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Intraspecific Variation in the Response of *Arabidopsis thaliana* Lines to Elevated Atmospheric CO_2

By

THOMAS A.W. VAN DER KOOIJ[1, 2], LUIT J. DE KOK[1] & INEKE STULEN[1]

Key words: *Arabidopsis thaliana* L., carbon dioxide, biomass production, relative growth rate, starch, specific leaf area.

Summary

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Since a study of the intraspecific variation in the response to elevated CO_2 of different genetic lines of one species might reveal the parameters essential for the response of a species to elevated CO_2, thirteen lines of *Arabidopsis thaliana* L. were exposed to elevated CO_2 (700 $\mu l\ l^{-1}$). All lines increased shoot biomass, leaf area and starch content and most lines decreased specific leaf area (SLA) upon exposure to elevated CO_2. The lines differed in the magnitude of their response to elevated CO_2 (ratio 700/350), viz. 1.09 to 1.68 for the increase in shoot biomass, 1.00 to 1.44 for the increase in leaf area, 1.40 to 1.71 for the increase in starch content and 1.02 to 0.84 for the change in SLA. Both soluble sugar and structural dry matter content were hardly affected by elevated CO_2. The changes in the various parameters are discussed in relation to the life strategy of *Arabidopsis thaliana* L.

Introduction

Carbon dioxide concentration in the atmosphere is gradually increasing as a consequence of the increase in human fossil energy consumption (NEFTEL & al. 1985), and in the next century a doubling of the present concentration can be expected (HOUGHTON & al. 1990). Exposure of plants to elevated CO_2 usually results in increased photosynthetic activity, biomass production, carbohydrate

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[1] Department of Plant Biology, University of Groningen, P.O. Box 14, 9750 AA, Haren, The Netherlands.

[2] Department of Genetics, University of Groningen, P.O. Box 14, 9750 AA, Haren, The Netherlands.

content and water use efficiency, and in changes in leaf morphology (KIMBALL 1983, CURE & ACOCK 1986, LAWLOR & MITCHELL 1991, WOODWARD & al. 1991, HUNT & al. 1993, STULEN & al. 1998). However, there is considerable variation in CO_2 response between species, which may be related to differences in leaf morphology and growth strategy (POORTER 1993, HUNT & al. 1993, LOEHLE 1995, POORTER & al. 1996, STULEN & al. 1998). The increase in biomass production at elevated CO_2 is the result of a transient increase in relative growth rate (RGR), which may last from a few days to a couple of weeks, depending on the plant species (STULEN & al. 1998). Various factors might be involved in the transient nature of this stimulation, as increased self shading, depletion of nutrients and/or photosynthetic acclimation (POORTER & al. 1988, SAGE & al. 1989, STULEN & al. 1998). The plant's ability to create a continuous sink and/or the ability to create new sinks for the increased carbohydrate production at elevated CO_2 might be decisive in determining the duration of the stimulation of the RGR upon exposure to elevated CO_2 (STULEN & al. 1998).

Exposure of *Arabidopsis thaliana* cv. Landsberg to 700 $\mu l\ l^{-1}$ CO_2 resulted in an increase in biomass and seed production, respectively. The transient period of the stimulation of the RGR lasted only one to three days (VAN DER KOOIJ & DE KOK 1996, VAN DER KOOIJ & al. 1999). Exposure of *A. thaliana* to atmospheric CO_2 concentrations from 390 to 1680 $\mu l\ l^{-1}$ showed that the maximal increase in shoot biomass production was already reached at 560 $\mu l\ l^{-1}$ (VAN DER KOOIJ & al. 1999). Over the same range of CO_2 concentrations a 5 to 17 % increase in shoot dry matter content was found, which could be accounted for by the increase in shoot starch content. Shoot soluble sugar content was not affected. In contrast to observations with other species (SAGE & al. 1989), down-regulation of photosynthesis did not occur in *A. thaliana* (VAN DER KOOIJ & DE KOK 1996, VAN DER KOOIJ & al. 1999).

The response of plants to elevated CO_2 is very variable (POORTER 1993, POORTER & al. 1996). A study of the variation in CO_2 response between different genetic lines of one species might be more successful in finding parameters essential for the individual CO_2 response of a species than comparing different species with variability due to phylogenetic differences or life strategies. Furthermore, knowledge on the variation in CO_2 response within a species is important to predict possible population genetic consequences for plant populations exposed to a gradual increasing CO_2 concentration (WULFF & ALEXANDER 1985, WOODWARD & al. 1991). In the present paper thirteen lines of *A. thaliana* from different origin were exposed to ambient (350) or 700 $\mu l\ l^{-1}$ CO_2. The response to elevated CO_2 of the lines with respect to shoot biomass production, dry matter content, leaf area, specific leaf area (SLA) and non-structural carbohydrate content was determined. The changes in the various parameters are evaluated in relation to the magnitude of the increase in shoot biomass (ratio 700/350) of various lines to elevated CO_2.

Materials and Methods

Thirteen different lines of *Arabidopsis thaliana* L. from various locations were used in the present experiments (Table 1). The seeds originated from self reproduced single seed propagated lines (F1-generation) of the original line material. Most lines were obtained from the Nottingham *Arabidopsis* Stock Centre (University of Nottingham, Nottingham, UK) and the *Arabidopsis* Biological Resource Center at Ohio State (Ohio State University, Columbus, USA). The line Landsberg (erecta) was obtained from Prof. Dr. Ir. M. KOORNNEEF (Agricultural University, Wageningen, The Netherlands). The line Gasteren was collected in The Netherlands near Gasteren (Drenthe), at a sandy field site along a wheat field.

Seeds were sown on commercial potting soil (Terosol, Intervema B.V., Eelde, The Netherlands) in either 2 l or 0.25 l plastic pots. Seeds were covered with a thin layer of white sand. The pots were transferred to a cold room (4°C) in the dark for four days in order to vernalize the seeds and synchronise germination. Thereafter, plants were pre-cultivated in a climate-controlled room, with a day and night temperature of 24 and 18°C, respectively, and a relative humidity of 80 %. The photoperiod was 14 h at a photon flux density of 280 μmol m^{-2} s^{-1} (within the 400-700 nm range), provided by fluorescent lights (Osram L58W/21). Plants were daily watered with tap water. Seven days after sowing the number of plants was reduced to either seven plants in the 2 l pots or one plant in the 0.25 l pots.

Plants were transferred to a climate-controlled room kept at 350 ± 10 μl l^{-1} CO_2 for three days, before half of the plants was transferred to an identical climate room, kept at 700 ± 10 μl l^{-1} CO_2. The CO_2 concentrations were controlled as described by DEN HERTOG & al. 1993. The climate-controlled rooms were kept at a day and night temperature of 20°C, and a relative humidity of 75 %. Photon flux density was 380 ± 20 μmol m^{-2} s^{-1} (within the 400-700 nm range), provided by Philips HPI-T (400 W) and Osram incandescent lamps (60W).

All thirteen lines were exposed to 350 and 700 μl l^{-1} CO_2 during their vegetative growth phase for eight days. At the start of the exposure two plants were harvested so that five plants remained in each 2 l pot. After eight days all plant shoots were harvested and fresh weight, dry weight and leaf area were determined as described by VAN DER KOOIJ & DE KOK 1996. The relative growth rate (RGR) over this period was calculated from the ln transformed initial and end weights. The specific leaf area (SLA) was calculated as the ratio of total leaf area and shoot fresh weight. Seven lines, grown in 0.25 l pots, containing a single plant, were exposed to 350 and 700 μl l^{-1} CO_2 for eleven days. After that period all plant shoots were harvested and dry matter, starch and soluble sugar content (non-structural carbohydrates) were determined. Structural dry matter content was calculated as dry matter minus non-structural carbohydrate content (soluble sugars + starch).

Dried shoots were ground in a mortar and the soluble sugars were extracted from the powdered plant material in 80 % ethanol. The soluble and insoluble fraction was separated by centrifugation. The pellets of the 80 % ethanol extracts were incubated in 1 N HCl for 3 h in order to degrade starch (DEN HERTOG & al. 1996). Sugar content was determined after FALES 1951, using glucose as a standard.

Differences between the lines were statistically analysed by a one way ANOVA using Graphpad Instat, Differences between CO_2 treatments within a line were statistically analysed with Student's t-test. Linear regression equations were calculated with Graphpad Prism2, GraphPad Software, Inc.

Results and Discussion

The *A. thaliana* lines showed variation in RGR, leaf morphology, dry matter content and soluble sugar content when grown at 350 μl l^{-1} CO_2. The relative growth rates (RGR) varied between 0.38 and 0.42 g g^{-1} day^{-1} (Table 1). The differences in RGR between the lines were significant ($P < 0.0001$). The differences in shoot biomass (P <0.0001; results not shown), leaf area (P <0.0001), specific leaf area (SLA; p <0.0001), dry matter content (p = 0.0005; results not shown) and soluble sugar content (P = 0.0017) were also significant (Table 1, 3 and 4). Differences between the lines in shoot starch content, the main storage carbohydrate pool, were not significant (Table 4). Since differences in initial weight between the lines were significant (Table 1), differences during early development (germination rate) must have occurred.

Exposure of the lines to 700 µl l^{-1} CO_2 for eight days resulted in an increase in shoot fresh and dry weight in all lines compared to the plants grown at 350 µl l^{-1} CO_2. The difference between shoot biomass production at 350 and 700 µl l^{-1} CO_2 can be expressed as a weight ratio (700/350). This ratio varied between the lines, viz. from 1.09-1.68 and from 1.26-1.93 for fresh and dry weight, respectively (Table 1). Apparently, some lines profited more from the increased atmospheric CO_2 concentration than other lines. Despite the relatively small differences in RGR, the slower growing lines profited more from elevated CO_2, since a significant negative correlation between the RGR at 350 µl l^{-1} CO_2 and the weight ratio (700/350) of the shoot was observed (Table 2). Previous experiments with *A. thaliana* showed that the stimulation of shoot biomass production after transfer of the plants from ambient to elevated CO_2 could be attributed to a short transient stimulation of the RGR (VAN DER KOOIJ & DE KOK 1996, VAN DER KOOIJ & al. 1999).

Table 1. Origin, initial fresh weight (FW), relative growth rate at 350 µl l^{-1} CO_2 on a fresh weight basis (RGR_{FW}) in g g^{-1} day and weight ratio's of the shoot (700/350) on a fresh weight (FW) and dry weight (DW) basis of *Arabidopsis thaliana* lines from various origins. [1]Rhon, [2]Kashmir, [3]Copenhagen, [4]Lisbon, [5]Marlborough, [6]Brittany, [7]Seattle, [8]Gasteren.

Line	Origin	Initial FW	RGR_{Fw}	FW ratio	DW ratio
Landsberg	laboratory line	12.3 ± 3.5	0.39 ± 0.02	1.24	1.45
N900	Germany[1]	7.7 ± 2.3	0.43 ± 0.02	1.15	1.27
N903	India[2]	10.5 ± 3.0	0.43 ± 0.01	1.09	1.26
N904	Poland	4.5 ± 1.8	0.38 ± 0.02	1.68	1.93
N921	Tadjikistan	10.1 ± 1.8	0.41 ± 0.02	1.27	1.48
N922	Tadjikistan	16.6 ± 2.2	0.41 ± 0.02	1.09	1.23
N929	Tadjikistan	14.1 ± 2.4	0.39 ± 0.01	1.39	1.58
N3109	Denmark[3]	9.3 ± 1.2	0.40 ± 0.01	1.28	1.59
Cs3180	Portugal[4]	5.8 ± 1.6	0.43 ± 0.02	1.18	1.46
Cs6075	U.K.[5]	5.7 ± 1.9	0.42 ± 0.01	1.48	1.68
Cs6094	France[6]	7.8 ± 2.2	0.41 ± 0.01	1.54	1.72
Cs6188	U.S.A.[7]	10.1 ± 2.7	0.42 ± 0.01	1.11	1.29
Gasteren	The Netherlands[8]	13.1 ± 2.4	0.42 ± 0.02	1.24	1.40

The variation between the lines in weight ratio (700/350), therefore, might be attributed to differences in degree and duration of the stimulation of the RGR, which could not be measured in the present experimental set-up. The variation might also be caused by small differences in physiological age between the different lines at the time of the start of the exposure to elevated CO_2. The latter seems plausible, since a significant negative correlation was observed between shoot weight ratio (700/350) and initial shoot weight (Table 2).

Table 2. Slope, correlation coefficient (r^2) and significance level (P) for the linear regressions between the weight ratio (FW_{700}/FW_{350}) and the dependent variables RGR_{350} (RGR at 350 µl l^{-1} CO_2), initial fresh weight (FW_{init}) and the ratio (700/350) of total leaf area ($LA_{700/350}$). The correlations were derived from data, expressed on a fresh weight basis, to avoid interference by the accumulation of non-structural carbohydrates in the interpretation of the results (STULEN & al. 1998).

	weight ratio (700/350)		
Variable	slope	r^2	P
RGR_{350}	- 0.054	0.358	0.031
FW_{init}	- 0.059	0.385	0.024
$LA_{700/350}$	0.687	0.691	0.0004

POORTER 1993 and POORTER & al. 1996 concluded from literature compilations, derived from experiments with various species with a wide range of RGR values, performed under different climatic conditions, that there is interspecific variation in CO_2 response within C_3 species. Potentially fast-growing wild species increased more in weight than slow-growing species. The dry weight ratios (700/350) ranged from 1.00-1.46 and 1.11-1.72, for the slow-growing and fast-growing species, respectively. In the present experiments intraspecific variation within a single species, with a narrower range of RGR values, but grown under the same climatic conditions was measured. The dry weight ratios (700/350) of the *Arabidopsis* lines, which can all be considered as fast-growing, compared to the data set given by POORTER 1993 and POORTER & al. 1996, ranged from 1.23-1.93 (Table 2). In the present experiments the relatively slower growing *Arabidopsis* lines were able to respond to elevated CO_2 by increasing shoot biomass production relatively more, while the weight ratio's (700/350) also depended on the initial fresh weights (Table 3). These findings may be related to the fact that *A. thaliana* is a species with a determinate growth pattern.

Nearly all lines increased their leaf area (LA) and most lines decreased their specific leaf area (SLA) upon exposure to elevated CO_2 (Table 3). The relative change in LA and SLA of the various lines grown at 700 and 350 µl l^{-1} CO_2 (700/350 ratio) was different, and ranged from 1.00-1.44 and 1.02- 0.84, respectively (Table 4). The increase in LA at elevated CO_2 could be ascribed to the increase in shoot biomass at elevated CO_2, since a significant positive correlation between the weight ratio (700/350) of the shoot and the ratio (700/350) of LA was observed (Table 2). A decrease in SLA in response to elevated CO_2 exposure has been reported for many species (POORTER 1993, DEN HERTOG & al. 1996), and is primarily due to accumulation of starch (WONG 1990) and/or ontogenetic drift as a result of the transient stimulation of the RGR (DEN HERTOG & al. 1996).

Shoot soluble sugar content was not significantly affected by exposure to elevated CO_2 in five out of seven tested lines (Table 4). Two lines, N900 and Cs6094, responded to elevated CO_2 with a slight increase in soluble sugar content. A strong increase in leaf starch content, and hence an increase in shoot dry matter content was observed in all lines (Table 4). After correction of the dry matter content for the extra starch, the calculated structural dry matter content was not affected in any line (results not shown). An increase in shoot storage carbohydrate content upon exposure of plants to elevated CO_2 has been reported for many species (STULEN & al. 1998). However, in most species both soluble and insoluble sugars are affected, while in *A. thaliana* the increase was exclusively due to starch accumulation, as was previously reported for cv. Landsberg (VAN DER KOOIJ & DE KOK 1996, VAN DER KOOIJ & al. 1999). The combination of a well-regulated soluble sugar content and a high storage capacity for starch makes that this species can profit to a large extent from the opportunity to increase its carbon gain at elevated CO_2. The continuously higher carbon gain at elevated CO_2 might directly be coupled to its life strategy as a short-lived annual. The vegetative plant produces as much carbohydrates as possible in its short growth period, which carbohydrates will later be used in seed production in the reproductive growth stage (VAN DER KOOIJ & DE KOK 1996).

Table 3. Leaf area (LA) and specific leaf area (SLA) of *Arabidopsis thaliana* lines, grown at 350 or 700 $\mu l\ l^{-1}$ CO_2 for eight days. Data represent the mean of ten shoots (± SD). Significant changes ($p<0.05$) between means are indicated by an asterisk (*).

Line	LA (cm^2)		SLA ($m^2\ kg^{-1}$ FW)	
	350 $\mu l\ l^{-1}$	700 $\mu l\ l^{-1}$	350 $\mu l\ l^{-1}$	700 $\mu l\ l^{-1}$
Landsberg	9.4 ± 1.5	10.9 ± 1.3*	3.38 ± 0.12	3.15 ± 0.10*
N900	8.2 ± 1.3	9.0 ± 2.2	3.48 ± 0.14	3.33 ± 0.14*
N903	12.2 ± 3.0	11.9 ± 2.1	3.71 ± 0.14	3.33 ± 0.28*
N904	3.9 ± 1.2	5.4 ± 1.9*	4.03 ± 0.11	3.38 ± 0.24*
N921	8.9 ± 2.6	12.6 ± 1.8*	3.24 ± 0.16	3.25 ± 0.22
N922	14.3 ± 2.2	15.7 ± 2.9	3.35 ± 0.24	3.35 ± 0.33
N929	8.9 ± 1.8	12.6 ± 1.8*	2.81 ± 0.21	2.86 ± 0.11
N3109	9.2 ± 1.6	10.9 ± 1.4	3.94 ± 0.12	3.63 ± 0.22*
Cs3180	6.1 ± 1.1	6.8 ± 2.1	3.53 ± 0.20	3.35 ± 0.21
Cs6075	5.8 ± 1.3	7.9 ± 0.7*	3.76 ± 0.29	3.43 ± 0.05*
Cs6094	7.7 ± 2.0	11.1 ± 1.4*	3.86 ± 0.23	3.60 ± 0.22*
Cs6188	8.8 ± 1.2	9.8 ± 2.4	3.21 ± 0.16	3.29 ± 0.33
Gasteren	13.2 ± 1.7	15.7 ± 1.8*	3.57 ± 0.21	3.05 ± 0.34*

A prerequisite for plant adaptation to a future elevation of the CO_2 concentration is the presence of genetic variation in general and variation in response to elevated CO_2 in particular (WULFF & ALEXANDER 1985, WOODWARD & al. 1991). Therefore, information on intraspecific variation is important. WARD & STRAIN 1997 investigated the response of *Arabidopsis* genotypes from different elevations to low and elevated CO_2. They found that the genotypes showed limited variation in the production of biomass to changes in atmospheric CO_2, indicating that genotypes did not differ in their relative abilities to assimilate carbon at low and elevated CO_2. NORTON & al. 1995 investigated ecotypic differentiation in CO_2 response of five *A. thaliana* lines. The CO_2 x ecotype interaction they found was mainly due to the growth enhancement of a single ecotype.

Table 4. Soluble sugar and starch content of *Arabidopsis thaliana* lines, grown at 350 or 700 μl l^{-1} CO_2 for eleven days. Data represent the mean of four shoots (± SD). Significant differences ($p<0.05$) between means are indicated by an asterisk (*).

	Soluble sugar (mg g^{-1} FW)		Starch (mg g^{-1} FW)	
Line	350 μl l^{-1}	700 μl l^{-1}	350 μl l^{-1}	700 μl l^{-1}
Landsberg	2.99 ± 0.11	2.76 ± 0.16	19.0 ± 1.6	27.5 ± 4.1*
N900	3.59 ± 0.12	4.20 ± 0.28*	19.2 ± 3.1	26.9 ± 3.8*
N921	3.25 ± 0.29	3.51 ± 0.21*	17.3 ± 0.6	26.5 ± 4.2*
Cs3180	3.41 ± 0.23	3.62 ± 0.11	19.5 ± 1.9	27.8 ± 2.7
Cs6075	3.21 ± 0.22	3.34 ± 0.11	17.2 ± 1.0	25.6 ± 1.5*
Cs6094	3.25 ± 0.20	3.95 ± 0.20*	19.7 ± 0.9	33.6 ± 2.2*
Cs6188	2.89 ± 0.22	3.16 ± 0.20	19.3 ± 0.8	26.5 ± 3.1

The total amount of genetic variation is low within natural populations of *A. thaliana*. This is due to its strict selfing and the low rate of outcrossing in natural populations (ABBOTT & GOMES 1989). *A. thaliana* occurs in dense populations, consisting of a distinct but low number of different genotypes. Individuals have to compete for space, light and nutrients. This population structure, in combination with the reported importance of leaf area development for the reproductive output (SCHULZE & al. 1994) and the direct correlation between fitness and biomass stimulation (VAN DER KOOIJ & DE KOK 1996), means that even small differences in relative response to elevated CO_2 might affect the process of natural selection. Genotypes, which profit more from the extra CO_2, by producing larger shoots with higher leaf area in a shorter period, will easily outcompete the less responsive genotypes. The observed negative correlation between weight ratio (700/350) of the shoot and RGR implies, however, that existing differences in biomass production between different lines of *A. thaliana* might become smaller in a future world with elevated atmospheric CO_2 concentrations. The diminishing differences in biomass production of the different lines at elevated CO_2 means that selection towards other environmental factors than CO_2 will become more important in the future.

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