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REVIEW

Ecophysiological Analysis on Effect of Planting Pattern on Biomass Production and Grain Yield in Rice

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Abstract

Increasing the biomass productivity of rice is a critical research target for improving the yield potential. This paper reviews ecophysiological studies on biomass production as affected by agronomic techniques and cultivars. In addition, we examined the effects of the planting pattern on the biomass production using cv. Takanari, a high-yielding and lodging resistant cultivar. The results showed that greater biomass production and grain yield were observed in plants with the combination of one plant per hill, high hill density and square hill arrangement. The factors responsible for high biomass production in this combination are; (1) vigorous tiller increase at the tillering stage resulting in higher capture of solar radiation, (2) erect leaves in the canopy after the panicle formation stage resulting in an improved light-intercepting character or smaller extinction coefficient, and (3) larger nitrogen accumulation during the ripening period resulting in a smaller decline of photosynthesis as well as a smaller midday and afternoon depression of photosynthesis possibly related to the larger water uptake ability of roots owing to better root-system development. Our results implied that an improvement in biomass production and yield is possible by optimizing the planting pattern and nitrogen management using high-yielding and lodging resistant cultivars in transplanted and direct-sown rice.

Discipline: Crop production
Additional key words: light extinction coefficient, light interception, photosynthesis

Introduction

Rice is an indispensable staple food for half of the World's population, especially in Asia. During the last half century, rice production increased approximately 2.5 fold in Asia[8]. This increase has been related to the expansion in area of cultivable land and the increase of yield per unit area[7]. The latter has been the main factor contributing to the increase in production. With the rapidly increasing population in Asia and only limited land available for rice cultivation, there is an urgent need to increase grain yield per unit area. However, the rate of the increase of grain yield per unit area has been limited in recent years. Therefore, scientific techniques are needed to break through the current yield potential. In Japan, where rice self-sufficiency has been achieved, improvements in productivity of financial inputs and land are important because the industry is developed. Rice also has potential uses other than white rice as human food, for example, as a source of forage and biomass for energy etc. In recent years, the utilization of not only grain, but also rice residue such as straw as an energy resource has been seriously considered for alternative energy production systems that reduce CO_2 production[32]. Therefore, increasing biomass productivity of rice is a critical research target.

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An increase in grain yield can be achieved by increasing the harvest index, which indicates the partitioning of assimilation products to grain, and/or total biomass production[7,47]. Improvements in grain yield by breeding during the last half century have been achieved mainly through improving the harvest index[7]. However, further increases in grain yield require improvements in biomass production[28]. In this paper, we focused on increasing weight of dry matter for higher grain yield and biomass for various purposes. The authors will review the characteristics of dry matter production and discuss our results.

Ecophysiological factors for determining biomass production

1. LAI, canopy photosynthesis

Biomass production is considered to be a function of the amount of solar radiation, interception rate of solar radiation by leaves and conversion factor of intercepted solar energy to biomass production[10]. In the first half of the 20th century, theoretical studies of biomass production were carried out and the concept of the growth analysis of canopy was suggested. At the beginning, the growth analysis demonstrated that the biomass production was mainly regulated by the leaf area index (LAI)[10]. Boysen−Jensen[3] showed that when the canopy closes completely, the photosynthesis of the canopy is also affected by the canopy structure, such as inclination of leaves, distribution of leaves and light environment inside the canopy. The light environment in the leaf canopy has been expressed in various ways. The simple index, light extinction coefficient, which was first proposed by Monsi and Saeki[34], has been most commonly used. The efficiency of solar radiation use by the canopy is determined by leaf area index and the light extinction coefficient[34]. As the photosynthesis measurement technique has been developed and improved, effects of environmental factors and physiological factors on photosynthesis were clarified and the advantage of C4 photosynthesis over C3 was discovered. With the advancement of ecophysiological researches on photosynthesis and biomass production, there have been intensive studies in rice about the relationship between photosynthesis and biomass productivity. Those studies are summarized below.

When the LAI is small, canopy CO_2 assimilation rate increases linearly with the increase in the LAI[15,35]. This is due to the increase in light interception by the canopy. Therefore, crop growth rate (CGR)[15] and the rate of photosynthesis of the canopy[35] are primarily determined by the LAI in any cultivar and any growing condition. F_1 hybrid rice has higher biomass production as a result of vigorous early growth and earlier leaf expansion at the tillering stage[20,58].

After the LAI reaches the value that makes mutual leaf shading possible, canopy CO_2 assimilation does not increase in proportion with LAI. After light interception by the canopy reaches the maximum at some level of LAI, the canopy CO_2 assimilation is not affected anymore, or rather decreases in some cases when LAI increases beyond the LAI of maximum light interception, which are defined as the critical LAI and the optimum LAI, respectively. Rice shows the typical saturated light response curve in photosynthesis of individual leaves[69]. At this point, the inclination of leaves affects the penetration of solar radiation into the canopy in which significant mutual shading occurs[12]. The larger the penetration of solar radiation, the larger the canopy photosynthesis. Therefore, the net assimilation rate (NAR) is higher in the canopy with more erect leaves at a given LAI[12]. A canopy that has more erect leaves and a smaller extinction coefficient, and therefore with better light-intercepting structure, has a larger critical or optimum LAI and a higher maximum canopy photosynthesis rate. After the heading stage, the light extinction coefficient of the canopy increases because of the horizontal inclination of flag leaves and an increase in light absorption by the panicle[12].

The canopy structure affects not only the light-intercepting characteristics of the canopy, but also CO_2 concentration inside the canopy during daytime. It is suggested that genotypes with long stems and smaller leaf area density have advantages to enhance CO_2 concentration in the canopy[29].

It is said that optimum LAI is determined mainly by the balance of photosynthesis and respiration, and appears when excessive LAI increases respiration more than photosynthesis. Excessive and luxuriant growth may deteriorate canopy structure and increase the extinction coefficient of the canopy, causing a decrease in canopy photosynthesis. Lodging of plants with larger LAI at the ripening stage induces serious reduction in light penetration into the canopy and CO_2 diffusion efficiency of the canopy, causing a decrease in photosynthesis of the canopy and biomass production. These also can be a cause of the appearance of the optimum LAI.

2. Photosynthesis of single leaf

The photosynthetic rate of an individual leaf contains some important aspects as follows: (1) the rate of leaf photosynthesis immediately after full expansion under optimum conditions (the maximum capacity of leaf photosynthesis)[35], (2) the rate of leaf photosynthesis under stress conditions[19,24], and (3) the rate of leaf photosynthesis during senescence[24,31]. 1) The rate of leaf photosynthesis usually reaches maximum immediately after full expansion. Maximum leaf photosynthesis rate is closely correlated with the level of leaf nitrogen because higher leaf nitrogen increases diffusion conductance of CO_2[18] and phosphate carboxylase/oxygenase (Rubisco) content which is a key enzyme in leaf photosynthesis in C3 plants[30,31]. 2) Environmental stresses, such as low temperature[36], high light intensity and so on, reduce leaf photosynthesis. There are many studies about the effect of water stress on photosynthesis. On clear days, leaf stomatal conductance and the leaf photosynthesis rate decrease at midday because of water stress due to intense transpiration. This process occurs in rice even when plants are grown under submerged soil conditions[19]. The degree of midday and afternoon depression in photosynthesis is affected significantly by the root water uptake capacity, which relates to root activity and morphological development[13,19,24]. 3) After fully expanded, the rate of photosynthesis decreases gradually during ripening period[31]. This decline is due to the decrease in the process of photochemical carboxylation and CO_2 diffusion. The closest correlation was observed between the level of Rubisco and the rate of photosynthesis at the ripening stage[31]. Delaying such leaf senescence is important to improve biomass production[23,24]. In plants showing a slow decrease in the rate of photosynthesis at the ripening stage, the level of Rubisco could be kept high by a larger accumulation of nitrogen in plants and a larger partitioning of nitrogen to the leaf[42]. Increased transport of cytokinins from root to aboveground parts during ripening is also associated with the maintenance of photosynthesis in rice[43,56,57].

The findings above suggest that an improvement in biomass production can be achieved by; (1) faster leaf area expansion at early growth stages, (2) canopy structure that has a small light extinction coefficient and high efficiency of CO_2 diffusion, (3) higher leaf photosynthesis resulting from the maintenance of higher levels of Rubisco and nitrogen until late growth stages, and (4) smaller midday and afternoon depressions of photosynthesis with better-developed root systems.

3. Breeding strategy for high yielding cultivars

The characteristics of high yielding cultivars have also been studied in terms of the photosynthesis and biomass production in aspects of breeding. In Japan, various strategies have been proposed for the improvement of biomass production and yield after the 1940's. The cultivars with shorter plant height, erect leaf blades and many panicles were developed for higher lodging resistance, better canopy structure or smaller extinction coefficient, and higher harvest index (HI) after the 1950's. IR8, a semi-dwarf cultivar with high panicle number was bred in 1966 at International Rice Research Institute and made a tremendous impact on rice production in tropical Asia. There was a large difference in the response to nitrogen between the old and these new cultivars with short stems. The cultivars after the 1950's showed better canopy structure for light interception and lodging resistance even under high nitrogen levels, that is, they could maintain a short stem length and erect leaf angle as compared with older cultivars[22,60,61,64]. The rate of photosynthesis during the ripening stage was higher in new cultivars than old cultivars under a high nitrogen level[46,48,63,65]. These characters led to high response of new cultivars in grain yields under heavy nitrogen application[11,45].

After the 1980's, the short culm and panicle weight type cultivars with thick stems were developed to further improve lodging resistance. These cultivars were bred as super-high yielding cultivars mainly for multipurpose uses. Takanari, one of the representative cultivars in this group, has been developed from indica germplasms[16]. Takanari is one of the cultivars which have shown the highest yield potential in Japan at present. These new higher yield cultivars possess better early growth, better light intercepting characteristics and higher photosynthesis during ripening stage[21,28]. No single cultivar possesses all of these beneficial characters. This indicates the opportunity to accumulate the beneficial characters to further improve biomass productivity[21].

In recent years, new long culm type cultivars with a superior lodging resistance and stronger stems have been developed mainly for animal forage[44]. Higher plant stature with strong and long stems leads to larger biomass of vegetative parts, such as stems and leaves. It is also expected to improve CO_2 diffusion within a canopy that is advantageous to enhance canopy photosynthesis.

Cultivation methods for improvement of biomass production and grain yield

1. Nitrogen management for biomass production and grain yield

The improvement of nitrogen management has been made based on the research on photosynthesis and dry matter production and this has contributed tremendously to the improvement in productivity since the 1950's together with breeding of high-yielding cultivars[33]. After the high-yielding cultivars with high panicle number had been released, greater emphasis was placed on nitrogen application in the late growth stage[38]. The principle of this nitrogen application is to limit excessive number of tiller during the early growth stage and this suppresses lower inter-node elongation to reduce lodging. More emphasis is put on topdressing that ensures the necessary number of spikelets and the maintenance of individual leaf photosynthesis and canopy photosynthesis during ripening.

2. Effects of planting pattern and planting density on biomass production

Planting pattern and planting density, referred simply to here as planting pattern, is the other factor that affects the biomass production and grain yield[2]. Planting pattern consists of hill density, the number of plants per hill and the conformation of hills. High hill density or a high number of plants per hill are generally advantageous in early growth. At the tillering stage, the number of tillers per square meter increased as the hill density or number of plants per hill increased[6,41,66,70]. Introduction of mechanized transplanter, which was employed rapidly during the 1970's-1980's in transplanting rice cultivation in Japan, enabled higher hill density as compared with manual transplanting, which resulted in increased grain yield[14].

On the other hand, there are negative aspects in high hill density and high number of plants per hill in later stages, such as the reduction of percentage of productive stems and smaller number of spikelets per panicle[1,6,17,41]. In addition, excessive vegetative growth[1,70], lowered nitrogen concentration in plants and shallow root systems[62] occurred. As a result, the differences in final biomass and grain yield are generally smaller among various planting patterns as compared with early growth. Topdressing for improving deteriorated growth sometimes induces lodging.

Direct sowing is one of the labor-saving practices. Direct seeded rice usually shows higher LAI owing to the production of a larger number of tillers and absence of transplanting shock as compared with transplanted rice[4,5,54]. These characteristics do not necessarily lead to higher final biomass and grain yield because of luxuriant growth inducing deteriorated canopy structure in later stages, lower rate of productive tillers and smaller number of spikelets per panicle[71]. Excessive early growth also leads to lower plant nitrogen levels after late tillering stages[4,54]. In addition, lodging is more frequent in direct-sowing due to high number of tillers and shallow root systems[27].

Although there are many studies that investigated the effect of planting pattern on biomass production, analysis from the aspect of light interception and leaf photosynthesis is limited except for the report showing that the higher hill densities led to a lower light extinction coefficient in spite of the larger LAI[37].

Effects of planting pattern on biomass production and ecophysiological characteristics in high yielding and lodging-resistant varieties

1. Effect of planting pattern on biomass production in direct-sown plants

As mentioned above, the panicle weight type cultivars with high lodging resistance have been released since the 1980's. However, optimum managements for these cultivars were not well investigated. We examined the effects of the planting pattern on biomass production by varying the hill density, the number of plants per hill and the conformation of hills, using Takanari as a high-yielding and lodging-resistant cultivar[49] in the transplanted and the direct-sown plants.

Firstly, we examined the effects of planting pattern with various hill densities, number of plants per hill, and row spacing on the biomass production and yield in direct-sown plants[53]. The planting patterns are shown in Table 1. Among the treatments, there was no significant difference in harvest index which indicated that higher biomass production led to higher grain yield (Table 2) and a close correlation was observed between dry weight of aboveground parts at harvest and grain yield (r = 0.937). When number of plants per hill was constant (D, E and C), total dry weight and yield were higher in the plots with higher hill density. When hill density was constant (A, B and C), total dry weight and the grain yield were higher in the plots with higher number of plants. When hill density was low, increasing the number of plants per hill had a compensating effect to increase the dry weight. Between the

Table 1. Planting patterns

Plot	Hill density (hills m^{-2})	Spatial arrangement of hills	No. of plants per hill	Plant density (plants m^{-2})
A	20.7	22 cm × 22 cm	5	103.3
B	20.7	22 cm × 22 cm	3	62.0
C	20.7	22 cm × 22 cm	1	20.7
D	82.6	11 cm × 11 cm	1	82.6
E	44.4	15 cm × 15 cm	1	44.4
F	44.4	7.5 cm × 30 cm	1	44.4

Table 2. Dry matter accumulation, grain yield and harvest index

Plot	Dry weight (g m^{-2})	Yield (g m^{-2})	Harvest index (%)
A	2,007 b	886 b	44.6 a
B	1,944 b	877 bc	43.2 a
C	1,788 c	834 c	45.1 a
D	2,293 a	929 a	42.1 a
E	2,094 ab	919 a	43.8 a
F	1,845 b	825 c	43.9 a

Dry weight is for aboveground parts at harvest. Unit area sampling yield is for brown rice with a grain thickness of more than 1.8 mm. Yield is given for a water content of 14.5%. Harvest index was calculated by dividing the dry weight of brown rice by the dry weight of aboveground parts. Means followed by same letters are not significantly different at the 5% level by Tukey test (n = 3).

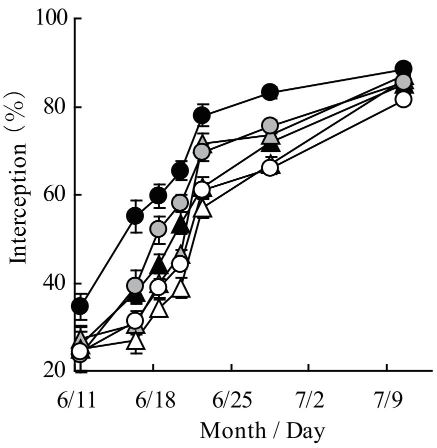

Fig. 1. Changes in the interception of solar radiation by the canopy

▲: A, △: B, △: C, ●: D, ◉: E, ○: F.
Vertical bars represent standard errors (n = 3).

Table 3. Light extinction coefficients of canopy (K) at the first ripening stage

Plot	K
A	0.53 b*
B	0.55 b
C	0.69 a
D	0.42 c
E	0.38 c
F	0.50 b

Light extinction coefficients are given for canopy layers higher than 60 cm above the ground.
*: Means followed by the same letters are not significantly different at the 5% level by Tukey's test (n = 3).

plots with square arrangement of hills, total weight and grain yield was larger in the plots with high hill density even at the same plant density. Between the plots with different arrangements of hills with the same number of plants per hill and the same hill density (E and F), the square arrangement showed the highest dry weight and yield.

In order to analyze the factors responsible for the difference in the dry matter production between the planting patterns, the rate of interception of solar radiation by the canopy and the light extinction coefficient of the canopy were compared. The treatment having the highest yield, with one plant per hill, higher plant density and square arrangement of hills, showed larger interception of solar radiation at the tillering stage (Fig. 1) owing to the greater number of tillers and larger LAI. This treatment also showed the smaller light extinction coefficient at the early ripening stage indicating better canopy structure (Table 3). This was due to the large stem inclination angle and this also caused a large leaf inclination angle in the plants with higher plant density and square arrangement (data not shown). These results suggested that one reason for higher dry weight in the plots with high hill density with one plant per hill and square arrangement of hills was better light intercepting characters throughout growth.

2. Effect of planting pattern on biomass production in transplanted plants

We investigated the dry matter production and associated characteristics of transplanted plants (TP) with different planting patterns as well as direct-sown plants (DSP)[50,51]. The cultivation methods and planting patterns are shown in Table 4. At the tillering stage, the number of tillers and, therefore, the LAI increased rapidly and the interception of solar radiation by the canopy was larger in plants of pattern I (one plant per hill) than in those of pattern III (three plants per hill) in TP as well as DSP. How-

Table 4. Cultivation methods and planting patterns

Plot	Cultivation method	Hill density (hills m^{-2})	Spatial arrangement of hills	No. of plants per hill	Plant density (plants m^{-2})
DSP I	DSP	51.3	13 cm × 15 cm	1	51.3
DSP III	DSP	17.5	19 cm × 30 cm	3	52.3
TP I	TP	51.3	13 cm × 15 cm	1	51.3
TP III	TP	17.5	19 cm × 30 cm	3	52.3

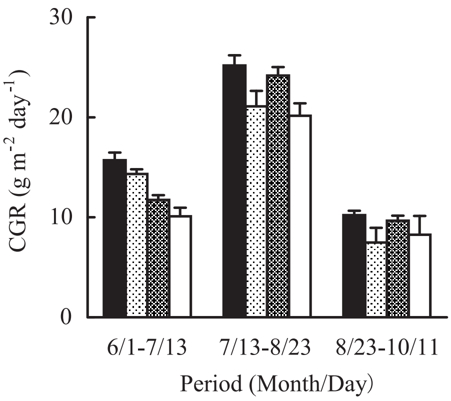

Fig. 2. Crop growth rate (CGR)
Vertical bars represent standard errors (n = 3).
■: DSP-I, ▩: DSP-III, ▦: TP-I, □: TP-III.

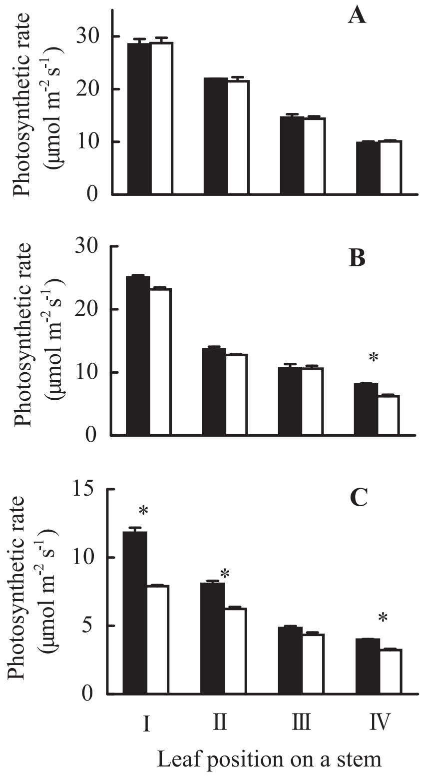

Fig. 3. The rate of photosynthesis on Aug. 15-17 (A), Sep. 12-14 (B) and Oct. 3-6 (C)
Measurements were taken at an ambient CO_2 concentration of 350 μl l^{-1}.
In the leaf position, I, II, III, and IV indicate the first (flag), second, third, and fourth leaf, respectively. Vertical bars represent the standard errors (n = 3). Three leaves were used for the measurements for each replicate.
■: Pattern I, □: Pattern III.
*: Values are significantly different at 5% level by t-test.

ever, the increase in tiller number, LAI and the solar radiation interception were larger in the DSP than in the TP, irrespective of the planting pattern (data not shown). These factors caused the higher CGR in the DSP than in the TP (Fig. 2). After the panicle formation stage, when the canopy closed completely and the interception of solar radiation exceeded 90%, the canopy consisted of more erect leaves and the extinction coefficient was smaller in pattern I than in pattern III, irrespective of the cultivation method. These features were responsible for the larger CGR of plants in pattern I than in pattern III (Fig. 2). The effect of planting patterns was larger than that of cultivation methods after the panicle formation stage.

3. Effect of planting pattern on photosynthesis and root function

We compared the rate of leaf photosynthesis and related physiological processes after heading in the direct-sown rice plants with different planting patterns[52]. The rate of photosynthesis was similar at full heading in pattern I and III (Fig. 3). However, pattern I maintained a higher rate of photosynthesis than in pattern III at the middle to late ripening stages. The difference was found not only in the flag leaf, but also the leaves in lower positions. These findings implied that higher photosynthesis at later stages contributed more to higher biomass production in pattern I. Rubisco is a key enzyme in leaf photosynthesis during senescence[30,31]. Photosynthesis during senescence is closely correlated with Rubisco levels in the leaves[31]. During the ripening stage, the levels of Rubisco were kept higher in pattern I than in pattern III (data not shown). A close linear relationship was observed between leaf nitrogen and the rate of photosynthesis, and Rubisco (Fig. 4).

Table 5. Nitrogen accumulation by plants

Stage	Planting pattern	Leaf blade (g m^{-2})$^{a)}$	Stem and leaf sheath (g m^{-2})	Panicle (g m^{-2})	Dead part (g m^{-2})	Total (g m^{-2})	Accumulated nitrogen after heading$^{b)}$ (g m^{-2})
Heading	I	8.39	7.32	—	—	15.71	—
(7 Aug.)	III	6.93	5.41	—	—	12.34	—
		*	*			*	
Late ripening	I	4.89	4.42	12.45	0.32	22.07	6.61
(23 Sep.)	III	3.32	3.75	9.75	0.43	17.25	4.91
		*	*	*	n.s.	*	*

*: Indicates significant difference at the 5% level by t-test.
n.s.: Indicates no significant difference at the 5% level by t-test.
a): g m^{-2} of land area.
b): The amount of accumulated nitrogen after heading was estimated from the difference between the total nitrogen content on August 7 and September 23.

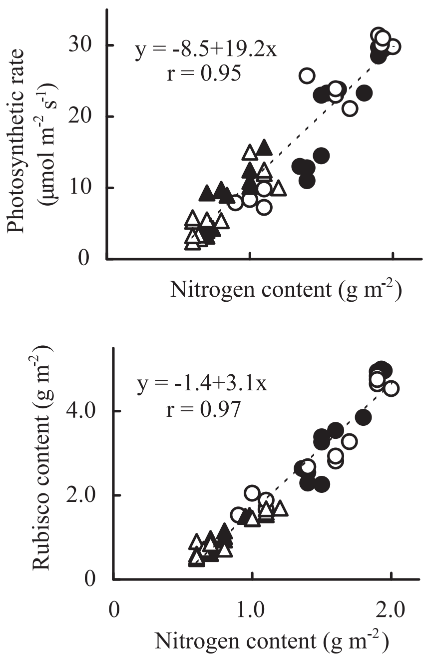

Fig. 4. Relationships between nitrogen content and the rate of photosynthesis, and Rubisco content of the flag and fourth leaves

The rate of photosynthesis was measured at an intercellular CO_2 concentration of 270 µl l^{-1}.
●: Flag leaf-Pattern I, ○: Flag leaf-Pattern III, ▲: Fourth leaf-Pattern I, △: Fourth leaf-Pattern III.

Leaf nitrogen is determined by aboveground nitrogen accumulation and nitrogen partitioning to the leaf. Higher leaf nitrogen in pattern I was attributed to both high nitrogen accumulation in aboveground parts and partitioning of nitrogen to leaves as compared with pattern III at late ripening stage (Table 5). In addition, the reduction in the

Table 6. The number of crown roots

Stage	Planting pattern	Roots (per stem)	Roots$^{a)}$ ($\times 10^4$ m^{-2})
Heading	I	57.0	2.0
(11 Aug.)	III	35.3	1.1
		*	*
Harvest	I	51.9	1.7
(11 Oct.)	III	40.5	1.1
		*	*

*: Indicates significant differences at the 5% level by t-test.
a): Number of roots per m^2 of land area.

rate of photosynthesis was not large in the midday and afternoon of clear days in the plants with pattern I compared with the plants with pattern III in the ripening stage (data not shown). The resistance to water transport from soil through root to leaf was lower in the plants with pattern I than in those with pattern III (data not shown). The high water uptake capacity of roots possibly leads to reducing the midday and afternoon depression in the plants with pattern I.

We found differences in root-system development and cytokinin transport from root to shoot between planting patterns. The number of crown roots per stem (Table 6) and the root length density (data not shown) were larger in the plants with pattern I than in those with pattern III. The latter resulted from the higher density of branched roots. The cytokinin flux from root to shoot was maintained at higher levels in the plants with pattern I than in those with pattern III after the middle ripening stage (Table 7). Exogenous cytokinin maintained high levels of

Table 7. Changes in concentration and fluxes of cytokinins per stem for exudates based on an *Amaranthus betacyanin* bioassay

Stage	Exudation rate per stem (ml h^{-1})			Concentration (nM BA eq.)			Flux per stem (pmol BA eq. h^{-1})		
	I	III		I	III		I	III	
Heading	0.27	0.24	n.s.	7.32	6.69	n.s.	1.85	1.59	n.s.
Middle ripening	0.24	0.18	*	6.01	5.89	n.s.	1.42	1.04	*
Late ripening	0.13	0.08	*	4.98	4.81	n.s.	0.63	0.41	*

Xylem exudates were collected between approximately 6 p.m. and 6 a.m. on Aug. 7 to 8, Sep. 12 to 13 and Sep. 23 to 24 for first heading time, middle ripening stage and late ripening stage, respectively.
*: Indicates significant differences at the 5% level by t-test.
n.s.: Indicates no significant difference at the 5% level by t-test.

leaf nitrogen during ripening by enhancing the partitioning of nitrogen to leaves[9,26,39,40,43,55]. Cytokinins promote the accumulation of transcripts of the gene for Rubisco[43]. Our findings together with these findings suggested the possibility that larger root development and high cytokinin production in the root contributed to keeping high leaf nitrogen in the plants with pattern I at the ripening stage.

Future research

Our results indicated that planting pattern has a significant impact on biomass production by affecting light interception, single leaf photosynthesis, and the root function in high yielding and lodging-resistant cultivars. Biomass production and the grain yield might increase approximately 10% or more by increasing hill density from conventional practices (about 22 hills per square meter in hill density and about 30 cm in row distance). The need to increase the biomass productivity of rice is increasing as utilization of rice as a source of forage and biomass for energy production etc. has been seriously considered in recent years. The findings in this study can be potentially utilized to improve biomass production of rice. However, when this technique is transferred to actual practices, several considerations have to be made. Increase in hill density by decreasing row distance as currently used with rice transplanter may not be feasible. Direct seeding is one option to realize higher hill density. Especially when employing direct seeding in rice cultivation, high hill density has a strong potential to improve biomass and grain production. In this case, as generally pointed out, ensuring high seedling establishment is critically important as well as lodging resistance.

Another aspect is varietal adaptability. Large increase in biomass production under high hill densities in this study might be partly due to the varietal characteristics of cv. Takanari which has relatively low stem production and high lodging resistance. According to our preliminary research, in cv. Kinuhikari[25] and Dontokoi[67], both of which are intermediate (between panicle-number and panicle-weight) type cultivars with lodging resistance, plants in the planting pattern with high hill density and square hill arrangement at the same plant density produced heavy biomass and grain compared with conventional planting pattern (data not shown). However, we do not know whether the results observed were restricted to the special cultivar, Takanari or the cultivars of panicle-weight type and/or the plants of indica type with well developed root systems, or if this could be widely adapted to the cultivars with lodging resistance. Further investigation on the optimum planting method with different plant types is needed.

Another point is adaptability to climatic conditions. In warmer conditions, high hill density and high number of plants per hill generally have a negative effect on final biomass. This is due to excessive early growth that results in longer lag phase between maximum tillering and panicle initiation and lower productive tillers[59,68]. To minimize these negative effects, timing of top dressing is critical. Optimum planting methods are needed to be established with different climatic conditions in combination with nitrogen management.

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