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Elevated atmospheric CO_2: a nurse plant substitute for oak seedlings establishing in old fields

MARK A. DAVIS*, PETER B. REICH†, MARY J. B. KNOLL*, LEE DOOLEY*, MARJORIE HUNDTOFT* and INGRID ATTLESON*

**Department of Biology, Macalester College, 1600 Grand Avenue, Saint Paul, MN 55105, USA, †Department of Forest Resources, University of Minnesota, Saint Paul, MN 55108, USA*

Abstract

It has been hypothesized that elevated levels of atmospheric CO_2 (*e*CO_2) may facilitate the encroachment of woody plants into grasslands by reducing water stress. In east-central Minnesota, sandy soils frequently create drought conditions for plants, and water limitation inhibits the establishment of oaks into old fields situated on these soils. Some have argued that *e*CO_2 should slow secondary succession by favoring fast-growing early successional species. However, if oak encroachment into old fields is being inhibited by water stress, then *e*CO_2 could accelerate old-field succession in this region. The purpose of this study was to test the hypothesis that *e*CO_2 will increase the establishment success of oak seedlings in an old field environment. The study was conducted with CO_2 levels controlled by free air CO_2 enrichment (FACE). In May 1999, four oak (*Quercus ellipsoidalis*) acorns were planted in each of 24 plots in each of six experimental FACE rings ($n = 576$), three of which received elevated levels (550 ppm) of CO_2. Half the plots in each ring were weeded during the first three summers of the experiment. In summer 2000, water input was manipulated during a 3.5-week period, during which half the plots received regular watering while the other half received no water. Summer 2001 was dry, receiving 35% less rainfall than the mean level. Under hot and dry conditions, *e*CO_2 increased soil water levels in unweeded plots and enhanced oak establishment (survival and growth) in weeded plots. In 2006, after the eighth growing season following planting, survival was five times greater under elevated than ambient CO_2. The results showed that under hot and dry conditions, *e*CO_2 can act like a nurse plant for tree seedlings growing in bare and unshaded areas, increasing seedling survival and growth, and thereby expanding the establishment window for trees encroaching into a grassland environment.

Keywords: drought, elevated CO_2, FACE, grasslands, old fields, *Quercus*, succession, woody encroachment

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Introduction

Woody vegetation is encroaching into grasslands throughout many regions of the world (Archer, 1989; Van Auken, 2000; Roques *et al.*, 2001; Silva *et al.*, 2001; Fensham *et al.*, 2005). Explanations for this phenomenon have included the introduction of domestic grazing animals, which are thought to reduce competition from grasses (Brown & Archer, 1999), the reduction in fire frequency, often due to high grazing pressure which reduces fuel loads (Roques *et al.*, 2001; Briggs *et al.*, 2005), and global change, including increases in precipitation (Fensham *et al.*, 2005) and elevated levels of atmospheric CO_2 (*e*CO_2) (Idso, 1992; Polley *et al.*, 2003).

In semiarid grasslands, limited soil water availability is believed to inhibit the ability of many woody plants to become established (Fensham *et al.*, 2005; Sankaran *et al.*, 2005; Ward, 2005). In some instances, plant establishment in harsh environments is facilitated by nurse plants, which have been found to increase seed germination and seedling survival, a result of a reduction in water stress due to the shade produced by the nurse

Correspondence: Mark A. Davis, tel. +651 696 6102, fax +651 696 6442, e-mail: davis@macalester.edu

plant (Holmgren *et al.*, 1997; Stachowicz, 2001; Castro *et al.*, 2002).

Studies have shown that eCO_2 can increase the water-use efficiency of plants, thereby increasing levels of soil moisture, and reducing water stress (Centritto *et al.*, 2002; Widodo *et al.*, 2003; Nelson *et al.*, 2004). As a result, under dry conditions, it has been hypothesized that eCO_2 can facilitate the encroachment of shrubs and trees into semiarid grasslands (Bond & Midgley, 2000; Dugas *et al.*, 2001; Polley *et al.*, 2003; Padilla & Pugnaire, 2006).

To date, most North American research on the effects of eCO_2 on woody plant encroachment into grasslands have been conducted in the American southwest, where water limitation is believed to be an important factor in inhibiting woody plant establishment (Van Auken, 2000; Polley *et al.*, 2003). However, mesic grasslands experience frequent periods of drought as well (Morgan *et al.*, 2004), and drought impacts on vegetation in these environments will be exacerbated by well-drained soils. Cedar Creek Natural History Area, located in east-central Minnesota, is situated on the Anoka sand plain, a glacial outwash area. The most common terrestrial habitats at Cedar Creek include oak savannas and woodlands and old fields. Many Cedar Creek old fields have persisted with little woody plant establishment for several decades (Inouye *et al.*, 1994; Lawson *et al.*, 1999). Studies at Cedar Creek have shown that water limitation represents a significant obstacle to the establishment of oaks in the site's old fields (Davis *et al.*, 1998, 1999, 2005), and drought conditions have been shown to reduce woody seedling establishment in other old field studies (de Steven, 1991). Some researchers have argued that eCO_2 should slow secondary succession because it should favor the fast-growing early successional species (Potvin & Vasseur, 1997; Niklaus *et al.*, 2001). However, if oak encroachment into Cedar Creek's old fields is inhibited by water stress, then it is possible that eCO_2 could accelerate, not further retard, old field succession. The purpose of this study was to examine this possibility. Specifically, this study tested the following two hypotheses: (1) because it is expected that plants will utilize water more efficiently under eCO_2, soil water levels during drought periods should be higher in eCO_2 conditions; (2) oak seedling establishment success should be greater under eCO_2 conditions.

Methods

The study was conducted at Cedar Creek Natural History Area (CCNHA), Bethel, MN (45°24′N, 93°12′W). CCNHA, a Long Term Ecological Research site, is situated on the Anoka Sandplain, a glacial outwash area that is characterized by coarse textured soils low in nitrogen (Grigal *et al.*, 1974). This area is located in the transition zone between the central grasslands and the eastern deciduous forest of North America. Before settlement by Europeans, dry oak savanna and barrens were the dominant vegetation types, with bur oak (*Quercus macrocarpa* Michx.) and northern pin oak (*Q. ellipsoidalis* E. J. Hill), being the two dominant tree species (Wovcha *et al.*, 1995). Today, upland, herbaceous dominated communities at CCNHA include old fields and natural openings in remnant oak savanna/woodland habitat. Dominant grasses in old fields are C3 species: *Agropyron repens* L., *Bromus inermis* L., and *Poa pratensis* L. Although east-central Minnesota is not considered a semiarid environment based on climate (mean precipitation during the summer months is 33.3 cm), little summer precipitation is retained for long in the sandy soils, and the vegetation of the Anoka Sandplain frequently experiences periods of drought.

This study was conducted in the field with atmospheric CO_2 levels controlled by free air CO_2 enrichment (FACE). The FACE technology, set up in an abandoned agricultural field in 1997, consists of six rings (28 m diameter) and has been the site of Cedar Creek's long-term BioCON experiment, in which the interactive effects of CO_2 concentrations (ambient: 360 ppm, elevated: 550 ppm), soil N, and species richness on a variety of community and ecosystem properties and processes have been studied (Reich *et al.*, 2001a, b, 2004). Within the FACE rings, but outside the BioCON plots, the soil, which had been cleared of vegetation during the construction of the FACE rings, has been naturally recolonized by old field vegetation and by some of the species planted in the BioCON plots. The experiment reported here was conducted in plots set up in this naturally reestablishing vegetation. During 1999–2001, these plots were dominated primarily by forbs. However, by 2006 old field grasses dominated most plots.

In each ring, 12 plots (1.5 m × 2 m) were established in May 1999. A portion of each plot (0.5 m × 0.5 m) was hand weeded and kept free of vegetation through August 2001. In May, 1999, eight pin oak (*Q. ellipsoidalis*) acorns were planted, four in the vegetated portion of the plot and four in the weeded portion, each portion considered a subplot. Acorns were planted 30 cm apart in each vegetation type.

Cedar Creek received 35.93 cm of rain during summer 1999 (June–August), approximately 8% more than the 30-year mean. Since it was expected than any benefit of eCO_2 is likely to occur during drought conditions, in summer 2000 water input was controlled for a 3.5-week period (July 19–August 14). Half of the 12 plots in each ring were randomly designated as wet plots and half as dry plots. During the 3.5-week period, rain tarps, which were put on before a rain event and taken off once the rain event was over, were used to prevent any water input to the dry plots. The wet plots received 1 cm of water (hand watering) every other day, unless it had rained a comparable amount during the preceding 24 h. Summer 2001 began dry and continued much drier than normal throughout the entire summer. Similar drought and wet conditions were planned for summer 2001, however problems with the irrigation system prevented the application of water supplements. Thus, no water treatments were applied in 2001 and all plots experienced the drought effects. (Summer 2001 precipitation was 22.17 cm, 33.5% drier than the annual mean.) No weeding or water manipulation took place after 2001. However, the seedlings were left in the plots and continued to experience either ambient or elevated levels of CO_2 during subsequent growing seasons.

Emergence rates were recorded on 23 July 1999 and survival and height of those seedlings that germinated were recorded on 23 September 1999. In 2000, seedling survival and height were recorded immediately before and after the 3.5 weeks water manipulation (19 July–14 August). In 2001, seedling survival and height were recorded on 5 June and 16 August. In May 2006, plots were recensused and all surviving seedlings were recorded and measured for height.

Soil water content of both weeded and unweeded portions of plots were measured weekly from 19 July to 16 Aug in 1999, and every 4 days from 17 July to 10 August in 2000 by measuring percent volumetric soil water content, θ, using a portable time domain reflectometry system (Trime FM™, Mesa Systems Co., Mefield, MA, USA). Twenty centimeter probes were inserted vertically into the soil surface near the center of each weeded and unweeded area of a plot. At many sites, soil water (matric) potential ψ_s is a better measure of availability of soil water to plants than volumetric soil water, θ. In this study field, because the coarse soil texture is extremely uniform and the field is flat, analyses using θ and ψ_s have produced identical results (Davis *et al*., 1999; Davis & Pelsor, 2001). Thus, findings were analyzed and are presented based on θ.

Data were analyzed using JMP™ (SAS Institute Inc.) based on a nested or double-nested design (depending on whether or not both the water and weeding treatments were included in the analysis). Survival data (percent survival) for each treatment combination were arcsine transformed before analysis to meet distribution normality requirements (Zar, 1996), and mean height and growth of surviving seedlings in the treatment combinations were used in the analysis. Differences between multiple means in ANOVAs were tested using the Tukey test ($P < 0.05$). All errors presented are standard errors.

Results

The first summer, 1999, was wetter than usual and there was no CO_2 effect on the number of emerged seedlings in a subplot ($F = 0.23$, $P = 0.65$), the survival of emerged seedlings ($F = 0.07$, $P = 0.81$), or height ($F = 0.11$, $P = 0.76$) of emerged seedlings (Fig. 1). However, there was a weeding effect on all three of these responses. Weeding reduced the emergence rate in subplots (weeded: 76.7 ± 3.0%; unweeded: 87.8 ± 2.4%; $F = 9.07$, $P = 0.0032$), the first summer survival rates of emerged seedlings (weeded: 85.3 ± 3.0%; unweeded: 93.0 ± 1.9%; $F = 4.55$, $P = 0.035$) and height of surviving seedlings (weeded: 3.88 ± 0.15 cm; unweeded: 5.13 ± 0.14 cm; $F = 32.45$, $P < 0001$; Fig. 1). The lower emergence rate in weeded plots was due primarily to increased predation on the acorns, most likely by small rodents. Specifically, acorns in the weeded plots, but not the vegetated plots, were frequently found excavated or removed entirely from the plots.

Only nine of the 362 seedlings alive at the start of the 3.5 weeks water input experiment in July 2000 died during this experimental period. All nine were in the dry treatment, which resulted in a significant water treatment effect ($F = 10.00$, $P = 0.002$), however even in the experimental drought plots, survival was very high, at least 94% (Fig. 2). There was no CO_2 or weeding effect on survival (CO_2: $F = 0.004$, $P = 0.95$; weeding: $F = 0.07$, $P = 0.79$; Fig. 2) and no CO_2, water, or weeding effects on growth (increase in height) (CO_2: $F = 0.02$, $P = 0.90$; water: $F = 0.64$, $P = 0.47$; weeding: $F = 0.92$, $P = 0.34$).

During the drought summer of 2001, there was a significant CO_2 × weeding interaction on both survival ($F = 4.42$, $P = 0.0382$) and growth ($F = 6.29$, $P = 0.0136$). Specifically, although both survival and growth were lower in the weeded than unweeded plots under ambient CO_2 conditions, survival and growth were not compromised in the weeded plots in the eCO_2 environment (Fig. 3). Hence, in the vegetated plots (that include potential nurse plants), survival was virtually unchanged by eCO_2, whereas in the weeded plots, survival of seedlings grown in eCO_2 was 50% greater than that of seedlings grown in ambient levels of CO_2 (aCO_2).

In May 2006, 19 seedlings were still alive, 16 of which were growing in eCO_2 conditions. The surviving seedlings growing in the eCO_2 environment averaged approximately 50% taller than those growing in aCO_2 conditions (eCO_2: 74.6 ± 5.7 cm; aCO_2: 48.0 ± 10.0 cm; $t = 1.90$, $P = 0.0745$; Fig. 4), although with only three surviving seedlings in the aCO_2 conditions, one must interpret the height result with caution. Evaluated on the basis of emerged seedlings in 1999, the difference between the number surviving in the enriched and ambient CO_2 conditions is significant ($F = 10.32$,

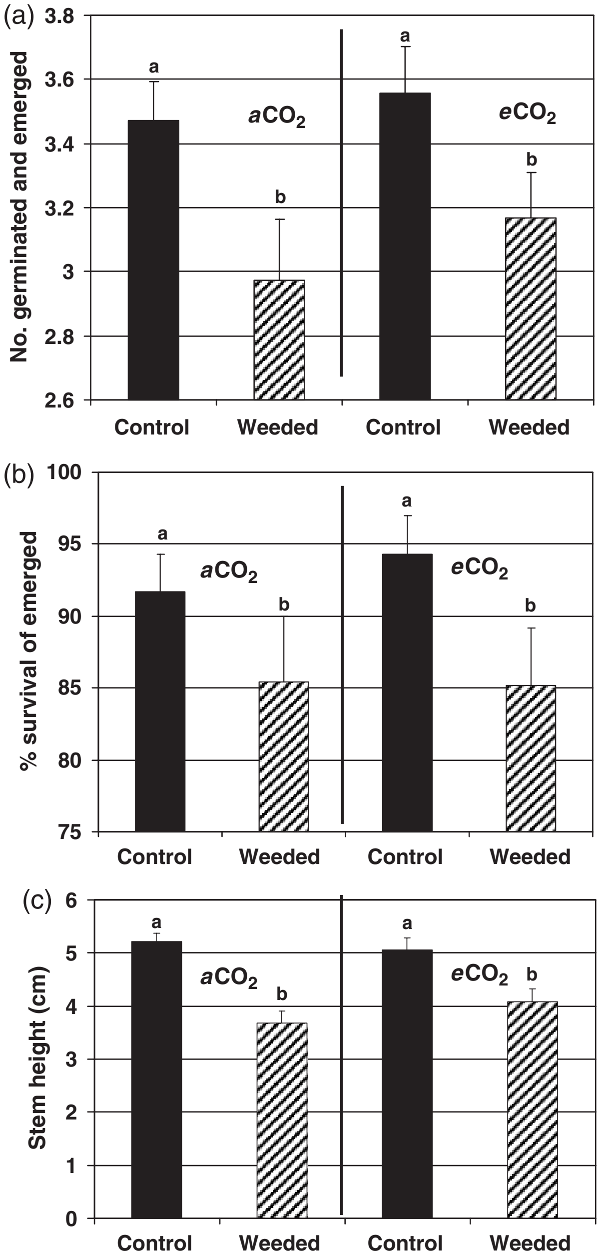

Fig. 1 Establishment success of oak seedlings during the first summer. (a) The number of acorns (of the original four that were planted) that germinated and emerged in weeded and unweeded plots in both enhanced and ambient levels of CO_2; (b) percent first summer survival of the emerging acorns in the four treatments; (c) height of surviving seedlings at the end of the first summer. In all three cases, there was a significant weeding effect but no CO_2 effect.

$P = 0.03251$, Fig. 4), indicating that CO_2 effects were detected across a span of eight growing seasons. However, based on those seedlings alive at the end of summer 2001 (at which time more seedlings were present in the eCO_2 plots), there was no significant subsequent CO_2 effect on survival, [i.e. from 2001 to 2006 ($F = 2.34$, $P = 0.200$)], suggesting that the enhanced survival trajectory under eCO_2 was due to effects and responses in the first few years following emergence.

The 1999 soil water measurements showed that there were no CO_2 effects on soil water under moderately wet to wet conditions (at least 17 mm of rain during the preceding week) (Fig. 5) or under very dry conditions (e.g. 1 mm of rain during preceding week) (Fig. 6). However, under dry (but not extremely dry) conditions (e.g. approximately 10 mm of rain during preceding week), there was a significant $CO_2 \times$ weeding effect ($F = 6.45$, $P = 0.0122$), with soil water being significantly lower in the vegetated than weeded plots in the ambient CO_2 plots, while soil water did not differ between vegetated and weeded plots in the eCO_2 plots (Fig. 6). While there was no significant weeding effect on soil water under moderately wet to wet conditions, there was a significant weeding effect under very dry conditions ($F = 39.94$, $P < 0.0001$). Naturally, there was a highly significant effect of the water treatments on soil water during the 2000 water input experiment ($P < 0.0001$), with soil water in the dry plots averaging around 5% while the wet plots averaged approximately 12%.

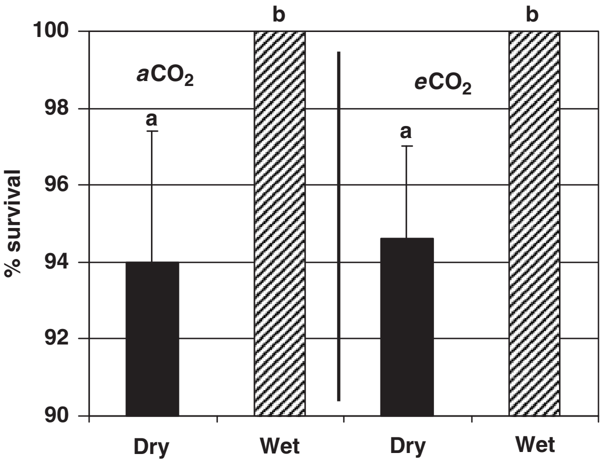

Fig. 2 Percent survival of seedlings during the 3.5 weeks experimental water period during the second summer. There was a significant water effect but no CO_2 effect on survival.

Discussion

The results showed that during their first three summers, pin oak seedlings benefited from a nurse plant effect from surrounding herbaceous vegetation. Acorns planted in these vegetated plots experienced less

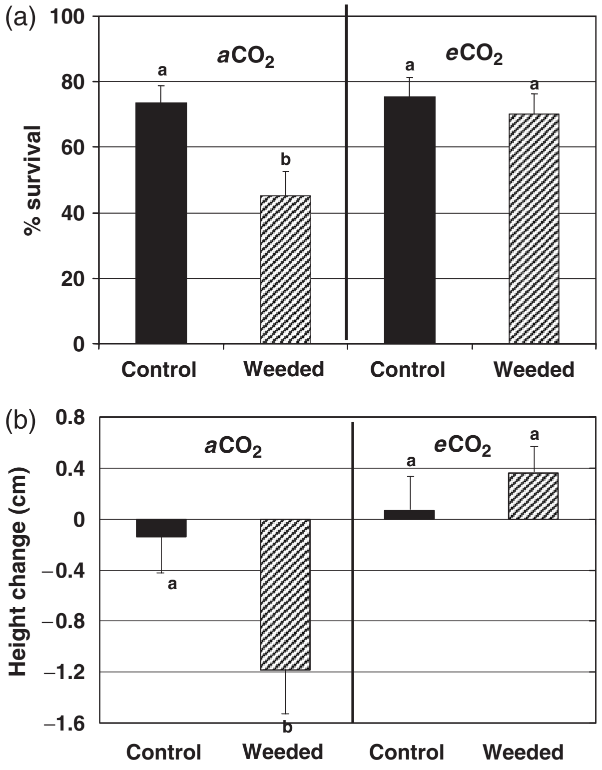

Fig. 3 Establishment success of oak seedlings during the third summer, which was 35% drier than normal. Both survival and growth are based on seedlings that were alive at the beginning of the third summer. (a) Percent survival of seedlings during the dry third summer showing a significant $CO_2 \times$ weeding interaction; (b) change in seedling height during the same summer, also showing a significant $CO_2 \times$ weeding interaction. In both cases, although success (survival or growth) was significantly reduced in weeded plots in ambient CO_2 conditions, under elevated CO_2 conditions, seedlings in the exposed weeded plots performed just as well as did the seedlings benefiting from a nurse plant effect in the unweeded plots.

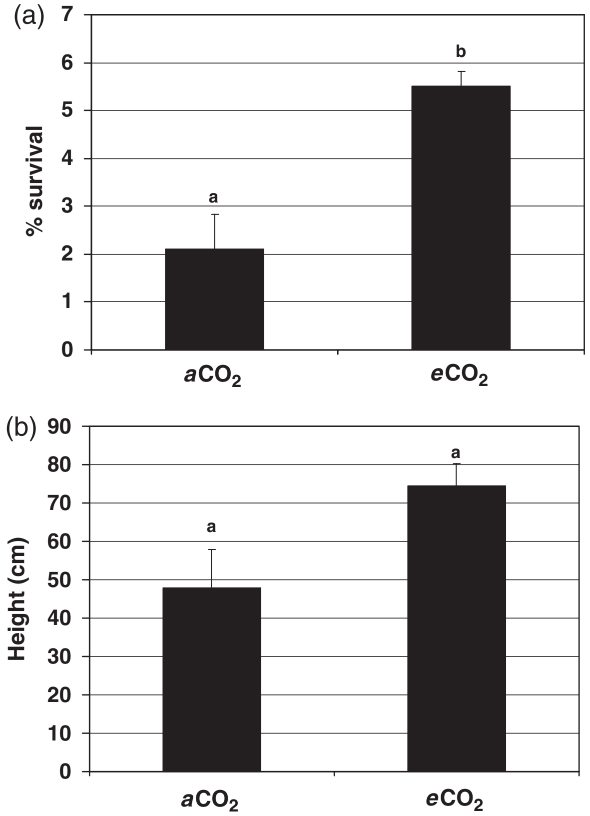

Fig. 4 Survival (a) and height (b) of the surviving seedlings in May 2006, 7 years following the experiment's inception. CO_2 level had a significant effect on survival based on those seedlings that germinated and emerged in 1999. Height differences approached significance ($P = 0.0745$).

predation, and the oak seedlings exhibited higher survival and growth rates in the vegetated plots. Due to the small size of the weeded plots and the fact that the plots were kept free of vegetation through weeding, which often left below-ground tissue of the herbaceous vegetation intact, it is not likely that the herbaceous vegetation was facilitating the seedlings through underground processes. Shade has been shown to reduce heat and water stress on tree seedlings and to increase seedling success of woody plants (Holmgren *et al*., 1997; Davis *et al*., 1999), and it is likely that these benefits were also conferred by the herbaceous plants in this study, which were much taller than the oak seedlings.

As predicted, the results showed that while *e*CO_2 did not provide any benefit to the establishing oak seedlings under wet conditions, it did benefit seedlings during periods of drought. However, under these dry conditions, *e*CO_2 enhanced seedling success only in weeded plots (Fig. 3). Specifically, *e*CO_2 increased both survival and growth of pin oak seedlings growing in weeded plots during the drought summer of 2001. No *e*CO_2 effect on the oak seedlings was documented in plots containing herbaceous vegetation, even during dry periods. Thus, during the hot, dry summer of 2001, *e*CO_2 essentially acted as a nurse plant substitute for the seedlings growing in the weeded plots, enabling these seedlings to exhibit growth and survival rates comparable to those growing in the vegetated plots at both ambient and elevated levels of CO_2.

As predicted, *e*CO_2 increased soil water levels under dry (but not very dry) conditions, presumably due to reduced water uptake by the herbaceous vegetation, which is predicted to occur under *e*CO_2 conditions (Morgan *et al*., 2004). The lack of effect of *e*CO_2 on soil water under very dry conditions has been documented by others (Morgan, *et al*. 2004, Nelson *et al*., 2004), and is most likely due to the fact that, under extreme drought

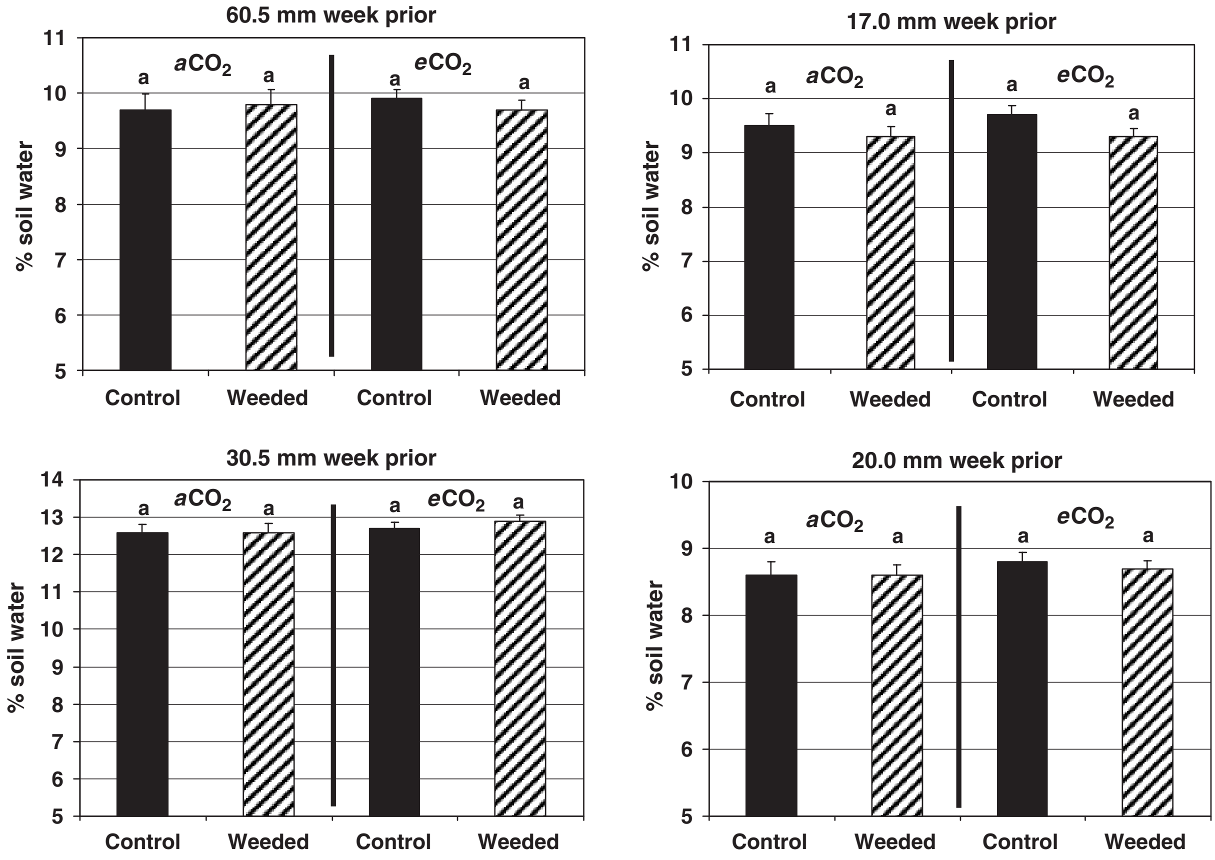

Fig. 5 Percent volumetric soil water for both weeded and unweeded plots in both CO_2 levels when plots experienced moderate to high levels of rain (17–60 mm) during the preceding week [data from 1999: 60.5 mm (20 July—27 July), 17 mm (28 July–2 August), 30.5 mm (3 Aug–10 Aug), 20 mm (11 Aug–16 Aug)]. As shown, there are no treatment effects.

conditions, most plants adopt a more or less a dormant state. Soil water levels in weeded plots were not affected by eCO_2, which one would expect due to the absence of any demand from herbaceous plants.

There have been few long-term studies of the effects of eCO_2 on seedling establishment success in woody plants. Thus, it is noteworthy that after eight growing seasons, seedling survival was five times higher in the elevated than ambient CO_2 plots (6.6% vs. 1.3%). The fact that CO_2 did not enhance survival from 2002 through 2006, which included two summers that were drier than the drought summer of 2001, suggests that the facilitative impact of eCO_2 is likely to be most important during the first few years of tree establishment, which makes sense because this is the time that the seedlings are most vulnerable drought and desiccation.

Our results support the view that eCO_2 is more likely to benefit plants during dry periods (Morgan *et al.*, 2004). Although the results support our predictions involving soil water levels and seedling success, changes in the two were not always coincident. For example, while soil water levels in vegetated plots were higher in the eCO_2 plots during dry conditions, the benefits to the oak seedlings growing in eCO_2 occurred in the weeded plots, where measured soil water levels were not affected by eCO_2. It is possible that the soil water measurements, recorded as the mean soil water content in the top 20 cm of soil, did not fully characterize water availability to the individual seedlings.

Prior studies have shown that oak seedling establishment in Cedar Creek's old fields is inhibited by herbaceous vegetation under dry conditions (Davis *et al.*, 1998, 1999, 2005). The difference between those results with those reported here is likely due to the difference in the composition of the herbaceous vegetation involved. In the previous studies, the seedlings were planted in plots dominated by grasses. During 1999–2001, the dominant herbaceous species in the FACE plots were forbs, which had naturally colonized and established from the surrounding old field and from other FACE plots to which they had been sown as part of other experiments. The

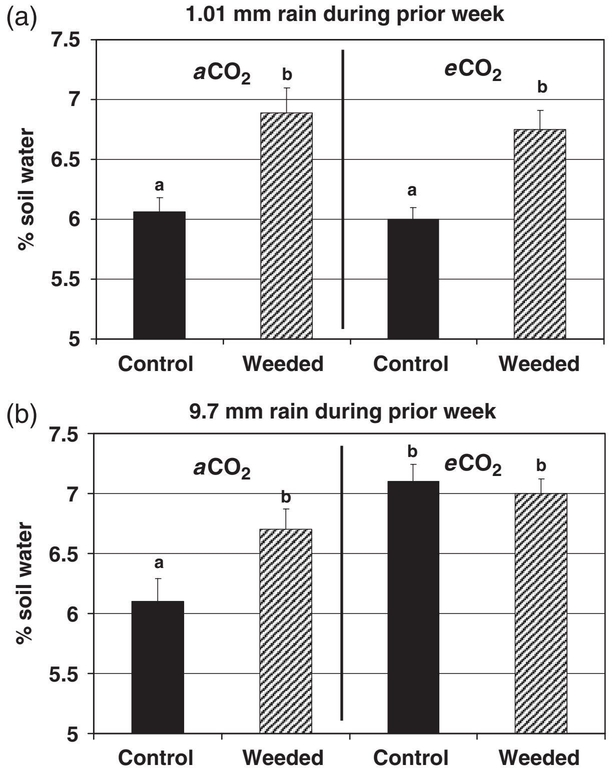

Fig. 6 Percent volumetric soil water for both weeded and unweeded plots in both CO_2 levels when (a) plots received almost no rain input (1 mm) during the preceding week (10 July–17 July 2000), and (b) when plots received approximately 10 mm (12 July–19 July 1999). There was a significant weeding effect when plots experienced almost no water input, with vegetated plots exhibiting lower levels of soil water than the weeded plots. However, when plots received approximately 10 mm of rain during the prior week (still a dry week), there was a significant $CO_2 \times$ weeding effect, with the soil water levels in the vegetated plots in the elevated CO_2 conditions remaining comparable to those in the weeded plots.

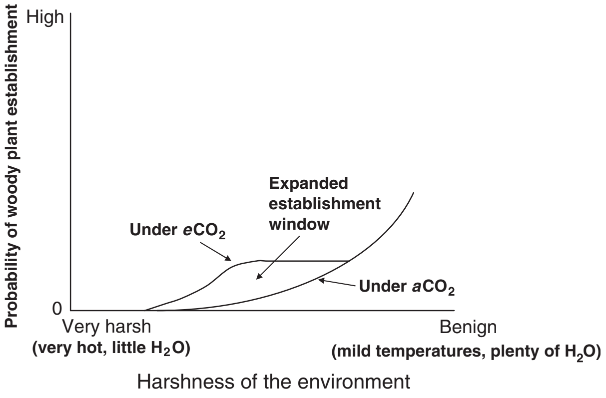

Fig. 7 An illustration showing how elevated levels of CO_2 are predicted to facilitate the encroachment of woody plants into grasslands, based on the hypothesis that eCO_2 reduces heat and/or water stress in dry environments. The illustration shows that under extremely hot and dry conditions, eCO_2 is unable to moderate the extreme conditions sufficiently to permit woody plant establishment. Under wet conditions, woody plants are likely not experiencing high levels of water or heat stress and thus eCO_2 does not confer any added benefit in these areas. However, under dry (but not too dry) conditions, eCO_2 can make a difference. Based on the results of this study, in semiarid conditions eCO_2 acts like a nurse plant substitute, buffering physical stressors which previously had been inhibiting the establishment of woody plants, thereby expanding the establishment window for these plants and facilitating encroachment.

prior studies (Davis *et al*., 1998, 1999, 2005) showed that oak establishment in grass-dominated plots was due to primarily to underground processes, particularly root competition for water. Forbs often lack the dense matrix of roots exhibited by grasses (Craine *et al*., 2002) and this is especially true for the species in the BioCON plots (Reich *et al*., 2001a, b). Thus during 1999–2001, the oak seedlings were able to reap the benefits provided by the shade from the forbs without experiencing the costs of intense root competition.

In most grassland environments, bare soil patches are common, whether due to burrowing animals (Platt, 1975; Inouye *et al*., 1997) or to low productivity and plant cover, (e.g. in most semiarid grasslands). At Cedar Creek in other extant grasslands, native and anthropogenic, in east-central Minnesota, pocket gophers are abundant and hence bare soil patches, which last for several years, are very common. Thus, if oak encroachment into Cedar Creek's old fields is being inhibited by intense competition with grasses for water in vegetated areas, and by heat and water stress in unvegetated areas, then, according to the results of this study, increasing atmospheric levels of CO_2 may be able to kick-start oak establishment into Cedar Creek's old fields. In sum, this study has shown that under hot and dry conditions, eCO_2 can act like a nurse plant for tree seedlings growing in bare and unshaded areas, increasing seedling survival and growth, and thereby expanding the establishment window for the trees and facilitating woody encroachment into some grassland environments (Fig. 7).

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