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Submission to the

New Inquiry into Australia's Biodiversity in a Changing Climate

conducted by the

House of Representatives Standing Committee on Climate Change, Environment and the Arts

Submission by

Mark J. Hovenden PhD

Associate Professor in Plant Ecology

School of Plant Science

University of Tasmania

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EXECUTIVE SUMMARY

I make this submission to the House of Representatives Standing Committee on Climate Change, Environment and the Arts for their New Inquiry into Australia's Biodiversity in a Changing Climate. In respect of the terms of reference of the committee, my submission directly addresses terrestrial biodiversity in Australia as well as how climate change impacts on biodiversity may flow on to affect human communities and the economy. In making my submission, I draw on my own professional expertise in the area as well as the results of my research and that of my research group, but also on the published work of other scientists, both Australian and foreign, whose work is relevant to this enquiry. Where my submission draws on published work of others, this work is cited and a full reference list provided at the end of my submission. This submission is a revised and updated copy of an earlier report written for the Federal Department of Climate Change.

The Standing Committee will no doubt receive many submissions covering the whole gamut of climate change but most especially alterations of average and extreme temperatures and precipitation distribution and abundance. These factors are extremely important but will no doubt be covered extensively in other submissions. Therefore, my submission will not deal with these factors. Instead by submission will focus on the direct and indirect impacts of the rising concentration of carbon dioxide ([CO_2]) in the atmosphere, irrespective of any change in other climatic factors. My submission will only deal with changes in temperature and precipitation where these factors are likely to interact with the impacts of the rising [CO_2] itself. My submission begins with a detailed examination of why the rising concentration of CO_2 must be considered important in its own right irrespective of its impact on the physical climate.

The increasing concentration of CO_2 in the atmosphere as a result of fossil fuel use and land use changes has the potential to impact on Australia's biodiversity. As CO_2 is the primary substrate for the production of carbohydrates through photosynthesis, and this process forms the basis of the entire terrestrial food web, there is substantial potential for both small and large scale changes in the abundance of organisms, community composition and ecosystem structure and function. This is important in terms of the maintenance of biodiversity and the productivity and carbon sequestration potential of Australia's terrestrial ecosystems.

From the published literature, supplemented with material from University libraries and archives, our knowledge of the likely impacts of the increasing [CO_2] on native species is extremely low for all organisms other than vascular plants. Studies on the impacts of [CO_2] on any aspect of an organism's biology have been published for 70 species, covering less than 0.05% of organisms native to Australia. Of these 70 species reported, 68 are vascular plants. While this is understandable, since plant responses to the increasing [CO_2] mediate nearly all other changes in the ecosystem, several important groups of organisms are badly under-represented. Of these, the most important are Australia's native invertebrates and browsing mammals, which are most likely to be affected by the rising [CO_2] over the coming decades. A second, extremely important group that has been largely ignored is the soil community. This is particular concern, since ecosystem level responses to the rising [CO_2] are most likely to be mediated through changes in the performance and/or composition of the soil microbial flora and fauna.

There have been only two ecosystem level investigations of the impacts of the rising [CO_2] in native ecosystems in Australia. One of these, the OzFACE experiment from North Queensland, has ceased operation and been decommissioned. The other experiment, the

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TasFACE experiment in Tasmania, is currently continuing. Both of these experiments investigate both the responses of individual organisms but also provide assessments at the population, community and ecosystem level. Such experiments are vital for predicting the long-term impacts of the increasing [CO_2], as the responses of long-term processes and feedbacks such as biogeochemical cycles to the increasing [CO_2] may well determine the response of entire ecosystems. Further, such experiments provide the only realistic projections of species behaviour into the future, as the responses of species to changes in [CO_2] when grown in isolation, divorced from normal ecological interactions, are often not predictive of the responses in the natural environment. Both the TasFACE and the OzFACE experiment are located in native grasslands/rangelands, so that the assessment of ecosystem processes to the rising [CO_2] is unavailable for all other Australian terrestrial ecosystems.

From the analysis of all research on Australia's native species, it can be determined that changes in biodiversity and ecosystem structure and function are most likely at the boundaries between deserts and grasslands, grasslands and woodlands and woodlands and forests. The increasing [CO_2] is likely to increase the plant water use efficiency thereby increasing plant cover in arid and semi-arid zones. The increasing [CO_2] will also increase the growth of woody species more than that of grasses, therefore allowing shrubs and trees to invade grasslands and grassy woodlands, a process known as vegetation thickening. There is also substantial reason to believe that major changes in community structure and function are likely to occur in Australia's unique and diverse shrublands as a result of the increasing [CO_2], despite the fact that there are no studies of any shrubland species to [CO_2]. This is an area of extreme concern and should be remedied as soon as practicable. It appears unlikely that the increasing [CO_2] will have substantial impacts upon the cool, wet ecosystems such as those in sub-alpine, alpine and subantarctic environments.

The most overwhelming responses to an increased [CO_2] observed in Australian plant species are a reduction in plant nitrogen concentration and an increase in the production of plant secondary metabolites. While many plant species also displayed increased growth rates at higher [CO_2], this was far from universal. Indeed, the only group that displayed a uniform increase in growth with increasing [CO_2] was the temperate trees, with all other species types investigated varying in responsiveness to an increase in [CO_2]. It is possible that this variation in response to increased [CO_2] will lead to changes in competition and community composition, structure and function. Such changes in the vegetation will lead to alterations of habitat quality for various other organisms. From the few ecosystem-level investigations that exist it is clear that currently widespread and abundant species may rapidly become vulnerable as a result of their particular physiological response to the rising [CO_2]. I point the Committee members to my study of the widespread and economically important Australian wallaby grass, *Austrodanthonia caespitosa,* described on p. 23 of this submission.

The strong and universal response of plant nitrogen concentration to increased [CO_2] will have ramifications for herbivorous animals, especially when coupled with the increase in the levels of plant secondary metabolites. Many plant secondary metabolites serve to reduce herbivory and may be toxic or repellent. Increasing concentrations of secondary metabolites, coupled with reduced plant nutritional quality, is certain to affect the health and behaviour of herbivores. This is of particular concern for Australia's unique herbivorous and granivorous marsupials, for which no information is available with the most vulnerable being the arboreal folivores, namely the koala, tree kangaroos and species of possum and glider. Changes in herbivore abundance and/or health is likely to feed into other trophic levels, such as predators, but the information available is too scant to allow further predictions.

I contend that several Australian terrestrial ecosystems are most important to consider in terms of response to the rising [CO_2]. These are the biodiverse tropical forests and perhaps more critically temperate heathlands, particularly those of south-west Western Australia, one of the world's biodiversity hotspots. The species-rich heathland is particularly susceptible given the highly specialised nutrient requirements of these species and the possibility of major changes in the community composition from small differences in response to the rising [CO_2]. Targeted research in this ecosystem is vital if we are to predict impacts.

In conclusion, there is sufficient information available to be certain that the increasing [CO_2] will impact upon Australia's native biodiversity. However, the amount of research required to formulate predictions concerning the long-term future of almost all organisms is far in excess of that currently available. Further research into targeted ecosystems and groups of organisms is required. It is essential that a framework be developed for coordinating research efforts into the impacts of the increasing [CO_2] on Australia's native biodiversity and ecosystems and for archiving existing and future data. Future experiments need to assess the responses of species in realistic environments, where normal ecological processes and environmental stresses occur and where long-term feedbacks can develop. Such experiments must be underlain by a modelling framework, devised so that generalised predictions of impacts for many species and communities will be possible. Only when such data are available will it be possible to predict the impacts of the inevitable future increases in [CO_2] and to take the management action necessary to prevent extinctions and widespread alteration of ecosystem function.

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BACKGROUND

The concentration of the greenhouse gas carbon dioxide (CO_2) has risen from pre-industrial concentrations of 280 μmol mol^{-1} to its present concentration of over 390 μmol mol^{-1}, and it is expected that the concentration in 2050 will be in the range of 500 – 600 μmol mol^{-1} (IPCC 2007b). Aside from its influence on global surface temperatures and associated changes to weather and ocean circulation patterns, the increasing atmospheric concentration of CO_2 ([CO_2]) also has both direct and indirect effects on living organisms in its own right. This is mostly due to the fact that CO_2 is the main substrate for the process of photosynthesis, the process whereby plants and some microbial organisms use solar energy to convert CO_2 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 CO_2 whenever its atmospheric concentration is below approximately 1000 μmol mol^{-1} (i.e. approximately three times the current concentration) (Jones 1992). Therefore, the increasing [CO_2] directly influences the photosynthetic rate, which in turn influences growth rates and the manner in which the plant allocates biomass, invests in reproduction and the production of 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 stimulation of photosynthetic primary production in terrestrial ecosystems by the increasing [CO_2] also increases the ability of these ecosystems to sequester carbon and act as carbon sinks (Woodward and Lomas 2004). Therefore, the response of plants to [CO_2] 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 [CO_2] and, therefore, the changing [CO_2] 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 [CO_2] are likely to become either more or less abundant, due to alterations of competition levels (Körner and Bazzaz 1996). This means that some species may become threatened because of their response to [CO_2] (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 and 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 and 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). These changes in hydrology and biogeochemistry have the potential to influence the CO_2-productivity relationship, as do changes in community structure (Reich *et al.* 2006). Responses to [CO_2] therefore have the potential to offset, reverse or exacerbate the effects of global warming and associated climatic change.

Australia has diverse and unique native species and communities. Many of Australia's species are endemic; some of them have no functionally similar or closely related analogues in other regions. Australia's native biodiversity therefore has great intrinsic value from many points of view. The response of these species and ecosystems to the increasing [CO_2] is, therefore, of enormous significance.

PROCESSES WHEREBY ELEVATED CO_2 MIGHT AFFECT BIODIVERSITY

Introduction

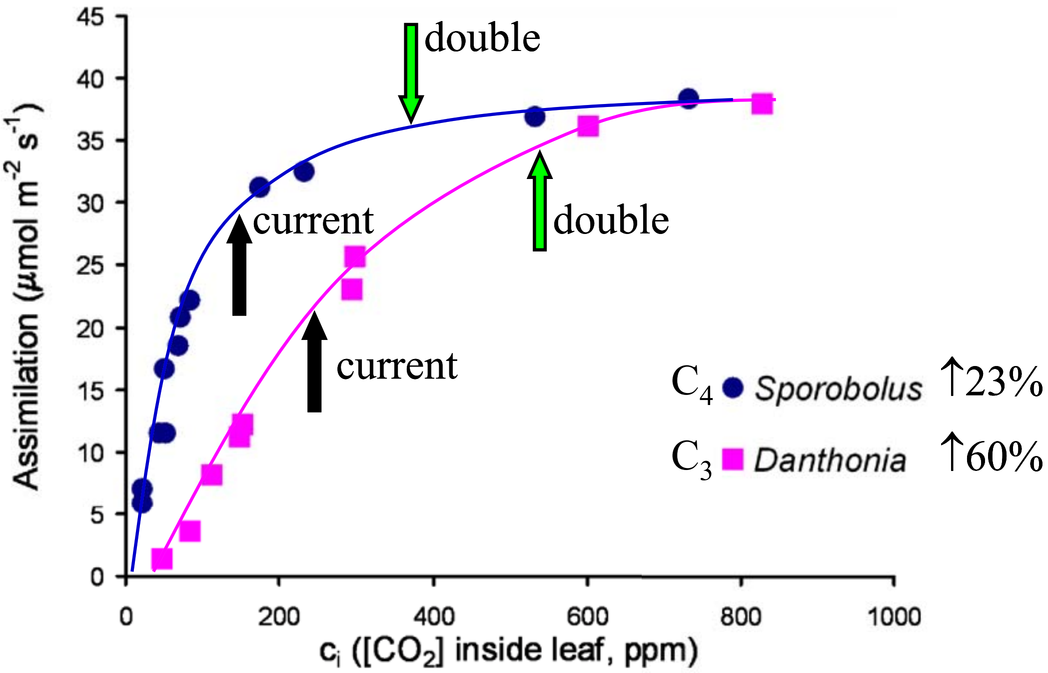
As plants form the basis of practically all terrestrial trophic networks, or food webs, the responses of most other organisms to [CO_2] are dependent upon the responses of the plants, such that most of the impacts of elevated [CO_2] on animals and other heterotrophic organisms can be considered indirect or plant-mediated (Pritchard *et al.* 2007). However, there are some specific direct impacts of elevated CO_2 on heterotrophic organisms and these will be addressed as well, albeit to a more minor extent. Therefore, the responses of plants and plant communities to elevated CO_2 are fundamental and largely govern the responses at all other trophic levels (Pritchard *et al.* 2007). The responses of plants to elevated CO_2 will thus form the bulk of this submission. The following section will detail the underlying theory and existing knowledge of the general processes whereby [CO_2] influences plant biology.

Impacts on plants

As mentioned in the Background section, CO_2 is the prime substrate for photosynthesis and the rate of photosynthesis is not saturated at current atmospheric [CO_2] in most plant species (Fig. 1) (Jones 1992). Therefore, the rate of photosynthesis in any plant will increase as [CO_2] rises (Jones 1992). The most immediate, direct effect of this is an increase in the rate of carbon uptake in the leaf, which will usually contribute to an increase in plant growth rate (Long *et al.* 2004). However, plants vary widely in their detailed photosynthetic physiology and this directly influences the magnitude of the photosynthetic response to [CO_2] increase (Medlyn *et al.* 1999). Variation in photosynthetic biochemistry leads to differences in the photosynthetic [CO_2] response between conifers and flowering plants, broad leaves and grasses, but most spectacularly between plants with the C_4 photosynthetic carbon concentrating mechanism (called C_4 plants) and all others (called C_3 plants) (Long *et al.* 2004). The specialised anatomy of plants possessing the C_4 pathway effectively isolates the primary C-fixing enzyme, Rubisco, from the atmosphere, where the C_4 biochemical pathway concentrates CO_2 (Kanai and Edwards 1999). This means that the photosynthetic rate of C_4 plants is higher in current conditions and is less sensitive to increases in [CO_2] (Fig. 1) (Sage and Kubien 2003).

The increasing [CO_2] affects C-assimilation not only by directly increasing the rates of the C-fixation reactions, but also by affecting the biochemical behaviour of Rubisco, the primary C-fixing enzyme (Sage and Kubien 2003). Under ideal conditions, Rubisco catalyses the carboxylation of the 5-C compound RuBP (Jones 1992). However, the high concentration of oxygen in the atmosphere leads Rubisco to catalyse a second reaction involving RuBP; namely its oxygenation (Jones 1992). The oxygenation of RuBP leads to the loss of fixed C from the plant and an energetically costly set of reactions known as photorespiration (Jones 1992). The ratio of carboxylation of RuBP to its oxygenation declines with increasing temperature, and thus the costs to the plant in terms of reduced net carbon assimilation and energy expenditure increase with increasing ambient temperature (Jones 1992). Since the C_4 pathway involves additional biochemical reactions and cellular energy expenditure, plants with the C_4 pathway incur metabolic costs above those of C_3 plants (Kanai and Edwards 1999). Therefore, the C_4 pathway is only beneficial when the costs of the C-concentrating steps are outweighed by the photorespiratory and C-release costs of the oxygenation of RuBP (Kanai and Edwards 1999). Since the rate of RuBP oxygenation increases with increasing temperature, C_4 plants tend to be most successful at high temperatures (Sage *et al.* 1999). The C_4 pathway has additional benefits in terms of improved efficiency of plant water use, since C_4 plants can photosynthesise effectively with a reduced stomatal aperture. Hence, C_4 plants are also successful in semi-arid and arid zones (Sage *et al.* 1999).

Fig. 1. The response of photosynthetic carbon assimilation (A) to [CO_2] in two grasses; *Danthonia*, a C_3 species (pink squares and line) and *Sporobolus*, a C_4 species (blue circles and line). The black arrows indicate rates at current [CO_2] and the green arrows indicate rates at twice current [CO_2]. The numbers indicate the percentage stimulation of carbon assimilation of each species with a doubling of [CO_2].



Increasing [CO_2] also increases a plant's water use efficiency, since an increased [CO_2] tends to reduce stomatal aperture, thus reducing water loss (Long 1991). Stomata act to maximise carbon assimilation while minimising water loss, so an increase in atmospheric [CO_2] will result in both increased carbon assimilation rates and reduced water loss (Long 1991).

In general, it is widely accepted that the increasing [CO_2] should increase plant growth rates and hence stimulate net ecosystem productivity (Woodward and Lomas 2004). This is true of both C_3 and C_4 plants, although the stimulation is considered to be stronger and less species-dependent in C_3 plants (Sage and Kubien 2003). Growth stimulation can occur both by the direct influence of CO_2, as described above, and, in water limited environments, by extending the growing season by improving plant water use efficiency, which would tend to favour growth of later seasonal species, many of which are C_4 plants (Wand *et al.* 1999). In many instances, the stimulation of growth by higher [CO_2] is greater below ground than above ground, with plants quite reliably having a greater root:shoot ratio and faster root turnover at elevated [CO_2] (Ceulemans *et al.* 1999). It is thought that a preferential increase in investment belowground leads to improved soil exploration and thus access to greater supplies of soil nutrients and water, which will further increase growth rates (Ceulemans *et al.* 1999).

Plants are quite plastic in their allocation of resources, which responds to environmental variation (Poorter and Nagel 2000). Of particular interest for the response to [CO_2] is the allocation of nitrogen (N) within the plant. N is often limiting to plants, hence plants readily re-allocate N from one organ or tissue to another (van Heerwaarden *et al.* 2005). Plants hold the greatest fraction of N in their leaves, where the largest single fraction is contained in Rubisco (Jones 1992). By stimulating the rate of photosynthetic C assimilation, the increasing [CO_2] may well encourage the re-allocation of N away from the photosynthetic machinery in general and Rubisco in particular (Bowes 1993). This redistribution of N away from the photosynthetic apparatus accompanies a reduction in the maximum photosynthetic rate of the leaf and is therefore termed photosynthetic down-regulation (Bowes 1993). While there is contention about whether down-regulation is an artefact of pot-based experimentation (Sage 1994), there is evidence that down-regulation occurs under field conditions (von Caemmerer *et al.* 2001). There is also evidence that plants vary in their tendency to down-regulate photosynthesis in response to higher [CO_2] (von Caemmerer *et al.* 2001). Whatever the case, elevated [CO_2] must result in an alteration of the efficiency with which plants use N, since a plant either (i) does not down-regulate but fixes greater amounts of C, thereby increasing the C:N ratio and, by definition, its N use efficiency, or (ii) down-regulates photosynthesis, reducing leaf N, but still maintaining a similar or greater actual rate of net C assimilation, due to the higher rate of photosynthesis and lower rate of photorespiration. C_3 and C_4 plants also differ in their fundamental N use efficiency, since C_4 plants typically maintain high photosynthetic rates with substantially reduced leaf Rubisco contents (Sage and Kubien 2003). C_4 plants are able to have lowered levels of Rubisco, and hence lower total leaf N, than C_3 plants because Rubisco works more efficiently in C_4 plants because of the generally high [CO_2] at Rubisco due to the operation of the C_4 C-concentrating steps. Thus, once again, as elevated [CO_2] is expected to increase N use efficiency, it is believed this will advantage plants with currently lower N use efficiency (Sage and Kubien 2003).

Any increase in the rate of photosynthetic C assimilation will result in an increase in the accumulation of the reaction products. If these products accumulate at the site of the reactions, it is possible that the equilibrium of the reactions will be unbalanced, leading to product-inhibition of C assimilation (Reekie *et al.* 1998). Therefore, the ability of a plant to maintain the CO_2-induced stimulation of C assimilation depends upon its ability to export fixed C from the leaf, which in turn depends upon the strength of its C sinks (Reekie *et al.* 1998). Therefore, it is expected that plants with strong C sinks will maintain a high photosynthetic rate at elevated CO_2 (Hovenden 2003b; Long *et al.* 2004). It is possible that the tendency for a species to down-regulate photosynthesis in response to elevated [CO_2] (as discussed above) is dependent upon its sink strength, so sink strength may be an important contributor to the overall response of a species to the increasing [CO_2] (Long *et al.* 2004).

Plants allocate both C and N resources for various functions, including reproduction and protection from herbivores. An important sink of both C and N is the production of plant secondary metabolites (O'Reilly-Wapstra *et al.* 2004). Secondary metabolites play a variety of roles in the plant from defence from herbivory and pathogens, to antioxidants and sunscreens. It is possible that an increased production of secondary metabolites in response to elevated [CO_2] could help prevent product-inhibition of photosynthesis and thus secondary metabolites might be beneficial in maintaining the CO_2-induced stimulation of productivity. Any increases in the production of secondary metabolites will have ramifications for both the plant and other organisms, since many secondary metabolites have repellent or toxic properties (Gleadow *et al.* 1998; O'Reilly-Wapstra *et* *al.* 2004). This topic will be considered in more detail below, where impacts on animals and other organisms are considered.

Since increasing [CO_2] is likely to enhance carbon assimilation and improve N use efficiency (Long *et al.* 2004), in the future plants may be able to allocate C and/or N differently to in the past. One of the major sinks for both C and N in plants is reproduction. Flowers, pollinator rewards such as nectar, fruits and seeds all involve a substantial investment of both C and N; it is likely that plants will allocate more of both C and N to reproduction at higher [CO_2] (Jablonski *et al.* 2002). This could mean that population dynamics will change, with the potential for the production of more and/or heavier, better provisioned seeds (Jablonski *et al.* 2002). Heavier seeds tend to produce more vigorous seedlings (Couvillon 2002), so it is possible that the increasing [CO_2] will stimulate population growth. However, if the allocation of C and N to the seeds is such that seed N content declines (Jablonski *et al.* 2002), then it is possible that seedling vigour will be lower, leading to greater seedling mortality and, eventually, reductions in population growth (Naegle *et al.* 2005). The availability of water during flowering and seed production is a crucial determinant of seed viability and subsequent seedling vigour (Boutraa and Sanders 2001). Since an increased [CO_2] is likely to improve soil water content in seasonally dry environments, there could be indirect benefits to plants in environments where seed production occurs during the onset of seasonal droughts. Clearly, there is great scope for interspecific differences in the manner in which plants allocate resources to reproduction, with potentially dramatic consequences (Jablonski *et al.* 2002).

Flowering phenology could also be changed by alterations to [CO_2] (Springer and Ward 2007). In some species, flowering is controlled by the availability of resources within the plant (Springer and Ward 2007). Therefore, enhanced growth could lead to earlier flowering. In some species, however, elevated [CO_2] acts to increase vegetative growth but to delay flowering (Springer and Ward 2007), in a manner similar to the results of excess application of soil nutrients (Taiz and Zeiger 2006). The anti-transpirational effects of elevated [CO_2] should also affect leaf temperature by reducing evapotranspirational cooling, which could lead to earlier flowering in species where flowering is controlled by the cumulative thermal load on a plant (Springer and Ward 2007). The extent to which the commencement of flowering is regulated by day-length, temperature and [CO_2] varies both among and within species, with potential for community level changes to flowering times with ramifications up to the level of the ecosystem (Springer and Ward 2007).

Because of the strong dependence of photosynthesis, photorespiration, water use and N use efficiency on [CO_2], there are strong reasons to believe that the increasing [CO_2] will lead to alterations of the competitive success within plant communities (Polley *et al.* 1996). Plants whose physiology is more responsive to the increasing [CO_2] may be expected to derive a greater growth advantage from an atmosphere richer in CO_2, when compared to those that are less responsive (Polley *et al.* 1996). This could lead to an alteration of plant communities by increasing the competitive advantage of one species or group of species at the expense of others. At the very least this should lead to alterations of relative abundance of some species in plant communities and changes in species' ranges. In extreme conditions, the increasing [CO_2] could lead to the decline and extinction of some species (Possingham 1993).

While variation in all of these responses could occur at the level of individual organisms and species, there is sufficient physiological evidence to expect that the increasing [CO_2] should lead to the following generalisations:

- C_3 species should be more advantaged than C_4 species, with the extent of the relative change increasing with increasing ambient temperature;

- dicots should be more advantaged than monocots;

- angiosperms should be more advantaged than gymnosperms;

- profligate water users should be more advantaged than conservative water users;

- in seasonally dry habitats, late-seasonal species should be more advantaged than early seasonal species;

- plants with strong C sink strength (e.g. woody species) should be more advantaged than those with low C sink strength (herbaceous species);

- N-fixing species should be more advantaged than non-N-fixing species;

- in N-limited ecosystems, species with lower N use efficiency should be more advantaged than those with higher N use efficiency.

Thus, the composition of plant communities should be expected to change, with corresponding alterations of community structure and function, which will affect ecosystem function.

Impacts on animals

While plants are far more responsive to [CO_2] than are nearly all other organisms, the increasing level of CO_2 in the atmosphere is likely to have both direct and indirect effects on other organisms, including animals. However, the main impacts of elevated [CO_2] on animals are likely to be indirect and mediated through plant responses. This is because animal physiology is mostly unaffected by [CO_2] within the range that is likely in the coming century (Sage 2002), but there are some notable exceptions, most especially amongst invertebrates (Stange 1996).

Direct effects

The most important direct effect of increasing [CO_2] on animals is likely to be olfactory sensing of prey by insects (Stange 1996). Both soil dwelling and aerial insects use gradients in [CO_2] to track and locate their food sources. In the soil, the [CO_2] is normally far in excess of atmospheric levels, so it is unlikely that the increasing atmospheric [CO_2] will have any direct impact on soil dwelling invertebrates (Stange 1996). However, olfactory sensing of [CO_2] by aerial insects may be disrupted by the increasing [CO_2], affecting the ability to search successfully for food in both herbivorous and blood-sucking insects (Stange 1996). Blood-sucking insects, such as ticks and mosquitoes, locate hosts by sensing local increases in [CO_2] resulting from exhalation of respiratory CO_2. Such insects can detect changes in [CO_2] from background levels as low as ~10 μmol mol^{-1} but generally do not actively move towards hosts until substantially higher elevations of [CO_2] are encountered (Stange 1996). Therefore, while blood-sucking insects are likely to experience changes to their olfactory perception because of the increasing [CO_2], it is unlikely that this will have major impacts on their ability to locate hosts, as the levels of CO_2 involved in host-location are generally high (>~3000 μmol mol^{-1}).

The situation with herbivorous insects, particularly those from the Order Lepidoptera (moths and butterflies), is different. Such insects are able to distinguish minute changes (<1 μmol mol^{-1}) in [CO_2] and are thus able to detect and locate photosynthesising plants. Caterpillars of one species of moth, *Helicoverpa armigera*, can discriminate between leaves and fruit on the basis of differences in carbon metabolism, since photosynthesising leaves reduce the local [CO_2] by CO_2 assimilation whereas growing, respiring fruit elevate local [CO_2] (Rasch and Rembold 1994). While the CO_2-sensing abilities of relatively few insects have been studied, results indicate that the CO_2 sensors of herbivorous insects become saturated at approximately [CO_2] of ~800 μmol mol^{-1} (Rasch and Rembold 1994; Sage 2002). Thus, the rising [CO_2] is likely to reduce the ability of these insects to detect hosts as the background [CO_2] approaches saturation point of their CO_2-sensors. It is exceedingly likely, therefore, that the increasing [CO_2] will affect the success and long-term population stability of many species of lepidopteran insects.

Indirect effects

Most of the secondary, or indirect, effects of the rising [CO_2] on animals are mediated through the various responses of plants detailed above. 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 whole ecosystem level, including animals.

Plant water content, particularly of leaf material, is likely to increase as a result of improved plant water use efficiency at elevated [CO_2]. The water content of fodder is an

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important determinant of herbivore digestive efficiency, with increasing water content increasing the digestion and assimilation of nutrients, particularly N, in most herbivorous insects (Coviella and Trumble 1999). Thus, elevated [CO_2] impacts on plant water content are likely to improve the health and growth-rates of herbivorous insects. This impact may be increased in situations where the plant growing season is extended through retention of soil water associated with improved plant water use efficiency at elevated [CO_2]. Further, it is possible that the extension of the growing season may allow smaller, later seasonal insect larvae to reach the size and lifecycle stage necessary for survival (Coviella and Trumble 1999).

The positive impacts for herbivores of improved plant water content at elevated [CO_2] are opposite to the impacts likely from the [CO_2]-mediated changes in plant nutrient content described above. The reduction in plant N concentrations, particularly in the leaves, at elevated [CO_2] is likely to have major consequences for herbivores (Roth and Lindroth 1995; Bezemer and Jones 1998; Ehleringer *et al.* 2002). Browsing by herbivorous animals, particularly invertebrates, is strongly related to animal protein intake. Thus, animals will tend to feed until they have eaten a certain amount of protein, rather than a set mass of plant matter. As plants almost universally have lower leaf N concentration at elevated [CO_2] (Long *et al.* 2004), this means that herbivores will need to eat more plant tissue to reach their protein requirement. This will mean that herbivores will spend longer feeding and browse plants more heavily (Bezemer and Jones 1998). The increased feeding time (as opposed to resting and hiding time) will have obvious consequences in terms of likelihood of predation and parasitism and the increased food intake will both increase the likelihood of ingesting pathogens and increase the herbivore's exposure to plant defensive chemicals. Increased herbivory at elevated [CO_2] would also have impacts on plants, since plants may become more heavily grazed at elevated [CO_2] (Stacey and Fellowes 2002).

Plant secondary metabolites 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, then herbivores will be exposed to higher levels of these compounds, with deleterious effects on the animal. It is also possible that increased plant C assimilation at elevated [CO_2] will alter the mixture of secondary metabolites, with plants perhaps increasing C-based compounds to a greater extent than they will of N-based compounds. This would alter the plant's toxin-profile, perhaps altering 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 [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 [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 determinant of the herbivore response. On balance, it is likely that the negative consequences for herbivores of increased allocation to defensive compounds at elevated [CO_2] will overwhelm the positive effects of increased plant water content (Ehleringer *et al.* 2002; Percy *et al.* 2002; Hamilton *et al.* 2004). This is extremely important as the responses of the plant will determine the level of herbivory it receives as well as affecting animal fecundity and mortality. Field studies at elevated [CO_2] indicate that at elevated [CO_2] herbivore abundance on plants is lower, herbivore mortality is higher and the levels of parasitoids on herbivores is higher, compared to control conditions (Stiling *et al.* 2002). However, a study on soybean grown as a crop has shown that elevated

[CO_2] unexpectedly prevented the production of jasmonic acid, a major plant secondary metabolite, in the leaves, with a consequent dramatic increase in the level of insect attack and increases in herbivore abundance, fecundity and lifespan (Zavala *et al.* 2008). Thus, it appears that the responses of plants to elevated [CO_2] in terms of the production of secondary metabolites may well be species-specific.

Herbivorous mammals will be susceptible to the same elevated [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 [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 [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 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 [CO_2] will affect pollinators if their phenology is not similarly altered (Post and Inouye 2008). Plant flowering times have already responded to global warming, as evidenced by many long-term observational studies (Fitter and Fitter 2002) and supported by experimental results (Price and Waser 1998). The emergence time of pollinating insects tends to be synchronised with flowering of their food species, and in many species phenology in both partners is largely controlled by a cumulative thermal load for a season (Post and Inouye 2008). As detailed above, it is possible that the increasing [CO_2] will interact to alter the response of flowering times to ambient temperatures (Springer and 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. This would have drastic consequences for both the plants, which will have reduced reproductive success, and the animals, which will have reduced access to preferred food sources (Post and Inouye 2008). It is possible that this will result in shifts in which species of animal pollinate which species of plants. In generalist species of both plants and pollinators, this is unlikely to have dramatic consequences because both have a variety of partners. However, in those species with specialist partnerships, the ramifications of such a shift would be profound and rapid, resulting in population decline and perhaps even extinction of both the plant and pollinator. This would have ramifications to other trophic levels, affecting, for example, herbivores and fungi dependent upon the plant species and insectivores dependent upon the pollinator.

The effects of increasing [CO_2] at trophic levels higher than herbivores, have rarely been examined and there are also almost no investigations of the responses of omnivorous species. It is possible that omnivores will respond to reductions in plant feed quality by increasing their levels of predation and reducing herbivory, but the lack of data in this area prevents anything but the most basic speculation.

The increasing [CO_2] has the potential to alter predator-prey interactions in several ways. Firstly, the higher [CO_2] may increase plant size, leaf area and architecture, reducing predator searching efficiency (Coll and Hughes 2008). Secondly, reduced herbivore growth, protein content or size at elevated [CO_2] may make them a less suitable food

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source. Herbivores may also accumulate plant secondary metabolites at a greater rate or to a greater extent at elevated [CO_2], influencing their palatability or nutritional value to predators. Conversely, increased herbivore foraging time at elevated [CO_2], as discussed above, may make finding prey easier for predators. It is also likely that some herbivores will be advantaged over others at elevated [CO_2], changing herbivore community composition, which may in turn alter predator composition. Predictions of the responses to the increasing [CO_2] 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 [CO_2] have been found to increase (Stiling *et al.* 1999; Stiling *et al.* 2002; Chen *et al.* 2005; Chen *et al.* 2007), decrease (Roth and Lindroth 1995; Sanders *et al.* 2004) or remain unchanged (Bezemer and Jones 1998; Percy *et al.* 2002; Stacey and Fellowes 2002; Holton *et al.* 2003; Hoover and Newman 2004) or vary annually when compared with control [CO_2] (Percy *et al.* 2002).

Plants almost universally increase their belowground proportional biomass allocation at elevated [CO_2], 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 [CO_2], with experiments demonstrating both increases (Yeates *et al.* 2003) and decreases or no change (Niklaus *et al.* 2003) in the abundance of root-feeding invertebrates. The soil micro-invertebrate community is complex and contains herbivores, fungivores, microbial grazers and predators. There is scant information on the impacts of elevated [CO_2] on belowground 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 [CO_2] (Yeates *et al.* 2003).

Alterations of the production rates and chemical composition of plant litter at elevated [CO_2] is likely to influence decomposer organisms in both the soil and litter. The quality of leaf litter in terms of N content varies in responsiveness to [CO_2] because of varying degrees of nutrient resorption in different species (Hoorens *et al.* 2002), the quantity of litter produced and the levels of secondary metabolites in the litter (Hoorens *et al.* 2002) are both likely to affect the abundance and community composition of detritovores 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; Gahrooee 1998; Dukes and Field 2000). Thus, it appears that the impacts of elevated [CO_2] 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

Direct effects

The known direct impacts of the increasing [CO_2] on fungi are restricted to impacts on spore-bearing material of Basidiomycetous fungi (e.g. mushrooms and toadstools). In many commercial species of mushroom, mushroom cap size is reduced and stalk-length increased by exposure to a [CO_2] of twice to three times ambient (Sage 2002). It is unknown how the fungal material senses or responds to [CO_2] but it appears likely that the response is part of a mechanism for placing sporulating material well into the bulk air stream where spore dispersal is likely to be successful (Sage 2002). It is unlikely that other fungal material would be affected by the increasing [CO_2] since these materials largely exist in soils or decomposing organic matter in which the [CO_2] is normally very high. However, it is not know if aerial sporulating material of types of fungi other than Basidiomycetes is affected by [CO_2].

Indirect effects

Increased plant C-assimilation at elevated [CO_2] 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 (AMF) (Rillig *et al.* 1998b; Rillig *et al.* 1999; Rillig *et al.* 2000; Rillig and Field 2003) and ectomycorrhizal fungi (EMF) (Rouhier and Read 1999; Gorissen and Kuyper 2000; Alberton *et al.* 2005). It is therefore generally believed that the diversity of root-associated fungi will be maintained or even increased in an atmosphere high in [CO_2] (Rillig *et al.* 1998a; Alberton *et al.* 2005). However, there is strong evidence that these responses are species-specific and therefore should not be generalised (Rillig *et al.* 1998a; Alberton *et al.* 2005).

In the short term, plant pathogen effects at elevated [CO_2] are determined by the opposing influences of enhanced host resistance that slows host invasion versus enlarged plant canopy that offers more infection sites and produces a microclimate conducive to disease development (Chakraborty and Datta 2003). More importantly, in the long term, higher pathogen fecundity, inoculum trapping by an enlarged plant canopy, and a higher number of infection cycles interact with the effects of enhanced host plant resistance to determine host-pathogen adaptation (Chakraborty and Datta 2003). While a range of growth cabinet and glasshouse experiments indicate that disease severity is generally increased at elevated [CO_2], field experiments in which [CO_2] is manipulated do not support this generalisation. Once again, it appears that the impacts of elevated [CO_2] 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 and Datta 2003). For instance, leaf blight of rice caused by the pathogen *Magnaporthe oryzae* was significantly higher at elevated [CO_2] 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 and Leuchtmann 2000; McElrone *et al.* 2005; Aldea *et al.* 2006; Strengbom and Reich 2006) have indicated that pathogens generally are less abundant and virulent at elevated [CO_2] (Chakraborty *et al.* 2008 *in prep*). However, the results of Aldea *et al.* (Aldea *et al.* 2006) on the impact of fungal pathogens on leaf photosynthetic efficiency under both elevated [CO_2] and control conditions, indicated that each separate lesion at elevated [CO_2] had an impact up to five times greater than a similarly lesion in control conditions. Thus, while the incidence of infection at elevated [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 belowground, could increase the food supply for saprophytic organisms, including bacteria and fungi, but increases in plant secondary metabolites could slow the rate of organic matter decomposition. Plants also commonly respond to elevated [CO_2] by increasing the exudation of sugars from the roots. It would be expected that this would increase fungal and/or microbial biomass in the rhizosphere. Reports of responses of biomass of soil microbes and fungi to elevated [CO_2] are contradictory and variable across years and highly dependent upon the plant species present (Dhillion *et al.* 1996; Chung *et al.* 2007; Van Groenigen *et al.* 2007). Therefore, it is difficult to generalise responses of soil saprophytes, although most reports to indicate that the total hyphal length of saprophytic fungi is higher at elevated [CO_2] (Dhillion *et al.* 1996; Rillig *et al.* 1999; Rillig *et al.* 2000; Rillig and Field 2003). Thus, it is possible that the diversity of saprophytic fungi will benefit from the increasing [CO_2].

All soil dwelling organisms are also likely to benefit from the increased soil water levels at elevated [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 [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.

Impacts of alterations in plant community composition

All of the indirect impacts of the changing [CO_2] outlined above for animals and other organisms are largely based on changes in existing plant species. It is very likely, however, that the increasing [CO_2] will affect the population dynamics of various plant species differently (Williams *et al.* 2007), thereby changing plant community composition, which will alter community 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 [CO_2]. This is an area that is little researched internationally, and any changes in community composition are likely to be to the benefit of some species and the detriment of others, so it is impossible to generalise responses. However, it would be possible to predict likely changes in plant community composition with increasing [CO_2], then to predict the impacts of those changes on particular species or groups of species, on a case-by-case basis. Such an approach might be particularly important when considering the impacts of increasing [CO_2] on threatened species.

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. The field of ecosystem level ecology is still in its infancy and, apart from investigations of energy flow through food webs and certain biogeochemical cycles, most ecosystem interactions remain largely unstudied and poorly understood.

However, despite our lack of a mechanistic understanding of ecosystem dynamics, it is clear that certain interactions are likely to change as [CO_2] increases. As detailed above under plant responses, certain types of plants are likely to increase in relative abundance at the expense of others. 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 [CO_2] will change biogeochemical cycling. Of special importance in this respect is the response of N cycling. At elevated [CO_2], more N is likely to be partitioned into biomass and into slowly turning-over soil organic matter (Luo *et al.* 2004). 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 [CO_2]-induced changes to the functioning of terrestrial ecosystems. The processes involved in PNL are only beginning to be understood and the system of long-term feedbacks on ecosystem function is not yet understood (Reich *et al.* 2001; Reich *et al.* 2006). However, a reduction in soil N would increase the competitive ability of plants with high N use efficiency, such as C_4 plants, in such a way as to counteract the impacts on N use efficiency of elevated [CO_2].

The area of ecological interactions and ecological processes and rising [CO_2] is perhaps the area that is most in need of further research as the ultimate responses of terrestrial biodiversity to the increasing [CO_2] may be more dependent upon secondary changes, such as PNL, than to the primary responses to the change in [CO_2] itself.

Interactions between the rising [CO_2] and other global changes

The ways that the increasing [CO_2] is likely to interact with other dominant global changes, such as global warming and alterations of rainfall, are considered throughout the discussion above. However, it is worth drawing some specific conclusions concerning the potential for interactions among global changes.

Since the effect of increasing [CO_2] on plant photosynthesis, and hence on growth, C-allocation, water and N use efficiency, is directly related to average temperature in the growing season, the impact of elevated [CO_2] 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 [CO_2] will become more and more important as global temperatures rise. Therefore, while it is extremely unlikely that the increase in [CO_2] will be able to counteract the effects of increased evaporative demand due to global warming, the increase in [CO_2] 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 2007a).

Global warming and the increasing [CO_2] are likely to have opposing impacts on nutrient cycling processes, particularly in the case of N (Reich *et al.* 2006). While the increasing [CO_2] 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 are unknown, as there is only a single published study that has investigated the interaction of warming and elevated [CO_2] 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 [CO_2] and warming stimulate the relative allocation of biomass belowground. Therefore, there is the potential for plants to have substantially increased soil exploration in warmed, elevated [CO_2] conditions. This is likely to confer improved nutrient acquisition and increased drought tolerance, both of which are increased by greater soil exploration. Thus, elevated [CO_2] might improve plant drought tolerance not only by reducing transpiration, but by promoting root growth, thereby increasing plant access to additional water sources.

A potentially overwhelming factor in most of Australia's terrestrial ecosystems is that between fire and the rising [CO_2]. If the rising [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 [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 are more flammable. 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 [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 [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). 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 and Slatyer 1980; Gill 1981). The increasing [CO_2] may reduce this crucial period if growth rates are increased or if plants allocate proportionally more biomass to reproduction at elevated [CO_2]. 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 [CO_2] and fire frequency is vital if future ecosystem processes are to be predicted.

RESEARCH INTO ELEVATED CO_2 IMPACTS ON AUSTRALIA'S NATIVE BIODIVERSITY

The extent of research into elevated CO_2 impacts on Australia's biodiversity

Research 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 [CO_2] is extremely low. There have been no studies of the impacts of elevated [CO_2] 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 [CO_2] will impact on the highly endemic vertebrate fauna.

Table 1. The number of native Australian species and how many have been investigated as to the impact of elevated [CO_2].

Taxonomic group	No. Australian native species[1]	No. spp. investigated for CO_2 impacts[3]	% of species investigated for CO_2 impact
Vertebrates	7558	0	0.0%
Invertebrates	114600	2	0.002%
Vascular plants	18140	68	0.37%
Non-vascular plants	1852	0	0.0%
Lichens	3227	0	0.0%
Fungi	5672	0	0.0%
Bacteria[2]	~40 000	0	0.0%
Cyanophytes[2]	270	0	0.0%
TOTAL	**151319**	**70**	**0.046%**

[1]-No. of species used is the actual number of described species, but see notes 2 and 3.
[2]-No. of species used for bacteria and cyanophytes is the estimated no. of species.
[3]-These numbers are the numbers of species for which published data are available.

Evidence of impacts of elevated CO_2 on native species

Introduction

Most investigations of the impacts of elevated [CO_2] have concentrated on single species, with only occasional investigations comparing multiple species. Therefore, it is most relevant to review the information on a species by species basis, grouping species at higher taxonomic levels.

Impacts on plants

Grasses

Worldwide, the grasses (Family Poaceae) have been far better studied in terms of their CO_2-response than any other group of organisms; this is exactly the same in Australia. Part of the reason for the concentration of information on grasses is the fact that grasses contain both C_3 and C_4 species, as well as all three of the C_4 sub-types. Grasses are also economically important both as crops and pasture species, are extremely abundant in nearly all ecosystems and are convenient for experimentation because of their rapid growth, small stature and hardiness.

Of the approximately 1300 species of grasses that are considered native to Australia, the [CO_2]-response has been studied for 24 or 1.85% (Table 2). However, the response to elevated [CO_2] has been assessed in a field setting for only nine of those species (Table 2).

Table 2. Australian grass species examined for [CO_2] response. Those species indicated with an asterisk (*) have been examined in a field setting.

Astrebla lappacea	*Bothriochloa biloba*
Astrebla pectinata	*Bothriochloa blahdii*
Astrebla squarrosa	*Dichanthium sericeum*
*Austrodanthonia caespitosa**	*Dichelachne crinita*
*Austrodanthonia carphoides**	*Digitaria brownii*
Austrodanthonia eriantha	*Ehrharta stipoides*
*Austrodanthonia tenuior**	*Elymus scaber**
Austrodanthonia richardsonii	*Panicum decompositum*
*Austrostipa mollis**	*Pennisetum alopecuroides.*
*Austrostipa nodosa**	*Poa labillardierei*
Austrostipa pubinodis	*Poa rodwayi**
*Austrostipa rudis**	*Themeda triandra**

Impacts by species: Widespread grasses

Austrodanthonia caespitosa

This C_3 perennial grass species is one of the widest spread grass species in southern Australia, extending across the entire southern half of the continent. The response of *Austrodanthonia caespitosa* to elevated [CO_2] has been studied in detail in growth-cabinet (Hovenden 2003a), glasshouse (Hovenden *et al.* 2008b) and field conditions (Hovenden *et al.* 2007; Williams *et al.* 2007; Hovenden *et al.* 2008b; Hovenden *et al.* 2008c). A growth-cabinet investigation with species grown singly in pots indicated that photosynthesis of *A. caespitosa* was only slightly down-regulated, water use efficiency was higher and biomass of 7-week old plants grown at elevated [CO_2] was virtually double that of plants grown in control conditions (Hovenden 2003a), thus indicating that this species should be expected to thrive as the [CO_2] rises. However, the potential growth stimulation by elevated [CO_2] was not realised when plants growing in a natural plant community were exposed to elevated [CO_2] in the TasFACE experiment (Hovenden *et al.* 2006). Indeed, under natural conditions, the population growth of *A. caespitosa* was significantly reduced by elevated [CO_2], most particularly when combined with warming of 2ºC (Williams *et al.* 2007). This was due to the production of fewer seeds and the emergence of substantially fewer seedlings at elevated [CO_2] compared to control conditions. Quite simply, the physiological response of this species to higher [CO_2] was to produce fewer seeds, with lower protein content. These changes resulted in reduced seed germination rates because a greater proportion of seeds were inviable (Hovenden *et al.* 2008b). Thus, exposure to elevated [CO_2] dramatically reduced the success of this species in a species-rich community, indicating that it is extremely vulnerable to any rise in CO_2 concentration because the species will fail to recruit new individuals to the population, leading to its decline and perhaps extinction.

Themeda triandra

This C_4 species is widespread across the entire Australian continent, occurring in all states from Cape York to southern Tasmania, from the coast to the arid interior. The same species also occurs across tropical and southern Africa as well as tropical and temperate Asia. A controlled environment study in which *T. triandra* plants were grown singly in pots in both elevated [CO_2] and control conditions, indicated that the photosynthetic C-assimilation rate was not significantly affected by exposure to elevated [CO_2], but stomatal conductance was greatly reduced, resulting in a substantially increased water use efficiency (Hovenden 2003a). This increased water use efficiency allowed *T. triandra* plants to have substantially increased growth at elevated [CO_2] in conditions in which the pots soil was allowed to dry down between watering events. Similarly, the growth of *T. triandra* plants in the field was significantly increased by elevated [CO_2] in the OzFACE experiment located in a tropical rangeland (C. Stokes, pers. comm.). This was different to the case in the TasFACE experiment in which growth of *T. triandra* in a temperate grassland was not stimulated by elevated [CO_2] in five years out of seven, which is related to the timing of rainfall (Hovenden, unpublished data). In the southern Tasmanian grassland where TasFACE is located, most rainfall occurs in the cool months during which time *T. triandra* is inactive. In the two years with substantial summer rainfall, however, growth of *T. triandra* was significantly stimulated by elevated [CO_2] (Hovenden, unpublished data). The population dynamics of *T. triandra* has also been largely unaffected by elevated [CO_2] exposure, but population growth rate was stimulated by the combination of elevated [CO_2] and 2ºC warming (Williams *et al.* 2007). Flowering, seed production and mean seed mass of *T. triandra* were not significantly affected by exposure to elevated [CO_2] (Hovenden *et al.* 2007).

<u>Impacts by species: Grasses from temperate regions</u>

Austrodanthonia carphoides
Flowering, seed production and mean seed mass in this perennial C_3 grass were not significantly affected by [CO_2] when grown in a natural community in the field in the TasFACE experiment (Hovenden *et al.* 2007).

Austrodanthonia eriantha
Growth was stimulated in this temperate C_3 grass by elevated [CO_2] at 20/10ºC day/night temperatures but not at 23/13ºC. Elevated [CO_2] did not alter the outcome when *Austrodanthonia eriantha* was grown in competition with the invasive C_3 grass *Vulpia myuros*, however, as growth of *A. eriantha* was strongly suppressed by the presence of *V. myuros* in both elevated [CO_2] and control conditions (Hely and Roxburgh 2005).

Austrodanthonia tenuior
Flowering and seed production in this perennial C_3 grass were not significantly affected by [CO_2] when grown in a natural community in the field in the TasFACE experiment (Hovenden *et al.* 2007).

Austrodanthonia richardsonii
The supply of phosphorus (P) to this C_3 grass of temperate southeastern Australia was found to determine the growth response to elevated [CO_2] (Barrett and Gifford 1999). When P was supplied in insoluble form at a concentration of greater than 8 mg/kg soil, elevated [CO_2] increased root production and thus the total efflux of citrate from the roots, which is known to increase P availability thereby increasing P uptake. This increased plant photosynthetic C-assimilation, thereby increasing biomass accumulation over a period of between 55 and 63 days. At P concentrations lower than 8 mg/kg, citrate efflux was limited by the low P availability, and thus exposure to elevated [CO_2] did not affect photosynthetic C gain or growth. This important research demonstrated that the chronically low P availability of many Australian soils may prevent elevated [CO_2] from stimulating growth of many Australian plant species.

Austrostipa mollis
The proportion of the population flowering in this perennial C_3 grass was substantially reduced by elevated [CO_2] in both a dry and a wet year when grown in a natural community in the field in the TasFACE experiment. This reduction occurred only in unwarmed plots, however. In warmed plots, elevated [CO_2] significantly increased the proportion of the population that flowered in the dry year and had no effect in the wet year. Flower and seed production per plant and mean seed mass were not significantly affected by [CO_2] (Hovenden *et al.* 2007).

Austrostipa nodosa
Flowering and seed production in this perennial C_3 grass were not significantly affected by [CO_2] when grown in a natural community in the field in the TasFACE experiment (Hovenden *et al.* 2007).

Austrostipa pubinodis
Doubling [CO_2] from 370 μmol mol^{-1} to 750 μmol mol^{-1} almost trebled the biomass of seven week old plants of this perennial C_3 grass when plants were grown singly in pots in growth chambers (Hovenden 2003).

Austrostipa rudis

Flowering and seed production in this perennial C_3 grass were not significantly affected by [CO_2] when grown in a natural community in the field in the TasFACE experiment (Hovenden *et al.* 2007).

Dichanthium sericeum
Elevated [CO_2] had no impact on the growth of this C_4 grass, but it did significantly increase plant water use (Ghannoum *et al.* 2001). Plants in this experiment were all grown without competition and with abundant water availability.

Dichelachne crinita
This widespread perennial C_3 grass showed only a very slight photosynthetic down-regulation of C-assimilation when grown at elevated [CO_2]. *Dichelachne crinita* biomass after seven weeks was also only slightly increased by elevated [CO_2] as compared to plants grown in control conditions (Hovenden 2003).

Elymus scaber
Flowering and seed production in this perennial C_3 grass were not significantly affected by [CO_2] when grown in a natural community in the field in the TasFACE experiment. Elevated [CO_2] increased mean seed mass, however, by three-fold in unwarmed plots and over five-fold in warmed plots (Hovenden *et al.* 2007).

Poa labillardierei
This dominant C_3 perennial grass of southern Australia had an exceptionally high stimulation of biomass production at elevated [CO_2] when grown singly in pots in a growth cabinet experiment (Hovenden 2003). *Poa labillardierei* plants grown at elevated [CO_2] also had a substantially lower C-assimilation efficiency than control plants, indicating substantial down-regulation of photosynthesis in response to elevated [CO_2]. When exposed to elevated [CO_2] in a field setting in the TasFACE experiment, both flowering and seed production were unaffected by [CO_2] (Hovenden *et al.* 2007).

<u>Impacts by species: Grasses from semi-arid and arid zones</u>

Astrebla lappacea
The impact of elevated [CO_2] on leaf temperature was assessed in this widespread C_4 grass from the semi-arid and arid zones of the northern half of Australia (Siebke *et al.* 2002). Leaves on plants grown at elevated [CO_2] were up to 0.4°C warmer than leaves on plants grown in control conditions, but the degree of temperature elevation was strongly dependent upon both the ambient light and humidity levels. When grown with abundant water and without competition in a glasshouse experiment, growth and water use of *Astrebla lappacea* were not significantly affected by [CO_2] (Ghannoum *et al.* 2001).

Astrebla pectinata
Elevated [CO_2] had no impact on the growth of this C_4 grass, nor did it significantly alter plant water use (Ghannoum *et al.* 2001). Plants in this experiment were all grown without competition and with abundant water availability.

Astrebla squarrosa
While elevated [CO_2] had no impact on the growth of this C_4 grass, it did significantly reduce plant water use (Ghannoum *et al.* 2001). Plants in this experiment were all grown without competition and with abundant water availability.

Bothriochloa biloba

Elevated [CO_2] had no impact on the growth of this C_4 grass, nor did it significantly alter plant water use (Ghannoum *et al.* 2001). Plants in this experiment were all grown without competition and with abundant water availability.

Bothriochloa blahdii
The impact of elevated [CO_2] on leaf temperature was assessed in this widespread C_4 grass from the monsoonal tropics of northern Australia (Siebke *et al.* 2002). Leaves on plants grown at elevated [CO_2] were up to 0.5°C warmer than leaves on plants grown in control conditions, but the degree of temperature elevation was strongly dependent upon both the ambient light and humidity levels. When grown with abundant water and without competition in a glasshouse experiment, growth of *Bothriochloa blahdii* was significantly increased by elevated [CO_2] but plant water use was unaffected by [CO_2] (Ghannoum *et al.* 2001).

Digitaria brownii
Elevated [CO_2] had no impact on the growth of this C_4 grass, nor did it significantly alter plant water use (Ghannoum *et al.* 2001). Plants in this experiment were all grown without competition and with abundant water availability.

Panicum decompositum
When grown with abundant water and without competition in a glasshouse experiment, growth of this C_4 grass was significantly increased, but plant water use was unaffected, by elevated [CO_2] (Ghannoum *et al.* 2001).

Pennisetum alopecuroides
Elevated [CO_2] had no impact on the growth of this C_4 grass, nor did it significantly alter plant water use (Ghannoum *et al.* 2001). Plants in this experiment were all grown without competition and with abundant water availability.

Trees

Research into the impacts of elevated [CO_2] on trees falls second only to the grasses in terms of research effort and output, both globally and in Australia. However, in terms of species number, there are published accounts of the impact of elevated [CO_2] on the more species of Australian trees than of grasses, with publications involving 28 Australian tree species, from a range of families covering the tropics to the cool temperate regions of southern Australia (Table 2). Of the 28 species whose responses to elevated [CO_2] have been investigated, eleven are eucalypts and ten are members of the genus *Acacia*, commonly known as wattles. 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 recently established Hawkesbury Forest Experiment will investigate the responses of *Eucalyptus saligna* using whole tree chambers, which will allow the plants to grow to a large size REF. No published results are yet available from the Hawkesbury Forest Experiment.

<u>Impacts by species: Trees of the tropics</u>

Alphitonia petriei
The impact of [CO_2] on foliar characteristics relevant to its palatability to vertebrate folivores was investigated in *Alphitonia petriei* in a glasshouse experiment. The results are discussed below in the section concerning Impacts on Animals – Vertebrates.

Brachychiton populneum
This species is widespread from tropical Queensland to Victoria, mostly occurring on the drier slopes west of the Great Dividing Range, but is extremely popular as a street plant in many areas because of its drought and frost tolerance. When grown in an open-top chamber experiment with abundant water supplies, elevated [CO_2] increased photosynthetic C-assimilation and reduced dark respiration of *Brachychiton populneum* (Idso and Kimball 1993).

Flindersia brayleyana
The impact of [CO_2] on foliar characteristics relevant to its palatability to vertebrate folivores was investigated in *Flindersia brayleyana* in the same glasshouse experiment as for *Alphitonia petriei*. The results are discussed below in the section concerning Impacts on Animals – Vertebrates.

Eucalyptus miniata
Growth biomass allocation and foliar nutrient content was assessed in plants grown from seed for 32 weeks in controlled environment tents at elevated and control [CO_2] with adequate water and nutrients (Duff *et al.* 1994). Elevated [CO_2] caused no significant changes to virtually any measured character in this tropical eucalypt, indicating that its growth, biomass allocation and foliar chemistry is insensitive to [CO_2].

Eucalyptus tetrodonta
In the same experiment as for *E. miniata*, Duff *et al.* (1994) discovered that the tropical eucalypt *E. tetrodonta* was very responsive to [CO_2]. Elevated [CO_2] increased the growth of *E. tetrodonta* in terms of both biomass and height and increased the relative allocation of biomass to the wood and leaves of the main stem while reducing allocation to wood and leaves in branches. Foliar N, phosphorus and Manganese content was also lower at elevated [CO_2] than in control conditions but there was no effect of [CO_2] on foliar soluble protein, calcium, potassium or magnesium contents. Elevated [CO_2]-grown *E. tetrodonta* plants also had a higher leaf water potential than control plants (Eamus *et al.* 1995).

Growth in elevated [CO_2] also altered the responses of stomatal conductance to temperature in this species, with stomatal conductance declining less sharply with increasing leaf temperature in plants grown in elevated [CO_2] than in control plants (Berryman *et al.* 1994). Interestingly, [CO_2] did not alter the response of stomatal conductance to humidity in this species (Berryman *et al.* 1994).

Eucalyptus tereticornis
Plants were grown in controlled environment cabinets exposed to both [CO_2] and drought treatments with biomass and xylem vessel development measured. Elevated [CO_2] increased growth of both droughted and watered plants but this was only sustained in the droughted plants (Atwell *et al.* 2007). Thus elevated [CO_2] is likely to increase growth of this species in water-limited environments. Earlier work on this species (Lawler *et al.* 1997) investigated the impacts of elevated [CO_2] on leaf nutrient content and the implications of these changes for a folivorous insect. These results are discussed in more detail in the section *Impacts on Animals*.

Eucalyptus microtheca
Elevated [CO_2] increased photosynthetic C-assimilation and reduced dark respiration in this tropical eucalypt when grown in an open top chamber experiment with abundant water (Idso and Kimball 1993).

Eucalyptus grandis
The impact of nutrient levels on the growth response of the widely distributed species *Eucalyptus grandis* to elevated [CO_2] was examined in a growth cabinet experiment (Conroy *et al.* 1992). The results indicated that growth of *E. grandis* was stimulated by elevated [CO_2] across a wide range of N and phosphorus (P) availability, but the magnitude of the stimulation was dependent upon nutrient levels. The degree of growth stimulation by elevated [CO_2] was inversely related to P availability, with the greatest stimulation occurring at the lowest P levels, which was different to results for other (exotic) species, in which low P availability prevented the stimulation of growth by elevated [CO_2]. The situation with N was completely different, with the magnitude of the growth stimulation by elevated [CO_2] being directly related to N availability, with the greatest stimulation occurring at high N availability. Foliage N and P content was lower in leaves from plants grown at elevated [CO_2]. Interestingly, the impact of elevated [CO_2] on plant demand for P and N was also different, with *E. grandis* plants having increased demand for P at elevated [CO_2] whereas N demand was either unchanged by [CO_2] or lower at elevated [CO_2]. Together, these results indicate that plants will have an altered nutrient demand and perhaps an increased demand for P relative to N at elevated [CO_2].

Maranthes corymbosa
The growth of the tropical tree *Maranthes corymbosa* was increased by exposure to elevated [CO_2] in terms of total biomass, leaf area, number and mass (Berryman *et al.* 1993). This tree from the tropical monsoonal rainforests also had increased branching at elevated [CO_2] but lower foliar N levels and increased N use efficiency. The foliar nutrient content of P, K, Mg, Mn and Ca was not affected by [CO_2]. The growth response of *M. corymbosa* to [CO_2] is partly related to its physiological and morphological responses. At elevated [CO_2], leaves of *M. corymbosa* had reduced stomatal density and specific leaf area, meaning that leaves were thicker. Under high light conditions, such as exist in the tropics, thicker leaves assimilate more C while losing less water, so plants grown at elevated [CO_2] maintain lower stomatal conductance, higher C assimilation and hence higher water use efficiency than those grown in control conditions (Eamus *et al.* 1993). Plants grown at elevated [CO_2] also had lower whole plant hydraulic conductivity and

higher leaf water potential than control plants as a result of the changes to water use efficiency.

Impacts by species: Mangroves

Rhizophora apiculata and *R. stylosa*
These two tropical to subtropical mangrove species were grown in a factorial glasshouse experiment at both current and elevated [CO_2] with high and low salinity and high and low humidity (Ball *et al.* 1997). Both species were shown to have a small growth response to elevated [CO_2] when growth rate was limited by salinity, but growth was strongly stimulated by elevated [CO_2] when low humidity limited growth rate. These responses were underlain by both photosynthetic changes (increased water use efficiency and net assimilation rate) and changes in leaf area. Growth of the less salt-tolerant but faster growing species, *R. apiculata*, was stimulated by elevated [CO_2] to a greater extent, indicating that the increasing [CO_2] could well alter competitive interactions along the current salinity-aridity gradient.

Impacts by species: Trees of the temperate zones

Acacia spp.
The following *Acacia* species were examined at the same time in a series of glasshouse experiments and all had largely similar responses to [CO_2] enrichment. Therefore, each species is only dealt with briefly. The growth results of Atkin *et al.* (1999), however, are unlikely to be predictive as the plants were all grown in sterilised soils, preventing them from forming the root nodule symbiotic partnership with N-fixing bacteria, which will surely influence the growth response to elevated [CO_2].

Acacia dealbata
Elevated [CO_2] increased both the relative growth rate and final biomass of *A. dealbata* without nodules after 12 weeks, relative to those grown in control conditions (Atkin *et al.* 1999). Plant N content was unchanged and phyllodes (analogous to leaves in *Acacia* spp.) were thicker, having a lower area per unit weight, at elevated [CO_2] than in control conditions. When nodulated plants were tested, elevated [CO_2] stimulated relative growth rate, decreased plant N concentration and had no impact on the total amount of N fixed by the plant (Schortemeyer *et al.* 2002). [CO_2] had no impact on the N fixation rate per nodule, nor on the relative contribution of fixed N to plant total N (Schortemeyer *et al.* 1999).

Acacia implexa
Elevated [CO_2] increased both the relative growth rate and final biomass of *A. implexa* after 12 weeks, relative to those grown in control conditions (Atkin *et al.* 1999). Plant N content was unchanged and phyllodes (analogous to leaves in *Acacia* spp.) were thicker, having a lower area per unit weight, at elevated [CO_2] than in control conditions. When nodulated plants were tested, elevated [CO_2] stimulated relative growth rate, decreased plant N concentration but increased the total amount of N fixed by the plant (Schortemeyer *et al.* 2002).

Acacia irrorata

Elevated [CO_2] increased the final biomass of *A. irrorata* after 12 weeks, relative to those grown in control conditions, but did not significantly increase the relative growth rate (Atkin *et al.* 1999). Plant N content was unchanged and phyllodes (analogous to leaves in *Acacia* spp.) were thicker, having a lower area per unit weight, at elevated [CO_2] than in control conditions. When nodulated plants were tested, elevated [CO_2] stimulated relative growth rate, decreased plant N concentration but increased the total amount of N fixed by the plant (Schortemeyer *et al.* 2002).

Acacia mearnsii
Elevated [CO_2] increased both the relative growth rate and final biomass of *A. mearnsii* after 12 weeks, relative to those grown in control conditions (Atkin *et al.* 1999). Plant N content was unchanged and phyllodes (analogous to leaves in *Acacia* spp.) were thicker, having a lower area per unit weight, at elevated [CO_2] than in control conditions. When nodulated plants were tested, elevated [CO_2] stimulated relative growth rate, decreased plant N concentration but increased the total amount of N fixed by the plant (Schortemeyer *et al.* 2002). [CO_2] had no impact on the N fixation rate per nodule, nor on the relative contribution of fixed N to plant total N (Schortemeyer *et al.* 1999).

Acacia melanoxylon
Elevated [CO_2] increased both the relative growth rate and final biomass of *A. melanoxylon* after 12 weeks, relative to those grown in control conditions (Atkin *et al.* 1999). Plant N content was unchanged and phyllodes (analogous to leaves in *Acacia* spp.) were thicker, having a lower area per unit weight, at elevated [CO_2] than in control conditions. When nodulated plants were tested, elevated [CO_2] stimulated relative growth rate, decreased plant N concentration but increased the total amount of N fixed by the plant (Schortemeyer *et al.* 2002). In a separate experiment in which *A. melanoxylon* plants were grown in hydroponic culture and inoculated with N-fixing bacteria, [CO_2] had no impact on the N fixation rate per nodule, nor on the relative contribution of fixed N to plant total N (Schortemeyer *et al.* 1999).

Acacia saligna
Elevated [CO_2] increased both the relative growth rate and final biomass of *A. saligna* after 12 weeks, relative to those grown in control conditions (Atkin *et al.* 1999). Plant N content was unchanged and phyllodes (analogous to leaves in *Acacia* spp.) were thicker, having a lower area per unit weight, at elevated [CO_2] than in control conditions. When nodulated plants were tested, elevated [CO_2] stimulated relative growth rate, decreased plant N concentration but increased the total amount of N fixed by the plant (Schortemeyer *et al.* 2002).

Acmena smithii
Growth of this warm temperate rainforest tree was stimulated by elevated [CO_2], which also induced photosynthetic down-regulation when compared to plants grown under control conditions (Roden *et al.* 1997).

Doryphora sassafras
Elevated [CO_2] caused a substantial reduction of photosynthetic efficiency in this warm temperate rainforest tree, in which growth was stimulated by 41% compared to plants grown in control conditions (Roden *et al.* 1997).

Eucalyptus cladocalyx
The southern Australian eucalypt *Eucalyptus cladocalyx* produces large quantities of cyanogenic compounds, the most abundant of which is prunasin. N-based defensive

compounds are costly in terms of N, so it is possible that a decreased photosynthetic demand for N at elevated [CO_2] might alter N allocation patterns within leaves. In a glasshouse experiment, Gleadow *et al.* (1998) grew *E. cladocalyx* plants for six months and determined the impact of elevated [CO_2] on growth, biomass allocation and the total and relative allocation of N to prunasin. The results indicated that elevated [CO_2] increased plant height and mass and reduced the allocation of biomass to the leaves. Elevated [CO_2] also reduced leaf N content but did not alter the foliar prunasin content. Therefore, plants allocated relatively more N to prunasin at elevated [CO_2] than under control conditions. These results are important both for understanding the N allocation responses of plants to elevated [CO_2] and also for predicting the likely impacts of elevated [CO_2] on browsing animals.

Eucalyptus macrorhyncha
In a unique experiment, Roden and Ball (1996b; Roden and Ball 1996a) investigated the impact of elevated [CO_2] on the impacts of high temperature, high light events and drought stress on the growth and physiology of two south-east Australian eucalypts, *E. macrorhyncha* and *E. rossii* grown in glasshouse conditions. Elevated [CO_2] increased growth of *E. macrorhyncha* in both well-watered and droughted conditions (Roden and Ball 1996a). Elevated [CO_2] reduced the water stress placed on *E. macrorhyncha* plants by drought conditions by reducing stomatal conductance and therefore transpiration. Elevated [CO_2] also resulted in photosynthetic down-regulation in well-watered but not in drought conditions, which was related to the accumulation of non-structural carbohydrates.

Eucalyptus polyanthemos
Elevated [CO_2] increased photosynthetic C-assimilation and reduced dark respiration in this temperate eucalypt of south-eastern Australia, when grown in an open top chamber experiment with abundant water (Idso and Kimball 1993).

Eucalyptus regnans var. *fastigata (*published as *Eucalyptus fastigata)*
Austin (1992) produced a model investigation of the environmental controls of current distribution to describe niche requirements. The work discusses the implications for including the impact on the niche of elevated [CO_2], in terms of tool development, but does not make any predictions of impacts.

Eucalyptus rossii
In the same experiments as for *Eucalyptus macrorhyncha,* Roden and Ball (1996a,b) examined the responses of *E. rossii*. The results for *E. rossii* were largely the same as for *E. macrorhyncha,* although growth of *E. rossii*, the species which was less stressed by the high temperature event, appeared to be stimulated to a greater extent by elevated [CO_2] than was the case for *E. macrorhyncha*.

Impacts by species: Trees/shrubs of the arid and semi-arid zones

The only experimental investigation of the responses to [CO_2] in woody plants from either the arid or semi-arid zones was a series of glasshouse experiments on *Acacia* species (Atkin *et al.* 1999; Schortemeyer *et al.* 1999; Evans *et al.* 2000; Schortemeyer *et al.* 2002). Four arid zone Acacia species, namely *Acacia aneura, A. colei, A. coriacea* and *A. tetragonophylla*, were grown from seed for 12 weeks in order to assess the maximum possible response of relative growth rate to [CO_2] (Atkin *et al.* 1999). The plants were grown in sterilized soil to prevent the formation of nodules and were supplied with N in solution so that differences in N-fixation rates would not confound the growth results. Of the four species, elevated [CO_2] increased the relative growth rate only in *A. coriacea* although both *A. colei* and *A. tetragonophylla* also had a significantly higher final biomass at elevated [CO_2] than in control conditions. However, when nodulated *A. aneura* plants were grown in control and elevated [CO_2] conditions, plants grown in elevated [CO_2] had substantially increased relative growth rate (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 [CO_2]. The same is not the case with *A. tetragonophylla*, however, in which elevated [CO_2] did not significantly increase relative growth rate in either nodulated (Schortemeyer *et al.* 2002) or un-nodulated (Atkin *et al.* 1999) plants.

Impacts by species: Trees of the sub-alpine zone

Eucalyptus pauciflora

Several publications have dealt with the results from a field experiment in which young *Eucalyptus pauciflora* trees were exposed to control and elevated [CO_2] in Open Top Chambers (OTC) (Lutze *et al.* 1998; Roden *et al.* 1999; Barker *et al.* 2005; Loveys *et al.* 2006). [CO_2] had little effect on leaf gas exchange or growth, apart from during the spring when seedlings grown at elevated [CO_2] 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 [CO_2] 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 [CO_2]-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 [CO_2]-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 [CO_2]-grown plants than to controls, with subsequent reductions in growth of seedlings at elevated [CO_2] (Barker *et al.* 2005). This work suggests that the extra carbon gained by evergreen trees because of the increasing [CO_2] may be offset by increases in loss of leaf tissue from higher levels of frost injury in frost-prone environments.

Impacts by species: Other plants of the temperate zones

There are several forbs and some sub-shrubs present in the TasFACE experiment. Details on the impact of elevated [CO_2] are available for some aspects of the biology of these species growing in a natural community.

Acaena echinata
Elevated [CO_2] did not affect flowering or seed production of this perennial forb in the TasFACE experiment (Hovenden *et al.* 2007).

Bossiaea prostrata
This twining, prostrate member of the Family Fabaceae is widespread in temperate grasslands and shrublands in southeastern Australia. The only investigations of the impact of elevated [CO_2] on this N-fixing species are from the TasFACE experiment. In this field experiment, elevated [CO_2] significantly reduced the proportion of plants in the population that produced flowers in a moist year but not during a dry year. However, in those plants that did produce flowers, elevated [CO_2] substantially increased the number of seeds produced per plant, but only when elevated [CO_2] was combined with 2ºC warming and only in the dry year. Mean seed mass was unaffected by [CO_2] (Hovenden *et al.* 2007).

Calocephalus citreus
The proportion of the population that flowered in this perennial forb from the family Asteraceae was more than doubled by elevated [CO_2], both in warmed and unwarmed plots during a dry spring. There was no impact, however, of elevated [CO_2] on flowering of *Calocephalus citreus* in a wet year (Hovenden *et al.* 2007).

Carex breviculmis
Flowering of this perennial graminoid was unaffected by [CO_2] (Hovenden *et al.* 2007).

Convolvulus angustissimus
Flowering of this perennial, twining forb was unaffected by [CO_2] (Hovenden *et al.* 2007).

Eryngium ovinum
Flowering of this perennial forb was unaffected by [CO_2] (Hovenden *et al.* 2007).

Geranium retrorsum
Flowering of this perennial forb was unaffected by [CO_2] (Hovenden *et al.* 2007).

Hibbertia hirsuta
Flowering of this perennial grassland sub-shrub was substantially increased by elevated [CO_2] in both a wet and a dry year. Total seed production per plant was also increased by a factor of three by elevated [CO_2]. The addition of warming, however, completely prevented the stimulation of flowering and seed production in both the wet and dry years. Mean seed mass was unaffected by [CO_2] (Hovenden *et al.* 2007).

Hypoxis vaginata
Flowering of this perennial graminoid was unaffected by [CO_2] (Hovenden *et al.* 2007).

Leptorhynchos squamatus
Elevated [CO_2] significantly increased the number of seeds produced per plant in this small perennial forb from the Family Fabaceae, with the impact of elevated [CO_2] being greater in warmed plots than in unwarmed plots. Elevated [CO_2] only increased seed production of *Leptorhynchos squamatus* during a dry spring with no impact occurring in a wet year. Mean seed mass was significantly increased by elevated [CO_2], with the impact of elevated [CO_2] being greater in plots warmed by 2ºC than in unwarmed plots (Hovenden *et al.* 2007).

Oxalis exilis
The proportion of the population flowering in this perennial forb was substantially reduced by elevated [CO_2] during both a dry and a wet year, but this result was only statistically significant in the dry year. The reduction of flowering by elevated [CO_2] was greater in unwarmed plots than in those warmed by 2ºC (Hovenden *et al.* 2007).

Plantago varia
Flowering of this perennial forb was unaffected by [CO_2] (Hovenden *et al.* 2007).

Sebaea ovata
Elevated [CO_2] significantly reduced flowering in this annual forb in the TasFACE experiment, with the reduction being greater in warmed than in unwarmed plots (Hovenden *et al.* 2007). Mean seed mass was unaffected by [CO_2].

Solenogyne dominii
Flowering of this perennial forb from the Family Asteraceae was unaffected by [CO_2] (Hovenden *et al.* 2007).

Wurmbea dioica
Flowering of this perennial graminoid was unaffected by [CO_2] (Hovenden *et al.* 2007).

Impacts on animals

Vertebrates

The only published study that has investigated the impacts of elevated [CO_2] on any Australian vertebrate was a study of the impacts of elevated [CO_2] on leaf chemistry of 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 μmol mol^{-1} and 790 μmol mol^{-1} [CO_2] on a nutrient rich (basalt) and a nutrient poor (rhyolite) soil in a glasshouse. The results shown largely match expectations of reductions in foliar N levels (by 25% in *A. petriei* and 29% in *F. brayleyana)* and increases in plant secondary metabolites in *F. brayleyana*. Interestingly, foliar cation concentrations (Na, Ca, K) and P levels were reduced by exposure to elevated [CO_2] by 19-28% in *F. brayleyana* but not affected in *A. petriei*. Leaves were both tougher and thicker on plants grown at elevated [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 [CO_2] than the co-occurring *F. brayleyana*, it is possible that folivores will feed preferentially upon this species at elevated [CO_2], perhaps reducing plant performance and success and eventually reducing the abundance of this species.

Insects

The insect folivore *Chrysophtharta flaveola* was fed foliage from *Eucalyptus tereticornis* grown at ambient (350 μmol mol^{-1}) and elevated (800 μmol mol^{-1}) [CO_2], with two nutrient and two light levels in a glasshouse experiment (Lawler *et al.* 1997). Foliage from plants grown at 800 μmol mol^{-1} [CO_2] had significantly reduced N content, higher C:N ratio and generally higher levels of phenolics than foliage from plants grown at a [CO_2] of 350 μmol mol^{-1}. At low nutrient levels, leaf relative water content was lower at elevated [CO_2] than at ambient, but at high nutrient levels there was no impact of [CO_2] on leaf water content.

The changes in leaf chemistry induced by the treatments affected the performance of 4th-instar larvae of *Chrysophtharta 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 [CO_2] at low nutrient levels, such as may well be expected under field conditions.

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 [CO_2] of 360 μmol mol^{-1} and 700 μmol mol^{-1} (Coll and Hughes 2008). This research demonstrated that *Oechalia schellenbergii* as a generalist predatory omnivore benefited from elevated [CO_2] 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 [CO_2].

In a study of the responses of *Eucalyptus cladocalyx* to elevated [CO_2], it was found that the foliar N content was lower at elevated [CO_2] than in controls whereas levels of the cyanogenic glycoside prunasin was unchanged (Gleadow *et al.* 1998). Since leaf N content is lower at elevated [CO_2], 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 fungi and microbes

In the only published account of the impacts of elevated [CO_2] on fungi or microbes, Grayston *et al.* (1998) discovered that elevated [CO_2] changed the soil microbial community growing in the rhizosphere of *Austrodanthonia richardsonii* plants that had been exposed to either elevated [CO_2] or control conditions for four years. The microbial community at elevated [CO_2] was different to that in control conditions. There was also a preferential stimulation of fungal growth at elevated [CO_2]. It appears from this single study that bacterial metabolic activity, and not population size, was stimulated by the additional flow of C to the soil at elevated [CO_2].

Unpublished results from the OzFACE experiment indicate that mycorrhizal fungi have lower abundance at elevated [CO_2] compared to control conditions (C. Stokes, pers. comm.).

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Research on Australian ecosystems

The impacts of the increasing [CO_2] 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 [CO_2] but few investigations globally have examined the responses of natural ecosystems to elevated [CO_2]. In Australia, the investigation of the likely impacts of elevated [CO_2] 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 of the rising [CO_2] 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, the results for most species listed in the preceding pages are analyses of how [CO_2] affects a species growth potential, thus they are analyses of how increasing [CO_2] influences the *physiological* niche. While this does provide important and necessary information, it does present substantial problems with scaling responses up to natural ecosystems. The main problem lies with the growth conditions used, particularly where plants are provided with abundant supplies of nutrients and water. The second is the lack of competition and other normal ecological processes. 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. In the field, factors such as competition can dramatically alter a species' response to an environmental factor, thus the species has a different niche in its natural environment to that in an artificial environment; this is its *realised* niche. Thus, it is possible, and even very likely, that a species' response to the increasing [CO_2] will be different in a natural environment to that in an artificial environment because of altered levels of competition, for example. This is well presented in the cases of *Themeda triandra* and *Austrodanthonia caespitosa*. These two co-occurring species had very similar growth responses to doubled [CO_2] in a growth cabinet study (Hovenden 2003a) 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 [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.

However, there is still merit in analysing the variety of responses among species in their fundamental response to the increasing [CO_2], particularly when considering species from different ecosystems. The following sections present an overall analysis of the likely impacts of the increasing [CO_2] on Australian ecosystems based on the results from individual species given in the preceding pages, together with ecosystem-level assessments where they are available.

Tropical Forests

There is a long record of research into the impacts of elevated [CO_2] on Australian forest tree species and these species remain a focus of research effort. However, there have been no published accounts of the impacts of elevated [CO_2] on forest ecosystem processes. The impacts of elevated [CO_2] on individual tropical forest species are dealt with in the previous section. From these reports it would appear that changes in species composition are likely due to differences in responsiveness to elevated [CO_2], foliage nutritional quality is extremely likely to decline as protein content decreases and concentration of secondary metabolites increases in response to increasing [CO_2].

Temperate Forests

All results concerning the impacts of elevated [CO_2] on temperate forests come from trees grown singly. However, the temperate forest species examined uniformly show significantly increased growth rates at elevated [CO_2]. Leaf N concentration also was reduced by elevated [CO_2] in all temperate species. Foliage nutritional quality is likely to decline with lower protein content and higher concentrations of secondary metabolites at elevated [CO_2]. All temperate members of the N-fixing trees and shrubs of the genus *Acacia* examined showed growth stimulation, reduced N concentration but increased total N-fixation at elevated [CO_2]. This indicates that N supply to temperate forests that contain *Acacia* species may be increased by the increasing [CO_2].

Woodlands

Alterations in canopy species dominance are likely to occur as [CO_2] increases, as evidenced by the substantially different responses to elevated [CO_2] of the trees *Eucalyptus tetrodonta* and *E. miniata* (Duff *et al.* 1994). Foliage nutritional quality is likely to decline with lower protein content and higher concentrations of secondary metabolites.

Increases in the cover and frequency of trees and shrubs in rangelands, including grassland and grassy woodlands, has been termed "vegetation thickening". There is evidence from several regions of northern Australia that vegetation thickening has occurred over the past decades and century (Vigilante and Bowman 2004; Fensham and Fairfax 2005; Lawson *et al.* 2007). A modelling study has indicated that this is partly due to the increased competitive ability of woody plants in the grassy ecosystem due to the increasing [CO_2] (Berry and Roderick 2002). However, vegetation thickening is not evident in all areas (Fensham 2008), indicating that there are limitations on the impact of elevated [CO_2] on the tree-grass competitive interaction. The modelling results indicate, however, that the predicted increased success of woody dicots in grassy ecosystems under elevated [CO_2] already appears to be occurring. Thus, further increases in vegetation thickening at the margins of grasslands and rangelands are to be expected as the [CO_2] rises further.

As a result of this increased competitive ability of woody species against grasses with rising [CO_2], it is likely that woodland areas will increase in area as woodland trees invade adjacent grasslands. It is also likely that woodland canopy cover will increase as the vegetation thickens. Woodlands may therefore become more like forests and grassy woodlands more like dry sclerophyll woodlands, as shrubs become more dominant at the expense of grasses.

Shrublands and Heathlands

No investigations have been made of the likely impacts of the increasing [CO_2] on Australia's shrublands or heathlands; neither has any publication dealt with the impacts on native Australian shrubland or heathland species. 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 of elevated [CO_2] impacts 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 [CO_2]. Shrublands tend to be seasonally very dry, often occur on sandy soils with poor nutritional and water holding capacity. Growth rate is also extremely important in fire-prone shrublands, since competition is fierce in the years immediately following fire and long-term survival depends upon rapid production of perennating buds or seeds, so the increasing [CO_2] may well reduce the minimum time needed between successive fires as growth rates increase. Australian shrublands also contain large numbers of species with specialised adaptations for maximising nutrient uptake. It is possible that these species will be able to take advantage of the increased [CO_2] by increasing nutrient mobilisation from the soil (e.g. members of the families Proteaceae and Ericaceae); such species may outcompete co-occurring species without such adaptations at elevated [CO_2]. N-fixing species form a large component of many Australian shrublands, and, as discussed under the section on temperate forests, temperate N-fixing species respond uniformly to elevated [CO_2] with increased growth.

Therefore, it is likely that shrubland community composition, structure and productivity will all respond strongly to the increasing [CO_2]. Therefore, it is also likely that habitat quality for shrubland animal species will also change as the [CO_2] increases. The lack of experimental data, however, prevents anything but supposition concerning this important and widespread vegetation type.

Rangeland and grassland ecosystems

Results at the ecosystem level are restricted to field experiments, of which there have been two in Australia, both in grassland ecosystems. There have been no formal publications of results from the OzFACE experiment, however, growth of the three dominant C_4 grasses, *Themeda triandra*, *Chrysopogon fallax* and *Eriachne obtusa*, has been shown to respond positively and very strongly to elevated [CO_2] exposure (C. Stokes, pers. comm.). Results from the TasFACE experiment have shown that flowering (Hovenden *et al.* 2007), seed production (Hovenden *et al.* 2007) and flowering phenology (Hovenden *et al.* 2008c) are all largely unaltered by exposure to elevated [CO_2]. However, some species did respond significantly to elevated [CO_2] and the response of some species showed a significant interaction between elevated [CO_2] and warming treatment (Hovenden *et al.* 2007). As a result, the population dynamics of different species varies in response to the global change treatments (Williams *et al.* 2007). These species-specific responses to elevated [CO_2] are likely to produce alterations in competition and result in changes in community composition and structure, which have indeed been observed (Hovenden, unpublished data).

There is also strong evidence from both the OzFACE and the TasFACE experiment of CO_2-induced alterations to nutrient cycling, supporting the PNL hypothesis. In the TasFACE experiment, elevated [CO_2] in the absence of warming reduced the availability of mineral N by 47% after four years and 50% after five years (Hovenden *et al.* 2008a). Interesting, the addition of 2ºC warming to the elevated [CO_2] treatment completely prevented the reduction in soil N availability (Hovenden *et al.* 2008a). Thus, it appears that warming may counteract the elevated [CO_2]-induced reduction of soil N in this ecosystem.

There is overwhelming evidence from Australian and international studies that both leaf N and seed N concentrations will decline with increasing [CO_2]. This will reduce food quality for both herbivores and granivores.

Increases in the cover and frequency of trees and shrubs in rangelands, including grassland and grassy woodlands, has been termed "vegetation thickening". There is evidence from several regions of northern Australia that vegetation thickening has occurred over the past decades and century (Vigilante and Bowman 2004; Fensham and Fairfax 2005; Lawson *et al.* 2007). A modelling study has indicated that this is partly due to the increased competitive ability of woody plants in the grassy ecosystem due to the increasing [CO_2] (Berry and Roderick 2002). However, vegetation thickening is not evident in all areas (Fensham 2008), indicating that there are limitations on the impact of elevated [CO_2] on the tree-grass competitive interaction. The modelling results indicate, however, that the predicted increased success of woody dicots in grassy ecosystems under elevated [CO_2] already appears to be occurring. Thus, further increases in vegetation thickening at the margins of grasslands and rangelands are to be expected as the [CO_2] rises further.

As detailed above under "woodlands", it is likely that the increasing [CO_2] will promote the invasion of woodland trees into adjacent grasslands. Thus, grassy vegetation may reduce in extent through conversion to woodland and shrubland as a result of the increasing [CO_2]. However, it is possible that grassy vegetation may extend into more arid zones as a result of potential improvements in water use efficiency due to the increasing [CO_2]. This is dealt with in greater detail in the following section on Deserts.

Deserts

No investigations have been made of the likely impacts of the increasing [CO_2] on Australia's arid zone ecosystems. However, it would appear likely that some degree of increased vegetation cover would be expected with the hypothesised improvement in water use efficiency at higher [CO_2].

As noted above, it is possible that these physiological changes brought about by the increasing [CO_2] may lead to the extension of grasslands and rangelands into arid and semi-arid ecosystems. However, from the eight grasses from arid and semi-arid environments assessed so far, only a single species, *Astrebla squarrosa*, had improved whole plant water use at elevated [CO_2], with the other seven species showing no impact of [CO_2] on overall water use. However, in two of these seven species, namely *Bothriochloa blahdii* and *Digitaria brownii*, growth was significantly increased by exposure to elevated [CO_2]. Thus, for three of the eight species investigated, elevated [CO_2] increased either growth or water use efficiency. Thus, it is possible that particular grasses of the semi-arid and arid zones will increase in abundance while others will not. It is therefore reasonable to assume that some degree of increase in grass cover will occur in semi-arid and arid regions as a result of the increasing [CO_2].

In addition to the grasses, information is also available on the [CO_2]-response of four species of semi-arid and arid-zone *Acacia* spp. Of these four *Acacia* species, however, only two, *A. aneura* and *A. tetragonophylla*, were grown with their nodule-forming symbionts, so only results from these two species can be considered predictive in any way. Elevated [CO_2] substantially increased the growth rate of *A. aneura* but not of *A. tetragonophylla*, so it is possible that at least one species will increase in abundance with the increasing [CO_2], so some degree of vegetation thickening is likely in Australia's deserts as a result of the increasing [CO_2].

However, all of the studies mentioned above, both on *Acacia* spp. and grasses, grew plants in conditions with abundant water and no competition. Therefore, applying these results to natural desert conditions must be done with extreme care. The only results worldwide that are directly relevant to the likely impacts of the increasing [CO_2] on desert ecosystems come from the desert FACE system in the USA (Huxman *et al.* 1999; Jordan *et al.* 1999; Smith *et al.* 2000; Morgan *et al.* 2004). In this system both biomass production and plant water use efficiency was either unaffected or improved by exposure to elevated [CO_2], depending upon both species and year. For example shoot production in a dominant perennial shrub, *Larrea tridentata*, was doubled by a 50% increase in [CO_2] in a wet year but had no effect in a dry year (Smith *et al.* 2000). In same experiment, biomass production and seed rain was increased by elevated [CO_2] to a greater extent in a single exotic C_3 grass species than in several native C_3 species (Smith *et al.* 2000). However, overall species composition was not changed, even though elevated [CO_2] lead to an increased abundance of a single invasive C_3 grass species in at least one year.

Thus, it appears that elevated [CO_2] is likely to result in increased biomass production, improved water use efficiency and possibly increased seasonal abundance of ephemeral species in desert ecosystems. These changes in the vegetation are likely to increase food availability for desert animals, at least seasonally. The impacts of elevated [CO_2] on food quality, however, it totally unknown in this extreme environment.

Alpine and subalpine ecosystems

No investigations have been made of the likely impacts of the increasing [CO_2] on Australia's alpine ecosystems; neither have any publications dealt with the impacts on native Australian alpine species. The only subalpine species to be investigated is the snow gum, *Eucalyptus pauciflora*. It appears that elevated [CO_2] is unlikely to alter the competitive ability of *E. pauciflora* in the subalpine plant community (Roden *et al.* 1999). Results from alpine and sub-alpine environments in other countries have also shown very little change in vegetation cover (Schäppi and Körner 1996; Schäppi and Körner 1997; Hattenschwiler and Zumbrunn 2006), so that although some species are definitely more responsive than others (Hattenschwiler and Zumbrunn 2006), it appears that the changes in overall vegetation structure and function are likely to be slight. Thus, it would appear that elevated [CO_2] is unlikely to affect the extent, productivity or botanical composition of alpine vegetation.

Subantarctic ecosystems

No investigations have been made of the likely impacts of the increasing [CO_2] on Australia's subantarctic ecosystems; neither have any publications dealt with the impacts on native Australian subantarctic species. However, it would appear that, similar with the responses of alpine and sub-alpine species, the low temperatures, very high water availability and lack of N-fixing species mean that there is very little potential for the increasing [CO_2] to affect physiology or ecological processes dramatically. The impact of [CO_2] on photosynthetic rates are very low at low temperatures, since photorespiration rates are negligible, and the improvements in water use efficiency will have little impact in a permanently wet environment such as occurs on the generally low lying subantarctic islands (Selkirk *et al.* 1990). While no research has looked into the impacts in subantarctic environments globally, it can probably be assumed that these cool, dim, wet terrestrial ecosystems would be amongst the least responsive on earth to the increasing [CO_2].

LIKELY IMPACTS OF ELEVATED CO_2 ON ECOLOGICAL PROCESSES RELEVANT TO ALL AUSTRALIAN ECOSYSTEMS

Introduction

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. This following section deals with some of the most important general principles governing natural ecosystem responses to elevated [CO_2] and summarises our overall level of understanding of how these processes, which affect all ecosystems, will change as the [CO_2] rises.

Community level processes

Competition

Generalisations about the responses of different functional or phylogenetic groups of species to the increasing [CO_2] abound (Table 2). However, several of these are apparently contradictory, such as the distinction between monocots and dicots and slow and fast growing species; many monocots are extremely fast growing. Therefore, there is no *a priori* reason to believe that a particular monocot will be less responsive to the increasing [CO_2] than a particular dicot, as other factors, such as growth rate, also influence the response. However, in cases where other factors are judged as being equal, certain of the generalisations listed in Table 2 do seem to be predictive, especially in simple systems. Thus, growth of an herbaceous dicot would be expected to be stimulated to a greater extent than that of a co-occurring herbaceous monocot with a similar growth rate in current conditions.

Therefore, the rising [CO_2] is likely to alter competitive processes in multi-species communities, due to differences in functional attributes among species. Such alterations in species composition have been observed in both artificial (Hely and Roxburgh 2005) and natural communities exposed to elevated [CO_2] (Owensby *et al.* 1999; Edwards *et al.* 2001; Teyssonneyre *et al.* 2002). However, predictions of the impacts of the increasing [CO_2] on community composition and structure require the classification of all component species according to several functional traits. Further, nutrient status, water availability and climate all interact to alter the competitive outcomes. Therefore, our knowledge of the impacts of elevated [CO_2] on community level processes is still inadequate to make realistic predictions for any actual plant community.

However, it is likely that species composition will change in response to the increasing [CO_2] in some plant communities, most importantly those in which competition is intense. Thus communities like grasslands, shrublands, and forests and woodlands following disturbance such as fire, are likely to respond strongly to the increasing [CO_2] through changes in species composition, whereas communities in more stressful environments, like deserts, are less likely to have alterations in community structure and function.

Table 2. Generalised attributes of species more and less likely to respond positively to the increasing [CO_2].

Less responsive to elevated [CO_2]	More responsive to elevated [CO_2]
C_4 species	C_3 species
Monocots	Dicots
Slow growing species	Fast growing species
Species with high NUE	Species with low NUE
Non-N-fixers	N-fixers
Herbaceous species	Woody species

Invasive species

The likely impact of the increasing [CO_2] on the invasiveness of exotic plant species in native ecosystems is complex and impossible to generalise. The basic tenets that describe the relative responsiveness of different plant species to the increasing [CO_2] (Table 2) applies equally to native and exotic species. Thus, the question of whether the invasiveness and dominance of a particular exotic species is likely to increase as a result of increasing [CO_2] depends upon the functional attributes of the exotic species and the plant community it is invading. While certain reviews have posed the question of whether invasive species are likely to become more aggressive in an elevated [CO_2] world (Dukes 2000), there is no *a priori* reason to believe that exotic species will be more advantaged at high [CO_2] than they are currently, as the response to elevated [CO_2] depends upon a number of interacting attributes in both the invader and the invaded community (Dukes 2000).

Most experimental investigations have considered a small number of species, being most commonly artificial competition experiments between a single exotic and a single native species. The results from these experiments are mostly predictable on the basis of the attributes of each species. For instance, Navie *et al.* (2005) found that a C_3 species, *Parthenium hysterophorus*, increased its competitive dominance over a C_4 species, *Cenchrus ciliaris*, when exposed to elevated [CO_2], a result easily predicted from their functional attributes. Similar, predictable results were obtained by others working with similar species pairs (e.g. Ziska 2001). Similar results have been obtained from field studies (e.g. Ziska and Goins 2006), supporting an attribute-based approach to examining competitive interactions. However, competition experiments using functionally similar native and exotic species have shown that [CO_2] does not affect competitive interactions (Hely and Roxburgh 2005; Ziska and Goins 2006), suggesting that there is nothing about exotic species *per se* that is likely to lend them a particular advantage in a high [CO_2] world.

There is, however, the distinct possibility that particular invasive species will possess a suite of functional attributes that will confer a competitive advantage in a high [CO_2] world. It is also possible that particular ecosystems are dominated by species that are prone to invasion. Therefore, an attribute-based assessment of potential invasive species for each ecosystem is extremely important if weed threats to native biodiversity are to be predicted.

The efficacy of this type of analytical modelling work has been demonstrated in the case of the exotic, invasive C_3 species *Acacia nilotica* ssp. *indica*, which is a problem in semi-arid rangelands and is likely to become increasingly aggressive as [CO_2] increases (Kriticos *et al.* 2003).

Clearly, this topic is one of the most pressing as vast sums and considerable community effort are expended annually on weed eradication programmes. Knowing which species or types of species are most likely to benefit or suffer from the rising [CO_2] is of immense practical, economic and strategic importance to Australia.

Ecosystem level processes

Biogeochemistry

As detailed above, the increasing [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.* 2004). Results from the TasFACE experiment indicate that PNL occurs in response to elevated [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 [CO_2] and warming on soil nutrient availability (Hovenden *et al.* 2008a). These results indicate that the addition of 2ºC warming completely prevents the strong (up to 60%) reduction of soil N availability that occurs in the presence of elevated [CO_2] without warming. Thus, it appears that the rising [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 [CO_2] on biogeochemistry where there is substantial inputs of new N through symbiotic N fixation are currently unknown for Australia.

Food webs

Although, the only study of food webs in an Australian context is that of Coll and Hughes (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 [CO_2] on trophic interactions can be applied to tissue chemical analyses of Australian native plants. Elevated [CO_2] almost universally decreases plant N content and in most Australian species examined, increases the concentration of plant secondary metabolites. In Australia, many plant species possess high to lethal levels of toxic secondary metabolites under current conditions, and the levels of these toxins limits 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 [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 [CO_2], such that some secondary metabolites are increased more than others as [CO_2] rises. This could impact on the community of herbivores that will feed on a plant. 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 [CO_2] on higher trophic levels, however, is currently prevented by the lack of experimental results. Therefore, the overall impacts of the increasing [CO_2] on trophic interactions in Australian ecosystems is currently unknown.

CONCLUSIONS AND RECOMMENDATIONS

Conclusions

General conclusions

After a comprehensive analysis of all published information regarding the responses of Australia's native biodiversity to the rising [CO_2], the following general conclusions are made:

- The proportion of Australian native species in which the impacts of the increasing [CO_2] has been examined in any way is low for all taxonomic groups other than vascular plants.
- Investigations of the impacts of the rising [CO_2] on plant nutritional content uniformly indicates that feed quality is almost certain to be lower in a future, high [CO_2] environment. However, the impact of this change on Australian native animals has been assessed in only two invertebrate species. In particular, the impacts of the rising [CO_2] on Australia's unique and diverse marsupial fauna has not been assessed in any manner for any species.
- Most of the experimental investigations of the impact of the rising [CO_2] on Australian plant species have assessed the responses of plants growing individually, in pots, with abundant nutrients and water supplies and no competition with other plants.
- No analyses have been published on the impacts of the rising [CO_2] on ecosystem processes including nutrient cycling, water use and food webs for any Australian ecosystem other than for a single temperate grassland.
- There is only a single long-term study of the impacts of elevated [CO_2] on a native ecosystem in Australia.
- There is a great potential for elevated [CO_2] to change the composition, structure and function of Australia's natural terrestrial ecosystems, but some ecosystems are likely to change more dramatically than others.
- The responses of plants to the increasing [CO_2] will determine the responses of the entire Australian landscape.
- There is no understanding of which functional characteristics determine the response of a plant species to the increasing [CO_2].
- There is no national coordination of the research effort into the impacts of the rising [CO_2] on Australian native species and ecosystems, neither is there any central repository or database of published information in this field.

Ecosystem specific conclusions

The rising [CO_2] is likely to have the following impacts on Australian terrestrial ecosystems:

Tropical Forests

Changes in botanical composition are likely. Foliage feed quality is likely to decline.

Temperate Forests

Changes in botanical composition may well be slight. Growth rates are very likely to be stimulated in most species, particularly N-fixing species. Ecosystem N-fixation rates are likely to increase, further supporting a sustained enhancement of temperate forest growth. Foliage feed quality is likely to decline although foliage production may increase.

Woodlands

Changes in botanical composition within the canopy are likely. The understorey of grassy woodlands is likely to become increasingly dominated by shrubs, altering habitat quality for animals. Woodland structure and function is likely to change dramatically at current boundaries, with woodlands becoming forests in wetter regions and invading grasslands in drier regions. Woodland feed quality is likely to decline.

Shrublands and Heathlands

Botanical composition is very likely to change, altering ecosystem structure, function and habitat quality. Insufficient experimental data are available to draw any further conclusions.

Rangeland and grassland ecosystems

Vegetation thickening is extremely likely as is reduction of grassland extent due to encroachment by shrublands and woodlands. Grasslands are likely to extend into desert systems. Changes in botanical composition are extremely likely with potential for dramatic decline in some currently abundant species. Grassland productivity is likely to increase in warmer regions and in cooler regions when warm season rains are sufficient, increasing food availability. Feed quality, both of foliage and seeds, is extremely likely to decline.

Deserts

Vegetation thickening and extension of grasslands into desert areas is likely. Biomass production during wet years is likely to be increased, increasing food supplies to herbivorous animals. Changes in botanical composition are likely.

Alpine and subalpine ecosystems

Changes in extent, productivity and botanical composition are likely to be slight.

Subantarctic ecosystems

Changes in extent, productivity and botanical composition are likely to be extremely slight.

RECOMMENDATIONS

After a comprehensive analysis of all published information regarding the responses of Australia's native biodiversity to the rising [CO_2], the following recommendations are made:

- As a matter of urgency, the impact of the rising [CO_2] on Australian shrubland species and ecosystems be examined.
- As a matter of urgency, the impact of the rising [CO_2] on Australian native marsupial species be examined. Specifically, the impact on native marsupials of changes in plant nutritional quality in response to the increasing [CO_2] should be examined.
- A coordinated project be instigated to investigate the functional characteristics that determine the response to the rising [CO_2] of plant species in the natural environment. This will allow the predictions of likely responses of a wide range of plant species to the increasing [CO_2] and must consist of planned experiments supported by an underlying modelling framework.
- Investigations of the impacts of the increasing [CO_2] on Australian native plant species grown in the absence of competitors, pathogens and enemies and with abundant nutrients and water be discouraged in favour of investigations in which species are grown in the presence of competitors, pathogens and enemies and with native soil conditions, including water and nutrient availability.
- Existing experiments investigating the impacts of the rising [CO_2] on ecosystem processes continue to be supported and specific new projects be instigated in selected ecosystems. It is specifically recommended that projects be instigated in shrubland and at the woodland/grassland boundary ecotone.
- A national repository or database of published information on the responses of Australian native species and ecosystems to the increasing [CO_2] be established. Such a database could also indicate current areas of research activity.

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