Growth and reproductive characteristics of C4 weeds under climatic conditions of the Czech Republic

J. Satrapová[1], T. Hyvönen[2], V. Venclová[1], J. Soukup[1]

[1]Department of Agroecology and Biometeorology, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Prague, Czech Republic
[2]MTT Agrifood Research Finland, Plant Production Research, Jokioinen, Finland

ABSTRACT

Climate change could promote the altitudinal spread of C4 weed species since they can benefit from warmer climate. The effects of altitude and climatic conditions (the sum of temperatures above 5°C and precipitation) on the biomass and seed production of two annual C4 weeds – *Amaranthus retroflexus* L. and *Echinochloa crus-galli* (L.) P. Beauv. – were studied in the Czech Republic. We included both temperature and precipitation variables in the study since they both serve as basic indicators of climate change and thus they have the greatest impact on plant development. The experiment was carried out by sowing both weed species on m^2 area with four replicates in seven localities differing in altitude in 2010 and 2011. We found no significant impacts due to altitude on any variables measured. However, climatic factors explained 44.5% of the variation in plant dry biomass and 41.4% of the seed number produced by *A. retroflexus*. The same variables did not significantly contribute to the variation in above-ground biomass or seed number of *E. crus-galli*. These results show the impact of climate conditions to vary between species and not to limit reproduction at high altitudes.

Keywords: *Amaranthus retroflexus* L.; *Echinochloa crus-galli* (L.) P. Beauv.; biomass; seeds; climate change

Global warming causes numerous negative effects to the environment and corresponding ecosystem functions (Pretel and Vácha 2003). Invasion of harmful alien plant species as a consequence of climate change is of concern (Walther et al. 2009). In arable ecosystems, the expansion range of C4 weed species is of particular interest since they comprise a majority of the 'world's worst weeds' (Holm et al. 1977) and prefer warm climate conditions (Sage and Kubien 2003).

Temperature is one of the main factors determining the distribution and productivity of C4 plants (Wang 2006, Sage and Kubien 2007). This is one reason why they are more common in tropical areas compared to temperate areas, and are especially prevalent in drier tropical climates (Fubrank and Taylor 1995, Sage and Monson 1999); these climatic conditions prevail in many subtropical regions of the world (Ehleringe and Bjorkman 1977). In Europe, the distribution of C4 weeds includes temperate regions (Holm et al. 1977, Hyvönen et al. 2011) because C4 plants are better adapted to the more intense temperature and light conditions relative to C3 species and thus exhibit greater water use efficiency (WUE). An optimum temperature for the photosynthesis of C4 species ranges from 25°C to 40°C (Sage and Monson 1999). These physiological adaptations result in different responses to climate change compared to C3 species. Unlike C3 plants, C4 plants do not benefit in terms of increased carbon intake, as a result of rising atmospheric CO_2 (Pearcy et al. 1981, Ziska 2001). This is likely due to their evolutionary response to lower levels of atmospheric

Supported by the Ministry of Education, Youth and Sports of the Czech Republic, Project S.

CO_2, which began during the Cretaceous period and continued until the Miocene (Ehleringer et al. 1991). For C4 weeds, rise in the temperature and long-term droughts are likely to be beneficial, however, the final benefits of climate change are based on the timing of warming, which can be more critical than the warming itself (Sage and Kubien 2003). Nonetheless, climate change can be hypothesized to lead to both latitudinal and altitudinal range expansion of C4 weeds in future (Hyvönen et al. 2011).

Here, we studied the climatic responses of two annual C4 weed species – *Amaranthus retroflexus* L. (AMARE) and *Echinochloa crus-galli* (L.) P. Beauv. (ECHCG) at different altitudes in the Czech Republic. These species are the most widely distributed and harmful C4 weeds in the Czech Republic (Jursik et al. 2004a,b). Both species are summer annuals competing especially in root crops and maize (Martinkova and Honek 1998). *E. crus-galli* is a grass species native to Europe and India (Maun and Barrett 1986, Holm et al. 1977). It mainly occurs in the lowlands, but is also found in the foothills of the Czech Republic (Kohout 1997). *A. retroflexus* is a dicot belonging to the family Amaranthaceae, and it is native to North America (Holm et al. 1997). It is the most harmful weed in the root crops in the warmer regions of the Czech Republic (Holec et al. 2004), but is rarely found in the mountain areas (Hejny and Slavik 2003). Understanding the climatic demands of these species at different altitudes will facilitate assessment of current altitudinal distributions and allow us to determine whether this distribution is limited by climatic factors. If this is the case, this information can be used in climate change models to help develop more robust predictions about how C4 plants in general, and these species specifically, might expand altitudinally in the future.

We expected *E. crus-galli* to prefer lower altitudes and warmer climate conditions than *A. retroflexus* due to its narrower distribution in the Czech Republic.

MATERIAL AND METHODS

Field experiment. A field experiment was started in 2009 with collection of seeds from both plant species from South Moravia, Czech Republic (Chvalovice – 48°47'N, 16°5'E 222 m a.s.l.). This location is the warmest area with the lowest precipitation. The seeds were stored in the plastic bottles in the dark. The seeds were used in the field experiments during 2010 and 2011. The seeds were sown in four localities with different altitudes: Praha-Suchdol, Brezany I, Horice, Dobra Voda in 2010 and three locations in 2011: Doksany, Praha-Suchdol, Sperice (Table 1). The climatic data were obtained from meteorological stations situated within a 0.5–25 km distance from the experimental plots. The sum of temperatures above 5°C ($x1$), the sum of precipitation (measured in millimeters; $x2$) from sowing to harvest of weeds in years 2010 and 2011 (data from National Climatic Data Centre – NCDC) were included in the analysis. The locality Praha-Suchdol was used as a reference locality for exploring the influence of time (year).

Experimental plots were established on maize fields in all localities, because the weed species

Table 1. Overview of the experimental sites used in the study – Climatological standard normal (1961–1990)

Localities	Latitude		Altitude (m a.s.l.)	Mean annual temperature (°C)	Annual amount of precipitation (mm)	Sum of temperatures above 5°C from sowing to harvest of weeds in 2010–2011		Sum of precipitation (mm) from sowing to harvest of weeds 2010–2011	
	N	E				AMARE	ECHCG	AMARE	ECHCG
Doksany	14°09'	50°27'	158	8.5	456	2109	–	405	–
Brezany I	15°04'	50°02'	240	8.5	617	1931	1574	523	418
Prague -Suchdol	14°22'	50°07'	285	7.9	526	1809	1492	395	329
Horice	15°12'	49°35'	468	6.6	675	1601	1482	626	555
Sperice	15°17'	49°34'	560	6.6	675	1798	1409	449	334
Dobra Voda	15°01'	49°23'	624	5.7	762	1579	1467	626	555

AMARE – *Amaranthus retroflexus* L.; ECHCG –*Echinochloa crus-galli* (L.) P. Beauv.

typically occur in maize fields. Each weed species were seeded in 1 m^2 (1 m × 1 m) area with four replicates (four 1 m^2 plots in each locality). Experimental plots were placed on crop free area. Sowing of weed seeds was carried out on 19^{th} or 20^{th} April at each site in both years (typical time for sowing of maize). The seeds were sown in marked regular pattern to avoid admixture of plants from soil seed bank. Throughout the experiment, the plots as well as the surroundings were consistently maintained weed-free by hand weeding (each 14 days); to avoid intraspecific competition, the number of sown plants was randomly gradually reduced to one plant individual per plot. The experiment was terminated at plant maturity, when the plants were ripen and started to die (18–27 weeks after sowing). The harvest of *A. retroflexus* was started on 6^{th} October and finished on 12^{th} October in 2010. In 2011, the harvest started on 24^{th} October in Doksany and Sperice and 30^{th} September at Suchdol. *E. crus-galli* was harvested between 25^{th} August and 15^{th} September in 2010 and 17^{th} August and 31^{st} August in 2011.

Dry above-ground biomass and the number of seeds per plant were measured at the end of the experiment. Mature seeds were gradually harvested by cutting of the mature parts of the panicles of *E. crus-galli* to prevent the seed rain. By *A. retroflexus*, the falling seeds were caught in the white non-woven fabric placed under the plants and collected regularly. Finally, the dead plants were harvested and transported to the laboratory for the separation of remaining seeds and biomass analyses. The weed samples were dried at 105°C for 48 h in the automatic drying room and weighed. The seeds were cleaned by using an air purifier and the number of seeds per plant was counted.

Statistical analysis. The relationship between climatic factors and the weed biomass as well as seed number was studied using linear and multiple linear regressions. A Mann-Whitney *U*-test was used for determination of differences between years in Praha-Suchdol. Both dry above-ground plant biomass and seed number per plant in both species appeared not to differ statistically significantly ($P > 0.05$) between years 2010 and 2011. Therefore, we chose to pool the data across years. The impact of altitude was analysed by linear regression. The impact of climatic factors was studied by multiple linear regression and included the sum of temperatures above 5°C ($x1$), the sum of precipitation ($x2$) (data from NCDC) in the analyses. Data were analyzed using the software Statistica 9 (www.statsoft.com).

RESULTS AND DISCUSSION

Altitude. Positive correlations between dry biomass and number of seeds were found to be high both for *A. retroflexus* and *E. crus-galli* ($r = 0.979$ and $r = 0.699$, respectively), i.e. larger plants produced more seeds for both weed species. The production of biomass and seeds showed a decreasing trend with altitude for *A. retroflexus* and a slightly increasing trend for *E. crus-galli* (Figure 1). However, none of the relationships were statistically significant at the level of $P < 0.05$ with the exception of *A. retroflexus* seed production which was marginally significant (i.e. $P < 0.1$) (Table 2). Plants of *E. crus-galli* did not emerge in the locality Doksany in 2011 and thus were not included in the analysis.

Low seed production and above-ground biomass weight of *E. crus-galli* on the experimental site Brezany was very likely caused by the phenomenon called ‘flash drought’ characterized by moisture deficits and abnormally high temperatures (Mozny et al. 2011). This could have had a negative effect on the seed production since *E. crus-galli* prefers wet soils (Holm et al. 1977).

In contrast to our expectations, neither of the studied weed species showed statistically significant relationships between seed production and altitude. However, the results showed both species capable of reproducing at the highest altitudes (i.e. > 600 m a.s.l.) included in the study. This altitude exceeds the altitudes in which these species are commonly found in the Czech Republic because they are most common in the lowlands (Hejny and Slavik 2003). Therefore, the results suggest that both of the species have a potential to succeed outside their current range.

Seed production appeared to be positively correlated with plant biomass in both species. This is in accordance with previous findings (e.g. Chauhan and Johnson 2010) demonstrating that reproductive effort can be a result of the number of primary stems per unit stem mass (Wang et al. 2006). Both species produced seeds more than reported earlier for *A. retroflexus*, Costea et al. (2003). They reported that *A. retroflexus* seed production varied in response to growing conditions such as the severity of crop competition. They also reported

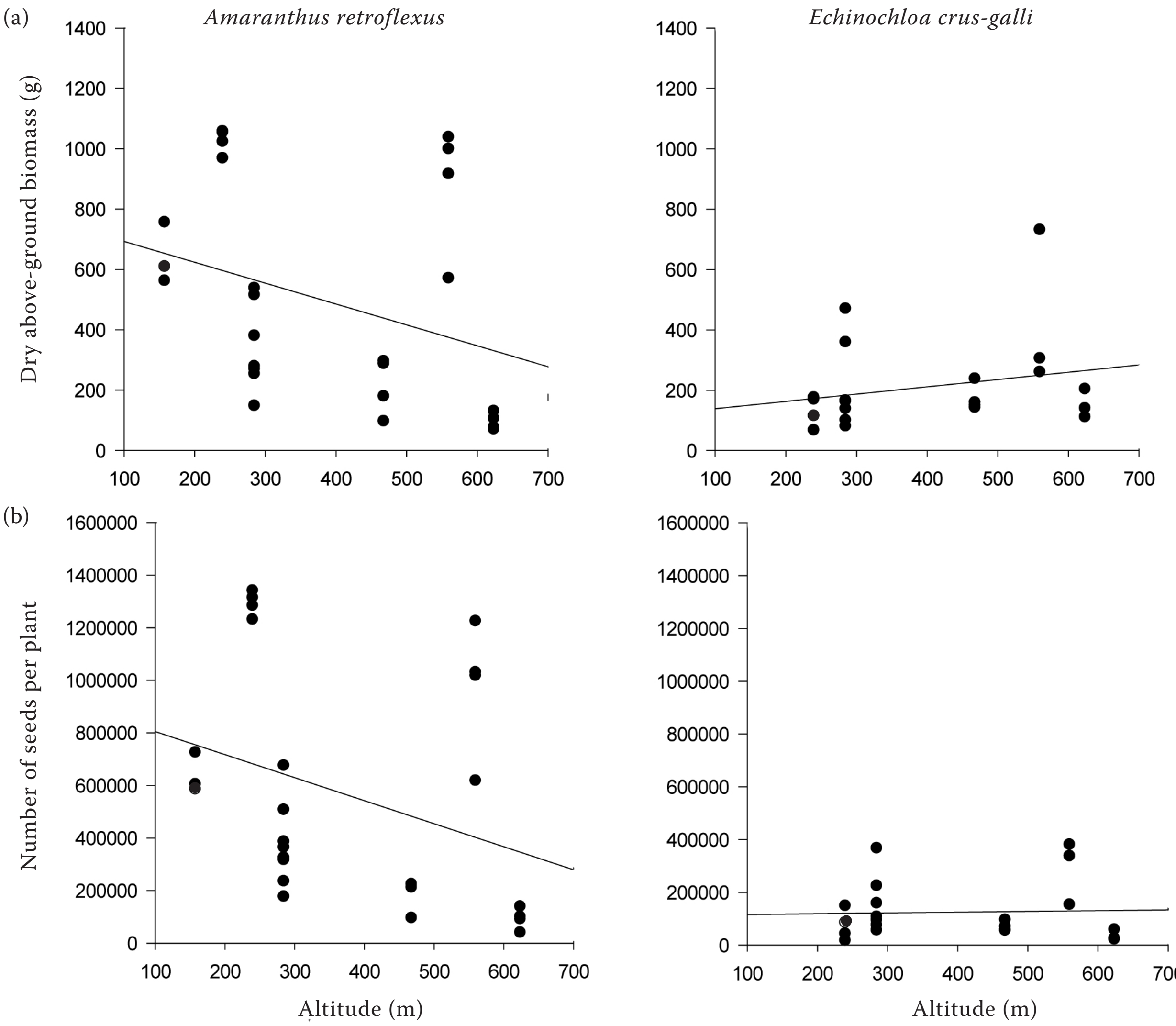

Figure 1. (a) The relationship between the dry biomass and the altitude, and (b) the relationship between the number of seeds and the altitude

that seed production per plant was, on average, 100 000 seeds. This value is much less than in our experiment (more than 1 000 000 seeds per plant). In *E. crus-galli*, the seed number was also ten times higher than reported previously (40 000 seeds per plant in Holm et al. (1977) compared to 370 000 seeds per plant in our experiment). Martinkova and Honek (1992) found out a strong relationship between seed production and above-ground biomass of *E. crus-galli* in maize. The plants produced about 650 seeds per 1 g of above-ground biomass in their study.

In the current study, the seed production was measured without competition by a crop species, which may partly explain the high seed production (Maun and Barrett 1986) and thus result in an overestimate of the effects of climate warming on the fitness of C4 species (Hyvönen 2011).

Climatic factors. The monitoring period was characterized by a slightly above-average air temperatures and higher precipitation especially during the summer.

In the case of *A. retroflexus*, the regression models including the independent variables (i.e. the sum of precipitation and the sum of temperature) showed positive responses both for the biomass and the seed production and explained 44.5% and 41.4% of their variation, respectively (Table 3).

In the case of *E. crus-galli*, precipitation had a negative effect and temperature a positive effect on seed production per plant as well as biomass production; the resulting model explaining 4.0% and 25.9% of the variation of the seed production per plant and the biomass, respectively (Table 3).

A. retroflexus shows a positive relationship in terms of temperature on biomass and seed produc-

Table 2. Linear regression results for altitude, plant dry biomass and seed number of *A. retroflexus* and *E. crus-galli*

	Amaranthus retroflexus		*Echinochloa crus-galli*	
	dry biomass	seed production	dry biomass	seed production
r	–0.319	–0.329	0.233	0.039
P	0.105	0.094	0.309	0.868

tion. These results are consistent with the finding of Guo and Al-Khatib (2003) who also found higher biomass production positively correlated with higher temperatures. Increased precipitation also resulted in higher production of biomass and seeds. These results are not consistent with the findings of Öztrürk et al. (1981). They reported severely diminished dry, shoot weight in plants exposed to relatively higher moisture levels. We assume the sum of precipitation was not as high and thus did not cause a negative impact on plants at our sites. Unfortunately, in our experiment the relative effects of temperature and precipitation could not be separated.

Previous research repeatedly demonstrated that *E. crus-galli* prefers wet soil (e.g. Wiese and Vandiver 1970, Holm et al. 1977) and grows better in wet condition relative to other C4 species (Singh et al. 1983). However, in our study, precipitation had a negative influence on seed production and biomass production though the interactions were not statistically significant (Table 3). Temperature had a positive influence on production of biomass and seeds. Our results suggest we need to consider a greater influence on *E. crus-galli* due to non-climatic factors not included in the study (e.g. soil type and other factors) because we could not find a relationship other factors maybe important and we should focus them.

Climate change. In conclusion, our results demonstrate a species-specific response of C4 plant species to climatic variables. Increases in temperature appear to be a reason for the spread of C4 plants to higher altitudes (Skillman et al. 2008) and may even be the case for *A. retroflexus*. These species, like most plants defined as weed species are known to be plastic regarding their seed production and growth response to climate change (Patterson 1995). Our findings suggest that the species we studied and possibly the other C4 plants can also reproduce in sub-optimal climate conditions enabling potential spread of these species to localities where there they are not currently found.

Over past 20 years the average number of tropical days in the summer season has increased in more than 1.5 times in Central lowlands region in the Czech Republic (Potop 2010). Since climate change models predict increases in the mean temperature and precipitation at higher altitudes in the Czech Republic we may expect to see an increase in C4 plants with indirect effects to agronomic production and weed control system. Interestingly, precipitation appeared to have a negative impact on

Table 3. Multiple linear regression model for dry biomass and seeds number per plant of *A. retroflexus* and *E. crus-galli*.

		r	*F*	*P*	Error of estimate
Amaranthus retroflexus					
Dry biomass	$r^2 = 0.445$	0.667	9.604	0.000	275.3
Seed number per plant	$r^2 = 0.414$	0.644	8.484	0.002	347801.1
Dry above-ground biomass	$y = -2954.64 + 1.72x_1 + 0.76x_2$				
Number of seeds per plant	$y = -3619197 + 2060x_1 + 981x_2$				
Echinochloa crus-galli					
Dry biomass	$r^2 = 0.040$	0.201	0.379	0.689	158.3
Seed number per plant	$r^2 = 0.259$	0.509	3.148	0.067	101007.2
Dry above-ground biomass	$y = -143.8 + 0.13x_1 - 0.27x_2$				
Number of seeds per plant	$y = -101522 + 170.3x_1 - 546.7x_2$				

the seed production of *E. crus-galli* in our study. Thus, conclusions about the success of both species in response to climate change must be considered in light of the multifaceted components of climate change, e.g. precipitation frequency, amount of rainfall, duration and frequency of drought, etc. Nonetheless, altitudinal range expansion of C4 species is a plausible expectation in response to future climate change and should be included in the development of climate change models specific to agronomic and plant/habitat conservation concerns.

REFERENCES

Chauhan S.B., Johnson D.E. (2010): Implications of narrow crop row spacing and delayed *Echinochloa colona* and *Echinochloa crus-galli* emergence for weed growth and crop yield loss in aerobic rice. Field Crops Research, *117*: 177–182.

Costea M., Weaver E.S., Tardif J.F. (2003): The biology of Canadian weeds. 130. *Amaranthus retroflexus* L., *A. powellii* S.Watson and *A. hybridus* L. Canadian Journal of Plant Science, *84*: 631–668.

Ehleringer J.R., Sage R.F., Flanagan L.B., Pearcy R.W. (1991): Climate change and the evolution of C_4 photosynthesis. Trends in Ecology and Evolution, *6*: 95–99.

Furbank R.T., Taylor W.C. (1995): Regulation of photosynthesis in C_3 and C_4 plants: A molecular approach. The Plant Cell, *7*: 797–807.

Guo P., Al-Kharib K. (2003): Temperature effects on germination and growth of redroot pigweed (*Amaranthus retroflexus*), Palmer amaranth (*A. palmeri*), and common waterhemp (*A. rudis*). Weed Science, *51*: 869–875.

Hejny S., Slavik B. (2003): Flora of the Czech Republic. Academia, Praha. (In Czech)

Holec J., Soukup J., Jursik M., Hamouz P. (2004): Invasive weed species on arable land in the Czech Republic. Journal of Plant Diseases and Protection, *19* (Special Issue): 231–236.

Holm L., Doll J., Holm E., Pancho J., Herberger J. (1997): World Weeds – Natural Histories and Distribution. John Wiley & Sons, New York.

Holm L.G., Pluckenett D.L., Pancho J.V., Herberger J.P. (1977): The World's Worst Weeds. Distribution and Biology. The University Press of Hawaii, Honolulu.

Hyvönen T. (2011): Impact of temperature and germination time on the success of a C_4 weed in a C_3 crop: *Amaranthus retroflexus* and spring barley. Agricultural and Food Science, *20*: 183–190.

Hyvönen T., Glemnitz M., Radics L., Hoffmann J. (2011): Impact of climate and land use type on the distribution of Finnish casual arable weeds in Europe. Weed Research, *51*: 201–208.

Kohout V. (1997): Weeds of Fields and Gardens. Agrospoj, Prague. (In Czech)

Jursik M., Soukup J., Holec J. (2004a): Biology and control of sugar beet significant weeds – redroot pigweed (*Amaranthus retroflexus* L.). Listy cukrovarnicke a reparske, *120*: 87–91. (In Czech)

Jursik M., Soukup J., Holec J. (2004b): Biology and control of sugar beet significant weeds Barnyard grass (*Echinochloa crus-galli* L.). Listy cukrovarnicke a reparske, *120*: 47–51. (In Czech)

Martinkova Z., Honek A. (1992): Effect of plant size on the number of caryopses in barnyard grass, *Echinochloa crus-galli* (Poaceae). Preslia, *64*: 171–176.

Martinkova Z., Honek A. (1998): Competition between maize and barnyard grass (*Echinochloa crus-galli*) at different moisture regime. Rostlinná výroba, *44*: 65–69.

Maun M.A., Barrett S.C.H. (1986): The biology of canadian weeds: 77. *Echinochloa crus-galli* (L.) Beauv. Canadian Journal of Plant Science, *66*: 739–759.

Mozny M., Trnka M., Zalud Z., Hlavinka P., Nekovar J., Potop V., Virag M. (2011): Use of a soil moisture network for drought monitoring in the Czech Republic. Theoretical and Applied Climatology, *107*: 99–111.

National climatic data centre (2012): NOAA Satellite and Information Service. Available at http://www.ncdc.noaa.gov/oa/ncdc.html

Öztürk M., Rehder H., Ziegler H. (1981): Biomass production of C_3- and C_4-plant species in pure and mixed culture with different water supply. Oecologia, *50*: 73–81.

Patterson D.T. (1995): Weeds in a changing climate. Weed Science, *43*: 685–701.

Pearcy R.W., Tumosa N., Williams K. (1981): Relationships between growth, photosynthesis and competitive interactions for a C_3 and a C_4 plant. Oecologia, *48*: 371–376.

Potop V. (2010): Temporal variability of daily climate extremes of temperature and precipitation in the middle Polabí (Elbeland) lowland region. Scientia Agriculturae Bohemica, *3*: 140–148.

Pretel J., Vácha D. (2003): Climate. Study for the Ministry of Environment, a Separate Department of Climate Changes. Available at http://www.chmi.cz/cc/inf/index.html

Sage R.F., Kubien D.S. (2003): Quo vadis C_4? An ecophysiological perspective on global change and the future of C_4 plants. Photosynthesis Research, *77*: 209–225.

Sage R.F., Kubien D.S. (2007): The temperature response of C_3 and C_4 photosynthesis. Plant, Cell and Environment, *30*: 1086–1106.

Sage R.F., Monson R.K. (1999): C_4 Plant Biology. Academic Press, San Diego.

Singh R.D., Sarkar P.A., Ghosh A.K. (1983): Tolerance of rice weeds for natural floodwater submergence. International Rice Research Newsletter, *8*: 19–20.

Skillman J.B., Sage R.F., Meyer A. (2008): Do C_3 and C_4 plants respond similarly to climate change? Comparative studies with the C_4 grass *Muhlenbergia richardsonis* at high elevations in California's White Mountains, Climate, Ecosystems, and Resources in Eastern California (CEREC). In: White Mountain Research Station Symposium, November 5–8, Bishop, 47.

Walther G.R., Roques A., Hulme P.E., Sykes M.T., Pysek P., Kühn I., Zobel M., Bacher S., Botta-Dukat Z., Bugmann H., Czucz B., Dauber J., Hickler T., Jarosik V., Kenis M., Klotz S., Minchin D., Moora M., Nentwig W., Ott J., Panov V.E., Reineking B., Robinet C., Semenchenko V., Solarz W., Thuiller W., Vila M., Vohland K., Settele J. (2009): Alien species in a warmer world: Risks and opportunities. Trends in Ecology and Evolution, *24*: 686–693.

Wang R.Z. (2006): The occurrence of C_4 plants and their morphological functional types in the vegetation of Xinjiang, China. Photosynthetica, *44*: 293–298.

Wang T., Zhou D., Wang P., Zhang H. (2006): Size-dependent reproductive effort in *Amaranthus retroflexus*: The influence of planting density and sowing date. Canadian Journal of Botany, *84*: 485–492.

Weber G.R. (1994): On the seasonal variation of local relationships between temperature, temperature range, sunshine and cloudiness. Theoretical and Applied Climatology, *50*: 15–22.

Wiese A.F., Vandiver C.W. (1970): Soil moisture effects on competitive ability of weeds. Weed Science, *18*: 518–519.

Ziska L.H. (2001): Changes in competitive ability between a C_4 crop and a C_3 weed with elevated carbon dioxide. Weed Science, *49*: 622–627.

Received on January 30, 2013
Accepted on May 14, 2013

Corresponding author:

Ing. Jitka Satrapová, Česká zemědělská univerzita v Praze, Fakulta agrobiologie, potravinových a přírodních zdrojů, Katedra agroekologie a biometeorologie, Kamýcká 129, 165 21 Praha, Česká republika
e-mail: satrapovaj@af.czu.cz