

The impacts of rising CO₂ concentrations on Australian terrestrial species and ecosystems

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Abstract The increasing atmospheric concentration of carbon dioxide ([CO₂]) contributes to global warming and the accompanying shifts in climate. However, [CO₂] itself has the potential to impact on Australia's terrestrial biodiversity, due to its importance in the photosynthetic process, which underlies all terrestrial food webs. Here, we review our knowledge regarding the impacts of elevated [CO₂] on native terrestrial species and ecosystems, and suggest key areas in which we have little information on this topic. Experimental information exists for 70 (or less than 0.05%) of Australia's native terrestrial plant and animal species. Of these, 68 are vascular plants. The growth of Australian woody species is more reliably increased by elevated [CO₂] than it is in grasses. At the species level, the most overwhelming responses to increased [CO₂] are a reduction in plant nitrogen concentration and an increase in the production of secondary metabolites. This is of particular concern for Australia's unique herbivorous and granivorous marsupials, for which no information is available. While many plant species also displayed increased growth rates at higher [CO₂], this was far from universal, indicating that changes in community structure and function are likely, leading to alterations of habitat quality. Future research should be directed to key knowledge gaps including the relationship between [CO₂], fire frequency and fire tolerance and the impacts of increasing [CO₂] for Australia's iconic browsing mammals. We also know virtually nothing of the impacts of the increasing [CO₂] on Australia's unique shrublands and semi-arid/arid rangelands. In conclusion, there is sufficient information available to be certain that the increasing [CO₂] will affect Australia's native biodiversity. However, the information required to formulate predictions concerning the long-term future of almost all organisms is far in excess of that currently available.

Key words: biodiversity, ecological processes, elevated CO₂, global change.

INTRODUCTION

The concentration of the greenhouse gas carbon dioxide (CO₂) has risen from pre-industrial concentrations of 280 µmol mol⁻¹ to its present concentration of over 380 µmol mol⁻¹, and it is expected that the concentration in 2050 will be in the range of 500–600 µmol mol⁻¹ (Coll & Hughes 2008). Aside from its influence on global surface temperatures and associated changes to weather and ocean circulation patterns (IPCC (Intergovernmental Panel on Climate Change) 2007), the increasing atmospheric concentration of CO₂ ([CO₂]) has both direct and indirect effects on living organisms in its own right. This is mostly due to the fact that CO₂ is the main substrate for photosynthesis, the process whereby plants and some prokaryotic organisms use solar energy to convert CO₂ and simple minerals to sugars, which are then converted to other carbohydrates, proteins, fats and eventually all food on the planet (Jones 1992).

For most photosynthetic organisms, the rate of photosynthesis is limited by the availability of CO₂

whenever its atmospheric concentration is below approximately 1000 µmol mol⁻¹ (i.e. approximately three times the current concentration) (Jones 1992). Therefore, the increasing [CO₂] directly influences the photosynthetic rate, which potentially influences growth rates and the manner in which the plant allocates biomass, invests in reproduction and produces secondary metabolites (Long 1991; Long *et al.* 2004). All of these changes have ramifications for ecosystem functioning, as plants are the base of the food web, providing the nutrition, either directly or indirectly, for nearly all other organisms in an ecosystem. The potential stimulation of photosynthetic primary production in terrestrial ecosystems by the increasing [CO₂] also increases the ability of these ecosystems to sequester carbon and act as carbon sinks (Woodward & Lomas 2004). Therefore, the response of plants to [CO₂] plays a vital role in both global climate and climate change.

Plant species and genotypes within a species vary in their responsiveness to the increasing [CO₂], which therefore has the potential to alter both inter- and intra-specific competition, changing both the structure and function of plant communities (Long *et al.* 2004). Species that are more responsive to the increasing

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[CO₂] are likely to become either more or less abundant, due to alterations of competition levels (Körner & Bazzaz 1996), and indeed some species may become threatened (Possingham 1993). Changes in plant community structure and function will also affect the organisms that rely on those communities, whether it be for food or habitat (Körner & Bazzaz 1996). Therefore, changes to the way that plants are constructed, behave, grow and reproduce have the potential to ramify through the entire ecosystem, affecting organisms at every trophic level (Körner & Bazzaz 1996).

These changes in plant communities, together with the changes in the biochemistry and physiology of individual plants and species, will also have ramifications at the ecosystem level, due to the sensitivity of ecosystem nutrient and water cycling (Hungate 1999). Changes in hydrology and biogeochemistry have the potential to influence the CO₂-productivity relationship, as do changes in community structure (Reich *et al.* 2006b). Responses to [CO₂] therefore have the potential to offset, reverse or exacerbate the effects of global warming and associated climatic change.

Why Australia?

Australian plants are no different in fundamental physiology from plants from anywhere else. Thus, any research concerning the fundamental responses of plants to the rising [CO₂] is relevant for Australian plants. Thus, it could easily be argued that a review of the impacts of elevated [CO₂] on Australian plants and ecosystems is unnecessary. However, as pointed out by Körner (2006), the experimental conditions and community stage in which experiments are done have an overwhelming importance in the interpretation of any elevated [CO₂] effects. Of particular importance in this respect is the environment's nutrient status and the plant community's occupation of available resources, including space. In these respects, Australian systems are unlike those in many parts of the world, and very different from nearly all existing sites where elevated [CO₂] impacts have been investigated (Long *et al.* 2004). For instance, Australian soils are generally very old, highly weathered and nutrient impoverished (Attiwill & Leeper 1987), which is associated with the prevalence of sclerophylls in the Australian flora (Beadle 1966). Nutrient limitation has been shown to restrict or even eliminate the response of plant growth and ecosystem primary production to elevated [CO₂] (McMurtrie *et al.* 2008), and since most Australian soils have very low nutrient levels, it is possible that elevated [CO₂] effects will be different in Australian situations than in those where nutrients are more abundant. Thus, in Australian systems, growth responses to elevated [CO₂] may be less important than

other responses, such as changes in water use, leaf chemistry and biomass allocation.

A second important and dominant feature of Australian ecosystems is the prevalence of fire. Work in southern Africa has demonstrated that [CO₂] has probably had a crucial role in the competition between trees and grasses in savanna systems (Bond & Midgley 2000; Bond *et al.* 2003, 2005). Bond and co-workers argued that the control of tree abundance in mixed tree/grass ecosystems by fire is greater at lower [CO₂] since reductions in tree growth increase the inter-fire period required for successful recovery (Bond & Midgley 2000). Most Australian ecosystems are subject to frequent fire so the possible impacts of the increasing [CO₂] on fire frequency and the ability of various life forms and species to withstand burning is more important here than on any other continent. The IPCC Fourth Assessment Report predicts substantial increases in woody vegetation cover in Australian rangelands (Hennessy *et al.* 2007), so this issue is of extreme relevance. The fire-[CO₂] relationship is also complex. Körner (2006) identified three basic ecosystem types with respect to the influence of elevated [CO₂], based on exploitation of resources and 'coupling' of nutrient cycling. Fire-prone systems oscillate between uncoupled, or low competition, relatively nutrient-rich conditions and tightly coupled, competitive, nutrient-poor conditions. Each of these conditions has a demonstrably different ecosystem response to elevated [CO₂] (Körner 2006), so ecosystems prone to recurrent fire are likely to have responses to the increasing [CO₂] that vary with time since fire. Increased [CO₂], by accelerating resource exploitation, is also likely to reduce the time that a recently burnt ecosystem spends in the uncoupled condition. Australian plants have a wide variety of adaptations to fire, so the impacts of changes in [CO₂] on successional processes are crucial for most of Australia, and particularly in iconic landscapes such as the biodiversity hotspot in the south-west of Western Australia (Myers *et al.* 2000).

The effect of elevated [CO₂] is likely to be extremely important for Australian herbivores since the nutritional quality of the sclerophyllous vegetation, particularly that of eucalypts, differs from that of other plant types. Australian herbivores, particularly browsing mammals, survive on foliage that is physically tougher, lower in nutrients and higher in secondary metabolites than in most other parts of the world (Hume 1999). All of these factors are likely to be sensitive to [CO₂], with strong implications for browsing mammal health and ramifications across trophic levels.

Given the above-mentioned reasons, it is reasonable to determine if Australian ecosystems respond differently to changes in [CO₂] than ecosystems elsewhere. To date, the potential impacts of the rising [CO₂] have been examined for very few Australian ecosystems,

many of which have no analogues in the northern hemisphere, where most elevated [CO₂] research has been done. Therefore, it is worth examining the elevated [CO₂] research that has been done for Australian organisms and ecosystems as well as identifying ways in which Australian plants and ecosystems might differ in terms of elevated [CO₂] responses from those elsewhere. By doing this, it is possible to identify gaps in existing knowledge and make recommendations for future research to ensure the information required for the management of Australia's ecosystems into the future is available.

PROCESSES WHEREBY ELEVATED CO₂ MIGHT AFFECT BIODIVERSITY

As plants form the basis of practically all terrestrial trophic networks, or food webs, the responses of most other organisms to [CO₂] are dependent upon the responses of plants, such that most impacts of elevated [CO₂] on animals and other heterotrophic organisms can be considered indirect or plant-mediated (Pritchard *et al.* 2007). While there are some specific direct impacts of elevated [CO₂] on heterotrophic organisms, these generally seem to be less important than the indirect effects. Therefore, the responses of plants and plant communities to elevated [CO₂] are fundamental and largely govern the responses at all other trophic levels (Pritchard *et al.* 2007). The basics of plant responses to the rising [CO₂] have been reviewed many times before, so they will not be repeated here. However, many of the ecosystem-level responses to the rising [CO₂] depend upon the plant responses, so a very brief account is necessary. See Drake *et al.* (1997), Körner (2003a,b, 2006), Körner and Miglietta (1994), Long (1991), Long *et al.* (2004) and Long and Drake (1992) for full accounts of the impacts of [CO₂] on plant photosynthesis, water use efficiency, growth and biomass allocation.

Physiological responses to the rising [CO₂]

Since photosynthetic carbon assimilation is not saturated at current [CO₂], any increase in [CO₂] will result in an increased photosynthetic rate (Long & Drake 1992). Variation in photosynthetic biochemistry leads to differences in the degree of stimulation of photosynthesis by a rising [CO₂] between conifers and flowering plants, broad leaves and grasses, but most spectacularly between plants with the C₄ photosynthetic carbon concentrating mechanism and all others (Long *et al.* 2004). Furthermore, increasing [CO₂] increases a plant's water use efficiency, since increased [CO₂] tends to reduce stomatal aperture, thus reducing water loss without substantially reducing carbon

assimilation (Long 1991). Improved plant water use efficiency can increase soil water content, which can, in water limited environments, extend the growing season, favouring growth of later seasonal species (Wand *et al.* 1999).

Plants allocate both C and N resources for various functions, including reproduction and protection from herbivores. By stimulating the rate of photosynthetic C assimilation, the increasing [CO₂] encourages the re-allocation of N away from the leaf in some species (Bowes 1993; von Caemmerer *et al.* 2001). An important sink of both C and N is the production of plant secondary metabolites (PSM) (O'Reilly-Wapstra *et al.* 2004). Secondary metabolites play a variety of roles in the plant, from defence from herbivory and pathogens, to anti-oxidants and sunscreens. Elevated [CO₂] is known to increase the production of secondary metabolites in a range of plant species (Coley *et al.* 2002), with important ramifications across trophic levels.

Because of the dependence of photosynthesis, photorespiration, water use and N use efficiency on [CO₂], there are strong reasons to believe that the increasing [CO₂] will lead to alterations of the competitive success within plant communities (Polley *et al.* 1996). Plants whose physiology is more responsive to the increasing [CO₂] may be expected to derive a greater growth advantage from an atmosphere richer in CO₂, when compared with those that are less responsive (Polley *et al.* 1996). This could lead to an alteration of plant communities, at the very least altering relative abundances. In extreme conditions, the increasing [CO₂] could lead to the decline and extinction of some species (Possingham 1993).

Impacts on animals

The direct effects of [CO₂] on animals have been reviewed in detail by Sage (2002) and Stange (1996, 1997). In short, animal physiology is mostly unaffected by [CO₂] within the range that is likely in the coming century, with the main exceptions being CO₂-sensing insects, particularly amongst the order Lepidoptera (moths and butterflies), whose CO₂ sensors appear to become saturated at a [CO₂] of approximately ~800 µmol mol⁻¹ (Rasch & Rembold 1994; Sage 2002). Therefore, most of the effects of the rising [CO₂] on animals are mediated through the various responses of plants. Many of the physiological and chemical changes that occur in individual plants will affect animals that depend upon plants for food and changes in community structure as a result of the differential responses of different plant species will have implications at the ecosystem level. In general, it is believed that the improved plant water use efficiency at elevated [CO₂] will increase plant tissue water

content, thereby improving herbivore digestive efficiency (Coviella & Trumble 1999). In contrast, the reduction in plant nutrient concentrations at elevated $[\text{CO}_2]$, particularly that of N, is likely to have strongly negative effects on herbivores (Roth & Lindroth 1995; Bezemer *et al.* 1998; Ehleringer *et al.* 2002; Levy *et al.* 2004). Of direct relevance to Australian situations, PSM act to reduce herbivory in a variety of ways, from repelling herbivores to reducing digestive efficiency and even acting as toxins (Fraenkel 1959; Harborne 1991). Obviously, if plants invest more heavily in the production of secondary metabolites as $[\text{CO}_2]$ increases, then herbivores will be exposed to higher levels of these compounds, with likely deleterious effects. It is also possible that increased plant C assimilation at elevated $[\text{CO}_2]$ will alter the mixture of secondary metabolites, with plants perhaps increasing production of C-based compounds to a greater extent than N-based compounds. This would alter the plant's toxin-profile, perhaps changing the suite of animals that can feed on the plant. Increases in the variety and concentration of secondary metabolites in plant material in response to increasing $[\text{CO}_2]$ will probably lengthen the developmental time, increase mortality and reduce adult size and fecundity in insect herbivores (Coley *et al.* 2002), especially as herbivores will need to eat greater quantities of plant matter in order to acquire sufficient N.

The impacts of elevated $[\text{CO}_2]$ on insect herbivores will depend upon the relative strength of the various plant responses with the final level of plant N and secondary metabolites in the fodder being most important determinants. On balance, it is likely that the negative consequences for herbivores of increased allocation to defensive compounds at elevated $[\text{CO}_2]$ will overwhelm the positive effects of increased plant water content (Ehleringer *et al.* 2002; Percy *et al.* 2002; Hamilton *et al.* 2004). Field studies indicate that at elevated $[\text{CO}_2]$ insect herbivore abundance on plants is lower, herbivore mortality is higher and the levels of parasitoids on herbivores is higher, compared with control conditions (Stiling *et al.* 2002). However, studies on field-grown soybean have shown that the level of insect attack and herbivore abundance, fecundity and lifespan were all greater at elevated $[\text{CO}_2]$ than in controls (Casteel *et al.* 2008; DeLucia *et al.* 2008; Dermody *et al.* 2008; O'Neill *et al.* 2008; Zavala *et al.* 2008, 2009). The authors of these studies have been quoted as stating that in soybean 'leaves grown under high CO_2 lose their ability to produce jasmonic acid, and that whole defense pathway is shut down.' (*ScienceDaily*. Retrieved September 3, 2008, <http://www.sciencedaily.com/releases/2008/03/080324173612.htm>). However, the published results do not support such a statement, demonstrating instead that elevated $[\text{CO}_2]$ reduced expression levels of key defensive chemistry genes

from the jasmonic acid pathway by approximately 30% (Zavala *et al.* 2008). This in turn reduced cysteine proteinase inhibitors, which are specific deterrents to herbivorous coleopteran larvae, with corresponding differences in the activity of cysteine proteinases in the guts of insects feeding on foliage from differently treated plants (Zavala *et al.* 2008). Thus, it appears that in some species $[\text{CO}_2]$ might affect gene expression and the pathways of secondary metabolite production resulting in changes in insect attack, but there is as yet no evidence that elevated $[\text{CO}_2]$ can completely inhibit defensive chemical pathways.

Herbivorous mammals will be susceptible to the same elevated $[\text{CO}_2]$ -induced changes in plant C/N ratios and the production of secondary metabolites (Ehleringer *et al.* 2002), although in most cases the impacts on the animals are likely to be far less severe. Currently, there are very few published analyses of the impacts of elevated $[\text{CO}_2]$ on the growth and health of mammalian herbivores. However, analyses of traditional agronomic 'feed quality' indicators, such as acid digestible fibre and crude protein, indicate that elevated $[\text{CO}_2]$ should result in slight reductions in the health and growth of mammalian herbivores (Owensby *et al.* 1996). These analyses come from agricultural situations, so it is possible that impacts of changes in plant chemistry and feed quality will be more dramatic in native mammalian herbivores, particularly arboreal folivores, already living on low protein diets. In these cases, arboreal folivores cannot overcome the reduction in foliage N concentration by increasing consumption, because such a strategy would lead to elevated and unsustainable losses of faecal nitrogen (Cork 1996; Hughes 2003).

Changes to flowering and fruiting times in response to elevated $[\text{CO}_2]$ will affect pollinators if their phenology is not similarly altered (Springer & Ward 2007; Post & Inouye 2008). The increasing $[\text{CO}_2]$ might alter flowering times in some species by effects on growth rates and carbon allocation or impacts on leaf temperature because of reduced transpiration (Springer & Ward 2007). Because the insect pollinators are likely to maintain their response to ambient thermal load, it is possible that flowering of some species will occur before or after the emergence of their pollinators, with potential consequences for plant-pollinator relationships (Springer & Ward 2007; Post & Inouye 2008). In generalist species of both plants and pollinators, this is unlikely to have dramatic consequences because both have a variety of partners. Memmott (2002) demonstrated that the majority of plant-pollinator reactions are general but some involve complex webs of plant-pollinator interactions. Thus, while animal and plant species will still have pollination options, the complex species interaction networks are likely to be altered by increases in $[\text{CO}_2]$. For specialist pollination partnerships, the ramifications of shifts in flowering times in

response to rising [CO₂] would be profound and rapid, resulting in population decline and perhaps even extinction of both the plant and pollinator with ramifications across trophic levels.

The increasing [CO₂] has the potential to alter predator-prey interactions in several ways. Firstly, the higher [CO₂] may increase plant size, leaf area and architecture, reducing predator searching efficiency (Coll & Hughes 2008). Secondly, reduced herbivore growth, protein content or size and altered chemical composition at elevated [CO₂] may make them a less suitable food source. Conversely, increased herbivore foraging time at elevated [CO₂] may make finding prey easier for predators. It is also likely that some herbivores will be advantaged over others at elevated [CO₂], changing herbivore community composition, which may in turn alter predator composition. Predictions of the responses to the increasing [CO₂] become increasingly difficult at higher trophic levels as the number of potential responses multiply, thus the few studies that have examined higher order responses are extremely valuable, but unsurprisingly contradictory. Predator and parasitoid performance and population levels at elevated [CO₂] have been found to increase (Stiling *et al.* 1999, 2002, Chen *et al.* 2005, 2007), decrease (Roth & Lindroth 1995; Sanders *et al.* 2004) or remain unchanged (Bezemer *et al.* 1998; Percy *et al.* 2002; Stacey & Fellowes 2002; Holton *et al.* 2003; Hoover & Newman 2004) or vary annually when compared with control [CO₂] (Percy *et al.* 2002).

Plants almost universally increase their below-ground proportional biomass allocation at elevated [CO₂], with both increased root growth and increased root turnover. Such increases might be expected to increase population densities of root-feeding invertebrates, such as nematodes. Current evidence indicates that the soil micro-invertebrate community does change with exposure to elevated [CO₂], with experiments demonstrating both increases (Yeates *et al.* 2003), decreases or no change (Niklaus *et al.* 2003) in the abundance of root-feeding invertebrates. There is scant information on the impacts of elevated [CO₂] on below-ground food webs with the only detailed examinations showing either no changes (Niklaus *et al.* 2003) or that nearly all groups increased in abundance at elevated [CO₂] (Yeates *et al.* 2003).

Alterations in the production rates and chemical composition of plant litter at elevated [CO₂] is likely to influence decomposer organisms in both the soil and litter. The N content of leaf litter varies in responsiveness to [CO₂], because of varying degrees of nutrient resorption in different species (Hoorens *et al.* 2002), and the quantity of litter produced and its content of secondary metabolites (Hoorens *et al.* 2002) are both likely to affect the abundance and community composition of detritivores in much the same manner as for herbivores. Thus, greater quantities of litter and roots

will increase food supply but secondary metabolites are likely to reduce the quality of the food resource. However, there is sufficient evidence to indicate that the general reduction in litter N concentrations do not affect decomposition rates as strongly as would be expected (Franck *et al.* 1997; Hirschel *et al.* 1997; Gahrooe 1998; Dukes & Field 2000). Thus, it appears that the impacts of elevated [CO₂] on litter decomposition rates might not be as strong as predicted from analyses of litter chemistry alone (Knops *et al.* 2007).

Impacts on fungi and microbes

Little is known of the impacts of increasing [CO₂] on fungi, although it appears that mushroom cap size is reduced and stalk-length increased by elevated [CO₂] in several commercial mushroom species (Sage 2002). It is unlikely that non-aerial fungal material would be affected directly by increased [CO₂] since these materials largely exist in soils or decomposing organic matter in which the [CO₂] is normally very high. Increased plant C-assimilation at elevated [CO₂] could lead to an increased allocation to mycorrhizal partners in plant roots and there is evidence that this is, indeed, the case for both arbuscular mycorrhizal fungi (Rillig & Allen 1998; Rillig *et al.* 1999, 2000, Rillig & Field 2003) and ectomycorrhizal fungi (Rouhier & Read 1999; Gorissen & Kuyper 2000; Alberton *et al.* 2005). Therefore, while responses seem to be species-specific (Rillig & Allen 1998; Alberton *et al.* 2005), it is generally believed that the diversity of root-associated fungi will be maintained or even increased in an atmosphere high in [CO₂] (Rillig & Allen 1998; Alberton *et al.* 2005).

While a range of growth cabinet and glasshouse experiments indicate that disease severity is generally increased at elevated [CO₂], field experiments in which [CO₂] is manipulated do not support this generalization. Once again, it appears that the impacts of elevated [CO₂] on plant disease severity in the field are dependent upon the plant species and the particular pathogen involved as well as the site of infection (Chakraborty & Datta 2003). For instance, leaf blight of rice caused by the pathogen *Magnaporthe oryzae* was significantly higher at elevated [CO₂] but panicle blight caused by the same organism was not higher (Kobayashi *et al.* 2006). However, various investigations of plant diseases in field experiments (Meijer & Leuchtmann 2000; McElrone *et al.* 2005; Aldea *et al.* 2006; Strengbom & Reich 2006) have indicated that pathogens generally are less abundant and virulent at elevated [CO₂] (Chakraborty *et al.* 2008). On the other hand, the results of Aldea *et al.* (2006), on the impact of fungal pathogens, indicated that each separate lesion at elevated [CO₂] had an impact on leaf

photosynthesis up to five times greater than a similar lesion in control conditions. Thus, while the incidence of infection at elevated $[\text{CO}_2]$ might be lower or similar to that in control conditions, the impacts might be far more severe. This area has been examined only rarely but is immensely important from both an agricultural and ecological perspective.

Increased production of plant litter, both above and below-ground, could increase the food supply for saprophytic organisms, including bacteria and fungi, but increases in PSM could slow the rate of organic matter decomposition. Reports of responses of biomass of soil microbes and fungi to elevated $[\text{CO}_2]$ are contradictory and variable across years and are highly dependent upon the plant species present (Dhillon *et al.* 1996; Chung *et al.* 2007; Van Groenigen *et al.* 2007). Therefore, it is difficult to generalize responses of soil saprophytes, although most reports indicate that the total hyphal length of saprophytic fungi is higher at elevated $[\text{CO}_2]$ (Dhillon *et al.* 1996; Rillig & Allen 1999; Rillig *et al.* 2000; Rillig & Field 2003). Thus, it is possible that the diversity of saprophytic fungi will benefit from the increasing $[\text{CO}_2]$. All soil-dwelling organisms are also likely to benefit from the increased soil water levels at elevated $[\text{CO}_2]$ and the impact of this is likely to be greatest in seasonally dry environments or those with unreliable rainfall. The impacts of increased $[\text{CO}_2]$ on fungal and microbial competition and succession are currently unknown but of extreme importance for long-term sustainability, both of productivity and biodiversity.

The indirect impacts of the changing $[\text{CO}_2]$ outlined previously are based on changes in physiology or behaviour of existing plant species. It is very likely, however, that the increasing $[\text{CO}_2]$ will differentially affect plant population dynamics (Williams *et al.* 2007) thereby changing plant community composition, structure and function. These changes are likely to have impacts on the organisms that use the plant communities for habitat or food sources and add further to the complexity of responses to changes in $[\text{CO}_2]$.

Impacts of alterations in ecological interactions

Terrestrial organisms exist in complex ecosystems where each organism interacts with many others, often in complex and non-intuitive ways. However, it is clear that certain interactions are likely to change as $[\text{CO}_2]$ increases. As detailed previously, plant community composition is likely to change. It is also likely that the stimulation of net ecosystem productivity, alterations of plant and litter chemistry and the stimulation of microbial and fungal biomass by elevated $[\text{CO}_2]$ will change biogeochemical cycling. Of special importance in this respect is the response of N cycling. At elevated

$[\text{CO}_2]$, more N is likely to be partitioned into biomass and into slowly turning-over soil organic matter (Luo *et al.* 2004a). This is likely to reduce the availability of N to plants through a process termed progressive nitrogen limitation (PNL). Reductions in available N are likely to drive changes in plant community composition and further exacerbate elevated $[\text{CO}_2]$ -induced changes to the functioning of terrestrial ecosystems.

A potentially overwhelming factor in most of Australia's terrestrial ecosystems is the interaction between fire and the rising $[\text{CO}_2]$. If rising $[\text{CO}_2]$ stimulates productivity, especially in fire-promoting species like eucalypts, then fires may become increasingly frequent and/or severe. Plants often invest in more leaf secondary compounds, such as phenolics, at elevated $[\text{CO}_2]$ and several classes of secondary compounds, such as leaf oils, are flammable (Coley *et al.* 2002). Therefore, it is possible that fires could be more likely not only because of an increased production of fuels but also because those fuels have greater flammability. However, it is also possible that increased plant water contents through reduced transpiration will suppress fires, but this is only likely to have any effect under marginal conditions, with fires still being extremely likely under most environmental conditions. However, while elevated $[\text{CO}_2]$ may stimulate fire frequency, it may also reduce the sensitivity of native plant species to fire. This could be achieved through several mechanisms related to specific fire adaptations of Australian plants. Many Australian woody plants survive fire through protected buds, either in lignotubers or below the bark (Gill 1981). Elevated $[\text{CO}_2]$ may allow plants to allocate more resources to these protected buds thus reducing the period required between successive fires for long-lived individuals to recover sufficiently. The same mechanism may allow seedlings to develop more rapidly to a size sufficient to survive their first fire, either in terms of bark thickness or lignotuber development (Gill 1981; Bond & Midgley 2000; Bond *et al.* 2003). Many other plant species do not survive the fire but rapidly develop a seedbank of fire resistant or protected seeds. The time between successive fires is even more important to these species as a single fire can cause local extinction of one of these species if it occurs too soon after another fire for a seedbank to have been established (Noble & Slatyer 1980; Gill 1981). The increasing $[\text{CO}_2]$ may reduce this crucial period if growth rates are increased or if plants allocate proportionally more biomass to reproduction at elevated $[\text{CO}_2]$ (Bond & Midgley 2000; Bond *et al.* 2003). This important area of the ecology of Australian ecosystems has received little consideration and no actual research effort. However, an understanding of the interactions between the increasing $[\text{CO}_2]$ and fire frequency is vital if future ecosystem processes are to be predicted.

Interactions between the rising [CO₂] and other global changes

Since the effects of increasing [CO₂] on plant photosynthesis, and hence on growth, C-allocation, water and N use efficiency, are directly related to average temperature in the growing season, the impact of elevated [CO₂] on all areas of plant biology should be expected to increase as the global temperature rises. Of particular importance in this respect is the increased water use efficiency. Increasing temperature always increases the evapotranspirational demand on plants, so the increased water use efficiency, and the concomitant increase in soil water retention and growing season, generated by the increasing [CO₂] will become more and more important as global temperatures rise. Therefore, while it is extremely unlikely that the increase in [CO₂] will be able to counteract the effects of increased evaporative demand due to global warming, it will undoubtedly reduce the severity of the impact. Increased water use efficiency is also important in offsetting the impacts of reduced precipitation that are likely across large areas of Australia (IPCC 2007).

Global warming and the increasing [CO₂] are likely to have opposing impacts on nutrient cycling processes, particularly in the case of N (Reich *et al.* 2006a). While the increasing [CO₂] causes the accumulation of N in biomass and soil organic matter pools with long residence times, soil warming is likely to increase nutrient turnover rates and stimulate microbial activity (Hovenden *et al.* 2008a). The extent of these changes is unknown, as there is only a single published study that has investigated the interaction of warming and elevated [CO₂] on soil nutrient availability and cycling processes (Hovenden *et al.* 2008a); however, it is possible that the opposing effects will counteract each other. Therefore, it is possible that global changes will have little effect on soil nutrient

cycling in Australia and other areas where increased nutrient deposition does not occur.

Both elevated [CO₂] and warming stimulate the relative allocation of biomass below-ground. Therefore, there is the potential for plants to have substantially increased soil exploration in warmed, elevated [CO₂] conditions. This is likely to confer improved nutrient acquisition and increased drought tolerance, both of which are increased by greater soil exploration. Thus, elevated [CO₂] might improve plant drought tolerance not only by reducing transpiration, but by promoting root growth, thereby increasing plant access to additional water sources.

CO₂ IMPACTS ON AUSTRALIAN SPECIES

Considering all possible methods, all available published data, and including all current but unpublished areas of research, the number of Australian species and ecosystems investigated as to their responses to elevated [CO₂] is extremely low. There have been no studies of the impacts of elevated [CO₂] on any Australian organisms other than vascular plants, of which approximately 0.4% of named Australian species have been investigated, and invertebrates, of which only two native species have been investigated (Table 1). In total, approximately 0.05% of Australian species (excluding algae, viruses and protoctists) have been investigated. Of substantial concern for biodiversity conservation is the total lack of knowledge of how elevated [CO₂] will affect the highly endemic vertebrate fauna.

Impacts on Australian plants

The impact of elevated [CO₂] has been investigated in 68 species of plants native to Australia, all of which are

Table 1. The number of native Australian species and the number and proportion of species in which the impact of elevated [CO₂] has been investigated

Taxonomic group	No. Australian native species [†]	No. spp. investigated for CO ₂ impacts [‡]	% of species investigated for CO ₂ impact
Vertebrates	7 558	0	0.0%
Invertebrates	114 600	2	0.002%
Vascular plants	18 140	68	0.37%
Non-vascular plants	1 852	0	0.0%
Lichens	3 227	0	0.0%
Fungi	5 672	0	0.0%
Bacteria [§]	~40 000	0	0.0%
Cyanophytes [§]	270	0	0.0%
Total	151 319	70	0.046%

[†]No. of species used is the actual number of described species, but see [‡] and [§]. [‡]These numbers are the numbers of species for which published data are available. [§]No. of species used for bacteria and cyanophytes is the estimated no. of species.

angiosperms. These studies have predominantly come from glasshouse or growth cabinet experiments, in which 43 species have been investigated. There have also been open-top chamber (OTC) experiments, in which plants are grown in the soil in natural or semi-natural conditions and surrounded by a cylindrical chamber, for four species. Published accounts from Free Air Carbon dioxide Enrichment (FACE) experiments exist for a single experiment, the TasFACE experiment in southern Tasmania. However, this single experiment has presented data on the responses of 23 native plant species to elevated $[\text{CO}_2]$ over several years in natural conditions.

The responses of plants to elevated $[\text{CO}_2]$ have been investigated at several different levels, with various classes of variables being studied (Appendix S1). Overall, the most comprehensively investigated variable is that of growth response, including relative growth rate as well as final biomass after an allotted period, which has been assessed in 36 species, representing 52.9% of species studied. The next most widely studied variable is the response of reproduction, including flower production, seed production and seed mass and nutrient content, in which the response of 31 species is known. Leaf gas exchange (26 species) and foliar nutrient content (20 species) responses to elevated $[\text{CO}_2]$ are also known for a range of species.

Overall, the responses of a wide range of variables are known, but generally in a very uneven and haphazard manner, with the responses of very few species being examined in a comprehensive fashion. Of the 68 species investigated, 30 have been investigated with respect to a single class of variable and a further 10 species for which the response of only two variable classes has been investigated. The responses of only seven species (*Acacia dealbata*, *A. implexa*, *A. irrorata*, *A. mearnsii*, *A. melanoxylon*, *Eucalyptus tereticornis* and *Maranthos corymbosa*) are known in a comprehensive fashion, as defined by having five or more categories of response investigated. All seven of these species are trees and have been investigated only in highly artificial glasshouse conditions in the absence of competition and natural soil processes.

Grasses

Of the approximately 1300 species of grasses that are considered native to Australia (Mallett & Orchard 2002), the $[\text{CO}_2]$ -response has been studied for 23, or 1.8% (Table 2). However, the response to elevated $[\text{CO}_2]$ has been assessed in a field setting for only nine of those species (Appendix S1). Moreover, only physiological and growth responses to elevated $[\text{CO}_2]$ have been examined for 13 of the 23 species studied (Table 2), with many of these investigations being of plants grown singly in pots with abundant nutrients

and water. Hence the ecological conclusions that can be drawn from these investigations are somewhat limited. However, it can be seen from Table 2 that some generalities of response do emerge and these serve to form useful conclusions. For instance, elevated $[\text{CO}_2]$ would be expected to increase growth rates or biomass accumulation, especially when plants are grown in the absence of competition and with abundant nutrients and water, as detailed previously. However, this was only observed in less than half (41%) of the cases, with elevated $[\text{CO}_2]$ having no significant effect as commonly as increasing growth, both of which occurred at a rate of approximately 41% (Table 2), in a fashion that was not related to photosynthetic pathway. In almost 18% of cases, the growth response to elevated $[\text{CO}_2]$ depended upon the level of some other experimental factor/s, such as temperature or water availability. Therefore, there is no reason to expect that increasing $[\text{CO}_2]$ will necessarily increase growth in native grasses. Similarly, elevated $[\text{CO}_2]$ is expected to reduce stomatal aperture, thereby reducing transpiration rates and reducing overall plant water use. This was not seen to occur in the majority of Australian grasses examined, with $[\text{CO}_2]$ having no significant effect on transpiration in 69% of cases and no effect on water use efficiency in 58% of cases (Table 2). For those species in which non-physiological responses to $[\text{CO}_2]$ were examined, it also appeared that the rising $[\text{CO}_2]$ had little effect in most cases. For instance, flowering and seed production was unaffected in 75% of cases and seed mass was unaffected in 60% of cases (Table 2).

Most of the multi-factor experiments found that many responses of grass species to elevated $[\text{CO}_2]$ were dependent upon other factors (Table 2). A prime example of this is that of the temperate C_3 grass *Austrodanthonia racemosa*, in which the responses of growth rate, photosynthesis, transpiration, water use efficiency and foliar N concentration to elevated $[\text{CO}_2]$ were strongly dependent upon water availability (Hely 2008). *Austrodanthonia richardsonii* however, showed a more uniform response to elevated $[\text{CO}_2]$, with carbon accumulation occurring regardless of N availability, and the effect of elevated $[\text{CO}_2]$ on carbon content did not diminish with time (Lutze & Gifford 1998).

However, in the grass species most studied, namely *Austrodanthonia caespitosa*, in which a range of variables have been examined in both glasshouse and field conditions with and without warming, elevated $[\text{CO}_2]$ did have a substantial impact on both physiological and ecological performance. In this species, which is a dominant grass over much of southern Australia, while elevated $[\text{CO}_2]$ increased growth rates, it reduced photosynthetic efficiency (defined throughout as carboxylation efficiency or the increase in rate of carbon assimilation per unit increase in $[\text{CO}_2]$), transpiration (Hovenden 2003), flowering (Hovenden *et al.* 2007),

Table 2. The responses of Australian grass species to elevated [CO₂] together with their photosynthetic pathway (C₃/C₄)

Species	C ₃ /C ₄	Growth/ biomass	C assimilation efficiency	Transpiration	Water Use efficiency	Foliage N	Seed production	Seed mass	Seed N	Population growth	Competitive ability
Arid/Semi-arid zone species											
<i>Asrebla lappacea</i>	C ₄	0		0	0						
<i>Asrebla pectinata</i>	C ₄	0		0	0						
<i>Asrebla squarrosa</i>	C ₄	0		–	+						
<i>Bothriochloa biloba</i>	C ₄	0		0	0						
<i>Bothriochloa bladhii</i>	C ₄	+		0	+						
<i>Digitaria brownii</i>	C ₄	0		0	0						
<i>Panicum decompositum</i>	C ₄	+		0	+						
Temperate zone species											
<i>Austrodanthonia caespitosa</i>	C ₃	+	–	–			–	–	–	–	
<i>Austrodanthonia carphoides</i>	C ₃						0	0			
<i>Austrodanthonia eriantha</i>	C ₃	v									0
<i>Austrodanthonia racemosa</i>	C ₃	v	v	v	v	v					0
<i>Austrodanthonia richardsonii</i>	C ₃	v	–								
<i>Austrodanthonia tenuior</i>	C ₃						0				
<i>Austrostipa mollis</i>	C ₃						v	0			
<i>Austrostipa nodosa</i>	C ₃						0				
<i>Austrostipa pubinodis</i>	C ₃	+					0				
<i>Austrostipa rudis</i>	C ₃						0				
<i>Dichanthium sericeum</i>	C ₃	0			–						
<i>Dichelachne crinita</i>	C ₃	+	0	0	0		0				
<i>Elymus scaber</i>	C ₃	+	–	0	0			+			
<i>Poa labillardierei</i>	C ₃	+		0	0						
<i>Pennisetum alopecuroides</i>	C ₄	0		0	0						
Widespread species											
<i>Themeda triandra</i>	C ₄	+	0	–	+		0	0	0	v	

Impacts are indicated as stimulation (+), reduction (–) or no significant effect (0) by elevated [CO₂] as compared to controls. Responses dependent upon other factors are shown as variable (v). Data from publications listed in Appendix.

seed mass (Hovenden *et al.* 2007, 2008b), seed N content (Hovenden *et al.* 2008b) and consequently reduced population growth rates in the field (Williams *et al.* 2007). Thus, while the literature suggests that many Australian grass species are largely insensitive to the increasing [CO₂], the responses of the few could be dramatic.

Trees

In terms of the number of species, there are more examinations of the impact of elevated [CO₂] on

Australian trees than there are of Australian grasses, with studies involving 28 Australian tree species, from a range of families covering the tropics to the cool temperate regions of southern Australia (Table 3). Of the 28 species whose responses to elevated [CO₂] have been investigated, 11 are eucalypts and 10 are members of the genus *Acacia* (Table 3). Eleven of the tree species studied occur in the tropical and sub-tropical regions, including the two mangroves *Rhizophora apiculata* and *R. stylosa*. The remaining species investigated consist of 13 from moist, temperate regions, four from semi-arid/arid zones and a single species, *Eucalyptus pauciflora*, from the sub-alpine zone

Table 3. The responses of Australian tree species to elevated [CO₂]

Species	Growth/ biomass	C assimilation efficiency	Transpiration	Water Use efficiency	Foliage N	PSM
Tropical zone species						
<i>Alphitonia petriei</i>					–	+
<i>Brachychiton populneum</i>		+				
<i>Eucalyptus grandis</i>	+				–	
<i>Eucalyptus microtheca</i>	+					
<i>Eucalyptus miniata</i>	0	0	0		0	
<i>Eucalyptus tereticornis</i>	v				–	+
<i>Eucalyptus tetradonta</i>	+		–	+	–	
<i>Flindersia brayleyana</i>					–	+
<i>Maranthes corymbosa</i>	+	+	–	+	–	
<i>Rhizophora apiculata</i>	v	v	v	+		
<i>Rhizophora stylosa</i>	v	v	v	+		
Arid/Semi-arid zone species						
<i>Acacia aneura</i> (–nod)	0	–	–	+		
<i>Acacia aneura</i> (+nod)	+					
<i>Acacia colei</i> (–nod)	+	0	–	+		
<i>Acacia coriacea</i> (–nod)	+	0	–	+		
<i>Acacia tetragonophylla</i> (–nod)	+	–	0	+		
<i>Acacia tetragonophylla</i> (+nod)	0					
<i>Acacia dealbata</i> (–nod)	+	–	0	+	0	
<i>Acacia dealbata</i> (+nod)	+				–	
<i>Acacia implexa</i> (–nod)	+	–	+	–	0	
<i>Acacia implexa</i> (+nod)	+				–	
<i>Acacia irrorata</i> (–nod)	+	–	–	+	0	
<i>Acacia irrorata</i> (+nod)	+				–	
<i>Acacia mearnsii</i> (–nod)	+	–	–	+	0	
<i>Acacia mearnsii</i> (+nod)	+				–	
<i>Acacia melanoxylon</i> (–nod)	+	–	–	+	0	
<i>Acacia melanoxylon</i> (+nod)	+				–	
<i>Acacia saligna</i> (–nod)	+	–	0	0	0	
<i>Acacia saligna</i> (+nod)	+				–	
<i>Acmena smithii</i>	+	–				
<i>Doryphora sassafras</i>	+	–				
<i>Eucalyptus cladocalyx</i>	+				–	0
<i>Eucalyptus macrorhyncha</i>	+	v	–	+		
<i>Eucalyptus polyanthemus</i>	+					
<i>Eucalyptus rossii</i>	+	v	–	+		
Sub-alpine zone species						
<i>Eucalyptus pauciflora</i>	v	0				

Elevated [CO₂] impacts are indicated as stimulation (+), reduction (–), no significant effect (0) or variable effect (v). Nodulation state of *Acacia* species during experiment is indicated (±nod). PSM, plant secondary metabolites. Data from publications listed in Appendix.

(Table 3). In nearly every case, the responses of tree species have been assessed on seedlings or small saplings only, as the examinations have been restricted to controlled environment cabinets or glasshouses with obvious size restrictions. The examinations have also been almost exclusively focused on physiological and growth responses (Table 3, Appendix S1). The Hawkesbury Forest Experiment in the north-western outskirts of Sydney, NSW, is investigating the responses of *Eucalyptus saligna* using whole tree chambers, which will allow the plants to grow relatively large. However, even this experiment will be unable to examine many ecologically relevant aspects of tree biology, such as reproduction, recruitment and competition.

In contrast to the responses of Australian grasses, growth at an elevated [CO₂] has a strong impact on most of the Australian tree species investigated (Table 3). The growth rate or biomass accumulation was significantly increased by elevated [CO₂] in nearly 80% of cases (Table 3). This was accompanied by an increase in water use efficiency at elevated [CO₂] in 87.5% of cases and a reduction in transpiration or stomatal conductance in nearly 60% of cases. However, the response of photosynthetic carbon assimilation was similar in trees and grasses, with 50% of species showing a reduction in photosynthetic efficiency at elevated [CO₂] (Table 3). The foliage N content of trees was reduced by elevated [CO₂] in nearly 65% of cases, with foliage N in the remainder of species being unaffected (Table 3). In the four instances where the response of PSM to [CO₂] was examined, elevated [CO₂] increased the PSM content in three species and had no effect on the fourth.

The responses of the 11 tropical trees investigated varied to a greater extent than did those of species from temperate and arid/semi-arid regions (Table 3). Thus, 100% of temperate zone trees and 66.7% of arid/semi-arid zone trees grew significantly faster or larger at elevated [CO₂] than they did under control conditions, whereas only 50% of tropical species reacted in this way. Interestingly, this corresponds with differences in responses to elevated [CO₂] of both photosynthetic efficiency and foliar N content (Table 3). Thus, photosynthetic efficiency was reduced at elevated [CO₂] in 80% of temperate zone tree species and 50% of arid/semi-arid zone species but not in any of the tropical zone tree species (Table 3). In much the same way, foliar N was reduced by growth at elevated [CO₂] in approximately half of the tree species investigated from both the temperate and arid/semi-arid zones, but in 86% of tropical zone species. It is normally assumed that reductions in foliar N content caused by elevated [CO₂] are at least partially due to photosynthetic down-regulation (Bowes 1993), but this does not seem to be the case for Australian tropical trees, in which leaf N concentrations were reduced at

elevated [CO₂] but photosynthetic efficiency was not. Thus, it seems likely that the reduction in N concentration at elevated [CO₂] in the tropical tree species is due to a dilution of leaf N caused by the extra carbohydrates fixed (Sage 1994). The impacts of elevated [CO₂] on water use efficiency were far more uniform, with almost all tree species investigated having a substantially increased water use efficiency at elevated [CO₂] (Table 3).

The responses of woody plants from the arid/semi-arid zones to [CO₂] are particularly worthy of mention. The only investigations of this type were a series of glasshouse experiments on four *Acacia* species, namely *Acacia aneura*, *A. colei*, *A. coriacea* and *A. tetragonophylla* (Atkin *et al.* 1999; Schortemeyer *et al.* 1999, 2002; Evans *et al.* 2000). This series of experiments investigated the growth response of un-nodulated plants of all species, as well as nodulated plants of *A. aneura* and *A. tetragonophylla*. In the un-nodulated state, elevated [CO₂] increased the relative growth rate only in *A. coriacea* although both *A. colei* and *A. tetragonophylla* also had a significantly higher final biomass than in control conditions. However, nodulated *A. aneura* plants had a substantially increased relative growth rate when grown at elevated [CO₂] (Schortemeyer *et al.* 2002), which is totally different to the response when plants were prevented from nodulating (Atkin *et al.* 1999). Nodulation therefore plays an important role in the response of *A. aneura* to elevated [CO₂]. The same is not the case with *A. tetragonophylla*, however, in which elevated [CO₂] did not significantly increase relative growth rate in either nodulated (Schortemeyer *et al.* 2002) or unnodulated (Atkin *et al.* 1999) plants.

Also of interest is the response to elevated [CO₂] of the single sub-alpine tree species investigated, *E. pauciflora*, which has been examined in several publications resulting from a field experiment in which young trees were grown in OTC (Lutze *et al.* 1998; Roden *et al.* 1999; Barker *et al.* 2005; Loveys *et al.* 2006). [CO₂] had little effect on leaf gas exchange or growth, apart from during the spring when seedlings grown at elevated [CO₂] had a higher growth rate (Roden *et al.* 1999). However, the stimulation of growth during the spring may be offset by freezing damage during the autumn, which was greater in seedlings at elevated [CO₂] than those in control chambers (Lutze *et al.* 1998; Barker *et al.* 2005; Loveys *et al.* 2006). The reasons for this were that foliage on elevated [CO₂]-grown plants had a higher ice nucleation temperature and therefore greater levels of frost damage (Lutze *et al.* 1998), which was probably due to higher day time leaf temperatures of elevated [CO₂]-grown plants (Loveys *et al.* 2006). These results were supported by the responses to a late-spring frost, which caused greater amounts of damage to elevated [CO₂]-grown plants than to controls, with subsequent

reductions in growth of seedlings at elevated $[\text{CO}_2]$ (Barker *et al.* 2005). Woldendorp *et al.* (2008) suggested that while increases in temperature meant fewer days below 0°C , there would still be just as many frost damaging events as the warmer leaf temperature of plants grown in elevated $[\text{CO}_2]$ means that the plants will not be acclimated to the low temperatures of a frost. This work suggests that the extra carbon gained by evergreen trees because of the increasing $[\text{CO}_2]$ may be offset by increases in loss of leaf tissue from higher levels of frost injury in frost-prone environments.

From the range of responses examined, it appears that the most uniform response of Australian tree species to the increasing $[\text{CO}_2]$ is the increase in plant water use efficiency. While the vast majority of tree species investigated also increased growth rate or biomass accumulation in response to an increased $[\text{CO}_2]$, the trend was most reliable in temperate zone species.

Other plant growth forms

There are several forbs and two species of sub-shrubs present in the TasFACE experiment. Published details on the impact of elevated $[\text{CO}_2]$ are available for aspects of the reproductive biology of these species growing in a natural community (Table 4). Elevated $[\text{CO}_2]$ had no effect on flowering and seed production

Table 4. The responses of Australian forb, geophyte and sub-shrub species to elevated $[\text{CO}_2]$

Species	Flower production	Flowering phenology	Seed mass
Temperate forbs			
<i>Acaena echinata</i>	0		
<i>Calocephalus citreus</i>	v	0	
<i>Convolvulus angustissimus</i>	0	0	
<i>Eryngium ovinum</i>	0	0	
<i>Geranium retrorsum</i>	0	0	
<i>Leptorhynchus squamatus</i>	+	v	0
<i>Oxalis exilis</i>	–		
<i>Plantago varia</i>	0		
<i>Sebaea ovata</i>	–		
<i>Solenogyne dominii</i>	0		0
Temperate geophytes			
<i>Carex breviculmis</i>	0		
<i>Hypoxis vaginata</i>	0	0	
<i>Wurmbea dioica</i>	0		
Temperate sub-shrubs			
<i>Bossiaea prostrata</i>	v	0	0
<i>Hibbertia hirsuta</i>	v	v	

Impacts are indicated as stimulation (+), reduction (–) or no significant effect (0) or variable effect (v) by elevated $[\text{CO}_2]$ as compared to controls.

in any of the three species of geophyte investigated or on six of the 10 species of forb investigated. Of the remaining four species of forb investigated, reproduction was significantly stimulated in one species, reduced in two and the effect was variable in one species (Table 4). The response of flowering and seed production in two sub-shrubs was also variable depending upon both year and warming treatments (Hovenden *et al.* 2007).

Impacts on Australian animals

Vertebrates

The only published study that has investigated the impacts of elevated $[\text{CO}_2]$ on any Australian vertebrate was a study of leaf chemistry in two pioneer tree species from tropical rainforests of north Queensland (Kanowski 2001). This study examined the foliar chemistry of seedlings of *Flindersia brayleyana* and *Alphitonia petriei* grown at $350 \mu\text{mol mol}^{-1}$ and $790 \mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ on a nutrient rich (basalt) and a nutrient poor (rhyolite) soil in a glasshouse. The results largely match expectations of reductions in foliar N levels (by 25% in *A. petriei* and 29% in *F. brayleyana*) and increases in PSM in *F. brayleyana* under high $[\text{CO}_2]$. Interestingly, foliar cation concentrations (Na^+ , Ca^{2+} , K^+) and P levels were reduced by exposure to elevated $[\text{CO}_2]$ by 19–28% in *F. brayleyana*, but were not affected in *A. petriei*. Leaves were both tougher and thicker on plants grown at elevated $[\text{CO}_2]$ than in controls, for both *A. petriei* and *F. brayleyana*. Kanowski (2001) concluded that folivores would become less abundant in tropical forests if these results were widely applicable to tropical tree species in the longer term. Given that foliar chemistry of *A. petriei* was generally less responsive to elevated $[\text{CO}_2]$ than in the co-occurring *F. brayleyana*, it is possible that folivores will feed preferentially upon this species at elevated $[\text{CO}_2]$, perhaps reducing plant performance and success and eventually reducing the abundance of this species.

Insects

The insect folivore *Paropsisterna flaveola* (published as *Chrysophtharta flaveola*) was fed foliage from *E. tereticornis* grown at ambient ($350 \mu\text{mol mol}^{-1}$) and elevated ($800 \mu\text{mol mol}^{-1}$) $[\text{CO}_2]$, with two nutrient and two light levels in a glasshouse experiment (Lawler *et al.* 1997). Foliage from plants grown at $800 \mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ had significantly reduced N content, higher C : N ratio and generally higher levels of phenolics than foliage from plants grown at a

[CO₂] of 350 µmol mol⁻¹. At low nutrient levels, leaf relative water content was unexpectedly lower at elevated [CO₂] than at ambient, but at high nutrient levels there was no impact of [CO₂] on leaf water content.

The changes in leaf chemistry induced by the treatments affected the performance of 4th-instar larvae of *P. flaveola* fed on the leaves (Lawler *et al.* 1997). Increased C : N ratios of leaves reduced digestive efficiencies and pupal body sizes and increased mortality. Below a threshold nitrogen concentration of approximately 1% dry mass, severe reductions in the performance of larvae were recorded. These extremely low N concentrations occurred at elevated [CO₂] at low nutrient levels, such as may well be expected under field conditions.

In a single study of an omnivorous Australian insect, a simple community consisting of the Australian omnivorous bug *Oechalia schellenbergii*, living with garden pea (*Pisum sativum*) and an introduced caterpillar pest, *Helicoverpa armigera*, common in Australian crops such as cotton, was raised in controlled environment growth cabinets at [CO₂] of 360 µmol mol⁻¹ and 700 µmol mol⁻¹ (Coll & Hughes 2008). This research demonstrated that *O. schellenbergii* as a generalist predatory omnivore benefited from elevated [CO₂] because it reduced the size and strength of the caterpillars by reducing foliage quality. Thus, it is possible that predatory insects will be advantaged by the increasing [CO₂].

In a study of the responses of *Eucalyptus cladocalyx* to elevated [CO₂], it was found that the foliar N content was lower at elevated [CO₂] than in controls whereas levels of the cyanogenic glycoside prunasin were unchanged (Gleadow *et al.* 1998). Since leaf N content is lower at elevated [CO₂], both mammalian and insect herbivores are likely to be exposed to higher levels of the extremely toxic prunasin as they ingest greater quantities of foliage to obtain necessary protein quantities. It is also possible that herbivores will avoid browsing *E. cladocalyx* altogether, perhaps placing greater browsing loads on co-occurring species and increasing competition for fodder with low toxicity.

Impacts on Australian fungi and microbes

In the only published account of the impacts of elevated [CO₂] on fungi or microbes, Grayston *et al.* (1998) discovered that elevated [CO₂] changed the soil microbial community growing in the rhizosphere of *Austrodanthonia richardsonii* plants that had been exposed to either elevated [CO₂] or control conditions for 4 years. The microbial community at elevated [CO₂] was different to that in control conditions. There was also a preferential stimulation of fungal growth at elevated [CO₂]. It appears from this single study that bacterial metabolic activity, and not popu-

lation size, was stimulated by the additional flow of C to the soil at elevated [CO₂].

Unpublished results from the OzFACE experiment in northern Queensland indicate that mycorrhizal fungi have lower abundance at elevated [CO₂] compared with control conditions (C. Stokes, pers. comm.).

RESEARCH ON AUSTRALIAN ECOSYSTEMS AND ECOSYSTEM PROCESSES

The impacts of the increasing [CO₂] on ecological processes and ecosystem composition, structure and function is far less studied, both globally and in Australia, than the responses of individual species. Modelling studies have investigated the likely responses of model or artificial ecosystems to elevated [CO₂] but few investigations globally have examined the responses of natural ecosystems. In Australia, investigation of the likely impacts of elevated [CO₂] on ecological processes and ecosystem properties are restricted to two field experiments and several modelling and conceptual investigations.

One of the main problems with determining the likely impact on Australian ecosystems is that the majority of research done to date concerns plants grown individually or in monocultures in pots in the absence of pathogens, competitors and other natural enemies such as herbivorous animals. Most experiments also supply abundant, or at least adequate, nutrients and water, whereas in the field both are often limiting. Thus, because the results for most species listed previously are analyses of how [CO₂] affects a species' growth potential, they are actually analyses of how [CO₂] influences the *physiological* niche. While this does provide important and necessary information, it does present substantial problems with scaling responses up to natural ecosystems. It is well established that the response of a species' physiological niche to variation in any environmental factor is different from that in the field. Indeed, species occupy a different niche in their natural environment to that in an artificial environment; this is termed the *realized* niche. Thus, it is possible, and even very likely, that a species' response to the increasing [CO₂] will be different in a natural environment to that in an artificial environment. This is well presented in the cases of the temperate grasses *Themeda triandra* and *A. caespitosa*. These two co-occurring species had very similar growth responses to doubled [CO₂] in a growth cabinet study (Hovenden 2003) and would therefore be predicted to have similar responses in the field. However, when grown in the field in the TasFACE experiment over several years, *A. caespitosa* had reduced population growth rate, particularly when

exposed to a combination of warming and elevated $[\text{CO}_2]$ (Williams *et al.* 2007). The consequent reduction in competition from *A. caespitosa* allowed *T. triandra* population growth to increase. This example illustrates the difficulties in predicting community and ecosystem level outcomes from single-species experiments.

Ecosystem level processes

Biogeochemistry

As detailed previously, the increasing $[\text{CO}_2]$ is believed to stimulate the sequestration of N into biomass and soil organic matter fractions with long residence times, a process known as progressive nitrogen limitation, PNL (Luo *et al.* 2004b). Results from the TasFACE experiment indicate that PNL occurs in response to elevated $[\text{CO}_2]$ in an Australian temperate grassland (Hovenden *et al.* 2008a). However, the impacts of warming on biogeochemical cycling are largely unknown and the data from the TasFACE experiment comprise the only published examination of the interaction between elevated $[\text{CO}_2]$ and warming on soil nutrient availability (Hovenden *et al.* 2008a). These results indicate that the addition of 2°C warming completely prevents the strong (up to 60%) reduction of soil N availability that occurs in the presence of elevated $[\text{CO}_2]$ without warming. Thus, it appears that the rising $[\text{CO}_2]$ potentially could affect biogeochemical cycling dramatically, but the rising temperature may well offset these impacts. The TasFACE site contains practically no N fixing species, so the impacts of the increasing $[\text{CO}_2]$ on biogeochemistry where there are substantial inputs of new N through symbiotic N fixation are currently unknown for Australia.

Food webs

Although the only study of the CO_2 -sensitivity of food webs in an Australian context is that of Coll and Hughes (2008), where a native omnivorous bug was grown in a simple ecosystem with an exotic plant and an exotic caterpillar, our general understanding of the likely impacts of the increasing $[\text{CO}_2]$ on trophic interactions can be applied to tissue chemical analyses of Australian native plants. In Australia, many plant species possess high to lethal levels of toxic secondary metabolites under current conditions, and the levels of these toxins limit the amount of plant material that can be ingested by an animal. Further, many plant species possess a wide range of secondary metabolites that have various effects on different types of animals, in order to protect the plant from a range of herbivorous

animals. The evidence from investigations of Australian plant species is that the increasing $[\text{CO}_2]$ is extremely likely to make plants more toxic and less nutritious to all herbivorous animals. There is also evidence that the composition of a suite of secondary metabolites in a species is sensitive to $[\text{CO}_2]$, such that some secondary metabolites are increased more than others as $[\text{CO}_2]$ rises, and this could also have an impact on herbivore community composition. Herbivores may also move to other species or alter their diet from leaves to other plant parts, such as flowers and fruits, with ramifications for the plants. It would appear likely that plants will be more heavily browsed by certain animals but these animals will have increased mortality due to both toxins and attack by predators and pathogens. Analysis of the impacts of elevated $[\text{CO}_2]$ on higher trophic levels, however, is currently prevented by the lack of experimental results. Therefore, the overall impacts of the increasing $[\text{CO}_2]$ on trophic interactions in Australian ecosystems is currently unknown.

RESEARCH GAPS AND SUGGESTIONS FOR FUTURE RESEARCH

It is clear that the rising $[\text{CO}_2]$ has the potential to alter the performance of individual species, the interactions of species and the biotic and abiotic environment and even ecosystem structure and function. Further, these changes are already happening as the $[\text{CO}_2]$ has risen dramatically over the past century. International research into ecosystem processes and the ways that the increasing $[\text{CO}_2]$ will affect them have direct relevance to the Australian system. Thus, Australian contributions to the area of ecological interactions and ecological processes and rising $[\text{CO}_2]$ should be maintained as the ultimate responses of terrestrial biodiversity to the increasing $[\text{CO}_2]$ may be more dependent upon secondary changes, such as PNL, than on the primary changes that occur. However, it is also clear that important aspects of the Australian environment differ from those studied elsewhere, making local research targeted at local ecosystems vital. Since budgets, research capability and time are limited, research effort and funds should be directed at key ecosystems and processes either likely to be most affected or most dissimilar to those studied elsewhere. Therefore, we propose the following priorities for research into the effects of the increasing $[\text{CO}_2]$.

1. Interactions with fire and rising $[\text{CO}_2]$

Since most of Australia's surface area is prone to recurrent fire and many of Australia's plant species, including the ubiquitous eucalypts, are fire-promoting,

the single largest question about the impact of the rising [CO₂] concerns the impact it will have on vegetation-fire relationships. Will increased biomass production, fuel accumulation and production of secondary metabolites increase the frequency and/or intensity of fires? Will rising [CO₂] make plants more resistant to fire or more able to cope with an increased fire frequency? Will higher [CO₂] allow seedlings to develop more rapidly to a size sufficient to survive their first fire or reduce the juvenile period and increase reproductive output in fire-sensitive species? These important questions have received little consideration and no actual research effort. However, an understanding of the interactions between the increasing [CO₂] and fire frequency is vital for most Australian ecosystems. Such questions require a concerted research program combining both experimental and modelling studies.

2. Impacts of rising [CO₂] on mammalian herbivores

One of the most universal responses to the rising [CO₂] is a reduction of plant foliar N levels. Most of the Australian plants investigated also increase foliar concentration of secondary metabolites in elevated [CO₂]. Together, these factors are likely to have dramatic consequences for all herbivores. Australia has unique and iconic mammalian herbivores including macropods, wombats, possums, greater gliders and koalas. While grazing mammals are likely to be affected by CO₂-driven changes in leaf quality, the greatest impacts are likely to be on browsing mammals. This is particularly important in those species reliant upon eucalypts, given the low levels of N coupled with the high levels of toxic secondary metabolites in foliage of these species under current conditions. The fact that we know absolutely nothing about the impact of rising [CO₂] on physiology, health and reproduction of Australia's unique browsing mammals needs to be addressed as a matter of urgency.

3. Interactions between P limitation and rising [CO₂]

The impact of nitrogen limitation on [CO₂] effects has been studied extensively and it is possible that PNL will be of dramatic importance in Australia's generally nutrient impoverished soils. However, of perhaps greater importance is the role of phosphorus limitation. Little work has investigated the impacts of low P availability on [CO₂] responses nor on whether the increasing [CO₂] could help alleviate P deficiency. Mycorrhizal fungi play a crucial role in plant P nutrition by providing access to P that would otherwise

be unavailable. Since elevated [CO₂] quite reliably increases mycorrhizal abundance, it is possible that it will alleviate to some extent the chronic P limitation that occurs in most Australian ecosystems. Investigating the relationship between [CO₂], plants, fungi and P availability is a key research area for Australian ecosystems.

4. Invasive plant species and rising [CO₂]

The issue of invasive plant species is particularly important in Australia. Each year, vast sums and considerable community effort are expended on weed eradication programmes. Knowing which species or types of species are most likely to benefit or suffer from the rising [CO₂] is of immense practical, economic and strategic importance to Australia. Despite this fact, there has been little actual research in this area. The question of whether the invasiveness and dominance of a particular exotic species is likely to increase as a result of increasing [CO₂] depends upon the functional attributes of the exotic species and the plant community it is invading. This level of enquiry demands a case-by-case analysis, and has been particularly successful for certain problem species, such as *Acacia nilotica* ssp. *indica*, which invades Australian semi-arid rangelands and is likely to become increasingly aggressive as [CO₂] increases (Kriticos *et al.* 2003). However, this approach is not particularly efficient when considering the large number of weeds in Australia. Therefore, the question of whether invasive species per se are likely to become more aggressive in an elevated [CO₂] world is of great ecological and economic relevance (Dukes 2000). There is good reason to believe that as the [CO₂] rises, any increases in net primary productivity will lead to increased diversity capacity, thus promoting invasion (Woodward & Kelly 2008). Determining whether exotic species will be more likely than natives to fill this increased diversity capacity is vitally important to the prevention of weed invasion.

5. Key ecosystems and taxa

As well as the general process-related research gaps identified previously, there are a few key Australian terrestrial ecosystems that deserve special attention. For instance, no investigations have been made of the likely impacts of the increasing [CO₂] on Australia's shrublands or heathlands or on the individual species found in those ecosystems, despite their importance for Australian biodiversity. Australian shrublands and heathlands tend to be dominated by species very different in biology and phylogeny to those in northern hemisphere environments and thus the few studies on

shrublands from other countries have little relevance here, other than in the most general terms. Despite this lack of knowledge, Australian shrublands are potentially very responsive to the increasing $[\text{CO}_2]$ and particularly to the interactions between $[\text{CO}_2]$ and fire.

Similarly, no investigations have been made of the likely impacts of the increasing $[\text{CO}_2]$ on Australia's arid zone ecosystems. These systems are typically low density, low competition environments, which have the greatest potential to respond to the increasing $[\text{CO}_2]$ (i.e. Type I environment, Körner 2006). The IPCC Fourth Assessment Report for Australia and New Zealand (Hennessy *et al.* 2007) predicts dramatic increases in woody plant cover in arid and semi-arid Australia. These predictions are based on simple physiological models and improved water use efficiency and are not supported by any experimental evidence. Again, the interaction between $[\text{CO}_2]$ and fire is crucial to the end result of rising $[\text{CO}_2]$ in this environment.

Finally, it is worth mentioning that by far the majority of Australia's woodlands and forests are dominated by the single taxon *Eucalyptus*. If any single Australian genus deserves concerted research effort into the impacts of the increasing $[\text{CO}_2]$ on its ecological interactions, it is certainly *Eucalyptus*. Despite the fact that several studies over several decades have examined the effects of $[\text{CO}_2]$ on various eucalypt species, none of them has examined actual competitive interactions.

CONCLUSIONS

It is clear that much work needs to be done before any clear predictions can be made concerning the impacts of the rising atmospheric $[\text{CO}_2]$ on Australia's native species and ecosystems. This is particularly the case for organisms other than vascular plants. However, from the research so far, it is possible to draw several conclusions about the responses of vascular plants. Woody plants, particularly from temperate regions, are likely to respond strongly to the increasing $[\text{CO}_2]$, as a result of both increased growth rates and improved water use efficiency. The greater and more uniform stimulation of trees above other growth forms indicates that vegetation thickening is likely, with grasslands and grassy woodlands likely to be invaded or have thickened canopies in response to the rising $[\text{CO}_2]$. The almost uniform response of leaf nitrogen content and secondary metabolite concentrations, across both region and lifeform, indicates that feed quality for herbivores is almost certain to be lower in a future, high $[\text{CO}_2]$ environment. However, the impact of this change on Australian native animals has been assessed in only two invertebrate species and in particular, the impacts of the rising $[\text{CO}_2]$ on Australia's unique and diverse marsupial fauna has not been assessed in any manner for any species. This is of grave concern as many such

organisms are already under threat from other factors such as land clearance and disease.

Nearly all of the research on the impacts of $[\text{CO}_2]$ on Australian species has come from experiments in glass-houses or growth cabinets with extremely artificial conditions and with few interacting factors. The lack of field-based, multi-factorial experiments hampers any predictions of likely future impacts. However, such experiments are expensive and require long-term commitment of both funds and researcher time, which means that they are rarely instigated. Much of the current push for increasing our understanding of the responses of ecosystems to global changes ignores the rising concentration of CO_2 in the atmosphere, or relegates the responses as interesting irrelevances and concentrates on rising temperature and altered precipitation instead, given the scale of changes in both climate and climatic variability. While FACE facilities are necessary for determining long-term ecosystem feedbacks and the way elevated $[\text{CO}_2]$ interacts with stochastic factors such as drought and fire, carefully controlled and realistic chamber or glasshouse experiments are cheaper and can more rapidly address several of the key research priorities mentioned previously. Such experiments need to be designed to take account of resource availability and species interactions to be useful for predictions.

One of the central goals of ecological research is to identify the unifying processes that control the structure and function of ecosystems. A particular aspect of this search for unifying processes is the study of the responses of ecological processes to the physical and chemical environment. While research effort does need to be guided towards increasing our understanding of the impacts of the rising $[\text{CO}_2]$ on ecosystem processes, it is also vital that high quality, basic research into the ways that ecosystems operate is well-supported. Such apparently 'interest-driven' or 'blue-skies' research underpins all impacts related research and provides the necessary context for the interpretation of experimental and modelling results, thus allowing policy to be set. It is clear that leaf-level plant gas exchange responses to $[\text{CO}_2]$ are well progressed for a range of Australian plant species. This review demonstrates that the rising $[\text{CO}_2]$ could have dramatic and potentially disastrous consequences for the sustainability of Australia's terrestrial ecosystems, yet we know almost nothing of the effect of $[\text{CO}_2]$ on the ecological processes most relevant to this continent. We ignore this at peril to ourselves, our country and the organisms with which we share it.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. All Australian plant species for which the impacts of elevated [CO₂] have been published, their life form and habitat together with measured response variables, method of investigation and any interacting factors. Measured responses for each species are indicated by an asterisk (*). For method of study, GH = glasshouse/growth cabinet, OTC = Open Top Chamber, FACE = Free Air CO₂ Enrichment. For other factors, C = competition, H = heating, L = light, N = nutrients, RH = relative humidity, S = salinity, T = temperature, W = water availability, Y = year. References given are those listed in the article reference list.