Jpn. J. Crop Sci. 60(4) : 529—536 (1991)

Varietal Difference in Leaf Senescence during Ripening Period of Advanced Indica Rice*

Yoshiharu WADA and Genshichi WADA**
(*Utsunomiya University, Utsunomiya 321, Japan ; ** International Rice Research Institute, P.O. Box 933 Manila, Philippines*)
Received January 25, 1991.

Abstract : The study has been carried out to evaluate varietal difference in leaf senescence during the ripening period in relation to sink size and nitrogen application. Leaf senescence was early in the medium-duration lines. Among the short-duration types, there were both early and late aging lines. The medium-duration lines had larger leaf area and higher sink sizes at the anthesis than short-duration types. The pattern of leaf area reduction during the ripening period in the short duration line, with relatively higher sink size, was almost similar with that in the medium-duration lines. However, in the short-duration lines with relatively small sink size, no significant leaf area reduction was observed until two weeks after the anthesis, and then the leaf area began to decrease rapidly in these lines. Decrease in leaf area during the ripening period varied with the rate of basal nitrogen (N). Higher basal N increased the rate of leaf area reduction by increasing the sink size. On the other hand, N-topdressing at the anthesis decreased the rate of leaf area reduction during the ripening period. Likewise, the reduction in sink size as imposed by removal of spikelets decreased the rate of leaf area reduction during the ripening period. Significant correlation coefficients between the sink size and the amount of N remobilized from leaves to panicles, and between the decrease in leaf area and the amount of N remobilized from leaves to panicles were observed. Therefore, the decrease in the leaf area during the ripening period is mainly governed by the amount of N remobilized from leaves to panicles, which is affected by the N requirement of grains for ripening and the amount of N absorbed during this period.
Key words : Indica rice, Leaf senescence, Nitrogen, *Oryza sativa* L., Sink size.

改良インディカ水稲における出穂後の葉の老化の品種間差：和田義春・和田源七**（宇都宮大学・**国際イネ研究所）

要　旨：国際イネ研究所の改良インディカ水稲の出穂後における葉の老化の品種間差を，シンクの大きさおよび窒素（N）施用との関連から調査した．中生系統は葉の老化が早く，早生系統の中には老化の早い系統と遅い系統とが存在した．中生系統は早生系統に比して出穂期の葉面積が大であり，またシンクサイズも大きかった．一方，早生系統の中では大きなシンクを形成した系統ほど出穂後の葉の老化が早かった．基肥N施用量が多い場合には大きなシンクを形成し，同時に出穂期以降の葉の老化が早かった．また，出穂期のN追肥は葉の老化防止に効果があった．実験的に穂切除や籾数制御を行ってシンクを小さくすると葉の老化が抑えられた．シンクサイズと登熟期に葉から穂に再転流したN量，およびこの時期の葉面積の減少量との間にはいずれも有意な正の相関がみられた．以上の結果から，登熟期の葉の老化は，籾のN要求量と登熟期のN吸収量によって決定される葉からの再転流N量の大小に主に支配されると考えられた．
キーワード：イネ，インディカ，シンクサイズ，窒素，葉の老化．

In the tropics, it has been reported that the yield of rice is mainly governed by the sink size and can be easily increased by increasing sink size, especially in short duration varieties[26,28,29,30,32]. However, when the plant holds higher sink size, the yield is sometimes affected by percentage of ripened grain[8,23], and the latter is mainly governed by the amount of photosynthate produced during the ripening period[11,12]. However, in this period, a large amount of nitrogen (N) is accumulated in panicle with photosynthate[25]. Since the amount of N supplied from the soil is very small compared with the amount of N accumulated in the panicle[26], a large amount of N should be translocated from shoot to panicle and this results in a rapid decrease of leaf area and photosynthetic activity (leaf senescence). Needless to say, such rapid leaf senescence is unfavorable from the view point of production of photosynthate, which is necessary for grain filling.

* This work is a part of the collaborative project between the Government of Japan and IRRI on "Low Input Rice Cultivation Technology" sponsored by the Government of Japan. A part of this paper was presented at the 189th meeting of the Crop Science Society of Japan, April 3, 1990.

** Present address : Nippon Koei Co. Ltd, Tokyo 102 Japan.

Until now, limited information has been available on the varietal difference in leaf senescence and the relationship between leaf senescence and yield components in the tropics. This study has been carried out (1) to evaluate the varietal difference in sink formation, the rate of leaf senescence and ripening of IR short-and medium-duration lines, (2) to clarify the effect of sink size and the amount of N absorption during the ripening period on the progress in leaf senescence.

Materials and Methods

Two field experiments (Exp. 1 and 2) and a pot experiment (Exp. 3) were carried out during the 1989 wet season (WS) at the International Rice Research Institute (IRRI).

Experiment 1.

Four short-duration (96-106 days maturity) and four medium-duration (119-130 days maturity) genotypes were used in the study (Table 1). A randomized complete block design with three replications was employed. Germinated seeds were sown in seedling trays (2 seeds cm^{-3} soil) on July 8, 1989, and transplanted at 16 days after seeding at 20 x 20 cm spacing (Plot size 15.2 m^2). Fertilizers (6 gN $\cdot$ m^{-2}, 4 gP $\cdot$ m^{-2} and 4 gK $\cdot$ m^{-2}) were incorporated in the soil at about 10 cm depth at two days before transplanting. Thirty hills were collected from each plot at weekly interval from the anthesis to the maturity. Three hills with an average number of panicles were selected from 30 hills and leaf area of these plants was determined by an automatic leaf area meter (AAM 8, Hayashi-Denko, Tokyo). These plants were separated to three parts (leaf blades, leaf sheaths+culms and panicles), and dried at 80°C for a week. The dry weight of plants and specific leaf area (SLA) were determined. Leaf area index (LAI) was estimated by two ways; (1) calculated from leaf area of the representative three hills and (2) calculated from leaf dry weight of thirty hills and SLA of the representative three hills. There was no big difference between LAI values estimated by the two different methods. LAI determined by the leaf area of the three representative hills was used in this study. The nitrogen content of each part was determined by the micro Kjeldahl distillation method. Potential sink, sink, and yield were determined as in the previous report[26].

Table 1. Variety and lines used in Experiment 1.

*	Variety/Lines	Growth duration (days)	Sink (g/m^2)
	Short duration		
○	IR39357-133-3-2-2-2	96	623
□	IR25588-7-3-1	98	735
△	IR29658-69-2-1-2	98	668
▽	IR29692-65-2-3-3	98	750
	Medium duration		
●	IR28228-96-3-2-1-3	119	867
■	IR38	119	685
▲	IR29723-143-3-2-1	124	895
▼	IR36892-163-1-2-2-1	126	733

Yield trial in 1988 WS at IRRI.
* ; Symbols used in figures.

Experiment 2.

Rice genotype IR36892-163-1-2-2-1 was employed. Cultural practice was as the same as in Exp. 1. A split plot design with two replications was employed; in a main plot, three basal N levels, 6, 12 and 24 gN $\cdot$ m^{-2} and in a subplot, two top-dressed N levels at the anthesis, 0 and 3 gN $\cdot$ m^{-2}. Each plot size was 25 m^2. Sampling procedure and the determination of dry weight and leaf area were the same as in Exp. 1.

Experiment 3.

Rice genotype IR29658-69-2-1-2 was employed. Sixteen days old seedlings were transplanted in a/5000 pots at two hills, with two plants a hill. Fertilizers (4 g of ammonium sulfate, 2 g of triple super phosphate and 2 g of muriate potash) were incorporated into the soil at one day before transplanting. At the anthesis, pots were grouped into four. The treatments were as follows, (1) all panicles were removed, (2) each panicle was cut to have a half number of spikelet, (3) two grammes of ammonium sulfate was applied and (4) control. At the anthesis and at three weeks after anthesis, leaf area of green leaves of six shoots with an average number of spikelets and an average value of flag leaf length was determined. The experiment was carried out in a green house.

Results and Discussion

Experiment 1.

A significant difference in LAI at the anthesis among the genotypes was observed, the larger value was observed in the medium-duration lines than in the short-duration lines (Table 2). A significant difference in the decreasing pattern of leaf area among genotypes was also observed. Leaf area of the medium-duration lines started to decrease just after the anthesis and decreased week by week. Among the short duration lines, IR25588-7-3-1, which had a relatively large sink size, showed the same decreasing pattern of leaf area as in the medium-duration lines. On the other hand, the other short-duration lines, which had a relatively small sink size, did not show any significant change in leaf area one week after anthesis. The significant decrease in leaf area was observed for the first time at two weeks after anthesis for IR29658-69-2-1-2 and IR29692-65-2-3-3, and at three weeks after anthesis for IR39357-133-3-2-2-2. Table 3 shows the growth duration, potential sink, sink and yield of the eight genotypes in 1989 WS. Comparing the values in 1989 WS with those in 1988 WS (Table 1), the growth

Table 2. Chages in LAI during ripening period.

Variety/Lines	Weeks after unthesis			
	0	1	2	3
Short duration				
IR39357-133-3-2-2-2	2.76 d A	2.51 d A	2.46 ab A	1.68 ab B
IR25588-7-3-1	3.19 cd A	2.70 cd B	2.08 bc C	1.23 b D
IR29658-69-2-1-2	3.46 bc A	3.38 ab A	2.78 a B	1.96 a C
IR29692-65-2-3-3	2.73 d A	2.57 cd A	1.95 c B	1.47 ab C
Medium duration				
IR28228-96-3-2-1-3	3.91 ab A	3.00 bc B	2.42 ab C	1.82 a D
IR38	3.85 ab A	3.32 ab B	2.20 bc C	1.73 a D
IR29723-143-3-2-1	3.72 ab A	3.19 ab B	2.33 abc C	1.66 a D
IR36892-163-1-2-2-1	4.00 a A	3.54 a B	2.77 a C	1.85 a D

A common capital letter and a common small letter are not significantly different by Duncan's new multiple range test at P=0.05 in a row and in a column, respectively.

Table 3. Growth duration, potential sink, sink and yield of the eigtht genotypes in 1989 WS.

Variety/Lines	Growth duration (days)	Potential sink ($g \cdot m^{-2}$)	Sink ($g \cdot m^{-2}$)	Yield ($g \cdot m^{-2}$)
Short duration				
IR39357-133-3-2-2-2	106	581	461	381
IR25588-7-3-1	106	951	587	495
IR29658-69-2-1-2	106	860	564	383
IR29692-65-2-3-3	106	752	485	330
Medium duration				
IR28228-96-3-2-1-3	126	965	628	382
IR38	126	752	605	397
IR29723-143-3-2-1	130	1066	678	448
IR36892-163-1-2-2-1	130	1109	629	412

Values are means of three replications.

durations were longer and sink sizes were smaller in 1989 WS in all the genotypes. However, the genotype order of these values was almost the same in both 1988 and 1989 WS. A significant correlation coefficient was observed between the sink size and the decreased leaf area during two weeks after anthesis ($r=0.840$, $P<0.01$ Fig. 1).

Nitrogen content (on dry basis) of rice plant at the anthesis and at two weeks after anthesis was shown in Table 4. Nitrogen contents of panicles were almost constant at about 1% and there was no significant difference among the genotypes and between 0 and 2 weeks after anthesis. Therefore the genotype with larger sink size required more amount of N for the ripening of grains.

There are two sources of N for the developing grain ; soil nitrogen absorbed by root and translocated to shoot (absorbed N), and redistribution of N accumulated in vegetative tissue before anthesis (remobilized N). The amount of remobilized N from shoot to panicle was much higher than the amount of N absorbed during this period in all the genotypes (Table 5). The amount of N absorbed during two weeks after anthesis was not related with the sink sizes of the genotypes. A significant correlation coefficient between sink size and the amount of remobilized N was observed (Fig. 2). Both the amount of remobilized N from leaf blades and from leaf sheaths+culms were highly correlated with sink size ($P<0.01$, Fig. 2). The amount of remobilized N from leaf blades to grains was larger than those of remobilized N from leaf sheaths and culms (Table 5). About 66% of total remobilized N in panicle was estimated to be derived from leaf blades (Fig. 2). The decrease in leaf area during this period was also highly correlated with the amount of N remobilized from leaf blades to panicles ($P<0.01$, Fig. 3). Therefore it can be concluded that the varietal difference in leaf senescence (evaluated by leaf area reduction) is primarily governed by the amount of N remobilized from shoot (mainly

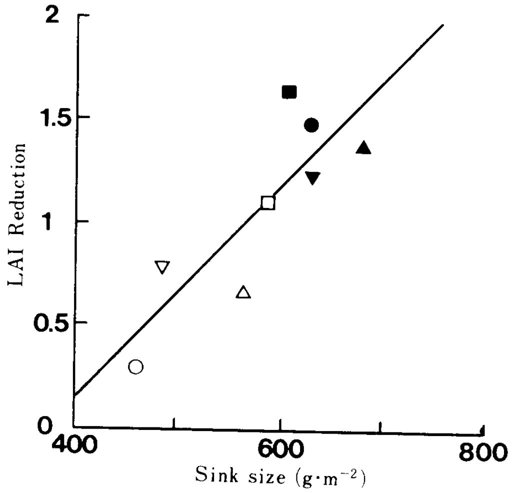

Fig. 1. Relationship between sink size and LAI reduction during two weeks after anthesis.
Symbols are the same in Table 1.
$y=-1.93+5.19\times10^{-3}x$, $r=0.840^{**}$.

Table 4. Nitrogen content (% on dry weight basis) of panicles (P), leaf blades (LB), and leaf sheaths+culms (LS+C) of the eight genotypes after 0 and 2 weeks from anthesis.

Variety/Lines	0 week			2 weeks		
	P	LB	LS+C	P	LB	LS+C
Short duration						
IR39357-133-3-2-2-2	1.26	2.46	0.88	1.17	2.08	0.64
IR25588-7-3-1	1.07	2.54	0.89	1.03	2.03	0.61
IR29658-69-2-1-2	1.11	2.58	0.85	0.95	1.99	0.59
IR29692-65-2-3-3	1.08	2.26	0.72	0.99	1.93	0.56
Medium duration						
IR28228-96-3-2-1-3	0.96	1.84	0.56	1.00	1.63	0.46
IR38	1.11	2.18	0.70	1.14	1.57	0.55
IR29723-143-3-2-1	1.03	1.89	0.57	1.03	1.54	0.48
IR36892-163-1-2-2-1	0.98	2.12	0.58	1.06	1.83	0.56

Values are means of 9 replications over 3 plots.

Table 5. Absorbed and remobilized nitrogen during two weeks after anthesis (mg • hill^{-1}).

Variety/Lines	Absorbed N	Remobilized N LB	LS+C	Total
Short duration				
IR39357-133-3-2-2-2	48.0	32.0	27.1	59.1
IR25588-7-3-1	31.8	58.4	35.0	93.4
IR29658-69-2-1-2	21.6	52.1	24.8	76.9
IR29692-65-2-3-3	34.3	43.2	23.4	66.6
Medium duration				
IR28228-96-3-2-1-3	54.1	53.1	33.3	86.4
IR38	13.8	71.7	42.6	114.3
IR29723-143-3-2-1	33.2	71.3	46.6	117.9
IR36892-163-1-2-2-1	32.2	62.0	36.1	98.1

Values are calculated from the data on Table 4.
LB; Leaf blades, LS+C; Leaf sheaths+culms.

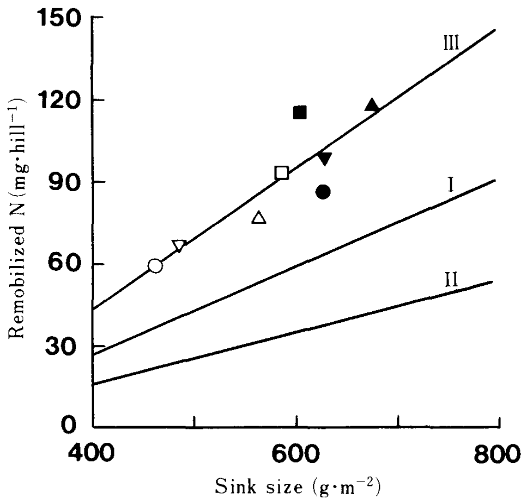

Fig. 2. Relationships between sink size and remobilized N during two weeks after anthesis.
Symbols are the same in Table 1.
I; Remobilized N from leaf blades ($y=-38.0+0.161x$, $r=0.880^{**}$), II; Remobilized N from leaf sheaths+culms ($y=-20.3+0.093x$, $r=0.811^{**}$), III; Total remobilized N (I+II, $y=-58.3+0.245x$, $r=0.881^{**}$).

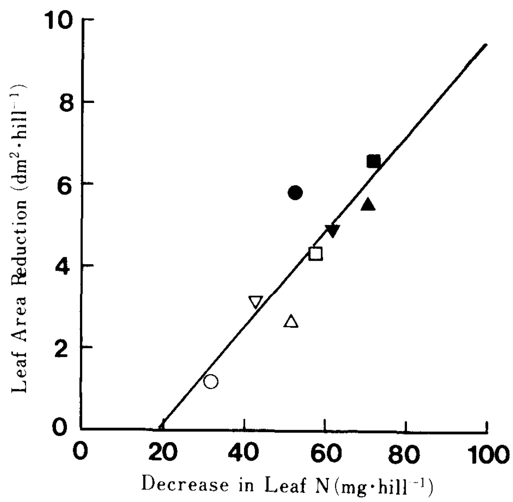

Fig. 3. Relationship between the decrease in leaf blade N and leaf area reduction during two weeks after anthesis.
Symbols are the same in Table 1.
$y=-218.4+11.7x$, $r=0.875^{**}$.

from leaf blades) to panicle which is affected by sink size.

Experiment 2.

The effects of the rate of basal N and top-dressed N at the anthesis on the decrease in LAI during the ripening period is summarized in Table 6. At the anthesis, higher LAI was observed in the plants grown under a higher rate of basal N. Without N top-dressing, LAI values of the 3 basal N did not show any significant difference at 2 and 4 weeks after anthesis. Therefore, higher rate of LAI reduction during the ripening period occurred in the plants grown under a higher rate of basal N without N top-dressing. Since sink size is correlated with an amount of N in plant at the anthesis[22,26,30], the plants grown under a higher rate of basal N have larger sink size and require larger amount of N for ripening. This result shows large sink size promotes LAI reduction (leaf senescence) during the ripening period. Top-dressing of N at the anthesis decreased the rate of LAI reduction during the ripening period, especially in the plants grown under higher rate of basal N. This means when large sink is produced, it requres a large amount of supplied N for maintaining LAI after anthesis.

Experiment 3.

Decrease in leaf area of the plants with half the amount of sink size of control plant and with no panicle were significantly lower than that of the control plant (Table 7). Furthermore, N top-dressing at the anthesis decreased the rate of leaf area reduction.

It has been reported that the removal of panicle or decreasing sink size retards leaf senescence[2,5,13,16,20,31]. One of the biggest effects of panicle removal or decreasing sink size on leaf senescence is to decrease the rate of translocatory loss of N from leaves[31]. In this experiment, the effect of panicle removal on leaf area reduction was shown to be similar to that of top-dressing of N at the anthesis (Table 7).

Based on the Exps. 1, 2 and 3, it can be said that the observed varietal difference in leaf senescence during the ripening period is related with the amount of N remobilized from leaf to panicle, which is determined by the sink size and the amount of N absorbed during the ripening period. These results are in good agreement with the results obtained in Japonica rice[24].

During the progress of leaf senescence of rice plant, nitrogenius compounds in leaves are degraded and remobilized to other parts of the plant[7,18]. Under N deficient conditions, it is well known that leaf senescence is accelerated[9,21]. Since Molish proposed the idea that leaf senescence of plant was induced as a result of diversion of nutrient from leaves to the developing fruits[10], until now, a lot of hypotheses concerning on the monocarpic senescence were presented, and these hypoth-

Table 6. The effect of basal N and top-dressed N at the anthesis on LAI reduction after anthesis in IR36892-163-1-2-2-1 (Exp. 2).

Weeks	Basal/Top-dressed N ($g \cdot m^{-2}$)					
	6/0	12/0	24/0	6/3	12/3	24/3
0	4.6 b	5.6 b	7.5 a	4.6 b	5.6 b	7.5 a
2	2.4 b	3.3 ab	3.3 ab	2.8 b	3.5 ab	4.1 a
4	0.8 b	1.0 b	ND	0.9 b	1.7 a	ND

Values are means of two plots.
ND; Not determined.
In a row, common letters are not significantly different by Duncan's new multiple range test at $P=0.05$.

Table 7. The effect of sink reduction and N top-dressing at the anthesis on leaf senescence (green leaf area) of IR29658-69-2-1-2 grown in pots (Exp. 3).

Weeks	Treatment	Grain number per panicle	Green leaf area ($cm^2 \cdot tiller^{-1}$)
0	Control	63.0±2.5	178.7± 6.7
3	Control	65.7±3.4	96.3± 6.9
	1/2 panicle	31.7±2.4	115.9±10.0
	No panicle	0	118.3±10.2
	N top-dressed	64.0±2.9	114.0±14.4

Values are mean±SE of six replications.

eses were summarized in recent reviews[14,17,19]. The cause of monocarpic leaf senescence may be different among plant species. In rice plants, it was reported that the translocation of metabolites and minerals from leaf to grain results in a deprivative stress in leaves[1,16]. Furthermore, leaf senescence is affected by environmental conditions as well as genetic properties of plants. Under the field conditions, generally the amount of N absorbed by plant after anthesis is small compared to the amount of N required by grains for ripening[22,25,26]. The shortage of nutrients do play a role in monocarpic senescence of leaves. The results of the study support this hypothesis. For keeping leaves at a high level of photosynthesis and high leaf area duration, it is important to decrease the translocatory loss of N in leaves by increasing N absorption during the ripening period. In order to increase the yield by increasing sink size, a large amount of N should be required before the anthesis. However, farmers in developing countries cannot use a large amount of fertilizer due to its steadily increasing cost as compared with paddy prices. Therefore, N-use efficiency of rice genotype[3,4,30], and fertilizer application practice[6,11,15,26] become very important. In this respect, the contribution of plant N at the anthesis and at maturity is the most important in the tropics, but in turn, the higher contribution of plant N at the anthesis to sink size may promote leaf senescence and may reduce the production of photosynthates during the ripening period. Therefore, leaf senescence must be studied further in relation to optimization of the use of plant N.

Acknowledgments

The authors wish to thank the staff members of the "Low Input Rice Production Technology" porgram, IRRI, for their kind help during the time that the work for this study was conducted. The authors wish to express our gratitude to Dr. K. Watanabe, Professor of Utsunomiya University, for his critical readings of the manuscript.

References

1. Biswas, A.K. and M.A. Choudhuri 1980. Mechanism of monocarpic senescence in rice. Plant Physiol. 65 : 340—345.
2. Cho, D., S. Yokoi and Y. Murata 1981. Studies on the photosynthesis and dry matter production of rice plants. III. Influence of whole or partial removal of panicles at heading on photosynthesis, dry matter production and yield components. Jpn. J. Crop Sci. 50 : 67—71*.
3. De Datta, S.K. and F.E. Broadbent 1988. Methodology for evaluating nitrogen utilization efficiency by rice genotypes. Agron. J. 80 : 793—798.
4. ——— and ——— 1990. Nitrogen-use efficiency of 24 rice genotypes on an N-deficient soil. Field Crops Res. 23 : 81—92.
5. Ishihara, K., H. Nakaya and T. Hirasawa 1989. Effect of panicle removal on production and distribution of dry matter and flag leaf photosynthesis in rice plants. Jpn. J. Crop Sci. 58 (Extra issue 2) : 105—106**.
6. Kimura, J. and H. Chiba 1943. Studies on the efficiency of nitrogen absorbed by the rice plant for yield of grains and straw. J. Sci. Soil Manure, Japan 17 : 480—497*.
7. Mae, T. and K. Ohira 1981. The remobilization of nitrogen related to leaf growth and senescence in rice plants (*Oryza sativa* L.). Plant Cell Physiol. 22 : 1067—1074.
8. Matsushima, S. and G. Wada 1958. Analysis of developmental factors determining yield and its application to yield prediction and culture improvement of lowland rice. XLVIII. Studies on the mechanism of ripening (9). Relation of the amount of carbohydrates stored by the time of heading, that of carbohydrates accumulated after heading and the nitrogen content at heading time. Proc. Crop Sci. Soc. Japan 27 : 201—203*.
9. Mei, H.S. and K.V. Thimann 1984. The relation between nitrogen deficiency and leaf senescence. Physiol. Plant. 62 : 157—161.
10. Molish, H. 1929. Über die Mittel, das Leben der Pflanze zu verlängern. In Die Lebensdauer der Pflanze. Jena Verlag von Gustav Fisher 98—115.
11. Murata, Y. and A. Osada 1959. Studies on photosynthesis in rice plant. XII. The effect of three major nutrient element supply upon the photosynthesis activity of rice leaves. Proc. Crop Sci. Soc. Japan 28 : 184—187*.
12. ——— and S. Matsushima 1975. Rice. In Crop Physiology. Some Case Histories (Ed.) L.T. Evans, Cambridge Univ. Press, London 73—99.
13. Nakaya, H., K. Ishihara and T. Hirasawa 1989. Physiological response to flag leaf photosynthesis to panicle removal in plants. Jpn. J. Crop Sci. 58 (Extra issue 2) 107—108**.
14. Noodĕn, L.D. 1980. Senescence in the whole plant. In Senescence in Plants. (Ed.) K.V. Thimann, CRC Press, Boca Raton, Florida. 219—258.
15. Prasad, R. and S.K. De Datta 1979. Increasing

fertilizer efficiency in wetland rice. In Nitrogen and Rice. IRRI, Los Baños, the Philippines. 465—487.

16. Ray, S. and M.A. Choudhuri 1981. Mobilization of metabolites from leaves to grains as the cause of monocarpic senescence in rice. Plant Physiol. 68 : 1345—1348.
17. Stoddart, J.L. and H. Thomas 1982. Leaf senescence. In Encyclopedia of Plant Physiology 14A (Eds.) D. Boulter and B. Parthier, Springer-Verlag, Berlin. 592—636.
18. Tanaka, A. 1959. Studies on the characteristics of physiological function of leaf at definite position on stem of rice plant (Part 3). Relation between nitrogen metabolism and physiological function of leaf at definite position. J. Sci. Soil Manure, Japan 26 : 413—418*.
19. Thomas, H. and J.L. Stoddart 1980. Leaf senescence. Ann. Rev. Plant Physiol. 31 : 83—111.
20. Tsuno, Y. and T. Shimizu 1962. Studies on yield forecast in main crops. VI. On the relation between nitrogen content in leaves and photosynthetic ability of rice plant at ripening stage. Proc. Crop Sci. Soc. Japan 30 : 325—328*.
21. Uchida, N., Y. Wada and Y. Murata 1982. Studies on the changes in photosynthetic activity of a crop leaf during its development and senescence. II. Effect of nitrogen deficiency on the changes in the senescing leaf of rice. Jpn. J. Crop Sci. 51 : 577—583*.
22. Wada, G. 1969. The effect of nitrogen nutrition on the yield-determining process of rice plant. Bull. Natl. Inst. Agric. Sci. A16 : 27—167*.
23. ——— and S. Matsushima 1969. Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. XCVI. Relation of the number of spikelets per unit field area to the percentage of ripened grains and the yield with special reference to the optimum number of spikelets per field area and the optimum percentage of ripened grains for maximizing the yield of rice. Proc. Crop Sci. Soc. Japan 38 : 294—298*.
24. ———, C. Kominami and S. Katoh 1973. Effect of nitrogen on leaf area duration during ripening period. Proc. Crop Sci. Soc. Japan 42 (Extra issue 2) : 87—88**.
25. ———, S. Shoji and J. Takahashi 1973. The fate of fertilizer nitrogen applied to the paddy field and its absorption by rice plant. 4. Distribution of basal and top-dressed nitrogen in rice plant. Proc. Crop Sci. Soc. Japan 42 : 84—90*.
26. ———, ——— and T. Mae 1986. Relationship between nitrogen absorption and growth and yield of rice plants. JARQ 20 : 135—145.
27. ———, D.V. Aragones and P. Sta. Cruz 1987. Physiological aspects of short duration varieties. Jpn. J. Crop Sci. 56 (Extra issue 1) : 4—5.
28. ———, ——— and R.C. Aragones 1989. Nitrogen absorption pattern of rice plant in the tropics. Jpn. J. Crop Sci. 58 : 225—231.
29. ——— and P.C. Sta. Cruz 1989. Varietal differences in nitrogen response of rice plants with special reference to growth duration. Jpn. J. Crop Sci. 58 : 732—739.
30. ——— and ——— 1990. Nitrogen response of rice varieties with reference to nitrogen absorption at early growth stage. Jpn. J. Crop Sci. 59 : 540—547.
31. Wada, Y., K. Watanabe and K. Miura 1990. The effects of source to sink ratio on carbohydrate production and leaf senescence during ripening period of rice. I. The effect on ripening, senescence of the flag leaf and the partitioning of carbohydrates and nitrogen in plant. Jpn. J. Crop Sci. 59 (Extra issue 1) : 170—171**.
32. Yoshida, S. 1981. Fundamentals of Rice Crop Science. IRRI, Los Baños, the Philippines. 213—230.

* In Japanese with English summary.

** In Japanese. Translocated by present authors.