**Biogeosciences
Discussions**

Plant communities as drivers of soil respiration: pathways, mechanisms, and significance for global change

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Abstract

Understanding the impacts of plant community characteristics on soil carbon dioxide efflux (R) is a key prerequisite for accurate prediction of the future carbon balance of terrestrial ecosystems under climate change. In this review, we synthesize relevant in-
5   formation from a wide spectrum of sources to evaluate the current state of knowledge about plant community effects on R, examine how this information is incorporated into global climate models, and highlight priorities for future research. Plant species consistently exhibit cohesive suites of traits, linked to contrasting life history strategies, which exert a variety of impacts on R. As such, we propose that plant community shifts to-
10 wards dominance by fast growing plants with nutrient rich litter could provide a major, though often neglected, positive feedback to climate change. Within vegetation types, belowground carbon flux will mainly be controlled by photosynthesis, while amongst vegetation types this flux will be more dependent upon the specific characteristics of the plant life form. We also make the case that community composition, rather than
15 diversity, is usually the dominant control on ecosystem processes in natural systems. Individual species impacts on R may be largest where the species accounts for most of the biomass in the ecosystem, has very distinct traits to the rest of the community, or modulates the occurrence of major natural disturbances. We show that climate-vegetation models incorporate a number of pathways whereby plants can affect R, but
20 that simplifications regarding allocation schemes and drivers of litter decomposition may limit model accuracy. This situation could, however, be relatively easily improved with targeted experimental and field studies. Finally, we identify key gaps in knowledge and recommend them as priorities for future work. These include the patterns of photosynthate partitioning amongst belowground components, ecosystem level effects
25 of individual plant traits, and the importance of trophic interactions and species invasions or extinctions for ecosystem processes. A final, overarching challenge is how to link these observations and drivers across spatio-temporal scales to predict regional or global changes in R over long time periods. A more unified approach to understanding

R, which integrates information about plant traits and community dynamics, will be essential for better understanding, simulating and predicting feedbacks to R across terrestrial ecosystems and the earth-climate system.

1 Introduction

Understanding and predicting the impacts of global climate change on terrestrial ecosystems is one of the main research challenges of the 21st century. Progress towards this goal has focussed on modelling the impacts of a wide array of climate change agents on key ecosystem level processes such as carbon (C) (Cramer et al., 2001; Friedlingstein et al., 2006) and nutrient cycling (Gruber and Galloway, 2008). However, these large scale processes are mediated via the plant community present within the system, which is also likely to change in response to climate shifts (Neilson et al., 2005). As such, many of the effects of climate change on ecosystem processes may be manifested through shifts in plant community properties. A large body of literature has developed, particularly over the last two decades, on the effects of plant community composition and diversity on a range of ecosystem processes (Hooper and Vitousek, 1998; Tylianakis et al., 2008; de Deyn et al., 2008). Understanding the process of ecosystem C sequestration is particularly important, because this information underpins government strategies aimed at limiting green house gas emissions in line with their Kyoto protocol commitments. Soil carbon dioxide (CO_2) efflux (R) is the largest single source of CO_2 from terrestrial ecosystems globally (Raich and Potter, 1995), and is about ten times greater than anthropogenic fossil fuel combustion (Boden et al., 2009). It is therefore a key determinant of ecosystem C sequestration, atmospheric CO_2 concentrations and climate change. Yet relatively little is known about interactions between R and plant community properties such as species composition and diversity.

Most studies which have directly investigated the effects of plant community diversity and composition upon R have been conducted in grasslands (Craine et al., 2001; de

Boeck et al., 2007; Dias et al., 2010), and these have yielded conflicting results. In common with all research on R, making useful inferences from these studies is hampered by the fact that R is a complex signal that integrates myriad interactions amongst heterogeneous populations of microbes, fungi and plants and the physical structure of the

5 soil matrix (Kuzyakov, 2006). Sources of R fall broadly into two distinct categories with fundamentally different drivers and behaviour: those sources which utilize old C (microbial respiration of organic matter) and those which largely depend upon recent plant photosynthate (respiration of live roots, mycorrhizae and some microbes subsisting on root exudates). The first group is relatively amenable to controlled experimentation, re-

10 sponds predictably to changes in temperature and moisture, and has thus been readily incorporated into models simulating R (Davidson and Janssens, 2006). However, the sources in the second category are partly decoupled from local soil conditions because they are driven by patterns of plant C assimilation, production and allocation (Högberg et al., 2001, Janssens et al., 2001) which are more difficult to measure and represent

15 within existing model frameworks. This remains a major impediment to understanding and predicting R in natural ecosystems, because belowground C allocation from plants may contribute over 50% of total R, shows substantial seasonal variation, and is responsive to a variety of drivers (Litton and Giardina, 2008).

A wide range of studies have been conducted which, whilst not directly investigating

20 the link between plant species and R, provide valuable insights into potential mechanisms. The purpose of this review is to draw together these studies, so as to identify overarching patterns of how plant species influence R, as well as the underlying mechanisms responsible for these effects. We focus on the following three distinct but interlinked topics which are each relevant to understanding how plant community prop-

25 erties affect R: 1) plant traits (Wardle et al., 2004; Cornwell et al., 2008; de Deyn et al., 2008), 2) plant invasions and range expansions (Peltzer et al., 2010), and 3) plant diversity (Hättenschwiler et al., 2005; Hooper et al., 2005). Finally, given the likelihood of future large scale shifts in the distribution, composition and diversity of plant communities driven by climate change (Neilson et al., 2005), we discuss the contrasting

approaches taken by major models to simulate species effects on ecosystem C cycling (Cramer et al., 2001; Friedlingstein et al., 2006; Reu et al., 2010). In doing so, we highlight potentially important ecological processes currently missing from the model frameworks, evaluate approaches to integrating field data into effective model representations of the processes in question, and suggest priorities for future research.

2 Plant traits and soil carbon cycling

It has long been recognized that a wide variety of plant anatomical, physiological and chemical traits covary together, reflecting fundamental evolutionary tradeoffs between alternative life history strategies (e.g., Grime et al., 1974; Wright et al., 2004). At one end of the spectrum are plants with a suite of traits maximizing rapid resource acquisition that are favoured in fertile or productive environments (Fig. 1). At the other end are plants with traits prioritizing resource conservation which dominate in infertile and or unproductive environments (Fig. 1). Over the last decade, many studies have focused on linking this spectrum of traits to a range of ecosystem level processes and properties (e.g., Chapin, 2003; Diaz et al., 2004; de Deyn et al., 2008). With respect to R, the plant traits of importance may be broadly grouped into traits controlling (1) the amount and chemical composition of organic matter deposited onto the soil surface, (2) the amount and destination of plant C allocated belowground, and (3) the physical properties of the soil and near surface atmosphere. We now discuss each of these in turn.

2.1 Effects on aboveground litter quantity and quality

Faster growing plants generally produce more litter, richer in nitrogen (N) but poorer in C rich structural compounds, which is more easily broken down by soil microbes and hence respired as R (Fig. 1). Slow growing plants not only acquire less C via photosynthesis but release less over time in recalcitrant litter forms that suppress decomposition

and R (Fig. 1). Further, the breakdown products of some recalcitrant compounds form complexes with amino acids and enzymes which inhibit decomposition (Hättenschwiler and Vitousek, 2000). Plant production is generally highest in warm, wet climates (Fig. 2c), which are the same abiotic conditions that also promote R. Global syntheses show that there is a consistent positive relationship between R and different measures of plant production (Raich and Schlesinger, 1992). While some of this relationship may be correlative rather than causal in nature, it is likely that existing plant community level variation in productivity amplifies the differences in R amongst biomes that would occur simply as a result of abiotic variation. At finer spatial scales, the link between plant productivity and R often weakens or breaks down entirely (e.g., Jurik et al., 1991; Ruess, 1996) probably because other factors become more important, as we discuss later. Over this century, rising CO_2 levels and N deposition are predicted to enhance plant productivity (Holland et al., 1997; Rustad et al., 2001), both via direct fertilization effects and indirectly through gradual shifts in plant community composition towards greater dominance of faster growing species or those with rapid turnover. This rise in plant productivity due to climate change could constitute an important positive feedback to R.

Physical and chemical properties of plant litter vary greatly both among and within plant communities and may serve as powerful drivers of R by determining litter mass loss rates (Fig. 2e). Cornwell et al. (2008) analyzed results from 14 studies spanning contrasting climatic zones which each measured litter decomposition of at least 20 species at a local scale. These revealed consistent correlations between decomposition and leaf nutrient content, thickness and lignin content, which underlay large differences in decomposition rates between different plant functional and taxonomic groups. For example, decomposition of litter from bryophytes and ferns was significantly slower than that from eudicot plants, decomposition of woody deciduous plant litter was much faster than that from evergreen species, and decomposition of herbaceous forb litter was faster than that from graminoids. Yet despite these differences, no clear current biome level differences in litter decomposition emerged. The observed

18.4 fold variability in decomposition rates among species within sites (Cornwell et al., 2008) reinforces other syntheses highlighting the very high local scale variation in leaf traits amongst coexisting species (e.g., Hättenschwiler et al., 2008, Richardson et al., 2008). By comparison, decomposition of standardized litter material across continental or global climatic gradients displayed only a 5 fold variation, (Berg et al., 1993; Parton et al., 2007). However, other processes also show strong variation with climate and soil types which influence the rate of incorporation of litter material into soils. For example, herbivores and soil macrofauna are often more abundant in warm, fertile sites dominated by faster growing plants maximizing resource acquisition. Herbivores can alter ecosystems in a large number of ways with important consequences for R (Bardgett and Wardle, 2003). The most consistent single effect is excretion of plant material in labile C and N forms which facilitates rapid microbial respiration. Macrofauna further contribute to this process by physically mixing and breaking apart litter (González and Seastedt, 2001), which enhances the accessibility of organic matter for microbes and fungi. Therefore, direct climate effects on decomposition rates, while significant, will likely be exceeded by indirect effects manifested through plant community composition and the structure and dynamics of the community food web, again amplifying the variation in R that is directly attributable to abiotic drivers.

2.2 Effects on plant allocation belowground

Total belowground C flux (TBCF) is governed in the first instance by the total amount of C acquired by photosynthesis (gross primary productivity or GPP), which is likely to be higher for species that prioritize resource acquisition, and which have both more leaf area and higher photosynthetic rates per unit leaf area (Fig. 1). Plants also vary in the proportion of GPP diverted to TBCF, which can be highest for those species with a suite of traits which together maximize resource retention (Fig. 1). These species tend to prevail in arid or infertile environments where there are considerable benefits in allocating more C belowground to enhance uptake of soil resources (Cannell and Dewar, 1994).

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Most detailed vegetation C budgets have focussed on forests and have examined impacts of different environmental factors at the level of the whole ecosystem rather than at the species or functional group level. Results suggest that GPP and the proportion of GPP invested in TBCF often show opposing responses to shifts in site fertility and water availability, with consistent trends among different tree species (Litton et al., 2007; Litton and Giardina, 2008). However, across forests worldwide, TBCF as a proportion of GPP shows only a relatively slight decrease from around 0.6 to 0.4 over a six fold increase in GPP (Litton et al., 2007). It therefore seems that over broad scales across structurally similar, undisturbed vegetation types, TBCF will likely be driven mainly by differences in GPP rather than the proportion GPP partitioned to TBCF (Figs. 2b,d, 3). How well this generalization applies to vegetation types other than forests has not been extensively tested. Changes in plant community composition within a particular vegetation type (or one dominated by a particular plant life form) that involve an increase in the relative abundance of more photosynthetically active plants adapted for rapid resource acquisition should therefore lead to an increase in GPP, TBCF and thus R. Possible examples of this situation include increased liana abundance across the Amazon rainforest (Phillips et al., 2002), and encroachment of temperate hardwoods into the southern limits of evergreen pine dominated forests in Northern Europe (Sykes and Prentice, 1996).

In contrast, if environmental changes are sufficient to cause shifts in the abundance of fundamentally different plant life forms, differences in the proportion of GPP diverted to TBCF amongst these life forms will potentially play a much greater role in determining R. Consequences of these shifts for R will be more difficult to predict, and will depend largely upon species or group specific anatomy, physiology and allocation strategy. For example, trees tend to construct more coarse structural roots to enhance plant stability. Coarser roots are usually longer lived with low respiratory rates, are better physically defended from herbivores, and decompose more slowly once dead (in the order of years to decades), which would collectively serve to suppress root contributions to R. In contrast, grasses and forbs often produce finer roots with higher

respiratory rates, and of higher chemical quality which turnover within weeks to years (Gill and Jackson, 2000; Comas et al., 2002), resulting in root litter which is preferentially targeted by herbivores and decomposes relatively rapidly (Silver and Miya, 2001; Bardgett and Wardle, 2003). This could help to explain why R in grasslands is generally higher than in forests under comparable climates and soils (Raich and Tufekcioglu, 2000), despite often having similar or lower aboveground productivity. Potential examples of this, more substantial, plant community transformation include predicted replacement of large expanses of Amazon rainforest with savannah as the region becomes drier (Zelazowski et al., 2011), or large reductions in moss and lichen cover and increasing tree and shrub cover in arctic tundra associated with rising temperatures (Chapin et al., 1995; Cornelissen et al., 2001). Ascertaining impacts of climate driven community shifts on R will be further complicated by species specific tissue respiration responses to temperature change, and for each species, the degree to which respiration acclimates over time under the new climate regime (Atkin et al., 2008).

Thus far, we have focused on factors determining the *amount* of TBCF (Fig. 3). However, an important source of plant species specific influence over soil C cycling arises from differences in how TBCF is partitioned amongst roots, mycorrhizae and soil exudates (de Deyn et al., 2008). Amongst forest systems globally, the estimated proportion of TBCF used for root growth increases from 0.26 to 0.53 as mean annual site temperature rises from −5 to 30 °C (Litton and Giardina, 2008). Root structure and chemistry vary substantially amongst plant functional groups, as discussed above. Recent evidence from an arctic tundra community suggests that this root trait variation is closely related to aboveground plant properties (Freschet et al., 2010). Further work in other systems is required to examine the extent to which aboveground traits can be used to predict belowground plant characteristics. Similarly to decomposition patterns of aboveground litter, root decomposition rates vary widely primarily due to tissue chemistry, with climate playing only a secondary role (Silver and Miya, 2001). Root herbivores proliferate in warm, fertile soils where they selectively consume high quality root material, most commonly associated with fast growing, resource acquisition prioritizing

plants, which is then excreted in relatively labile C forms easily utilized by soil microbes (Bardgett and Wardle, 2003). Therefore, plant functional differences in root properties may drive shifts in soil food webs that can also impact upon R.

From data showing a shift in the proportion of TBCF diverted to root growth across
5 forests worldwide (Litton and Giardina, 2008), we hypothesise that a greater proportion of TBCF is dedicated to maintaining mycorrhizae in cold climate forests compared to those in warmer climates. We note that this pattern could be related to a number of factors (e.g., vegetation, soil type) that covary with temperature at the global scale. This is consistent with independent, experimental observations that the proportion of TBCF di-
10 verted to mycorrhizae tends to be higher in slower growing plants on infertile soil (Hobbie, 2006). In comparison with fine roots, mycorrhizal hyphae turnover relatively quickly (Godbold et al., 2006), are more dependent on recent plant photosynthate (Högberg et al., 2001, 2010) and contain more recalcitrant structural compounds that inhibit decomposition (Langley and Hungate, 2003). In addition, mycorrhizal colonization affects
15 losses of C from the root system via respiration, decomposition and consumption (Langley and Hungate, 2003; Hughes et al., 2008). Therefore, the abundance and types of mycorrhizae occurring in an ecosystem have a potentially large influence on R. In a survey of 83 British plants of known mycorrhizal affiliation, plant species forming associations with arbuscular mycorrhizae were shown to have traits linked with the
20 maximization of resource acquisition (Fig. 1), such as high seedling growth rates, elevated leaf nutrient concentrations and high tissue decomposability (Cornelissen et al., 2001). By comparison, plants forming ericoid and ectomycorrhizal associations tended to have traits associated with resource retention. Thus plant and mycorrhizal traits may act in concert to regulate soil biogeochemistry. For example, in environments where
25 mineral N is in short supply (e.g., boreal forests and tundra) mycorrhizae enable plants to compete more effectively with soil microbes and saprotrophic fungi for a wide range of soil nutrients, including complex organic compounds (Persson and Näsholm, 2001), and often suppress decomposition (and thus nutrient supply for other plants) through a variety of mechanisms (Bending et al., 2003; Langley and Hungate, 2003). Such

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plants often also possess litter traits characteristic of a resource conservation strategy (Fig. 1) which serve to further reduce rates of soil C cycling and hence R. Thus, plant-mycorrhizal associations may serve to reinforce and amplify existing differences in R driven by environmental factors and other plant traits.

Root exudates are a diverse group of compounds which interact in numerous ways with plant roots, soil microbes and macrofauna, and can represent a substantial proportion of belowground C allocation for herbaceous plant species (Inderjit and Weston, 2003). In some cases, root exudates may promote microbial breakdown of previously inaccessible soil C compounds and thereby further boost R (Kuzyakov et al., 2006). However, the functional significance of many exudates is still poorly understood and some have been found to contain toxins which suppress microbial activity (Inderjit and Weston, 2003). The amount and composition of exudates appear to vary greatly amongst species and growth strategies (Grayston et al., 1996) but further research is required before any general pattern between plant functional type and exudate production can be identified with sufficient confidence to predict the consequences for R.

2.3 Effects on microclimate and soil structure

Plant traits can have a diverse range of effects on soil properties and habitat microclimate (Chapin, 2003). Our aim here is not to provide an exhaustive list, but to highlight the most widespread and important effects with respect to R. In particular, vegetation effects on soil temperature and moisture are important because these factors are key physical drivers of microbial activity and hence R (Davidson and Janssens, 2006). Dense vegetation canopies are often dominated by light demanding, resource acquisition prioritizing plants. Such canopies often reduce ground level radiation and soil evaporation rates which maintain greater soil moisture levels and lower temperatures that both, in turn, potentially affect R (Pierson and Wight, 1991; Breshears et al., 1997, 1998). Canopy and soil albedo can vary substantially amongst plant communities, with important consequences for soil properties (Gao et al., 2005). Interactive effects of vegetation and albedo can be particularly powerful in boreal systems where snowpack

depth and the duration of winter snow cover are key determinants of R (Brooks et al., 2004). Another important, but underappreciated, effect of plants lies in their potential to influence the spatial distribution and timing of R by affecting the speed with which CO_2 diffuses from the soil. For example, dense canopies can impede air circulation (particularly at night), causing subcanopy accumulation of CO_2 to concentrations up to 90% more than in the above canopy atmosphere (de Araújo et al., 2008). At a broad scale this may not matter since this CO_2 will likely emerge somewhere else or at some later time, but for interpreting spatially patchy, instantaneous records of R it has important consequences. The patterns described above operate at relatively broad scales as the integrated product of a plant community. Effects of an individual species on microclimate will become significant where the species is the dominant constituent of the community. The wide diversity of possible mechanisms whereby plant traits could influence soil and vegetation structure means that no consistent, integrated effect on R can be ascribed to a specific plant functional type. Instead, effects will be highly context dependant, resulting from interactions between particular combinations of plants, their associated biota, and the physical environment.

3 Plant invasions and range expansions

Shifts in plant species distribution via invasions and range expansions are currently widespread and likely to increase further due to climate changes (Neilson et al., 2005). Such shifts can serve as natural experiments which provide valuable insights into the myriad effects of individual plant species on ecosystem structure and function. A growing number of studies have shown that even single plant species can drive major changes in ecosystem wide C cycling (Bradley et al., 2006; Litton et al., 2008; Peltzer et al., 2010). In a survey of 94 experimental studies, invaded ecosystems on average had 83% higher productivity and 117% faster litter decomposition rates (Liao et al., 2008), often driven in part by consistent trait differences between invading species and native species. While there is little direct information on the effects of plant invasions

on R, these shifts in production and decomposition suggest that invaded ecosystems would on average have higher R.

Two contrasting hypotheses, which are relevant to understanding and predicting average effects of species invasions on ecosystem processes, have each gathered some support from experiments and field observations. The first, the "mass ratio" hypothesis, asserts that species which account for a high proportion of the total ecosystem biomass should exert a greater influence on ecosystem processes, such as R, than uncommon, low biomass species (Grime et al., 1998). One example of this is the invasion of conifers throughout treeless ecosystems in the Southern Hemisphere (Richardson and Rejmánek, 2004). The second and opposing hypothesis predicts that even locally rare, low biomass species may have significant impacts on ecosystem processes when they possess key traits that differ substantially from the surrounding community. For example, compared to native dominant trees in Hawaii, the invading N fixer *Myrica faya* has foliage with a higher photosynthetic rate, and produces litter with a lower C to N ratio which decomposes faster (Matson, 1990), all of which might be expected to promote R. In a New Zealand shrub dominated floodplain, Peltzer et al. (2009) found that the removal of several exotic species with distinct life history and leaf traits, but comprising less than 3% of total plant biomass, caused significant reductions in surface litter, soil C and basal respiration, and major shifts in soil microbial and macrofaunal populations.

Some plant species with low biomass and broadly similar traits to other species in the community can nevertheless regulate ecosystem processes like R by controlling the frequency and or severity of large scale disturbance events such as fires (Mack and D'Antonio, 1998). For example, invasion of exotic grass species through many tree dominated systems has caused a large rise in fire frequency through changes in ground litter flammability (D'Antonio and Vitousek, 1992). Conversely, encroachment of trees into grass or shrub dominated systems may reduce surface fuel loads thereby suppressing fire (Braithwaite et al., 1989; Doren and Whiteaker, 1990). Fire affects soil C cycling in a large number of ways over different time scales (Certini, 2005), which makes it very difficult to reliably predict the net effect of these changes in fire regime

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on R. The existence of complex, context dependant interactions between species and disturbance agents and other factors, means that the effects of individual species on R, while potentially large, cannot be confidently predicted from general principles but should be examined on a case by case basis.

4 Plant community diversity

With biodiversity of many groups of organisms declining a thousand times faster now than at any time in the fossil record (Millenium Assessment, 2005), attention has turned to the effects of this loss upon key ecosystem processes (see syntheses by Hooper et al., 2005; Balvanera et al., 2006; Cardinale et al., 2006). A large number of experimental studies have used synthetic species assemblages varying in species richness to show that some ecosystem processes, notably productivity, increase with richness (Hooper et al., 2005), but reach an asymptote at richness levels that are lower than most natural systems. If this is the case, then a decline in species richness in low diversity systems may lead to decreased R as productivity and hence organic litter input to soil declines. However, such studies may have limited relevance for understanding natural communities in which species composition and species losses are determined by environmental pressures, species recruitment, extinction, dispersal patterns and traits of the constituent species (Huston, 1997; Grime, 1998). For this reason, experimental removal of key species or functional groups from natural systems may provide a better picture of how ecosystem processes, such as R, may be influenced by nonrandom species losses from plant communities (Diaz et al., 2003). Further, there is still relatively little direct evidence from natural gradients for the sort of strong biodiversity-function relationships frequently predicted from experimental studies (Levine and D'Antonio, 1999; Mittelbach et al., 2001). Indeed, the largest and clearest terrestrial diversity gradient on the planet- increasing from the poles to the tropics- is not clearly related to latitudinal variation in productivity or R (Fig. 2c,f; Huston and Wolverton, 2009).

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A smaller, but rapidly growing, number of studies have specifically examined plant diversity impacts on soil processes. Results indicate that key facets of soil functioning such as decomposition, microbial nutrient cycling, and R are often more dependent upon the functional traits of the dominant plant species than diversity *per se* (Wardle et al., 1999; Bardgett and Shine, 1999; Hector et al., 2000; Johnson et al., 2008). Where a link between diversity and R has been found, this has often been mediated via the effect of diversity on plant production (e.g., Zak et al., 2003; Craine et al., 2001; Dias et al., 2010). Other studies highlight the importance of particular species or functional groups, rather than diversity, in determining ecosystem level patterns of R (de Boeck et al., 2007; Johnson et al., 2008; Ward et al., 2009). For example, Johnson et al. (2008) found consistent differences in R amongst established grassland mesocosms driven by functional group rather than diversity. As such, forb dominated mesocosms had higher R while sedge dominated communities with relatively high biomass had low R. The lack of any clear link between R and plant biomass, either above or belowground, indicates that R in these systems may be controlled by other functional group specific mechanisms (e.g., soil water availability, mycorrhizal association).

Plant removal experiments further illustrate the potential importance and complexity of the interactions between community composition, nonrandom species loss and R in natural systems. For example, in a removal experiment along a boreal forest succession, the presence of tree roots or the shrub *Vaccinnium vitis-idaea* were both linked to increased litter decomposition and soil microbial respiration, and therefore potentially also with R, but only at the early stages of vegetation succession (Wardle and Zackrisson, 2005). In contrast, plots with and without removal of *V. myrtillus* had similar levels of soil microbial respiration across the whole gradient. In a similar plant community, removal of ericoid shrubs more than doubled both ecosystem respiration (R and above ground plant respiration) and photosynthesis, and increased the rate of photosynthate transfer through the plant and soil (Ward et al., 2010). Isotopic labelling showed that this effect was largely driven by the graminoids that dominated in ericoid free plots, which showed relatively high innate rates of $^{13}CO_2$ uptake and turnover, and were

suppressed by the presence of ericoid shrubs. Effects of species can persist long after they have disappeared from the community: 40 years after selective logging of a single forest tree species in New Zealand, consistent and significant differences in soil chemical and biological properties were observed around the tree stumps compared with the surrounding forest (Wardle et al., 2008).

Given that the majority of plant biomass is returned to the soil as litter, plant diversity effects on decomposition and hence R may often be manifested through mixing of litter from different species. Respiration rates of single species litter are usually well correlated with species specific litter chemistry and structure (Aerts and de Caluwe, 1997). However, litter mixing studies frequently reveal different patterns of respiration for the mix as a whole than would be expected from the respiration rates of each species in isolation (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Among and even within studies, a range of effects of litter mixing on respiration rates have been reported, ranging from strong negative "antagonistic" to strong positive "synergistic" effects depending on species (Gartner and Cardon, 2004) and environmental context (Jonsson and Wardle, 2010). There is little information about the mechanisms underpinning litter mixing effects on decomposition and respiration but the most likely explanations involve effects of nutrients, soluble carbon and secondary metabolites from some litters on others, as well as alteration of decomposer trophic links and microhabitats (Hättenschwiler et al., 2005). Given the prevalence of contrasting respiratory responses among mixtures with identical species number but different composition (Gartner and Cardon, 2004), it appears that species or functional group specific litter qualities, rather than the number of species in the litter mix, are the most important determinants of litter respiration and hence R. Therefore, the overall message emerging from the literature on plant diversity effects upon productivity, belowground functioning and litter mixing is that plant community composition is usually the key driver of R in natural systems, with diversity playing a secondary role, and then only under certain circumstances.

5 Towards model integration of species effects

Simulation models are essential for integrating multiple sources of ecological information, often gathered over small spatio-temporal scales and unevenly distributed across biomes, to derive regional or global estimates of key ecological processes over long time periods. Several recent syntheses of outputs from Dynamic Global Vegetation Models (DGVM's) provide key insights into the causes and consequences for inter-model discrepancies, and highlight important areas for future research (Cramer et al., 2001; Friedlingstein et al., 2006). In all models, plant community processes introduce a wide range of feedbacks into the global C cycle, often via their effect on R. In the remainder of this section, we review the status of DGVM's and assess their ability to represent the previously discussed impacts of plant community on R. We focus on the following sample of widely used DGVM's, all of which remain in a state of continuous development: TRIFFID (Cox, 2001), LPJ-GUESS (Smith et al., 2001), ED (Moorcroft et al., 2001), LPJ (Sitch et al., 2003), CTEM (Arora, 2003), sDGVM (Woodward and Lomas, 2004), ORCHIDEE (Krinner et al., 2005), CLM-CN (Thornton et al., 2007), aDGVM (Schieter and Higgins, 2009), and O-CN (Zaehle and Friend, 2010).

5.1 Modelling plant trait effects

In all vegetation models, litter production is controlled by plant productivity, so that the first order relationship between production and R is simulated by default. However, influences of plant type on litter quality are more variable amongst models. Plant litter traits, such as C to N ratios and tissue specific decomposition rates, vary with plant type in some DGVM's (e.g., O-CN, CLM-CN, sDGVM and CTEM). In other cases, litter decomposition is simulated as a function of abiotic conditions and tissue type (LPJ, LPJ-GUESS, SEIB-DGVM, aDGVM), while some do not even explicitly simulate a litter pool independent of the soil carbon pool (TRIFFID). Further, no models simulate interactions between abiotic drivers and populations of aboveground or soil fauna that may, in some cases, be important drivers of soil C cycling. Models that exclude the

potential for feedbacks between litter type and decomposition, or interactions that involve different trophic groups within the community, may underestimate the alterations in R generated by climate changes.

Vegetation models also vary in how they determine the fate of C allocated to roots and exudates. As such, some models use a single allometric relationship between the quantities of C partitioned aboveground and belowground (ED, SEIB-DGVM), but the majority of models now vary the proportion of GPP diverted belowground according to estimated soil water or nutrient limitations (e.g., O-CN, LPJ , LPJ-GUESS, aDGVM, sDGVM, CLM-CN, and ORCHIDEE). Shifts in root production will impact on R partly via altered supply of root litter. Only O-CN and LPJ distinguish between above and belowground dead organic matter pools, whereas all other models treat these pools together. The impact of this simplification is unclear, but in the LPJ model, decomposition of aboveground litter is driven by air temperature, and belowground litter by soil temperature, which might have an important effect in ecosystems with very large diurnal air temperature fluctuations.

The majority of vegetation models calculate plant tissue respiration based on on an exponential temperature response curve. However, this function is more appropriate for instantaneous temperature responses, and does not take into account the potential for differential acclimation of respiration amongst plant functional groups to longer term temperature variations. Acclimation equations should be simple to implement in the majority of DGVM's (e.g., Atkin et al., 2008), and would provide a better simulation of this widely observed phenomenon and the consequences for R. However, their implementation could be problematic in the absence of a better understanding of photosynthetic temperature acclimation amongst species, which may produce impacts that negate those of respiratory acclimation (Sage and Kubien, 2007).

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To simulate the impact of plants on microclimate, and hence potentially R, all models represent differences in albedo amongst vegetation types, and simulate the consequences for near surface air temperatures. Other interactions that are typically resolved by land surface models include: (1) the impact of vegetation on radiation interception
5   and albedo, and thus snowpack depth, which enhances soil insulation and increases winter R where snow is thicker; (2) the extraction of water by roots from deep soil layers, which increases the latent heat fraction and reduces overall surface air temperatures in seasonally dry environments; and (3) the impact of canopy shading on soil surface evaporation, which maintains wetter surface soils and thus stimulates R. Pro-
10 cesses that are typically not resolved, which might affect R, include the redistribution of soil moisture by deep root systems (but see Harper et al., 2010), the impact of plant canopies, ground litter and waterlogging on the circulation of CO_2 within soil and the near surface atmosphere, and litter moisture content. In all models, the moisture availability constraint on litter decomposition is that of the soil moisture of the top layer of
15 the soil, and not of the litter layer itself. Given that the litter layer often contains much of the labile C in the soil, and may experience very different moisture regimes to the soil layers below, this simplification could confound attempts to accurately simulate R.

5.2   Modelling effects of plant invasions and diversity

The effects of individual invasive plant species on ecosystem processes, such as R,
20 cannot usually be captured by generic DGVM's parameterized at the scale of whole biomes. This is partly due to deficiencies in model structure, but also attributable to inadequate information about the factors determining invasion success and the mechanisms underlying observed ecosystem level impacts of most invasive plant species. The basis for the dominance of a particular invasive plant in its new range may not
25 be related to easily identifiable ecosystem or species properties that could feasibly be represented within DGVM's. However, inclusion of already widespread species, whose large impact on R can be demonstrated and for which the mechanisms of dominance are understood, should be considered. For example, many invasive species

that become abundant are symbiotic N fixers and inclusion of N fixers as a separate plant functional type is now possible in some vegetation models (Fisher et al., 2010). Thus, the potential exists to simulate plant invasion and range shifts for some broad, easily identifiable plant types and their impacts on R via alterations in soil conditions and plant productivity.

The existing structure of vegetation models, with less than 20 plant functional types used to represent all plant species globally, is inappropriate for simulating interactions between plant diversity and R. The first-order solution to this issue is to include a greater variety of plant types in vegetation models. However, in most simulations that include a feedback between plant growth and plant success, simply increasing the number of available plant types does not necessarily increase the simulated diversity, as exclusion of slow growing plants by fast growing plants is a likely outcome of the competitive process simulated. Clark et al. (2007) argue that within species variation in plant properties can explain and alleviate this problem, and that the standard approach of using mean species properties to drive DGVM's is flawed, because coexistence is greatly facilitated by within species (or plant type) genetic and environmentally modulated heterogeneity. One promising framework is provided by the JeDi model (Reu et al., 2010) that generates a theoretical plant community whose traits vary along twelve functional trade-off gradients. A coupled plant physiology model selects a subset of plant physiological strategies that survive under a given set of climate conditions. This approach has met with some success at predicting global patterns of plant diversity, although it has yet to be coupled to a model that simulates the potential for coexistence of the theoretically plausible plant types. Once this is achieved, then a model based exploration of the interactions between plant diversity and emergent ecosystem properties, such as R, might become a plausible goal.

6 Conclusions

Plant communities influence R via many mechanisms over a range of spatial and temporal scales. The most obvious and direct mechanism is plant control of the quantity and quality of organic inputs to the soil. There is often a clear link between plant production and R (Raich and Schlesinger, 1992), which could contribute to a positive climate feedback in those systems for which productivity may rise due to increasing temperatures and N availability (Holland et al., 1997; Rustad et al., 2001). Further, plant species traits determine the quality of resource input to the soil both within and among communities, which may influence R and feedbacks to the earth climate system (de Deyn et al., 2008). Abiotic drivers of global change may also accelerate decomposition rates of organic litter, but this effect will likely be complicated by changes in litter traits associated with shifts in community composition and possibly diversity. The impacts of species shifts on R may be particularly large where they involve species that account for most plant biomass in the system, as well as subordinate species that have very different traits (e.g., litter chemistry, N fixation ability) to the rest of the community. Large impacts can also occur when particular species mediate the frequency and severity of large scale disturbance events such as fire or insect attacks. In addition, plant effects on R can operate via changes in the amount of photosynthetic C channelled belowground. There is evidence from forests that the rate of canopy level C assimilation, rather than the pattern of photosynthate partitioning, is the dominant control upon the amount of C diverted belowground within vegetation types (Litton et al., 2007), but this has yet to be broadly verified for non forested vegetation. Across ecosystems of contrasting vegetation type, or within ecosystems where fundamental shifts in dominant plant life forms occur over time, species or functional-group specific differences in the proportion of photosynthate allocated belowground will play a greater role in explaining patterns of R. A diverse range of potentially very important plant impacts on R operate via effects upon soil surface temperature and moisture levels, and other aspects of microclimate. Climate vegetation models take a variety of approaches

to simulating differences amongst plant functional types in terms of litter decomposition, belowground C flux, and microclimate alteration. These mechanisms provide a range of model pathways through which plants may impact upon R. Key areas for potential improvement include allocation schemes, regulation of litter decomposition and the extent and speed of respiratory acclimation to temperature increases. A cohesive framework for prediction of plant impacts on R is urgently required to inform model simulations of climate-vegetation interactions and design effective mitigation strategies. We outline the following areas as critical gaps in ongoing efforts to construct such a framework:

– The fate of belowground carbon. A key uncertainty, in determining the effects of shifts in belowground C flux on R, is how this C is partitioned amongst roots, fungi and microbes. Each compartment has distinct sensitivities, C turnover rates and trophic interactions with soil biota that can affect the amount of C released from soil as R. Combination of whole plant isotopic labelling with techniques that isolate C in specific soil fractions (e.g., Högberg et al., 2010) will make significant advances in this field.

– Linking plant traits to ecosystem effects. The wide diversity of plant function and form can, to some extent, be simplified along fundamental trait axes that describe contrasting life history strategies. Improved knowledge of how these traits simultaneously determine plant responses to environmental change and plant effects upon ecosystem processes (Suding et al., 2008) will increase our ability to link climate changes with shifts in R mediated via plant community characteristics.

– Biotic interactions. Idiosyncratic ecological outcomes, which are particularly challenging to predict (and, when necessary, to prevent or mitigate), often result from complex interactions of organisms with each other and with their environment. Identifying when, where, and why these nonlinear feedbacks occur will be critical for successfully modelling and managing CO_2 emissions from R in terrestrial ecosystems.

– Species gains and losses. For a variety of aesthetic and economic reasons, there is considerable interest in the wider ecosystem effects of species extinctions and invasions. While there have been important advances in developing general principles about how plant species invasions may affect ecosystem processes relevant to R, our understanding of how species losses in real ecosystems affects these processes remains more limited. Further application of promising approaches such as species removal experiments and species specific isotopic labelling will help to tease apart the myriad factors determining the effects of individual species or functional groups on R.

– Integrating across scales. Soil C models are mainly driven by soil temperature and moisture. These factors are often excellent predictors of R over short temporal scales and under particular conditions (Davidson, 2010). Over larger spatio-temporal scales, plant activity and other factors become increasingly important. Thus, regional or global scale modelling of R will be particularly dependent upon an accurate representation of seasonal variation in plant C allocation amongst different functional groups.

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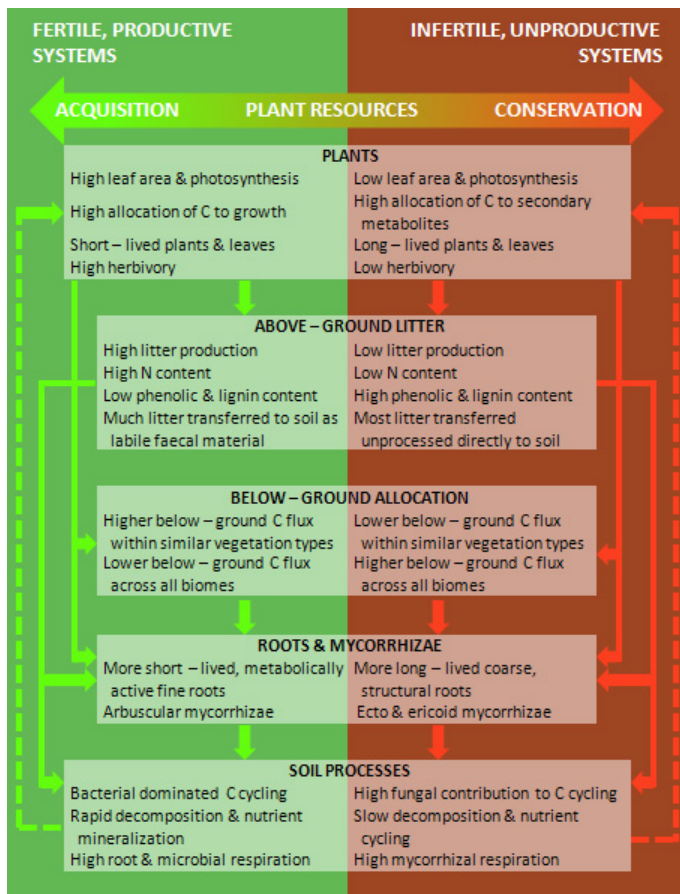
Fig. 1. Conceptual framework of linkages amongst plant traits and key plant and soil processes that affect soil CO_2 efflux in contrasting terrestrial ecosystems. Note that these are generalizations with many exceptions. Modified from Wardle et al. (2004).
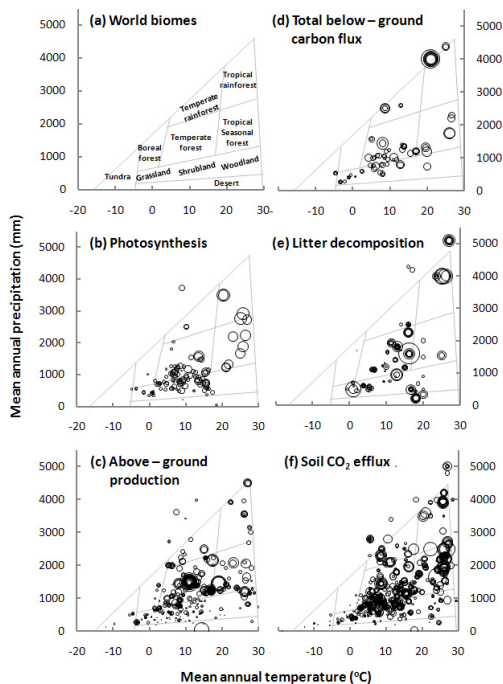
Fig. 2. Distribution of plant biomes[1] **(a)**, annual gross primary productivity[2] **(b)**, annual above-ground plant productivity[3] **(c)**, total annual belowground carbon flux[4] **(d)**, litter decomposition rate[5] **(e)** and soil CO_2 efflux[6] **(f)** in relation to mean annual site air temperature and rainfall. Note that a number of factors (e.g., vegetation and/or soil type) covary with global temperature and moisture gradients. Belowground carbon flux is presented only for forest ecosystems, the other variables span all ecosystems for which data are available. Soil CO_2 efflux data is presented only for unmodified, natural systems. The diameter of the circles denotes the magnitude of the values. Data sources: [1] Whittaker (1975); [2] Luyssaert et al. (2007); [3] Ohnson et al. (2001); [4] Litton and Giardina (2008); [5] Zhang et al. (2008); [6] Bond-Lamberty (2010).

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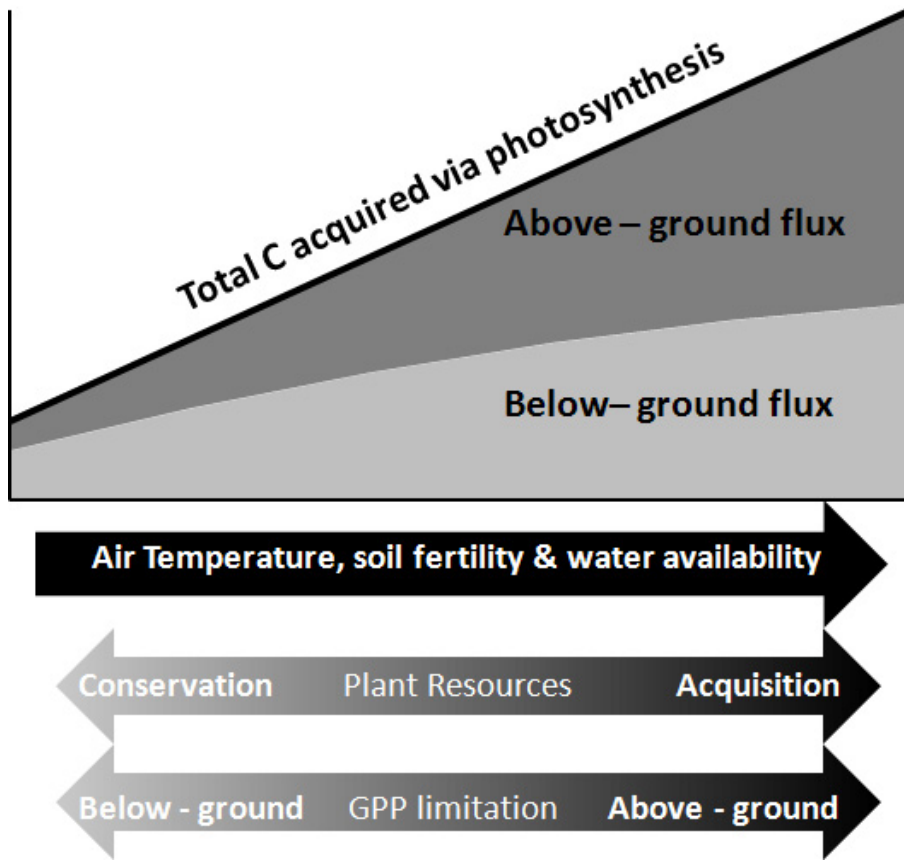
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Fig. 3. Hypothesized relationships between GPP partitioning and abiotic factors, plant functional type and limitations to photosynthesis. Modified from Litton and Giardina (2008).