

Controls of Canopy Activities on Roots and Soil Carbon Dynamics in a Young Ponderosa Pine Forest

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Summary

Our research at the Blodgett Forest Ameriflux site in California's Sierra Nevada addresses the issue of aboveground controls on root turnover and soil carbon sequestration in a mid-elevation, young ponderosa pine plantation with an understory of shrubs (*Arctostaphylos* sp. and *Ceanothus* sp.). This research includes canopy flux measurements using the eddy covariance method. Soil respiration was measured by both chamber and solid-state gradient measurement sensors. Root dynamics was evaluated using periodic measurements with minirhizotron videography. During the 2003 vegetation period, the leaf area index of ponderosa pine increased from ~3.0 to ~3.5, while the shrubs leaf area index increased from ~0.70 to ~1.2. The photosynthetic capacity of *Ceanothus* sp. and *Arctostaphylos* sp. was two times (winter) to five times (summer) higher than ponderosa pine per-unit leaf area. Both above- and sub-canopy daily flux integrals of CO₂ showed significant uptake of carbon from the atmosphere. The daily sub-canopy CO₂ uptake was 10% of the above canopy in spring and 50% in midsummer. During summer, around 60% of the outgoing energy flux was from the sub-canopy level. Soil respiration was driven by temperature and soil moisture: daily average respiration increased steadily from 1.44 $\mu\text{mol } \mu\text{m}^{-2} \text{ s}^{-1}$ in March to 5.20 $\mu\text{mol } \text{m}^{-2} \text{ s}^{-1}$ in August. Tree stems started to expand at the beginning of May, and shoots to elongate in mid-May. The photosynthetic capacity of the trees and shrubs started to increase at the end of May. The roots didn't exhibit substantial growth until mid-June, probably because the soil was too cold: the daily minimum temperature stayed below 5°C until mid-May. The new needle elongation followed root growth closely. The root dynamics in this plantation were decoupled from photosynthetic activity in the short term, but probably strongly linked with photosynthesis in the medium term via regulating root demography. Fine root dynamics showed a month-long growth pulse, with negligible prior or subsequent growth, which contradicts existing studies that show relatively uniform fine root growth patterns throughout the growing season. Soil respiration was strongly linked with root development: no significant increases of soil CO₂ efflux was detected during the most active period of root growth, despite the constantly rising average temperature, which may indicate the presence of a negative priming effect. Further analysis of our extensive datasets will focus on testing this hypothesis more thoroughly.

Keywords: carbon dynamics, ponderosa pine, soil respiration, root turnover

Objectives

1. Our first project objective is to better understand how the stand-scale fluxes of carbon, water vapor and energy of a mid-elevation semi-arid ponderosa pine plantation vary interannually

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in response to climate variability, and how these fluxes are impacted by management practices such as shrub removal and thinning.

2. The second objective is to study how root dynamics (initiation, growth, and death) exert control over the spatial and seasonal patterns of the CO₂ efflux, and to show that such control is most apparent when roots are active.
3. Our third objective is to address the issue of aboveground controls on root turnover and soil carbon sequestration by combining the ongoing canopy scale and soil chamber gas flux measurements at the Blodgett forest research site with measurements of root dynamics using a minirhizotron approach.

Approaches and Procedures

The three groups involved in the ongoing project were actively integrating their efforts to acquire a very comprehensive and unique dataset, including canopy scale flux measurements (Goldstein and Misson), soil CO₂ fluxes (Qi and Tang) and root demography (Cheng and Gershenson).

Canopy Scale Measurements

Canopy flux was measured using the eddy covariance method at two levels: above canopy at ~6m above the tree top from 1997 to now, and sub-canopy (1.3 m), at the transition between the lower branches of the trees and the top of the shrubs in 2003. The sub-canopy system was an addition to what was promised in the original proposal. Environmental parameters such as wind direction and speed, air temperature and humidity, net and photosynthetically active radiation (R_n and PAR, respectively), soil temperature, soil moisture, soil heat flux, rain, and atmospheric pressure also were monitored. Vertical profiles of wind speed, air temperature, relative humidity, and CO₂ have been measured since 1998.

Root Dynamics and Growth Phenology

Two plots (15 x15 m each) were marked out in the footprint area of the canopy flux measurements. In each plot, root dynamics including root density, growth rate, death rate, and diameter classes were measured by minirhizotron imaging. Nine minirhizotron tubes (1.5 m in length, 5 cm in inside diameter) were installed in each plot at a 45-degree angle in the spring and fall of 2002. Briefly, images of a narrow strip (18-mm wide) of the upper soil-tube interface were captured and digitized incrementally using an on-site digitizing system with an indexing handle (Bartz Technologies minirhizotron combined with a “Video Capture Essentials” s-video capture card and software from ImperX.). The image changes through time at each exact tube position have been recorded monthly starting in April of 2003. All digitized images were analyzed using RooTracker 2.0.3 (Duke U. National Phytotron). RooTracker is a recognized standard in the field; it allows manual digitizing of minirhizotron images, as well as calculation of diameter, surface area, and volume of the roots. We used this software to analyze the obtained images for root density, growth rate, death rate, and diameter classes.

Belowground production was measured by minirhizotron and will be calibrated by soil core analysis. When calibrated with root coring data, minirhizotron data can provide reliable measures of belowground net primary productivity (Cheng et al. 1990, Hendrick and Pregitzer 1993a). Quarterly standing crop of roots was assessed using a coring procedure. We took 15 cores (25

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cm in diameter, 30 cm in depth) per plot to estimate fine root biomass. This will allow for existing minirhizotron data to be calibrated with core data and belowground NPP to be estimated. Roots from cores will be separated into diameter classes (coarse roots: >2mm; large fine roots: <2mm and >0.5 mm; small fine roots: <0.5mm) before any further analysis.

Additionally to what was promised in the original proposal, stem growth was recorded on 13 trees every five days in 2003 by visual readout of manual band dendrometers. These constant band tension instruments are capable of reading 0.1 mm changes in circumference. Needle and shoot elongation was recorded as well on the same trees.

Soil Chamber Measurements

Soil CO₂ efflux was measured using soil chambers (Licor 6400) at 24 sampling points co-located with the minirhizotron plots, so that the spatial pattern of roots can be directly related to the spatial pattern of CO₂ efflux. The sampling points were distributed within the tower footprint and the measurements were comparable to those taken since 1998 (Xu and Qi 2001a and b). In 2003, soil respiration was sampled every month, except in winter when snow covered the ground. Soil temperature and moisture were measured at each sampling point. Soil respiration was also measured on a trenched plot (or root exclusion experiment), which allowed us to remove the influence of root autotrophic respiration on total soil respiration. Bole respiration was measured as well using the Licor 6400 and collars installed on stem surface.

Soil CO₂ Profile

In addition to what was promised in the original proposal, we installed solid-state CO₂ sensors (GMT222, Vaisala, Finland) to measure CO₂ profiles in the soil during the 2003 vegetation period (Tang et al. 2003). The sensor is a new silicon-based, non-dispersive infra-red (NDIR) device for the measurement of CO₂ based on the patented CARBOCAP® technique. It assesses CO₂ concentration by detecting the attenuate of single-beam dual-wavelength infra-red light across a fixed distance. The probe provided us with a new means of measuring gradient of soil CO₂ concentration and deducing continuous estimates of CO₂ efflux. We buried three sensors at depths of 2 cm, 8 cm and 16 cm in a trenched plot (root exclusion) and in an unmanipulated location. At each depth, soil temperature and moisture was recorded as well.

Soil Incubation

In addition to what was proposed in the original project, a controlled lab experiment is ongoing to quantify the control of soil moisture and temperature on soil respiration efflux, and on the turnover rate of labile soil carbon pools. Soil was sampled at Blodgett and at the Oak/Savanna site and has been incubated at three different soil moistures and three different temperatures over the past three months with weekly measurements of respiration.

Leaf Gas Exchange

Also in addition to what was promised in the original proposal, A/Ci and A/PAR response curves were measured in 2003 by chamber measurements (Licor 6400). Four to six trees and shrubs were measured every month. The status of the photosynthetic system (carboxylation efficiency and maximum rates of electron transport) was determined from the response curves of net

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photosynthesis versus leaf internal CO₂ concentration. The Farquhar photosynthesis model was fit according to the equations and parameters given in De Pury and Farquhar (1997). Quantum efficiency was determined by regression analysis of the light-limited portion of the light curve. Light saturated photosynthetic rates were determined from the light-saturated portion of the curve.

Results

Even during winter, the young ponderosa pine plantation at Blodgett acted mainly as a sink of carbon. Strong variations in winter carbon sequestration occurred due to changes in leaf area index and frequency of freezing temperatures. Interannual variations in springtime carbon flux occurred mainly due to differences in the timing of seasonally increasing temperatures. Drought is a regular feature of the California climate, making water availability the major controller of gas exchange in summer and fall. In late summer 2001, drought stress reduced ecosystem carbon uptake by 1/5, while the Bowen ratio increased by 1/3.

Thinning is a widespread procedure in plantation management carried out to reduce stand density, improve forest health, and optimize tree growth. In spring 2000, 2/3 of the trees were removed by mastication, the process of mechanically chewing up unwanted trees, which is becoming a widespread method for pre-commercial thinning in the United States. During and after thinning, the plantation remained a sink of carbon. Thinning at the Blodgett site reduced the leaf area index from ~3 to ~2 m² m⁻², and created branch and stem debris of 400-500 g m⁻². During summer 2000, mastication decreased ecosystem carbon uptake by 1/3. Ecosystem water use efficiency decreased by 1/5, and the Bowen ratio increased by 1/3. This indicates the increasing heat lost as sensible versus latent heat as the water flux decreased due to the reduction in leaf area index.

After thinning, leaf area index rapidly increased again. As a result, the uptake of carbon by the ecosystem increased by 1/3 in early summer 2001, in comparison to the pre-thinning value. By summer 2001, the Bowen ratio returned to its pre-thinning value, and the ecosystem water use efficiency increased by 1/3. Higher ecosystem water use efficiency was maintained in summer 2002 and 2003, indicating that the thinning led to better optimization of ecosystem water use for at least the following three years, increasing the ratio of carbon gained to water lost over the growing season.

Based on the field measurement of all samples of soil CO₂ efflux in non-trenched plots and a trenched plot, we averaged spatial samples of both the non-trenched plots and trenched plot, and calculated the daily mean values. CO₂ efflux in the non-trenched plots is from total soil respiration; CO₂ efflux in the trenched plot is from heterotrophic respiration; and the difference from above is autotrophic respiration.

Daily mean soil respiration peaked in May-June at about 3.8 μmol m⁻² s⁻¹, and then decreased to about 1.6 μmol m⁻² s⁻¹ in the winter. Soil heterotrophic respiration had a similar seasonal variation, peaking in the early summer at about 3.0 μmol m⁻² s⁻¹ and going down to 1.2 μmol m⁻² s⁻¹ in the winter. Autotrophic respiration was estimated as the difference between soil respiration and heterotrophic respiration. Autotrophic respiration had a different variation from both total soil respiration and heterotrophic respiration. In 2002, it peaked in June-July at 1.4 μmol m⁻² s⁻¹

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and decreased into the winter to $0.67 \mu\text{mol m}^{-2} \text{s}^{-1}$. The ratio of autotrophic respiration to total respiration varied from 0.11 to 0.40.

We explored the correlation between respiration and its influencing factors, such as root density per ground area, soil organic carbon content, and soil nitrogen content of each sample location. The correlation coefficient (R^2) between soil respiration and root density was 0.46, greater than the R^2 for respiration and nitrogen content (0.36), and respiration and carbon content (0.26).

During the 2003 vegetation period, the leaf area index of ponderosa pine increased from ~ 3.5 to ~ 5.0 , while the shrubs leaf area index increased from ~ 0.70 to ~ 1.2 . After the dormant season, the photosynthetic capacity of the three species started to increase in May (data not shown). V_{cmax}

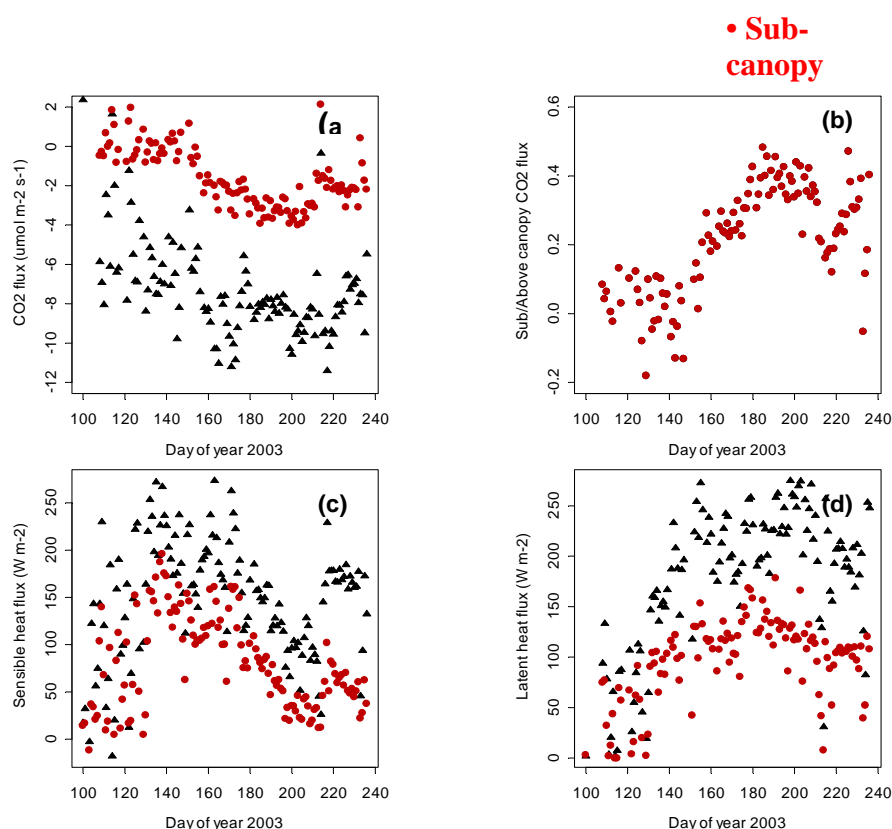


Figure 1. (a,b) Daily average CO_2 fluxes and (c,d) energy fluxes above- and sub-canopy in 2003.

of *Ceanothus* sp. and *Arctostaphylos* sp. was two times (winter) to five times (summer) higher than ponderosa pine per unit leaf area. Both above- and sub-canopy daily flux integrals of CO_2 showed significant uptake of carbon from the atmosphere (fig. 1a). The daily sub-canopy net CO_2 uptake was near zero in spring and up to 40% of the total canopy uptake in mid-summer (fig. 1b). During summer, around 60% of the outgoing energy flux was from the sub-canopy level (fig. 1cd).

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Tree stems started to expand at the beginning of May, and shoots to elongate in mid-May (*fig. 2c*). The photosynthetic capacity of the trees and shrubs started to increase at the end of May. The roots didn't exhibit substantial growth until mid-June, probably because the soil was too cold: the daily minimum temperature stayed below 5°C until mid-May (*fig. 4a, fig. 2ab*). The new needle elongation followed root growth closely (*fig. 2d*). Root growth stopped in July, with no substantial additions of new roots during the remainder of the season. Root death was observed primarily in the first month after emergence, if at all (*fig. 2ab*). The net number of roots was the highest during the period between June and July, after which we observed a slow but continuous decline. Minimal fine roots appear over the winter period, although additional observation will be necessary for confirmation. The root dynamics in this plantation were decoupled from photosynthetic activity in the short-term, but probably strongly linked with photosynthesis in the medium-term via regulating root demography.

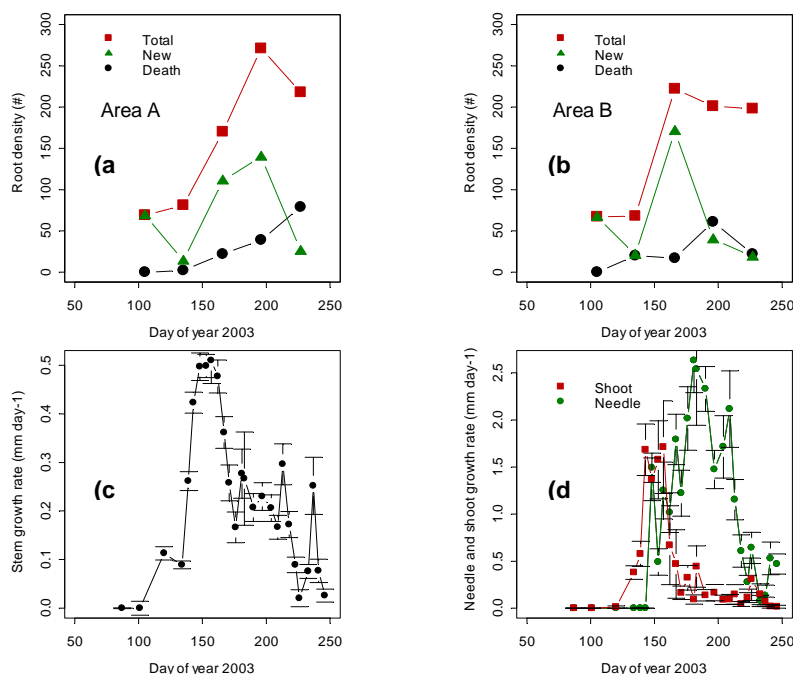


Figure 2. (a,b) Root density (#), (c) Stem growth, (d) Leaf and shoot elongation in 2003.

The CO₂ concentration gradient from 16-cm soil depth to the air at sub-canopy level drove the soil CO₂ efflux, both daily and seasonally (*fig. 3*). During the spring, soil respiration was primarily driven by temperature and soil moisture (*fig. 4ab*). Soil respiration stabilized during the early summer, even though new roots appeared rapidly during this period, suggesting presence of a negative rhizosphere priming effect (as defined by Kuzyakov and Cheng, in press). In July and August, soil respiration was coupled to root development: a significant increase of soil CO₂ efflux was detected while soil temperature was stable and soil moisture has dropped to 10%. (*fig. 4bc*). Further analysis of our datasets will focus on testing more thoroughly the link between photosynthesis, root growth, and soil respiration.

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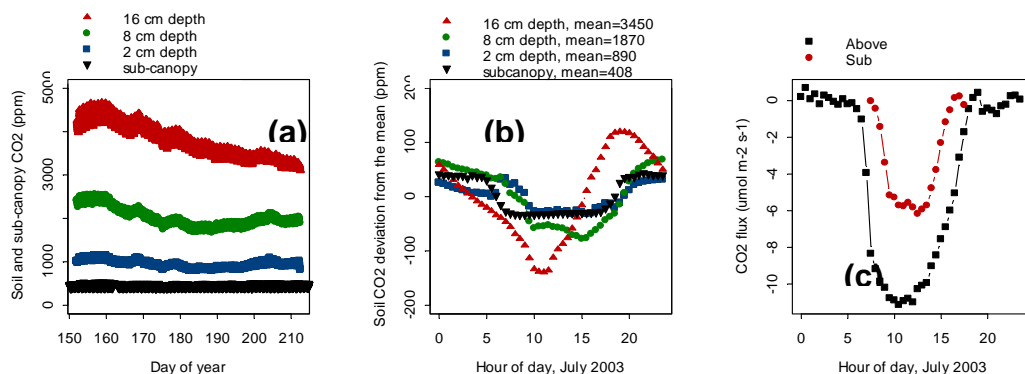


Figure 3. (a) Seasonal variation of soil and sub-canopy [CO₂], (b) Mean diurnal cycle of [CO₂], (c) Mean diurnal cycle of canopy CO₂ fluxes (#).

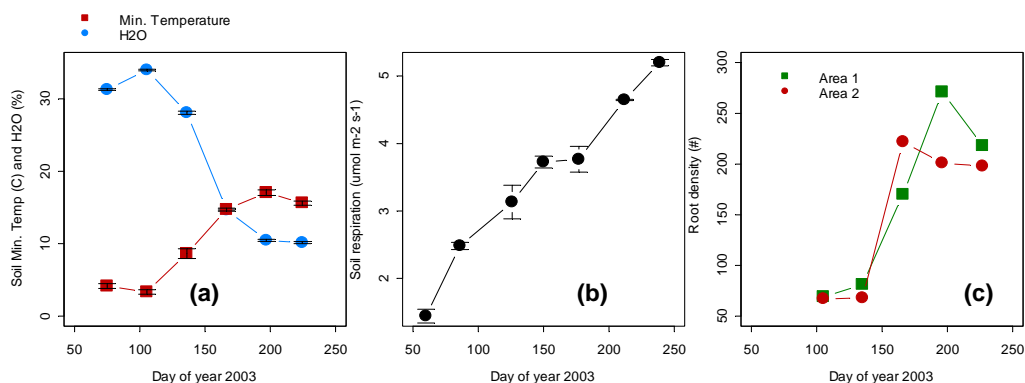


Figure 4. (a) Monthly average of daily minimum temperature and soil moisture, (b) Daily average of soil CO₂ flux by chamber measurements, (c) Root density (#).

Discussion

Several studies have demonstrated that root activities are tightly coupled with photosynthesis in annual plants (Bilbrough and Caldwell 1995, Craine et al. 1999, Kuzyakov and Cheng 2001) with very short time lags (minutes to hours). As shown in a study by Horwath et al. (1994), the time lags in the linkage between aboveground photosynthesis and root respiration can be as short as a few days for very young hybrid poplars. Beyond the immediate time scale, phenological changes of root dynamics and carbohydrate storage will be ultimately linked to photosynthesis. For northeastern hard woods, new root initiation, growth and mortality occur concomitantly throughout the growing season (Hendrick and Pregitzer 1992). Our results showed a very different pattern, with a sharply pronounced growth peak, which occurred immediately after daily minimum temperatures rose above 5°C, and ended a month and a half later. No significant root growth was recorded before June or after July.

Our study showed that root growth occurs in spring after aboveground growth has slowed down. Greater root mortality occurs at the end of the summer and not in the fall as illustrated in

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other studies (Kuhns et al. 1985, Hendrick and Pregitzer 1996, Wells and Eisenstat 2001, Pregitzer et al. 2000b). This seasonality tends to follow phenological leaf development. Carbon allocation to roots and leaf is probably delayed until carbon demand to construct new stem and branches in the spring is reduced. High root mortality in mid to late summer is most likely associated with loss of carbon fixation because of a decrease in photosynthetic capacity due to drought stress. Other studies showed that high root mortality in fall was associated a decrease in photosynthetic capacity due to leaf senescence (McClaugherty et al. 1982, Kurtz and Kimmins 1987, Hendrick and Pregitzer 1992, 1993, 1996, Joslin et al. 2001).

Associated with phenological variation are both changing environmental conditions (e.g., soil warming in the spring and summer) and alteration in resource availability (e.g., nutrients and water). In studies with highly determinate patterns of tree growth, such as sugar maple, fine root growth tends to be much more continuous and exhibits greater plasticity than shoot and leaf growth (Hendrick and Pregitzer 1992, 1993a, 1996, Pregitzer 2000b). In our case, we showed that initiation of root growth is highly controlled by soil temperature and that low soil moisture content influence root mortality in the mid to late summer. These findings could be of great importance in the future if, as predicted by some climate change models, the timing and the amount of precipitation will change, potentially closing a very narrow window available for production of new roots.

Our study showed that rhizosphere respiration is the most important belowground process responsible for carbon release. These results are in accordance with a recent study that shows rhizosphere respiration contributes 54% of the total soil CO₂ efflux (Högberg et al, 2001). Conceptually, the amount of live root biomass and the specific activity of live roots may largely control rhizosphere-associated CO₂ release. Our study showed that the seasonal and diurnal patterns of soil CO₂ efflux are mostly explained by soil temperature and moisture. However, these two environmental factors play a minor role in affecting the spatial pattern. Instead, we found that the fine-root biomass, microbial biomass and other soil organic matter are the most important factors controlling the spatial pattern of soil surface CO₂ efflux once the fine roots become active in early June. The mechanism by which the temporal pattern is controlled by temperature and moisture may lie in their effect on root activity.

These results contribute greatly to the goals of the mission of the Kearney Foundation: **(1)** to understand mechanisms and processes governing the storage and flow of carbon in soils, and **(2)** to assess the roles of soils in emissions and consumption of greenhouse carbon gases. However, a large amount of collected data still needs to be processed and analyzed from this project in order to draw definitive conclusions. This includes calculating root biomass dynamics from root demography and soil cores, calculating continuous soil respiration fluxes from the soil CO₂ concentration gradient, calculating photosynthetic parameters for the pine and shrubs, and calculating soil respiration fluxes of autotrophs and heterotrophs using the root exclusion experiment. We will be able to analyze a very comprehensive and unique dataset, including data on CO₂ fluxes from all the components of the ecosystem (tree, shrubs, soil, heterotrophic and autotrophic partitioning), high temporal resolution of canopy photosynthetic and ecosystem respiration rates, and carbon allocation (leaf, stem, shoot, root).

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