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BRIEF COMMUNICATION

Maintenance respiration of *Oryza sativa* leaves at different growth stages as influenced by nitrogen supply

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Abstract

Maintenance respiration rate, R_M, irrespective of growth stages, increased with increase in nitrogen supply. The R_M increased almost in proportion with net photosynthetic rate, P_N, and biomass production during early growth stages, while it declined after anthesis. Significant positive correlation was observed between biomass production and P_N at all growth stages except tillering. Though R_M was positively correlated with biomass production during early growth stages, it was negatively correlated with the rate of increase in shoot biomass after flowering, which could indicate a possibility to identify certain cultivars endowed with low maintenance expenses despite building up biomass.

Additional key words: biomass production, diurnal variation, photosynthetic rate, rice cultivars.

Respiration rates, mainly on plant or canopy level, have sometimes been studied with respect to photosynthate utilization using the concept of growth and maintenance respiration proposed by McCree (1970), and later used by more than 300 authors (*cf.* Šesták and Čatský 1974-1998, Čatský and Šesták 1997). Briefly, in growth respiration, R_G, photosynthates are used to provide the energy required for the synthesis of structural and storage compounds. The R_G may be related directly to the net photosynthetic rate, P_N. In maintenance respiration, R_M, photosynthates are used in energy-consuming processes that are necessary to maintain the plant structure. The R_M is proportional to leaf dry mass (*cf.* Tichá *et al.* 1985, Sekerka 1991). Rather little information is available on R_G and R_M on the leaf level, because the principle of measuring these values may be criticized for different reasons.

The aim of this study was to determine diurnal changes in R_M, in relation to P_N, of the rice leaves at different growth stages, as influenced by different N supply.

Two high yielding rice (*Oryza sativa* L.) cultivars, Swarnaprabha and Ratna, were grown for 120 - 130 d under 4 different N concentrations in the field at Central Rice Research Institute, Cuttack during wet seasons of 1993 and 1994 (alluvial sandy loam of the Mahanadi river delta, pH 6.8, organic C 0.83 %, total N 0.09 %, available P 22 kg ha^{-1}, and available K 128 kg ha^{-1}). Thirty-day-old seedlings were transplanted at 10 × 15 cm spacing in 3 replications in a randomised block design. K and P were applied in equal doses (30 kg ha^{-1} each) while N was applied in 4 different doses (30, 60, 90, and 120 kg ha^{-1}) and in three equal splits at planting, maximum tillering and primordial initiation stages. Recommended plant protection measures were taken as and when required.

R_M was measured at different growth stages like maximum tillering, primordial initiation, flowering and 15 d after flowering (DAF). *Differential Respirometer* (*Gilson*, Middleton, USA) was used to assess CO_2 evolution rate using traditional experimental procedure. Leaves excised in the evening and kept for 12-h in darkness were used, as recommended by Penning de Vries (1975a). Day and night variations in R_M under four nitrogen concentrations were assessed during flowering stage at 4-h interval. Diurnal variation of the same at 2-h interval was also observed during vegetative and flowering stages under 60 kg(N) ha^{-1} only. Total dry mass production was recorded taking 10 randomly selected samples from each plot at every stage. P_N of single intact leaf was measured by portable photosynthetic system (*LI-COR 6000*, Lincoln, USA).

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Abbreviations: DAF - days after flowering; P_N - net photosynthetic rate; R_G - growth respiration rate; R_M - maintenance respiration rate.

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R_M and P_N were determined in the two rice cultivars at maximum tillering, primordial initiation, flowering and 15 d after flowering (DAF). Irrespective of growth stages, both R_M and P_N increased with increasing soil nitrogen content. Further, the rate of both the traits increased with growth stages from maximum tillering to flowering and declined thereafter (Table 1). This decline might be associated with senescence of the crop. R_M of Swarnaprabha was slower than of Ratna during maximum tillering and panicle initiation, while at flowering and at 15 DAF Swarnaprabha respired more than Ratna (Table 1). P_N was always higher in Swarnaprabha than in Ratna. R_M followed similar trends as P_N (Baker *et al.* 1990). Stahl and McCree (1988) reported a large decline in R_M from panicle initiation to maturity.

Table 1. Net photosynthetic rate (P_N) and maintenance respiration rate (R_M) [μmol(CO_2) m^{-2} s^{-1}] of two rice cultivars at various growth stages and under different nitrogen supply [kg ha^{-1}]. F-values * - significant at 5 % level, ** - significant at 1 % level, ^{NS} - not significant.

Cultivar	N supply	Tillering		Primordial initiation		Flowering		15 DAF	
		P_N	R_M	P_N	R_M	P_N	R_M	P_N	R_M
Ratna	30	19.1	0.086	20.5	0.111	21.0	0.126	17.8	0.124
	60	21.0	0.096	22.0	0.126	22.6	0.145	18.7	0.135
	90	21.9	0.118	22.2	0.137	23.0	0.170	19.8	0.165
	120	22.3	0.144	22.7	0.163	23.6	0.189	19.1	0.193
Swarnaprabha	30	21.5	0.080	22.3	0.093	23.2	0.134	20.6	0.120
	60	22.2	0.089	23.2	0.107	24.2	0.160	20.9	0.125
	90	24.1	0.110	25.6	0.126	26.1	0.184	22.9	0.151
	120	25.0	0.131	26.9	0.146	27.3	0.224	23.7	0.183
F_C		<1	50.57**	93.75**	<1	21.87**	6.61*	622.63**	805.00**
F_a		<1	411.89**	29.97**	1.11^{NS}	64.98**	44.84**	76.11**	7854.18**
$F_{C\times A}$		<1	1.69^{NS}	6.52**	1.02^{NS}	6.72**	2.51**	16.10**	39.50**

Table 2. Total biomass production of two rice cultivars [g m^{-2}(soil)] at successive growth stages under different nitrogen supply [kg ha^{-1}]. F-values * - significant at 5 % level, ** - significant at 1 % level, ^{NS} - not significant.

Cultivar	N supply	Tillering	Primordial initiation	Flowring	15 DAF	Maturity
Ratna	30	109	302	607	655	713
	60	110	333	645	707	759
	90	148	348	696	771	810
	120	172	410	721	797	832
Swarnaprabha	30	95	419	663	824	883
	60	124	445	769	926	982
	90	141	512	819	984	1040
	120	179	590	836	994	1036
F_C		146.26**	106.93**	102.77**	51.09**	86.90**
F_a		2.40^{NS}	592.58**	277.36**	409.55**	948.89**
$F_{C\times A}$		11.12**	8.99**	7.18**	1.23^{NS}	3.72*

Differences in total biomass production among cultivars, nitrogen rates (except at maximum tillering), and their interaction (except at 15 DAF) were highly significant at different growth stages. Total biomass increased with increase in N rate along with progressive growth stages of the crop till maturity (Table 2). Swarnaprabha proved superior to Ratna at flowering and post flowering stages. Maximum biomass was recorded in Swarnaprabha followed by Ratna under 120 kg(N) ha^{-1} at maturity. Stahl and McCree (1988) found that the efficiency for biomass production increased with plant age. In rice, Baker *et al.* (1992) reported that canopy dark respiration rate reached maximum 30 – 50 d after planting followed by a gradual decline with time until the end of growing season. A positive correlation between R_G and dry mass increase was observed in rice by Hirai *et al.* (1997). In rice cultivars Ratna and Swarnaprabha significant positive correlation was observed between biomass production and P_N at all growth stages except maximum tillering (r = 0.966, 0.964 and 0.956 at PI, flowering and 15 DAF, respectively). Though R_M indicated significant positive correlation with biomass production at early growth stages (r = 0.955 at tillering), the R_M was negatively associated (r = -0.728) with the rate of increase in shoot biomass after flowering.

Diurnal variation in R_M at both vegetative and flowering stages starting from 06:00 to 18:00 at 2-h interval was assessed in both cultivars. In general, R_M was high during the morning (06:00 - 08:00), declined stiffly until mid-day and again increased till 18:00 (Fig. 1). The rate of protein turnover in mature leaves is maximal in the morning, after the onset of light (Penning de Vries 1975b). This may be due to the induction of enzyme synthesis which causes an increase in energy requirement, and thus in R_D. Decline in R_D during the mid-day could be attributed to high CO_2 concentration, high temperature and low substrate level. There is evidence that R_D is sensitive to the instantaneous CO_2 concentration and may decrease with increasing CO_2 (*e.g.* Bunce 1990, Amthor 1991). Although the pattern of diurnal variation was bimodal in both the cultivars, R_M in Swarnaprabha was found to be lower than in Ratna.

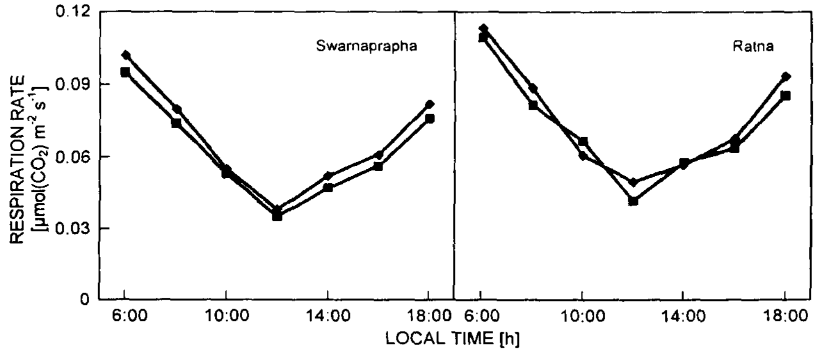

Fig. 1. Diurnal variation in maintenance respiration rate (R_M) at vegetative (*squares*) and flowering (*diamonds*) stages of rice cultivars Swarnaprabha and Ratna under N supply 60 kg ha^{-1}.

Day and night variation in R_M under different N concentrations was studied at flowering stage only. In the present study no significant change in R_M was observed with time during the night hours especially till mid-night (20:00 - 24:00) and maintained a plateau till 04:00, after which the rate increased towards morning and reached maximum at 06:00 - 08:00 (Fig. 2).

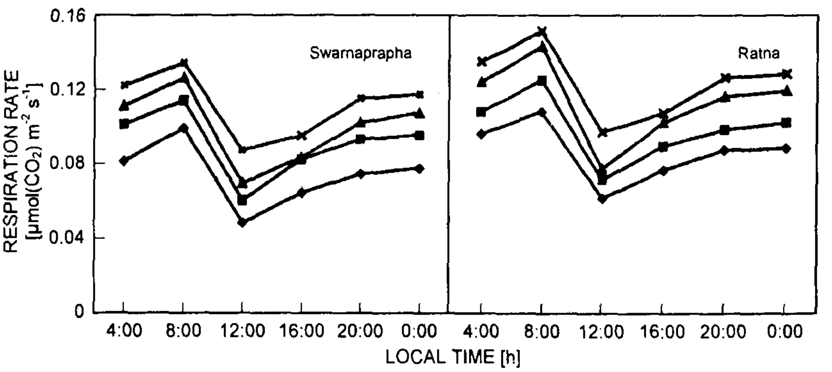

Fig. 2. Day and night variation in maintenance respiration rate (R_M) at flowering stage under nitrogen supply 30 (*diamonds*), 60 (*squares*), 90 (*triangles*) and 120 (*crosses*) kg ha^{-1}.

Pearman *et al.* (1981) found that if a sizable fraction of respiration is not linked to growth or essential maintenance, it could be possible to increase yield by decreasing respiration. Heichel (1970) and Wilson (1975) also observed that increased growth of maize and ryegrass has been associated with decreased respiration. There is very little scope to alter R_D or photorespiration rate and thus improvement of cultivars in terms of higher biomass production and productivity will depend to a reasonable extent on R_M. The differences in R_M between the two cultivars were noticed in these experiments, and they were influenced considerably by plant age and soil N content. This suggests that future scope for aligning R_M with optimum N management through conventional breeding or advanced biotechnological tools may be possible to augment biomass and grain production.

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