Regulation of Plant Type and Carbon Assimilation of Rice

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Since grain yield is the product of number of spikelets per unit field area and percentage of ripened grains (ripening percentage), it is necessary to increase these two yield-components for increasing yield. However, as there exists a negative correlation between these two factors in general, remarkable yield increase may not be expected without breaking such correlation. For that purpose, the ripening percentage must be increased at a high level of spikelet number per unit field area by increasing carbon assimilation during the ripening stage.

Basic components of carbon assimilation are photosynthetic ability per unit leaf area and the size of leaf area; the first and the second factor respectively. In addition, carbon assimilation of plant community is influenced by light intensity at individual leaves so that plant type (light-receiving structure) constitutes the third factor. For the first and second factors, nutrient supply was proved directly effective, whereas varietal improvement rather than cultural methods has been considered predominantly in relation to the third factor. However, it seems to be possible to regulate plant type by means of nutrient supply because the determinant of plant type is leaf growth itself.

An increase of leaf area is inevitable for producing sufficient number of spikelets for increasing yield, but at the same time the main cause of lowering light intensity inside plant community is leaf area itself. Therefore, it is most important in rice culture how to obtain higher light-receiving efficiency than expected from the size of leaf area at the stage of maximum leaf area. From this point of view, the author carried out a series of research to establish a rational cultural method for higher yield by means of plant type regulation. Some of the major results are presented in this paper.

State of single leaf and carbon assimilation

Carbon assimilation of plant community is the sum of carbon assimilation of individual leaves, which differ in photosynthetic ability according to leaf position on stem and in environmental conditions, and which perform carbon assimilation depending on their ability and environmental conditions. Each leaf in plant community receives light not only on upper surface (adaxial side) but also on lower surface (abaxial side), and the total light intensity varys with degree of luxuriance of community and the state of each leaf. In view

Table 1. Relation between the light intensity on adaxial and abaxial sides and CO_2 abosorption of a whole leaf

Light intensity on the abaxial side, cal/cm²/min	Light intensity on the adxial side, cal/cm²/min: 0	0. 2	0. 4	0. 6
0		10. 64	22. 92	29. 50
0. 2	11. 27	27. 27	39. 42	38. 02
0. 4	21. 69	39. 87	41. 30	
0. 6	28. 92	39. 79		

Note: Used variety is Norin No. 25. Numerals in the table show CO_2 absorption in CO_2 mg/dm²/hr.

of this, carbon assimilation of single leaf as affected by light intensity at abaxial and adaxial side of the leaf was examined.

Table 1 shows carbon assimilation of single leaf measured under an artificial illumination with light intensity changed independently for abaxial and adaxial sides of leaves. Interesting is that carbon assimilation of leaf exposed to light at one side is different from that of leaf exposed to light at both sides even when the total light intensity is equal for both cases. Apparently, the latter leaf which received ½ of light intensity at both sides showed higher carbon assimilation than the former exposed to strong light intensity at only one side. This difference was found more remarkable with leaves having higher nitrogen content and greater leaf thickness. This fact gives an interesting and important view point for the efficiency of light energy utilization and for the state of plant community. Namely, the plant community with horizontally oriented leaves, showing great angles between leaves and stems (leaf angle), causes not only a reduction of light penetration inside the community but also a decrease of carbon assimilation because leaves at the upper layer of the community receive strong sunlight (direct and diffused) only at the upper surface but very weak reflected light (from other leaves and ground surface) at the lower side of the leaves, giving carbon assimilation close to that of one-side lighted leaves. On the contrary, the plant community with vertically oriented leaves at small leaf angles gives better penetration of light and higher carbon assimilation as compared to the former, because both sides of leaves are exposed to light, i.e., direct sunlight and diffused light at one side and sufficient diffused light on the other side.

Thus, for obtaining high yield, state of leaves that enables full expression of photosynthetic ability, i.e., an erect state receiving sufficient light at both sides of leaves is necessary.

State of plant community and carbon assimilation

To know what state of plant community is able to increase light receiving efficiency and hence carbon assimilation under high degree of luxuriance, a relationship between carbon assimilation and leaf angle and leaf curvature was examined using plant communities with the same degree of luxuriance. A plant community with leaf area index (LAI) of 7.1 and erect upper leaves was divided into two plots at the heading stage. After carbon assimilation of both plots was measured, all leaves in one plot were artificially drooped by attaching small lead balls to the tip of all leaves (drooped leaf plot), while no such treatment was given to an other plot (erect leaf plot), as shown in Fig. 1, and carbon assimilation was compared. Before the treatment, both plots showed carbon assimilation increased with the increase of light intensity up to the maximum of that day, 1.0 cal/cm^2/min, giving no light-saturation. However, after the treatment, the drooped leaf plot showed an apparent light-saturation at about 0.6 cal/cm^2/min, without an increase of carbon assimilation beyond that light intensity, whereas the light-curve of the erect leaf plot was unchanged, showing a similar trend as that measured before the treatment (Fig. 2).

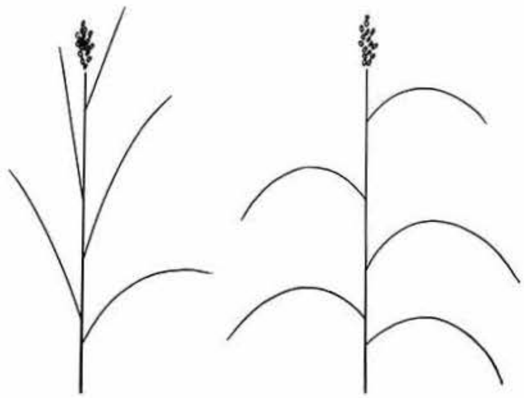


Fig. 1. Schematic illustration of plants with erect or drooping leaves

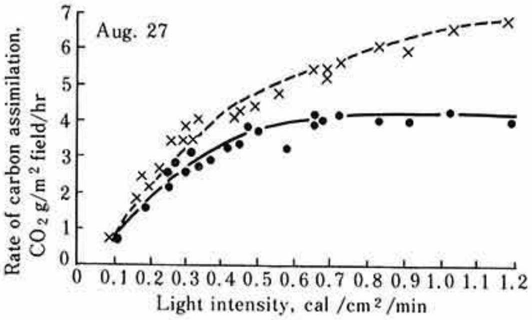


Fig. 2. Light-curves of carbon assimilation of rice plant communities with different plant type.

Note : X...Plant community with straight and erect leaves.

● ...Plant community with curved and drooped leaves.

Measurement of light received by individual leaves made it clear that such a difference in the light-curve was caused by the difference of light receiving state between two plots. In the drooped leaf plot, an increase of incident light intensity hardly causes an increased carbon assimilation of the community because it results in the occurrence of light-saturation with upper leaves and only limited increase of carbon assimilation of lower leaves as the upper leaves restrict the light penetration to the lower leaves. Contrary to this, in the erect leaf plot lower leaves are exposed to more light intensity increases because of an easy light penetration into the community.

Thus, it was proved that carbon assimilation of plant community differs very much depending on their light-receiving structure even when the degree of luxuriance and photosynthetic ability of individual leaves are the same. Yield and yield components of the two plots are shown in Table 2. The yield of the drooped leaf plot was reduced 32.5% as compared to the erect leaf plot. Among yield components, the largest decrease occurred with ripening percentage followed by weight of 1000 grains (brown rice), showing 25% and 7.1% decrease, respectively. This result indicates that the reduced yield is attributable to lowered carbon assimilation caused by worsened state of plant community. Thus, the erect leaf is an important characteristic of plant community for obtaining high yield.

Table 2. Comparison of yield and yield-components between a plant community with straight and erect leaves and that with curved and drooped leaves

	C	D	E	F	G	H	I
A	18. 0	75	1350	70. 0%	24. 4 g	22. 9 g	100%
B	18. 5	73	1355	50. 9	22. 9	15. 8	68. 5

Note: A…Plant community with straight and erect leaves.
B…Plant community with curved and drooped leaves.
C…Number of panicles per hill.
D…Number of spikelets per panicle.
E…Number of spikelets per hill.
F…Percentage of ripened grains.
G…Weight of 1000 grains.
H…Grain weight per hill.
I…Ratio of grain yield.

State of plant community and ripening percentage

To make clear the effect of the state of plant community on ripening percentage, communities with different plant type were prepared by various treatments such as nitrogen application at different growth stages, prevention of nitrogen absorption by plants by means of root prunning, chemical treatment, replanting treatment or intensive midseason drainage etc. to examine the relation between community state and ripening percentage. As a result, it was recognized that length of leaf blade (Fig. 3), leaf curvature (Fig. 4) and angles of leaf blade to stem (Fig. 5) of the flag leaf and the following second leaf have negative correlations to ripening percentage. Particularly the sum of these values of the flag leaf and the second leaf was strongly correlated to ripening percentage, indicating that the state with short and erect leaf blade of upper leaves is an essential factor for increasing ripening percentage.

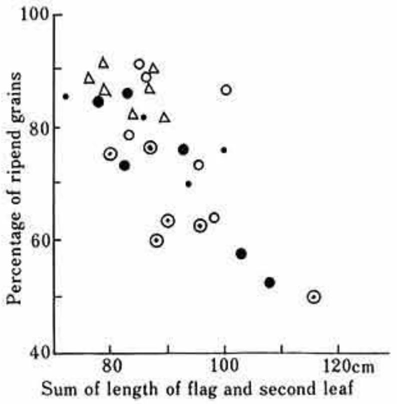


Fig. 3. Relation between the percentage of ripened grains and the sum of length of the flag and the second leaf-blade.

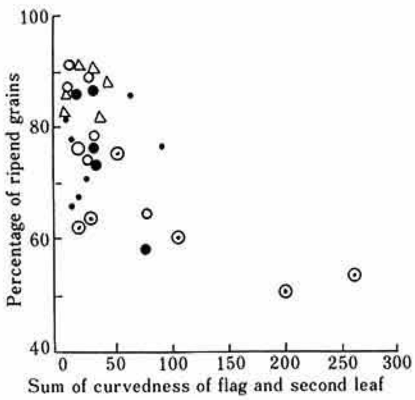
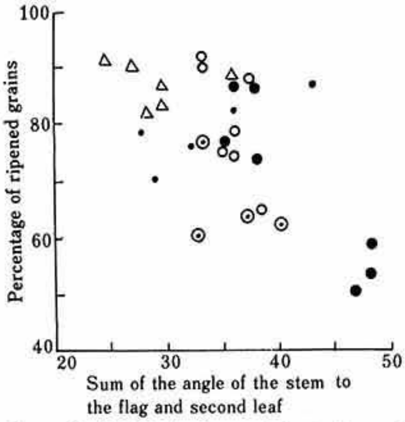


Fig. 4. Relation between the percentage of ripened grains and the sum of curvedness of the flag and the second leaf-blade.



Note: Symbols in the figures indicate the number of spikelets as follows:

⊙ 35,000 ~ 38,000.
● 33,000,
• 31,000,
○ 29,000,
△ 27,000/m^2

Fig. 5. Relation between the percentage of ripened grains and the sum of the angle of the stem to the flag and the second leaf.

Methods of regulating plant type

To attain the plant type with erect leaves is inevitable for increasing yield as shown above, so that the following experiments were carried out to know how the plant type can be regulated as desired.

Rice plants grown in pots were taken out from the pots at four successive growth stages with an interval of one leaf age. Roots were washed to remove soil and kept in tap water for 6 days in order to give nitrogen depletion during that period. Then, the plants were replanted to pots, and examined to know what portion of the plants was shortened (Fig. 6). The result clearly showed that the nitrogen depletion for 6 days caused the most remarkable shortening for the leaf blade just emerging and elongating at that period, and the leaf sheath of the following second leaf as well as the third internode counted from the internode enclosed by that leaf sheath. All of them are the portions which elongate simultaneously.

By giving top dressing of nitrogen or nitrogen depletion treatments as mentioned above at different growth stage, portions of plant that were shortened or lengthened as compared to the control plant were examined. When the leaf blade and sheath of the first (flag leaf), second, third and forth leaf from the top of the plant are signified as B_1, B_2, B_3, B_4, and S_1, S_2, S_3, S_4, respectively, and internodes as N_0, N_1, N_2, N_3 in order of their position from the top, taking the uppermost internode (between ear-neck node and the node of flag leaf) as N_0, the following sets

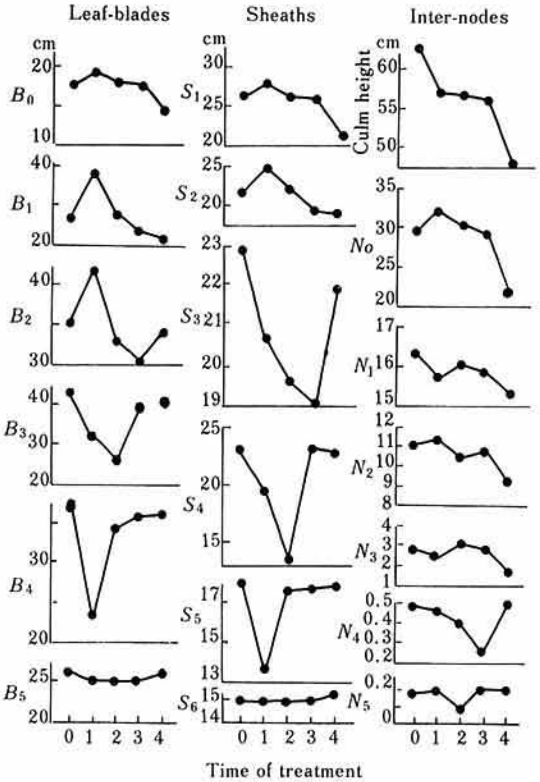


Fig. 6. Effects of nitrogen depletion during various growth periods on the length of leaf-blades, sheaths and inter-nodes.

Note:

Time of treatment	Time of treatment shown by plant age as expressed by number of leaves on main stem	
	Begining	End
0	Untreated control	
1	12. 1	12. 8
2	13. 2	13. 9
3	14. 4	15. 0
4	15. 1	16. 0

The variety produced a total of 16 leaves on a main stem

of organs were influenced simultaneously by the treatments, because organs of each set grew simultaneously: (B_1, S_2, N_3), (B_2, S_3, N_4) and (B_3, S_4, N_5). Thus, the time of treatment for regulating a given organ can be known based on leaf blade position. For example, to regulate the growth of S_4, a treatment should be made at the time when B_3 is growing. To make upper three leaves (flag leaf to the third leaf) short and erect with a variety which produces a total of 16 leaves on main culm nitrogen depletion treatment should be given at plant age* of 11.1–12.1 leaves (leaf age index** 70–76) and continued at least to plant age of 14.1 (leaf age index 88), by considering that the treatment exhibits its effect on the leaf subsequent to the emerged and elongating leaf.

This principle obtained by pot experiments was tested for field applicability. It was confirmed that to shorten a given leaf blade, B_n, nitrogen depletion treatment such as strong midseason drainage, etc. should be applied immediately before or at the time of the emergence of that leaf and to lengthen a given leaf blade nitrogen should be applied at the time when a preceding leaf blade, B_{n+1}, begins to emerge.

Plant type regulated at different growth stages

As it was proved possible to make plant type closer to an ideal type by regulating artificially the elongation of leaf blade, leaf sheath and internode, an experiment was carried out to increase carbon assimilation of plant community during the ripening period by regulating plant type at different growth stages. Plant communities at three levels each of planting density and rate of basic dressing of nitrogen were treated by nitrogen depletion or supply at the middle growth stage (leaf age index 69–92) and the later stage (leaf age index 92–maturity), and carbon assimilation, dry matter production and grain yield were examined.

Dense planting caused a rapid increase of leaf area at an early stage, resulting in an increase in carbon assimilation, dry matter

* Plant age as expressed by number of leaves produced on main culm.

** Leaf age index$=\frac{\text{(Plant age expressed by leaves at a given time)}}{\text{(Total No. of leaves on main culm, specific to a variety)}}\times 100$

production and number of panicles. As number of spikelets/m^2 has a close positive correlation to the product of dry matter weight and nitrogen content at the spikelet differentiation stage, sufficient number of spikelets can be obtained by the increased dry matter at the early stage, even though nitrogen content is lowered in the middle growth stage. Thus, the increase of dry matter at the early stage has an important bearing to the high yield. In addition, an increased dry matter production at the early stage, associated with the rapid absorption of nitrogen by plants, is liable to induce nitrogen shortage at the middle growth stage, resulting in a benefit of natural regulation of plant type.

Nitrogen restriction at the middle growth stage reduced carbon assimilation in that stage, and hence retarded dry matter and leaf area increase at that stage. But, it prevented leaf area from becoming excessive in the later stage and made the upper three leaves short and erect. Nitrogen applied at the panicle initiation stage after the nitrogen restriction treatment was effective in preventing spikelet degeneration, in increasing photosynthetic ability per unit leaf area and consequently increasing carbohydrate reserve before heading. Top dressing of nitrogen at the full heading stage was possible to increase ripening percentage and weight of 1000 grains by an increased carbon assimilation caused by sustained active leaf area and photosynthetic ability per unit leaf area during the ripening period.

On the contrary, top dressing of nitrogen at the middle growth stage caused a marked increase of carbon assimilation and dry matter production in that stage. More dry matter was distributed to leaves, due to high nitrogen content, causing a rapid increase of leaf area with long and drooping upper leaves. Such plant type reduced markedly carbon assimilation at the later stage with a result of lowered ripening percentage, 1000 grain weight and consequently lowered yield.

In summary, it was proved important to regulate plant type so as to have short and erect upper leaves by lowering nitrogen content at the middle growth stage, although it lowered dry matter production at that stage, for increasing carbon assimilation and dry matter production in the ripening stage.

Conclusion

From the aobev results, the followings are regarded important cultural techniques to regulate plant type for increasing yield: Firstly, dense planting and cultural managements to promote an early growth are important in obtaining sufficient number of tillers and leaf area, secondly the restricted nitrogen supply at the middle growth stage is required for achieving plant type which leads to an increased carbon assimilation at the later stage, and thirdly top dressing of nitrogen at the spikelet initiation stage and at the full heading stage is required to maintain active leaf area and photosynthetic ability during the ripening stage.

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