Lotus corniculatus L. response to carbon dioxide concentration and radiation level variations

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Abstract

Carbon dioxide concentration and light conditions may greatly vary between mountainous and lowland areas determining the photosynthetic performance of plants species. This paper aimed to evaluate the photosynthetic responses of Lotus corniculatus, growing in a mountain and a lowland grassland, under low and high radiation and CO$_2$ concentration. Net photosynthetic rate, stomatal conductance, transpiration rate, and intercellular CO$_2$ concentration were measured while the water-use efficiency and the ratio of variable to maximal fluorescence were calculated. Photosynthetic response curves to different levels of radiation and intercellular CO$_2$ partial pressure were estimated. Our results showed that high radiation and CO$_2$ concentration enhanced water-use efficiency of plants at both sites, enabling them to use more efficiently the available water reserves under drought conditions. The increase of radiation and CO$_2$ concentration would enhance the photosynthetic performance of the mountainous population of L. corniculatus, which overall seems to express higher phenotypic plasticity.

Additional key words: ambient conditions; birdsfoot trefoil; elevation; light; photosynthetic rate; plasticity index.

Introduction

Grasslands represent 13.2% of the total area in 27 countries of the European Union (Trnka et al. 2011) including plant species with a high economic value (Allen-Diaz et al. 1996, Alkemade et al. 2013). They also cover a large area of Greece constituting an important component of the mountainous ecosystems. In addition, intermediate and high elevation grasslands represent a valuable resource for the transhumant livestock system (Karatassiou et al. 2014).

In mountain ecosystems, vegetation is composed of surrounding species that have dispersed to higher elevation and became capable of adapting to highland conditions (Price et al. 2013). In mountain areas, which are considered particularly vulnerable to climate change, the CO$_2$ concentration and temperature generally decrease with altitude, while irradiance increases (Kumar et al. 2005). Despite the sensitivity of photosynthesis to short-term variation in temperature, leaf properties minimize the differences in leaf temperature between ecosystems, and plants may become acclimated and adapted. Thus, there is no clear relationship between temperature and average photosynthetic rate in the field, when ecosystems are compared (Chapin et al. 2011). Since CO$_2$ concentration plays a crucial role in plant photosynthesis, it is important to understand plant response to elevated CO$_2$ concentration in order to predict grassland structure and function in the future. Light, another critical component of photosynthesis, on the other hand, is not frequently considered an important limiting resource for the photosynthetic performance of grasslands. Nevertheless, forage species are often subjected to limited irradiance conditions (e.g. shading by neighboring species, increased cloud cover etc.) (Humphreys 1991, Dias-Filho 2002), which may impact plant performance.

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Abbreviations: AQE – apparent quantum efficiency; $C_i$ – intercellular CO$_2$ concentration; CE – carboxylation efficiency; CO$_2$ CP – CO$_2$ compensation point; $E$ – transpiration rate; $F_v/F_m$ – ratio of variable to maximal fluorescence; $g_s$ – stomatal conductance; LCP – photosynthetic light-compensation point; LSP – photosynthetic light-saturation point; $P_N$ – net photosynthetic rate; $P_{\text{Nmax}}$ – light-saturated (maximum) photosynthetic rate; $P_{\text{Nsat}}$ – photosynthesis at saturating CO$_2$; $R_D$ – dark respiration rate; RDPI – relative distance plasticity index; RH – relative humidity; $T_a$ – air temperature; VPD – vapor pressure deficit; WUE – instantaneous water-use efficiency.
Lotus corniculatus L. (birdsfoot trefoil), a species of the Fabaceae family, grows under a wide range of environmental conditions (Escaray et al. 2012). It is a common herbaceous species in Greece persisting and thriving in a variety of soil conditions, including hardpan, dry, moist, acid, saline, infertile soils (Peterson et al. 1992, Escaray et al. 2012). It is agronomically important because of its high nutritive value, and the nonbloating features when grazed directly by livestock. It is a drought resistant species, well adapted to marginal environments (Carter et al. 1997, Frame et al. 1998, Escaray et al. 2012). Winter hardiness of L. corniculatus depends on cultivar provenance, while its optimum summer temperature for growth is approximately 24°C. Nevertheless, it is intolerant of shading, especially during establishment, requiring a day length of more than 16 h for assuming peak of flowering (Beuselinck and Grant 1995, Frame et al. 1998).

In the current study, we measured the photosynthetic response of L. corniculatus, growing in mountainous and lowland areas of northern Greece, to different CO₂ concentrations and irradiance level variations. We tested the hypothesis that the lowland population of L. corniculatus outweighs the mountainous one in terms of photosynthetic performance, exhibiting higher adaptability to an environment with elevated CO₂ concentration and radiation.

Materials and methods

Experimental sites: A mountainous grassland and a lowland grassland were selected. The mountainous grassland (site 1) was located near the village Filippaiou (Mountain Smolikas), approximately 225 km west of Thessaloniki (Greece) (1,200–1,300 m a.s.l.). The climate of this region is characterized as submediterranean and belongs to the humid bioclimatic floor with severe winter (Mavromatis 1978). The mean annual precipitation is 1,079 mm and the mean annual air temperature 8.09°C. The mean annual air temperature 12.2°C. Both grasslands are grazed mainly by sheep and goats (Karatassiou et al. 2014, Parissi et al. 2014) and their soil has a pH of approximately 6. At each site, five transects at five-meter intervals were used according to Cornelissen et al. (2003). A plant that fell first on each line was chosen and one leaf per plant was selected for measurements. At each site, a total of five plants were used for each set of measurements.

Microclimatic conditions in the study sites were measured under ambient conditions, when the gas-exchange measurements were taken as average of five measurements. Air temperature (Tₐ) and relative humidity (RH) were acquired using the microclimatic sensor Novasima MS1 (Novatron Scientific Ltd, Horsham, UK). Vapor pressure deficit (VPD) was calculated according to Abtew and Melesse (2012). At site 1, the Tₐ, RH, and VPD were 24.1 ± 0.2°C, 32.8 ± 2.1%, and 2.05 ± 0.23 kPa, respectively, while at site 2, the Tₐ, RH, and VPD were 25.1 ± 0.3°C, 29.2 ± 1.5%, and 2.26 ± 0.18 kPa, respectively.

Gas-exchange measurements were carried out from late spring to early summer 2014. Plants from the site 2 were measured earlier in a season than those from the site 1 in order to achieve similar phenological stage of the plants at both sites. In each grassland, gas-exchange parameters of L. corniculatus, such as net photosynthetic rate (Pₙ), transpiration rate (E), stomatal conductance (gₛ), and intercellular CO₂ concentration (Cᵢ), were measured under: (1) ambient conditions, (2) low [300 μmol(photon) m⁻² s⁻¹] and high [1,400 μmol(photon) m⁻² s⁻¹] PPFD with the CO₂ concentration fixed at 380 μmol(CO₂) mol⁻¹, and c) under ambient [380 μmol(CO₂) mol⁻¹] and high [800 μmol(CO₂) mol⁻¹] CO₂ concentration with the PPFD fixed at 1,400 μmol(photon) m⁻² s⁻¹. All measurements were taken using a portable photosynthesis system (LCpro-SD, ADC Bioscientific Ltd, Hoddesdon, UK) from 10:00 to 12:00 h on five mature, intact, fully expanded, upper leaves. Water-use efficiency (WUE) was calculated from the ratio Pₙ/E (Jones 2004).

Photosynthetic light-response curves (Pₙ-PPFD) were recorded on five fully expanded leaves (one leaf per plant) from each site. Sampled leaves were placed in the leaf chamber of the above mentioned photosynthesis system and illuminated by the built-in light unit attached to the sensor head, acclimating for approximately 10 min before gas-exchange measurements. These measurements were taken at different PPFD [1,800; 1,500; 1,200; 900, 700, 400, 200, 100, 40, and 0 μmol(photon) m⁻² s⁻¹], following a 7-min acclimation. During the measurements the ambient CO₂ concentration in the chamber was maintained at 380 μmol(CO₂) mol⁻¹ and the temperature at 25 ± 1.0°C.

Pₙ was also measured in response to changes in Cᵢ. Photosynthetic CO₂ response curves (Pₙ-Cᵢ) were recorded on five fully expanded leaves (one leaf per plant) in each site at different Cᵢ [700, 550, 450, 350, 200, 100, 50, and 0 μmol(CO₂) mol⁻¹] following a 7-min acclimation process. During the gas-exchange measurements the PPFD in the chamber was maintained at 1,500 μmol(photon) m⁻² s⁻¹ and temperature at 25 ± 1.0°C.

Light-saturated photosynthetic rate (Pₙmax), dark respi-
ration rate ($R_0$), apparent quantum efficiency (AQE), photosynthetic light-compensation point (LCP), photosynthetic light-saturation point (LSP), $CO_2$-compensation point ($CO_2$ CP), photosynthesis at saturating $CO_2$ ($P_{N\text{sat}}$), and carboxylation efficiency (CE) were estimated by Photosyn Assistant, software, version 1.1.2 (Dundee Scientific, Dundee, UK), that determines these parameters by fitting the light-response data to a model function expressed as a quadratic equation (Prioul and Chartier 1977). The variables were estimated using least squares fitting regression and the Nelder-Mead minimization routine (Nelder and Mead 1965).

Chlorophyll (Chl) fluorescence: In vivo Chl fluorescence was measured in the same leaves used for the above mentioned curves using the saturation pulse method (Schreiber et al. 1994) with a Chl fluorometer (OS-30p, Opti-Sciences Inc., Hudson, USA) at 30-min dark-adapted leaves. The ratio of variable to maximal fluorescence ($F_v/F_m$), expressing the maximum quantum yield of PSII (Maxwell and Johnson 2000), was measured in five plants from each experimental site.

Plasticity index: The “relative distance plasticity index” (RDPI) (Valladares et al. 2006) was used in order to compare the phenotypic plasticity of the populations from the two sites under ambient and high $CO_2$ and PPFD conditions. RDPI was calculated as

$$RDPI = \sum_{ij} (d_{ij} - d_{i'j'}) / (x_{ij} + x_{i'j'}) / n$$

where $d_{ij} - d_{i'j'}$ is the absolute value of the difference ($x_{ij} - x_{i'j'}$), $n$ is the total number of distances, $x_{ij}$ is the trait value of a given individual $j$ ($j = 1,...,3$) subjected to $i$ treatment (ambient concentration of $CO_2$ or radiation) and $x_{i'j'}$ is the trait value of a given individual $j'$ ($j' = 1,...,3$) subjected to treatment $i'$ (high $CO_2$ or PPFD).

Statistical analysis: In order to determine differences in the ecophysiological response of *L. corniculatus* between the two sites, one-way analysis of variance (ANOVA) was performed on all parameters studied (Steel and Torrie 1980). Pearson’s $r$ was used for the correlation analysis of the physiological data under ambient conditions. All statistical analyses were carried out with the SPSS® statistical software v. 22.0 (SPSS Inc., Chicago, IL, USA).

Results

**Ambient conditions**: The ANOVA revealed significant differences for $C_i$, $P_N$, and WUE between the two sites under ambient conditions (Table 1). However, $E$ and $g_s$ were not significantly different at the two sites. Plants from the site 1 exhibited significantly higher $C_i$ compared to plants from the site 2. On the other hand, plants from

<table>
<thead>
<tr>
<th>Site</th>
<th>$E$ [mmol(H$_2$O) m$^{-2}$ s$^{-1}$]</th>
<th>$g_s$ [mol(H$_2$O) m$^{-2}$ s$^{-1}$]</th>
<th>$C_i$ [μmol(CO$_2$) mol$^{-1}$]</th>
<th>$P_N$ [μmol m$^{-2}$ s$^{-1}$]</th>
<th>WUE [μmol(CO$_2$) mol$^{-1}$(H$_2$O)]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 1</td>
<td>2.18 ± 0.37</td>
<td>0.12 ± 0.03</td>
<td>278.8 ± 10.5</td>
<td>3.64 ± 0.48</td>
<td>1.79 ± 0.28</td>
</tr>
<tr>
<td>Site 2</td>
<td>1.97 ± 0.35</td>
<td>0.11 ± 0.03</td>
<td>205.8 ± 21.2</td>
<td>8.30 ± 0.88</td>
<td>4.71 ± 0.95</td>
</tr>
<tr>
<td>$F$</td>
<td>0.18</td>
<td>0.05</td>
<td>9.5</td>
<td>21.58</td>
<td>8.63</td>
</tr>
<tr>
<td>Significance</td>
<td>ns</td>
<td>ns</td>
<td>$P&lt;0.05$</td>
<td>$P&lt;0.01$</td>
<td>$P&lt;0.05$</td>
</tr>
</tbody>
</table>

Table 1. Mean values ± SE ($n = 5$) and level of significance for transpiration rate ($E$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration ($C_i$), net photosynthetic rate ($P_N$), and water-use efficiency (WUE) of *Lotus corniculatus* plants located in a mountainous (site 1) and a lowland (site 2) grassland under ambient conditions.

Fig. 1. Response curves of net photosynthetic rate ($P_N$) in relation to elevated irradiation (PPFD) of *Lotus corniculatus* plants located in a mountainous (site 1) and a lowland (site 2) grassland of northern Greece. Points represent mean values ± SE, $n = 5$.  

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Fig. 2. Mean values ± SE (n = 5) of light-compensation point (LCP), light-saturation estimate (LSE), dark respiration (Rd), apparent quantum efficiency (AQE), maximum photosynthetic rate (P_{\text{Nmax}}), and ratio of variable to maximal chlorophyll fluorescence (F_{v}/F_{m}) of Lotus corniculatus plants located in a mountainous (site 1) and a lowland (site 2) grassland of northern Greece. Columns accompanied by different letters differ significantly at P<0.05.

the site 2 showed significantly higher values of P_N and WUE. Correlation analysis revealed a significant association between C_i and WUE (site 1: r = –0.948, P<0.05), g_s and E (site 1: r = 0.991, site 2: r = 0.975, P<0.01), and F_{v}/F_{m} and P_N only for the site 2 (r = 0.912, P<0.05).

**Light curves:** The P_N-PPFD curves (Fig. 1) showed significantly higher values of P_N for the site 1 compared to the site 2. P_{\text{Nmax}} (Fig. 2E) was 13.4 and 11.3 μmol m^{-2} s^{-1} at the site 1 and site 2, respectively. LCP (Fig. 2A) was significantly higher at the site 2 [108 μmol(photon) m^{-2} s^{-1}] compared to the site 1 [37 μmol(photon) m^{-2} s^{-1}]. Rd was also significantly higher in the site 2 [−2.2 μmol m^{-2} s^{-1}] compared to the site 1 [−0.8 μmol m^{-2} s^{-1}] (Fig. 2C), while LSE, AQE, and F_{v}/F_{m} (Fig. 2B,D,F) did not differ significantly between the two sites.

**P_N-C_i curves:** For CO_2 concentrations higher than 100 μmol mol^{-1}, the P_N of L. corniculatus plants was significantly higher at the site 1 than that in the site 2 (Fig. 3). Significant differences between the two sites were also found for CE and P_{\text{Nsat}}, with plants from the site 1 showing higher values (Table 2). On the contrary, plants from the site 2 had significantly higher CO_2 CP compared to those from the site 1 (Table 2).

**Gas-exchange responses to elevated radiation:** Gas-exchange responses of L. corniculatus plants under low and high PPFD (Fig. 4) demonstrated that all parameters, except C_i, increased under high PPFD. In particular, plants from the site 1 had a higher increase in E and g_s (48 and 37%, respectively) compared to the site 2, where the increase in E and g_s was 28 and 21%, respectively. Under high PPFD, plants from the site 2 showed a higher increase of P_N and WUE (446 and 325%, respectively) compared to plants from the site 1 (226% for P_N and 120% for WUE), while plants from the site 1 had higher g_s, P_N, and WUE compared to plants from the site 2 (Fig. 4). Plants from both sites had similar E and C_i.
Fig. 3. Response curves of net photosynthetic rate ($P_N$) in relation to elevating CO$_2$ concentration of *Lotus corniculatus* plants located in a mountainous (site 1) and a lowland (site 2) grassland of northern Greece. Points represent mean values ± SE, $n = 5$.

Table 2. Mean values ± SE ($n = 5$) of carboxylation efficiency (CE), photosynthesis at saturating CO$_2$ ($P_{N_{sat}}$) and CO$_2$ compensation point (CP) for *Lotus corniculatus* plants located in a mountainous (site 1) and a lowland (site 2) grassland.

<table>
<thead>
<tr>
<th>CE</th>
<th>$P_{N_{sat}}$ [μmol m$^{-2}$ s$^{-1}$]</th>
<th>CO$_2$ CP [μmol(CO$_2$) mol$^{-1}$]</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 1</td>
<td>0.516 ± 0.013</td>
<td>74.12 ± 5.18</td>
<td>$P&lt;0.01$</td>
</tr>
<tr>
<td>Site 2</td>
<td>0.389 ± 0.009</td>
<td>49.19 ± 1.07</td>
<td>$P&lt;0.01$</td>
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**Gas-exchange responses to elevated CO$_2$:** Plants of *L. corniculatus* from both sites expressed slightly reduced $E$ under an elevated CO$_2$ [800 μmol(CO$_2$) mol$^{-1}$] concentration (Fig. 5) (site 1: 15%, site 2: 3%), while $g_s$ decreased by 4% at the site 1 and increased by 14% at the site 2. From 380 to 800 μmol(CO$_2$) mol$^{-1}$, $C_i$ increased by 90% at the site 1 and by 122% at the site 2. A similar increase of $P_N$ (about 80%) was found for plants from both sites under elevated CO$_2$ concentration, while WUE increased by 116% at the site 1 and 85% in the site 2. Under elevated CO$_2$ concentration (Fig. 5) plants from the site 1 demonstrated higher values of $g_s$, $P_N$, and WUE. On the contrary, plants from the site 2 showed higher $C_i$, while plants from both sites showed similar values of $E$.

**Phenotypic plasticity index:** The comparison of plant phenotypic plasticity of the two populations between ambient and high PPFD level (Fig. 6A) showed significant differences of RDPI only for $P_N$, which was higher for the site 1 compared to site 2. No significant differences were found between the two sites for the other gas-exchange parameters. The comparison of plant phenotypic plasticity of the two populations between ambient and high CO$_2$ (Fig. 6B) showed significant differences of RDPI for $C_i$, $P_N$, and WUE; higher values of RDPI were found at the site 1 for $P_N$ and WUE, while the site 2 had higher RDPI for $C_i$.

**Discussion**

The results of the current study suggest that under ambient conditions, *L. corniculatus* plants from both sites demonstrated similar values of $g_s$ and $E$. However, those from the site 2 expressed 2-fold higher $P_N$, and consequently also much higher WUE compared to plants from the site 1. Nevertheless, no significant correlation between $P_N$ and $g_s$ was found at both sites. Probably at high elevation sites under natural rainfall conditions other attributes (e.g., the allocation pattern, particular environmental conditions) and/or the previous grazing history often play a more important role than the photosynthetic mechanism alone (Pearcy and Ehleringer 1984, Karatassiou and Noitsakis 2010).

To our knowledge there are scarce reports concerning the photosynthetic responses of grassland species to elevated irradiation and CO$_2$ concentration, making comparisons within and between taxonomic groups rather difficult. The photosynthetic light-response curves from both sites saturated at irradiances of about 650 μmol (photon) m$^{-2}$ s$^{-1}$. Saturation at higher irradiances is usually reported for sun-adapted, early successional species (Bazzaz and Carlson 1982, Awada *et al.* 2003). Plants grown under high light show some ability for photosynthetic acclimation as evidenced by the higher
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Fig. 4. Mean values ± SE (n = 5) of A: transpiration rate (E), B: stomatal conductance (gs), C: internal CO2 concentration (Ci), D: net photosynthetic rate (PN), and E: water-use efficiency (WUE) of Lotus corniculatus plants from a mountainous (site 1) and a lowland (site 2) grassland under low [300 μmol(photon) m⁻² s⁻¹] and high [1,400 μmol(photon) mol⁻¹] radiation (PPFD).

light-saturated rate of CO₂ assimilation (Horton and Neufeld 1998). On the other hand, plants from the site 1 expressed lower LCP and RΔ values compared to plants from the site 2, which is typical of plants exposed to shade (Dalmolin et al. 2013), allowing them to maintain a small but positive carbon gain during long periods of low light in the understory (Horton and Neufeld 1998). Plants from the site 2 expressed also significantly higher values of PNmax. Maximum photosynthetic capacity reflects the rate of diffusion of CO₂ to Rubisco, the activity of Rubisco and/or the rate of ribulose-1,5-bisphosphate (RuBP) regeneration (Farquhar et al. 1980). Differences in PNmax have been attributed to differences in the biochemical efficiency of carboxylation, rather than to differences in CO₂ supply to the intercellular spaces (Reich et al. 1998, Shangguan et al. 2000). In addition, Fv/Fm, which is proportional to the quantum yield of photosynthesis, was similar at both sites. This ratio is usually ranging from 0.79 to 0.84 in nonstressed terrestrial leaves (Bjorkman and Demmig 1987). Changes in Fv/Fm are very sensitive and inversely proportional to physiological stress and might indicate the beginning of a slowly reversible photoinhibition (Osmond and Grace 1995). Since Fv/Fm and PN showed a significant correlation in the site 2, the lower photosynthetic performance of plants from the site 2, as expressed by the lower PN values in the PN-PPFD curve and the lower PNmax values, is pointing towards the existence of additional factors that inhibit photosynthesis of L. corniculatus plants in this particular site compared to the mountainous one.

The increase in the PPFD exerted a positive effect in all measured physiological parameters, except Ci. Generally in grasslands, both PN and gs have been found to parallel PPFD (Bollig and Feller 2014). Interestingly, plants from both sites increased their WUE at the higher PPFD. Working with different cultivars of L. corniculatus, Inostroza et al. (2015) demonstrated that the highest WUE was also accompanied by the highest dry matter yield under water stress conditions. Therefore, the increment of WUE under high radiation could be beneficial to the plants, enabling them to use more efficiently the available water reserves and to express higher performance under drought conditions, which are very common in the Mediterranean area.

The photosynthetic PN-Ci response curves of L. corniculatus revealed a photosynthetic upregulation by elevated
CO₂ at both sites. C₃ plants show a significant positive response to photosynthetic acclimation to elevated CO₂ (Bernacchi et al. 2003, Reddy et al. 2010). Elevated CO₂ concentration increases the carboxylation efficiency and, therefore, reduces photorespiration (Reddy et al. 2010). Working with L. corniculatus, Carter et al. (1997) found that doubling of CO₂ concentration [up to 700 μmol(CO₂) mol⁻¹] resulted in the increase of the growth rate, shoot biomass, and WUE, and in the reduction of the flowering time, specific leaf area, and Chl content of plants.

On the other hand, elevated CO₂ concentration did not affect the gₛ of plants from the site 1, while it resulted in the slight increase of gₛ of plants from the site 2. Variable effects of elevated CO₂ concentration on gₛ have been previously reported, most likely depending on plant species (Medlyn et al. 2001, Reich et al. 2001, Lewis et al. 2002, Maherali et al. 2002, Ainsworth et al. 2004, Long et al. 2004).

Furthermore, the Pₘₐₓ-Cᵢ response curves of plants in the site 1 saturated at higher values of CO₂ and demonstrated higher CE and lower CO₂-compensation point compared to the site 2. Other studies have also demonstrated increased CE at higher altitudes (Körner et al. 1988, Kumar et al. 2005). In addition, the rise in CO₂ concentration led to the increase of WUE in both sites; the higher increase was found in plants from the site 1. Elevated CO₂ concentration can increase WUE, in part by decreasing gₛ and E (Ainsworth et al. 2002). In the current study, a decrease of E under elevated CO₂ concentration was also observed at least for plants from the site 1. Lower E along with increased WUE can support plants to overcome water stress conditions and become more antagonistic in drought periods that are usually experienced in the Mediterranean zone during the summer.

Our results clearly showed that plants of L. corniculatus originating from the mountainous site had higher photosynthetic performance under elevated radiation and CO₂ concentration. In a number of studies, a decrease in plant performance with elevation in altitude was found, mainly as a result of lower temperature and a shorter growing season (Koerner 2003). To the best of our knowledge there are no studies addressing the performance of L. corniculatus plants at different altitudes. Working with different species, Frei et al. (2014) found that Ranunculus bulbosus, Trifolium montanum, and Briza media responded differently with respect to their
Fig. 6. Mean relative distance plasticity index (RDPI) of gas-exchange parameters of *Lotus corniculatus* plants from a mountainous (site 1) and a lowland (site 2) site between: A: ambient and high [1,400 μmol(photon) mol⁻¹] radiation (PPFD) and B: ambient and elevated [800 μmol(CO₂) mol⁻¹] CO₂ concentration. (n = 5).

altitude of origin indicating genetic differentiation. Other studies report that high-altitude plants have higher photosynthetic efficiency than the low-altitude ones (Körner and Diemer 1987, 1994; Friend and Woodward 1995: Impacts, Adaptations and Mitigation of Climate Change). Pp. 131-158. Cambridge University Press, 2016). According to our findings plants from the mountainous site (site 1) showed higher phenotypic plasticity for *Pₜ* both under different CO₂ and PPFD levels. Plants from the site 1 also showed higher phenotypic plasticity for WUE under different CO₂.

In conclusion, our results showed that the increase of CO₂ concentration and radiation enhanced the photosynthetic performance of the mountainous population of *L. corniculatus*. Nevertheless, further studies using plants from both sites growing under the same environmental conditions, are needed in order to investigate whether the differentiation of *L. corniculatus* photosynthetic performance found in the present study derived from genetic differentiation between the two populations and/or from their phenotypic adaptation to the local environment of each site.

References


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