Gas exchange variability and water use efficiency of thirty landraces of rice still under cultivation in Kumaun region of the Indian Central Himalaya

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ABSTRACT

Gas exchange characteristics of thirty landraces of rice (*Oryza sativa* L.) along with an introduced variety VL-206 (recommended high yielding variety for rainfed uplands of the Indian Central Himalaya, ICH), grown in earthen pots and kept in the open at the Institute nursery at Kosi (1150m amsl, 79°38'10"E and 29°38'15"N) were studied. The photosynthetic rate (Pn) and other related parameters were found to vary considerably among landraces. Based on the comparison of Pn of landraces with that of VL-206, these were categorized into two groups: i) high ($>6.0 \mu\text{mol m}^{-2}\text{s}^{-1}$), and ii) low ($<6.0 \mu\text{mol m}^{-2}\text{s}^{-1}$) Pn groups. Overall the landraces belonging to the high Pn group (Saurajubawan, Syaudhan and Taichin) which had higher stomatal conductance (gs), transpiration rate (E), water use efficiency (WUE), mesophyll efficiency (low Ci/gs ratio) and chlorophyll (Chl) content in comparison to landraces in the low Pn group. However, significant differences were not found in the intercellular CO₂ concentration (Ci) between landraces belonging to the high and low Pn groups. Differences among landraces were found with regard to dark respiration; landraces with low Pn respired proportionately more of the carbon fixed than those of high Pn group. Based on the studied gas exchange characteristics Saurajubawan, Syaudhan and Taichin, local landraces of rice, may be identified as potential cultivars with high Pn and WUE. [Physiol. Mol. Biol. Plants 2009; 15(4) : 303-310] E-mail : rk_agnihotri@rediffmail.com

Key words : landraces, net photosynthetic rate, *Oryza sativa*, rainfed mountain areas, water stress, water use efficiency.

Abbreviations : Ca – atmospheric CO₂ concentration; Ci – intercellular CO₂ concentration; Ci/gs – mesophyll efficiency; Chl – chlorophyll; E – transpiration rate; gs – stomatal conductance; Pn – net photosynthetic rate; WUE – water use efficiency.

INTRODUCTION

Based on the soil and water conditions in which rice is grown, it has been classified into four broad categories viz., irrigated or flooded paddy rice, lowland rainfed rice, upland rice and deep-water rice. Out of 140-145 million hectares of land area planted under rice annually, about 53 % is grown as irrigated, 25 % as rainfed lowland rice, 10-14 % as upland rice and about 6 % as

deep water rice (IRRI, 1984). Excluding irrigated rice, about half of the world's rice cultivation depends on rainfall and thus often subjected to water stress. This is due to seasonal monsoonal rainfall, which has become highly variable and unpredictable. Significant reduction in rice yield has been observed in rainfed lowland areas in south and south-east Asia compared to areas with adequate water supply (Cabuslay *et al.*, 2002). In the higher reaches (rainfed areas) of the Indian Central Himalaya (ICH), rice is the most important rainy season crop and provides food for the humans and fodder for the livestock. In view of the prevailing agro-economic conditions of the region, landraces which provide higher

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biomass as well as higher grain yield, and also exhibit higher water use efficiency (WUE) are preferred by the marginal farmers of this region.

Growth and productivity of a plant depends on the net carbon dioxide fixed (Zelitch, 1982). In view of a close relationship between photosynthetic rate and productivity and existence of genetic variability in photosynthetic characteristics in plants, these can be used as criteria for early selection of higher yielding landraces or varieties (Joshi and Palni 1998).

While literature on rainfed landraces and/or other varieties of rice in the ICH is confined to limited reports of their occurrence (Pant and Negi, 1997), information on their biological attributes is missing. This study was, therefore, carried out to examine variability in selected physiological traits such as photosynthetic characteristics among thirty landraces of rice still under cultivation in Kumaun region of ICH; VL-206, a variety released for the region by the Indian Council of Agricultural Research (ICAR), was used for comparison.

MATERIALS AND METHODS

Plant material

Thirty landraces of rice (*Oryza sativa* L.) were collected during March–April, 1998 from 13 villages in Kumaun, Uttaranchal. VL-206 (a recommended high yielding variety for rainfed uplands of the Himalayan region) was obtained from VPKAS (Vivekanad Parvatiya Krishi Anushandhan Sansthan), a hill laboratory of the ICAR, Hawalbagh, Almora (Agnihotri *et al.*, 2003). The seeds were sown in May, 1998 in earthen pots (top dia 30 cm; ht 30 cm), containing equal parts of farmyard manure, sand and soil. Three sets (15 plants per set) of each landrace and VL 206 were grown under identical conditions, in the open, at the Institute nursery in Kosi (1150m amsl; 79°38'10"E longitude and 29°28'15"N latitude); pots were watered occasionally to maintain minimum soil moisture (around 25 %) for seed germination. Once seeds had germinated, watering was not done and the plants were allowed to experience rainfed conditions.

Gas exchange measurements

During a preliminary investigation, two landraces of rice (Saurajubawan, Taichin) and VL-206 were examined at 40, 65, 90 and 105 (± 5) days after seed sowing in order to find out their photosynthetic capacity at different times. The peak photosynthetic CO₂ fixation

was found to be 90 days after sowing. Therefore, all subsequent measurements on gas exchange characteristics were conducted 90 (± 5) days after sowing (between 1st September to mid September). Photosynthetic measurements were made with an open flow gas exchange system (LI-6400, LI-COR, Nebraska, USA) equipped with LED red light emitting source (LI-6400-02, LI-COR, Lincoln, Nebraska, USA) fixed on the top of the leaf chamber. The measurements were done at the cuvette air temperature of 25 °C, relative humidity of 50–55 %, irradiance of 800 $\mu\text{mol m}^{-2}\text{s}^{-1}$ at the leaf level, and the gas flow rate was 500 mmol s^{-1} . Relatively low irradiance was used since most days were cloudy during the monsoon season when the measurements were done. The rate of dark respiration was measured by maintaining the leaf at zero irradiance in the leaf chamber. Since the steady state photosynthesis reaches within 30 to 45 minutes, the leaves were kept for about one hour under each set of conditions, before the observations were recorded. Different parameters viz. rates of net photosynthesis (Pn), dark respiration, transpiration (E), and stomatal conductance for water and CO₂ (gs) and intercellular CO₂ concentration (Ci) were calculated according to Von Caemmerer and Farquhar (1981); water use efficiency (WUE) was calculated as the ratio of rate of photosynthesis and transpiration and a ratio of Ci and gs (Ci/gs) was used as an indicator of mesophyll efficiency.

Chlorophyll (Chl) content

Leaves used for the photosynthetic gas exchange measurements were harvested afterwards for the determination of Chl a, b and total Chl following the method of Holm (1954).

Environmental parameters

Temperature (maximum and minimum) was recorded with the help of an automatic weather station and data logger (Campbell Scientific, USA), whereas total sunshine hours were recorded manually. Total rainfall was recorded using Symon's rain gauge fixed one meter above ground; data on rainfall was collected at 8.30 am every day and used to calculate the monthly average.

Statistical analysis

Gas and water vapour exchange experiments were carried out on healthy flag leaves of three plants from each set (each pot) and three pots were used for each landrace. Therefore, nine replicates of each measurement were used for analyses. Further, the same exercise was repeated for chlorophyll estimation. Correlation was

estimated between different physiological traits with the help of SYSTAT programme of SPSS Inc., Chicago, USA.

RESULTS

Environmental parameters

Details of the experimental site for the entire life cycle of the rice plants are given in Fig. 1. Mean maximum air temperature of the site was close to 32 °C during May and June whereas mean minimum air temperature was 6 °C in March. Maximum rainfall was recorded (257 mm) in August whereas it was minimum (63 mm) in April. Total average sunshine hours were maximum (10 hrs a day) during May and minimum (3.8 hrs) during August.

Gas exchange rates

The changes in leaf Pn and E in relation to plant age in Saurajubawan, Taichin and VL-206 are shown in Fig. 2; maximum activity in respect to Pn was found around 90 days after seed sowing. In all cases Pn and E decreased significantly at 105 days after sowing, relative to maximal values recorded at 90 days.

Table 1 shows data of 30 landraces of rice along with VL-206 for Pn, dark respiration, E, gs and Ci, and landraces were found to differ considerably in respect of these parameters. The photosynthetic rate varied from 2.21 (Anjani) to 9.45 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Taichin). Based on the rate of photosynthetic CO_2 uptake and in view of the values recorded for VL-206 (7.22 $\text{mmol m}^{-2}\text{s}^{-1}$), studied landraces were categorised into two groups: (a)

high Pn group (CO_2 uptake rate $>6.0 \mu\text{mol m}^{-2}\text{s}^{-1}$, e.g. Saurajubawan, Syauidhan and Taichin), and (b) low Pn group (CO_2 uptake rate $<6.0 \mu\text{mol m}^{-2}\text{s}^{-1}$) (Table 1). Among high Pn landraces, Taichin was found to have the highest Pn (9.45 $\mu\text{mol m}^{-2}\text{s}^{-1}$) followed by Saurajubawan (8.10 $\mu\text{mol m}^{-2}\text{s}^{-1}$) and Syauidhan (6.30 $\mu\text{mol m}^{-2}\text{s}^{-1}$). The lowest and highest Pn in the low Pn group were recorded in Anjani (2.21 $\mu\text{mol m}^{-2}\text{s}^{-1}$) and Nauli (5.37 $\mu\text{mol m}^{-2}\text{s}^{-1}$), respectively.

Differences among landraces were also found with regard to dark respiration which varied from 0.61 (Bauran) to 2.47 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Taichin). Compared to the rate of photosynthesis, dark respiration rate was relatively higher in the low Pn group, with a few exceptions, than in the high Pn group (Table 1). On an average, approximately 39 % of the assimilated CO_2 was lost through dark respiration in low Pn group, whereas this loss was 24 % in case of the high Pn group, indicating a negative association between Pn and respiratory rates.

Fig. 1. Environmental data of the experimental site for the entire growth period (during the months of March to October) of different landraces of rice for 1998.

Fig. 2. Effect of leaf age on (A) net photosynthesis (Pn), and (B) transpiration (E) in two landraces of rice and VL-206 recorded at 25 °C and 800 $\mu\text{mol m}^{-2}\text{s}^{-1}$ light intensity. The values for Pn and E have been calculated as % of the maximum values observed at 90 (± 5 days after sowing with $\pm$ SD of three replications).

Table 1. Net photosynthetic rate, Pn ($\mu\text{mol m}^{-2}\text{s}^{-1}$), transpiration rate, E ($\text{mmol m}^{-2}\text{s}^{-1}$), stomatal conductance, gs ($\text{mmol m}^{-2}\text{s}^{-1}$) and intercellular CO_2 concentration, Ci ($\mu\text{mol mol}^{-1}$) in flag leaves of different landraces of rice. Landraces have been arranged in decreasing order of Pn. All values are means of nine observations $\pm$ S.E. Values in parentheses denote response at 0 irradiance.

Landraces	Pn	E	gs	Ci	Chl a	Chl b	Total Chl
High Photosynthesis Group							
Saurajubawan	8.1 $\pm$ 0.58 (-2.09 $\pm$ 0.35)	2.39 $\pm$ 0.06 (0.87 $\pm$ 0.04)	122.0 $\pm$ 6.07 (42.9 $\pm$ 97.10)	190.0 $\pm$ 9.48 (389.0 $\pm$ 11.75)	1.13 $\pm$ 0.11	0.21 $\pm$ 0.03	1.32 $\pm$ 0.14
Syaudhan	6.30 $\pm$ 0.40 (-1.84 $\pm$ 0.14)	2.56 $\pm$ 0.32 (0.64 $\pm$ 0.05)	149.0 $\pm$ 10.46 (39.17 $\pm$ 9.10)	239.0 $\pm$ 8.80 (381.0 $\pm$ 14.7)	0.68 $\pm$ 0.09	0.34 $\pm$ 0.03	1.01 $\pm$ 0.12
Taichin	9.45 $\pm$ 0.44 (-2.47 $\pm$ 0.27)	3.48 $\pm$ 0.01 (0.87 $\pm$ 0.05)	230.5 $\pm$ 13.9 (46.4 $\pm$ 13.21)	228.0 $\pm$ 8.67 (391.0 $\pm$ 7.84)	1.33 $\pm$ 0.12	0.23 $\pm$ 0.06	1.56 $\pm$ 0.18
VL-206	7.22 $\pm$ 0.90 (-1.27 $\pm$ 0.23)	2.69 $\pm$ 0.44 (0.58 $\pm$ 0.12)	161.10 $\pm$ 2.34 (32.10 $\pm$ 7.11)	239.0 $\pm$ 124.0 (381.0 $\pm$ 8.21)	0.84 $\pm$ 0.15	0.38 $\pm$ 0.14	1.22 $\pm$ 0.28
Low Photosynthesis Group							
Anjani	2.21 $\pm$ 0.12 (-0.97 $\pm$ 0.24)	0.83 $\pm$ 0.07 (0.46 $\pm$ 0.09)	34.80 $\pm$ 3.91 (25.24 $\pm$ 5.00)	253.0 $\pm$ 8.111 (393.0 $\pm$ 17.08)	0.59 $\pm$ 0.06	0.25 $\pm$ 0.03	0.84 $\pm$ 0.09
Bauran	4.70 $\pm$ 0.50 (-0.61 $\pm$ 0.07)	2.89 $\pm$ 0.27 (0.48 $\pm$ 0.08)	127.20 $\pm$ 12.60 (22.84 $\pm$ 2.76)	245.0 $\pm$ 11.13 (352.0 $\pm$ 9.85)	0.66 $\pm$ 0.19	0.26 $\pm$ 0.06	0.92 $\pm$ 0.26
Bauria	4.8 $\pm$ 0.03 (-1.65 $\pm$ 0.50)	1.49 $\pm$ 0.22 (0.56 $\pm$ 0.02)	73.50 $\pm$ 1.26 (30.80 $\pm$ 7.49)	220.0 $\pm$ 19.42 (404.0 $\pm$ 26.02)	0.71 $\pm$ 0.17	0.32 $\pm$ 0.07	1.03 $\pm$ 0.24
Bindudhan	2.53 $\pm$ 0.57 (-1.49 $\pm$ 0.37)	1.30 $\pm$ 0.10 (0.53 $\pm$ 0.05)	51.30 $\pm$ 5.80 (30.67 $\pm$ 4.51)	233.0 $\pm$ 17.45 (383.0 $\pm$ 7.11)	0.34 $\pm$ 0.05	0.15 $\pm$ 0.01	0.48 $\pm$ 0.07
Chhatuli	2.61 $\pm$ 0.47 (-1.45 $\pm$ 0.22)	1.50 $\pm$ 0.05 (0.58 $\pm$ 0.09)	53.91 $\pm$ 2.76 (37.80 $\pm$ 5.64)	242.0 $\pm$ 13.77 (386.0 $\pm$ 7.89)	0.61 $\pm$ 0.15	0.23 $\pm$ 0.05	0.85 $\pm$ 0.20
Chhotiya	2.27 $\pm$ 0.15 (-1.28 $\pm$ 0.10)	0.81 $\pm$ 0.02 (0.43 $\pm$ 0.02)	32.60 $\pm$ 2.30 (23.30 $\pm$ 1.20)	211.0 $\pm$ 10.64 (389.0 $\pm$ 9.26)	0.50 $\pm$ 0.14	0.22 $\pm$ 0.06	0.72 $\pm$ 0.20
Dalbadal	3.12 $\pm$ 0.50 (-1.25 $\pm$ 0.15)	1.48 $\pm$ 0.09 (0.68 $\pm$ 0.05)	67.70 $\pm$ 4.00 (35.80 $\pm$ 2.10)	227.0 $\pm$ 17.8 (367.0 $\pm$ 11.40)	0.83 $\pm$ 0.20	0.31 $\pm$ 0.08	1.14 $\pm$ 0.28
Danbasmati	3.35 $\pm$ 0.46 (-1.12 $\pm$ 0.07)	1.36 $\pm$ 0.24 (0.49 $\pm$ 0.02)	66.70 $\pm$ 1.30 (25.45 $\pm$ 1.07)	225.0 $\pm$ 9.73 (373.0 $\pm$ 3.31)	0.88 $\pm$ 0.15	0.34 $\pm$ 0.05	1.22 $\pm$ 0.21
Dehradooni basmati	2.60 $\pm$ 0.41 (-0.64 $\pm$ 0.03)	1.18 $\pm$ 0.04 (0.46 $\pm$ 0.02)	56.71 $\pm$ 3.50 (24.18 $\pm$ 2.34)	255.0 $\pm$ 9.89 (361.0 $\pm$ 6.02)	0.58 $\pm$ 0.06	0.26 $\pm$ 0.02	0.84 $\pm$ 0.06
Dudhikapkoti	3.76 $\pm$ 0.44 (-0.93 $\pm$ 0.04)	1.26 $\pm$ 0.02 (0.24 $\pm$ 0.01)	72.70 $\pm$ 5.48 (16.00 $\pm$ 5.90)	229.0 $\pm$ 10.17 (421.0 $\pm$ 10.95)	0.70 $\pm$ 0.03	0.14 $\pm$ 0.02	0.84 $\pm$ 0.05
Dutiau	2.44 $\pm$ 0.38 (-1.28 $\pm$ 0.27)	1.12 $\pm$ 0.11 (0.56 $\pm$ 0.01)	50.20 $\pm$ 2.81 (26.90 $\pm$ 5.90)	253.0 $\pm$ 14.92 (388.0 $\pm$ 32.90)	0.34 $\pm$ 0.06	0.14 $\pm$ 0.10	0.48 $\pm$ 0.07
Jhungia	2.46 $\pm$ 0.36 (-1.42 $\pm$ 0.14)	1.34 $\pm$ 0.06 (0.51 $\pm$ 0.03)	63.11 $\pm$ 2.82 (27.34 $\pm$ 1.87)	247.0 $\pm$ 10.03 (403.0 $\pm$ 9.41)	0.91 $\pm$ 0.15	0.45 $\pm$ 0.06	1.36 $\pm$ 0.20
Kaladur	2.60 $\pm$ 0.55 (-1.31 $\pm$ 0.25)	1.82 $\pm$ 0.13 (0.76 $\pm$ 0.09)	88.81 $\pm$ 4.94 (38.20 $\pm$ 3.90)	241.0 $\pm$ 9.59 (365.0 $\pm$ 6.30)	0.85 $\pm$ 0.02	0.41 $\pm$ 0.03	1.26 $\pm$ 0.04

Table 1. Continued

Landraces	Pn	E	gs	Ci	Chl a	Chl b	Total Chl
Kantolia	3.22±0.60 (-1.32±0.13)	1.73±0.17 (0.48±0.09)	78.00±7.97 (25.00±3.60)	233.0±10.00 (402.0±4.92)	0.69±0.08	0.25±0.02	0.95±0.10
Kaunkaun	2.30±0.24 (-1.28±0.08)	0.87±0.03 (0.53±0.03)	45.20±2.87 (31.42±1.97)	227.0±12.30 (381.0±18.7)	1.06±0.28	0.40±0.95	1.46±0.37
Khudinandhani	2.26±0.80 (-1.11±0.15)	0.82±0.07 (0.44±0.04)	43.40±2.00 (30.87±3.24)	257.0±5.52 (388.0±5.13)	0.68±0.05	0.28±0.01	0.97±0.06
Kururidhan	2.73±0.70 (-1.29±0.13)	1.37±0.04 (0.53±0.03)	65.60±2.98 (33.42±4.27)	244.0±17.99 (373.0±528.0)	0.50±0.12	0.21±0.05	0.71±0.17
Laldhan	4.58±0.39 (-1.37±0.37)	1.96±0.07 (0.56±0.07)	116.00±2.34 (34.28±4.51)	232.0±14.7 (369.0±12.27)	0.55±0.11	0.23±0.04	0.78±0.15
Nandhani	2.42±0.47 (-1.41±0.29)	1.60±0.05 (0.51±0.06)	53.00±2.60 (27.20±7.60)	237.0±11.44 (395.0±21.26)	0.64±0.26	0.17±0.02	0.81±0.11
Nauli	5.37±0.45 (-1.19±0.12)	2.20±0.09 (0.50±0.06)	122.80±4.10 (28.27±5.14)	219.0±5.92 (370.0±8.48)	1.26±0.04	0.28±0.03	1.55±0.07
Patoli	4.15±0.41 (-1.30±0.20)	1.62±0.01 (0.48±0.14)	78.00±1.80 (30.20±9.00)	209.0±4.64 (375.0±7.49)	0.88±0.07	0.19±0.03	1.06±0.14
Sabhawati	3.18±0.41 (-1.19±0.16)	1.17±0.05 (0.69±0.02)	59.81±2.61 (37.70±4.91)	227.0±17.02 (368.0±6.64)	0.64±0.08	0.35±0.07	1.08±0.06
Sailani	5.27±0.28 (-1.12±0.05)	2.45±0.16 (0.53±0.07)	136.80±10.70 (30.00±3.14)	243.0±5.95 (374.0±6.20)	0.90±0.12	0.24±0.05	1.14±0.16
Santoli	2.36±0.12 (-1.76±0.12)	1.57±0.09 (0.70±0.09)	68.51±5.01 (36.50±4.31)	248.0±7.46 (386.0±10.46)	0.84±0.10	0.25±0.09	1.10±0.17
Saunji	3.64±0.44 (-1.40±0.18)	2.38±0.18 (0.46±0.10)	116.50±8.03 (27.21±3.12)	258.0±4.16 (391.0±12.24)	0.50±0.18	0.21±0.06	0.72±0.24
Thapchini	3.57±0.39 (-1.08±0.07)	1.90±0.09 (0.47±0.01)	96.50±6.27 (23.71±4.0)	242.0±8.79 (382.0±6.76)	1.00±0.19	0.38±0.07	1.38±0.26
Tilansi	2.29±0.45 (-1.89±0.64)	1.45±0.02 (0.59±0.09)	71.10±4.90 (29.12±5.90)	255.0±8.73 (413.0±29.19)	0.73±0.11	0.31±0.06	1.05±0.17

Both gs and E were considerably higher in the high Pn group in comparison to the low Pn group (Table 1). As in case of Pn, E ($3.48 \text{ mmol m}^{-2}\text{s}^{-1}$) and gs ($230.5 \text{ mmol m}^{-2}\text{s}^{-1}$) were highest in Taichin, whereas lowest values ($2.39 \text{ mmol m}^{-2}\text{s}^{-1}$ and $122.80 \text{ mmol m}^{-2}\text{s}^{-1}$, respectively) were recorded in Saurajubawan, among the landraces of the high Pn group. The lowest ($0.81 \text{ mmol m}^{-2}\text{s}^{-1}$ and $32.60 \text{ mmol m}^{-2}\text{s}^{-1}$) and highest ($2.99 \text{ mmol m}^{-2}\text{s}^{-1}$ and $127.20 \text{ mmol m}^{-2}\text{s}^{-1}$) values for E and gs were recorded in Chhotiya and Bauran, respectively among the low Pn group. Analysis of correlation matrix between Pn, gs and E (Table 2) showed significant

positive correlation between Pn and gs ($r = 0.90$, $P \leq 0.01$) and between gs and E ($r = 0.952$, $P \leq 0.001$).

Intercellular CO_2 concentration (Ci) in the high Pn group landraces was 6 % lower than that of the low Pn group. Among the high Pn group highest Ci was recorded in VL-206 ($239 \mu\text{mol mol}^{-1}$) and lowest in Saurajubawan ($190 \mu\text{mol mol}^{-1}$), whereas Patoli ($209 \text{ mmol mol}^{-1}$) and Saunji ($258 \mu\text{mol mol}^{-1}$), landraces of the low Pn group, exhibited lowest and highest values, respectively (Table 1). A similar trend was observed for Ci/Ca ratio (Fig. 3), and significant ($P \leq 0.02$) but

negative correlation ($r = -0.439$ and -0.428) was observed between Pn and Ci, and between Pn and Ci/Ca ratio (Table 2).

Water use efficiency (WUE) of different landraces is shown in Fig. 3. It is apparent that WUE of the high Pn group landraces was considerably greater than that of the low Pn group. The greater WUE of the high Pn group could be attributed to their higher Pn.

In respect of the mesophyll efficiency, data reveal that the landraces with high Pn possess low Ci/gs ratio (high mesophyll efficiency) and a reverse trend was observed for the low Pn landraces (Fig. 3).

Chl Content

Chl a, b and total Chl contents for different landraces are shown in Table 1. Chl a and total Chl contents were highest in Taichin (1.33 and 1.56 g kg⁻¹ f.w., respectively) and lowest in Syaudhan (0.68 and 1.01 g kg⁻¹ f.w., respectively) among the high Pn group landraces. However, Chl b was found to be lowest in Saurajubawan (0.21 g kg⁻¹ f.w.) and highest in VL-206 (0.38 g kg⁻¹ f.w.). It was interesting to note that both total Chl and Chl a contents were relatively lower in

the low Pn group landraces. However, difference between the two groups of landraces with regard to Chl b were negligible.

DISCUSSION

Changes in the gas exchange characteristics could potentially be used as a screening indicator of drought tolerance in plants (Ni and Pallardy, 1991). According to Chauhan *et al.* (1996), the active period of growth for rice landraces lies between 45 days (post germination) and before the onset of flowering. The relationship between water deficit stress, gs and Pn has been often used to assess the degree of drought tolerance in plants. The results of this study on thirty landraces of rice reveal that the rate of photosynthesis varies considerably among landraces. Overall the average Pn of landraces in the high Pn group (Saurajubawan, Syaudhan and Taichin) was about 242 % higher than that of landraces in the low Pn group. Further, the pattern of changes in leaf Pn and E with age in high Pn landraces showed a similar trend with that of VL-206, with maximum activity around 90 ± 5 days after sowing. The observed variability in Pn found in different landraces

Fig. 3. Water use efficiency (WUE), mesophyll efficiency (Ci/gs ratio) and the ratio of intercellular to ambient CO₂ concentration (Ci/Ca) in different landraces of rice and VL - 206.

Table 2. Correlation matrix of some physiological traits and chlorophyll content in different landraces of rice.

	Pn	E	gCO ₂	Ci	Ci/Ca	Ci/gs	WUE	Chl a	Chl b	Chl total
Pn	1	0.835****	0.904****	-0.439****	-0.428****	-0.752****	0.532****	0.507****	0.20	0.432****
E		1	0.952****	-0.107	-0.103	-0.859****	0.122	0.389**	0.034	0.339*
gCO ₂			1	-0.137	-0.146	-0.842****	0.252	0.463****	0.086	0.419****
Ci				1	0.667****	0.227	-0.543****	-0.407**	0.047	-0.323*
Ci/Ca					1	0.132	-0.559****	-0.191	0.246	-0.087
Ci/gs						1	-0.092	-0.449**	-0.128	-0.422
WUE							1	0.205	-0.093	0.155
Chl a								1	0.423****	0.957****
Chl b									1	0.661****
Chl total										1

*, **, ***, **** = significant at 0.05, 0.025, 0.02 and 0.01 levels.

of upland rice is in line with such variation found in different cultivars of some other species (Boyer, 1996). The present findings suggest that photosynthetic response of rainfed rice landraces to water deficit stress differs as also reported for several other species, cultivars and landraces (Morgan, 1984).

Comparison of photosynthetic parameters such as g_s , C_i , mesophyll efficiency (C_i/g_s) and WUE between landraces of low and high Pn groups reveal marked differences in these parameters. The stomatal rate of transpiration and conductance of high Pn landraces were about 181 and 225 % higher than that of the low Pn landraces, respectively. Significant positive correlations between g_s and Pn and g_s and E were observed in the present study. Further, landraces from the high Pn group also exhibited higher WUE (approx. 127 % greater) than landraces of the low Pn group. Water use efficiency has been regarded as a desirable trait under both irrigated and rainfed conditions. Jones (1992) has reported that under drought conditions, plants with a high WUE should have higher productivity or a greater ability to survive than plants with a low WUE.

In the present investigation higher WUE in the high Pn group may be attributed to both; for a given g_s , rate of Pn was greater than that of E in high Pn landraces, as also observed by Hsiao (1973). While higher WUE has been associated with plants maintaining lower C_i (Jones, 1992), there were no significant differences in C_i values as well as C_i/C_a ratio between landraces of the low and high Pn groups; the C_i values were slightly higher (by 6 %) in the low Pn landraces, probably representing differences in their mesophyll conductance. Intercellular CO₂ concentrations in turn can be generally regulated by g_s and/or by intrinsic photosynthetic capacity (i.e., non-stomatal factors). It was found that high Pn landraces also showed higher intrinsic leaf photosynthetic capacity as for a given C_i , the net photosynthetic rate was higher in the high Pn landraces in comparison to low Pn landraces. This implies that the photosynthetic system of high Pn landraces is less susceptible to drought stress. Further, C_i/g_s ratio, a reflection of mesophyll efficiency (Sheshshayee *et al.*, 1996), also suggests a greater mesophyll efficiency (lower C_i/g_s ratio) in high Pn landraces. Further studies on the relative contribution of different components regulating Pn in rice landraces may, therefore, be useful for rice breeding/improvement programmes as also suggested by Jones (1985).

In addition, Chl content was much higher in the high Pn group than in the low Pn group. A positive correlation

between Pn and chl content ($P < 0.01$) was recorded. Similar results have been reported by Swain and Murthy (1997) for high yielding varieties of rice. Further, dark respiration rate was relatively higher in the low Pn group than in the high Pn group. It has also been recognized that crop yield/productivity can be increased by reducing respiratory loss (Lambers, 1985), and successful efforts have also been made to select lines with low respiration rates (Robson 1982).

In conclusion, it may be pointed out that great variability in Pn and a number of related parameters was observed in 30 landraces of rice grown in the rainfed areas of ICH, and high Pn and WUE were invariably associated with high yielding landraces. Significant positive correlations between Pn and gs, WUE and chl content imply that these parameters could also be used as criteria for selection of high yielding landraces of rice suitable for rainfed areas.

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