A Varietal Difference in Coleoptile Growth is Correlated with Seedling Establishment of Direct Seeded Rice in Submerged Field under Low-Temperature Conditions

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Abstract: To elucidate the physiological characteristics relating to better seedling establishment in submerged field under low-temperature conditions, we compared the time required to reach various growth stages after seed imbibition among rice (Oryza sativa L.) varieties differing in the performance of seedling establishment. Two experiments were conducted. In the field experiment, the percentage of seedlings with expanded second leaf at 30 days after sowing (PSSL) was measured and regarded as the index of establishment rate for each variety. In agar-bed experiment, the number of germinated seeds, the seedlings with the coleoptile elongated to the medium surface, and the seedlings with the 1st leaf apparent were counted daily under a 16°C condition. A sigmoid model was applied to the above values to evaluate the time requirements. There was a significant correlation between the duration from 50% germination to 50% emergence in the agar-bed experiment and PSSL in the field experiments. However, the duration from imbibition to 50% germination, and that from 50% emergence to 50% appearance of the first leaf were not significantly correlated with PSSL. We found that fast growth of the coleoptile is an important characteristic for the varieties that can provide stable and excellent seedling establishment at low temperature.

Key words: Coleoptile growth, Direct seeding, First-leaf growth, Germination, Low temperature, Rice (Oryza sativa L.), Seedling establishment.

In direct seeded rice plants (Oryza sativa L.), the percentage of seedling establishment is drastically low when the soil temperature is below 17°C under a submerged condition (Kurosawa, 1975; Kurosawa and Higashi, 1976; Dakeishi and Fukuda, 1990). Many studies (Nishiyama, 1975, 1978; Sasaki, 1979; Maruyama and Tajima, 1986; Sasahara and Ikarakahi, 1989; Hagiwara and Irmura, 1991, 1993) have also shown that physiologically critical temperature for the germination and early seedling growth is around 17°C.

On the other hand, many workers have pointed out that there is a wide varietal difference in the seedling establishment at low temperatures (Sasaki and Yamazaki, 1971; Ikehashi, 1973; Jones and Peterson, 1976; Li and Rutgar, 1980; Kotaka and Abe, 1988; Kowata et al., 1992; Amano et al., 1993; Redona and Mackill, 1996; Inoue et al., 1997). The genetic improvement of seedling establishment at low temperatures is considered to be possible by using several varieties superior in seedling establishment as genetic resources. Detailed analysis of varietal difference in seedling growth is indispensable to the rapid breeding using advanced technologies such as genetic markers and QTL analysis. The information about the critical growth stage for better seedling establishment under low temperature and submerged conditions is important not only for the breeding but also for the improvement of direct sowing cultivation system in submerged paddy fields.

There may exist three morphologically and physiologically distinctive growth stages from sowing to seedling establishment in submerged paddy fields; the 1st is the germination, the 2nd is the coleoptile elongation under low oxygen tension, and the 3rd is the elongation and appearance of the 1st leaf and radicle after enough oxygen being supplied through the coleoptile (Kordan, 1972; Kordan, 1974; Alpi and Beevers, 1983; Alpi et al., 1985; Setter et al., 1994). Although the relationship between seedling vigor and seedling length at certain days after sowing (Sasaki and Yamazaki, 1971; Ikehashi, 1973; Jones and Peterson, 1976; Li and Rutgar, 1980; Kotaka and Abe, 1988; Kowata et al., 1992; Amano et al., 1993; Redona and Mackill, 1996) and the relationship between seedling vigor and germination index (Kotaka and Abe, 1988; Kowata et al., 1992) have been studied, few physiological studies focusing on the above 3 distinctive growth stages under submerged conditions have been reported.

The objective of the present study is to clarify the effects of low temperature on the relationships between seedling establishment and the rapidity of germination, coleoptile elongation, and the elongation and appearance of the 1st leaf under submerged conditions. For this purpose, two experiments were conducted. One is the nursery box experiment conducted in the field (field

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Abbreviations: E50, 50% emergence; E50-F50, duration from 50% emergence to 50% appearance of 1st leaf; F50, 1st leaf appeared in 50% of sown seeds; G50, 50% germination; G50-E50, duration from 50% germination to 50% emergence; IMB, imbibition; IMB-G50, duration from imbibition to 50% germination; PSSL, percentage of seedlings with expanded second leaf at 30 days after sowing.
Table 1. Percentage of seedlings with expanded second leaf at 30 days after sowing (PSSL) in the field experiment.

<table>
<thead>
<tr>
<th>Variety</th>
<th>1995 May,15&lt;sup&gt;(16.9°C)&lt;/sup&gt;</th>
<th>1997 Apr,26&lt;sup&gt;(16.1°C)&lt;/sup&gt;</th>
<th>1998 Apr,27&lt;sup&gt;(15.5°C)&lt;/sup&gt;</th>
<th>Average PSSL</th>
<th>Agar-bed&lt;sup&gt;6&lt;/sup&gt; experiment ’95 ’97 ’98</th>
<th>Origin</th>
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<tr>
<td>Arroz da Terra</td>
<td>93.8</td>
<td>87.4</td>
<td>92.6</td>
<td>91.3</td>
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<td>Szarvosi Korai</td>
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<td>85.6</td>
<td>86.4</td>
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<td>Hungary</td>
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<tr>
<td>Thankote Dhan</td>
<td>80.3</td>
<td>85.3</td>
<td>82.8</td>
<td>82.8</td>
<td>○ ○ ○</td>
<td>Nepal</td>
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<tr>
<td>Koukoutouji</td>
<td>85.0</td>
<td>80.1</td>
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<td>86.2</td>
<td>○ ○ ○</td>
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<td>87.1</td>
<td>96.7</td>
<td>82.2</td>
<td>○ ○ ○</td>
<td>Italy</td>
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<tr>
<td>Calrose</td>
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<td>70.3</td>
<td>73.0</td>
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<tr>
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<td>70.2</td>
<td>65.1</td>
<td>65.1</td>
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<tr>
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<td>61.3</td>
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<td>Calrose76</td>
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<td>77.2</td>
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<td>59.8</td>
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<td>S-201</td>
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<td>11.4</td>
<td>21.8</td>
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<td>10.3</td>
<td>1.2</td>
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<td>Bluebellie</td>
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<td>3.4</td>
<td>3.4</td>
<td>○ ○ │ USA</td>
<td></td>
</tr>
</tbody>
</table>

1) Varieties are shown in reverse order of average PSSL. 2) Date of sowing. 3) Average soil temperature within 15 days after sowing. 4) ○ ○ ○ indicates the varieties chosen for agar bed experiment. *** Significant at 0.1% level.

2. Field experiment using nursery boxes

Nursery boxes with small compartments (“Kabumakipot”, Fujimoto Kagaku Kogyo Co., Tokyo, Japan) were used to make an uniform seed bed and sowing depth. A box was divided into 17×34 compartments of 10 mm×10 mm×30 mm (width×width×depth), with a hole in the bottom. The 4×17 compartments made one plot, and one nursery box had 7 plots. For each variety (Table 1), 4 or 5 replications were provided in one experiment. Sieved soil was filled in nursery boxes to approximately 2 to 3 mm below the top edge of the box to attain a 4-mm thick soil covering.

Seeds were sterilized with 50-fold diluted antiformin containing 100 ppm Triton X-100 for 4 hr at room temperature. After the sterilization, seeds were soaked in flowing tap water (ca. 9°C) for 36 hr. One seed was put on the surface of the soil in each compartment of the nursery box after fully watered. Seeds were placed so as to face the embryo to the horizontal direction. After seeds were covered with the sieved soil to the top edge of the refrigerator at 4°C after packed in a sealed bottle. Experiments were carried out in 1995, 1997, and 1998 using the seeds harvested in the previous year.

1. Seeds

Japanese, European and US varieties were used as materials in this study except for one variety from Nepal and another one variety from China (Table 1). European and the U.S. varieties were included because of their superior seedling growth (Jones and Peterson 1976; Kotaka and Abe 1988; Kowata et al., 1992; Amano et al., 1993; Redoma and Mackill 1996). The seeds of all varieties used in this study (Table 1) were harvested in the experimental paddy fields of the Department of Lowland Farming, Tohoku National Agricultural Experiment Station (Omagari, Akita Prefecture, Japan). Seeds were selected by specific gravity (>1.13), and stored in the refrigerator at 4°C after packed in a sealed bottle.
the box, all boxes were placed in the continuously irrigated paddy field. The water level was kept around 5 cm from the top edge of the box. Soil temperature at ca. 1 cm deep was recorded every 1 hr (in 1995) or 10 min (in 1997 and 1998) during the experiments.

The percentage of the seedlings with the expanded second leaf was determined at 30 days after sowing (PSSL), and this was regarded as the indicator of the percentage of established seedlings. Actual soil cover depth estimated by measuring the length of the white part in the base of the 1st leaf of cv. Haenuki, was around 3 mm in every experiment.

Seeds were sown on May 1, 15, and 29 in 1995, on April 26 and May 8 in 1997, and on April 27 and May 7 in 1998. In the following analysis, we used the data obtained from the experiment in which the average soil temperature during 15 days after sowing was the lowest among experiments carried out in the same year. The soil temperature during the first 15 days after sowing are shown in Table 1.

3. The agar-bed experiment

According to the result of the field experiment, 6 varieties in 1995, 10 varieties in 1997, and 12 varieties in 1998 were chosen for the agar-bed experiments as shown in Table 1. These varieties were chosen to include varieties with different PSSL ranges; higher than 80%, 60~80%, 40~60%, and lower than 40%. Some varieties, including Szarvasi Korai and Thankote Dhan, were excluded from further analysis in spite of their high PSSL, because they did not produce seeds with enough quality for precise analysis.

Seeds of these varieties were sterilized with 50-fold diluted antifomrin containing 100 ppm Trition X-100 for 4 hr at room temperature. After sterilization, seeds were washed thoroughly with sterilized distilled water, and soaked in sterilized distilled water over night at 16°C before incubation. In the polycarbonate pots for plant tissue culture (“Agripot”, Iwaki Glass Co., 6 cm φ×12 cm high, with ventilation through a filter), 0.5% (w/v) agar-beds (bed volume was 40 to 50 mL) were prepared and sterilized by autoclaving. No nutrients were added. Twenty-five seeds were sown in one polycarbonate pot. The seeds were placed in the agar-bed with their embryo up. The depth of the embryo in the medium was 7-8 mm from the surface. After sowing, a small amount of sterilized distilled water was added to the pots. The pots were placed in an incubator controlled at 16°C, and kept in the continuous dark till 80% of the seeds in the pot emerged. After 80% emergence, the pots were moved to another incubator pot by pot, and exposed to fluorescent light (180 μmol m⁻² s⁻¹) for 14 hr a day at the same temperature. In one experiment, 4 or 5 polycarbonate pots were used for each variety.

For every pot, the number of germinated seeds, the number of seedlings with coleoptile emerged, the number of seedlings with the 1st leaf apparent, and the number of seedlings with the radicle apparent were counted once a day. In this experiment, the germination was defined as the appearance of the tip of coleoptile from embryonic axis. The emergence was defined as the reaching of the coleoptile to the surface of the medium. The appearance of the 1st leaf and the beginning of radicle growth were defined as the appearance of the tip of 1st leaf from the coleoptile and the appearance of the tip of radicle, respectively. A sigmoid model was applied to the increase of each number, and regression analysis was conducted between estimated values by the model and the observed values. The time in hour from the beginning of imbibition (IMB) to the 50% germination (G50), to the 50% emergence (E50), and to the 50% appearance of the 1st leaf (F50) were computed based on each sigmoid model. According to these values, the duration from the beginning of imbibition to the 50% germination (IMB-G50), from the 50% germination to the 50% emergence (G50-E50), and from the 50% emergence to the 50% first-leaf appearance (E50-F50), were estimated for each variety.

4. Rank correlation analysis

The ranking of each cultivar among 6, 10 and 12 varieties (Table 1), which were used in the agar-bed experiments in 1995, 1997, and 1998, respectively, was determined in the field for each experimental year. The rankings in IMB-G50, G50-E50, and E50-F50 in the agar-bed experiment, were also determined among the same varieties. In this case, the rankings in PSSL in 1995 and 1998 were determined as the average of values obtained from two independent agar-bed experiments, and that in 1997 from the result of single experiment. The above rankings were standardized as follows; The ranking in PSSL were linearly converted to the scores (ranking score) between 0.0 (the lowest in PSSL) and 1.0 (the highest in PSSL). The ranking in IMB-G50, G50-E50, and E50-F50 were also converted linearly to the ranking score between 0.0 (the longest in IMB-G50, G50-E50, and E50-F50) and 1.0 (the shortest in IMB-G50, G50-E50, and E50-F50). Correlation analysis was conducted between two kinds of ranking scores.

Results

1. Evaluation of seedling establishment in submerged field condition

The average soil temperature during 15 days after sowing in each field experiment for three years ranged from 15.5 to 16.9°C. This was lower than 17°C, a critical temperature for seedling establishment (Nishiyama 1975, 1978; Sasaki 1979; Maruyama and Tajima 1986; Sasahara and Ikarashi 1989; Hagiwara and Imura 1991, 1993). In every experiment, PSSL of listed varieties were widely distributed from less than 20% to higher than 80%, and the varietal difference was significant at 0.1% level in variant analysis (Table 1).

PSSL value in each variety fluctuated from year to
year. However, the variances due to the change of experimental year were relatively small compared with the difference in PSSL among varieties (Table 1). Correlation between PSSL in 1997 and that in 1995 was highly significant (\( y = 0.77x + 21.4, r^2 = 0.812, P < 0.0001 \)) for 14 varieties (Fig. 1). A significant correlation (\( y = 0.92x + 8.2, r^2 = 0.800, P < 0.0001 \)) was also observed between PSSL in 1997 and 1998 for 20 varieties (Fig. 1). Therefore, PSSL value in 1997 experiment, in which the largest number of varieties were examined, was thought to be valid to describe the performance of seedling establishment in each variety. The result of 1997 will be used principally to describe the seedling establishment trait, hereafter.

PSSLs in European varieties, Arroz da Terra, Szarvasi Korai, and Italica Livorno, were higher than those in other varieties in 1997, and comparable to those in Th ankote Dhan, an indigenous variety cultivated in highland of Nepal (it was collected at the altitude 2500 m above sea level), and a Chinese indigenous variety, Koukoutouji (Kushibuchi et al., 1971). It is noteworthy that Arroz da Terra recorded the highest PSSL among varieties in 1997. This variety also recorded thig PSSL in 1995 and 1998. It indicates the superiority and stability of this variety in the performance of seedling establishment under low temperature.

Among modern Japanese varieties, Haenuki and Snow Pearl recorded relatively higher PSSL, 55.6% and 62.1%, respectively in 1997, however, these varieties were inferior to a Japanese indigenous variety Iburiwase. Among nine U.S. varieties tested in this experiment, Calrose, M-101, and Calrose76 recorded a PSSL higher than 50%, while, in the other 6 varieties, PSSL was lower than 50%. Two long grain tropical japonica type varieties (Sato, 1997a, b) from southern U.S.A., Blue Bonnet and Bluebell, recorded especially low PSSL, 1.2% and 3.2%, respectively, in 1997.

2. Germination, and elongation of the coleoptile and the 1st leaf in agar-bed

The time-courses of germination, emergence, appearance of the 1st leaf, and that of the radicle in Arroz da Terra, Haenuki, and Blue Bonnet are shown in Fig. 2 with the sigmoid model applied to each growth stage. These varieties showed high, medium, and low PSSL, respectively, in the field experiment. A high correlation was found between the estimated values with the sigmoid model and the observed values irrespective for growth stages and variety. The correlation coefficients between the estimated and observed values ranged from 0.953 to 0.999 in all examined varieties and stages. Thus, the sigmoid model was considered to be appropriate to estimate the time course of development in young rice seedlings.

Based on the sigmoid model, the time in hours required from the beginning of imbibition to 50% germination (IMB-G50), G50–E30, E50–F50, were estimated to compare each duration among varieties. The radicle appearance was excluded from our analysis, because the radicle appeared immediately after emergence, and the curve of the radicle appearance was almost in parallel to that of emergence in all varieties (Fig. 2).

Table 2 shows the result in 1997. There was a significant varietal difference in IMB-G50 at 1% level in variant analysis. IMB-G50 in S201 and Bluebell was 81.3 hr and 82.6 hr, respectively, and shorter than that in the other 8 varieties. The duration in Arroz da Terra, Blue Bonnet, Calrose and L202 was almost the same (87.5 to 90.5 h) without a significant difference. IMB-G50 in M-201 and M-202 was around 110 hr, the longest duration among examined varieties.

There was also a significant varietal difference in G50–E30 at 1% level (Table 2). The shortest was found in Arroz da Terra, which recorded 73.2 hr. G50–E50 in Calrose, Haenuki, M–202, and S-201 was relatively shorter, ranging from 87.2 hr to 90.9 hr, next to that in Arroz da Terra, and that in the other varieties was longer than 100 hr. Bluebell and Blue Bonnet recorded an outstandingly long G50–E50.

A significant varietal difference was found in E50–F50, although F-value for this duration was lower than that for IMB-G50 and G50–E50 (Table 2). Bluebell record-
ed 65.2 hr, the shortest among the varieties tested. On the other hand, E50–F50 in Arroz da Terra and S-201 was longer than 105 hr.

3. Relationship between PSSL in the field experiment and the duration of each growth stage

To investigate the relationships between PSSL and the duration for each growth stage, correlation analysis was conducted using data for 1997 in the field (Table 1) and the agar-bed experiment (Table 2). A significant positive correlation was found between G50–E50 and PSSL \( (r^2 = 0.736, p < 0.0001) \). In contrast, no significant correlation was found between IMB-G50 and PSSL, or between E50–F50 and PSSL.

Table 2 showed that Arroz da Terra which recorded the highest PSSL in 1997 field experiment, recorded only 73.2 hr for G50–E50, which was significantly shorter than that in other varieties. Fukuhibiki, M201, and L202, which showed a relatively low PSSL in field experiment, recorded longer than 100 hr for G50–E50. Bluebell and Blue Bonnet, in which PSSL was lower than 10%, showed the longest G50–E50 among tested varieties (Table 2).

In order to ascertain the above results, we analyzed the correlation between ranking score in PSSL and the duration of three growth stages using the data obtained from experiments for three years (Fig. 3). Each dot in Fig. 3 represents the ranking score of respective variety in the field experiment plotted against the score for the agar-bed experiment.

There was a significant positive correlation \( (y = 0.890x + 0.121, r^2 = 0.740, p < 0.0001) \) between the ranking scores in PSSL and those in G50–E50. By contrast, no significant correlation was found between PSSL and IMB-G50 nor E50–F50.

**Discussion**

In the present study, a field evaluation method using
Fig. 3. Correlations between the ranking score of PSSL in the field experiments and that of IMB-G50, G50-E50, or E50-F50 estimated in the agar bed experiments. PSSL, percentage of the seedlings with expanded second leaf at 30 days after sowing; IMB-G50, duration from inhibition to 50% germination; G50-E50, duration from 50% germination to 50% emergence; E50-F50, duration from 50% emergence to 50% appearance of the first leaf. Field experiments and agar-bed experiments were carried out in 1995 (▲), 1997 (□), and 1998 (○), using seeds harvested in previous year, respectively. Varieties subjected to this analysis are shown in Table 1. See text for methods of ranking and scoring.

nursery boxes was used to eliminate the disturbance caused by the variation of soil cover depth, and to make a better field screening for PSSL. This method provided significant and stable varietal differences in PSSL in experiments carried out for three years (Table 1), and made it possible to select the varieties showing different performance of seedling establishment for further analysis.

In the agar-bed experiment, the index of IMB-G50 had no correlation with PSSL (Fig. 3). Sasaki and Yamazaki (1971), and Kotaka and Abe (1988) reported that faster germinating varieties showed better seedling establishment at low temperatures. However, they compared the seedling growth only with Hokkaido varieties which are very early-maturing japonica type. Kotaka and Abe (1988) also found that several lowland rice varieties collected from the south western region of Japan and some upland rice varieties in Japan showed poor seedling establishment in spite of their rapid germination. The results of the present study obtained using a wide range of genotypes indicated that rapid germination is not an essential trait for the good performance of seedling establishment (Fig. 3). This is in agreement with an observation of Tanaka and Yamazaki (1989).

The duration from emergence to the appearance of the 1st leaf (E50–F50) also did not correlate with PSSL in the field experiment (Fig. 3). In our observation, when the coleoptile opened, the 1st leaf inside already reached 15–20 mm long in Arroz da Terra and Italic Livorno, while that was only 3–7 mm in Bluebell and Blue Bonnet. Thus the appearance of the 1st leaf might not be parallel to the growth of the 1st leaf. Further experiments are required for the evaluation of this stage.

On the other hand, a significant correlation was observed between the ranking score in PSSL and that in G50–E50 (Fig. 3). Since the elongation of mesocotyl was not observed in any varieties, the G50–E50 was thought to be the index relating with the growth rate of coleoptile. Thus this result leads to the conclusion that the rate of coleoptile elongation is an important factor affecting PSSL at low temperature. Tanaka and Yamazaki (1989) also pointed out the importance of coleoptile growth for seedling establishment based on their finding that the seedling establishment was more severely hindered by irrigating with cold water during the coleoptile elongation than during germination.

Coleoptile is considered to be an essential organ to absorb oxygen from air or oxygen rich water (Kordas, 1977). Only after enough oxygen become available, aerobic respiration in mitochondria resumes (Shibasaka and Tsuji, 1988), and the 1st leaf and seminal root begin to grow (Kordas, 1974; Setter and Ella, 1994). Oxygen uptake through the emerging coleoptile is indispensable to further seedling growth. It may be possible to infer that faster elongation of coleoptile in high PSSL variety contributes to the survival of seedlings under submerged condition at low temperature through a faster transition to aerobic condition.

In the agar-bed experiment, almost all seeds of the tested varieties developed the first leaf within 20 days after imbibition (Fig. 2). This indicates that only a few seedlings died during this period in the sterile condition. Seedlings might die of accidental contamination with microorganisms. Therefore a low temperature around 16°C is not lethal to rice seedlings, but is low enough to impede the growth of seedlings. Although there is no direct evidence, the slow growth may increase the risk of microorganism hazards in paddy field conditions as suggested by Jones and Peterson (1976).
Introducing rapid germinating trait from some varieties like Italica Livorno to modern palatable varieties has been carried out by many breeders, and this method already produced several promising pedigree lines for direct seeding cultivation (Sasaki and Yamazaki, 1971; Fukuoka et al., 1999). However, rapid germination is a risky characteristic because it increases a chance of vivipary which may harm the quality of products. The results of this study indicate that the rapid growth of coleoptile is important for the better establishment of seedlings, rather than rapid germination. This suggests that the genetic improvement for better seedling establishment at low temperatures can be achieved without increasing the risk of vivipary.

References


*In Japanese with English abstract.
**In Japanese with English summary.
***In Japanese.