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Carbon Flow Through Root and Microbial Respiration in Vineyards and Adjacent Oak Woodland Grassland Communities

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Summary

Extensive areas of coastal California have undergone conversion from oak woodlands or oak woodland-grassland to vineyards (Merenlender et al. 2000). Orchards or other cropping systems often preceded conversion to vineyards. Although grapevines are perennial taxa, they are more diminutive than trees, and vineyard floors are generally managed under some form of tillage. Thus, the carbon cycle has undoubtedly undergone substantial alterations as a consequence of these changes. In comparison to conversion of forest or prairie ecosystems in the Midwest, little is known about how conversion from natural to perennial agricultural ecosystems influences the carbon cycle in California's Mediterranean climates.

The primary aim of this investigation was to document changes that have occurred in carbon flow following conversion of oak woodland–grasslands to vineyard systems. Nearly all carbon that cycles through soils does so through the activity of microbial communities, while root deposition and root respiration represent substantial input and loss. For this reason, we worked to understand carbon flow through these two pathways. Our research findings during the course of this investigation provided invaluable information on differences in carbon flow in oak-woodlands versus adjacent vineyards growing on the same soil.

The highlights of this research indicate that:

- A loss of carbon in the first 30 centimeters of soil equivalent to approximately 33 tons per hectare has occurred over time. Such loss of carbon could have a substantial long-term impact on the sustainability of these soils.
- Carbon loss in the form of soil CO_2 respiration has declined to a point where these soils may actually represent net sinks for atmospheric CO_2, depending on the depth to which grapevine roots are able to grow as well as the longevity and quantity of carbon stored in deep roots.
- Cultivation of these soils apparently altered their effective diffusion coefficients. This may have accounted for diminished net rates of CO_2 efflux and points to a need to examine subsurface hydrologic carbon flows.

Objectives

The key objective of this project was to document historical changes that have occurred as a result of conversion of oak woodland-grassland to vineyards in the Oakville Region of the Napa Valley. Two specific objectives were proposed and addressed. The first objective involved the documentation of the magnitude of seasonal CO_2 fluxes from both an oak woodland-grassland

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and a research vineyard in close proximity. The second objective addresses the separation of such fluxes into root and microbial respiratory components. A parallel project examines root population dynamics (turnover) to a depth of 1.4 meters as viewed through clear plastic minirhizotron observation tubes using digital imaging with fiber optics.

Approach and Procedures

To determine the annual soil CO_2 emission budgets for undisturbed oak woodland-grasslands and adjacent lands converted to vineyards, CO_2 fluxes were measured every two weeks using a Licor 6400 with a 6400-09 soil chamber attachment (LI-COR, Lincoln, NE). Measurements were taken bi-weekly at six oak woodland-grassland sites composed mainly of *Quercus lobata*, and six adjacent vineyard sites. All sites in this study were located on the same soil type, a Bale (variant) gravelly loam (Fine-loamy, mixed, superactive, thermic Cumulic Ultic Haploxeroll). To establish the isotopic signature of the carbon pools being utilized at a range of soil depths in the field and determine the concentration of CO_2 along a soil profile, soil gas was also sampled bi-weekly from an array of permanently established stainless steel soil gas sampling tubes (Piñol et al. 1995) at six depths, starting at 15 cm down from the surface to 105 cm. Intact cores of soil (8 cm diameter x 6 cm depth) were removed from areas adjacent to the efflux measurement sites to directly measure the diffusion coefficients (Ralston 2002). These data were used to verify field observations of net efflux measurements as well as the soil profile [CO_2] data.

For the second objective, separating rhizosphere from litter and soil organic matter respiration, soil to a depth of 20 cm was collected from two oak and four vineyard sites (two row sites and two berm sites) and sieved (2 mm mesh) and to isolate the fine fraction. All roots were removed prior to the initiation of the soil incubation. Although all litter was removed from the soil surface, the O horizon graded into the A horizon, so it is possible that the oak soils may have increased organic matter due to incorporation of the O horizon. Vineyard berms have a different management than do vineyard rows. Berms are sprayed with herbicides to prevent all vegetative growth and are not tilled. Rows are often grown with a cover crop and are tilled several times annually. All soils were brought to the same gravimetric moisture content. These soils were monitored for C loss, $^{13}CO_2$ emission, and NO_3^- mobilization during a more than 250 days *in vitro* laboratory incubation (Hart et al. 1994). Soil respiration and changes in the isotopic ^{13}C signature were used to discern shifts in utilization of carbon pools as microbes apparently oxidize different and increasingly more recalcitrant sources (Abelson 1961; Macko 1987; Rochette 1999). The effects of changes in available soil carbon on nutrient cycling were concurrently evaluated by analyzing nitrogen pools.

Results

To infer a land-use effect upon soil and vegetation properties using a comparative study of this kind, it is imperative that initial site and soil conditions are similar, and that the vineyard sites experienced similar kinds of disturbance and management. These histories are nearly impossible to know. Nonetheless, soils (0-20 cm depth) in the vineyards and the oak woodlands were very similar in terms of texture and mineral composition, but showed substantial variation in total N and total C content (*table 1*). Total carbon in the oak woodland-grassland was 4.63% and in the vineyard soils, the total carbon was 2.21% to 2.48%. The 4.63% value for total C in the oak closely matches the total C value (4.4%) in Quercus Douglasii woodlands (Dahlgren et al. 2003)

Total nitrogen followed a similar pattern with the oak woodland grassland having slightly elevated levels (0.35%) versus that of the vineyard (0.21%). There were also some minor differences in base cations (*table 1*), and it is likely these differences exist as a consequence of vineyard fertilization. Differences between the oak and vineyard sites seem largely due to changes in land management because the only known alteration that has occurred over approximately the past 50 years was conversion of oak woodland sites to orchards and then to vineyards.

Table 1*: Shown are the means and the standard errors of the means (n = 6) for total soil C, total soil N, 1 M KCl extractable* NH_4^+*-N, 1 M KCl extractable* NO_3^-*-N, potassium (sulfuric acid), Mg and Ca (ammonium acetate) texture (% sand, silt, clay), and bulk density.*

		Row	**Berm**	**Oak**
Total-C	%	2.21± 0.08	2.48 ± 0.03	4.63 ± 0.13
Total-N	%	0.21 ± 0.01	0.21 ± 0.01	0.35 ± 0.01
NH_4^+-N	ppm	3.98 ± 0.31	3.02 ± 0.25	12.23 ± 1.36
NO_3^--N	ppm	8.32 ± 1.10	2.75 ± 0.26	2.20 ± 0.14
K	ppm	417.5 ± 7.0	387.2 ± 4.5	273.3 ± 1.5
Mg	meq/100 g	2.87 ± 0.05	3.60 ± 0.06	2.77 ± 0.05
Ca	meq/100 g	10.33 ± 0.19	10.02 ± 0.12	8.18 ± 0.04
Sand	%	50.67 ± 1.63	49.33 ± 1.03	49.67 ± 1.37
Silt	%	32.17 ± 1.17	33.67 ± 1.23	37.67 ± 1.21
Clay	%	17.17 ± 1.17	17.00 ± 0.01	12.67 ± 0.52
Bulk Density	g/cm3	1.207±.076	1.246±0.061	1.023±0.048

Comparison of Land Use Impacts on Carbon Dynamics in the Field

The oak sites had significantly greater soil CO_2 efflux rates than did the vineyard sites over the course of one year (*fig. 1*). A spike in the efflux rates in November of both 2002 and 2003 (*fig. 1*) corresponded to the first rainfall of each season. The efflux rates in the oak woodland-grassland increased from 0.89 µmoles $m^{-2} s^{-1}$ before the rainfall to 7.43 µmoles $m^{-2} s^{-1}$ after the rainfall event in 2002 and 1.71 µmoles $m^{-2} s^{-1}$ to 6.27 µmoles $m^{-2} s^{-1}$ in 2003. The corresponding change for the vineyard was 1.66 umoles $m^{-2} s^{-1}$ before the rainfall event to 2.96 umoles/$m^2 s^{-1}$ afterwards in 2002 and 1.68 µmoles $m^{-2} s^{-1}$ to 3.84 µmoles $m^{-2} s^{-1}$ in 2003. After the initial release of CO_2, the efflux rates decreased to a lower baseline than during the mid to late fall, varying from 5.10 to 3.15 µmoles $m^{-2} s^{-1}$ for the oak woodland-grasslands and 2.33 to 1.79 µmoles $m^{-2} s^{-1}$ for the vineyard. Efflux rates gradually increased until a peak was reached in the middle of May. Soils were wet, and the soil temperatures were high (19.67 °C for the oak sites, and 21.89 °C for the vineyard sites). Warm and wet conditions were especially conducive to CO_2 production in the oak sites with values of 9.53 µmoles $m^{-2} s^{-1}$ versus 2.77 µmoles $m^{-2} s^{-1}$ for the vineyard sites. The oak sites had significantly greater CO_2 efflux than did the vineyard sites over the course of the year ($p = 0.0055$). At only a few points in the fall did the oak soil CO_2 efflux fall below that of the vineyards

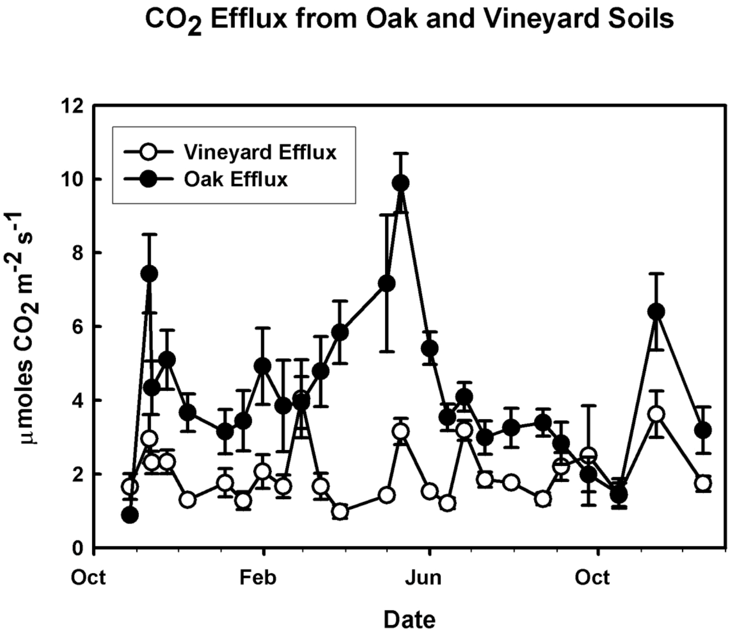

Figure 1. Shown are the means and standard errors of the means (n = 9 for each symbol) for seasonal soil CO_2 efflux for six vineyard and six adjacent undisturbed oak woodland sites growing in similar Bale series clay loam soil.

The soil profile CO_2 measurements showed some interesting trends. At depth, vineyard soils contained greater amounts of CO_2 than did oak soils by a substantial margin (*fig. 2*). However, the oak soils had a larger [CO_2] gradient between 15 cm and the surface. Profile ^{13}C distributions were also not significantly different between the oak and vineyard sites (*fig. 3*). The $\delta^{13}C$ ratios varied significantly with depth ($p < 0.05$), with the CO_2 becoming more depleted in ^{13}C with depth. Sample date was also significant ($p < 0.01$) with the upper depths becoming increasingly enriched in ^{13}C from winter until fall. The profile CO_2 was more enriched in ^{13}C than was expected. Diffusion coefficients were determined for a limited number of samples for the top 12 cm (*table 2*). Oak sites tended to have larger diffusion coefficients than the vineyard sites. Modeled values (see Ralston 2002) showed the exact same trend, although they were higher than the measured values. The oak soils had a larger diffusion coefficient than did the vineyards.

Table 2. *Measured and theoretical values for soil CO_2 diffusion coefficients in vineyard and oak soils.*

	Measured Dg	Measured Dg	Theoretical Dg	Theoretical Dg
Site	0-6 cm (cm^2/s)	6-12 cm (cm^2/s)	0-6 cm (cm^2/s)	6-12 cm (cm^2/s)
Vineyard Berm 1	0.00168	0.00072	0.00581	0.00211
Vineyard Berm 2	0.00402	0.00288	0.01132	0.00674
Vineyard Berm 3	0.00408		0.01184	0.01051
Oak 1	0.00186	0.00162	0.00824	0.00501
Oak 2	0.00336	0.00246	0.00998	0.00483
Oak 3	0.01194	0.00666	0.01455	0.01013

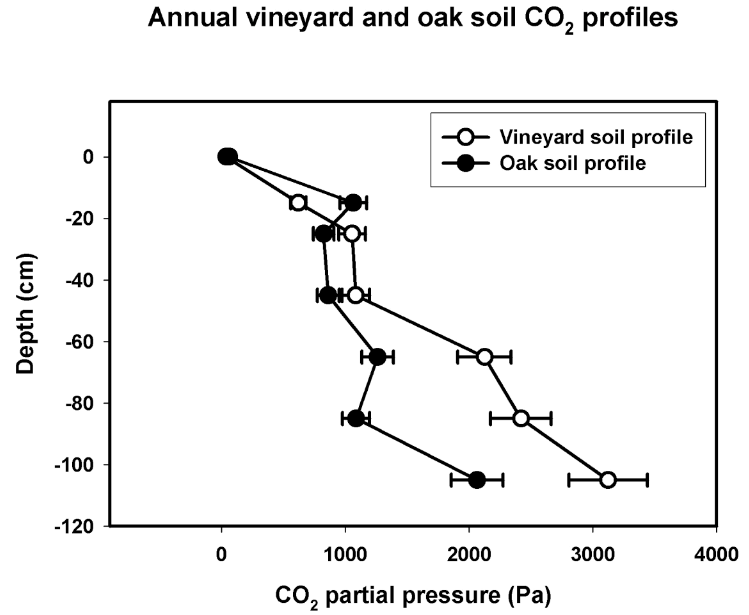
Annual vineyard and oak soil CO_2 profiles

Figure 2. Means and standard errors for soil profile CO_2 samples collected from three vineyard and three oak woodland sites located near the soil CO_2 efflux sites over one year (n = 36 for each symbol)

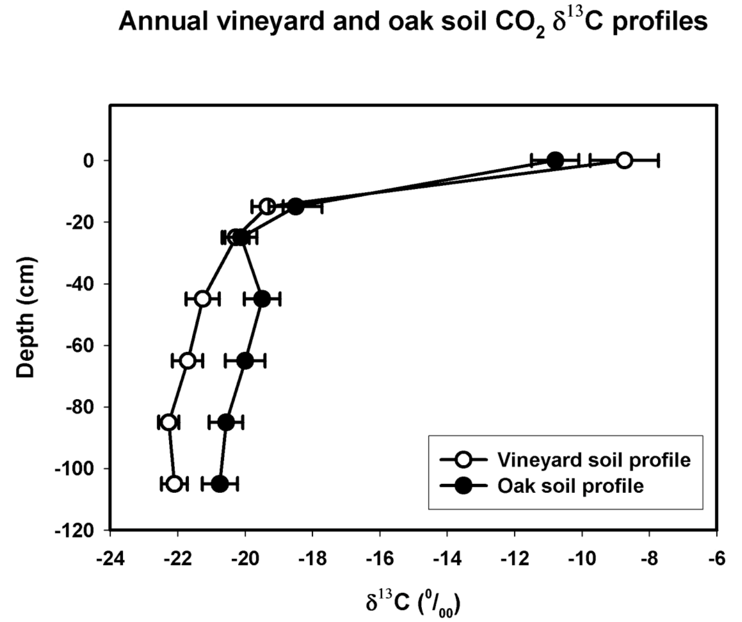
Annual vineyard and oak soil CO_2 $\delta^{13}C$ profiles

Figure 3. Means and standard errors for soil profile CO_2 $\delta^{13}C$ samples collected from three vineyard and three oak woodland sites located near the soil CO_2 efflux sites over one year (n = 36 for each symbol).

Microbial $^{13}CO_2$ Production During Soil C Mineralization

Incubation respiration data showed that CO_2 production by the oak soils was significantly greater than that produced by the vineyard row or vineyard berm soils ($p < 0.001$) at the onset of the experiment (*fig. 4*). The vineyard berm and row soils were not different from each other despite differences in management. Respiration rates fell off throughout the duration of the incubation for all soils. Oak soil respiration was still significantly greater at the end of the eight months incubation ($p < 0.001$).

Vineyard and oak incubation respiration CO_2 concentration data

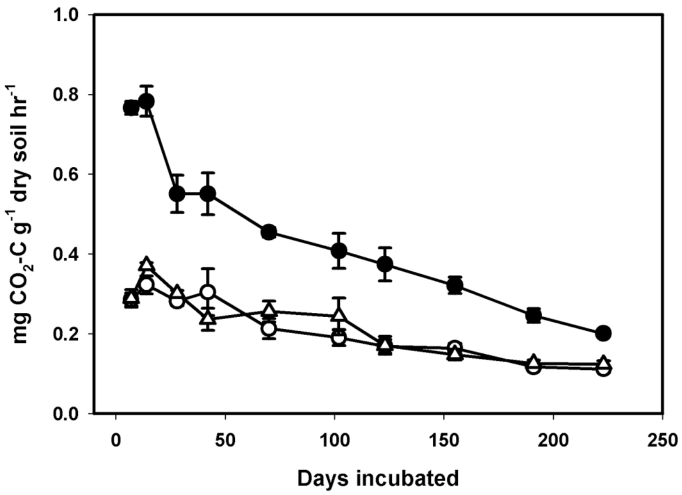

Figure 4. Means and standard errors of carbon mineralization for soils collected from two oak woodland sites and two vineyard sites (n = 12 for each symbol) in the Oakville Region of the Napa Valley.

Measured ^{13}C ratios of the respired CO_2 from the oak soils were significantly greater than that of the vineyard berm soils ($p < 0.01$), but not statistically different from the vineyard row soils (fig. 5). ^{13}C ratios of the vineyard berm or row soils were not significantly different from each other. Also, no significant change in respiration $\delta^{13}C$ ratios occurred over the incubation period for any of the soils.

Nitrate levels from the laboratory incubation portion of the project increased for all the sites as the incubation progressed (fig. 6). Nitrate levels were similar among the oak woodland-grassland and vineyard row and berm soils at the initiation of the incubation, although the amount of nitrate released by oak woodland soils after eight months of incubation ($p < 0.001$). The two vineyard management types, the rows and berms, were not significantly different from one another, but contained significantly ($P = 0.001$) less nitrate than did the oak soils at all time periods.

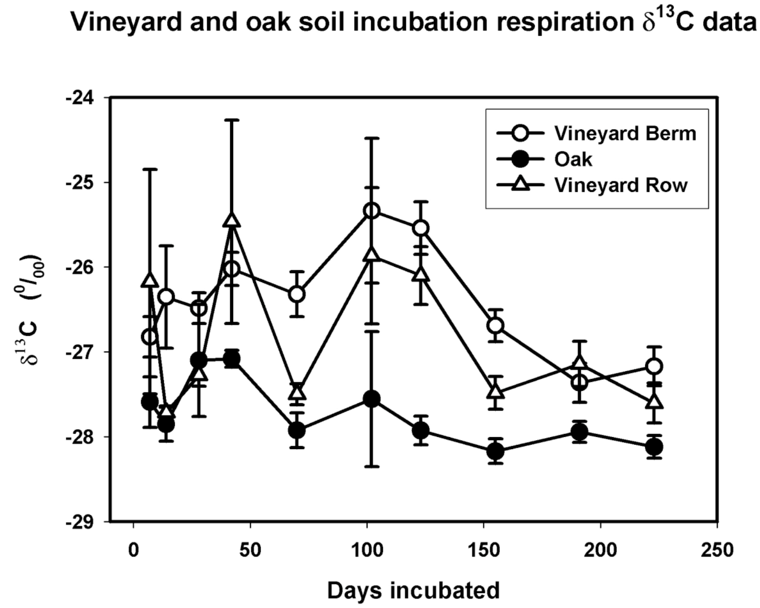

Figure 5. Means and standard errors for incubation respiration δ^{13}C values of soils collected from two oak woodland sites and two vineyard sites (n = 12 for each symbol) in the Oakville Region of the Napa Valley.

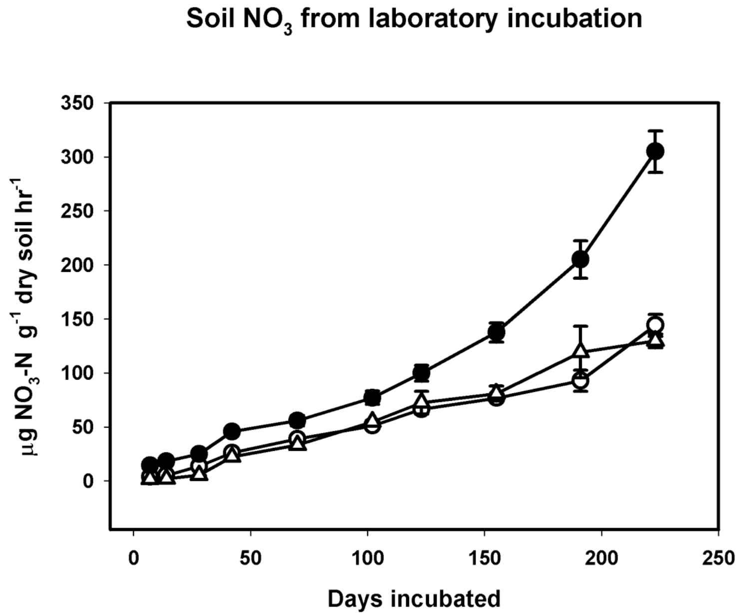

Figure 6. Means and standard errors for nitrate accumulation of soils collected from two oak woodland sites and two vineyard sites (n = 8 for each symbol) in the Oakville Region of the Napa Valley.

Discussion

The primary aim of this project was to document how historical changes have altered carbon flow following conversion of oak woodland-grasslands to vineyards. The first major objective involved monitoring soil respiration in three oak woodland-grassland sites and adjacent vineyards that were converted from such woodlands. The second major objective involved experiments that were to allow us to partition such respiration into microbial and root respiratory components. A third objective considers carbon as a controlling factor in the cycling of nitrogen and is represented by ongoing experiments.

Our data have shown that soil respiration, the major flow of carbon from soils, differs between the vineyard and oak woodland-grassland sites (fig. 1). After the first rain of the season, the oak sites began to respire substantially more than did the vineyard sites. This initial spike in soil CO_2 efflux has been observed twice after the first sizeable rainfall event. Following the initial pulse, efflux rates decreased to a lower but elevated level, gradually increasing as the soil moisture level and temperature increased. The initial pulse of more rapid CO_2 emissions, as well as the continued higher baseline rates thereafter, can be attributed to a number of factors. The influx of water results in a physical displacement of the soil atmosphere, releasing accumulated CO_2 in the soil air space (Smart and Penuelas 2003). Rewetting also causes previously lysed cells to release more labile carbon into soil, and thus increase microbial mineralization activity and soil concentrations of dissolved organic carbon (DOC) (Van Gestel et al. 1993; Lundquist et al. 1999).

Oak woodland-grasslands consistently exhibited a substantially higher efflux rate than did the vineyard sites after the first rainfall. Carbon inputs were presumably much greater in the oak woodland-grassland sites than in the vineyard sites. This is in large part due to the management activities of the vineyard. The oak sites received litter from leaves and senescing annual grassland vegetation as well as root deposition. However, the vineyard berm sites only received carbon inputs from root deposition and turnover as much of the usual carbon inputs (fruit, bark, and canes) are removed from the vineyard. Vineyard management activities at which our vineyard sites were located may further limit CO_2 efflux from vineyard berm, as there is a dearth of annual grass and forb biomass due to herbicide applications. Decomposing annual plant biomass may be a substantial contributor to the total oak woodland-grassland CO_2 efflux. The absence of tillage disturbance in the oak woodland-grassland has implications for the rate at which litter is decomposed. Plant residues left on the surface of the oak soil help regulate temperatures and retain soil moisture while providing a more lasting source of carbon (Neher 1999). Litter that is incorporated into the soil through tillage has a higher short-term impact on respiration, which fades and results in lower average microbial activity (Neher 1999). Tillage also decreases microbial biomass, a labile pool of carbon, in the first several cms of soil (Woods 1989).

The vineyard soils have diminished rates of CO_2 emission in comparison to the oak woodland soils (*fig. 1*). These data suggest that the vineyards may be acting as CO_2 sinks (Sperow et al. 2003) – during the 2002 and 2003 seasons approximately 4.5 mt C ha^{-1} was removed from the vineyards in leaves, fruit and cane wood (this does not include wood increment and root production). This C was less than 2.0 metric tons C ha^{-1} lower than the CO_2-C lost from the vineyard soils by soil respiration. This points to the real potential for agricultural ecosystems to serve as C sinks, and so help mitigate the observed increase of CO_2 concentration in the atmosphere (Sperow et al. 2003). Global terrestrial ecosystems represent the major potential sink for atmospheric CO_2, and may account for the 'missing sink,' or discrepancy between CO_2 inputs into the atmosphere and atmospheric CO_2 increase (at 1 to 2 Gt C y^{-1}; Friedlingstein et al. 1995). Eve et al. (2001) reviewed known reports of CO_2 emissions and carbon inputs for cropland soils and found that most soils under cultivation in the United States were, in fact, acting as C sinks. Estimates of the potential for cropland soils to sequester C range from about 0.1 to 2 Gt C y^{-1} (Lal et al. 2003; Fan et al. 1998; Pacala et al. 2001; Sperow et al. 2003). Assuming biomass produced in literfall and aboveground understory grasses have a carbon content of approximately 45%, then 5.3 mt C ha^{-1} in annual production is estimated from oak woodland grasslands (Dahlgren et al. 1997). Thus, our initial measures of vineyard production lag behind the potential ability to serve as a carbon sink, and also points to the clear need to develop a more acute understanding of the contribution of below ground production in perennial cropping systems.

Soil profile [CO_2] indicated that the presence of vineyards and the accompanying management schemes may have altered the effective diffusion coefficients of these soils. The presence of high concentrations of soil CO_2 in the vineyards versus the much lower concentrations in the oak woodlands appear to indicate that there is some physical process that is retarding the movement of CO_2 through the vineyard soil profile. The higher concentration of CO_2 at 15-cm depth in the oaks is probably a function of the presence of greater amounts of organic matter and the resulting greater oxidation rates that accompany it. Much of the microbial activity takes place in that region of the soil as well. The difference between the incubation $\delta\,^{13}C$ and the profile $\delta\,^{13}C$ was greater than the $4.4^{0}/_{00}$ enrichment normally found in soil profiles due to the physical discrimination against ^{13}C movement in the soil (Amundson 1998). It seems likely that the difference was due to movement of atmospheric air into the soil profile. Oak sites showed greater relative enrichment than did the vineyard sites. This would be the case if the enrichment was the result of atmospheric CO_2 with a $\delta^{13}C$ of $-8^{0}/_{00}$ were mixing with the soil atmosphere. Oaks with the larger diffusion coefficient should show a larger effect of the mixing. The $\delta^{13}C$ ratios observed during the experiment showed similar seasonal trends to other studies of European beech and silver conifer forests (Certini et al. 2003) and old-growth conifer forests in the Pacific Northwest (Fessenden and Ehleringer 2003). Fessenden and Ehleringer (2003) found that water stress during the summer months resulted in an enrichment in soil $\delta^{13}C$ in the upper soil profile as well as in soil respired $^{13}CO_2$. This is similar to the trend showed in the soil profiles of our sites

The results for carbon are intriguing. As organic matter decomposes, polysaccharides and amino acids are preferentially consumed giving way to older, more recalcitrant carbon sources like lignin (Benner et al. 1987). Due to ^{13}C fractionation during biosynthesis of phenylalanine and tyrosine (Abelson and Hoering 1961; Macko et al. 1987), two key substrates utilized in lignin biosynthesis, lignin and humic materials are relatively depleted in ^{13}C. Heterotrophic respiration does not fractionate against ^{13}C (Lin and Ehleringer 1997); thus, the ^{13}C abundance of soil respired CO_2 declines after recently fixed photosynthate rhizodeposited in soils is consumed (Rochette et al. 1999; Ehleringer et al. 2000). We predicted that the isotopic signature of ^{13}C in CO_2 would decline over the course of the incubation until it converged on a value for recalcitrant SOM, but this has not been the case (*fig. 5*). As C mineralization proceeded the CO_2-C has shown little change in $\delta^{13}C$ ratios. At this time, the stable isotopic ratios for respired $^{13}CO_2$ were not sufficiently resolvable to provide a tool for separating microbial from root respiration. It is unlikely this situation will change under field conditions for either the oak woodlands or the vineyards. For example, when we observed an increase in soil respiration during spring root flushes (as observed in a parallel project that examines root proliferation using minirhizotron observation tubes) we did not observe corresponding shifts in soil CO_2 efflux.

Nitrate levels, which were recorded to track the effects of soil carbon on N dynamics, have shown a systematic increase during the course of the laboratory incubation. The increases were especially high in the oak soils. Given the greater total C and the presumably higher above- and belowground annual inputs of plant biomass, one would expect that the oak woodland-grassland soils would mineralize significantly more N than the two vineyard soils. In a comparison of N dynamics in a conventional (no organic matter additions) vs. an organically-managed (compost added) agricultural field, microbial NO_3^--N uptake was greater in the organically-managed field, presumably because nitrate assimilation is energetically costly, and sufficient labile C must be available to support this activity (Burger et al. submitted). The rate and timing of the increase in NO_3^- in the oak soils is very similar to that seen in a conifer forest (Hart et al. 1994).

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