gradually downward soil drying conditions. The total water used by cultivars was the same up to the post anthesis stage of growth when plants were harvested. However, Asakaze used more water from emergence to the beginning of the stem elongation period of growth and BR9 used more after that period up to the post anthesis stage. Cultivars showed significant differences in root length at different soil depths. Asakaze was predicted to use more water from topsoil layers compared to BR9 and BR10. On the other hand, BR9 was expected to use more water from deep layers in comparison to Asakaze. These were suggested to be the effect of the higher root density of each cultivar in the top and deep soil layers. It is also suggested that higher root length density in deep soil layers could be targeted as a favorable trait for breeding wheat Cultivars, which are growing under gradually downward soil drying conditions.

Keywords: Root, Water extraction pattern, Wheat.

INTRODUCTION

Wheat root characteristics are considered as plant features, which have the potential to increase drought resistance. [23, 14, 12 and 26] Results from Blum *et al*. suggest that it is the higher root length which, in part, keeps the wheat yield stable across different moisture regimes. [4] A larger root system may benefit from a higher capacity for water uptake under dry conditions. [14, 28, 9] but the cost of more assimilate transferred to the roots may exceed the benefits of more assimilate fixed in shoot parts due to more wa-

ter absorbed. [18] Therefore, it seems that root growth and development needs to be optimized in relation to the water demand of the shoot parts in order to maximize the efficiency of water used to produce grain yield. [18] Significant genotypic variation has been found in the wheat root pattern of growth. [6, 7] It has been argued that different rooting patterns may result in different amounts of soil water available to the plant. [18] A significant correlation coefficient has been found between root distribution and the amount of water extracted from different depths of the soil. [20, 7] It is also reported

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that even a small difference in root density in the deeper layers may cause a greater difference in soil water content than in the upper layers [7]. Passioura suggested that seminal roots of spring wheat cultivars, which penetrate more deeply into the soil, have a higher hydraulic resistance that reduces the rate of water use and thereby increases grain yields [17]. The seminal root length of the wheat cultivars was shown to be significantly different after 4 weeks of growth [16]. They concluded that it is possible to modify the development of the seminal roots toward an optimum root development pattern. Oat plants selected for their longer seminal roots produced higher grain yield [3]. Wheat cultivars with more extensive deep root systems are shown to absorb more nutrients than cultivars with less extended root systems [11]. It has also been shown that roots of some wheat cultivars penetrate more quickly into the soil than the others under both wet and dry conditions [8].

In drought prone environments the natural pattern of water supply does not usually promise to meet the pattern of the crop water requirement to needed maximize the harvest index and grain yield. Hence, regulation of the use of water stored in the soil by the plant would be critical. Since seminal roots penetrating into deep soil layers [13, 21] and root length density are of two the major factors determining the ability of roots to extract water, [18] cultivars with a higher root density in deep soil seem to be suitable for this situation. The objectives of this study were to compare different drought resistant cultivars in terms of yield for possible differences in water extraction patterns and to find its relationship with the root development pattern.

MATERIALS AND METHODS

Three wheat (*Triticum aestivum* L.) cultivars were grown in pots during 1997. These were BR9 (a tall, drought tolerant cultivar from Brazil), BR10 (a semi-dwarf cultivar)

and Asakaze kumugi (a non-tolerant dwarf one from Mexico and Japan, respectively).

This experiment was conducted under a rain-shelter in the field at Tokyo University. PVC tubes (10.7 cm diameter) were used for the construction of the pots. Each pot included three 30 cm long and one 10 cm long tubes. The shorter one was sealed at the base with PVC plates ($144cm^2$) and served as the bottom part of the pots. A gap ($0.2 \times 2cm^2$) was made 5 cm above the bottom of each part and an additional one was made in the middle of one of the long parts. A gypsum block ($5.2 \times 5.3 \times 1.2$ cm^3) was placed in the tubes near each gap and its wire passed through the gap to the outside of the tube. Silicon stick was inserted into the gap and around the wire to keep them water and air tight.

A sun-dried soil mixture (8% W/W soil water content) was added to the bottom part, which was further lengthened by tapping the other long parts which, in turn, filled stepwisely with the soil. The same amount of soil (7,800g) was used in each pot so that the topsoil was located at 5cm below the top of the pots after applying equal vibration to them. The parts were arranged on each other was so that, at the final stage, gypsum blocks were located at soil depths of 10, 20, 30, 60, and 90 cm. Care was taken to keep the gypsum blocks in a vertical position during the filling of the tubes with soil. Pots were covered with Aluminum foil to prevent heating from solar radiation. Half-strength Hogland solution (3,600g) was added stepwisely to each pot. Twenty-four hours later, the electrical resistance of the gypsum blocks was measured using a soil moisture meter. In all pots electrical resistance was low except for the bottom ones, which showed very high values. This indicated that the water had not penetrated to the bottom layers of the soil, and so 800g more of the solution was added to each pot. After 24 hours, three seeds were placed on the top of the soil and covered with100g soil (3 cm) which, in turn was wetted by 40g water. Pots were replicated four times for each cultivar and arranged in a complete randomized

block design. No more water was added to the pots during plant growth. In order to estimate the direct evaporation from the soil surface, three unplanted pots were made and placed nearby the pots.

Four days after emergence, the seedlings were thinned to one per pot and a 3-cm layer of Perlite was added to the top of all the pots, including the unplanted ones. The amount of water lost by each pot was determined by measuring their weight every 2 to 3 days. Plants were small in size during 30 days after emergence, and so direct evaporation of water from the soil may contribute more to the water lost compared to the amount of water which is lost due to plant transpiration. Therefore, water used by each plant expressed as the difference between the water lost by the planted and the mean of the amount of water lost by unplanted pots until 30 days after emergence and thereafter as the amount of water lost by each pot. The electrical resistance of the gypsum blocks was measured regularly and the soil water content for each measurement was determined using calibration graphs, which had already been prepared for each of them. Changes in soil water content were used to predict the amount of water used by plants at different soil depths.

Plants were cut out at the soil surface 64 days after emergence when they were under severe stress conditions. Shoot parts were dried at 80°C for 24 hours. Pots were divided into parts and the soil contained in each part was the extracted and sieved using a fine screen to remove the roots. Roots were then washed carefully over the screen to remove the excess soil and stored in a 70% Ethanol solution at 4°C. Root length at different depths was measured using a root measuring system (Comair Root Length Scanner, Commonwealth Aircraft Corp. Ltd., Australia). The dry weight of the root samples was measured after drying the samples at 80°C for 24 hours. Root length density at each depth was expressed as the total root length of each part divided by the soil volume.

Data were subjected to analysis of variance and correlation analysis[29]. Dancan's multiple range test was used to compare differences between cultivar means. The amount of water used at each soil layer was predicted according to the relevant changes in the soil water content. More precise analysis of the relationships between water used and root length at each depth was performed by partitioning the correlation coefficients into path coefficients in order to determine the importance of root length at each layer on the water used, by solution of the following matrix equation: [29]

$$P = (X'X)^{-1}.X'Y$$

where P and Y are the vectors of path coefficients and the correlation coefficients of root length at different depths with the amount of water used, respectively, and X is the matrix of correlation between traits. Unexplained variations in water used were computed using the following equation;

$$r^2_{uy} = 1-(p^2_{1y}+p^2_{2y}+ p^2_{3y}+2p_{1y}p_{2y}r_{12} +2p_{1y}p_{3y}r_{13}+ 2p_{2y}p_{3y}r_{23})$$

where y is substituted for the water used during each period and 1, 2, and 3 are substituted for root length at 0-55, 55-95, and 0-95cm depths. u is a dummy variable, which represents the effect of all other unknown sources of variation in the amount of water used by plants.

RESULTS

Cumulative water used by wheat cultivars and the predicted amounts of water used are shown in Figure 1. The predicted water used was, on average, 38% more than the measured amount due in part, to the adjustment of the water used for evaporation from the soil surface and errors in reading the electrical resistance of the gypsum blocks. However, there was a good agreement between the measured and predicted amounts of water used in the pattern of water use. There was also a close relation between the predicted water used by cultivars with the root dry matter at each soil depth (Figure 2). Nevertheless, the predicted water used in the top layers was less than the amount used in the
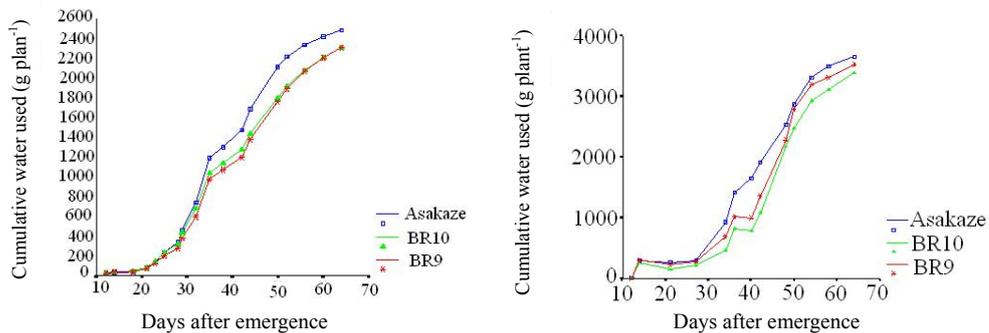
Figure 1. (Left) Cumulative water used by wheat cultivars grown in pots under gradually down-ward soil-drying conditions during growth. Data obtained by regular measurements of weight of the pots. (Right) Predicted cumulative water used by wheat cultivars grown in pots under continued soil-drying conditions. Data calculated using soil water contents at different depth measured using the gypsum block method.

deep layers, even though more roots were found in the top layers.

The total water used during the growth period was almost the same for all cultivars (Table 1). However, Asakaze used significantly more water during the period from seedling emergence to the beginning of stem elongation, while the amount of water used by BR9 was highest in the period from the beginning of stem elongation to anthesis (Table 1).

Changes in soil water content at different soil depths for wheat cultivars and control pots are shown in Figure 3. At 10cm soil depth, water content remained almost the

same for all cultivars until 28 days after emergence and, thereafter, Asakaze started to separate by reduc soil water content faster than the others. Similar results were found at 20, 30, and 60cm depths but the separation started after 30, 32, and 35 days after emergence. BR9 had the lowest soil water content at a depth of 90cm, which started about 37 days after emergence.

Root length and dry matter were significantly higher in Asakaze compared to the others, mainly due to higher root length in the top layers (Table 2). BR9 that had fewer roots in the top layers produced higher numbers of roots in the deep layers. Since the
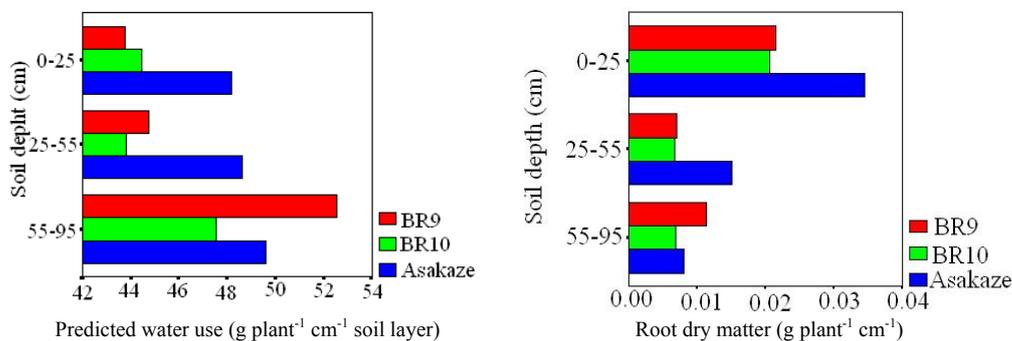

Figure 2. (Left) Predicted water used (gr) by wheat cultivars from different soil depths. Data calculated based on changes in the soil water content at each depth during plant growth. (Right) Amounts of root dry matter (gr/plant/cm of soil layer) of three wheat cultivars at different soil depths.

Table 1. Mean water used (g/plant) at different periods during growth for wheat cultivars grown in pots under gradually downward soil drying conditions.

Cultivars	Mean water used (g/plant)		
Periods	(0-38)	(38-64)	(0-64)
Asakaze	2108.65a	513.2b	2621.85a
BR10	1800.02a	717.08a	2517.1a
BR9	1760.86b	759.8a	2520.69a

Means followed by different alphabets are significantly different at 5% level based on the Duncan's multiple range test.

shoot dry matter of cultivars was almost the same, the root: shoot ratio was also significantly higher in Asakaze (Table 2).

A significant negative correlation coefficient was found between the water used from emergence to the beginning of stem elongation and the water used from stem elongation to the post-anthesis stage (-0.998, P≤ 0.001) However, the total water used was positively correlated with water used during the first period (+0.991, P≤ 0.001).

DISCUSSION

Genetic variations in root characteristics have been reported among wheat germplasms. [26,29,8,12,23,16,21] In this study, genetic variations for root length and dry matter were found at different soil depths suggesting that selection and breeding for these features is possible in wheat.

Under rainfed conditions soil drying usually takes place from top to the deep layers. Therefore, roots in the upper layers lose

and even may exude some water to dry soil. [2, 5] Deeper roots in wheat have been shown to become increasingly more efficient in water extraction as soil gradually becomes dry from the surface to deep layers [20]. However, in a study with three cereal crops it was found that even though root dry weight in the deep layers is less in triticale and rye compared to wheat, triticale could extract more water from the deep layers than wheat. It has been suggested that different root systems are of little importance in determining the water uptake pattern of the plants[25]. The downward drying of soil that is also observed in this study seems to be related to root density and, to some extent, to the time of arrival of roots in the different layers. It is suggested that cultivars like Asakaze with a high root in the at top layers may lose their advantages in water absorption when the soil of the top layers gradually dries. On the other hand, cultivars with a dense root at deep layers like BR9 may benefit from of delaying the high water use rate to the later growth stages by sending

Table 2. Mean shoot and root dry matter (g) and root to shoot ratio and root length density (cm/cm3) at different soil depths for wheat cultivars grown in pots under gradually downward soil drying conditions.

Cultivars	Dry matter (g/plant)			Root length density (cm/cm3)		
	Shoot	Root	R/S ratio	(0-55)	(55-95)	(0-95)
Asakaze	5.51a	1.44a	0.26a	3.36a	1.26ab	2.54a
BR10	5.13a	0.84b	0.18b	2.09b	0.94b.	1.39c
BR9	5.55a	0.99b	0.18b	1.63b	1.50a	1.92b

Means followed by different alphabets are significantly different at 5% level based on the Duncans multiple range test.

their effectiveness in water absorption [1]

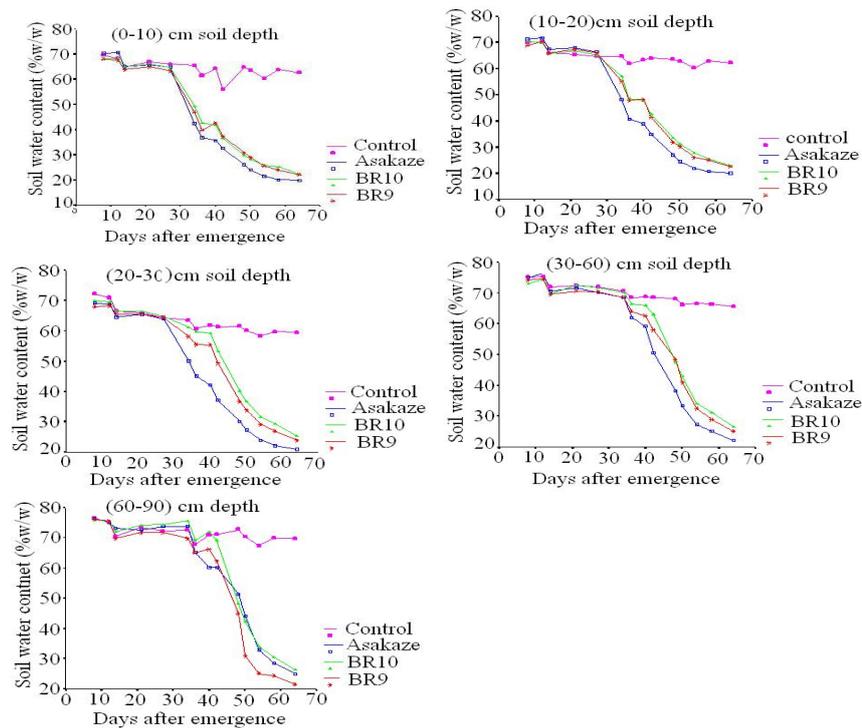their denser root system to the deeper layers.

Figure 3. Changes in the soil water content at different soil depths during the growth period of wheat cultivars grown in pots under gradually downward soil-drying conditions.

It has been suggested that a large root system with a high density in the topsoil layers might be beneficial in Mediterranean climates. [14] However, in their experiment, the higher grain yield of cultivar Karel with a high root density in the top layers compared to Capeity8 with a deeper root system is suggested to be the result of using 30 mm rain that fell after a prolonged period of drought [14]. Such rainfall is not normal after the start of the dry season in Mediterranean environments. The taller size of Capeity8, which might induce a higher transpiration rate, is also supposed to be another reason to decrease its yield [14]. However, in this study, BR9 with its more extended root system in the deep layers indeed had a slightly lower transpiration rate per unit of leaf area as measured only once during the growth (results are shown). BR9 has been shown to produce as much as double the grain yield as the cultivars Asakaze and

BR10 under progressive soil drying conditions. [30] As a drought tolerance mechanism, osmoregulation has been shown to exist in BR9. [31] However, a denser root system in deep soil also might be the reason under such conditions.

When plants rely on the water stored in the soil it would be much more beneficial to their yield if the absorption of more water is regulated so to as take place at later growth stages, particularly after anthesis, when there is no more potential for root growth. Regulation of the water extraction pattern by the plant seems to be possible through the action of some plant and environmental factors. Root morphology and development seems to play an important role in this regulation. Many nodal roots which originate from the crown are densely developed in the upper layers of the soil, since they tend to develop more horizontally [13] and make those layers gradually become dry during the period

Table 3. Path coefficients in the relationships between total water used and root length density at different soil depths.

Traits	Direct effect	Indirect effect via		
		RL(0-55)	TRL(55-95)	TRL
RL (0-55)	1.07	--	-0.080	-0.015
RL (55-95)	-0.240	0.376	--	-0.008
TRL	-0.015	1.046	0.131	--

$r^2_{uy} = -0.004$

of low evapotranspiration demand at early growth stages. Chemical messages, which are argued to be produced by stressed roots, [15] may play a role in the regulation of water use by decreasing the leaf expansion rate. On the other hand few seminal roots which are produced by coleorhiza, sparsely penetrating into deep soil layers, are usually still wet at anthesis [13]. If seminal roots play the major part in water absorption during the period from anthesis to the end of the grain filling stage, they need to be able to perform two main functions: i) To regulate the rate of water uptake. Previous findings show that they have the capacity to be genetically manipulated so that their hydraulic resistance changes via changes in the diameter of their main xylem vessel [23]. Interestingly, this regulation only works under dry conditions. [20] ii) To have the ability to extract the maximum available water stored in the deep soil. Root length density is the main plant factor determining the rate of water uptake by the plant. Jordan and Miller [10] found that sorghum root length density is too low in deep layers to extract all soil available water. Results of this study suggest that cultivars with denser root systems in the deep layers may have the ability to extract more water from those deep layers.

Even though the number of the genotypes used in this study was too few to have just one degree of freedom for correlation analysis, they provide a wide range of root density in the top and deep soil layers. Therefore, some correlation analyses appear to be interesting. The direct effect of root length at 0-55 cm depth on the total water used was much higher than that of a root length from 55-95 cm and also than the total root length (Table 3). This implies that the root length in the top layers is more important in determining the total water used under progressive soil drying. In the other words, the higher the number of roots in the top soil layers, the grater their contribution to the total amount of water used by the plants. It is the top layer's roots which strongly affect the rate of stored water use. It has been shown that root dry matter in the top layers, which are usually formed during the early growth stages, has been reduced in modern cultivars [19]. It has also been shown that cultivars with a less dense root system in the top layers would be beneficial for decreasing the amount of the water used in order for save it for later use [19].

CONCLUSIONS

This study showed that significant genotypic differences might exist in the pattern of root length of wheat cultivars at different soil depths. As these patterns are correlated with the patterns of water use from different depths it can be concluded that breeding cultivars with a denser root system in the deep layers in order to regulate the pattern of water use is possible.

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اختلاف در الگوی استخراج آب از اعماق مختلف خاک توسط سه واریته گندم (Triticum aestivum L.) در شرایط خشک شدن تدریجی خاک به طرف عمق

ع.ا. مقصودی مود و ت. یاماگیشی

چکیده

در مناطقی که در معرض خشکی قرار دارند رشد و تولید محصول گندم تا حد زیادی وابسته به مقدار آب ذخیره شده در خاک در مرحله قبل از گرده‌افشانی بوده و با وجود اینکه پس از برداشت محصول مقداری آب در خاک باقی می‌ماند، بوته‌ها تحت تاثیر خشکی قرار می‌گیرند. به منظور بررسی تاثیر الگوی مصرف آب به عنوان یک صفت گیاهی بر نحوه استفاده از آب ذخیره شده در خاک سه واریته گندم (Asakaze, BR9, BR10) که از لحاظ مبدا و مقاومت به خشکی بر اساس میزان عملکرد دانه متفاوت بودند در گلدان‌هایی که رطوبت آنها به تدریج به طرف لایه‌های پایین خاک خشک می‌شد کشت گردیدند. کل آب مصرف شده توسط واریته‌ها تا مرحله بعد ازگرده‌افشانی یعنی هنگامی که بوته‌ها برداشت گردیدند مشابه بود. با این وجود Asakaze از موقع سبز شدن تا شروع مرحله طویل شدن ساقه‌ها آب بیشتری مصرف نمود در حالیکه BR9 بعد از طویل شدن ساقه‌ها تا بعد از گرده‌افشانی آب بیشتری مصرف نمود. از لحاظ مقدار ریشه در اعماق مختلف خاک اختلافات معنی‌داری بین واریته‌ها وجود داشت. طبق محاسبات انجام شده آب مصرفی از لایه‌های سطحی خاک توسط واریته Asakaze بیشتر از BR9 و BR10 بود. از طرف دیگر مطابق محاسبات آب مصرف‌شده توسط BR9 از لایه‌های عمقی خاک بیشتر از Asakaze بود. بر اساس نتایج بدست آمده می‌توان چنین اظهار نمود که این اختلاف در مصرف آب می‌تواند ناشی از اختلاف در تراکم ریشه بین واریته‌ها در لایه‌های عمقی و سطحی خاک باشد. همچنین می‌توان اظهار نمود که تراکم ریشه بیشتر در لایه‌های عمقی خاک می‌تواند به عنوان یک صفت مطلوب برای واریته‌هایی که در خاک‌هایی که به تدریج خشک می‌شوند، کشت می‌گردند، در برنامه‌های اصلاحی مورد استفاده قرار گیرد.