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Review

Impact of defoliation in temperate eucalypt plantations: Physiological perspectives and management implications

Alieta Eyles[a,b,c,*], Karen M. Barry[a,b], Audrey Quentin[d], Elizabeth A. Pinkard[a,b,d]

[a] Cooperative Research Centre for Forestry, Private Bag 12, Hobart, Tasmania 7001, Australia
[b] Tasmanian Institute of Agriculture/School of Agricultural Science, University of Tasmania, Private Bag 98, Hobart, Tasmania 7001, Australia
[c] School of Plant Science, University of Tasmania, Private Bag 55, Hobart 7001, Australia
[d] CSIRO Ecosystems Sciences and CSIRO Sustainable Agriculture Flagship, Private Bag 12, Hobart, Tasmania 7001, Australia

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ABSTRACT

The loss of live foliage to browsing mammals, insects and foliar pathogens can reduce plantation productivity. It remains difficult to define damage thresholds that trigger lost productivity because tree responses to defoliation are influenced by abiotic stresses, such as nutrient or water limitation, as well as the frequency, severity, seasonality and pattern of defoliation by these biotic agents. This review provides a detailed synthesis of the key physiological mechanisms underpinning defoliation-related growth responses in temperate eucalypts. It illustrates how this understanding can assist in developing decision tools to quantify rotation-length pest impacts across a range of growing conditions and identifies management strategies that may promote recovery from defoliation and minimise impact. We examine host and pest interactions that influence growth responses, host defence mechanisms that reduce susceptibility, leaf-level and whole-tree physiological processes associated with recovery, and the interactive effects of defoliation and environment. We conclude by highlighting the knowledge gaps that need to be addressed to build capacity to predict and model the impacts of defoliation on productivity, especially under new environments associated with climate change.

Contents

* Corresponding author at: Tasmanian Institute of Agriculture/School of Agricultural Science, University of Tasmania, Private Bag 98, Hobart, Tasmania 7001, Australia. Tel.: +61 03 62262668; fax: +61 03 62267444.
E-mail address: aeyles@utas.edu.au (A. Eyles).

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1. Introduction

Pest activity in the form of periodic large-scale outbreaks can have substantial impacts on the ecology, carbon balance and productivity of natural and managed forests (Berg et al., 2006; Kurz et al., 2008; Brown et al., 2012). Forests can, for example, switch from being a carbon sink to a carbon source, both during and immediately after an outbreak (Kurz et al., 2008). The prediction that affected forests are likely to remain carbon sources for several years after an insect epidemic (Kurz et al., 2008) was recently questioned when the pine forests of northern America were found to show faster than expected recovery following extensive outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) (Brown et al., 2012); this was related to increased gross ecosystem photosynthesis, unchanging ecosystem respiration, and increased solar radiation transmissivity at the stand level. Further, increases in tree vigour were attributed to leaf-level increases in photosynthetic capacity of the surviving trees and vegetation. Greater carbon-fixing capacity of the remaining crown is just one of a range of compensatory mechanisms that enable defoliated trees to maintain similar rates of growth to undefoliated trees despite substantial reductions in leaf area (Pinkard, 2003, Pinkard et al., 2007; Eyles et al., 2009a, 2012; Quentin et al., 2010).

The genus *Eucalyptus* comprises over 700 species and includes some of the most widely planted hardwood crops worldwide. Approximately 35% of intensively managed eucalypt plantations are in the temperate and Mediterranean zones of Argentina, Australia, Chile, Portugal and Spain (Forrester et al., 2012). The temperate *Eucalyptus* species that are grown commercially and managed in plantations exhibit superior early growth, broad adaptability and multipurpose wood properties (Beadle et al., 2008). Average annual production of wood volume can reach 35 m^3 ha^{-1} $year^{-1}$ in temperate environments allowing them to be harvested in as little as 20 years for pulpwood (Whitehead and Beadle, 2004). While potential productivity is high, maximum rates are rarely achieved because of limitations due to drought, nutrient availability and biotic disturbances. Outbreaks of herbivorous insects or foliar pathogens are common in eucalypt plantations (Loch and Matsuki, 2010) and a recent review has described the main damaging pests of eucalypts including both native and introduced insect herbivores and pathogens (Paine et al., 2011). Current methods of pest management in plantations vary greatly depending on the pest type and resources available (Elek and Wardlaw, 2010). Management options may rely on host resistance (deployment of resistant genotypes), chemical control (application of broad-spectrum or targeted pesticides, pheromones, or poisons for browsing mammals), biological control (e.g. egg parasitoids for insect pests), cultural control (e.g. avoidance of sites with high pest risk, nutrient management, thinning of stands) or a combination of these strategies as part of an integrated pest management system (Stone, 1991; Elek and Wardlaw, 2010). In reality few of these practices are implemented because of economic and environmental constraints, and damage from defoliating pests is therefore a regular occurrence.

In this review, we explore how a deeper understanding of the underlying physiological processes determining tree responses to defoliation can provide a robust process-based framework upon which to identify damage thresholds and management strategies to reduce the impact of defoliation on eucalypt plantation productivity. The framework for the review is outlined in Fig. 1. Our review draws from the accumulated knowledge gained over two decades of defoliation studies in temperate Australia, and generalises the results of these studies to make them relevant to temperate eucalypt plantations more broadly. These studies primarily focused on the two most common temperate *Eucalyptus* species planted globally, *E. globulus* and *E. nitens*. Where necessary, we cite examples regardless of the causal agent of defoliation, whether that be by invertebrate or vertebrate herbivores (Jordan et al., 2002; Rapley et al., 2009) diseases (Pinkard and Mohammed, 2006), or by deliberate management (e.g. green pruning; Pinkard, 2003; Forrester et al., 2012).

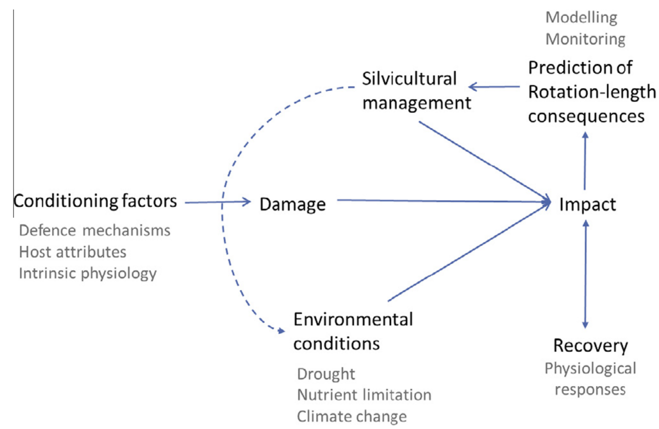

Fig. 1. Conceptual diagram of the factors influencing eucalypt responses to defoliation.

We firstly provide a summary of growth impacts in eucalypts, then discuss the host and pest characteristics that influence eucalypt growth responses (Section 2). We summarise the available information on host defence mechanisms in eucalypt–herbivore interactions (Section 3), followed by a discussion of physiological processes associated with recovery from defoliation (Section 4). In Section 5, the interactive effects of defoliation and environmental conditions are explored. Management strategies to promote recovery in *Eucalyptus* spp. following defoliation are analysed in Section 6, including the conditions under which these management strategies might be effective in reducing pest impacts. In Section 7, we highlight knowledge gaps that currently hinder our capacity to predict defoliation effects on productivity or develop management strategies to counter defoliation impacts.

2. Impact of defoliation on growth

2.1. Defoliation characteristics that influence growth outcomes

The severity of defoliation is typically negatively correlated to growth but the point where growth is reduced, and the length of