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Original Article

Morphological and anatomical characteristics of Indonesian rice roots from East Nusa Tenggara contribute to drought tolerance

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Abstract

The ability of rice plants to cope with drought is supported by several parameters, including the structure of the root organ for water absorption. This study aimed to analyze the characteristics of the root tissues that play a role in supporting local rice plants during drought. This study was conducted by comparing 18 East Nusa Tenggara (Nusa Tenggara Timur [NTT]) local rice cultivars with two comparative drought-tolerant and drought-susceptible cultivars under drought stress treatment using the fraction of transpirable soil water method with levels 1 (control) and 0.2 (severe stress). Morphological measurement of plant growth and root phenotype, including root length and root dry weight, as well as plant height, number of leaves, and number of tillers, was conducted in the vegetative phase (46 days after planting). The collected root samples were prepared for anatomical slides using the paraffin embedding method and observed microscopically. Results showed the tendency of drought-tolerant plants to exhibit low reduction of the growth characteristics. In this study, drought tolerant rice cultivars (Pak Mutin, Boawae 100 Malam, and Kisol) tend to have root anatomical structure characterized by smaller root diameter, root area, cortical radius, vascular cylinder diameter, smaller cross-sectional of the vascular cylinder, and smaller metaxylem diameter with the higher number of metaxylem cells. In addition, thicker root epidermal cells and more schlerenchyma cell layers were also observed.

Keywords: Drought tolerance, Nusa Tenggara Timur, Local rice, Root anatomy

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Introduction

Rice (*Oryza sativa* L.) is a crop widely cultivated in the world and is a staple food for one third of the world's population (Priya et al., 2019). In Indonesia, rice is the staple food for most of its population. To increase food production in this region, the need for agricultural sectors to manage the development of drought-tolerant rice is considered to be crucial. In line with this, the selection of rice cultivars that are naturally adapted to dry climate conditions is highly recommended. Dry climate prevelance in East Nusa Tenggara (Nusa Tenggara Timur [NTT]) province of Indonesia, and the study of several local rice cultivars that adapt to drought conditions in terms of morphophysiological changes has also been previously studied (Salsinha et al., 2020).

One of the main characteristics considered in the selection of drought-tolerant rice cultivars is root system (Phule et al., 2019). Given that rice roots tend to have lower hydraulic conductivity than the roots of other crop plants, rice roots are generally unable to extract water from drying soil as much as herbaceous crops, including the common bean (Grondin et al., 2016).

With regard to drought tolerance, one of the supporting parameters of plant tolerance to dehydration conditions is the root organ (Purushothaman et al., 2013). According to the research conducted by Afzal et al. (2019), some of the characteristics that are considered in determining the tolerance of rice plants to cope with abiotic stress consist of water-utilizing ability, sizes and dimensions of leaves, yield of seeds, and root architecture. An understanding of root development is related to the response of plants to adapt to diverse soil moisture conditions and to function under drought conditions to ensure optimum growth (Kano-Nakata et al., 2019).

The analysis of the anatomical characteristics of the root organ provides a new perspective on the effect of stress on the structural conditions of the root. The research conducted by Phule et al. (2019) showed that some root tissue characteristics, such as aerenchyma formation, root thickening, and xylem area, and root length were critically affected by flooding and drought conditions. Research on the physical effects of soils, such as soil depth and consistency (Kundur et al., 2015), as well as the effect of hypoxia, edaphic stress like low nitrogen and drought stress (De Bauw et al, 2019), on the structure of rice root cortical aerenchyma (RCA) that compose intercellular space has also been conducted. Those studies (Kundur et al., 2015; De Bauw et al, 2019) showed that the addition of certain protective layers and the differentiation of cortical tissue around the root system contribute to rice plant tolerance under certain abiotic stress conditions. Drought avoidance is one of the drought tolerance strategies demonstrated through structural adaptations of plants (Kundur et al., 2015). Because the roots are the organs responsible for water absorption, the root architecture and anatomical characteristics are key to crossbreeding strategies in drought avoidance and drought adaptation (Gowda et al., 2011; Hazman and Brown, 2018). The morphological characteristics of plants that possibly increase its ability to avoid drought include root length, root hair density, and small root diameter, which enable deeper root penetration (Wassmann et al., 2009).

Under normal conditions, rice plants root consist of vascular cylinder, epidermal cells in the form of long tubular-shaped outgrowths that develop into root hairs, and cortex, which is composed of four layers of cells with different functions. The first layer of the cortex undergoes sclerenchyma thickening and is called the exodermis (Kadam et al., 2015). The second layer of the cortex contains parenchyma cells, which undergo differentiation to form aerenchyma (Afzal et al., 2019). The third layer of the cortex is between the endodermis and the aerenchyma and has a rectangular shape (O'Toole and Bland, 1987). The endodermis develops into the last layer of the cortex, which is characterized by the tight junction between cells compared with that of the pericycle. In this layer, the Casparian band appears as U-shaped thickening. Meanwhile, the stele consists of the pericycle with irregular parenchymal cells differentiated in uniseriate lines. A group of protoxylem, metaxylem, and phloem are also found in the stele section (Yang et al., 2014).

The research conducted by Gu et al. (2017) and Nurrahma et al. (2017) showed that abiotic stress on roots directly affects the morphological and phenotypic characteristics of plants. Under drought conditions, dehydration stimulates rapid root growth in certain cultivars despite having low biomass and short root length compared with that under optimum watering conditions (Uga et al., 2009; Wassmann et al., 2009; Kato et al., 2014). Several studies showed that, under drought conditions, upland rice cultivars have thicker and more deeply penetrating roots than lowland rice cultivars, which is supported by high root density, large root volume, and long root length (Uga et al., 2009; Grondin et al., 2016; Phule et al., 2019).

Through the analysis of the differences in tissue structure of plant roots from various cultivars under optimum watering and drought conditions, the possible contribution of root structure to the drought tolerance of rice cultivar can be explained briefly. This study aimed to characterize the roots anatomical structures of candidate drought tolerance rice cultivars from NTT.

Material and Methods

This study was conducted by observing the root anatomical characteristics from 20 rice cultivars consisting of two control cultivars, namely, “Ciherang” (drought-susceptible rice) and “Situ Bagendit” (drought-tolerant rice) and 18 NTT local rice cultivars consisted of Pak Morin, Shintara, Gogo Pulut Merah, Mapan, Pak Mutin, Hare Tora, Gogo Fatuhao, Gogo Jak, Padi Merah Noemuti, Gogo Metan, Kisol Manggarai, Boawae 100 Malam, Padi Merah Kuatnana, Padi Putih Kuatnana, Padi Hitam Maumere, Padi Putih Maumere, Gogo Sikka, and Padi Merah Malaka. This research was conducted at Sawitsari Research Station, Faculty of Biology, Universitas Gadjah Mada (7°45′22″ S, 110°23′18″ E with an altitude of 114 m above sea level) with sunlight intensity from approximately 5,500 lx to 11,000 lx during the day, temperatures between 24 ºC and 34 ºC, and average rainfall of 250–350 mm in October–December 2019, with the minimum rainfall of 2 mm in July and maximum at 720 mm in January as the beginning of rice growing season.

Planting and Treatment: Each 21 days-old seedling was transferred into 15 cm (diameter pot) containing 1 kg of growth media containing a mixture of soil and compost (3:1). The total number of plants used in this experiment were 120 plants (includes two level treatments, 20 cultivars, and three replications) which were arranged according to a randomized complete block design and acclimatized at 100% field capacity for 7 days. Drought stress treatment was conducted using the fraction of transpirable soil water (FTSW) method (Serraj et al., 2008) with two levels of stress, namely, FTSW 1 (control) and FTSW 0.2 (severe drought). To get the exact weight of pot and soil of each FTSW level, each cultivar was first treated with 100% field capacity (gravimetry method) and grown until permanent wilting point has reached to examine the total transpirable soil water (TTSW) of each cultivar. The TTSW were determined by the difference between initial weight of pot and plant (P0) and the weight of pot and plant at the permanent wilting point (Pi). The exact weight of pot and plant at any given time (Pt) and the water amount should be kept for each FTSW level (Wt) then calculated using formula:

$$TTSW = P0 - Pi$$
$$Pt = P0 - (TTSW - Wt)$$
$$Wt = FTSW \times TTSW$$

The FTSW treatment was started when the plants reached the water availability standards according to their respective FTSW at 14 days after planting (DAP).

Growth Characteristics: The final growth characteristics, including plant height, number of leaves, number of tillers, root length and root weight were observed when plant reached 46 DAP with three biological replications. To determine the level of drought tolerance of each cultivar, the percentage reduction values for several major growth and physiological parameters were determined including root density and plant height. The smallest percentage of parameter reduction indicates the greatest tolerance level for drought. The reduction percentage value is calculated by finding the difference between the parameter values in FTSW 1 (Control) and FTSW 0.2 (Stress) according to the formula:

$$Reduction\ percentage\ (\%) = \frac{(Control\ - Stress)}{Control} \times 100$$

Anatomical Characteristics: Plant roots from each treatment were collected at 46 DAP with three replications for each group of treatment. Sample preparation was performed by cutting the roots (5 cm from the base). Samples were collected and placed in a flask containing 70% alcohol.

Anatomical preparations of the transverse sections of the roots were conducted using an embedding method (Sutikno, 2018) with paraffin and a simple staining method with safranin. Initially, the samples were fixed with formalin-aceto-alcohol solution and incubated for 24 h. Then, the dehydration and washing processes were conducted with gradual dehydration using 70%, 80%, 95%, and 100% alcohol, with the incubation period of 30 min each. Subsequently, the dealcoholization process was conducted using 3:1 alcohol/xylol, 1:1 alcohol/xylol, 1:3 alcohol/xylol, and xylol, with the incubation period of 30 min each.

Finally, the samples were incubated in a 1:9 xylol/paraffin mixture at 57 ºC for 24 h.

Infiltration was conducted by replacing the xylol/paraffin mixture with pure paraffin and incubating at 57 ºC for 24 h. Before the samples were blocked, the paraffin mixture was replaced with pure paraffin and incubated for 1 h. The printed block was sliced using a rotary microtome (Shibuya Co. Ltd.) (with a slice thickness of 6–12 µm). The slice was mounted on a glass object with two drops of glycerin/albumin mixed with water and placed on a hot plate (45ºC) (Scilogex, MS7-H550-S).

The mounted samples were stained in stages of gradual replacement of xylol, alcohol/xylol, and 100% to 70% alcohol with the incubation period of 3 min each, 1% safranin in 70% alcohol with the incubation period of 1 h, and 70% to 100% alcohol, alcohol/xylol, and xylol with the incubation period of 1 min each. The sample section was closed with a covered glass with Canadian Balsam and dried with 45ºC on a hot plate.

The observation of the root anatomical characteristics was conducted using a binocular light microscope (Boeco BM-180/SP, Germany) and Optilab Viewer 1.0 (Miconos) with the objective lens magnifications of ×4, ×10, and ×40. The analysis of the root anatomical characteristics was performed using the Optilab and Image Raster 3.0 (Miconos).

Statistical Analysis: The significance of the data and interactions between treatments and cultivars on each parameter was statistically analyzed using Two-Way ANOVA and Duncan's multiple range test at the 95% confidence level (IBM-SPSS Ver. 25.00.US).

Results and Discussion

Drought in grass crops is a condition in which the available water in the growth medium is less than approximately 6.5 mm of water per day (FAO, 2019). Figure 1 shows that, under drought conditions (FTSW 0.2), several cultivars experienced a decrease in root morphology.

The effect of drought was confirmed in Table 1, which shows the following morphological parameters: plant height, leaf number, tiller number, root length, and root dry weight. Among all cultivars, the lowest reduction (i.e., 8% to 25%) of each growth parameter was observed in Mapan, Pak Mutin, Kisol, and Boawae 100 Malam, with a significant difference of $p < 0.05$ among all cultivars and treatments compared with Situ Bagendit, which exhibited the highest tolerance to drought.

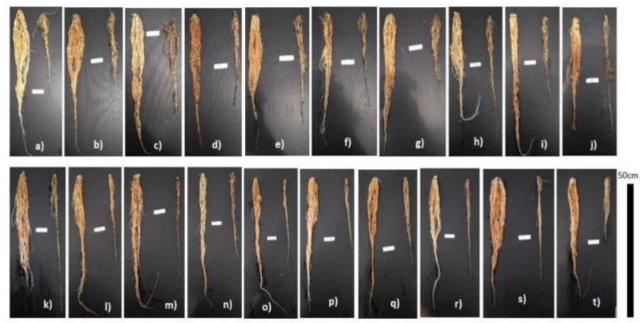

Figure-1. Root morphology of the *O. sativa* plant (Bars = 5 cm, Left: FTSW 1 and Right: FTSW 0.2): a) Pak Morin, b) Shintara, c) Gogo Pulut Merah, d) Mapan, e) Pak Mutin, f) Hare Tora, g) Gogo Fatuhao, h) Gogo Jak, i) Padi Merah Noemuti, j) Gogo Metan, k) Kisol, l) Boawae 100 Malam, m) Padi Merah Kuatnana, n) Padi Putih Kuatnana, o) Padi Hitam Maumere, p) Padi Putih Maumere, q) Gogo Sikka, r) Padi Merah Malaka, s) Situ Bagendit (drought tolerant), and t) Ciherang (drought susceptible).

Drought reduced the plant water content, turgor potential, stomatal activity, and leaf water potential, leading to the reduction in the percentage of plant growth (Salsinha et al., 2020). In this study, this effects has been recorded in growth parameters of plant height, leaf number, tiller number, and root dry weight. This effect occurs through physiological changes, including ion and water uptake, respiration, and photosynthesis. Once cells experience water loss through the cell membrane, the ability to maintain growth and cell division are also reduced (Dien et al., 2017; Salsinha et al., 2020). This process leads to the reduction in the leaf and tiller numbers and plant height under drought conditions (Kato et al., 2014). The data presented in Table 1 specifically indicate that Pak Mutin, Kisol, and Boawae 100 Malam show a decrease in root dry weight and root length from control condition (FTSW 1) to stress condition (FTSW 0.2) with low reduction (<25%) compares to the others (>39%).

Table-1. Phenotypic characteristics of the roots from 18 NTT local rice cultivars and control rice plants subjected to drought stress treatment by the FTSW method in the vegetative phase

Cultivar	Plant Height (cm)		Leaf Number		Tiller Number		Root Dry Weight (g)		Root Length (cm)	
	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2
Pak Morin	87.0^{klm}	58.0^{abcdef}	11.0^{abcdefgh}	6.8^{a}	2.5^{abcde}	1.5^{a}	0.9^{abc}	0.6^{abc}	44.2^{H}	27.3^{l}
Shintara	74.3^{ghij}	55.8^{abc}	18.3^{lmn}	11.0^{abcdefgh}	3.3^{def}	2.5^{abcde}	2.1^{gh}	0.7^{abc}	31.9^{u}	17.7^{b}
Gogo Pulut Merah	83.9^{jklm}	66.0^{bcdefgh}	13.8^{fghijk}	10.5^{abcdefgh}	2.3^{abcd}	2.3^{abcd}	2.1^{gh}	0.6^{abc}	40.7^{D}	30.5^{s}
Mapan	69.0^{efghi}	59.4^{abcdef}	15.0^{ijklm}	9.0^{abcde}	2.8^{bcdef}	2.5^{abcde}	2.2^{gh}	0.7^{abc}	25.9^{i}	19.7^{d}
Pak Mutin	69.6^{efghi}	53.0^{a}	20.0^{n}	11.8^{cdefghijk}	3.8^{f}	2.8^{bcdef}	2.1^{gh}	0.7^{abc}	27.3^{l}	27.1^{k}
Hare Tora	75.1^{hijk}	60.0^{abcdef}	10.5^{abcdefgh}	7.3^{ab}	2.5^{abcde}	1.5^{a}	1.8^{efgh}	0.5^{ab}	29.1^{p}	26.1^{j}
Gogo Fatuhao	66.8^{bcdefgh}	56.1^{abcd}	15.5^{jklm}	11.8^{cdefghijk}	2.3^{abcd}	2.8^{bcdef}	1.9^{fgh}	0.6^{abc}	30.0^{r}	19.1^{c}
Gogo Jak	88.6^{lm}	65.0^{abcdefgh}	12.5^{defghijk}	9.3^{abcde}	2.3^{abcd}	2.0^{abc}	2.4^{h}	0.7^{abc}	33.1^{v}	22.7^{g}
Padi Merah Noemuti	61.9^{abcdefg}	54.3^{ab}	14.0^{ghijk}	9.5^{abcdef}	3.0^{cdef}	2.0^{abc}	1.9^{fgh}	0.7^{abc}	39.3^{B}	24.3^{h}
Gogo Metan	90.1^{m}	57.5^{abcde}	14.8^{hijkl}	10.3^{abcdefg}	3.0^{cdef}	1.8^{ab}	2.1^{gh}	0.4^{ab}	32.0^{u}	29.2^{q}
Kisol	83.6^{jklm}	67.1^{cdefgh}	12.8^{efghijk}	9.0^{abcde}	3.0^{cdef}	2.0^{abc}	0.8^{abc}	0.4^{ab}	38.2^{A}	34.3^{x}
Boawae 100 Malam	92.3^{m}	69.0^{efghi}	12.5^{defghijk}	7.5^{abc}	2.5^{abcde}	1.5^{a}	1.1^{bcde}	0.5^{abc}	36.8^{z}	22.2^{f}
Padi Merah Kuatnana	83.3^{jklm}	59.8^{abcdef}	12.8^{efghijk}	8.3^{abcd}	3.0^{cdef}	2.0^{abc}	0.6^{abc}	0.3^{a}	57.6^{J}	31.6^{t}
Padi Putih Kuatnana	86.6^{klm}	66.8^{bcdefgh}	9.3^{abcde}	9.5^{abcdef}	1.5^{a}	1.8^{ab}	0.6^{abc}	0.4^{a}	44.3^{I}	28.8^{n}
Padi Hitam Maumere	83.3^{jklm}	68.3^{cdefghi}	10.5^{abcdefgh}	8.3^{abcd}	2.3^{abcd}	1.5^{a}	1.0^{abcd}	0.6^{abc}	41.3^{F}	22.2^{f}
Padi Putih Maumere	77.1^{hijkl}	57.3^{abcde}	11.3^{bcdefghij}	8.8^{abcde}	2.3^{abcd}	2.3^{abcd}	1.6^{defg}	0.7^{abc}	39.6^{C}	22.1^{e}
Gogo Sikka	68.8^{defghi}	60.0^{abcdef}	18.5^{lmn}	12.8^{efghijk}	3.5^{ef}	3.0^{cdef}	1.2^{cdef}	0.7^{abc}	43.7^{G}	29.0^{o}
Hare Tora Merah	80.3^{ijklm}	69.1^{efghi}	10.3^{abcdefg}	8.8^{abcde}	2.0^{abc}	1.8^{ab}	1.0^{abcd}	0.6^{abc}	41.0^{E}	28.5^{m}
Ciherang (Susceptible)	65.3^{abcdefgh}	57.5^{abcde}	15.8^{klm}	11.0^{abcdefgh}	3.0^{cdef}	2.3^{abcd}	1.8^{efgh}	0.6^{abc}	36.5^{y}	14.6^{a}
Situ Bagendit (Tolerant)	70.4^{fghi}	65.1^{abcdefgh}	19.0^{mn}	15.5^{jklm}	3.5^{ef}	3.0^{cdef}	2.3^{gh}	0.7^{abc}	34.2^{w}	29.1^{p}

The mean value from 3 replication (n=3) followed by the same letters in the column and row in each parameter shows no significant difference at the 95% confidence level based on Two-Way ANOVA and Duncan's multiple range test. FTSW 1 = Control, FTSW 0.2 = Severe drought. For the root length parameter, the letters a–z and A–J indicate the significant differences from shorter to longer root length.

Rice plants are characterized by a deep and dense root system known to be tolerant to drought stress. Under drought conditions, tolerant plants exhibit root plasticity (Hodge, 2004; Dien et al., 2017) that can be observed through morphological and anatomical changes, as well as metabolic and physiological changes, during the dehydration phase, which has an important role in drought adaptation (O'Toole and Bland, 1987; Dien et al., 2017; Kano-Nakata et al., 2019).

Under normal conditions (Figure 2), the root tissue of submerged rice consists of one to two layers of protective tissue (epidermis), sclerenchyma, large cortical aerenchyma, endodermis, and stele with a large diameter, which is composed of a few vessels (protoxylem and metaxylem). This structure was arranged to support the ability of plants to maintain water absorption and transportation under submerged conditions with the lack of oxygen and large amount of water (Yang et al., 2014; Kano-Nakata et al., 2019; Phule et al., 2019).

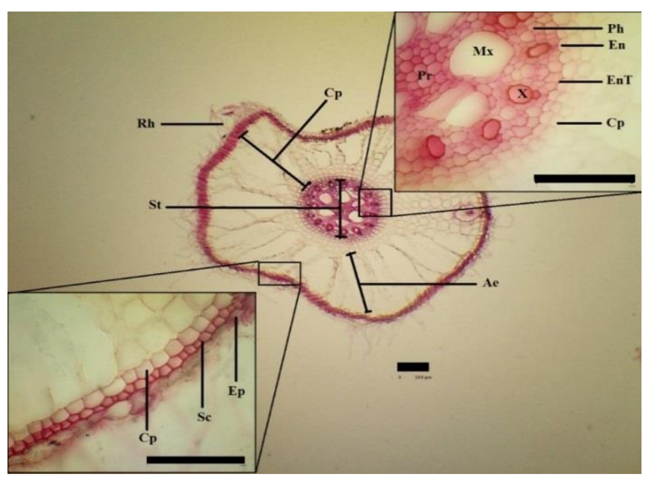

Figure-2. Anatomical structure of submerged *O. sativa* roots under normal condition (Bar = 100 µm). Note: Rh = Root hair, Ep = Epidermis, Sc = Sclerenchyma, CP = Cortical parenchyma, Ae = Aerenchyma, En = Edodermis, EnT = Endodermis cell thickening, Ph = Phloem, X = Xylem, MX = Metaxylem, Pr = Parenchyma.

Table-2. Root diameter, root area, and cortical radius of the roots from 18 NTT local rice cultivars and control rice plants subjected to drought stress treatment by the FTSW method in the vegetative phase

Cultivar	Root Diameter (µm)		Root Area (µm^2)		Cortical Radius (µm)	
	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2
Pak Morin	1,119.63^{opq}	726.58^{cde}	1,120,535.1^{qr}	432,334.56^{cde}	397.96^{op}	219.27^{cde}
Shintara	978.97^{jklm}	651.91^{ab}	719,067.4^{kl}	395,380.23^{cd}	321.43^{jkl}	224.41^{def}
Gogo Pulut Merah	1,151.84^{opqr}	851.32^{fghi}	1,200,349.7^{r}	561,652.54^{fghi}	394.83^{op}	310.53^{jk}
Mapan	1,094.03^{nopq}	668.77^{ab}	958,409.1^{op}	405,329.90^{cd}	380.19^{nop}	208.93^{cd}
Pak Mutin	959.78^{jkl}	493.44^{a}	713,912.6^{kl}	132,134.03^{a}	343.26^{klm}	155.08^{a}
Hare Tora	986.84^{jklm}	831.14^{fgh}	761,335.8^{lm}	542,224.14^{efgh}	239.79^{defg}	288.51^{hij}
Gogo Fatuhao	1,181.71^{pqr}	770.48^{def}	1,046,784.0^{pq}	457,004.02^{def}	411.71^{p}	246.13^{efg}
Gogo Jak	1,009.04^{klmn}	1,087.83^{nop}	845,630.4^{mn}	995,460.97^{op}	314.89^{jk}	351.68^{lmn}
Padi Merah Noemuti	809.50^{efg}	884.15^{ghij}	537,763.4^{efgh}	585,492.71^{ghij}	299.56^{ij}	266.58^{ghi}
Gogo Metan	900.70^{ghij}	613.93^{b}	640,868.6^{ghijk}	282,910.94^{b}	290.26^{hij}	173.18^{ab}
Kisol	1,514.96^{t}	897.83^{ghij}	1,894,316.4^{t}	653,890.38^{hijkl}	519.16^{r}	244.26^{efg}
Boawae 100 Malam	1,387.90^{s}	852.77^{fghi}	1,505,485.6^{s}	555,502.39^{fghi}	447.70^{q}	247.59^{efg}
Padi Merah Kuatnana	1,222.99^{r}	952.73^{ijk}	1,170,128.6^{r}	696,244.36^{jkl}	360.74^{mn}	293.75^{ij}
Padi Putih Kuatnana	1,188.35^{qr}	928.00^{hijk}	1,120,251.8^{qr}	670,420.86^{ijkl}	354.85^{lmn}	267.93^{ghi}
Padi Hitam Maumere	1,060.99^{mno}	827.96^{fgh}	996,888.7^{op}	530,189.87^{efg}	351.09^{lmn}	243.58^{efg}
Padi Putih Maumere	1,075.41^{mno}	594.58^{b}	910,590.6^{no}	276,958.31^{b}	364.27^{mno}	172.08^{ab}
Gogo Sikka	1,142.80^{opqr}	625.75^{b}	1,039,200.6^{pq}	332,527.03^{bc}	398.48^{op}	189.51^{bc}
Hare Tora Merah	1,409.76^{s}	1,053.15^{lmno}	1,555,920.2^{s}	844,161.11^{mn}	453.98^{q}	304.41^{j}
Ciherang (Susceptible)	941.02^{ijk}	819.34^{efg}	707,737.5^{kl}	561,209.79^{fghi}	355.04^{lmn}	258.14^{fgh}
Situ Bagendit (Tolerant)	947.79^{ijk}	679.88^{abc}	763,601.9^{lm}	389,388.22^{cd}	324.69^{jkl}	158.27^{ab}

The mean value from 3 replication (n=3) followed by the same letters in the column and row in each parameter shows no significant difference at the 95% confidence level based on Two-Way ANOVA and Duncan's multiple range test. FTSW 1 = Control, FTSW 0.2 = Severe drought.

By contrast, under drought conditions, the water absorption efficiency of the root is a key factor in determining the rate of transpiration and developing various adaptation strategies (Purushothaman et al., 2013). Monocotyledonous roots have developed some tissues that determine its water absorption capability (Ai-hua et al., 2017). For example, endodermic tissue was highly developed and characterized by a unicellular and compact structure with no air space that contributes to filtration and water absorption. This section contains cells that are thickened with lignin and suberin to support the impermeability of cells to ions and water (Uga et al., 2009; Purushothaman et al., 2013).

Thus, the ability of plants to maintain water absorption depends on the root anatomical characteristics. The root anatomical characteristics, including root diameter, cross-sectional area of the root, cortical radius, epidermis layer thickness, and sclerenchyma layer thickness, decreased along with the increase in drought treatment, with significant differences ($p < 0.05$) among all cultivars (Tables 2 and 3). As the amount of water and the turgidity of the cell decreased, the cell proliferation and differentiation rates of the plant also decrease (Kano et al., 2011; Kato et al., 2014), which leads to the decrease in the quantitative growth characteristics (Kulkarni et al., 2017), including the root diameter and root area, of each cultivar.

Tables 2 and 3 show the significant differences in the root anatomical characteristics ($p < 0.05$) between each cultivar subjected to drought stress treatment (FTSW 0.2) and the control (FTSW 1). Table 2 shows that Pak Mutin, Kisol, and Gogo Sikka have high tolerance to drought, with the ability of the plant to maintain a small root diameter, root area, and cortical radius and a low reduction of each parameter during drought stress. These three local rice cultivars were also compared with the control cultivars that can tolerate drought (Situ Bagendit) and are susceptible to drought (Ciherang). The comparison of the anatomical characteristics of these cultivars (Figures 3) shows that the root characteristics of the Situ Bagendit cultivar was dominated by smaller diameter, cross-sectional area, and cortical radius than the Ciherang cultivar. The large size or cross-sectional area of the root of the Ciherang cultivar, as shown in Table 2, is an adaptation to the irrigated conditions in which the cortex layer allows the root tissue to store more air for root respiration before passing through the impermeable endodermic layer. By contrast, the Situ Bagendit cultivar maintains a small size or cross-sectional area of the root to adapt to the high tension during water absorption and transportation under drought conditions.

Table-3. Epidermis thickness, sclerenchyma thickness, vascular cylinder diameter, and vascular cylinder area of the roots from 18 NTT local rice cultivars and control rice plants subjected to drought stress treatment by the FTSW method in the vegetative phase

Cultivar	Epidermis Thickness (μm)		Sclerenchyma Thickness (μm)		Vascular Cylinder Diameter (μm)		Vascular Cylinder Area (μm^2)	
	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2
Pak Morin	25.47^{cdefg}	21.62^{bcdef}	12.82^{fgh}	7.94^{abcde}	278.8^{no}	223.8^{ijk}	$67,390.6^{pqr}$	$38,756.2^{ijkl}$
Shintara	27.64^{defg}	14.44^{ab}	7.80^{abcde}	7.94^{abcde}	198.9^{efgh}	165.7^{bc}	$31,219.8^{defghi}$	$24,718.0^{bcd}$
Gogo Pulut Merah	29.33^{fg}	17.91^{abcde}	$9.60^{abcdefg}$	7.44^{abcd}	324.6^{q}	188.1^{def}	$88,558.3^{s}$	$27,177.3^{cdef}$
Mapan	21.73^{bcdefg}	18.78^{abcdef}	6.24^{ab}	8.04^{abcde}	214.8^{hij}	188.8^{def}	$36,787.7^{hijk}$	$30,821.6^{defghi}$
Pak Mutin	23.82^{bcdefg}	16.84^{abc}	15.43^{h}	$8.77^{abcdefg}$	205.6^{efghi}	117.7^{a}	$33,140.5^{efghi}$	$10,803.5^{a}$
Hare Tora	28.01^{efg}	21.71^{bcdefg}	11.47^{cdefgh}	7.62^{abcde}	275.3^{no}	260.1^{mn}	$66,139.4^{pqr}$	$52,688.8^{no}$
Gogo Fatuhao	22.56^{bcdefg}	32.32^{g}	$9.36^{abcdefg}$	$9.13^{abcdefg}$	213.6^{ghij}	175.3^{cd}	$36,122.1^{ghijk}$	$25,829.4^{cde}$
Gogo Jak	22.54^{bcdefg}	24.07^{bcdefg}	$9.95^{abcdefg}$	13.06^{gh}	276.4^{no}	301.5^{p}	$59,795.0^{op}$	$73,525.1^{r}$
Padi Merah Noemuti	20.83^{abcdef}	25.90^{cdefg}	6.82^{ab}	10.47^{bcdefg}	186.3^{de}	236.2^{kl}	$26,681.1^{cdef}$	$42,455.4^{jklm}$
Gogo Metan	22.51^{bcdefg}	18.31^{abcde}	7.43^{abcd}	8.27^{abcde}	208.6^{fghi}	164.0^{bc}	$34,741.0^{fghij}$	$20,611.3^{bc}$
Kisol	16.22^{abc}	23.49^{bcdefg}	8.46^{abcdef}	8.11^{abcde}	356.6^{r}	266.9^{mno}	$99,275.9^{t}$	$55,828.4^{o}$
Boawae 100 Malam	17.21^{abcd}	24.41^{bcdefg}	8.11^{abcde}	12.11^{efgh}	391.8^{s}	233.5^{jkl}	$120,024.6^{u}$	$42,894.3^{klm}$
Padi Merah Kuatnana	21.88^{bcdefg}	26.15^{cdefg}	$9.87^{abcdefg}$	$9.24^{abcdefg}$	334.2^{q}	267.2^{mno}	$87,942.0^{s}$	$55,153.9^{no}$
Padi Putih Kuatnana	23.63^{bcdefg}	20.62^{abcdef}	8.46^{abcdef}	8.48^{abcdef}	339.5^{qr}	299.9^{p}	$91,426.6^{s}$	$67,406.3^{pqr}$
Padi Hitam Maumere	21.24^{abcdef}	27.84^{efg}	7.91^{abcde}	11.84^{defgh}	284.4^{op}	240.5^{kl}	$65,462.7^{pq}$	$45,009.3^{lm}$
Padi Putih Maumere	16.09^{abc}	16.18^{abc}	5.68^{a}	5.81^{a}	247.4^{lm}	153.2^{b}	$48,122.5^{mn}$	$17,904.2^{ab}$
Gogo Sikka	22.46^{bcdefg}	19.96^{abcdef}	7.20^{abc}	$8.62^{abcdefg}$	232.6^{jkl}	164.1^{bc}	$42,985.9^{klm}$	$20,180.5^{bc}$
Hare Tora Merah	20.41^{abcdef}	14.65^{ab}	7.74^{abcde}	$9.06^{abcdefg}$	334.6^{q}	301.3^{p}	$87,828.5^{s}$	$68,921.4^{qr}$
Ciherang (Susceptible)	18.37^{abcde}	10.91^{a}	6.33^{ab}	$9.55^{abcdefg}$	193.0^{defg}	207.0^{efghi}	$29,792.7^{defgh}$	$31,991.8^{defghi}$
Situ Bagendit (Tolerant)	25.52^{cdefg}	22.54^{bcdefg}	6.74^{ab}	7.58^{abcde}	186.2^{de}	109.9^{a}	$27,951.8^{cdefg}$	$10,590.4^{a}$

The mean value from 3 replication (n=3) followed by the same letters in the column and row in each parameter shows no significant difference at the 95% confidence level based on Two-Way ANOVA and Duncan's multiple range test . FTSW 1 = Control, FTSW 0.2 = Severe drought.

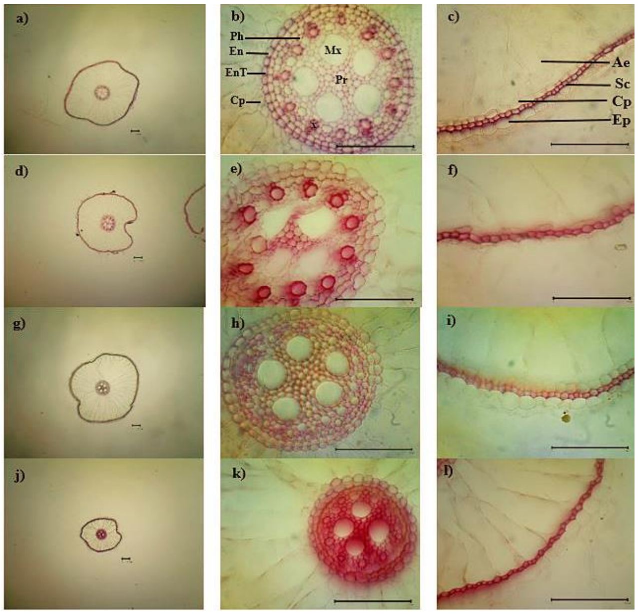

Figure-3. Root anatomy of *O. sativa* control cultivars treated with a,b,c) Ciherang- drought susceptible (FTSW 1), d,e,f) Ciherang-drought susceptible (FTSW 0.2), g,h,i) Situ Bagendit-drought tolerant (FTSW 1), j,k,l) Situ Bagendit-drought tolerant (FTSW 0.2).Bars = 100 µm. Note: Ep = Epidermis, Sc = Sclerenchyma, Cp = Cortical parenchyma, Ae = Aerenchyma, En = Edodermis, EnT = Endodermis cell thickening, Ph = Phloem, X = Xylem, MX = Metaxylem, Pr = Parenchyma.

Previous research on the characteristics of the cortical tissue layer (Lima et al., 2015; Grondin et al., 2016) showed that the formation of aerenchyma in the cortex layer is not only regarded as hypoxic adaptation of submerged plants but also assumed to reduce the radial flow of water and regulate oxygenation under irrigated conditions so that it does not reach higher acidification conditions. Meanwhile, under dry conditions, the presence of aerenchyma indicated by the cortical radius size is associated with physical barriers that slow down the absorption process (Grondin et al., 2016). Thus, the cultivars with small cortical radius sizes have high water absorption efficiency.

The ability of plants to maintain water absorption was also monitored from the thickness of the epidermis and sclerenchyma layers. Both of these tissue layers were observed to be thicker in drought-tolerant cultivars. Previous research (Yang et al., 2014; Phule et al., 2019) showed that drought stress causes abrasion on the outer surface of the roots and damage to the underlying tissues, which decrease the water absorption efficiency of plants. With a thick protective layer, the cultivar can maintain its cell structure to support maximum water absorption. This characteristic was exhibited by the Pak Mutin and Boawae 100 Malam cultivars (Table 3).

Previous research on monocotyledonous plants (Kulkarni et al., 2017; Kano-Nakata et al., 2019) showed that drought-tolerant plants developed a root system with the stele having a small diameter. Table 3 shows that drought-tolerant cultivars tend to have a small vascular cylinder diameter and vascular cylinder area, which leads to high pressure supporting water absorption and transportation to the shoots. The same cultivars, i.e., Gogo Pulut Merah, Pak Mutin, and Boawae 100 Malam, exhibited this adaptation.

During drought stress, plants also have a small xylem area and low metaxylem number. Root attributes, including small root xylem vessel diameters, have been observed in rice. This characteristic was observed to have a beneficial effect during drought stress by reducing the risk of xylem vessel cavitation (Cal et al., 2019). Table 4 shows a decrease in the xylem number and xylem vessel area in several cultivars, although the xylem number was not significantly different ($p > 0.05$) among all cultivars. The cultivars that exhibited a decrease in xylem number and xylem vessel area include Boawae 100 Malam, Pak Mutin, and Padi Putih Maumere.

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Table-4. Metaxylem number, xylem number, metaxylem vessel diameter, and metaxylem vessel area of the roots from 18 NTT local rice cultivars and control rice plants subjected to drought stress treatment by the FTSW method in the vegetative phase

Cultivar	Metaxylem number		Xylem number		Metaxylem Vessel Diameter (µm)		Metaxylem Vessel Area (µm^2)	
	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2	FTSW 1	FTSW 0.2
Pak Morin	5^{gh}	5^{fg}	15^{defgh}	13^{bcde}	54.6^{klmno}	45.5^{efghi}	2,397.3^{kl}	1,632.3^{efgh}
Shintara	4^{cde}	3^{ab}	12^{abcde}	19^{h}	45.7^{efghi}	42.5^{defgh}	1,651.2^{efgh}	1,659.6^{efgh}
Gogo Pulut Merah	5^{efg}	4^{cde}	13^{bcde}	13^{bcde}	70.7^{s}	41.0^{cdef}	3,985.7^{q}	1,320.3^{cdef}
Mapan	4^{cde}	4^{cde}	13^{bcde}	16^{efg}	48.4^{hijk}	41.4^{cdefg}	1,851.5^{ghij}	1,409.0^{cdefg}
Pak Mutin	4^{cde}	3^{ab}	11^{abcd}	8^{a}	45.8^{efghi}	26.0^{a}	1,649.4^{efgh}	554.2^{a}
Hare Tora	6^{h}	6^{h}	16^{efgh}	15^{defgh}	57.4^{mnop}	50.0^{ijkl}	2,517.2^{klm}	1,962.1^{hij}
Gogo Fatuhao	4^{bcd}	3^{a}	14^{bcdefg}	8^{a}	45.3^{efghi}	46.9^{fghij}	1,535.6^{defgh}	1,714.9^{efghi}
Gogo Jak	5^{fg}	6^{h}	14^{bcdefg}	16^{efg}	69.4^{rs}	53.2^{jklmno}	3,562.5^{p}	2,483.3^{klm}
Padi Merah Noemuti	5^{fg}	5^{fg}	12^{abcde}	12^{abcde}	35.2^{bc}	47.0^{fghij}	1,013.5^{bc}	1,747.5^{fghij}
Gogo Metan	5^{fg}	3^{ab}	15^{defgh}	14^{cdefg}	47.8^{ghij}	40.0^{cde}	1,724.5^{efghi}	1,336.9^{cdef}
Kisol	6^{h}	5^{fg}	15^{defgh}	12^{abcde}	71.3^{s}	55.5^{lmno}	4,013.1^{q}	2,785.9^{lmn}
Boawae 100 Malam	10^{k}	3^{abc}	17^{fgh}	11^{abcd}	63.0^{pq}	41.9^{defgh}	3,155.1^{nop}	1,937.5^{hij}
Padi Merah Kuatnana	9^{jk}	5^{fg}	19^{h}	12^{abcde}	51.0^{ijklm}	59.0^{op}	2,176.6^{jk}	2,758.6^{lmn}
Padi Putih Kuatnana	9^{j}	6^{h}	19^{h}	28^{i}	66.5^{qrs}	58.1^{nop}	3,506.9^{p}	3,413.5^{p}
Padi Hitam Maumere	6^{h}	5^{fg}	25^{i}	13^{bcde}	59.6^{op}	51.9^{ijklmn}	2,832.0^{mno}	2,179.1^{jk}
Padi Putih Maumere	6^{h}	3^{ab}	14^{bcdefg}	10^{abc}	51.8^{ijklmn}	22.8^{a}	2,115.8^{ijk}	708.1^{ab}
Gogo Sikka	4^{cde}	5^{gh}	18^{h}	10^{ab}	46.7^{fghij}	31.7^{b}	1,767.8^{fghij}	855.7^{ab}
Hare Tora Merah	8^{i}	6^{h}	18^{gh}	14^{bcdefg}	62.8^{pq}	63.7^{pqr}	3,199.1^{op}	3,208.3^{op}
Ciherang (Susceptible)	5^{fg}	4^{cde}	12^{abcde}	11^{abcd}	40.2^{cdef}	32.0^{b}	1,282.5^{cde}	1,277.4^{cde}
Situ Bagendit (Tolerant)	5^{fg}	4^{bcd}	14^{bcdef}	14^{bcdef}	37.9^{bcd}	33.8^{b}	1,123.9^{bcd}	972.9^{bc}

The mean value from 3 replication (n=3) followed by the same letters in the column and row in each parameter shows no significant difference at the 95% confidence level based on Two-Way ANOVA and Duncan's multiple range test . FTSW 1 = Control, FTSW 0.2 = Severe drought.

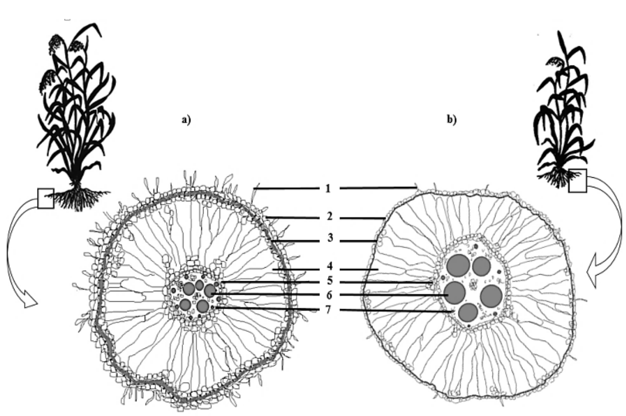

Figure-4. Schematic differences in the anatomical root structure of a) drought-tolerant cultivar and b) drought-susceptible cultivars subjected to drought stress treatment (FTSW 0.2) in the vegetative phase. MX = Metaxylem. The root anatomical characteristics of drought-tolerant and drought-tolerant cultivars, including 1) root hair, 2) epidermis, 3) schlerenchyma, 4) cortex, 5) endodermis, 6) metaxylem, and 7) xylem, were compared.

As a submerged plant, rice exhibits root plasticity to cope with drought conditions. The root anatomical characteristics are generally composed of specific tissue that reduces acidification due to flooding and regulates water absorption at the optimum limit. When a rice cultivar is subjected to drought stress, some root anatomical characteristics such as smaller root diameter, root area, and cortical radius and a low reduction of each parameter during drought stress will enable the plant to adapt to drought environment as stated in Pak Mutin, Kisol, and Gogo Sikka cultivar indicated have high tolerance to drought. Moreover, differences in anatomical response, such as root plasticity, enable a cultivar to tolerate drought. This study showed that plants with the ability to adapt to drought can be classified on the basis of the anatomical structure of the root, including some changes to the root characteristics (Figure 4). Some root phenotypic characteristics that contribute to drought tolerance include high root dry weight and long root length, in line with the low reduction of plant height, leaf number, and tiller number.

Based on the root morphological characters, the reduction of growth percentage and the roots anatomical characters, this study classified classified 18 NTT local rice cultivars into three classifications of drought tolerant, moderate and susceptible rice cultivars. Drought tolerant rice cultivars include Pak Mutin, Kisol, Boawae 100 Malam, Gogo Fatuhao and Padi Putih Kuatnana (with reduction percentage about 8.8 – 23.5 %); drought moderate cultivars include Padi Merah Kuatnana, Gogo Jak, Gogo Pulut Merah, Mapan, Gogo Sikka, Padi Putih Maumere, Hare Tora Merah (with reduction percentage about 26.1- 39.4%) and drought susceptible cultivars includes Pak Morin, Gogo Metan, Padi Merah Noemuti, Hara Tora, Padi Hitam Maumere, and Shintara (with reduction percentage about 40.8-58 %).

Conclusion

Some root phenotypic characteristics that contribute to drought tolerance include high root dry weight and long root length. Meanwhile, the root anatomical characteristics of drought-tolerant cultivars are smaller root diameter, smaller cross-sectional area of the root, smaller cortical radius, smaller vascular cylinder diameter, smaller cross-sectional area of the vascular cylinder, and lower xylem number compared to drought susceptible cultivar. On the basis of these characteristics, the Pak Mutin, Boawae 100 Malam, and Kisol cultivars were determined to be drought-tolerant NTT local rice cultivars.

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Contribution of Authors

Salsinha YCF: Conceived Idea, designed research methodology, data collection and manuscript writing
Maryani M: Designed research methodology, data collection and data interpretation
Indradewa, D: Literature review, data interpretation, and statistical analysis
Purwestri, YA: Manuscript writing, data collection, and data interpretation
Rachmawati, D: Conceived idea, statistical analysis, manuscript final reading and approval