

高いバイオマス生産をあげるイネの生態生理

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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):

$$Y = Q \times I_c \times \varepsilon \times H \quad (1)$$

where Q is the total quantity of incident solar radiation received over the growing period of the crop; I_c , the fraction of Q that is intercepted by the canopy; ε , 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 CO₂ 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.

Growth stage	Characteristics	Corresponding term in eq. (1)	High-yielding cultivars with these characteristics ¹⁾
Tillering stage	Rapid increase in leaf area.	lc	Nanjing 11 and high-yielding hybrid
After the panicle formation stage	(1) Canopy structure well suited to light interception. (2) Canopy structure well suited to CO ₂ diffusion into canopy.	ϵ	(1) Milyang 23 and Takanari (2) Tainung 67
Late ripening stage	Large leaf area during ripening.	lc	Akenohoshi
Throughout plant growth	Photosynthesis by canopy leaves. (1) High photosynthetic capacity. (2) High rate of photosynthesis in the afternoon. (3) High rate of photosynthesis during ripening.	ϵ	(1) Takanari (2) Akenohoshi and Takanari (3) Akenohoshi

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

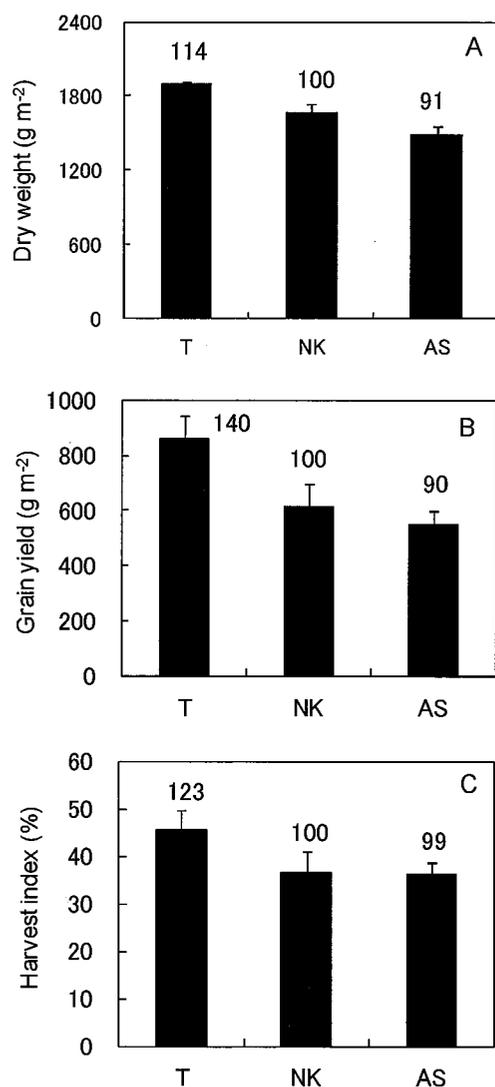


Fig. 1. Comparisons of (A) total dry weight of above-ground plant parts at harvest, (B) grain yield, and (C) harvest index of cultivars from different eras grown in a paddy field (adapted from Taylaran et al. 2009). Data are averages of three years (2002, 2005, and 2006); error bars indicate standard 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

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.

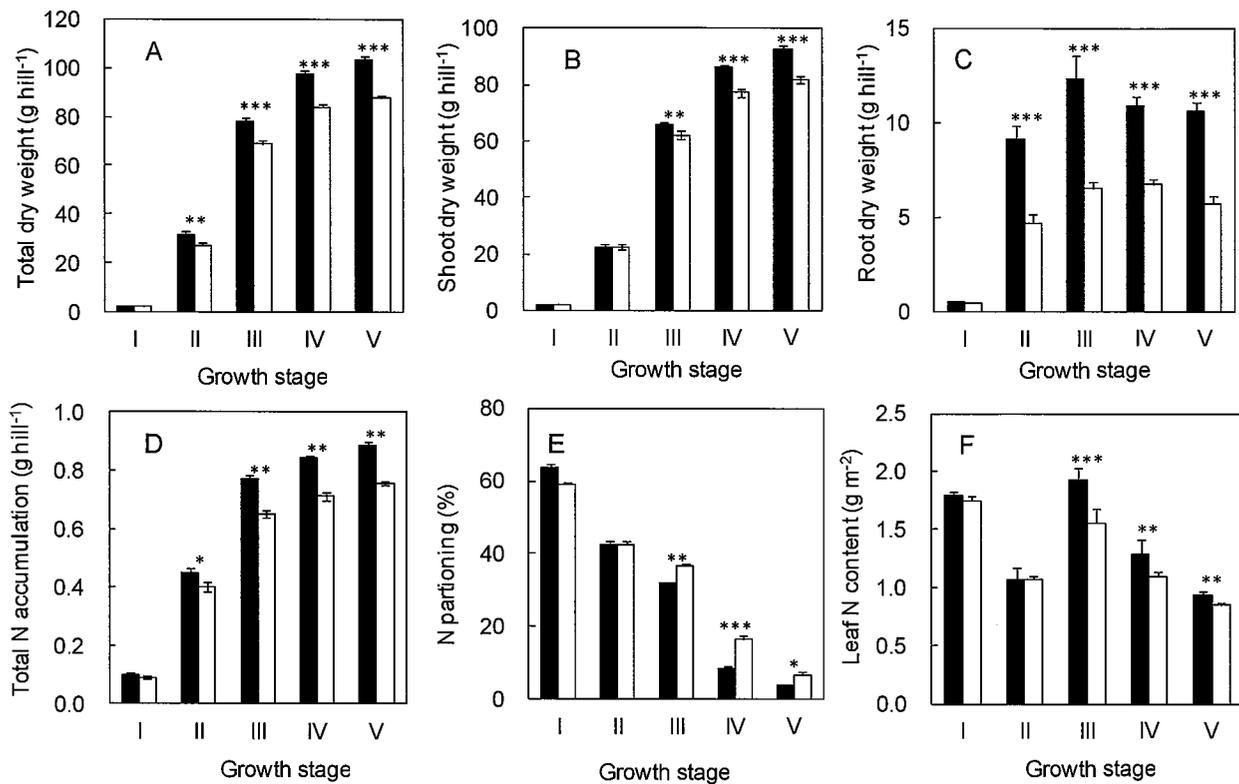


Fig. 2. Changes in (A) total dry weight, (B) shoot dry weight, (C) root dry weight, (D) total N accumulation, (E) N partitioning to the leaves, and (F) leaf N content in Takanari (■) and Koshihikari (□) grown in 12-L pots (adapted from Taylaran et al. 2011). Growth stages: I, tillering (3 weeks after transplanting); II, panicle formation (7 weeks after transplanting); III, heading; IV, 2.5 weeks after heading; and V, 4.5 weeks after heading. Koshihikari 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 Koshihikari 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 Koshihikari 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 Koshihikari 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 Koshihikari.

(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 Koshihikari from the panicle-formation stage to the ripening stage (Fig. 3A). Rates of leaf photosynthesis at an ambient CO_2 concentration of $370 \mu\text{mol mol}^{-1}$ 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 Koshihikari at all leaf N levels examined. The stomatal conductance at ambient CO_2 concentration was also greater in Takanari than in Koshihikari at heading (Fig. 4A) and ripening

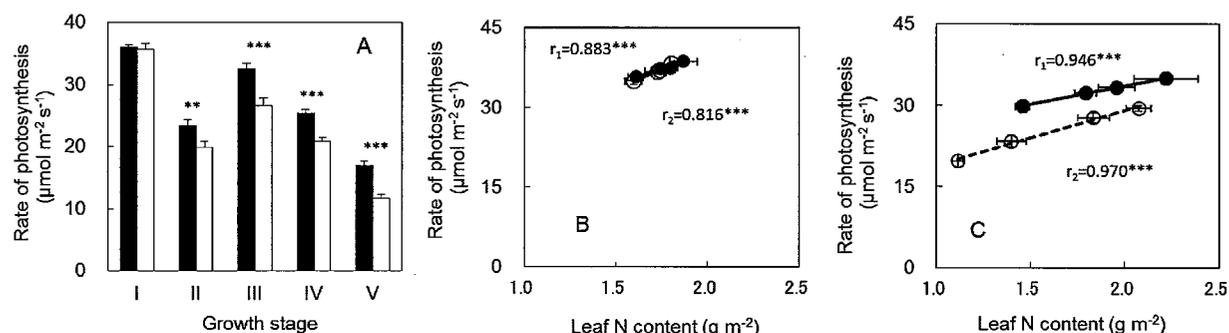


Fig. 3. Changes in (A) the rate of leaf photosynthesis and (B, C) relationships between leaf N content and rate of photosynthesis at (B) tillering and (C) full heading of the uppermost fully expanded leaf in Takanari (■, ●) and Koshihikari (□, ○) grown in 12-L pots (adapted from Taylaran et al. 2011). Rates of photosynthesis were measured at an ambient CO_2 concentration of $370 \mu\text{mol mol}^{-1}$. 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 CO_2 concentration of $280 \pm 2 \mu\text{mol mol}^{-1}$ 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.

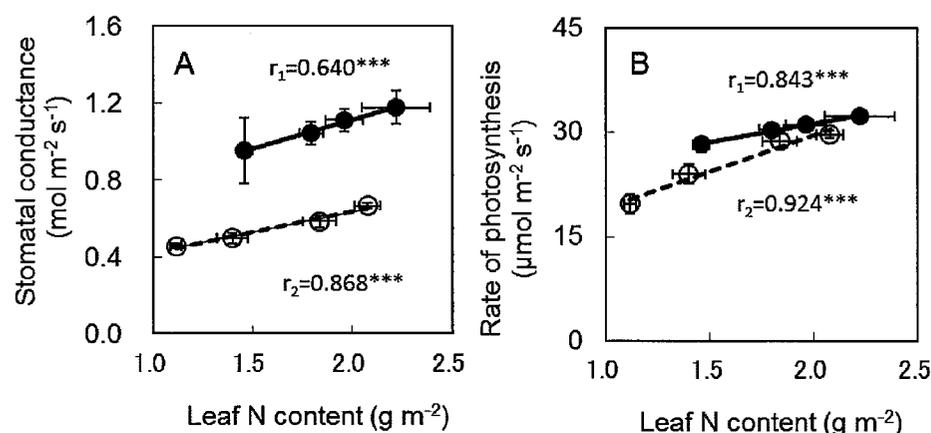


Fig. 4. Relationship between leaf N content and (A) stomatal conductance at an ambient CO_2 concentration of $370 \mu\text{mol mol}^{-1}$ or (B) rate of flag leaf photosynthesis at an intercellular CO_2 concentration of $280 \pm 2 \mu\text{mol mol}^{-1}$ at heading in Takanari (●) and Koshihikari (○) 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 ($n = 5$). r_1 and r_2 are correlation coefficients for Takanari and Koshihikari, respectively. *** indicates significance at the 0.1% level.

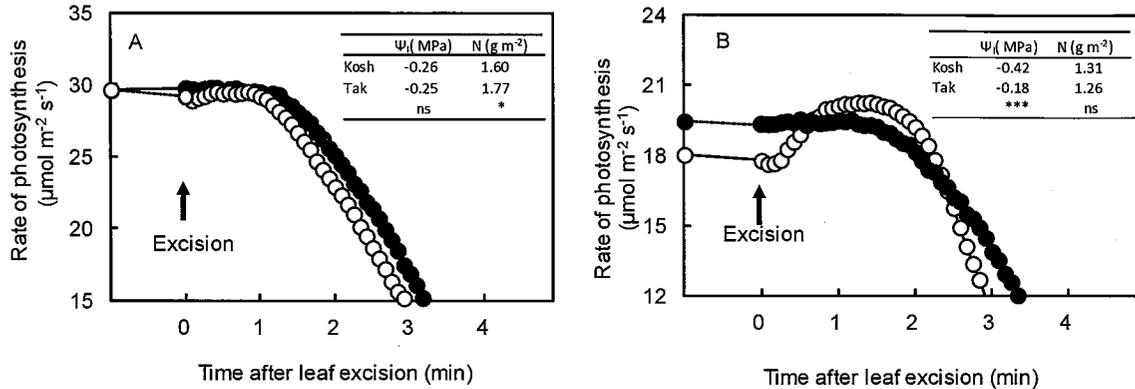


Fig. 5. Changes in rates of photosynthesis after leaf excision in Takanari (●) and Koshihikari (○) grown in 3-L pots at (A) tillering and (B) heading (adapted from Taylaran et al. 2011). Each leaf was excised at the base of the leaf blade after leaf gas exchange had reached a steady state. The ambient CO_2 concentration and leaf–air vapor pressure difference before leaf excision were $370 \mu\text{mol mol}^{-1}$ and $\sim 1.5 \text{ kPa}$, 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_l) and leaf N content (N) of Takanari (Tak) and Koshihikari (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_l) of the flag leaf in Koshihikari 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 hydrostatic pressure in the xylem, which was done after leaf gas exchange had reached a steady state, the rate of photosynthesis in Koshihikari 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 Koshihikari (Taylaran et al. 2011). The hydraulic conductance from roots to leaves (C_{pp}) was far higher in Takanari than in Koshihikari (Taylaran et al. 2011), but there was no difference in hydraulic conductivity (L_p) between the two cultivars. Taylaran et al. (2011) suggested that the larger root surface 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 Koshihikari 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 C_{pp} was small between Koshihikari 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 Koshihikari, 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_c and ϵ 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at an ambient CO_2 concentration of 370 to 400 $\mu\text{mol mol}^{-1}$ (Kanemura et al. 2007; Hirasawa et al. 2010; Jahn et al. 2011). The highest recorded rate of leaf photosynthesis in rice, approximately 30 to 33 $\mu\text{mol m}^{-2} \text{s}^{-1}$, was observed in Takanari (Hirasawa 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$. 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。

$$Y = Q \times I_c \times \epsilon \times H \quad (1)$$

ここで、 Q は作物全生育期間中に入射する太陽光エネルギー、 I_c は入射した太陽放射に対する作物個体群が受ける割合、 ϵ 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わる。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)受光態勢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、出穂期以降の個体群受光態勢が良く、個葉光合成速度が高い。

3. バイオマス生産量の更なる向上の可能性

個体群受光態勢、個体群内への CO_2 の拡散、個葉光合成速度、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られる。(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 $AP01$ であること、が最近明らかにされている。