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The interactive effect of irradiance and source of nitrogen on growth and root respiration of *Calamagrostis epigejos*

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SUMMARY

Growth and respiratory processes of *Calamagrostis epigejos* (L.) Roth were studied as part of a comprehensive ecological project aimed at explaining the acclimation potential of some perennial grasses upon changes in climatic and edaphic factors after logging activity in forests. We investigated the relative growth rate (RGR), the respiration rate and the contribution of the different respiratory pathways in roots of *Calamagrostis epigejos* grown at two levels of irradiance and with nitrate or ammonium as N-source. The respiration rate as well as the RGR decreased significantly but the leaf area ratio (LAR) increased upon transfer to shade. The LAR increase was caused by both a greater specific leaf area (SLA) and a greater leaf weight ratio (LWR). The relative contribution of the alternative (AP) and the cytochrome pathways to total respiration rate was the same in both radiation regimes. The ammonium form of N-nutrition had a significant stimulative effect on AP activity in shaded plants. The AP capacity was significantly higher in ammonium-fed plants grown at both irradiance levels. A possible role of the AP in plants with low energy input and with ammonium ions as N-source is discussed.

Key words: Nitrogen nutrition, irradiance, growth rate, respiratory pathways, shade-tolerance.

INTRODUCTION

Calamagrostis epigejos is a perennial rhizomatous grass with a wide distribution in coniferous forests on acid soils in central Europe. Associated with its high morphological and physiological plasticity (Gloser & Gloser, 1996) is its remarkable ability to survive in deep shade beneath the tree canopy and expand quickly after tree cutting. What connection does respiration have with acclimation to different radiation regimes? It is generally accepted that carbon economy is of crucial importance for shade-tolerant plants (Givnish, 1988; Pearcy & Sims, 1994). As found in our previous study , acclimatory changes in the net photosynthetic rate (per unit of leaf area) are not sufficient to explain the relatively fast growth of *C. epigejos* at extremely low irradiance (Gloser & Gloser, 1996).

Respiration is another important part of the plant's carbon budget,as more than one quarter of recently fixed carbon is usually respired in the same time period (Van der Werf, Poorter & Lambers, 1994). It is well known that respiration rate is much decreased in shade-grown plants (Björkman, 1981; Givnish, 1988) as a consequence of low availability of newly formed carbohydrates. Changes in the efficiency of respiration caused by the contribution of the different respiratory pathways might also play a role in acclimation to environmental variability. Taking into account the possible function of the AP as an 'energy overflow' (Lambers, 1985), we could hypothesize that the contribution of this pathway will be very low or non-existent under light-limiting conditions (deep shade). Differences in mineral nutrition can interfere with responses of *Calamagrostis epigejos* to the radiation regime in field conditions. The relative abundance of nitrate or ammonium as nitrogen source is of particular importance for the carbon balance and growth rate of plants (Bloom *et al.*, 1989; Bloom, Sukrapanna & Warner, 1992). Ammonium ions are much more

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abundant than nitrate in acid soils with *C. epigejos* (J. Gloser, unpublished). Less energy-demanding assimilation of ammonium ions (at least theoretically, cf. Thornley & Johnson, 1990) as well as the very efficient uptake mechanism by roots (Marschner, 1995) should be particularly advantageous for extremely shaded plants, the growth of which is primarily limited by energy capture and use. On the other hand, it is well known that efficient uptake and assimilation of ammonium ions in roots depends on sufficient supply of carbohydrates from the shoot. If there are not enough carbohydrates, toxic effects of ammonium may occur (Haynes & Goh, 1978).

The effect of different nitrogen forms on the rate and efficiency of respiration is not well understood. Cramer & Lewis (1993) reported increased oxygen uptake in roots of ammonium-fed plants, but CO_2 output was significantly higher in plants supplied with nitrate. Barneix, Breteler & Van de Geijn (1984) reported both increased oxygen consumption and carbon dioxide release in ammonium-fed plants, which was connected with significant stimulation of AP activity. De Visser, Spreen Brouwer & Posthumus (1986) found that AP-mediated increased uptake of oxygen both in nitrate and ammonium nutrition after transfer from N-free nutrient solution. All the above-mentioned experiments were made, however, only with plants grown at high light availability.

The objective of this work was to determine the rate of root respiration and the engagement of the AP in plants grown at two radiation regimes and with two types of nitrogen nutrition (with ammonium or nitrate as the sole sources of nitrogen). The relationship between relative growth rate and respiration rate was also examined.

MATERIALS AND METHODS

Plant cultivation

Caryopses of *Calamagrostis epigejos* (L.) Roth. were collected in a forest clearing west of Brno, Czech Republic and were germinated on filter paper moistened with deionized water. After germination, the seedlings were transferred to fine sand moistened with half-strength nutrient solution of the same type as that used later for hydroponic cultivation. Ten-d-old seedlings were placed into aerated full nutrient solution (603 μM $Ca(NO_3)_2$, 795 μM KNO_3, 190 μM KH_2PO_4, 270 μM $MgSO_4$, 2 μM $MgSO_4$, 0·85 μM $ZnSO_4$, 0·15 μM $CuSO_4$, 20 μM H_3BO_3, 0·25 μM Na_2MoO_4, 40·5 μM FeNa–EDTA) (Poorter, Remkes & Lambers, 1990) in plastic containers. The nutrient solution was renewed weekly and its pH was adjusted daily to 5·8 with H_2SO_4. The photosynthetic photon flux (PPF) was 300 ± 40 μmol m^{-2} s^{-1} for 14 h, temperature $20 \pm 0{\cdot}5$ °C, r.h. 70 %. Light was provided by fluorescent lamps (Philips TL-33-RS, 215 W, Eindhoven, The Netherlands) and incandescent bulbs (Philips, 40 W, Eindhoven, the Netherlands) in a ratio 4:1. Plants were rotated each week within the growth chamber. The total duration of cultivation in the nutrient solution was 35 d.

After 20 d of growth in the hydroponic solutions, the plants were divided randomly into four groups with different light and nutrition treatments. One half of the plants was left under the same PPF as given above (control light treatment, CL). The other half of the plants was shaded with a neutral shade cloth (low light treatment, LL). The PPF in the middle of the canopy of the LL treatment was 90 ± 15 μmol m^{-2} s^{-1}. Half of the plants from each of these groups was transferred after 6 d to a modified nutrient solution with ammonium instead of nitrate as the source of nitrogen: 250 μM $(NH_4)_2SO_4$, 280 μM KH_2PO_4, 540 μM $MgSO_4$, 454 μM $CaSO_4$, 2 μM $MnSO_4$, 0·85 μM $ZnSO_4$, 0·15 μM $CuSO_4$, 20 μM H_3BO_3, 0·25 μM Na_2MoO_4, 40·5 μM FeNa–EDTA. Plant roots were washed with demineralized water before transfer.

Growth analysis

An analysis of growth was carried out simultaneously with measurements of respiration during the last 15 d of plant cultivation. A set of 12 plants was harvested subsequently at days 0, 7 and 15 after the transfer of plants to low irradiance. Each plant was divided into 'roots' (roots + rhizomes), 'stems' (leaf basis + leaf sheaths) and 'leaves' (leaf blades). Leaf area was determined by a leaf area meter (Li-3000, LI-COR, Lincoln, NE, USA). Samples were dried at 80 °C for 48 h. The RGR of the plants was calculated according to the formula described in Evans (1972), for both time intervals (days 0–7, days 7–15) and also over the whole harvesting period (days 0–15). For a better estimation of plant RGR in the middle of the sampling period, when the respiratory measurements were conducted, its mean value for the three time intervals was calculated. Other parameters were calculated according to the classical approach (Evans, 1972). LAR is the product of SLA (the amount of leaf area per unit leaf mass) and the LWR (the fraction of total plant biomass allocated to leaves). Thus:

$$\text{LAR} = \text{SLA} \times \text{LWR}.$$

The fraction of total plant biomass allocated to roots is denoted as root weight ratio (RWR). The data of LAR, SLA, LWR and RWR from the last harvest (at day 15) are presented.

Root respiration

The measurements of root respiration started 3 h after the onset of the light period in the growth chamber and continued *c.* 8 h. Intact plant 'roots',

Table 1. *Relative growth rate (RGR) and some growth characteristics of* Calamagrostis epigejos *grown at control or low irradiance (CONTROL LIGHT, LOW LIGHT) and with different source of nitrogen (NO_3^-, NH_4^+)*

Variable	Control light		Low light	
	NO_3^-	NH_4^+	NO_3^-	NH_4^+
RGR_{plant} (mg g^{-1} d^{-1})	159 ± 27 ab	174 ± 13 a	102 ± 24 bc	88 ± 17 c
RGR_{shoot} (mg g^{-1} d^{-1})	159 ± 26 ab	175 ± 12 a	112 ± 34 bc	99 ± 30 c
RGR_{root} (mg g^{-1} d^{-1})	157 ± 28 a	171 ± 21 a	77 ± 2 b	62 ± 12 b
LAR (m^2 kg^{-1})	11·3 ± 0·36 a	10·8 ± 0·27 a	18·7 ± 0·42 b	18·4 ± 0·67 b
SLA (m^2 kg^{-1}	26·0 ± 0·89 a	23·9 ± 0·55 a	38·0 ± 0·92 b	37·7 ± 1·03 b
LWR (g g^{-1})	0·44 ± 0·01 a	0·45 ± 0·01 a	0·49 ± 0·01 b	0·49 ± 0·01 b
RWR (g g^{-1})	0·32 ± 0·01 a	0·30 ± 0·01 a	0·24 ± 0·01 b	0·25 ± 0·01 b

Mean values of three and 12 determinations (±SE) for RGR and other characteristics, respectively. For further explanation see text. Significantly different values ($P \leqslant 0{\cdot}5$) are followed by different letters.

excised from the shoot immediately before the measurements, were placed in a respiration cuvette with aerated nutrient solution of the same composition as used for cultivation during the last period of growth, with the exception of iron. The solution was buffered with 10 mM 2-(*N*-morpholino) ethansulphonic acid (MES) and the pH was set at 5·8 using KOH. The decrease of the oxygen concentration in a closed system was measured with a Clark-type O_2 electrode (Yellow Springs Instruments, OH, USA) connected to an oxygen monitor at 20 °C. The duration of all measurements with each sample did not exceed 30 min for which the respiration rate was assumed to be constant. The total respiration rate (v_{tot}) consists of three separate components:

$$v_{tot} = v_{alt\,(min)} + v_{cyt} + v_{res}.$$

The minimum activity of the AP ($v_{alt\,(min)}$) was estimated from the decrease of total respiration rate after addition of an inhibitor of the alternative oxidase (salicylhydroxamic acid, SHAM). The maximum cytochrome pathway activity (v_{cyt}) was estimated from the further decrease in respiration rate in the presence of the SHAM, after addition of a specific inhibitor of the cytochrome pathway (KCN). The maximum activity of the cytochrome path equalled the actual activity in our experiments, since titration analysis indicated full engagement of this pathway (cf. Atkin, Villar & Lambers, 1995). Consequently, the estimated minimum activity of the AP equalled the actual activity. At the end of the measurement, in the presence of both inhibitors, some respiratory activity remained: the residual component of respiration (v_{res}) (Møller *et al.*, 1988). The maximum capacity of the AP ($V_{alt\,(max)}$) was determined as the difference between respiration rate of the sample in the presence of the specific inhibitor of the cytochrome path (KCN) and the residual respiratory component of the sample.

Addition of SHAM to the roots was done by replacement of the whole volume of standard nutrient solution in the cuvette by the new solution with the same nutrient concentration and the desired concentration of SHAM. KCN was injected directly into the measuring cuvette from a 0·5 M stock solution. The appropriate concentration of SHAM, which fully inhibits the AP, was determined by the method of titration with different SHAM concentrations in the absence and presence of KCN, a specific inhibitor of the cytochrome pathway (Møller *et al.*, 1988). The cytochrome pathway engagement was examined by titration with different KCN concentrations in the absence and in presence of optimal concentration of SHAM (Møller *et al.*, 1988; Atkin *et al.*, 1995). Both titrations were done with CL–NO_3 plants. For all respiratory measurements four independent samples were used.

Statistics

For a statistical evaluation of results, the program STATGRAPHICS v. 6.0 (Statistical and Graphics Corp., 1992) was used. The influence of experimental factors on plants was tested by multifactorial ANOVA. The homogeneity of variances was checked by Bartlett's and Cochran's tests and non-homogeneous sets of data were log-transformed before calculation. The multiple comparison of means was based on the method of LSD-contrasts.

RESULTS

Relative growth rate

Shading reduced the relative growth rate of the whole plants, and especially that of the roots (Table 1). The drop in RGR of the above-ground part was not significant. Of the components affecting the magnitude of RGR, LAR was analysed in detail. The shaded plants had significantly higher values of LAR than those grown at control light (Table 1). The increase in LAR was due mainly to a SLA and to a lesser extent to a higher LWR in the shaded plants.

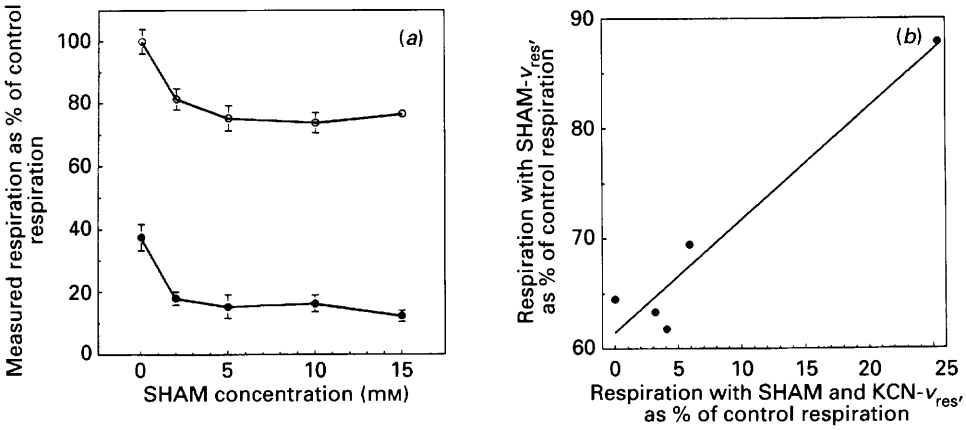

Figure 1 (*a*) The effect of SHAM in the absence (○) and presence (●) of 0·5 mM KCN on the respiration of detached, intact roots of *Calamagrostis epigejos*. Each point represents the mean value of four independent determinations (±SE). 100 % = 41·0 nmol O_2 g^{-1} d. wt s^{-1}. (*b*) The data of the respiration rate of roots in the absence of KCN plotted against the respiration rate in the presence of KCN (ρ-plot, after Møller *et al.* 1988). The residual respiration has been subtracted from the values from (*a*) before being plotted in (*b*). The slope of the line (ρ_{alt}) indicates the fraction of the total capacity of the AP that is engaged ($r^2 = 0{\cdot}97$, $\rho_{alt} = 1{\cdot}0 \pm 0{\cdot}16$, ρ_{alt} is not significantly different from 1 ($P \leqslant 0{\cdot}05$)).

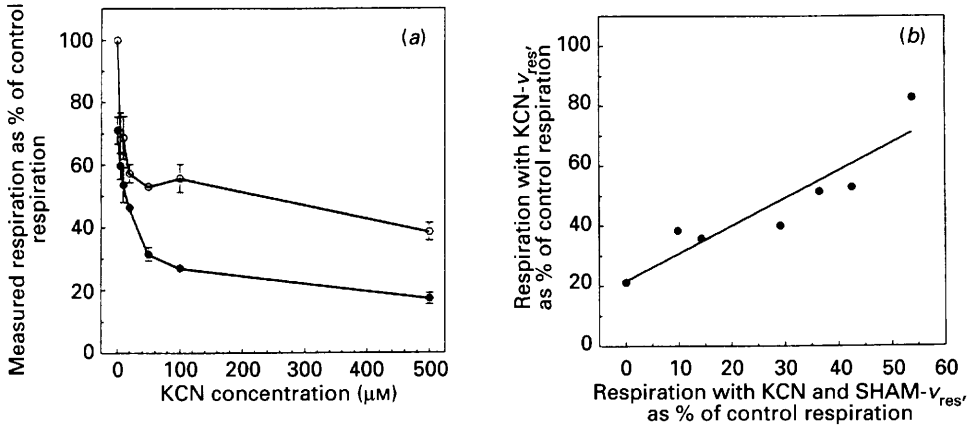

Figure 2. Effect of KCN on the rate of root respiration of *C. epigejos*. (*a*) Respiration in the absence (○) and presence (●) of 10 mM SHAM. Each point represents the mean value of four independent determinations (±SE). 100 % = 51·3 nmol O_2 g^{-1} d. wt s^{-1}. (*b*) The data from (*a*) were plotted in a similar way as in Fig. 1*b* producing a KCN ρ-plot. The residual respiration has been subtracted from the values from (*a*) before being plotted in (*b*). The slope of the line (ρ_{cyt}) indicates the fraction of the total capacity of the cytochrome pathway that is engaged ($r^2 = 0{\cdot}92$, $\rho_{cyt} = 0{\cdot}92 \pm 0{\cdot}17$, ρ_{cyt} is not significantly different from 1 ($P \leqslant 0{\cdot}05$)).

The source of nitrogen did not significantly affect the RGR of plants and also had no significant effect on LAR, or on its components (Table 1). The reduced PPF decreased the root weight ratio, irrespective of the source of nitrogen in the medium.

Respiration rate

To assess possible side effects of the inhibitors and to determine the contribution of the two respiratory pathways, a titration with SHAM was carried out (Møller *et al.*, 1988; Atkin *et al.*, 1995). The titration curve (Fig. 1) showed a relatively broad range of SHAM concentrations capable of fully blocking the AP (2–15 mM). For further determinations a concentration of 10 mM was chosen, at which SHAM also penetrates quickly into thick parts of the roots. The titration curve as well as the ρ-plot (Fig. 2) showed no side effects of SHAM in this concentration range. The AP was engaged with its maximum capacity ($\rho_{alt} = 1$) so that SHAM inhibition must give a reliable estimate of the activity of the alternative path. The residual respiration was about 17 % of the total respiration rate.

There was a significant effect of the source of nitrogen in the cultivation medium on the total respiration rate (Table 2). The ammonium-grown plants exhibited a higher root respiration rate in control irradiance. The respiration rate of roots of shaded plants was only 80–90 % of that of plants grown at control light (Table 2). This was associated with a decline in the activities of both respiration

Table 2. *The rate of total root respiration (v_{tot}) and some other characteristics describing the different respiratory pathways in detached roots of experimental plants*

Variable	Control light		Low light	
	NO_3^-	NH_4^+	NO_3^-	NH_4^+
v_{tot} (nmol O_2 g^{-1} s^{-1})	37·0 ± 1·6 a	44·2 ± 1·4 b	32·8 ± 2·1 a	34·8 ± 2·0 a
v_{cyt} (% of v_{tot})	49·2 ± 3·7 ab	56·3 ± 2·1 a	48·2 ± 2·2 b	49·4 ± 1·4 ab
$v_{alt\ (min)}$ (% of v_{tot})	26·1 ± 3·3 a	28·0 ± 2·4 a	27·3 ± 0·9 a	35·9 ± 1·5 b
$V_{alt\ (max)}$ (% of v_{tot})	18·6 ± 2·2 a	37·3 ± 5·5 bc	30·6 ± 4·0 b	46·9 ± 4·0 c
v_{res} (% of v_{tot})	18·7 ± 1·9 ab	14·2 ± 2·4 a	23·3 ± 2·8 b	14·3 ± 1·2 a

Each value represents the mean of four determinations (± SE). Significantly different values ($P \leq$) are followed by different letters. For further description see Table 1 and text.

pathways (alternative and cytochrome paths), so that the contribution of each to the total respiration rate was unchanged (Table 2). The nitrogen source had a significant effect on AP activity only under low irradiance: LL–NH_4^+ plants showed higher AP activity than LL–NO_3^- plants. There were significant effects of both irradiance and N-source on the AP capacity. The plants with ammonium as the source of nitrogen had a significantly higher AP capacity than the NO_3^--grown plants, irrespective of radiation regime during cultivation. The LL–NO_3^- plants showed also a significantly higher AP capacity in comparison with the CL–NO_3^- plants.

DISCUSSION

The RGR of shaded plants of *Calamagrostis epigejos* was *c.* 40–60 % lower than that of the CL plants. The acclimatory changes of photosynthetic characteristics of shade-grown plants of the genus *Calamagrostis* and their importance for the whole-plant carbon balance were discussed previously (Gloser & Gloser, 1996). The changes in respiratory processes in shaded plants were less known and, therefore, worth a more detailed study.

The decline in total root respiration rate of shaded plants is in accordance with responses found in some other species (Lambers, 1985). Root growth is a major sink for respiratory energy in roots (Poorter *et al.*, 1991). The decline of the growth rate of shaded plants is usually reflected in the decrease of rate of respiratory processes due to control mechanisms, in which the concentrations of both carbohydrates and adenylates play a role (Lambers, Atkin & Scheurwater, 1996).

After acclimation of our plants to low irradiance, the respiratory processes did not become more efficient by a decrease of the AP engagement. The relative share of $v_{alt\ min}$ in the total respiration rate was very similar in plants grown at control or low PPF. High activity of the AP, even under conditions of limited supply of photosynthates, seems to disagree with its assumed function as an 'energy overflow' under excess of energy (Lambers, 1985). However, a transient decrease of the activity of AP may have occurred after shading, whereas upon a long-term exposure it might stabilize again at the value corresponding to its relative contribution before shading (Lambers *et al.*, 1996). This phenomenon is possibly associated with the new steady state in the plant corresponding to another allocation pattern (higher LAR) and respiratory energy requirement.

Causal analysis of the interactions between nitrogen source, growth rate and respiratory processes in perennial grasses including *Calamagrostis epigejos* is complicated not only by different biochemistry and energy requirements of NO_3^- and NH_4^+-assimilation, but also by different location of N-assimilation within a plant. Most of the nitrate taken up by grasses is reduced in leaves using energy and reductant supplied by photosynthesis (Abrol, Sawhney & Naik, 1983), whereas the assimilation of NH_4^+ takes place only in the roots (Andrews *et al.*, 1992). Nitrate assimilation demands much more energy than NH_4^+-assimilation, and its negative impact on whole-plant carbon balance could be particularly pronounced under light-limiting conditions. This was, however, not found in our experiments.

Different forms of nitrogen in the nutrient solution had a significant effect on the total root respiration rate (v_{tot}) of plants from control light treatment. The root respiration rate in plants supplied with NO_3^- nutrition was lower than that in the presence of NH_4^+ as the sole nitrogen source, which is in accordance with the findings of Cramer & Lewis (1993). They suggested that the assimilation of NO_3^- might compete with the mitochondrial electron transport chain for reduced pyridine nucleotides. Our analysis of activity of different respiratory pathways revealed that the regulation is probably more complex.

Relative changes in the engagement of different respiratory pathways in roots of *Calamagrostis epigejos* grown in the presence of different N-forms were found under low-light conditions. The AP activity in LL–NH_4^+ plants was higher than in LL–NO_3^- plants. There was also a significant effect

of N-source on AP capacity. Roots of NH_4^+-treated plants showed higher AP capacity than roots of NO_3^--treated plants, irrespective level of the irradiance. The increased proportion of AP in total respiration in LL–NH_4^+ plants seems to contradict their rather low carbon input.

However, it seems probable that the demand for energy in root metabolism was not of primary importance in our LL–NH_4^+ plants. A considerable amount of carbon skeletons in the form of keto-acids is essential for NH_4^+-assimilation in roots, and their production must be provided by a high activity of the TCA cycle (Turpin & Weger, 1990). Maintenance of enhanced activity of the TCA cycle requires continued oxidation of NADH and $FADH_2$. The energy gained from their oxidation can be fully used for synthetic and maintenance processes only in fast-growing plants (CL–NH_4^+ treatment), not in seriously growth-limited plants (LL–NH_4^+-treatment). The root growth rate in the shaded plants was most probably reduced by diminished photosynthesis and small amount of assimilates translocated to the roots. The relative overproduction of reductant in roots as a consequence of high utilization of TCA-cycle intermediates in amino-acid synthesis, and, simultaneously, a low demand for energy for growth processes, might lead to increased activity of AP which could help to maintain the balance.

The higher AP capacity in plants with NH_4^+-nutrition could be connected with higher levels of organic acids (e.g. isocitrate and malate) within the roots assimilating ammonium and with the effect of these acids on the alternative oxidase (Vanlerberghe *et al.*, 1995). The higher AP capacity might then contribute to high ecological plasticity of the plants.

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