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Extensive belowground carbon storage supports roots and mycorrhizae in regenerating scrub oaks

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Abstract Portions of a regenerating scrub oak ecosystem were enclosed in open-top chambers and exposed to elevated CO_2. The distinct ^{13}C signal of the supplemental CO_2 was used to trace the rate of C integration into various ecosystem components. Oak foliage, stems, roots and ectomycorrhizae were sampled over 3 years and were analyzed for ^{13}C composition. The aboveground tissue ^{13}C equilibrated to the novel ^{13}C signal in the first season, while the belowground components displayed extremely slow integration of the new C. Roots taken from ingrowth cores showed that 33% of the C in newly formed roots originated from a source other than recent photosynthesis inside the chamber. In this highly fire-prone system, the oaks re-establish primarily by re-sprouting from large rhizomes. Remobilization from belowground C stores may support fine roots and mycorrhizae for several years into stand re-establishment and, therefore, may explain why belowground tissues contain less of the new photosynthate than expected. Though it has been shown that long-term cycles of C storage are theoretically advantageous for plants in systems with frequent and severe disturbances, such patterns have not been previously examined in wild systems.

Keywords Carbon remobilization · Ectomycorrhizae · Rhizomes · Scrub oak · Storage

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Introduction

Storing available C and energy reduces immediate plant C allocation to growth and reproduction but allows for biosynthesis and respiration when photosynthesis is restricted. Accumulation and remobilization of C reservoirs can occur on physiological time scales such as day to night or over decades as with forest regeneration over a disturbance cycle. The optimal size and location of C reservoirs within the plant depend on the severity, frequency and regularity of disturbances that can restrict photosynthesis. Though the biochemistry and physiology of plant C storage in agricultural species have been well studied, ecological consequences of C flux into and out of reserves in wild plants remain largely unexplored (Chapin et al. 1990).

Woody perennials tend to store and remobilize C over long time scales, particularly where periodic disturbances make such patterns favorable. The location within the plant of long-term reservoirs varies. Plants in ecosystems that are subjected to periodic and severe disturbances tend to store resources in the portion of the plant that will have the most stable environment from which to regenerate (Lacey 1974; James 1984). While any perennial portion of a plant can serve as a C reservoir, belowground tissue most consistently serves as the primary long-term storage organ (James 1984; Loescher et al. 1990). Belowground organs are often better suited for storage because they can sustain an array of severe disturbances such as fire and extreme weather. Physically protected belowground structures afford plants a mechanism for rapid post-disturbance regeneration that is not severely constrained by initially low photosynthetic capacities. Systems that are prone to greater frequency or intensity of defoliation generally contain dominant plant species that are more reliant on belowground C reserves (Iwasa and Kubo 1997).

Long-term patterns of photosynthate reallocation have been estimated in horticultural species by correlating fluctuations in concentrations of accessible C storage compounds with shoot growth (Priestley 1970; Wargo et

al. 1972; Rodgers et al. 1995). Generalizations made from such observational studies have proven faulty when tested quantitatively (Chapin et al. 1990). More sophisticated techniques are required to resolve specific questions about the timing and magnitude of C flow between storage structures and actively growing tissues. Storage and transport compounds vary greatly among species and remain unknown for many plants (Glerum 1980). Studies that focus on a limited range of carbohydrates could overlook patterns of total C flow. Additionally, the primary long-term storage organs are unknown for many species. Trees can utilize a variety of organs as primary C reservoirs including boles (Sakai and Sakai 1998), burls (James 1984), rhizomes (Lacey 1974), lignotubers (Mesleard and Lepart 1989), thick roots (Rodgers et al. 1995) or intermediate roots (Woods et al. 1959). C in "storage organs" is not always remobilizable, while C in other organs considered static may actually be mobile (Chapin et al. 1990). The extent of C mobility is unknown; C could be as dynamic as other plant resources such as N and P in stressed individuals.

Belowground growth and maintenance could consume as much C as aboveground sinks and should be considered as potential sinks for remobilized C. While aboveground sprouting initially relies exclusively on storage, root regrowth may rely more heavily on C reservoirs for longer periods of time (Kramer and Kozlowski 1979). Roots and mycorrhizae remain strong C sinks throughout stand development (Bloomfield et al. 1996), while aboveground tissue can rapidly become a net source of C shortly following initial leaf establishment (Priestley 1970; Hansen 1971). C sinks first deplete stocks that are near the site of utilization (Kramer and Kozlowski 1979). Further, the prevailing direction of C flow is from above to belowground. There may be an extra cost associated with remobilizing stored C from roots in the reverse direction over greater distances, especially when the strongest sinks lie belowground.

In this study, 16 open-top chambers were constructed over a regenerating Florida scrub oak system following a controlled burn. Half of the chambers were exposed to elevated CO_2 concentrations. We utilized the fortuitous ^{13}C signal present in CO_2-fertilized chambers to investigate patterns of C allocation over 3 years. While aboveground plant tissues rapidly integrated the novel ^{13}C signal, belowground oak tissue expressed only a small fraction of the new signal 2 years into the experiment, much less than would be expected from even very slow root turnover. We hypothesize that stored C, which had been fixed at least 2 years previous to the study period, is remobilized to support belowground structures. This hypothesis is consistent with empirical data and natural history. This system is known to have a short fire-return cycle, roughly 7–10 years, and rapid subsequent resprouting (Schmalzer and Hinkle 1996), both of which are traits indicative of systems heavily reliant on belowground C storage.

Materials and methods

Site description

The study site is at the Merritt Island National Wildlife Refuge off the east coast of central Florida (28 38′N, 80 42′W). The coastal scrub oak system lies on well-drained, infertile, sandy soils (Arenic Haplohumod) with low nutrients and low pH (3.9–4.1). Organic matter is largely confined to the top 30 cm, most of it in the top 15 cm (Schmalzer and Hinkle 1996). The site is dominated by three similar species of scrub oak, myrtle oak (*Quercus myrtifolia* Willd.), sand live oak (*Q. geminata* Sargent), and Chapman oak (*Q. chapmanii* Small). Saw palmetto (*Serenoa repens* Small) and *Galactia elliottii* Nuttall, an N-fixing vine, also occur in most of the chambers. The natural fire cycle is thought to be approximately 7–10 years (Schmalzer and Hinkle 1996) though it has been subject to human suppression over the last 50 years. A controlled burn was executed in the spring of 1996, after which 16 octagonal open-top chambers, each covering 9.4 m^2 and 3.8 m tall, were erected over the charred ground. Eight of the chambers are exposed to ambient air and eight are exposed to ambient air+350 ppm CO_2 [for further details of the experimental setup, see Johnson et al. (2001)]. The oaks re-established in the first summer by resprouting from intact root systems and after 3 years neared canopy closure at a height of 1.5 m and a density of 60 shoots m^{-2} (Dijkstra et al. 2002).

Sampling

At each of five sampling dates (June, July, September, December 1998 and September 1999), three cores (0.9 cm internal diameter×15 cm depth) were bulked from each of the 16 chambers (n=6–8) and stored at 4°C until processing. Air-dried soil was sieved through a 1-mm sieve to remove mineral soil. From the >1 mm fraction, brittle, red roots from *Serenoa repens* and fibrous, white roots from *Galactia elliottii*, and organic debris were manually removed based on visual and textural characteristics. The remaining sample consisting of oak roots and their associated ectomycorrhizae was weighed. Because the matter had dried, an accurate live-dead distinction could not be made; therefore, this group included live and dead structures, but not visibly decomposing ones. The ectomycorrhizal portion (that colonized by ectomycorrhizae) was separated from a subsample of this oak root fraction using extra fine forceps under a dissecting microscope. Fine oak roots (<1 mm) and ectomycorrhizal root tips were analyzed on a Carlo Erba elemental analyzer coupled to a Finnegan Delta Plus isotopic ratio mass spectrometer (Finnegan, Germany). At each coring date, foliage and stems were sampled from each of the dominant species and analyzed for ^{13}C composition. Archived *Quercus* foliar tissue (n=3) from December 1996 and July 1997 was also analyzed to ensure a stable aboveground ^{13}C signal throughout the experiment.

Three cylindrical (5 cm diameter×10 cm length) root ingrowth bags (1 mm mesh) were filled with root-free sand from the C horizon (50–100 cm) and were buried in situ into the A horizon (0–15 cm) of each chamber at the beginning of the experiment in May 1996. Therefore, any root or root-associated tissue harvested from the ingrowth bags had grown since they were buried in May 1996. The first set of bags was harvested in December 1998. The contents were sorted as described above. Roots and ectomycorrhizal tips were weighed separately and analyzed for ^{13}C content. The ^{13}C integration of this newly formed root matter was compared to that of tissue from cores, which contained new and old root matter.

^{13}C Signal

In the elevated-CO_2 chambers, supplemental bottled CO_2 is mixed with the existing ambient CO_2 at a ratio of approximately 1:1. Once the air mixes and C is fractionated during photosynthesis,

the average $\delta^{13}C$ signal of oak stems in the elevated-CO_2 chambers reflects the lighter isotopic composition of the supplemental CO_2. Tissue from the unlabeled, ambient chambers was used to account for naturally occurring isotopic differences among tissue types. The difference between labeled and unlabeled (individual labeled sample $\delta^{13}C$ minus the tissue average $\delta^{13}C$ of control samples) is referred to as $\Delta\delta$ and is used for all subsequent calculations and statistical analyses (Table 1). Variance of the $\Delta\delta$ term, therefore, equaled that from labeled plots, which was over 45 times greater than $\Delta\delta$ variance in unlabeled plots. A two-source mixing model (graphically depicted in Fig. 1) based on $\Delta\delta$ was used to determine the percentage of C derived from recent photosynthesis:

$$N = 100\% \times (\Delta\delta_{root}/\Delta\delta_{stem})$$

where N is the percentage of newly fixed high-CO_2-chamber C. Whereas soil cores contained new and old roots, root tissue in ingrowth bags was formed since the application of the depleted ^{13}C signal in May 1996. We assumed all C in ingrowth roots was derived either from storage or new photosynthesis. By eliminating the possibility of residual root matter, the percentage of C ingrown matter derived from storage was estimated as:

$$X_{ingrowth} = 100 - N_{ingrowth}$$

where X is the percentage of C remobilized from storage. To estimate C source distribution in core-derived tissue, we assumed that root tissue taken from cores received the same proportion of its C from storage reservoirs as matter taken from ingrowth cores.

In September 1999, one soil core was taken at both 5 cm and 30 cm outside four random elevated-CO_2 chambers (n=4). Root and mycorrhizal tissues were removed as described above and analyzed for ^{13}C. Using a linear relationship based on the mean ^{13}C values of these samples taken outside the chamber, we calculated the amount of new chamber-fixed C in root tissue cored outside the chamber. Assuming equilateral C flow, we estimated how much C in roots sampled >30 cm inside the chamber could have originated from photosynthesis occurring outside the chamber.

A two-way ANOVA was performed on the difference between control and labeled $\delta^{13}C$ values in material harvested in December 1998 to evaluate the effects of matter (mycorrhizal or root) and tissue age (ingrowth or core). A t-test was used to compare fine root and mycorrhizal tissue $\Delta\delta$ in cores over all four sampling dates. A special variance formula tailored for isotopic mixing models was used to estimate error on the C-source partitioning model (Phillips and Gregg 2001).

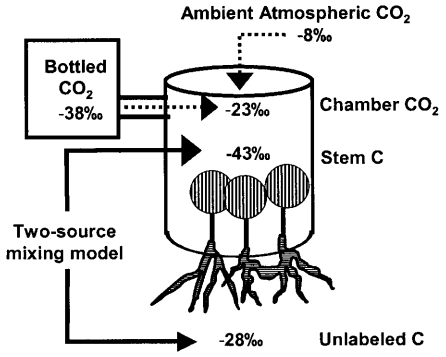

Fig. 1 Diagram of the two-source mixing model used to determine the origin of C in root tissue in elevated chambers. Following photosynthetic discrimination, labeled photosynthate has a $\delta^{13}C$ value approximately 15‰ depleted compared to unlabeled tissue. Belowground tissue ^{13}C fell between labeled stem ^{13}C and natural abundance

Results

The depleted ^{13}C signal of the elevated-CO_2 chambers was incorporated into aboveground tissue (leaves and stems) within the first season, but was integrated much more slowly into belowground fractions (Fig. 2). Root and mycorrhizal tissue taken from ingrowth bags was lower in $\delta^{13}C$ than corresponding matter taken from soil cores (Fig. 3) (P<0.001; two-way ANOVA). Though the ingrown roots and associated fungi had $\delta^{13}C$ values much nearer to the newly fixed, aboveground C, they retained much of the old ^{13}C signature. No such relationship was apparent in the N-fixing vine, *Galactia elliottii*, ensuring that procedural differences in collecting root versus stem tissue did not seriously affect isotopic composition (Table 1). Ectomycorrhizal roots had more new C than nonmycorrhizal fine roots over all the sampling dates (P<0.01, t-test). These two fractions were not different in December 1998 (two-way ANOVA). However,

Table 1 Mean $\delta^{13}C$ values for the above- and belowground tissues sampled in December 1998

Sampling method	Matter sampled	Control $\delta^{13}C$ (‰)[a]	SE	Labeled $\delta^{13}C$ (‰)	SE	$\Delta\delta$ (‰)[b]	SE
Quercus							
Ingrowth	Roots[c]	–28.2	0.14	–38.4	1.70	10.2	1.70
Ingrowth	Mycorrhizae	–28.0	0.46	–38.9	1.41	10.9	1.41
Core	Roots	–27.4	0.39	–30.1	0.79	2.7	0.79
Core	Mycorrhizae	–28.4	0.41	–33.0	1.08	5.8	1.08
Clipped	Oak foliage	–29.2	0.25	–43.9	0.25	14.7	0.25
Clipped	Oak stem	–27.6	0.21	–43.2	0.29	15.6	0.29
Galactia							
Clipped	Foliage	–29.4	0.21	–41.5	0.82	12.1	0.82
Ingrowth	Root	–25.5	0.87	–40.3	1.14	14.8	1.14

[a] Isotopic δ values are reported in ‰=$[(R_{sample}/R_{standard})-1]\times1{,}000$, where R=$^{13}C/^{12}C$ and the standard is Pee Dee Belemnite

[b] $\Delta\delta$ is the mean difference between the mean $\delta^{13}C$ of the control tissue and each individual labeled value

[c] Roots are non-ectomycorrhizal portions of fine roots, while mycorrhizae are the portions of fine roots colonized by ectomycorrhizal fungi

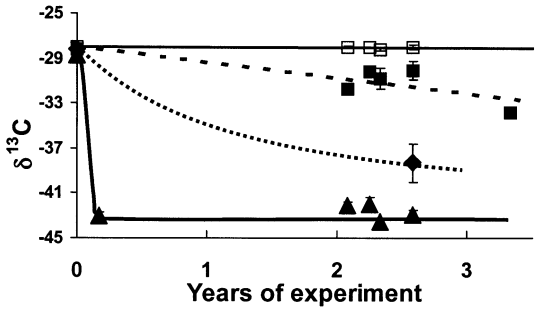

Fig. 2 ^{13}C composition of *Quercus* tissues from May 1996 to September 1999. Tissues displayed include control roots (□), roots taken from cores (■), ingrown roots (◆), and stem tissue (▲) (n=5–8). Ingrowth roots that grew since fumigation with labeled CO_2 adopted the signal much more quickly than the samples from cores, which include a mix of new and old roots

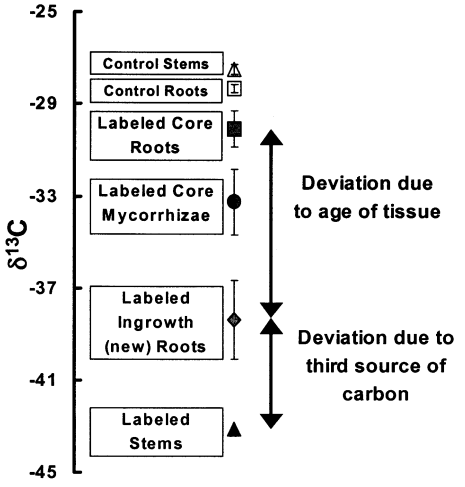

Fig. 3 $\delta^{13}C$ composition (mean±SE, n=5–8) of *Quercus* tissues in December 1998. Roots in cores have a mean $\delta^{13}C$ value that is scarcely lower than that of the unlabeled control roots. Ingrowth roots have a signal much more similar to the expected aboveground value, but still 4.8‰ greater, a difference that is attributed to the remobilization of unlabeled C from storage

a comparison of individual means showed that mycorrhizae had marginally lower $\delta^{13}C$ than fine roots when harvested from cores (P=0.07), but not when taken from ingrowth bags (P=0.78) (One-way ANOVA, least significant difference mean comparison).

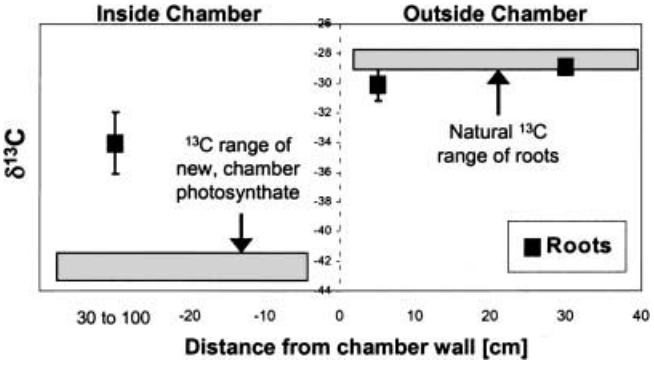

Fig. 4 The magnitude of C transfer belowground in roots (?) taken at various positions relative to the chamber. Newly fixed C inside elevated-CO_2 chambers (*lower left*) has ^{13}C values approximately 15‰ lower than the natural abundance ^{13}C range (*upper right*). To measure the magnitude of lateral belowground C flux, samples (n=4) were taken at 5 cm and 30 cm outside the chamber walls. While the labeled C is detectable at 5 cm outside the chamber wall, very little is present 30 cm away. All roots harvested in the primary study were taken at least 30 cm inside the chamber wall. Assuming equilateral transfer, we estimated that <1% of the C in sampled chamber roots is derived from stems outside the perimeter of the chamber, far too little to explain the high root ^{13}C. Error bars represent ±1 SE

Estimates of the amount of root tissue C derived from storage were calculated based on the $\Delta\delta^{13}C$ of root matter in ingrowth bags, soil cores and aboveground matter all harvested in December 1998 (Table 1). Ingrowth bags contained no root tissue residing from before the chambers were erected but still had higher-than-expected $\delta^{13}C$ values. Over a third of the C in the newly formed ingrowth roots was derived from a source other than recent photosynthesis (Fig. 3).

Tissue $\delta^{13}C$ measurements from the ambient CO_2 plots indicated that isotopic fractionation from stems to roots to mycorrhizae may occur but is extremely slight (all values fall within 2‰), particularly in the context of the large deviations caused by ^{13}C labeling. Naturally occurring ^{13}C variation among groups of tissues should not interfere with C-source estimates because the $\Delta\delta$ term accounts for the difference between $\delta^{13}C$ values of the control tissue and corresponding labeled tissue (Table 1). The subsequent calculations of C source distribution (Table 2) are based on this fractionation-corrected term.

Table 2 Percentages of the three-source model for belowground oak C

	New	Unlabeled[a]	Storage[b]	Residual	SE
Ingrowth root	65.5	34.5	34.5	0.0	11.8
Ingrowth mycorrhizae	70.3	29.7	29.7	0.0	8.3
Core root	17.4	82.6	34.5	48.1	5.3
Core mycorrhizae	37.2	62.8	29.7	33.1	5.2

[a] All chamber C is either new or unlabeled. Unlabeled C is divided into two categories, that in root tissue which has persisted from before the chambers were constructed (residual) and that which is derived from storage

[b] The numbers shown represent the C-source distribution assuming core roots derive the same proportion of C from storage as do ingrowth roots

Lateral transfer of unlabeled C into the roots of labeled plots could have produced a ^{13}C signal deviation in the direction witnessed. Roots from cores taken at 5 cm outside the wall of the chamber had a $\delta^{13}C$ value of –30.0‰ and roots 30 cm outside a value of –28.9‰, i.e. 0.8‰ depleted compared to roots from non-chamber reference plots (Fig. 4). From a linear relationship based on these numbers, we calculated that all roots outside the chamber had 14.5% new, labeled C relative to roots inside the chamber. Roots that were further than 30 cm from the outside edge of the labeling chamber accounted for 7% of the total exported C. With equilateral C flow, roots that are >30 cm inside receive <1% of their C from photosynthesis outside the chamber.

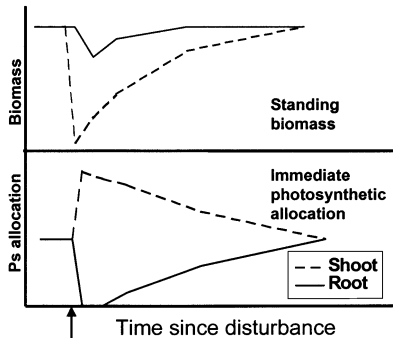

Fig. 5 Hypothesized relationships between root and shoot biomass, and relative photosynthate allocation to each, following aboveground disturbance (↑). Root biomass remains greater than shoot biomass after disturbance though allocation to roots is comparatively small

Discussion

C remobilization from storage is most consistent with the deviation of root ingrowth $\delta^{13}C$ from the expected (aboveground) values (Fig. 3). C fractionation can occur between photosynthetic structures and their belowground subsidiaries (Hobbie et al. 1999); however minimal, such fractionation is apparent among unlabeled ambient-CO_2 stem, root and mycorrhizal tissue (Table 1). Saprotrophy and lateral C transfer were also considered but neither of these hypotheses proved sufficient to explain the patterns observed. If the mycorrhizae were partially saprotrophic, they could potentially break down old organic matter that is relatively enriched in ^{13}C. The reported ability of ectomycorrhizal fungi to facultatively utilize organic matter for C is thought to be limited and activated primarily when ectomycorrhizal fungi grow independently of plant hosts (Bending and Read 1997). When ectomycorrhizal fungi have access to a rich source of plant C, as do the fungi forming root tips sampled, C obtained from other sources is minimal. Mycorrhizal roots tended to have a higher percentage of new C than the corresponding non-mycorrhizal roots (Table 2). Because C transfer from ectomycorrhizal fungi to plants is not thought to occur on a meaningful scale, fungal saprotrophy was eliminated as a viable explanation for the deviation of the ^{13}C signal.

C transfer between plants rooted inside and those outside the chambers could dilute the isotopic signal and cause a deviation in the direction witnessed, but this effect proved to be minimal. Roots sampled outside the chamber had <15% labeled C by mass relative to the roots inside the chamber. All cores in the primary analysis were taken *at least* 30 cm from the wall inside the chambers. Assuming that C flow is equilateral on average, <1% of the C in tissues sampled in the chambers was fixed outside the chamber (Fig. 4). This C transfer test was performed in September 1999, 3.5 years into the study; the cumulative extent of exchange was greater than when the original samples were collected (up until 2.5 years into the study). Dilution of the added ^{13}C signal does perhaps occur in part as a result of C transport from outside to inside the chambers, but the magnitude is far too low to explain the higher-than-expected root $\delta^{13}C$.

Storage

Similar species of rhizomatous oaks have been reported to store enough C belowground that repeated, complete aboveground harvests may not kill the rhizomes (Woods et al. 1959). It has been suggested that plant species can develop prolific belowground root structures not as a conduit for C transfer, but primarily as an accessible C pool to support regrowth following severe aerial disturbances (Lacey 1974; Landa et al. 1992; Matlack 1997). Our study demonstrated that the belowground ^{13}C signal does not distribute over a broad lateral range (Fig. 3), nor is it apparent in aboveground tissues (Table 1). This entire system was burned prior to elevated CO_2 application. Over 2.5 years later, the system continues to develop. Actively growing roots could be predominantly supported by storage, particularly in the early stages of development. Perhaps only later in development will new, labeled photosynthate replenish C stores and overcome the residual, higher $\delta^{13}C$-C. Studies of tree C storage have traditionally centered on seasonal time frames of reservoir variation (see Loescher et al. 1990).

Ingrown tissue $\delta^{13}C$ values demonstrated that remobilization occurs to a great extent, though the magnitude of this in the core tissues is not certain. The slow integration of the novel ^{13}C signature in cores could have resulted from some combination of slow photosynthate integration and slow root turnover. Our estimation of C-source distribution (Table 2) hinges on the assumption that core tissues receive the same amount of C from storage as do ingrown tissues. The disturbance associated with the ingrowth bag implementation could have lead to over- or underestimation of the importance of stored C for the undisturbed root crop. Also, the core tissue is older and may not have received the same amount of C from storage reserves. Regardless, the assumption allows for a reasonable first estimation of the amount of old C in core tissues that was derived from storage and how much lies in residual root tissue.

Feasibility of maintaining large storage reserves

The oaks in this fire-prone Florida system maintain large root systems throughout the entire disturbance regime. The stored C is used briefly to establish initial aboveground sprouts immediately following disturbance, but is primarily allocated to root growth and maintenance. Because belowground structures do not require as much rebuilding as aboveground ones, the plants may allocate a smaller fraction of immediate photosynthate to them throughout stand development (Fig. 5). The extent of C storage we estimated from the ^{13}C method is much greater than expected and eclipses what has been considered evolutionarily advantageous for seasonal resprouting following annual defoliation (Kozlowski and Uchmanski 1987; Pugliese and Kozlowski 1990).

Advantages of maintaining large storage reserves may be overlooked if one considers only short-term advantages of storage over the lifespan of aboveground structures and not that of the entire organism (Sakai et al. 1997). Iwasa and Kubo (1997) used an allocation model to decipher the optimal size of belowground storage for plants in environments subjected to unpredictable aerial disturbance. They assumed that plants adopted the lifestyle with the greatest lifetime reproductive success. Instead of considering only aboveground lifespan, their "lifetime" extended throughout recoverable disturbances (e.g., fire), but ended with the less frequent fatal disturbances (e.g., volcanic eruption). The ratio of resources in storage pools to the resources allocated to production organs increased as the plant approached maximal size, and also increased with the harshness of the environment. That is, plants in an environment with low productivity and with frequent, severe disturbances, will allocate a large proportion of resources to long-term storage (Iwasa and Kubo 1997).

The Florida scrub oak site fits the theoretical description of a system that would rely heavily on stored resources in a long-term remobilization cycle. The oaks regenerate quickly after disturbance. Canopy closure occurs when the oaks reach only a modest stature (ca. 2 m). Net aboveground production diminishes rapidly (<10 years) following disturbance, allowing for replenishment of belowground stores.

Clonal species, which can rely heavily on belowground C remobilization, dominate one-third of the world's forests and over half of non-forest ecosystems (Oborny and Bartha 1995). Most other perennial vegetation types, and especially grasses, depend on accessible belowground stores to support regrowth following aboveground defoliation. Long-term fluxes into and out of storage organs may skew global NPP estimates if not considered. Calculations will be particularly erroneous for systems at stages of development when net C flux into or out of the reservoir is large, perhaps following disturbance.

Aside from skewing NPP estimates in natural systems, the magnitude and timing of stored C cycling could itself respond to global change. The effects of elevated CO_2 on the economy of C storage could not be evaluated in our study because the traceable ^{13}C signal was only available in the elevated-CO_2 chambers. It is unlikely that the CO_2 treatment profoundly altered the C allocation pathways, though the magnitude in natural systems could be different. Elevated CO_2 could accelerate the progression of stand development and cause plants to divert more C to supporting immediate growth and less to storage. Because CO_2 enrichment increases photosynthetic capacity in many species, storage of C may not be as critical for rapid establishment of vegetative cover. Also, C storage could be coupled to storage of mineral nutrients, such as N, which could respond to a change in future nutrient availability (Ameziane 1997). Any alteration of plant allocation to belowground structures could have serious consequences for global C and nutrient cycling. Experiments that employ a label in all treatments (e.g., van Kessel et al. 2000), as well as those that consider the progression of regrowth (Bernston and Bazzaz 1998), are required to specifically test effects of global change on C allocation patterns.

Fine roots vs. ectomycorrhizal roots

We found that ectomycorrhizal roots contained more new C than uncolonized portions of fine roots in the core samples (Fig. 4). Fractionation can occur between plants and mycorrhizae (Henn and Chapela 2001), but our data from the control chamber tissue suggest that little such fractionation occurs in this system. The trend could result from the tissues' age. Bloomfield et al. (1996) reported that the lifespan of fine roots will increase upon ectomycorrhizal colonization, a claim that has been suggested elsewhere (Smith and Read 1997). The tendency towards greater amounts of new C in mycorrhizal tissue (Table 2) argues against enhanced longevity of mycorrhizal roots, though some of the new C could be transient, passing through a structure composed of older C. Mycorrhizal roots could have a shorter lifespan, or plants may allocate more new C to mycorrhizal roots than nonmycorrhizal ones to support enhanced respirational demands. A third possibility is that post-senescent mycorrhizae degenerate more rapidly, existing in a recognizable form for a shorter span of time than nonmycorrhizal roots. Though mycorrhizal fungi are rich in N, little is known about their decomposition rates (Treseder and Allen 2000).

Conclusions

Oak roots taken from cores received <20% of their C from recent photosynthesis in the chamber (Table 2). Half of their C was estimated to be residual in roots that were formed before the label was applied and persisted since then. ^{13}C analysis of roots taken from ingrowth cores showed that these roots may derive a large portion of their C from long-term, belowground C reserves. Belowground oak tissues rely heavily upon reserve C for

growth and respiration throughout much of their early establishment. Over 2.5 years since the fire, considering all tissues, we believe the oaks have roughly equivalent amounts of newly assimilated and previously assimilated C including aboveground tissues. Such lengthy temporal patterns of C storage are theoretically beneficial, but have never been experimentally examined in intact ecosystems. More labeling experimentation as well as methods for representative sampling of large belowground organs are needed in this system and other storage-dependent systems to refine the magnitude and timing of long-term reserve resource cycling.

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