



Review and synthesis

The Tree Decline Recovery Seesaw; a conceptual model of the decline and recovery of drought stressed plantation trees



G. Whyte, K. Howard, G.E.St.J. Hardy, T.I. Burgess*

School of Veterinary and Life Sciences, Murdoch University, 6150, Australia

ARTICLE INFO

Article history:

Received 3 September 2015
 Received in revised form 18 March 2016
 Accepted 19 March 2016
 Available online 6 April 2016

Keywords:

Stressors
 Tree vigour
 Decline
 Recovery
 Mortality
 Plantation

ABSTRACT

Worldwide tree plantations face prolonged drought periods that are predicted to increase in duration and intensity under climate change scenarios. Trees stressed by drought are susceptible to secondary stressors including pests and pathogens. Depending on the timing and intensity of these stressors, their impact may be persistent or acute, with varied temporal and spatial responses by different hosts. There are complex processes involved in tree performance and mortality, and often it can be difficult to identify the leading cause of growth decline and death. However, it is important to recognise that often death can be a gradual process with periods of recovery. While previous models have focussed on the decline of the tree in response to stress, there has been little focus on the recovery from stress. Hence, the development here of the **Tree Decline Recovery Seesaw model**. This conceptual model is based on the premise that drought stressed trees may alternate between different stages of health through time, particularly those facing intermittent drought over extended periods. This approach takes into account that recovery periods allow for the tree to regain health, and potentially create new opportunities for pest and disease outbreaks. The *Tree Decline Recovery Seesaw* model provides researchers with the understanding of the complexity of drought/pest/pathogen interactions, allowing them to assess the order and severity of the stressors to determine the likely outcome. This paper provides a vital step towards the development of predictive tools for plantation managers. While our model has focussed on eucalypt plantation trees, there is potential to apply the model to other tree species and forms of plant stress.

Crown Copyright © 2016 Published by Elsevier B.V. All rights reserved.

Contents

1. Introduction	103
2. The Tree Decline Recovery Seesaw model	104
2.1. Plant Stress Hypothesis	106
2.2. Plant Vigour Hypothesis	106
2.3. Levels of host stress have differing effects on insect feeding guilds	106
2.3.1. Root pathogens	107
2.3.2. Leaf diseases	108
2.4. Cankers and fungal endophytes	108
2.5. Feedback Loop Mechanisms	109
2.6. The Pulsed Stress Hypothesis	110
3. Conclusion	110
Acknowledgements	110
References	111

* Corresponding author.

E-mail address: tburgess@murdoch.edu.au (T.I. Burgess).

1. Introduction

There are complex processes involved in tree performance and mortality, and often it can be difficult to identify the leading cause of growth decline and death (Amoroso et al., 2012). Trees face a diverse range of abiotic and biotic stressors, and based on the order, timing and intensity of these stressors, their impact may be persistent or acute, with varied temporal and spatial expression (Mitchell et al., 2013a). Often death can be a gradual process (Waring, 1987). Response to stress, and subsequent recovery, reflects the history of stressors on growth (Bansal et al., 2013), which may influence the severity of future stressors on survivorship (Niinemets, 2010). However, while the effect of an individual stressor can be predicted, it is very difficult to extrapolate the interactive and the potential additive impact of multiple stressors, which may occur sequentially or simultaneously (Niinemets, 2010). Bansal et al. (2013) examined the role of independent stressors and the combined impact of drought and herbivory, and demonstrated that the impacts of multiple stressors can be antagonistic so are not always equal to the sum of the impacts of the

individual stressors. They showed the influence of multiple stressors was dependent on the stress intensity of one or both of the stressors, for example, the combined impacts of drought and herbivory at moderate intensity reduced radial growth in *Pinus* to a larger extent than when either of these stressors affected the host independently (Bansal et al., 2013). Furthermore, acclimation to previous stress can alter plant response to subsequent stressors, for example heat stress tolerance can be enhanced after trees suffer drought stress, or drought stress tolerance can be increased after mild drought if there is sufficient recovery time to enhance root growth, however multifactor tolerance to environmental factors is rare in trees (Niinemets, 2010).

Several conceptual models have been developed to elucidate reasons for tree death. However, the lack of knowledge of tree decline limits the ability of models to predict tree mortality events. The decline spiral model, a multi-factor sequential decline model, divided the interactions into predisposing, inciting and contributing factors (Manion, 1991). Manion's model only considers the “negative influences that predispose, contribute to or incite tree death” and does not account for environmental change (Wang

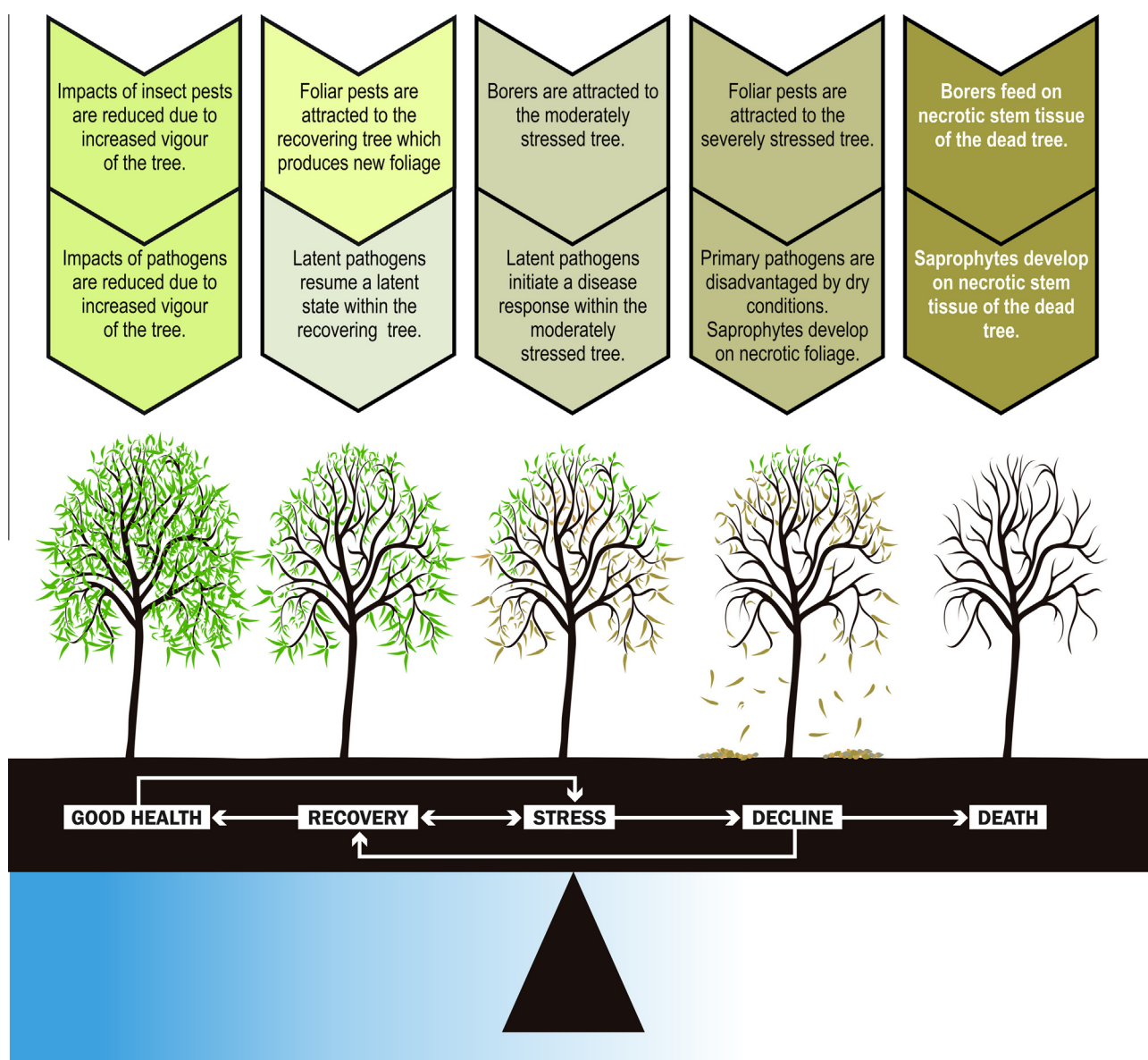


Fig. 1. The Tree Decline Recovery Seesaw model showing a drought stressed tree which may shift between different stages of health, where physical changes occur such as leaf regrowth (recovery), stress or leaf loss (decline), which determines the types of insect pests and pathogens that may exploit the tree.

et al., 2012). Wang et al. (2012) extended Manion's framework to include positive influences from climate change and proposes that drought may play a contributing role but not an inciting role in tree death. However, the spiral models suggest that decline is a continuous process, and does not account for recovery. In order to take a more holistic approach and investigate the decline/recovery aspect of plantation trees a conceptual model; the *Tree Decline Recovery Seesaw* was developed (Fig. 1).

2. The Tree Decline Recovery Seesaw model

The *Tree Decline Recovery Seesaw* model predicts how plantation trees respond to pests and pathogens at various stages of health during periods of drought stress. This model allows for the positive and negative impacts of climate, as well as recovery after damaging events. This model has been developed using both existing knowledge of pests and pathogens from published research and independent observations made during field surveys in eucalypt plantations in southern Queensland after a decade of drought came to an end (Whyte et al., 2011; Whyte, 2012). Eucalypts are the focus of this study, as it is believed that the genus has a narrow safety margin to climatic extremes in comparison to other groups such as gymnosperms (Choat et al., 2012; Mitchell et al., 2013b).

Eucalypt Plantations

The global area of tree plantations has expanded by almost 50% in the last 20 years (Kroger, 2012) to an estimated 109 M ha of productive tree plantations (Farley and Bremer, 2010). It is predicted that the total area of industrial forest plantations in the world will almost double in the next 40 years (Barua et al., 2014). Eucalypts are the most widely planted hardwood species, and plantations have been established in more than 90 countries (Booth, 2013) on more than 20 M ha (FAO, 2013; GIT Forestry Consulting, 2014). Eucalypts are mostly endemic to Australia, and grown for fuel wood, poles, timber, biomass and essential oil. India (22%), Brazil (20%) and China (14%) contain more than half of the world's Eucalypt plantations (GIT Forestry Consulting, 2014). Of the 894 taxa of *Eucalyptus*, nine species, and their hybrids, account for >95% of plantation eucalypts; *E. globulus*, *E. grandis*, *E. urophylla*, *E. saligna*, *E. pellita*, *E. nitens*, *E. dunnii*, *E. camaldulensis* and *E. tereticornis* (Harwood, 2011; Silva-Junior et al., 2015). Plantations are managed to optimise primary productivity by understanding, and potentially controlling, multiple abiotic and biotic stresses which may limit growth and quality (Barry and Pinkard, 2013). They are usually even aged monocultures of species selected for their fast growing properties and tree species are often planted far outside their natural range, leaving them vulnerable to stress.

Along with changing climate trends, where trees are exposed to gradual change, extreme events are increasing in frequency and magnitude and often result in an increase in mortality (Jentsch et al., 2007). The IPCC has identified an increase in the frequency and magnitude of droughts in many parts of the world linked to higher temperatures (IPCC, 2014). Drought, often in combination with other abiotic and biotic factors, has been implicated in many large-scale mortality events in forests over the past century (Allen et al., 2010). Exposure to drought makes trees more vulnerable to pathogens (Niinemets, 2010). Allen et al. (2010) provided evidence of 88 examples of forest mortality from 5 major regions of the

world that were driven by climatic drought/heat stress since 1970. Plantations are more susceptible than natural ecosystems, due to the planting regimes (site conditions, monocultures, even aged, stocking density and competition). Practices to increase yield can leave the trees with an increased drought risk due to progressive soil drying with increasing stand age and larger canopies (White, 2009; White et al., 2014). While eucalypt plantations are only considered moderately vulnerable to changing climatic conditions due to short rotation times (Booth, 2013), it is the extreme events, and the unpredictability of the system (Bale et al., 2002) that can tip the balance. The plantations grown in the tropical areas, are reporting more frequent droughts. It is expected that there will be increases in variability of water availability (Bale et al., 2002). In the drier regions of Brazil, where drought occurs, plantations face problems from introduced pests (psyllid *Glycaspis*, bronze bug *Thaumastocoris* and gall wasp *Leptocybe*) which are now widely spread through Brazil (Gonçalves et al., 2013). China also has serious forest pest problems (Ji et al., 2011) and suffered severe and extensive droughts in 2006, 2009 and 2010–2011 (Wang et al., 2014) in the southwest where there are large eucalypt plantations. However, there are no reports on plantation losses, as yet. There are extended droughts forecast for southern China before 2020 (Zhou and Xiao, 2014) with increasing drying in the southeast (Wang et al., 2014). Australia contains around 5% of the total eucalypt plantations (GIT Forestry Consulting, 2014) and extended droughts are affecting these plantations. The plantations in southwest Western Australia face prospects of increased drying and extreme weather events, as do other Mediterranean regions (IPCC, 2007), but this region has already seen a long term decrease in rainfall and increased warming (Bates et al., 2008) resulting in an unparalleled forest collapse (Matusick et al., 2013). For the plantations on the east coast of Australia the decline in rainfall associated with El Niño is not linear and this region has recently suffered near record droughts (Wang and Hendon, 2007).

A conceptual model of drought induced tree mortality was introduced by Wang et al. (2012). In response to drought, adaptations in biochemistry, morphology and physiology occurs affecting plant tolerance, often in a complex way (Massad and Dyer, 2010). Prolonged, severe stress can strongly inhibit growth (Niinemets, 2010). Without entering into the current debate on the exact physiological cause of drought induced mortality, briefly, drought events can trigger several effects on trees leading to defoliation and the impact of drought on mortality also depends on the length and intensity of the drought. In the short-term (days) or during moderate levels of drought, the tree's water use is controlled by the reduction of stomatal conductance. In the medium term (weeks or months), a reduction of leaf area occurs and there is an alteration of biomass allocation, shifting towards higher root to shoot ratios (Medlyn et al., 2011). During the longer-term (months or years) or during high levels of drought intensity, xylem embolism occurs, leaf shedding takes place and finally death occurs (Medlyn et al., 2011; Choat et al., 2012; McDowell et al., 2013). However, during drought conditions stomatal conductance slows but does not stop the decline of xylem pressure and hydraulic capacity, so if soil water is replenished before complete hydraulic failure occurs then the tree may recover (Choat et al., 2012). The physiological response to waterlogging is considered to be similar to that induced by drought (Bradford and Hsiao, 1982). The response of the tree to stress is driven by stress length, severity and history, tree reserves and exposure to multiple stresses (Niinemets, 2010). The transient effect of drought stress on surviving trees will have long-term consequences for productivity especially in situations where this matters economically as in industrial plantation estates.

Drought tolerance of species of eucalypts has been attributed to a variety of genotypic and phenotypic responses (Poot and Veneklaas, 2013). Species with a root system composed mainly of surface lateral roots are often more susceptible to drought stress than species with deep tap roots. *Eucalyptus camaldulensis*, for example, has good drought resistance due to the development of an extensive and deep root system (Hulme, 2008). Foliar characteristics can also influence drought resistance. *E. globulus* is more susceptible to drought stress than *E. nitens* because the stomatal conductance of *E. globulus* foliage is slower to respond to drought stress (White, 1996) and this species has a high leaf area to sapwood ratio (White et al., 1998). Although many eucalypt species are adapted to survive in dry arid regions, most species used for plantations are native to high rainfall areas (Weston et al., 1991; Madeira et al., 2002). Fast-growing eucalypts have extravagant water-use strategies, which predispose them to rapid hydraulic failure (Mitchell et al., 2013b). In drought conditions, their overall non-structural carbohydrates remain unchanged at mortality, in contrast to the slower growing *Pinus* with its very conservative water-use strategies, which have significantly depleted reserves at mortality (O'Grady et al., 2013; Mitchell et al., 2013b). While droughts may have a short duration, the effects can be long lasting, manifesting for years.

The conceptual *Tree Decline Recovery Seesaw* model is based on the premise that drought stressed trees may alternate between different stages of health through time. Environmental influence (i.e. water availability or drought) will determine which direction the seesaw is likely to tip. As the stressed tree moves between various stages of health, physical changes occur such as leaf regrowth (recovery), leaf necrosis/stress or leaf loss (decline), which determines the types of pests and pathogens that may exploit the tree (Fig. 1). To demonstrate the opposing outcomes in eucalypt plantations of tree decline and recovery and the associated pests and pathogens after initial drought stress (indicated by S) we refer to stages of decline (*D* and *D*⁺) and stages of recovery (*R* and *R*⁺) as illustrated in Fig. 2.

Of the many reviews that examine the influence of drought stress on tree hosts and their associated insect pests (Mattson and Haack, 1987; Larsson, 1989; Koricheva et al., 1998; Huberty and Denno, 2004; Lieutier, 2004; Jactel et al., 2012; Anderegg et al., 2015), most describe two opposing hypotheses; the *Plant Vigour Hypothesis* (PVH) and the *Plant Stress Hypothesis* (PSH). The *Plant Vigour Hypothesis* predicts that plants or plant components with greater vigour are more attractive to insect herbivores (Price, 1991), while the *Plant Stress Hypothesis* proposes that stressed plants are more susceptible to attack by insect herbivores than healthy plants because plant stress can result in increased nutrient availability to the pest and/or inhibits the production of anti-herbivore chemicals (White, 1969). These hypotheses were developed to describe the effects of drought stress on insect herbivores that fall into two groups: senescence or flush feeders (White, 2009).

The mechanisms of the *Tree Decline Recovery Seesaw* are consistent with hypotheses and explanations in the literature. Some of the more important inclusions of the model are as follows;

- 2.1. The mechanism of tree decline is consistent with the *Plant Stress Hypothesis*
- 2.2. The mechanism of tree recovery is consistent with the *Plant Vigour Hypothesis*
- 2.3. The model recognises that levels of host stress (moderate to severe) have differing effects on insect feeding guilds (foliar pests and borers)
- 2.4. The model recognises that levels of host stress (moderate to severe) have differing effects on fungal guilds (latent pathogens, primary pathogens and saprophytic fungi)
- 2.5. Stressed trees may alternate between decline and recovery before eventually dying. This is consistent with the description of Feedback Loop Mechanisms.
- 2.6. Drought can occur intermittently – this is consistent with the description of the *Pulsed Stress Hypothesis*.

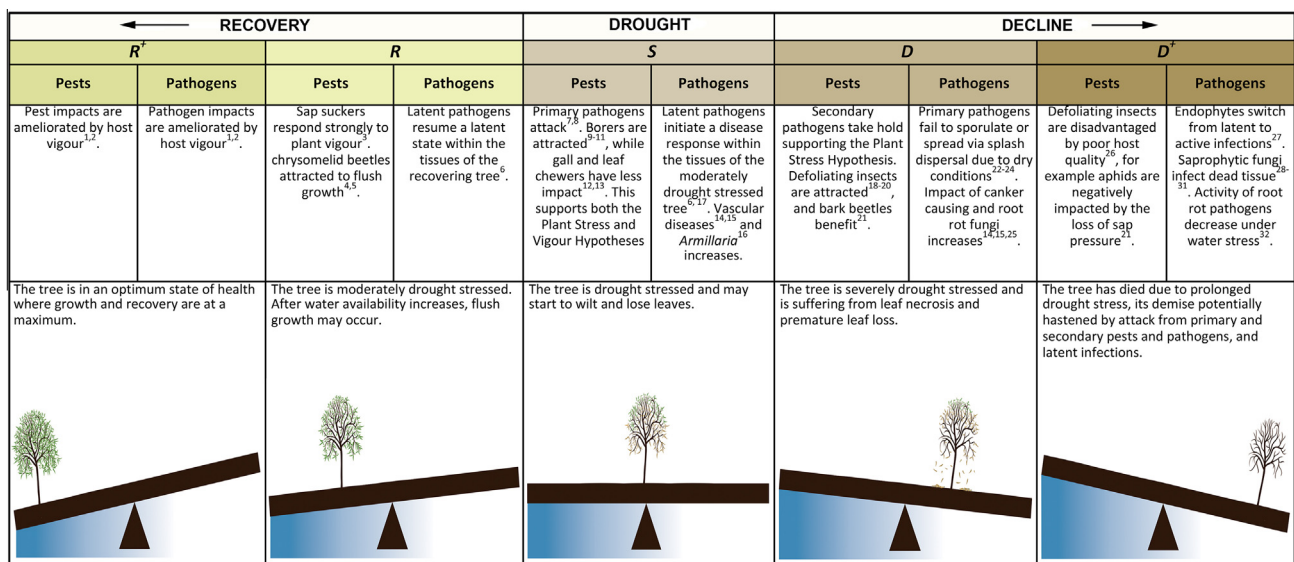


Fig. 2. The Tree Decline Recovery Seesaw illustrating the outcome of recovery and decline of a drought stressed tree in response to impacts by insect pests and diseases, and the influence of sufficient water availability. ¹ Benson and Hager, 1993; ² Stone, 2001; ³ Cornelissen et al., 2008; ⁴ Edwards, 1992; ⁵ Whyte et al., 2011; ⁶ Anselmi et al., 2007; ⁷ Stone and Bacon, 1994; ⁸ Landsberg, 1990; ⁹ Lieutier, 2002; ¹⁰ Wardlaw and Bashford, 2007; ¹¹ Jactel et al., 2012; ¹² Koricheva et al., 1998; ¹³ Huberty and Denno, 2004; ¹⁴ Schoeneweiss, 1981; ¹⁵ Brown and Hendrix, 1981; ¹⁶ Sturrock et al., 2011; ¹⁷ Carnegie, 2007; ¹⁸ White, 1969; ¹⁹ Mattson and Haack, 1987; ²⁰ Larsson and Björkman, 1993; ²¹ Netherer and Schopf, 2010; ²² Walklate et al., 1989; ²³ Wilks and Shen, 1991; ²⁴ Agrios, 2005; ²⁵ Ghini et al., 2011; ²⁶ Rouault et al., 2006; ²⁷ Sieber, 2007; ²⁸ Griffin, 1977; ²⁹ Rayner and Boddy, 1988; ³⁰ Bettucci and Alonso, 1997; ³¹ Bettucci et al., 1999; ³² Brouwers et al., 2013.

2.1. Plant Stress Hypothesis

The *Plant Stress Hypothesis* (PSH) was formulated on psyllid outbreaks on water-stressed eucalypts (White, 1969) as they accumulated higher nitrogen containing compounds that were available to insects (Huberty and Denno, 2004). The PSH predicts that stressed plants are more susceptible to attack by insect herbivores than healthy plants because plant stress can inhibit the production of anti-herbivore chemicals (White, 1969, 1984; Louda and Collinge, 1992; Koricheva et al., 1998). It is hypothesised that stressed plants may shift resources away from defence mechanisms to enhance survival (Gutbrodt et al., 2012) resulting in the plants presenting a higher quality resource to herbivores (Huberty and Denno, 2004; Cornelissen et al., 2008; Fig. 2R). Slow accumulation and low concentrations of phytoalexins, delayed formation of necrophylactic periderm, less effective compartmentalisation and callus development has been reported in drought stressed trees (Jactel et al., 2012). Stem borers (e.g. *Phorocantha*) may be attracted to drought stressed eucalypts (Wardlaw and Bashford, 2007) because of reduced concentrations of secondary defence compounds found in tree stems as a response to drought (Desprez-Loustau et al., 2006). Among eucalypt species the secondary metabolites vary quantitatively and qualitatively (Li et al., 1996; Nicolle et al., 1998; Steinbauer, 2010) and amongst provenances (Andrew et al., 2007). It is important to realise that the concentrations of plant secondary metabolites affected by water stress can be experiment, species and compound specific (McKiernan et al., 2014) and defensive chemicals have a range of effects on feeding insects (Taylor, 1997; Strauss and Agrawal, 1999; Sanson et al., 2001). Toxic compounds such as cyanide may act as a direct deterrent to insects, while other compounds such as tannins may bind to nutrients such as nitrogen and reduce their availability within plant tissues. However, few studies actually demonstrate a decrease of chemically mediated induced resistance in stressed plants (Gutbrodt et al., 2012).

2.2. Plant Vigour Hypothesis

Price (1991) hypothesised that more vigorously growing plants may have greater resources, higher food quality and a lack of defensive compounds. The *Plant Vigour Hypothesis* (PVH) was originally designed based on gall forming insects (Price, 1991) but has been extended to encompass other insect feeding guilds that attack leaves and stems (Cornelissen et al., 2008). Meta-analysis has shown there is a stronger preference by insect herbivores for more vigorous plants than stressed plants (Koricheva et al., 1998; Huberty and Denno, 2004; Cornelissen et al., 2008; Fig. 2R) however, there is not always a strong relationship between preference for vigorous growth and insect performance (Cornelissen et al., 2008). Insect pests often prefer the active growing parts of a plant to feed upon (Price, 1991), as they are flush feeders (White, 2009; Fig. 2R). Nitrogen availability is one of the most important factors in plant-insect associations (Stone and Bacon, 1995; Landsberg and Cork, 1997). Generally, nitrogenous primary metabolites decline in concentration as leaves age while plant secondary metabolites (potentially defensive) rise (Brunt et al., 2006), and flush growth often occurs in eucalypts after a drought breaks. A moth herbivore has shown attraction to the tallest trees, which have the most rapid growth (Cunningham and Floyd, 2005). Unfortunately, pests can be attracted to vigorous growth (Fig. 2R) resulting in high levels of herbivore damage which can result in a reduced yield and a decline in health (Fig. 2D).

Plant Stress Hypothesis vs the Plant Vigour Hypothesis – flush and senescence feeders

In the last decade, investigation into individual insect pest cases reveals that the interactions of drought-stressed plants and their herbivores are complex (Glynn et al., 2004; Gutbrodt et al., 2011). White (2009) points out the *Plant Stress* and *Plant Vigour Hypotheses* are not “two alternative, mutually exclusive hypotheses”. Fitting insect feeding guilds to either of these hypotheses in order to predict the interaction during drought (or other stressors) is difficult due to variable plant responses, the degree of specialisation of the insect pest, changes in insect feeding mode, the intensity of the drought (Gutbrodt et al., 2011), and the impact that predators may have on the pests.

Sap suckers are adversely affected by water stressed hosts, while chewers and leaf miners have inconsistent responses (Huberty and Denno, 2004), and sap suckers respond strongly to plant vigour (Cornelissen et al., 2008; Fig. 2R). These generalisations were expounded by White (2009) who indicates that sap suckers, leaf-chewers and -miners may be flush or senescence feeders, or may even switch from one feeding mode to the other within their life cycle. This is confirmed by Gutbrodt et al. (2011) who demonstrated that responses can vary significantly according to the pest's degree of specialisation. The generalist pests preferred drought stressed plants where there was a reduction in plant secondary defence compounds, while the specialist's preference was for well-watered plants. Therefore, the PSH may only explain outbreaks of senescence-feeders in response to changes in host physiology due to stress, while the PVH only refers to flush feeders (White, 2009).

In stressed eucalypts the ratio of juvenile to adult leaves (heteroblasty) is altered. Chrysomelid beetles prefer flush growth rather than tough adult leaves and may feed more intensively on stressed hosts which produce epicormic (juvenile) growth (Edwards, 1982; Edwards and Wanjura, 1990; Fig. 2R). In north-eastern Australia, *E. dunnii* have a rapid turnover of leaves due to seasonal dry conditions, with the flush foliage supporting the multivoltine Chrysomelids while the dry period prevents population build up (personal observations; Angel et al., 2008; Whyte et al., 2011). Stressed trees may be continually defoliated which leads to canopy dieback or even death (Landsberg, 1990a; Larsson and Ohmart, 1988; Fig. 2D, D*). These processes support the *Plant Stress Hypothesis*, however, some authors offer simpler explanations, such as that the impact of pests may only appear greater on stressed hosts due to reduced growth and recovery (Stone and Bacon, 1995). The high diversity of insects found on eucalypts in Australia, and high defoliation rates experienced by many eucalypt species, suggest either that the insects have gained an advantage over their hosts, or that an equilibrium has been established (personal observations; Edwards, 1982).

2.3. Levels of host stress have differing effects on insect feeding guilds

A recent meta-analysis confirmed that insect pests caused more damage on drought-stressed trees compared to control trees (Jactel et al., 2012). They revealed that, irrespective of drought severity, primary damaging pests or pathogens living on foliar organs caused significantly more damage to stressed trees than those living in woody organs. In contrast, damage caused by secondary

pests and pathogens on drought stressed trees increased with stress intensity. In cases of mild to severe drought stress primary agents result in decreased damage to foliage but increased damage to woody organs, while secondary agents only increase damage to woody organs under severe water stress (Jactel et al., 2012). However, in the case of sequential multiple stressors, the response of the plant will depend on which stress occurs first and the degree that the plant has acclimated to the first stress factor (Niinemets, 2010).

The effects of host stress on insects may vary depending on the type of association. Larsson (1989) suggests that sap-sucking species would benefit more from feeding on stressed hosts than defoliating species due to their more intimate association. For example, aphids generally have increased rates of reproduction on moderately drought stressed plants (Huberty and Denno, 2004; Fig. 2S, R). However, aphids were negatively affected on severely drought stressed hosts, in response to the availability of nitrogen decreasing due to loss of turgor (Netherer and Schopf, 2010; Fig. 2D*). It has also been shown that the effects of host stress may differ between borers and defoliators depending on the level of the stress. Moderate host stress may benefit borer species (Lieutier, 2002; Koricheva et al., 1998; Jactel et al., 2012; Fig. 2S), while defoliator species may benefit more from severe stress if it leads to increased available nitrogen in foliage (White, 1969, 1986; Mattson and Haack, 1987; Larsson, 1989; Larsson and Bjorkman, 1993; Fig. 2D). On hosts under moderate drought stress, gall makers and leaf chewers were negatively affected in their performance (Koricheva et al., 1998; Huberty and Denno, 2004; Fig. 2S). Scolytid bark beetles are likely to benefit from severely stressed hosts as host defences are reduced (Netherer and Schopf, 2010; Fig. 2D). Eventually, severe stress may disadvantage both borers and defoliators if it leads to poor host quality (Rouault et al., 2006; Fig. 2D*). Interestingly, it was considered that sap suckers were performing better on stressed trees (Koricheva et al., 1998) whereas the opposite was found by Huberty and Denno (2004).

It has been recognised that herbivore abundance can be affected by plant stress but this is dependent on the type of plant and

damage, herbivore feeding guild and species, stress intensity and duration (Larsson, 1989; Huberty and Denno, 2004; Cornelissen et al., 2008; Mody et al., 2009; White, 2009). A modification of the *Plant Stress Hypothesis* (insect performance hypothesis) predicts that there is a nonlinear relationship between herbivore performance and drought-stressed plants, which is maximised at medium stress levels (Larsson, 1989).

The duration and timing of stress influences host-root pathogen interactions (Desprez-Loustau et al., 2006) and will have differing effects on fungal guilds such as root, leaf or canker pathogens. Age and size (ontogeny) influences the resilience of the tree to fungal attacks (Fleischmann et al., 2009). However, the biggest influence on fungal disease is how temperature and moisture affect host susceptibility and also simultaneously influence pathogen growth, reproduction and infection. The direct effects of drought on tree pathogens are generally considered negative, as water availability is an important factor for pathogen development (Desprez-Loustau et al., 2006; Jactel et al., 2012). However, studies on the influence of stress on disease susceptibility often focus on disease development rather than the probability of infection (Walker and Stahmann, 1955; Cook and Papendick, 1972). Drought can significantly alter disease incidence and severity by causing changes to the distribution and phenology of events of infection (Sturrock et al., 2011). For instance, the flush growth that occurs after the drought breaks presents a greater proportion of young/juvenile foliage that can be largely unprotected from fungal attack (Fig. 2R). If environmental conditions provide humidity that results in wet foliage then leaf disease outbreaks can occur. Unfortunately, most work on tree pathogens reported in the literature is conducted in the greenhouse, and experiments conducted on mature trees are scarce (Desprez-Loustau et al., 2006).

2.3.1. Root pathogens

Root pathogens attack fine roots (e.g. *Phytophthora* spp.) and/or large roots (e.g. *Armillaria* and *Phytophthora* spp.) and directly

***Heteronyx* in *Eucalyptus globulus* plantation – an example of drought decline exacerbated by insect defoliation**

Moderate, but continued, drought stress east of Albany in Western Australia and leaf feeding by adult *Heteronyx* (Scarabaeidae) beetles have been attributed to the low productivity of *Eucalyptus globulus* plantations (Fig. 3). In some areas, the trees were severely defoliated and did not recover. Low yields have caused companies losses of \$400 million (The West Australian, 2012). Damaging defoliation by *Heteronyx* has also been noted in Northern Tasmania. These swarming, nocturnal scarab beetles can also affect young plantations as the larvae can feed on roots, particularly where old pasture land has been used.



Fig. 3. Low productivity in *Eucalyptus globulus* plantation caused by continued moderate drought stress combined with *Heteronyx* beetle defoliation. Image M. Matsuki, Integrated Pest Management Group.

interfere with the trees' water use. Trees can generally cope with fine root losses when there is adequate water, but when drought occurs these trees are substantially affected. While soil borne root and collar pathogens generally require soil moisture to move, sporulate and germinate near hosts, trees that are already infected are most at risk and increasing water stress results in increasing disease severity (Crombie and Tippet, 1990; Desprez-Loustau et al., 2006; Fig. 2D).

In Eucalypts, an increase in disease severity caused by root and vascular pathogens *Ceratocystis fimbriata*, *Cylindrocladium*, *Ralstonia solanacearum* and *Xanthomonas* species is expected with increased temperatures and stressed plants (Ghini et al., 2011; Fig. 2D). Although *Armillaria* spp. have not caused significant losses in plantations, this secondary pathogen can infect drought stressed trees as host stress increases susceptibility to the pathogen (Palzer, 1981; Wardlaw, 2006; Fig. 2D) and disease is predicted to increase during drought (Sturrock et al., 2011; Fig. 2S).

In contrast, root rot caused by *Phytophthora cinnamomi* is expected to decrease. In south-western Australia, where the climate has been drying for the last 30 years a reduction of *P. cinnamomi* activity has been noticed, however, there is a higher incidence of *P. cinnamomi* induced mortality with drought stress (Brouwers et al., 2013; Fig. 2D⁺). Trees infected with *P. cinnamomi* have a higher vulnerability to water deficits (Crombie and Tippet, 1990; Maurel et al., 2001), as these trees have almost no root regenerating capacity (Desprez-Loustau et al., 2006). However, lesions caused by *P. cinnamomi* were smaller in drought-affected eucalypts (Tippet et al., 1987) showing that water deficit within the tree can hamper this pathogen (Fig. 2D), but the infection compounds the stress the tree is under. So, while the root rotting pathogens might be directly negatively affected by drought, drought might exacerbate disease in trees that are already infected. If Eucalyptus plantations are established with species susceptible to *Phytophthora*, increased tree death could be expected during drought.

2.3.2. Leaf diseases

Foliar diseases in eucalypts are mainly caused by fungi and there have been instances where destructive epidemics have occurred in plantations in Australia, New Zealand, South Africa, Brazil and India where the humid conditions favour the pathogen (Park et al., 2000). It is envisaged that leaf diseases will decrease during drought (Fig. 2S,D), current infections can be exacerbated, but once the leaves are dropped new infections should not occur. For example, a primary pathogen *Puccinia* which causes rust leaf disease is one of the most significant eucalypt pathogens in South America (Tommerup et al., 2003) but disease incidence should decrease during periods of drought. The incidence of *Puccinia*, which is not normally associated with drought stressed trees, will have decreased opportunities to infect as it requires high humidity for germination and requires free water on the host surface spore germination. However, as one of the infection targets of this pathogen is juvenile leaves (Lana et al., 2012) flush foliage after drought may present opportunities for infection (Fig. 2R).

2.4. Cankers and fungal endophytes

Many pathogens that cause damage in stressed trees are endophytes in healthy trees (Manion, 1991; Linares et al., 2010). All forest trees host endophytic fungi, and some of these fungi have been evolving with their hosts for millions of years (Sieber, 2007). Endophytes infect healthy hosts in the absence of a disease response (Carroll and Carroll, 1978; Fisher and Petrini, 1992; Kendrick, 1992; Carroll, 1988; Arnold et al., 2000). Some endophytes are better described as 'latent pathogens' (Anselmi et al., 2007; Fig. 2R,S); they switch from latent phase to a pathogenic state when conditions are favourable for the endophyte and/or unfavourable for the host (Sieber, 2007; Fig. 2D⁺). Saprophytic fungi only infect dead tissue; however, some opportunistic saprophytes may cause disease in living tissue if the host is severely stressed (Griffin, 1977; Rayner and Boddy, 1988; Bettucci and Alonso, 1997; Bettucci et al., 1999; Fig. 2D⁺).

Teratosphaeria leaf blight – an example of the effect of drought on eucalypt plantation pathogens

Mycosphaerella spp. and *Teratosphaeria* spp. are considered important pathogens in eucalypt plantations (Park et al., 2000; Burgess et al., 2007; Carnegie, 2007; Barber et al., 2008; Hunter et al., 2011; Páez et al., 2014). Given their requirement for leaf wetness to infect, these diseases should decrease during drought (Fig. 2D) but may also present problems after drought if conditions are conducive. For example, during the extended drought in Queensland from 1995 to 2007, leaf diseases were minimal (Whyte et al., 2011). However, when the drought broke in 2008 there was a flush of new growth and this led to an epidemic of *Teratosphaeria* Leaf Disease (Andjic et al., 2010; Fig. 2R). As the disease increased annually, the trees had insufficient recovery time (Fig. 4), resulting in 25 000 ha of plantations unlikely to yield a commercial return (ABC Rural News, 2010).



Fig. 4. Typical symptoms of repeated defoliation caused by *Teratosphaeria* spp. Image T. Burgess.

High incidence and severity of cankers in eucalypts are associated with drought (Shearer et al., 1987; Whyte et al., 2011; Fig. 2D). More than 60% of 100 fungal pathogen-forest tree studies demonstrated an increase in disease due to drought, mostly due to cankers and vascular diseases (Desprez-Loustau et al., 2006; Fig. 2R) attributed to stress increasing host susceptibility to the pathogens (Sturrock et al., 2011).

It has been predicted that drought would reduce tree resilience and recovery from pathogen attack, predisposing trees to stem canker fungi (Old and Stone, 2005; Fig. 2D). Schoeneweiss (1981) and Brown and Hendrix (1981) showed that canker-causing fungi caused substantial damage to trees weakened by heat and drought stress, and predict that during drought stress these pathogens would be more likely to reach epidemic levels (Fig. 2S,D). *Chrysosporthe cubensis* is a canker pathogen of eucalypt plantations grown in high rainfall areas (van Heerden and Wingfield, 2002). By measuring cambial lesions on *Eucalyptus grandis* seedlings, Swart and Conradie (1992) demonstrated that the pathogenicity of *C. cubensis* was greater on healthy hosts rather than drought stressed hosts (Plant Vigour Hypothesis).

The most common canker-associated fungi are the Botryosphaeriaceae, which are considered weak, opportunistic pathogens that cause disease in stressed trees (Slippers and Wingfield, 2007; Fig. 2D), and include *Botryosphaeria*, *Neofusicoccum*, *Pseudofusicoccum* and *Lasiodiplodia* (Chen et al., 2011). Indirect effects of drought, through changes to host physiology, may be the predominant cause of occurrence of these diseases as the stressed hosts trigger the shift from latent to pathogenic stages. For example, species of Botryosphaeriaceae are not considered primary pathogens in eucalypt plantations in Australia but they can cause significant damage and low levels of mortality, particularly after drought (Carnegie, 2007; Slippers et al., 2009; Fig. 2S). Drought stress has been identified as the most common reason for *Botryosphaeria* disease expression in trees posing a significant threat to plantations, particularly in non-native areas (Sieber, 2007; Slippers and Wingfield, 2007).

2.5. Feedback Loop Mechanisms

Interaction between plants and herbivores can alternate between positive and negative feedback loops. For instance, the density of the pest may increase in a positive feedback cycle until damage exceeds the limits of the plant to compensate for tissue loss, and then a negative feedback loop may be initiated (Craig, 2010).

Due to the generalised responses of plants to damage, positive feedback loops (resource regulation) can be established to favour the defoliators of the current or future generations. This resource regulation cycle can be altered in times of drought. Damage caused by browsing pests can stimulate dormant buds resulting in vigorous juvenile growth, which may be a preferred food source (Craig, 2010; Fig. 2R). Defoliators manipulate the plants' source-sink relationships and can alter plant nutrition or defensive chemistry which may result in higher susceptibility to defoliation (Craig, 2010; Fig. 2D).

Long term herbivory altering plant architecture and the resultant sink-source change can decrease tree yield substantially. Resource regulation (Craig, 2010) occurs in some eucalypts where severe, repeated damage produces juvenile-form foliage which has higher levels of herbivory than adult foliage (Fox and Morrow, 1983; Steinbauer et al., 1998). Juvenile foliage on damaged trees can be more nutritious and poorly defended than unaffected trees (Landsberg, 1990a), thus, resulting in a positive feedback mechanism produced by repeated defoliation (Craig, 2010). Often trees that have been heavily defoliated produce larger quantities of flush growth when conditions are conducive, initiating a feedback loop of increasing susceptibility to defoliation (Landsberg, 1990a; Fig. 2R,D). While there may be no difference in consumption of foliage by insects between stressed and healthy plants, the impact of herbivory may be greater on stressed plants, because of their reduced growth (Stone and Bacon, 1995; Thomson et al., 2001). In frost damaged *E. globulus*, the abundance of insect herbivores on a tree was affected mainly by the number of new leaves and although severely damaged trees produced smaller and thinner

Canker pathogens in southern Queensland

The establishment of *Eucalyptus dunnii* plantations in southern Queensland coincided with the 'Millennium Drought' which lasted from 2001 to 2009 (van Dijk et al., 2013). Adequate water and occasional strong rain events promoted early growth, but at 2–4 years of age huge basal cankers were observed (Fig. 5). These cankers were very similar in appearance to those caused by *Chrysosporthe cubensis* and were of great concern because this pathogen was considered a serious biosecurity risk. However, while symptoms were the same, the organisms recovered were *Holocryphia eucalypti* and various *Neofusicoccum* species, which are well known endophytes and latent pathogens (Gryzenhout et al., 2009; Slippers et al., 2009). These observations demonstrated that trees alternated between periods of intense water stress, where they stopped growing and lost most of leaves, to flush growth where they grew very fast. In the drying phases, the bark cracked allowing the expression of usually benign endophytes and the formation of large basal cankers (Fig. 2D). After rain most cankers healed over and the trees continued to grow.



Fig. 5. Basal cankers seen in drought affected *Eucalyptus dunnii* plantations. Image T. Burgess.

leaves than healthier trees (Landsberg, 1990a,b,c), the total number of new leaves was not influenced by prior frost damage. However, superior growth rates of the larvae of the herbivores indicated that previously damaged trees provide tissues that are of higher nutritional value although they did not attract more insects (Thomson et al., 2001).

2.6. The Pulsed Stress Hypothesis

The *Pulsed Stress Hypothesis* proposed by Huberty and Denno (2004) addresses the occurrence of intermittent drought, which describes many natural situations. We found following drought stress all plantations of *E. dunnii* produced juvenile foliage which was also lost rapidly during further water stress (Whyte et al., 2011). The meta-analysis by Huberty and Denno (2004) demonstrated that phloem feeding insects had more impact on intermittently- than continuously-stressed plants. During intermittent drought stress there were large population increases, while densities remained low in comparison to controls in continually stressed plants. They propose that drought stress mediates nitrogen availability. Intermittent plant stress provides a more favourable food source for herbivore pests when nitrogen accumulates in the foliage during the previous drought period. This hypothesis predicts a better performance of phloem feeders on intermittently water-stressed plants where there is a recovery of turgor pressure compared with continuously stressed plants (Huberty and Denno, 2004). In the case of *E. dunnii*, multivoltine Chrysomelids were present most of the year, so flush occurrences resulted in increased damage by these defoliators (Whyte et al., 2011; Fig. 2R). Positive responses have also been demonstrated for leaf-chewing lepidopteran larvae by Mody et al. (2009), and Gutbrodt et al. (2011) showed that herbivores were able to distinguish differences between the degree of drought-induced stress in individual plants. Bauerfeind and Fischer (2013) suggest that the effects of drought are non-linear effects and that the level of stress determines whether the impact on the herbivore is positive or negative.

3. Conclusion

The *Tree Decline Recovery Seesaw* provides a unique approach to understanding the complex interactions of stressed trees and their associated pests and pathogens. Given that each stage of the model presents a unique set of conditions, the model allows the coexistence of opposing hypotheses such as the *Plant Vigour Hypothesis* and the *Plant Stress Hypothesis*. The staging of tree health can also be seen as a mechanism of niche partitioning, which is implicated as an important factor for the co-occurrence of species (Schoener, 1974).

While there are many reports of tree mortality in relation to drought and other stressors, most plant/pest models have overlooked the importance of recovery periods between stress events, and only the *Pulsed Stress Hypothesis* has considered the intermittent nature of moderate to severe droughts. The *Tree Decline Recovery Seesaw* model provides researchers with the understanding of the complexity of drought/pest/pathogen interactions, allowing them to assess the order and severity of the stressors to determine the likely outcome. For instance, a severe insect attack before a drought might be worse than drought followed by severe insect attack. This may help direct future research with the goal of producing predictive tools for plantation managers to use to maximise productivity.

Mathematical models and remote sensing are effective tools for predicting and assessing plantation productivity. However, further development of current models and the use different systems may be required in order to provide a powerful predictive tool for

plantation managers. We already have many of the necessary components to determine the status of the plantations, for example; models are routinely used to determine wood yield via basal area and height; repeated measures of stem diameter variations have been used to investigate response of trees to drought (Turcotte et al., 2009; Biondi and Rossi, 2014; Belien et al., 2014; Van der Maaten, 2013) and if coupled with biophysical modelling (e.g. soil water availability) the direct response to drought (amount of stress) can be determined (De Swaef et al., 2015). Meanwhile, LiDAR has been used to estimate reductions in canopy vigour with relation to climate and using environmental elements (solar radiation, elevation and location) as covariates (Van Gunst et al., 2016). Dynamic feedback models were developed by Guneralp and Gertner (2007) to incorporate feedback loops into Bossel's (1986) sudden death hypothesis models by utilising eigenvalue elasticity analysis to determine how the tree responds to various stressors, and thus incorporating Manion's (1991) gradual decline hypothesis. They investigated the physiological responses of a tree in the presence of varying degrees of stress under the assumptions of the two model frameworks. Pinkard et al. (2010) took this further by using CLIMEX to generate leaf disease severity and frequency scenarios over different seasons and sites, this data was then fed into the CABALA tree growth model with climate projections and varying nitrogen and water availability. Recent developments in remote sensing of drought show that the Atmospheric Infrared Sounder mission has the potential to improve early warnings of drought (AghaKouchak et al., 2015).

Future research to support this conceptual model should focus on quantifying the impact of drought, and pests and pathogen outbreaks on plantation productivity as there have been few experiments or data surveys that do this. By linking with entomological studies and models of pests and disease, the effects of drought and the subsequent recovery periods can help to predict outcomes and determine the appropriate actions to be taken. Anderegg et al. (2015) has reviewed the development of drought/insect interaction models in forest settings and provided a conceptual model. Further developments of spectral imaging, monitoring volatile compound emissions or the plant's non-structural carbon reserves to determine tree health during the effects of multiple consecutive and separate stresses (Niinemets, 2010) is needed. Furthermore, it is suggested that experiments and surveys are conducted in the field, rather than in the glasshouse, as drought tolerance and acclimation to stressors increases with age (Niinemets, 2010). Our observations indicate that older plantation trees can retain damaged foliage, so age must also be taken into account. Along with research to provide data on stress in plantations, there is a need for development of models and algorithms to combine multiple data sets (complex interactions) to test our conceptual model of tree decline and provide adaptive capacity for plantation managers. It is a complex task, but progress has been made.

There is potential to apply the *Tree Decline Recovery Seesaw* model to other forms of plant stress, such as that caused by nutrient deficiency, or other environmental parameters, and it could be adapted for use with other plantation tree species such as *Pinus radiata* and to other tree decline where drought stress plays an important role.

Acknowledgements

GW was a recipient of an Australian Postgraduate Award Industry (APAI) on an Australian Research Council funded project LP0349190, 'Fungal pathogens threatening the sub-tropical eucalypt plantation industry in Australia'. Figures 1 and 2 were produced by Jodi Burgess (<http://jajographics.com.au/>). The authors thank the two anonymous reviewers for their helpful comments and suggestions.

References

- ABC Rural News, 2010, May. Investors lose as fungus shuts down Elders forests. <<http://www.abc.net.au/site-archive/rural/news/content/201005/s2888836.htm>>.
- AghaKouchak, A., Farahmand, A., Melton, F.S., Teixeira, J.M., Anderson, C., Wardlow, B.D., Hain, C.R., 2015. Remote sensing of drought: progress, challenges and opportunities. *Rev. Geophys.* 53, 452–480. <http://dx.doi.org/10.1002/2014RG000456>.
- Agrios, G.N., 2005. *Plant Pathology*, fifth ed. Academic Press, New York.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684.
- Amoroso, M.M., Daniels, L.D., Larson, B.C., 2012. Temporal patterns of radial growth in declining *Austrocedrus chilensis* forests in Northern Patagonia: the use of tree-rings as an indicator of forest decline. *For. Ecol. Manage.* 265, 62–70.
- Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.A., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J.D., Stephenson, N.L., Tague, C., Zeppel, M., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol.* 208, 674–683.
- Andjic, V., Pegg, G.S., Carnegie, A.J., Callister, A., Hardy, G.E.S., Burgess, T.I., 2010. *Teratosphaeria pseudoecalypti*, new cryptic species responsible for leaf blight of *Eucalyptus* in subtropical and tropical Australia. *Plant. Pathol.* 59, 900–912.
- Andrew, R.L., Wallis, I.R., Harwood, C.E., Henson, M., Foley, W.J., 2007. Heritable variation in the foliar secondary metabolite sideroxylonal in *Eucalyptus* confers cross-resistance to herbivores. *Oecologia* 153, 891–901.
- Angel, P.J., Nichols, J.D., Stone, C., 2008. Biology of *Creiis liturae* Froggatt: (Hemiptera: Psyllidae), pest on *Eucalyptus dunnii* Maiden in plantations: morphology, life cycle and parasitism. *Aust. For.* 71, 311–316.
- Anselmi, N., Nasini, M., Mazzaglia, A., Librandi, A., Rocco, E., Ravaioli, F., 2007. Correlation between the occurrence of pathogenic fungal endophytes in healthy oak trees and oak decline. *J. Plant Pathol.* 89, S28.
- Arnold, A.E., Maynard, Z., Gilbert, G.S., 2000. Are tropical fungal endophytes hyperdiverse? *Ecol. Lett.* 3, 267–274.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S.E., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biol.* 8, 1–16.
- Bansal, S., Halliday, G., Löfvenius, M.O., Nilsson, M.-C., 2013. Synergistic, additive and antagonistic impacts of drought on herbivory on *Pinus sylvestris*: leaf, tissue and whole-plant responses and recovery. *Tree Physiol.* 33, 451–463.
- Barber, P.A., Carnegie, A.J., Burgess, T.I., Keane, P.J., 2008. Leaf diseases caused by *Mycosphaerella* species in *Eucalyptus globulus* plantations and nearby native forest in the Green Triangle Region of southern Australia. *Australas. Plant Pathol.* 37, 472–481.
- Barry, K.M., Pinkard, E.A., 2013. Growth and photosynthetic responses following defoliation and bud removal in eucalypts. *For. Ecol. Manage.* 293, 9–16.
- Barua, S.K., Lehtonen, P., Pahasalo, T., 2014. Plantation vision: potentials, challenges and policy options for global industrial forest plantation development. *Int. For. Rev.* 16, 117–127.
- Bates, B.C., Hope, P., Ryan, B., Smith, I., Charles, S., 2008. Key findings from the Indian Ocean Climate Initiative and their impact on policy development in Australia. *Clim. Change* 89, 339–354.
- Bauerfeind, S.S., Fischer, K., 2013. Testing the plant stress hypothesis: stressed plants offer better food to an insect herbivore. *Entomol. Experimentalis et Applicata* 149, 148–158.
- Belien, E., Rossi, S., Morin, H., Deslauriers, A., 2014. High-resolution analysis of stem radius variations in black spruce [*Picea mariana* (Mill.) BSP] subjected to rain exclusion for three summers. *Trees* 28, 1257–1265.
- Benson, J.S., Hager, T.G., 1993. The distribution, abundance and habitat of *Eucalyptus dunnii* (Myrtaceae) (Dun's white gum) in New South Wales. *Cunninghamiana* 3 (1), 123–144.
- Bettucci, L., Alonso, R., 1997. A comparative study of fungal populations in healthy and symptomatic twigs of *Eucalyptus grandis* in Uruguay. *Mycol. Res.* 101, 1060–1064.
- Bettucci, L., Alonso, R., Tiscornia, S., 1999. Endophytic mycobiota of healthy twigs and the assemblage of species associated with twig lesions of *Eucalyptus globulus* and *E. grandis* in Uruguay. *Mycol. Res.* 103 (4), 468–472.
- Biondi, F., Rossi, S., 2014. Plant-water relationships in the Great Basin Desert of North America derived from *Pinus monophylla* hourly den-drometer records. *Int. J. Biometeorol.* 59, 939–953.
- Booth, T.H., 2013. Eucalypt plantations and climate change. *For. Ecol. Manage.* 301, 28–34.
- Bossel, H., 1986. Dynamics of forest dieback: systems analysis and simulation. *Ecol. Model.* 34, 259–288.
- Bradford, K.J., Hsiao, T.C., 1982. Stomatal behaviour and water relations of waterlogged tomato plants. *Plant Physiol.* 70, 1508–1513.
- Brouwers, N., Matusick, G., Ruthrof, K., Lyons, T., Hardy, G., 2013. Landscape-scale assessment of tree crown dieback following extreme drought and heat in a Mediterranean eucalypt forest ecosystem. *Landscape Ecol.* 28, 69–80.
- Brown II, E.A., Hendrix, F.F., 1981. Pathogenicity and histopathology of *Botryosphaeria dothidea* on apple stems. *Phytopathology* 71, 375–379.
- Brunt, C., Read, J., Sanson, G.D., 2006. Changes in resource concentration and defence during leaf development in a tough-leaved (*Nothofagus moorei*) and soft-leaved (*Toona ciliata*) species. *Oecologia* 148, 583–592.
- Burgess, T.I., Barber, P.A., Sufaati, S., Xu, D., Hardy, G.E.St.J., Dell, B., 2007. *Mycosphaerella* spp. on *Eucalyptus* in Asia; new species, new hosts and new records. *Fungal Div.* 24, 135–157.
- Carnegie, A.J., 2007. Forest health condition in New South Wales, Australia, 1996–2005. II. Fungal damage recorded in eucalypt plantations during forest health surveys and their management. *Australas. Plant Pathol.* 36, 225–239.
- Carroll, G.C., 1988. Fungal endophytes in stems and leaves. From latent pathogens to mutualistic symbiont. *Ecology* 69, 2–9.
- Carroll, G.C., Carroll, F.E., 1978. Studies on the incidence of Coniferous needle endophytes in the Pacific North West. *Can. J. Bot.* 56, 3034–3040.
- Chen, S.F., Pavlic, D., Roux, J., Slippers, B., Xie, Y.J., Wingfield, M.J., Zhou, X.D., 2011. Characterization of *Botryosphaeriaceae* from plantation-grown *Eucalyptus* species in South China. *Plant. Pathol.* 60, 739–751.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Field, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491, 752–755.
- Cook, R.J., Papendick, R.I., 1972. Influence of water potential of soils and plants on root disease. *Ann. Rev. Phytopathol.* 10, 349–374.
- Cornelissen, T., Fernandes, G.W., Vasconcellos-Neto, J., 2008. Size does matter: variation in herbivory between and within plants and the plant vigor hypothesis. *Oikos* 117, 1121–1130.
- Craig, T.P., 2010. The resource regulation hypothesis and positive feedback loops in plant-herbivore interactions. *Pop. Ecol.* 52, 461–473.
- Crombie, D.S., Tippet, J.T., 1990. A comparison of water relations, visual symptoms, and changes in stem girth for evaluating impact of *Phytophthora cinnamomi* dieback on *Eucalyptus marginata*. *Can. J. For. Res.* 20, 233–240.
- Cunningham, S.A., Floyd, R.B., 2005. *Toona ciliata* that suffer frequent height-reducing herbivore damage by a shoot-boring moth (*Hypsipyla robusta*) are taller. *For. Ecol. Manage.* 225, 400–403.
- Desprez-Loustau, M.-L., Marçais, B., Nageleisen, L.-M., Piou, D., Vannini, A., 2006. Interactive effects of drought and pathogens in forest trees. *Ann. For. Sci.* 63, 597–612.
- De Swaef, T., De Schepper, V., Vandegehuchte, M.W., Steppe, K., 2015. Stem diameter variations as a versatile research tool in ecophysiology. *Tree Physiol.* 35, 1047–1061.
- Edwards, P.B., 1982. Do waxes on juvenile eucalypt leaves provide protection from grazing insects? *Aust. J. Ecol.* 7, 347–352.
- Edwards, P.B., Wanjura, W.J., 1990. Physical attributes of eucalypt leaves and the host range of chrysomelid beetles. *Synop. Biol. Hung.* 39, 227–236.
- FAO, 2013. Global Forest Resources Assessment 2010. In: FAO Technical Paper. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 378.
- Farley, K.A., Bremer, L., 2010. Timber plantations. In: Warf, B. (Ed.), *Encyclopedia of Geography*. SAGE Publications, Inc. <http://dx.doi.org/10.4135/9781412939591>.
- Fisher, P.J., Petrini, O., 1992. Fungal saprobes and pathogens as endophytes of rice (*Oryza sativa* L.). *New Phytol.* 120, 137–143.
- Fleischmann, F., Winkler, J.B., Oßwald, W., 2009. Effects of ozone and *Phytophthora citricola* on non-structural carbohydrates of European beech (*Fagus sylvatica*) saplings. *Plant Soil* 323, 75–84.
- Fox, L.R., Morrow, P.A., 1983. Estimates of damage by herbivorous insects on eucalyptus trees. *Aust. J. Ecol.* 8, 139–147.
- Ghini, R., Bettiol, W., Hamada, E., 2011. Diseases in tropical and plantation crops as affected by climate changes: current knowledge and perspectives. *Plant. Pathol.* 60, 122–132.
- GIT Forestry Consulting, 2014. <http://git-forestry.com/download_git_eucalyptus_map.htm> (Accessed July, 2015).
- Glynn, C., Ronnberg-Wästljung, A.-C., Julkenen-Tiitto, R., Wieh, M., 2004. Willow genotype, but not drought treatment, affects foliar phenolic concentrations and leaf-beetle resistance. *Entomol. Experimentalis et Applicata* 113, 1–14.
- Gonçalves, J.L.M., Alvares, C.A., Higa, A.R., Silva, L.D., Alfenas, A.C., Stahl, J., Ferraz, S. F.B., Lima, W.P., Brancalion, P.H.S., Hubner, A., Bouillet, J.P.D., Laclau, J.P., Nouvellon, Y., Epron, D., 2013. Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. *For. Ecol. Manage.* 301, 6–27.
- Griffin, D.M., 1977. Water potential and wood-decay fungi. *Ann. Rev. Phytopathol.* 15, 319–329.
- Gryzenhout, M., Wingfield, B.D., Wingfield, M.J., 2009. Taxonomy, Phylogeny, and Ecology of Bark-inhabiting and Tree-pathogenic Fungi in the Cryphonectriaceae (p. 119). American Phytopathological Society Press, St. Paul, MN, p. 136.
- Gutbrodt, B., Mody, K., Dorn, S., 2011. Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. *Oikos* 120, 1732–1740.
- Gutbrodt, B., Dorn, S., Unsicker, S.B., Mody, K., 2012. Species-specific responses of herbivores to within-plant and environmentally mediated between-plant variability in plant chemistry. *Chemoecology* 22, 101–111.
- Guneralp, B., Gertner, G., 2007. Feedback loop dominance analysis of two tree mortality models: relationship between structure and behaviour. *Tree Physiol.* 27, 269–280.
- Harwood, C., 2011. New introductions – doing it right. In: Walker, J. (Ed.), *Developing a Eucalypt Resource: Learning from Australia and Elsewhere:*

- University of Canterbury. Wood Technology Research Centre, Christchurch, New Zealand, pp. 43–54.
- Huberty, A.F., Denno, R.F., 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* 85, 1383–1398.
- Hulme, K.A., 2008. *Eucalyptus camaldulensis* Biogeochemistry: An Innovative Tool for Mineral Exploration in the Curnamona Province and Adjacent Regions (Ph.D. thesis). University of Adelaide, School of Earth and Environmental Sciences.
- Hunter, G.C., Crous, P.W., Carnegie, A.J., Burgess, T.I., Wingfield, M.J., 2011. *Mycosphaerella* and *Teratosphaeria* diseases of Eucalyptus; easily confused and with serious consequences. *Fungal Divers.* 50, 145–166.
- IPCC, 2007. Climate change 2007: impacts, adaptation and vulnerability. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, p. 976.
- IPCC, 2014. Climate change 2014: synthesis report. In: Pachauri, R.K., Meyer, L.A. (Eds.), Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, p. 151.
- Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A., Koricheva, J., 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biol.* 18, 267–276.
- Jentsch, A., Kreyling, J., Beierkuhnlein, C., 2007. A new generation of climate-change experiments: events, not trends. *Front. Ecol. Evol.* 5 (7), 365–374.
- Ji, L., Wang, Z., Wang, X., An, L., 2011. Forest insect pest management and forest management in China: an overview. *Environ. Manage.* 48, 1107–1121. <http://dx.doi.org/10.1007/s00267-011-9697-1>.
- Kendrick, B., 1992. Fungal plant pathology in agriculture and forestry. In: The Fifth Kingdom. Mycologue Publications, pp. 193–212.
- Koricheva, J., Larsson, S., Haukioja, E., 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. *Ann. Rev. Entomol.* 43, 195–216.
- Kroger, M., 2012. Global tree plantation expansion: a review. In: Initiatives in Critical Agrarian Studies Review Paper Series No. 3. University of Helsinki.
- Lana, V.M., Mafra, R.G., Ferreira, M.A., Sartório, R.C., Zauza, E.A.V., Mounteer, A.H., Alfenas, A.C., 2012. Survival and dispersal of *Puccinia psidii* spores in eucalypt wood products. *Australas. Plant Pathol.* 41, 229–238.
- Landsberg, J.J., 1990a. Dieback of rural eucalypts: does insect herbivory relate to dietary quality of tree foliage. *Aust. J. Ecol.* 15, 73–87.
- Landsberg, J.J., 1990b. Dieback of rural eucalypts: response of foliar dietary quality and herbivory to defoliation. *Aust. J. Ecol.* 15, 89–96.
- Landsberg, J.J., 1990c. Dieback of rural eucalypts: the effect of stress on the nutritional quality of foliage. *Aust. J. Ecol.* 15, 97–107.
- Landsberg, J.J., Cork, S.J., 1997. Herbivory: interactions between eucalypts and the vertebrates and invertebrates that feed on them. In: Williams, J.E., Woinarski, J. C.Z. (Eds.), *Eucalypt Ecology: Individuals to Ecosystems*. Cambridge University Press, Australia, pp. 342–372.
- Larsson, S., 1989. Stressful times for the plant-stress performance hypothesis. *Oikos* 56, 277–283.
- Larsson, S., Björkman, C., 1993. Performance of chewing and phloem feeding insects on stressed trees. *Scand. J. For. Res.* 8, 550–559.
- Larsson, S., Ohmart, C.P., 1988. Leaf age and larval performance of the leaf beetle *Paropsis atomaria*. *Ecol. Entomol.* 13, 19–24.
- Li, H., Madden, J.L., Potts, B.M., 1996. Variation in volatile leaf oils of the Tasmanian *Eucalyptus* species II. Subgenus *Symphyomyrtus*. *Biochem. Syst. Ecol.* 24, 547–569.
- Lieutier, F., 2002. Mechanisms of resistance in conifers and bark beetle attack strategies. In: Wagner, M.R., Clancy, K.M., Lieutier, F., Paine, T.D. (Eds.), *Mechanisms and Deployment of Resistance in Trees to Insects*. Kluwer Academic Publishers, Dordrecht.
- Lieutier, F., 2004. Bark and wood boring insects in living trees in Europe: a synthesis. In: *Host Resistance to Bark Beetles and Its Variations*. Kluwer Academic Publishers, Dordrecht.
- Linares, J.C., Camarero, J.J., Carreira, J.A., 2010. Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *J. Ecol.* 98, 592–603.
- Louda, S.M., Collinge, S.K., 1992. Plant resistance to insect herbivores: a field test of the environmental stress hypothesis. *Ecology* 73, 153–169.
- Madeira, M.V., Fabião, A., Pereira, J.S., Araújo, M.C., Ribeiro, C., 2002. Changes in carbon stocks in *Eucalyptus globulus* Labill. plantations induced by different water and nutrient availability. *For. Ecol. Manage.* 171 (1–2), 75–85.
- Manion, P.D., 1991. *Tree Disease Concepts*, second ed. Prentice-Hall, New Jersey, USA.
- Massad, T.J., Dyer, L.A., 2010. A meta-analysis of the effects of global environmental change on plant-herbivore interactions. *Arthropod. Plant Interact.* 4, 181–188.
- Mattson, W.J., Haack, R.A., 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37, 110–118.
- Matusick, G., Ruthrof, K.X., Brouwers, N.C., Dell, B., Hardy, G., St. J., 2013. Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt forest in southwestern Australia. *Eur. J. For. Res.* 132, 497–510.
- Maurel, M., Robin, C., Capdevielle, X., Loustau, D., Desprez-Loustau, M.L., 2001. Effects of variable root damage caused by *Phytophthora cinnamomi* on water relations of chestnut saplings. *Ann. Sci. For.* 58, 639–651.
- McDowell, N.G., Fisher, R.A., Xu, C., Domec, J.C., Holtta, T., Mackay, D.S., Sperry, J.S., Boutz, A., Dickman, L., Gehres, N., Limousin, J.M., Macalady, A., Ogee, J., Pangle, R.E., Rasse, D.P., Ryan, M.G., Sevanto, S., Waring, R.H., Williams, A.P., Yezzer, E.A., Pockman, W.T., 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel–experiment framework. *New Phytol.* 200, 304–321.
- McKiernan, A.B., Hovenden, M.J., Brodribb, T.J., Potts, B.M., Davies, N.W., O'Reilly-Wapstra, J.M., 2014. Effect of limited water availability on foliar plant secondary metabolites of two *Eucalyptus* species. *Environ. Exp. Bot.* 105, 55–64.
- Medlyn, B.E., Zeppel, M., Brouwers, N.C., Howard, K., O'Gara, E., Hardy, G., Lyons, T., Li, L., Evans, B., 2011. Biophysical impacts of climate change on Australia's forests. In: Contribution of Work Package 2 to the Forest Vulnerability Assessment. National Climate Change Adaptation Research Facility, Australia.
- Mitchell, P.J., Battaglia, M., Pinkard, E.A., 2013a. Counting the costs of multiple stressors: is the whole greater than the sum of the parts? *Tree Physiol.* 33, 447–450.
- Mitchell, P.J., O'Grady, A.P., Tissue, D.T., White, D.A., Ottenschlaeger, M.L., Pinkard, E.A., 2013b. Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. *New Phytol.* 197 (3), 862–872.
- Modý, K., Eichenberger, D., Dorn, S., 2009. Stress magnitude matters: different intensities of pulsed water stress produce non-monotonic resistance responses of host plants to insect herbivores. *Ecol. Entomol.* 34, 133–134.
- Netherer, S., Schopf, A., 2010. Potential effects of climate change on insect herbivores in European forests—general aspects and the pine processionary moth as specific example. *For. Ecol. Manage.*, 831–838.
- Nicoll, D., Dunlop, P.J., Bignell, C.M., 1998. A study of the variation with time of the compositions of the essential leaf oils of 16 *Eucalyptus* species. *Flavour. Frag. J.* 13, 324–328.
- Niinemets, Ü., 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *For. Ecol. Manage.* 260, 1623–1639.
- O'Grady, A.P., Mitchell, P.J.M., Pinkard, E.A., Tissue, D.T., 2013. Thirsty roots and hungry leaves: unravelling the roles of carbon and water dynamics in tree mortality. *New Phytol.* 200, 294–297.
- Old, K.M., Stone, C., 2005. Vulnerability of Australian Forest Carbon Sinks to Pests and Pathogens in a Changing Climate. Australian Greenhouse Office, Canberra.
- Palzer, C., 1981. Aetiology of gully dieback. In: Old, K.M., Kile, G.A., Ohmart, C.P. (Eds.), *Eucalypt Dieback in Forests and Woodlands*. CSIRO, Melbourne, pp. 174–178.
- Park, R.F., Keane, P.J., Wingfield, M.J., Crous, P.W., 2000. Fungal diseases of eucalypt foliage. In: Keane, P.J., Kile, G.A., Podger, F.D., Brown, B.N. (Eds.), *Diseases and Pathogens of Eucalypts*. CSIRO, Australia, pp. 153–239.
- Pérez, G., Burgess, T.I., Slippers, B., Carnegie, A.J., Wingfield, B.D., Wingfield, M.J., 2014. *Teratosphaeria pseudonubilosa* sp. nov., a serious *Eucalyptus* leaf pathogen in the *Teratosphaeria nubilosa* species complex. *Austral. Plant Pathol.* 43, 67–77.
- Pinkard, E.A., Battaglia, M., Bruce, J., Leriche, A., Kriticos, D.J., 2010. Process-based modelling of the severity and impact of foliar pest attack on eucalypt plantation productivity under current and future climates. *For. Ecol. Manage.* 259, 839–847.
- Poot, P., Veneklaas, E.J., 2013. Species distribution and crown decline are associated with contrasting water relations in four common sympatric eucalypt species in southwestern Australia. *Plant Soil* 364, 409–423.
- Price, P.W., 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62, 244–251.
- Rayner, A.D.M., Boddy, L., 1988. *Fungal Decomposition of Wood: Its Biology and Ecology*. John Wiley and Sons, New York.
- Rouault, G., Candau, J.N., Lieutier, F., Nageleisen, L.M., Martin, J.C., Warzée, N., 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Ann. For. Sci.* 63, 613–624.
- Sanson, G., Read, J., Aranwela, N., Clissold, F., Peeters, P., 2001. Measurement of leaf biochemical properties in studies of herbivory: opportunities, problems and procedures. *Austral. Ecol.* 26, 535–546.
- Schoener, T.W., 1974. Resource partitioning in ecological communities. *Science* 185, 27–39.
- Schoeneweiss, D.F., 1981. The role of environmental stress in diseases of woody plants. *Plant Dis.* 65, 308–314.
- Shearer, B.L., Tippet, J.T., Bartle, J.R., 1987. *Botryosphaeria ribis* infection associated with death of *Eucalyptus radiata* in species selection trials. *Plant Dis.* 71, 140–145.
- Sieber, T.N., 2007. Endophytic fungi in forest trees: are they mutualists? *Fungal Biol. Rev.* 21, 75–89.
- Silva-Junior, O.B., Faria, D.A., Grattapaglia, D., 2015. A flexible multi-species genome-wide 60K SNP chip developed from pooled resequencing of 240 *Eucalyptus* tree genomes across 12 species. *New Phytol.* 206, 1527–1540.
- Slippers, B., Wingfield, M.J., 2007. *Botryosphaeriaceae* as endophytes and latent pathogens of woody plants: diversity, ecology and impact. *Fungal Biol. Rev.* 21, 90–106.
- Slippers, B., Burgess, T.I., Pavlic, D., Ahumada, R., Maleme, H., Mohali, S.R., Rodas, C., Wingfield, M.J., 2009. A diverse assemblage of *Botryosphaeriaceae* infect *Eucalyptus* in native and non-native environments. *South. For.* 71, 101–110.
- Steinbauer, M.J., 2010. Latitudinal trends in foliar oils of eucalypts: environmental correlates and diversity of chrysomelid leaf-beetles. *Austral. Ecol.* 35, 204–213.
- Steinbauer, M.J., Clarke, A.R., Madden, J.L., 1998. Oviposition preference of a *Eucalyptus* herbivore and the importance of leaf age on interspecific host choice. *Ecol. Entomol.* 23, 201–206.
- Stone, C., Bacon, P.E., 1994. Relationships among moisture stress, insect herbivory, foliar cineole content and the growth of river red gum *Eucalyptus camaldulensis*. *J. Appl. Ecol.* 31, 604–612.

- Stone, C., Bacon, P.E., 1995. Influence of insect herbivory on the decline of black box (*Eucalyptus largiflorens*). *Aust. J. Bot.* 43, 555–564.
- Stone, C., 2001. Reducing the impact of insect herbivory in eucalypt plantations through management of intrinsic influences on tree vigour. *Austral Ecol.* 26, 482–488.
- Strauss, S.Y., Agrawal, A.A., 1999. The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.* 14 (5), 179–185.
- Sturrock, R.N., Franke, S.J., Brown, A.V., Hennon, P.E., Kliejunas, J.T., Lewis, K.E., Worral, J.J., Woods, A.J., 2011. Climate change and forest diseases. *Plant. Pathol.* 60, 133–149.
- Swart, W.J., Conradie, E., 1992. Effects of water stress on the development of cambial lesions caused by *Cryphonectria cubensis* on *Eucalyptus grandis*. *Plant Dis.* 76 (7), 744–746.
- Taylor, G.S., 1997. Effect of plant compounds on the population dynamics of the lerp insect, *Cardiaspina albitextura* Taylor (Psylloidea, Spondyliaspidae) on eucalypts. In: Raman, A. (Ed.), *Ecology and Evolution of Plant Feeding Insects in Natural and Manmade Environments*. International Scientific Publications, New Delhi, pp. 37–57.
- The West Australian, 2012, November. Company burnt by foray into forestry sector. <<https://au.news.yahoo.com/thewest/countryman/a/15262797/company-burnt-by-foray-into-forestry-sector/>>.
- Thomson, V.P., Nicotra, A.B., Steinbauer, M.J., 2001. Influence of previous frost damage on tree growth and insect herbivory of *Eucalyptus globulus globulus*. *Austral Ecol.* 26, 489–499.
- Tippett, J.Y., Crombie, D.S., Hill, T.C., 1987. Effect of phloem water relations on the growth of *Phytophthora cinnamomi*. *Phytopathology* 77, 246–250.
- Tommerup, I.C., Alfenas, A.C., Old, K.M., 2003. Guava rust in Brazil – a threat to *Eucalyptus* and other Myrtaceae. *NZ J. For. Sci.* 33, 420–428.
- Turcotte, A., Morin, H., Krause, C., Deslauriers, A., Thibeault-Martel, M., 2009. The timing of spring rehydration and its relation with the onset of wood formation in black spruce. *Agric. For. Meteorol.* 149, 1403–1409.
- Van der Maaten, E., 2013. Thinning prolongs growth duration of Euro-pean beech (*Fagus sylvatica* L.) across a valley in southwestern Ger-many. *For. Ecol. Manage.* 306, 135–141.
- van Dijk, A.I.J.M., Beck, H.E., Crosbie, R.S., de Jeu, R.A.M., Liu, Y.Y., Podger, G.M., Timbal, B., Viney, N.R., 2013. The Millennium Drought in southeast Australia (2001–2009): natural and human causes and implications for water resources, ecosystems, economy, and society. *Water Resour. Res.* 49, 1040–1057.
- Van Gunst, K.J., Weisberg, P.J., Yang, J., Fan, Y., 2016. Do denser forests have greater risk of tree mortality: a remote sensing analysis of density-dependent forest mortality. *For. Ecol. Manage.* 359, 19–32.
- van Heerden, S.W., Wingfield, M.J., 2002. Effect of environment on the response of *Eucalyptus* clones to inoculation by *Cryphonectria cubensis*. *For. Pathol.* 32, 295–402.
- Walker, J.C., Stahmann, M.A., 1955. Chemical nature of disease resistance. *Ann. Rev. Plant Physiol.* 6, 351–366.
- Walklate, P.J., McCartney, H.A., Fitt, B.D.L., 1989. Vertical dispersal of plant pathogens by splashing. Part II: Experimental study of the relationship between raindrop size and the maximum splash height. *Plant. Pathol.* 38 (1), 64–70.
- Wang, G., Hendon, H.H., 2007. Sensitivity of Australian rainfall to inter-El Niño variations. *J. Clim.* 20, 4211–4217.
- Wang, W., Peng, C., Kneeshaw, D.D., Larocque, G.R., Luo, Z., 2012. Drought-induced tree mortality: ecological consequences, causes, and modelling. *Environ. Rev.* 20, 109–121.
- Wang, L., Chen, W., Zhou, W., 2014. Assessment of future drought in southwest China based on CMIP5 multimodel projections. *Adv. Atmos. Sci.* 31, 1035–1050.
- Wardlaw, T., 2006. Managing diseases in plantations. In: Davidson, N., Volker, P., Leech, M., Lyons, A., Beadle, C. (Eds.), *Farm Forestry—A Technical and Business Handbook*. University of Tasmania, Australia, pp. 241–245.
- Wardlaw, T.J., Bashford, D., 2007. The effectiveness of thinning eucalypts in reducing losses from stem-boring insects and fungal rots. In: *Borers and Rots in Eucalypts Conference Proceedings, Commercial Management Issues, IFA – WA Division, Western Australia*.
- Waring, G.L., 1987. *Plant Stress and the Ecology of Gallforming Insects* (Ph.D. dissertation). Northern Arizona University Flagstaff, Arizona.
- Weston, C.J., Attiwill, P.M., Cameron, J.N., 1991. Growth and nutrition of eucalypts in relation to soil type and former land use in Gippsland, Victoria. In: Schonau, A.P. G. (Ed.), *Intensive Forestry: The Role of Eucalypt*. IUFRO Symposim. South African Institute of Forestry, Durban, pp. 480–491.
- White, D., Beadle, C., Worledge, D., Honeysett, J., Cherry, M., 1998. The influence of drought on the relationship between leaf and conducting sapwood area in *Eucalyptus globulus* and *Eucalyptus nitens*. *Trees-Struct. Funct.* 12, 406–414.
- White, D.A., 1996. *Physiological Responses to Drought of Eucalyptus globulus and E. nitens in Plantations* (Ph.D. thesis). University of Tasmania.
- White, D.A., Crombie, D.S., Kinal, J., Battaglia, M., McGrath, J.F., Mendham, D.S., Walker, S.N., 2014a. Managing productivity and drought risk in *Eucalyptus globulus* plantations in south-western Australia. *For. Ecol. Manage.* 259, 33–44.
- White, D.A., McGrath, J.F., Ryan, M.G., Battaglia, M., Mendham, D.S., Kinal, J., Downes, G.M., Crombie, D.S., Hunt, M.E., 2014b. Managing for water-use efficient wood production in *Eucalyptus globulus* plantations. *For. Ecol. Manage.* 331, 272–280.
- White, T.C.R., 1969. An index to measure weather induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* 50, 905–909.
- White, T.C.R., 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63, 90–105.
- White, T.C.R., 1986. Weather, *Eucalyptus* dieback in New England, and a general hypothesis of the cause of dieback. *Pac. Sci.* 40, 58–78.
- White, T.C.R., 2009. Plant vigour versus plant stress: a false dichotomy. *Oikos* 118, 807–808.
- Whyte, G., Howard, K., Hardy, G., Burgess, T., 2011. Foliar pests and pathogens of *Eucalyptus dunnii* plantations in southern Queensland. *Aust. For.* 74 (3), 901–909.
- Whyte, G., 2012. *The Ecology of Insect Pests and Fungal Pathogens of Drought Stressed Eucalypt Plantations in Southern Queensland* (Ph.D. thesis). Murdoch University, Western Australia.
- Wilks, D.S., Shen, K.W., 1991. Threshold relative humidity forecasts for plant disease prediction. *J. Appl. Meteorol.* 30, 463–477.
- Zhou, X.H., Xiao, Z.N., 2014. Climate projection over Yunnan province and the surrounding regions based on CMIP5 data. *Clim. Environ. Res.* 19, 601–613 (in Chinese with English abstract).