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Root production and demography in a california annual grassland under elevated atmospheric carbon dioxide

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Abstract

This study examined root production and turnover in a California grassland during the third year of a long-term experiment with ambient (LO) and twice-ambient atmospheric CO_2 (HI), using harvests, ingrowth cores, and minirhizotrons. Based on one-time harvest data, root biomass was 32% greater in the HI treatment, comparable to the stimulation of aboveground production during the study year. However, the 30–70% increase in photosynthesis under elevated CO_2 for the dominant species in our system is considerably larger than the combined increase in above and belowground biomass. One possible explanation is, increased root turnover, which could be a sink for the additional fixed carbon. Cumulative root production in ingrowth cores from both treatments harvested at four dates was 2–3 times that in the single harvested cores, suggesting substantial root turnover within the growing season. Minirhizotron data confirmed this result, demonstrating that production and mortality occurred simultaneously through much of the season. As a result, cumulative root production was 54%, 47% and 44% greater than peak standing root length for the no chamber (X), LO, and HI plots, respectively. Elevated CO_2, however, had little effect on rates of turnover (i.e. rates of turnover were equal in the LO and HI plots throughout most of the year) and cumulative root production was unaffected by treatment. Elevated CO_2 increased monthly production of new root length (59%) only at the end of the season (April–June) when root growth had largely ceased in the LO plots but continued in the HI plots. This end-of-season increase in production coincided with an 18% greater soil moisture content in the HI plots previously described. Total standing root length was not affected by CO_2 treatment. Root mortality was unaffected by elevated CO_2 in all months except April, in which plants grown in the HI plots had higher mortality rates. Together, these results demonstrate that root turnover is considerable in the grassland community and easily missed by destructive soil coring. However, increased fine root turnover under elevated CO_2 is apparently not a major sink for extra photosynthate in this system.

Keywords: carbon allocation, carbon budget, carbon dioxide enrichment, minirhizotron, root turnover, water-use-efficiency

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Introduction

In general, plant growth under elevated CO_2 leads to a sustained enhancement in leaf-level photosynthesis, a reduction in stomatal conductance and a consequent increase in leaf-level water-use-efficiency (Curtis, 1996), though not for all species (Saxe *et al*., 1998). In the grassland ecosystem we study, CO_2 enrichment leads to 30–70% increases in mid-day photosynthesis for abundant species (Jackson *et al*., 1994; Lund *et al*., 2002) but responses of aboveground biomass are inconsistent

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(Field *et al*., 1996). The large CO_2 response of photosynthesis relative to that of biomass is common to numerous CO_2 enrichment studies (Canadell *et al*., 1996), leading to questions about the fate of the extra fixed carbon (Luo *et al*., 1997).

One possible explanation is that typical root analysis underestimates belowground carbon allocation and root response to CO_2 enrichment. The usual tools for root analysis, destructive soil coring and root harvests, do not permit simultaneous measurement of root production and mortality and therefore do not account for turnover (Eissenstat & Yanai, 1997). In some ecosystems, at least 1/3 of fine root production and mortality occur simultaneously (Hendrick & Pregitzer, 1993b; Rytter & Rytter, 1998), leading one-time harvests to underestimate root production. Therefore, changes in belowground allocation of carbon that may accompany CO_2 enrichment could be underestimated by a failure to include root turnover. Indeed, accurate measurements of net primary production, allocation of biomass and nutrients, and transfer of carbon and nutrients from plants to soil all depend on credible estimates of root turnover (Eissenstat *et al*., 2000). Non-destructive root observations, with minirhizotrons and other facilities, provide approaches for frequently observing roots in near-natural environments (Maertens, 1987; Cheng *et al*., 1991) and can be used to account for root turnover.

Carbon dioxide enrichment increases the rate of fine root production and mortality in numerous studies (Curtis *et al*., 1994; Pregitzer *et al*., 1995; Fitter *et al*., 1996; Berntson & Bazzaz, 1997; Fitter *et al*., 1997; Thomas *et al*., 1999; Pregitzer *et al*., 2000; Zak *et al*., 2000). In others, however, elevated CO_2 leads to increases in either production (Allen *et al*., 2000) or mortality (Kasurinen *et al*., 1999) but not both. Elevated CO_2 can also reduce root mortality (Tingey *et al*., 1997; Arnone *et al*., 2000; Johnson *et al*., 2000).

In this study, we used minirhizotrons, ingrowth cores, and biomass harvests to determine whether elevated CO_2 concentrations altered standing live root length, the timing or quantity of new root production, and root mortality. We also examined how the CO_2 effect varies with soil depth, since interactions of CO_2 with water availability and many other environmental factors may not be constant through the soil profile.

Materials and methods

Study site

Stanford University's Jasper Ridge Biological Preserve (37°24′-N, 122°13′-W) has a mediterranean-type climate with cool wet winters and hot dry summers. The Jasper Ridge CO_2 Experiment (Field *et al*., 1996) consists of three field treatments: a no-chamber control (X), an open-top chamber control with ambient CO_2 concentration (LO), and an open-top chamber treatment with elevated CO_2 concentrations (ambient plus 360 ppm, HI). Each treatment is replicated ten times over the communities growing on two distinct soil types, a relatively high nutrient sandstone soil—dominated by Eurasian annual grasses (Baker, 1989) and a relatively low nutrient serpentine soil (not considered in this study). In the spring of 1994, we installed 60 acrylic minirhizotron tubes (2 tubes per plot) at 45° to a depth of approximately 0.3 m in the 30 sandstone field plots. Each plot is 0.65 m in diameter and contains approximately one thousand individual plants. Carbon dioxide enrichment began in January 1992. It was continuous from then through April 1997, except for the summer of 1992.

Harvests and ingrowth cores

We collected soil cores near the end of the winter-spring growing season (May 4, 1995) in each of the LO and HI plots. The core had a diameter of six centimeters and was inserted to a depth of 15 cm. Stem material was removed and the remaining organic material was divided into root, bulb, and litter fractions. Each fraction was then dried and weighed. Results were analysed using a single factor ANOVA. Regression analysis compared soil harvest data with root ingrowth core and minirhizotron data, respectively.

We placed root-free ingrowth cores in the ground in June of 1994 and initially exchanged them in October of 1994. No roots were found in the cores exchanged in October 1994. Ingrowth cores were removed and replaced four additional times throughout the 1994–95 growing season (February 14, March 17, May 12, and June 28). The cores had a 2.3 cm diameter, and sampled roots to a depth of 20 cm. Root samples were dried in an oven at 65 °C and weighed. Comparison between treatments for each sampling date was conducted by analysis of variance (ANOVA). We compared the May root ingrowth core data with the soil core data by linear regression. Aboveground biomass was estimated from a complete harvest of 80 cm^2 from each plot ($n = 10$) at the time of peak biomass (early May). Biomass samples were dried at 60 °C and sorted to species.

Minirhizotron analysis

Images were gathered monthly using a method similar to that described by Cheng *et al*. (1991), using a minirhizotron microvideo camera system (BTC-2, Bartz Technology, Santa Barbara, CA) and a HI8 VCR (EV-C100, Sony, Tokyo, Japan) and a monitor. Images were recorded every cetimeter along the upper surface of the tube

from the soil surface to a depth of approximately 20 cm. Individual images covered an area of approximately 13.5 by 18 mm, of which we analysed the central 10.86 by 14.49 mm.

Images were then analysed with a program that transfers root information from images to a database (ROOTRACKER, 1995 created by Craine + Tremmel at the Duke University Phytotron). Each live root was assigned to one of two condition classes, white or yellow, based on appearance. Roots that were black, very dark, or that disappeared were considered dead.

Many frames had gaps between the tube and the soil. We analysed only those frames that had uniform contact between the soil and tube. In general, frames that had good soil contact at the beginning of the analysis (November 1994, 8 months after the tube installation) were usable throughout the study period. We rejected the time series of images for a location if any image from the time series had gaps amounting to more than 5% of the analysis area.

We analysed images from four depth zones (frames 8–12, 13–17, 18–22, and 23–25, hereafter referred to as frame depths 10, 15, 20 and 25). The centres of these zones correspond to actual depths in the soil of roughly 7, 11, 14, and 17 cm, respectively. Images from frames shallower than frame 8 seldom had good contact with soil. For each depth zone in each tube, we selected the frame with the best soil/tube interface for detailed analysis. If more than one had a good soil/tube interface, we selected the one closest to frame 10, 15, 20, or 25, respectively. If none of the frames from a depth zone in a tube had a good soil/tube interface, we dropped that zone of that tube from the analysis.

We collected 500 images per month over the 12 month period. 140 of these were outside the depth zones we examined. From the 360 remaining images, we selected 62 frames in the X plots (13 at zone 10, 14 at zone 15, 18 at zone 20, and 17 at zone 25), 70 frames in the LO plots (14 at zone 10, 18 at zone 15, 19 at zone 20, and 19 at zone 25), and 72 frames in the HI plots (17 at frame depth 10, 16 at frame depth 15, 19 at frame depth 20, and 20 at frame depth 25) for monthly analysis based on the criteria described in the preceding paragraph. The analysis in this paper covers data collected from November 1994 through October 1995.

All lengths are presented per unit of view area (m/m^2), calculated based on the area of each frame subjected to analysis. We estimated root density (root length per soil volume) based on the assumption that the observation zone extends 2 mm into the soil (Klepper *et al*., 1973; Taylor & Klepper, 1973), yielding a soil volume per frame of 314.72 mm^3.

'Standing live root length' is a measure of the live root length at a particular time. It is the sum of the lengths of all live roots in a frame, independent of condition or production date (i.e. it is a static measure that does not account for turnover). We used multiway, repeated measures ANOVA to test for effects of treatment, date and depth. To explore the relationship between sample size, size of the CO_2 effect, and probability of detecting the CO_2 effect, we calculated statistical power (Glantz, 1992).

We compared the soil core and minirhizotron results by linear regression. Root length was summed for the frame depths 10, 15, & 20 (corresponding to the depth of our soil cores) and for both tubes in a single plot. Since the soil cores were taken between the April and May imaging dates, we compared the soil core data to total standing root length for April, May, and the average of April and May

To estimate root biomass at the end of the growing season from image data, we assumed roots are cylindrical. Mass per length is estimated from the measured radius and an assumption that mass per volume is 0.2 g/cm^3. These estimates were integrated to a depth of 0.17 m, assuming that each measured image was representative of its depth zone.

'New root length production' was calculated for each interval as the sum of the length of roots not present in the previous month, plus the extension of existing roots. We used multiway repeated measures ANOVA to evaluate effects of treatment, date and depth. Survivorship was calculated as the fraction of roots produced in each month that were still alive by some future month. By dealing with the roots produced in each month as an independent cohort, it is possible to examine both the age dependence and the date dependence of survivorship. The sample sizes of roots in each production cohort were insufficient to support analyses of survivorship by depth, so data were pooled over the four depths. Differences in survivorship were examined using Gehan's generalized Wilcoxon test as described by (Lee, 1992), and (Pyke & Thompson, 1986).

Results

Ingrowth cores and end of season root biomass

The end of season soil cores revealed average root densities of 36.4 g/m^2 (SD = 16.5) and 48.0 g/m^2 (SD = 26.6) for the LO and HI treatments, respectively (Table 1), a 32% difference that was not statistically significant ($P = 0.304$). Root ingrowth core data (Fig. 1) indicated relatively constant rates of root production for samples collected in February (39.2, 37.9, and 31.8 g/m^2), March (30.1, 22.1, 22.3 g/m^2), and May (30.8, 40.1, and 37.3 g/m^2 for the X, LO and HI treatments, respectively). Productivity declined after May for all treatments (3.9,

4.3, and 6.6 g/m^2 for the X, LO, and HI treatments, respectively).

Summing over all four sampling dates produces a measure of cumulative production of 103.9, 104.3, and 98.0 g/m^2 for the X, LO, and HI plots, respectively. These cumulative values for root production are 187 and 104% higher than the end of season harvest values (36.4 g/m^2 and 48.0 g/m^2) for the LO and HI plots, respectively. The regression between the soil core and root ingrowth core data was not significant ($r^2 = 0.06$).

Minirhizotrons

Standing live root length

In each treatment, standing live root length reached a single peak in spring, at levels 5–10 times larger than the initial lengths in November (Fig. 2). Standing length in the HI treatment peaked in June (119.7 m/m^2), while the peaks for the X (122.6 m/m^2) and LO (109.1 m/m^2) plots were in April and May, respectively. The total number of live roots followed a similar pattern (data not shown). Averaged over sampling dates, the rooting depth profiles in all three treatments were similar, but roots in the LO treatment were more concentrated at the top of the profile (Fig. 3).

Standing root length varied significantly with date ($P < 0.0001$) but not with depth ($P = 0.217$). There were no significant effects of treatment (CO_2 or presence of a chamber) over the entire year or at any single date. The only significant interaction was between depth and date (Table 2).

At the time of maximum root abundance (April – June), root densities reached peak values of 6.43, 5.45, and 5.99 cm/cm^3, corresponding to estimated biomass of 97.25, 85.75, and 92.25 g/m^2, for the X, LO, and HI plots, respectively. This rough estimate (Maertens, 1987) is very close to the seasonal totals from the ingrowth cores but more than twice the biomass recovered from the soil cores. Regressions between soil core data and minithizoton root length for the average of April and May ($r^2 = 0.18$) and for April alone ($r^2 = 0.26$) were not significant.

New root length production

New root length production was greatest for all treatments in April (Fig. 4a), reaching values of 44.6, 29.8, and 44.1 m/m^2 in the X, LO, and HI plots, respectively. This pattern was, however, noisy enough that it could not be identified at each depth (data not shown). Very little new production occurred after June in any of the treatments (2.9 m/m^2 in X, 4.5 m/m^2 in LO, and 4.9 m/m^2 in HI). The total number of new roots paralleled the pattern in new root length (Table 3).

Cumulative new root length production (Fig. 4b) was 189.1, 160.4 and 172.1 m/m^2 for the X, LO and HI plots, respectively. Prior to May, cumulative root production was greater in the LO than the HI plots, but from May through the end of the season, this pattern reversed, and

Table 1 Above and below-ground biomass from the 1994–95 season (grams) with SD. Below-ground values are from the soil cores extracted in May of 1995. Root biomass differences are not significant based on analysis of variance

	Above-ground			Below-ground		
Treatment	Biomass	SD	Root Mass	SD	Litter	SD
X	261	117				
LO	408	193	36	17	299	83
HI	361	142	48	27	322	21

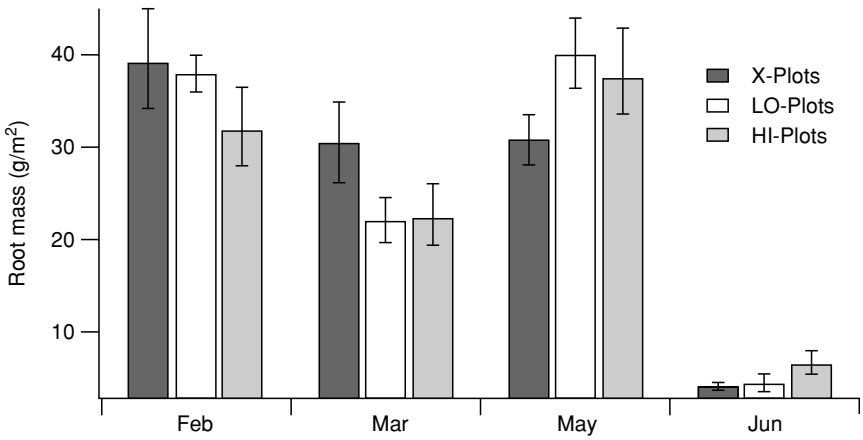


Fig. 1 Root ingrowth core mass from November 1994 through October 1995 for the no-chamber (X), ambient CO_2 (LO), and elevated CO_2 (ambient plus 360 ppm, HI) treatments. Root mass per unit of ground area is integrated from the surface to a depth of 20 cm. The error bars represent SE.

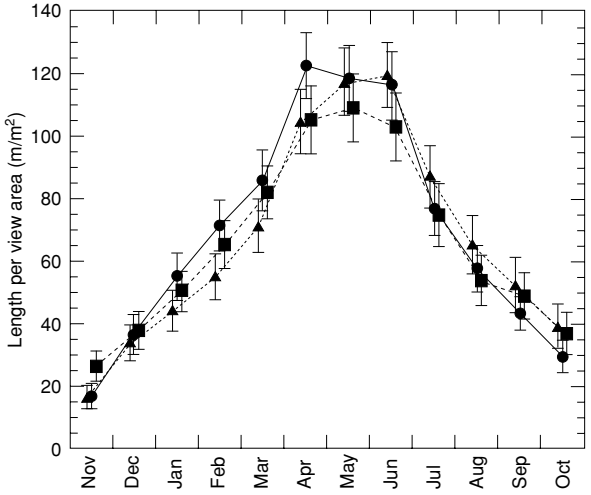


Fig. 2 Standing root length per unit of view area as measured by minirhizotron imaging from November 1994 through October 1995 for the X (●), LO (■) and HI (▲) plots. The error bars represent SE.

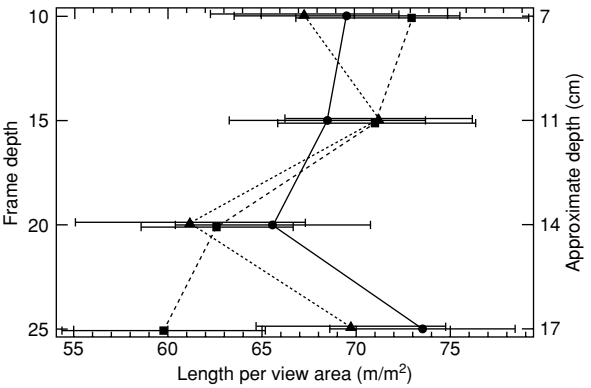


Fig. 3 Standing root length per unit of view area from minirhizotron observations at frame depth 10, 15, 20, and 25 averaged over time for the X (●), LO (■) and HI (▲) treatments. The error bars represent SE. Note that the horizontal scale does not begin at the origin.

Table 2 Standing root length *P*-values based on repeated measures analysis of variance

	X/LO/HI
Treatment (date)	0.951
Depth (date)	0.217
Date	0.000
Treat (date)*Depth (date)	0.993
Treat (date)*Date	0.148
Depth (date)*Date	0.000
Treat (date)*Depth (date)*Date	0.786

cumulative root production was greater in the HI than the LO plots. These cumulative values of root production are 54%, 47%, and 44% higher than the peak standing root values (122.6, 109.1, and 119.7 m/m^2) for the X, LO, and HI plots, respectively.

Comparison between LO and HI chambers shows that CO_2 had a significant effect on new length production ($P = 0.013$) for the period from April to June, leading to a 58.6% increase. However, there was no significant CO_2 effect on new length production for the year as a whole ($P = 0.593$) or for any other period during the year. Among all treatments, date did have a significant effect on new length production ($P < 0.001$, Table 4).

Root mortality

Roots produced in January, February, May, and June, did not have significant differences in survivorship for any treatment pair (Figs 5b.c.f.g). Survivorship for roots produced in April in the HI and X plots was significantly decreased, compared to roots grown in LO plots ($P < 0.05$) (Fig. 5e). Survivorship for roots produced in December and March in the LO and HI treatments had significantly decreased mortality relative to the X treatment ($P < 0.05$). There was, however, no significant difference between LO and HI treatments for December and March (Figs 5a.d).

Time until half the roots died remained fairly constant for roots produced prior to May, with early cohorts tending to survive 3–5 months vs. 2.5–3.5 months for roots from May and June. Root longevity appears to be only slightly sensitive to season and water limitation, at least in years with above average such as the 1994–95 season.

Discussion

Each of the three techniques used in this study (soil cores, ingrowth cores, and minirhizotrons), has strengths and weaknesses for determining belowground carbon allocation (Gill & Jackson, 2000). Taken together, the three methods show a substantial amount of concurrent production and mortality not accounted by destructive harvests. Therefore, soil core data alone would result in an underestimate of production in the grassland.

Based on the minirhizotron data, cumulative annual root production was about 50% greater than peak standing crop. This is slightly larger than the result of Hendrick & Pregitzer (1993a), who found that 1/3 of new root production and root mortality occurs simultaneously in the northern hardwood ecosystem that they studied. Comparing the ingrowth cores with the soil cores, cumulative production was 2–3 fold the peak standing crop. This difference could imply decreased

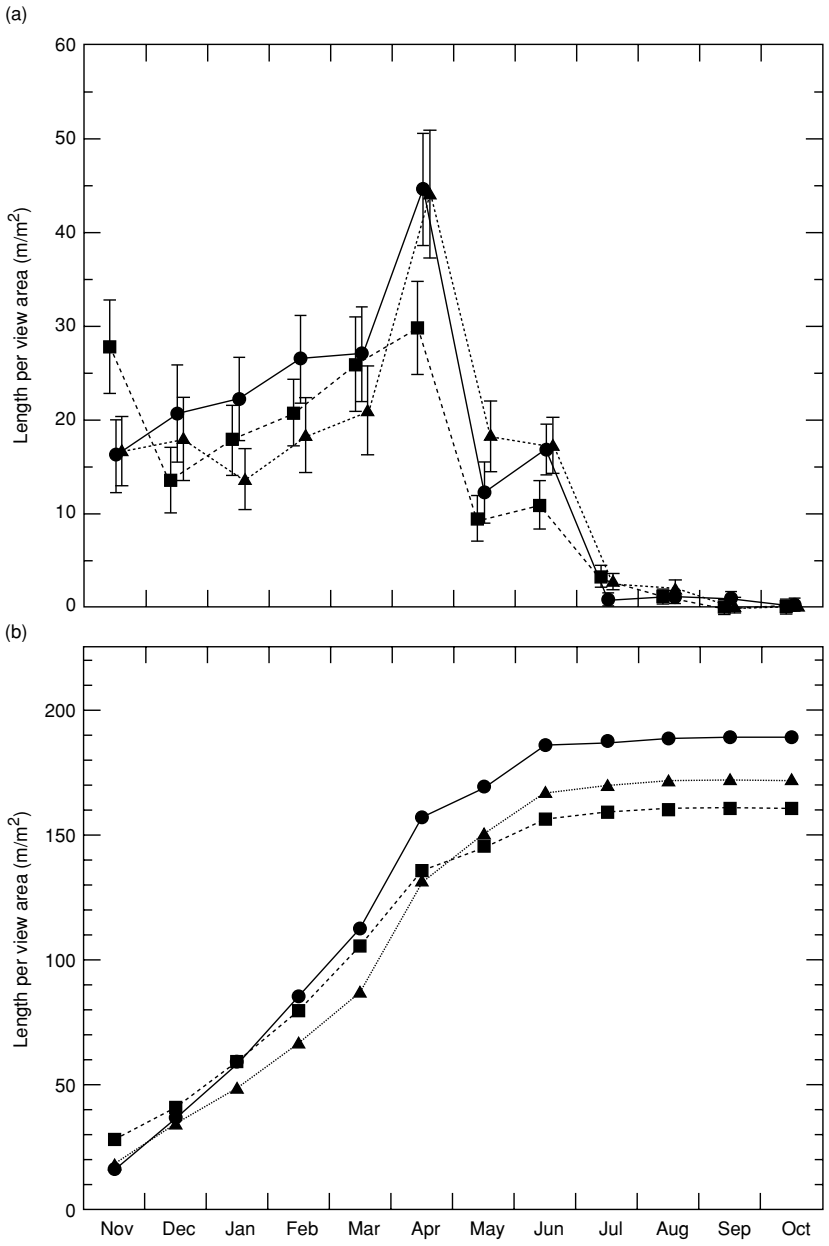


Fig. 4 Production of new root length per unit of view area from minirhizotron observations from November 1994 through October 1995 in the X (●), LO (■) and HI (▲) plots. (A) Monthly production (B) cumulative production. The error bars in (A) represent SE.

root turnover near the minirhizotron tubes, but the more likely explanation is that the ingrowth cores stimulated production.

As indicated in Table 1, aboveground biomass for the 94–95 season was similar among the treatments. Thus, the increase in carbon fixation that typically accompanies CO_2 enrichment in our system, 30–70% for the dominant species (Jackson *et al*., 1994; Lund, 2002) (but not measured in 1994–95) was not invested in an increase in above-ground growth. The high rate of root turnover could potentially account for the extra carbon fixed by plants grown under elevated CO_2. Rates of root turnover

Table 3 Number of roots in each cohort for each treatment (each column is the number of roots initiated during that time period)

Date	X-Plots	LO-Plots	HI-Plots
Dec−94	37	20	31
Jan−95	40	33	20
Feb−95	38	34	31
Mar−95	52	50	41
Apr−95	78	53	77
May−95	27	25	38
Jun−95	41	24	47

Table 4 New root length production *P*-values from repeated measures analysis of variance

	11/94–10/95	11/94–2/95	3/95–6/95	7/95–10/95	4/95–6/95
X/LO/HI	0.306	0.264	0.145	0.564	0.026
Treatment (date)					
Depth (date)	0.038	0.003	0.722	0.553	0.486
Date	0.000	0.518	0.000	0.002	0.000
Treat (date)*Depth (date)	0.992	0.719	0.617	0.547	0.315
Treat (date)*Date	0.111	0.242	0.305	0.124	0.700
Depth (date)*Date	0.022	0.296	0.091	0.037	0.050
Treat*Depth*Date	0.354	0.740	0.169	0.405	0.061

were, however, unaffected by elevated CO_2 except near the end of the season. Any increase in carbon allocation to roots from increased photosynthesis should lead to increased root production throughout the year. Instead we see a CO_2-mediated increase in productivity only at the end of growing season coinciding with soil moisture differences (discussed below). The total magnitude of the late-season extra root production under elevated CO_2 was less than 15% of the live root length at that time. This small increment of root production can account for some, but not all of the increase in carbon fixation that accompanies CO_2 enrichment (consistent with the results of Arnone *et al*., 2000).

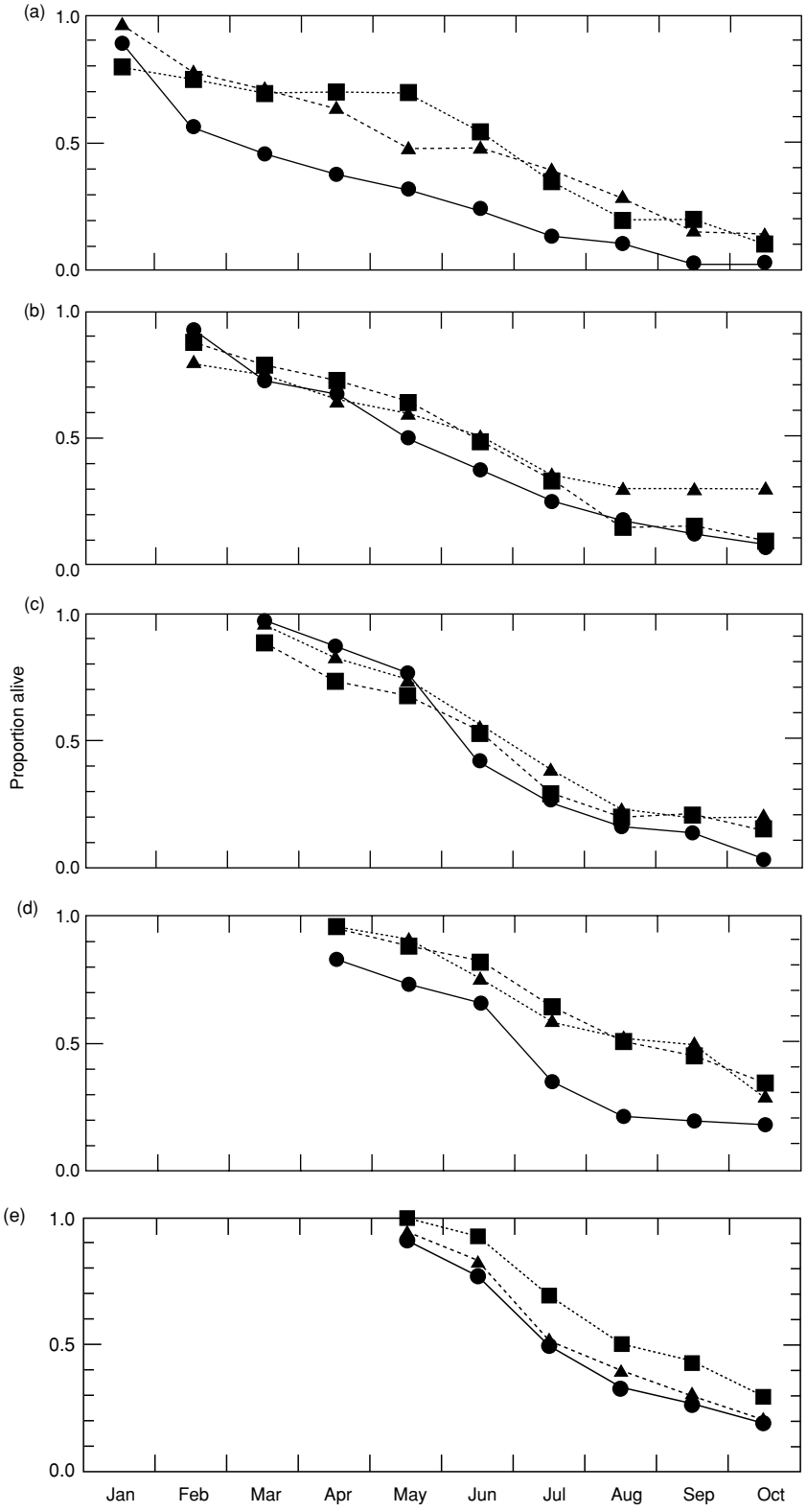
Elevated CO_2 did cause a 58.6% increase in new root production from April to June. This is the period when soil moisture is 18% greater in the HI than the LO plots (Fredeen *et al*., 1997; Lund, 2002), suggesting that at least part of the CO_2 effect is mediated through the effect on soil moisture. The late-season root production under elevated CO_2 could be a direct response to the relatively favourable root environment, or it could be an indirect effect of persistent photosynthetic activity (Jackson *et al*., 1994).

The importance of soil moisture for root production is further supported by the comparison between the X and LO treatments. The chambers reduced new root production by approximately 15% at the end of the season. Results from previous years show that the LO plots dry from roughly 10–28 days faster than the X plots (Fredeen *et al*., 1997; Lund, 2002), indicating that an increase in soil moisture alone is sufficient to increase late-season root production.

If CO_2 reduces H_20 stress, or enables plants to cope with moisture stress more effectively (Owensby *et al*., 1993; Volk *et al*., 2000), CO_2 effects on root turnover or standing root length may have been hidden by the higher than normal soil moisture late in the season. The 1994–95 season was very wet (1042 mm, precipitation), which may have reduced mid to late season water stress (Lund, 2002).

Others have found changes in the vertical distribution of roots in response to elevated CO_2 (Day *et al*., 1996; Thomas *et al*., 1999; Arnone *et al*., 2000). However, we did not detect an effect of elevated CO_2 on the depth distribution of the roots, partly as a consequence of limited statistical power. The greatest difference in mean standing root lengths was 16.7% at frame depth 25 (Fig. 3). Thus, if there were a CO_2 effect on depth distribution, it was small. Statistical power also limits our ability to detect treatment effects on total standing root length, but we are able to conclude that if there were a CO_2 effect on standing root length, it was small.

Increases in atmospheric CO_2 can cause increases in photosynthesis and carbon allocation to plant roots (Pregitzer *et al*., 1995; Arnone & Körner, 1995; Fitter *et al*., 1997). This increased allocation could lead to increased root growth directly or because of an increase in the C:N ratio, which may lead to increased nitrogen demand and soil exploration. Alternatively, higher WUE may reduce H_2O demand leading to decreased soil exploration and root growth. Excess carbon could also be lost through exudation, thus leaving the roots themselves unchanged. Finally, others have suggested that higher C/N ratios of plants grown at higher CO_2 could result in microbial immobilization of nutrients, which would cause a dampening of growth response (Schimel, 1990; Pregitzer *et al*., 1995). Our findings confirm that root turnover is considerable in the grassland community and easily missed by destructive soil coring. Rates of turnover are, however, largely unaffected by elevated CO_2 so the increase in carbon fixation that accompanies CO_2 enrichment cannot be entirely accounted by increased fine root turnover.


(a)
(b)
(c)
(d)
(e)
1.0
0.5
0.0
Proportion alive
Jan
Feb
Mar
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Jul
Aug
Sep
Oct

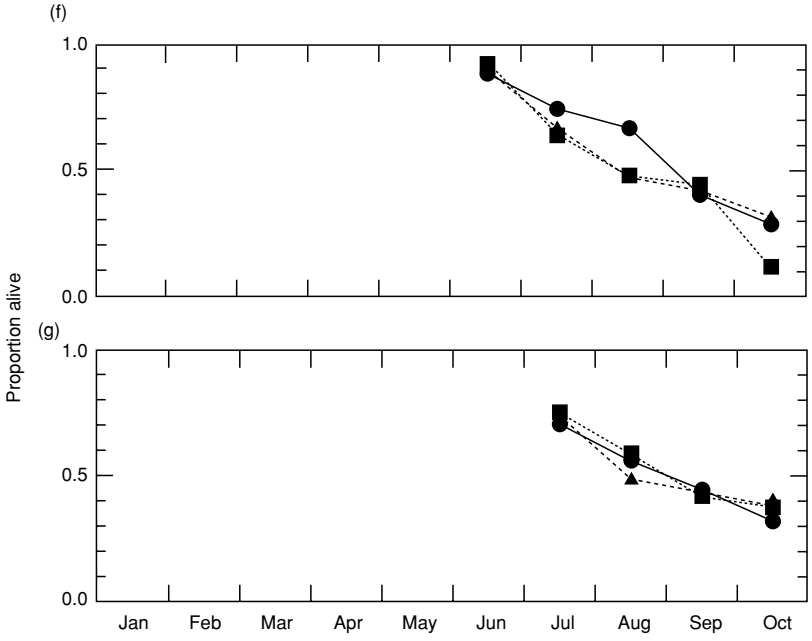

Fig. 5 Survivorship for roots produced in December (a), January (b), February (c), March (d), April (e), May (f), and June (g) for the X (●), LO (■) and HI (▲) plots.

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