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Photosynthesis and growth response of *Calamagrostis arundinacea* and *C. villosa* to enhanced UV-B radiation

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Abstract

Calamagrostis arundinacea L. (Roth.) and *C. villosa* (Chaix.) J.F. Gmel are two grass species substituting forest communities on deforested areas in Central Europe. They were exposed to enhanced ultraviolet-B (UV-B, λ = 290–320 nm) radiation during 22 weeks. A system of modulated lamps operating under field conditions was used to simulate a 25 % increase of incident UV-B radiation. CO_2 assimilation seemed to be limited by a decrease of stomatal conductance (g_s) in *C. arundinacea*, whereas carboxylation activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) was not affected. On the contrary, g_s and RuBPCO activity decreased in *C. villosa*. These physiological adjustments resulted in growth changes; above-ground biomass decreased in *C. villosa* (prevailing negative effect) and significantly increased in *C. arundinacea* (prevailing positive effect) in response to enhanced UV-B radiation.

Additional key words: biomass; field experiment; stomatal conductance; ultraviolet radiation.

Introduction

Ultraviolet-B (UV-B; 290–320 nm) radiation has negative effect on plant physiology and morphology due to damages of nucleic acids and gene expression (Mackerness 2000), and destruction of photosynthetic pigments and alteration of xanthophyll cycle (Tevini *et al.* 1981, Šprtová *et al.* 2000). Moreover, decrease of net photosynthetic rate (P_N) is induced *via* processes of photosystem 2 deactivation, reduction of D1 polypeptide turnover, photo-destruction of electron transport carriers, and reduction of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) amount and activity (Vu *et al.* 1984, Caldwell *et al.* 1995, Šprtová *et al.* 1999, Mackerness 2000). UV-B treatment increases contents of UV-absorbing pigments (*e.g.* flavonoids) and phenolic compounds (Rozema *et al.* 2002, van de Staaij *et al.* 2002). Pollen germination, growth inhibition, and anatomical and morphological alterations have been reviewed (*e.g.* Caldwell *et al.* 1995) in many herbaceous and tree species.

Literature on photosynthesis and growth of *Calamagrosti*s sp. in response to enhanced UV-B radiation is contradictory. Oudejans *et al.* (2001) underline a reduction of *Calamagrostis epigejos* aboveground portion in a dune system (*i.e.* leaf mass and surface and tiller number) in response to enhanced UV-B, whereas Tosserams and Rozema (1995) show increased total biomass of the same species related to leaf anatomical changes.

The objective of this research was to evaluate *Calamagrostis* species response to enhanced UV-B radiation in the field. Grasses such as tuft forming *Calamagrostis arundinacea* and rhizomatous *C. villosa* play an important role as temporary substitutes of forest communities in the mountains of Central Europe. These species have an important anti-erosion function, accumulating a great amount of nutrients in their biomass, and reducing nutrient losses (Fiala *et al.* 1998).

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Abbreviations: C_i – intercellular CO_2 concentration; D/T – dry mass of dead leaves to total leaf dry mass ratio; g_s – stomatal conductance; I – photosynthetically active irradiance; J_{max} (V_{Cmax}) – maximum electron transport (carboxylation) rate; LAR – leaf area ratio; LMR – leaf mass ratio; P_N – net photosynthetic rate; R_D – leaf dark respiration; R/S – ratio between below- and above-ground mass; RuBPCO – ribulose-1,5-bisphosphate carboxylase/oxygenase; SLA – specific leaf area; UV – ultraviolet radiation; α – apparent quantum efficiency; Γ_I – compensation irradiance.
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Materials and methods

Experimental site and plants: Experiments were carried out in the Moravian-Silesian Beskydy Mts. (Bílý Kříž, 49°33´N, 18°32´E, 908 m a.s.l., NE of the Czech Republic). The climate of the area is characterised by an annual mean temperature of 5.5 °C, an annual mean relative air humidity of 80 %, and a total rainfall of 1 000–1 400 mm. The UV-B enhancement was provided with a modulated lamp system in the field, according to Caldwell *et al.* (1983) and Šprtová *et al.* (1999). The system consisted of a 1.5×3.0 m light bank containing 12 fluorescent lamps (*UV-B-313*, *Q-Panel*, USA) filtered with pre-solarised 0.13 mm thick cellulose diacetate film to prevent the transmission of UV-C (<290 nm) radiation. The cellulose diacetate film was regularly replaced every 10 d. The system monitored (vacuum photodiode *SED-240*, *Starna*, Austria) the incident UV-B intensity of the lamp-bank adjusting it to the preset level (25 % enhancement) by a feedback and amplification circuit.

Potted samplings of *Calamagrostis arundinacea* L. (Roth.) and *C. villosa* (Chaix.) J.F. Gmel (local soil-ferric-podzols, loamy/sand-loamy, 30–40 % of gravel; 0.05 m^3 volume) were exposed to ambient (control; non-functioning UV lamps) or enhanced (UV-B+25 % of the control) UV-B irradiances. Plants with similar initial biomass were chosen and the statistically insignificant differences of their assimilation characteristics were verified at the beginning of the experiment (data not shown). The experiment was carried out from middle of May to October 2000 (22 weeks). Twenty pots per species and treatment were considered.

Gas exchange at steady state was measured on segments (6 cm^2 each) of the second leaf (n = 6) in two periods during the vegetative season: May (after 3 d of UV-B treatment) and September (after 15 weeks of UV-B treatment). The portable infra-red gas analyser *CIRAS-1* (*PP Systems*, UK) was used to calculate the relationship between P_N and the intercellular CO_2 concentration (C_i) or photosynthetically active irradiance (I). P_N-C_i curves were obtained under the fully saturating irradiances (1 300–1 500 μmol m^{-2} s^{-1}) within the interval of ambient CO_2 concentrations 0–1 900 μmol(CO_2) mol^{-1}. The P_N-*I* curves were obtained at constant ambient CO_2 concentration, *i.e.* 365 μmol(CO_2) mol^{-1}, under a predetermined (0–1 300 μmol m^{-2} s^{-1}) set of irradiances. Moreover, P_N values were obtained at steady-state g_s (*ca.* 10 min after the exposure). Leaf temperature and relative air humidity inside the leaf chamber were kept constant at 18–21 °C and 50–55 %, respectively.

Both assimilation response curves were modelled by a quadratic equation on the base of biochemical model of photosynthesis (Caemmerer 2000); maximum carboxylation (V_{Cmax}) and maximum electron transport (J_{max}) rates were calculated from the P_N-C_i curves. The Keen and Spain (1992) model was used to fit the relationship between g_s and *I*.

Biomass: Above- and below-ground samples were collected after 22 weeks of UV-B treatment. The number of shoots per pot and live and dead leaves per shoot were considered. The length of shoots (five of the highest shoots per pot), the width and length of second leaf from the top, and the total leaf area of these five shoots were determined by the leaf area meter *LI-3000A* (*LiCor*, USA). Plants were dried to constant mass at 80 °C for 48 h. Specific leaf area (SLA; leaf area per leaf dry mass), leaf area ratio (LAR; leaf area per total plant dry mass), leaf mass ratio (LMR; leaf dry mass to total plant dry mass ratio), the ratio of dry mass of dead leaves to total leaf dry mass (D/T), and the ratio between below- and above-ground masses (R/S) were calculated.

Statistical analysis: LSD test (*ANOVA*) was used to evaluate the statistically significant differences in above-mentioned parameters among UV-B treatments. All statistical tests were performed using *STATISTICA* software.

Results

Gas exchange: The P_N-*I* response curves under the UV-B treatment showed 18 % decrease (p>0.05) of the maximum assimilation rate (P_{Nmax}; at ambient CO_2 concentration and saturating *I*) in *C. arundinacea* (Fig. 1*A*). However, *C. arundinacea* treated plants showed a 23 % increase of the maximum of carboxylation rate (V_{Cmax}) (Table 1) demonstrating a significant (p<0.01) increase of RuBPCO carboxylase activity.

Low irradiances ($I \approx 300$ μmol m^{-2} s^{-1}) led to the full opening of the stomata in the control; maximum stomatal conductance (g_{smax}) was reached at above 1 000 μmol m^{-2} s^{-1} irradiance in *C. arundinacea* (Fig. 1*C*). In UV-B treated plants, g_{smax} decreased by 35 %, followed by a decrease of C_i from 285±5 μmol(CO_2) mol^{-1} in control to 250±5 μmol(CO_2) mol^{-1} in UV-B treatment, *i.e.* by 12 %. The P_N-C_i relationship and P_N calculated by V_{Cmax} demonstrated that this difference in C_i explained the 26 % P_N decrease in UV-B plants of *C. arundinacea* compared to the control ones.

In *C. villosa*, V_{Cmax} and CO_2 concentration in mesophyll cells decreased by 13 and 12 %, respectively (Table 1). P_{Nmax} (Fig. 1*B*) and g_{smax} (Fig. 1*D*) significantly decreased (up to 45 %, p<0.01) in UV-B treated plants compared to control plants. P_N (Fig. 1*A*,*B*) and g_s (Fig. 1*C*,*D*) exerted higher decreases in UV-B treated plants of *C. villosa* than of *C. arundinacea*.

Likewise, other parameters of P_N-I and P_N-C_i response curves, *e.g.* apparent quantum efficiency (α), demonstrated a stronger damage of assimilation apparatus in *C. villosa* than in *C. arundinacea* (Table 1). Lower assimilate production of *C. villosa* was also reflected in significantly lower values of leaf dark respiration (R_D; 29 %). An estimation of CO_2 assimilation capacity [P_{Nsat}; at saturating I>1 000 μmol m^{-2} s^{-1} and C_i>800 μmol(CO_2) mol^{-1}] demonstrated significant increase for *C. arundinacea* (26 %), while P_{Nsat} for *C. villosa* did not change under the UV-B treatment. These adjustments are relative to changes of maximal electron transport rates (J_{max}); the increase of 26 % for *C. arundinacea* and the decrease of 6 % for *C. villosa* (Table 1).

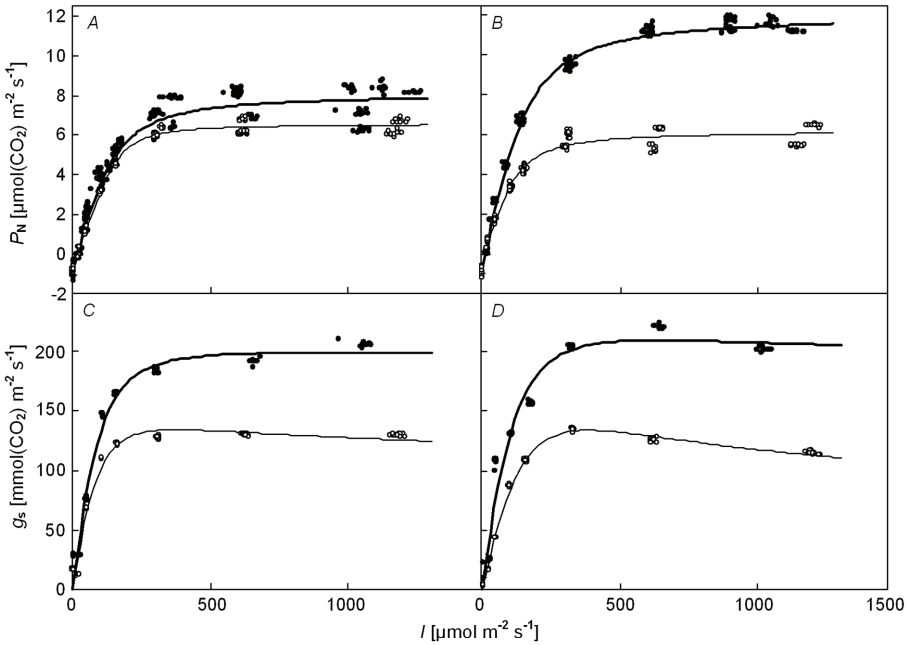

Fig. 1. Relationship between net photosynthetic rate, P_N (*A, B*) or stomatal conductance, g_s (*C, D*) and photosynthetically active irradiance (*I*) at ambient CO_2 concentration [365 μmol(CO_2) mol^{-1}] in *C. arundinacea* (*A, C*) or *C. villosa* (*B, D*). ● (○) measured control (UV-B exposed), ▬ (–) mathematical regression (Caemmerer 2000 or Keen and Spain 1992). n = 6.

Table 1. Mean values ± standard deviation of P_{Nmax} = net photosynthetic rate at ambient CO_2 concentration and saturating irradiance, α = apparent quantum efficiency, Γ_I = compensation irradiance, R_D = leaf dark respiration rate, P_{Nsat} = net photosynthetic rate at saturating intercellular CO_2 concentration and saturating irradiance, V_{Cmax} (J_{max}) = maximum rate of carboxylation (electron transport) calculated from gas exchange measurement; *, ** – statistically significant differences at levels of 0.05, 0.01 (*ANOVA* LSD test); n = 6. Diff in % = Percentage differences shows an increase (+) or a decrease (–) of selected parameter under UV-B treatment in comparison with the control and ambient conditions.

Parameter	*C. arundinacea*				*C. villosa*			
	Control	+UV-B	Diff. [%]	Sign.	Control	+UV-B	Diff. [%]	Sign.
P_{Nmax} [μmol(CO_2) m^{-2} s^{-1}]	9.0±1.2	7.4±0.2	–18	**	13.0±1.0	7.1±0.8	–45	**
α [μmol(CO_2) mol(photon)$^{-1}$]	0.051±0.008	0.041±0.001	–20	**	0.073±0.004	0.041±0.001	–44	**
Γ_I [μmol m^{-2} s^{-1}]	16.0±1.4	20.0±1.7	+25	*	17.0±1.1	18.0±3.4	+6	
R_D [μmol(CO_2) m^{-2} s^{-1}]	–0.9±0.3	–0.8±0.1	–11		–1.3±0.1	–0.9±0.2	–29	**
P_{Nsat} [μmol(CO_2) m^{-2} s^{-1}]	14.0±1.9	17.3±0.5	+24	**	17.0±2.4	17.0±0.7	0	
V_{Cmax} [μmol(CO_2) m^{-2} s^{-1}]	22.0±1.8	27.0±1.2	+23	**	31.0±5.3	27.0±1.4	–13	
J_{max} [μmol(electrons) m^{-2} s^{-1}]	68.0±6.1	85.5±0.4	+26	**	94.0±15.4	89.0±5.6	–6	

Biomass: The differences of production and morphological parameters between control and UV-B exposed plants are summarised in Tables 2 and 3. UV-B treatment led to 20 % significant increase of above-ground biomass in *C. arundinacea* (p<0.05) and the 12 % reduction in *C. villosa* (p>0.05). No significant effects of UV-B treatment on below-ground biomass were observed in both plant species.

Enhanced UV-B had no significant effect on shoot density and total leaf number of *C. arundinacea* and *C. villosa*. A significant increase of the leaf width (16 %; p<0.05) was recorded in *C. arundinacea*; the increase of

Table 2. Mean values ± 95 % confidence limits of production parameters of *C. arundinacea* and *C. villosa* under ambient and enhanced UV-B irradiance. Δ [%] = per cent difference shows an increase (+) or a decrease (–) of the selected parameter under UV-B treatment in comparison with the control and ambient conditions. *The same letters* indicate no statistical difference at $p<0.05$ (*ANOVA* LSD test); $n = 10$.

Dry mass	*C. arundinacea*			*C. villosa*		
[g per pot]	Control	+UV-B	Δ [%]	Control	+UV-B	Δ [%]
Stems	0.53 a (0.33–0.73)	0.71 ab (0.21–1.22)	+34	1.19 c (0.97–1.40)	1.01 bc (0.50–1.51)	–15
Live leaves	1.28 b (0.56–1.98)	1.69 b (0.79–2.58)	+32	0.54 a (0.38–0.70)	0.61 a (0.41–0.80)	+13
Dead leaves	0.82 a (0.69–0.94)	0.81 a (0.32–1.30)	–1	1.18 b (0.90–1.45)	0.95 ab (0.67–1.24)	–19
Total leaves	2.10 ab (1.49–2.70)	2.50 b (1.63–3.37)	+9	1.72 a (1.50–1.93)	1.56 a (1.14–1.98)	–9
Litter	1.08 b (0.84–1.33)	1.23 b (0.62–1.84)	+14	0.61 a (0.22–1.00)	0.51 a (0.32–0.71)	–16
Above-ground biomass	3.71 a (2.92–4.50)	4.44 b (3.63–5.25)	+20	3.52 a (2.95–4.08)	3.08 a (2.35–3.81)	–12
Roots	6.17 a (2.94–4.50)	6.60 a (5.03–8.16)	+7	7.76 a (3.66–11.85)	7.10 a (6.39–7.81)	–8
Bases or rhizomes	3.82 a (2.69–4.96)	3.91 a (2.72–5.10)	+2	6.50 b (3.34–9.67)	5.70 ab (3.47–7.93)	–12
Below-ground biomass	9.99 a (5.64–14.34)	10.51 a (7.79–13.22)	+5	14.26 a (7.00–21.52)	12.80 a (10.24–15.36)	–10
Roots/shoots	2.80 ab (0.91–4.70)	2.37 a (1.92–2.82)	–15	4.05 bc (2.22–5.87)	4.19 c (3.24–5.14)	+3
Total dry biomass	13.7 a (9.94–17.45)	14.95 a (11.7–18.23)	+9	17.78 a (10.27–25.28)	15.88 a (12.88–18.89)	–11

Table 3. Mean values ± 95 % confidence limits of the selected morphometric parameters of *C. arundinacea* and *C. villosa* under control ambient and enhanced UV-B irradiance; specific leaf area (SLA), leaf area ratio (LAR), and leaf mass ratio (LMR). Δ [%] = per cent difference shows an increase (+) or a decrease (–) of the selected parameter under UV-B treatment in comparison with the control and ambient conditions. *The same letters* indicate no statistical difference at $p<0.05$ (*ANOVA* LSD test). $n = 10$.

	C. arundinacea			*C. villosa*		
	Control	+UV-B	Δ [%]	Control	+UV-B	Δ [%]
Shoot density per pot	28.3 ab (18.4–38.1)	26.0 a (17.8–34.2)	–8	36.5 b (27.3–45.7)	35.5 ab (23.0–48.0)	–3
Shoot length [cm]	45.0 a (41.4–48.6)	47.1 a (44.0–50.2)	+5	48.3 a (45.6–51.0)	45.2 a (41.5–48.8)	–6
Leaf length [cm]	33.2 b (30.1–36.2)	35.0 b (32.3–37.6)	+5	24.4 a (23.1–25.7)	22.8 a (20.7–24.8)	–7
Leaf width [cm]	5.5 a (5.1–6.0	6.4 b (6.0–6.8)	+16	6.2 b (5.8–6.6)	5.8 ab (5.4–6.3)	–7
Leaf area [cm^2 per pot]	236 ab (104.7–367.8)	333 b (190.4–474.7)	+41	158 a (99.1–215.9)	174 a (117.8–230.4)	+11
SLA [$m^2\ kg^{-1}$]	18.5 a (15.72–21.22)	20.4 a (15.10–25.63)	+10	29.0 b (26.42–31.64)	28.7 b (26.13–31.20)	–0.3
LAR [$m^2\ kg^{-1}$]	1.80 bc (0.66–2.94)	2.24 c (1.24–3.23)	+24	0.96 a (0.29–1.62)	1.09 ab (0.83–1.36)	+15
LMR [$kg\ kg^{-1}$]	0.16 b (0.09–0.23)	0.17 b (0.13–0.20)	+6	0.10 a (0.07–0.13)	0.10 a (0.08–0.12)	0
Leaves per shoot	2.9 a (2.5–3.2)	2.7 a (2.4–3.0)	–4	4.5 b (4.1–4.9)	4.3 b (3.9–4.7)	–4

total leaf area per pot (up to 41 %), was not statistically significant (Table 2). Also, difference of SLA, LAR, and LMR between *C. arundinacea* and *C. villosa* were not statistically significant (Table 3).

Although most of growth parameters of both species were not significantly ($p>0.05$) affected by enhanced UV-B radiation, we conclude that *C. arundinacea* manifested a slightly positive response (in 16 out of 20 items), while *C. villosa* showed a negative one (in 15 out of 20 ones) over the vegetation season.

Discussion

In contrast to many other experiments, the grasses were exposed to supplemental UV-B radiation at an outdoor facility under treatment of cellulose diacetate-filtered lamps which also produced UV-A (320–400 nm) radiation that may facilitate the set of repairing mechanisms (Caldwell *et al.* 1995, Norton *et al.* 1999).

Gas exchange: The asymptotic part of the P_N-I curve ($I>500$ μmol $m^{-2}\ s^{-1}$) is predominantly limited by RuBPCO (*e.g.* Caemmerer 2000), hypothesising a decrease of RuBPCO amount and/or activity in both *C. arundinacea* (Fig. 1*A*) and *C. villosa* (Fig. 1*B*). Also, Vu *et al*. (1984) demonstrated a decrease of RuBPCO carboxylase activity in pea and soybean leaves in response to increased UV-B. However, treated plants of *C. arundinacea* showed a 23 % increase of the maximum of carboxylation rate (V_{Cmax}) (Table 1) demonstrating a significant ($p<0.01$) increase of RuBPCO carboxylase activity. This discrepancy could be explained by changes of stomata opening and subsequent decrease of C_i under enhanced UV-B radiation.

Decrease of g_s is in accordance with results of Nogués *et al*. (1999) showing a substantial decrease of adaxial and abaxial g_s (*ca*. 80 and 40 %, respectively) of *Pisum sativum* plants under UV-B treatment. Moreover, Dai *et al*. (1995) demonstrated that difference in four cultivars

of *Oryza sativa* dry mass between UV-B treated and control plants was significantly correlated with the reduction in stomatal opening and density on adaxial leaf surface under UV-B treatment.

Likewise, values of apparent quantum efficiency (α; Table 1) demonstrate a stronger damage of assimilation apparatus on the level of photon absorption and photochemical utilization in *C. villosa* (decrease by 44 %) compared to *C. arundinacea* (decrease by 20 %). Decrease of both primary and secondary phases of photosynthesis necessitated lower production of assimilates. It may be demonstrated by significantly lower R_D (Table 1) in *C. villosa* (29 %) compared to *C. arundinacea* (11 %). Contrariwise, Gwynn-Jones (2001) reported a significant increase of respiration in young and mature leaves of *C. purpurea*. This increase was accompanied by alterations in the allocation of plant assimilates.

Hence we conclude that assimilation reactions of *C. villosa* to enhanced UV-B radiation are more sensitive than those of *C. arundinacea*. P_N of *C. arundinacea* was predominantly limited by the decrease of g_s, whereas in *C. villosa* both the carboxylation activity of RuBPCO and g_s were reduced.

Biomass: The above mentioned changes of assimilation rates resulted in appropriate changes of total biomass formation. However, earlier studies have often shown no UV-B effects on overall plant productivity (Ziska *et al*. 1993, Norton *et al*. 1999).

The differences between control and UV-B exposed variants were mainly not statistically significant; there is an obvious positive effect on biomass parameters of *C. arundinacea* (increases by up to 34 %), while the same treatment performed prevailing negative effects in *C. villosa* (decrease by up to 19 %). Most studies show inhibition of growth and overall mass production under enhanced UV-B (*e.g*. Caldwell *et al*. 1995), although Musil (1996), Tosserams and Rozema (1995), or Allen *et al*. (1999) have reported higher biomass production with consequent changes of morphometrical parameters. However, these positive short-term effects could diminish over the long-term treatments (Teramura *et al*. 1990). A significant reduction due to UV-B supplementation in number of tillers and total above-ground dry mass per soil area unit was also found for *C. epigejos* (Oudejans *et al*. 2001).

Differences in the sensitivity of both studied grass species were noticed in many morphological parameters reflecting their different character of growth and reproduction (Holub 2003). Reduced formation of total plant dry mass in two sub-arctic species *Calamagrostis purpurea* (Trin.) Trin. and *Calamagrostis lapponica* (Wahlenb.) Hartman, after an increase of incident UV-B radiation, was accompanied by significant increases in shoot to root ratio, LAR, and LMR, which were due to changes in both SLA and root growth (Gwynn-Jones and Johanson 1996). Similarly, in *C. lapponica* there were reductions in total dry mass of UV-B treated plants, although differences in partitioning were observed only in LMR which was significantly greater than in the non UV-B treatment. Also Deckmyn and Impens (1998) have observed no significant UV-B effect on LMR values of *Bromus catherticus*, but there was a stronger negative effect on generative growth than on vegetative growth.

In accordance with the variety of results mentioned in the literature, we conclude that *C. arundinacea* manifested a slightly positive response, while *C. villosa* showed a negative one to enhanced UV-B radiation over the vegetation season.

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