

Photosynthetic characteristics of *Hordeum*, *Triticum*, *Rumex*, and *Trifolium* species at contrasting altitudes

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Abstract

Photosynthetic characteristics were compared between plants of low altitude (LA) grown at LA (Palampur; 1 300 m) and at high altitude, HA (Kibber; 4 200 m), and plants naturally occurring at different altitudes (Palampur, 1 300 m; Palchan, 2 250 m; and Marhi, 3 250 m). Net photosynthetic rate (P_N) was not significantly different between altitudes. However, the slopes of the curve relating P_N to intercellular CO_2 concentration (C_i) were higher in plants at Palchan, Marhi, and Kibber compared to those at Palampur, indicating that plants had higher efficiency of carbon uptake (the initial slope of P_N/C_i curve is an indication) at HA. They had also higher stomatal conductance (g_s), transpiration rate, and lower water use efficiency at HA. g_s was insensitive to photosynthetic photon flux density (PPFD) for plants naturally occurring at Palampur, Palchan, and Marhi, whereas plants from LA grown at Palampur and Kibber responded linearly to increasing PPFD. Insensitivity of g_s to PPFD could be one of the adaptive features allowing wider altitudinal distribution of the plants.

Additional key words: intercellular CO_2 concentration; net photosynthetic rate; photosynthetic photon flux density; stomatal conductance.

Introduction

High altitude (HA) environment is characterized by high solar radiation, low mean temperature, rapid temperature changes, and low partial pressure (P_a) of air (Streb *et al.* 1998). The change in any of these parameters affects plant performance. The relationship between altitude and photosynthesis is of great interest to plant physiologists, ecologists, and palaeobotanists.

Studies have shown that HA plants have higher photosynthetic efficiency than the low altitude (LA) ones (Körner and Diemer 1987, 1994, Körner *et al.* 1988). The leaves of HA plants are capable of positive net photosynthetic rate (P_N) at lower CO_2 concentrations and lower temperatures than LA plants (Friend and Woodward 1990). At HA, leaves achieve maximal photosynthetic rate (P_{Nmax}) at higher irradiance than those at LA (Friend and Woodward 1990). The CO_2 concentration and temperature both generally fall with altitude, and irradiance

often increases. Carbon 13/12 isotope ratios have been determined from leaves of 146 C_3 plant species from all major mountain ranges (Körner *et al.* 1988): the amount of ^{13}C increased with increasing altitude, *i.e.* overall discrimination against the heavy isotope was reduced at HA indicating higher efficiency of carbon uptake (ECU) than at LA (Körner *et al.* 1988). The $\delta^{13}C$ isotope discrimination effect is significant for altitude, but no effect was observed for latitude (Kelly and Woodward 1995).

Most of the previous studies were carried out on plants that naturally grow at HA (Friend and Woodward 1990, Purohit 2003). However, there are scanty reports for LA plants grown at HA (Kumar *et al.* 2004). Therefore, we compared the photosynthetic characteristics of crop plants from LA by growing them at LA or HA and plants growing in natural habitat at different altitudes.

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Abbreviations: C_a – ambient CO_2 concentration; C_i – intercellular CO_2 concentration; E – transpiration rate; ECU – efficiency of carbon uptake; g_s – stomatal conductance; HA – high altitude; LA – low altitude; P_a – partial pressure of air; P_{CO_2} – partial pressure of CO_2 ; P_N – net photosynthetic rate; P_{Nmax} – maximum photosynthetic rate; PPFD – photosynthetic photon flux density; PS – photosystem; WUE – water use efficiency.

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Materials and methods

Locations: Studies were conducted at Palampur (Distt. Kangra, Himachal Pradesh), Palchan and Marhi (Distt. Kullu, Himachal Pradesh), and Kibber (Distt. Lahul and Spiti, Himachal Pradesh). The characteristic features of these locations are summarized in Table 1.

LA plants: Barley (*Hordeum vulgare* L., cv. HBL-113) and wheat (*Triticum aestivum* L., cv. VL-116) were sown at Palampur (LA) during the month of October, while at Kibber (HA; a location representing about 40 % decrease in P_a compared to Palampur) the seeds were sown in May. These are the conventional sowing seasons for the plant species under study. Various physiological analyses of flag leaves were done 85 d after sowing. Mean

monthly day temperatures during the month of data recording at Kibber and Palampur were 18.6 ± 2.5 and 19.2 ± 2.2 °C, respectively.

Plants naturally occurring at different altitudes: Studies were also carried out on *Rumex nepalensis* Spreng. and *Trifolium repens* L. growing in natural conditions at Palampur, Palchan, and Marhi. These two species naturally grow on wide altitudinal range (Ansari *et al.* 1999, Singh 2000, Bahar 2002). Measurements were carried out during last week of July to the 2nd week of August. Mean monthly day temperatures during the month of data recording at Palchan and Marhi were 17.5 ± 1.7 and 12.2 ± 3.2 °C, respectively.

Table 1. Characteristic features of locations where studies were carried out.

Characteristics	Locations			
	Palampur	Palchan	Marhi	Kibber
Altitude [m]	1300	2250	3250	4200
Latitude	32°06'32"N	32°17'41"N	32°20'47"N	32°20'11"N
Longitude	76°33'43"E	77°10'76"E	77°13'17"E	78°00'52"E
Atmospheric pressure [kPa]	86.8	78.4	68.1	61.1
PPFD [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	1 500–1 700	2 000–2 300	2 200–2 500	2 300–2 700

Gas exchange was measured on 10 plants from each cultivar. P_N was measured at ambient CO_2 concentration (C_a) at all the altitudes using a portable open gas exchange system *LI-6400* (*Li-COR*, Lincoln, USA). The instrument was equipped with a transducer to measure atmospheric pressure, which was used to calculate CO_2 concentration (*LI-6400* technical note, Eqs. 1 and 8–9). Infrared gas analyzers were zeroed for CO_2 and H_2O using a CO_2 scrubber and desiccant, respectively, before calibrating span for CO_2 and H_2O . Spans for CO_2 and H_2O were adjusted using a calibrated gas ($505 \text{ cm}^3 \text{ m}^{-3}$; *Li-COR*) and a portable dew point generator (*LI-610*; *Li-COR*), respectively, at all the altitudes. P_N per unit leaf area was determined at different photosynthetic photon flux density (PPFD) ranging at $0\text{--}3\,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ at C_a . The same instrument was used to construct P_N versus C_i (intercellular CO_2 concentration) curve, wherein C_i of different levels was generated using *6400-01* CO_2 injector and a CO_2 mixer supplied along with the instrument. Temperature of the chamber was maintained at 25 °C through a Peltier cooling and heating system, and PPFD was maintained at $2\,000 \mu\text{mol m}^{-2} \text{s}^{-1}$. A cool light source (*6400-02 LED*) fitted on top of the leaf chamber, capable

of providing software adjustable quanta ranging at $0\text{--}3\,000 \mu\text{mol m}^{-2} \text{s}^{-1}$, served as the irradiation source. These curves were generated using an automatic logging system with cuvette temperature set at 25 °C and set to match the sample and reference analysers before recording each new observation. Leaves were allowed to equilibrate for 90 s before any measurement. Replicates were obtained using automatic logging for each data set.

LI-6400 computes stomatal conductance (g_s) and transpiration rate (E) by measuring air flow rate and chamber H_2O concentration, leaf area, and mole fraction of water in chamber and in stomata. $P_{N\text{max}}$ represents maximum P_N at $2\,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD while measuring P_N at various C_i . Water use efficiency (WUE) was computed by *LI-6400* using the data of P_N and g_s (Polley *et al.* 1993).

Statistical analysis: Data for P_N , $P_{N\text{max}}$, g_s , E , and WUE, and g_s at different C_i and C_i at different PPFD of plants at all altitudes was analyzed using two-way method of variance (ANOVA) as described by Gomez and Gomez (1984). Differences between means were tested against critical difference at $p < 0.05$.

Results

The photosynthetic characteristics of plants from Palampur, Palchan, Marhi, and Kibber are summarized in

Tables 2 and 3. Slope (from P_N/C_i curve), g_s , P_N , $P_{N\text{max}}$, E , and WUE were evaluated by two-way analysis. P_N was

not significantly different between the altitudes (Tables 2 and 3). P_N at different C_i showed a significant increase of the slopes by 20.8 and 23.8 % in *R. nepalensis*, and by 20.5 and 36.7 % in *T. repens* at Palchan and Marhi as compared to those at Palampur, respectively (Fig. 1 and Table 2). In LA plants, the slopes were 14.9 and 20.4 % higher in barley HBL-113 and wheat VL-616, respectively, at Kibber compared to Palampur (Table 3). g_s at various C_i values increased significantly at HA (Fig. 2). At ambient CO_2 , g_s was 40.0 and 91.4 % higher in *R. nepalensis*, and 95.4 and 121.8 % higher in *T. repens* at Palchan and Marhi compared to Palampur, respectively

(Table 2). E increased by 38.1 and 94.2 % in *R. nepalensis*, and by 52.0 and 108.2 % in *T. repens* at Palchan and Marhi compared to Palampur, respectively (Table 2). In LA plants, g_s was higher by 66.1 % in barley HBL-113 and 19.7 % in wheat VL-116 at Kibber compared to those plants grown at Palampur (Table 3). WUE was 31.4 and 33.1 % lower in *R. nepalensis*, and 40.1 and 45.4 % lower in *T. repens* at Palchan and Marhi as compared to Palampur, respectively (Table 2). Differences in E and WUE were statistically insignificant in LA plants at both the altitudes (Table 3).

C_i at different PPFD showed significant differences at

Table 2. Net photosynthetic rate, P_N and P_{Nmax} [$\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$], stomatal conductance (g_s) and transpiration rate (E) [$\text{mmol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$], and water use efficiency, WUE [$\mu\text{mol}(\text{CO}_2) \text{ mol}^{-1}(\text{H}_2\text{O})$] of *R. nepalensis* and *T. repens* naturally occurring at Palampur, Palchan, and Marhi. Values are $\pm\text{SE}$ ($n = 4$). Values indicated by different letters in the superscript, to be compared with corresponding row values, show significant difference at $p < 0.05$. Values in parentheses show the % increase at Palchan and Marhi as compared to Palampur.

	<i>Rumex nepalensis</i>			<i>Trifolium repens</i>		
	Palampur	Palchan	Marhi	Palampur	Palchan	Marhi
P_N	13.70 ^a \pm 2.14	14.30 ^{ab} \pm 1.67 (4.3)	14.70 ^{ab} \pm 1.56 (7.2)	15.20 ^{ab} \pm 1.78	14.40 ^{ab} \pm 2.71 (-7.0)	16.70 ^b \pm 1.43 (4.4)
P_{Nmax}	14.30 ^c \pm 1.46	17.00 ^c \pm 0.67 (18.8)	20.40 ^b \pm 1.32 (42.6)	16.20 ^{de} \pm 1.45	20.90 ^b \pm 0.52 (29.0)	23.80 ^a \pm 0.89 (46.9)
g_s	247.0 ^d \pm 16.8	346.0 ^c \pm 9.4 (40.0)	473.0 ^b \pm 23.2 (91.4)	261.0 ^d \pm 23.62	510.0 ^{ab} \pm 32.7 (95.4)	579.0 ^a \pm 27.9 (121.8)
E	5.51 ^{de} \pm 0.67	7.61 ^{bc} \pm 1.21 (38.1)	10.70 ^a \pm 1.54 (94.2)	4.46 ^c \pm 0.67	6.78 ^{cd} \pm 1.21 (52.0)	9.29 ^{ab} \pm 1.78 (108.2)
WUE	50.90 ^a \pm 5.68	34.90 ^b \pm 4.78 (-31.4)	34.06 ^b \pm 6.24 (-33.0)	55.76 ^a \pm 6.89	33.41 ^b \pm 7.81 (-40.0)	30.45 ^b \pm 4.32 (-45.3)
Slope	0.07 ^c \pm 0.01	0.08 ^b \pm 0.01 (20.8)	0.08 ^b \pm 0.01 (23.8)	0.07 ^c \pm 0.01	0.08 ^b \pm 0.01 (20.5)	0.09 ^a \pm 0.01 (36.7)

Table 3. Different photosynthetic parameters of low altitude plants grown at Palampur and Kibber. Values are $\pm\text{SE}$ ($n = 4$). Values indicated by different letters in the superscript, to be compared with corresponding row values, show significant difference at $p < 0.05$. Values in parentheses show the % increase at Kibber as compared to Palampur.

Parameters	<i>Hordeum vulgare</i> cv. HBL-113		<i>Triticum aestivum</i> , cv. VL-616	
	Palampur	Kibber	Palampur	Kibber
P_N [$\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$]	14.10 ^a \pm 2.45	15.40 ^a \pm 1.67 (9.02)	14.10 ^a \pm 0.56	15.00 ^a \pm 1.91 (6.3)
P_{Nmax} [$\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$]	15.80 ^a \pm 1.10	17.80 ^b \pm 0.72 (12.6)	14.80 ^a \pm 1.44	17.60 ^b \pm 0.45 (18.9)
g_s [$\text{mmol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$]	136.0 ^c \pm 20.9	226.0 ^a \pm 16.8 (66.1)	167.0 ^{bc} \pm 12.6	200.0 ^{ab} \pm 10.3 (19.7)
E [$\text{mmol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$]	6.66 ^a \pm 1.52	8.62 ^a \pm 0.54 (29.4)	6.10 ^a \pm 0.65	7.80 ^a \pm 0.83 (27.8)
WUE [$\mu\text{mol}(\text{CO}_2) \text{ mol}^{-1}(\text{H}_2\text{O})$]	109.5 ^a \pm 17.5	67.33 ^a \pm 11.73 (-38.1)	86.50 ^a \pm 11.78	80.50 ^a \pm 5.89 (-7.0)
Slope (P_N versus C_i)	0.11 ^{bc} \pm 0.01	0.13 ^a \pm 0.01 (14.9)	0.08 ^d \pm 0.01	0.10 ^{bc} \pm 0.01 (20.4)

HA as compared to those at Palampur (Fig. 3). There was no significant correlation between g_s and PPFD in *R. nepalensis* and *T. repens* at all the altitudes (Fig. 4A,B). However, strong correlation between g_s and PPFD was found in plants from LA (barley HBL-113 and wheat VL-

116) at both altitudes (Fig. 4C,D). Further, a plot between P_N and g_s showed that plants at HA functioned at higher g_s and this relationship was more pronounced in the plants naturally occurring at wider altitudinal gradient compared to the LA plants (Fig. 5).

Discussion

In spite of about 30 % reduction in P_a at Kibber, and 9.7 and 21.5 % at Palchan and Marhi as compared to Palampur, P_N was not significantly different between altitudes. As revealed by the slope of P_N/C_i curves, the plants have higher ECU at HA than at LA. Körner and Diemer (1987) have shown in 12 pairs of altitudinally separated herbaceous plants that plants at HA had higher

ECU compared to those at LA. An analysis of more than the 100 plant species showed a decreased $^{13}\text{C}/^{12}\text{C}$ ratio with increase in altitude suggesting higher ECU at HA (Körner *et al.* 1988). $\delta^{13}\text{C}$ value for *Polygonum cuspidatum* was higher at HA than at LA (Kogami *et al.* 2001).

The g_s and E increased with altitude (Fig. 2 and Tables 2 and 3). As g_s and E are directly correlated with

P_N , plotting P_N at various g_s clearly showed the behaviour of the stomata (Fig. 5). Plants naturally occurring at wider altitudinal range had more pronounced effects on stomatal openings than LA plants at HA. Plants that naturally occur at wider altitudinal range had higher P_{Nmax} than the LA plants. Moreover, the difference of P_{Nmax} between LA and HA was larger for *R. nepalensis* and *T. repens* than for LA plants barley and wheat (Table 3). Higher P_{Nmax} of

HA plants might be due to higher g_s . Earlier studies have also shown that HA plants have higher g_s (Woodward and Bazzaz 1988, Hovenden and Brodribb 2000). Alpine species have higher g_s than LA land plants (Körner *et al.* 1986); they have higher evapotranspiration rate than the LA plants (Hovenden and Brodribb 2000). The high E is beneficial for plants to protect photosystem 2 (PS2) from high energy solar radiation at HA.

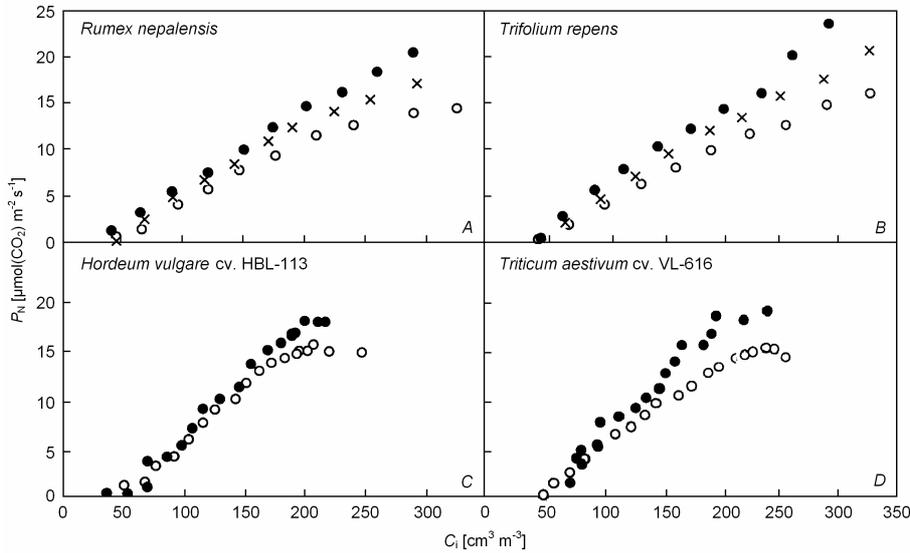


Fig. 1. Net photosynthetic rate vs. intercellular CO₂ concentration (P_N/C_i) curves of plant species (A, B) that naturally occur across altitudinal gradient at Palampur (○), Palchan (×), and Marhi (●), and low altitude species (C, D) grown at Palampur (○) and Kibber (●). Pooled from measurements of 6–8 different individuals per plant species.

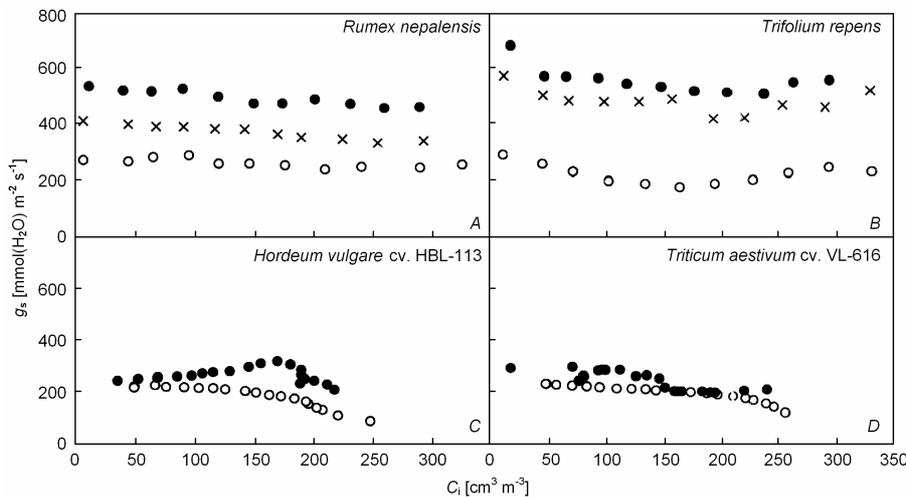


Fig. 2. Stomatal conductance (g_s) at various intercellular CO₂ concentrations (C_i) of plant species (A, B) that naturally occur across altitudinal gradient at Palampur (○), Palchan (×), and Marhi (●), and low altitude species (C, D) grown at Palampur (○) and Kibber (●). Pooled from measurements of 6–8 different individuals per plant species.

Plants at Palchan and Marhi had lower WUE than at Palampur (Table 2). The increases in leaf E will improve the plant water relation and hence will lower the WUE. The production of plant mass as well as the collective

plant surface area of communities in the alpine is low (Tranquillini 1964). This inverse relationship between WUE and P_{CO_2} is known (Polley *et al.* 1993). With increase in C_a from 15 to 35 P_a , WUE in oats, mustard, and

two cultivars of wheat increased by 40–100 % (Polley *et al.* 1993). When CO₂ concentration was elevated to 55 P_a, WUE of wheat increased by 76 and 86 % in two full growing seasons. WUE of C₃ plants increased by 27 %

over the past 200 years and ≈100 % since Last Glacial Maximum (Polley *et al.* 1993), the period during which P_{CO2} increased substantially.

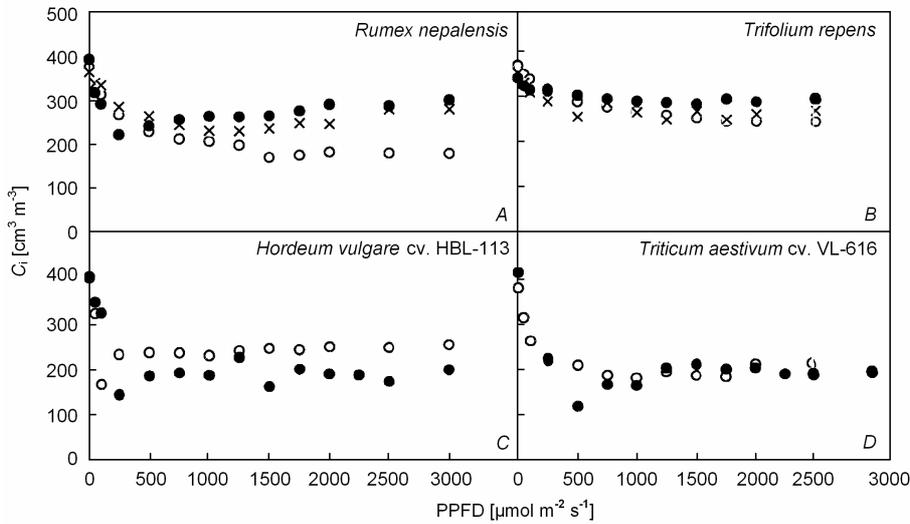


Fig. 3. Intercellular CO₂ concentration (C_i) at various irradiances (PPFD) in plant species (A, B) that naturally occur across altitudinal gradient at Palampur (○), Palchan (×), and Marhi (●), and low altitude species (C, D) grown at Palampur (○) and Kibber (●). Pooled from measurements of 6–8 different individuals per plant species.

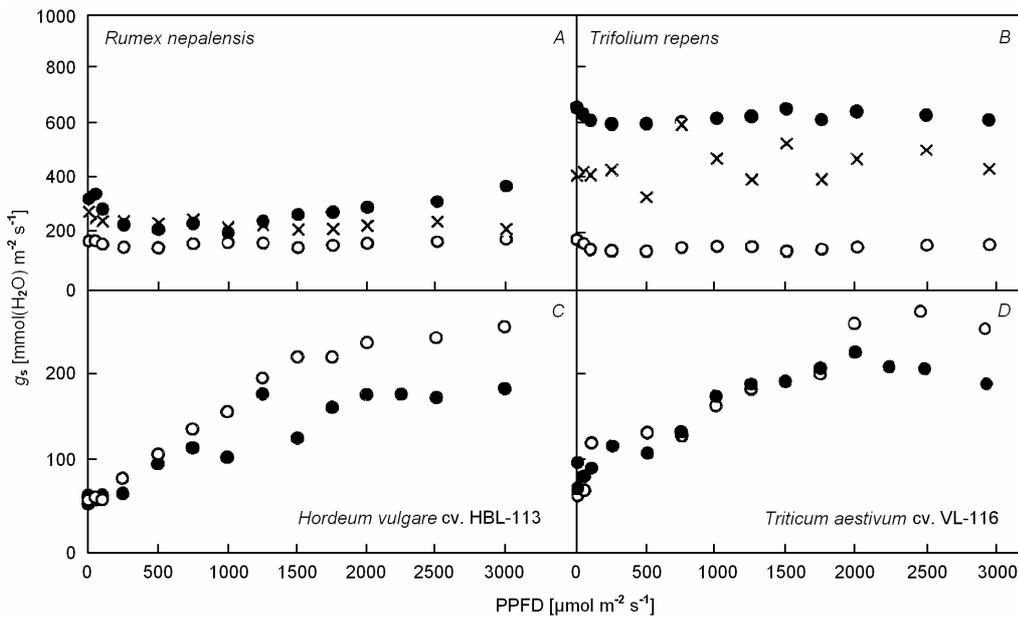


Fig. 4. Relationship of stomatal conductance (g_s) with irradiance (PPFD) in plant species (A, B) that naturally occur across altitudinal gradient at Palampur (r = 0.683 and 0.611, p < 0.01) (○), Palchan (r = -0.386 and 0.501, p < 0.01) (×), and Marhi (r = 0.538 and 0.253, p < 0.01) (●), and low altitude species (C, D) grown at Palampur (r = 0.917 and 0.952, p < 0.01) (○) and Kibber (r = 0.956 and 0.873, p < 0.01) (●). Pooled from measurements of 6–8 different individuals per plant species.

In the plants growing naturally along the altitudinal gradient, C_i was higher at Palchan and Marhi compared to Palampur at different PPFD (Fig. 3A,B). However, no significant correlation was observed between g_s and

PPFD at all altitudes for these plants (Fig. 4A,B). Unaltered g_s at different PPFD suggested that the stomata of these plants were insensitive to irradiance. This could be the reason that these plants are adapted to altitude ranging

between 400–4 000 m where they can sustain strong fluctuations in irradiance (Ansari *et al.* 1999, Singh 2000, Bahar 2002). The increase in C_i with increasing irradiance suggested an increase in photorespiration rate at HA (Pandey *et al.* 2003). HA plants have higher photorespiration rates, which is beneficial for plants to protect

PS2 from high energy solar radiation (Streb *et al.* 1998, Taub *et al.* 2000). Stomata of LA plants were sensitive to irradiance, g_s was low at low irradiance, increased linearly with increase in PPFD, and then declined at high PPFD indicating closure of stomata at high PPFD (Fig. 4C,D).

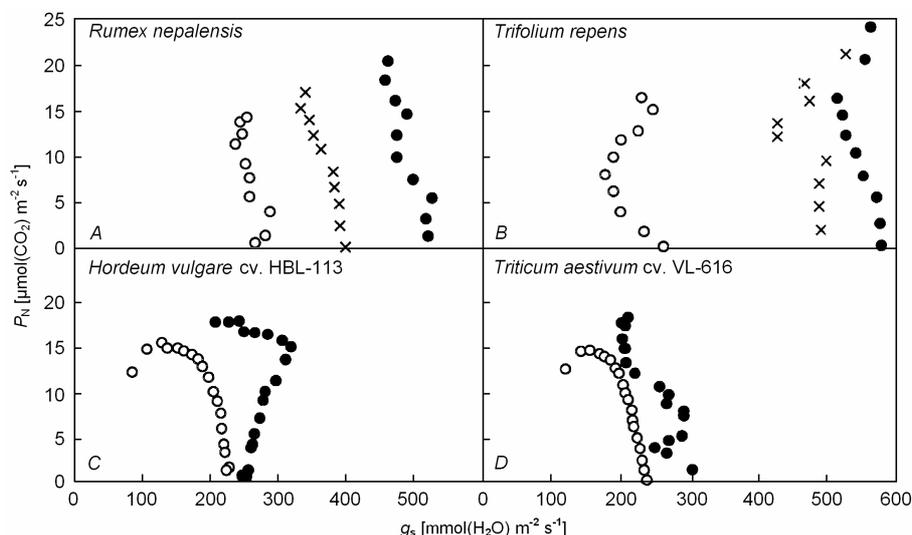


Fig. 5. Net photosynthetic rate (P_N) at various stomatal conductances (g_s) in plant species (A, B) that naturally occur across altitudinal gradient at Palampur (\circ), Palchan (\times), and Marhi (\bullet), and low altitude species (C, D) grown at Palampur (\circ) and Kibber (\bullet). Pooled from measurements of 6–8 different individuals per plant species.

We conclude that the plants that naturally occur along a wide range of altitude have g_s , which is insensitive to PPFD, whereas LA plants respond linearly to increase in

PPFD. Insensitivity of g_s to PPFD could be one of the adaptive features allowing wider altitudinal distribution to the plants.

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