Field Crops Research 108 (2008) 54–59

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Three-year field evaluation of early and late 20th century spring wheat cultivars to projected increases in atmospheric carbon dioxide

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ARTICLE INFO

Article history:
Received 25 October 2007
Received in revised form 26 February 2008
Accepted 21 March 2008

Keywords:
Breeding
Carbon dioxide
Wheat

ABSTRACT

Carbon dioxide (CO_2), along with light, water and nutrients, represents an essential resource needed for plant growth and reproduction. Projected and recent increases in atmospheric carbon dioxide may allow breeders and agronomists to begin intra-specific selection for yield traits associated with CO_2 sensitivity. However, selection for maximum yield, particularly for cereals, is continuous, and it is possible that modern cereal cultivars are, in fact, the most CO_2 sensitive. To test CO_2 responsiveness, we examined two contrasting spring wheat cultivars, Marquis and Oxen, over a 3-year period under field conditions at two different planting densities. Marquis was introduced into North America in 1903, and is taller, with greater tiller plasticity (i.e. greater variation in tiller production), smaller seed and lower harvest index relative to modern wheat cultivars. Oxen, a modern cultivar released in 1996, produces fewer tillers, and has larger seed with a higher harvest index relative to Marquis. As would be expected, under ambient CO_2 conditions, Oxen produced more seed than Marquis for all 3 years. However, at a CO_2 concentration 250 μmol mol^{-1} above ambient (a concentration anticipated in the next 50–100 years), no differences were observed in seed yield between the two cultivars, and vegetative above ground biomass (e.g. tillers), was significantly higher for Marquis relative to Oxen in 2006 and 2007. Significant CO_2 by cultivar interaction was observed as a result of greater tiller production and an increased percentage of tillers bearing panicles for the Marquis relative to the Oxen cultivar at elevated carbon dioxide. This greater increase in tiller bearing panicles also resulted in a significant increase in harvest index for the Marquis cultivar as CO_2 increased. While preliminary, these results intimate that newer cultivars are not intrinsically more CO_2 responsive; rather, that yield sensitivity may be dependent on the availability of reproductive sinks to assimilate additional carbon. Overall, understanding and characterizing vegetative vs. reproductive sink capacity between cultivars may offer new opportunities for breeders to exploit and adapt varieties of wheat to projected increases in atmospheric carbon dioxide concentration.

Published by Elsevier B.V.

1. Introduction

Since 1958, atmospheric carbon dioxide has increased by ~24% to a current level of 385 μmol mol^{-1} (NOAA, 2007), with projected increases to 700–800 μmol mol^{-1} CO_2 by the end of the current century (IPCC, 2007). Ongoing and projected changes in atmospheric carbon dioxide and other greenhouse gases may result in uncertain climatic changes related to temperature, precipitation, etc., with negative consequences for global food supply (e.g. Lobell and Field, 2007).

Identification of possible preventive measures to either mitigate or adapt to climate change is one of the challenges for agricultural researchers in the 21st century. In that regard, carbon dioxide is not only a greenhouse gas, but a necessary plant resource since it supplies carbon for photosynthesis and growth. Do opportunities exist then, whereby agricultural scientists can begin to select for intra-specific variability within a given cultivated crop that could exploit this resource as a means to adapt to climatic uncertainty?

From an agronomic standpoint, intra-specific selection with respect to CO_2 sensitivity could provide benefits regarding seed yield. Significant variation in yield response with a doubling of current CO_2 levels has been observed in cultivars of cowpea (Ahmed et al., 1993), rice (Ziska et al., 1996; Moya et al., 1998), and soybean (Ziska and Bunce, 2000).

Although wheat is recognized as a global staple for human and animal nutrition, only a few studies have examined intra-specific yield variability to recent or projected changes in atmospheric CO_2 concentration, [CO_2]. Using a [CO_2] gradient tunnel, Mayeux et al. (1997) examined the yield response of modern wheat cultivars to

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0378-4290/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.fcr.2008.03.006

recent 20th century increases in CO_2. Ziska et al. (2004) examined spring wheat varieties released during the 20th century to recent and projected CO_2 increases using plants in environmental growth chambers. Mandersheid and Weigel (1997) evaluated six contrasting cultivars of spring wheat that had been introduced in Germany between 1890 and 1988 using open-top chambers in field conditions, but for plants grown in pots. However, none of these published reports evaluated intra-specific yield responses to projected increases in atmospheric carbon dioxide in a field setting for wheat grown using standard agronomic practices. Although these data (Mandersheid and Weigel, 1997; Ziska et al., 2004) had indicated that older cultivars could, potentially, yield as much as a modern cultivar at projected, elevated levels of atmospheric carbon dioxide, it was unclear if similar results could be observed under field conditions.

To determine if intra-specific variability to [CO_2] exists *in situ*, two contrasting spring wheat cultivars were grown under field conditions for a 3-year period at different planting densities. The objective of the study was twofold: first to determine if intra-specific variability of yield and/or biomass existed between wheat cultivars to anticipated levels of elevated [CO_2] and, if variability did exist, to determine, at least in part, a possible basis for the different responses.

2. Materials and methods

The experiment was conducted from 2005 to 2007 at Beltsville, Maryland agricultural research center farm site. Twelve experimental aluminum chambers (3 m in diameter and 2.25 m in height) covering an area of 7.2 m^2 were placed at regular intervals within the field. Because of the chamber size, a modified suspended chamber top was necessary to prevent wind intrusion and to maintain a stable CO_2 concentration. For each year of the study individual chambers were randomly assigned one of two [CO_2] treatments, ambient or ambient +250 μmol mol^{-1} CO_2.

For all 3 years of the study, [CO_2] treatments were maintained 24 h d^{-1} from sowing until physiological maturity. Air was supplied through perforations in the inner wall of the lower half of the chamber. Air was adjusted to the desired CO_2 concentration with pure CO_2 supplied from a 5 ton liquid CO_2 tank. Gas samples were withdrawn from all elevated and one ambient CO_2 chamber at 4 min intervals at canopy height and adjustments to the elevated [CO_2] were made daily. Carbon dioxide concentration [CO_2], determined using an absolute CO_2 analyzer (Li-Cor 6252, Li-Cor Corporation, Lincoln, NE, USA), indicated average daytime [CO_2] (6:00 a.m. to 7:00 p.m.) values of 394 ± 14, 404 ± 13 and 396 ± 21 μmol mol^{-1} and, average nighttime values of 488 ± 27, 506 ± 15 and 478 ± 30 μmol mol^{-1} for the ambient CO_2 treatment from 2005 to 2007. Elevated [CO_2] values for 2005–2007 were 662 ± 9, 668 ± 14 and 661 ± 31 (daytime) and 780 ± 13, 779 ± 18 and 756 ± 43 μmol mol^{-1} (nighttime), respectively. Micro-meteorological conditions of photosynthetic photon flux indicated that the chamber transmitted ~88% of all incoming light, with an average daytime temperature increase of 0.9, 1.1 and 1.1 °C above the outside ambient temperature for 2005, 2006 and 2007, respectively.

Seed from two cultivars of hard-red spring wheat (*Triticum aestivum* L.) introduced during the 20th century, Marquis (1903), and Oxen (1996) were sown in late April for each year of the experiment and thinned to one of two planting densities, 19 or 33 plants per meter of row (low and high planting densities, respectively), within the chambers and in external plots. Row widths were ~20 cm for all experimental plots. All plots were hand weeded, and a nearby weather station was used to estimate the difference between precipitation and evapotranspiration (ET) on a weekly basis. If ET was greater than precipitation, plots were irrigated to make up the difference. This occurred three times in 2005, once in 2006, and twice in 2007. Field soil was classified as a Cordurus silt-loam (*Cordurus harboro*), pH 5.5 with high availability of potash and phosphate. Yearly soil analysis to a depth of 15 cm prior to planting showed N-NO_3 values between 7 and 15 ppm, indicating the need for supplemental N. This is a critical requirement since the response of wheat to [CO_2] may be nitrogen dependent (Jamieson et al., 2000). To meet this need, additional nitrogen (~36 g N m^{-2}) as ammonium nitrate was added seasonally as a split application (20 and 16 g N m^{-2}) as per Maryland extension recommendations (Sammons et al., 1989) for each year of the study.

All plants were grown until maturity which was determined by leaf senescence and kernel hardness. Oxen matured approximately 2 weeks earlier than Marquis. However, elevated [CO_2] did result in earlier maturity for both cultivars for all 3 years of the experiment, increasing maturity by 6 and 8 days for the Oxen and Marquis cultivars, respectively. At maturity, 2, 1 m rows were cut at ground level for all experimental plots. Plants and tillers were counted, and panicles removed. Following drying at 68 °C, for 48 h, vegetative mass was weighed. Panicles were threshed, seeds were collected and weighed, and a sub-sample of 50 seed was weighed separately to determine individual seed weight.

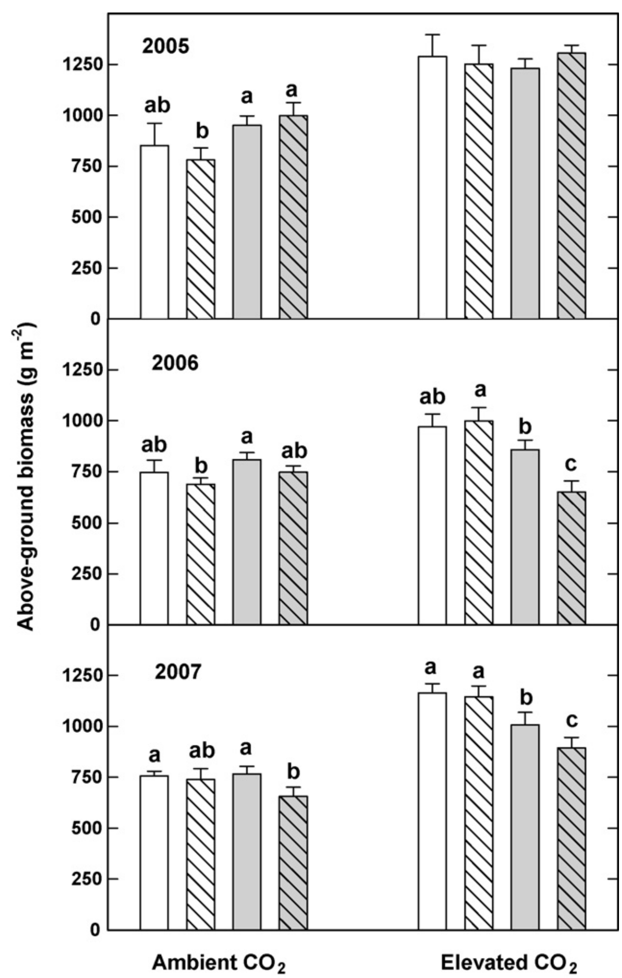

Fig. 1. Above ground biomass per m^2 for two spring wheat cultivars, Marquis, (clear bars) released in 1908 and Oxen (shaded bars) released in 1996. Each cultivar was grown at one of two planting densities, high (open bars) and low (striped bars) at two CO_2 concentrations (ambient and elevated, ambient +250 μmol mol^{-1}) over a 3-year period (2005–2007). Error bars are ±S.E. Different letters indicate a statistically significant difference between means for a given year and CO_2 treatment.

The study was arranged in a completely randomized block for the 12 chambers at the field site. There were three replications of the two [CO_2], and two cultivars (3 replications, 2× [CO_2] 2× cultivars) with two planting densities of a given cultivar arranged in a split plot design within a chamber (i.e. only one cultivar per chamber). Above ground biomass at maturity was assessed as vegetative (tiller number, tiller weight, panicle weight and number) and reproductive characteristics (seed weight, harvest index) in order to determine if planting density or cultivar affected [CO_2] sensitivity. A three-way analysis of variance (density, cultivar, [CO_2]) was used to analyze vegetative and reproductive parameters for each year, and a four-way (including year) analysis was also conducted. A Fisher's least significant difference (lsd) was used to separate treatment effects.

3. Results

Above ground biomass did not significantly differ between cultivars irrespective of planting density when grown under ambient [CO_2] (Fig. 1). However, seed yield at ambient [CO_2] was greater for Oxen relative to Marquis for all 3 years of the experiment (Fig. 2). Conversely, at the elevated [CO_2] treatment, total above ground biomass was significantly greater for Marquis relative to Oxen in 2006, and 2007, and no difference in seed yield was observed between cultivars for those years (Figs. 1 and 2).

Overall the relative increase in vegetative dry weight was greater than that for seed weight for Oxen in response to elevated [CO_2] when averaged for all 3 years of the study (22 vs. 16%, respectively). In contrast, for Marquis, the relative response of vegetative and seed weight was significantly greater than Oxen, averaging 49 and 64% over the experiment, with a greater relative increase in seed relative to vegetative dry weight (Table 1).

Both [CO_2] and cultivar showed significant effects on vegetative and reproductive parameters (Table 2). Significant [CO_2] × cultivar interactions were also noted for tiller weight and number of panicles (heads) throughout the experiment. When averaged for all 3 years, a significant interaction was also observed for tiller number. Cultivar × density and cultivar × density × [CO_2] interactions were also observed, but were not consistent from year to year during the study.

[CO_2] × cultivar interactions are a result of the greater observed sensitivity of both vegetative growth and seed yield for the Marquis relative to the Oxen cultivar in response to elevated carbon dioxide. This increase was not related to greater individual seed weight or to increased tiller production per se (Table 1). Rather, the percent tillers with seed bearing panicles increased significantly for Marquis, but not Oxen in response to elevated [CO_2] when averaged for the entire study (Fig. 3). This result is consistent with the [CO_2] × cultivar interaction observed for tiller weight and panicles, as well as the noted increase in harvest index (P = 0.08 when averaged from 2005 to 2007) for Marquis (Table 2, Fig. 3).

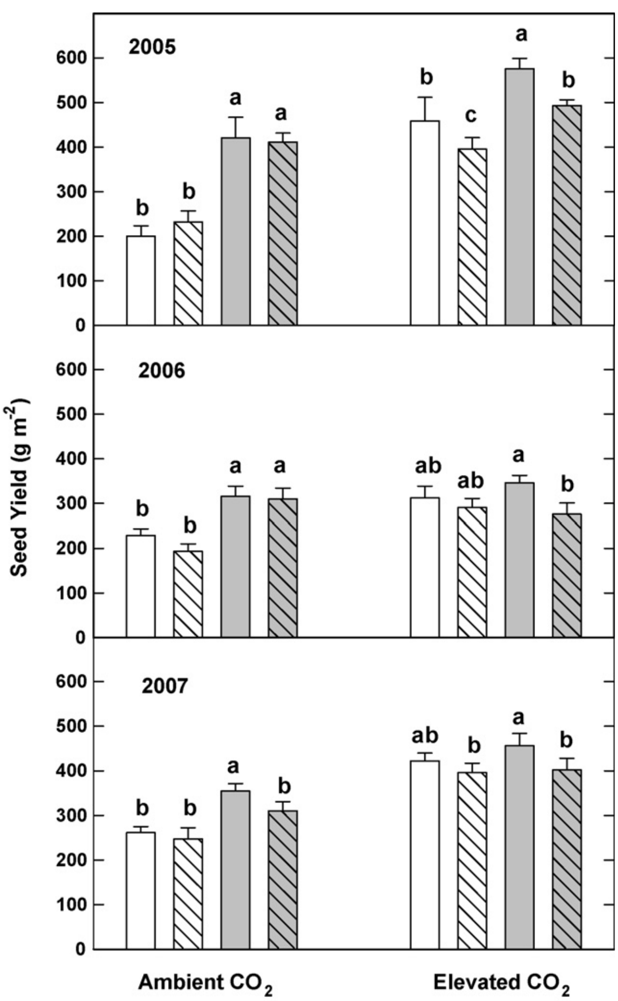

Fig. 2. Same as Fig. 1, but for seed yield.

4. Discussion

The current study attempts to elucidate key questions related to intra-specific variability of spring wheat to climate change, specifically: Do cultivars of wheat, released at the beginning and end of the 20th century, differing in development and morphology, show dissimilar yield sensitivities to recent and projected increases in [CO_2]? What is the basis for these differences? Can such differences be quantified and exploited by breeders as a means to adapt to climate change?

Marquis was introduced in southern Canada in 1903 (Morison, 1960). It had yields superior to any previously released spring wheat variety and by the early 1920s was so popular that 90% of spring wheat in Canada was composed of Marquis (Morison, 1960). Oxen, in contrast, reflected breeding choices of the "green revolution" during the 1960s and 1970s; i.e. shorter in stature, with larger average seed size and greater harvest index. Oxen was released in 1996, as a spring wheat cultivar with earlier maturity and leaf rust resistance. Given a 100 years of breeding, and improved agronomic practices, it is not surprising that Oxen would out yield Marquis.

What is of interest however, is the current observation that Marquis productivity at elevated [CO_2] is equal (seed yield) or superior to (above ground biomass) that of Oxen. Given this result, it is advantageous to elucidate the underlying causes for the greater degree of [CO_2] sensitivity exhibited by Marquis since inclusion of [CO_2] responsive traits could be used to exploit recent and projected increases in atmospheric carbon dioxide as a means to increase yield of spring wheat globally. One multi-year trial with two cultivars cannot, of course, clarify all of the biological parameters associated with [CO_2] sensitivity for spring wheat. Nevertheless, the differences observed between Marquis and Oxen may be illustrative, a least in part, of how elevated [CO_2] may alter plant morphology and source–sink relations intra-specifically.

Marquis, for example, when given additional carbon dioxide, produces not only additional tillers per plant, but from a reproductive standpoint, additional heads (panicles) for these tillers with a subsequent increase in HI. In contrast, Oxen also produced more tillers with increased [CO_2] (although fewer than

Table 1
Vegetative and reproductive parameters for two Spring wheat cultivars, "Marquis" and "Oxen" released in 1903 and 1996, respectively; grown at two different planting densities ("low" and "high", 19 and 33 plants per meter of row, respectively) and at ambient and ambient + 250 μmol mol^{-1} CO_2 (ambient and elevated, respectively)

Parameter	Cultivar		CO_2		Density		CO_2 × cultivar			
	Marquis	Oxen	Ambient	Elevated	Low	High	Marquis		Oxen	
							Ambient	Elevated	Ambient	Elevated
(2005)										
Tiller no.	753	792	697	856	730	820	675	846	719	864
Tiller wt.	522	388	380	530	451	456	419	626	354	434
Head no.	645	817	656	840	683	795	549	778	704	815
Head wt.	502	725	517	742	622	620	395	633	629	830
% w/heads	82	99	86	99	96	89	72	93	98	94
50 seed wt.	1.20	1.46	1.28	1.39	1.34	1.33	1.15	1.26	1.41	1.52
HI	.30	.43	.35	.39	.35	.39	.27	.35	.43	.43
(2006)										
Tiller no.	673	658	644	687	622	709	615	730	673	643
Tiller wt.	472	317	351	438	381	409	394	551	309	325
Head no.	543	626	531	638	573	596	419	667	643	608
Head wt.	378	450	396	431	390	437	323	433	469	430
% w/heads	80	95	82	93	92	83	68	91	96	95
50 seed wt.	0.89	1.22	1.05	1.06	1.03	1.08	0.89	0.89	1.19	1.23
HI	.30	.41	.35	.36	.35	.36	.29	.37	.40	.41
(2007)										
Tiller no.	732	691	630	793	652	770	641	823	618	763
Tiller wt.	485	285	308	462	404	366	375	595	241	330
Head no.	592	665	497	759	585	671	398	785	597	733
Head wt.	466	546	421	591	492	520	373	470	561	621
% w/heads	79	96	80	96	86	90	63	96	97	96
50 seed wt.	1.08	1.28	1.19	1.18	1.22	1.15	1.12	1.05	1.26	1.31
HI	.35	.46	.40	.40	.40	.41	.33	.36	.47	.45

% w/heads is the percentage of tillers that have a panicle. HI is harvest index: seed weight divided by head plus tiller weight. 50 seed weight is in g. Data for tillers and heads are per m^2. Statistics are shown in Table 2.

Marquis; +23 vs. +12% when averaged over the study), but the percentage of tillers with seed heads was unaffected.

It is also interesting to note the importance of planting density in each cultivar's ability to respond to elevated [CO_2]. For example, with the exception of seed yield in 2005, the ability of Marquis to respond to [CO_2] is independent of planting density. Conversely, for Oxen, the largest relative response of yield or biomass to [CO_2] is observed for the high planting density treatment. These data may reflect phenotypic differences related to tiller plasticity (Ziska et al., 2004). This is, older cultivars (i.e. pre-green revolution) are variable with respect to tiller production, increasing or decreasing depending on resource availability, whereas tiller production in newer cultivars may be more static in cereals (e.g. oat varieties released during the 20th century, Ziska and Blumenthal, 2007).

[CO_2] induced morphological changes in reproduction that would increase the ratio of reproductive carbon sinks to vegetative sources (e.g. the increase in HI observed for Marquis), could be advantageous for a given cultivar with a future, higher [CO_2] atmosphere. Previous work in evaluating plant response to rising [CO_2] levels has emphasized the importance of sink strength as a

Table 2
Statistical significance for variables associated with Table 1

Year	Variables	Cultivar	CO_2	Density	Cultivar × CO_2	Density × CO_2	Cultivar × density	Cultivar × density × CO_2
2005	Tiller no.		***	(*)				
	Tiller wt.	***	***		*			
	Head no.	***	***	**	(*)			
	Head wt.	***	***				(*)	
	50 seed	***	***			**		(*)
	HI	***			(*)	*		
2006	Tiller no.		*	***	***		**	
	Tiller wt.	***	***		***		*	(*)
	Head no.	***	***		***	(*)	***	
	Head wt.	***	(*)	*	***			
	50 seed	***						
	HI	***			(*)		**	
2007	Tiller no.		***	***				
	Tiller wt.	***	***	*	***			
	Head no.	***	***	***	***		**	
	Head wt.	***	***					
	50 seed	***		*	(*)			(*)
	HI	***			(*)			

Values are per plant. (*)$P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

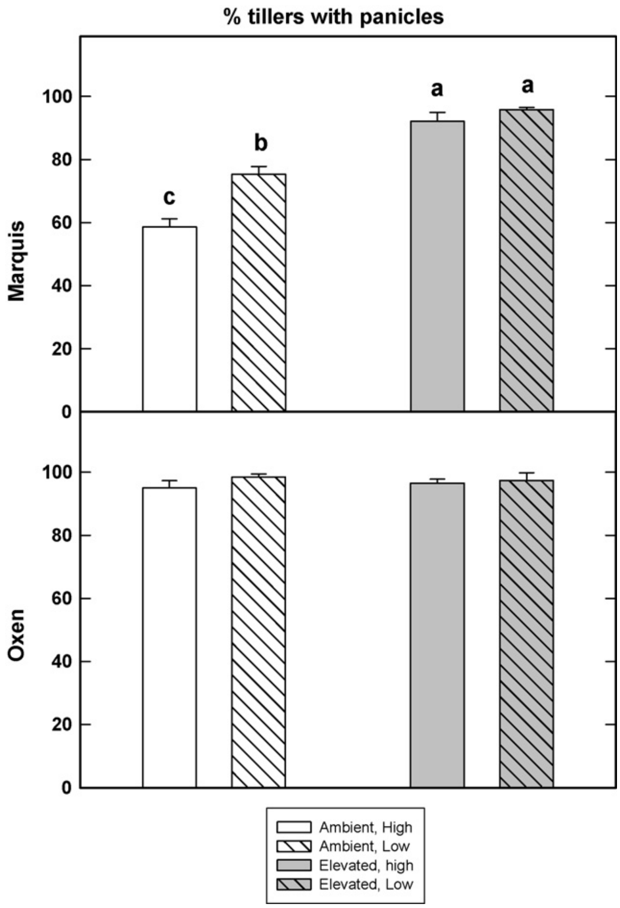

Fig. 3. Change in the percentage of panicle bearing tillers averaged over the 2005–2007 seasons for Marquis and Oxen as a function of CO_2 concentration and planting density. Error bars are ±S.E. Different letters indicate a statistically significant difference between means for a given year and CO_2 treatment.

means to avoid photosynthetic down regulation (acclimation) and boost plant growth (e.g. Arp, 1991; Hall and Allen, 1993). In the current experiment, the ability of Marquis to form new tillers when additional carbon is made available is consistent with this hypothesis.

However, in spite of the greater CO_2 responsiveness of Marquis relative to Oxen, seed yield of the two cultivars did not differ at elevated CO_2. This emphasizes the difference between the relative and absolute responses to CO_2. The fact that seed yield did not differ could suggest a biological constraint in exploiting additional carbon dioxide into seed yield. Alternatively, as suggested by Hall and Allen (1993), crop cultivars with a high HI (e.g. Oxen) and hence, greater carbohydrate sink, could be inherently more suitable for a higher [CO_2] atmosphere.

In that regard, while Marquis shows an interesting shift in reproductive sinks with additional carbon dioxide, a more thorough evaluation of seed yield/[CO_2] among a wider collection of diverse spring wheat cultivars would be needed to identify CO_2 sensitive traits. There are a number of key questions which remain to be addressed; but, given increases in photosynthetic rate in an elevated [CO_2] atmosphere and more assimilate (i.e. greater source availability), could selection for greater assimilate transfer to developing reproductive sinks and a subsequent increase in HI be possible for wheat? How can we begin to accept the challenge of increasing yield potential (e.g. Sinclair et al., 2004) as a specific means to adapt to climate change?

Overall, in response to the basic questions addressed in the current study, the rapid increase in atmospheric [CO_2] represents an essential resource needed by plants. Exploitation of carbon dioxide therefore, as a possible means to mitigate or adapt to climatic change, should be an appealing one for plant scientists. Overall, questions related to the utilization of additional atmospheric carbon dioxide as a potential resource in plant breeding are just beginning to be addressed (e.g. Hall and Ziska, 2000; Sage and Coleman, 2001; Newton and Edwards, 2007). To date, there have been few attempts to determine the specific characteristics that increase the responsiveness of seed yield in spring wheat to atmospheric [CO_2]. Although it is difficult to draw generalizations from a comparison of only two cultivars, the present study is, in fact, the first multi-year evaluation of yield and biomass responses of contrasting spring wheat varieties to elevated [CO_2] under field conditions in North America. These data cannot elucidate all desirable physiological, morphological or phenological traits associated with [CO_2] responsiveness; but do indicate that [CO_2] responsiveness differs among wheat cultivars under field conditions. Furthermore, these data, while limited, indicate that it should not be assumed, *a priori*, that newer wheat culitvars are the most [CO_2] sensitive (e.g. Ziska et al., 2004). However, specific mechanisms associated with absolute increases in seed yield among wheat varieties as atmospheric [CO_2] increases will require further experimentation.

Acknowledgements

I thank Dr. JA Bunce for editorial suggestions. I also thank Mr. Ernie Goins, Mr. Jon Clark and Ms. Martha Tomecek for expert technical assistance.

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