Relative Contribution of Hetero-and Auto-trophic Growth to Genotypic Variation of Seedling Vigor in Rice (*Oryza sativa* L.)

Tatsuhiko Shiraiwa, Eiko Watatsu and Takeshi Horie

(Graduate School of Agriculture, Kyoto University, Japan)

Abstract: To elucidate the major physiological process to cause genotypic variation in the seedling vigor of rice, we analyzed the dry matter accumulation in the seedling for diverse cultivars distinguishing hetero- and auto-trophic growth. Four cultivars in Exp. 1 and 63 cultivars in Exp. 2 were grown in a glasshouse by hydroponics for about three weeks. In Exp. 1, heterotrophic dry weight (DWh) was regressed against thermal time (T, °C d) by logistic functions, in which the final heterotrophic dry weight (DWh_max) was considered the primary determinant of heterotrophic growth rate. The increase of autotrophic dry weight (DWa, DWt (total DW)-DWh) was regressed to the exponential function of T with a fairly stable parameter, relative growth rate (RGR). The variation of DWt among cultivars and seed-sizes was well represented by combining the DWh and DW models. In Exp. 2, DWt varied among cultivars from 51 to 116 mg pl⁻¹. The effects of cultivar-specific parameters, DWh_max (final DWh) and RGR, were evaluated by calculating the standard DWt with the mean DWh_max and RGR, and then substituting one of the two cultivar-specific parameters for every cultivar. The results showed that those cultivars whose superior DWt was attributable to DWh_max were limited to very large-seed cultivars. If they were excluded, the estimated effect of RGR (autotrophic process) on DWt was evidently greater than that of DWh_max (heterotrophic process).

Key words: Autotrophic growth, Genotypic variation, Heterotrophic growth, *Oryza sativa*, L., Relative growth rate, Seed reserve, Seedling vigor.

Seedling vigor is a desirable trait for improving and stabilizing crop productivity especially under resource-limited conditions. Genotypic variability and heritability of seedling vigor in rice have been recognized in a number of studies (Chen et al., 1986; Lee et al., 1986; Sasahara et al., 1986; Redona and Mackill, 1996a; Mackill and Lei, 1997) and identification of genetic factors for this trait has recently been attempted by QTL approaches (Redona and Mackill, 1996b; Cui et al., 2002; Zhang et al., 2005). However, the presumed genomic regions for seedling vigor varied depending on genetic background of the studied populations and a number of epistatic effects (Zhang et al., 2005). In this respect, we still need to understand major physiological processes that cause variation in this trait and to quantify the effects of important factors, as a prerequisite for determination of major genetic factor and its utilization in the breeding programs.

Close correlations have been reported between seed size and seedling growth (Chen et al., 1986; Lafond and Baker, 1986; Sasahara et al., 1986), indicating that seedling vigor of the plant is strongly affected by the seed reserve utilization, i.e., heterotrophic growth. However, the extent to which heterotrophic growth contributes to genotypic variation of seedling growth has not been quantified and hence the significance of autotrophic process for the variation is not clear.

The initial growth of rice plant immediately after germination is completely heterotrophic and the autotrophic process starts after the establishment of photosynthetically active organs, but the heterotrophic process also continues until the seed reserve is consumed (Sasaki and Hoshikawa, 1997; Salam et al., 1997, 1999; Asch et al., 1999). Due to the existence of this "transit phase", it is not easy to directly determine whether a vigorous seedling growth resulted from its seed reserve as the initial capital or photosynthetic activity as the compound interest. In this study, seedling growth of rice was analyzed distinguishing hetero- and auto-trophic dry weight gain. The objective was to determine the relative contribution of hetero- and auto-trophic growth to the variability of seedling vigor among diverse rice cultivars.

Materials and Methods

In Experiment 1, four cultivars were intensively observed from 27 May to 15 June 1999 in order to...
establish a formula of growth analysis distinguishing between the hetero- and autotrophic growth. Experiment 2 was conducted from 23 September to 16 October 1999 with 63 diverse cultivars to quantify variability of seedling vigor among cultivars and analyze it in reference to the effects of hetero- and autotrophic growth activity. In both experiments, plants were grown hydroponically in a greenhouse at Kyoto University, Japan. The mean air temperature was 26.9 and 19.9°C during the periods of Experiment 1 and 2, respectively. The seeds harvested in 1998 and 1997 were stored at 15°C and 40% relative humidity. The seeds with a specific gravity greater than 1.06 g cm$^{-3}$ were first sterilized by N-propyl-N-[2-(2,4,6-trichlorophenoxy) ethyl] imidazole-1-carboxyamide and then soaked in water for 96 hours at 12°C. They were then incubated in two growth cabinets for about 40 hours, during which the status of the seeds was frequently checked and the temperature for each cultivar was changed to ensure synchronized germination of all the cultivars. Seeds were sown on the floating beds with the plastic mesh attached to the Styrofoam float (22 cm × 22 cm × 1.5 cm), and was placed on the water in the tanks 1.8 m in length, 0.9 m in width and 0.3 m in depth. From each float bed four seeding rows 2 cm in width and 18 cm in length were cut out at 3.5 cm intervals, and the rows were underlaid with the mesh. The culture solution was changed weekly and contained 0.7 μg L$^{-1}$ nitrogen (N) as ammonium sulfate, 1μg L$^{-1}$ phosphorous (P) as sodium dihydrogen phosphate, 4.3μg L$^{-1}$ potassium (K) as potassium chloride, 4.3 μg L$^{-1}$ calcium (Ca) as calcium chloride, 4.3μg L$^{-1}$ magnesium (Mg) as magnesium sulfate, 2μg L$^{-1}$ iron (Fe) as ethylenediamine-tetra acetic acid-Fe and 1μg L$^{-1}$ manganese as manganese chloride.

### Experiment 1

Nipponbare (semi-dwarf, japonica), Suweon 258 (semi-dwarf, indica), Black Gora (tall statured, indica) and Ch86 (tall statured, indica) were used. Before seed preparation, the individual grain weight was measured and the seeds were divided equally into three categories, the heaviest 33 %, the lightest 33 % and the rest, namely large, small and intermediate seeds. Only the large and small seeds were used to create as great variation in the seed size as possible. The initial seed dry weight (SWini) of each group is listed in Table 1.

| Seed size | SWini | GE | DW$h_{\text{max}}$ | DWt | DWem | RGR |
|-----------|-------|----|-------------------|-----|------|-----|
| Nipponbare (semi-dwarf, japonica) | Large | 25.8 | 0.61 | 11.7 ** | 58 | 0.51 | 9.0 ns. |
| | Small | 21.8 | 0.63 | 10.2 | 53 | 0.44 | 9.2 |
| Sewon 258 (semi-dwarf, indica) | Large | 25.8 | 0.63 | 11.5 ** | 56 | 0.44 | 9.4 ns. |
| | Small | 21.8 | 0.63 | 10.1 | 55 | 0.49 | 9.4 |
| Black Gora (tall statured, indica) | Large | 29.4 | 0.66 | 13.8 ** | 74 | 0.46 | 9.5 ns. |
| | Small | 23.3 | 0.68 | 11.5 | 73 | 0.44 | 10.0 |
| Ch86 (tall statured, indica) | Large | 25.2 | 0.62 | 11.3 ** | 70 | 0.62 | 9.8 ns. |
| | Small | 21.6 | 0.66 | 10.0 | 65 | 0.66 | 10.1 |

** and ns. mean that significant at 0.01 level and non-significant differences existed between large and small seeds for each cultivar.

### Table 1.

Seed dry weight (SWini), growth efficiency (GE), the final heterotrophic dry weight (DW$h_{\text{max}}$), total dry weight (DWt) at 312T (19DAG), embryo dry weight (DWem) of the seed and relative growth rate (RGR) in Experiment 1.
the randomized complete block design with four replications.

An additional experiment was conducted to determine growth efficiency (GE) of each cultivar. The large and small seeds of the four cultivars were sown on the beds floated on the culture solution in the plastic trays and grown under dark condition in a growth cabinet, in which daily mean temperatures were adjusted to the mean value of the main experiment. The experiment was conducted with four replications assigning one row for each, using 32 rows in total (8 floating beds); the seeding rate was 40 seeds per row. Eight or ten plants were harvested in each replicate at 2, 4 and 12DAG. GE was obtained by the linear regression between DWt in the dark and reduction of seed dry weight (SW lost) (Tanaka and Yamaguchi, 1968).

**Experiment 2**

Sixty-three rice cultivars including old and modern cultivars of japonica, tropical japonica and indica, were classified into nine groups as shown in Table 2. They were grown on floating beds as described in Exp. 1, and placed in two hydro-culture tanks. One row in the bed was assigned for each replicate. The seeding rate was 30 seeds per row, and the four rows on a float bed were used for four different cultivars located randomly.

Dry weights of the seed and growing plant organs were measured three times harvesting ten and four plants per replication for the first two (4 and 11DAG) and the last (23DAG) harvests, respectively. Leaf area (LA) was also measured in the second and third harvests. DWem was determined for every cultivar in the same way as in Experiment 1.

Two water tanks were separated into two blocks, and the 63 cultivars were randomly located in each block. The effect of cultivar was analyzed with the randomized complete block design with four replications. The effect of cultivar was analyzed with the randomized complete block design with four replications.

**Calculation of hetero- and auto-trophic dry weight and model analysis**

Following Yoshida (1973), heterotrophic dry weight (DWh, mg pl⁻¹) at a given harvesting time was calculated multiplying GE by SWlost.

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**Table 2.** Cultivars studied in Experiment 2 and total plant dry weight (mg pl⁻¹) at 320T (23DAG).

| Japonica | Tropical Japonica | Indica |
|----------|-------------------|--------|
| **Japanese modern cv.** | **U.S.A. cv.** | **Modern cv.** |
| 1 Nipponbare | 66.3 | 18 M201 | 84.6 | 22 Lemont | 54.1 | 40 Suweon258 | 79.7 |
| 2 Akitakomachi | 61.7 | 19 M202 | 96.6 | 23 Bonnet73 | 57.6 | 41 Miyang23 | 68.8 |
| 3 Hinohikari | 61.1 | 20 Calrose76 | 85.2 | Asian and non-fam. cv. | 42 Nanjing11 | 96.5 |
| 4 Koshihikari | 65.5 | 21 Calrose | 68.1 | 31 Banten | 94.5 | 43 Takanari | 72.5 |
| 5 Ohchikara | 99.0 | Asian and Euro-cv. | 32 Ketan Nangka | 95.5 | 44 IR72 | 87.5 |
| 6 Nekken 2 | 68.7 | 24Kr7 | 73.5 | 33 Sile-wah | 81.8 | 45 IR20 | 50.9 |
| 7 Tanginbozu | 53.8 | 25Ch19 | 99.6 | 34 Kha0 Pick Laos | 116.2 | 46 IR24 | 77.3 |
| **Japanese old cv.** | **U.S.A. cv.** | **Modern cv.** |
| 8 Ginbozu | 56.6 | 27 Arroz da Terra | 104.9 | 36 P10 | 73.5 | 48 IR39323-182-2-3-3-2 | 82.8 |
| 9 Asahi | 85.0 | 28 Cavcna/Fortuna6-103-15 | 60.7 | 37 In23 | 82.4 | 49 IR13429-150-3-2-1-2 | 74.2 |
| 10 Shinriki | 75.6 | 29 BGI | 100.5 | 38 Bm6 | 80.4 | 50 IR65600-127-6-2-3 | 71.0 |
| 11 Omachi | 86.5 | 30 Arborio | 108.7 | 39 Ba11 | 65.5 | 51 IR66160-121-4-1-1 | 84.9 |
| 12 Kamenoo | 67.5 | **Japanese upland cv.** | **U.S.A. cv.** | **Modern cv.** |
| 13 Ohkawawase | 73.1 | **Asian and non-fam. cv.** | **Modern cv.** |
| 14 Hatafusa-mochi | 76.7 | 54 BG380-2 | 88.6 |
| 15 Rikuto-norin-mochi26 | 83.8 | 55 IRGA409 | 82.2 |
| 16 Sensho | 86.3 | **Japanese upland cv.** | **Old cv.** |
| 17 Sankanka | 113.1 | 56 Basmati370 | 53.4 |

LSD(5%)=9.1 mg pl⁻¹

*, Local lines collected by Y. Satoh, Kyoto Univ. and the names are from registration codes in his collection.

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The large and small seeds of the four cultivars were sown on the beds floated on the culture solution in the plastic trays and grown under dark condition in a growth cabinet, in which daily mean temperatures were adjusted to the mean value of the main experiment. The experiment was conducted with four replications assigning one row for each, using 32 rows in total (8 floating beds); the seeding rate was 40 seeds per row. Eight or ten plants were harvested in each replicate at 2, 4 and 12DAG. GE was obtained by the linear regression between DWt in the dark and reduction of seed dry weight (SWlost) (Tanaka and Yamaguchi, 1968).
GE was measured in darkness as mentioned above for the four cultivars in Experiment 1. In Experiment 2, however, GE was not determined for individual cultivars, and the averaged value from Experiment 1 (0.64 mg mg\(^{-1}\)) was used as a fixed GE to calculate DWh.

Plant dry weight produced by leaf photosynthesis (autotrophic dry weight, DW\(_a\), mg pl\(^{-1}\)) was then obtained by subtracting DWh from the total plant dry weight, DW\(_t\).

\[
DW_a = DW_t - DWh
\]

Since the rate of early growth is strongly affected by temperature (Yoshida, 1973), changes in SW\(_t\), DW\(_t\), DW\(_h\), and DW\(_a\) were presented as the functions of thermal time (T), which was calculated in a degree-day unit (°C d) by summing the difference between the daily mean temperature and a fixed base temperature. The base temperature was set to 9°C following the similar experiments by Salam et al. (1997 and 1999) to ease comparison of results between studies.

For the analysis of total seedling growth taking heterotrophic input into account, we described growth rates on T basis (mg pl\(^{-1}\) °C\(^{-1}\) d\(^{-1}\)) in the heterotrophic, transition and autotrophic growth rates by the following equations.

\[
\frac{dDWh}{dT} = \text{\footnotesize{(Heterotrophic)}}
\]

\[
\frac{dDWt}{dT} = \frac{dDWh}{dT} \cdot (\text{T<100})
\]

\[
\frac{dDWa}{dT} = \text{\footnotesize{(Autotrophic)}}
\]

The change in DWh was regressed against T in the first-order logistic function and the heterotrophic growth rate (\(\frac{dDWh}{dT}\), mg pl\(^{-1}\) °C\(^{-1}\) d\(^{-1}\)) was expressed by the following equation.

\[
\frac{dDWh}{dT} = DW_h \cdot b \cdot (1-DWh/DWh_{Max}) \quad (4)
\]

where, b is the parameter to represent the initial rise of the curve and it was fixed at 0.04 (°C\(^{-1}\) d\(^{-1}\)). The calculation of DWh was started at 45T after germination and DW\(_{em}\) was used as the initial value, because in Experiment 1 the plant weight of the emerging shoot reached their DW\(_{em}\) approximately at 45T.

The autotrophic growth was described by the exponential curve, and the growth rate was expressed by the product of relative growth rate (RGR, °C\(^{-1}\) d\(^{-1}\)) and the current DW\(_t\) (mg pl\(^{-1}\)).

\[
\frac{dDWa}{dT} = \text{RGR} \cdot DW_t \quad (5)
\]

However, in the transit phase DW\(_t\) is derived not only from autotrophic growth but also from conversion of seed reserve. Then DW\(_t\) in equation (5) was replaced by DWh+DW\(_a\).

\[
\frac{dDWa}{dT} = \text{RGR} \cdot (DWh+DW_a) \quad (6)
\]

where DW\(_h\) was calculated from equation (4). The calculation of DW\(_a\) was started at 100T using the current DW\(_t\) value provided by the DW\(_h\) at that moment and with DWh + DW\(_a\) afterward.

**Results and Discussion**

1. **Growth of the four cultivars (Experiment 1)**

The GE values used for calculation of DWh ranged from 0.61 to 0.68 mg mg\(^{-1}\) (Table 1) and this range was close to the values determined by Tanaka and Yamaguchi (1969) determined with the rice seedlings under various temperature conditions. Although cv. Black Gora tended to show higher GE than the other cultivars, there were no significant differences with the cultivar or seed size. As has been characterized by Tanaka and Yamaguchi (1995), GE of young rice seedling can be regarded as a quite stable trait.

Fig. 1 shows the changes in DWh and DW\(_a\) for the small and large seeds in the four tested cultivars. Autotrophic growth started at about 100T. Heterotrophic growth was completed more than 90% at 190T. Thereafter, there was very little seed reserve utilization as expressed by SW\(_{em}\) minus SW. Thus the transition phase occurred between 100T and 200T. As Salam et al. (1997, 1999) have already noted, the time course of the phasic development was similar among
cultivars and seed size treatments.

The final value of heterotrophic dry weight (DW_{h,\text{Max}}) was determined by the final measurement of DW_h at 312T (19DAG) (Table 1). DW_{h,\text{Max}} varied from 10.0 (Ch86, small) to 13.8mg pl^{-1} (Black Gora, large) and DW_t at 312T ranged from 53 (Nipponbare, small) to 74mg pl^{-1} (Black Gora, large), respectively. There were significant differences among cultivars in DW_t for both large and small seeds. But the effect of seed size on DW_t was not significant, although that for DW_{h,\text{Max}} was significant.

2. Model analysis for the four cultivars (Experiment 1)

The change of DW_h was calculated by equation (4) using the measured DW_em as the initial DW_h, which ranged from 0.44 mg pl^{-1} in the large seed of Suweon 258 to 0.66 mg pl^{-1} in the small seed of Ch86 (Table 1). This logistic model satisfactorily described the heterotrophic growth of seedlings (Fig. 1). The result of the calculation using a fixed DW_em (the mean value) instead of measured DW_em values scarcely varied even when DW_h was estimated for each cultivar and seed-size (data not shown). This indicates that DW_{h,\text{Max}} is the primary determinant of heterotrophic growth.

The parameter RGR was first determined for every harvesting interval after the autotrophic growth started. Though RGR changed with seedling growth, the change was moderate and there was a significant correlation between RGR values determined separately for the periods in transition and autotrophic phases (r=0.81). Thus, a single value of RGR derived from the average of RGRs across observation period was used to represent the entire autotrophic growth of the seedling, as a parameter specific to cultivar and seed-size.

Fig. 1 shows the estimated changes of DW_t. The exponential model described the observed values fairly well. A major discrepancy was the overestimate of DW_t for Nipponbare and Suweon258 in the initial autotrophic growth. This is presumably because the onset time of autotrophic growth was fixed to 100T. Based on an intensive observation of rice seedling growth, Asch et al. (1999) found a difference in the onset time of autotrophic growth between *Oryza glaberrima* and *O. sativa* genotypes and suggested that it could be one factor in the differential seedling vigor. The harvest interval of this study was not frequent enough to determine the precise onset time of autography and requires further study.

The estimated DW_t, the sum of DW_h determined by the logistic model and DW_t determined by the exponential model, met with DW_t measured at 237T ($R^2 = 0.93$, (n=8) and DW_t at 312T ($R^2 =0.91$) (data not shown). Thus, seedling growth was well represented by the three parameters, DW_em for the initial DW, DW_{h,\text{Max}} for the heterotrophic growth and RGR for the autotrophic growth. This simple model should be used for the analysis of seedling vigor variation among diverse cultivars.

3. Variability of seedling vigor among diverse rice cultivars (Experiment 2)

The seedling DW_t at 320T ranged from 50 mg pl^{-1} of IR20 (#45, modern indica) to 116 mg pl^{-1} of Khao Pick Laos (#34, tropical japonica). Thus, more than two fold difference was observed among cultivars in the seedling dry matter accumulation. Seedling weights of Japanese upland rice and tropical japonica were generally greater than those of the modern cultivars of both japonica and indica, indicating that the cultivars adapted to upland culture tend to exhibit superior seedling growth. Also, among indica cultivars, the old group had greater DW_t than modern cultivars on the average. However, the variation within each group was large and any of japonica, tropical japonica and indica groups included more than a few cultivars with superior seedling growth. Therefore, it appears that the vigor trait of the cultivar does not depend on the subspecies to which it belongs and this is consistent with the evaluation of 27 cultivars by Redona and Mackill (1996a).

### Table 3. The ranges of the parameters, DW_{h,\text{Max}}, RGR and DW_em for the 63 cultivars (Experiment 2) and the variation of seedling growth (DW_t at 320T) estimated by the model based on the observed values of each parameter the other parameters being fixed to the mean values.

| Parameter   | Observed range | Unit    | Variation of estimated DW_t due to the individual parameters |
|-------------|----------------|---------|-------------------------------------------------------------|
|             |                 |         | Range of estimates C.V. \(^\gamma\)                        |
| DW_{h,\text{Max}} | 8.1–22.4       | mg pl\(^{-1}\) | 66–111 (83\(^*\)) 18.4 (12.3\(^*\)) %                   |
| RGR         | 8.6–11.4       | °C\(^{-1}\)\(\text{d}\^{-1}\) | 69–117 21.7                                     |
| DW_em      | 0.18–0.71      | mg pl\(^{-1}\) | 66–73 4.3                                                 |

\(^\gamma\): Coefficient of variance among 63 estimates.

\(^*\): The value when the four large-seed cultivars are excluded.
4. Contribution of hetero- and auto-trophic growth to seedling vigor (Experiment 2)

The seedling growth of 63 cultivars was analyzed by equations (3), (4) and (6). For the calculation of DW, for each cultivar, three cultivar-specific parameters were used; i.e., DW_{h, Max} as the determinant of heterotrophic growth, RGR to represent autotrophic growth activity and DW_{em} as the initial DW. DW_{h, Max} was calculated by equation (1) using the SW value at the second harvesting (at 190T) and a fixed GE, the average of the four cultivars in Experiment 1 (0.64mg mg^{-1}). RGR was calculated from the seedling DW, of the second and third harvests at 190T and 320T, respectively, when virtually no heterotrophic growth occurred. The initial DW, was given by the embryo dry weight (DW_{em}) of each cultivar.

DWh.Max, RGR and DW_em varied among 63 cultivars from 8 to 22 mg pl^{-1}, from 8.6 to 11.4 ºC^{-1}d^{-1} and from 0.18 to 0.71 mg pl^{-1}, respectively (Table 3). The seedling DWt at 320T (23DAG) was calculated for every cultivar by the model using the three cultivar-specific parameters. The estimated DW, (y) as a function of cumulative effective temperature coincided with the measured value (x) with a linear regression; y = 1.12x -20.6 (R^2 = 0.74, n = 63) and the standard error of 15.4 mg pl^{-1}. Thus, the variation of seedling growth among diverse cultivars was represented fairly well by the model.

For evaluation of relative effects of growth parameters, one of DW_{h, Max}, RGR and DW_{em} measured for individual cultivars was given to the equations the other parameters being fixed for the mean values of 63 cultivars. Table 3 shows the calculated variation among cultivars of DWt at 320T due to each parameter. Seedling growth estimated using measured DWh.Max and RGR showed a variation similar to that of the measured DW_{h, Max} and RGR, respectively. The coefficients of variance (C.V.) of estimated DW, with varied DWh.Max and RGR were 18 and 22%, respectively. On the other hand, the effect of DW_{em} was smaller than the other two parameters resulting in the C.V. of only 4%. Although the embryo size may have some importance in the initial growth (Sasahara et al., 1986; Lopez-Castaneda et al. 1996), this result suggested that the contribution of embryo weight may be limited compared to those of DWh.Max and RGR. One possible explanation is that the larger embryo cultivar tended to have a larger DWh.Max with r=0.43 (P<0.01). Thus, the occasionally observed correlation between embryo size and DW, (Sasahara et al., 1986, for javanica cvs.) may be in part attributed to the larger DWh.Max.

The estimated effects of the two parameters on DW, in individual cultivars are presented in Fig. 2 by the percent increase or decrease of estimated DW, by substituting the cultivar-specific value for the fixed DWh.Max or RGR (mean of 63 cultivars). In each calculation, the other two parameters, RGR or DWh.Max and DW_{em} were fixed at the mean values. The positive effect of DWh.Max was particularly large in four cultivars. They are cultivars Ohchikara (#5), BGI (#29),
Arborio (#30) and Khao Vay (#57) and are unique for exceptionally large seed size; their SW ini was from 41 to 52 mg per seed as compared with the average of all cultivars, 26 mg per seed. Thus, it is evident that the existence of these large-seed cultivars is the major source of variation in DWt. In the other cultivars, the SW ini varied among cultivars from 17 mg (IR20, modern indica) to 52 mg (BG1, japonica). Although it was quite consistent regardless to varied seed sizes it was notably smaller than that due to RGR, 21.7 % (Table 3).

The most vigorous ten cultivars in terms of DWt at 320T are indicated by black bars in Fig. 2. Of those cultivars, six cultivars, Sankanka (#17), Ch19 (#25), Italic Livorno (#26), Arroz da Terra (#27), Khao Pick Laos (#34) and In33 (#61) achieved their great DWt due to superior RGR and the above mentioned four cultivars due to superior DW h,Max. These results indicate that the contribution of RGR to seedling vigor in terms of dry matter accumulation was relatively greater than that of DW h,Max. Although the trait of large DW h,Max could certainly be a dominating factor to increase seedling DWt, the effect of the large DW h,Max tended to be masked by the effect of RGR unless DW h,Max was extremely large.

Fig. 2 indicates that the inferior growth of Japanese japonica was due to inferior RGR, and that of the modern indica group was due to inferior DW h,Max and/or RGR. It also shows that the RGR-dependent variation of DWt was especially large in the japonica cultivars. This result is consistent with the evaluation made on 117 cultivars based on the 9 degree ratings (Mackill and Lei 1997), and suggests the existence of a relatively great opportunity for japonica to be improved in seedling vigor through the traits related to autotrophic process.

Previous studies have demonstrated correlations between α-amylase enzyme activity with germination rate and/or initial plant growth (Williams and Peterson, 1973; Sasahara et al., 1986; Lee et al., 1986; Karrer et al., 1993). The present study included Italic Livorno (#26), Arroz da Terra (#27) and M202 (#19) reputed to exhibit high amylase activity and Calrose (#21) and Lemont (#22) evaluated for low activity (Williams and Peterson, 1973; Karrer et al., 1993, Ogawa and Terashima, 1996). According to Williams and Peterson (1973), the effect of high amylase activity would be realized in the rapid utilization of seed reserve. This aspect may be represented by parameter "b" in equation (4), which determines the initial rise of the DWt increase curve (logistic curve). However, this parameter was fixed in the calculations in this study. In fact, DWt was more or less under-estimated by the model for the three cultivars of high amylase activity (data not shown). Thus, there remains a need to account for fastness of seed reserve utilization depending on amylase activity and consequent earlier onset of autotrophic growth for more accurate evaluation of limiting factors of seedling growth.

5. Characteristics related to seedling vigor (Experiment 2)

DW h,Max can be described as the product of the three components.

\[
DW_{h,\text{Max}} = GE \cdot \text{SW}_{\text{lost,Max}}/\text{SW}_{\text{ini}} \cdot \text{SW}_{\text{ini}} 
\]

where, SW lost,Max is the final value of seed DW reduction and represents the total consumption of seed dry matter through heterotrophic growth of the plant. The ranges among 63 cultivars for SW ini and SW lost,Max/SW ini in Experiment 2 are presented in Table 4 along with their correlations with DW h,Max. Another component, GE was not measured in the Experiment 2, because it was quite consistent regardless to varied seed sizes and cultivars in the Experiment 1 as discussed before. The SW ini varied among cultivars from 17 mg (IR20, modern indica) to 52 mg (BG1, japonica). Although there was a significant difference among cultivars, the ratio SW lost,Max/SW ini did not largely differ among cultivars with the range from 0.62 to 0.79 and its average and standard deviation of 0.74±0.04 (mg mg⁻¹) (data not shown). Consequently, SW lost,Max/SW ini did not appear to play a major role to cause genotypic variation of DW h,Max. In contrast, SW ini correlated closely with DW h,Max (r=0.97) (Table 4), indicating DW h,Max is determined primarily by seed size.

RGR is conventionally resolved into three components.

\[
RGR = \text{NAR} \cdot \text{SLA} \cdot \text{DWl/DWt} 
\]

where, NAR is the net assimilation rate, SLA is specific leaf area; DWl/DWt, ratio leaf dry weight per total dry weight.
glaberrima cultivar was attributable partly to these two traits (Ash et al., 1999). On the other hand, NAR is generally considered to reflect photosynthetic activity of leaves. As shown in Table 4, NAR, SLA and DW/DR ranged from 35 to 83 mg cm$^{-2}$ C d$^{-1}$, from 0.28 to 0.54 cm$^2$ mg$^{-1}$ and from 0.41 to 0.61 mg mg$^{-1}$, respectively, and the cultivar difference was significant for all the three components (P<0.01). However, the component that showed significant correlation with RGR was only NAR (r = 0.39, P<0.01). This result suggests that the fast development of leaf area is not the only factor to achieve vigorous seedling growth and leaf photosynthetic activity also might be an important factor to determine the growth of seedling plant.

It must be noted that, in this study, plants were grown by hydroponics and hence water and nutrient supply was not limited. In the field condition, especially in direct seeding, various factors, such as elongation of leaves and root growth, would be important for the plant to adapt to the changing environment. This study examined the factors affecting potential growth activity of diverse cultivars in terms of dry matter accumulation and compared relative contribution of hetero- and auto-trophic processes to the growth activity, which have not been quantitatively analyzed previously.

Conclusions

Diverse rice cultivars were grown hydroponically and their seedling growth was analyzed. Dry-matter accumulation of the seedling was well represented by a function of thermal time using the cultivar-specific parameters, embryo dry weight, final heterotrophic weight and relative growth rate. A more than two-fold difference in the seedling weight was observed among 63 diverse cultivars. The result of model analysis conducted substituting cultivar-specific parameters indicated that the contribution of heterotrophic process to genotypic variation in seedling growth was relatively limited as compared with that of autotrophic process.

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