

## Commentary

# Symbiotic fungi and clonal plant physiology

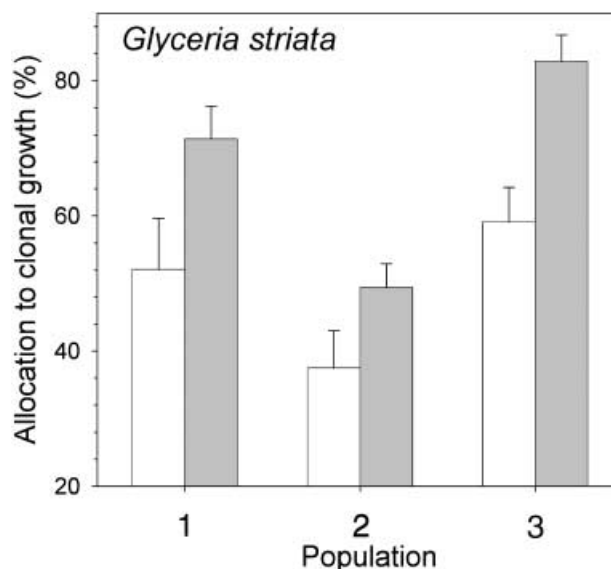
Fungal symbionts commonly occur in plants influencing host growth, physiology, and ecology (Carlile *et al.*, 2001). However, while whole-plant growth responses to biotrophic fungi are readily demonstrated, it has been much more difficult to identify and detect the physiological mechanisms responsible. Previous work on the clonal grass *Glyceria striata* has revealed that the systemic fungal endophyte *Epichloë glyceriae* has a positive effect on clonal growth of its host (Pan & Clay, 2002; 2003). The latest study from these authors, in this issue (pp. 467–475), now suggests that increased carbon movement in hosts infected by *E. glyceriae* may function as one mechanism by which endophytic fungi could increase plant growth. Given the widespread distribution of both clonal plants and symbiotic fungi, this research will have implications for our understanding of the ecology and evolution of fungus–plant associations in natural communities.

### Clonal plants and fungal symbionts

Well over 80% of vascular plant species form symbiotic associations with arbuscular mycorrhizal fungi (AMF) within their roots (Smith & Read, 1997). Also, AMF and leaf-inhabiting fungal endophytes are widely distributed in some ecologically important groups, such as the grasses (Newsham & Watkinson, 1998; Clay & Schardl, 2002). Given the preponderance of clonal plants in many habitats worldwide, the potential for fungal symbionts to impact plant population and community dynamics is enormous. In addition, by differentially affecting the sexual or asexual reproduction of host genotypes, infection by symbiotic fungi (whether pathogenic or mutualistic) is likely to influence microevolutionary processes within plant populations.

For clonal plants, clonal growth is a major determinant of genet fitness through its effects on genet persistence and new ramet and seed production (Pan & Price, 2002). Only a few studies have described the potential role of symbiotic fungi in the growth and asexual reproduction of clonal plants. Streitwolf-Engel *et al.* (2001) showed that, for the stoloniferous herb *Prunella vulgaris*, AMF explained more of the variation in clonal traits such as ramet production than did host genotype. They concluded that the effects of AMF on plant growth and clonal reproduction were great enough to ‘affect population size and variation of clonal plants in communities’. For the stoloniferous grass *Glyceria striata*, Pan and

Clay (2002) reported that plants infected by the systemic endophyte *Epichloë glyceriae* produced more stolons and clonal growth mass than uninfected plants. The results suggest that infected (+E) *Glyceria* genotypes should be spatially larger due to increased lateral spread than uninfected (–E) genotypes in natural communities. However, infection and host genotype were confounded because only naturally infected or uninfected individuals were utilized. In a follow-up study (Pan & Clay, 2003), effects of infection and host genotype were experimentally separated through the use of +E and –E replicates of the same host genotypes. This was achieved by manual separation of +E individuals into two ramet groups, one of which was treated with the systemic fungicide Benomyl®. Two host genotypes were replicated for each of three populations in southern Indiana, USA. Total dry mass did not differ between +E and –E plants; however, stolon numbers and lengths were significantly greater in +E plants (Pan & Clay, 2003). Furthermore, +E hosts allocated more of their total mass to clonal growth in all three populations (Fig. 1). Clearly in this system there was a shift in resource allocation associated with fungal infection. Putative physiological mechanisms that might account for this effect remained elusive.



**Fig. 1** Mean (+ SE) percent of the total genet biomass allocated to clonal growth (stolons and daughter ramets) in three populations of the clonal grass *Glyceria striata* infected (shaded bars) or not infected (open bars) by the systemic fungal endophyte *Epichloë glyceriae*. Four infected and four uninfected replicates of two genotypes were used in each population. Data supplied by J.J. Pan, based on research reported in Pan & Clay (2003).

## The *Epichloë*–*Glyceria* symbiosis

*Epichloë* (Clavicipitaceae; Ascomycotina) and its asexual derivatives (*Neotyphodium*) are systemic fungal endophytes of cool-season grasses with effects on their hosts that span the continuum from antagonism to mutualism (Schardl, 1996; Schardl *et al.*, 2004). Host benefits include protection from herbivores due to four classes of alkaloids produced by the endophyte; improved abiotic stress tolerance; and enhanced growth (Clay & Schardl, 2002). Antagonistic aspects to the symbiosis are due to the abortion of host inflorescences during stroma formation, which is part of the fungal sexual cycle (Schardl, 1996). The fungal hyphae are only located between the leaf cells of the host and do not penetrate host cell walls. Presumably, endophytic hyphae are able to utilize simple sugars, amino acids or other metabolites located within the intercellular spaces as nutrient sources (Clay & Schardl, 2002).

The clonal grass *Glyceria striata* is widely distributed throughout most of the United States, typically occurring in moist woodlands or marshes (Gould & Shaw, 1983). An individual genet grows vegetatively by basal tiller production to form a clump of ramets, but can also exhibit lateral spread during clonal growth by ramet production along extending stolons. Tillers can develop large, open inflorescences (panicles) for sexual reproduction, but only when they are not infected by *Epichloë glyceriae*. In their paper in this issue, Pan & Clay note that, due to the replacement of inflorescences by fungal fruiting bodies (stromata), fertile inflorescences are never found on *Epichloë*-infected hosts. Hence, *G. striata* is sexually sterile when infected, but remains quite capable of vigorous clonal growth and asexual reproduction (Pan & Clay, 2003; Fig. 1).

## The dynamics of carbon

In efforts to document and understand physiological integration, that is, the sharing of resources between connected ramets within a genet, clonal plant biologists have often used  $^{14}\text{C}$  to trace the movement of carbon compounds (Jónsdóttir & Watson, 1997). Physiological integration may be ecologically advantageous to clonal plants in resource-poor environments (Jónsdóttir & Watson, 1997) or highly competitive communities (Gough *et al.*, 2002).

The new paper by Pan & Clay extends clonal plant research a bit further by asking whether or not changes in physiological integration can be mediated by a symbiotic fungus. Because they had shown previously that infection by *Epichloë* increased clonal growth of the host *Glyceria striata* (Pan & Clay, 2002, 2003), they hypothesized that increased resource movement in infected plants could be part of the mechanism responsible.

Both severed and intact stolons of *G. striata* that were infected (+E) or not infected (–E) by *Epichloë* were labeled

with  $^{14}\text{C}$  during the thirteenth week of the glasshouse experiment. Two weeks later, above-ground biomass was harvested; labeled stolons were divided into segments; and these were analyzed to determine the pattern of assimilate distribution. Stolon segments both proximal and distal to the original  $^{14}\text{C}$ -labeled leaf were assessed for radioactivity.

Pan & Clay found that both proximal and distal movement of  $^{14}\text{C}$  away from the labeled leaf was greater for +E stolons; in contrast, more assimilate was retained by the labeled leaf of –E stolons. Although carbon movement was greater along +E stolons, there was no difference in stolon growth or new ramet production between +E and –E hosts, suggesting that the observed level of physiological integration did not play a major role in improving clonal growth in this study.

The results of Pan & Clay's efforts are exciting because, by showing that symbiotic fungi change the dynamics of carbon within the host, they have opened up new avenues for research into the mechanistic basis for such an effect. The physiological reasons for the increase in carbon translocation in infected hosts is currently unknown, but Pan & Clay speculate that hormones or enzymes produced by *Epichloë* could be responsible. Although not explicitly mentioned by the authors, fungal-mediated changes in cytokinin levels may be a possibility, especially as cytokinins have been implicated in the regulation of source–sink relations in plants (Roitsch & Ehneß, 2000). Furthermore, both phytopathogenic and mycorrhizal fungi have been shown to produce cytokinins (Jameson, 2000).

It is therefore possible that the endophyte affects assimilate partitioning by increasing the sink strength of meristems, which provide a nutrient-rich environment for hyphal growth (Schardl *et al.*, 2004). Active uptake of carbon compounds by the fungus in regions of active host growth should increase sink strength. Alternatively, source strength may be increased if the endophyte somehow enhances leaf photosynthesis. Indeed, there is some evidence for greater photosynthetic rates in endophyte-infected tall fescue (e.g. Marks & Clay, 1996), but it is not certain that such effects would increase carbon translocation. However, assimilate movement is clearly driven by the pressure gradient between source and sink regions (Oparka & Santa Cruz, 2000), and the possibility that endophyte infection can alter source–sink relations cannot be discounted. Future investigations into the carbon physiology of the endophyte–grass symbiosis should consider fungal-mediated effects on carbohydrate production (Marks & Clay, 1996); translocation (Pan & Clay); and storage (Cheplick & Cho, 2003).

## Ecological ramifications

Pan & Clay's new study provides a nice starting point for further investigations into the potentially important role that symbiotic fungi play in the physiology and ecology of

clonal plants. There is no doubt that the ability to integrate resources impacts the population dynamics of clonal plants (Jónsdóttir & Watson, 1997). Provisioning of carbohydrate resources to new ramets by established genet should improve the probability of ramet- and whole-genet survival in a heterogeneous environment. Symbiotic endophytes might improve the odds for genet spread and persistence within the local community.

It is also increasingly recognized that symbiotic associations can be significant determinants of plant community structure (Clay, 2001). Mycorrhizal associations, for example, can affect the ecology of clonal species (Streitwolf-Engel *et al.*, 2001; Watson *et al.*, 2002) and entire plant communities (Newsham *et al.*, 1995). The community and ecosystem-level consequences of fungal endophyte infection are only just beginning to be documented and explored by ecologists (Clay & Schardl, 2002; Rudgers *et al.*, 2004).

### Gregory P. Cheplick

Department of Biology, College of Staten Island,  
City University of New York, Staten Island,  
NY 10314, USA  
(tel 1718 9823931; fax 1718 9823852;  
email cheplick@mail.csi.cuny.edu)

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**Key words:** carbon translocation, clonal plants, endophytes, *Glyceria striata*, symbiotic fungi.

## Plant and arbuscular mycorrhizal fungal diversity – are we looking at the relevant levels of diversity and are we using the right techniques?

A strong emphasis in modern ecology is placed on an experimental approach to understanding mechanisms that explain patterns actually observed in nature. Testing the relevant hypotheses experimentally can often draw on a wealth of descriptive ecological information that exists for a large number of plants and animals, much of which was probably collected before descriptive ecology became less fashionable. Thus the observation of patterns in nature typically precedes the experimental tests of which mechanisms might explain

their existence. Experimental ecologists may often take such descriptive data for granted. However, for those of us working on organisms where we do not have the necessary information at hand about these patterns in nature, then testing the relevant hypotheses can be a bit like going fishing: before we start, we don't know whether we will get anything and even if we are successful, perhaps there is always the elusive 'one that got away' (the more important or the more ecologically relevant hypothesis that we did not think to test). Working on the ecology of arbuscular mycorrhizal fungi (AMF; Glomeromycota) falls into this latter category of organisms, where descriptive data on their community structure in different environments and in relation to the community structure of their host plants is sadly lacking. In this issue (pp. 493–504), Landis *et al.* present descriptive data showing the correlation in Wisconsin oak savannas between AMF species richness and plant community composition. This relationship should exist in natural communities if a number of experimental studies testing the relationship between these two factors were correct and were, indeed, testing ecologically relevant hypotheses.

The study by Landis *et al.* also raises two issues that deserve some further discussion. The first of these is raised by the authors themselves and concerns the reconstruction of AMF species richness by using, controversially, the morphology of AMF spores, rather than molecular techniques to measure AMF species richness. The second concerns the ecologically relevant measure of AMF diversity: is it interspecific or intraspecific AMF diversity that is ecologically important?

### The relationship between the diversity of plants and their fungal symbionts

Few would doubt the ecological importance of arbuscular mycorrhizal fungi, given that they improve plant nutrition and growth and are found in symbiosis with the roots of the majority of land plants (Smith & Read, 1997; van der Heijden & Sanders, 2002). Over the past two decades, a number of key experimental studies have indicated that AMF affect plant community structure, diversity and productivity. Grime *et al.* (1987) first showed that the presence of AMF can increase the diversity of plants in experimental plant communities and subsequently, using a similar design, van der Heijden *et al.* (1998) showed that increasing AMF species richness led to an alteration in the plant community structure and an increase in plant productivity and diversity. Vice versa, by manipulating the diversity of the plant community, Burrows and Pflieger (2002) saw an effect on the structure of the AMF community. So it appears that a change in the community of either one of the symbionts affects the other.

There are also some elegant conceptual models that explain the effects of each symbiont on the other, such as the negative feedback model (Bever *et al.*, 1997; Bever, 2003), which

also predicts that a change in the diversity of one symbiont should affect the diversity of the other. Experimental investigations also support this model (Bever, 2002). However, if the experimental ecologists have got it right, and the relationships between the diversity of plants and AMF are not obscured by other factors that were not considered, then we should see some correlations between the diversity of these two groups of organisms in natural ecosystems. It is therefore encouraging that this is exactly what Landis *et al.* show in their study. As the authors are fully aware, the study is based on correlations, meaning that one cannot say whether plant diversity directly affects fungal diversity or *vice versa* and it must be pointed out that both are also co-correlated with soil texture and soil nitrogen content.

### Morphological vs molecular descriptions of AMF communities

One aspect that is controversial regarding the study is the use of morphological techniques to measure AMF species richness rather than PCR-based molecular identification methods. AMF spores can be sieved from the soil and then classified into different morphological types. These can then either be counted in order to obtain their abundance and then used to reconstruct the AMF community structure or they can simply be recorded as present/absent in order to obtain a measure of AMF species richness (as favoured by Landis *et al.*). The problems with this approach are numerous. An AMF species could be present in low frequency but produce many spores. Another could be very abundant but hardly produce any spores. This is why Landis *et al.* do not favour this measurement for AMF abundance. However, what Landis *et al.* do not point out is that there are a number of other reasons why the method may be seriously flawed.

First, the environment may affect sporulation. Thus, the comparison of AMF species richness in different environments may reflect differences in which, and how many, AMF species sporulate in the different environments, even though the same fungi could potentially be present in all environments. In this case, the existence of a correlation between these two factors would be a red herring in the search for patterns that match the experimental predictions. Second, AMF spores are notoriously difficult to identify when sieved directly from the soil and some AMF taxonomists only consider identification to be reliable when the fungi have first been established in pot culture, from which many replicate spores of the same fungus can be observed. Even then, it can take a skilled researcher many hours to correctly mount samples of one fungus and observe the spore wall structure for correct identification. Third, we now know from molecular based studies of AMF communities in plant roots that many AMF are present in roots, although spores of these fungi have never been found using the techniques proposed by Landis *et al.* One of the clearest examples of this comes

from a study that was also published in *New Phytologist*. Clapp *et al.* (1995) used molecular techniques to show that the roots of one of the common understorey plants in a woodland in north Yorkshire, UK consistently contained AMF for which no spores had been found. There are several other studies that document similar findings.

However, a more recent study provides even more worrying data for the proponents of the spore morphology-based methods. Rosendahl and Stukenbrock (2004) have sequenced AMF ribosomal DNA (rDNA) from plants in a Danish grassland community on a sand dune. Using a phylogenetic analysis, they found that the sequences fitted into 11 clades within the Glomeromycota. Of these 11 clades, only four matched to known AMF for which species have been described on the basis of their spore morphology. Furthermore, within the four clades of known AMF, very few of the spore morphotypes were actually found at the Danish grassland site that match to those sequences, although they are known from other locations. This study indicates that AMF species richness, based on spore counts, is probably only scratching the surface of what really occurs in plant roots. Landis *et al.* partly justify their chosen methodology because they claim that sporulation is an important part of the AMF life-cycle. The molecular data, however, indicate that some AMF species are obviously not sporulating very often, if at all, and the importance of sporulation may be much less than has previously been assumed.

As Landis *et al.* point out, the molecular methods available for AMF identification are by no means problem-free. The most precise of the methods, to date, involves amplifying parts of the AMF ribosomal DNA from roots and then sequencing the DNA. This can be both costly and time consuming, given the diversity of sequences that can be found in the root system of one plant. But the real problem with all of the molecular methods is the amount of genetic variation within an AMF species and even within an AMF individual. It is well known that high sequence variation for a given region of DNA occurs in AMF, even within single spores (Sanders, 2002). For ecologists this is problematic because when two or more different AMF sequences are obtained from a root system we don't know whether those sequences originate from one, two or several different AMF individuals. Furthermore, without knowing the true extent of the genetic variation within an individual, among individuals of the same species and among different AMF species, it is very difficult to know exactly what this sequence diversity actually represents.

The amount of genetic variation in an AMF spore or in an AMF species is in itself a controversial issue. The reconstruction of AMF phylogeny using rDNA sequences relies on the underlying assumption that the variation in rDNA is so low that distinguishing among AMF morphotypes with rDNA sequences is not problematic. However, the failure of so many attempts to make true AMF morphotype-specific or species-specific primers suggests that it is not quite so

simple. Other studies, however, indicate that the diversity of rDNA sequences within a morphotype is so large that such identification on the basis of one or a few sequences could be very misleading (Rodriguez *et al.*, 2004b). In fact, Rodriguez *et al.* (2004b) found that several isolates of two different morphotypes of AMF harboured extremely diverse rDNA sequences. However, they also found that the two morphotypes also shared some identical sequences. They claim that low sequence variation suggested by some researchers is simply due to the fact that they have not sequenced intensively enough to see some of the low frequency variants (Rodriguez *et al.*, 2004a). Furthermore, the first quantification of genome-wide molecular variation among isolates of one species of an AMF shows extremely high genetic variation, even in a very small field (Koch *et al.*, 2004). The study was not based on rDNA variation but on 250 different polymorphic markers. The issues about genetic variation in AMF are clearly not yet sufficiently resolved such that we know exactly what we are dealing with when we pull a few AMF rDNA sequences out of the roots of a plant.

### Should we actually be trying to measure AMF species or morphotype diversity?

The study of within species genetic variation in AMF (Koch *et al.*, 2004) highlights a final concern about studies that measure AMF diversity. Many of these studies, whichever method they employ, justify the ecological relevance of their study because of the experimentally demonstrated relationship between AMF species richness and plant diversity (van der Heijden *et al.*, 1998). However, most of such experiments have used one AMF isolate (often originating from one spore) to represent an AMF species and have ignored the variation in plant growth that could be due to within-AMF species variation. The study of Koch *et al.* (2004) shows that there is very large genetic variation within an AMF species, even within a small field, and that variation in how the fungi grow also has a genetic basis. A recent study by Munkvold *et al.* (2004) has shown that different isolates of one AMF species can supply very different levels of phosphorus to the plant. Perhaps the relationship might exist between the number of genetically different AMF in the field and the diversity of plant species; the distinction as to whether this is due to variation among or within AMF species or morphotypes may be largely irrelevant. I would certainly want to know the answer to this before embarking on an extensive and probably very costly survey of AMF species or morphotype variation in the field. The methods employed by Landis *et al.* will not be able to tackle this question, but molecular methods based on quantification of molecular variation within the AMF community, when further refined, along with a better understanding of AMF genetics and levels of genetic variation, may provide the answers.

## Perspectives

The methods that are currently available for AMF identification in ecological studies are problematic. I remain sceptical regarding the validity of the occurrence of spores in the soil as a measure of AMF species richness. Despite my criticisms I was, however, struck by the following sentence of Landis *et al.* 'However, we find it extremely hard to believe that the striking correlations among AMF community composition and species richness, plant community composition and richness, and environmental factors that are demonstrated in this paper by our use of spore morphology could be artefacts'. We may well find in the future that the correlations observed by Landis *et al.* between plant diversity and AMF species richness may not exist when we measure the true richness that occurs in roots. It may turn out that the results reflect changes in the numbers of AMF that sporulate with changes in plant diversity, and that the sporulating AMF mask completely different underlying levels of AMF diversity/richness of nonsporulating AMF. Indeed, the correlations observed by Landis *et al.* are unlikely to be artefacts and it will be exciting to find out in the future what is the underlying mechanism for their existence.

Ian R. Sanders

Department of Ecology and Evolution, University of  
Lausanne, 1015 Lausanne, Switzerland  
(tel +41 21 6924261; fax +41 21 6924265;  
email ian.sanders@unil.ch)

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**Key words:** AMF species richness, AMF spore morphology, arbuscular mycorrhizal fungal diversity, molecular techniques, oak savannas, plant community composition, plant diversity.

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## Meetings

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### The human footprint in ecology – past, present and future

#### Ecological Society of America, 89th Annual Meeting, Lessons of Lewis & Clark: Ecological Exploration of Inhabited Landscapes, Portland, OR, USA, August 2004

The Sustainable Biosphere Initiative, initiated by the Ecological Society of America (ESA) in 1988 and launched officially in 1991, outlined a new series of research priorities for ecology, with an emphasis on the global nature of environmental pressures and human impact on the environment (Sala, 1992). There has been a growing awareness of the importance of human impact in both managed and natural ecosystems, and from local to global scales. Coupled with this growing awareness has been an increasing need to evaluate and understand how humans are modulating the ecosystems in which they live. Finally, and most recently, ecologists increasingly feel a sense of responsibility to transmit that information to the public at large and to policy makers, who are currently making a number of decisions where relevant ecological understanding is the basis of an informed decision (Bazzaz *et al.*, 1998).

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*'Ecologists must take their science in bold new directions if humans and the natural systems on which they depend are to coexist in the future.'*

*(ESA Visions Report, Box 1)*

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The ESA annual meeting was held in Portland, Oregon from August 1–6, with over 4000 participants from all walks of the ecological spectrum: academics, representatives from nongovernmental organizations, students, and government researchers. Human impact on the environment was a central theme in the thinking and research presented at this society's meeting. A simple overview of the abstracts and talk titles is particularly revealing. From approximately 2800 oral and poster presentations at this meeting, over 60% were in some way related to human impact on the environment. Topics ranged across anthropogenic disturbance and land-use change, urban ecology, invasions, biodiversity loss, and interacting drivers of global change. Taken together, the resounding message of this meeting focused on the human footprint on the land- and waterscapes across the globe and what could be done to understand and mitigate this impact in the future. The current ESA president, William Schlesinger (Duke University, NC, USA), even went a step further emphasizing not only the scientific contract for ecologists, but the need for political motivation and responsibility as well.

#### The past: human legacy on the landscape

The idea that humans manipulate their environment is not new; however, the novel ways in which we view and interpret that impact was shown in a number of presentations, both in symposiums and contributed oral sessions. Peter Vitousek (Stanford University, CA, USA) presented evidence demonstrating how the interaction of soil fertility and climate determined practices of dryland agriculture in the Hawaiian islands. Dr Vitousek and colleagues, collecting soils from under field walls constructed by native Hawaiians approximately 500 years ago, found very high levels of available soil phosphorus (P), suggesting a 'sweet spot' for agricultural activity due to the effect of plants absorbing P from the soils and depositing nutrient-rich litter at the soil surface (Vitousek *et al.*, 2004). But

#### Box 1 Ecological science and sustainability for a crowded planet – the ESA Visions Report

In May of this year, the ESA published a new report (Palmer *et al.*, 2004a) which recognized the need to identify the future of research priorities in ecology and that this future inevitably must incorporate the effect of human activity on the environment. The goals of the Visions Committee, led by Margaret Palmer (University of Maryland, MD, USA) were established to go beyond simple assessment of environmental issues, in an attempt to outline a conceptual framework to apply our power of prediction to combat environmental problems from local to global scales (Palmer *et al.*, 2004b). In essence, this report is a call to action for ecologists worldwide to recognize the fundamental role of ecology in our collective future prompting all members of this society, and the public at large, to participate in the effort.

interestingly, the fact that the early agriculturists of Hawaii had cultivated this area for dryland agriculture was the reverse of what we might imagine – they did not manipulate the environment to increase yield of these areas, but rather took advantage of preexisting conditions of fertility due to the interacting effects of climate and vegetation on soil nutrient status.

A second perspective of the human legacy at the global scale stemming from agricultural activity came from James White (University of Colorado, CO, USA) who presented a look back at the global methane budget over the last 2000 years using air extracted from ice cores in Antarctica. Dr White showed that during this period, there has been a marked increase in methane concentrations in the last 200 years (over three-fold), but that additionally, the global methane budget was not in balance over the entire period of record. Other lines of paleoecological evidence, including isotopic ratio measurements of  $^{13}\text{CH}_4$  enrichment attributable to anthropogenic activity, and overlapping cores from other parts of the world, corroborate this finding of increased methane concentrations in the atmosphere. Mixing models suggest that these increases in global methane concentrations can be attributed to increased biomass burning and subsequent cultivation resulting in biogenically increased sources of methane production from rice cultivation and ruminant activity.

### The present: urban ecosystems

Urban zones, which presently occupy approximately 2% of the land surface and are conservatively estimated to cover 3–4% over the next 30 years, have arrived as a central focus of ecological research. The long-term ecological research (LTER) network program in the United States (<http://lternet.edu/>), begun in 1980 by the National Science Foundation, established a network of sites across the United States in natural ecosystems in an effort to examine long-term trends in ecological research and at large spatial scales. The most recent additions to the network have been two urban zones: one in the metropolitan area of Baltimore, Maryland (<http://www.beslter.org/>); and the other in the greater metropolitan area of Phoenix in the arid matrix of central Arizona (<http://caplter.asu.edu/>). Urban zones have been largely ignored as part of traditional ecological research precisely because of the extensive human influence and 'nonnatural' conditions that surround these areas. It has become increasingly clear, however, that ecologists must better understand these fast-growing urbanized areas, as a result of the increasing importance of land area and the disproportionate effect of urban zones on adjacent ecosystems (Austin *et al.*, 2003). Nancy Grimm (Arizona State University, AZ, USA), director of the Central Arizona-Phoenix LTER and president-elect of the ESA, presented the provocative idea that understanding biogeochemistry in urban zones may require a change in our theoretical

understanding of element interactions and ecosystem functioning (Grimm *et al.*, 2000). Dr Grimm argued that increased concentrations of nitrogen (N) due to N deposition and trace metals from industrial activities may fundamentally disrupt the element interactions in both terrestrial and aquatic ecosystems that are part of and interface with urban zones, and that this may result in shifts in fundamental nutrient limitations and novel biogeochemical interactions. This suggests that our predictive power for understanding urban ecology may be limited due to the profound human impact on the landscape and the creation of novel ecological conditions and interactions.

Two presentations from different study sites highlighted the same conclusion of the importance of nonnative species creating new ecological interactions. Katalin Szlavecz (John Hopkins University, MD, USA) presented data from the Baltimore Ecosystem LTER that showed dramatic changes in the soil invertebrate communities in comparing rural and urban forests and lawns. However, contrary to the general belief that urban environments are impoverished in biodiversity, urban forests had the highest levels of species richness, in large part due to the introduction of nonnative species in these environments. The importance of the exotic fauna varied by taxonomic group but largely explained the shifts in community structure, particularly earthworm abundance in urban environments. Margaret Carreiro (University of Louisville, KY, USA) demonstrated that decomposition was altered along urban-rural gradients due to changes in: litter quality from increased nutrient deposition; species composition; and soil community structure, particularly nonnative earthworm abundance. Dr Carreiro suggested that the combined effects of these multiple changes are only beginning to be documented and that comparative studies across a number of urban zones will be necessary before we can begin to understand the impact of urbanization on ecosystem processes.

### The future: global change and interdisciplinary science

Ecology as a field of study has, almost by definition, been an interdisciplinary endeavor, but never has it been more clearly demonstrated than in some of the research presented at this ESA meeting. Recent research on a number of topics incorporated work not only from other scientific disciplines but also the social sciences, including economics, human demography, and sociology. An entire oral session, Estimating Carbon Dynamics in Forested and Deforested Landscapes of Costa Rica – organized by Flint Hughes (Institute of Pacific Islands Forestry USDA Forest Service, HI, USA), Boone Kauffman (Institute of Pacific Islands Forestry USDA Forest Service, HI, USA) and Alex Pfaff (Columbia University, NY, USA) – focused on the necessity to integrate economic models and scientific information in order to



understand how carbon sequestration in tropical forests and the potential for carbon trading under the Kyoto protocol for non-Annex 1 countries could impact both ecosystems and human society. A variety of presentations demonstrated the ecological challenges of calculating carbon pools, particularly with forest-to-grassland conversion (Judith Jobse, Oregon State University, OR, USA) and the potential for carbon accumulation in secondary tropical forests (Miguel Cifuentes Jara, Oregon State University, OR, USA). But one of the newest approaches was by Alexander Pfaff (Columbia University, NY, USA), an environmental economist, who presented an integrated model of the pressures for development and deforestation in Costa Rica. Dr Pfaff and colleagues have identified the difficulties in establishing carbon and land-use baselines in tropical forests due to the scarcity of ecological information regarding regional carbon sinks (Pfaff *et al.*, 2000). He presented a model, combining ecological knowledge with economic parameters including the effects of transport costs and poverty, to extrapolate a 'new' assessment of deforestation rates that circumvent some of the largest uncertainties in our current estimates of carbon baselines. The model highlighted the need to incorporate both the ecological and economic sides of the equation in an integrated model of land-use change.

It has become clear that, as we think about the future impact of global change, one of the largest uncertainties is how these major anthropogenic changes will interact and affect ecological processes. There are a number of large research projects aimed at trying to understand exactly that; not only the direct effects of each factor in isolation, but also the complexity of considering multiple global change effects simultaneously. One oral presentation came from the Jasper Ridge Global Change Experiment, a multifactorial experiment with manipulation of four global change parameters – elevated CO<sub>2</sub>, elevated N deposition, elevated temperature, and changes in water availability. Elsa Cleland (Stanford University, CA, USA) conducted litter decomposition experiments in this experimental framework. She showed that, while warming increased decomposition, elevated CO<sub>2</sub> attenuated this effect, resulting in nonadditive effects of the interaction. In contrast, Shiqiang Wan (Oak Ridge National Laboratory, TN, USA) presented data on soil respiration under conditions of elevated CO<sub>2</sub>, elevated temperature and water availability, demonstrating additive effects of CO<sub>2</sub> and temperature with increased soil respiration in the combination treatments. The range of studies and diversity of results suggest that the complexity of the response of these interacting factors will challenge ecologists in the coming years to understand the impact of realized global change.

### Biogeosciences: the big picture

One of the newest additions at ESA has been the formation of the Biogeosciences Section, focused on biogeochemistry

and earth sciences, and the impact of global change. In line with the growing need to integrate the biological and earth sciences, also occurring at the American Geophysical Union (AGU) (Curtis, 2004), the section arose from an effort undertaken by Robert Jackson (Duke University, NC, USA) and Lars Hedin (Princeton University, NJ, USA) to capture the interest of a large number of ecologists working at the interface of biogeochemistry, earth sciences and global change research. Lars Hedin, the current Biogeosciences Section president, hopes that the new section can serve as an outlet for advocacy of interdisciplinary science within the ESA, as well as educating decision makers and funding agencies. It is yet another indication of how the future of ecology must indeed go in bold new directions and the dynamic nature of what was seen at this ESA meeting exemplified in many ways the changing face of ecology in the 21st century.

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**Amy T. Austin**

Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura (IFEVA), Faculty of Agronomy and CONICET, University of Buenos Aires, Avenida San Martín 4453, Buenos Aires C1417DSE, Argentina  
(tel +54 11 4524–8070; fax +54 11 4514–8730;  
email austin@agro.uba.ar)

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