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RESEARCH PAPER

Evaluation of the growth response of six invasive species to past, present and future atmospheric carbon dioxide

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Abstract

The response of plant species to future atmospheric carbon dioxide concentrations [CO_2] has been determined for hundreds of crop and tree species. However, no data are currently available regarding the response of invasive weedy species to past or future atmospheric [CO_2]. In the current study, the growth of six species which are widely recognized as among the most invasive weeds in the continental United States, Canada thistle (*Cirsium arvense* (L.) Scop.), field bindweed (*Convolvulus arvensis* L.), leafy spurge (*Euphorbia esula* L.), perennial sowthistle (*Sonchus arvensis* L.), spotted knapweed (*Centaurea maculosa* Lam.), and yellow star thistle (*Centaurea solstitialis* L.) were grown from seed at either 284, 380 or 719 μmol mol^{-1} [CO_2] until the onset of sexual reproduction (i.e. the vegetative period). The CO_2 concentrations corresponded roughly to the CO_2 concentrations which existed at the beginning of the 20th century, the current [CO_2], and the future [CO_2] projected for the end of the 21st century, respectively. The average stimulation of plant biomass among invasive species from current to future [CO_2] averaged 46%, with the largest response (+72%) observed for Canada thistle. However, the growth response among these species to the recent [CO_2] increase during the 20th century was significantly higher, averaging 110%, with Canada thistle again (+180%) showing the largest response. Overall, the CO_2-induced stimulation of growth for these species during the 20th century (285–382 μmol mol^{-1}) was about 3× greater than for any species examined previously. Although additional data are needed, the current study suggests the possibility that recent increases in atmospheric CO_2 during the 20th century may have been a factor in the selection of these species.

Key words: Carbon dioxide, invasive weeds, leaf area ratio, net assimilation rate, relative growth rate.

Introduction

Invasive plants are generally recognized as those species, usually non-native for a given system, whose introduction, commonly by human transport, results in economic or environmental harm. Although the impact of such species on native plant communities is well documented (Rejmanek and Randall, 1994), introduced plant species also present a threat to agronomic productivity. In agriculture, invasive plants out-compete crops for soil and water resources, reduce crop quality, interfere with harvesting operations, and reduce land values. The US Department of Agriculture estimates the annual productivity loss of 64 crops due to invasive or 'noxious' species at $7.4 billion (USDA-NRCS, 1999).

Of course, not all introduced plant species become invasive. What then are the characteristics associated with successful invasive species? Understanding these characteristics is crucial since, if they can be identified, future invasions could be identified and controlled. While attention has been given to the lack of native predators or parasites (Vitousek *et al.*, 1996), less work has focused on the role of the abiotic environment per se in invasions (D'Antonio and Vitousek, 1992)

One aspect of the environment which is of obvious interest is global climate change. The concentration of atmospheric CO_2 has already risen 30% during the 20th century from ~285 μmol mol^{-1} to a current estimate of 370 μmol mol^{-1} with most of the increase occurring since the

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1950s (Keeling and Whorf. 2001). The United Nations Intergovernmental Panel on Climate Change (UN-IPCC) predicts that [CO_2] could exceed 700 μmol mol^{-1} by the end of the current century (Houghton *et al.*, 1996). Recent IPCC reports provide strong evidence that rising CO_2 and other trace gases could lead to a 3–12 °C increase in global surface temperatures with subsequent effects on climate, although the degree of temperature/climatic change remains uncertain (Kaiser, 2001).

While the extent of temperature increases remains speculative, there is acknowledged consensus on the direct physiological impact of increasing [CO_2] on plant photosynthesis and metabolism (see reviews by Stitt, 1991; Bowes, 1996). Increasing [CO_2] has been shown to stimulate growth and development significantly in hundreds of plant species (see Kimball, 1983; Kimball *et al.*, 1993; Poorter, 1993, for reviews examining the response to future CO_2 concentrations; Sage, 1995, for a review of the response to pre-industrial CO_2 concentrations).

Based on these reviews, it is clear that plant species respond differently to the ongoing increase in atmospheric [CO_2]. In fact, differential response of C_3 and C_4 plant species to increasing CO_2 during the 20th century has been suggested as one potential explanation for recent invasions of native C_4 grasslands in North America by woody C_3 species (Johnson *et al.*, 1993). However, a specific evaluation of growth responses among recognized invasive plant species to past, present and future CO_2 concentrations is not available.

To determine the relative extent of potential growth stimulation systematically, six widely acknowledged North American invasive weeds, Canada thistle (*Cirsium arvense* (L.) Scop.), field bindweed (*Convolvulus arvensis* L.), leafy spurge (*Euphorbia esula* L.), perennial sowthistle (*Sonchus arvensis* L.), spotted knapweed (*Centaurea maculosa* Lam.), and yellow star thistle (*Centaurea solstitialis* L.) were grown from seed at either 284, 380 or 719 μmol mol^{-1} [CO_2] until the onset of sexual reproduction (i.e. the vegetative period). These CO_2 values correspond approximately to those which existed at the beginning of the 20th century, those which exist today, and those which are predicted to occur by the end of the 21st century. Vegetative growth was considered critical since early development is a key factor in determining crop/weed competition (Kropff and Spitters, 1991).

Materials and methods

Seeds from six weedy species, Canada thistle, field bindweed, leafy spurge, perennial sowthistle, spotted knapweed, and yellow star thistle, were grown using three controlled environmental chambers (EGC Corp., Chagrin Falls, OH, USA) with each chamber kept at one of three 24 h carbon dioxide concentrations set-points, 285, 380 or 720 μmol mol^{-1} (actual [CO_2] values averaged on a 24 h basis through the experiment were 284±18, 380±10 or 719±6 μmol mol^{-1} CO_2). Five to ten seeds of each species were sown in 0.6 l pots filled with vermiculite and were thinned to one seedling 4–6 d after emergence. For each [CO_2] treatment 24–26 plants of a given species were used. Pots were rotated biweekly inside the chambers and arranged to avoid shading from other plants. All pots were watered to the drip point daily with a complete nutrient solution containing 14.5 mMol m^{-3} nitrogen (Robinson, 1984). All seed was obtained from Herbiseed (Herbiseed Corp., Berkshire, UK).

For all environmental chambers, temperature was altered in a diurnal fashion from an overnight low of 20 °C to a maximum afternoon value of 30 °C, with an average daily (24 h) value of 23.1 °C. Similarly, light (photosynthetically active radiation, *PAR*) was also altered diurnally in conjunction with temperature, with the highest *PAR* value (~1200 μmol m^{-2} s^{-1}) occurring during the afternoon. Daily *PAR* was 15 h, supplied by a mixture of high pressure sodium and metal halide lamps and averaged 38 mol m^{-2} d^{-1} for all chambers. The CO_2 concentration of the air was controlled by adding either CO_2 or CO_2-free air to maintain the desired CO_2 concentration. Injection of CO_2 and CO_2-free air was controlled by a TC-2 controller using input from an absolute infrared gas analyser (WMA-2, PP Systems, Haverhill, MA, USA). Temperature, humidity and [CO_2] were recorded every 15 min, and daily averages determined for a given experimental run. Additional details concerning the operating system can be found in Ziska *et al.* (2001).

Plants were grown until 54–60 d after sowing (DAS) at which time, depending on species, initiation of floral spikes or reproductive development was evident. Reproductive development occurred 2–3 d earlier at 284 μmol mol^{-1} CO_2 for spotted knapweed and yellow star thistle relative to ambient CO_2 conditions, but was approximately equivalent for all other species among CO_2 treatments. Because of different growth rates and timing of reproductive development, Canada thistle, field bindweed and yellow star thistle were harvested at 17, 23, 35, and 54 DAS, while leafy spurge, spotted knapweed and perennial sowthistle were harvested at 23, 35, 54, and 60 DAS. To minimize root binding, all species were transplanted to 21.1 l pots by 36 DAS. With the exception of leafy spurge, leaf area was determined photometrically on all leaves at 17, 23 and 35 DAS using a leaf area meter (model 3100, Li-Cor Corp., Lincoln NE, USA). Because of the large leaf area at 54 and 60 DAS, subsamples of 10 leaves per CO_2 treatment and species were placed in moistened paper towels to prevent leaf rolling and leaf area was determined as described previously. These leaves were then dried at 65 °C and total leaf area per plant and specific leaf weight estimated by the linear regression of leaf area to leaf dry weight (r^2>0.91 for all species) obtained from these leaves. Because of the milky latex and the subsequent difficulty in running leaves of leafy spurge through the leaf area meter, this technique was also used to determine total leaf area per plant for this species at 54 and 60 DAS. In addition to leaf area, dry mass was determined separately for all leaves, stems and roots at each harvest for all species and [CO_2] treatments after drying at 65 °C for a minimum of 48 h or until dry mass was constant. Relative growth rate (*RGR*), net assimilation rate (*NAR*) and leaf area ratio (*LAR*) were calculated according to Jones (1983). Because *NAR* is determined on a per leaf area basis, *NAR* of whole plants (*NARp*) was also determined by multiplying *NAR* by existing leaf area at a given harvest.

Because only three chambers were available, a randomized complete block design was used with runs over time as replications (blocks). Each chamber was assigned one of the three CO_2 treatments. At the end of a given run (i.e. 60 DAS), CO_2 treatments were randomly assigned to a given chamber and the entire experiment was repeated. The entire experiment was repeated three times, and the mean value from each run used as a single replicate. Growth characteristics, biomass and vegetative characteristics were analysed using a one-way ANOVA with CO_2 as the independent variable. To determine differences as a function of [CO_2] for a given species and harvest date, a Student's *t*-test (assuming unequal variances) was used. Unless otherwise stated, significant differences for any measured parameter were determined as significant at the $P \leq 0.05$ level.

Results

Increasing [CO_2] above levels present at the beginning of the 20th century (i.e. 285 μmol mol^{-1}) stimulated *NAR* at either 23 and/or 35 DAS for all invasive species except for spotted knapweed (Table 1). By 54–60 DAS, the additional stimulation of *NAR* by [CO_2] was no longer consistent among species (and had actually declined for perennial sowthistle) (Table 1). Although this would suggest increasing insensitivity to assimilation with increasing CO_2, *NAR* is expressed per unit leaf area. Consequently, if total leaf area per plant is taken into consideration, increasing [CO_2] from either 284 to 380 or from 380 to 719 μmol mol^{-1} resulted in significant stimulation of *NAR* per plant (*NARp*) through 54 or 60 DAS for all species except leafy spurge with no evidence of a decline in the relative stimulation through this period as a function of [CO_2] (Table 2).

Leaf area was also significantly stimulated with increasing [CO_2] with a greater relative increase from early 20th century to current CO_2 than from current to projected [CO_2] levels (Fig. 1). *LAR* in contrast, increased with decreased [CO_2], especially during the early part of the growing season for five out of the six species (Fig. 2). That is, at 284 μmol mol^{-1} CO_2, *LAR* significantly increased for Canada thistle, field bindweed, perennial sowthistle, spotted knapweed, and yellow star thistle between 17–35 DAS. Increased *LAR* for the lowest [CO_2] was also observed for leafy spurge at 54 and 60 DAS. The increase in *LAR* indicates a greater allocation to leaf production during early development for the lowest [CO_2] (Fig. 2).

The CO_2-induced stimulation of plant biomass was consistent with that observed for leaf area, with a greater relative increase from 284 to 380 than from 380 to 719 μmol mol^{-1} CO_2 (Table 3). Yellow star thistle and perennial sowthistle showed the largest absolute increase in plant biomass at 54 and 60 DAS, respectively. The smallest absolute response was observed for leafy spurge, with no significant increase in biomass observed at 60 DAS between current and future [CO_2]. By the final harvest date (i.e. either 54 or 60 DAS), significant increases in leaf, stem and root weight were also observed in all species with increasing [CO_2], with the exception of root weight in leafy spurge (Table 3). The largest relative increase, averaged across all species was observed for root biomass (~120% from 284 to 389 μmol mol^{-1}; 55% from 380 to 719 μmol mol^{-1}). While there is a significant effect of [CO_2] on R:S ratio averaged for all species, for individual species, no consistent effect of [CO_2] was observed for root:shoot ratio (Table 3).

Although there are clear differences in plant biomass and its components as a consequence of [CO_2], little actual change in *RGR* as a function of [CO_2] was observed for a given sampling date (Table 4). Although *RGR* did decline over time, overall *RGR* did not differ as a function of CO_2

Table 1. *Change in net assimilation rate* (NAR, $g\ cm^{-2}\ d^{-1} \times 10^3$) *for six noxious weed species grown at either 284, 380 or 719 μmol mol^{-1} CO_2*

Different letters indicate significant differences between CO_2 treatments for a given sampling date and species.

Species	CO_2	DAS			
		23	35	54	60
Canada thistle	284	1.16 b	1.74 c	1.45 b	
(*Cirsium arvense*)	380	1.85 a	2.10 b	1.68 ab	
	719	1.08 b	2.55 a	1.74 a	
Field bindweed	284	1.32 b	1.55	1.03 b	
(*Convolvulus arvensis*)	380	1.28 b	1.78	1.07 b	
	719	2.54 a	1.95	1.49 a	
Leafy spurge	284		NA	0.92 b	1.01
(*Euphorbia esula*)	380		NA	1.21 ab	0.90
	719		NA	1.48 a	1.10
Perennial sowthistle	284		1.31 b	1.61 a	0.70 c
(*Sonchus arvensis*)	380		1.76 a	1.31 ab	1.16 b
	719		2.00 a	1.18 b	1.50 a
Spotted knapweed	284		2.23	1.27 b	0.65 b
(*Centaurea maculosa*)	380		2.13	1.41 ab	1.29 a
	719		2.55	1.55 a	1.15 ab
Yellow star thistle	284	2.73 a	1.74	1.29	
(*Centaurea solstitialis*)	380	2.17 b	2.02	1.26	
	719	2.53 ab	2.10	1.28	
Average	284	1.74 b	1.71 b	1.26	0.79 b
	380	1.77 b	1.96 b	1.32	1.12 ba
	719	2.05 a	2.23 a	1.45	1.25 a

Table 2. *Change in net assimilation rate on a per plant basis* (NARp, *g plant*$^{-1}$ *d*$^{-1}$) *for six noxious weed species grown at either 284, 380 or 719 μmol mol*$^{-1}$ CO_2

Different letters indicate significant differences between CO_2 treatments for a given sampling date and species.

Species	CO_2	DAS			
		23	35	54	60
Canada thistle	284	0.014 b	0.249 c	1.532 c	
(*Cirsium arvense*)	380	0.056 a	0.543 b	3.332 b	
	719	0.052 a	1.016 a	5.424 a	
Field bindweed	284	0.057 b	0.488 b	2.177 c	
(*Convolvulus arvensis*)	380	0.078 b	0.866 a	3.383 b	
	719	0.245 a	1.164 a	4.293 a	
Leafy spurge	284		NA	0.270 c	0.650 ab
(*Euphorbia esula*)	380		NA	0.608 a	0.450 b
	719		NA	0.721 a	0.928 a
Perennial sowthistle	284		0.165 c	1.491 c	0.895 c
(*Sonchus arvensis*)	380		0.526 b	2.537 b	2.966 b
	719		0.891 a	3.592 a	6.279 a
Spotted knapweed	284		0.265 c	1.672 c	0.742 b
(*Centaurea maculosa*)	380		0.453 b	2.775 b	3.627 a
	719		0.837 a	4.162 a	4.418 a
Yellow star thistle	284	0.106 b	0.473 c	2.108 b	
(*Centaurea solstitialis*)	380	0.111 b	0.804 b	4.279 a	
	719	0.211 a	1.356 a	4.642 a	
Average	284	0.059 b	0.328 c	1.542 c	0.762 c
	380	0.082 b	0.638 b	2.819 b	2.348 b
	719	0.169 a	1.053 a	3.806 a	3.875 a

treatment during the measured growth interval. Since there are obvious biomass differences as a result of [CO_2] by the end of the experiment, the actual change in *RGR* resulting from [CO_2] must have occurred prior to 17 DAS for Canada thistle, field bindweed and yellow star thistle and prior to 23 DAS for leafy spurge, perennial sowthistle and spotted knapweed.

Discussion

Because of the recent increase in atmospheric [CO_2], and its importance in plant physiology, the response of plant species to future levels of CO_2 has been the object of numerous studies (for reviews see Poorter, 1993; Kimball *et al.*, 1993; Curtis and Wang, 1998; *inter alia*). In examining the species listed in these reviews, it is clear that a principal focus of many studies has been on commercially important species (i.e. crops and trees). Although weeds have been investigated (see Patterson, 1995, for a review), specific evaluations of the growth response of recognized invasive or noxious weeds to past, present or future CO_2 concentrations are not available.

The invasive species chosen for this study were taken from Skinner *et al.* (2000) who ranked noxious weeds from surveys of the United States and Southern Canada. ('Noxious' refers to the fact that these plants have been deemed harmful in a legal sense and not that the plants are poisonous.) Their inclusion in such a list recognizes the detrimental nature of such species and their wide-spread occurrence. Obviously a plant known to be noxious and invasive is likely to be regulated by law in order to prevent its introduction or spread into new areas. Six of the top 15 weeds determined by Skinner *et al.* (2000) (all C_3 species) were used in the current study. Among these, Canada thistle, is recognized as the most noxious weed, occurring on 33 noxious lists (the next closest weed, musk thistle, occurs on 24 lists) (Skinner *et al.*, 2000).

Relative to other species, do invasive species show a stronger or lesser response to increasing atmospheric [CO_2]? What is the expected response? One of the earliest attempts to integrate plant response to elevated [CO_2] was published by Kimball (1983) who examined 430 previous studies. Bases on his analysis he determined that the average response of plants (±SE) to future elevated CO_2 conditions was 34±6% (330–360 μmol mol^{-1} for ambient versus 600–1000 μmol mol^{-1} for future elevated; Kimball, 1983). Other studies which have quantified the variation in the response of plants to future [CO_2] show similar results (e.g. 37% for 156 plant species; Poorter, 1993). In the current experiment with invasive weeds, the average response after 54 DAS was ~45%, similar to previously published values (Fig. 3A). For individual weedy species, only Canada thistle (+72%) and spotted knapweed (+60%) indicate a substantially stronger than expected response to future elevated [CO_2] relative to the baseline devised by Kimball (1983). The strong response to future elevated [CO_2] relative to current ambient levels observed for these two species is consistent with the observed stimulation of *NARp* (+63% and +50% for Canada thistle and spotted

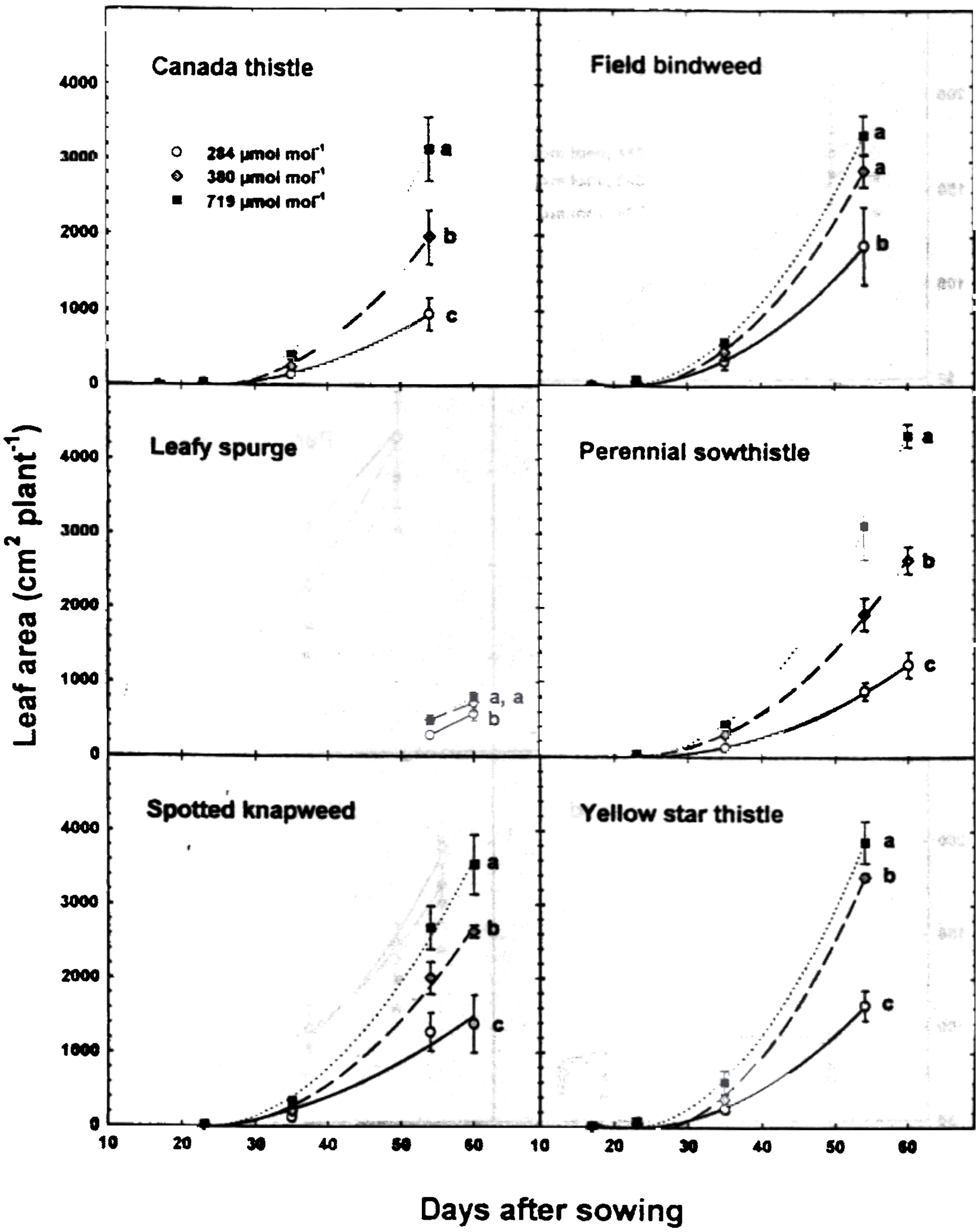

Fig. 1. Leaf area for six invasive weedy species, Canada thistle (*Cirsium arvense*), field bindweed (*Convolvulus arvensis*), leafy spurge (*Euphorbia esula*), perennial sowthistle (*Sonchus arvensis*), spotted knapweed (*Centaurea maculosa*), and yellow star thistle (*Centaurea solstitialis*) as a function of 284, 380 and 719 µmol mol^{-1} [CO_2]. Each point is the average of 15–18 plants averaged over three runs. Bars are ±SE. Different letters indicate significant differences on the last day of harvest (54–60 DAS) as a function of [CO_2].

knapweed, respectively, from ambient to future elevated [CO_2]), but could not be predicted based on relative biomass allocation (e.g. R/S, alterations in source:sink). Overall, the response of the invasive weeds examined here to projected future increases in atmospheric [CO_2], does not differ considerably from that of other species.

But the 'current' [CO_2] is in flux. Atmospheric carbon dioxide has already risen from ~285 to 378 µmol mol^{-1} during the 20th century, with most of the observed increase coming since the late 1950s (*c.* 312 µmol mol^{-1} in 1959) (Keeling and Whorf, 2001). Prior to 1900, [CO_2] fluctuated between 180–290 µmol mol^{-1} for at least 220 000 years (Barnola *et al.*, 1987; Jouzel *et al.*, 1993). With respect to the recent and rapid increase in atmospheric [CO_2] during the 20th century, do invasive species show a stronger than expected response?

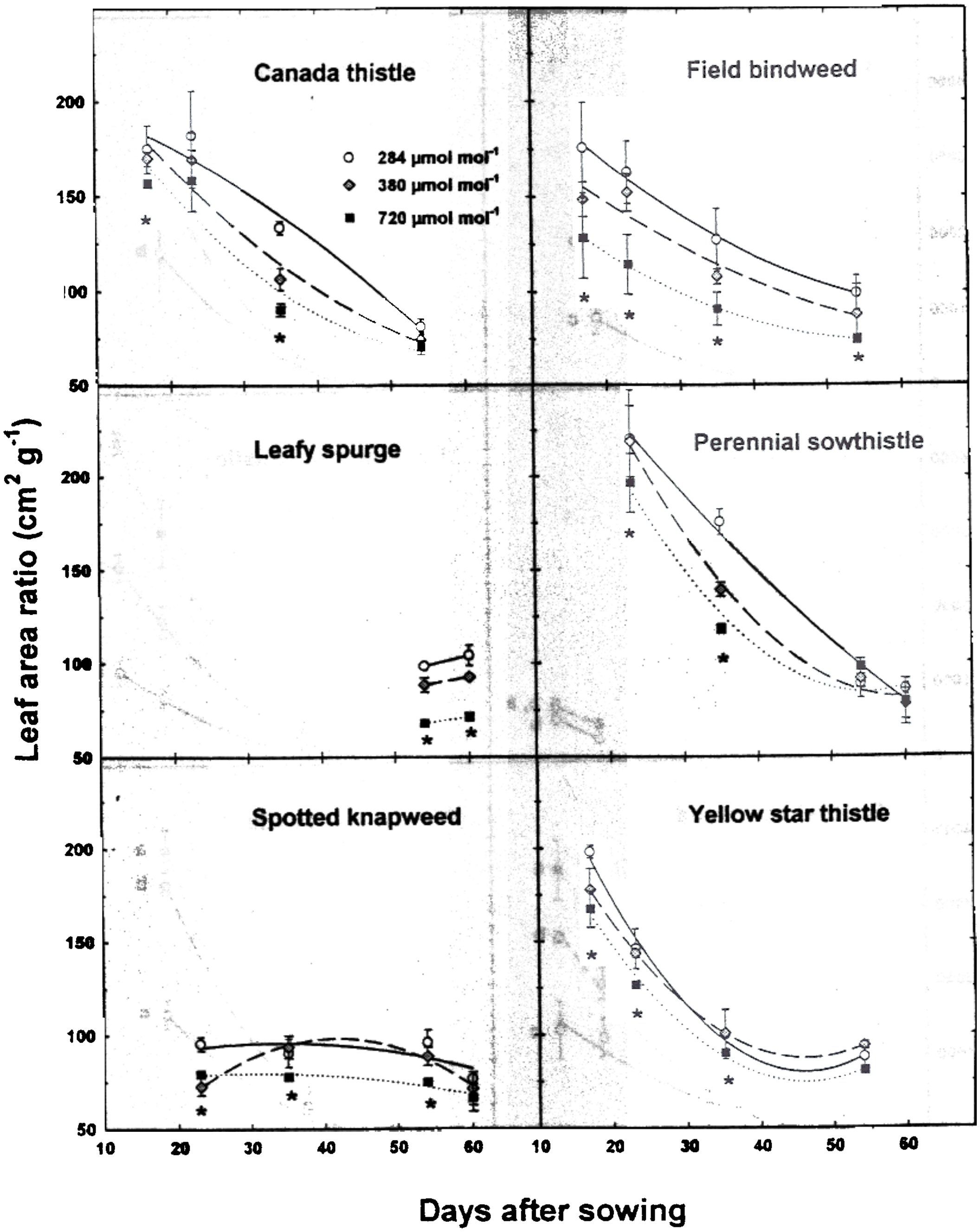

Fig. 2. Leaf area ratio (*LAR*) determined as the ratio of existing leaf area to above-ground plant biomass at different harvest dates for six invasive weedy species, Canada thistle (*Cirsium arvense*), field bindweed (*Convolvulus arvensis*), leafy spurge (*Euphorbia esula*), perennial sowthistle (*Sonchus arvensis*), spotted knapweed (*Centaurea maculosa*), and yellow star thistle (*Centaurea solstitialis*) as a function of 284, 380 and 719 µmol mol^{-1} [CO_2]. * Indicates a significant difference relative to the 284 µmol mol^{-1} value for the 719 µmol mol^{-1} treatment.

In contrast to future elevated CO_2 levels, less work has integrated the response of plants to the recent increase in atmospheric [CO_2], even though it is recognized that leaf and plant photosynthesis can be particularly sensitive to the low [CO_2] concentrations of the past (Polley *et al.*, 1993). This is due in part to technical considerations since it is more difficult to scrub CO_2 than it is to add it. Nevertheless, Sage (1995) summarized 12 studies over the range of preindustrial relative to current levels. Including only C_3 species, the estimated average relative biomass response between 270 and 380 µmol mol^{-1} is approximately 29% (see Fig. 3b in Sage, 1995). If this response is updated to include more recent reports, (i.e. wheat varieties Seri M82 and Yaqui; Mayeux *et al.*, 1997; *Albutilon theophrasti*; Dippery *et al.*, 1995; Ward *et al.*, 1999), the average relative growth response (±SD) is 33±11% for

Table 3. *Final biomass characteristics for six noxious weeds*

Canada thistle, field bindweed and yellow star thistle were harvested at 54 DAS; leafy spurge, perennial sowthistle and spotted knapweed were harvested at 60 DAS. Weeds were grown from sowing at either 284, 380 or 719 μmol mol^{-1} CO_2. Values are expressed as g $plant^{-1}$. R:S is the ratio of root to shoot biomass. Different letters indicate significant differences as a function of CO_2 concentration for a given parameter and species.

Species	[CO_2]	Leaf wt.	Stem wt.	Root wt.	R:S
Canada thistle		6.79 c			0.50
(*Cirsium arvense*)		15.02 b			0.42
		24.71 a			0.44
Field bindweed		8.38 c			0.51 c
(*Convolvulus arvensis*)		12.31 b			0.71 a
		17.52 a			0.64 b
Leafy spurge		2.75 c			0.49 a
(*Euphorbia esula*)		4.21 b			0.43 ab
		6.13 a			0.35 b
Perennial sowthistle		7.33 c			0.58 b
(*Sonchus arvensis*)		16.17 b			0.88 a
		25.89 a			0.86 a
Spotted knapweed		10.81 c			0.26 b
(*Centaurea maculosa*)		21.72 b			0.38 a
		30.03 a			0.46 a
Yellow star thistle		11.43 b			0.42 ab
(*Centaurea solstitialis*)		21.01 a			0.36 b
		24.63 a			0.46 a
Average		7.92 c			0.49 b
		15.07 b			0.52 b
		21.49 a			0.56 a

Table 4. *Change in relative growth rate (RGR, g g^{-1} d^{-1}) for six noxious weed species grown at either 284, 380 or 719 μmol mol^{-1} CO_2*

Different letters indicate significant differences between CO_2 treatments for a given sampling date and species.

Species	CO_2	DAS			
		23	35	54	60
Canada thistle	284	0.210 b	0.232	0.118	
(*Cirsium arvense*)	380	0.307 a	0.224	0.126	
	719	0.169 a	0.232	0.122	
Field bindweed	284	0.214 b	0.191	0.103	
(*Convolvulus arvensis*)	380	0.192 b	0.193	0.107	
	719	0.283 a	0.177	0.099	
Leafy spurge	284		0.160	0.091	0.105
(*Euphorbia esula*)	380		0.150	0.106	0.065
	719		0.137	0.101	0.077
Perennial sowthistle	284		0.230	0.139	0.059 b
(*Sonchus arvensis*)	380		0.245	0.120	0.083 a
	719		0.236	0.114	0.098 a
Spotted knapweed	284		0.197	0.121	0.044 b
(*Centaurea maculosa*)	380		0.200	0.124	0.096 a
	719		0.198	0.116	0.080 a
Yellow star thistle	284	0.395 a	0.173	0.113	
(*Centaurea solstitialis*)	380	0.311 b	0.194	0.119	
	719	0.321 b	0.190	0.103	
Average	284	0.273	0.197	0.114	0.069
	380	0.270	0.201	0.117	0.081
	719	0.258	0.195	0.109	0.085

[CO_2] values between 250–270 μmol mol^{-1} and 360–380 μmol mol^{-1}.

In the current study, the response of the six invasive weeds to recent increases in [CO_2] (i.e. since the beginning of the 20th century) averaged 110%. Although only a limited number of preindustrial studies are available, the responses from the current experiment are considerably higher than previously reported for any plant species over this [CO_2] range (Fig. 3b). It could be argued that limitations of nutrients or water could limit the response of these species to atmospheric CO_2 in the field; however, many of these

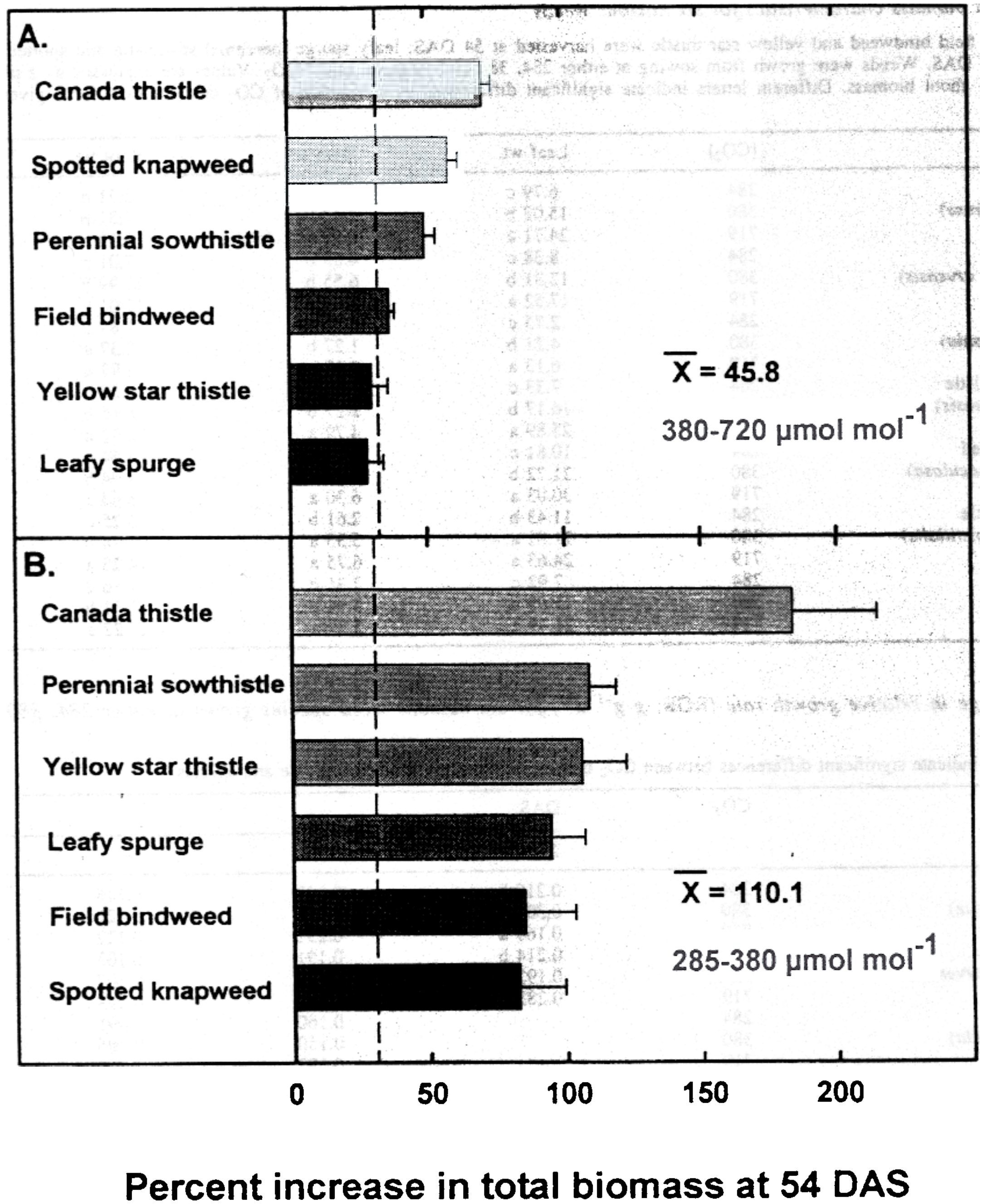

Fig. 3. (A) The average relative increase (%) determined from the ratio of dry weight at elevated (719 μmol mol^{-1}), relative to ambient (380 μmol mol^{-1}) CO_2 for three experimental runs for each of six invasive weeds, Canada thistle (*Cirsium arvense*), field bindweed (*Convolvulus arvensis*), leafy spurge (*Euphorbia esula*), perennial sowthistle (*Sonchus arvensis*), spotted knapweed (*Centaurea maculosa*), and yellow star thistle (*Centaurea solstitialis*) at a common harvest date of 54 DAS. Dotted line is the average response of plants as reported by Kimball (1983). (B) Same as (A), but for [CO_2] of 284 and 380 μmol mol^{-1} CO_2. Dotted line is the published response of plants from 270–380 μmol mol^{-1} (Sage, 1995). See text for additional details.

species are associated with managed agronomic environments where water and nutrients would be optimal (Patterson, 1995).

For individual species, Canada thistle again showed the largest relative increase (+180%), but no species showed a relative growth increase less than 80%. There was a larger relative increase in leaf area and *NARp* between 284 and 380 than from 380 to 719 when averaged for all species, but the relative response of *NARp*, or other growth characteristics from 284 to 380 μmol mol^{-1} was independent of the CO_2-induced stimulation of growth observed at 54 DAS for individual species.

Why such a strong response to recent increases in atmospheric [CO_2]? It has been shown in numerous studies that below-ground growth can show dramatic increases with increased [CO_2] (Rogers *et al.*, 1986; Bernsten and Woodward, 1992; Prior *et al.*, 1994). Interestingly, of the most noxious weedy species listed by Skinner *et al.* (2000), many have a strong below-ground root or rhizome system (e.g. Canada thistle, purple loosestrife, field bindweed, leafy spurge, Russian knapweed, whitetop, perennial sowthistle, quackgrass, dalmation toadflax) which can generate new stems from below-ground structures. Averaged among all species in the current experiment, below-ground biomass showed the strongest relative increase to the recent [CO_2] increase (+121% versus 54% for CO_2 concentrations from 284–380 versus 380–719 μmol mol^{-1}, respectively, see Table 3).

It is possible that substantial below-ground sinks contributed to the large growth stimulation from 284 to 380 μmol mol^{-1} providing a link between invasiveness and CO_2 responsiveness. However, at this time, the selection of propagation by vegetative means over floral reproduction remains only an intriguing possibility. The evolutionary role of increasing [CO_2] in the recent past cannot be fully elucidated by a single study done under growth chamber conditions for individual species. Clearly, the responses of the species considered here will vary *in situ* as a function of competition and environment with other factors antagonistic to the direction of selection (Etterson and Shaw, 2001). Additional field experiments to clarify the response to recent increases in [CO_2] are difficult due to technical considerations (cf. Mayeux *et al.*, 1993). Nevertheless, understanding the role of climate, particularly the sudden and dramatic rise in atmospheric carbon dioxide within recent decades, as a possible factor in the invasiveness of the these species deserves additional consideration. Such an assessment may be crucial in quantifying the response and potential agronomic threat posed by invasive weeds as atmospheric [CO_2] continues to increase.

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References

Barnola JM, Raynaud D, Korotkevich YS, Lorius CD. 1987. Vostok ice core provides 160 000 year record of atmospheric CO_2. *Nature* **329**, 408–414.

Bernsten GN, Woodward FI. 1992. The root system architecture and development of *Senecio vulgaris* in elevated CO_2 and drought. *Functional Ecology* **6**, 324–333.

Bowes G. 1996. Photosynthetic responses to changing atmospheric carbon dioxide concentration. In: NR Baker, ed. *Photosynthesis and the environment*. Dordrecht: Kluwer Academic Publishers, 387–407.

Curtis PC, Wang X. 1998. A meta-analysis of elevated CO_2 effects on woody plant mass, form and physiology. *Oecologia* **113**, 299–313.

D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass-fire cycle and global change. *Annual Review of Ecology and Systematics* **23**, 63–87.

Dippery JK, Tissue DT, Thomas RB, Strain BR. 1995. Effects of low and elevated CO_2 on C_3 and C_4 annuals. *Oecologia* **101**, 13–20.

Etterson JR, Shaw RG. 2001. Constraint to adaptive evolution in response to global warming. *Science* **294**, 151–54.

Houghton JT, Meira-Filho LG, Callander BA, Harris N, Kattenburg A, Maskell K. 1996. *IPCC climate change assessment 1995: the science of climate change*. Cambridge: Cambridge University Press.

Johnson HB, Polley HW, Mayeux HS. 1993. Increasing CO_2 and plant-plant interactions: effects on natural vegetation. *Vegetatio* **104/105**, 157–170.

Jones HG. 1983. *Plants and microclimate*. Cambridge: Cambridge University Press.

Jouzel J, Barkov NI, Barnola JM. 1993. Extending the Vostok ice-core record of the paleoclimate to the penultimate glacial period. *Nature* **364**, 407–412.

Kaiser J. 2001. Seventeen national academies endorse Kyoto. *Science* **292**, 275–277.

Keeling CD, Whorf TP. 2001. Atmospheric CO_2 records from sites in the SIO air sampling network. In: *Trends: a compendium of data on global change*. Oak Ridge, Tennessee, USA: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy.

Kimball BA. 1983. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal* **75**, 779–788.

Kimball BA, Mauney JR, Nakayama FS, Idso SB. 1993. Effects of increasing atmospheric CO_2 on vegetation. *Vegetatio* **104/105**, 65–75.

Kropff MJ, Spitters CJT. 1991. A simple model of crop loss by weed competition from early observations on relative leaf area of the weeds. *Weed Research* **31**, 97–105.

Mayeux HS, Johnson HB, Polley HW, Dumesnil MJ, Spanel GS. 1993. A controlled environment chamber for growing plants across a sub-ambient CO_2 gradient. *Functional Ecology* **7**, 125–133.

Mayeux HS, Johnson HB, Polley HW, Malone SR. 1997. Yield of wheat across a sub-ambient carbon dioxide gradient. *Global Change Biology* **3**, 269–278.

Patterson DT. 1995. Weeds in a changing climate. *Weed Science* **43**, 685–701.

Polley HW, Johnson HB, Marino BD, Mayeux HS. 1993. Increase in C_3 plant water-use efficiency and biomass over Glacial to present CO_2 concentrations. *Nature* **361**, 61–64.

Poorter H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. *Vegetatio* **104/105**, 77–97.

Prior SA, Rogers HH, Runion GB, Mauney JR. 1994. Effects of free-air enrichment on cotton root growth. *Agriculture and Forest Meteorology* **70**, 69–86.

Rejmanek M, Randall J. 1994. Invasive alien plants in California: 1993 summary and comparison with other areas in North America. *Madrono* **41**, 161–177.

Robinson JM. 1984. Photosynthetic carbon metabolism in leaves and isolated chloroplasts from spinach plants grown under short and intermediate photosynthetic periods. *Plant Physiology* **75**, 397–409.

Rogers HH, Cure JD, Smith JM. 1986. Soybean growth and yield response to elevated carbon dioxide. *Agriculture, Ecosystems and Environment* **16**, 112–128.

Sage RF. 1995. Was low atmospheric CO_2 during the Pleistocene a limiting factor for the origin of agriculture? *Global Change Biology* **1**, 93–106.

Skinner K, Smith L, Rice P. 2000. Using noxious weed lists to prioritize targets for developing weed management strategies. *Weed Science* **48**, 640–644.

Stitt M. 1991. Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. *Plant, Cell and Environment* **14**, 741–762.

USDA-NRCS (**US Department of Agriculture, Natural Resources Conservation Service**). 1999. The PLANTS Database (http://plants.usda.gov/plants Baton Rouge, LA: National Plant Data Center. Accessed 27September 2001.

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R. 1996. Biological invasions as global environmental change. *American Scientist* **84**, 468–478.

Ward JK, Tissue DT, Thomas RB, Strain BR. 1999. Comparative responses of model C_3 and C_4 plants to drought in low and elevated CO_2. *Global Change Biology* **5**, 857–857.

Ziska LH, Ghannoum O, Baker JT, Conroy J, Bunce JA, Kobayashi K, Okada M. 2001. A global perspective of ground level 'ambient' carbon dioxide for assessing the response of plants to atmospheric CO_2. *Global Change Biology* **7**, 789–796.