# Modelling the impact of defoliation and leaf damage on forest plantation function and production

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## ABSTRACT

After presenting a short review of process-based model requirements to capture the plant dynamic response to defoliation, this paper describes the development and testing of a model of crown damage and defoliation for *Eucalyptus*. A model that calculates light interception and photosynthetic production for canopies that vary spatially and temporally in leaf area and photosynthetic properties is linked to the forest growth model CABALA. The process of photosynthetic up-regulation following defoliation is modelled with a simple conditional switch that triggers up-regulation when foliar damage or removal causes the ratio of functional leaf area to living tissue in the tree to change.

We show that the model predicts satisfactorily when validated with trees of *Eucalyptus nitens* and *Eucalyptus globulus* from a range of sites of different ages, subject to different types of stress and different types of defoliation events ($R^2 = 0.96$ across a range of sites). However, the complexity of particular situations can cause the model to fail (e.g. very heavy defoliation events where branch death occurs).

It is concluded that while the model will not cope with all situations, an appropriate level of generality has been captured to represent many of the physiological processes and feedbacks that occur following defoliation or leaf damage. This makes the model useful for guiding management interventions following pest attack and allows the development of scenarios including climate change impact analyses and decision-making on the merits of post-defoliation fertilisation to expedite recovery.

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## 1. Introduction

Few attempts to model the impacts of leaf damage or defoliation on tree growth with process-based models have been published, though a rich history of empirical modelling has occurred (e.g. Candy et al., 1992; Erdle and MacLean, 1999; Dobbertin and Brang, 2001). At the leaf scale the process of infection and plant response is well understood (Ayres, 1981; Manter et al., 2003). How infection affects whole canopy production and tree performance in subsequent years is more problematic and less studied (but see Béasse et al., 2000; Bethenod et al., 2005; Le May et al., 2005). Some attempts have been made to model the impacts of the simpler intervention of green pruning on subsequent production (Nygren et al., 1996; Génard et al., 1998; Pinkard et al., 1999; Balandier et al., 2000). Kirschbaum et al. (2007) managed to simulate the effect of defoliation on net primary production using time variant discounts on production and respiration.

If we are to predict the impacts of given levels of leaf damage, or infection, on subsequent growth attention needs to be paid to particular physiological responses. Studies show that leaf necrosis, damage or loss result in variable gas exchange responses ranging from a reduction to an increase in leaf-level gas exchange and changes in respiration rates. Necrotic leaves are often retained for some time after damage and the effect of shading of residual healthy foliage, and the subsequent reduction in light interception, will affect subsequent canopy production. Defoliation can affect different portions of the crown, affecting canopy zones with differing contribution to overall photosynthetic production. Following defoliation trees change patterns of biomass allocation and remobilise nutrient and carbohydrate reserves from storage pools with influence on the pattern, rate and timing of re-foliation and photosynthetic recovery.

Collectively, these considerations indicate the complexity associated with scaling from leaf to crown in heterogeneous canopies. In these situations, 'big-leaf' models, that assume canopy heterogeneity can be ignored and that leaves in a stand can be treated in aggregate as a single, continuous leaf, are inappropriate. Similarly, the complexity of whole-tree regulation suggests that models that use fixed patterns of biomass allocations, or

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allometric relationships, alone to determine allocation to tree biomass pools may struggle to simulate the totality of defoliation response.

Few process-based models routinely used for forest management are suitable for exploring the combined effect of defoliation responses. Models are always designed with an end-use in mind, and as such, their unsuitability to a particular application should not reflect poorly on the intended model use. Array models such as MAESTRA (Wang and Jarvis, 1990) are well suited to calculating the effect on light interception and net canopy production. However, unless linked to allocation and growth models, they are not useful for asking forest management, risk analysis and impact questions (though many good examples of such links exist). More easily applied process-based forest management models such as 3PG (Landsberg and Waring, 1997) lack the links and flexibility within the sub-modules of allocation, light interception or nutrition to deal with discontinuous canopies and altered tree physiology that occur following defoliation. SimWal (Balandier et al., 2000) requires detailed branch and root architectural information, which though powerful is difficult to apply without sophisticated tree scanning. The carbon balance model of Génard et al. (1998) is a single season model and makes highly simplified assumptions such as fixed photosynthetic rates that are not suitable for forests growing through highly variable conditions of water stress, frost and marked seasonality in temperature. Recent modifications to CenW (Kirschbaum et al., 2007) are an exception, and success was achieved in modelling pest impacts on carbon flux. However, in that modelling exercise biomass partitioning responses and the rate of recovery from damage were user-defined inputs, rather than emergent from the model, and this limits the usefulness of the model in dynamic applications.

The process-based model CABALA (Battaglia et al., 2004) has many of the components at suitable scale and degree of generality necessary to model the impacts of loss of leaf area on forest production. Carbon, water and nitrogen cycles are linked so that simultaneous impacts of leaf area loss on biomass allocation, transpiration and water use and nitrogen reallocation can be assessed. While the model allows for different spacing arrangements, in its published form it makes assumptions of uniform leaf area density and a fixed attenuation pattern of photosynthetic capacity within the crown. This paper details modifications to CABALA to extend the light interception and photosynthetic sub-modules to allow the impacts of leaf area damage and loss to be assessed. It also describes the approach used to regrow leaf area in the crown. We test the model with a wide range of data sets in which trees have been defoliated or damaged by pests or where pest damage has been mimicked artificially.

The modified CABALA allows the assessment of rotation length impacts of defoliation to guide interventions such as spraying or post-defoliation fertilisation to mitigate the impacts of pest attacks. Similarly we hope that this tool will provide a process-based framework to assess effects of changes in pest frequency and severity of attack from climate change (e.g. Pinkard et al., 2010). In this work we give an example of how the model may be used to understand the complex interaction of site, silviculture and pest attack as a guide to intervention management. Empirical decision support tools have been produced and applied to manage pest attacks (e.g. budworm, Hennigar et al., 2007; Gray, 2008; gypsy moth, Ghent et al., 1996). Empirical models are ultimately based on the assumption that host–pest responses observed in the past are accurate indicators of future performance. Our intention with this work is to create a framework that, being based on the physiological interaction in trees at leaf scale, can simulate the interaction of the new conditions of climate, atmospheric $CO_2$ and pest attack that may occur in the future beyond historical precedent.

## 2. Methods

### 2.1. Assumptions in modelling

The CABALA model (Battaglia et al., 2004) is a daily time step model.[1] Photosynthetic production is calculated using the model of Sands (1995) with trees within a plantation initially treated as non-interacting crowns, that then merge within rows to form non-interacting hedgerows and finally after canopy closure are treated as a 'big-leaf'. Tree water-use is the minimum of water uptake, calculated through a relationship between fine-root length density and soil water content, and atmospheric demand calculated with the Penman–Monteith equation (after McNaughton and Jarvis, 1991). The Ball–Berry equation (Ball et al., 1987) is used to simultaneously constrain stomatal conductance for $CO_2$ and $H_2O$ effects. Respiration is calculated from tissue type, mass, temperature and nitrogen content. Allocation is the resultant of backward looking optimisation for above- and below-ground resource captured in the manner of Chen and Reynolds (1997) constrained by biomechanical constraints (West et al., 1989) and conservation of mass and nitrogen. Nitrogen mineralisation is calculated using the CERES-N model (Goodwin and Jones, 1991) with a simple uptake model based on soil nitrogen concentration and fine root mass.

To extend the CABALA model to the prediction of the effect of loss of leaf area on production and number of assumptions are made about processes and stand representation.

First it is assumed that a stand is composed of identical individual trees and that all trees in the stand are equally affected by defoliation, or decline in photosynthetic capacity. This assumption is necessary since CABALA models light interception and allocation for the 'typical' tree and aggregates to the stand level. This assumption may lead to errors where infection or damage varies markedly from tree to tree because of the non-linear response of canopy assimilation to light interception. In situations where damage changes gradationally, or is in discrete patches, it may be sensible to conduct separate simulations for particular levels of damage and spatially average the results.

When we calculate photosynthetic production the tree is broken up into radial and vertical crown zones. Following canopy closure the canopy is assumed to be composed of continuous vertical zones. Within each crown zone, leaf properties (leaf area distribution and extinction coefficient) are identical. In the implementation developed in this manuscript 2 radial and 3 vertical zones are used.

In simulations, damaged leaves are either removed by defoliation or else remain on the tree for their normal longevity with reduced photosynthetic capacity. The capacity of trees to produce new leaves is not reduced (no bud or branch loss). Leaves with reduced photosynthetic capacity (or dead leaves retained on the tree) will shade other leaves in the crown. Cohorts of live and dead leaves are held as state variables in each crown zone and used in radiation interception and transmission calculations. The assumption that only leaves are damaged means that if biotic, or abiotic, damage destroys or damages buds, or leads to branch death, then the model will over-predict production.

New leaf area is added to each leaf zone proportional to the volumetric enlargement of that zone – so that when trees are expanding laterally as well as vertically leaf area will be added to all outer leaf zones, but once closure within and between rows has taken place leaf area is only added to the top zones of trees. As new leaf area is added the proportion of damaged leaf area, or the leaf area of each radial and vertical zone, is adjusted for both the added leaf area and for branch extension and crown lift.

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