Gamma Field Symposia

Semicentennial
(Number 50, 2011)

Can Mutations Increase Plant Biomass?

INSTITUTE OF RADIATION BREEDING

NIAS

Hitachi-Omiya, Ibaraki-ken
Japan
Can Mutations Increase Plant Biomass?

Report of Symposium
held on
July 13-14, 2011

Institute of Radiation Breeding
NIAS

Hitachi-Omiya, Ibaraki-ken
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(50th GF Symposium)

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Foreword

There’s no water, there’s no electricity, there’s no convenient bathroom, food isn’t readily available, and gasoline is running out... These were first-time experiences for everyone. That was the year that the Great East Japan Earthquake occurred, and it was just when the 50th commemorative symposium should have been held, a half-century since the first Gamma Field Symposium in 1962. Although no staff members were hurt at the Institute of Radiation Breeding, the earthquake registered over M6 and caused substantial damage to facilities and fields.

The earthquake and tsunami were followed by the onslaught of a third disaster: the Fukushima nuclear accident. People became more sensitive to the word “radiation.” At a time of such chaos throughout Japan, some people argued that we should exercise “self-restraint,” and accordingly, one view was that perhaps the symposium should be called off this time. On the other hand, some said that we should “carry on as usual,” especially at such times. Amid these opposing views, we received encouragement from the Tsukuba office and decided to hold the symposium. Although preparations were delayed beyond the usual timetable, we received a great deal of support from many people.

The Gamma Field Symposia have been held to present the latest research results and mutation-related information in thremmatology, genetics, radiation biology, molecular biology, and related research fields, as a summer school for researchers, engineers, and students to widely share their knowledge with each other, and as a venue for information exchange among industry, academia, and government. The symposia, which have been held every year, marked its 50th meeting in 2011. At first they were often held in the Institute of Radiation Breeding, and the symposia were “hand-prepared” by the institute’s staff, but after a while they were held at venues such as hotels, and in recent years we have commissioned a conference services company to organize them.

This symposium comprises two parts. The first day is a lecture open to the public on “Selective Breeding and Mutations,” and the theme for the second day is “Can mutations increase biomass?” Lecture topics are decided by the Gamma Field Symposium Committee. Presentations have been compiled in English as Gamma Field Symposia and distributed to related institutions in Japan and abroad. On this occasion, discussions were held on whether or not to continue the symposia, and it was decided to continue the event but make this publication the last. As such, we have produced a special compilation of the symposia in a 50th anniversary commemorative volume. In addition to including English-language versions of the lectures as usual, the publication includes features such as the approximately 10 years of research results produced by the Institute of Radiation Breeding since the publication of A 40-Year History of the Institute of Radiation Breeding, as well as materials on the Gamma Field Symposia, outside experts’ views on the direction of research by the Institute of Radiation Breeding, a description of the damage incurred in the Great East Japan Earthquake, the long process of recovery and reconstruction, and more.

Over the last 18 months, we have benefited from the encouragement and assistance of very many people inside and outside the institute, and we have somehow begun to see the path to recovery and reconstruction. Furthermore, during the last half century, the symposia and lectures have been achieved with the cooperation of a very large number of people in Japan and other countries. This will be the final symposium publication, although the symposia themselves will continue. The record of our journey in this publication is our expression of gratitude to everyone.

The Symposium Committee, Chairperson, Minoru Nishimura
PROGRAM

Opening address: M. Nishimura
Congratulatory address: T. Ishige

Special lecture
Chairperson: Y. Nagato
Induced Mutations Will Help Mold the Future of Food T. Tanisaka

Session 1
Chairperson: N. Tsutsumi
Ecophysiological Characterization of Rice Plants for Breeding High-Biomass Cultivars T. Hirasawa

Session 2
Chairperson: H. Kitano
Breeding of High-Yielding Rice Cultivars in Japan H. Nemoto

Session 3
Chairperson: H. Nakagawao
Isolation and Analysis of Sorghum Mutants by Gamma-Ray Irradiation T. Sazuka

Session 4
Chairperson: T. Meshi
Biotechnology and Mutation Breeding M. Miyata

Session 5
Chairperson: T. Nishio
General discussion

Closing address: Y. Nagato
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Induced Mutations Will Help Mold the Future of Food

Takuji TSUKIYAMA, Hiroki SAITO, Ken NAITO, Masayoshi TERAISHI, Yuki MONDEN and Takatoshi TANISAKA

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Introduction

Scientific plant breeding started immediately after the rediscovery of Mendel's laws of heredity in 1900. Since then, the efficiency of plant breeding rapidly increased, and a large number of elite cultivars have been developed. For the past 110 years, the grain yields per area of two of the most important crops worldwide, rice and wheat, have almost tripled. Thus, plant breeding has obtained dazzling results up until now. Recently, however, obtaining further marked increases in grain yield per area has become difficult: grain yield per area is thought to have reached its upper limit unless novel gene sources are exploited.

Recent breeding in rice and wheat has achieved high grain yields by increasing the harvest index of semidwarf cultivars, which have a short, stiff culm and strong lodging resistance. Harvest index, however, seems to have reached a maximum (0.6–0.65). This is the chief reason why grain yield in rice and wheat is thought to have reached a maximum, if we continue semidwarf breeding dependent on a few semidwarfing genes. Thus, the exploitation of novel genetic factors that confer higher yields than the currently used semidwarfing genes has been an important subject worldwide since the 1990s. Needless to say, stress resistance and regional adaptability are also very important for stable crop production: exploitation of genetic resources containing these traits should be done along with breeding for higher yield performance.

Stadler (1928a, b) successfully induced mutations by X-ray irradiation in barley and maize. In those days, there was an academic controversy over the effectiveness of induced mutations in plant breeding that continued until the 1940s. With the development of many excellent cultivars in barley in Northern Europe, however, “mutation breeding” became the center of plant breeders’ attention, and a number of elite cultivars in various crops were developed one after another. Thus, mutation breeding was highly regarded as a useful method of plant breeding at one time, but its use has gradually decreased in practical breeding since the 1980s because of its low efficiency of producing useful mutants without also introducing unfavorable mutations.

In spite of its decreased use in practical breeding programs, the utilization of artificial mutations is becoming more and more frequent in the fundamental plant sciences. In Arabidopsis, regarded as a model for analyzing the genome structure of dicots, a number of genetic and physiological studies have been made utilizing a large number of mutants induced in various ecotypes. Consequently, the physiological and biochemical functions of various kinds of genes have been described. Various kinds of mutants are easily obtained in Arabidopsis because of several important characteristics of this plant: diploid inheritance, very small genome size, and short period from germination to seed maturity.

There are two broad classes of mutations: spontaneous and induced. The former arise from a variety of sources, including errors in DNA replication, spontaneous lesions, and transposable elements (transposons, retrotransposons). The latter are caused by mutagens. However, there is no great difference in the patterns of chromosome and molecular changes between spontaneous and induced mutations (except for insertional mutagenesis by transposable elements), between spontaneous and induced mutations (except for insertional mutagenesis by transposable elements),
although induced mutations are more likely to result in loss of function. Humans have improved crops for a long time using spontaneous variations. To date, however, most of the existing useful genes seem to have already been introduced into modern cultivars. It may be inevitable that induced mutations will play a greater role in plant breeding in the near future. In this report, based on our studies, we show that induction of mutations is an effective way of obtaining useful genes, and we propose that the use of induced mutations should be promoted as a means of expanding the narrow useful gene source base.

**Induction of mutant genes isoallelic to existing genes**

Modern plant breeding has successfully developed a number of elite cultivars using a great variety of mutations that have arisen naturally. Our previous studies suggested that mutant genes with phenotypic effects similar to those of spontaneous mutant genes can be induced by mutagens, although it is highly unlikely that an induced mutant gene would have the same DNA sequence as a spontaneous mutant gene at the same locus. Here we show a few examples of useful mutations that arose at agronomically important loci. These examples support the idea that even if sources of useful genes are somehow lost, genes with a similar effect can be recovered by mutagenic treatments.

**Late-flowering-time gene ef1-h in HS169**

We first describe the mutant allele ef1-h at the Ef1 (Early flowering-1, functional allele) locus in rice (*Oryza sativa* L.). Flowering time (heading time) plays a principal role in the regional adaptability of rice cultivars (Okumoto et al. 1991, 1992a, b, 1996; Tanisaka et al. 1992; Ichitani et al. 1997, 1998, 2002). Preflowering development of rice is divided into three successive phases: the basic vegetative growth phase (BVP), the photoperiod-sensitive phase (PSP), and the reproductive phase (RP) (Yin et al. 1997; Nishida et al. 2001). The durations of the first two (BVP and PSP) show great intervarietal variation, while the duration of the third (RP) is almost constant at 35 days, regardless of cultivar or photoperiod (Vergara and Chang 1985). Because PSP can be completely eliminated under optimum photoperiod conditions, heading time of rice has been considered to be primarily determined by the duration of the basic vegetative growth period (BVG period, nearly equal to the duration of BVP plus RP) under optimum photoperiod conditions, expressed in days to heading (Hosoi 1981; Tanisaka et al. 1992). To date, seven loci involved in determining the BVG period have been reported: Ef1 on chromosome 10 (Tsai 1986), Ef2 on chromosome 9 (Khn et al. 2005b), Ef3 (chromosome unknown; Tsai 1991), Ef4 on chromosome 3 (Khn et al. 2005a), Ef5 on chromosome 6 (Khn et al. 2004), Ef6 on chromosome 7 (Khn et al. 2006), and Ehdl (Early heading 1) on chromosome 10 (Doi et al. 2004).

Among these loci, Ef1 was the first identified BVG locus. It was detected in the progeny of crosses of the Taiwanese cultivar Taichung 65 (T65) (ef1) and early-heading experimental lines (Ef1): the dominant allele Ef1 confers a short BVG period, while the recessive allele ef1 confers an extremely long BVG period (Tsai 1986, 1991). This locus has been extensively investigated in several studies aiming to identify the allele present in certain *japonica* cultivars and to observe the gene’s effect on preflowering developmental phases and its interactive effects with other loci (Sato and Hayashi 1985; Inoue et al. 1998; Nishida et al. 2001; Ichitani et al. 2002). These studies have shown that Ef1 is a key locus dividing *japonica* rice cultivars into two groups: an *ef1* group, found in subtropical latitudes (21–26°N), and an *Ef1* group, found in temperate zones (25–39°N).

*ef1* has played a very important role in rice production development in Taiwan. Until the first decade of the twentieth century, when Japanese *japonica* cultivars from the southern and middle part of Japan (25–39°N) were introduced into Taiwan, the rice cultivars predominantly grown in Taiwan (21–26°N) were *indica* cultivars. Because most of the introduced Japanese cultivars were strongly photoperiod-sensitive,
their introduction into Taiwan did not improve Taiwanese rice production. Instead, the strong photoperiod sensitivity inevitably resulted in heading before the plants had achieved sufficient vegetative growth, resulting in low grain yields (Ito 1963). This problem was overcome in 1936, however, with the development and release of Taichung 65 (T65), which was derived from a cross between two Japanese japonica cultivars, Kameji and Shinriki. T65 has an extremely long BVG period (conferred by ef1) and weak photoperiod sensitivity. Since its release, T65 has been used as a cross parent in the development of many elite cultivars that are well adapted to the climatic conditions and especially the photoperiods in Taiwan (11.0–13.0 h), and Taiwan now reliably produces japonica rice with a high grain yield. According to Lin (1991a, b), of the 99 japonica cultivars developed between the 1940s and the 1980s, 80 were descendants of T65, and most of them exhibited an extremely long BVG period. This suggests that ef1 is widely distributed among Taiwanese japonica cultivars and has made a significant contribution to rice production in Taiwan.

A late-heading mutant line, HS169, which was induced by gamma irradiation of seeds of the Japanese japonica cultivar Gimbozu (Fig. 1A, B), also has an

Fig. 1. A) Phenotypes of the ef1-h mutant (line HS169) and its original cultivar Gimbozu (WT) at the heading time of Gimbozu. B) Days to flowering under different photoperiodic conditions. L, light; D, dark. Values are means (n = 10). C) Location of the ef1-h region on chromosome 6. White boxes, untranslated regions (UTRs); black boxes, exons; lines connecting black boxes, introns. The ef1-h mutant gene in line HS169 has an insertion of mPing (miniature Ping; gray rectangle) in exon 2.
extremely long BVG period (Tanisaka et al. 1992; Nishida et al. 2002; Saito et al. 2009). Genetic analysis using an F2 population from a cross of HS169/Gimbozu showed that the late heading of HS169 was caused by a single recessive mutant gene. The subsequent analysis of heading responses of HS169, Gimbozu, and six heading-time tester lines to five photoperiods (10–16 h) revealed that the mutant gene confers an extremely long BVG regardless of genetic background and photoperiod. This mutant gene was found to be a nonfunctional allele at the Ef1 locus on chromosome 10. We designated this mutant gene ef1-h (Nishida et al. 2002).

We examined the allelic relationship between Ef1 and Ehdl (Early heading date 1; Doi et al. 2004), because both showed similar phenotypic effects and were located in almost the same region on chromosome 10. The Ehdl locus was originally identified in an experiment using the progeny from a cross between T65 and African rice (Oryza glaberrima Steud.; Acc. IRGC 104038). The functional allele Ehdl-gla from the African rice encodes a B-type response regulator that shortens the BVG period, whereas the nonfunctional ehdl from T65 greatly prolongs the BVG period (Doi et al. 2004). Ehdl and ehdl can easily be discriminated from each other by the number of GARP (Golden2, Arabidopsis RESPONSE REGULATOR [ARR], and Chlamydomonas regulator protein of P-starvation acclimatization response [Psrl]) DNA-binding domains in the middle of them: Ehdl harbors a single Ddel restriction site in the sequence encoding the GARP domain, while ehdl harbors two Ddel restriction sites, one of which reflects a nucleotide substitution from G to A that causes an amino acid substitution from Gly to Arg (Doi et al. 2004). Our conventional genetic analysis using F2 and F3 populations and subsequent CAPS (cleaved amplified polymorphic sequence) analysis based on the amino acid sequences of Ehdl and ehdl showed that Ef1 and Ehdl were at the same locus, and that ehdl and ef1 were the same allele (Saito et al. 2009). The CAPS analysis also showed that the Taiwanese japonica cultivars with extremely long BVG periods all harbor ef1 (ehdl), but that this allele does not exist among indica and japonica cultivars grown at low latitudes. Since ef1 has not been found in any japonica cultivars outside Taiwan, this allele might have originated in Taiwan. The parental cultivars of T65, Kameji and Shinriki, do not harbor ef1. Accordingly, there is a high possibility that ef1 was a spontaneous mutant gene induced during the process of developing T65.

According to Nishida et al. (2002), ef1 permits some residual function to accelerate heading, whereas ef1-h causes the complete loss of function. Sequence analysis revealed that ef1-h, which prolongs the BVG period even more than ef1 does (ca. 20 days longer), does not encode a Gly-to-Arg substitution in the GARP DNA-binding domain, but instead has an insertion of an mPing (miniature Ping) substitution in exon 2 (Fig. 1C). Except for this mPing insertion, ef1-h has the same sequence as Ef1; thus, it appears that the complete loss of function of ef1-h relies on the insertion of mPing. A recently established rice breeding program for low latitudes, where short photoperiod (SP) conditions occur throughout the year, aims to develop cultivars with extremely long BVG periods and weak photoperiod sensitivities. Our results indicate that both the ef1 and ef1-h alleles can be used in this program to develop rice cultivars with extremely long BVG periods for low latitudes.

Late-flowering-time gene ef1 in HS276

Like HS169, HS276 is a late-heading mutant line, which was induced by gamma irradiation of seeds of Gimbozu, exhibits an extremely long BVG period (Fig. 2A, 2B) (Tanisaka et al. 1992). A genetic analysis using an F2 population from an HS276/Gimbozu cross showed that the late heading of HS276 is governed by a single recessive mutant gene (Yuan et al. 2009). The subsequent analysis of heading responses of HS276, Gimbozu, and heading-time tester lines to four photoperiods (12–15 h) and a photoperiodic transfer treatment from a long photoperiod (LP; 14 h) to SP (10 h) revealed that the mutant gene confers an extremely long BVP and increases photoperiod sensitivity under long photoperiods.
Fig. 2. A) Phenotypes of the ef7 mutant (line HS276) and its original cultivar Gimbozu (WT) at the heading time of Gimbozu. B) Days to flowering under different photoperiodic conditions. L, light; D, dark. Values are means (n = 10). C) Schematic diagram of the Ef7 locus and polymorphism between HS276 and Gimbozu (WT). White boxes, untranslated regions (UTRs); black boxes, exons; lines connecting black boxes, introns. The ef7 mutant harbors two 8 bp deletions (indicated by dashes) and three 1 bp substitutions (indicated by asterisks) relative to Gimbozu.

(14 and 15 h). The BVP durations of HS276 and Gimbozu were estimated at 30.1 and 16.0 days, respectively; thus, the mutant gene elongates the duration of BVP by 14 days. In the transfer treatments, 13 pots for each cultivar/line were initially kept under a 14-h photoperiod at 0, 7, 14, 21, 28, 35, 42, 49, 56, 63, 80, and 90 days after sowing, one pot per cultivar/line was transferred to a 10-h photoperiod and grown until heading. We estimated the duration of BVP according to the model of Ellis et al. (1992), using the data set from the transfer treatments. Linkage analysis showed that the mutant gene is located in the 129-kb region between INDEL markers INDELAP0399_6 and INDELAP3487_2, on the distal part of the short arm of chromosome 6 (Fig. 2C). No other BVP genes are located in this region; therefore, we designated this newly detected mutant gene ef7.

Subsequently, we attempted to characterize Ef7 (the functional allele at the ef7 locus). Ef7 is a rice ortholog of Arabidopsis ELF3 (EARLY FLOWERING 3), which plays important roles in maintaining circadian rhythms (Saito et al. 2012). HS276 flowered later than Gimbozu under both SP and LP conditions. Expression analyses of flowering time–related genes demonstrated that Ef7 negatively regulates the expression of Ghd7 (Grain number, plant height and
heading date 7), a repressor of the photoperiodic control of rice flowering (Xue et al. 2008), and consequently up-regulates the expression of the downstream Ehd1 (Ef1) and FT-like genes (Arabidopsis flowering time-like genes) under both SP and LP conditions (Saito et al. 2012). Genetic analyses with a nonfunctional allele, ghd7, provided further evidence that the delayed flowering of HS276 (ef7ef7/Ghd7Ghd7) is mediated through the Ghd7 pathway. The analysis of light-induced expression of Ghd7 revealed that HS276 was more sensitive to red light than Gimbozu (Ef7Ef7/Ghd7Ghd7), but the gate of Ghd7 expression was unchanged. Thus, Ef7 functions as a floral promoter by repressing Ghd7 expression under both SP and LP conditions. The quantitative trait locus (QTL) Hd17 (Heading date 17) is associated with a difference in flowering time between Japanese japonica rice cultivars, and the difference may result from a single-nucleotide polymorphism within a putative gene that encodes a homolog of Arabidopsis ELF3. We have not yet investigated the allelic relationship between Ef7 and Hd17, but we hypothesize that these two genes are at the same locus, because they encode the same protein and are located in the same region (Matsubara et al. 2012). However, the recessive allele at the Hd17 locus reported by Matsubara et al. (2012) does not have a great effect on heading time, whereas the ef7 allele described here delays heading markedly by lengthening BVP by 14 days.

Like ef1-h, ef7 will be useful in breeding rice for low latitudes, because it confers an extremely long BVP duration and only slightly enhances photoperiod sensitivity under SP conditions.

**Semi-dwarfing mutant genes sd1, d49(t), and sd1-h**

At the sd1 (semi-dwarfing l) locus (Rutger et al. 1976; Foster and Rutger 1978), several semi-dwarfing (nonfunctional) alleles have been identified. Most of these alleles have been used for semi-dwarf rice breeding in each cultivation area. One of them, a spontaneous mutant allele, d47 (later renamed sd1), found in the Taiwanese indica cultivar Dee-Geo-Woo-Gen, greatly contributed to the Green Revolution in rice (Aquino and Jennings 1966), and has been widely used for rice breeding in Southern Asia. Recently it has come into use in Japanese breeding programs, though not frequently. The induced mutant allele d49(t) (later renamed sd1) of the semi-dwarf mutation cultivar Reimei, which was developed by gamma irradiation of seeds of the Japanese tall japonica cultivar Fujiminori, has been used in semi-dwarf breeding in the Tohoku district of Japan (Futsuhara 1968). The induced mutant allele sd1 of the semi-dwarf mutation cultivar Calrose 76, which was induced in the Californian tall japonica cultivar Calrose, has greatly contributed to rice production in California, USA (Rutger et al. 1976; Foster and Rutger 1978). In addition to these three alleles, at least three others are known: the Jikkoku allele (spontaneous; Kikuchi et al. 1985), the 1-Geo-Nan-Te allele (spontaneous), and the HS90 allele (induced; Tanisaka et al. 1994). These facts suggest that the sd1 mutants are easily induced both spontaneously and artificially.

HS90 is a short-culmed mutant line that was induced by gamma irradiation of seeds of Gimbozu (Fig. 3). HS90 harbors two semi-dwarfing genes: one is an incomplete recessive mutant allele (sd1-h) at the sd1 locus, and the other is an incomplete recessive
semidwarfing gene (sd9) (Tanisaka et al. 1994). According to our studies on plant height, sd9 is widely distributed among Japanese japonica rice cultivars. Plant breeders in Japan started breeding semidwarf rice about 20 years earlier than in any other country, which seems to be explained by the fact that many Japanese native cultivars with a high grain yield harbor the sd9 gene, and that Japanese plant breeders had great foresight. The F1 plants from crosses between HS90 and Gimbozu exhibit a culm length (80 cm) that falls within the range of semidwarf stature that is optimum for the present cultivation methods (Fig. 3); hence, the genotype of these F1 plants, Sd1sd1-hisd9sd9, is considered favorable for F1 hybrid cultivars. We propose that Sd1sd1/sd9sd9 and Sd1sd1/sd9sd9 are favorable genotypes for female (short culm: 50 cm) and male (long culm: 90 cm) parents, respectively, for the production of semidwarf F1 cultivars. We confirmed that the double-recessive genotype (sdl1sd1/sd9sd9) produced sufficient seeds when used as the female parent (Tanisaka et al. 1994).

**Novel genes induced by mutagenesis**

*Early-flowering mutant allele sel3*

The mutant line X61, which was induced by gamma
irradiation, flowers 35 days earlier than the original cultivar Gimbozu when grown in Kyoto (35°01′N) (Fig. 4A, B). We attempted to identify the causal gene(s) of the extremely early flowering in this line. Experimental results showed that the early flowering of X61 was caused by a complete loss of photoperiodic response due to a novel single recessive mutant gene, sel3 (Fig. 4B) (Saito et al. 2011). This locus interacts with two crucial photoperiod sensitivity loci, Sel and E1. Wild-type alleles at these two loci do not function when the sel3 mutant allele is in a homozygous state, suggesting that the product of Sel3 functions upstream of the products of Sel1 and E1. Linkage analysis showed that Sel3 is located in the 110-kb region between markers INDEL3735_1 and INDEL3735_3 on chromosome 1. A database search suggested that Sel3 is identical to AK101395 (= OsHY2), which encodes phytochromobilin synthase, a key enzyme in phytochrome chromophore biosynthesis. Subsequent sequence analysis revealed that X61 harbors a 1 bp insertion in exon 1 of OsHY2, which induces a frameshift mutation producing a premature stop codon (Fig. 4C). We therefore conclude that the complete loss of photoperiodic response of X61 is caused by a loss of function of Sel3 (OsHY2), the product of which is involved in phytochrome chromophore biosynthesis. According to our previous studies, the nonfunctional alleles el and sel confer reduced photoperiod sensitivity, but they never eliminated photoperiod sensitivity completely (Nishida et al. 2001; Tanisaka et al. 1992; Yamagata et al. 1986). Izawa et al. (2000) reported that the se5 mutant is completely deficient in photoperiodic response and shows extremely early heading even under long photoperiods. This is because se5, whose wild-type allele is an ortholog of the Arabidopsis HY1 gene, disturbs the conversion of heme to BV IXa in phytochrome chromophore biosynthesis. Sel3 (OsHY2) functions in the conversion of BV IXa to ΦΦB. We conclude that the complete deficiency of the photoperiodic response of X61 is caused by the loss of function of Sel3 (OsHY2), which is essential for photo-interconversion between Pr and Pfr. sel3, unlike se5, does not disturb chlorophyll formation. For this reason, the mutant gene sel3, which eliminates photoperiod sensitivity completely without the aid of other photoperiod-insensitivity genes, will be helpful in the development of suitable cultivars for both high and low latitudes.

**Discovery of a useful spontaneous mutant gene**

In China, the “7, 8, 9 Super Rice Project” for developing super-high-yielding rice cultivars started in 1996. The project has been going according to plan for all rice categories, namely hybrid rice, inbred (pure line) japonica rice, and inbred (pure line) indica rice. Among these, the category of inbred japonica rice seems to have made the greatest progress, by developing high-yielding cultivars with erect-pose panicles (EP) (Fig. 5). Nowadays, such cultivars cover ca. 70% of the japonica rice cultivation area in the northern part of China. The EP cultivars exhibit strong lodging resistance due to stiff, thick culms, although the culms are long. The Japanese maxim that “rice bows its head with the advance of seed-filling” does not apply to the EP cultivars.

We conducted a genetic analysis using an F2 population from a cross between Liaoqing5, the first japonica EP cultivar in China, and the Japanese japonica cultivar Toyonishiki (with normal-pose

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**Fig. 5.** A cultivar with erect-pose panicles developed at Shenyang Agriculture University, China.
panicles). We showed that the EP trait is governed by the incompletely dominant gene EP (Wang et al. 2009), which was derived from the Italian *japonica* cultivar Balilla. Subsequently, map-based cloning of the EP locus was conducted using Liaojing5, Toyonishiki, the F2 population, ZF14 (*EPEP*), and WF14 (++), and the sequence-tagged site (STS) marker H90 was found to segregate completely with panicle pose. H90 is located in cDNA AK101247 in the database (http://rapdb.dna.affrc.go.jp/). The AK101247 sequence in the wild-type allele has a 637-bp sequence in exon 5 that is replaced by a 12-bp sequence in Liaojing5. It therefore appears that AK101247 represents the wild-type allele at the EP locus, and that the sequence substitution in exon 5 of Liaojing5 is crucial for expression of the EP mutant phenotype. The sequence of this gene was also identified by Huang et al. (2009).

The effects of *EP* on agronomic traits were investigated using Liaojing5, Toyonishiki, and two near-isogenic pairs developed from the cross between Liaojing5 and Toyonishiki (Wang et al. 2009): ZF6 (*EPEP*) and WF6 (++) are a near-isogenic pair derived from a single *EP*-heterozygous F2 plant, and ZF14 (*EPEP*) and WF14 (++) are a near-isogenic pair derived from a single *EP*-heterozygous F12 plant. The EP mutant allele significantly increased grain yield, chiefly by increasing the number of secondary branches and the number of grains on each secondary branch (Table 1). It also produced a remarkable increase in grain density (grains/cm). In a subsequent experiment, the grain yields of EP cultivars increased with increasing fertilizer levels, especially nitrogen, and reached ca. 1200kg/ha. Farmers in northern China have been using six to eight times as much fertilizer as Japanese farmers do, and have achieved far higher productivity than ever before.

Until now, the normal-pose panicle has been

<table>
<thead>
<tr>
<th>Traits</th>
<th>ZF14 (<em>EPEP</em>)</th>
<th>WF14 (+++)</th>
<th>ZF6 (<em>EPEP</em>)</th>
<th>WF6 (++)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grain yield (g/m²)</td>
<td>559.7c</td>
<td>508.1d</td>
<td>605.2b</td>
<td>558.9c</td>
</tr>
<tr>
<td>Number of grains per panicle</td>
<td>137.2b</td>
<td>113.2d,e</td>
<td>145.6a</td>
<td>107.7e</td>
</tr>
<tr>
<td>Number of filled grains per panicle</td>
<td>126.0a</td>
<td>106.3c</td>
<td>131.8a</td>
<td>101.0c,d</td>
</tr>
<tr>
<td>Filled grain percentage</td>
<td>91.9a,b</td>
<td>93.9a</td>
<td>90.5b</td>
<td>93.8a</td>
</tr>
<tr>
<td>1,000-grain weight (g)</td>
<td>22.9b</td>
<td>25.3a</td>
<td>22.5b,c</td>
<td>25.6a</td>
</tr>
<tr>
<td>Number of primary branches per panicle</td>
<td>11.5b</td>
<td>11.3b</td>
<td>12.5a</td>
<td>11.0b</td>
</tr>
<tr>
<td>Number of secondary branches per panicle</td>
<td>23.9a</td>
<td>17.2c</td>
<td>24.9a</td>
<td>15.5c</td>
</tr>
<tr>
<td>Number of grains on primary branch</td>
<td>66.4b</td>
<td>64.1b</td>
<td>72.8a</td>
<td>63.4b</td>
</tr>
<tr>
<td>Number of grains on each secondary branch</td>
<td>70.8a</td>
<td>49.2c</td>
<td>72.9a</td>
<td>44.4c</td>
</tr>
<tr>
<td>Grain density (grains/cm)</td>
<td>8.4b</td>
<td>5.4d</td>
<td>9.4a</td>
<td>5.6d</td>
</tr>
<tr>
<td>Number of panicles/m²</td>
<td>291.4d</td>
<td>283.0d,e</td>
<td>304.9c</td>
<td>325.8b</td>
</tr>
</tbody>
</table>

1) ZF14/WF14 and ZF6/WF6 are two near-isogenic pairs; see text for details.
2) Means were compared using Tukey's test. Values within a row followed by different letters are significantly different at the 5% level.
considered as an ideal phenotype for high-yielding rice cultivars. The successful spread of EP cultivars in northern China, however, suggests that unconventional ideas are necessary for breaking the barriers to achieving even higher-yielding rice.

**Insertional mutagenesis by transposable elements**

*Discovery of MITE mobilization through genetic analysis of a mutable slender-glume mutation*

Both induced and spontaneous mutations often arise through the addition of one or more nucleotides into the DNA. The insertion of transposable elements and errors during the replication of repeating elements usually induce mutations. An insertion in the coding region of a gene may cause a shift in the reading frame or alter mRNA splicing; an insertion in a promoter region often represses the expression of a gene. Transposable elements are divided into two groups according to their transposition mechanism and mode of propagation (amplification): retrotransposons (class I elements) transpose via mRNA, whereas DNA transposable elements (class II elements) move by excision and reintegration (Kunze et al. 1997). Active DNA transposable elements are often excised from their original genome site and inserted into another genome site.

With the development of complete genome sequence determination in many eukaryotes, miniature inverted-repeat transposable elements (MITEs) have become noted by many transposon researchers, because they are numerically the most prominent type of transposable element in plants (Feng et al. 2002; Feschotte et al. 2002). For example, sequence analysis of rice chromosome 4 has shown that MITEs account for nearly half of all repetitive DNA sequences (Feng et al. 2002). Their mobilization, however, had not been detected until our discovery in 2003 (Nakazaki et al. 2003). We verified that one of the MITEs, *mPing*, is mobile in the genome of whole rice plants grown under natural conditions, by analyzing the mutability of a slender-glume mutation. At the same time, two other groups demonstrated the mobilization of *mPing* under tissue culture conditions (Jiang et al. 2003; Kikuchi et al. 2003). Because *mPing* has no coding region, the transposase required to catalyze its transposition has to be provided in *trans* (Feschotte et al. 2002; Jiang et al. 2003, 2004). Both *Ping* and *Pong* are now considered to be transposase-encoding elements (autonomous elements) for *mPing* mobilization.

A mutable slender-glume mutant (mutant line IM294) was induced by gamma irradiation of seeds of the *japonica* rice cultivar Gimbozu (Fig. 6) (Teraishi et al. 1999). This mutant character is governed by a recessive mutant allele *slg* (*slender glume*) at the *slg* locus and has not been fixed (made homozygous) in spite of repeated self-propagation (Teraishi et al. 1999). In successive generations, both normal-glume (wild-type) plants and plants chimeric for glume shape occur at a low frequency (ca. 1%) (Fig. 7). Conventional linkage analyses revealed that the *slg* locus was located close to the *rfs* (*rolled fine stripe leaf*) locus on chromosome 7. In a subsequent restriction fragment length polymorphism (RFLP) analysis, the *slg* locus was found to be located between two RFLP loci, XNpb33 and R1440, on chromosome 7 with recombination values of 3.1% and 1.0%, respectively (Teraishi et al. 1999, 2001). Through

![Gimbozu(WT) Normal glume IM294 Slender glume](image)

**Fig. 6.** Glume shapes in the *japonica* cultivar Gimbozu (WT) (left) and the slender-glume mutant line IM294 (right). In addition to its characteristic glume shape, IM294 exhibits abnormal phenotypes such as late heading time and partial seed sterility.
the use of these two RFLP loci as probes, five YAC (yeast artificial chromosome) clones containing one or the other locus were selected from a YAC library. Subsequently, both end fragments of these YAC clones were amplified by the inverse PCR (IPCR) method and used to select new YAC clones more closely linked to the slg locus. After repeating this procedure several times (chromosome walking), we successfully constructed a 6-cM YAC contig, identified four overlapping YAC clones covering the slg locus, and narrowed down the genomic location of slg to a region with a physical distance of less than 280 kb between the right-end fragments of YAC clones Y1774 and Y3356.

To pinpoint the genomic location of slg, we searched for loci in the overlapping region of YAC clones Y1774 and Y3356 and found a single-copy RFLP locus, R430. By carrying out a BLAST search with a partial cDNA sequence, D23858, found in the R430 locus, we identified four cDNA sequences, including AU101270, at the R430 locus. In PCR analyses with the primers designed by sequencing nucleotides 2 to 655 of AU101270, IM294 and Gimbozu both yielded a single PCR product, but the product from IM294 was larger than that from Gimbozu. This suggests that IM294 and Gimbozu have different alleles at the R430 locus. Sequencing analysis of the PCR products showed that the Gimbozu allele contains three introns and an open reading frame (ORF) with the same sequence as AU101270. The deduced amino acid sequence of the Gimbozu allele was not homologous to any plant proteins,
but shared homology (41% identity) with the product of the yeast gene urm1 (ubiquitin-related modifier-1) (Furukawa et al. 2000). We therefore named the R430 locus rice ubiquitin-related modifier-1 (Rurml), and designated the Gimbozu allele as Rurml and the IM294 allele as Rurml-m. We found that the two alleles had the same nucleotide sequence except for a 433-bp insertion sequence in exon 4 in Rurml-m. The insertion sequence included 15-bp terminal inverted repeats (TIRs) and a 3-bp target-site duplication (TSD) of TAA, which suggests that it belongs to the Tourist-like superfamily of MITEs (Bureau and Wessler 1992; Bureau et al. 1996), but its TIR was not homologous to that of any of the known Tourist-like elements (Jurka and Kapitonov 2001). In a BLAST search, we identified 34 sequences with high nucleotide similarity to the insertion sequence in the genome of Nipponbare, a japonica rice cultivar that is closely related to Gimbozu. The TSDs of these sequences formed two groups: one group had the sequence TAA; the other had its complementary sequence TTA. In addition to these similarities in the TSD, 4 of the 34 sequences were identical to the insertion sequence of Rurml-m; 27 differed from it by a single base (T to C) at the same position; and 3 differed from it at more than two bases. Thus, these sequences, including the insertion sequence found in Rurml, constituted a previously unknown family of MITEs, which we called mPing (miniature Ping). Subsequent analyses revealed that excision of mPing from slg results in reversion to a wild-type phenotype, confirming that Rurml-m and slg are the same. Thus, we discovered that mPing excised from the original site (exon 4 of Rurml-m) to another genome site. This was the first discovery that MITEs are mobile in organisms.

Transposable elements with a high copy number comprise the majority of eukaryotic genomes, where they are major contributors to gene and genome evolution (Feschotte 2008; Oki et al. 2008). We found that the Gimbozu (strain EG4) genome has over 1000 mPing elements, whereas the sequenced Nipponbare genome has only 54, and that in a few cultivars, including Gimbozu, the copy number of mPing was increasing by ~40 per plant per generation (Naito et al. 2006). Naito et al. (2009) assessed the impact of mPing insertion on the expression of 710 genes by comparative microarray analysis, and found that the vast majority of transposable element insertions either upregulate or have no detectable effect on gene transcription. The modest impact reflects a surprising deficit of mPing insertions into exons and a preference for insertion into 5'-flanking sequences of genes. In addition, Naito et al. (2009) verified the generation of new regulatory networks by a subset of mPing insertions that render adjacent genes stress inducible. Thus, this study provided evidence for models previously proposed for the involvement of transposable elements and other repetitive sequences in genome restructuring and gene regulation (Britten and Davidson 1971; McClintok 1984).

Use of transposable elements as gene tags

The use of mobile transposable elements as gene tags in whole plants is a powerful tool for functional analysis, because transposable element insertions often inactivate genes. Before the mid-1990s, various kinds of transposable elements had been reported in the rice genome, but their mobility had not been investigated. One of the retrotransposons, Tos17, is the first transposable element whose mobilization was demonstrated in rice. Tos17 becomes active under tissue culture conditions (Hirochik et al. 1996), and has been used to develop a large-scale series of rice mutants in the Japanese MAFF (Ministry of Agriculture, Forestry and Fisheries) Genome Research Project (Hirochik et al. 2001).

Although this mutant series is a useful tool for analyzing gene function, its gene-tagging efficiency is very low (5%–10%), owing to the presence of mutations induced by other factors under tissue culture conditions (Kumar and Hirochik 2001). In addition, tissue culture techniques for indica rice have not been fully developed. Thus, the mobility of the mPing transposon in whole rice plants will provide a useful alternative tool for analyses based on reverse genetics in both the indica and japonica subspecies. A search of the Nipponbare genome identified 54 sequences with high nucleotide similarity to mPing, indicating that
mPing represents a family of transposable elements. The low copy number of mPing will be a great advantage in efficient gene-tagging procedures for detecting newly inserted sequences in the rice genome.

**Use of mPing as a DNA marker system**

QTL analysis is widely performed to isolate agronomically important genes, but it has been difficult to obtain molecular markers that are polymorphic between individuals with similar phenotypes. As described above, we verified that the miniature inverted-repeat transposable element mPing is active in the japonica rice cultivar Gimbozu (strain EG4), which has accumulated more than 1000 copies (Naito et al. 2006). In contrast, most other japonica cultivars, including Nipponbare, have 50 or fewer mPing insertions in the genome (Naito et al. 2006). By using the polymorphism of mPing insertion sites, we generated more than 150 PCR markers (mPing-SCAR [sequence characterized amplified region] markers) in a cross between the closely related Nipponbare and Gimbozu (EG4) (Monden et al. 2009). These new markers were distributed in genic regions throughout the genome and showed significantly higher polymorphism in this cross (150 polymorphic loci/183 marker loci) than the other molecular marker types tested, including simple sequence repeat (SSR) markers (46/661). We have successfully mapped many genes, including a heading-date QTL on the short arm of chromosome 6 and culm-length QTLs on the short arms of chromosomes 3 and 10, by using recombinant inbred lines (RILs) derived from the Nipponbare/Gimbozu cross (Asami et al. 2009; Monden et al. 2009). Unlike other DNA markers used for temperate japonica crosses, the mPing-SCAR markers were highly polymorphic and covered almost the whole genome without any marker clusters. mPing-SCAR markers allow us to easily map candidate loci in a very short time. For genotyping each marker, only 15 min of electrophoresis in 1% agarose gel is required after PCR, which is a simpler and easier procedure than for other molecular marker types, including SSRs, single-nucleotide polymorphisms (SNPs), and RFLPs. It should be emphasized that all characterized japonica cultivars other than Gimbozu have ~50 or fewer mPing copies. By crossing Gimbozu with other japonica cultivars, linkage map construction and QTL analysis can easily be achieved.

**Conclusions**

The future of humankind greatly depends on a sufficient and stable food supply. The most effective way of achieving this is to develop cultivars with superior agronomic characteristics, especially high yield. As described above, a marked increase in grain yield in rice and wheat will probably be difficult if we continue semidwarf crop breeding utilizing existing semidwarfing genes, viz., sd1 and sd9 in rice, and Rht1 and Rht2 in wheat (Gale 1985). Thus, it is very important to exploit other useful genes related to yield and other agronomically important traits. In this report, we show that a great variety of mutations, including novel gene mutations, can be induced by mutagenic treatment. We propose that we should attempt to induce a great number of mutant genes as well as to identify useful genes from existing genetic resources, and that we should collect and stock these mutants at a research institute in charge. We have described the mPing transposon in detail in this report. As discussed here, transposable elements and other repetitive sequences are involved in gene and genome restructuring and in gene regulation (Tomita and Tanisaka 2010). For this reason, the use of transposable elements should be considered in future plant breeding efforts.

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突然変異に食の未来を託す

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Mendelの遺伝法則の再発見（1900）を契機として、遺伝学に基礎を置く科学的育種が始まり、これによってイネやコムギを中心に作物の品種改良は急速な勢いで活発になった。しかし、1990年代に入ると、この伸びは急に鈍化し、食の確保に対する不安が明らかになり、実在のものとなった。近年のイネ、コムギの多収化、半永久性という草型を基本骨格とし、収穫指数を高めることによって実現した。しかし、収穫指数が限界に達したとみられる今日、従来の半永久性遺伝子を利用した育種を行う限り、これ以上の多収は望めないとされている。このため、多収を実現する新規有用遺伝子の開発が世界的な重要課題となっている。これには突然変異の誘発が大きな役割を担うと考えられている。突然変異には、突然突然変異と誘発突然変異があるが、分子あるいは染色体レベルでそれらを特徴づけることはできない。人間は長い間、自然突然変異を利用して作物改良を行ってきた。これらの遺伝資源が利用できつつある今、新たな有用遺伝子の開発を誘発突然変異に求めることは自然のなりゆきであろう。本文発では、まず、農業上利用な遺伝子の大半が地球上から消失することがあっても、放射線や化学変異原、さらにはゲノムの中に存在する転移因子によってそれらとほぼ同じ機能（表現型）をもつ同類対立遺伝子を誘発できることを、台湾の稲作に著しい生産性の向上と安定をもたらした、基本栄養成長期遺伝子座E/F1座の機能喪失型アレル15f1Iと同類対立遺伝子の関係にある誘発突然変異アレルef1-h、およびわが国イネ品種の出穂期の変異に関わるHd7座の劣性アレルより機能喪失度の大きい同定の誘発突然変異アレルef7、さらに、緑の革命のイネ品に寄与した半永久性遺伝子d47の突然変異（同類対立遺伝子d49）およびsd1を例にとって説明する。つまり、突然変異原処理によって新たな有用遺伝子が誘発できることを、日長耐性を完全に消失させ、著しい早生化をもたらす遺伝子se13 を例にとって、また、これまで有用性が認識されていたかった遺伝子のなかにも、視点を変えれば有用遺伝子になる可能性のある遺伝子があることを、中国における固定型ジャボニカ品種の超多収化に貢献する直立傾遺伝子EPを例にとって説明する。また、転移因子のなかでも、その数の多さから遺伝子やゲノムの進化に大きく関わっていると考えられている MITE（miniature inverted repeat transposable elements）のなかで現在、もっとも活発に転移を繰り返しているイネのmPingの発現の経緯とその遺伝学的特徴、さらにその育種上の利用について説明する。
質疑応答

長戸：mPing は銀塩主では非常に増えやすく、日本ではあまりコピー数が増えない。それは要するに、たぶん日本ではトランスポゾンの増殖に関するレギュレーションがかかっていますが、そのメカニズムは何かわかりますか。

谷坂：いま探っている最中です。が、一つの候補として Ping の数があげられます。Ping の数は銀塩主が7個で日本是1つです。Ping は mPing の自律性因子のことです。

長戸：銀塩主と日本はF2を展開してもそうなりますか。

谷坂：F2を展開して、その実験をしております。一応、QTL も出てまいります。QTL が目的のものであれば、トランスポゾンの転移を制御できるのではないかと思っています。

長戸：マーカーとしては使えるのですけど、コピーは毎年かなり増えますか。

谷坂：増えますが、そんなに気にすることはありません。

長戸：マーカーが抜け出してしまうこともあります。

谷坂：抜け出ることはまずありません。増えることはあっても、抜け出ることは理論的にほとんどありません。

草場：mPing がどんどんもすごく飛んでいくとのことでですが、そこで最大どの程度まで飛びうるのかということ、ゲノムサイズに非常に影響する程飛んでいくとすると、進化的に何か役割がありうるのかということもお聞きしたい。

谷坂：この mPing は新しいトランスポゾンだと思っております。今まさに増えている最中で、この100年で50くらいから1000くらいになったと考えています。それは、銀塩主という品種ができたきさつと、その親になった愛国の mPing の数を見ると、だいたい1年で40コピーぐらい増えてきたと推定されます。進化との関係ですが、これは質先生の方が詳しいと思いますが、このMITEというのは進化とかなり関係があると言われています。我々が確認した所、いっぱい飛び出していても、ほとんどの場合修復されます。それでもその配列に戻りますが、修復がうまくいかない場合というのがこれもまた結構あります。その時にいったい最大で5000bpの変化が起こります。ですから進化にかなりかかわっているのだろうと思います。進化に関わっていると考えるトランスポゾン研究者の方が、多いのではないかと思います。
Ecophysiological Characterization of Rice Plants

for Breeding High-Biomass Cultivars

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Introduction

Rice is one of the most important staple foods in the world. Increasing rice yields from the existing arable land to meet the demands of rapidly growing populations presents a major challenge (IRRI 2008; www.irri.org), because the land area available for rice cultivation is unlikely to increase significantly in the future. In Japan, where self-sufficiency in rice was achieved more than 40 years ago, rice is also grown to produce products such as flour and animal feed. More recently, rice has been used in the production of biofuels, further increasing the need to improve yields to reduce production costs.

Since more than 90% of plant dry matter is derived from photosynthesis, crop yield \((Y)\) can be expressed as follows (Ishihara 1996; Hay and Porter 2006):

\[
Y = Q \times l_c \times e \times H \quad (1)
\]

where \(Q\) is the total quantity of incident solar radiation received over the growing period of the crop; \(l_c\), the fraction of \(Q\) that is intercepted by the canopy; \(e\), the overall photosynthetic efficiency of the crop; and \(H\), the harvest index of the crop. On the basis of equation (1), we can construct images of the plant canopy and the individual leaves that compose the canopy, as shown in Table 1 (Gardner et al. 1985). At early growth stages, the rate of leaf growth is proportional to the rate of biomass production. Once the field area is completely covered by leaves, canopy architecture becomes an important factor in light penetration and CO\(_2\) diffusion into the canopy, both of which affect dry matter production. It is considered desirable to have high rates of leaf photosynthesis from the seedling to the ripening stages to maximize biomass production. The harvest index (i.e., the ratio of harvested material to total aboveground biomass) represents the combined effects of numerous processes, including photosynthesis. Modern semi-dwarf rice cultivars generally have very high harvest index values (Evans 1993). However, as harvest indices have approached the theoretical maximum, increases in total biomass production are considered central to increasing rice yield (Mann 1999).

In Japan, brown rice yields increased by approximately 1000 kg ha\(^{-1}\) over the 20 years since the late 1940s, which is equivalent to the rate of increase in rice yield in Asia during the Green Revolution. Since the 1970s, when Japan attained self-sufficiency in rice, the increase in grain yields decreased in response to a shift in the eating habits of Japanese consumers, i.e., the quality of rice for consumption became more important than yield. In the 1970s, several high-yielding rice cultivars were released in Korea to produce rice for human consumption. In the 1980s, similar very-high-yielding cultivars were released in Japan for uses other than human consumption. The yield of these cultivars was approximately 20% to 30% higher than that of the cultivars grown in Japan for eating at that time (Ishihara 1996).

Characteristics of improved cultivars for eating

We compared the yields of several Japanese rice cultivars grown under identical conditions (Fig. 1). The yields of Nipponbare and Koshihikari, which were released about 50 years ago and which are still grown for human consumption, were higher than those of the leading cultivars grown in the Kanto area more than
Table 1 Characteristics affecting increased dry matter production in high-yielding rice cultivars.

<table>
<thead>
<tr>
<th>Growth stage</th>
<th>Characteristics</th>
<th>Corresponding term in eq. (1)</th>
<th>High-yielding cultivars with these characteristics (^1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiller stage</td>
<td>Rapid increase in leaf area.</td>
<td>(l_c)</td>
<td>Nanjing 11 and high-yielding hybrid</td>
</tr>
<tr>
<td>After the panicle formation stage</td>
<td>(1) Canopy structure well suited to light interception. (2) Canopy structure well suited to CO(_2) diffusion into canopy.</td>
<td>(\varepsilon)</td>
<td>(1) Milyang 23 and Takanari (2) Tainung 67</td>
</tr>
<tr>
<td>Late ripening stage</td>
<td>Large leaf area during ripening.</td>
<td>(l_c)</td>
<td>Akenohoshi</td>
</tr>
<tr>
<td>Throughout plant growth</td>
<td>Photosynthesis by canopy leaves. (1) High photosynthetic capacity. (2) High rate of photosynthesis in the afternoon. (3) High rate of photosynthesis during ripening.</td>
<td>(\varepsilon)</td>
<td>(1) Takanari (2) Akenohoshi and Takanari (3) Akenohoshi</td>
</tr>
</tbody>
</table>

\(^1\) Adapted from Ishihara (1996).

100 years ago, but none of these were as high as the yield of Takanari, which was released about 20 years ago. This increase in yield over time shows the results of breeding. In the cultivars used in the experiment, the increase in yield resulted from an increase in dry matter production rather than from an increase in harvest index. Comparing rice cultivars currently grown in Japan with older cultivars, Kumura (1995) noted the following:

1) The extinction coefficient of the canopy, which is an indicator of its light-intercepting characteristics, is smaller in currently grown cultivars than in older cultivars.

2) With nitrogen (N) topdressing, the level of leaf N and the rate of leaf photosynthesis increase significantly more in currently grown cultivars than in older cultivars.

3) Currently grown cultivars have a shorter culm and show higher lodging resistance than older cultivars.

Characteristics of Takanari, one of the most productive cultivars in Japan

Compared with the cultivars currently grown in Japan for eating, the high-yielding cultivars that were released in Korea and Japan since the 1970s had one or more superior characteristics related to canopy photosynthesis (Table 1). The indica cultivar Takanari is considered to be one of the most productive cultivars in Japan, with consistently higher grain yields and dry matter production than any of the new or older commercial japonica cultivars cultivated in the country (Fig. 1). Specifically, Takanari can produce 8–9 t ha\(^{-1}\) grain and 19–21 t ha\(^{-1}\) total dry matter under normal field conditions (San-oh et al. 2004; Taylaran et al. 2009). As shown in Table 1, its superior characteristics for canopy photosynthesis are considered to be the canopy structure that affects light interception (Xu et al. 1997; Taylaran et al. 2009; Soda et al. 2010a), leaf photosynthetic capacity (Xu et al. 1997; Ohsumi et al. 2008, Hirasawa et al. 2010), and the rate of leaf photosynthesis at midday and in the afternoon (Xu et al. 1997). Compared
with other high-yielding cultivars, Takanari has many superior characteristics related to canopy photosynthesis, which may explain why it can produce more dry matter than many other high-yielding cultivars (Ishihara 1996).

The superiority of Takanari in dry matter production is most apparent after heading, when approximately 70% of the final carbohydrates in the rice grain are derived from photosynthate. The greater dry matter production after heading would also increase the harvest index of Takanari compared with the *japonica* cultivars that have been examined to date. It has been suggested that the higher rates of canopy photosynthesis observed from heading through ripening in Takanari can be attributed to the enhanced light-intercepting characteristics of the canopy (Xu et al. 1997; Taylaran et al. 2009) and the higher rate of photosynthesis of individual leaves in the canopy (Xu et al. 1997; Ohsumi et al. 2008; Hirasawa et al. 2010).

**Reasons for the higher rate of leaf photosynthesis in Takanari**

The higher rate of leaf photosynthesis in Takanari can generally be attributed to its higher levels of leaf N and larger leaf stomatal conductance (Hirasawa et al. 2010). Possible reasons for these features have been investigated in detail by comparing them (at plant stages between the tillering and ripening stages) with those of Koshihikari (Taylaran et al. 2011).

**1) Dry matter and N accumulation, N partitioning to leaves, and levels of leaf N**

The superiority of Takanari over Koshihikari in terms of total dry matter production is evident at the panicle-formation stage (II) and persists through to the ripening stage (V) (Fig. 2A). No significant difference between the cultivars in shoot dry weight was apparent before the heading stage (Fig. 2B), but the dry weight of Takanari roots was significantly greater than that of Koshihikari from the panicle-formation stage through the ripening stage (Fig. 2C).

Both cultivars accumulated N rapidly before heading and then more slowly during ripening (Fig.

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**Fig. 1.** Comparisons of (A) total dry weight of above-ground plant parts at harvest, (B) grain yield, and (C) harvest index of cultivars from different eras grown in a paddy field (adapted from Taylaran et al. 2009). Data are averages of three years (2002, 2005, and 2006); error bars indicate standard deviations. T: Takanari, a high-yielding *indica* rice cultivar released in 1990. NK: Average values for Nipponbare and Koshihikari, *japonica* cultivars currently grown in Japan for eating that were released in 1963 and 1956, respectively. AS: Average values for Aikoku and Sekitori, *japonica* cultivars released in 1882 and 1848, respectively. The number above each bar represents the value for that trait relative to that of NK, which was set at 100.
Fig. 2. Changes in (A) total dry weight, (B) shoot dry weight, (C) root dry weight, (D) total N accumulation, (E) N partitioning to the leaves, and (F) leaf N content in Takanari (■) and Koshiihikari (□) grown in 12-L pots (adapted from Taylaran et al. 2011). Growth stages: I, tillering (3 weeks after transplanting); II, panicle formation (7 weeks after transplanting); III, heading; IV, 2.5 weeks after heading; and V, 4.5 weeks after heading. Koshiihikari and Takanari headed on 14 and 21 August, respectively. Error bars represent the standard deviation (n = 5). * *, ** and *** indicate statistical significance at the 5%, 1% and 0.1% levels, respectively.

2D). Takanari accumulated more N than Koshiihikari from the panicle-formation stage onward, and this amount remained higher through the ripening stage. The relative partitioning of N to leaves was somewhat lower in Takanari than in Koshiihikari after heading (stage III and later; Fig. 2E). No significant difference in leaf N content was apparent at the tillering and panicle-formation stages (Fig. 2F). The leaf N content of Takanari was significantly higher than that of Koshiihikari after heading. Taken together, these results indicate that the higher level of leaf N in Takanari may result from its ability to accumulate N more efficiently than Koshiihikari.

2) Rates of leaf photosynthesis

Although there was no observable difference between the cultivars in the rate of leaf photosynthesis at the tillering stage, the rate in Takanari was higher than that in Koshiihikari from the panicle-formation stage to the ripening stage (Fig. 3A). Rates of leaf photosynthesis at an ambient CO₂ concentration of 370 μmol mol⁻¹ were closely correlated with leaf N content in each cultivar at the tillering and full-heading stages (Fig. 3B, C). At the tillering stage, there was no varietal difference in the relationship between the rate of photosynthesis and leaf N content (Fig. 3B). However, the rate of leaf photosynthesis at the heading (Fig. 3C) and ripening stages (Taylaran et al. 2011) was higher in Takanari than in Koshiihikari at all leaf N levels examined. The stomatal conductance at ambient CO₂ concentration was also greater in Takanari than in Koshiihikari at heading (Fig. 4A) and ripening
Fig. 3. Changes in (A) the rate of leaf photosynthesis and (B, C) relationships between leaf N content and rate of photosynthesis at (B) tillering and (C) full heading of the uppermost fully expanded leaf in Takanari (■, •) and Koshihikari (□, ◦) grown in 12-L pots (adapted from Taylaran et al. 2011). Rates of photosynthesis were measured at an ambient CO₂ concentration of 370 μmol mol⁻¹. Vertical and horizontal bars represent the standard deviations for rate of photosynthesis and leaf N content, respectively (n = 5). Definitions for stages I–V are the same as those in Fig. 2. ** and *** indicate statistical significance at the 1% and 0.1% levels, respectively. (Taylaran et al. 2011). In both cultivars, the relationships between the rate of photosynthesis and leaf N content at an intercellular CO₂ concentration of 280 ± 2 μmol mol⁻¹ were very similar at the heading stage (Fig. 4B) and at the ripening stage (Taylaran et al. 2011), implying that leaf photosynthetic activity was very similar when leaf N contents were identical in the two cultivars. The levels of leaf rubisco were also very similar in the two cultivars (Taylaran et al. 2011). Thus, the higher rates of photosynthesis in Takanari after heading may have been due to increased stomatal conductance and higher leaf N content.

Fig. 4. Relationship between leaf N content and (A) stomatal conductance at an ambient CO₂ concentration of 370 μmol mol⁻¹ or (B) rate of flag leaf photosynthesis at an intercellular CO₂ concentration of 280 ± 2 μmol mol⁻¹ at heading in Takanari (●) and Koshihikari (○) grown in 12-L pots (Taylaran et al. 2011). Measurements were taken once the panicle of a main stem emerged completely. Vertical and horizontal bars represent the standard deviations for rate of photosynthesis and leaf N content, respectively (n = 5). r₁ and r₂ are correlation coefficients for Takanari and Koshihikari, respectively. *** indicates significance at the 0.1% level.
Fig. 5. Changes in rates of photosynthesis after leaf excision in Takanari (●) and Koshikihari (○) grown in 3-L pots at (A) tillering and (B) heading (adapted from Taylaran et al. 2011). Each leaf was excised at the base of the leaf blade after leaf gas exchange had reached a steady state. The ambient CO₂ concentration and leaf–air vapor pressure difference before leaf excision were 370 µmol mol⁻¹ and ~1.5 kPa, respectively, but were not controlled after leaf excision. Measurements at heading were taken when a panicle of the main stem emerged completely. Inserted tables show leaf water potential (Ψ) and leaf N content (N) of Takanari (Tak) and Koshikihari (Kosh). * and *** indicate statistical significance at the 5% and 0.1% levels, respectively. ns, no significant difference.

(3) Leaf water potential and root water uptake capacity

At the full-heading stage, the water potential (Ψ) of the flag leaf in Koshikihari decreased significantly compared with that in Takanari despite the fact that plants of both cultivars were growing under submerged conditions and the difference in leaf–air vapor pressure was as low as 1.5 kPa. After excision of a leaf at its base and release of the hydrostationary pressure in the xylem, which was done after leaf gas exchange had reached a steady state, the rate of photosynthesis in Koshikihari increased within a few minutes to that in Takanari (a phenomenon known as the Ivanov effect; Slavik 1974), while there was little increase in Takanari itself (Fig. 5B). At the full-heading stage, the root surface area in Takanari was approximately twice that in Koshikihari (Taylaran et al. 2011). The hydraulic conductance from roots to leaves (Cₚₘ) was far higher in Takanari than in Koshikihari (Taylaran et al. 2011), but there was no difference in hydraulic conductivity (Ｚₖ) between the two cultivars. Taylaran et al. (2011) suggested that the larger root area might be responsible for the higher hydraulic conductance of Takanari.

In contrast, at the tillering stage, no differences were observed in leaf water potential between Koshikihari and Takanari, and no clear increases in the rate of leaf photosynthesis after the leaf excision were observed in either cultivar (Fig. 5A). The difference in Cₚₘ was small between Koshikihari and Takanari at the tillering stage and there was also no difference in root surface area between the cultivars (Taylaran et al. 2011).

In conclusion, the higher rate of photosynthesis in Takanari appeared to result from both the greater leaf N content and the greater stomatal conductance than those in Koshikihari, even under the same level of N application and even at the same level of leaf N, respectively. The increased N uptake and hydraulic conductance might be caused by the larger root surface area, which might contribute to the higher rate of leaf photosynthesis in Takanari. The larger root surface area of Takanari might be a target trait in future rice breeding for increasing dry matter production through the improvement of leaf photosynthetic rate.
Further increasing biomass production in Takanari

Increasing parameters $I_e$ and $c$ in equation (1) may be key to increasing biomass production. Takanari is not superior to other high-yielding cultivars in all of the characteristics listed in Table 1. Consequently, if it were possible to improve others of these characteristics in Takanari, its biomass production might be increased further.

(1) Light-intercepting characteristics of the canopy

Compared with the Japanese cultivars cultivated for human consumption, Takanari and the high-yielding * japonica × indica* hybrid cultivar, Milyang 23 both have erect leaves and small canopy extinction coefficients at the heading stage. However, because of Takanari’s large, downward-pointing panicles, its canopy extinction coefficient during the ripening stage was larger than that of Milyang 23 (Soda et al. 2010a).

(2) Rate of photosynthesis in fully expanded young leaves

When measured under light-saturating and unstressed conditions, the rate of photosynthesis in young expanded rice leaves shows varietal differences. For example, the rate of photosynthesis can range from approximately 20 to 30 $\mu$mol m$^{-2}$ s$^{-1}$ at an ambient CO$_2$ concentration of 370 to 400 $\mu$mol mol$^{-1}$ (Kanemura et al. 2007; Hirasaawa et al. 2010; Jahn et al. 2011). The highest recorded rate of leaf photosynthesis in rice, approximately 30 to 33 $\mu$mol m$^{-2}$ s$^{-1}$, was observed in Takanari (Hirasaawa et al. 2010; Taylaran et al. 2011). Conversely, Koshihikari, which is the most popular rice cultivar in Japan, has a relatively low photosynthetic rate of 25 to 28 $\mu$mol m$^{-2}$ s$^{-1}$. Among backcross inbred lines (BILs) derived from a cross between Takanari and Koshihikari (Koshihikari/Takanari//Takanari), we identified lines with leaf photosynthesis values that were approximately 20% higher than that observed in Takanari (Adachi et al. 2013). These lines had mesophyll cells with large surface areas and unprecedented rates of leaf photosynthesis, which were achieved by greater diffusion of CO$_2$ from intercellular air spaces to chloroplasts, combined with increased diffusion of atmospheric CO$_2$ into these intercellular spaces through high levels of stomatal conductance (Adachi et al. 2013).

(3) Reduced rates of leaf photosynthesis associated with senescence

Compared with Nipponbare, the high-yielding cultivar Akenohoshi maintains high rates of leaf photosynthesis during ripening; however, Takanari does not. If we could lessen the reduction in the rate of leaf photosynthesis during senescence at the ripening stage in Takanari, it might produce more dry matter and higher grain yield.

(4) Lodging resistance and CO$_2$ diffusion into the canopy

As aboveground biomass increases, so does the bending moment. Increasing the bending moment of the basal internode at breaking is considered to be important for lodging resistance in transplanted rice. This value is significantly larger in the high-biomass-producing cultivar Leaf Star than in Takanari, owing to the larger section modulus in Leaf Star (Ookawa et al. 2010a).

Since Takanari is shorter than Leaf Star, the canopy leaf area density of Takanari is greater, which has the effect of decreasing CO$_2$ diffusion into the canopy (Ookawa et al. 2010a). If the culm of Takanari could be made longer and stronger, then Takanari might produce greater dry matter and support more aboveground biomass (Kuroda et al. 1989).

Genetic analysis of the traits responsible for biomass production: Concluding remarks

If the characteristics affecting biomass production listed in Table 1 could be improved, then, in addition to increasing biomass production in commercial cultivars that are currently grown for eating, we could increase biomass production in Takanari and other high-yielding cultivars. The greatest concern is how to improve these
characteristics effectively, because they are assumed to be quantitative traits. Since selection by eye would not be possible for characteristics such as increased culm breaking strength or increased rate of leaf photosynthesis, a marker-assisted approach would likely be one of the most effective approaches for improving these traits. Indeed, the current identification of numerous important quantitative traits would be useful in this effort (Yamamoto et al. 2009). In this regard, several assessments of quantitative trait loci (QTL) for the inclination angles of leaf blades, rate of photosynthesis, and culm-breaking strength have been undertaken to date.

(1) Inclination angle of leaf blade

By using BILs derived from Koshihikari and Takanari (Koshihikari/Takanari//Takanari and Koshihikari/Takanari//Koshihikari), Soda et al. (2010b) found that at least two genetic regions on chromosomes 1 and 4 were responsible for increasing the inclination angle of leaf blades.

(2) Rate of leaf photosynthesis

The analysis of chromosome segment substitution lines (CSSLs) derived from crosses of cultivars Sasanishiki and Habataki showed that four genetic regions on chromosomes 4, 5, 8, and 11 were responsible for increasing the rate of leaf photosynthesis (Adachi et al. 2011b). In progeny populations and selected lines derived from a cross between Koshihikari and Habataki, genomic regions responsible for the rate of photosynthesis were identified in regions of 2.1 Mb on the long arm of chromosome 4, 1.2 Mb on the short arm of chromosome 8, and 0.12 Mb on the long arm of chromosome 11 (Adachi et al. 2011a; Kanno et al. 2011). For each QTL, the chromosome region contributed by Habataki was associated with an increase in leaf N content or hydraulic conductance; specifically, the Habataki regions increased leaf N content as well as root hydraulic conductance (chromosome 4), root hydraulic conductivity (chromosome 8), and leaf N content (chromosome 11).

The rate of leaf photosynthesis was further improved by combining the two QTLs on chromosomes 4 and 8. In addition, Koshihikari alleles on chromosomes 1 and 7 increased the rate of photosynthesis significantly in plants with a Takanari genetic background (Nakae et al. 2011).

(3) Lodging resistance

An effective QTL for culm strength, designated SCM2, was identified by using CSSLs. Positional cloning revealed that SCM2 was identical to APO1 (ABERRANT PANICLE ORGANIZATION) (Ikeda et al. 2007; Ookawa et al. 2010b). A near-isogenic line carrying SCM2 showed enhanced culm strength and increased spikelet number, considered to be a pleiotropic effect of the gene.

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高いバイオマス生産をあげるイネの生態生理

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作物の乾物重の90％以上は光合成産物によって構成されるので、収量（Y）は概念的には次式で表わされる。

\[ Y = Q \cdot Ic \times \epsilon \times H \]  (1)

ここで、Qは作物全生産期中に入射する太陽光エネルギー、Icは入射した太陽放射に対する作物個体群が受ける割合、\( \epsilon \)は個体群が受ける太陽放射の乾物への変換効率、Hは収穫指数である。Qには栽培地の気象条件や作物の早晩性などが関与する。これに基づいて、これまでイネの収量、バイオマス生産量の増加を支えてきた形質を整理し、バイオマス生産量の一層の増加に向けて今後の研究の展開方向とその可能性を考える。

1. わが国で現在栽培されている水稲品種の性質

わが国で食（飯）用に現在栽培されている水稲品種（「現在品種」）は、これらより以前に育成された古い品種（「旧品種」）と比較して、収量が高い。その理由に、(1)受光効率を表す個体群吸光係数が「現在品種」では葉身がより直立することによって「旧品種」に比較して小さいこと、(2)「現在品種」は「旧品種」に比較して、追肥によって葉身の窒素含量が高まり、光合成速度が高くなり、これが穂ばらみ期以降のバイオマス生産量を高め、収量と収穫指数を高めること、(3)「現在品種」は「旧品種」に比較して、稈長が短いことによって倒伏抵抗性が高いこと、があげられる。

2. インド型多収性品種タカナリの特徴

多用途利用の目的などで近年育成された多収性品種（「多収性品種」）は、「現在品種」と比較して収量あるいはバイオマス生産量が20〜30％、あるいはそれ以上に高い。それぞれの「多収性品種」はいずれも、個体群光合成速度を高めることに関わる優れた性質をもつ。現在最もバイオマス生産量、収量の高い品種の一つであるタカナリは「現在品種」と比較すると、出穗期以降の個体群受光態度が良く、個体光合成速度が高い。

3. バイオマス生産量の更なる向上の可能性

個体群受光態度、個体群内へのCO₂の拡散、個体葉光合成速度、倒伏抵抗性などに関して、タカナリに勝る優れた性質が他の「多収性品種」や系統に見出されている。このことは、タカナリを上回るバイオマス生産量をあげるイネを育成できる可能性を示すものである。

4. バイオマス生産に関わる形質の遺伝解析と今後の展望

バイオマス生産に関わる形質の遺伝子座、遺伝子を同定していくことによって、「現在品種」、「多収性品種」のバイオマス生産量、収量を効率的に大きく向上させることが可能となるものと考える。(1)個葉光合成速度では、第4、5、8、11染色体に光合成速度を高めるQTLが存在し、これらは、根量を増し窒素蓄積量と根の水伝導度を高める（第4染色体）、根の表面積当たりの水伝導度を高める（第8染色体）、窒素蓄積量を高める（第11染色体）作用を有すること、(2) 倒伏抵抗性に関しては、稈の断面係数を高めるQTLが第1、6染色体に存在し、後者の原因遺伝子はAPO1であること、が最近明らかにされている。
質疑応答

堤：タカカリのバイオマスが大きいというのは、窒素含量とホモテンシャルの両方という話でよろしいでしょうか。

平沢：これまでの検討に基づきますと、タカカリのバイオマスがわが国の多くの食用品種に比較して大きいのは、受光態勢が良好ことと個葉の光合成速度が高いことによくあります。光合成から見ますと、葉の窒素含量が植物体全体の窒素吸収窒素量が多いことによって高くなり、そしてこのことによって葉内の光合成活性が高くなることが一つの理由で、もう一つは、根の吸水能力が大きく気孔が開くことによることになります。根の量の違いがまず最初に現れ、その後窒素吸収量と気孔伝導度に違いが出てくることからすると、おそらく、根の量が多くなって窒素吸収量と吸水能力高くなり、その結果、光合成に効いているのではないかと考えております。

堤：そうすると根の張り方で、水吸収も高まり気孔の気孔伝導も高まって、窒素含量が高まり、個葉の光合成能力が高くなるということですね。

平沢：はい、そのように考えております。

松原：先程の谷坂先生のお話にありましたように、出穂期がバイオマスには深く関わっていると思像でできますが、こうした研究の中では、そこはどのように制御されるとお考えになって進めて来られてますでしょうか。

平沢：圃場で解析的な仕事ををする上で、出穂期が遅しまうと、いろいろな要因が入ってくる中で大変になりくくなります。そこで、今日ご紹介した気温を新しい品種まででの比較において、できるだけ出穂期のそろっている品種を選定して行いました。出穂期が変わるとどういうことになるかというのももちろん重要なテーマだと思います。が、ままず同じ生育期間で比べてみることが、いろいろな特性を解明するのに都合が良いと思っております。

田中：作物研究でイネの育種をやっております。根量が全然違うという話が非常に興味深く何かわざわざ聞かせていただきました。我々育種家をやっている中で実際に根量が正確にしかも（なかなか難しいでしょうけど）簡単に計れると、選抜に非常に役に立ったのですから、実際どのように計られているのかというところ、簡単な計測法というのはあるのか、あるいは考えられるのか、それについて先生のお考えをお聞きしたいと思います。

平沢：圃場条件で根の分を正確に把握するのはなかなか大変で、いろいろな方法で推定されています。我々がタカカリと他の品種の根の量を比べる時には、筒状に土壌（コア）を数多く採取し、その中に含まれる根の量を測定し、根系の発達程度を推定しております。しかし、実際に根の機能を見ようとする時には、根の量だけではなくて根の量あたりの機能というのも重要になってきますが、圃場では根を全量取り出すのは大変難しいです。そこで割り切って、ポット栽培で根の全量を把握し、併せてその機能を計ることによって根の量のいか質なのかということを検討するようにしています。

谷坂：バイオマス生産を上げていくために幾つかの要因があげられていると思うのです、それぞれの寄与率、どの程度の割合で1個1個がいていくかが、ある意味では育種の方法にすごく大事な情報になると思うのですが、もし整理されておられましたら教えていただきたいと思います。

平沢：大変重要ですが、なかなか難しいです。現在、圃場でそれぞれがどれだけ効くかという推定は難しいと思います。しかし、これからはいろいろなNITが作られていくと思いますので、これを使っって量的な評価ができるものと考えております。先程少しご紹介しましたが、第12染色体の光合成に関わる領域（まだ幅は広いですが）を導入した時に、1個1個50％とか乾物生産が増えておりますので、光合成の増える増える乾物生産の増加というのではなく関係にあるのではないかと思っております。

谷坂：タカカリとコシヒカリの後代を使わせて遺伝分析されていますが、タカカリはインディカでコシヒカリはジャパンヒカリであり、かなりバックグランドが違います。したがって、収量性に関わるような遺伝要因を見つけるのは難しいようにも思えます。むしろインディカはインディカと交配する（ジャパンヒカリ同士はマーカーがないから難しいかもしれないですが）、タカカリとの交配には例えばIR24とかIR36を使われた方がすんなりとした結果が出てくるように思えるのですが、されていますか。

平沢：まだいません。コシヒカリの染色体断片をタカカリに入れると光合成速度の著しく高い系統が
出ってきたので、それぞれの組み合わせについて、まずは材料を徹底的に解析していくことが大切と考えております。役に立つ品種が育成できるか否かについて、最終的にどのようになるかはよくわかりません。いただいたご意見は今後参考にさせていただきたいと思います。
Breeding of High-Yielding Rice Cultivars in Japan

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Introduction

The yield ability of each major crop is considered to be an index of the level of development of agriculture in a country. In Japan, the average yield of brown rice, which had been 1.78 t/ha in 1883, reached 5.32 t/ha in 2005 through improvements in both cultivars and cultivation technology. This increase means that the accumulation of long-term studies is necessary to improve yield ability.

Breeding of rice cultivars with high yielding ability in Japan

High yield is the most important breeding objective in crop research, but it is difficult to improve yield dramatically without using various genetic resources. The introgression of yield-related characteristics of indica cultivars, such as total grain number and grain filling ability, is expected to improve the yield potential of domestic rice cultivars (KATO 2008). However, tropical indica cultivars tend to have insufficient tolerance to cold temperature and blast. The combination of the high yield potential of indica cultivars and the yield stability of domestic japonica cultivars is a basic strategy by which to establish high-yielding, stable cultivars suitable for cultivation in Japan.

Established rice cultivars with high yielding ability

1. Rice cultivars with high grain yields

We carried out several research projects to develop high-yielding cultivars suitable for utilization as animal feed or processing materials (SAKAI et al. 2003). By 2009, we had released a series of high-yielding cultivars adapted for each part of the country.

Brown rice yields of more than 8 t/ha have been achieved by several high-yielding cultivars such as ‘Takanari’ (IMBE et al. 2004), ‘Hokuriku 193’ (GOTO et al. 2009), and ‘Momiroman’ (HIRABAYASHI et al. 2010). The yields of these cultivars are up to 38% higher than those of ordinary cultivars. Their eating quality is moderate compared with that of more widely grown cultivars; however, their superior yielding ability is expected to expand the utilization of rice or other purposes. The high yielding ability of these cultivars is based on their large panicle, solid culm, and superior grain-filling ability. For example, the average brown rice yield of early-maturing ‘Bekoaoba’, which is suitable for the Toboku area, was 9.2 t/ha in performance tests from 2001 to 2008 in Akita prefecture. In addition, ‘Hokuriku 193’, which had been utilized for bioethanol production, had brown rice yields of 7 to 9 t/ha in three years of performance tests in farmers’ fields in Niigata prefecture (Fig. 1). However, cultivars derived from indica cultivars tend to be susceptible to cold and blast. The improvement of these shortcomings is needed to stabilize the yields of high-yielding rice cultivars.

Fig. 1. ‘Hokuriku 193’

2. Rice cultivars with high whole-plant yields

For whole-crop silage use, the entire aerial part of the plant (consisting of grains, leaves, and stems) is harvested at the yellow-ripe stage. The total digestible nutrient (TDN) yields of high-yielding rice cultivars are around 1.2 t/ha, which are 3% to 27% higher than those of ordinary cultivars, and similar to those of forage maize. There are two types of rice cultivars with high...
whole-plant yield: grain-type and leafy-type. The grain-type cultivars have a high proportion of grain that contributes to high whole-plant yield: examples include ‘Hoshiaoba’ and ‘Yumeaoba’. The leafy-type cultivars have a high proportion of leaves and stems: examples include ‘Takisuzuka’ and ‘Leaf Star’. The leafy-type cultivars are also expected to serve as unique materials for cellulose production because of their high content of nonstructural carbohydrate in the stem and leaf sheath.

**Established high-yielding rice cultivars**

1. ‘Momiroman’, a cultivar with high grain yield

   ‘Saikai 203’ (‘Mizuhochikara’) is a cultivar with large panicles that has the potential to produce a large number of grains; however, its grain filling is insufficient to produce superior grain yield. ‘Momiroman’ was selected to improve the grain filling of ‘Saikai 203’ by the introduction of New Plant Type. The high yield of ‘Momiroman’ was confirmed in multi-location performance tests, and this cultivar has been released for use as feed rice and for the production of flour for rice noodles.

   ‘Momiroman’ has a superior growth volume and a solid culm (Fig. 2). However, its grain filling is still too low under low levels of solar radiation; thus, future improvement is needed to stabilize the yield of ‘Momiroman’ (HIRABAYASHI et al. 2010).

2. ‘Leaf Star’, a cultivar with high whole-plant yield

   ‘Leaf Star’ shows superior leaf and stem growth, but its grain yield is less than that of ordinary cultivars. Its parental cultivar ‘Chugoku 117’ was selected from a cross of a US cultivar with a strong stem and a Taiwanese cultivar with superior plant growth characteristics. ‘Leaf Star’ has shorter panicles and lower grain yield than ordinary cultivars. However, its whole-crop yield and TDN yield of the aerial parts are higher than those of ordinary cultivars. It is grown for high-quality whole-crop silage (KATO et al. 2010).

**Future research strategies for high yield**

Future improvement of yield will require both increases in plant grain number and improvement of grain-filling ability. In order to improve grain filling, new yield-related characteristics should be considered for study (for example, elongation of the ripening period) to complement basic studies of photosynthesis and translocation of photosynthate. One problem that must be urgently addressed is stabilization of blast resistance. Many high-yielding cultivars have inherited true resistance to blast, along with their high yielding ability, from indica cultivars. The risk of resistance breakdown is increasing because the cultivation areas of these cultivars are expanding. Thus, high-yielding cultivars with stable field resistance to blast should be developed as soon as possible.

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稲の多収性育種の現状と戦略

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育成された多収水稲品種

1）玄米多収品種

農研機構では飼料用や加工用に向けて米飯食味や玄米外観品質は劣るが、700〜1000kg/10aの高い収量性を示す多収性品種の開発を進め、2009年までにほぼ全国の稲作地域で栽培可能な多収性品種シリーズを育成した。こうした品種は陸重型の草型をもち、大きな穗を支える強い稈と、優れた登熟力により高い収量性を実現している。なかでも東北地方向けの「べこしごや」は2001年から90年に秋田県大仙市で行った極多肥栽培で、平均して920kg/10aの高い玄米重を示した。また、新潟県でのバイオエタノール原料稲栽培実証事業で利用されている「北陸193号」は新潟県三条市における3ヵ年の現地実証試験で700〜900kg/10aの粗玄米重を示した。しかし、インド型品種の多収性を導入した多収性品種は耐冷性や病害抵抗性が劣る傾向があり、今後のさらなる改良が必要である。

2）茎葉多収品種

茎葉と穂を一緒に収穫し、稲発酵粗飼料として家畜に供与するために、株全体の収量が高品質が開発されている。全重が多収の品種には「べこしごや」、「夢あおば」のように子実の割合が多い品種と、「たかすがや」、「リープスター」のように子実よりも茎葉の生育が全重多収に貢献している品種がある。茎葉が多収の品種は「茎葉型」と呼ばれ、成熟期に通常の品種ではコメに価値が付かない炭水化物が稲などにも多く蓄積し、消化性の良い稲発酵粗飼料の原料となる。

今後の多収戦略

さらに収量性を向上させるためには、穂数と増熟力の向上が求められる。一穂粒数の増加は耐倒伏性を維持するために稈質の強化も不可欠となり、玄米の収量増加に直結しない可能性が考えられる。そのため、穂数の増加に対する単位面積当たり穂数の増加を考慮する必要がある。さらに、増熟力を向上させるためには、光合成能力などの基礎的な研究に加えて、登熟期間の延長などの新しい収量形質の導入なども検討される必要がある。
質疑応答

谷坂：農業全体を見ると肥料のやりすぎが非常に大きな問題になっていると思います。イネは栽培面積が大きいですから少食化が求められていると思います。品種改良において少食化と多収化の狭間というのは非常に難しい所がありますが、どのようにお考えでしょうか。

根本：近年、化学肥料の価格が上がり気味で、沢山入れて沢山穀穂というのはちょっと無理がでてくるところもあります。こういった意味で私たちは、一方でこのような多収データを積み重ねることも一つの柱としていますが、他方で、ロインプットで（あまり肥料は入れないで）そこでの収穫を競うという研究も進めています。特に北海道のこの課題をいろいろ試してもらっております。

神田：多収米や飼料米を生産するにあたって低コスト栽培というのはキーワードとなっている。それにあたって直種栽培等が全国的に求められていると思うのですが、多収イネの育種にあたっての直種適性のよう部材への取り組み等があったら教えていただきたいと思います。

根本：このような多収品種では直種栽培が前提だと思っています。多収性系統の選抜では、移植栽培が加えて直種栽培での収量性を同じように評価しています。両方とも高くなれば開品種として出すのは踏襲しなければならないと思います。例えば、すでに品種になった多収品種のタカナリや新潟県で作っているバイオオーガニック用品種の北陸193号は実は直種にはあまりよくありません。休眠性が強くすぎて、苗立ちが悪いのが欠点です。これから出す品種につきましては、そういった苗立ち性の問題もなく高いレベルでの直種栽培適性を持つのが前提条件となると考えております。

谷坂：先程の平沢先生のお話で、幾つかのバイオマスを大きくする要因があったと思うのですが、それらはどの程度視野に入れて品種改良されていますか。

根本：バイオマスに関しては実際に研究を担当している作物研究所の加藤浩さんのご意見をうかがえればと思います。

加藤：（バイオマスを大きくする要因）全部ではないのですが、少なくとも葉の角度については仕方なく出てしまっております、ほとんどの立ったものを使っています。葉面積密度については、（株を）高くした方がエアレーションが良くなるので、茎葉多収型については、（株を高くする形質）だいぶ導入してきました。ただし、玄米で多収を穂らすという場合は、穂を大きくして背を高くするとモーメントが非常にかかすぎるので、少し難しい所があると思います。

北野：現在作られている反収が1トンを越えるような飼料イネなどの育成に関して、インディカやニューブランドタイプなどの品種限られた遺伝資源をもとにして、ある意味でかなり育種的に多収に係わる形質の集積されたようなものを母本にして日本稲に交配して新しいものを作ってきていると思います。そのように考えると、1トンの壁を既に越えてお次のステージに行こうとした時に、やはり遺伝資源が問題となってくると思うのです。先程最後の方のスライドにあったパケモノのようなイネも遺伝資源として使えるかどうか、次の世代の多収が可能かどうかということについて少しお考えがあれば紹介していただきたいと思います。

根本：今飼料用多収性品種をご紹介ができる理由は、今から30年前に韓国などから日印交雑の材料を大幅に導入して種改良をスタートしたもので、今になって実際に普及できる品種として育成出来てきたということです。30年かかったといえます。その意味で今後とも将来の育種のために遺伝資源を活かすという活動は続けていかなければならないと思います。例えば、野生稲などを使った染色体断片置換系統のセットなどもできていますので、そういったものから新しい収量性形質のようなものを期待しています。
総合討論

座長　西尾　剛（東北大学）

西尾：本日は5名の先生方にバイオマスに関してお話をお伺いしました。テーマは「突然変異はバイオマスを増大できるか」ということで突然変異とバイオマス生産という関連づけたことで議論を進められればと思いますが、まずはご講演後質問ができないかという方々がございましたら個別にご質問をいただければと思います。

草場：佐塚先生にお聞きしたいのですが、イネのゲノムのいろいろな知識がソルガムに利用できるということですが、ソルガムは非常に大きく、多分栽培なども非常に大変だと思うのですが、イネの知識を逆遺伝学的にどうやっていこうというようなアプローチを考えられているのか、もし行っているということであればどのように進んでいるのか、主にミュータントについて教えていただきたい。

佐塚：ソルガムを含めてイネ以外の作物でも幾つかあると思うのですけれども、その問題点の1つは形質転換です。イネは私たちは研究室でもルーチンで毎週形質転換をやっているのですが、ソルガムの形質転換は非常に難しく、組換え体を使ってというような発想に今のところなかなかならない状況です。一方で従来のやり方、例えばミュータントを沢山作っておいて、それをTILLINGのような方法で特定の遺伝子のアリルをとっていくような手法は充分に考えられます。それについては今実際にそこで踏み込んでやってはいっていませんが、だんだんとやれるような状況、リソースの蓄積はでてきております。

西尾：他にご質問が特にございませんでしたら議論に入れていきたいと思います。最初、谷坂先生は突然変異の形質、主に関核の早晩性に係わる遺伝子に関するお話が多かったと思います。平沢先生と谷坂先生は同じイネですが、バイオマス生産に及ぼす草種の問題とか、実際の多収性のイネの育種についてご講演いただきました。お三方はともイネの内容ですが、谷坂先生は突然変異の方面からお話をいただきましたが、平沢先生、根本先生はむしろ形質特性あるいは遺伝資源の利用というような観点でお話いただだと思われますので、突然変異という観点から少しお話いただければと思いますがいかがでしょうか。

根本：実際の品種育成を行っている立場で、突然変異育種をどのように利用していくかという点ですが、突然変異を使っていきなり多収性的品種を作り出そうとするのはなかなか簡単ではないと思っております。私たちの方で突然変異を利用するのは、まず最初の素材開発としてです。何か特徴的な素材を突然変異で誘導し、それを育種のパートとして利用するのが一般的です。その次に、マイナーな形質の改良では実際にかなり使われています。例えば、インド種品種の多収性を日本品種に入れた場合どうしても穀の脱粒性が残ってしまう場合があります。たとえば多収のタカカリや北陸193号は結構脱粒性で、そこで突然変異を使って脱粒性を改良するという育種はかなり行われ、品種でもできています。

平沢：私の専門分野は作物学ですので、いまのようなご質問に正答できるかどうかわかりませんが、バイオマス生産に関しては少なくて先程私が紹介したような範囲に形質を分けて整理できるということになります。そういった形質に関連した突然変異がどのようにできてくるのかということが、多収と直接結びつく、あるいは結びつくためには一番重要ではないかというふうに考えております。このことから、むしろ私の方から育種、イネの育種をやっている方々にお聞きしたいのは、突然変異でそういった形質に係わる変異が出るかどうか、その可能性をどのように考えているかということです。

中川：乾物収量で見た時に、バイオマスを突然変異で増やすのかどうかというのは、第一印象的には私は駄目だというふうに感じます。それは何かというと、遺伝子組換えから遺伝子を入れて何かを増やすほうがであろうけれども、突然変異というのは基本的に遺伝子を乱す、ノックアウトしてしまいます。ただし、いろいろなメカニズムがあってどこかで抑えているものがどれか大きなカギを開けるかもしれないからという人もいるんですが、そういうメカニズムはほとんどあり
ませんよという話をすむのです。）それがまず一
点です。ただし、例えば耐塩性を備えることによっ
て、塩の多いところで沢山作れるようになったとい
うこと、あるいは、成分を変えることによって特殊
になるのが増えたという場合です（これは昔から
良い例はいろいろあると思うのです。）。です
から、作物生産のメカニズムを見たときに、何かの
遺伝子が流れることによってバイオマスが急激に
上がるような例があるのだろうかということ
を含めて考えます。
谷坂：私は、突然変異体を作るために大いに万
個体を毎年植えてきました。その中にバイオマス
の大きいものが出てくるかどうかを調べてきました
が、やはり出ます。しかし、当然いろいろな変異
を持たれます。放射線の量と化学薬品の量が関係し
ますが、これは大きいなというのはかなり出ると思
います。40年近くやってまいりましたけど、そのよう
な実感は持っていません。
北野：突然変異をどのようにとらえていくかという
観点から最近少し思っているのは、今まではいろ
いろな変異を使った研究ということで見ていくには
すこしいい時代でした。しかし、育種という話にな
ると、どうも可能性がないという話が多く出て
きまして、それは例えばコンヒカリの収量を2倍に
あげましょうと仮に考えた時に、コンヒカリに放射
線をあてて一生涯寿命から2倍のものができる
かという問題だと思います。それが、今回のシンポ
ジウムにて少し驚いたのは、谷坂先生が紹介さ
れた、たったmPingが働くという1つの現象で、すこ
くインパクトのある他的写真のような変異体が出て
くる。これはまだ可能性があるということが私の
新しい発見です。もう1つ考え方は、バイオマス
をひっくり持って器をどこも基準にして考えるかで
す。佐塚先生がご紹介されたソルガムは、イネの世
界から見たとどまらない植物で、イネでは想像で
きないようにバイオマスを持っている。そういう
リソースを改良していく場合には、突然変異という
のはそれをコーディネートしたり増強をしたりと
いうことで、もっともバイオマスの潜在能力が高い
ものを変えていくという意味ではすごく重要だと思
います。しかし、もともとバイオマスの低いイネを
どうするかということに問題をとらえた時に、今
我々が日本の中で持っている優良な品種の候補と
いうものは、そのバイオマスの容量というのはで
てもなく低いのではないか。隣の中国とかあるいは
インドとかもっと稲作に歴史のある所は多分何千年
もかけてそういうバイオマスを集める、収量を上
げるというテーマの中でバイオマス能力を上げると
いうような育種が背景で行われている、今それを
使って育種をやっているのではないか。では日本は
どうするか、ということに関して何かいいアイディア
があれば是非教えていただきたいと思います。
谷坂：中国の東北三省で栽培されている直立穂
の品種は今作付面積の70％をカバーしています。
だいたい1.2トンとれます。このいわゆる直立穂と
いうのは誰も、日本の方もほとんど考えたことない
でしょうし、この国の方も考えていなかった。瀋
陽農業大学の陳先生が、これはもちろしあるもし
れないと、たまたま作ったのが確かに1976年のこと
なんです。それから30年くらい経つと1.2トンを越
えるようになりましたが、普通の感覚で品種改良し
ていると思います。思いつかなかったかも知れません。ですから、さっき講演でも言ったのですが、軍備の中に
眠っていると、おそらくこのままズルズル行っちゃ
うんだと思います。組換えも大事でしょうし、い
ろいろな可能性を求めてやっていく必要があると
思います。農研機構でも、今創薬利用などでイン
ディカの血を入れたりいろいろな形で作られてい
ると思いますが、やはりそういう形で変えていかな
いと今の日本のバイオマス中の遺伝的変異は非
常に小さいです。現品種のレベルを大きく超
えるような品種はできないだろうと思います。北野先生は
今、多収用のいろいろな遺伝子を創ら
れていると思います。そういう知見をぜひ育種の中
で活かしていただきたいと思います。
根本：ご指摘のように、バイオマスに限らないと思
うのですが、素材の幅を広げることが育種の中で
非常に大切な事です。今から30年前、私がどう
と入賞した頃の話なのですが、逆7・5・3計画に
よる農水省の超多収のプロジェクトが始まり、イン
ド型の品種を素材として使って多収を狙うために、
インド型品種を材料に使って育種を進めるように
という指示がありました。その時に、育種の現場か
ら強い反対がありました。コンヒカリを超える美味
しい品種を作らなくてはいけないので、インド型品
種を使った利用はないとするものです。インド型品
種を親に使うと、品質・収量が一端下がります。そこからまた新しい多収性を見分け、くみ上げていくというのは、ものすごい時間と労力が必要なので、反対があったのはよく覚えてています。ただ実際のうちに、そういった中で強引に、半分強引に進めたおかげで、今種の幅が広がっていると言えます。種品の産地は米粉パンに良いということ、研究にも広がっています。こういった面でも育種、品種が全てではないんです、こういう育種の幅を広げることによって、農業研究全体に良い影響が期待できるのではないかと考えておきましょう。

佐塚：私ちょっと今日はこの会に出させていただいた、やはりまだ突然変異の可能性はあるんだろうな、と、論議も含めて今回感じております。ただ一方で、これにソルガムに関しては、先程もご紹介したように、F1でのヘテロシーチスを使った育種というのが盛んに行われています。それでそれらのバイオマスの上げ幅と突然変異での上げ幅を比較すると、ヘテロシーチスの方が大きい感じがします。これはケースバイケースの話で、ソルガムの場合にはヘテロシーチスの方がやはり便利そうに思われます。ただ、ヘテロシーチスの仕組みにさらなるような変異の有無であるかもしれないということもあり、ちょっと、ということも含めて考えると、やはり遺伝子の問題も含めて育種の問題も含めて、やはりチャレンジしていく必要があるんだろうなと考えていま

西尾：今、雑種強勢の利用というのと突然変異の利用というのを並べてご意見いただいたのですが、雑種強勢を利用してするの突然変異というのは有効に使えないでしょうか。

佐塚：先程も説明したとおりです。結局F1の育種というのは親の育種になってくる。勿論、組合せ検定がそこには入って来るんですけれども、基本的には親の育種だと思います。親の育種の育種は両方同然インブレッドですので、その育種そのものには突然変異がスピード的にも早い、その場合はパイオマスを必要としませんので、むしろホールクロップのパイオマスが下がってでも種子収量がきちんとあればいいということですので、その育種には放射線の利用は向いているのかなと思うのが、今一番思っていることです。

西尾：元々論議を広げまして、最後に宮田先生にバイオテクノロジーと放射線育種というでお話いただきましたが、バイオテクノロジーを有効に利用するために放射線育種というのはどういう有効な利用法があるのか、うまく共存して利用していくのに何かいいアイディアとかお持ちではないでしょうか。

宮田：先程の遺伝資源とか突然変異のお話について、植物に限らず、いろいろ動物とか人間の遺伝学的研究がどんな進んでいると、我々がわかってっているのが本当にまだ少なく、大多分とかもそういう植物のことはもっと少なんじゃないかと思うております。そういう意味でさっきから議論されてますけど、これはマウスの1個の遺伝子を1個ずつ減していくという計画もありましたし、クロロプラスタナノックアウトの話もありましたし、放射線育種である遺伝子を欠失させて失うよによって何かのフェノタイプ（表現型）が変わってくるものは何かという研究はずっとやるべきだと思います。それは遺伝子機能の解析という意味で重要です。さらに解析をした遺伝子を、我々が集めている遺伝資源の中でホモロジーをサーチして、その中で一番強力な遺伝子を遺伝子組換えで元に戻すとか、そういうさまざまな再築運動がたぶんこれからされてくるんじゃないかと思っています。それから、遺伝子組換えで確立した品種をさらにチューンナップする為に放射線育種っていうのはありうるんじゃいかと。たとえば、花型の菊を遺伝子組換えで作って、抗ウィルス性と耐虫性を入れたんだけど、もうちょっと花色をピンクにしたいような研究開発です。だからそういう意味では品種育成のために、バイオテクノロジーと放射線育種を自在に組み合わせて、いかに早く目的の品種を得るのかというのが今後の重要なポイントになるのではないかと思っております。

西尾：最後の宮田先生のお話は世界レベルでの植物育種の広いお話でしたので、今後は突然変異育種を考えていく上で重要なお話だったと思いますが、その関連でみなさんご意見ご質問ございませんでしょうか。
中川：昨日鶴巻先生の話を聞かれたと思うんですけど、今、日本で多分、突然変異品種と呼ばれるようなものが260幾つくらい直接利用のものがいます。それはIAEAの統計データからいうと世界第3位になっている。1位が中国で、2位がインドで、3位が日本です。どれくらい日本の野菜植物で使われているかというと、2008年に調べた時には、間接利用品種も入れて、片親にたとえばレイメイが入っている時にその子供も突然変異品種という計算をすると、100品種くらいが1ha以上日本に植えられており、トータルの面積が12.4%あります。大豆も8品種あって、それは直接利用品種が4つと間接利用品種が4つなのでですが、あわせて9,000くらいになります。ですから先程の鶴巻とか味噌の話もありますが、ほとんど消費者が知らないうちに突然変異で作られてそれが利用されている一方では、先程申し上げたように、私はゴールド20世紀というのは放射線の大成果だと思いませんが、この前記の人に「鳥取県の20世紀の博物館にはまったくそういうことは書かれてませんよ」というようなコメントをされている、そこから考えしていて大いにいずれかということがあります。育種という面で見たときには、先程言いましたように突然変異品種のうちの8割はイオンビームも含めて放射線です。そのうちの8割、だいたい全体の6割はガンマ線照射ででています。ですから品種を作ることにはガンマ線というのは重要な役割を果たしてきた今後もいくらくらい、これからの方針についてはまったく宮田先生がおっしゃったのほとんどと同感で、そういった形で進歩できたら良いと思います。

西尾：それその時間がせまってまいりましたが最後にかかお一言、ご意見はありますでしょうか。

谷坂：宮田先生にぜひお聞きしたかったのですが、いろいろな科学技術が国民に理解されないとというのは、日本とそうです国だからずっと思ってきました。原因をいろいろ考えますとまずメディアがいけないと思います。まさにメディアにおられる方質問なんですが、メディアとそれから政府関係の、政治家の中、いわゆる官僚といわれる中に科学技術を最低10年やった人がいないとこのような現実になるのかなと。たとえばドイツの今の首相は物理学者ですね。そういった意味ではすごく科学に対応する理解力があってそういう形でいろいろなことを進めていくと。だけど日本というのは、メディアに申し訳ないんですけど、メディアに動かす人も本当に関心の世界の中にもいない。政治家の中にもいない。ほどんど経済学部とか法学科を出ている。そういう人たちがいろんな形で科学を変な形で報道してしまいます。そんな気がしてならないですね。宮田さんに日経を科学技術の新聞にする、経済新聞じゃなくて科学技術の新聞にするくらいの勢いで是非やっていただきたいなと思います。
ネットできっとした情報をまず発信するというこ
to, もしそれで自分の言いたいことだけを言うの
dけなくて、たとえばあるコミュニティーのような
所に説明して、対話をするようなインターネットのメ
ディアを作っていたくとありがたい。西ドイツやオ
ランダなんかでは遺伝子組換えの教育をする時ど
うするかというと、高校生を集めてパーソナルにア
メリカの農民と対話させるんですよ。それで対話さ
せた上で、自分はどう思ったか作文コンテストを
やってですね。そうすると、ものすごく親が作文書
いたりしなよ、親ぐるみコミュニティーぐるみの
行動になるんですね。科学コミュニケーションスキ
ルは私も下手ですし、みなさんも下手ですし、官
公庁も下手ですし。これ何とかしないとまずいで
す。そうとう苦しい思いをして。でもみなさんの一歩一
歩やってまいりましょう。そうじゃないとこの国は変
わりません。
西尾：最後になかなか論議が盛り上がっておもしろ
くってきたのがですが、残念ながら時間がまいり
ました。総合討論を終わりにしたいと思います。
今回のシンポジウムは「バイオマスを増大させ
る」という内容で、震災の影響でエネルギー不足
が心配される中、これからバイオエネルギーやい
うのは非常に重要になるという事が考えられま
すので、タイミングが良かったと思います。今回の
5名の先生方のご講演で得られました知識、あ
るいは今回の論議で得られました知識を、今後
のみなさんの研究の発展に繋がりますことを期
待しております。本日はどうもありがとうございま
した。（了）