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Coupling of canopy gas exchange with root and rhizosphere respiration in a semi-arid forest

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Abstract. The strength of coupling between canopy gas exchange and root respiration was examined in ~15-yr-old ponderosa pine (*Pinus ponderosa* Doug. Ex Laws.) growing under seasonally drought stressed conditions. By regularly watering part of the root system to reduce tree water stress and measuring soil CO_2 efflux on the dry, distant side of the tree, we were able to determine the strength of the relationship between soil autotrophic (root and rhizosphere) respiration and changes in canopy carbon uptake and water loss by comparison with control trees (no watering). After ~40 days the soil CO_2 efflux rate, relative to pre-treatment conditions, was twice that of the controls. This difference, attributable to root and rhizosphere respiration, was strongly correlated with differences in transpiration rates between treatments ($r^2 = 0.73$, $p < 0.01$). By the end of the period, transpiration of the irrigated treatment was twice that of controls. Periodic measurements of photosynthesis under non-light limited conditions paralleled the patterns of transpiration and were systematically higher in the irrigated treatment. We observed no evidence for a greater sensitivity of soil autotrophic respiration to temperature compared to the response of heterotrophic respiration to temperature; the Q_{10} for total soil respiration was 1.6 ($p > 0.99$) for both treatments. At the ecosystem scale, daily soil CO_2 efflux rate was linearly related to gross primary productivity (GPP) as measured by eddy-covariance technique ($r^2 = 0.55$, $p < 0.01$), suggesting patterns of soil CO_2 release appear strongly correlated to recent carbon assimilation in this young pine stand. Collectively the observed relationships suggest some consideration should be given to the inclusion of canopy processes in future models of soil respiration.

Introduction

Soil CO_2 efflux is the second largest flux of carbon in terrestrial ecosystems, second only to gross primary production (GPP). On average ~80% of GPP is respired in forest ecosystems releasing CO_2 back to the atmosphere (Janssens et al. 2001). Soil CO_2 efflux, widely referred to as soil respiration, accounts for greater than two-thirds of this respiratory flux (Law et al. 1999; Janssens et al. 2001; Xu et al. 2001), yet our understanding of the factors that control soil respiration is notably weaker compared to our understanding of GPP.

With current interest in determining the role of forest ecosystems in the terrestrial carbon cycle and how their ability to sequester carbon may change in response to climate change, it is becoming increasingly important to be able to

model respiratory fluxes on both seasonal and annual time scales. Currently most models of soil respiration are empirical and rely on correlations with temperature and water availability and while this approach may be adequate for making short-term predictions at a particular site or filling gaps between periodic measurements, the lack of a mechanistic foundation prevents robust extrapolation to other sites or environmental conditions.

Soil CO_2 efflux originates from both root (autotrophic) and microbial (heterotrophic) activity. Estimates of the contribution of root respiration to total soil CO_2 efflux have been reported to range from 10 to 90% (Hanson et al. 2000). Much of this variability may reflect problems with measurement techniques that often disturb the soil and roots (Hogberg et al. 2001). The carbon substrate for both autotrophic and heterotrophic respiration is plant based, however the timing between carbon fixation and its oxidation by living roots or decomposition in the bulk soil are distinct. If microbial activity constitutes a significant fraction of soil respiration, there may be large quantities of detrital material from root turnover and litter decomposition, such that current photosynthate plays only a minor role in determining current soil respiration. In this case there would be a large time lag between the fixation of a molecule of CO_2 and its release back to the atmosphere. However, if root respiration comprises a significant fraction of soil respiration then current rates of photosynthesis may be tightly coupled to current rates of soil respiration.

Few studies have examined these issues in forest ecosystems, yet to develop better models of soil respiration, information is required about the degree of coupling between above and below ground processes. Over large spatial scales, Reichstein et al. (2003) found the inclusion of leaf area index together with soil moisture and temperature improved predictions of soil respiration for forest and shrubland sites. They concluded that soil respiration was more correlated with factors related to site productivity, such as leaf area index, than estimates of carbon pools such as litter or soil carbon. While this approach remains empirical the inclusion of some measure of above ground productivity illustrates the importance of understanding the contribution of autotrophic respiration to total soil CO_2 efflux. More recently Campbell et al. (in press) found that across a strong climatic gradient, annual soil respiration was correlated with fine root mass, suggesting that root respiration plays a more significant role than decomposition in determining differences in soil respiration in the temperate evergreen forests.

Studies on annual crop plants or seedlings have shown that there are tight linkages between photosynthesis and carbohydrate supply to roots. Craine et al. (1999) demonstrated in a field experiment with grass that shading or clipping the plant canopy caused substantial reductions in soil and root respiration within two days. Whether such coupling between carbon fixation and soil respiration occurs in much larger and long-lived tree species is however less well studied. It is possible that storage of carbohydrates by tree species may result is less tight coupling. A novel study by Hogberg et al. (2001) that used tree girdling to stop phloem transport to the root system in $\sim$50-yr-old pine

trees found that soil respiration was reduced by almost 40% within 4 days compared to control plots, and that root respiration accounted for 65% of total soil CO_2 efflux (Bhupinderpal-Singh et al. 2003). Using isotopic techniques Ekblad and Hogberg (2001) and Bowling et al. (2002) concluded it took only several days for photosynthate to become available for root respiration. In studies on ponderosa pine we observed that seasonal patterns of soil respiration were correlated with seasonal patterns of tree transpiration (Irvine and Law 2002; Irvine et al. 2004). While this does not prove that current levels of GPP were controlling current rates of soil respiration it provided impetus for this study in which we attempt to demonstrate, using a novel approach, that patterns of canopy gas exchange are closely related to patterns soil autotrophic respiration.

In this study, we consider the term root respiration to include any CO_2 release that depends directly on labile carbon compounds leaked from roots, and thus technically includes respiration from roots and associated rhizosphere organisms. Heterotrophic respiration is considered to originate from other micro-organisms including fungi in the bulk soil that do not depend directly on compounds from the roots. To manipulate rates of root respiration independently of heterotrophic respiration, we make use of the response of young trees to seasonal soil water deficit that may be temporally relieved by irrigating part of the root system without disturbing soil heterotrophic respiration outside the irrigated zone. Because all parts of the tree are hydraulically connected, adding water in this manner will improve the water status of the trees including the root system in areas distant to the point of irrigation. By comparison with control trees, we were able to determine the relationship of root respiration to changes in canopy gas exchange.

Methods

Study site and experimental protocol

The site is located on the eastside of the Cascade Mountains, near Sisters, Oregon, (latitude 44°26′ N, longitude 121°34′ W) and regenerated naturally following logging in 1978. The stand had a density of ~1200 trees ha^{-1} and includes an understory of bitterbrush (*Purshia tridentata* (Pursh) D.C.) and manzanita (*Arctostaphylos patula* Greene) with a stand leaf area index of 1.1. The soils are freely draining sandy loams, classified as ultic haploxeralfs. Precipitation varies between approximately 300 and 600 mm yr^{-1}, the majority falling between November and April as a combination of rain and snowfall. The site is part of the AmeriFlux network of flux sites. Further site details and meteorological conditions were reported in Anthoni et al. (2002) and Law et al. (2001). Six trees ~15-yr-old and ranging in height between 1.9 and 3.0 m were selected and three assigned to the irrigated and three to the control treatment. The trees chosen had minimal competition with understory shrubs. The drip-

line of the tree canopies extended to 0.75 m from the tree boles. Between mid-June and mid-August 2003, continuous measurements of tree transpiration were made together with approximately weekly measurements of predawn foliage water potential, soil water content, soil CO_2 efflux and leaf photosynthesis. These measurements were typically made between dawn and the early afternoon. Directly following the measurements ~25 l (between mid-June and mid-July) or ~50 l (between mid-July and mid-August) of water was added to one side of each of the irrigated trees (Figure 1) over a surface area of ~0.6 m^{-2} . The first watering took place on the 17th June. Lateral surface flow was prevented by a 10 cm high metal strip formed into a ring and inserted ~2 cm into the soil. The highly sandy nature of the soil allowed the water to infiltrate within several minutes. Excavations below the irrigated zone in a preliminary experiment showed water did not move laterally more than a few centimeters from the area encompassed by the metal strip. Periodic soil moisture measurements on the dry side of the irrigated trees were made for further verification. At the start of the experimental treatment both stem radial increment and current needle expansion were ongoing and had not reached their seasonal maximum (based on previous years unpublished data). All data analysis was performed using SPLUS 6.1 (Insightful Corp, Seattle, WA). Comparisons between measured variables at specific points in time were computed using Student's *t*-tests.

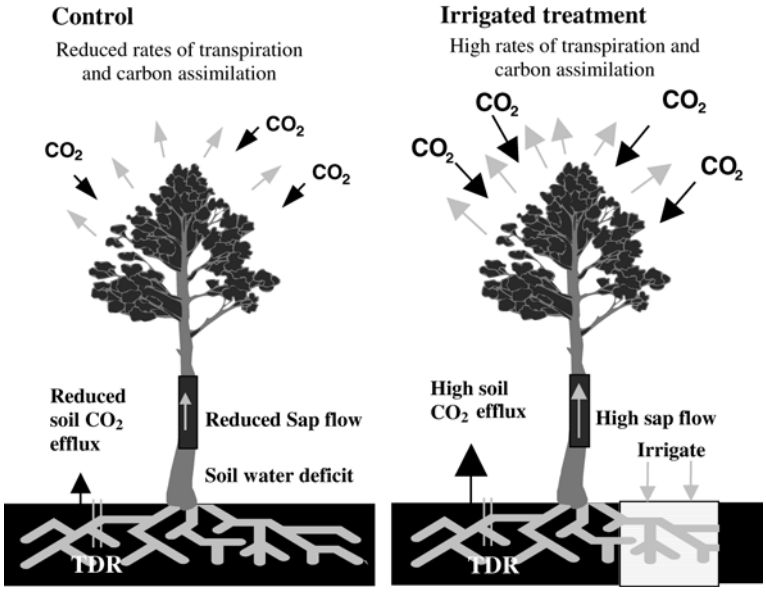

Figure 1. Experimental design with expected responses. TDR refers to soil water content measurements made using time-domain-reflectometry.

Tree transpiration

Sap flux was measured on the stems of all six trees below the first live branch using the heat dissipation technique as described by Irvine et al. (2004). Briefly, 20 mm long probes were inserted into the xylem and the temperature differential between the constantly heated upstream probe and an unheated reference probe were recorded every minute, averaged and stored every 10 min. Data was subsequently converted to sap flux densities using the equations developed by Granier (1987). In this study we were interested in the patterns of transpiration as influenced by the experimental treatment, rather than the absolute quantity of water transpired. Therefore daily average sap flux density was calculated for each tree and expressed relative to the value on the day of initiation of the irrigation treatment. Absolute tree transpiration from this stand during June was $\sim$1.0 mm d^{-1} (Irvine et al. 2004).

Soil CO_2 efflux

On one side of each tree soil CO_2 efflux measurements were made at three locations $\sim$50 cm from the stem using a Li-6400 with Li-6400-9 soil chamber (LI-COR inc, Lincoln, NE, USA). Soil temperature at 8 cm depth was recorded simultaneously. Measurements were made at all 18 locations using PVC collars that were approximately 5 cm tall and 10.7 cm in diameter. These were pushed into the soil leaving 2.5 cm protruding above the soil surface. The soil collars remained in place throughout the experiment. On the irrigated treatment the collars were placed on the distant side of the tree to the irrigated area. Soil CO_2 efflux is in general highly spatially variable but repeated measurements at a single location provides valuable information about treatment effects. Soil CO_2 efflux from each collar was expressed relative to the value on the day of initiation of the irrigation treatment, where the absolute values on the first day averaged 4.2 μmol m^{-2} s^{-1} (standard deviation = 2.7 μmol m^{-2} s^{-1}). Values were averaged across the three collars per tree.

Photosynthesis

Rates of photosynthesis were measured on two shoots per tree on fully expanded needles from the previous year. Measurements were made using a Li-6400 with Li-6400-02B LED light source set at 1200 μmol m^{-2} s^{-1}, a level that had previously been shown to be saturating in ponderosa pine. Measurements were made repeatedly on the same shoots throughout the experiment. Values were averaged by tree.

Soil water availability

To determine tree water availability, predawn needle water potentials were determined on two previous-year needles per tree on each measurement occasion. Values were averaged by tree. Direct measurements of soil water content across the top 30 cm depth of soil were made using time-domain-reflectometry (TDR) probes installed vertically close to the soil respiration collars by each tree. Measurements were made using a Tektronix cable-testing oscilloscope (1502B, Tektronix Corp, Beaverton, OR) in conjunction with a CR10X data logger and SMD1502 interface (Campbell Scientific).

Results and discussion

Between mid-June and mid-August, the period of the experimental treatment, 7 mm of rain was recorded. This small quantity was not unusual for summer conditions at this site and we observed a steady decline of soil water content in the control treatment (Figure 2, panel a). Before the first watering, soil water content measurements in the irrigated treatment were by chance slightly drier than the control treatment (the TDR probes may have sensed a greater proportion of stones for example), resulting in an offset in soil water content between treatments.

The approach of adding water to only one side of the tree in the irrigated treatment, so as not to stimulate heterotrophic respiration on the other side of the tree, was successful, as soil water content of the irrigated treatment paralleled that of the control treatment (Figure 2, panel a). Consequently any observed differences in soil CO_2 efflux between the two treatments can be attributed to differences in root (by our definition including rhizosphere) respiration as influenced by tree water status.

We detected no significant influence of irrigation on any of the variables measured during the first 9 days following the initial addition of water, suggesting water was not limiting in either treatment during this period. However, by day 16, predawn foliage water potentials ($p < 0.01$) and soil CO_2 efflux ($p < 0.07$) started to differ notably between the treatments (Figure 2, panels b and e respectively). From this point until ~day 40 large differences in soil CO_2 efflux and tree transpiration (Figure 2, panel c) developed between treatments, with the difference in transpiration strongly correlated with the difference in soil CO_2 efflux Figure 2, panel f). The relationship was linear (Δ soil CO_2 efflux = $0.08 + 0.80 \cdot \Delta$ transpiration, $r^2 = 0.76$, $p < 0.01$), the intercept was insignificant ($p < 0.01$). This relationship predicts that during the period maximum differences in soil efflux were observed (36–42 days after the start of irrigation) when transpiration in the irrigated treatment was on average 2.04 times that of the control, soil CO_2 efflux on the dry side of the irrigated trees was on average 2.11 times that of the controls.

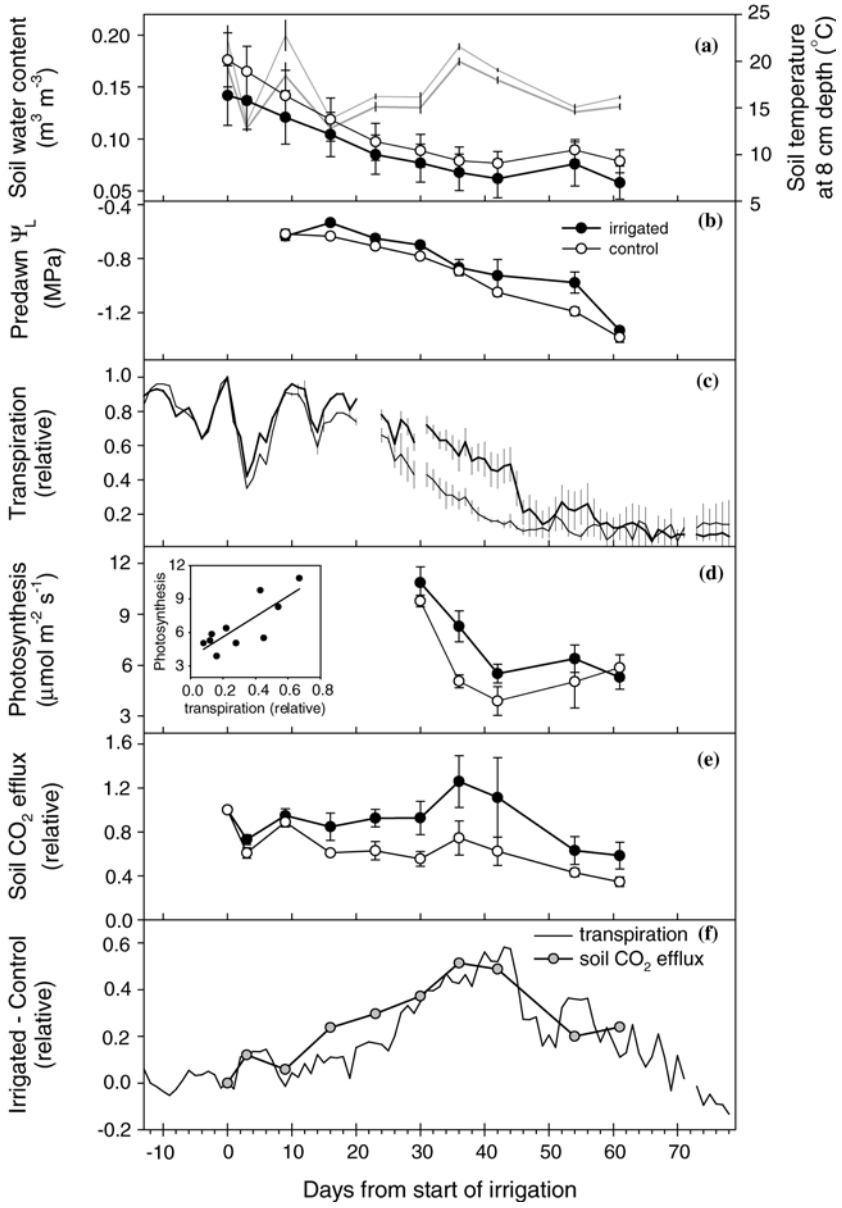

Figure 2. Canopy gas exchange and soil respiration response to the irrigation treatment (heavy lines, closed symbols) in comparison with controls (fine lines, open symbols). In the irrigated treatment both soil water content and soil CO_2 efflux were measured on the dry side of the trees. Soil temperature (panel a) is shown with gray lines. Transpiration and soil CO_2 efflux data are expressed relative to values on day zero (June 17th 2003). The difference in soil CO_2 efflux between treatments can be attributed to root respiration (panel f). Bars indicate ±1 SE (only after day nine for transpiration), three days missing transpiration data was filled by linear interpolation (panel f). The relationship between transpiration and photosynthesis (data from panels c and d respectively) is shown inset in panel d.

Measurements of photosynthesis were systematically higher in the irrigated treatment with the most significant difference between treatments ($p < 0.02$) corresponding with the largest difference in soil CO_2 efflux on day 36. Instantaneous photosynthesis was linearly related to daily transpiration ($r^2 = 0.65$, $p < 0.01$, Figure 2, panel d inset).

To remove the variability in soil CO_2 efflux due to changes in soil temperature across the experimental period, we expressed the relative soil CO_2 efflux to a common temperature using the exponential relationship between soil temperature at 8 cm depth and measured soil CO_2 efflux for the period the irrigation treatment was successful in reducing drought stress (Figure 2, days 0–42). We observed no significant difference in the temperature response of both treatments $Q_{10} = 1.6$ ($p > 0.99$), indicating that autotrophic and heterotropic respiration showed similar temperature sensitivity. It has been reported that soil autotrophic respiration exhibits a stronger temperature response than heterotrophic respiration (Boone et al. 1998). The lack of a difference in the response of soil respiration to soil temperature between treatments in this study would not support this contention. This result is in agreement with the findings of Baath and Wallender (2003) made on pine seedlings and the observations by Bhupinderpal-Singh et al. (2003) on girdled plots of Scots pine; both studies found no evidence of a greater sensitivity of root respiration to temperature compared to the response of soil heterotrophic respiration to temperature.

In the control treatment, the temperature normalized soil CO_2 efflux declined steadily after day 16 to less than half the initial value by day 61 Figure 3). In the irrigated treatment the temperature normalized soil CO_2 efflux increased after day 16 by ~30% and remained at these levels for ~30 days before declining to below the initial rates. This decline was correlated with transpiration in the irrigated treatment falling to the same levels as the controls

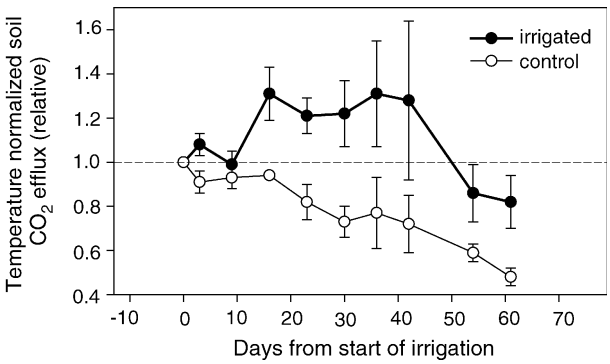

Figure 3. Soil CO_2 efflux normalized to a constant soil temperature, expressed relative to values on day zero. Bars indicate ±1 SE.

(Figure 2, panel c). The irrigation treatment only partially and temporally reduced tree water stress in this experiment and ultimately no difference in tree water status was observed on day 61. In split-root experiments in the laboratory, even though part of a root system is well watered, it is not uncommon to observe drought stress-related changes in canopy processes. We suspect similar mechanisms prevented long-term amelioration of water stress in this study. The temporary extent to which water stress was reduced, however, resulted in significant changes in canopy gas exchange and root respiration distant to the irrigated zone. The decline in temperature normalized soil CO_2 efflux in the control treatment was likely due to a combination of a decline in both autotrophic and heterotrophic respiration as drought stress developed. The increase in temperature normalized soil CO_2 efflux on the dry side of the irrigated trees was most likely due to root respiration, since the bulk soil progressively dried across the period, which results in strong declines in heterotrophic respiration at this site (Kelliher et al. 2004). Fine root growth peaks during June at this site (C. Andersen, pers. comm.) and we might expect that these roots be maintained longer in the dry soil of irrigated treatment due to internal hydraulic redistribution. Conversely we might expect fine root mortality to occur earlier in the control trees due to the more rapid onset of drought stress.

It has been shown that root conductivity and hence root function declines during the summer period at this site (Domec et al. 2004); hence it could be argued that the improved water status of roots in the dry soil of the irrigated treatment as a result of hydraulic redistribution could have led to the observed increase in respiration without any additional availability of photosynthates due to the higher stomatal conductance. We cannot exclude this possibility, however, the gradual increase in the difference in autotrophic respiration between treatments was correlated with a gradual increase in the difference in transpiration between treatments when the plant water status (as determined from predawn foliage water potentials) showed only small and rather static differences between treatments. We suggest that if the changes in autotrophic respiration over time were solely in response to improved root water status, then autotrophic respiration would not have increased as much as we observed. A direct response of autotrophic respiration to root water status independent of photo-assimilates would also be dependent on the availability of non-structural carbohydrates as a substrate for respiration. Hoberg et al. (2001) calculated that during a large-scale tree girdling study, root starch could account for 10–20% of the respiratory efflux during the first month after stopping the flow of photosynthates to the roots, with a decline in starch reserves beyond this period. In the absence of non-structural carbohydrate data for this study, if we were to assume that proportionally similar starch reserves were available in roots at our site, the direct response of autotrophic respiration to improved water status would not have accounted for the large increase in autotrophic respiration that was observed.

The technique adopted in this experiment does not provide a quantitative estimate of the contribution from root respiration to soil CO_2 efflux, but rather

examines in a non-intrusive manner the degree of correlation between canopy gas exchange and root respiration. At this young ponderosa pine stand Law et al. (2001) estimated that roots contribute ~50% of total soil CO_2 efflux in summer, using measurements of total soil CO_2 efflux and respiration rate of the excised roots, substantial enough to cause the observed increase in respiration in response to irrigation treatment. This study demonstrates a strong correlation between treatment differences in transpiration, photosynthesis, and soil respiration (which can be considered the difference in autotrophic respiration).

Such results add to the growing body of literature that demonstrates strong correlations between photosynthesis and root or total soil respiration. It has been demonstrated in laboratory studies on ponderosa pine seedlings that diel patterns of respiration from unsuberized roots can be manipulated by changing the light regime and hence carbohydrate supply (Lipp and Andersen 2003). In an innovative study on oak saplings pulsed delivery of carbohydrates to roots were highly correlated with soil respiration (Cardon et al. 2002).

Field studies in forest ecosystems on the controls of soil respiration by recent photo-assimilates are limited. To assess whether a strong correlation existed between photosynthesis at the forest scale and total soil CO_2 efflux, we examined GPP data measured by eddy-covariance and soil CO_2 efflux measured with an automated soil chamber system (Figure 4). Over a 3-year period we found that daily GPP was linearly correlated with daily soil respiration during the growing season. This relationship suggests that a significant fraction of soil respiration could be simply modeled as a fraction of carbon uptake during the growing season at this site. Whether such relationships hold across a

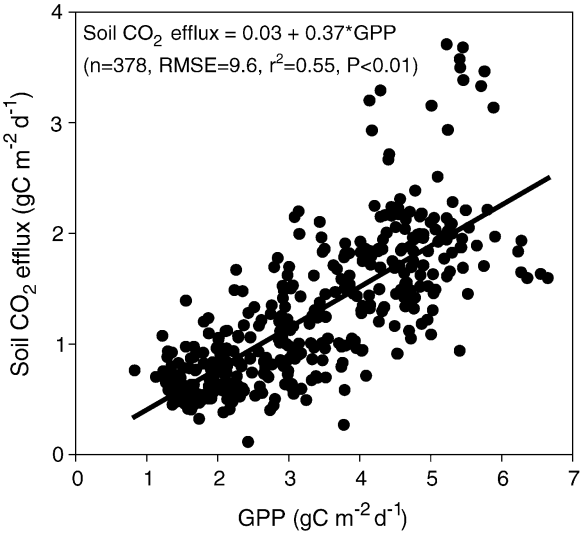

Figure 4. Correlation between soil respiration measured with an automated soil chamber system and gross primary productivity determined from eddy-covariance measurements across three growing seasons (2000–2002).

wider range of stand ages on less seasonal drought stressed sites remains to be demonstrated.

Currently, field techniques to separate soil autotrophic and heterotrophic respiration in a routine non-destructive manner are lacking, but much can be gained by examining such relationships. In addition, if new techniques to measure rates of phloem export can be developed they would also garner valuable information. Such measurements could be combined with high temporal resolution assessments of root growth and turnover and detailed evaluations of the seasonal use of stored carbohydrates. A combination of manipulative studies involving phloem blocking, trenching to exclude roots and schemes to change patterns of carbon allocation or rates of carbon assimilation may prove valuable in addition to routine measurements of soil CO_2 efflux. As more studies report on the strength of linkages between above and below ground processes, we will find ourselves in a better position to develop more mechanistic models of soil respiration and generate more robust estimates of soil CO_2 efflux.

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