Historical Changes in Grain Yield and Photosynthetic Rate of Rice Cultivars Released in the 20th Century in Tohoku Region

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Abstract: A retrospective analysis of the physiological basis of genetic yield improvement should provide us a direction for future yield improvement. The objectives of the present study were to evaluate the change in yield in leading rice cultivars that were bred and grown in the Tohoku region in the 20th century, and to find whether apparent photosynthetic rate (AP) is associated with the yield improvement. Ten leading rice cultivars were grown at low- and high-nitrogen conditions, Low-N and High-N, respectively, and three environmental conditions (two years in Sendai and one year in Kashimadai). Yields were higher under High-N than under Low-N in all the cultivars tested, and yield increase was greater in the newly bred cultivars released after 1960s (new cultivars) than in those released before 1960 (old cultivars). The genotypic improvement in yield under High-N was progressive year by year in the old cultivars whereas it was stagnated in the new cultivars. The cultivar difference in AP of the flag leaf one week after heading was small, but that three weeks after heading was larger in new cultivars than in old cultivars except for a few cultivars. A dependence of AP on leaf nitrogen concentration three weeks after heading was evident in the plants grown under High-N. The number of spikelets increased under High-N in all ten cultivars, where the percentage of ripened grains was lower in the old cultivars than in the new cultivars. These results suggest that yield improvement of rice cultivars in the 20th century in the Tohoku region has been accompanied by a greater AP during the ripening stage that might lead to a greater grain filling percentage.

Key words: Grain filling, Nitrogen application, Oryza sativa L., Photosynthesis, Rice, Yield improvement.

Worldwide demand for rice will increase at an estimated annual rate of 1.6% from 1992 to 2020 (Oga and Koyama, 1995). Given that an expansion of the acreage devoted to rice production is not likely, any further increase in rice production should be enhanced with continuing improvement of yield per unit area (Evans, 1999). In Japan, although rice production currently exceeds demand, achieving lowering production costs for rice growers will require further increases in yield.

The average rice yield in Japan has increased at a remarkable rate, from 2,250 kg ha⁻¹ at the beginning of the 20th century to 5,180 kg ha⁻¹ in 2000 (Ministry of Agriculture, Forestry and Fisheries, 2002). In the Tohoku region, where rice production currently accounts for about 25% of the total production of Japan, the average yield was lower than the national average in the first half of the 20th century, but exceeded it in the last few decades. The rapid increase in rice yields, both in the Tohoku region and Japan, appeared to slow down in the recent decades (Ministry of Agriculture, Forestry and Fisheries, 2002).

Crop yield is the outcome of many processes at all developmental stages, and no single process can play a major role in greater yield potential. Many different processes may limit the yield of a cultivar at different environmental conditions. Researchers have attempted to identify the dominant physiological traits which contributed to past yield increase and could be exploited in the future (Tanaka et al., 1968; Hayami, 1982, 1983a, 1983b; Takeda et al., 1983, 1984; Kuroda and Kumura, 1990a, 1990b, 1990c; Saitoh et al., 1991a, 1991b, 1993). The new cultivars released after the 1950s have high yield potentials resulting from high photosynthetic rate per leaf area (Hayami, 1982; Takeda et al., 1983; Kuroda and Kumura, 1990a), and from greater light interception by the canopy (Tanaka et al., 1968; Saitoh et al., 1993). However, most of these studies were conducted outside the Tohoku region. Interactions of genotypic and environmental factors are always significant; therefore, a proper evaluation of yield differences among cultivars should be made in the area where the cultivars are environmentally adapted. Hayami (1982, 1983a, 1983b) conducted such researches in the Tohoku region, but he used cultivars released before 1970.

The objectives of the present study were to evaluate the change in yield in leading rice cultivars that were bred in the Tohoku region in the 20th century, and to find whether the yield improvement is associated with photosynthetic rate.
Zhang and Kokubun — Yield Improvement in Rice in Tohoku Region

Materials and Methods

1. Plant materials

Experiments were conducted in Sendai (38°16’ N) for two years and in Kashimadai (38°28’ N) for one year. Ten leading rice cultivars in the Tohoku region in the 20th century were grown under low and high nitrogen conditions, Low-N and High-N, respectively (Table 1 and 2). Seeds were sown in nursery boxes at a rate of 120 g per box (30 cm × 60 cm) on April 19, 2001 and April 16, 2002 in Sendai, and April 15, 2002, in Kashimadai. The seedlings were transplanted 30 days after sowing, by hand in Sendai, and with a transplanter in Kashimadai. The planting density was 22.2 (30 × 15 cm) hills m⁻², each hill consisting of three plants in Sendai and 2 – 4 plants in Kashimadai. Nitrogen was applied as ammonium sulfate at 1.5 – 3 g N m⁻² (Low-N) and 3 – 8 g N m⁻² (High-N) (Table 2). Phosphorus and potassium were applied as superphosphate and potassium chloride, respectively, at the rates specified in Table 2. Nitrogen was applied twice (as basal and top-dressing), but other fertilizers were applied only as a basal dressing. Additional nitrogen was top-dressed at meiosis stage of respective cultivars, which was estimated by the distance between auricles of flag and penultimate leaves being zero (Matsushima, 1966). The soil was a fine-textured clayey Terrace Yellow soil in Sendai and was a fine-textured clayey Mottled Gley Lowland soil in Kashimadai (Classification Committee of Cultivated Soils, 1996). Weeds were removed manually when necessary, and irrigation was provided until maturity (yellowing of spikelets). Since some cultivars were susceptible to lodging when grown under High-N, they were supported by stretching tapes between rows at a height of about 50 cm above the ground.

Each plot was 10 m² in Sendai and 40 m² in Kashimadai, and cultivars were arranged randomly. Consistency of genotypic ranking in yields across the three environmental conditions was estimated using Spearman’s rank correlation coefficients.

2. Measurements

The dates of heading and maturity of each plot were recorded. The date of maturity was determined as a stage when 80% of spikelets became yellow. The number of tillers per hill was counted weekly after transplanting until heading and the number of panicles were determined at heading for ten hills of each plot. Five hills of each plot were collected at heading, and leaf blades were separated from the rest of the plant parts. The area of the leaf samples was measured with a leaf area meter (automatic area meter model AAM-7, Hayashi Denko Co. Ltd., Tokyo, Japan). At maturity, 30 hills from each plot were harvested, air dried, and the total weight of the plants was measured.

Table 1. Year of release and days from transplanting to heading and maturity of the cultivars used.

| Cultivar | Year of release | Transplanting - Heading Low-N | Transplanting - Heading High-N | Heading - Maturity Low-N | Heading - Maturity High-N | Transplanting - Maturity Low-N | Transplanting - Maturity High-N |
|----------|-----------------|-------------------------------|-------------------------------|--------------------------|--------------------------|-------------------------------|-------------------------------|
| No. | Name |                   | 76 | 84 | 42 | 62 | 117 | 145 |
| 1   | Kamenoo | 1893             | 76 | 84 | 42 | 62 | 117 | 145 |
| 2   | Riku 132 | 1921             | 76 | 84 | 42 | 61 | 117 | 145 |
| 3   | Fujisaka 5 | 1949             | 72 | 74 | 40 | 50 | 111 | 124 |
| 4   | Sasashigure | 1952             | 81 | 84 | 40 | 48 | 121 | 131 |
| 5   | Fujimori | 1960             | 73 | 74 | 38 | 44 | 111 | 118 |
| 6   | Sasanishiki | 1963             | 77 | 81 | 39 | 46 | 116 | 127 |
| 7   | Reimei | 1966             | 73 | 75 | 37 | 42 | 110 | 117 |
| 8   | Toyonishiki | 1970             | 81 | 84 | 37 | 42 | 118 | 126 |
| 9   | Akihikari | 1976             | 72 | 74 | 37 | 40 | 108 | 114 |
| 10  | Hitomebore | 1991             | 82 | 85 | 39 | 42 | 121 | 127 |

Values are means of data under three environmental conditions (two years in Sendai and one year in Kashimadai).

Table 2. Amounts of fertilizers applied under three environmental conditions.

| Year     | Location | Plot | N (g m⁻²) | P₂O₅ (g m⁻²) | K₂O (g m⁻²) |
|----------|----------|------|------------|---------------|-------------|
| 2001     | Sendai   | Low-N | 2 + 1      | 6             | 8           |
|          |          | High-N| 6 + 2      | 6             | 8           |
| 2002     | Sendai   | Low-N | 1 + 1      | 6             | 8           |
|          |          | High-N| 4 + 2      | 6             | 8           |
| 2002     | Kashimadai | Low-N | 1.5 + 0   | 3             | 3           |
|          |          | High-N| 3 + 0      | 3             | 3           |

Amounts of N: Basal + top-dressed at meiosis stage.
After threshing and hulling, grains screened with a rice grader (with strings of 1.8 mm apart) were weighed. Grain moisture after air-drying was in a range of 14 – 15%. For the measurements of yield components, five hills of medium growth were used. The number of spikelets per panicle was counted. After threshing, ripened grains were selected by soaking unhulled grains in a salt solution of 1.06 specific gravity, and the percentage of ripened grains was estimated. After hulling, the 1000-grain-weight of ripened grains after air-drying was measured.

Apparent photosynthesis (AP) of the flag leaf (L-1) was measured in five plants from each plot in Sendai using a LI6400 portable photosynthesis system (LI-COR, NE, USA). In 2001, the AP of L-1 of all cultivars was measured one week and three weeks after heading. In 2002, the AP of L-1 and the leaf two nodes below the flag leaf (L-3) of Rikuu 132 and Akihikari was weekly measured after heading for four weeks. The measurement was carried out between 1000 and 1300 hr. The flow rate of air in the leaf chamber was 500 µmol s⁻¹, and the CO₂ concentration was maintained at 350 µL L⁻¹. The irradiance on the measured leaves (6 cm²) was regulated at 1,500 µmol m⁻² s⁻¹ PPFD. The temperature of the chamber was kept at 28°C, and the relative humidity was maintained at about 60%. The CO₂ diffusive conductance (including stomatal and boundary layer) was measured and calculated as described by von Caemmerer and Farquhar (1981). After the measurement of AP, the leaves were excised, oven dried at 80°C for at least two days and weighed. The dried samples were ground in a mill and the N concentration was analyzed by the Kjeldahl-Gunning method.

Weather data were obtained from the website of Sendai District Meteorological Observatory.

**Results**

1. **Weather conditions**

In general, climatic conditions were not extreme in the three environmental conditions. Air temperatures in May, June and July in 2001 in Sendai (2001S) were 0.8 to 2.1°C higher than in 2002 in Sendai (2002S) and Kashimadai (2002K), but the temperature in August in 2001S was substantially lower than in the other two environments (Table 3). Duration of sunshine in 2001S was significantly longer in July but shorter in August than in the other two environments.

2. **Growth period, yield and harvest index**

In 2001, Kamenoo and Rikuu 132 lodged to a considerable extent under High-N, despite the plants were physically supported. The leaves and stems partly deteriorated, so that total plant weights of the two cultivars were excluded from the analysis of yield and plant weight relationship. The lodging of the above two cultivars was slight in 2002 and that of the other cultivars was insignificant under any environmental condition.

The period from transplanting to maturity was longer under High-N than under Low-N, irrespective of cultivar (Table 1), primarily due to the prolonged duration after heading. This period in Kamenoo and Rikuu 132 was markedly longer than that of the other cultivars.

There was a substantial difference in yield among cultivars and the three environmental conditions. In general, the yields were higher in 2001S than in 2002S and 2002K. Under Low-N, the yield variation among cultivars was 398 to 609 in 2001S, 384 to 480 in 2002S, and 359 to 500 g m⁻² in 2002K, respectively. Under High-N, the variation was 394 to 681 in 2001S, 456 to 594 in 2002S and 382 and 583 g m⁻² in 2002K, respectively. Under High-N, ranking in yield among the cultivars was significantly consistent across the different environmental conditions, whereas the consistency under Low-N was significant only between 2001S and 2002S (Table 4).

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Table 3. Monthly average of daily mean temperature and duration of sunshine during growth period under the three environmental conditions.

| Year | Location | May | June | July | Aug. | Sept. | May | June | July | Aug. | Sept. |
|------|----------|-----|------|------|------|-------|-----|------|------|------|-------|
| 2001 | Sendai   | 15.4| 19.3 | 24.7 | 21.8 | 20.1  | 156 | 140  | 208  | 78   | 128   |
| 2002 | Sendai   | 14.6| 17.9 | 23.3 | 24.4 | 20.5  | 184 | 160  | 126  | 147  | 141   |
| 2002 | Kashimadai | 14.1| 17.4 | 22.6 | 23.3 | 19.3  | 159 | 120  | 92   | 116  | 144   |

Table 4. Spearman’s rank correlation coefficients for the relationship between yields among cultivars across three environmental conditions.

| Year | Location | Low-N | High-N |
|------|----------|-------|--------|
| 2001 | Sendai (A) | 0.648* | 0.915** |
| 2002 | Sendai (B) | 0.248 | 0.661* |
| 2002 | Kashimadai (C) | 0.152 | 0.697* |

* and ** indicate a significant correlation at the 5% and 1% level, respectively.
Yields were generally higher under High-N than under Low-N, and the difference between High-N and Low-N was large for the new cultivars (Fig. 1). Sasashigure and Sasanishiki had the highest yields under Low-N, whereas Fujiminori, Reimei, and Toyonishiki showed the greatest N responsiveness.

Fig. 1. Average yield over the three environmental conditions. Ten cultivars were grown under Low-N and High-N. Vertical bars are means ± SE of three environmental conditions.

Fig. 2. Relationship between yield and total plant weight at maturity and harvest index. Ten cultivars were grown under Low-N and High-N in 2001 and 2002, in Sendai. * and ** indicate a significant correlation at the 5% and 1% level, respectively.
1 – 10: Cultivar number (see Table 1).
The genotypic improvement in yield under High-N with release year was progressive for the old cultivars whereas it was stagnated in the new cultivars.

The correlation between yield and total plant weight at maturity in Sendai was significant under Low-N irrespective of year, whereas under High-N it was significant in 2001 but not in 2002 (Fig. 2 upper). The correlation between yield and harvest index was consistently significant regardless of year or nitrogen treatment (Fig. 2 lower). Generally, the genotypic improvement in total plant weight and harvest index was progressed with release year, although the progression was not clear in the new cultivars (Fig. 2).

### 3. Yield components

Yield was significantly correlated with the number of panicles per m$^2$ and the number of spikelets per m$^2$ under Low-N (Table 5). Among cultivars, Sasashigure (No. 4) and Sasanishiki (No. 6) produced the greatest number of spikelets, leading to the higher yield of these cultivars at Low-N (Fig. 3). Under High-N, however, yield significantly correlated with the percentage of ripened grains (Table 5). Under Low-N, there was no significant relationship between the number of spikelets per unit field area and the percentage of ripened grains (Fig. 4). Under High-N, where the number of spikelets ranged between ca. 30,000 and 50,000 per m$^2$, depending on the cultivar, the ten cultivars fell into two groups: old cultivars (numbered 1 to 4) and new cultivars (numbered 5 to 10). The percentage of ripened grains was lower than 70% (2001) or 80% (2002) in the old cultivars, whereas that of the new cultivars was higher than 70% (2001) or 80% (2002).

### 4. Leaf photosynthesis, nitrogen content and sink/source ratio

The AP was higher under High-N than under Low-N irrespective of cultivar or growth stage (Fig. 5). At one week after heading, the cultivar difference in AP was negligible, except for Kamenoo and Rikuu 132. However, the cultivar difference was large at three weeks after heading. Of the ten cultivars measured, Fujiminori and Akihikari possessed the highest AP during the ripening stage when grown under High-N. The AP at three weeks after heading was positively

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**Table 5. Correlation coefficients between yields and yield components for two years in Sendai.**

| Plot    | Number of panicles per m$^2$ | Number of spikelets per panicle | Number of spikelets per m$^2$ | Percentage of ripened grains | Weight of 1,000 grains |
|---------|-------------------------------|---------------------------------|-------------------------------|------------------------------|------------------------|
| Low-N   |                               |                                 |                               |                              |                        |
| 2001    | 0.729*                        | -0.087                          | 0.816**                       | 0.389                        | -0.188                 |
| 2002    | 0.834**                       | -0.716*                         | 0.732*                        | 0.467                        | -0.222                 |
| High-N  |                               |                                 |                               |                              |                        |
| 2001    | 0.537                         | -0.394                          | -0.110                        | 0.933**                      | 0.608                  |
| 2002    | 0.485                         | -0.668*                         | -0.336                        | 0.843**                      | -0.175                 |

* and ** indicate a significant correlation at the 5% and 1% level, respectively.

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**Fig. 3. Relationship between yield and the total number of spikelets. Ten cultivars were grown under Low-N and High-N in 2001 and 2002, in Sendai.**

Open circles: Low-N, Closed circles: High-N.

* and ** indicate a significant correlation at the 5% and 1% level, respectively.

For cultivar identification, see Table 1.
Fig. 4. Relationship between the total number of spikelets and the percentage of ripened grains. Ten cultivars were grown under Low-N and High-N in 2001 and 2002, in Sendai. Open circles: Low-N, Closed circles: High-N. ** indicates a significant correlation at the 1% level. For cultivar identification, see Table 1.

Fig. 5. Photosynthetic rate of the flag leaf one week and three weeks after heading. Plants were grown under Low-N and High-N in 2001, in Sendai. Vertical bars are means ± SE of five plants.
correlated with leaf nitrogen concentration under High-N; but not under Low-N or at one week after heading for both N treatments (Fig. 6). The AP significantly depended on diffusive conductance at three weeks but not at one week after heading (Fig. 7).

The AP of L-1 and L-3 tended to be higher in Akihikari than in Rikuu 132, although the difference in the AP of L-1 was not significant at 0 and 14 days after heading (Fig. 8).

Under Low-N, the ratio of the number of spikelets to leaf area did not correlate with the year of release, but under High-N, it tended to be lower in the cultivars released after Sasashigure (Table 6). Among the cultivars tested, Hitomebore consistently exhibited the lowest ratios irrespective of year or N application rate.

**Discussion**

The warmer weather condition during vegetative growth stage as well as greater amount of basal N fertilizer in 2001S, might have produced greater total plant weights, leading to the higher grain yields than in 2002S and 2002K. In 2001S, the lower temperature along with the significantly short duration of sunshine in August might be responsible for the lower percentage of grain filling than in 2002S and 2002K.

These results indicate that a genotypic yield improvement with release year is evident until the 1960s, but not thereafter (Fig. 1). The new cultivars exhibited higher photosynthetic rates and higher grain filling percentages under High-N, leading to higher yields (Figs. 1, 5, 8). Among the cultivars tested, Sasanishiki, Toyonishiki and Akihikari exhibited the highest yields under High-N (Fig. 1).

Takeda et al. (1984) compared yields of various cultivars under warmer conditions in Kyushu and found a close association between yield and harvest index, but no correlation between yield and total plant weight. In our present study, yield was more dependent on harvest index than total weight, although in 2001S.
the dependence of yield on total weight was significant irrespective of nitrogen treatments (Fig. 2). In warm regions, rice plants tend to grow more vigorously than in cool region, leading to lodging, particularly when the plants are given a high nitrogen. Under these conditions, increased total weight may not always lead to a higher yield, and harvest index might be a more important yield determinant. In the Tohoku (a cool region), however, increased total weight often resulted in a higher yield.

A strong dependence of yield on harvest index has been recognized in rice (Ito, 1975; Takeda et al., 1984), wheat and barley (Evans, 1993). Sinclair (1998) indicated that a historical improvement in harvest index was closely associated with high levels of nitrogen accumulation in plants. It is unclear, however, whether there is much room for further improvement in harvest index in rice cultivars, since the harvest index has already been improved genetically to the highest level (Evans, 1993).

A concomitant decline of AP and leaf nitrogen concentration during a period from one to three weeks after heading was commonly observed (Figs. 5, 6 and 8). However, new cultivars such as Akihikari and Fujimiori maintained a higher leaf nitrogen concentration and AP than older cultivars during this period, and this appeared to be associated with the higher yields of these cultivars (Figs. 1, 5, 6 and 8). The AP of Sasanishiki and Toyonishiki was intermediate among the cultivars tested, but the yields of these cultivars were the highest. Therefore, the traits contributing to the higher yields of these cultivars are not attributable to AP. The association of higher AP and leaf nitrogen concentration with higher yield has been observed in previous studies conducted in Tohoku (Hayami, 1982, 1983a), Kanto (Kuroda and Kumura, 1990a, 1990c; Saitoh et al., 1991a; Sasaki and Ishii, 1992) and Kyushu (Takeda et al., 1983). Obviously, improved AP arising from high leaf nitrogen concentration contributed to yield improvement in the newer cultivars, irrespective of growing areas. Since decreased application of nitrogen fertilizer is recommended to avoid environmental pollution by nitrate, further improvement of AP cannot realistically be achieved through heavier application of nitrogen. Instead, more efficient utilization of absorbed nitrogen in plants might be a good target for future improvement of AP. To achieve this, biochemical modification of photosynthetic processes using biotechnology would be a possible option (Sheehy et al., 2000).

Since dry matter production during ripening was not examined in the present experiment, it is not clear whether a high AP of new cultivars contributed to an increase in yield through increase in total dry matter production or through increase in photosynthates translocated directly to caryopsis.

At three weeks after heading, diffusive conductance largely accounted for the cultivar difference in AP (Fig. 7). This phenomenon was previously observed by Kuroda and Kumura (1990a) and Saitoh et al. (1991a) in the cultivars including those bred in the Tohoku region. Kuroda and Kumura (1990b) emphasized the importance of root activity, which might regulate water absorption and thereby lead to increased diffusive conductance. The importance of root activity, in terms of nitrogen absorption, was similarly pointed out by Hayami (1983b).

Hayami (1983a) adopted two indices, the number of spikelets per nitrogen absorbed and the number of spikelets per leaf area, to evaluate the sink formation ability of rice cultivars that had been bred before the 1960s in the Tohoku region. He found that new cultivars exhibited a rise in the two indices, as well as in AP, when grown under a heavy nitrogen application. In our present study, which included cultivars released

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**Table 6. Ratio of the number of spikelets to leaf area (cm²) at heading in Sendai.**

| Cultivar | 2001     | 2002     |
|----------|----------|----------|
|          | Low-N    | High-N   | Low-N    | High-N   |
| 1 Kamenoo| 1.18     | 1.30     | 0.75     | 0.62     |
| 2 Rikuu  | 1.23     | 1.27     | 0.78     | 0.65     |
| 3 Fujisaka| 1.20     | 0.96     | 0.76     | 0.70     |
| 4 Sasshigure | 1.00   | 0.81     | 0.83     | 0.47     |
| 5 Fujimiori | 1.32    | 0.86     | 0.87     | 0.52     |
| 6 Sasanishiki | 0.98    | 0.89     | 0.67     | 0.44     |
| 7 Reimei  | 1.27     | 0.88     | 0.87     | 0.53     |
| 8 Toyonishiki | 1.22    | 0.93     | 1.05     | 0.63     |
| 9 Akihikari | 1.22    | 0.90     | 0.78     | 0.57     |
| 10 Hitomebore | 0.81    | 0.76     | 0.62     | 0.44     |

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Fig. 8. Time course of changes in photosynthetic rate of the flag leaf (L-1) and the leaf two nodes below the flag leaf (L-3) for two cultivars. Plants were grown under High-N in 2002, in Sendai. Bars indicate ± SE for five plants.
after the 1960s, we used the number of spikelets per leaf area as an index for evaluating sink formation ability. In our survey, this index did not change with the year of release (Table 6). The reason for this disagreement with the previous studies is not clear.

Under Low-N, Sasanishiki exhibited the highest yield (Fig. 1). This cultivar had a high tillering ability, and produced a greater number of spikelets per m² under Low-N (Fig. 3). For example, the panicle number of Sasanishiki was 18, whereas that of other cultivars ranged 11 to 17 per hill, as average values of two years in Sendai. In addition, Sasanishiki had a high grain filling percentage when grown under Low-N (Fig. 4). Since there is an increasing requirement to minimize the nitrogen application from environmental concern, Sasanishiki can be a superior breeding material in the future.

Acknowledgments

We thank T. Takita and K. Tanno for providing the seeds of the rice cultivars, Y. Cui and Y. Oki for the help in the measurements, and K. Otomo for the field management.

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