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Growth Response of Rice (*Oryza sativa* L.) to Drought

II. Varietal difference in transpiration under water stress and its related plant characteristics

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Abstract : Transpiration of a rice plant under a low water potential of rooting medium and low air-humidity conditions was studied in order to evaluate varietal difference in response to water stress. Water stress in the rooting zone was induced by polyethylene glycol 6000, and the whole plant's transpiration was determined gravimetrically under different air-humidity conditions.

Varietal difference in maintaining transpiration under water stress was observed, and the difference was significant under conditions of air humidity less than 45%. Transpiration measurement of plants exposed to low water potential of rooting medium under the low air-humidity was an effective method for evaluating varietal characteristics in water-use behavior.

Based on the decrease of transpiration and leaf-water content (LWC), 13 rice varieties could be classified into three groups : tolerant, moderate and susceptible to water stress. Under water stress conditions, tolerant varieties had more characteristics for maintaining higher transpiration and LWC than susceptible varieties. Varietal difference may arise from the differences in sugar accumulation between plants, which may be a result of degradation of starch during water stress. Varieties in which sugar content increased more during water stress could maintain a higher transpiration and LWC than those which accumulated less sugar. An ability to convert starch to sugar during water stress might be a characteristic related to drought tolerance in rice.
Key words : Drought tolerance, Humidity, Leaf-water content, Rice, Sugar content, Transpiration, Varietal difference.

イネの耐乾燥性に関する研究　第2報　水ストレス下における蒸散の品種間差とそれに係わる形質：土屋幹夫・MUNANDAR・小合龍夫（岡山大学農学部）

要　旨：水ストレスに対するイネの反応の品種間差異を評価するために，培地水ポテンシャルと空気湿度を組み合わせた条件で，個体当りの吸水蒸散量を重量法で調査した．培地水ポテンシャルはポリエチレングリコール 6000 を用いて設定した．水ストレス下での吸水蒸散量の品種間差異は，空気湿度 45% 以下で顕著で，低空気湿度下で培地水ポテンシャルを変えての吸水蒸散量の測定は，品種の水利用特性を評価する有効な方法と考えられた．吸水蒸散と葉身の含水率に基づいて，13 品種は 3 つのグループに分類され，従来耐乾燥程度が大きいとされた品種では小さい品種に比較して，低湿度低水ポテンシャル下での吸水蒸散量の低下が小さく，含水率が高く維持されていた．また，耐乾燥程度大の品種では，水ストレス処理によるデンプン含量の低下と糖含量の増大が認められ，水ストレス下でデンプンを糖に変える特性は浸透調節を通じて耐乾燥性の付与に係わる形質の一つと推定された．
キーワード：品種間差，イネ，蒸散，湿度，耐乾燥性，糖含量，葉身の含水率．

A high capacity for maintaining transpiration in a cultivated plant is considered one of the major parameters affecting drought resistance[8]. In terms of agricultural production, maintenance of a high actual evapotranspiration to a potential one is a strong determinant of overall crop growth and yield[3].

Under field conditions, water status of plants is governed by the humidity of surrounding air at the leaf boundary layer and soil moisture around roots[9]. Air humidity or vapor-pressure deficit between leaf and air are important not only because they define the driving force for transpiration but also because they appear to directly influence stomatal aperture[2].

Rice cultivars show different behavior in maintaining transpiration and water status. Cultivars adapted to dryland and rainfed cultures maintain significantly higher leaf-water potential during the peak period of evapotranspiration than cultivars selected in wetland and irrigated soil cultures[6,12].

The characteristics related to the mechanism of a plant in maintaining water uptake, transpiration and plant water status under low

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soil-water potential are the basis for understanding the improvement of drought tolerant cultivars[11]. Many mechanisms of plants are claimed to be the main attributes for high capacity to maintain water uptake, transpiration and plant-water status under decreasing soil-water content[7,12,15].

Osmotic adjustment of leaves, as a result of net increase in solute concentration, will keep stomata open and transpiration high to lower leaf-water potential and hence to lower soil-water potential[13]. Osmotic adjustment also will allow root growth to continue at low water potentials, this enables the plant to explore a greater volume of soif for water at depth[14].

In this study, the effect of air humidity and low water potential of rooting medium on transpiration of an individual plant of rice was studied in order to establish a method for evaluating plant response to water stress. Then, varietal difference of rice plants in capacity for maintaining transpiration and water uptake under water stress, and the relationship between capacity for maintaining transpiration and characteristics for accumulating sugar under water stress were investigated.

Materials and Methods

The experiment was conducted during the period of June to August 1987. Four varieties of rice (*Oryza sativa* L.), Rikuto Norin 12 and Rikuto Norin 21 (upland varieties), Norin 22 (lowland variety) and Dular (dual lowland-upland variety) were used to clarify the effect of air humidity and water potential in culture solution on transpiration of rice plant. Seeds were germinated on a plastic net in a container (33×25×10 cm) filled with water. At the 2—3 leaf stage, seedlings were transplanted at a spacing of 3×4 cm into holes of a styrofoam panel attached to a container (60×35×16 cm) filled with the standard concentration of Kimura B nutrient solution. Plants were placed in a glass house and cultivated until the 7—8 leaf stage, when transpiration and water uptake was determined.

Transpiration and water uptake was observed by exposing the whole plant to water stress of rooting zone under four levels of relative air-humidities, i.e. 85, 65, 45 and 25%. Polyethylene glycol 6000 (PEG 6000) was used to develop the treatments of water potential of −0.49, −0.75 and −1.09 MPa. Culture solution without adding PEG 6000 was used as 0 MPa treatment. Two plants were transplanted into a 500 m*l* plastic bottle filled with treatment solution. Plants were placed on the platform in growth chambers and the height of the platform in the chamber was adjusted so that the light intensity around the leaves would be 50 klux. Air temperature in the chamber was maintained at 30.0°C. Under the temperature, relative air humidity of 85, 65, 45, and 25% were equal to water-vapor pressure of −22.9, −60.7, −112.4 and −195.2 MPa. Air humidity in the chamber automatically controlled and changed from wet to dry conditions every hour. Transpiration of the two plants in the bottle was measured gravimetrically, and the same plant materials were used for measurements at four levels of air humidity. The measurements were carried out under different levels of water potential with three replications. Leaf area was measured by using Automatic Area Meter (Hayashi Denko : Model AAM7).

The second experiment was carried out to evaluate varietal difference in transpiration under water stress, and conducted during the period from May to August in 1988. Thirteen rice varieties of different hydrological adaptation were used. Rikuto Norin 12, Rikuto Norin 21, Toyohatamochi, and Esoshimamochi are upland varieties. Dular is dual lowland-upland variety, and Norin 22, IR 52, IR 58, BPI 76, Nona Bokra, Azucena, Binato and Kalarata 1—24 are lowland varieties. Plants were cultured in a glass house using the same method as experiment 1.

Transpiration and water uptake was studied by exposing plants for 4 hours to different levels of water stress conditions, i.e. 0, −0.32, −0.51, −0.67, and −1.09 MPa. Water stress conditions were prepared in the same way as experiment 1. Two plants were transplanted into a 300 m*l* plastic bottle filled with treatment solution, and were placed in a growth chamber. The condition in the chamber was maintained at 30.0°C of temperature, 45% of air humidity and 50 klux of light. Transpiration rate was determined gravimetrically with the same method as in experiment 1. Plant material was dried for 48 h at 80°C and weighed. Leaf-water content was determined on the dry weight basis.

In the third experiment, the relationship between transpiration ability and characteristics in capacity for accumulating sugar under water stress was investigated. On the basis of the result of experiment 2, of which the 13 rice varieties were classified into three groups according to different capacity in maintaining transpiration and leaf-water content, three varieties of rice, Dular, Norin 22 and Eso-shimamochi were chosen to represent each group. Dried leaf samples were ground finely and used for analysis of sugar and starch. Sugar and starch content were analyzed by using the Nelson-Somogyi method.

Results and discussion

1. Effect of air humidity on transpiration under water stress

Transpiration rate was presented in the relative value to the rate under 0 MPa of water potential and 85% relative air-humidity, as it was shown in Fig. 1. Under this condition, absolute values of transpiration rate for Dular, Norin 22, Rikuto Norin 21 and Rikuto Norin 12 were 0.86, 0.89, 1.19 and 0.80 g $dm^{-2}h^{-1}$. Transpiration rate almost linearly increased with the decrease of air humidity at 0 MPa, but under low water potential it only slightly increased with the decrease of air humidity. Varietal differences of transpiration in response to low water potential were observed at a lower level of air humidity. The transpiration rate at −0.49 MPa and less that 45% of relative humidity was significantly different among the varieties at the 5% level of probability, and it was higher in Dular and Norin 22 than in Rikuto Norin 12 and Rikuto Norin 21.

The result indicates that rice varieties may have different capacities to absorb water and to restrict transpiration under low water potential and low air-humidity. Another study[2] revealed that plant species show a different stomatal behavior in response to low air humidity ; some sharply close their stomata in dry air to conserve water at the expense of photosynthesis ; others exhibit only a moderate humidity response and maintain high photosynthesis in dry air at the expense of high water use.

The result of this experiment suggests that stomatal conductance of a rice seedling at 0 MPa is almost unaffected by air humidity and the transpiration rate increases with the vapor-pressure deficit. Also it suggests that low water potential of rooting medium primarily affects the flux of water through the plant and the transpiration rate does not increase even though the water-vapor pressure deficit increases. Therefore, the transpiration rate under low air-humidity and low water potential of root medium may express the water uptake ability of a plant.

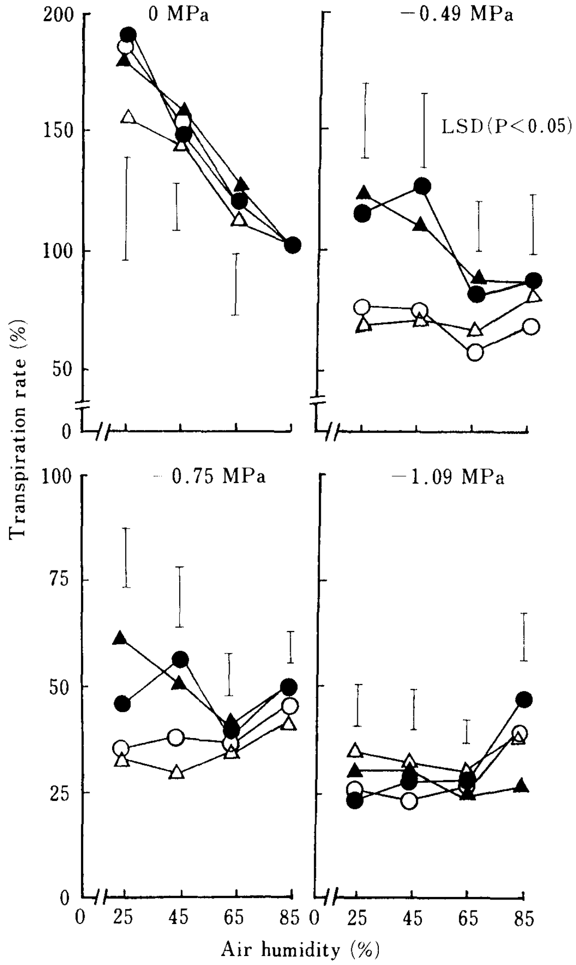

Fig. 1. Effect of air humidity on transpiration under different water potential of culture solution. Transpiration rate is presented in the relative value to the rate under 85% RH and 0 MPa water potential. Vertical bars represent LSD ($P<0.05$) among varieties for a level of air humidity.
● : Norin 22, ▲ : Dular,
○ : Rikuto Norin 12, △ : Rikuto Norin 21.

A measurement of the transpiration rate under increasing water-vapor pressure difference between leaf and surrounding air and decreasing water potential of rooting medium is considered an effective method for elucidat-

Table 1. Varietal difference in transpiration rate and leaf-water content in response to four levels of rooting medium water potential at 45% relative air humidity.

Varieties	Transpiration rate: Absolute values ($g\ dm^{-2}\ h^{-1}$)	Relative values[1)] (%)				Leaf-water content ($g\ g^{-1}$)
	0 MPa	−0.32 MPa	−0.51 MPa	−0.67 MPa	−1.09 MPa	0 MPa
Group 1						
Binato	2.72±0.75[2)]	89.5a[3)]	100.3a	80.3a	68.0a	2.83±0.35[2)]
IR 58	3.48±1.66	79.9ab	81.6ab	72.1ab	53.2ab	2.69±0.22
BPI 76	3.81±0.87	77.7ab	66.5abc	54.6bc	47.4ab	2.84±0.29
Dular	2.78±1.02	74.4abc	70.5abc	47.5c	43.3ab	3.06±0.07
Group 2						
Rikuto Norin 12	3.81±0.97	71.7abcd	50.2bcd	45.8c	34.8ab	2.91±0.57
IR 52	5.28±1.42	65.4bcde	50.3bcd	42.7cd	33.6ab	2.78±0.07
Rikuto Norin 21	4.17±1.81	59.7bcde	46.5bcd	38.3cde	29.1b	3.33±0.40
Norin 22	7.74±3.72	56.7cde	46.7bcd	35.7cde	26.8b	2.83±0.10
Group 3						
Toyohatamochi	5.03±0.87	60.0bcde	38.0cd	34.9cde	26.0b	2.95±0.07
Kalarata 1-24	4.45±1.07	53.9de	35.7cd	39.0cde	30.0ab	3.02±0.27
Nona Bokra	5.94±2.78	53.0de	42.8cd	36.2cde	28.4b	2.92±0.15
Esoshimamochi	8.54±1.17	52.0de	28.0d	27.7de	20.3b	2.77±0.22
Azucena	8.39±1.24	45.4de	29.5d	19.8e	22.0b	2.91±0.10

1) Relative to the rate under 0 MPa.
2) 95% confidence intervals.
3) Figures within a column followed with same letter are not significantly different at the 5% level by Duncan's multiple range test.

ing varietal characteristics in water-use behavior. So far, many studies on water stress evaluated a growth and water status of a plant exposed to low soil-water potential in field or pot experiments. It should be taken into consideration that experimental condition for clarifying plant response to water stress is not only the lowering water potential of a rooting medium but also the increasing water-vapor pressure difference between leaf and surrounding air.

2. Varietal difference in transpiration rate and leaf-water content

The absolute values of transpiration rate, leaf-water content at 0 MPa and the decrease of transpitation rate by lowering water potential of rooting medium were shown in Table 1. Varietal difference in maintaining transpiration under low water potential was discovered. Transpiration rates at −0.32, −0.51, −0.67 and −1.09 MPa of water potential were significantly correlated with the absolute value of transpiration rate at 0 MPa at the 1% level of probability. These correlation coefficients were −0.698**, −0.704**, −0.687** and −0.753**, respectively. This fact may imply that there is a varietal difference in water-use behavior, i.e. low- and high-transpiring varieties. Low-transpiring varieties have the characteristics of taking more water from the medium of low water potential compared with high-transpiring ones. Under the water stress conditions of the medium, increased capacity to conduct water from roots to leaves may be an adaptive mechanism that results in maintenance of relatively high plant-water status and transpiration[10)]. And also the varietal difference in transpiration rate under 0 MPa and low air-humidity may suggest the importance of leaf-surface structure and stomatal role in

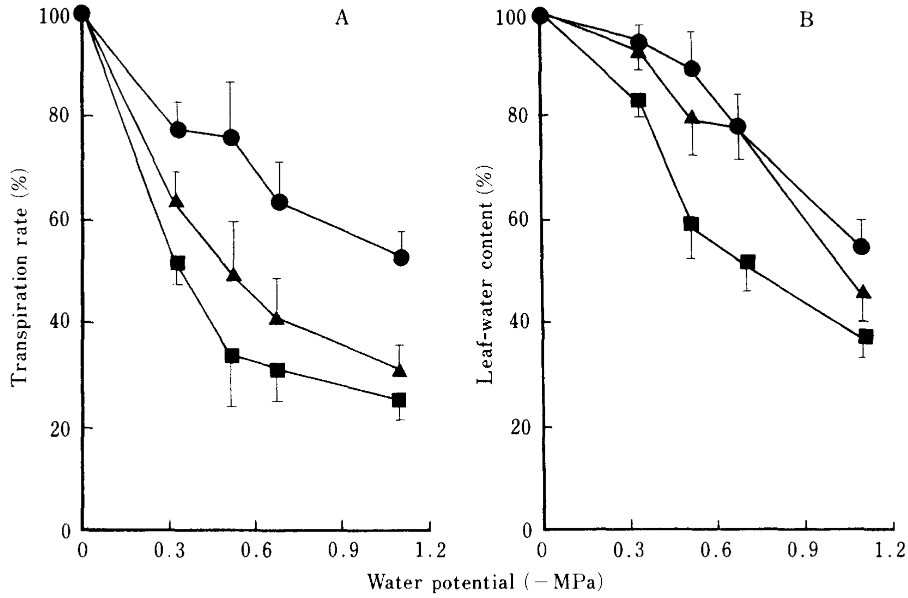

Fig. 2. Comparison of three varietal groups in response of transpiration (A) and leaf-water content (LWC) (B) to water potential of solution culture. Both transpiration and leaf-water content are presented in the relative value to the ones under 0 MPa. Vertical bars indicate 95% confidence intervals.
●: Group 1, ▲: Group 2 and ■: Group 3.

reducing water loss.

Though the varietal difference of transpiration rate at the four levels of low water potential was not always significant, 13 varieties used in this experiment could be broadly classified into three groups according to decrease in transpiration rate and leaf-water content by water stress (Table 1 and Fig. 2). The first group, which consisted of Dular, IR 58, BPI 76 and Binato, was considered the most tolerant to water stress. In this group, the decrease in transpiration rate was significantly less than that of the other two groups, and leaf-water content was highest at four levels of low water potential. The second group, which included varieties considered to have moderate tolerance, showed a larger decrease in the transpiration rate than the first group, but leaf-water content was almost the same as the first group. The varieties belonging to this group were Rikuto Norin 12, Rikuto Norin 21, Norin 22 and IR 52. The third group, which consisted of Esoshimamochi, Toyohatamochi, Kalarata 1—24, Azucena and Nona Bokra, was considered as the most susceptible to low water potential, of which both the transpiration rate and leaf-water content significantly and drastically decreased even at −0.32 MPa. An appearance of leaf wilting during the measurement of transpiration also showed a varietal difference in drought tolerance to some extent. While the varieties in group 1 and group 2 started to show wilting at −0.51 MPa, in group 3 varieties, it was already observed at −0.32 MPa.

This classification concurred with the results of a previous study[5], in which the varietal classification of drought tolerance might not be correlated with classification based on hydrological adaptation.

The results suggest that the change in transpiration rate and leaf-water content measured by lowering the water potential of the rooting medium under low air-humidity could be used as a sound basis for evaluating varietal difference in response to water stress. Also it is suggested that drought tolerant varieties had characteristics to uptake more water from the low-water-potential medium and to reduce water loss from leaf surface to low humidity air, compared with susceptible varieties.

3. Characteristics in capacity of accumulating sugar

Varietal differences in maintaining water status among rice varieties may arise from differences in capacity for accumulating

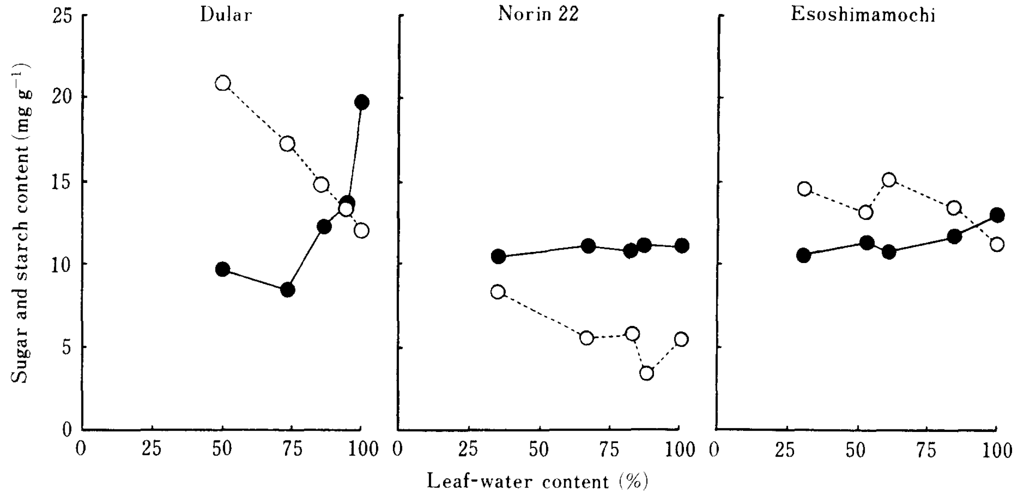

Fig. 3. Relationship between LWC and sugar content (open symbols), starch content (closed symbols) during water stress.

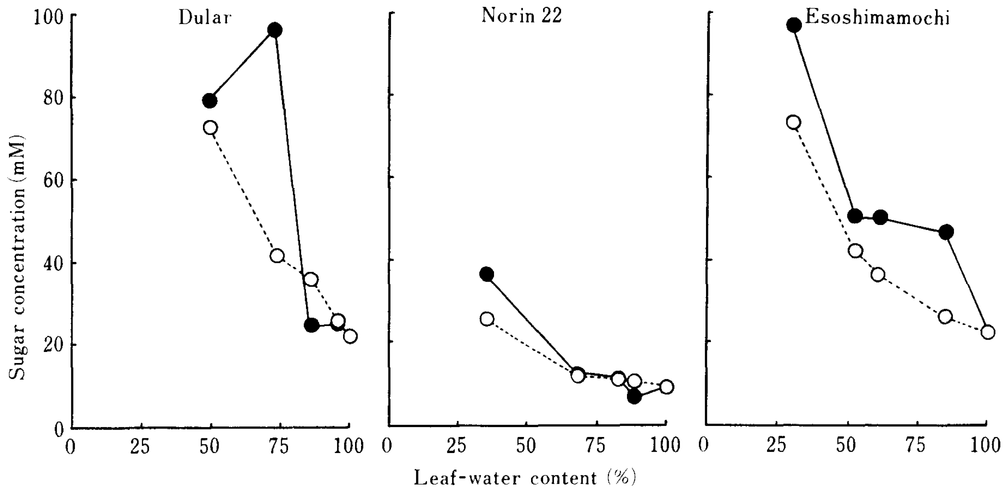

Fig. 4. Relationship between LWC and calculated sugar concentration (open symbols), actual sugar concentration (closed symbols).

solutes like sugar. Three varieties classified in terms of capacity to maintain transpiration under water stress showed a different capacity for accumulating sugar. Dular, which represented the group with a higher capacity for maintaining transpiration and leaf-water content during water stress produced more sugar than Esoshimamochi and Norin 22 (Fig. 3).

The increase in sugar content observed might occur through degradation of starch. Because, in Dular, as plant-water content decreased to 50%, sugar content increased about two times. At the same time, starch content decreased by 50%. But in Esoshimamochi and Norin 22, though water content decreased more, sugar and starch content were almost unchanged. Leaf sugar concentration in all varieties increased as water content decreased (Fig. 4). Though the increase of sugar content in Esoshimamochi and Norin 22 was mostly due to loss of water, in Dular it resulted from both increase of sugar content and loss of water.

This result indicates that a high capacity for accumulating sugar may be a characteristic responsible for the high ability of maintaining transpiration and leaf-water content during water stress. Some studies revealed that accumulation of a solute like sugar and proline acts as the main contributor of osmotic solutes, and as protection of protein denaturation that slows down the rate of drying and enhances dehydration tolerance[1,4,15].

However, the increased level of sugar content with water stress in Norin 22 was less than in Esoshimamochi, but its transpiration rate and leaf-water content were higher than those of Esoshimamochi. This means that this mechanism still can not completely explain the ability of maintaining transpiration and leaf-water content in the varieties of the second group. Plants in the second group may sharply close their stomata to restrict transpiration as a mechanism to conserve water under water stress. Other characteristics, such as rigidity of plant structure, may also be involved in the mechanism to maintain high transpiration rate and leaf-water content under water stress, especially in the varieties of the second group.

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