# Rapid root closure after fire limits fine root responses to elevated atmospheric $CO_2$ in a scrub oak ecosystem in central Florida, USA

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## Abstract

Elevated atmospheric carbon dioxide ($CO_2$) often stimulates the growth of fine roots, yet there are few reports of responses of intact root systems to long-term $CO_2$ exposure. We investigated the effects of elevated $CO_2$ on fine root growth using open top chambers in a scrub oak ecosystem at Kennedy Space Center, Florida for more than 7 years. $CO_2$ enrichment began immediately after a controlled burn, which simulated the natural disturbance that occurs in this system every 10–15 years. We hypothesized that (1) root abundance would increase in both treatments as the system recovered from fire; (2) elevated $CO_2$ would stimulate root growth; and (3) elevated $CO_2$ would alter root distribution. Minirhizotron tubes were used to measure fine root length density ($mm\,cm^{-2}$) every three months. During the first 2 years after fire recovery, fine root abundance increased in all treatments and elevated $CO_2$ significantly enhanced root abundance, causing a maximum stimulation of 181% after 20 months. The $CO_2$ stimulation was initially more pronounced in the top 10 cm and 38–49 cm below the soil surface. However, these responses completely disappeared during the third year of experimental treatment: elevated $CO_2$ had no effect on root abundance or on the depth distribution of fine roots during years 3–7. The results suggest that, within a few years following fire, fine roots in this scrub oak ecosystem reach closure, defined here as a dynamic equilibrium between production and mortality. These results further suggest that elevated $CO_2$ hastens root closure but does not affect maximum root abundance. Limitation of fine root growth by belowground resources – particularly nutrients in this nutrient-poor soil – may explain the transient response to elevated $CO_2$.

*Keywords:* Carbon dioxide, fine roots, fire, minirhizotrons, root closure, root length.

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## Introduction

Global carbon models suggest that some portion of excess atmospheric carbon is being sequestered by terrestrial plants as a result of carbon dioxide ($CO_2$) fertilization (Beedlow et al., 2004). Generally elevated $CO_2$ increases both root and shoot growth in the short-term (Norby, 1994; Curtis & Wang, 1998; Rogers et al., 1999). However, only long-term studies can determine whether this response persists or dissipates owing to environmental limitations, such as nutrients or water.

In our long-term study in a scrub oak ecosystem in Florida, we observed initial increases in above- and belowground production in response to elevated atmospheric $CO_2$. Four years after enrichment began, elevated $CO_2$ resulted in increased aboveground biomass; the relative $CO_2$ effect was 44% in the first year followed

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by 55%, 66%, and 75% (Dijkstra *et al.*, 2002). During the third and fourth year of exposure to elevated $CO_2$, *Quercus myrtifolia* (myrtle oak), the dominant oak in this ecosystem, exhibited a 72% increase in photosynthesis (Ainsworth *et al.*, 2002). During the first 20 months after initiation of $CO_2$ treatment, minirhizotron measurements revealed increased fine root length, production and mortality under elevated $CO_2$ (Dilustro *et al.*, 2002). A pilot study conducted before the current project also indicated increased root length and a shift in fine root distribution under elevated $CO_2$ with a greater response deeper in the soil profile over a year and a half period (Day *et al.*, 1996).

The scrub oak ecosystem has a natural burn cycle of 10–15 years. A controlled burn was implemented on the study site before initiation of $CO_2$ treatments. This resulted in the loss of all aboveground vegetation and a die back of fine roots; thus, vegetation regrowth occurred as part of system recovery. The initial belowground response indicated a $CO_2$ fertilization effect on fine root regrowth and recovery under elevated $CO_2$ conditions. However, how long might this response be expected to persist? Do environmental limitations cause the response to dissipate or does the response persist even after the number and mass of roots in the soil equilibrate?

Long-term stimulation of fine root growth may be limited by nutrients (especially nitrogen), water, exploitable soil volume (space), or greater allocation of production aboveground. A prevalent hypothesis is that initial stimulation of plant growth under elevated $CO_2$ could cause immobilization of N in plant biomass and soil organic matter, progressively reducing N availability to plants leading to progressive N limitation (Tingey *et al.*, 2000; Beedlow *et al.*, 2004; Hungate *et al.*, 2004; Luo *et al.*, 2004). An alternate hypothesis could be that carbon dioxide fertilization leads to increased plant growth, greater nutrient demands, higher fine root production, more soil volume explored by roots, and, therefore, increased nutrient acquisition to support more growth (Finzi *et al.*, 2001). Water could also become limiting. Another possibility is that roots could reach closure in a limited resource volume, and the growth response could subsequently shift to greater biomass allocation aboveground.

The primary objective of this study was to follow the recovery process belowground in the experimental chambers and test for $CO_2$ effects over a 7-year period. We hypothesized that (1) root abundance would increase in both treatments as the system recovered from fire; (2) elevated $CO_2$ would stimulate root growth; and (3) elevated $CO_2$ would alter root distribution.

We emphasize that the results reported here are for fine root length (a surrogate for abundance). A $CO_2$ effect could be expressed in other components of stored carbon, such as large coarse roots. Also, even though fine root abundance may not indicate a $CO_2$ effect, greater fine root turnover could be occurring, resulting in greater carbon transport into the soil and masking a possible treatment effect.

## Methods

The study site is on Merritt Island, an inland area of the northern part of Kennedy Space Center (KSC), Florida ($28°38'$ N$80°42'$W). Merritt Island is a barrier island with topography ranging from sea level to about 3 m. Precipitation averages $131\,cm\,yr^{-1}$ with high year-to-year variability (Schmalzer & Hinkle, 1987). A dry season occurs from April to May and is optimal for the occurrence of wild fire. A rainy season occurs from May to October; the rest of the year is relatively dry (Mailander, 1990). Mean daily temperatures are $22.3\,°C$ for January and $33.3\,°C$ for July; mean daily minimum temperatures are $9.6\,°C$ for January and $21.9\,°C$ for August (Mailander, 1990). The soils are excessively drained Poala sand (Spodic Quartzpsamment) and moderately well drained Pomello sand (Arenic Haplahumod) (Schmalzer & Hinkle, 1987). Both soils found on the site are acidic and nutrient poor with a mean N content of 0.01% N (Hungate *et al.*, 1999) and a spodic horizon (Bh).

The experimental site is dominated mainly by *Quercus myrtifolia* Wasd. (myrtle oak) (76%), *Quercus geminata* Small (sand live oak) (15%), *Quercus chapmanii* Sargent (Chapman oak) (7%), *Serenoa repens* (Bartram) Small (saw palmetto) and *Lyonia ferruginea* (Walt.) Nutt. (stagger-bush). The scrub oak system was chosen because the dominant vegetation is woody, perennial, deciduous, and thus has a nutrient cycle representative of mature forests while still being short enough to study using open top chambers. Belowground biomass of this system is greater than aboveground biomass (Schmalzer & Hinkle, 1996).

The scrub community is fire adapted and maintained with natural fire cycles of 10–15 years (Schmalzer & Hinkle, 1987). The stand selected for our experiment had burned 10 years earlier. The area was subjected to a controlled burn in February 1996 before the chambers were put in place. The fire-adapted scrub oak species and saw palmetto all resprout from roots and rhizomes after fire. Previous burns in these ecosystems demonstrated faster initial regrowth for saw palmetto than for the scrub oak species and showed a return to preburn community dominance values at 7–11 year intervals (Schmalzer & Hinkle, 1992).

Open top chambers were used to maintain enriched atmospheric $CO_2$ ($C_a$) concentrations (Drake *et al.*, 1989). The treatments, initiated May 14, 1996, were maintained at ambient ($C_a = 350\,ppm$) and elevated ($C_a = 700\,ppm$) $CO_2$ levels 24 hour a day. Open top chambers are

considered best suited for the study of small stature vegetation such as scrub oak communities (Mooney & Koch, 1994). Both ambient and elevated chambers had air continuously circulating through blower systems. The open top chambers had the air circulated from the bottom of the cylinder and out the top. The chambers are octagonal with sides of 139.9 cm, a maximum diameter of 365.6 cm, and a height of 365 cm. The experimental design consists of 16 chambers (eight enriched and eight ambient) and eight chamberless reference plots ($N = 8$). Treatments were randomly assigned within blocks consisting of three plots with similar initial aboveground biomass values that were determined before the control burn. All vegetation that resprouted from the time of the controlled burn until full deployment of the chambers (approximately a 3-month period) was clipped to ground level at the onset of the study.

Two cellulose acetate butyrate minirhizotron tubes (5.7 cm diameter) were installed in each of the 16 plots (early March 1996), and one tube was installed into each of eight reference plots (early June 1996) for a total of 40 minirhizotrons. The tubes were installed at a 45° angle to the soil surface. The portion of the tubes extending above the soil interface was painted, taped and capped to prevent light and water from entering. Each tube was etched with 159 numbered frames (9 mm × 13 mm) along the side. Sampling depth was one meter. Images were taped on Hi8 (mm) videotape with a Bartz Technology® BTC-2 minirhizotron camera system (Bartz Technology Co., Santa Barbara, CA, USA) aligned by the etched frames. The root images were digitized using a video capture board and analyzed using ROOTS® version 1.05 and more recently version 2.2 (Michigan State University Remote Sensing Laboratory) to identify phenological state and measure fine root length and width. Roots as small as 0.001 mm diameter were measured and most of the largest roots were typically less than 5 mm diameter. However, roots as large as 13 mm diameter were occasionally observed.

A repeated measures ANOVA was used to test the effects of CO$_2$ enrichment and depth on fine (<5 mm) root length (root length density, RLD). The MIXED procedure was used in SAS (SAS Institute, 1990) with chamber as the random effect and CO$_2$ treatment as the fixed effect. The ANOVA tables calculated by PROC MIXED lack the separate error term due to the estimation of the covariance parameters via the maximum likelihood approach (Khattree & Naik, 1999). When the three way interactions were calculated to be strongly nonsignificant ($Pr > F = 1$), the three-way interaction was removed from the model to conserve degrees of freedom (Khattree & Naik, 1999). The three-way ANOVA revealed a significant treatment × date interaction; so one-way ANOVA's were used to test for treatment effects

on individual dates. The reference plots were analyzed with the ambient chambers to test for chamber effects (the treatment term in this analysis represented chamber effect). Relative CO$_2$ effect was calculated as

$$\frac{\text{elevated RLD} - \text{ambient RLD}}{\text{ambient RLD}} \times 100.$$

## Results

Fine root abundance increased rapidly during the first 2 years as the system recovered after the burn (effect of time, $P < 0.001$, Fig. 1). In all treatments, fine root abundance reached a plateau during the third year after fire, reaching maximum values of 25–30 mm cm$^{-2}$. Fine root abundance declined in the autumn of 2002, but then increased slightly throughout 2003 in all treatments. High rainfall in early summer of 2002 and low rainfall during the fall of 2002 (especially September and October, Fig. 2) could possibly be responsible for the June peak in root abundance followed by the sudden drop in the fall. Longer time intervals between measurements in the 1998–2002 data compared with the
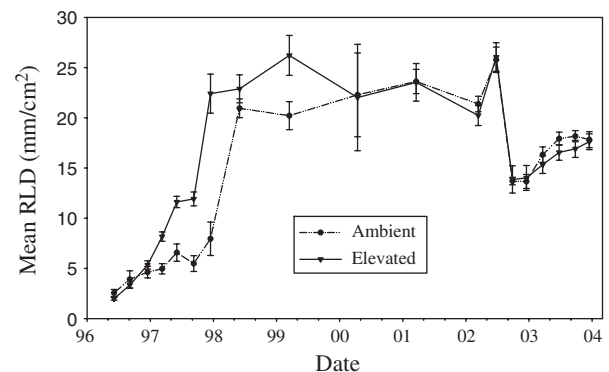


**Fig. 1** Fine root length expressed as root length density (mm cm$^2$) averaged across all frames digitized over the entire minirhizotron tube.
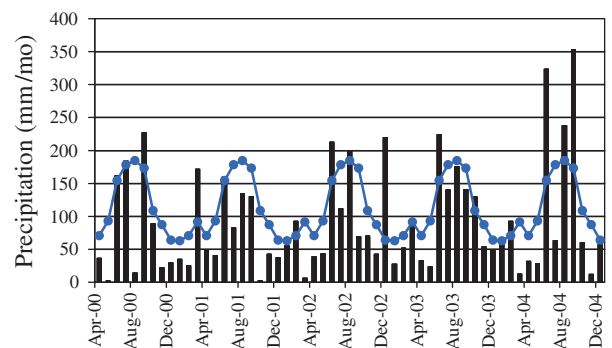


**Fig. 2** Monthly precipitation for the scrub oak site (bars) and long-term mean monthly precipitation from 1971 to 2000 (line graph).

2003 data make discerning correlations between environmental data and fine root abundance difficult.

The main effect of $CO_2$ was not significant in the 7-year data set, but there was a significant interaction between $CO_2$ and date, indicating that the effect of elevated $CO_2$ changed through time. Specifically, during the first year and a half of the study, elevated $CO_2$ substantially enhanced fine root abundance ($P < 0.01$ for the effect of $CO_2$ from March 1997 to December 1997, four sample dates). However, this effect diminished during years two and three and disappeared entirely after 4 years of experimental treatment, and the effect of $CO_2$ on fine root abundance has remained negligible since that time (Fig. 3). Overall, there was no significant chamber effect ($P < 0.288$).

For all dates, root length density decreased with soil depth ($P < 0.001$). The treatment × depth interaction was marginally significant ($P < 0.058$) in the main model, likely reflecting the proportionally greater effect of $CO_2$ in the top 12 cm of soil and at 38–49 cm depth during the early phase of the experiment (Fig. 4). In their analysis of this portion of the data set, Dilustro *et al.* (2002) observed no apparent proportional effect by depth, but they lumped the data into broader depth ranges. For our analysis we created more depth classes and teased out the apparent initial proportional response. This proportional effect quickly disappeared along with the main $CO_2$ effect. These results support what we found in an earlier pilot study on the same site (Day *et al.*, 1996) (Fig. 4). The pilot study also showed proportionally greater $CO_2$ effects in the top 12 cm of soil and at 38–49 cm within the same time frame of elevated $CO_2$ exposure, as well as an initial enhancement of overall fine root abundance. On the one hand, the consistency between the short-term responses is reassuring: results from global change field experiments can be repeatable. On the other hand, the disappearance
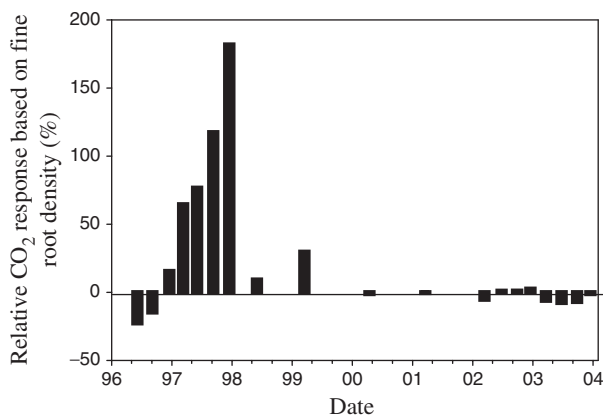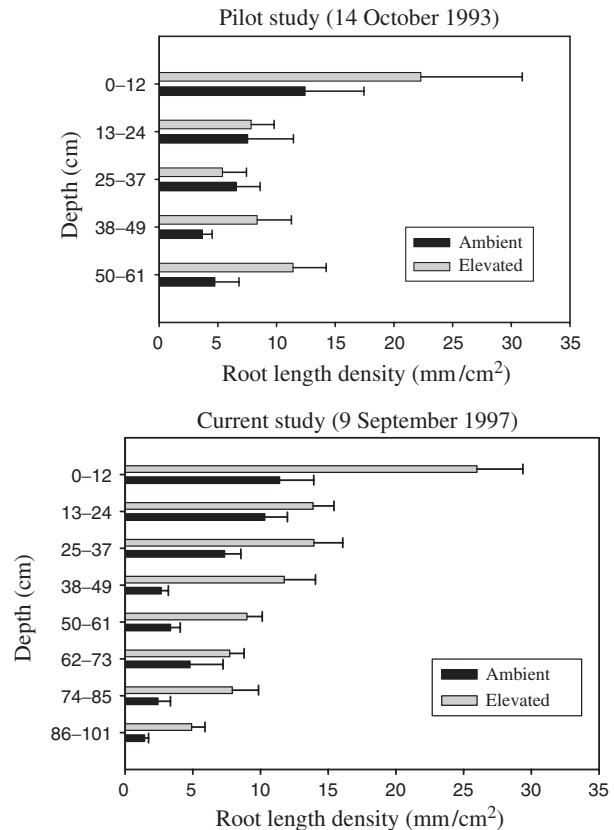


Fig. 4 Distribution of fine roots by depth about 1.5 years after initiation of treatments in the 1992–1993 pilot study and the current study. The minirhizotron tubes only extended to 61 cm depth in the pilot study.

of the $CO_2$ effect over time illustrates the serious challenges in extrapolating results from short-term experiments to predict longer-term responses to environmental forcing. Maintaining long-term field studies is clearly an essential component of global change research.

## Discussion

After rapidly increasing in abundance after fire for a 2-year period, fine roots in this ecosystem reached a plateau during the third year. Fine root abundance did not increase after this point, despite continued accumulation of aboveground biomass in all treatments (Dijkstra *et al.*, 2002; T.J. Sieler *et al.* unpublished data). This pattern indicates that fine root abundance reached a state of dynamic equilibrium, where production of new roots is matched by root mortality, such that total fine root abundance does not change. Our data suggest that this state of 'root closure' occurs well before canopy closure, as leaf area index continued to increase in the Florida scrub-oak system 5 years after fire (Hymus *et al.*,



Fig. 3 Relative carbon dioxide response based on fine root length density.

2002; B. G. Drake *et al.* unpublished data). In this nutrient-poor soil (Schmalzer & Hinkle, 1987, 1992, 1996; Johnson *et al.*, 2003), it is possible that nutrient availability declines rapidly after fire, and that fine roots deplete soil reserves within a few years. After this point, further investment in expanding the mass of fine roots may not pay off. The dominant oaks in this ecosystem resprout after fire, but maintain large belowground storage organs (Schmalzer & Hinkle, 1996; Langley *et al.*, 2002). The rapid equilibration of fine root abundance before canopy closure may indicate the importance of belowground storage of nutrient reserves that can be accessed after fine root closure to support further investment in aboveground tissues. Rapid development of fine roots could help replenish nutrient stores by taking up nutrients liberated immediately after fire.

McConnaughay & Bazzaz (1991) asked if physical space is a soil resource in a study of potted plants and suggested that individual roots in close proximity to each other may overlap zones of nutrient uptake resulting in competition. Numerous studies have indicated that root architecture and the size of root systems are related to soil resources in the space occupied and the spatial heterogeneity of those resources (Mou *et al.*, 1995; Mou *et al.*, 1997; Hutchings & John, 2003; Robinson *et al.*, 2003). De Kroon *et al.* (2003) suggested that competition is for space with resources secured from within that space. Hypothesizing that fine root density in a forest might reach a maximum value analogous to the aboveground canopy reaching a maximum leaf area index, Norby & Jackson (2000) questioned if a concept similar to 'canopy closure' can apply belowground. The idea that the number, mass and surface area of roots reaches a constant 'soil root capacity' under a given set of soil resource conditions has been around a long time (Coile, 1937; Stevenson, 1967; McGinty, 1976). Our data provide some support for such a concept.

Elevated CO$_2$ accelerates the rate of fine root recovery after fire by affording plants a greater supply of fixed carbon. Figure 1 shows that fine root biomass rapidly recovers within two growing seasons of fire. Recovery is about four months faster under elevated CO$_2$. Whatever limits root length density following recovery is likely the same under ambient and elevated CO$_2$, given the close correspondence between treatments following 1998.

Few studies have followed the response to elevated CO$_2$ in natural ecosystems over 8 years. Many published short-term observations (<3 years) match the initial response seen in our study in Florida. Two to 3 years after CO$_2$ enrichment began in the Duke FACE study of loblolly pine forest, minirhizotron observations showed 16% greater root length and 24% more roots per tube in elevated CO$_2$ conditions, though these effects were not statistically significant (Pritchard *et al.*, 2001a). In the third year of CO$_2$ treatment in California grassland, root biomass was 32% greater in the elevated treatment, but total root length was not affected (Higgins *et al.*, 2002). Carbon dioxide enriched plots in artificially constructed longleaf pine communities had 35% greater root length after 16 months and greater production and mortality, but only in the 10–30 cm depth range (Pritchard *et al.*, 2001b). During the first 3 years of CO$_2$ enrichment in a sweetgum forest, elevated CO$_2$ consistently increased net primary productivity by 21%, including production by fine roots (Norby *et al.*, 2002).

In our study in Florida, the treatment effect in fine roots dissipated over several years after the early CO$_2$ fertilization response. Farrar & Jones (2000) stressed the importance of distinguishing between a short-term response, which might be because of plants getting bigger, and a long-term response after plants begin to deplete soil resources (Lukac *et al.*, 2003). In the Italian *Populus* forest, the system was still expanding and at that stage it is not possible to equate to the reaction of a stable-state mature forest (Lukac *et al.*, 2003). Similarly in our Florida scrub oak system, the forest was recovering from the fire before the start of the study. During the rapid regrowth phase, elevated CO$_2$ accelerated regrowth, but the fine roots then seemed to reach closure at a 'carrying capacity' for the soil, possibly determined by nitrogen availability. The precipitous drop in the relative CO$_2$ effect in 1998 occurred at the point where growth was beginning to equilibrate between the two treatments.

Three findings suggest that reduced nitrogen availability may be responsible for the declining fine root responses to elevated CO$_2$ (McGuire *et al.*, 1995; Tingey *et al.*, 2000; Beedlow *et al.*, 2004; Luo *et al.*, 2004). First, Hungate *et al.* (1999) showed that elevated CO$_2$ decreased gross N mineralization and increased specific ammonium consumption (per unit microbial biomass) during the first year of the study (summer 1996 to summer 1997), a period when CO$_2$ enhanced photosynthesis and carbon allocation to roots (as our data illustrate). Second, elevated CO$_2$ also enhanced N immobilization by decomposing roots, suggesting increased N demand by soil microorganisms (Dilustro *et al.*, 2001). And third, by 2001, elevated CO$_2$ had enhanced nitrogen accumulation in the O horizon (Johnson *et al.*, 2003), coincident with a reduction in nitrogen in the labile fraction of underlying mineral soil (Hungate *et al.*, 2006). Together, these responses suggest that elevated CO$_2$ may have caused N availability to plants to decline, perhaps explaining the declining fine root response we observed. Elevated CO$_2$ has continued to stimulate aboveground growth in this ecosystem,

though the magnitude of that effect also appears to be declining (Dijkstra et al., 2002; Drake, 2004 and B. G. Drake, unpublished data). This response may also be driven by declining availability of N (Hungate et al., 2006), though it appears to be coupled with rainfall as well (Drake, 2004). We cannot yet ascribe with certainty a specific mechanism to the cause of the declining root growth response.

After 8 years of exposure to elevated $CO_2$, there was no significant effect of $CO_2$ on the depth distribution of fine roots. The apparent stimulation of fine root abundance near the soil surface and 38–49 cm below the surface that we observed initially was not statistically detectable after 8 years. We previously found that elevated $CO_2$ stimulated root length in this ecosystem during the first 1.5 years of experimental treatment, and that the response varied with depth with the greatest stimulation near the surface and at 38–49 cm depth (Day et al., 1996). A few other studies have also revealed a shift in vertical root distribution under elevated $CO_2$, with more roots at deeper depths (Pritchard et al., 2001b; Lukac et al., 2003). Rasse's model of nitrogen deposition and $CO_2$ effects on fine root dynamics simulated an increase in fine root biomass and predicted that the distribution of fine roots over the soil profile will be altered (Rasse, 2002). Yet, none of these studies have examined whether altered root distributions persist after chronic exposure to elevated $CO_2$. Our results indicate that short-term changes in root distribution may exaggerate changes seen in the long term.

Quantifying ecosystem-level root dynamics is difficult with minirhizotrons alone, considering they only measure fine roots (Pritchard et al., 2001a). Elevated $CO_2$ could be enhancing growth of large coarse roots, which our minirhizotron tubes cannot assess. Also, even though abundance or biomass may not indicate a long-term $CO_2$ effect, $CO_2$ could have altered fine root turnover. In some studies an increase in photosynthesis considerably larger than the combined increase in above and belowground biomass has been observed, possibly indicating increased root turnover (Higgins et al., 2002). We intend to further examine potential impacts on turnover and coarse roots. We also hope to burn the system again in accordance with its natural fire cycle and follow the $CO_2$ response in the second recovery cycle.

## Acknowledgements

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