Abstract: We propose a model of "premature tree decline whereby an absence of fire hastens the mortality of overstorey eucalypts in some forests. This model is relevant to some temperate Australian forests in which fire regimes have shifted from relatively frequent before European settlement to infrequent following settlement. The increased development of midstorey vegetation and litter accumulation has occurred since European settlement in some specific examples of Australian forests and woodlands. Our model proposes that in the long absence of fire: 1. midstorey vegetation reduces the availability of soil water for eucalypts and; 2. Eucalypts have less access to P and/or cations as these elements become locked up in soil, litter and midstorey biomass. We highlight important knowledge gaps and argue that research into ecological burning, for eucalypt health and other values such as biodiversity, is urgently required.

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Premature decline of *Eucalyptus* and altered ecosystem processes in the absence of fire in some Australian forests

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Abstract

We propose a model of 'premature tree decline' whereby an absence of fire hastens the mortality of overstorey eucalypts in some forests. This model is relevant to some temperate Australian forests in which fire regimes have shifted from relatively frequent before European settlement to infrequent following settlement. The increased development of midstorey vegetation and litter accumulation has occurred since European settlement in some specific examples of Asutralian forests and woodlands. Our model proposes that in the long absence of fire: 1. midstorey vegetation reduces the availability of soil water for eucalypts and; 2. Eucalypts have less access to P and/or cations as these elements become locked up in soil, litter and midstorey biomass. We highlight important knowledge gaps and argue that research into ecological burning, for eucalypt health and other values such as biodiversity, is urgently required.

Introduction

Aboriginal people used fire extensively and modified the pattern and structure of vegetation in Australia to improve access, to attract herbivores to 'green-pick', and to increase the abundance of food plants (Bowman 1998). It is generally accepted that the frequency of fire has decreased, and the intensity and scale of fire has increased since European settlement of some Australian temperate forests (Bowman 1998). Jackson (1968) developed the 'ecological drift' theory to describe how patterns of vegetation in western Tasmania are determined by fire interval, such that in a uniform landscape, low fire frequency is associated with the presence of rain forest, intermediate fire frequency is associated with eucalypt forest and high fire frequency is associated with button grass plain. A shift in mean fire frequency induces shifts (ecological drift) in vegetation composition and structure, and in soil physical and nutritional characteristics (Jackson 1968). In Jackson's model (1968) the ecological drift away from eucalypts involved the death of trees by intense fire or old age, but not through premature decline and mortality. However, eucalypts can be replaced prematurely (in terms of their potential life-span) by rainforest species that can regenerate in the absence of fire in wet, temperate forests (Ellis 1985, Werkman et al. 2008) and by *Allocasuarina* species in dry, temperate forests (Withers et al. 1978, Lunt 1998) in association with ecological drift in midstorey composition. These changes in the composition of midstorey vegetation have important implications for many forest values including biodiversity conservation, timber production, recreation, fire and water catchment management.

There is increasing evidence of premature decline of overstorey *Eucalyptus* in localised areas across a diverse range of forest types in temperate Australia (Archibald et al. 2005, Ellis 1971, 1985, Kirkpatrick 1986, Lunt 1998, Withers et al. 1978, Werkman et al. 2008). The forests in decline are not pathogen or pest affected, are not within agricultural landscapes, and have been subjected to changed fire regimes since European settlement. Below-average rainfall has prevailed across much of temperate Australia over the past three decades. However, the presence of declining forest adjacent to healthy forest (i.e., within identical soil and climatic environments), where the only difference is seemingly a management boundary (Davidson et al. 2007), suggests that reduced rainfall is not the sole or even the primary cause of premature and localised decline. Although anecdotal reports from forest and fire management authorities, coupled with our own observations, indicate that overstorey eucalypt decline is widespread in some forest types across temperate Australia (e.g. Jurskis 2005), we currently lack quantitative information on the extent of decline and there is a clear need to investigate both the scale of the phenomenon and the ecological processes that underpin it. We emphasise that the research reported is site and species specific and that our model is thus applicable to only a sub-set of Australian ecosystems. For example some eucalypt species (*Eucalyptus regnans* in eastern temperate Australia and *E. diversicolor* in western temperate Australia) growing in relatively fertile soils and under high rainfall do not appear to exhibit premature decline with the development of a dense, shade adapted midstorey. We stress that in no way do we wish to infer that one vegetation type is qualitatively 'preferred' over another, but instead focus on the ecophysiological processes associated with premature decline of temperate overstorey eucalypts in Australia.

In this paper, we review the limited, but robust, published evidence for the change in forest structure in Australia associated with the suppression of fire in the recent past,

and we highlight some ecological parallels and divergences between Australian eucalypt and some North American forests (Abrams et al. 1992, 2003, Covington et al. 1997, Hart et al. 2005, Nowacki and Abrams 2008). We propose a model of the ecophysiological processes that underpin premature decline of temperate overstorey eucalypts in Australia in the long absence of fire (Figure 1), and describe the implications of these changes for forest, fire and biodiversity management.

Ecosystem processes and premature decline of eucalypts in the absence of fire

Our model of premature eucalypt decline predicts the impacts of an absence of fire on ecosystem processes to be: 1. the significant development of midstorey trees and shrubs and soil surface litter; 2. significantly increased leaf area (leading to increased inter-specific competition for soil water); 3. relatively cool and humid conditions at the soil surface (which affect mycorrhizal dynamics) and; 4. decreased availability of plant nutrients (Figure 1).

1. Vegetation structure
There is strong evidence from a range of different forest types that a shift from historically frequent, low intensity fire to fire exclusion or infrequent, high intensity fire has promoted development of fire intolerant, shade tolerant midstorey trees and shrubs, soil surface litter accumulation and the premature decline of fire tolerant, shade intolerant overstorey eucalypt species. Ellis (1985, Table 1) and Werkman et al. (2008, Figure 2, Figure 3) have quantified a general pattern of premature decline of *E. delegatensis* and *E. coccifera* forests in Tasmania in the absence of fire. Decline has progressively developed following the cessation of aboriginal burning 160 years earlier and is associated with the development of a rainforest midstorey, significant soil litter accumulation, and alteration in the rooting environment and microbial community (Werkman et al. 2008). Ellis et al. (1980) further demonstrated a reversal of premature decline in *E. delegatensis* through removal of the rainforest mid-storey. Similarly Withers and Ashton (1977) reported increased dominance of shade tolerant *Allocasuarina* species, the development of a thick soil litter layer and the decline of the overstorey *E. viminalis* and *E. ovata* in remnant eucalypt woodland that had not been burnt for at least 90 years in the central south coast of Victoria. Lunt (1998) re-sampled Withers and Ashton's (1977) plots after an additional 25 years in the absence of fire, and showed that the density of shade tolerant *Allocasuarina* species had increased further (Table 1) and that the fire tolerant eucalypts had continued to decline over the period. Seedlings planted in plots that had been experimentally burnt by Withers and Ashton (1977) had survived, indicating that recruitment was possible where the thick litter layer was eliminated. Kirkpatrick (1986) described a similar pattern of *Allocasuarina/Eucalyptus* dynamics in dry Tasmanian woodland in the absence of fire (Table 1) and related poor eucalypt health with high total tree basal area (Kirkpatrick et al 2007).

In Western Australia, Archibald et al. (2005) studied *Eucalyptus gomphocephala* woodland in which fire frequency had declined since the Yalgorup National Park was declared in 1968. Fire had been suppressed since 1976, and by 2004 the mid-canopy vegetation structure had shifted to a lower density of the post-fire seed regenerator *Banksia attenuata* and a higher density of the shade tolerant *Agonis flexuosa* (Figure 4) in parallel with significant canopy decline across all mature age classes of the overstorey dominant, *E. gomphocephala*.

There are parallels between Australian eucalypt forests and North American pine and oak forests in the way vegetation structure is altered when fire becomes less frequent. Prior to 1900 there was a long history of frequent, low intensity fire in mixed-conifer forests dominated by *Pinus ponderosa* (2-15 year intervals) and *Pinus jeffreyi* (14-18 years) (McBride and Jacobs 1980). After 1900, livestock grazing and logging occurred in mixed species *P. ponderosa* forests and fire management focussed on suppression. This led to a shift from a bunchgrass or shrub-dominated understorey to a dense, suppressed midstorey of mixed woody species. Mortality in the over-stocked midstorey contributed to a large and elevated fuel load that facilitated the development of crown fires. Crown fire and competition with the developed midstorey reduced survival of remaining dominant *Pinus ponderosa* and vegetation composition shifted to include less fire-resistant species (Covington et al. 1997). Change in vegetation structure also encouraged development of thick litter layers. While these serve to reduce diversity and abundance of understorey species (Covington et al. 1997) and can cause 'stagnation' in nutrient cycling processes due to microbial immobilisation in the high lignin 'pine needle' environment (Hart et al. 2005), they may also become 'inconspicuous' sources of high concentrations of mineral nitrogen (N) and phosphorus (P) in surface runoff waters (Miller et al. 2005).

In the eastern U. S., vast expanses of deciduous forests were dominated by oak species throughout much of the Holocene epoch (Abrams 2003). Low to moderate intensity understorey fires every 5-20 years were a critical ecological factor in the historical development and perpetuation of oak forests (Abrams 1992, 1998, 2003). Factors such as thick bark, resprouting ability and the requirement of high-light, ash-bed conditions for seed germination and successful establishment (all of which parallel the ecological attributes of *Eucalyptus* species) led to the stability of oak populations on sites of extreme edaphic or climatic conditions, or areas that were periodically burned (Abrams 1992). Nearly complete suppression of fire in forests in the eastern U.S. during the 20th century resulted in dramatic reductions in recruitment of the dominant upland oaks on all but the most xeric and nutrient poor sites. Mixed-mesophytic and later successional hardwood genera, such as *Acer, Betula, Fagus, Nyssa, Tsuga,* and *Prunus* have rapidly replaced the oaks (Abrams 1992, 1998, 2003). In the absence of fire, the increase in non-oak, less pyrogenic species is creating cooler and moister forest microenvironments and altering the rate of decomposition of the litter layer (Nowacki and Abrams 2008).

2. Tree water-availability

Work investigating the effects of vegetation changes resulting from varied fire regimes on water availability for overstorey eucalypts is scant. Using sapflow technology, Hunt and Beadle (1998) showed that *Eucalyptus nitens* plantations with an *Acacia* midstorey transpired 30% more water than adjacent plantations without an *Acacia* midstorey. Kirkpatrick and Marks (1985) inferred that relatively high drought tolerance of *Allocasuarina* enabled it to displace eucalypts in a woodland of southern Tasmania. They further observed that fire, in eliminating a component of inter-specific competition, prevented drought damage to mature eucalypts (Kirkpatrick and Marks 1985). Our recent findings (Close et al. unpubl. data, Pfautsch and Adams 2008) indicate similar increases in total water use, and thus a putative increase in competition, due to the developed midstorey in mature forests of *E. regnans* in Victoria, *E. delegatensis* in Tasmania and *E. gomphocephala* in WA.

A parallel process has been demonstrated in *P. ponderosa* forests of the North American. Significant mortality of overstorey *P. ponderosa* has been attributed to water stress induced by competition from midstorey vegetation that developed in the absence of fire in Yosemite National Park (Guarín and Taylor 2005). In contrast, mortality of overstorey *P. ponderosa* was rare in northern Californian forest where the prevailing climatic conditions are similar to those in Yosemite National Park, but where prescribed fire was frequently applied (Guarín and Taylor 2005). Sala et al. (2001) investigated transpiration in stands in which the fire intolerant/shade tolerant *Abies lasiocarpa* had encroached into the fire tolerant/shade intolerant *Pinus albicaulis* forest in the absence of fire. Transpiration of invaded stands was significantly increased due to increased leaf area index and leaf area to sapwood area ratios of 0.8 in *Abies lasiocarpa* relative to 0.3 in *Pinus albicaulis*. Further, Sala et al. (2005) reported that 8-9 years after being thinned, *P. ponderosa* had higher water potentials and stomatal conductances and consequently faster rates of photosynthesis at the end of the dry season than when not thinned.

3. Soil microclimate and microflora
Changes to vegetation structure have marked effects on soil microclimate. For example, significant development of a rainforest midstorey and litter accumulation in a declining *E. delegatensis* forest reduced average surface temperatures by 2 °C and maximum soil temperatures by up to 8 °C. Consequently, surface soils held considerably more water in summer relative to nearby, healthy *E. delegatensis* forest that was not in decline and did not carry significant midstorey development (Ellis 1971). Note that this surface soil moisture accumulation occurred immediately under the relatively thick litter layer and was not necessarily indicative of plant water availability within the greater soil profile that plant roots access. This process is paralleled in eastern North American oak forests where the increased dominance of late-successional tree species has coincided with increased stand density and a microenvironment that is more shaded, humid and cooler. This has been termed the "mesophication" process, and it renders oak forests less likely to carry fire (Nowacki and Abrams 2008).

Fire directly influences soil microbial communities by decreasing total organism biomass and selecting for heat-tolerant soil microbes. However, given the strong links between plant species or functional groups and soil microbial communities, Hart et al. (2005) argued where frequent fire has shaped the evolutionary history of North American forests, the effects of fire on soil microbial communities are mediated primarily by fire-induced changes in the vegetative community. Ellis and Pennington (1992) investigated the growth of *E. delegatensis* seedlings in soils from: (a) stands with healthy eucalypt that had been burnt four years previously, (b) secondary rainforest with dead and dying eucalypts, and (c) rainforest. Eucalypt seedlings grown in soil from healthy stands had vigorous root systems, with ubiquitous ectomycorrhizae. Seedlings grown in rainforest soils had localised ectomycorrhizae with occluded root tips. By contrast, seedlings grown in soil from stands with unhealthy eucalypts had sparse primary roots, with few short roots and few or no ectomycorrhizae (Ellis and Pennington 1992). Inoculation of soil from unhealthy stands with soil from healthy stands resulted in increased seedling growth and favourable associations with ectomycorrhizae.

Evidence that fire-driven changes to vegetation modify soil microbial communities includes the significantly increased rates of soil respiration and nutrient-mineralizing enzymatic activities under grass (the pre-European dominant canopy type) than under *Pinus ponderosa* canopies that dominate southwestern North American ponderosa pine forests in the absence of frequent fire (Boyle et al. 2005). Hart et al. (2005) calculated that net N released directly via fire under the historical frequent surface fire regime provided far less plant-available N than did net N mineralisation from soil organic matter during the fire-free interval. Hart et al. (2005) further hypothesised that the relative importance of fire-induced changes to vegetation structure compared to post-fire nutrient mineralisation increases as the mean fire return interval increases.

4. Tree nutrient-availability

N Cycling
Soil N accumulates (via N fixation and atmospheric deposition) in the absence of fire. In wet temperate Australian forests, N-fixing *Acacia* can replace the soil N lost (via volatilisation) during fires within 10-20 years (Adams and Attiwill 1991). Turner and Lambert (2005) suggested that regenerating forests undergo three stages of stand development and soil N dynamics:
1. Initially, N losses, due to tree uptake, are greater than inputs, leading to a net decline in soil N.
2. N uptake declines and inputs become greater than outputs. Soil N and carbon (C) accumulate. Mineral N increases while C:N decreases – burning regulates this process.
3. N accumulates in the soil and large increases in mineral N lead to N saturation. At this stage, stands lose nitrate through leaching that can be measured in soil and runoff water.

Jurskis and Turner's (2002) model of stand dynamics predicts that eucalypt decline in the absence of fire occurs because "…increased soil moisture and N status stresses the roots of established eucalypt trees". However, no data support this model in undisturbed native forests, although decline of *E. ovata* and *E. camphora* has been postulated as due to increases in available N from nearby land uses in an intensively managed agricultural landscape (Granger et al. 1994). In contrast our recent results (Close et al. unpubl. data) suggest that soil N accumulation in the absence of fire did not translate to increased N uptake by overstorey eucalypts in trials in Tasmania (*E. delegatensis*) and Western Australia (*E. gomphocephala*). The question of whether total soil N accumulation in the absence of fire translates to increased plant-available soil nitrogen and increased eucalypt uptake of N is a key issue that remains to be answered.

P Cycling
Generally P becomes increasingly limiting over time relative to N in the humus layer, and this is subsequently followed by reduced concentrations of P in litterfall (Wardle et al. 2004). O'Connell and Mendham (2004) concluded that regular fire was critical for cycling P and maintaining plant P uptake in the *E. marginata* forest of south-west Western Australia. Fire converts soil organic P, and P immobilized in vegetation and litter, into plant-available orthophosphate, leading to significantly increased plant-available P (Adams and Byrne 1989). More recently, in a review of nutrient cycling, Adams (2007) noted that "widening (of) N:P without fire is the cause of large or even

wholesale changes in diversity and productivity". Wittkuhn (2002) reported that 28-43 % of P locked up in plant biomass pre-fire was plant-available in ash following low intensity fire in a *E. marginata* forest. These studies, and other studies that report increased availability of P in soils after fire (e.g. Tomkins et al. 1991), confirm that the vital P-mineralizing role of fire is an essential part of the ecology of eucalypt forests. We recently found that in a forest of *E. delegatensis* in premature decline with a rainforest midstorey, and where fire had been absent for > 120 years, foliar P was almost three-fold less than in adjacent healthy *E. delegatensis* (Close et al. unpubl. data). The result implicates altered ectomycorrhizal relations.

Soil pH and Exchangable Cations
Soil pH is usually increased following fire as a result of the oxidation of organic acids and the release of alkaline cations (Ca, Mg, K and Mn) previously bound to organic matter. Significant increases in soil pH (in excess of one pH unit for high fuel load treatments) were found following fire in a *E. obliqua/E. rubida* forest in Victoria (Tomkins et al. 1991). Increased soil pH after fire serves also to maintain availability of plant nutrients. Wittkuhn (2002) reported that 18-50% of cations and 27-85% of micronutrients were returned from plant detritus to ash after low intensity fire in *E. marginata* forest of south-west Australia. Significantly increased concentrations of Ca, Mg, Cu, Zn, S and B in leaf bases has been related to mineralisation and increased availability of those nutrients in fine ash following fire (eg. Tomkins et al. 1991). Consistent with this we noted significantly reduced concentrations of foliar Cu in prematurely declining *E. gomphocephala* over significantly developed midstorey in the long absence of fire, relative to healthy *E. gomphocephala* that had little midstorey due to frequent (every 10 years) burns (Close et al. unpubl. data). Further, we found that *E. gomphocephala* seedlings planted immediately following a prescribed burn had significantly higher foliar Cu than seedlings planted at the same time in adjacent, unburnt *E. gomphocephala* woodland (Close et al. unpubl. data).

Conclusions

The main conclusions drawn from this review underpin our model of premature decline of temperate Australian overstorey eucalypts (Figure 1). These are: (1) low fire frequencies since European settlement have promoted the development of dense, shade-tolerant midstorey vegetation (ecological drift) and the decline of overstorey eucalypts in particular areas across a wide range of forest types in temperate Australia. Where this occurs, the developed midstorey vegetation (2) competes with overstorey eucalypts for soil water, and (3) alters soil microclimate conditions that deleteriously affect overstorey eucalypt-ectomycorrhizal interactions. Thus, (4) fire plays a crucial role in controlling tree nutrient-availability by increasing soil pH and the availability of P and cations.

We highlight four clear parallels between the decline of northern American forests and Australian eucalypt forests in response to the long absence of fire: (1) the increased development of midstorey vegetation, the decline of fire tolerant tree species and the dominance of shade tolerant species; (2) increased total stand water use and increased mortality due to drought of fire tolerant/shade intolerant overstorey trees; (3) altered soil microclimate and microbial dynamics and; (4) increased occurrence and risk of wildfire in xeric *P. ponderosa* systems but decreased

occurrence and risk of wildfire in mesic oak systems (mesophication; Nowacki and Abrams 2008) – the latter is clearly similar to the mesophication of wet eucalypt forests, such as temperate *E. delegatensis* forests (Werkman et al. 2008). The main divergence between ecological processes appears to be the effect of a decrease in fire frequency on plant-availability of P and cations that occurs in Australian but not in North American forest systems. We speculate that this is due to inherently younger and generally less weathered soils in North American relative to Australian forest systems.

Our integrated model of premature tree decline in the absence of fire (Figure 1) provides a valuable synthesis of current research on forest dynamics and ecosystem functions, and provides a framework to guide research on this issue. Further research is required to document the spatial extent of temperate eucalypt decline in Australian forests, and to relate the potential for decline to environmental parameters; for example, can forests susceptible to eucalypt decline in the absence of fire be readily identified, in a similar manner to Nowacki and Abrams' (2008) model of forests susceptible to mesophication in the eastern United States? Such research would greatly assist forest planning and management. From a mechanistic perspective, key areas of research include the ecophysiology of inter-species competition for water, and the effects of structural vegetation change on tree-ectomycorrhizal relations, soil and tree nutrition. Additionally, we recommend that further research is urgently required to develop ecological fire regimes that address a wide range of forest attributes and values, including ecosystem processes, fuel dynamics and biodiversity conservation.

We have shown that ecological drift (*sensu* Jackson 1968) of midstorey composition and structure, and consequent mesophication and changes to the soil physical and chemical environment, has occurred in response to European fire management since settlement in Australia. In some forest types this alters competitive relationships between the midstorey and overstorey, leading to crown decline and premature mortality of the dominant overstorey trees.

Acknowledgements

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Table 1. Examples of increased density of fire intolerant species and decreased density of eucalypt species in the absence of fire in temperate Australia. All are based on individual stem density plot data except that of Ellis (1985), which is based on inference using dead stems to indicate past *E. delegatensis* forest.

Absence of fire (years)	Fire intolerant species	% change	Fire tolerant species	% change	Reference
160	*Nothofagus cunninghamii*	+77	*Eucalyptus delegatensis*	-73.5	Ellis (1985)
Urban remnant bushland 1-2 low intensity burns between 1975-1985	*Allocasuarina verticillata*	+257	*Eucalyptus viminalis*	-10	Kirkpatrick (1986)
115 (changes from 1975 to 2000)	*Allocasuarina verticillata*	+266	*Eucalyptus ovata*	-59	Lunt (1998)
	Allocasuarina littoralis	+633			

Figure 1. A model of premature decline of temperate overstorey eucalypts in temperate Australian eucalypt forests. 1. A long absence of fire (this timeframe varies between forest types, e.g. *ca*. 30 years in coastal *Eucalyptus gomphocephala* in the Mediterranean climate of south west Western Australia to 150 years in cool, wet, high altitude *Eucalyptus delegatensis* forests of Tasmania) leads to the development of dense midstorey vegetation. 2. The developed midstorey competes for soil available water with the overstorey eucalypts. Competition for soil water, coupled with periodic drought, causes water stress, leaf abscission, altered canopy structure, altered plant carbon balance and increased epicormic shoot development in overstorey eucalypts. 3. The absence of fire leads to a build up of soil surface litter that moderates soil surface temperatures leading to wetter, cooler soil surface conditions (mesophication; Nowacki and Abrams 2008) that may be less favourable to mycorrhizae of eucalypts that are particularly important for P acquisition. 4. Soil nitrogen accumulates via fixation and atmospheric deposition, and P, Zn, Mn, Fe and Mg become immobilised in soil surface litter (Hart et al. 2005). Overstorey eucalypts become deficient in P or soil-pH dependent micronutrients, limiting photosynthesis and causing leaf abscission that leads to further epicormic shoot development. The foliage of epicormic shoots is more susceptible to herbivory (Landsberg et al. 1990) due to decreased lignin and increased digestive value of foliage. Greater occurrence of herbivory further reduces crown leaf area and contributes to decline.

Epicormic regeneration
•Soft foliage

Herbivory

Crown decline
•Depletion of carbon reserves in the shoot
•Less carbohydrate available for leaf re-growth and for mycorrhizae

Reduced crown photosynthesis
•Less carbon fixation and storage

Increased crown damage

Increased water stress
•Drought, leaf abscision and altered canopy structure

Shoot nutrient imbalance
•Decrease in P and/or pH-dependent nutrients (Zn, Mn, Fe, Mg)

2. Tree water availability
•Increased competition with understorey for water

4. Tree soil-nutrient availability
•Increase in nitrogen (fixation, atmospheric deposition, no volatilisation)
•Decrease in P, Zn, Mn, Fe, Mg (immobilized in litter)
*Canopy declines are observed where soils are of inherently low nutrient status

1. Absence of fire and changes in vegetation structure
•Increase in midstorey trees and shrubs
•Increase in soil surface litter development
•Elevated transpirational leaf area

3. Soil microclimate and microflora
•Increased surface soil moisture (from mulch-effect of litter)
•Decreased surface soil temperature (from shade)
•Altered mycorrhizal associations