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Drought Stress Effects on Root Anatomical Characteristics of Rice Cultivars (*Oryza sativa* L.)

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Abstract: The objective of this study was to compare some aspects of root anatomy of rice cultivars under irrigation and submerged conditions. Seedling of three new rice cultivars (Zayande-Rood, 829 and 216) were transferred to 9 lysiometers (200×120×100 cm) according to a randomized block design with two treatments (submerged and aerated condition) in three replicates. The amount of water consumption was recorded during growing season. Cross-sections of plant roots were obtained at two different times; two and four months after seedling. The root samples were prepared from 20 mm of tip. Root cross-sections were successively stained with 1% aqueous solutions of Methyl green and Congo red. Figures of sections were made by LM. Anatomical differences were observed among the three cultivars submitted to water regimes regarding the amount of aerenchyma tissue and cell walls of secondary tissues. The irrigated roots of the three cultivars presented a decreasing tendency in the proportion of the area of the cortex destined for the aerenchyma besides thickening of the cell walls of endodermis, pith and sclerenchyma layer cells. The rate of aerenchyma disappearing in the irrigated plants suggested different behaviors in different cultivars. Zyande-Rood and 829 cultivars exhibited extensive aerenchyma disappearing when the plants was irrigated compared to others. The sclerenchyma layer cell walls in 2-month-old roots were higher in irrigated plants and also was higher in Zayande-Rood cultivar. The result of xylem vessels wall indicated that the thicknesses of xylem vessels under submerged and irrigated condition were 3.6 and 7.9 μ in Zyande-Rood cultivar respectively. The thicknesses of endoderm cell wall of the submerged roots ranged from 4.6 to 10.8 μ for Zyande-Rood cultivar in submerged and irrigated conditions respectively and were lower for other cultivars. The water consumptions were 43.04 and 82.5 cm in whole season for irrigated and submerged condition, respectively.

Key words: Drought stress, root anatomical characteristics, *Oryza sativa*, aerenchyma, endodermis cell wall, xylem cell wall, cavitation, fiber cell wall

INTRODUCTION

Drought has a major impact on plant growth and development, limiting crop production throughout the world. Plant tissue responses to water stress depend on the physiological properties of the cell components and the anatomic characteristics that regulate the transmission of the water stress effect to the cells (Matsuda and Rayan, 1990; Shinozaki *et al*., 2003; Xiong *et al*., 2002; Olmos *et al*., 2007). Consequently, it should be expected that species living in habitats where flooding and drought alternate, will be under a strong selective pressure to develop the ability to adjust their anatomy and physiology according to the stress under which they are growing. Rice (*Oryza sativa* L.) a semi-aquatic cereal, is adapted to a variety of climates. A number of morphological, physiological and phenological traits have been proposed to improve the performance of rice challenged either by drought or flooding (Guzmań and Zamora, 2008; Siopongco *et al*., 2008). A principal mechanism by which rice has become adapted to water deficiency is through the possession of a pronounced root system which maximizes water capture and allows access to water at depth (Babu *et al*., 2001; Asch *et al*., 2005). However the most studied plastic response to flooding is the formation of aerenchyma in the root cortex (Justin and Armstrong, 1987; Justin and Armstrong, 1991; Striker *et al*., 2007). The aerenchyma found in roots provides an interconnected system of air channels, enabling gases to diffuse or ventilate from above-ground to below-ground organs and thus helping to maintain aerobic respiration and rhizosphere oxygenation (Jackson and Armstrong, 1999; Colmer, 2003). Increased aerenchyma is a

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common adaptive response of plants to soil anoxia (Justin and Armstrong, 1987; Jackson and Armstrong, 1999; Jackson and Colmer, 2005). In *Oryza sativa*, aerenchyma produced under flooding is formed by cell lysis and cell deflation. However, the formation of additional aerenchyma in the root cortex produces large variations in the internal structure of the roots (Justin and Armstrong, 1987; Suralta *et al*., 2008), which might lead to a trade-off in root mechanical strength necessary to resist both natural and anthropogenic soil compressive forces (Engelaar *et al*., 1993). The aerenchyma arrangement in the root cortex in response to flooding is variable among genotype (species, as well as cultivar/accession) (Jusin and Armstrong, 1987; Jakson and Armstrong, 1991; Guzmani and Zamora, 2008; Shiono *et al*., 2008) and environmental conditions (Colmer, 2003). Additional studies have suggested that a positive relationship exists between the frequency of flooding experienced by a given species and the ability of that species to form aerenchyma (Visser *et al*., 2000). Similarly, increased aerenchyma formation is positively related to increased growth and survival under waterlogged conditions (McDlonald *et al*., 2002).

The plant vascular system is responsible for the transport of water, ions, carbohydrates and other nutrients. It has been the subject of numerous studies, because it may also constrain the distribution of resources within a plant (Oriansal and Jones, 2001; Orians *et al*., 2002; Zwieniecki *et al*., 2003). Multiple characteristics of vascular structures have been investigated, such as modifications to the wall architecture, ion composition, protein expression and alteration of the xylem/phloem ratio, all of which are thought to be involved in the resistance of the plant to environmental stresses (Saijo *et al*., 2001; Equiza and Tognetti, 2002; Child *et al*., 2003; Zwieniecki *et al*., 2003). In contrast, most investigations have focused on the structure of the root cylinder (Colmer, 2003; Hoale *et al*., 2001; Steudle, 2000), especially during environmental stresses.

Moreover, plant cell walls play essential roles in growth, development, response to environmental factors (Chen *et al*., 2006). Variations in the cell wall during the development of the plant provide an excellent model system for studies of the mechanisms that determine growth regulation and adaptation to different environmental conditions (Moore *et al*., 2002; Sabba and Lulai, 2002). Tissues exposed to environments with low water availability have generally shown reduction in cell size, increase in vascular tissue and cell wall thickness (lignification) (Pitman *et al*., 1983). Anatomical alterations may occur in plants under water deficit to protect and adapt the species to this stress. These alterations are probably due to lignin or suberin deposits found in the exodermis, endoderm and cell layers neighboring the root cortex and medulla (Baruch and Mérida, 1995) that protect against desiccation and cortex cell death (Sharp and Davies, 1985; Sharp, 1996; Vasellati *et al*., 2001; Pena-Valdivia *et al*., 2005).

One approach to improve crop performance in water-limited environments is to select for genotypes that have improved yield in these environments. This approach has proved partially successful, but difficult to accomplish due to the variability of rainfall and the polygenic nature of drought tolerance (Mullet and Whitsitt, 1997; Mullet *et al*., 2005; Ribaut and Ragot, 2007).

The objective of this study was to quantify differences in root anatomy among three rice cultivars under submerged (traditional cultivation) and irrigated condition. In this research, the effect of fewer water supplies to rice in root structure and its component will be evaluated. Consequently we show how the comparative analysis of differences in drought resistance between rice cultivars can be used as criterion for selection of cultivars differing in water stress resistance. In rice, a better understanding of the morpho-anatomical and physiological basis of such differences in water stress resistance could be used to select or create new varieties of crops to obtain a better productivity under water stress conditions. This information will serve to genetic improvement of water deficit resistance in rice and also has potential benefits to agricultural especially in arid region for rice production.

MATERIALS AND METHODS

This experiment was conducted in late April 2005 in glass house of Biology Department, University of Isfahan. Three new cultivars of rice including 216, 829 and Zyande-Rood were planted in separated pans to have seedling. In May of 2005, three rice cultivars' seedlings were transferred to 9 lysiometers (200×120×100 cm) according to a randomized block design with two treatments of submerged and aerated condition in three replicates. During the growing season, the water level kept up to 5 cm in submerged treatment but in irrigated plots the water applied as closely spaced borders type irrigation. The amount of water consumption was recorded during growing season. Plant samples were obtained in two different times, two and four months after seedling. The roots of plant samples were washed and then fixed in FAA (formaldehyde+acetic acid+ 70% ethylic alcohol) for 72 h and kept in 70% alcohol until cutting. The microscopic sections were obtained from one third of root tip and then aerenchyma formation was compared within treatments. Root cross-sections were prepared from plant samples using fixed roots. Cross-sections were taken at almost 20 mm distances from the root tip and material inclusion in stalk were later lightened in sodium hypochloride solution at 20% commercial product for a period of three to five minutes and then washed three times in distilled water. The material was then neutralized with acetic acid solution at 5% for one minute and the washing process was repeated. The samples were successively stained with 1% aqueous solutions of Methyl green and Congo red (Da Silva *et al.*, 2003). Figures of sections were made by LM (Olympus microscope model BX-50).

RESULTS

The water consumed during growing season show that in irrigated treatment the amount of water consumed was 43.04 cm and in submerged condition was 82.5 cm. This is almost 2-fold of water used in submerged condition. The numbers of irrigation in different treatments were 4 and 10 times in irrigated and submerged treatment respectively (Table 1). Although comparison for water and labor saving is more concerned in agricultural sector, in this paper anatomical aspect is more considered.

Aerenchyma: Fully developed aerenchyma was observed at 20 mm distance from tip in submerged roots (Fig. 1A, B). The results indicated that rice roots under submerged condition (traditional cultivation) consist of more aerenchyma and air spaces than plants under irrigated condition. Interestingly, the roots of plants grown in irrigated condition for four months generally had less aerenchyma than those of plants grown in submerged system for two months (Fig. 1C-F). Furthermore, Zyande-Rood and 829 cultivars exhibited extensive aerenchyma disappearing when the plants was irrigated compared to others. Consequently in aerated soils, the overall amount of aerenchyma in Zyande-Rood and 829 cultivars was lower than the 216 cultivar (Fig. 1).

Table 1: The average amounts of water consumed in irrigated and submerged treatments in lysiometer for rice production

Treatment	Times of irrigation	Water consumed in each irrigation (cm)	Total amount of water (cm)
Submerged	36	2.29	82.50
Irrigated	4	10.76	43.04

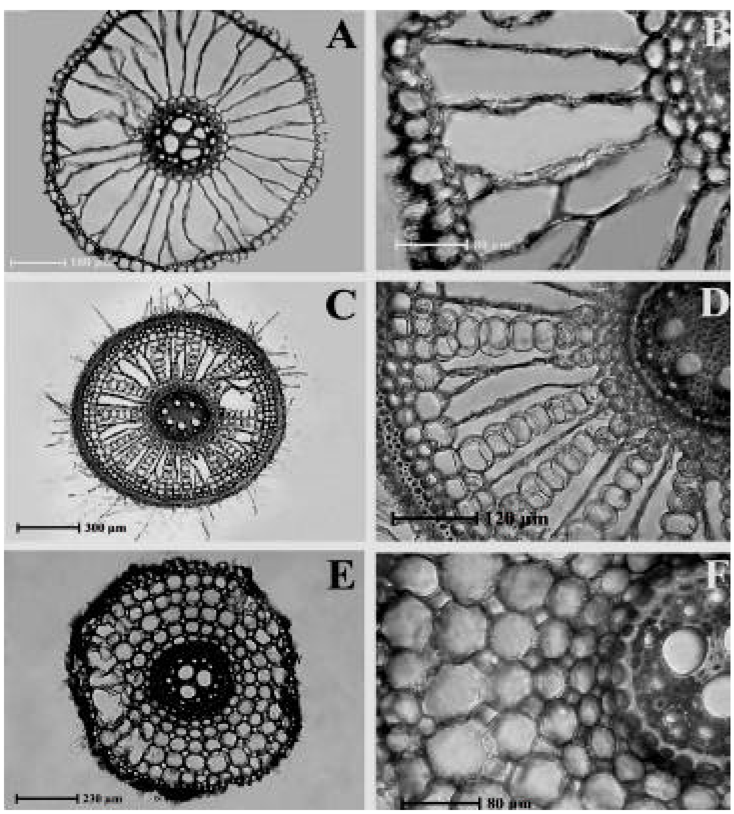

Fig. 1: Sections of roots of rice (*Oryza sativa*) plants cultivar Zayande-Rood (A-F). Aerenchyma formation at submergence (A and B), irrigated (2 months under treatment) (C and D) and irrigated (4 months under treatment) (E and F). The cross-sections were obtained at 20 mm from the root tip

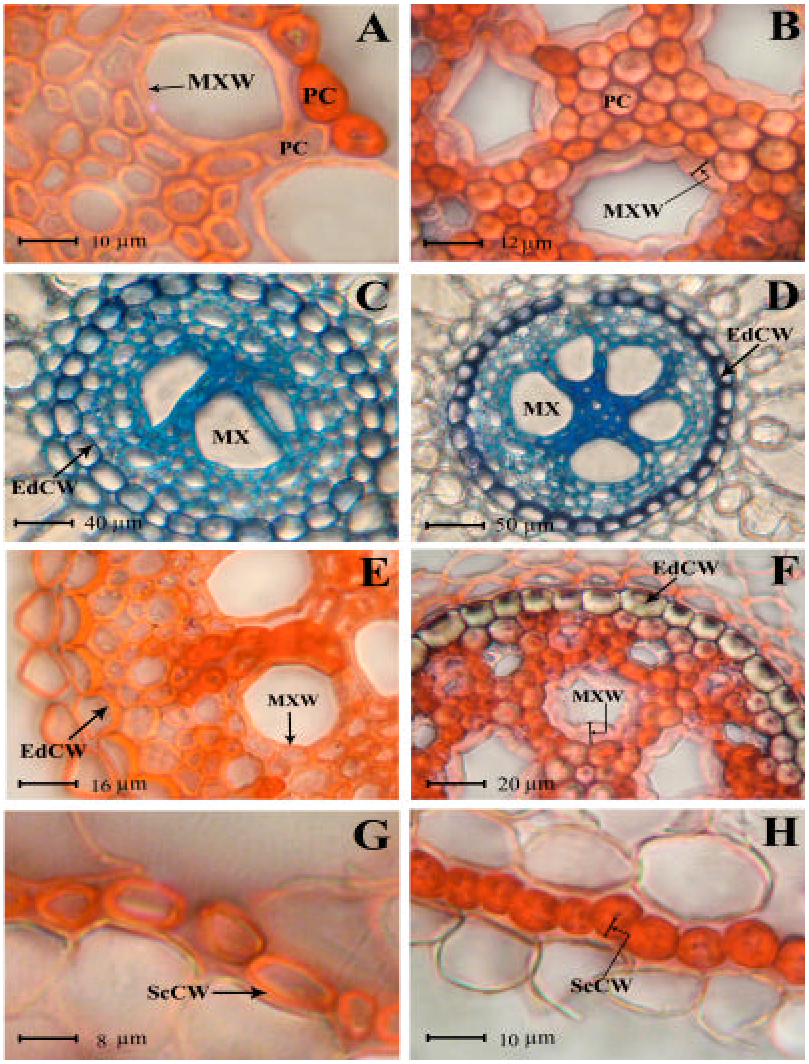

Fig. 2: Sections of root cylinder of rice (*Oryza sativa* L.) plants cultivar Zayande-Rood (A-F). MX : Meta Xylem, MXW: Meta Xylem Wall, PC: Pith Cell, EdCW: Endoderm Cell Wall, ScCW: Sclerenchyma Cell Wall Thickness of pith cell walls and xylem wall at submergence (A) and irrigated (B) treatments 30 mm from the root tip Microphotographs with details of the root cross-section showing the endoderm and casparian bound of rice in the submerged (C and E) and irrigated (D and F) root system treatments Freehand cross-sections were stained with methyl green (C and D) and Methyl green and Kongo red (A, B, E and F), The sclerenchyma layer in outer part of roots (OPR). G-H (2 months old) in submerged (G) and irrigated (H) treatments Freehand cross-sections taken at 30 mm from the root tip were stained with Kongo Red

Secondary tissues: The anatomical assessment of secondary tissues (xylem wall, endoderm cell wall and fiber cell wall) under irrigated system showed that the rice roots responded to this condition differently, presenting thickening in the secondary tissues of the cell wall compared to the submerged condition. Anatomical analysis of 4-month-old roots grown under irrigated condition shows significantly increase in the cell wall thickness of three cultivars specially Zyande-Rood cultivar (Table 2). However, the same result was observed for sclerenchyma layer cell walls in 2-month-old roots (Table 3). The result of xylem vessels wall indicated that the thicknesses of xylem vessels under submerged and irrigated condition were 3.6 and 7.9 µ in Zyande-Rood cultivar, respectively. The differences in xylem cell wall thickness were observed with less effect for different cultivars (829 and 216 cultivars) under different treatments.

Table 2: The changes in xylem pith and endoderm cell wall (µ) of rice at four months old plants in submerged and irrigated condition

	Xylem cell wall		Pith cell wall		Endoderm cell wall	
Cultivars	Submergence	Irrigated	Submergence	Irrigated	Submergence	Irrigated
Zayande Rood	3.6	7.9	1.2	3.7	4.6	10.8
829	3.9	6.8	1.2	3.2	4.7	8.9
216	3.7	5.5	1.1	3.2	4.5	7.2

The mean values were obtained from 20 samples

Table 3: The change in sclerenchyma layer thickness µ for two months old plants in submerged and irrigated condition

Cultivars	Submergence	Irrigated	Change (%)
Zayande Rood	1.6	3.4	112.5
829	1.8	2.8	55.6
216	1.6	2.3	43.8

The mean values were obtained from 20 samples

The cross-section of the root of plants shows massive secondary wall thickening of medulla cells and sclerenchyma layer (Fig. 2A, B, G, H). The results indicated that the thickness of fiber cell wall increased in three cultivars under irrigated condition.

This condition could accelerate the formation of secondary tissues components such as lignin, suberin and cellulose in the irrigated roots.

There were also differences in the thickness of endoderm cell walls of the rice roots under different treatments. It was observed that the endoderm cell wall under submerged condition was thickened compared to the irrigation condition. The effect of irrigation system on endoderm cell wall thickness was different in different cultivars. The highest difference was observed in Zayande-Rood cultivar and the lowest belongs to 216 cultivar. Plants grown for two months in submerged system, the endodermis at 20 mm distance from the root tip was not developed significantly (Fig. 2C, D). In contrast, the roots were grown for 4 month under submerged condition the endoderm cell wall was increased but it was not as much as the rate of roots under irrigated condition (Fig. 2E, F). The thicknesses of endoderm cell wall of the submerged roots ranged from 4.6 to 10.8 µ for Zyande-Rood cultivar in submerged and irrigated conditions, respectively (Table 2) and were lower for other cultivars.

DISCUSSION

Aerenchyma: A decrease in root's aerenchyma was observed in all cultivars in irrigated condition compared to the submerged treatment (control). However in Zyande-Rood and 829 is more extensive. The existence of aerenchymas helps the plants under conditions of excess water in the soils to maintain aerobic respiration by maintaining O_2 diffusion (Kawawse, 1981; Colmer, 2003). Although, under flooded condition, the formation of aerenchyma consider as a favorite characteristic, It can be appeared as a significant weakening factor under irrigated treatment (Striker *et al*., 2007). Roots commonly suffer mechanical stress during their lifespan (Bennie, 2002) due to water level fluctuation. Soil swelling-shrinkage as a result of repeated wetting-drying cycles is major factor producing mechanical stress on roots in grassland ecosystems.

Depending on the soil type and condition, such stresses can involve pressure ranging from 120 to 200 kPa because of soil shrinkage (Kirby and Bengough, 2002; Bengough *et al*., 2006). This type of mechanical stress can lead roots to collapse, therefore limiting water and nutrient uptake (Bengough *et al*., 2006).

Furthermore, in many grassland of the world, root systems could be exposed to the combination of antagonistic stress factors such as flooding and soil compaction as part of the natural disturbance regime.

In such conditions, the advantage of increased root porosity for oxygenation could endanger the mechanical strength of the roots, which helps them resist the subsequent soil shrinkage associated with the decrease of soil water content immediately after flooding. However, anatomical features that facilitate growth in waterlogged soils may cause limitations for root functioning under well-drained conditions (Stirker, 2007). Aerenchyma formation may weaken the root structure. After flooding, when the soil becomes more compacted, the aerenchymatous structure may collapse under external pressure and the amount of functional root tissue may be reduced (Engelaar *et al*., 1993).

Similar experiments show that The porosity in roots of wetland grasses increased 1-2 to 2-2 fold above these constitutive levels when grown in stagnant rather than aerated solution; a similar finding indicated a range of 1-5 to 3-0 fold increase in aerenchyma for several wetland grasses grown in flooded compared to drained sand. The adventitious root porosity previously reported for dry land grass species ranged from 6 to 9% in drained conditions to around 12% in waterlogged conditions (Smirnoff and Crawford, 1983) and from 1 to 6% in drained conditions to 2-18% in waterlogged conditions (Justin and Armstrong, 1987; Rubio *et al*., 1995). Loreti and Oesterheld (1996) also showed that root porosity increased under flooding and decreased under drought conditions.

Results of this experiment exhibited extensive aerenchyma disappearing when the irrigated plants compared to the submerged condition. These differences were different in different cultivars. However in submerged conditions their behaviors were almost the same and therefore the level of their resistance to anoxia condition would be the same. Consequently in irrigated conditions there could be expected different behavior for different cultivar. This may be considered as various disadvantages to the plants in aerated condition. The overall amount of aerenchyma in Zyande-Rood and 829 cultivars was lower than the 216 cultivar in aerated condition therefore these cultivars may exhibit more tolerance against soil mechanical pressure due to imposing irrigated condition.

Xylem wall: Secondary cell wall thickening and lignification are controlled to a significant extent by individual xylem elements and are regulated by environmental conditions (Donaldson, 1992, 2002; Gindl *et al*., 2000). In another word the internal diameter of these vessels depends on the thickness of the cell wall. The limit to xylem tension before cavitation takes place depends on, in part, conduit size (Atkinson and Taylor, 1996). Conduits with larger diameters are more prone to cavitation than those with smaller diameters (Vasellati *et al*., 2001).

Thus, a xylem with narrow vessels is physiologically better protected against cavitation (Jacobsen *et al*., 2005). Cavitation occurs when the axial water flow in the xylem vessels cannot keep up with the transpiration rate (Buckley, 2005) and causes to lower the water potential of xylem sap. More negative potential may cause additional cavitation, causing even steeper water potential gradients, unless water loss is reduced by stomatal closure (Tyree and Sperry, 1988; Jones and Sutherland, 1991; Sperry *et al*., 2003). The direct result of cavitation in plants is a reduced hydraulic conductivity and less water flux rate along the xylem. We now know that drought-induced xylem cavitation is by no means a rare event in submerged rice. However it has been shown to occur in roots (Sperry and Hacke, 2002), stems (Pockman and Sperry, 2000) and leaves (Salleo *et al*., 2001; Stiller *et al*., 2003).

Rice roots have been reported to be highly susceptible to cavitation (Stiller *et al*., 2003) and novel refilling may be crucial for restoring hydraulic conductivity (Stiller *et al*., 2005). Refilling despite negative water potential could be important for rice plants that are grown under upland (aerobically) or rain-fed lowland conditions because these plants are subjected to unpredictable periods of soil drought (Chaudhary and Rao, 1982). Refilling may therefore be more likely in species with smaller-diameter xylem vessels or tracheids where the volume of water required to fill the lumen is smaller. In addition, a larger proportion of smaller diameter vessels dramatically decreased root hydraulic conductance (Clearwater and Clark, 2003).

Present results exhibited xylem wall thickening in the root of irrigated plants compared to the submerged condition. The differences were not the same in three cultivars. However in submerged conditions thickness of the xylem wall in roots were almost the same and therefore the probability of cavitation in different cultivars would be equal consider that the vessel internal diameter was the same in three cultivars. In contrast, in irrigated condition different thicknesses of xylem wall could be expected for different cultivar. The thickness of xylem wall in Zyande-Rood cultivar was higher than the 216 and 829 cultivar in aerated condition. Therefore the diameter of root xylems' vessels in this cultivar would be lower than the others. These results indicated that in root's xylem of Zyande-Rood cultivar the creation probability of cavitations and consequently interruption of the connection of water between root and shoot would be lower than in 829 and 216 cultivars. Moreover, the 829 cultivar exhibit more xylem wall thickening in roots compared to 216 cultivar. Same results were obtained by Miyamoto *et al*. (2001). In their experiment *Paspalum dilatatum* responded to flooding by increasing root and leaf sheath aerenchyma and to drought by decreasing the diameter of metaxylem vessels. As a consequence of insufficient water supply, tensions may be created in the xylem that result in cavitation and in an interruption of the connection between root and shoot. Other experiment on *Paspalum dilatatum* show that the diameter of root xylem vessels decreased significantly under drought. Vessel diameter seems to be closely and positively correlated with the volume of water conveyed and inversely correlated with the `safety' of the conductive system (Salleo and Lo Gullo, 1986; Carlquist and Wilson, 1995; Koizumi *et al*., 2007).

Moreover, in vascular plants, secondary wall thickening plays a fundamental role in providing mechanical strength to support the plant body (Ye, 2002).

Endoderm and cell walls: More examinations on root cylinder reveal that some alterations were occurred in the medulla and outer part in roots of three cultivars, especially Zayande-Rood. The endoderm, pith and sclerenchyma cell walls were thickened in the irrigated root system treatments. This alteration was observed in the three cultivars, whereas in Zayande-Rood cultivar was more considerable. Baruch and Mérida (1995) studied the anatomy of four grasses under drought and flood conditions and obtained similar results for cell wall thickening in the endoderm, epiderm, cortex and medulla cells. Sharp and Davies (1985) and Stasovski and Peterson (1991) also observed thickening of the endoderm and exodermis of maize roots exposed to low water availability.

Several recent studies have shown that modifications of cell wall polymers help to create barriers to water, solutes, gases and pathogens in plants exposed to unfavorable biotic and abiotic stress conditions (Hose *et al*., 2001; Hartmann *et al*., 2002; Moore *et al*., 2002; Sabba and Lulai, 2002; Enstone *et al*., 2002) . Rice roots develop apoplastic barriers in the endodermis and exodermis and a sclerenchyma layer, which may impede the apoplastic component of water flow across the root cylinder (Clark and Harris, 1981; Miyamoto *et al*., 2001).

Researches show that the main apoplasmic resistances are the exodermis and endodermis which form the outer and inner boundaries of the root cortex, respectively. According to Van Fleet (1942) endodermal development (including suberization and wall thickening) is most effectively promoted by an alternation of dry and wet (aerated) conditions in several species of *Allium*.

Others have reported that endodermal and exodermal development is promoted by drought (Jupp and Newman, 1987; North and Nobel, 1991) and low temperature (Cruz *et al*., 1992). Cell wall thickness of root endodermis in a japonica-type lowland rice cultivar and two tropical japonica-type upland rice cultivars were measured by a Scanning Electron Microscope (SEM).

Moreover, It has been supposed that root endodermis play rolls of barrier for radial water movement in plant roots. Other experiments show that the cell size of endodermis was larger in the two upland rice cultivars than in the lowland rice cultivars and so the wall thickness. This result indicates that varietals difference in the cell-wall thickness of endodermis may determine the drought tolerance in these types of rice cultivars, because the secondary thickening of cell walls may prevent from water-leakage of roots. Moreover, the endodermis might be expected to have a protective function during drought (Peterson, 1992; Stasovski and Peterson, 1993). The presence of a conspicuous endodermis may play a role in preventing the collapse of the inner portion of the root and in protecting stellar tissues from desiccation, as has been found in roots exposed to drying soil (Sharp and Davies, 1985; Peterson, 1992; Allaway and Ashford, 1996).

The strength of vegetal organs, such as roots, depends on its structural type, size and constitutive materials (Aranwela *et al*., 1999). The resistance of the organ is expected to be higher if there is a presence of strong mechanical tissues beneath the epidermis, for example, the reported sclerenchymatous ring in rice stems (Li, 2003). The cell wall thickening could raised from activation of some genes that are involved in synthesis of the cell wall components (Pichon *et al*., 1998; Boerjan *et al*., 2003; Sofo *et al*., 2004; Fan *et al*., 2006).

Results show that the cell walls of endoderm, pith cells and sclerenchyma layer in all cultivars was thicker when the irrigated plants compared to the submerged condition. These differences were different in different cultivars. However in submerged conditions the thickness of cell walls in mentioned cells were almost the same. On the other hands, in irrigated treatment there could be expected different behavior for different cultivar. The thickness of cell walls in of endoderm, pith cells and sclerenchyma layer in Zayande-Rood cultivar was higher than the 820 and 216 cultivars in aerated condition therefore Zayande-Rood cultivar may exhibit more tolerance against water deficit and soil mechanical pressure irrigated treatment.

CONCLUSION

The anatomical assessment of rice under conditions of low water availability in the soil and root grown in submersion system showed that there were a same proportion of aerenchymas in the roots of plants with submerged root system in all cultivars. In contrast, in irrigated condition the amount of aerenchyma tissue decreased specially in Zayande-Rood and 829 cultivars.

Therefore, these cultivars are capable to tolerate the strength of soil pressure. Moreover, the root of different cultivars, responded to the irrigation conditions by producing thicker cell walls of the endoderm, xylem vessels, medulla and sclerenchyma layer cells. This response was observed in Zayande-Rood cultivar more than the other cultivars. This finding suggested that Zayande-Rood cultivar could be considered as more resistance cultivar against drought condition than 829 and 216 cultivars. Based on this study, genetic scientists may take this founding when selecting the drought tolerant cultivars of rice. Moreover, In arid condition which water is limited and dry land farming is necessary, Zayande-Rood could be selected as a tolerance cultivar.

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