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BRIEF COMMUNICATION

Photosynthetic response of *Podophyllum hexandrum* Royle from different altitudes in Himalayan ranges

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Abstract

Plants of *Podophyllum hexandrum*, collected from lower, mid, and upper distribution limits in alpine Himalaya were studied under greenhouse conditions to evaluate the photosynthetic response. Net photosynthetic rates (P_N), stomatal conductance (g_s), and efficiency of carbon uptake increased with altitude. The maximum P_N and g_s were measured in the considered population during the 3–6th week of development. P_N and g_s decreased on an average by 58 and 48 % from maximum rates reached around 4th week to the 10th week of growth, respectively. The photosynthetic response in the three ecotypes appeared to be genetically controlled.

Additional key words: efficiency of carbon uptake; intercellular CO_2 concentration; stomatal conductance.

Altitude influences environmental variables such as temperature and partial pressure of CO_2 (Hovenden and Brodribb 2000). A decrease in growth temperature may result in changes in leaf at the structural and biochemical level. Plants from greater elevation show higher assimilation rates and efficiency of carbon uptake (ECU) compared to plants growing at low altitudes (Körner and Diemer 1987, Friend and Woodward 1990, Hovenden and Brodribb 2000). Leaves developing at low temperatures exhibit higher specific activity of enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) (Björkman *et al*. 1978, Kumar *et al*. 2004), which influences ECU (Caemmerer and Farquhar 1981). However, high altitude plants have higher photosynthetic rates than lowland ones (de Lillis *et al*. 2004), especially when grown under controlled conditions (Mächler and Nösberger 1977). The difference in photosynthetic response of mountain plants is shaped by a complex mixture of environmental and genetic influences. Some mountain plants have evolved in response to their particular altitude but many of these features could occur without any genetic component (Friend and Woodward 1990). Species growing at different elevation sites and differentiating in photosynthetic characteristics such as P_N and ECU could be an indicator of their respective altitude.

The present study aimed to find if populations of *P. hexandrum* Royle, an endemic herbaceous species of the Himalayan ranges, collected from different altitudes, and grown in greenhouse differed in photosynthetic response. Gas exchange response was monitored during different developmental stages.

Plants of *P. hexandrum* were collected from three different elevations in the Himalayan ranges at Great Himalayan National Park (site A, GHNP; 31°45'N, 77°22'E; 2 400 m a.s.l.), and Kukumseri (site B, 32°42'N, 76°40'E; 2 800 m) and Koksar (site C, 32°24'N, 77°14'E; 3 200 m) in Indian western Himalaya (Kharakwal 2003). The plants were grown in a greenhouse (day temperature 24–28 °C, relative humidity 65–75 %) in the Institute of Himalayan Bioresource Technology at Palampur (32°06'N; 76°33'E; 1 300 m). Plants were grown in pots containing a mixture of garden soil, sand, and farmyard manure in equal proportion. Gas exchange was measured

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Abbreviations: C_i – intercellular CO_2 concentration; ECU – efficiency of carbon uptake; g_s – stomatal conductance; PPFD – photosynthetic photon flux density; P_N – net photosynthetic rate.

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after one year from the plantation, during the month of December 2002, starting around 10:00 (local time), after full sunlight was available in the glasshouse, till late in the afternoon, before sunlight started to fade. Maximum values of net photosynthetic rates (P_N) and stomatal conductance to water vapour diffusion (g_s) recorded during the forenoon were used for analysis.

A portable photosynthesis system *LI-6400* (*Li-COR*, Lincoln, NE, USA) was used to monitor gas exchange. 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. Span for CO_2 and H_2O was adjusted using a calibrated gas (505 cm^3 m^{-3}; *Li-COR*) and a portable dew point generator (*LI-610*; *Li-COR*), respectively. g_s and P_N were determined at different PPFD (photosynthetic photon flux density) ranging 0–2 000 µmol m^{-2} s^{-1}. P_N *versus* C_i (intercellular CO_2 concentration) curves were obtained using a *6400-01* CO_2 injector. A time interval of 90 s was given for leaf to equilibrate to the new conditions in each measurement. Replicates were obtained using automatic logging for each set.

Under the greenhouse condition, P_N was saturated at 1 000–1 500 µmol m^{-2} s^{-1}. For all measurements, therefore, this irradiance was maintained by a cool light source (*6400-02* LED) fitted on top of the leaf chamber, and the temperature of the chamber was maintained at 25 °C through a Peltier cooling and heating system. Gas exchange was measured weekly, starting from the stage of unfurled leaf up to 10 weeks (senescence phase). Gas exchange parameters were analysed by factorial analysis of variance using *SPSS* statistical package (*SPSS*, Chicago, USA) and general linear model procedures. Significant results were compared using Gabriel *post hoc* comparison.

The differences ($p<0.05$) in P_N and g_s among the considered ecotypes were evident during the 3rd–6th week of growth. P_N increased during the leaf development reaching maximum ($p<0.05$) in the 4–5th week after bud break (Fig. 1*A*). P_N decreased on an average by 58 % at the 10th week in all the three ecotypes. Similarly, highest ($p<0.05$) g_s was recorded during the 3rd–6th week of growth (Fig. 1*B*). g_s decreased by 48 % from the highest during 4th week to the lowest during 10th week in the three ecotypes.

In the considered ecotypes, P_N and g_s were significantly ($p<0.05$) different, with highest rates monitored in ecotype C (Fig. 2*A*). P_N and g_s were linearly related in the considered ecotypes. P_N increased significantly ($p<0.05$) with increase in C_i irrespective of the ecotype (Fig. 2*B*), whereas no clear trend was found in g_s (Fig. 2*C*). At the same C_i, the ecotype from higher altitude had a higher g_s compared to ecotype from lower altitude (Fig. 2*C*). Ecotype C showed higher ECU values than those from A and B ecotypes (A: 0.03775±0.00161; B: 0.04101±0.00105; C: 0.04468±0.00136).

Like most of the Himalayan alpine herbaceous species, *P. hexandrum* is subjected to a relatively short growing period (May–August; Polunin and Stainton 1984). A rapid increase in P_N during the earlier leaf developmental stage would be advantageous to support growth and development in other parts of plants (Sawada *et al.* 1982). The subsequent development of the photosynthetic apparatus, associated with increase in pigment content, contents and activities of photosynthetic enzymes, photophosphorylation, and activities of electron transport chain (Šesták 1985), could explain the maximum P_N achieved during 4–5th week of growth in *P. hexandrum*. The decline in P_N at the senescence phase of growth was an intrinsic characteristic of the species (Tichá *et al.* 1985).

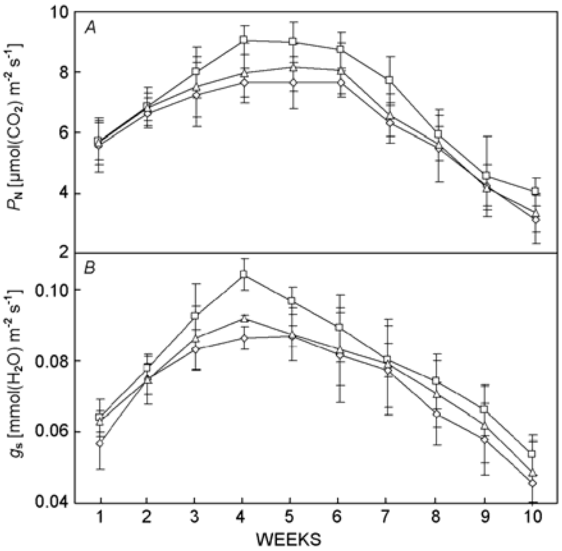

Fig. 1. Net photosynthetic rates (P_N, *A*) (y = 4.2 + 1.65 x – 0.178 x^2; *r* = 0.886) and stomatal conductance (g_s, *B*) (y = 0.05 + 0.016 x – 0.0016 x^2; *r* = 0.839) in *Podophyllum hexandrum* collected from site A (◇), site B (△), and site C (□) elevation in Himalayan ranges, and grown under glass house conditions. Means of 150 measurements.

The observed differences in the photosynthetic response of ecotypes from different altitude are in accordance with the results of Clebsch (1960), Billings *et al.* (1961), Mooney and Johnson (1965), Körner and Diemer (1987), and Hovenden and Brodribb (2000). As a function of increase in altitude, P_N and g_s increased significantly in *P. hexandrum*. High P_N is often correlated with high g_s (Mott *et al.* 1982). Yet P_N may not always respond to change in g_s. Studies across an altitudinal range of 20–1 300 m reported nearly constant photosynthetic rates in *Metrosideros polymorpha*, while g_s varied substantially (Meinzer *et al.* 1992). A significant relationship ($p<0.05$) between g_s and P_N in *P. hexandrum* grown in greenhouse indicated that g_s influenced P_N in the species, such that the high altitude ecotype was able to assimilate carbon more rapidly than ecotype with lower g_s. At different C_i, g_s did not show significant change, indicating the insensitivity of stomata to changing C_i.

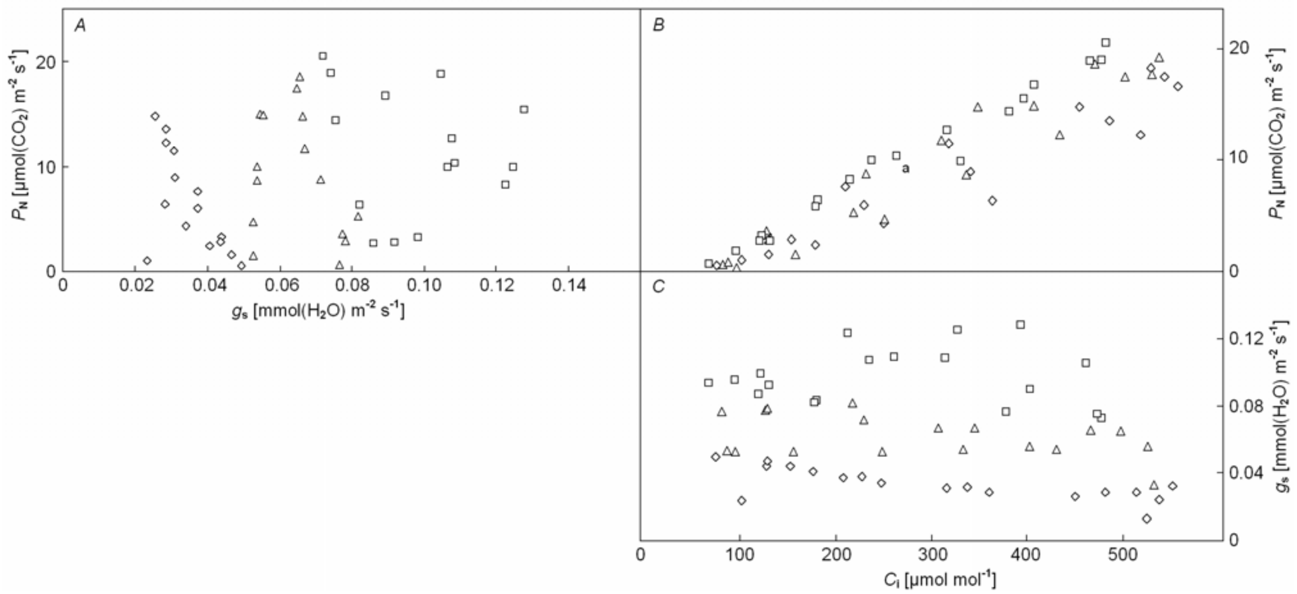

Fig. 2. Net photosynthetic rates (P_N, *A, B*) as a function of (*A*) stomatal conductance (g_s) (y = 6.64 + 33.22 x + 36.03 x^2; *r* = 0.191) or (*B*) leaf intercellular CO$_2$ concentration (C_i) (y = –1.63 + 2.289 x + 0.18 x^2; *r* = 0.966), and (*C*) g_s as a function of C_i (y = 0.055 + 0.01 x – 0.001 x^2; *r* = 0.200) in *Podophyllum hexandrum* collected at A (◇), B (Δ), and C (□) elevations in Himalayan ranges, and grown under glasshouse. Means of 45 (*A*) or 54 (*B, C*) measurements.

The increase in P_N along the rise in altitude may primarily be due to changes in ECU (Körner and Larcher 1988). ECU is largely controlled by the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) per unit leaf area (Caemmerer and Farquhar 1981). Higher RuBPCO activity was reported in the high altitude ecotype of *Selinum vaginatum* compared to that from lowland (Pandey *et al*. 1984). Species exhibiting higher ECU invariably show high maximum P_N (Friend and Woodward 1990).

The difference in ECU between plants at different altitudes could be induced environmentally or through genetic factors. A possibility of enhanced ECU with increased altitude could be due to influence of low temperature on leaf development (Friend and Woodward 1990). However, under the common growth conditions in the greenhouse, the high altitude ecotype C of *P. hexandrum* showed higher P_N and high ECU. The difference in the photosynthetic characteristics of the three ecotypes of *P. hexandrum* collected from different altitude showed that the species responded to increase in altitude through enhanced photosynthetic performance, and maintained the trait when grown at a low elevation (Körner and Diemer 1994, Hovenden and Brodribb 2000), suggesting a genetic control.

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