The effects of frequent burning on nutrient cycling and insect herbivory: implications for forest health

FIONA J. CHRISTIE[1,2], ALAN YORK [1,2]

1 The School of Forest and Ecosystem Science, The University of Melbourne, Water St Creswick, VIC 3363, Australia.

2 Bushfire CRC, Level 5, 340 Albert Street, East Melbourne, VIC 3002, Australia.

Author for correspondence: Fiona J Christie[1]
Phone: (61-3) 5321 4301
Fax: (61-3) 5321 4277
E-mail: fjc@unimelb.edu.au

Abstract

Low intensity fires are used extensively in forest management around Australia despite there being known about the long-term effects of repeated burning on ecological functioning. Understanding the impacts of disturbance on ecological functioning are fundamental to predicting the long term effects of repeated fire events on forest systems. Invertebrate herbivory is one of the most important ecological processes affecting forest health and hypotheses of Plant Vigour and Plant Stress have examined the responses of invertebrate herbivores to changes in foliar nutrient content. Prescribed burning may affect plant foliar chemistry through changes in nutrient availability which can subsequently influence herbivore feeding patterns. We examined the effects of different fire regimes on forest health and addressed the following questions: 1) what is the effect of different fire regime on soil, leaf litter and foliar nutrients; and 2) what is the effect of different fire regimes on levels of invertebrate herbivory? Eighteen independent sites (0.5 ha) were studied representing three experimental fire regimes: fire exclusion (at least 45 years), frequently burnt (every 3 years), and fire exclusion followed by the recent introduction of frequent burning (2 fires in 6 years). Soil, leaf litter and canopy leaves (Eucalyptus pilularis) were collected from each site and analysed for nutrients. Canopy leaves were further assessed for levels of invertebrate herbivore damage. Results show a trend for reduced levels of nitrogen in frequently burnt sites in soil, leaf litter and canopy foliage. Despite this we found no effect of frequent burning on herbivore damage in canopy leaves suggesting that frequent burning has not significantly affected this component of forest health. Long term studies such as these provide important insights into the long term effects of frequent fire on nutrient cycling and ecosystem function and have implications for the development of strategies for the management of prescribed burning.

Introduction

Alterations in fire frequency can have significant effects on primary productivity and carbon and nitrogen cycling in terrestrial ecosystems (Tilman *et al*., 2000; Reich *et al.*, 2001). In the short term fire has been found to enhance nitrogen mineralization (Hobbs *et al.,* 1991) with losses of nitrogen through frequent burning ultimately leading to long-term decreases in nitrogen availability (Blair, 1997) and cycling (Dijkstra *et al*., 2006). Reduced carbon (C) and nitrogen (N) cycling with increased fire frequency have been linked to long term effects of fire on forest systems and Net Primary Productivity (NPP) (Ojima *et al*., 1994) with N in particular found to be a limiting factor for productivity (Dijkstra *et al*., 2006).

Fire effects such as these have implications for flow on effects to other components of ecosystem function and processes, in particular leaf herbivory. Invertebrate herbivory is one of the most important ecological processes affecting forest health (Lill & Marquis, 2001; Stone, 2001) and resource availability models (Coley *et. al*, 1985) and hypotheses of Plant Vigour (Price, 1991) and Plant Stress (White, 1984) have examined the responses of invertebrate herbivores to changes in foliar nutrient content. Insect herbivory is strongly correlated with foliar nutrients, in particular N (McCullough & Kulman, 1991; Ohmart & Edwards, 1991; Throop & Lerdau, 2004) and available N has been shown to be one of the most important factors in limiting the performance and survival of invertebrate herbivores (White, 1984; Peeters, 2002). Increases in survival and fecundity of phytophagous insects in stressed environments has also been attributed to N enrichment (Landsberg, 1990).

Frequent low intensity prescribed burning in particular may affect plant foliar chemistry and foliar nutritional suitability through changes in nutrient availability which can influence herbivore feeding patterns (Adams & Rieske, 2003). Furthermore, transitory increases in foliar N in tree seedlings observed directly following prescribed fire in some systems (Reich *et al.,* 1990) has been attributed to a post-fire increase in available soil nutrients.

Low intensity prescribed fire is used extensively in forest management around the globe with little known about the long-term effects of repeated burning on ecological functioning. In Australia, such fires are often used specifically to achieve both fuel reduction and ecological outcomes, in particular the maintenance and conservation of biodiversity and key ecological process. For land mangers balancing these issues provides significant challenges and requires an understanding of the interactions between fire, biodiversity and ecological processes. This research investigates how prescribed burning affects forest health through changes in nutrient cycling. We determined the effect of fire frequency on total C and N and insect herbivory in eighteen plots of coastal blackbutt (*Eucalyptus pilularis*) forest subject to three different frequencies of experimental low intensity prescribed burning. We had three main objectives; the first was to determine the effects of low intensity prescribed fires on canopy foliar nutrients of *E. pilularis*. The second was to assess the level and type (chewing or surface) of leaf damage by invertebrate herbivores. Thirdly we determine how fire affects forest health through altering foliar nutrients.

Methods

Study Site

Field sites were located in Lorne State Forest on the mid-north coast of New South Wales, Australia (Van Loon, 1970; York, 1999; York, 2000). The forest consists of even-aged coastal blackbutt, *Eucalyptus pilularis* forest, with an average canopy height of 30 metres. Dominant canopy species being *Eucalyptus pilularis* (48%) and *Corymbia gummifera* (31%), with the remainder comprising of *Syncarpia glomulifera, E. resinifera*, and *E. punctata*. Eighteen independent sites (0.5 ha) were studied representing three experimental fire regimes: fire exclusion (at least 45 years), frequently burnt (every 3 years), and fire exclusion followed by the recent introduction of frequent burning (2 fires in 6 years). For the purposes of this paper "forest health" will refer the type, level and extent of insect damage.

Canopy Sampling

Within each study plot ten canopy trees of *E. pilularis* were randomly chosen for canopy sampling to determine foliar nutrients and assess levels of leaf damage by insect herbivores. We used a high powered .308 Sako rifle to shoot branches from canopy trees. Two terminal branches were selected for removal on each tree giving a total of 360 branches (18 plots x 10 trees x 2 branches). Leaves from both branches of each tree were removed and combined in one plastic bag providing one sample per tree.

Damage Assessments

Fifty fully expanded leaves were randomly selected from each bag. Approximately ten leaves were placed adaxial side down on a flatbed scanner and scanned to produce a digital image. Leaf damage was categorized as either chewing damage or surface damage. Chewing damage was characterised by part of the lamina physically missing, such as holes within leaves or incomplete leaf margins. Surface damage was characterised as all damage that had not physically reduced the extent of the lamina, such as necrosis, mining, skeletonising, galls and fungal damage.

Leaf images were imported into image analysis software for damage assessments. Levels of leaf chewing and surface damage were estimated using the Total Proportion Damaged (TPD) method (Landsberg, 1989). Software features were used to obtain measures of actual leaf area (ALA) for each leaf. Potential leaf area (PLA) was determined by estimating where the leaf would have grown in the absence of herbivory. The missing area and measure of leaf-chewing damage was calculated as the difference between the PLA and the ALA.

Nutrient Analysis

Leaves from each tree were oven dried at 60°C for 72 hours and ground to a fine powder. Total Nitrogen (N%) and Total Carbon (C%) content of leaves was then determined by a Leco-combustion method, using a CHN 2000 Leco Analyser.

Statistical Analysis

One-way analysis of variance was used to test for differences in the levels of chewing or surface damage of leaves, combined damage (surface and chewing), ALA, C and N content. In these analyses data from the ten trees were averaged for each site resulting in six replicates for each of FB, LU and LUB experimental fire treatments. Tukey HSD (honestly significant difference) pairwise comparison tests were used to determine the source of any differences observed.

Results

We found evidence of chewing damage in almost three quarters (73.4 %) of all leaves. The frequency of damage was consistent across FB (73.5%), LUB (76.2%) and LU (70.1%) treatments with no differences detected ($F_{2,15} = 1.44$; $p = 0.268$).

Leaf damage caused by mining was greater across all treatments compared to chewing damage (Figure 1). Chewing damage did not differ between fire treatments ($F_{2,15} = 0.18$; $p = 0.841$), nor was there any differences in levels of surface damage ($F_{2,15} = 1.33$; $p = 0.295$) (Figure 1) or combined leaf damage ($F_{2,15} = 0.54$; $p = 0.593$).

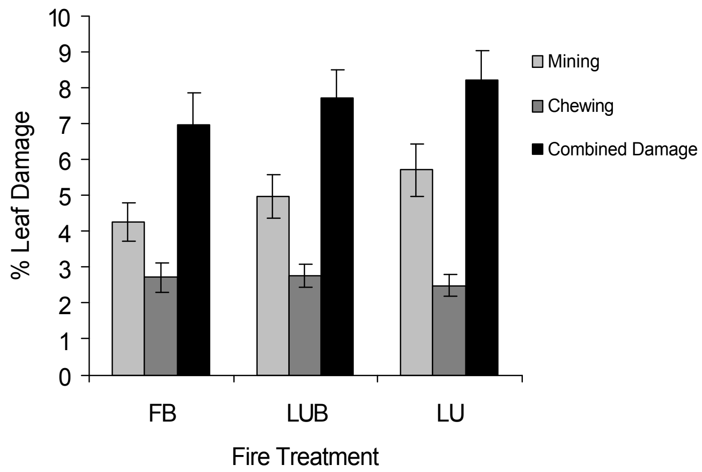

Figure 1: Percentage of leaves showing signs of mining and chewing and combined damage for each fire treatment. Error bars represent the standard error of the means.

Actual Leaf Area was not different between fire treatments ($F_{2,15} = 1.54$; $p = 0.247$) although there was a trend for larger leaves in FB sites (Figure 2). There were no significant differences between treatments for foliar carbon ($F_{2,15} = 1.29$; $p = 0.305$) or nitrogen ($F_{2,15} = 1.41$; $p = 0.274$).

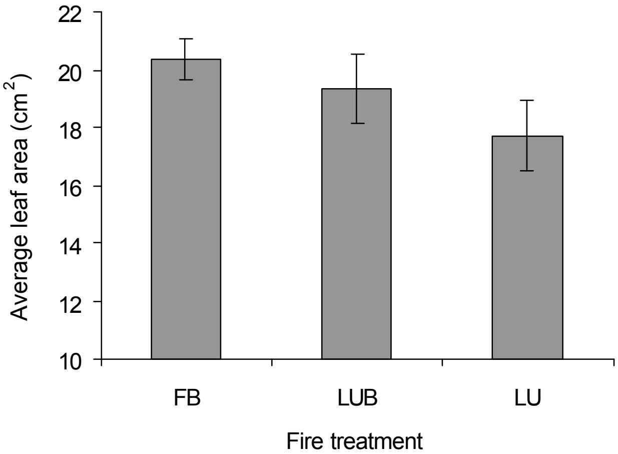

Figure 2: Average leaf area in cm^2 for each treatment. Error bars represent the standard error of the mean.

Discussion

We aimed to explore the long-term impacts of frequent (ten fires in 37 years) low intensity fires from a forest health perspective as measured by levels of insect damage and nutrient availability. Mature leaves of Eucalyptus pilularis on frequently burnt (FB) sites displayed only marginally lower levels of foliar nutrients (N and C) than those of long unburnt (LU) and long unburnt to burnt sites (LUB). Nitrogen is one of the potentially limiting factors to the performance and survival of invertebrate herbivores (White, 1984; Hanks & Denno, 1993; Peeters, 2002) and despite a corresponding trend for lower levels of overall damage in FB sites differences in herbivory were minor between fire treatments and the ecological significance questionable.

Overall the levels of leaf damage observed were far lower than demonstrated for Eucalyptus elsewhere in Australia (Burdon & Chilvers, 1974; Fox & Morrow, 1983; Landsberg *et al.,* 1983). Resource availability and plant anti-herbivore defence models suggest that plants growing in resource limited environments have lower levels of herbivory due to a greater investment in anti-herbivore defences. Research on other Eucalyptus species has supported these models (Close *et al*., 2005) and although we did not assess foliar chemical defences it is possible that trees in our study sites have increased allocation of plant secondary metabolites resulting in overall low levels of herbivore damage.

Fire has been found to impact soil, litter quality and nutrient cycling and ultimately determining host plant quality and suitability to potential herbivores (Rieske *et al.,* 2002). The soils of the forests in our plots are characteristically nutrient poor, with soils (Osborn, 2007) and leaf litter of FB sites having significantly lower levels on N compared to other fire treatments. Despite this, these differences were not reflected in either canopy foliar nutrients or herbivore damage.

Considering the nutrient depleting impacts of frequent fire coupled with naturally low resource (nutrient) availability we suggest FB plots in our study area are high stress environments. Mechanisms driving levels of herbivory are complex and it is difficult to identify one single factor as the primary force. We suggest that in this forest system several factors in combination, in particular nutrient limitation as a consequence of frequent fire may be influencing observed patterns and that sites display some resilience or resistance to disturbance events. This research was conducted on relatively small size plots and fires applied to them were at the low severity end of the prescribed burning spectrum. Using experimental evidence such as applied in this study to support hypotheses predicting how changes in nutrients and nutrient cycling may influence ecological processes and consequently affect ecosystem function and health will provide important insight for management initiatives and strengthen our understanding of complicated land systems. With projected changes in global climate change and predictions of increased fire frequencies, understanding the impacts of fire regimes is essential for global conservation.

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