Forest Ecology and Management 296 (2013) 98–107

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Seasonal dynamics in understorey abundance and carbohydrate concentration in relation to browsing and bark stripping of Tasmanian *Pinus radiata* plantations

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ARTICLE INFO

Article history:
Received 19 October 2012
Received in revised form 2 February 2013
Accepted 4 February 2013
Available online 22 March 2013

Keywords:
Understorey composition
Browsing
Diet selection
Herbivore
Browse management
Pine plantation

ABSTRACT

Bark stripping in *Pinus radiata* plantations by Bennett's wallaby (*M. rufrogriseus* subspecies *rufrogriseus*) triggers high rates of tree mortality and reduces crop productivity, causing significant economic losses to the Australian forest industry. Bark stripping shows a marked increase during winter which may be associated with concurrent increases in bark soluble sugar concentration. Seasonal abundance of alternative forage may also contribute to bark-stripping incidence. Relationships between seasonal variations in forage quantity and quality, and periods of increased bark stripping were assessed in two *P. radiata* plantations. Understorey composition, abundance, browsing pressure, and sugar, starch and total non-structural carbohydrate (TNC) concentrations were measured seasonally over a period of 12 months for each species in areas experiencing high and low levels of bark stripping. A strong general positive association of high soluble sugar concentrations, particularly in two exotic grasses *Poa annua* and *Holcus lanatus*, with elevated levels of browsing pressure was found. In contrast starch content was weakly and negatively associated with browsing pressure. Ratios of the concentration of soluble sugars to starch were significantly and positively correlated with browsing pressure. Understorey species were allocated to five sub-groups based on putative chemical and physical mechanisms of tolerance to, or defence against, herbivory. This sub-grouping lends support to the significant effect of sugar to starch ratios on browsing preference. The current study demonstrates that soluble sugar concentration of *P. radiata* bark was consistently higher than concentrations in native understorey species and that bark represents an available, apparent and high quality food source to wallaby. *P. annua* and *H. lanatus* had comparable concentrations of soluble sugars to *P. radiata* bark and are an alternative food source provided they remain in sufficient abundance. These results are indicative of a key mechanism driving bark stripping in Tasmania. The results lend credence to the implementation of two browser management strategies (1) in the short term, the provision of a diversionary feed and (2) limiting the abundance of alternative herbage so that over time the plantation landscape supports lower populations of browsers.

1. Introduction

A wide range of mammalian species are known to both strip and consume bark from standing trees in most forest-growing regions of the world (Lunney and O'Connell, 1989; le Mar and McArthur, 2005; Gill, 2006; Saint-Andrieux et al., 2009). Bark stripping of plantation-grown eucalypts (Ward et al., 2008) and *Pinus radiata* (D. Don) (radiata pine) is a significant problem in south-eastern Australia (Gonnet, 2007). *P. radiata* is most susceptible to damage from stripping during the first three-to-six years of growth, after which the bark becomes too thick for the majority of native browsers to remove (Wotherspoon, 2004).

The species of browser responsible for damage in Tasmanian *P. radiata* plantations is easily identified in the field. Bark stripping by Bennett's wallaby (*Macropus rufogriseus* subspecies *rufogriseus*) occurs on the lower stem (0–1 m). The larger grey kangaroo (*Macropus giganteus*) strips bark from higher up the stem (1–2 m); the smaller red-bellied pademelon (*Thylogale billardierii*), although not strong enough to remove bark, causes needle clipping and

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http://dx.doi.org/10.1016/j.foreco.2013.02.002

lateral branch damage; and the brushtail possum (*Trichosurus vulpecular*), generally targets older stands (8–15 years), removes the apical bud in the upper crown and causes stem breakage during travel through the canopy (Jacometti et al., 2007). Extensive surveys in Tasmanian *P. radiata* plantations reveal that most bark stripping injury occurs in the bottom metre stem, and therefore Bennett's wallaby is primarily responsible for the majority of the observed level of damage (Wotherspoon, 2004).

Bennett's wallaby is found throughout Tasmania and is a nocturnal, generalist herbivore (Calaby, 1983) with a diet of mainly grasses and broad-leaved forbs (Sprent and McArthur, 2002). At maturity, the animal can weigh up to 20 kg and attain a head-body length of 90 cm. Night time feeding in open grassland and young plantations, and daytime sheltering, often in older plantations is observed (le Mar and McArthur, 2005).

Numerous hypotheses have been proposed to explain the underlying causes of browsing selection and bark stripping in Tasmanian plantations. Small perimeter: area, higher degree of canopy closure in surrounding vegetation and greater proportion of stand perimeter adjoining forest are associated with high risk of browsing within eucalypt plantations (Bulinski and McArthur, 2003). Inter- (e.g. surrounding forest and vegetation types, altitude rainfall and soil) and intra- (e.g. planting density, stem diameter, tree branch number, internode length, browser density, patch characteristics such as alternate feed quality and structure) site factors also affect the incidence and severity of bark stripping (McArthur et al., 2003; Pietrzykowski et al., 2003; Jacometti et al., 2007; Miller et al., 2007). However it is not always possible to predict the risk of browsing damage in this way. Several studies show no relationship between bark stripping damage and scat deposition (scats/m^2/day), suggesting browser density and extent of damage do not correlate (Reimoser and Gossow, 1995; Bulinski and McArthur, 2003; Di Stefano et al., 2007). Yet it has been demonstrated by Sprent and McArthur (2002) that differences in browser density and species diversity result in selection for different diets within plantations. However it can be argued that this is due to responses to predation risk, rather than an interaction causing direct partitioning of food resources (While and McArthur, 2005).

While the above listed causes of herbivore selection have been extensively investigated, the nutritive benefits of bark stripping are yet to be fully understood (Verheyden-Tixier et al., 2008). Duncan's Nutritional Value Hypothesis (2007) predicts that bark is selected purely for its nutritive value. By eating bark, herbivores ingest carbohydrates (Faber, 1996; Randveer and Heikkilä, 1996), proteins (Santra et al., 2008), specific minerals (DeCrombrugghe, 1965; Ernst, 1975; Husak, 1985), and water (Camperio Ciani et al., 2001; Aregheore et al., 2006). Another suggested reason for bark stripping is the Digestion Benefit Hypothesis, which states that bark may assist in promoting digestion efficiency when the browser's diet has low fibre content (Keenan, 1986; Gill, 1992b) (Hutchings et al., 2006). Generalist herbivores are unable to produce the necessary enzymes required for plant cellulose and fibre degradation, and have evolved a range of symbiotic associations with a consortium of intestinal organisms for this purpose (Hume and Warner, 1980). Structural carbohydrates such as cellulose are broken down and non-structural carbohydrates are metabolised to Short Chain Fatty Acids (SFCAs) by microbial fermentation. SCFAs provide nutrition to gut epithelial cells (Stevens and Stettler, 1967) and in *M. rufogriseus* (red-necked wallaby), can account for up to 42% of overall maintenance energy requirements (Stevens and Hume, 1998). Therefore, non-structural carbohydrates are generally considered a major factor underlying food preference in herbivores and play an integral part in wallaby nutrition. (Tixier et al., 1997; Moser et al., 2006; Parsons et al., 2006). Bark also contains other compounds associated with defence against pests and diseases viz namely resin acids, terpenes, tannins and other phenolic compounds. As bark contains high concentrations of tannins, it could also have anti-parasitic properties (Meissner and Paulsmeier, 1995; Iason et al., 1996; Dearing, 1997).

Seasonal changes in carbohydrate concentrations occur in many plants, including *Pinus* species (Bonicel et al., 1987; Ashworth et al., 1993; Rinne et al., 1994; Barbaroux and Breda, 2002). The majority of soluble sugars produced by the photosynthetic process are utilised in summer by the strong sinks that result from vegetative plant growth (Gregory and Wargo, 1986). Following the growing period, a decrease in growth rate gives rise to lower sink strength. Sugar levels increase in the bark and foliage of a number of pine species throughout autumn as part of the "hardening process" (Levitt, 1980; Nguyen et al., 1990), resulting in increased tolerance to low winter temperatures (Faber, 1996; Kimball et al., 1998, 1999; Faber and Lavsund, 1999; Laska, 2001; Bulinski and McArthur, 2003; Gonnet, 2007). Larger reserves of sugars are also known to be associated with increased cold tolerance in *Pinus contorta* and *Pinus sylvestris* (Ogren et al., 1997; Ogren, 2001; Repo et al., 2004). Any excess soluble sugars are converted to the major reserve carbohydrate, starch. Previous studies have found that the root system is the main storage organ for starch (Landhausser and Lieffers, 2003), and that reserves of root starch peak late in autumn, and then decrease slowly over winter as a result of respiration (Loescher et al., 1990). Mohammed and Smith (2010) report a significant increase during winter and spring of bark-stripping damage due to Bennett's wallaby in Tasmanian *P. radiata* plantations, which parallels a two-to-three fold increase in bark total non-structural carbohydrates (TNCs) that most likely results from cold hardening.

Bark nutritional value can be similar to that of alternative food plants in planted forests (Storms et al., 2008). In winter, bark can serve as a supplementary source of energy (Gill, 1992a). The amount of energy available from bark-stripping herbivory is known to vary with tree species and life stage, stand productivity and biodiversity (Jactel and Brockerhoff, 2007). Nevertheless, it is well documented, particularly in temperate climates, that when alternative forage is scarce, browsers take advantage of the supplementary source of energy afforded by stripping bark (Gill, 1992a; Kowalczyk et al., 2011). The nutritional dynamics of understorey species and their influence on bark stripping of *P. radiata* is poorly understood.

Some 600–800 ha of pine plantations annually experience moderate to severe bark-stripping damage in Tasmania (Wotherspoon, 2004). This damage represents significant economic loss to forestry companies by triggering mortality in young plantations, reducing productivity in surviving trees, and causing an indirect impairment to wood quality through wounding responses. Levels of damage are such that industry is sensitive about divulging exact figures on losses; however an indication of its importance can be gauged by the AUD $48/ha that was being spent on poisoning vertebrate browsers (Wotherspoon, 2004).

The total ban on the use of sodium monofluoroacetate (1080 poison) in Tasmanian State Forests from December 2005 increased the need to find alternative management strategies for vertebrate browser pests, particularly in eucalypt and pine plantations (Walsh and Wardlaw, 2005). Current management depends on shooting or trapping which is expensive and less effective than poisoning (Wotherspoon, 2004; Miller et al., 2009). In order to successfully develop cost effective and publicly acceptable strategies it is necessary to gain a thorough understanding of the underlying mechanisms that influence the risk of plantations to bark stripping (Statham, 1983).

This study investigated the seasonal dynamics of abundance (food quantity), concentration of TNCs (as an index of food quality) and the severity of browsing (browsing pressure) of understorey species in relation to incidence and severity of *P. radiata* bark