BIOLOGIA PLANTARUM (PRAHA)

33 (2) : 105–114, 1991

Effect of Spikelet Removal on the Whole Plant Senescence of Rice

R. I. KHAN and M. A. CHOUDHURI

Botany Department, Burdwan University, Burdwan – 713 104, West Bengal, India

Abstract. The rice (*Oryza sativa* L.) cultivar IET 1444 showed a nonsequential mode of senescence as evident from the decline in chlorophyll and protein of the flag and second leaves at the senescent stage. Removal of 50, 75 and 100 % spikelets from the panicle of rice plant or emasculation of the panicle by hot water treatment induced the development of secondary branch from the axil of second leaf but 25 % removal had no effect. Similarly, removal of 75 and 100 per cent spikelets from the panicle of secondary branch induced tertiary branch development, while 25 and 50 per cent removal had no such effect. Similar treatments on tertiary branch had no effect on further branch production. The pattern of leaf senescence of the untreated (control) main tiller, secondary and tertiary branches was identical, *i. e.* nonsequential, which could be changed into the sequential type only by the development of additional sinks (*i. e.* side branch). The leaf area and the seed number of secondary and tertiary branches were gradually reduced and reached a critical value in the tertiary branch. The removal of spikelets or emasculation delayed leaf senescence of the main tiller and the secondary and tertiary branches. Also the longevity of the whole plant could be increased by 40 d *i. e.*, up to the senescence of the tertiary branch. Both leaves and reproductive parts control side branch production, which, in turn, controls the longevity of the whole rice plant.

The mechanism of monocarpic senescence has been studied in leguminous (Lindoo and Nooden 1977, Valio and Polo 1983, Grover *et al* 1985, Biswas and Mondal 1987) and graminaceous (Biswas and Choudhuri 1980, Ray and Choudhuri 1981, Mondal and Choudhuri 1984, Biswas and Mondal 1986) plants. For rice plants, Biswas and Choudhuri (1980) and Ray and Choudhuri (1981) suggest that the mobilization of metabolites from leaves to grains results in a deprivational stress in leaves, followed by a decrease in the ratio of cytokinin to abscisic acid leading to a hastening up of leaf senescence. However, the direct signal for actual triggering of senescence does not seem to be the mobilization of metabolites. Recently, Veierskov and Thimann (1988) suggested a probable hypothesis for the onset of senescence in oat leaf. According to them the protease initially does not have access to its substrates until the vacuolar membrane is impaired. This enables protease to enter the cytosol and attack the proteins there and in the organelles. Slabý and Šebánek (1987), on the other hand, showed that cytokinin-like substances increased in

Received October 2, 1989; accepted March 16, 1990

sunflower leaf and reached maximal value when the leaf blade area reached approximately 70 % of the final value and continuously decreased thereafter, with concomitant increase in the release of ethylene. It seems likely that early during leaf blade senescence, depletion of ethylene-antagonistic hormones, especially cytokinins and gibberellins, occurs. Such an event, in turn, probably releases controls on the production of ABA and ethylene and/or influences the ability of these two hormones to induce senescence (Mattoo and Aharoni 1988). From the experimental evidence it appears that senescence is brought about by an interaction between some or all of the five known phytohormones.

Prakash (1976), Lindoo and Nooden (1977), Kulkarni and Schwabe (1985) and Nooden (1988) have suggested that a "Senescence signal" may be responsible for the induction of senescence. Recently, Choudhuri and Mondal (1988) have suggested that senescence genes may be induced/activated during flowering, and senescence can be prevented only by checking flowering of photoperiod-sensitive plants by subjecting them to unfavourable conditions. Several workers have attempted to find out the effect of removal of flowers or fruits on whole plant senescence, but the results are mostly inconclusive. In pea (Grover *et al* 1985), wheat (Biswas and Mondal 1986), rice (Ray and Choudhuri 1981, Mondal and Choudhuri 1984) and soybean (Leopold *et al.* 1959, Wittenbach 1982), the removal of flowers and fruits has delayed leaf senescence, whereas, in maize (Allison and Weinmann 1970, Christensen *et al.* 1981) and *Capsicum annuum* (Hale and Brady 1977) such treatment accelerated senescence. Valio and Polo (1983) also demonstrated that removal of flowers on fruits in *Phaseolus vulgaris* delayed leaf senescence, depending on their number.

The present study tried to examine the effect of removal of spikelets on whole plant senescence of rice.

MATERIALS AND METHODS

Healthy and viable seeds of photoperiod-insensitive rice (*Oryza sativa* L. cv. IET 1444) were surface-sterilized by 0.1 % $HgCl_2$ for 1 min and allowed to germinate in plastic trays containing moistened blotting paper at 37 °C. Germinated seeds were sown in the seed-bed and 30-d-old seedlings were transplanted in earthen pots (height 25 cm and diameter 30 cm) filled with garden soil mixed with cowdung as the only fertilizer.

At the anthesis stage of the main tiller (98 d old plant), 25, 50, 75 and 100 % of the spikelets were removed manually from the panicle or emasculated by hot water treatment (55 °C for 5 min) from a lot of 10 plants in each group. Rice plants with untreated panicles served as control. The development of secondary branch at the axil of second leaf of these treated plants was recorded. The treatment was repeated with secondary and tertiary branches.

The senescence pattern of the first (flag) and the second leaf of the main tiller the

secondary and tertiary branches was noted by recording the changes in chlorophyll (Arnon 1949) and protein (Lowry *et al.* 1951) amounts, which served as reliable indicators of rice leaf senescence (Biswas and Choudhuri 1980). Their amounts were determined in leaves of rice plants at the anthesis stage (98, 119 and 138 d), grainfilling stage (105, 126 and 145 d), grain development stage (112, 133 and 152 d), grain maturation stage (119, 140 and 159 d) and senescent stage (126, 147 and 166 d) in the case of main tiller, secondary branch and tertiary branch, respectively (Mondal and Choudhuri 1985).

The leaf area of different leaves of the main tiller, secondary and tertiary branches were measured individually by graphical methods. In each case at least ten plants were taken for recording. Each treatment was repeated three times with three replicas for each set. The data were statistically analysed at the treatment and replication levels and the least significant difference (LSD at $P = 0.05$) values were calculated and entered in tables.

RESULTS AND DISCUSSION

The chlorophyll and protein contents of the flag leaf and the second leaf of the control main tiller, secondary branch and tertiary branch gradually decreased during reproductive development (Table 1). The studied cultivar of rice thus showed a nonsequential mode of leaf senescence of the main tiller and the secondary and tertiary branches, where the younger flag leaf senesced earlier than the older second leaf. Similar observations were made by Ray and Choudhuri (1981) and Mondal and Choudhuri (1984) in other rice cultivars. Hence the nonsequential pattern of leaf senescence was genetically controlled and only removal of reproductive parts could change it to a sequential mode.

The removal of 50, 75 and 100 % spikelets from the panicle or emasculation of the main tiller induced the development of the secondary branch, having only two leaves, from the axil of the second leaf (Table 2), but removal of 25 per cent spikelets did not induce it. Similarly, the removal of 75 and 100 percent spikelets from the panicle or emasculation of the secondary branch induced the development of the tertiary branch at the second leaf axil (Table 2), bearing two leaves. However, the removal of 25 and 50 % spikelets from the secondary branch had no effect on branch production. A similar treatment on the tertiary branch completely failed to induce further quaternary branch development. Thus the reproductive parts (panicle) exerted an inhibitory influence on branch development comparable with the phenomenon of "apical dominance". Nevertheless, the influence of factor(s) responsible for inducing branch development became limiting in the tertiary branch. As a consequence of this, there was no quaternary branch development and the plant completely senesced thereafter. Thus, the apical dominance-like effect as exerted by the panicle appears to regulate the onset of whole plant senescence. The removal of a higher percentage of spikelets was necessary for destroying the apical dominance-

Table 1

Changes in chlorophyll and protein [g kg^{-1} (f. m.)] contents in the flag and second leaves of the main tiller, secondary and tertiary branches of rice plant (cv. IET 1444) during reproductive development. Figures within parentheses indicate age of the plant at the development stage.

Percentage of spikelets removed	Leaf position	Reproductive stages and plant age [d]							
		Chloro-phyll	Protein	Chloro-phyll	Protein	Chloro-phyll	Protein	Chloro-phyll	Protein
		Grain-filling (105)		Grain development (112)		Grain maturation (119)		Senescent (126)	
Main tiller									
	Flag	1.18	78.4	0.73	64.8	0.25	51.8	0.07	39.8
0	Second	0.95	65.9	0.63	60.3	0.21	49.4	0.13	43.9
(Control)	LSD at 5% level	0.056	13.3	0.02	4.3	0.04	2.9	0.05	3.3
	Flag	1.1	81.6	0.75	64.3	0.24	50.6	0.08	40.2
25	Second	0.94	66.7	0.65	61.8	0.21	47.8	0.12	44.2
	LSD at 5% level	0.13	11	0.05	3.6	0.02	4.8	0.03	3.1
	Flag	1.08	76.1	0.76	65.1	0.26	54.8	0.14	44.69
50	Second	0.96	71.5	0.61	62.3	0.22	48.3	0.13	45.7
	LSD at 5% level	0.05	3.4	0.14	2.3	0.06	3.6	0.011	1.1
	Flag	1.01	76.9	0.83	66.6	0.33	55.1	0.15	50.5
75	Second	0.96	68.7	0.64	59.5	0.29	53.3	0.13	48.1
	LSD at 5% level	0.04	8.2	0.05	6.3	0.05	1.8	0.01	3.2
	Flag	1.11	80.1	0.8	68.1	0.34	60.2	0.21	52.7
100	Second	0.92	72.3	0.61	58.4	0.31	55.5	0.18	49.3
	LSD at 5% level	0.21	5.2	0.031	7.12	0.02	3.5	0.016	2.7
	Flag	1.03	80.2	0.81	66.1	0.32	62.8	0.21	51.3
Emasculated	Second	0.98	74.9	0.65	60.6	0.28	56.1	0.17	50.7
	LSD at 5% level	0.07	1.8	0.04	4.7	0.02	3.4	0.04	1.06

Secondary branch		(126)		(133)		(140)		(147)	
	Flag	0.99	72.2	0.71	62.9	0.29	50.2	0.11	38.2
0	Second	0.91	70.2	0.66	58.5	0.28	48.3	0.16	42.6
(Control)	LSD at 5% level	0.015	1.6	0.07	1.8	0.016	1.8	0.04	4.35
	Flag	0.93	73.2	0.68	63.6	0.305	52.1	0.11	38.5
25	Second	0.94	71.1	0.65	58.8	0.29	47.7	0.175	43.7
	LSD at 5% level	0.0042	2.1	0.07	4.1	0.011	4.1	0.045	3.41
	Flag	0.98	75.3	0.64	60.4	0.34	52.4	0.13	42.0
50	Second	0.91	69.3	0.69	59.9	0.33	50.3	0.18	44.5
	LSD at 5% level	0.02	6.3	0.08	1.13	0.022	1.2	0.038	2.14
	Flag	0.92	75.3	0.72	66.3	0.37	56.0	0.16	48.3
75	Second	0.92	64.1	0.66	56.6	0.34	52.2	0.131	44.65
	LSD at 5% level	0.001	5.6	0.01	3.1	0.039	1.7	0.031	2.65
	Flag	1.02	76.1	0.72	67.3	0.38	60.2	0.18	51.9
100	Second	0.93	66.6	0.67	58.5	0.34	55.3	0.17	47.8
	LSD at 5% level	0.009	5.6	0.03	7.7	0.021	5.6	0.002	3.8
	Flag	0.96	76.5	0.7	67.3	0.39	59.2	0.19	50.7
Emasculated	Second	0.93	65.5	0.65	60.3	0.35	58.8	0.16	48.5
	LSD at 5% level	0.02	11.3	0.02	3.7	0.035	1.4	0.022	1.65

Continued overleaf

Tertiary branch		(145)		(152)		(159)		(166)	
0	Flag	0.89	73.2	0.71	62.2	0.30	51.1	0.08	38.2
	Second	0.86	70.2	0.57	58.3	0.26	48.2	0.15	42.3
	LSD at 5% level	0.023	1.83	0.08	2.8	0.023	1.83	0.041	3.3
25	Flag	0.88	74.3	0.7	62.3	0.31	52.3	0.08	38.9
	Second	0.86	70.5	0.59	57.2	0.25	48.8	0.14	41.1
	LSD at 5% level	0.023	3.6	0.06	3.7	0.041	2.24	0.044	2.2
50	Flag	0.91	72.2	0.65	60.3	0.3	53.7	0.1	39.0
	Second	0.85	71.9	0.64	57.7	0.27	50.3	0.16	42.2
	LSD at 5% level	0.041	0.57	0.002	1.51	0.016	1.96	0.05	1.67
75	Flag	0.95	79.2	0.69	65.5	0.33	58.1	0.14	44.5
	Second	0.93	72.7	0.66	63.3	0.32	51.1	0.18	44.9
	LSD at 5% level	0.01	4.1	0.005	2.1	0.007	5.9	0.021	0.03
100	Flag	0.95	81.1	0.73	67.7	0.35	58.2	0.15	46.5
	Second	0.94	73.3	0.66	64.6	0.34	52.5	0.19	48.5
	LSD at 5% level	0.006	5.9	0.027	2.8	0.009	3.3	0.033	1.11
Emasculated	Flag	0.91	75.6	0.71	66.6	0.33	57.7	0.14	45.1
	Second	0.9	75.2	0.65	65.0	0.32	54.9	0.17	47.3
	LSD at 5% level	0.008	0.02	0.041	3.8	0.005	2.71	0.018	1.22

Table 2

Effect of removal of spikelets on branch development, leaf area and longevity of the whole plant of rice (cv. IET 1444). A = absence of branch production, P = presence of branch production.

Treatment	Main tiller (MT)				Secondary branch (SB)				Tertiary branch (TB)			
	Branch production	Leaf area [cm_2] Flag	Second	Longevity of MT [d]	Branch production	Leaf area [cm^2] Flag	Second	Longevity of plant [d] (MT + SB)	Branch production	Leaf area [cm^2] Flag	Second	Longevity of plant [d] (MT + SB + TB)
Control (intact)	A	28	39	126	A	18	19	147	A	13	14	166
25 % spikelets removed	A	28	39	126	A	18	19	147	A	13	14	166
50 % spikelets removed	P	28	39	126	A	18	19	147	A	13	14	166
75 % spikelets removed	P	28	39	129	P	18	19	149	A	13	14	166
100 % spikelets removed	P	28	39	133	P	18	19	154	A	13	14	173
Emasculation	P	28	39	133	P	18	19	154	A	13	14	173
Second leaf and spikelets removed	A	–	–	–	A	–	–	–	–	–	–	–

like effect and inducing the development of tertiary branch than what was necessary for the induction of secondary branch development.

The area of the flag and second leaves of the secondary and tertiary branches gradually decreased simultaneously with their seed production capacity (Table 2). Thus 82 ± 4, 62 ± 3 and 43 ± 3 seeds were produced by the main tiller, the secondary and tertiary branches, respectively. Hence, the initiation of side branches was a result of balance between the inhibitory influence from the spikelets and the promotive influence of the leaf subtending the branch (mediated by metabolites and phytohormones). The failure to induce branch development at the leaf axil of the tertiary branch even after 100 % spikelet removal or emasculation suggested that the branch-initiating factor(s) supplied by the second leaf of tertiary branch became limiting due to the reduction of leaf area below a critical level. That the leaf provides an essential factor(s) for side branch development can be corroborated by the finding that complete removal of both spikelets and the second leaf from the main tiller and similar treatment with the secondary branch failed to induce secondary and tertiary branch development (Table 2).

The 50, 75 and 100 % removal of spikelets from the panicle or emasculation of the main tiller delayed leaf senescence by maintaining chlorophyll and protein levels of the flag and the second leaf above that of the control plant, but such treatments caused in the main tiller a shift to the sequential mode of leaf senescence. The reason for change from the nonsequential to sequential leaf senescence in the main tiller was probably the formation of secondary branch as an additional sink. This confirms the earlier observations of Ray and Choudhuri (1981) and Mondal and Choudhuri (1984). The present study further showed that removal of only 25 % of total spikelets had no delaying effect on senescence and thus the reduction of sink demand was related with senescence development.

Similar results were also observed in the secondary branch (Table 1) where less than 50 % removal of spikelets did not delay leaf senescence but 75 and 100 % removal of spikelets and emasculation not only delayed leaf senescence but also induced a sequential mode of leaf senescence in that branch. Although removal of 75 and 100 % spikelets of emasculation of tertiary branch (Table 1) delayed leaf senescence, quaternary branches were not formed and the mode of leaf senescence behaviour was not changed.

The longevity of the main tiller (whole plant) was extended by about 40 d over the untreated control plant owing to side branch production at the second leaf axil (Table 2). Hence both leaves and reproductive parts might exert regulatory role on side branch production which, in turn, might control the longevity of the whole plant. The senescenceinducing substance, if formed in the subtending second leaf, was not transmitted to the leaves of the side branch. If that happened, the second leaf would have senesced earlier than the flag leaf of the side branch which was, however, not the case. Thus in rice, the failure of further branch production on removal of spikelets marks the end of the whole plant.

Acknowledgement

The authors acknowledge the financial assistance rendered by the Council of Scientific and Industrial Research in the form of a Junior research fellowship to RIK.

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Formation of adventitious roots has been of interest to plant sciences for many years and the interest still has not dropped especially due to the continually increasing number of economically important plants propagated by cuttings. In spite of concentrated effort of plant physiologists and biochemists to elucidate control mechanisms concerned with the initiation and development of new roots, much of the fundamental biology of these processes is still unsufficiently understood.

Because of intensive study the present literature on the subject is voluminous. The purpose of this book, as editors themselves declare, was to bring together, review, and interpret the research that has been done. According to my opinion, both authors and editors were exceedingly successful in fulfilment of their target. Twenty six contributors from 10 countries represent the entire range of plant sciences from plant physiology, genetics, molecular biology and biochemistry to horticulture and forestry concerning the biological and biochemical formation of roots.

The book has been divided into five sections: Development, Physiology and Biochemistry, Growth Regulators, Environmental Considerations, Future Outlook, comprising 22 chapters. The nature of rooting potential including possibilities for its affecting during maturation is especially dealt with in the first section. The second section brings information concerning some aspects of etiolation, mineral nutrition, photosynthesis, and water balance, related to adventitious rooting as well as roles of numerous enzymes and carbohydrates. The chapter about genetic effects on formation of adventitious roots is also a part of this section. The third section deals with an influence of auxins, gibberellins, cytokinins, ethylene, polyamines, growth inhibitors and other chemicals on adventitious rooting. The effects of the environment of stock plants, storage of unrooted cuttings and environmental conditions of cultivated cuttings on adventitious root formation are discussed in the fourth section. One must further appreciate valuable information on bioassays, immunochemical assays and physicochemical methods used in the rooting research, the possibilities of applying of microorganism *Agrobacterium rhizogenes* to stimulate rooting and data on the factors influencing rooting in tissue cultures. The last chapter deals with the future trends in adventitious rooting. The reader could miss concise survey of the anatomical data related to the root initiation and development but the editors refer to some excellent recent reviews.

Despite of the wide array of contributors the book can be considered exemplary in its compact style and balanced contents that demonstrates close co-operation and perfect action of both authors and editors. It could be of value as a rich information source, often exceeding the dealing topic, for plant physiologists, biochemists and genetists interested in theoretical aspects of adventitious root formation as well as for horticulturists, foresters, and agronomists using given data in practical applications.

L. Meravý (Praha)