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# Heterosis in Japonica/Indica $F_1$ Rice Hybrids with Special Reference to Nodal Root Function*

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**Abstract** : Although root system of japonica/indica $F_1$ hybrids of rice (*Oryza sativa* L.) must play an important role for expression of heterosis, few studies have been conducted. This study was carried out to evaluate how the function of root system in japonica/indica $F_1$ rice hybrids is related to heterosis for shoot growth. Two $F_1$ hybrids grown in culture solution for 45 days after sowing and $F_1$ hybrid cultured in soil-filled pots till full ripening were compared with parents. Shoot dry weight of $F_1$ hybrids was greater than that of parents when their stem and nodal root numbers were similar to those of parents. Heterobeltiosis for shoot dry weight reached the maximum 180 when the $F_1$ hybrid surpassed parents in the stem and nodal root numbers. $F_1$ hybrids were the same as one or both parents in S/R ratio, but dry weight of a single nodal root of $F_1$ hybrids exceeded that of parents in most cases. Moreover, nitrogen uptake rate of a single nodal root ($\mathbf{N}_{no}$) as well as leaf area and shoot dry weight of a single nodal root in $F_1$ hybrids was greater than those in parents during vegetative growth. Nitrogen uptake rate per root system dry weight ($\mathbf{N}_{dw}$), however, was much the same. These results strongly suggest that in japonica/indica $F_1$ hybrids, more photosynthate is partitioned to each nodal root, so that this enhances its function and consequently, the entire root system.
**Key words** : Dry matter partitioning, Heterosis, Japonica/indica $F_1$ hybrid, Nitrogen uptake, Rice, Root system, Single nodal root.

**ジャポニカ/インディカ $F_1$ 雑種水稲の雑種強勢とその節根の機能**：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**：一般に作物の雑種強勢において根系が重要な役割を果たしていると考えられる．にもかかわらず，ジャポニカ/インディカ $F_1$ 雑種水稲の根系に関する研究は極めて少ない．そこで，本研究は根系の機能が地上部の雑種強勢にどう関連しているかを明らかにするために行われた．播種から 45 日間水耕栽培した $F_1$ 雑種（MS 1003/密陽 23 号，MS 1003/新青矮 1 号）および成熟期までポットで土壌栽培した $F_1$ 雑種（MS (N)/密陽 23 号）を両親と比較した．$F_1$ 雑種では茎数や節根数が両親と同程度であっても地上部乾物重は両親を上回ったが，茎数や節根数が多かった場合には地上部乾物重の Heterobeltiosis は最高 180 に達した．栄養生長期には S/R 比は両親と大差なかったが，節根 1 本当たりの乾物重は生育初期から完熟期までのほとんどの場合両親より大きかった．さらに，栄養生長期には節根 1 本当たりの葉面積，地上部乾物重および窒素吸収速度が高かった．しかしながら，根系乾物重当たりの窒素吸収速度は両親と同様の値であった．以上の結果は，ジャポニカ/インディカ $F_1$ 雑種水稲では節根 1 本当たりの乾物分配量が多く，このことが節根 1 本当たりの機能を高め，結果として根系全体の機能も高くなることを強く示唆している．
**キーワード**：乾物分配，根系，雑種強勢，ジャポニカ/インディカ $F_1$ 雑種，節根 1 本当たりの機能，水稲，窒素吸収速度．

Since Jones[11] discovered heterosis in $F_1$ rice hybrid, a number of physiological studies on heterosis for their shoot growth[1,2,5,14,15,23~27] have been conducted.

Root system of $F_1$ rice hybrid must play an important role for expression of heterosis. Although root development[15,18,33], nutrient uptake[8~10,16,28], root RNA content[5], root ATP content and enzyme activity[33], root exudate[4,5,15,16], root density[33], root/whole plant dry weight ratio[13] and pulling force[7,20] of $F_1$ hybrids have already been investigated, the role of the root system is still unclear. Japonica/indica $F_1$ rice hybrids being developed at Hokuriku National Agricultural Experiment Station are expected to exhibit larger heterosis and higher yield. However, studies about the japonica/indica $F_1$ rice hybrids[18,28] are few in number.

Gramineous root systems consist of seminal and nodal root axes and lateral roots produced on those axes. It is thus important to elucidate relationship between dry matter partitioning

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and function of each seminal and nodal root. Therefore, the objective of this study is to evaluate how the function of root system in japonica/indica $F_1$ rice hybrids is related to heterosis for shoot growth with special reference to the function of a single nodal root including seminal root.

## Materials and Methods

### 1. Experiment 1

Two $F_1$ rice hybrids (MS1003/Milyang 23, MS1003/XinGingAi 1) and parents [Akihikari ; the maintainer line (japonica), Milyang 23 and XinGingAi 1 ; the restorer lines (indica)] were grown in Kasugai rice culture solution[12] in a greenhouse under natural light and temperature for 45 days. The cytoplasmic male sterile (CMS) line, MS1003, has the nuclear DNA of Akihikari and the cytoplasm of Chinsurah Boro II.

Seeds were selected with salt solution (specific gravity of 1.06) and sterilized with 1000-fold dilution of thiram and benomyl for 24 hours. Pregerminated seeds were sown on a stainless net floating in a container filled with 77 $l$ of 8-fold dilution of the culture solution {5ppm N as $(NH_4)_2SO_4$ ; 1.1ppm P as $Na_2HPO_4$ ; 3.1ppm K as KCI ; 0.36ppm Ca as $CaCl_2$ ; 0.45ppm Mg as $MgCl_2$ ; 0.43ppm Fe-Citrate ; 0.041ppm Mn as $MnCl_2$} on May 27 of 1989. The culture solution was prepared with tap water. The culture solution was renewed on the 7th day (Day 7) and the 10th day (Day 10) after sowing and then the pH of the culture solution was adjusted to 5.1 with 1N of hydrochloric acid and sodium hydroxide. On Day 14, two hundred seedlings were transplanted at a distance of 5cm×4.5cm into a bed (132 $l$ ; length 110cm, width 60cm, depth 20cm plus tank 168 $l$) filled with 40-fold dilution of the solution (1ppm N ; 0.22ppm P ; 0.62ppm K ; 0.72ppm Ca ; 0.90ppm Mg ; 0.86ppm Fe ; 0.082ppm Mn). Since the actual nitrogen concentration of the paddy soil solution in heavy clay of Hokuriku district (2ppm or less)[31] is very much lower than that of the usual rice culture solution (10—30ppm). The culture solution was circulated at the rate of 10$l$ per minute and renewed every week. The pH of the solution was abjusted daily to 5.1. Mutual shading among rice plants was negligible.

According to the plan size, five to eighty plants for each $F_1$ hybrid and parents were collected seven times beginning on Day 14 until Day 45. The leaf area and number of nodal roots including seminal root were determined. The plants were dried in an oven at 80°C for two days and the dry weights of the shoots and root systems were taken. The dried shoots were ground and their nitrogen content was determined by the semi-micro Kjeldahl digestion and Indophenol method[22] with Autoanalyzer (TRAACS-800, Technicon Industrial Systems, USA).

Since the linear relations between shoot nitrogen content and nodal root number or dry weight of root system were observed, nitrogen uptake rate of a single nodal root ($\mathbf{N}_{no}$) and per dry weight of root system ($\mathbf{N}_{dw}$) were estimated by a formula analogous to mean net assimilation rate used in growth analysis[19] :

$$\mathbf{N}_{no}=\frac{N_2\text{-}N_1}{RN_2\text{-}RN_1}\times\frac{\mathrm{Log_e}(RN_2)\text{-}\mathrm{Log_e}(RN_1)}{T_2\text{-}T_1}$$

$$\mathbf{N}_{dw}=\frac{N_2\text{-}N_1}{RW_2\text{-}RW_1}\times\frac{\mathrm{Log_e}(RW_2)\text{-}\mathrm{Log_e}(RW_1)}{T_2\text{-}T_1}$$

where $T_1$ and $T_2$ is Day $T_1$ and Day $T_2$, respectively, and $N_1$, $RN_1$, $RW_1$ and $N_2$, $RN_2$, $RW_2$ is shoot nitrogen content, number of nodal roots and dry weight of root system on Day $T_1$ and Day $T_2$, respectively.

### 2. Experiment 2

$F_1$ rice hybrid (MS (N)/Milyang 23) and parents [Nekken 2 ; the maintainer line (japonica) and Milyang 23] were cultured in pots under outdoor conditions till full ripening in 1990. The CMS line, MS (N), has the nuclear DNA of Nekken 2, in which wide-compatibility genes were incorporated[3], and the cytoplasm of Chinsurah Boro II.

Cylindrical plastic pots (diameter, 25cm, depth ; 30cm) were filled with 14.4kg of air-dried heavy clay soil, which was sieved through 5mm mesh. Sixteen g of crushed compound fertilizer (N ; 15%, P ; 6.5%, K ; 12%) was thoroughly mixed with the soil as basal dressing before filling the pots. Five pregerminated seeds of the varieties prepared in the same way as Experiment 1 were sown in a pot under upland conditions in a greenhouse on April 21. After seedling emergence the pots were waterlogged, and the seedlings were thinned into one plant per pot. The pots were

Table 1. Comparison of leaf area, dry weight, shoot nitrogen content and nodal root number of two $F_1$ hybrids and parents (Experiment 1).

| | Plant age in leaf number | Leaf area ($cm^2$/plant) | Dry weight (mg/plant) | | Shoot/root ratio | Shoot nitrogen content (mg/plant) | Number of nodal root |
|---|---|---|---|---|---|---|---|
| | | | Shoot | Root system | | | |
| Day 14 | | | | | | | |
| A | 3.0 | 0.79 b | 9.61 a | 4.90 a | 1.96 b | 0.279 a | 8.6 a |
| M | 3.0 | 0.65 b | 8.04 b | 3.81 b | 2.12 a | 0.231 b | 6.9 b |
| FM | 2.9 | 1.08 a | 10.15 a | 5.27 a | 1.93 b | 0.284 a | 6.1 b |
| | | (137) | (106) | (108) | (91) | (102) | (71) |
| A | 3.0 | 0.79 c | 9.61 b | 4.90 c | 1.96 a | 0.279 b | 8.6 a |
| X | 3.2 | 1.21 b | 8.86 c | 5.46 b | 1.62 b | 0.258 b | 8.7 a |
| FX | 3.1 | 1.55 a | 10.68 a | 6.63 a | 1.61 b | 0.315 a | 7.5 a |
| | | (129) | (111) | (121) | (82) | (113) | (86) |
| Day 24 | | | | | | | |
| A | 5.0 | 6.15 b | 37.5 b | 13.9 b | 2.70 a | 1.61 b | 13.8 a |
| M | 5.1 | 6.73 b | 35.8 b | 13.2 b | 2.71 a | 1.61 b | 13.9 a |
| FM | 5.0 | 9.26 a | 44.9 a | 16.3 a | 2.76 a | 2.05 a | 13.9 a |
| | | (138) | (120) | (117) | (102) | (127) | (100) |
| A | 5.0 | 6.15 b | 37.5 b | 13.9 b | 2.70 a | 1.61 b | 13.8 b |
| X | 5.9 | 8.60 a | 42.2 b | 17.7 a | 2.38 b | 2.04 a | 17.1 a |
| FX | 5.5 | 9.52 a | 48.8 a | 18.4 a | 2.65 a | 2.25 a | 16.2 a |
| | | (111) | (116) | (104) | (98) | (110) | (95) |
| Day 45 | | | | | | | |
| A | 9.8 | 141 b | 1180 b | 501 b | 2.36 a | 38.6 b | 95.4 a |
| M | 9.2 | 153 b | 945 c | 517 b | 1.83 b | 31.8 c | 61.4 c |
| FM | 9.0 | 207 a | 1458 a | 740 a | 1.99 b | 46.5 a | 77.0 b |
| | | (135) | (124) | (143) | (84) | (120) | (81) |
| A | 9.8 | 141 b | 1180 b | 501 b | 2.36 a | 38.6 ab | 95.4 a |
| X | 10.2 | 144 b | 934 c | 576 b | 1.62 c | 34.9 b | 72.2 c |
| FX | 9.3 | 205 a | 1422 a | 782 a | 1.82 b | 45.2 a | 83.4 b |
| | | (143) | (121) | (136) | (77) | (117) | (87) |

Day 0 : Sowing day, A : Akihikari, M : Milyang 23, FM : MS1003/Milyang 23, X : XinGingAi 1, FX : MS1003/XinGingAi 1. Values with the same letter in each combination are not significant at 5% level by Tukey's Studentized Test. Values in parentheses indicate heterobeltiosis [ $= F_1$/(better parent) $\times$ 100].

transferred outside the greenhouse on Day 20, and then grown as single plants which were free from mutual shading. On Day 92, 2.4g of ammonium sulfate was applied to each plant as top dressing.

In each sampling the number of stems and nodal roots and shoot dry weights were determined on three to five plants for $F_1$ hybrid and parents, respectively. Dry weights of root systems were measured by means of the ashing method[29] on one to four plants.

### 3. Data analysis

Data analysis was performed by the ANOVA (Analysis of Variance), the GLM (General Linear Model) and the TTEST (t-test) procedures of PC-SAS (Statistical Analysis Systems for Personal Computers, Verison 6.03, SAS Inc., USA)[21].

## Results

### 1. Experiment 1

Table 1 shows leaf area, dry weight, shoot

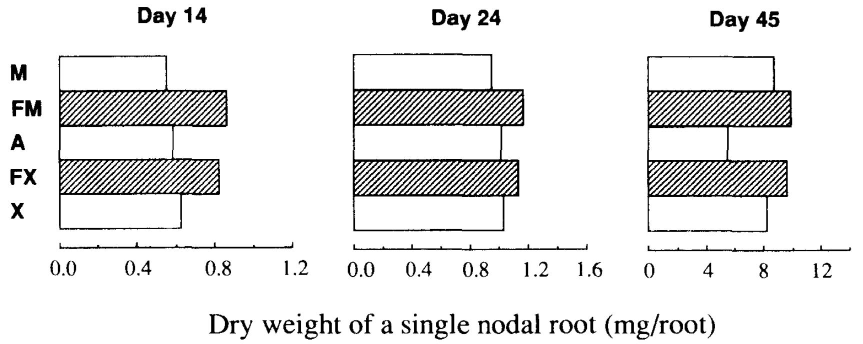


Fig. 1. Comparison of dry weight of a single nodal root of two $F_1$ hybrids and parents (Experiment 1).
M : Milyang 23, A : Akihikari, X : XinGingAi 1, FM : MS1003/Milyang 23, FX : MS1003/XinGingAi 1.

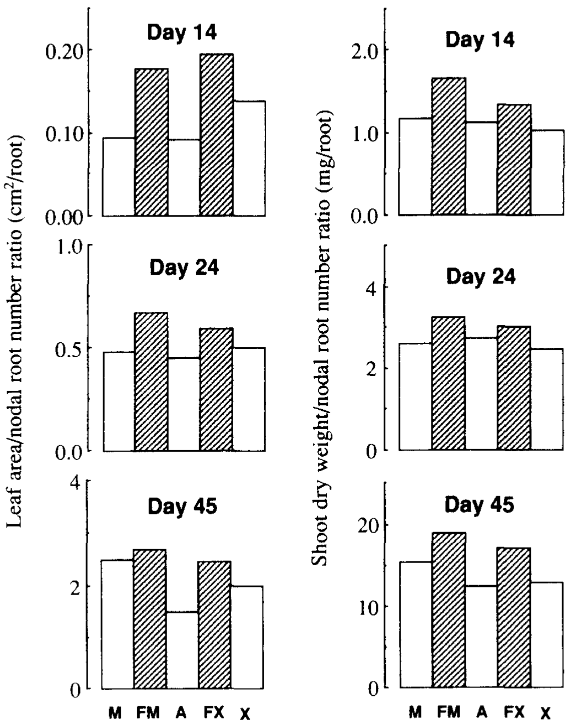


Fig. 2. Comparison of leaf area and shoot dry weight/number of nodal roots ratios of two $F_1$ hybrids and parents (Experiment 1). Abbreviations M, A, X, FM and FX, see Fig. 1.

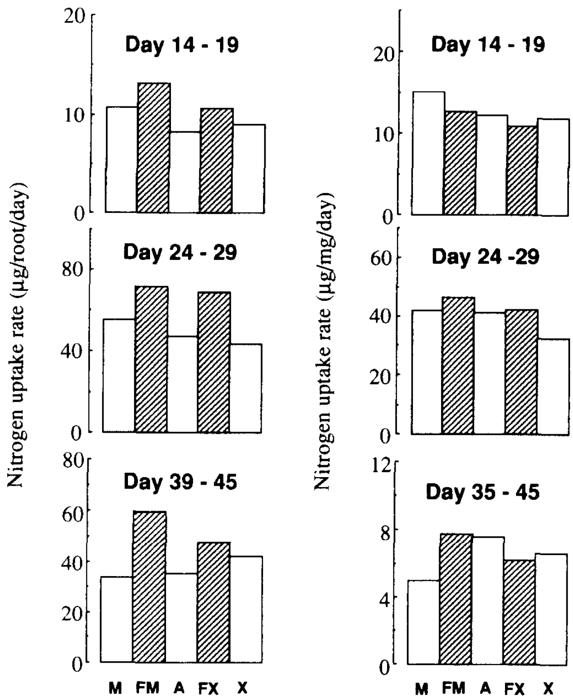


Fig. 3. Comparison of nitrogen uptake rate of a single nodal root ($\mathbf{N}_{no}$, left) and per root system dry weight ($\mathbf{N}_{dw}$, right) in two $F_1$ hybrids and parents (Experiment 1). Abbreviations M, A, X, FM and FX, see Fig. 1.

nitrogen content, and number of nodal roots on Day 14, Day 24 and Day 45. Shoot dry weight of both $F_1$ hybrids significantly surpassed that of parents. Leaf area, root system dry weight and shoot nitrogen content of both $F_1$ hybrids were all greater than those of parents as well, although not always significant.

On the other hand, the number of nodal roots of both $F_1$ hybrids was about same as that of either parent, or in between that of parents throughout the experimental period. The stem number of Akihikari, Milyang 23, MS1003/Milyang 23, XinGingAi 1 and MS1003/XinGingAi 1 on Day 45 was 7.2, 7.8, 8.0, 8.4 and 8.8, respectively, but significant differences between mean values was not observed. Shoot/root system dry weight ratio (S/R ratio) showed a similar trend to the number of nodal roots. However, dry weight of a single nodal root of both $F_1$ hybrids, calculated from dividing the root system dry

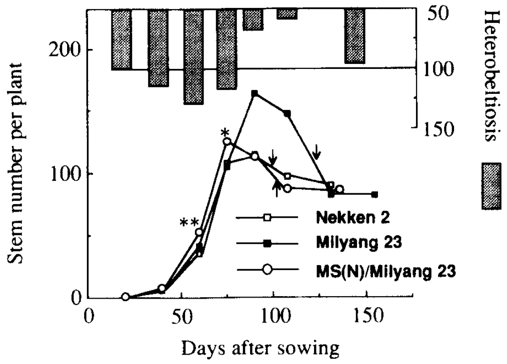


Fig. 4. Comparison of changes in stem number of $F_1$ hybrid and parents (Experiment 2). ○ with * and ** indicate that $F_1$ hybrid statistically surpassed parents at 5% and 1% level (t-test), respectively. ○ without * shows not significant. Arrows show the heading days.

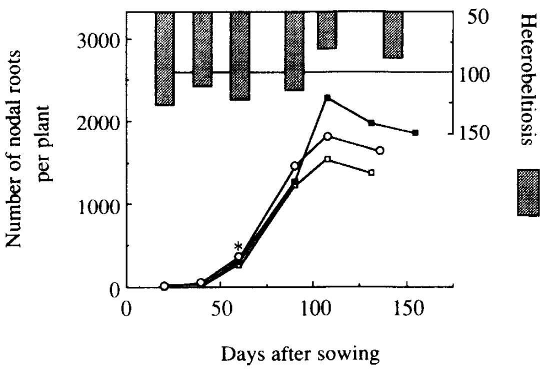


Fig. 5. Comparison of changes in number of nodal roots of $F_1$ hybrid and parents (Experiment 2). Symbols □, ■, ○, and *, see Fig. 4.

weight with the number of nodal roots, was larger than that of parents (Fig. 1).

The ratios of leaf area and shoot dry weight to number of nodal roots are shown in Fig. 2. Both leaf area and shoot dry weight of a single nodal root of $F_1$ hybrids were always greater than those of parents. Moreover, $\mathbf{N}_{no}$ of both $F_1$ hybrids always exceeded that of parents (Fig. 3). These results can be interpreted that the function of a single nodal root such as water and nutrient uptake is higher in $F_1$ hybrids than parents. $\mathbf{N}_{dw}$ of $F_1$ hybrids, however, was similar to that of parents (Fig. 3).

## 2. Experiment 2

Fig. 4 shows time-course changes in stem number of pot-grown $F_1$ hybrid (MS(N)/Milyang 23) and parents. Stem numbers of $F_1$ hybrid on Day 60 and Day 75 were greater than those of parents. Then, that of Milyang 23 still increased while that of Nekken 2 and $F_1$ hybrid decreased gradually, and the number on Day 90 was the highest in Milyang 23 followed by $F_1$ hybrid and Nekken 2. However, the final panicle number of the three varieties was similar. $F_1$ hybrid also exceeded parents in the number of nodal roots from Day 30 to Day 90, although not necessarily singnificant (Fig. 5). Number of nodal roots of the plants reached maximum on Day 108, and the order among the varieties was the same with that of the stem number. Thereafter, number of nodal roots of the plants gradually decreased toward full ripening.

Eventually, shoot dry weight of $F_1$ hybrid became significantly greater than that of parents from Day 30 to Day 108, and the heterobeltiosis attained 180 on Day 60. In addition, shoot dry weights of Milyang 23 and $F_1$ hybrid at full ripening were the same, although the growth period was 19 days longer in Milyang 23 (Fig. 6).

Fig. 7 indicates the dry weight of a single nodal root. The dry weight of $F_1$ hybrid was heavier than that of parents from Day 40 to full ripening of $F_1$ hybrid. However, the dry weight of Milyang 23 showed marked increase during late ripening stage. Since Milyang 23 belongs to late-maturing variety in Hokuriku district, the mean temperature during the stage was comparatively low (22.4°C). Therefore, surplus photosynthetic assimilates which were not translocated to panicles[30] may have been accumulated in the root system.

## Discussion

$F_1$ rice hybrids used in Experiment 1 exhibited obvious hybrid vigor for shoot growth during vegetative growth. The mean heterobeltiosis for shoot dry weight was 116 (Table 1), whereas the stem numer of $F_1$ hybrids on Day 45 was almost the same as that of parents. The numbers of nodal roots of $F_1$ hybrids were also similar to those of parents during the experimental period. On the other hand, $F_1$ hybrid selected for Experiment 2 was greater in the number of both stems and nodal roots than parents on Day 60 (Figs. 4 and 5), and heterobeltiosis for shoot dry weight reached 180 at that time (Fig. 6). Accordingly, an increase in stem number should result in an increase of nodal root number in $F_1$ hybrid,

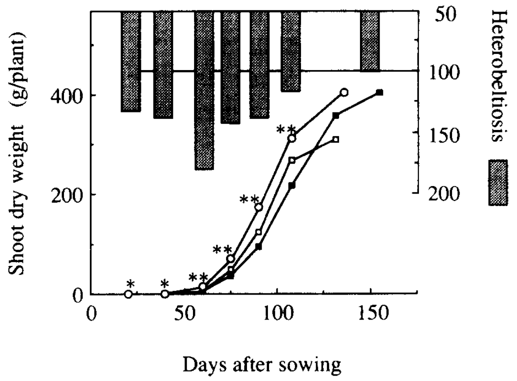


Fig. 6. Comparison of changes in shoot dry weight of $F_1$ hybrid and parents (Experiment 2). Symbols □, ■, ○, * and **, see Fig. 4.

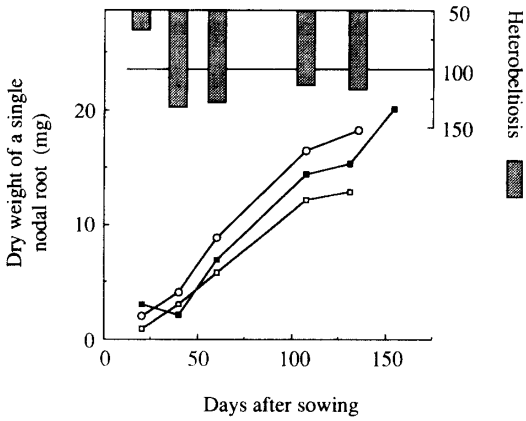


Fig. 7. Comparison of changes in dry weight of a single nodal root of $F_1$ hybrid and parents (Experiment 2). Symbols □, ■, ○, see Fig. 4.

and the degree of heterosis could become maximum during vegetative growth. The depression of tillering in Experiment 1 must be due to high temperature in the greenhouse[17].

Kawano et al.[13] reported that 22 out of 33 $F_1$ rice hybrids, which were grown in culture solution for seven weeks after transplanting, surpassed parents in the partitioning rate of dry matter to roots. In this study, however, S/R ratio of $F_1$ hybrids was the same as for either parent or in between parents (Table 1). This means the partitioning rate of dry matter to root system of japonica/indeca $F_1$ rice hybrids is much the same as that of parents during vegetative growth.

On the other hand, the dry weight of a single nodal root of $F_1$ hybrids exceeded that of parents from young seedling to full ripening stage with one exception (Figs. 1 and 7), whether the number of nodal roots of $F_1$ hybrids and parents was similar or not. According to our preliminary experiment where MS1003/Milyang 23 and parents were grown in 0.2, 2.0 and 20.0ppm $NH_4$-N of culture solution, the $F_1$ hybrid was from 1.2 to 1.3 times larger in cross sectional area of nodal root axes, and was from 1.0 to 1.2 times longer in nodal axis length than better parent. This indicates that the $F_1$ hybrids used partition more dry matter to each nodal root than parents, and form thicker and longer nodal root axes.

Ichii and Nakamura[9] showed that most of 25-day-old $F_1$ hybrids of japonica/japonica combination were higher than parents in $NH_4$-N, $NO_3$-N, P and K uptake rates (whole plant dry weight basis), whereas in whole plant dry weight the $F_1$ hybrids were much the same as either parent. However, $\mathbf{N}_{no}$ as well as leaf area and shoot dry weight of a single nodal root in $F_1$ hybrids was greater than those of parents in this study (Figs. 2 and 3). These results strongly suggest that in japonica/indica $F_1$ hybrids more photosynthate is partitioned to each nodal root, so that this enhances its function and consequently, the entire root system.

Suzuki et al.[28] reported that nitrogen uptake rate (whole plant dry weight basis) was much the same between $F_1$ hybrids and parents irrespective of japonica/japonica or japonica/indica combinations. They suggested that higher nirtogen uptake rate per plant of $F_1$ hybrids may not be due to higher uptake rate per dry weight, but due to their larger weight as a whole plant. In addition, in the present study, japonica/indica $F_1$ hybrids exhibited similar value to parents in $\mathbf{N}_{dw}$ during vegetative growth.

It is well-known that in gramineous crop plants which form fibrous root system lateral roots greatly contribute to the total length and surface area of the root system[6,32], although their dry weight may not be in large proportion. Therefore, it is indispensable to know how $F_1$ rice hybrids utilize more dry matter partitioned to each nodal root to produce lateral roots. However, no quantitative analysis of the root system in $F_1$ rice hybrids seems to be conducted. Thus, further study is needed to quantify development of the root system in $F_1$ rice hybrids.

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