

Impact of global climate change and fire on the occurrence and function of understorey legumes in forest ecosystems

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Abstract

The objective of this review was to provide a better understanding of how global climate change and fire influence the occurrence of understorey legumes and thereby biological nitrogen (N) fixation rates in forest ecosystems. Legumes are interesting models since they represent an interface between the soil-, plant-, and microbial-compartments, and are directly linked to nutrient cycles through their ability to fix N. As such, they are likely to be affected by environmental changes. Biological N fixation has been shown to increase under enriched CO₂ conditions, but is constrained by the availability of phosphorus and water. Climate change can also influence the species composition of legumes and their symbionts through warming, altered rainfall patterns or changes in soil physicochemistry, which could modify the effectiveness of the symbiosis. Additionally, global climate change may increase the occurrence and intensity of forest wildfires thereby further influencing the distribution of legumes. The establishment of leguminous species is generally favored by fire, as is N₂ fixation. This fixed N could therefore replenish the N lost through volatilization during the fire. However, fire may also generate shifts in the associated microbial community which could affect the outcome of the symbiosis. Understorey legumes, because they represent key ecological processes, respond rapidly to environmental changes and are closely associated with soil microbes, could be used to monitor the responses of forest ecosystems to global warming or fire. This would be helpful to accurately model ecosystem N budgets, and since N is often a limiting factor to plant growth and a major constraint on C storage in ecosystems, would allow us to assess more precisely the potential of these forests for C sequestration.

Keywords Global climate change • Nitrogen fixation • Fire • Rhizobia • Understorey legumes

1 Introduction

Legumes are broadly distributed across the globe and are important components of the understorey of forest ecosystems. They are especially present in Australian eucalypt-dominated forests, which represent 79% of the native forest estate of the continent (National Forest Inventory 2007). Understorey legumes are critical for the ecosystem functioning of these forests since they can fix nitrogen (N) through their association with N-fixing bacteria, and are able to increase the quantity of N and phosphorus (P) cycled through litterfall (Guinto et al. 2000; Forrester et al. 2005). These symbiotic associations, combined with other competitive physiological traits such as their resistance to drought, permit them to colonize disturbed lands and to quickly re-establish after fires. This makes understorey legumes adequate species for ecological restoration in the tropics (Adams et al. 2010). **Understorey legumes play a crucial role in the N balance of forest soils. However, relatively little information exists about the taxonomic and functional diversity of the interactions between native understorey legumes and their symbionts** (Hoque et al. 2011).

Biological N₂ fixation is the major natural process providing N inputs to the soil and as such, an important biogeochemical mechanism for forest productivity. It can occur through free-living or symbiotic microbial pathways (van Groenigen et al. 2006), and because it is one of the most energy-demanding biological processes on Earth, it closely depends on carbon (C) supply as an energy source. Furthermore, it requires 16 molecules of ATP per mole of N₂ fixed which makes it strongly constrained by P at molecular scales (Vitousek et al. 2002). The C, N and P biogeochemical cycles are essential to sustain life on Earth. Living organisms require these elements in exact proportions, especially because the cycles of C, N, and P are coupled from molecular to global scales (Gruber and Galloway 2008). This stoichiometric balance is fundamental for maintaining forest ecosystem diversity, functioning, and stability (Finzi et al. 2011). Environmental changes such as elevated atmospheric CO₂ and temperature, atmospheric N deposition, land-use change or forest fires, have modified this fragile balance. How forest ecosystems are responding to these modifications is still unclear, and it is necessary to understand the underlying processes regulating these responses in order to be able to predict how C and nutrient cycles will be affected in the long term (Beedlow et al. 2004; Magnani et al. 2007; Chen and Xu 2010; **Owens and Xu 2011**).

Soil microbial communities, because they are mainly heterotrophic and are parts of the belowground processes, are likely to be affected as well by the stoichiometry changes in C, N and P due to environmental change (Chen and Xu 2010). Although a large amount of information has been published on the influence of global environmental changes on forest ecosystems (e.g. Sitch et al. 2008; Allen et al. 2010; **Liu et al. 2011a**), most of it deals with the aboveground ecosystem components (Xu and Chen 2006; **Liu et al. 2011b**). There is increasing evidence that above- and below-ground processes are intimately linked (Heimann and Reichstein 2008) and it is therefore critical to adopt a change of framework in order to unravel the impacts of environmental alterations on plant-soil-microbe interactions and ultimately on ecosystem functioning. Understorey legumes and their associated microbiota represent a perfect example of the interrelations existing between the soil-, plant-, and microbial-compartments of forest ecosystems, and are directly linked to nutrient cycles through biological N₂ fixation. The objective of this review was to provide a better understanding of how environmental stressors, such as global climate change or fire, influence legume distribution and functioning in forest ecosystems. **We also**

comment on the potential role of understorey legumes to mitigate the impacts of such environmental changes and to monitor the responses of eucalypt-dominated forests to environmental changes.

2 The impact of global climate change on understorey legumes

2.1 Global climate change affects forest growth through photosynthesis and water use efficiency

Over the last century, fossil fuel burning and land-use change have caused atmospheric CO₂ concentration to increase globally by nearly 30% and temperature by approximately 0.6°C, and these increases are projected to continue even more rapidly (IPCC 2007). The impacts of global climate change on long-term forest growth and C sequestration have raised concern worldwide (Oren et al. 2001; Reich et al. 2006; Heimann and Reichstein 2008; Chen and Xu 2010). First, trees should be able to adjust their physiological responses over time to gradually changing environmental conditions (Dawson et al. 2011) but in the long-term, gradual and step increases in atmospheric CO₂ concentration could generate negative effects on plant photosynthesis (Sun et al. 2010). Because increased CO₂ did not occur in isolation but was accompanied by elevated N deposition and altered cycles of elements due to anthropogenic activities, the outcomes of global climate change are even more difficult to predict (Xu et al. 2009; Owens and Xu 2011). Most studies conclude that elevated CO₂ concentration should increase photosynthesis by stimulating the carboxylation rate of Rubisco and reducing photorespiration (Schimel 1995; Atkin et al. 1999), provided that available N and water are present in sufficient amounts (Liu et al. 2010, 2011a). As shown in Table 1, greater stimulation of photosynthesis and growth of legumes and actinorhizal plants, compared to non-N₂-fixers, is expected under elevated CO₂ concentration (Soussana and Hartwig 1996; Zanetti et al. 1996; Rogers et al. 2006; Tobita et al. 2010). Even when these physiological responses vary among N₂-fixing species and genotypes (Reich et al. 2001; West et al. 2005), they confer them with an advantage to cope with global climate change. This is due to the ability of N₂-fixers to maximize the benefits of elevated CO₂ concentration by counteracting N limitation and decreasing the negative impact of drought on biological N fixation (Rogers et al. 2009).

Water stress will thus become increasingly critical for the functioning of forest ecosystems. Water is closely coupled with the C cycle through photosynthesis and indirectly influences nutrient availability through soil moisture. The hydrological cycle is altered by global climate change through the increase in global temperature and its consequent effects on rainfall patterns. Seasonal variation in precipitation may deeply affect ecosystem productivity as any change in the frequency or timing of rainfall may determine whether water will be taken up by plants or lost by evaporation or run-off (Heimann and Reichstein 2008). Plant responses to water shortage, such as water use efficiency (WUE) and resilience to drier environmental conditions, will be crucial for maintaining forest productivity under elevated CO₂ concentrations. It has been predicted that the increase in plant photosynthesis and the reduction in stomatal conductance originating from rising CO₂ should result in lower transpiration rates and consequently in higher plant water use efficiency (Nelson et al. 2004; Peñuelas et al. 2009). Species with higher WUE may therefore possess an adaptive advantage to stand the expected drier conditions provoked by climate change in many parts of the world. Recently, Gebrekirstos et al. (2011) used stable C isotope techniques to investigate the ability of different *Acacia* species to withstand drought, and reported that species with lower water potentials and hence higher WUE demonstrated a conservative water use strategy under water stress conditions. However, this higher plant WUE might be offset by decreasing plant photosynthesis after the tipping point in forest productivity is passed (Xu et al. 2009; Laurance et al. 2011).

2.2 Influence of global climate change on N fixation and N₂-fixing microorganisms

Legumes and their associated soil microorganisms are sensitive to environmental changes, especially to increases in atmospheric CO₂ concentrations (Jablonski et al. 2002). Symbiotic N-fixing bacteria, such as rhizobia or the actinomycete *Frankia*, are known to benefit from plant growth under elevated CO₂ conditions (Rogers et al. 2009). The availability of N supplies is particularly relevant in order to delay the negative effects of elevated CO₂ concentrations on forest productivity. Enhanced biological N fixation has been therefore suggested as a means to provide the N necessary to support C accumulation under rising atmospheric CO₂ concentration (Finzi et al. 2007), which would make biological N fixation a key process for mitigating environmental change. Increases in the size of symbiotic rhizobial populations (Schortemeyer et al. 2002), in the size and number of root nodules (Serraj et al. 1998; Tobita et al. 2010) or in nitrogenase activity (Soussana and Hartwig 1996) are common effects of atmospheric CO₂ enrichment, provided P is supplied in sufficient amounts. Some studies showed that N fixing plants are also able to increase the availability of P in soil through their phosphatase activity (Houlton et al. 2008), though it might be of direct benefit for the legumes that produced that enzyme activity. This capacity to remobilize P implies that woody legumes are able to succeed in establishing where other plants may fail due to poor supplies of water and P.

The relative contribution of symbiotically-fixed N has been shown to increase under elevated CO₂ concentrations since the increasing plant demand for N, as a result of an enhanced growth, cannot be fulfilled by available mineral N (Lüscher et al. 2000). However, other studies reported that the presence of legumes does not prevent a gradual decrease in biomass response under elevated CO₂ and moderated the role of N₂ fixation in C storage (Reich et al. 2006). The enhancement of biological N fixation under such conditions may be species specific (West et al. 2005) and is constrained by the availability of other nutrients, such as P, potassium or molybdenum (Hungate et al. 2004; van Groenigen et al. 2006). The P-limitation of this increase in N₂ fixation has been demonstrated for actinorhizal plants as well (Tobita et al. 2010). Since biological N fixation is an energy-demanding process which requires P (Forrester et al. 2005), it is consequently closely linked to other nutrient cycles and is therefore likely to be influenced by any change in environmental conditions.

If the impact of CO₂ enrichment on N₂-fixing relationships is generally well documented, the effects of other environmental changes, such as warming and water shortage, are less studied. The N₂-fixing plants are indirectly influenced by warming since biological N fixation is strongly temperature dependent, with a maximum at around 25°C (Houlton et al. 2008; Adams et al. 2010). The N₂ fixation is enzymatic and energy-demanding, hence any temperature constraint could enhance its C cost (Vitousek and Field 1999). The magnitude of the effect of an increase in temperature may depend on the legume species and on their particular distribution. In his work about projected impacts of climate change in Australia, Hughes (2003) concluded that *Acacia* species may be relatively robust to modest warming, since only one species would be threatened by its bioclimate disappearance with a 0.5°C increase in global temperature. However, the bioclimates of 59% of *Acacia* species would be expected to disappear with a 1°C increase and would totally disappear with a 2°C warming.

Lack of rain and rising temperatures also increase the soil salinity, creating an osmotic stress which affects both the plant and its symbionts. Coping mechanisms include the accumulation in the bacterial cell of potassium or other low molecular weight organic solutes, which protect the cells against hyperosmotic stress or desiccation (Essendoubi et al. 2007). These solutes have been found in various rhizobial strains growing in drought-prone ecosystems (Zahrán 2001).

Because rhizobial strains vary in salt tolerance, shifts in symbiont community composition may have drastic effects for the ecological success of their hosts, hence mediating host adaptation to stressed environments (Thrall et al. 2009). Changes in environmental conditions due to climate change may also modify the plant dependence on the symbiosis, especially when the associated microorganisms themselves are sensitive to environmental change (Thrall et al. 2008). In harsher conditions, successful plant establishment may depend on the microbial adaptation to the environmental stressor, as in the case of salt-tolerant rhizobial strains. On the contrary, the cost of maintaining the symbiosis under environmental stress might become too high for the plant to sustain.

The increasing levels of CO₂ in the atmosphere are unlikely to directly affect soil organisms, since the concentration of CO₂ already present in pore spaces of most soils would probably buffer any atmospheric increase (Pritchard 2011). However, plant physiology is directly affected by CO₂ enrichment, which may therefore impact the plant belowground symbionts (Xu et al. 2009; Owens and Xu 2011). Trees growing in CO₂-enriched atmospheres have been reported to present significant increases in root production (e.g. Norby et al. 2004), which represents an increase in the resources made available to the soil microbial communities. The release of more labile organic compounds into the rhizosphere is expected to change the size and the activity of soil microbiota, increasing mycorrhizal or N₂-fixation associations, resulting in higher rhizosphere microbial activities per unit of root growth (Pritchard 2011). Increased activity may in turn enhance organic matter decomposition and increase N mineralization rates and N uptake by plants, as well as the loss of soil C (Fig. 1). This exchange of tree C for soil N, with the amount of C allocated to the soil determined by soil N availability, appears to maintain high forest productivity under elevated CO₂ (Drake et al. 2011). However, the greater immobilization of soil nutrients, in particular of soil N, due to the increasing organic C input to the soil, could soon lead to progressive nutrient limitations (Beedlow et al. 2004; Chen and Xu 2010). This would challenge the plant's capacity to respond to elevated atmospheric CO₂, thereby resulting in a decrease in plant productivity over time, as suggested by Drigo et al. (2008).

Different plant species may possess a different potential to adapt to warming and water stress. An increase in temperature due to climate change may thus change plant species composition and consequently alter their associated microbiota. Host community structure plays a fundamental role in shaping symbiotic interactions and effectiveness (Thrall et al. 2011) and therefore ecosystem productivity and diversity. Overall, the effect of global climate change on biological N fixation may probably be twofold since adverse conditions can alter both legumes and their symbiotic bacteria. Increasing atmospheric CO₂ concentrations are unlikely to stimulate all groups of soil organisms equally, and changes in soil community composition will probably occur. Studies about the influence of global climate change on soil microbial communities suggest that energy flows through fungal pathways may be enhanced relative to bacterial pathways by both warming and atmospheric CO₂ enrichment (Abera et al. 2011; Pritchard 2011). Fungi have lower N requirements than bacteria and may therefore be favored by higher litter C:N ratios and by the increased exudation of organic C compounds into the rhizosphere, although recent findings do not validate this hypothesis (Blankinship et al. 2011). Drake et al. (2011) demonstrated the importance of fungal community composition in ecosystems affected by warming and suggested that fungi, by conditioning soil nutrient availability, may mediate the effects of elevated CO₂ on forest productivity. In any case, a shift from bacterial- to fungal-dominated soil microbial communities would have important implications for N₂-fixing plants which form symbiotic associations with both and consequently for the ecosystem response to increasing CO₂ concentrations (Langley and Megonigal 2010).

3 The impact of fire on understorey legumes

3.1 Wildfires affect the establishment of understorey legumes

Forest fires represent an element of global climate change which enhances greenhouse gas concentrations through the release of C and N as gases and particulates into the atmosphere and might accelerate negative responses of forest ecosystems to climate change (Allen et al. 2010). Alternatively, global climate change may increase the occurrence and intensity of forest wildfires by changing rainfall, temperature and air humidity patterns, thus enhancing drought conditions (Neary et al. 1999). Feedbacks between physiological stress driven by climate change and other forest disturbance processes such as fire are poorly understood (Allen et al. 2010), especially because they intervene at different scales: whereas climate change acts at a global scale by increasing atmospheric CO₂ concentrations and temperatures, fire has a more local influence on forest ecosystems (Xu et al. 2009; Owens and Xu 2011).

Wildfires are frequent in ecosystems ranging from tropical semiarid savannas to American temperate forests, where N is often a common limiting factor for tree growth (Hains et al. 1999; Caldwell et al. 2002). Legumes are ubiquitous in fire-dependent ecosystems since they often need fire to germinate. As part of the understorey, they are directly affected by wildfires. Various studies reported that the establishment of N₂-fixing vegetation was promoted by frequent fires which decreased the competitive exclusion of legumes once established (Hendricks et al. 1999; Newland and DeLuca 2000). This higher density of legumes and actinorhizal plants following fire thereby increases biological N fixation rates, which in turn enhance the rates of soil N cycling through the input of higher quality litter to the soil (Hart et al. 2005). Other studies, however, showed that this increase in legume abundance was season-dependent, and that unlike winter fire, summer fire seemed to constrain N₂-fixing plants, probably due to its effect on flowering and seed production (Hains et al. 1999). Moreover, the dominance of legume species can in some cases cause problems for trees to re-establish, thereby delaying the replenishment of C pools (Johnson et al. 2005).

Wildfires also affect legume distribution through indirect pathways, by altering biogeochemical cycles (Fig. 2). N volatilization results in lower pools of plant available and total N, and some of the vegetation types which have been found to dominate post-fire ecosystems produce slowly-decomposing recalcitrant litter resulting in immobilization of N (Reich et al. 2001). The reduction in plant biomass following forest fires may induce changes in C dynamics since woody cover has been shown to promote the sequestration of both C and N (Coetsee et al. 2010). Furthermore, by modifying soil moisture conditions and elevating soil temperature, fire may generate some shifts in nutrient availability, as well in soil chemical and physical properties. The resulting loss of organic matter, the alteration of nutrient availability by leaching of soluble ions, and the modification of soil moisture levels will induce changes in the occurrence of leguminous species, which are known to vary in their tolerance to drought (Sprent 1995). Belowground processes will be affected as well (Guinto et al. 1999b), and losses of C due to the burning may be accelerated by increases in microbial activity due to elevated soil temperatures (Treseder et al. 2004). On the other hand, they may be counterbalanced through the deposition of charcoal in the soil, which contributes significantly to the soil C pool, especially in fire-maintained forest ecosystems (DeLuca and Aplet 2008). There may be a variety of other ecological and management factors which affect legume distribution, and a better understanding of the spatial and temporal responses of legume species to different burning regimes and resources is required. Furthermore, changes in the distribution and occurrence of N₂-fixing plants following fire are probably modifying as well the abundances

of their symbionts, ultimately altering the community composition and activities of other soil microorganisms (Table 1).

3.2 Wildfire impact on biological N fixation and N₂-fixing microorganisms

The impact of fire on biological N fixation has received much attention, especially because fire-adapted legumes may play a relevant role in replacing N lost by volatilization (Hendricks and Boring 1999). On low-fertility sites, even small N₂ fixation values can represent a long-term source to restore soil N levels following disturbance (Busse et al. 2007). N₂-fixing plants may also favor the input into the forest soil of higher quality litter with lower C:N ratio (Newland and DeLuca 2000). Fires have been showed to increase *Acacia* nodulation in eucalypt-dominated forests (Guinto et al. 2000) and may promote the ability of legumes to fix N₂ by making soil conditions more favorable. Low intensity fires reduce soil available N by N mineralization and enhance soil available P, both propitious to biological N fixation (Vitousek et al. 1999). However, N₂ fixation is often constrained by water shortage. Increasing drought stress under frequent fire events is likely to contribute to a decrease in leaf area, thereby reducing the quantity of photosynthates necessary to maintain nodule biomass and N₂ fixation rates (Hendricks and Boring 1999). Furthermore, frequent fires may not be as favorable to legumes, since the quantity of N fixed between fires would be smaller than the N lost during the fires. Newland and DeLuca (2000) concluded that a critical assessment of the temporal patterns of biological N fixation is necessary to develop reliable long term N budgets.

Direct fire impacts on rhizobial and actinorhizal communities may occur through heat-induced mortality. Furthermore, indirect effects are likely to arise due to the modification of the soil environment through heating, oxidation and new inputs to the soil system of charcoal, distillates metal oxides, and plant litter (Hart et al. 2005). Some groups of microbes are more sensitive to heating than others, which can result in shifts in the size, activity, and composition of the soil microbial community. Abera et al. (2011) showed that the microorganisms involved in soil N transformation processes have different sensitivity levels to water availability, which may modify community composition at the rhizosphere level. Bacteria are acknowledged to be more tolerant to heat than fungi, and since most legume species present symbiotic associations with both rhizobial bacteria and mycorrhizal fungi (Diédhiou et al. 2005; Adams et al. 2010), they would be directly affected by such changes in soil microbial community composition. Arbuscular mycorrhizal fungi have been shown to be more tolerant to heat than asymbiotic fungi (Hart et al. 2005). This symbiosis is especially relevant for P acquisition and could help overcome possible P-induced decreases in legume abundance and biological N fixation (Hains et al. 1999). Finally, the changes in plant communities occasioned by wildfires, similarly to the changes generated by CO₂ enrichment, will probably alter the relative competitive ability between plant and microbes for limiting nutrients, which may indirectly affect the soil microbiota and the outcome of symbiotic associations.

3.3 Prescribed burning as a management tool for forest ecosystems

Also relevant to forest functioning is the use of fire as a forest management tool, generally known as controlled or prescribed burning (Guinto et al. 1999b; Mao et al. 2002; Penman and York 2010). Prescribed burning usually involves low intensity, understorey fires (Fig. 3). It is used by forest managers to avoid devastating wildfires by reducing the amount of fuel, to reestablish ecosystem functioning, to control competition and facilitate regeneration, and to manage wildlife habitat (Hendricks and Boring 1999). Because the accumulation of fuels has also been shown to generate stagnation in nutrient

cycling (Caldwell et al. 2002), prescribed burning may be beneficial for forest functioning. As a forest management tool, periodic fire plays a crucial role in these ecosystems, and may reduce the potential feedbacks of wildfire on climate change. However, burning may act as an additional environmental stressor by affecting the functional interactions between soil biota and plants and favoring some plant or soil microbial species (Guinto et al. 1999a; Bastias et al. 2006a, b). Prescribed burning also generates N volatilization: Johnson et al. (1998) estimated that a fire of moderate-severity would volatilize about 200 kg N ha⁻¹ from a semi-arid forest ecosystem. Furthermore, it results in increased nutrient availability and in lower nutrient uptake by the plants, thereby increasing N leaching (Mohamed et al. 2007). Frequent or regular burning may further modify C and N cycling patterns by decreasing the quantity of soil organic matter, altering C allocations in plants, reducing N mineralization rates and ultimately altering plant succession and evapotranspiration rates (Neary et al. 1999). The frequency of prescribed burning is thus a critical parameter to take into account in forest management, since short fire-return intervals would result in greater N replacement needs, as would fires of higher severity (Busse et al. 2007). In such cases, additional N inputs from native legumes would therefore be needed to replace the N lost through volatilization, although extensive planting would probably be required to ensure the establishment and persistence of legume populations large enough to significantly increase N availability (Hendricks and Boring 1999).

4. Understorey legumes as potential indicator species in forest ecosystems

While there is a relatively large amount of studies focusing on the responses of forest trees to global climate change (Beedlow et al. 2004; Magnani et al. 2007; Bonan 2008), relatively little information has been generated on the understorey vegetation. Legumes are known to be important functional components of the understorey vegetation of forest ecosystems, and are acknowledged to play a crucial role in biological N fixation. Because N is often a limiting factor to plant growth and a major constraint on C storage in ecosystems, N₂-fixing plants are a key element in the N biogeochemical cycle and could mitigate the potential C:N imbalance caused by elevated CO₂ through N inputs into the soil system (Serraj et al. 1998; Forrester et al. 2005). This may be especially true for understorey legumes growing on nutrient-depleted soils, such as the ancient Australian forests soils where even small N inputs by biological N fixation may be significant (Guinto et al. 2000). Forest management practices thus increasingly consider understorey legumes as important to reestablish an adequate balance between inputs and outputs of N (Adams et al. 2010).

Understorey legumes will have to adapt to the new environmental conditions created by environmental disturbances. Sprent (1995) indicated that Australian acacias may have evolved due to variations in moisture regimes and hence that accelerated land degradation and desertification may continue to exert selection pressure and lead to more speciation. These pressures are likely to act on legume-associated bacteria as well. *Rhizobium* for instance possesses the ability to survive under stressed environments (Thorne and Williams 1997; Räsänen et al. 2004; Sarr and Lesueur 2007). However, because of the high diversity of nodule-forming bacteria associated with understorey legumes and to their broad distribution (Hoque et al. 2011), different species of symbionts may respond differently to global climate change or fire, which makes the impact of environmental changes on N-fixing microbes difficult to assess. Since legumes and their associated microbes are direct actors in nutrient cycling, they may respond more rapidly to changes in nutrient fluxes, especially because plant-microbes interactions are particularly sensitive to changes in plant physiology and belowground allocation (van der Heijden et al. 2003; Duponnois et al. 2005; Adams et al. 2010).

Acacia is a particularly important genus, with 955 species recorded in Australia. *Acacia* species possess the capacity to

accumulate relatively large quantities of cyclitols as a mechanism to cope with drought conditions (Adams et al. 2010), and may therefore be able to play a major role in land rehabilitation and C sequestration strategies. There is a great diversity in both host and microbial symbionts (formed by both rhizobia and mycorrhizal fungi) in *Acacia* symbioses. If biodiversity helps maintaining ecosystem functioning in complex environments and may buffer natural ecosystems against ecological impacts of nutrient pollution (Cardinale 2011), it may also help mitigating the negative effects of global climate change. Understorey legumes are important functional species, and even when they cannot reasonably be expected to reestablish nutrient balance in forest soils, they may be used as indicator species to monitor nutrient fluxes and the response of forest ecosystems to changing environmental conditions. *Acacia* species are sensitive to global climate change and fire management, play a direct role in nutrient cycling and are likely to respond rapidly to any environmental change in nutrient fluxes, and as such represent an interface between forest soils, soil microbes and major trees of the ecosystem. Their ability to fix N enables an adjustment of N availability close to the availability of other resources and thereby strongly relies on the fragile equilibrium of biogeochemical cycles (Vitousek and Field 1999). Understorey legumes are functional keystone species in forest ecosystems, and because they are sensitive to environmental changes, they may be good ecological indicators to monitor the response of these forests to enriched CO₂ conditions or to wildfires. Moreover, as shown previously, fungi may be favored over bacteria by warming and increasing N limitations. Since acacias are known to form symbiotic associations with both bacteria and mycorrhizal fungi, they would constitute the perfect model to study the influence of environmental disturbances on the relative abundance of bacterial and fungal communities present in its rhizosphere. **Plants may rely more strongly on their symbionts when subjected to stress and the outcome of the symbiosis is likely to change under harsher conditions. It is therefore necessary to study how environmental factors influence the effectiveness of the interaction (Sarr and Lesueur 2007). Finally, getting a better understanding about how environmental stressors affect biological N fixation is an essential requirement to accurately model ecosystem N budgets and ultimately for forest ecology and productivity and for ecosystem C storage (DeLuca et al. 2011).**

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Figure Captions

Fig. 1 Conceptual model describing the responses of understorey legumes and their associated microbes to global climate change. The increase in photosynthesis is expected to 1) lead to larger C inputs to the roots, enhancing microbial activity and consequently decomposition of litter and organic matter; and 2) increase the C:N ratio of the plants, hence enhancing N uptake and biological N fixation by the plants. The larger litter C:N ratio may in turn decrease litter decomposition rates and subsequent nutrient releases. The C sequestration by forest soils is directly linked with the soil organic matter decomposition rates.

Fig. 2 Conceptual model describing the responses of understorey legumes and their associated microbes to fire. Fire is expected to 1) generate a C and N loss by volatilization; 2) lead to changes in the species composition of legumes and associated symbionts, either directly or by altering soil nutrient availability; and 3) decreasing soil available N by N mineralization, which could enhance N₂ fixation and increase N inputs to the soil.

Fig. 3 A prescribed burning fire conducted on 11 August 2011 in a sub-urban forest of Brisbane, Australia.