Heterosis for Root System Development in Japonica/Indica F₁ Rice Hybrid*

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Abstract : Vigorous growth of F₁ hybrid of rice (*Oryza sativa* L.) may be partially attributed to the development and function of the root system, but only a few studies have been conducted in this aspect. This study was carried out to elucidate the root system development of heterotic F₁ hybrid seedlings grown in culture solution for 30 days. Dry weight of a single nodal root (SNR) of F₁ hybrid was always greater than that of parents, except 10 days after planting. Each representative root system of 20-day-old F₁ hybrid and parents was quantitatively analyzed. Total root length and total number of root apices of SNR were also greater than those of parents. From the viewpoint of the entire root system, F₁ hybrid surpassed parents in the total root length, root dry weight and total number of root apices, and each heterobeltiosis was 168, 123 and 139, respectively. As a result, the root system of F₁ hybrid was not only heavier in the dry weight but also greater in length/dry weight ratio (specific root length) than that of parents. We interpreted this result that F₁ hybrid had high efficiency in converting dry matter into root length increment, which may possibly ensure high nutrient collection capability.

Key words : Heterosis, Japonica/indica F₁ hybrid, Lateral root, Nodal root, Rice, Specific root length, Total root length.

ジャポニカ/インディカ F₁ 雑種水稻における根系発達の雑種強勢: 長谷川浩・金 忠男・河野恭広** (北陸農業試験場・**名古屋大学農学部)

要 旨 : F₁ 雑種水稻の活発な生長に対して根系の発達と機能とが密接に関与していると考えられるが, このような視点からの研究は少ない. そこで, 本研究は 30 日間水耕液で育てたジャポニカ/インディカ F₁ 雑種水稻の幼植物における根系発達を明らかにするために行われた. 節根 1 本当たりの乾物重は播種後 10 日目を除き, 常に両親より F₁ 雑種で高かった. 播種後 20 日目の根系を側根まで実測したところ, F₁ 雑種は両親と比べて節根 1 本当たりの全根長が長く全根数が多かった. 根系全体から見ると, F₁ 雑種の全根長, 根系乾物重および全根数は両親のそれらを大きく上回り, Heterobeltiosis (=F₁ 雑種/優良親×100) はそれぞれ 168, 123, 139 に達した. その結果, F₁ 雑種の根系は両親のそれより重いだけでなく, 全根長/根系乾物重比 (Specific root length) においても両親のそれを上回った. このことは, F₁ 雑種は両親と比べて乾物から根長への転換効率が高いことを示唆している.

キーワード : 雑種強勢, ジャポニカ/インディカ F₁ 雑種, 水稻, 節根, 全根長, 全根長/根系乾物重比, 側根.

Vigorous growth of heterotic F₁ hybrids of crop plants can be partially attributed to the superior development and function of their root systems. Kiesselbach and Weihing⁵⁾ found heterosis for penetration depth, maximum spread and mean diameter of nodal axes in F₁ maize hybrids at maturing. Heimsch et al.⁴⁾ observed the anatomy of nodal axes of F₁ maize hybrid, but it was found that heterosis for the anatomy was indistinct. McClure and Harvey⁷⁾ estimated the root development of F₁ sorghum hybrid grown in the field using the radiophosphorus method. Nielsen and Barber⁸⁾ reported that only one of four combinations of F₁ maize hybrids showed marked

heterosis in specific root length. Several researchers^{3,10,12,15,16)} reported that dry weights of the root systems of F₁ hybrids were greater than those of parents.

It has been reported that F₁ hybrids absorb more mineral nutrients than parents^{3,11,12,15,17)}. Rabideau et al.¹¹⁾ examined the functional significance of the root system development of F₁ maize hybrid, and suggested that the active absorption of phosphorus in F₁ maize hybrid was associated with the larger root system in weight, indicating that its root system has a high capability for mineral nutrient uptake. In the previous study³⁾, we also found that F₁ hybrids were greater than parents in the dry weight of SNR as well as in leaf area per SNR and nitrogen uptake rate of SNR. This suggested that F₁ hybrids were superior to parents

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in their ability for nutrient and water uptake of SNR. However, mineral nutrient uptake seems to be more closely related to root length than root dry weight, as indicated in a theoretical work by Nye and Tinker⁹⁾ and in an ecological review by Böhm¹⁾. In this aspect, Lin and Yuan⁶⁾, who qualitatively analyzed the root development of F₁ rice hybrid, found that F₁ rice hybrid surpassed parents in penetration rate, depth and width of the rooted zone, and the numbers of adventitious and lateral roots. However, for F₁ rice hybrid, no quantitative analysis of the root system, including total root length, seems to have been conducted.

According to the quantitative study of one-month-old cereal root systems¹⁸⁾, more than 95% of the total root length was accounted for by the lateral roots, although their dry weight may not be a large proportion. Thus, the objective of this study was to quantitatively analyze the root system development, including the lateral roots of japonica/indica F₁ rice hybrid, which is expected to exhibit large heterosis and high yield.

Materials and Methods

1. Plant materials

F₁ rice hybrid (MS1003/Milyang 23) and parents [Akihikari; the maintainer line (japonica), Milyang 23; the restorer line (indica)] were used. The cytoplasmic male sterile line, MS1003, has the nuclear DNA of Akihikari and cytoplasm of Chinsurah Boro II.

2. Growth and treatment conditions

The experiment was conducted for 30 days from May 19, 1990. The rice plants were grown in water culture units of 300 liters consisting of a bed of 132 liters (110cm long, 60cm wide, 25cm deep) and a tank of 168 liters placed in a greenhouse. The water culture units were transferred outside during daytime to avoid extremely high temperatures, except rainy days. Average daily air temperatures calculated from maximum and minimum daily air temperatures during the experimental period was 23.8°C.

The rice plants were grown in the rice culture solution of Yoshida et al.¹⁹⁾, but in the present experiment, concentration of N, P, K, Ca and Mg was modified to one twentieth. NH₄⁺-N which is the major nitrogen form in paddy fields was employed as a nitrogen

source, and its concentration was monitored by the Indophenol method¹⁴⁾ and maintained daily by addition of concentrated NH₄⁺ stock solution. The pH of the culture solution was also adjusted daily to 5.1 with HCl and NaOH. The culture solution was continuously circulated at the rate of 10 liters per minute, and was renewed every ten days.

Seeds were selected with salt solution (specific gravity of 1.06) and sterilized with a 1000-fold dilution of thiram and benomyl for 24 hours prior to pregermination. The seeds pregerminated for 7 hours at 30°C were sown on a stainless net floating in the bed. The rice plants were transplanted into the three water culture units 10 days after sowing (Day 10). Mutual shading among the rice plants was negligible throughout the experimental period.

3. Measurement of plant growth

The sampling and measurement for F₁ hybrid and parents were conducted on Day 10, 15, 20, 25 and 30, although the data only for Day 10, 20 and 30 were shown for simplicity. The number of plants sampled on Day 10, 15, 20, 25 and 30 was 25, 24, 18, 6 and 6, respectively. After counting the number of both stems and nodal roots, samples were dried in an oven at 80°C for two days and dry weights of shoots and root systems were determined. Dry weight of a single nodal root (SNR) was calculated by dividing the dry weight of the root system with the number of nodal roots.

On Day 20, additional nine to 12 plants for F₁ hybrid and parents were also harvested to determine root system development. One representative root system that showed average shoot and root system development was selected from the samples, and the number and length of all root system components, such as nodal root axes and lateral roots, were manually measured with a ruler. In the measurement, first and second order lateral roots were classified into L (long) and S (short) types following the procedure used by Yamauchi et al.¹⁸⁾.

4. Data analysis

Parametric data analysis was performed by the ANOVA and GLM procedures of PC-SAS (Statistical Analysis Systems for Personal Computers, Version 6.03, SAS Inc., USA)¹³⁾. The Ryan-Einot-Gabriel-Welsch option was used for a multiple range test.

Table 1 Heterosis for dry weight and the number of nodal roots.

	Dry weight (mg/plant)						Number of nodal roots per plant		
	Shoot			Root system					
	Day 10	Day 20	Day 30	Day 10	Day 20	Day 30	Day 10	Day 20	Day 30
Akihikari	7.00 b	83.3 c	426 c	3.91 a	31.8 c	184 c	4.6 a	18 b	48 a
Milyang 23	7.17 b	97.6 b	647 b	3.25 b	35.8 b	259 b	6.2 a	21 a	54 a
F ₁ hybrid	8.62 a	121.9 a	832 a	4.18 a	43.8 a	339 a	5.2 a	21 a	52 a
	(120)	(125)	(129)	(107)	(123)	(131)	(84)	(100)	(96)

Values with the same letter in the same day are not significant at 5% level by Ryan-Einot-Gabriel-Welsch multiple range test¹³⁾.

Numerals in parentheses indicate heterobeltiosis [=F₁/(better parent) × 100].

Table 2 Heterosis for the dry weight of a single nodal root (SNR, mg).

	Day 10	Day 20	Day 30
Akihikari	0.85	1.77	3.83
Milyang 23	0.52	1.66	4.80
F ₁ hybrid	0.80	2.03	6.52
	(95)	(115)	(136)

Numerals in parentheses show heterobeltiosis.

Results

Shoot dry weight of F₁ hybrid statistically surpassed that of parents throughout the experimental period. On the other hand, the dry weight of root system of F₁ hybrid was almost the same as that of better parent (Akihikari) on Day 10, but thereafter F₁ hybrid became significantly greater than parents (Table 1). The number of both stems (data not shown) and nodal roots (Table 1) showed similar value between F₁ hybrid and parents. The dry weight of SNR was heavier in F₁ hybrid than in parents, except that on Day 10 (Table 2). This can be interpreted that F₁ hybrid partitioned more dry matter to each nodal root than parents.

Fig. 1 shows distribution patterns of the total root length (1) and the total number of root apices (2) of SNR composed of a root system in each genotype examined. The root system of F₁ hybrid was composed of more SNRs whose total length and total number of root apices were relatively great when compared with that of parents. The mean values of

Fig. 1 Distribution patterns of the total root length (1) and the total number of root apices (2) of SNR composed of a root system in each genotype examined (Day 20). The horizontal bar in each column indicates each mean value. The number of nodal roots composed of a root system examined was 20 in Akihikari (A), 23 in Milyang 23 (M) and 24 in F₁ hybrid (F₁). Each plot indicates total root length or total number of root apices of each SNR, although parts of the plots overlapped each other.

the total root length and the total number of the root apices of SNR were also greater in F_1 hybrid than in parents (Fig. 1). Although the second order S type laterals emerged by Day 20, only a small portion (8% and less than) of the total root length and the total number of the root apices was accounted for by the first order L type laterals and second order S type laterals that emerged from them. Thus, the difference in the root system development between F_1 hybrid and parents can be mainly attributed to that in the development of nodal root axes and the first order S type laterals. Total length of the nodal root axes, which are the sites where lateral roots initiate, was longer in F_1 hybrid than in parents. Moreover, average length of the first order S type laterals of F_1 hybrid surpassed that of parents (Table 3).

The total length of seminal root in F_1 hybrid was much longer compared with that in parents. In the total number of the root apices, F_1 hybrid also surpassed parents. Consequently, F_1 hybrid had substantially longer root system than parents, and the heterobeltiosis attained 168 (Table 4).

Table 3 Heterosis for root system components (Day 20).

	Total length of nodal root axes (cm)	Average length of first order S type laterals (cm)
Akihikari	234	0.35
Milyang 23	242	0.32
F_1 hybrid	305 (126)	0.41 (117)

Numerals in parentheses show heterobeltiosis.

Fig. 2-1 shows the ratio of the total root length to the dry weight of the root system (specific root length). The specific root length of F_1 hybrid was greater than that of parents. Since the specific root length reflects the mean diameter of roots assuming that the specific gravity of the root system is constant²⁾, the result suggests that F_1 hybrid was composed of thinner roots. However, the percentage of the total length of the first and second order S type laterals to the total root length, which indicates the percentage of the thinner roots in

Fig. 2 Heterosis for the ratio of the total root length to the dry weight of the root system (specific root length, 1) and the percentage of the total length of S type laterals to the total root length (2, Day 20). Numerals in parentheses show heterobeltiosis.

Table 4 Heterosis for the total root length and total root apex number (Day 20).

	Total root length (cm)		Total root apex number per plant
	Root system	Seminal root	
Akihikari	1273	296	2977
Milyang 23	1293	319	3312
F_1 hybrid	2172 (168)	508 (159)	4613 (139)

Numerals in parentheses show heterobeltiosis.

the entire root system, were not greatly different between F_1 hybrid and parents (Fig. 2-2).

Discussion

In our previous study³⁾, it was found that F_1 hybrids were greater than parents in the dry weight of SNR as well as in leaf area per SNR and nitrogen uptake rate of SNR. We interpreted those results in such a way that F_1 hybrid was superior to parents in the function of SNR, and thus the entire root system. Throughout the experimental period, including Day 15 and Day 25 (data not shown) except only Day 10, the same result was also found in this study (Table 2). In addition, the total root length and the total number of the root apices of F_1 hybrid were also greater than those of parents. Thus, these may partially explain why the function of the root system of F_1 hybrid was possibly superior to that of parents.

According to the further analysis by the specific root length, F_1 hybrid was greater than parents (Fig. 2-1). Assuming that the specific gravity of the root system is constant²⁾, this result indicates that F_1 hybrid consists of thinner roots, and can be interpreted that F_1 hybrid had a high efficiency in converting the dry matter into root length increment. However, we found in the previous study that nodal root axes of F_1 hybrid were thicker than those of parents³⁾. In addition, the percentage of the total length of the first and second order S type laterals to the total root length, which indicates the percentage of the thinner roots in the entire root system, were not greatly different between F_1 hybrid and parents (Fig. 2-2). These facts lead us to conclude that F_1 hybrid may have produced thinner S type laterals than parents, again assuming the constant specific gravity. Further study is required.

McClure and Harvey⁷⁾ reported that only during maturing stage, F_1 sorghum hybrid surpassed parents in root system development. This was quite different from the present result. The root system of F_1 hybrid was already substantially longer in the total length than that of parents by Day 20, and the heterobeltiosis attained 168 (Table. 4). F_1 hybrid also surpassed parents in the total number of the root apices of the root system. (Table 4), although the degree of the heterobeltiosis (=139) was not as high as that for

total root length.

In the expression of heterosis in the earlier stage, the heterobeltiosis for the total length of the seminal root was almost the same as that for the entire root system (Table 4). Quantitative determination of the entire root system is laborious and time-consuming. Thus, the determination of the seminal root length might provide a speedy and early-stage selection method for heterotic root systems in F_1 rice hybrids.

In conclusion, compared with parents, SNR of F_1 hybrid was heavier in root dry weight and greater in total root length. Thus, this may partially explain why the function of SNR of F_1 hybrid was possibly superior to that of parents. Moreover, from the viewpoint of the entire root system, F_1 hybrid was already not only heavier in the dry weight but greater in the specific root length on Day 20, and thus was substantially greater in root system length. We interpreted this result in a such way that F_1 hybrid had a high efficiency in converting the dry matter into root length increment.

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