Empirical Selection of Cultivated Oat in Response to Rising Atmospheric Carbon Dioxide

L. H. Ziska⋆ and D. M. Blumenthal

ABSTRACT

Carbon dioxide is a principle resource for plant growth; as such, the ongoing increase in its concentration may allow breeders to begin selecting for optimal cultivars among current crop lines. Such a program may not be necessary, however, if breeders have, by empirical selection, already chosen the most responsive cultivars. To test this hypothesis, we examined the growth and vegetative characteristics of individual plants of cultivated oat (*Avena sativa* L.) from seven geographical locations to CO_2 concentration ([CO_2]) increases that corresponded roughly to the [CO_2] from the 1920s, the current [CO_2], and the [CO_2] projected for the middle of this century (300, 400, and 500 μmol mol^{-1}, respectively). In contrast to our predictions, newer lines were less responsive than older lines to rising [CO_2] in terms of both leaf area and tiller number. A comparison of phenotypic variability indicated that for almost all measured parameters, older lines had a greater degree of intraspecific variability (i.e., newer lines were more uniform). As a consequence, a number of CO_2-sensitive lines among older cultivars were identified with respect to parameters such as vegetative biomass or tiller production. Our results suggest that for oat: (i) newer lines are not intrinsically more responsive to rising CO_2 levels than older lines; and (ii) phenotypic homogenization among modern lines could hamper efforts to identify desirable characteristics associated with CO_2 responsiveness.

L.H. Ziska, USDA-ARS, Alternate Crop and Systems Lab., Beltsville, MD 20705; D.M. Blumenthal, USDA-ARS, Rangeland Resource Research Unit, Cheyenne, WY 82001. Received 27 Sept. 2006. ⋆Corresponding author (l.ziska@ars.usda.gov).

Abbreviations: PAR, photosynthetically active radiation.

RECORDS OBTAINED from the Mauna Loa observatory in Hawaii have shown an increase in CO_2 concentration ([CO_2]) of about 20%, from 311 to 375 μmol mol^{-1} since 1959 (Keeling and Whorf, 2001). Because 95% of all plants currently lack optimal levels of CO_2 for photosynthesis (i.e., those with the C_3 photosynthetic pathway), this anthropogenically driven increase in CO_2 represents a rapid increase in an available resource. Such a rapid change is likely to result in differential responses among plant populations and species with corresponding differences in biological and reproductive success.

From an agronomic standpoint, selection among crop lines with respect to CO_2 responsiveness could provide benefits regarding food supply. Initial data have indicated significant intraspecific variation in yield response with a doubling of current CO_2 levels in cowpea [*Vigna unguiculata* (L.) Walp.; Ahmed et al., 1993], rice (*Oryza sativa* L.; Ziska et al., 1996; Moya et al., 1998), wheat (*Triticum aestivum* L.; Mandersheid and Weigel, 1997), and soybean [*Glycine max* (L.) Merr.; Ziska et al., 2001].

Although genotypic and phenotypic variation in response to future, elevated CO_2 is evident from these initial studies, we could find no published report that reflects a systematic evaluation on the part of breeders or agronomists for selection of crop lines responsive to rising atmospheric CO_2. This may be due,

in part, to the argument that given the gradual increase in CO_2, empirical selection for yield will automatically choose the most CO_2-responsive plants over time (cf. Kimball, 1985; Lawlor and Mitchell, 2000). Unfortunately, it is difficult to separate CO_2 stimulation effects from technological and management advances that coincided with the rapid increase in CO_2 concentration since the 1940s (for a discussion, see Amthor, 1998), and separate assessments of growth and yield independent from recent CO_2 increases are generally not available (see Mayeux et al., 1997, for wheat).

To determine if, in fact, empirical selection has thus far chosen the most CO_2–responsive cultivars, we assessed the response of 14 different lines of cultivated oat (*Avena sativa* L.) from seven different geographical locations to recent and projected changes in atmospheric CO_2, comparing paired cultivars from each location released early and late in the 20th century. In general, sensitivity to CO_2 decreases with plant age in annual species (see Stitt, 1991; Ziska and Bunce, 1995); consequently, growth following seed emergence should show the greatest relative response to increasing $[CO_2]$. In addition, we were interested in the tiller data, because previous studies have shown that yield response to increased CO_2 concentration in rice and wheat is associated with an increase in the number of productive tillers (Ziska et al., 1996, 2004). Therefore, our overall goal was to examine initial vegetative and growth parameters following emergence to determine whether empirical selection has, de facto, chosen the most CO_2-responsive lines of cultivated oat.

MATERIALS AND METHODS

To simulate subambient $[CO_2]$, controlled environmental chambers (EGC Corp., Chagrin Falls, OH) were used. At present, field evaluations done at continuous subambient $[CO_2]$ are not possible (see Mayeux et al., 1993). For each chamber, temperature was varied in a diurnal mode from an overnight low of 12°C to a maximum afternoon value of 25°C, with an average daily (24-h) value of 17°C. Light (photosynthetically active radiation, PAR) was also altered diurnally in conjunction with temperature, with the highest PAR value ($\sim$1000 µmol m^{-2} s^{-1}) occurring during the afternoon. The daily light period was 14 h, supplied by a mixture of high-pressure Na and metal halide lamps, and averaged 24.4 mol m^{-2} d^{-1} for all chambers. The CO_2 concentration of the air was controlled by adding CO_2 or CO_2–free air either using injection of pure CO_2 or by a Ballston 75-60 type CO_2 scrubber (Ballston Filter Products, Lexington, MA). Injection of either CO_2 or CO_2–free air was determined using a TC-2 controller that monitored CO_2 values measured from an absolute infrared gas analyzer (WMA-2, PP Systems, Haverhill, MA). Carbon dioxide concentrations were set at 300, 400, and 500 µmol mol^{-1} d^{-1} (24 h). These concentrations approximated the $[CO_2]$ present at the beginning and end of the 20th century as well as that projected to occur sometime in the next 30 to 50 yr (Houghton et al., 1996). Actual 24-h $[CO_2]$ values ($\pm$ SD) averaged throughout the experiment were 311 $\pm$ 19.6, 412 $\pm$ 13.3, and 504 $\pm$ 17.0 µmol mol^{-1}. Temperature, humidity, and $[CO_2]$ were recorded every 15 min and averages determined on a daily basis for all experimental runs.

Seed of 14 cultivars from seven locations were grown using three controlled-environment chambers, with each chamber set at one of the $[CO_2]$. Two cultivars, one from the 1920s and one from the 1990s (old and "new," respectively) were obtained for each geographic location (Table 1). Oat is a self-pollinating grass with <0.5% outcrossing (Stoskopf, 1985), so it is unlikely that lines changed genetically with time. Two to three seeds of each cultivar were sown in 0.6-L pots filled with vermiculite and thinned to one seedling 4 to 6 d after emergence for each $[CO_2]$ treatment. All pots were watered to the drip point daily with a complete nutrient solution containing 14.5 mmol N m^{-3}.

Cultivars were harvested at four different growth stages during development: tiller initiation, leaf sheath elongation, flag leaf development, and panicle initiation (approximately 2.0, 4.5, 8.0, and 10.0 on the Feekes small grains scale, respectively). No consistent effect of $[CO_2]$ was observed with respect to timing of the various stages. The Russian and Idaho cultivars matured slightly (3–5 d) earlier relative to the other cultivars. To minimize root binding, all cultivars were transplanted to 4.5-L pots following sheath elongation. Plants from a given cultivar were grouped together, and groups were spaced so as to minimize mutual shading. Both individual plants and groups were rotated weekly inside the chambers to minimize border effects.

At each harvest, four to five plants per cultivar and $[CO_2]$ were sampled. Leaf area was determined photometrically on all leaves for the first three growth stages, and estimated from the relationship between leaf weight and area ($r^2 > 0.90$) from leaf samples for all cultivar–treatment combinations. In addition to leaf area, dry mass was determined separately for leaves, stems, and roots at each harvest for all cultivars and $[CO_2]$ treatments following drying at 65°C for a minimum of 48 h or until dry mass was constant. Root recovery fraction was estimated to be approximately 88%. Relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR) were calculated according to Jones (1985) for the last three vegetative harvests.

Given the limited number of chambers, and because pots do not represent valid replications, a randomized complete block design was used with runs with time as replications (blocks). That

Table 1. Name, geographical location, and release date for 14 lines of cultivated oat (*Avena sativa* L.) used in the experiment. Seeds were obtained by the U.S. National Plant Germplasm System.

Cultivar	Location	Release Date
Eclipse	California	1919
Bates 89	California	1996
Clydesdale	Ohio	1920
Burton	Ohio	1996
Kherson	Idaho	1920
Powell	Idaho	1998
Storm King	United Kingdom	1920
Colt	United Kingdom	1993
Osmo	Finland	1922
Katri	Finland	1997
Hatvan	Hungary	1925
Zalalovoi	Hungary	1997
Shatilovskij	Russia	1927
Drug	Russia	1992

is, each chamber was initially assigned one of the three CO_2 treatments for a given run with CO_2 treatments reassigned to another chamber and the entire experiment repeated at the end of each run (i.e., all CO_2 treatments occurred in all chambers for a total of three runs). Photosynthetically active radiation, humidity, and temperature were quantified before and at the end of each run to determine within-chamber and between-chamber variability. No differences in temperature, PAR, or humidity were observed between chambers or runs. All measured and calculated parameters were analyzed using analyses of variance including $[CO_2]$ and age (i.e., old vs. new) as fixed effects, experimental run and location as random effects, and appropriate interactions (PROC MIXED, SAS Institute, 1997). Where significant $[CO_2] \times$ age interactions were observed, linear contrasts were used to test for significant $[CO_2]$ effects separately among new and old lines; Bonferroni tests were used to correct for multiple comparisons (Moore and McCabe, 1989). An equality of variance F test was used to determine whether age (old vs. new) was a factor in the response to $[CO_2]$ (Statview, Cary, NC). Unless otherwise stated, differences for any parameter were deemed significant at the $P < 0.05$ level.

RESULTS

By the end of the vegetative stage of growth (panicle initiation, approximately 49 d after sowing), $[CO_2]$ had significantly increased total oat biomass; similar trends for other vegetative characteristics were not significant (Table 2). For calculated growth characteristics determined from the onset of tiller initiation, $[CO_2]$ significantly decreased LAR, but had no effect on NAR or RGR (Table 3). Averaged across $[CO_2]$ treatments, the only consistent effect of age was the higher RGR of older cultivars (Table 3).

Significant age $\times$ $[CO_2]$ interactions were observed for several variables. Both total leaf area and tiller number increased with rising $[CO_2]$ for old ($P < 0.001$) but not new cultivars (Table 2). Old lines also displayed greater plasticity in tiller number in response to CO_2 (Fig. 1). That is, although the newer lines had, on average, a greater number of tillers, tiller number did not respond to $[CO_2]$; in contrast, older lines demonstrated larger and more varied responses, with tiller number at the highest $[CO_2]$ exceeding those of the newer lines (e.g., 'Shatilouskji' and 'Powell,' the two cultivars from each age group with the greatest absolute number of tillers, averaged 46.1 and 39.0 tillers plant^{-1}, respectively, at 500 μmol mol^{-1} CO_2). A significant $CO_2 \times$ age interaction was also observed for weight per tiller, which tended to decrease with $[CO_2]$ for older cultivars, and increase with $[CO_2]$ for newer cultivars (trends not significant). As with tiller number, variability in weight per tiller was significantly greater for the older than newer lines (Table 4).

Overall, the degree of intraspecific variability as a function of age group was significantly greater for the older

Table 2. Vegetative characteristics for 14 cultivated lines of oat (*Avena sativa* L.) in response to previous, current, and projected atmospheric CO_2 concentrations (300, 400, or 500 μmol mol^{-1}, respectively) at 49 d after sowing. Lines were paired by release date as either old (released 1919–1927) or new (released 1992–1998) for seven different geographic locations in North America and Europe.

Variable	Average value per plant								P		
	300[†]	400[†]	500[†]	300	400	500	All CO$_2$ conc.		CO$_2$	Age	CO$_2$ × age
							New	Old			
Leaf area, cm²											
All cultivars				2385	2610	2736	2445	2709	NS[‡]	NS	*
Old	2421	2780	2924								
New	2349	2438	2507								
Leaf wt., g				12.3	14.4	15.7	13.5	14.8	NS	NS	NS
Tillers, no.											
All cultivars				23.8	24.3	29.1	31.0	20.4	NS	**	***
Old	15.2	18.2	27.7								
New	32.4	30.4	30.3								
Weight tiller^{-1}, g											
All cultivars				0.60	0.73	0.56	0.48	0.79	NS	*	***
Old	0.80	0.95	0.57								
New	0.40	0.48	0.54								
Tiller wt., g				11.0	13.6	14.8	13.8	12.4	NS	NS	NS
Root wt., g				13.8	17.1	17.6	15.2	17.1	NS	NS	NS
Root/shoot				0.59	0.61	0.58	0.56	0.63	NS	NS	NS
Total wt., g				37.1	45.2	48.0	42.6	44.3	*	NS	NS

*Significant at $P < 0.05$.

**Significant at $P < 0.01$.

***Significant at $P < 0.001$.

[†]Average values for old and new cultivars separated for variables with significant CO$_2$ × age interactions.

[‡]NS, not significant.

relative to the newer oat lines for eight vegetative and growth parameters (Table 4). The greater degree of variability is evident in the response of total plant biomass at panicle initiation for each age group (Fig. 2). Therefore, while the total plant weight between age groups was not significant in absolute terms (Table 2), the range of responses to increased $[CO_2]$ was greater for the older cultivars (Fig. 2).

DISCUSSION

Any increase in light, nutrients, water, or CO_2 will differentially affect individuals of the same or different species (Patterson and Flint, 1990); consequently, intra- or interspecific variability can be anticipated as atmospheric CO_2 increases globally. In unmanaged plant communities, for example,

Table 3. Growth characteristics for 14 cultivated lines of oat (*Avena sativa* L.) in response to previous, current, and projected atmospheric CO_2 concentrations (300, 400, or 500 µmol mol^{-1}, respectively) at 49 d after sowing. Lines were paired by release date as either old (released 1919–1927) or new (released 1992–1998) for seven different geographic locations in North America and Europe.

Variable[†]	Average value					P		
	300	400	500	New	Old	CO_2	Age	CO_2 × age
LAR, cm² g⁻¹	65.8	58.8	57.8	58.6	63.0	**	NS[‡]	NS
RGR, kg kg⁻¹ d⁻¹	0.128	0.135	0.134	0.125	0.140	NS	*	NS
NAR, mg cm⁻²	2.04	2.37	2.41	2.24	2.31	NS	NS	NS

*Significant at $P < 0.05$.

**Significant at $P < 0.01$.

[†]LAR, leaf area ratio; RGR, relative growth rate; NAR, net assimilation rate.

[‡]NS, not significant.

there has been recent evidence suggesting that rising $[CO_2]$ has, or could, favor the growth of certain plant species (Phillip et al., 2002; Mohan et al., 2006). Similarly, selection experiments have found high $[CO_2]$ to favor particular genotypes within plant species (Ward et al., 2000).

For agriculture, or managed plant communities, selection is principally by artificial (i.e., human) means. Some initial trials have suggested that intraspecific variability among cultivars in response to $[CO_2]$ could be substantial. For example, the relative response of seed yield among 17 rice cultivars varied from 0 to 150% when ambient $[CO_2]$ was increased to 660 µmol mol^{-1} (Ziska et al., 1996). Given the degree of intraspecific variability, artificial selection could, potentially, begin to significantly increase crop productivity by exploiting increasing levels of atmospheric CO_2.

But is such a selection program necessary? Breeders and agronomists have maintained that CO_2 responsiveness will occur with empirical selection for the fastest growing, highest yielding cultivars under current environmental conditions—conditions that would, over time, reflect changes in the background concentration of CO_2 (e.g., Lawlor and Mitchell, 2000).

If this argument is valid, recent crop lines should, on average, show greater $[CO_2]$ sensitivity relative to older cultivars. In our study, however, new cultivars were either similarly or less responsive to rising $[CO_2]$ than old cultivars, depending on the vegetative
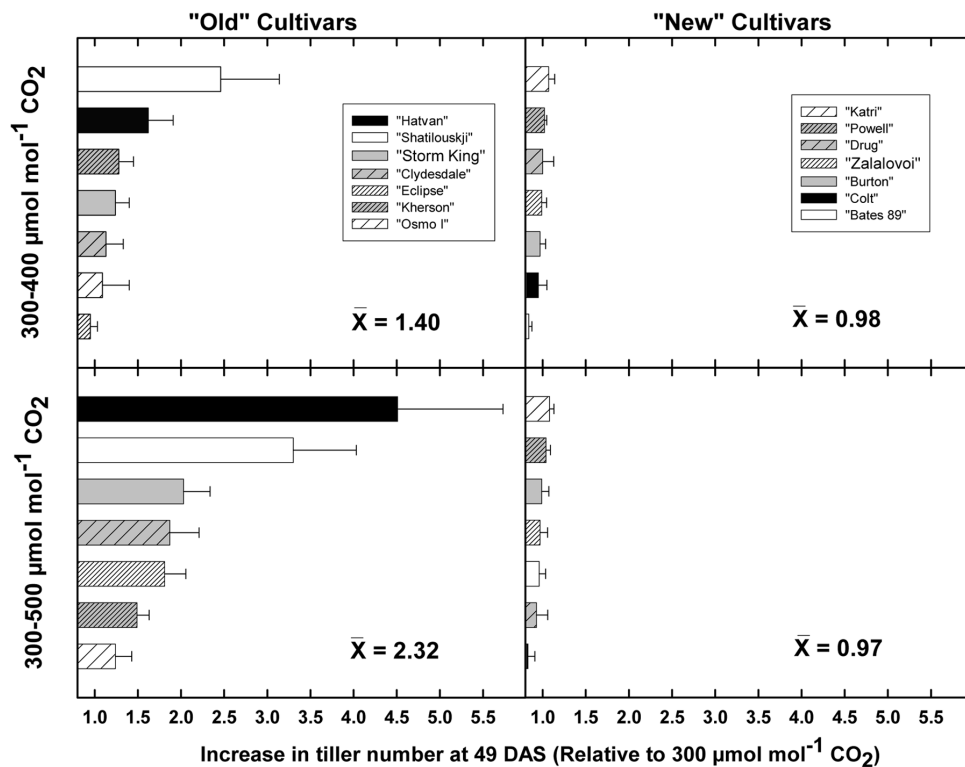

Figure 1. The relative increase in oat (*Avena sativa* L.) tiller numbers at 49 d after sowing (DAS) for seven old and new cultivars (see Table 1) relative to the 300 µmol mol^{-1} CO_2 concentration (e.g., a value of 2.0 indicates a doubling in tiller production). No effect of CO_2 concentration on tiller production was observed for any oat lines released during the 1990s.

characteristic measured (Table 2). For example, while new and old cultivars had similar mean leaf area at 300 μmol mol^{-1} CO_2, only old cultivars increased in leaf area in response to rising [CO_2]. Similarly, although new cultivars generally produced more tillers, only old cultivars increased tiller production in response to rising [CO_2], coming to resemble new cultivars at the highest [CO_2]. Although similar patterns were observed for root, leaf, and total biomass, these trends were not significant.

One could argue that such an evaluation of individual plant response among newer oat lines does not reflect [CO_2] sensitivity at the agronomic, or field, level. This is a valid point. Yield at the field level, however, is a consequence of both whole-plant response (e.g., harvest index) and agronomic practice (e.g., row spacing). Consequently, it seems reasonable to suggest that if some older lines show greater phenotypic variation (e.g., vegetative growth or tiller production) to increasing [CO_2] than newer lines at the whole-plant level, it may be possible to develop suitable agronomic practices that would convert these phenotypic differences into potential increases in productivity at the field level in a future, higher CO_2 environment.

The observation that phenotypic variance is reduced among newer lines (Fig. 1, Table 4) is not unexpected. Increasing uniformity for a given crop reflects, in part, the mechanized harvests and economic considerations associated with modern agriculture (Doyle, 1985). However, uniformity can also limit responses to selective factors, including rising CO_2 (Reich et al., 2001). The lower variance in response to ris-

Table 4. Significance of equality of variance for old and new oat (*Avena sativa* L.) cultivars for select vegetative and growth characteristics averaged across all CO_2 concentrations. Statistical significance indicates a greater degree of phenotypic variation. Root/shoot ratio, leaf area ratio, and net assimilation rate were not significant.

Variable	Old cultivars	New cultivars
Leaf area	*	NS[‡]
Leaf wt.	**	NS
Tiller wt.	**	NS
Weight tiller^{-1}	***	NS
Tiller no.	*	NS
Root wt.	*	NS
Total wt.	***	NS
Relative growth rate	**	NS

*Significant at $P < 0.05$.

**Significant at $P < 0.01$.

***Significant at $P < 0.001$.

‡NS, not significant.

ing CO_2 for new relative to old cultivars in this experiment suggests that the ability to respond to rising CO_2 may have been constrained through past breeding efforts. Among the many traits that were less variable among new relative to old cultivars, tiller number showed the strongest differences (Fig. 1, Table 4). Previous work with cereals (wheat and rice) has demonstrated that, at the whole-plant level, the ability to produce new tillers or leaf area per tiller is highly correlated to CO_2 responsiveness (Mitchell et al., 1993; Mandersheid and Weigel, 1997; Moya et al., 1998; Ziska et al., 2004). Yet,
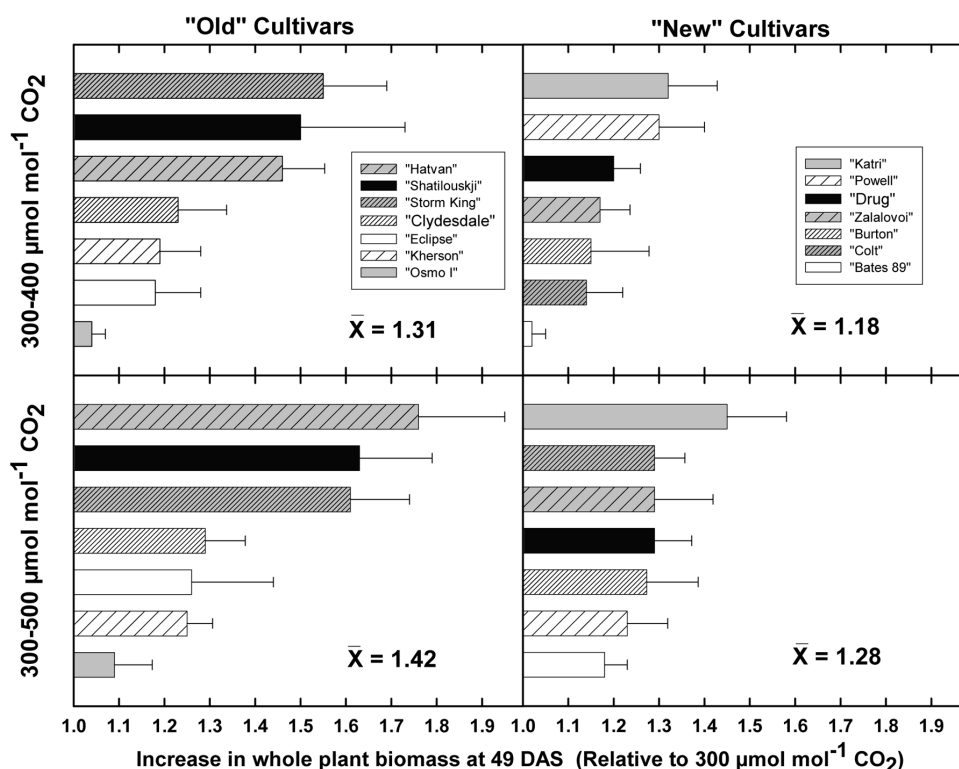

Figure 2. The relative increase in oat (*Avena sativa* L.) whole-plant biomass at 49 d after sowing (DAS) for seven old and new cultivars (see Table 1) relative to the 300 μmol mol^{-1} CO_2 concentration (e.g., a value of 2.0 indicates a doubling in biomass).

in the current experiment, none of the newer oat lines was able to produce additional tillers as [CO_2] increased above the 300 µmol mol^{-1} baseline.

Overall, in the current experiment, we could find no evidence that selection for modern lines of oat has, in fact, been associated with greater CO_2 sensitivity. Rather, modern, relative to older, oat lines appear to have greater phenotypic uniformity and decreased plasticity with respect to [CO_2], with potentially less opportunity to exploit increases in atmospheric CO_2.

These data and others (Ziska and Bunce, 2000; Ziska et al., 2001) argue that empirical selection may not be sufficient to choose the most CO_2-responsive crop lines. As a consequence, agronomic cultivars in current use could be inadequate to maximize productivity in response to increasing atmospheric CO_2, suggesting that a broader, more thorough evaluation of crop germplasm is necessary. At present, however, we are unaware of any such evaluation effort in regard to CO_2 at the government, university, or corporate level.

Acknowledgments

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