Chapter 3
Mycorrhizae and Global Change

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Abstract Mycorrhizal symbioses are essential components of terrestrial ecosystems. These symbioses are intimate associations between plants and fungi where the plant fixes C, exchanging it for nutrients and water from fungal hyphae that permeate and explore surrounding soil. Perturbations, whether acute (such as disturbance or cutting) or chronic (global change, N deposition) alter mycorrhizal functioning and thereby forest dynamics. Among these dynamics are C sequestration and alleviating nutrient stresses to optimize C:nutrient ratios. We explore three areas whereby global change might alter mycorrhizae, which in turn, will affect forest dynamics. First, increasing temperatures associated with elevated atmospheric CO_2 will increase soil temperature, thereby potentially increasing respiration. However, that may depend upon lags and the variation inherent in diel and seasonal variation. Second, the increased temperature will increase soil drying, and subsequently reduce the length of the growing season for mycorrhizal fungal hyphae. However, elevated CO_2 will simultaneously increase water-use efficiency, thereby increasing the length of the growing season. Third, mycorrhizae increase activity and nutrient uptake with elevated CO_2, negating some of the C:nutrient stress. This activity is dictated by both changing amounts of mycorrhizal hyphal growth and by shifting mycorrhizal fungal taxa, altering the strategies whereby nutrients are acquired and C allocated. This includes spatial (breadth and depth) as well as enzymatic shifts. Finally, we examine the longer-term implications of how global change can alter plant communities and plant dynamics on both ecological and evolutionary time scales.

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3.1 Introduction

Mycorrhizae play critical roles in all terrestrial ecosystems globally. The vast majority of plants are dependent upon mycorrhizae for acquisition of soil resources, largely because plant roots, including root hairs, are too large to thoroughly explore soils for water and nutrients. Mycorrhizal fungi require carbon (C) obtained from the plant in exchange for the nutrients the fungus provides (e.g., Allen 1991). In addition, because the fungi have the ability to cross soil air gaps and penetrate pores, down to large ultra-micropores, and because water flux occurs in response to potential gradients, the fungi can serve to exchange water between water pockets in soil and the host plants (Allen 2007). Plants that do not form mycorrhizae, largely annuals in the Caryophyllales, live in nutrient rich environments and rapidly exploit open patches of soil resources. For these plants, mycorrhizae are a net C drain (Allen and Allen 1990). A small group of plants form cluster roots, extremely fine roots that simulate mycorrhizal fungi, largely in extremely nutrient deficient soils, such as South Africa and Australia (e.g., Pate et al. 2001). For all other plants, mycorrhizae are the normal condition.

It is also important to remember that the mycorrhizal condition for fungi evolved multiple times, in multiple, independent lineages of fungi. The most common mycorrhiza is the arbuscular mycorrhiza (AM) formed between most plants and members of Glomales, a monophyletic group arising sometime in the Silurian, and expanding with land plants. The second most common mycorrhiza is an ectomycorrhiza (EM), which independently evolved many times among different plant groups, and among many fungi, including the Endogonales, Ascomycota, and Basidiomycota. A third mycorrhizal type, the ericoid mycorrhiza, merits consideration because it forms in extremely nutrient-deficient conditions, which may be altered by changing global conditions. There are specialized mycorrhizae, including orchid mycorrhizae that we will not address in this review. Thus, associations hinge upon diverse groups of fungi but only in the orchids are there interesting directional shifts within life stages, being important for biodiversity, but not global carbon management.

The impacts of global change are largely focused on increasing global temperatures (and resulting shifts in precipitation patterns) or on CO_2 directly. Increasing atmospheric temperature (T_a) increases fungal respiration (R_f) but it also increases evaporation, thereby reducing soil moisture (θ). Furthermore, changes in soil temperature (T_s) and θ could have dramatic effects on mycorrhizal composition and thereby mycorrhizal functioning. Changing CO_2 also has important consequences to mycorrhizal functioning. Increased atmospheric CO_2 increases water-use efficiency, delaying soil drying and increasing θ. Delays in soil drying are especially important in arid and semiarid environments. Shifting precipitation regimes also alter the depth distribution of soil moisture (Thomey et al. 2011), again a factor that is related to mycorrhizal dynamics (Querejeta et al. 2009). Finally, increasing atmospheric CO_2 alters the C:N and C:P ratios in soils, with dramatic impacts on mycorrhizae. During the history of terrestrial vegetation,

abrupt changes in atmospheric CO_2 have had important consequences to the evolution of mycorrhizae (Allen et al. 1995).

Global change is a complex suite of changes resulting from chronic anthropogenic perturbation. In the past, most human impacts have been acute: heavy metal deposition, tillage, and soil disturbance. Global change is different in that it proceeds across generations of organisms, including many fungi and plants. This means that there are ecological interactions between organisms (e.g., Klironomos et al. 2005), and likely evolutionary changes incurred (altered gene frequencies within a population). This time scale, coupled with the global nature of the perturbation, means that virtually every interaction between plant-fungus-soil-fungus-plant is altered. These changes include direct CO_2 effects on fixation and C allocation, global-regional-local temperature regimes (with impacts on respiration, water use, and growth), water-use efficiency (WUE), and nutrient-use efficiency (NUE). In addition, not only are humans increasing atmospheric CO_2 through fossil fuel burning and increasing deforestation and desertification, we are also increasing N deposition, at a more local scale, again through fossil fuel consumption and food production. Ecosystems are extremely sensitive to C:N ratios, so that it is the interactions between elements of global change that pose the greatest challenge to understanding and managing forest resources. Similarly, at the scale of an individual plant: fungus mycorrhiza, as either CO_2 increases, or a soil resource increases (e.g., N, P), and the C:N or C:P ratio is altered; the mycorrhizal activity is increased or decreased depending upon the relative ratio (Treseder and Allen 2002).

A final caveat is that most of the results we will present are from our field sites in the southwestern US, particularly the James Reserve, a UC NRS site located near Idyllwild, CA (http://www.jamesreserve.edu) and the Sky Oaks Reserve, (http://fs.sdsu.edu/kf/reserves/sofs/), a San Diego State University reserve near Warner Springs, CA. Other programs are also relevant, but these provide a perspective from a system that appears to be very sensitive to the changing global environment and for which sites have been studied for almost two decades.

3.2 Resource Acquisition and CO_2 Allocation

Water acquisition and nutrient acquisition are fundamentally different processes, and should be so thought of in the context of global change and mycorrhizae. However, both directly affect CO_2 acquisition and nutrient use, so both processes need to be understood as separate parts of the mycorrhizal system. We will first deal with the two individually, then examine how they interact later.

3.2.1 Temperature, Water and Global Change

Elevated global temperatures result from actually a very small increment in long-wave re-radiation (a global average of 3 Wm^{-2}). Given that the peak radiation for a site such as the James Reserve is as high as 1,400 Wm^{-2}, this value appears quite small. But, the change occurs primarily at night (re-radiation), thereby slightly increasing soil temperature (T_s). Every GCM (Global Circulation Model) run shows increased T_a over the next half-century to century (IPCC 2007; Hayhoe et al. 2004) including ecosystems within southern California. This change alters both evaporation, thereby reducing θ, and microbial and root respiration because of increased T_s. But concomitant increases in atmospheric CO_2 will likely negate some of that response by increasing water use efficiency (WUE) and thereby increasing θ. Both of these directional changes are subtle and will require careful new modeling efforts. Nevertheless, some interesting hypotheses can be generated (Fig. 3.1).

In EM ecosystems, net ecosystem exchange (NEE) and soil respiration (R_s) appear to be sensitive to changes in T (Vargas et al. 2010). AM systems may be less sensitive to changing T_a, but that may be because AM plants occupy such a broad range in T_a (from alpine to hot deserts). In any case, increased T, a consistent response among GCM's, will have complex impacts on mycorrhizae. In an experimental AM system, Staddon et al. (2003a) reported that % AM root length increased with summer drought and winter warming. But, we do not know if this was due to decreasing fine root production relative to AM inoculum density, or increased fungal activity. Their observation of reduced hyphal density suggests that we need additional information on production and mortality of both roots and fungi. In theory, increasing T_a should increase microbial activity and R_s (e.g., Pritchard 2011). Thus, increasing T_a should result in increased T_s, thereby increasing mycorrhizal growth, respiration, and mortality. Many studies support the notion that higher T_s increases activity of soil organisms, including mycorrhizae (see Pritchard 2011). At the James Reserve, our modeling of R_s (Vargas and Allen 2008; Hasselquist et al. 2010) suggests that shifting T_s upward by a few degrees could have a measurable indirect impact on mycorrhizae and soil dynamics. However, we do not know if the changing T_a will reasonably alter T_s enough to directly alter soil microbial or mycorrhizal functioning. Applying DayCent modeling (http://www.nrel.colostate.edu/projects/daycent/) to our system, we increased T_a by 2 °C (Kitajima and Allen, unpublished data). There are some interesting problems with DayCent modeling, mostly dealing with the consequences of soil depth and lags in response times that are not captured by the model. Nevertheless, the overall effect is instructive. Two particular responses are relevant here. First, heterotrophic respiration (R_h) increased by approximately 6 % with increasing T_a (and subsequently T_s). Secondly, NEP and NPP increased by approximately 8 %.

In looking at changing T_s with seasonal change, the response of variables such as fine root production and leaf production is similar given the projected change in T_s. Is this enough (6–8 %) to cause a detectable ecosystem response? That is an issue requiring additional research. T_s varies greatly at this site on both a diurnal and on a

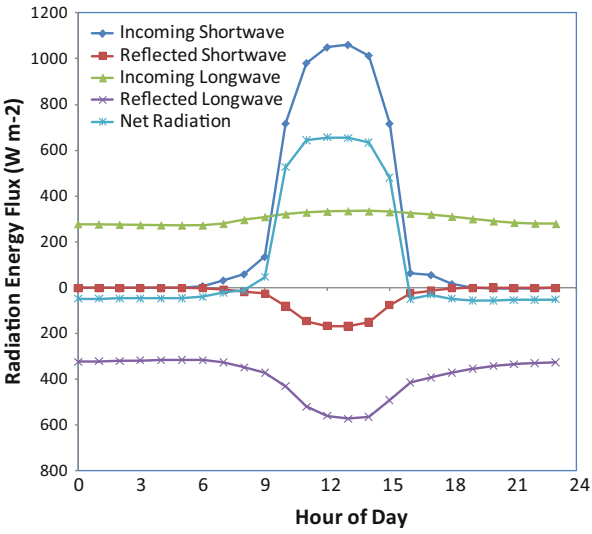

Fig. 3.1 Daily energy balance of James Reserve observed between May 1 and May 7, 2010

seasonal basis. Q_{10} analyses show a highly variable response within these ranges (Kitajima and Allen, unpublished data), in part associated with the hysteresis actually measured in the field (Vargas and Allen 2008). These differences can be greater than the 6–8 % responses measured.

This interpretation is also supported by the small variation in net radiation exhibited by elevated atmospheric CO_2 to 450 or 550 ppm at the scale of a single site (such as beyond 2,050 or 2,060). For values above these levels, variance estimates increase and predictability declines dramatically. However, we do not really know how this plays out with θ, especially as θ both deceases (higher evaporation) and increases (higher WUE with elevated CO_2). Hernandez and Allen (unpublished data) found that T_a will likely increase with all GCMs, scaled down to the James Reserve (Fig. 3.2). But precipitation varied greatly, depending upon both the model, and on the time element. The clearest signal was a T_a response that will likely modulate θ—presumably occurring via increased evaporation and longer dry seasons under a warming climate—in concert with a dynamic precipitation regime.

We ran two types of models. First, we looked at the ecosystem-scale responses to changing θ using both increasing and decreasing levels using DayCent, in comparison with direct measurements of NEP using eddy covariance (provided by M. Goulden, University of California-Irvine), sapflow, and fine-root dynamics. Second, we modeled R_s based on the Fick's second law of diffusion and measured CO_2 concentrations at three different soil depths (Tang et al. 2005). These relate to mycorrhizae as approximately 50 % of the R_s is newly fixed C based on $\delta^{14}C$ of respired soil CO_2 (Trumbore, personal communications). Further, in the case of this site, every root tip is mycorrhizal, so that we equate increasing fine root NPP with increasing mycorrhizal numbers (see Allen et al. 2010 for more discussion). The

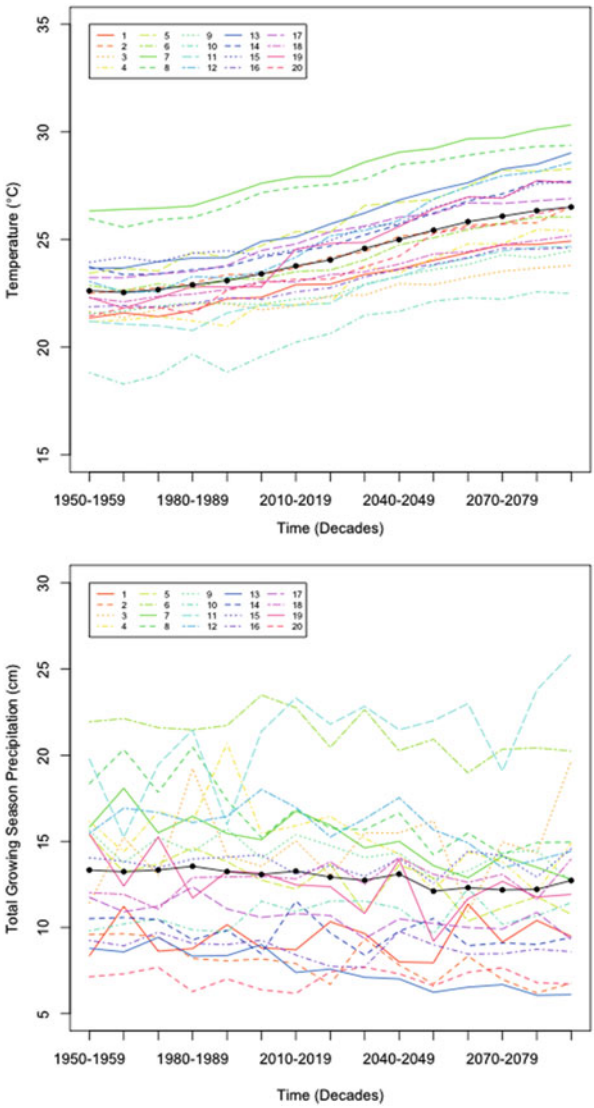

Fig. 3.2 Projected air temperature (°C) and total growing season precipitation (cm) based on individual global climate models (n = 20) and mean projected temperature (black points) averaged over each decade at UC James Reserve (Idyllwild, CA). Models include: (*1*) CCMA (cgcm3 1 t63); (*2*) CNRM (cm3); (*3*) CSIRO (mk3 0); (*4*) GFDL (cm2 0); (*5*) GFDL (cm2 1); (*6*) GISS (aom); (*7*) GISS (model e h); (*8*) GISS (model e r); (*9*) IAP (fgoals1 0 g); (*10*) INM (cm3 0); (*11*) IPSL (cm4); (*12*) MIROC3 (2 hires); (*13*) MIROC3 (2 medres); (*14*) MIUB (echo g); (*15*) MPI (echam5); (*16*) MRI (cgcm2); (*17*) NCAR (ccsm3); (*18*) NCAR (pcm1); (*19*) UKMO (hadcm3); (*20*) UKMO (hadgem1)

DayCent response of increasing precipitation (precipitation) is dramatic. Virtually all ecosystem parameters increased between 5 % and 10 %. These included NEP, NPP, fine and coarse root NPP, and R_s. As T_a increases, if precipitation also increases due to warming ocean temperatures (one of the GCM scenarios), then we can expect a dramatic increase in C allocation to roots and mycorrhizae, and subsequent sequestration in soils from fine root and mycorrhizal organic matter inputs (see Treseder and Allen 2000; Treseder et al. 2005b). Just as important, if

winter precipitation drops, and the recharge of soil moisture declines, all relevant activity declines 10–15 %.

Beyond simply the predictability issues, a key question will be whether these changes are enough to affect other ecosystem processes, including accumulation of fine fuels, drying of soil water with increasing leaf production, or tree mortality due to periodic droughts. As EM fungi consists of chitin and other complex C compounds, rising T could both increase C sequestration by facilitating production, however, it could also decrease soil C due to increased R_s.

AM-dominated ecosystems are sensitive to changes in θ (Vargas et al. 2010) but across a far broader range (deserts to tropical forests). But under global change scenarios, accounting for θ is complicated. Treseder et al. (2003) found small increases in θ because of the increased WUE with elevated CO_2 in chaparral. AM activity also increased, but separating the effects of slight increases in θ from the direct increases in AM due to increased C allocation to AM was not possible. A change in T_a could increase evaporation and thereby reduce θ, and the subsequent length of the growing season. However, in that study, we did not change T (Fig. 3.3).

In that vein, changes in T and θ may also play out in altering the duration of the growing season. Specifically, if T_s increases evaporation, or if θ declines or increases directly due to changing precipitation, then the dry season will be longer or shorter, respectively. If we can establish life spans of fine roots and mycorrhizal fungal hyphae, then we could model how changing conditions would affect total annual production and C inputs to soils.

Estimates in the literature based on laboratory studies appear wildly inaccurate for field studies. For example, Staddon et al. (2003b) estimated that hyphal turned over in 3 days. If all AM hyphae in a field site had this type of lifespan, then the AM hyphae alone, over a growing season, would require an order of magnitude more C than is allocated to root systems. Thus, field observations of hyphal dynamics and growth characteristics are needed.

Allen et al. (2003) developed a hyphal expansion model based on the growth of new roots (from Allen 2001). In this model, as a root tip grows, a new infection forms. Specifically, the extramatrical hyphae branch out from the infection point, transferring nutrients to the plant in exchange for C. In laboratory observations, the hyphae grew at approximately one branching unit per day and up to eight branching orders. Subsequently, the hyphae died back from the tips. The hyphal tips lived only a few days, but the base of the network would survive for 40–50 days, and the runner (or arterial) hyphae could survive for a growing season. Using this model we could better estimate hyphal growth and mortality if we could observe hyphae directly in the field. Such observations would also confer the ability to measure standing crop of AM and EM hyphae. For tracking, we observe the hyphae radiating from a root or EM for identification, especially for EM, where there are no morphological differences.

Using an automated minirhizotron (Allen et al. 2007), which can resolve hyphal dynamics on a daily basis, we found that the mean life span for AM hyphae in the field was 46 days in a meadow at the James Reserve (unpublished data, Hernandez

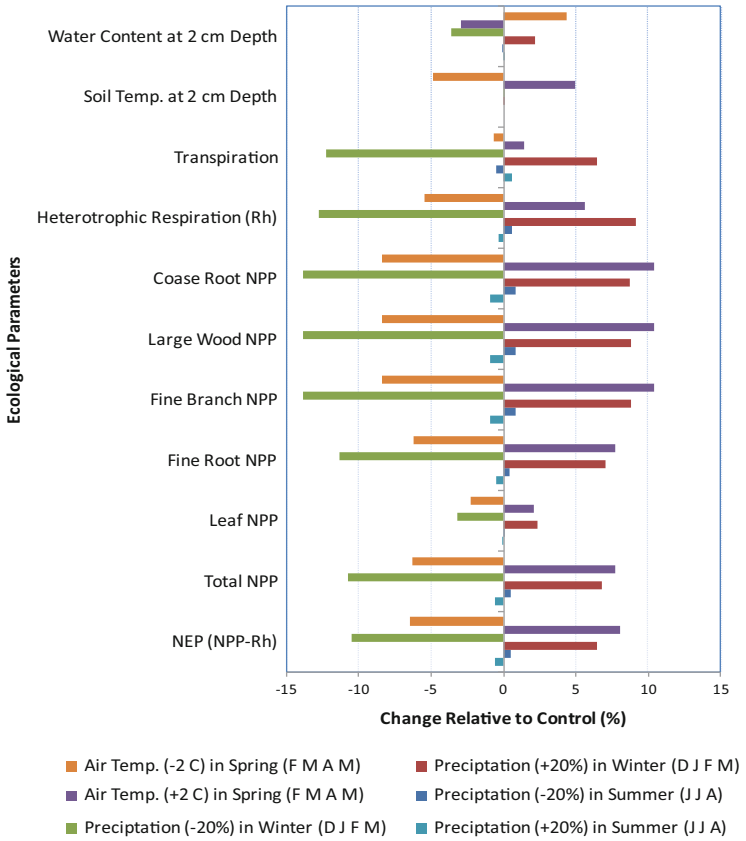

Fig. 3.3 Percent changes of various ecosystem components modeled with DayCent relative to the values estimated from the historical weather condition at the James Reserve (between 1943 and 2010). Six hypothetical weather conditions were simulated: increased/decreased air temperature in spring (Feb–May), precipitation in winter (Dec–Mar), and precipitation in summer (Jun–Aug)

and Allen). This is quite different from the estimate of 3 days from a grassland microcosm study (Staddon et al. 2003b). In the direct observations of individual hyphae, some lived only hours whereas others persisted for a full growing season, generally supporting the model of Allen et al. (2003). In addition, those observations throughout a growing season showed that the AM hyphae rapidly grow with the onset of winter rains. The average remains high throughout the growing season, although both production and mortality occur in response to weather events (Fig. 3.4). At the end of the growing season, in late spring, as T increases and θ declines, the AM hyphae rapidly disappear. In general, this pattern conforms to analyses from soil cores (Allen et al. 2005b) of AM dynamics through growing seasons in a shrubland. With these results, we can model the production of AM fungal hyphal C based on the standing crop and turnover, using traditional ecosystem calculations. This value could also be contrasted with fine root production and

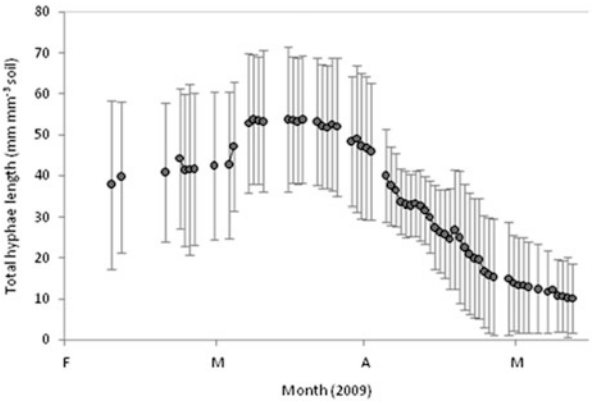

Fig. 3.4 Total hyphae length (mm) per mm^3 of soil as observed using an automated minirhizotron (n = 6) in a mixed conifer forest (UC James Reserve, Idyllwild, CA). Error bars are 95 % CI

mortality at the same site. Using this approach, we estimate that the mean standing crop of AM fungi was 20 g m^{-2} during the growing season, (compared with a peak standing crop of 21 g m^{-2} measured from soil cores, as per Allen et al. 2005). Assuming an average growing season length of 8 months, then the total allocation to AM fungi would be approximately 100 g m^{-2}, a value similar to that of fine root production, where the life span was slightly less than a single growing season (Kitajima et al. 2010). Based on this analysis, then, the annual allocation of C to mycorrhizal fungi may approach that of fine roots. Changes in T or θ that alter the growing season of AM fungi, or the total number of fine root new tips (that support the mycorrhizal fungi, Allen 2001) could dramatically affect C balance estimates, not to mention ecosystem dynamics.

In a final analysis, in modeled projections of environmental change, precipitation was extremely variable both among models and within each model through time (unpublished data, Hernandez and Allen). This is an extremely critical outcome. Increasing variability in precipitation even under decreased total precipitation may mean more biologically effective θ (Thomey et al. 2011). This result occurs because larger (even less frequent) storms increase the depth to which water infiltrates. Soils at the James Reserve are quite shallow, to the point where they are unable to store enough moisture to support the current growth of trees, including both oaks and conifers, through the dry season. Egerton-Warburton et al. (2003) found that trees, such as live oaks, utilized water in granite bedrock during the dry season. Egerton-Warburton et al. (2003) and Bornyasz et al. (2005) observed mycorrhizal roots in bedrock fractures and individual hyphae extending into the granite bedrock matrix. We analyzed the isotopic signatures of the water in the plant stems at the end of the growing season (Allen 2006). Mature plants were using water from the bedrock that had been deposited during winter rains. It is unlikely that the water diffused from the granite matrix to the roots, because of the extreme tortuosity of the material. However, the hyphae grow across these gaps, and provide a rapid pathway for water flow through that matrix (Allen 2007). Thus, if water increases infiltration with depth in response to greater storm variability (Thomey

et al. 2011) or in response to greater precipitation, then mycorrhizae will play a critical role in acquiring that water for plant production and survival.

Just as important, both AM and EM fungi benefit from the water provided by hydraulic lift (Querejeta et al. 2003, 2007, 2009). Thus, the seasonal life spans of the mycorrhizal fungi can be extended beyond the growing season predicted by precipitation and T alone. Indeed, in our sapflow and R_s measurements, this was illustrated by an extension of activity into the summer drought, likely using water provided by hydraulic lift, and a result not predicted by the DayCent model.

3.2.2 Nutrients and Global Change

CO_2 fixation is linearly related to N concentration in the leaves, and curve-linearly related to P. Yet, CO_2 is taken up by the plant from the atmosphere, while water, N, and P (as well as other elements) from the soil. Uptake of CO_2 by the plant is direct, and depends upon its physiological status. The plant must either acquire soil resources through rather inefficient structures (roots) or "bargain" with the fungus for N or P. The exception being the formation of cluster roots by the plant, in which root systems are so fine as to co-opt mycorrhizal functioning (e.g., Adams et al. 2002) in surface area, and rhizosphere chemistry.

One clear fact emerges, however, and that is as atmospheric CO_2 increases, the need for N and, to a lesser extent P, increases. This creates a greater dependency by the plant on mycorrhizal fungi to acquire nutrients (e.g., Allen et al. 2003). We found that more C went through the mycorrhizal fungal energy channel under elevated CO_2 than in control model ecosystems in both sagebrush and *Populus tremuloides* (Klironomos et al. 1996, 1997). Further, elevated CO_2 altered the allocation of C within the mycorrhizal system (Rillig et al. 1998a, b, 1999). Alberton et al. (2007) also postulated that the increased C flow to mycorrhizal fungi requires increased N in the increased fungal mass, setting up a negative feedback to the host from the mycorrhizal fungi. However, whether mycorrhizal fungi increase soil C sequestration under elevated CO_2 is surprisingly controversial. Treseder and Allen (2000) and Treseder et al. (2005) proposed that as plants require more N and P, they allocate more C to mycorrhizal fungi, and the slower-decomposing compounds in the fungi remain, increasing soil C sequestration. Alternatively, Heinemeyer et al. (2007) argued that simply more C was respired by the mycorrhizal symbiosis; i.e., there was simply greater C throughput from plant to atmosphere. We argue that while throughput might increase, it is inconceivable that the increased mycorrhizal fungal C allocation would not add soil C based on the fungal chemical composition. Compounds like glomalin and chitin will remain in the soil well after the active life of the hypha. While it is likely that R_s increases with elevated CO_2, it is likely less than the net fixed. Indeed, studies of N additions, that reduce mycorrhizal activity, reduce soil C (Allen et al. 2010), evidenced by declining soil C age (measured by $\delta^{14}C$ analysis, Trumbore, personal

communications) probably from increased saprotrophic activity, and decomposition of older carbon.

In a chaparral shrubland, we increased atmospheric CO_2 in 100 ppm increments (Allen et al. 2005) over a four growing season period. As atmospheric CO_2 increased, N became more limited in the host plant. N fixation in *Ceanothus greggii* (an actinorhizal-associated plant) increased, and uptake and transfer of N by EM, as estimated by isotopic fractionation increased. Root biomass and AM fungal mass increased. The amount of new C fixed into soil aggregates and glomalin also increased indicating that more C was being deposited in the soil through mycorrhizal fungi (Rillig et al. 1999; Treseder et al. 2003) in both the chaparral shrubland and in experimental annual forb/grasslands. In AM plants, the dominant fungi shifted, particularly from *Glomus* spp. to taxa in the Gigasporeaceae that form extensive mycelia networks. Production and soil functioning crashed under severe N limitation somewhere between 600 and 750 ppm atmospheric CO_2, a level projected (without CO_2 limits) to occur sometime in the next century.

These responses suggest that there is a response curve between soil resources and atmospheric CO_2 that will regulate mycorrhizal functioning along a changing global environment. Treseder and Allen (2002) described such a response surface in an experimental analysis of mycorrhizal response to and N and P gradient. Applying that curve to a CO_2 by N by P (or other limiting nutrient) response provides useful information on mycorrhizal responses to a variety of global change parameters (Fig. 3.5) but especially the impacts of CO_2. In one perspective, adding N deposition in an elevated CO_2 atmosphere, drives many processes back to pre-industrial relationships, albeit towards a more eutrophic environment overall.

Nitrogen is the next critical plant resource after T and θ in most ecosystems. Leaf N is linearly related to photosynthesis, such that as N increases, photosynthesis increases. But, if N is added, particularly through N fertilization or through anthropogenic N deposition, the plant does not need to exchange N with the mycorrhizal fungus to obtain the critical resource. Alternatively, if it declines (in a high CO_2 environment) the plant will be more dependent upon mycorrhizae. In most AM dominated ecosystems (Egerton-Warburton and Allen 2000, 2001; Egerton-Warburton et al. 2007; Johnson et al. 2008), as soil N increases through anthropogenic additions, AM activity of many plants declined (e.g., *Andropogon gerardii*, *Panicum virgatum*, *Bouteloua gracilis*, *B. eriopoda*). However, AM do not always decline. Some AM plants (*Juniperus monospermum*, *Elymus elymoides*, *Agropyron repens*) simply respond by increasing total production (Johnson et al. 2008; Corkidi et al. 2008; Allen et al. 2010). EM systems are less well measured for soil activity, but are likely very sensitive. In an N fertilization experiment, EM functioning declined in *Pinus edulis*, as measured both by total mycorrhizal root tips and by N fractionation between hyphae and leaf, although AM juniper showed increased production (Allen et al. 2010), as did mortality in red pine (Johnson et al. 2008; Corkidi et al. 2008; Allen et al. 2010). Mortality in red pine at the Harvard Forest was also observable with high levels of N fertilization, although AM angiosperms increased in production (Allen, unpublished observations). Theoretically, as CO_2 increases, and the ratio again shifts toward higher C:N ratios, mycorrhizal activity

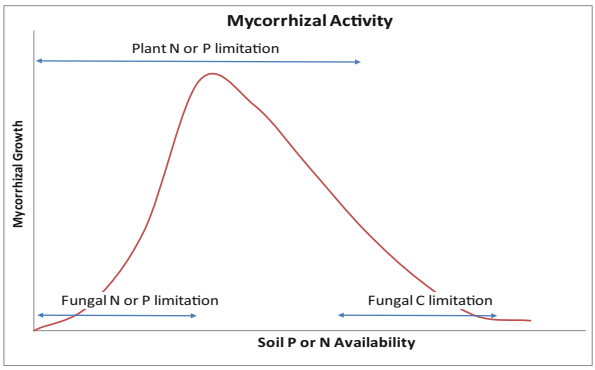

Fig. 3.5 The interaction of plant and fungal nutrient limitation on the biomass of mycorrhizal fungi. At high nutrient levels, fungi will receive little carbon from plants and will be C-limited. At lower nutrient levels, plants will be N- or P-limited and will allocate C to mycorrhizal fungi. At the same time, if N or P concentrations are sufficient for fungal growth, mycorrhizal fungi will proliferate. At the lowest nutrient levels, both fungi and plants should be nutrient limited, and fungal biomass will be low regardless of C allocation to the fungi by plants (Redrawn from Treseder and Allen 2002)

should again increase, and as N deposition increases, mycorrhizal functioning declines. If N deposition is controlled, then mycorrhizae should again become more important.

In addition, as atmospheric CO_2 increases, P becomes more limiting. Treseder and Allen (2002) found that shifting N:P ratios shifted AM fungal composition. In other studies, the Konza prairie has been noted as a model ecosystem for studying AM functioning. However, N fertilization actually increased AM activity (Johnson et al. 2008). This site has calcareous soil, which makes soil nutrients N and P extremely limiting, resembling high CO_2 in the case of both soil nutrients. Based on the Treseder and Allen (2002) model, the Konza prairie may exist nearer the extremely low nutrient condition end of the spectrum, and nutrient additions stimulate mycorrhizal activity, in a similar mechanism to increasing atmospheric CO_2. Mycorrhizae can also shift activity in response to altered P conditions. In a high P, but clayey soil, AM fungi produced oxalate crystals that enhanced P uptake by mycorrhizal fungi (Jurinak et al. 1986) but in sandy soils with high available P, AM fungi apparently did not produce oxalate crystals, although EM fungi did (Allen et al. 1996). Sites with serious nutrient deficiencies may make important test models for environments being altered by increasing CO_2 levels.

Mediterranean climate forest and shrubland ecosystems may be a useful test case system. Above ground, there is a large literature on convergent evolution because the climate has driven similarities in leaf structure and physiognomy between very different groups of plants in the different regions (the Mediterranean Basin, South Africa, Australia, Chilean coast, California coast). However, belowground, these ecosystems radically diverge in mycorrhizal types largely because soil nutrient conditions also differ. Australia and South Africa contain many plants forming

cluster roots, a mechanism to acquire nutrients under extreme nutrient deficiencies when even mycorrhizae are limiting. There are a few legumes forming cluster roots in P deficient calcareous soil in the Mediterranean Basin. Many of these sites also contain plants forming ericoid mycorrhizae. These associations are especially effective at acquiring organic N in bogs and other highly organic environments. Interestingly, in Australia, South Africa, and (a few) in the Mediterranean Basin, these associations exist in arid soils with little organic matter, but where that organic matter is still critical for N cycling. In all regions, ectomycorrhizal and arbuscular mycorrhizal plants abound. In California and Chile, there is a special abundance of nonmycotrophic annual plants (e.g., annual Chenopodiaceae, Brassicaceae- although perennial taxa in these families are mycorrhizal, e.g., Allen and Allen 1990, unpublished observations) and many other invasive plants in particular that show minimal response to mycorrhizae such as annual grasses (*Bromus* spp., *Avena* spp.). There are no comparative studies among ecosystems to explore these dynamics, an area ripe for comparative research.

3.3 Global Change and Biodiversity

3.3.1 Shifting Fungal Composition

Measuring ecosystem response is a complex task, particularly teasing apart the multiple impacts of global change in highly variable environments, where daily values may exceed the change in response. However, organisms tend to track extremes and variation, often better than instrumentation and models. Fungi tolerate incredible variation in T, θ and nutrients. However, in a competitive environment, they may be readily overtaken by fungi less sensitive to altered conditions. In general, individual hyphae are presumed to have relatively short lives, although a mycelial network may be long-lived. This interpretation has also been applied to mycorrhizal fungi, as most studies of mycorrhizae are limited to short-lived pot culture studies (e.g., Staddon et al. 2003b). An outcome resulting from this assumption is that hyphae turn over rapidly and composition can likely change rapidly in time as one fungus replaces another following environmental change. Another problem is that assessments of mycorrhizal activity tend to be made from relatively infrequent coring in which space cannot be distinguished from time. Soils are remarkably heterogeneous, and even neighboring cores a few centimeters apart can result in very different communities (Allen and MacMahon 1985; Klironomos et al. 1999).

Allen et al. (2003) developed a simple stochastic model to study shifting the relative production under shifting ratios of C, N and P. This approach was built around known variation in physiological dynamics of different fungal taxa. Interestingly, this model showed a complex array of outcomes in nutrient allocation, plant growth, and fungal growth dependent upon the fungal physiology. Although

increased diversity of mycorrhizal fungi is often related to increased plant performance (e.g., Van der Heijden et al. 1998), that is not the only outcome. In multiple stochastic runs of our stoichiometry model, in some cases, increasing fungal richness increased productivity. In others, increasing richness caused no change, or even reduced plant productivity, depending upon the characteristics of the individual fungi (Allen et al. 2003). These multiple outcomes can be observed in other published studies of plant growth responses to fungal diversity (Allen et al. 2003). We proposed that understanding the individual physiological characteristics of the participants under shifting environments is crucial to understanding the outcomes of global change.

A few experimental studies have demonstrated a change in mycorrhizal fungi in response to elevated CO_2. In a plant × AM fungal experiment, Wolfe et al. (2003) reported complex changes in AM fungal communities to increasing CO_2. In annual communities with a mix of invasive and native species, complex changes in the fungal communities emerged (Rillig et al. 1998a, 1999). In chaparral, Treseder et al. (2003) found that AM fungi shifted from a predominance of *Glomus* spp. in low to ambient CO_2 levels, to a predominance in Acaulosporaceae and Gigasporaceae in high atmospheric CO_2 levels. Apparently, the increased N and P deficiencies associated with elevated CO_2 increased the dependency upon AM fungi known to form an extensive mycelial network (Allen et al. 2005). However, only recently have molecular sequencing techniques been developed for AM fungi allowing for more extensive species-level community analyses. These have not yet been applied to AM fungal communities altered by elevated CO_2 experiments.

EM communities are far more complex and difficult to assess. Parent et al. (2006) found changes in EM fungal communities in response to elevated CO_2. However, there was a shift toward EM fungi located deeper in the soil profile (Pritchard et al. 2008). Alberton and Kuyper (2009) showed that two fungi with different N strategies (one nitrophilous, one not so) resulted in very different outcomes in N allocation and immobilization in response to elevated CO_2. A site like the James Reserve probably has somewhere between 40 and 200 species in a stand of plants (Allen et al. 2002). However, we have very little information on how the community composition changes in response to elevated CO_2, increasing T, or altered θ. Alternatively, as a test system, we might look at the impacts of N deposition on EM communities with the hypothesis of hindcasting back to higher C:N ratios (Hoeksema et al. 2010). If this model is appropriate, we have a few studies in which to examine mycorrhizal composition and even functional change.

In an early study, Karen et al. (1997) found that although there was a large decline in sporocarp production (see also Arnolds 1991), an analysis of root tips using RFLP analyses showed that a high diversity actually remained at the site. This result has been duplicated in other ecosystems (e.g., Lilleskov et al. 2001). In a cross-continent study, Lansing (2003), using an RFLP analysis of the ITSF region, found that richness declined slightly with high N fertilization, showing a shift in the species increment curve, but that species overlap between N-fertilized and control plots was low.

One hypothesis is that the turnover of EM would be increased under high N, such that individual mycorrhizal tips last shorter, returning the C back to the atmosphere more rapidly. We were unable to demonstrate a consistent response, however (Treseder et al. 2004). In response to fertilization, some fungi increased their C accumulation lifespan and others decreased. Another approach is needed to tease this community level dynamic apart.

Allen et al. (2010) found that with N fertilization, the total numbers and richness of EM declined. In the control plots, the pines obtained approximately 35 % of their N from mycorrhizal fungi, while allocating 20 % of the leaf NPP to the fungi in exchange for that N, based on Hobbie and Hobbie (2006). However, with fertilization, the needle biomass dramatically increased, making the ratio of leaf:root tip increase dramatically. N isotopic fractionation data showed that the trees could obtain all their N from the added fertilizers, and the EM were reduced to improving P uptake, or simply existing as commensalists or even parasites. The fungi might be C starved, as no fruiting of EM was found during the duration of the study in the N fertilized plots, although they continued fruiting in control plots and in the surrounding forest. Alternatively, in *Adenostoma fasciculatum*, under elevated CO_2, $\delta^{15}N$ fractionation between the leaf tissue and soils indicated that mycorrhizal fungi increased the fraction of N available for aboveground productivity (Allen et al. 2005).

Examination of high N deposition-fertilization studies in southern California also show interesting patterns that we can use to understand the implications of N deposition and, indirectly, develop testable hypotheses to elevated CO_2., using the Hobbie and Hobbie (2006) model of N and C allocation based on isotopic fractionation. Pinaceae appear to be particularly sensitive to N deposition, in part because aboveground productivity tends to increase beyond the sustainability of the root/mycorrhiza system to sustain water and P uptake (see Allen et al. 2010). In the San Bernardino Mountains, where N deposition has been studied extensively (Sirajuddin 2009, Allen, Sirajuddin and Fenn in preparation), we developed a regional phylogeny for the Transverse Ranges in southern California, focusing on a low N input site (Camp Osceola), a high N site (Camp Pavika) and with additional N fertilization at both sites (Fenn and Bytnerowicz 1993) along with the James Reserve, an intermediate depositional site. In the low N control site, we estimated that the trees obtain approximately 35 % of their N from mycorrhizal fungi (based on the Hobbie and Hobbie fractionation model). To obtain that N, the trees allocated approximately 21 % of the total NPP. In turn, the fungi allocated 41 % of their N to obtain that C. This value is within the expected allocation range for the allocation of C to mycorrhizal fungi. In the high N treatments, we could not generate an allocation. The dominant shift was from fungi such as *Rhizopogon* sp., *Russula acrifolia*, and *Cortinarius* sp. No fruiting was observed, although this may be compounded by the severe 2001–2002 drought. But, in both the high N deposition site, and following long-term N fertilization, the dominant fungi were *Cenococcum* sp. and unknown Thelephoraceae species found on the root tips. Sporocarps of *Cenococcum* have not been found and we were unable to find sporocarps of *Thelephora* spp. Our preliminary analysis suggests that the total

allocation may remain similar, but the NPP of the sites increased dramatically with added N (Fengming Yuan, personal communication). Trees in the region did suffer high rates of mortality during the 2001–2002 severe drought.

Angiosperms, including oak (*Quercus agrifolia*), may simply increase production in response to added N, but alter their C allocation patterns. Again, using the Hobbie and Hobbie (2006) model and examining isotopic data from sporocarps collected from high and low N deposition sites (Allen et al. 2005) and the isotopic signatures in oak leaves (Cario 2005), we were able to determine changing allocation of C and N patterns. In a low N area (the Sky Oaks reserve), the trees received 35 % of their N from EM fungi, while allocating 20 % of the aboveground NPP (estimated as per Arbaugh et al. 1998) to the EM fungi in exchange. With N deposition (at the San Dimas Experimental Range), the plants only needed 23 % of their N from EM fungi and allocated only 10 % of their aboveground NPP.

Importantly, few of the fungi found in the control plots actually disappeared from the N added areas, although they did shift relative dominance. Those EM fungi lost could have simply been missed in the sampling. Species increment curves demonstrated that not all EM fungi present at any of the sites were accounted for. As CO_2 continues to increase, and potentially N deposition is controlled, will the species' relative abundances shift back or adjust to a new composition remains an interesting question.

One aspect that could be undertaken is to study individual fungi and use these to parameterize currently hypothetical stoichiometric models (Allen et al. 2003). In examining AMR images, we identified two EM morphotypes that correspond to morphotypes isolated by coring and identified by sequencing. Both were from our James Reserve site, a moderate N deposition location. We have analyzed the fungi, plants and soils for $\delta^{15}N$ and $\delta^{13}C$, along with soils and plants to evaluate dynamics and change. Hoeksema and Kummel (2003) found that turnover rates of fungi increased with elevated CO_2, although Treseder and colleagues (2004) did not find a consistent change with N fertilization in either sporocarp and root tip age or rhizomorph lifespans, respectively. Hobbie and Agerer (2010) developed a means to evaluate comparative strategies among fungi based on $\delta^{15}N$ fractionation. Two fungi in particular were identified at the James Reserve, located near each other. The first was *Russula acrifolia*. This fungus has only a small isotopic fractionation, suggesting that it is more exploratory, probably utilizing the same N sources as the plant (NO_3^-, NH_4^+, and amino acids). The other fungus is an unknown taxon of *Cortinarius*. This fungus has a high fractionation, suggesting that it is taking up organic N, fractionating, and transporting proteins to the plant. Based on the stoichiometric model, these two fungi together increase the ability of the plant to acquire multiple forms of N. If one or more of these strategies are lost, then we could expect important shifts in plant nutrient relationships to emerge. By coupling observations of individual tip and hyphal dynamics from AMR units, with sequencing for both identification and specific gene activities, and with isotopic analyses, hypothetical models such as the stoichiometric approaches could be accurately parameterized. With time and with experimental treatment,

patterns of individual fungal behaviors might emerge that would provide the critical answers to this difficult question.

3.3.2 Shifting Plant Composition

There are numerous studies on the impacts of increased N and CO_2 on plant communities. We will not deal with this specific issue here, except as they relate to mycorrhizal functioning. Wolf et al. (2003) reported that elevated CO_2 altered the diversity of plants, which in turn changed the composition of AM fungi. Unfortunately, the site had been sterilized with methyl bromide prior to the imposition of the elevated CO_2 compromising what could have been a very important study.

The interesting shift in vegetation in response to elevated CO_2 relating to mycorrhizal dynamics occurred in the Mojave Desert FACE (Free Air CO_2 Enrichment) study. There, Smith et al. (2000) found that for a wet period, there was a dramatic increase in *Bromus tectorum*. This pattern was not consistent through time, but *Bromus* dominance appears to cycle (Salo 2004) with precipitation, and has important implications for mycorrhizal functioning. We would have expected to see an increase in AM fungal activity and even a potential shift in the species composition in response to elevated CO_2. But no change in percent infection, or glomalin (an indication of long term AM fungal activity) was found (Clark et al. 2009). Importantly, all species of *Bromus* are also considered nitrophilous, and often replace native shrubs and forbs under N deposition or fertilization (e.g., Allen 2004). *Bromus tectorum* seems to have little response to AM, although the relationships are formed (Wolfe et al. 2003). In other species of *Bromus*, the AM fungi shift in response to elevated CO_2 and to N (Rillig et al. 1998a, b, 1999), but the plant appears relatively unaffected. Clearly more work on the relationships between mycorrhizae, elevated CO_2, and plant community dynamics is needed.

3.3.3 Adaptation: A Missing Element from Global Change Studies

The rate of change in atmospheric is very rapid. There are many calls that although CO_2 levels are nowhere near highest levels geologically, the rate of change is unprecedented. As we do not know past rates of change (such as the elevated CO_2 shift from the Paleocene to Eocene with high CO_2 inputs), it is difficult to know if ecological or evolutionary adaptations can occur within the timescales of the current rate of change.

Across the long history of mycorrhizal symbioses, major changes in new mycorrhizal types occur at times of elevated CO_2 (Allen 1996). When the land was first

invaded, atmospheric CO_2 was high, and nutrients in short supply. AM fungi, which were already present, possibly living symbiotically with algal communities as *Geosiphon* does today (Schuessler and Kluge 2001). During the Carboniferous Period, globally high levels of CO_2 were found (as high as 2,000 ppm). This is also the time period when there was a major change in the Pinales (i.e., order comprising extant conifers). Specifically, the EM Pinaceae separated from the Cupressaceae. The Cupressaceae and all other northern hemisphere gymnosperms are AM whereas the Pinaceae forms EM. The fungi forming AM are Glomeromycota, a distinct monophyletic of ancient fungi, whereas EM are Ascomycota and Basidiomycota (plus one advanced Zygomycota, the Endogonales). The timing of this event corresponds to a spike in atmospheric CO_2. On one final note, nonmycotrophic annual plants in the Caryophyllales are modern plants. They rapidly spread in high fertility soils during the Pleistocene, when atmospheric CO_2 levels were particularly low (180 ppm).

Klironomos et al. (2005) found, by looking at mycorrhizal infection over several generations of short-lived plants, that if the imposition of elevated CO_2 occurred abruptly, then a marked change in mycorrhizal activity and composition occurred. However, if the imposition of elevated CO_2 occurred gradually across multiple generations, then neither parameter changed significantly. This experiment suggests that we need to think about our systems and interpretations of rates of change. The advantage of this study was that it went across generations of plants. For many plants, changes in CO_2 levels, and warming conditions will occur across generations, unlike the immediate imposition of FACE and growth chamber experiments. However, for many tree species, the changes humans are imposing are well within a generation. Many old growth forests were initiated under atmospheric CO_2 at approximately 300 ppm, and individual trees will be alive as we exceed 450 ppm and beyond.

Whether the fungi are adapting across generations, or even evolutionary is an important question that deserves consideration. The Glomeromycota do not have cross walls, such that the mycelial network has unbounded, large numbers of nuclei scattered through the hyphae. There is still debate as to whether these are identical or vary within an "individual" but even within an individual there must be some mutation of individual haploid nuclei. In EM in the higher fungi, the dikaryons have variation upon which there can be changing gene frequencies under environmental change condition. Thus there is a potential for both ecological and evolutionary adjustment that cannot be studied in growth chamber studies or short term field enrichments.

3.4 Altered Environments: A Global View

Mycorrhizae contribute a large fraction of the sequestered C in soils. Further, soils contain approximately three times as much C as in the atmosphere; imparting small changes in soil processes with potential to confer dramatic impacts on the

atmospheric CO_2 concentrations, and feedback effects such as climate change and C:nutrient dynamics. However, soil ecological research, and mycorrhizal research in particular suffers from a strong aversion to getting in the field and determining what is actually occurring. It is far easier to continue to run pot culture studies than to investigate belowground processes as they happen. There is a further notion that the tools of the 1970s, coring and laboratory measurement, are adequate to study soil processes. Unfortunately, these perspectives are hindering our understanding of C dynamics at ecosystem to global scales.

Measuring aboveground processes and subtracting to extract soil "differences" are extremely inaccurate. Even the best eddy co-variance system dumps much of the phenomena data (using best Ameriflux standards), much of which we believe is tied to soil dynamic processes. Coring is completely inadequate, manifesting as almost a classic Heisenberg uncertainty principle. As soon as the soil is extracted, it is changed. One can never take two cores in time, because the second core changes space as well. We know enough about soil communities to know that two cores samples differ in organisms, compositions, and structure (Allen and MacMahon 1985; Klironomos et al. 1999; Allen et al. 2007). At the very least, coring should be coupled with sensor technology to actually determine what is happening in the field, not what might happen based on theory.

There is a large research base with background information on the impacts of acute anthropogenic perturbation on mycorrhizae, from disturbance, to N and P fertilization, as well as immediately enriched CO_2 environments. The impacts of chronic change, in particular N deposition and increasing atmospheric CO_2 that changes at decadal to century scale adjustments are much more difficult. We often try to relate changes occurring today with those in the geological record, but we do not know if those occurred at the century or millennial scale. We can model (e.g., DayCent) and we can hindcast (e.g., Egerton-Warburton et al. 2001), but we need a combination of real long-term monitoring and perturbation studies focused on the soil environment and soil environmental change. New tools from soil observatories (Allen et al. 2007) to next generation sequencing capacity (Nilsson et al. 2011), with the ability to resolve processes, not just composition, provide incredible opportunities to study the impacts of global change. Observatories such as NEON and Ameriflux (and their international collaborations) have the potential to incorporate such exciting new technologies and ideas, but those programs must not be allowed to continue to flounder on past approaches, because it is easier for the entrenched bureaucracy, agency personnel, and entitlements to particular groups of scientists to continue with business as usual.

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