Varietal Difference in Growth Directions of Rice Crown Roots and Relation to Gravitropic Response and Diameter of Crown Roots

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The growth direction of four crown roots of rice varieties belonging to Indian ecotypes (*aus*, *aman* and *boro*), Indonesian ecotypes (*bulu* and *tjereh*) and Japanese lowland and upland varieties was examined in darkness at the seedling stage. In the *aus* varieties the growth direction of crown roots varied markedly. Part of these varieties which belonged to the *indica* showed rather larger ratio of crown roots growing horizontally compared with the other groups. In the *aman* and *boro* varieties, the crown roots grew horizontally. Crown roots growing upward were detected in the Indonesian ecotypes. In some of the *tjereh* varieties, however, crown roots grew horizontally as in the case of the Indian ecotypes. The crown roots of the Japanese lowland and upland rice varieties grew downward and this tendency was more conspicuous for lowland rice. The growth direction of the rice crown roots differed between *indica* and *japonica*, and was also related to the cultivation conditions. Under dark conditions, the varieties with crown roots growing downward showed a stronger gravitropic response and had thicker crown roots than the varieties with crown roots growing horizontally. Although the crown roots of the *bulu* varieties showed only limited gravitropic responses, they were the thickest among the ecotypes used in this experiment. Under illumination conditions, the crown roots of all the varieties grew downward and showed a gravitropic response. The diameter of the crown roots was longer in the illuminated plants than in the dark-treated ones. The growth direction of the crown root appears to be more related to the gravitropic response than to the diameter of the root.

KEY WORDS: *Oryza sativa*, crown root, ecotype, gravitropic response, growth direction.

Introduction

Varietal differences in the root structure have been investigated in maize (SPENCER 1940), wheat (HURD 1968), barley (HACKETT 1968) and rice (CHANG *et al.* 1972). Among these crops, rice displays the largest variability in the root structure (RUSSELL 1977). It is well known that the structure of roots differs between upland and lowland rice varieties (CHANG *et al.* 1972). Furthermore, it has been reported that native Indonesian rice varieties form aerial roots (UENO and SATO 1989a). The wide variation in the direction of crown root growth of rice may be related to the differences in the conditions of cultivation.

The growth direction of crown roots in rice is correlated with the gravitropic response (KAWATA *et al.* 1980) and diameter of the roots (YAMAZAKI *et al.* 1981). TAKITA and KUSHIBUCHI (1983) and TERASHIMA *et al.* (1986) reported that the roots, which were formed near the soil surface, were thinner than those growing downward. We have observed thick crown roots, however, around the tillers of *bulu* varieties over the paddy soil.

Only one Japanese rice variety was used for the experiments in the relation of the growth direction with the gravitropic response (KAWATA *et al.* 1980), or with the diameter of the

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crown root (YAMAZAKI *et al.* 1981), respectively. So far, it remains to be determined how varietal differences in the crown root growth are related to the gravitropic response or to the diameter of the crown roots. In this experiment, we analyzed the growth direction of crown roots of various rice ecotypes. Then we analyzed the gravitropic response and the diameter of the crown roots which differed in the growth direction in 36 varieties.

Materials and Methods

Varietal differences in the growth direction of crown roots

The rice varieties used were; ecotype *aus* (26 varieties), *aman* (12) and *boro* (5) for Indi-

Table 1. The varieties used in this study.

Ecotype	Variety's name							
<i>aus</i>	aus 3 ¹⁾	aus 4 ¹⁾	aus 5 ¹⁾	aus 6 ¹⁾	aus 9 ¹⁾	aus 10 ¹⁾	aus 11 ¹⁾	aus 13 ¹⁾
	aus 14 ¹⁾	aus 18 ¹⁾	aus 20 ¹⁾	aus 24 ¹⁾	aus 25 ¹⁾	aus 30 ¹⁾	aus 34 ¹⁾	
	aus 35 ¹⁾	aus 36 ¹⁾	aus 42 ¹⁾	aus 43 ¹⁾	aus 44 ¹⁾	Dular	Kataktara	
	Kele	Marich-bati	Pusur	Surjamukhi				
<i>aman</i>	Ba 15 ¹⁾	Ba 18 ¹⁾	Ba 20 ¹⁾	Ba 21 ¹⁾	Ba 24 ¹⁾	Badshabhog		
	Bhasamanik	Blue Stick	Daudin	Daudkhani	Hatishail			
	Patnai-23							
<i>boro</i>	Assam IV	Bhutmuri 36	Chinsurah Boro I	Chinsurah Boro II				
	Tepa I							
<i>bulu</i>	Baok	Bayan	Benong 130	Berganti	Brondol Putih			
	Cita Wati	Dara Cambong	Deli	Gemdjah Beton	Gendjah Ratji			
	Gowabi	Gropak Gedeh	Jenning Kuning	Kapel	Kesimbukan			
	Keta	Ketan Bumain	Ketan Gadjih	Ketan Saman	Manca Wuri			
	Manda Putih	Pannongha Gilang	Pekto	Simbukan	Sipulut Bajangguh			
	Sri Untung	Sukanandi						
<i>tjereh</i>	Banjar Tinggi	Bendang Putih	Cantik Nanis	Gog Gundul				
	Hetan Hitan	Hoing Gringsing	Hoing Jaher	Kaciak Naibah	Kanila			
	Ketan Gajih	Ketan Serang	Kuning Haibah	Lagos				
	Lantik Candung	Lati Sail	PB Sani	Peta	Pulut Hitan			
	Pulut Hitan (red)	Putih Lontik	Ratih	Rijal	Salak	Seratus Malam		
	Seribu Naik	Si Jangkong	Si Rendah Herah	Si Rondong Kuning				
	Simandiri	Skrivimankoti	Tjahaja	Ube Gerang				
Japanese lowland rice	Akiyutaka	Daikoku wase	Fujiminori	Fukoku	Genroku	Kamenoo		
	Kiyonishiki	Koshihikari	Nihonbare	Norin No.1	Ootori	Ouu No.195		
	Ouu No.200	Sasaminori	Sekiyama	Shimizu mochi	Somewake			
Japanese upland rice	Aogara	Damattero	Daisen	Kirishima	Okabo	Norin No.11(upland)		
	Norin No.14(upland)		Norin No.19(upland)	Sensyo	Toga	Yakan		

¹⁾: from Nat. Inst. Genet. The variety's name is unknown.

The varieties in boldface were used in *gravitropic response and diameter of crown roots*.

an rice, *bulu* (27) and *tjereh* (32) for Indonesian rice as well as Japanese lowland (17) and upland (11) rice varieties (Table 1). Seeds were sterilized with a 2.5% sodium hypochlorite solution for 15 min., then rinsed with distilled water. The seeds were germinated in darkness at 28°C in Petri dishes. Boiled 0.2% agar (200 ml) was injected into a cylindrical, clear glass jar (97 mm × 180 mm). A germinated seed was planted on the solidified agar of that jar. Thereafter, the top of the jar was sealed with aluminum foil and 5 holes were perforated with a needle, then the jar was maintained at 28°C under darkness. After 5 days, the growth direction of four crown roots for a plant was measured with a protractor. Five plants for each variety were measured and the ratio of the root number in 5 groups was calculated. Each ecotype was evaluated based on the variety mean value of the ratio in 5 groups (Fig. 1). The growth direction of the crown roots of each variety was analyzed in the report of UENO and SATO (1989b). The varieties in which the growth direction of the crown roots was evaluated was classified into *indica*, *japonica* and other groups by the method of UENO *et al.* (1990).

Gravitropic response and diameter of crown roots

Six *aus*, 6 *aman*, 4 *boro*, 7 *bulu*, 7 *tjereh* and 6 Japanese rice varieties were used (Table 1). Boiled 0.34% agar (80 ml) was injected into a 100 ml Erlenmeyer flask. A germinated seed was sown on the solidified agar, then the flask was sealed with aluminum foil and maintained at 28°C. When the first crown root grew to a length of about 1 cm, the flask was inclined at 45°. Before and after the inclination for 4 hr., the growth direction and bend angle were determined with a protractor. We used this bend angle for the evaluation of the gravitropic response of crown root. Then the diameter of the crown root was measured using a microscope (25-fold magnification) at a distance of 5 mm from the connection with the stem. Since light is known to influence the gravitropic response in some species (LAKE and SLACK 1961, SHEN-MILLER 1978), cultivation was performed under darkness or under illumination conditions (6,500 lux). Dim green light was used in darkness for the inclination of the flask. Measurements were performed in five plants for each variety and the mean values were used for the evaluation.

Results

Varietal difference in the growth direction of crown roots

The varieties of each ecotype were classified into typical *indica*, typical *japonica* and other groups (see, UENO *et al.* 1990). The results are shown in Table 2 with each cultivation area. *Aus* showed wide variations in the growth direction of the crown roots (Fig. 1). Some of the *aus* varieties belonging to the typical *indica*, exhibited a larger ratio of horizontally grown crown roots than other types of *aus*, in which many crown roots grew downward. Most of the *aman* and *boro* varieties belonged to the typical *indica*, and in these types many crown roots grew horizontally. Parts of the crown roots of *bulu* grew upward as well as two thirds of the *bulu* varieties belonging to other groups (Table 2). *Tjereh* was characterized by the presence of typical *indica* and other groups, each of which consisted of varieties with crown roots growing upward. Japanese lowland and upland rice varieties mainly belonged to the typical *japonica* and other groups, respectively. In each of the Japanese rice varieties,

Table 2. Classification of varieties by the method of UENO *et al.* (1990)

Area	Ecotypes	<i>indica</i>	<i>japonica</i>	other groups	total
India	<i>aus</i>	12	2	12	26
	<i>aman</i>	11	0	1	12
	<i>boro</i>	5	0	0	5
Indonesia	<i>bulu</i>	0	8	19	27
	<i>tjereh</i>	21	1	10	32
Japan	lowland	0	15	2	17
	upland	0	2	9	11

Fig. 1. Growth direction of crown roots. A: Indian ecotypes, B: Indonesian ecotypes, C: Japanese rice varieties. The numbers with minus symbol denote upward direction.

crown roots grew downward. This tendency was more conspicuous in lowland rice than in upland rice (Fig. 1).

Gravitropic response and diameter of crown roots

Dark conditions

The correlation of the growth direction with the gravitropic response and also with the diameter of the crown root was positive ($r = 0.87^{**}$, $r = 0.35^*$, **: 1% level, *: 5% level, Figs. 2-1 and 2-2). The crown roots of the Japanese rice and *aus* varieties showed stronger gravitropic responses and were thicker than those of the *aman*, *boro* and *tjereh* ecotypes. The gravitropic response of the crown roots was significantly different between the Japanese rice and *bulu* varieties, unlike the diameter.

Illumination conditions

The correlation of the growth direction was significant with the gravitropic response of the crown root ($r = 0.33^*$), but not with the diameter (Figs. 3-1 and 3-2). All the crown roots

Fig. 2-1. Relation between growth direction and gravitropic response of crown roots under dark conditions.

Fig. 2-2. Relation between growth direction and diameter of crown roots under dark conditions.

which we examined in this experiment grew downward, showed a stronger gravitropic response, and became thicker with illumination.

Discussion

In this report, we described the varietal differences in the growth direction of rice crown roots which developed just after germination. In the case of wheat, the growth direction of the roots changed in each plant, even if the plants belonged to the same genotype (UENO and OIKAWA 1992). In the case of rice, however, since the difference between plants with the same genotype was minimal, the characteristics of each variety were clearly defined (UENO and SATO 1989b).

The varieties which belonged to the typical *indica*, namely the *aman*, *boro* and almost half of the *aus* ecotypes exhibits a high ratio of crown roots with horizontal growth. The Japanese lowland rice varieties belonged to the typical *japonica* and the crown roots grew downward.

Most crown roots of the Indian ecotypes grew horizontally. Half of the *aus* varieties, however, showed a high ratio of crown roots with downward growth. The *aus* ecotype can be divided into Highland *aus* and Lowland *aus* (HECTOR 1930). The wide variation in the growth direction of the crown roots in the *aus* ecotype may be ascribed to the genetic

Fig. 3-1. Relation between growth direction and gravitropic response of crown roots under illumination conditions.

Fig. 3-2. Relation between growth direction and diameter of crown roots under illumination conditions.

diversity which arose through adaptation to the cultivation conditions. Crown roots with upward growth were detected in the Indonesian ecotypes. *Tjereh* has been introduced into Indonesia from China or India in recent years (NAKAGAHRA 1985). *Tjereh* and *aman* mainly belonged to the typical *indica* and many of their characters were similar to each other (TAKAHASHI and KAIMORI 1978, KATAYAMA *et al.* 1982), although the direction of the growth of the crown roots differed. It is suggested that after introduction to Indonesia, the crown roots of *tjereh* may have started to grow upward. The crown roots of the Japanese lowland and upland rice varieties grew downward. Since the oxygen concentration is lower in deeper soil, the Japanese rice roots may show a higher tolerance to low oxygen stress than the Indian and Indonesian rice varieties.

The direction of the crown root growth is likely to differ between the typical *indica* and typical *japonica*. Moreover, it was suggested that the growth direction of the crown roots was related to the environmental conditions where the varieties had been grown.

TAKITA and KUSHIBUCHI (1983) and TERASHIMA *et al.* (1986) who examined varietal differences in root characters, reported that the diameter of the crown root is related to the direction of growth. The correlation coefficients of the growth direction with the gravitropic response were higher than with the diameter of the crown roots (Figs. 2 and 3). *Bulu* had

thick crown roots, which did not grow downward and also did not respond to a gravitropic stimulus. The direction of the crown root growth was more related to the gravitropic response than to the diameter of the roots. YAMAZAKI *et al.* (1981) suggested that the growth direction of roots may be affected by the quantity of assimilates translocated from the shoot. Although the crown roots of *bulu* are thick, the translocation capacity of the assimilates may be low.

The crown roots of the typical *indica* and Japanese rice varieties at the reproductive stage grew near the soil surface. Once these roots grew on the soil surface, they were stimulated by light and grew downward (Fig. 3-1). The crown roots of the Indonesian rice varieties also exhibited a gravitropic response associated with the light stimulus (Fig. 3-1). On the other hand the crown roots of the Indonesian varieties spread on the soil surface (UENO and SATO 1989a). It is possible to consider that the light-stimulated roots of the Indonesian varieties may grow upward again for some unknown reason(s).

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イネの冠根の伸長方向の品種間差異および伸長方向におよぼす冠根の重力反応と太さの影響

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イネの生態型である *aus*, *aman*, *boro* (インド在来), *bulu*, *tjereh* (インドネシア在来) に属するイネおよび日本の水稻と陸稲を用い, 播種直後に生じた4本の冠根の伸長方向を暗条件下で検討した. *aus* に属するイネ品種は冠根の伸長方向において広い変異を持っていた. *aus* の中でインド型に属する品種はインド型に属さない品種に比べ, 冠根が水平方向へ伸長する傾向があった. *aman* と *boro* に属するイネ品種の冠根は水平方向へ伸長した (Fig. 1). インドネシアの生態型には冠根の一部が上方向へ伸長する品種が見いだされた. *bulu* は古くからインドネシアで栽培されてきた生態型であるのに対し, *tjereh* は比較的近年にインドや中国よりインドネシアに入ったと考えられている. *tjereh* は *aman* と多くの形質において似ているが, 上方向へ伸長する冠根を持つ品種の割合においては異なった. 日本の水稻と陸稲の冠根はおもに下方向へ伸長した. 水稻は陸稲より冠根を下方向へ伸長させる傾向があった (Fig. 1). *aman* と *boro* はインド型に属し, 日本の水稻は日本型に属している (Table 2). イネの冠根の伸長方向はインド型と日本型とで異なる傾向があることが分かった. また生育地域により冠根の伸長方向は異なる傾向もあった.

冠根の伸長方向に影響を与える要因として, 冠根の重力反応と太さについて検討した. 暗条件下において, 冠根の伸長方向は冠根の太さおよび重力反応と有意な正の相関を示した. しかし *bulu* の冠根は太いにも関わらず, 水平もしくは上方向へ伸長した (Figs. 2-1, 2-2). 明条件下ではすべての品種の冠根は下方向へ伸長し, 重力反応を示した. 伸長方向と重力反応の相関は有意であったが, 伸長方向と太さの相関は有意でなかった (Figs. 3-1, 3-2). イネの冠根の伸長方向の品種間差異は明条件下よりも暗条件下で明瞭となることが分かった. また, 冠根の伸長方向は冠根の太さとよりも, 重力反応と強い相関を示すことが分かった.