http://www.zju.edu.cn/jzus;　E-mail: jzus@zju.edu.cn
ISSN 1009-3095 *Journal of Zhejiang University SCIENCE* V.4, No.4, P.469-473, July-Aug., 2003

Seminal, adventitious and lateral root growth and physiological responses in rice to upland conditions*

YANG Ling(杨　玲), ZHENG Bing-song(郑炳松), MAO Chuan-zao(毛传澡),
YI Ke-ke(易可可), Wu Yun-rong(吴运荣), WU Ping(吴　平)†,
TAO Qin-nan(陶勤南)

(*College of Life Sciences, Zhejiang University, Hangzhou 310029, China*)

†E-mail: docpwu@cls.zju.edu.cn

Received Sept. 12, 2002; revision accepted Dec. 2, 2002

Abstract: Understanding the growth and physiological responses of rice to upland conditions would be helpful for designing treatments to improve the tolerance of rice under a rainfed system. The objective of this study was to investigate the initiation, elongation and membrane stability of seminal, lateral and adventitious roots of upland rice after 9-d upland condition treatment. Compared with control roots under waterlogged conditions, upland water deficiency conditions favor seminal and lateral root growth over adventitious root growth by accelerating seminal root elongation, promoting lateral root initiation and elongation, and reducing the elongation and number of adventitious roots. Enhanced total root number and length resulted in increase of total root dry weight and thereby increasing the root-to-shoot ratio. Organic compound leakage from seminal root tips and adventitious roots increased progressively to some extent with upland culture duration, while significant increases in seminal root tips were the consequence of loss of membrane integrity caused by the upland-condition enhanced growth.

Key words: *Oryza sativa* L., Root growth, Upland conditions
Document code: A　　**CLC number:** Q945

INTRODUCTION

Oryza sativa L. rice is a semi-aquatic species adapted to a variety of climates. Upland rice depends mainly on rainfall, is often exposed to drought, and has developed drought resistant traits. A principal mechanism by which rice adapts to water deficiency is through the possession of a pronounced root system which maximizes water capture and allows access to water at considerable depth (Price and Tomos, 1997). Upland rice often has a deeper root system compared with lowland rice (Zhang *et al.*, 2001).

The root system of rice consists mainly of seminal, adventitious and lateral roots. Upland rice is usually directly planted under rainfed conditions; the growth of seminal roots is important for the establishment of seedlings (Zhang *et al.*, 2001). Lateral and adventitious roots are formed in response to environmental conditions and, in fact, comprise the major portion of most mature root systems; and strongly determine a plant's survival and productive capability (Mergemann *et al.*, 2000). The differences among these roots are not as great as those among the heterorhizal roots, hence little attention is generally given to the differences in their morphological and physiological functions (Miyamoto *et al.*, 2001). Different types of roots for the same genotype can exhibit differential growth response to limited soil moisture (Yamauchi *et al.*, 1996). Knowledge of the morphological and physiological adaptations of different types of roots to upland conditions could be usefully applied to selection of traits that improve the productivity of rice under a rainfed system. The objective of this study is to compare the root growth and organic compound leakage response to upland and re-waterlogged conditions among different types of roots for a selected upland rice genotype.

---

* Project (No. G1999011700) supported by National Key Basic Resench Special (863) Foundation of China

MATERIALS AND METHODS

1. Plant material and upland condition treatment

Azucena, an upland drought tolerant variety was used in this study. Uniformly germinated seeds were transplanted to plastic pots (10 cm in diameter and 24 cm in height) with holes at the bottom and containing quartz sand and then grown under waterlogged conditions for 8 d before the upland condition treatment was started. The entire experiment was conducted in a greenhouse with daily maximum and minimum temperature of 30℃ and 22℃ and relative humidity of 65% – 85%. A 12-h photoperiod of approximately 158 μmol. m^{-2}. s^{-1} light intensity was provided by dysprosium lamps.

The experiment consisted of two soil moisture treatments: (i) waterlogged conditions: water level was kept 5 mm above sand surface and (ii) upland conditions: pots were taken out of tanks, drained and the sand allowed to dry for 9 d, then re-waterlogged for 2 d. Sand water content (SWC) was measured every other day by weighing.

Plants from three pots in each treatment were harvested 1, 3, 5, 7, 9 and 11 d after treatment. Eight seedlings per pot were dug out and the roots were recovered by removing sand particles with a brush for relative water content (RWC) measurement. The entire root systems of other seedlings were rapidly washed free of sand.

2. Growth measurement of three types of roots

The seminal, lateral and adventitious root lengths were measured with a ruler and adventitious roots were counted. The total length and number of lateral roots on seminal roots were measured with an image analysis system (WinRHIZO, Regent Instruments Inc, Canada). The root-to-shoot ratio was calculated based on dry weight.

The seminal root tips (0 – 1.0 cm) were fixed in formaldehyde: glacial acetic acid: ethanol 1: 1: 18 (v/v/v), treated with 1 mol/L NaOH and stained with 1% safranine. Cortical cell lengths of the elongation zone were measured under light microscope (Olympus BH-2).

3. Determination of organic compound leakage from roots

Seminal root tip (10-mm section from the root tip), lateral root (4-cm section of the middle of seminal root) and adventitious root were separated with a razor blade. Four roots from the same type were placed together and used for measuring the amount of UV-absorbing organic substances leaked from roots with a spectrophotometer (Du 640, Beckman) (Huang and Gao, 2000).

4. Histochemical analyses

The location of lipid peroxidation and the loss of plasma membrane integrity were detected by staining with Schiff's reagent and Evans blue, respectively, as described by Yamamoto (2001). The stained roots were observed under a light microscope (Model S4E; LEICA, Germany).

5. Statistical analyses

Each experiment repeated at least three times yielded similar results. One-way ANOVA (SAS/6.11, GLM) was used to test significant differences between control and treatment in all replications.

RESULTS

1. Water status

Fig. 1a shows the changes in SWC at different depth after treatment was initiated. The

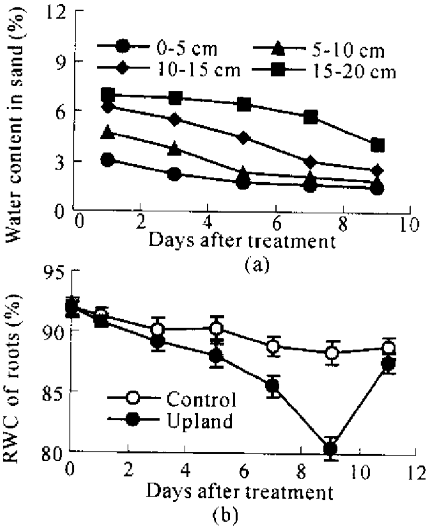

Fig. 1 Water content of sand at different depth (a) and relative water content of root (b) after upland condition treatment. Error bars represent SE from six roots

sharp decline in SWC during the first 1 d was mainly due to drainage after treatment； thereafter， the decline in SWC was due to root absorption. Although water removal from the surface layer involved water evaporation from the sand， the water depletion rate in the 5 – 10 cm layer was higher than that in the surface 5 cm dry layer at 5 d. The water depletion rate in the 10 – 15 cm layer was greater than that in the 5 – 10 cm layer at 7 d， and that in the 15 – 20 cm layer was the greatest among various soil depths at 9 d of treatment.

The root RWC in upland – condition plants was significantly lower （$P < 0.01$） than that in control plants after 5， 7 and 9 d of treatment. By 9 d， the reduction in root RWC was 7.6% of control level （Fig. 1b）.

2. Root growth

Lateral root elongation was stimulated （$P < 0.05$） throughout the upland condition treatment （Fig. 2b）， whereas seminal root elongation was promoted significantly （$P < 0.01$） until 5 d of treatment and decreased slightly relative to waterlogged control at 9 d of treatment （Fig. 2a）. Adventitious root elongation was inhibited throughout the upland condition treatment （Fig. 2c）， and was due to the sharp decline of SWC in the upper 10 – cm of sand. All seminal， lateral and adventitious root elongation recovered to control level after being re-waterlogged for 2 d （Fig. 2）. The mean cell lengths of the elongation zone （100.4 μm ± 19.6） were significantly longer in roots grown for 3 d under upland conditions compared with those （75.7 μm ± 13.6） grown under waterlogged conditions.

Total root number was found to increase under both waterlogged and upland conditions， and starting from 3 d after dry-down， was significantly higher （$P < 0.01$） than that of control plants. Compared to waterlogged conditions， Azucena had many more lateral roots， but fewer adventitious roots under upland conditions （Fig. 3b）.

Starting from 3 d after dry-down， the total root length was significantly higher than that of control plants. Adventitious roots accounted for most of the differences in total root length under waterlogged conditions， whereas lateral roots accounted for most of the differences in root length under upland conditions. For example， at 7th d of treatment， upland conditions reduced adventitious root length by 31%， and increased lateral root length by 42% （Fig. 3a）.

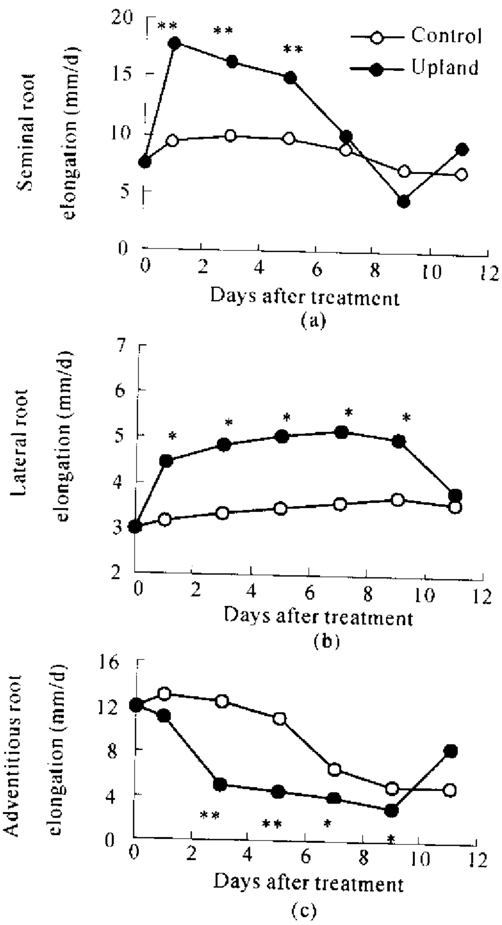

Fig. 2 Time course of the changes in the elongation rate of seminal root （a）， lateral root （b） and adventitious root （c） under waterlogged and upland conditions. In （b） and （c）， the three longest laterals and adventitious roots are presented. Means followed by an asterisk and double ones are significantly different from control at $P < 0.05$ and $P < 0.01$， respectively

Dry weight accumulation of seminal root with lateral roots and adventitious roots followed the same pattern as that of root length （Fig. 4a）. Root-to-shoot ratios were significantly higher beginning 3 d after dry-down compared with the ratios under waterlogged conditions （Fig. 4b）.

Root length， number and dry weight， however， increased significantly after re-waterlogging for 2 d， which was accompanied by rapid new adventitious roots and lateral root initiation； followed by new root growth which even exceeded that of the control （Fig. 3， 4a）.

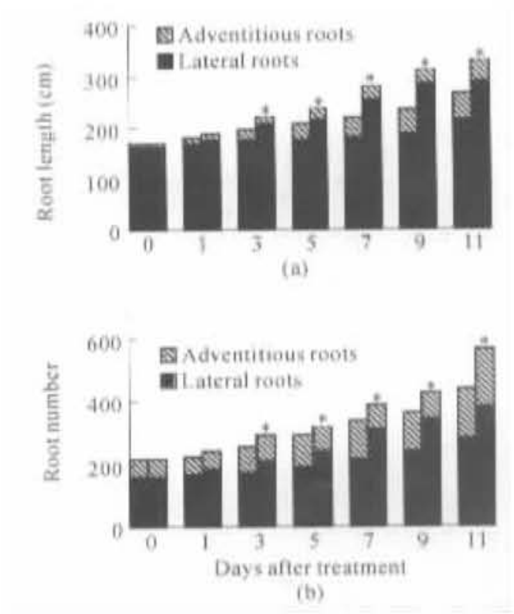

Fig.3 The length (a) and number (b) of lateral and adventitious roots under waterlogged (left column) and upland conditions (right column). In (b), the number of adventitious roots is twenty times of actual values

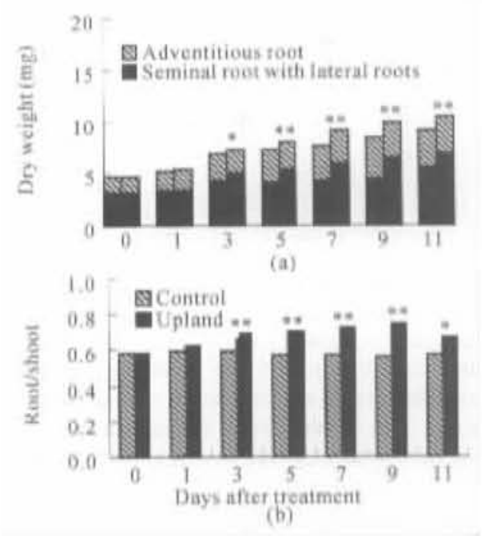

Fig.4 Time course of the changes in root dry weight and root-to-shoot ratio under waterlogged and upland conditions

3. Root cell membrane stability

Compared with control roots under waterlogged conditions, the relative leakage level of organic compounds from adventitious roots and seminal root tips were higher in upland-condition treated roots. Significantly notable increases in leakage from seminal root tips and adventitious roots were observed after 5 d to 7 d of treatment. In contrast, upland condition treatment significantly decreased the degree of leakage in lateral roots during the first 5 d treatment. A significant decline of organic compound leakage was observed 2 d after re-waterlogging (Fig.5).

The distribution of the histochemical stains of lipid peroxidation under waterlogged conditions was similar to that of upland conditions (Fig. 6a). The Evan blue staining patterns observed on the root surface at the root apex in squamae and staining area were bigger under upland conditions than under waterlogged conditions (Fig.6b).

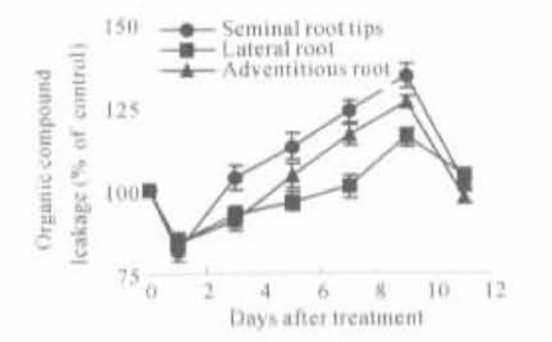

Fig.5 Time course of the relative changes of organic compound leakage from three types of roots during upland condition treatment

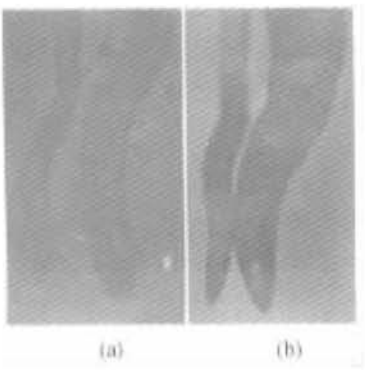

Fig.6 Histochemical detection of lipid peroxidation (a) and plasma membrane integrity (b) in seminal root tips caused by upland conditions. The seedlings were grown under waterlogged (a) and upland (b) conditions for 3 d. ×30

DISCUSSION

Simulated upland conditions in the natural drain-off system were used in this experiment to assess the growth and physiological responses of different types of roots to water shortage. This experiment demonstrated that upland conditions clearly affected the root system architecture in rice. Individual root types within a root system respond independently to upland conditions. Short-duration of upland conditions favor seminal and lateral root growth over adventitious root growth by accelerating seminal root elongation, promoting lateral root initiation and elongation, and reducing adventitious root elongation and number. The mean cell length of the elongation zone in seminal root under upland conditions was 32% increased compared with that under waterlogged conditions; mirrors the change in seminal root length under upland and waterlogged conditions.

Increased seminal root thickness under upland conditions (Fig.6) improves drought resistance as the roots can increase water uptake by producing more and larger root branches, and enable roots to penetrate compacted soil layers (Price and Tomos, 1997). Enhanced total root number and length resulted in increase of total root dry weight.

The organic compounds leakage from cells or tissues during stress can be used as a measure of membrane stability (Huang and Gao, 2000). Upland condition treatment significantly decreased the degree of leakage from lateral roots during the first 5 d treatment. The relative organic compound leakage level in seminal root tips under upland conditions was higher than that under waterlogged conditions. The loss of membrane integrity in seminal root tips under upland conditions was sharper than that under waterlogged conditions, but lipid peroxidation was not different under either condition (Fig.6). So the membrane damage could be due to mechanical disruption of elongation zone epidermal cells which was likely caused by rapid cell expansion. These results suggested that a significant part of the upland-condition caused reduction in cell membrane stability (at least in seminal root tips) , which seemed to be a secondary consequence of the upland-condition caused enhanced growth in the elongation zone, not the primary damage related to water deficit.

After re-waterlogging for 2 d, the elongation rate, dry weight and cell membrane stability recovered nearly to control level, and roots rapidly regenerated.

In summary, enhanced root growth and activity under upland environmental conditions may have adaptive significance in water acquisition by increasing the contact area between the root and the surrounding soil before soil becomes very dry, and by increasing water uptake rate in the deeper soil profile as compensation for the reduced water uptake at the surface soil layer. The divergence under upland conditions observed among root types within a root system suggested that there may be differences in adaptive mechanisms among root types.

References

Huang, B., Johnson, J. W., Box, J. E. and NeSmith, D. S., 1997. Root characteristics and hormone activity of wheat in response to hypoxia and ethylene. *Crop Sci.*, **37**: 812 – 818.

Huang, B. and Gao, H., 2000. Root physiological characteristics associated with drought resistance in tall fescue cultivars. *Crop Sci.*, **40**: 196 – 203.

Mergemann, H. and Sauter, M., 2000. Ethylene induces epidermal cell death at the site of adventitious root emergence in rice. *Plant Physiol*, **124**: 609 – 614.

Miyamoto, N., Steudle, E., Hirasawa, T. and Lafitte, R., 2001. Hydraulic conductivity of rice roots. *J. Exp. Bot*, **52**: 1835 – 1846.

Price, A. H. and Tomos, A. D., 1997. Genetic dissection of root growth in rice II: mapping quantitative trait loci using molecular markers. *Theor. Appl. Genet.*, **95**: 143 – 152.

Yamamoto, Y., Kobayashi, Y. and Matsumoto, H., 2001. Lipid peroxidation is an early symptom triggered by aluminum, but not the primary cause of elongation inhibition in pea roots. *Plant Physiol.*, **125**: 199 – 208

Yamauchi, A., Pardales, J. R. and Kono, Y., 1996. Root System Structure and Its Relation to Stress Tolerance. *In*: Ito, O., Johansen, C., Adu-Gyamfi, J. J., *et al.*, eds. Dynamics of roots and nitrogen in cropping systems of the semi-arid tropics, p.211 – 233.

Zhang, W. P., Shen, X. Y., Wu, P., Hu, B. and Liao, C. Y., 2001. QTLs and epistasis for seminal root length under a different water supply in rice. *Theor. Appl. Genet*, **103**: 118 – 123.