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Effect of thinning, pruning and nitrogen fertiliser application on transpiration, photosynthesis and water-use efficiency in a young *Eucalyptus nitens* plantation

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ABSTRACT

Interactions between thinning, pruning and fertiliser application in forestry are rarely examined, even though these treatments are often applied simultaneously in practice. Understanding these interactions can facilitate the design of regimes to best exploit such silvicultural interventions. The effects of these treatments on stand transpiration (*E*), photosynthesis and water-use efficiency (AGB-WUE, defined as the above-ground biomass production per unit transpiration) were measured in a *Eucalyptus nitens* plantation in south-eastern Australia. Two levels of each treatment were applied at age 3.2 years and transpiration was measured between ages 5.3 and 6.3 years. Treatments were: unthinned, or thinned from ca. 900 to 300 trees ha^{-1}; unpruned, or 50% of the live crown length pruned of the 300 largest-diameter potential sawlog crop trees ha^{-1}; and nil, or 300 kg ha^{-1} N fertiliser. There were no significant treatment interactions on growth, *E* or AGB-WUE. Thinning and pruning reduced *E* by 45% and 12%, respectively, and fertiliser application increased *E* by 21%. Transpiration was linearly related to stand leaf area, which explained more than 90% of the variation across treatments. Thinning and pruning also increased AGB-WUE by 23% and 21%, respectively, while fertiliser application had no significant effect. There was a small increase in AGB-WUE with increasing tree size, such that in unthinned stands the largest 50% of trees were 7% more efficient than the smallest 50% of trees. Thinning increased AGB-WUE by increasing the light available to the lower canopy and pruning increased AGB-WUE by removing the least efficient lower canopy foliage and increasing the efficiency of the remaining foliage. All treatments also modified the hydraulic architecture of the trees by changing leaf area to sapwood area ratios and radial sap flux density profiles. This study shows how silvicultural treatments can be used to modify stand transpiration and AGB-WUE of *E. nitens* plantations, potentially reducing their drought susceptibility while making more efficient use of the sites water resources.

1. Introduction

Silvicultural interventions such as thinning, pruning and fertiliser application are commonly applied to forests and plantations to increase growth rates and improve sawlog wood quality and value of retained trees (Forrester et al., 2010c). Each of these interventions work mechanistically to produce these outcomes in different ways, and if they are applied simultaneously as often happens, there may be interactions that are difficult to predict from studies that focus on each intervention in isolation (Forrester and Baker, in press). Understanding how silvicultural interventions affect water use of forests is crucial for managing water fluxes in forests and for making efficient use of water for wood production. This study examines all three treatments and their interactions on the transpiration and water-use efficiency of a *Eucalyptus nitens* plantation.

Thinning, pruning and fertiliser application can alter crown architecture and stand structure. This can change microclimatic variables such as light penetration, temperature, vapour pressure deficit (*D*) and windspeed (Gary, 1974; Tang et al., 1999; Landsberg and Sands, 2011) and water supply from the soil (Bréda et al., 1995). Increases in each of these variables can increase rates of transpiration of leaves and trees (Phillips et al., 2001; Medhurst et al., 2002; Hubbard et al., 2004; Morris et al., 2004). Trees can acclimate to these changes and maintain a homeostatic balance

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between stomatal conductance, the soil-to-leaf water pressure gradient ($\Delta\Psi$), and hydraulic architecture parameters including whole-tree hydraulic conductance per unit sapwood area (k_s), leaf area (A_l), sapwood area (A_s) and their ratio (A_l:A_s) (Whitehead et al., 1984a,b).

Thinning increases soil moisture availability and reduces plant water stress by reducing stand transpiration and losses from rainfall interception (Aussenac and Granier, 1988; Stogsdill et al., 1992; Bréda et al., 1995; White et al., 2009). Conversely, thinning can lead to higher soil evaporation as soil temperatures increase, and increased understorey leaf areas and hence transpiration (Black et al., 1980; Macfarlane et al., 2010). The atmospheric demand for water, and thus tree transpiration, may also increase because more open canopies can have a higher tree boundary layer conductance and be more coupled with the atmosphere (Teklehaimanot et al., 1991; Medhurst et al., 2002). This may make them more sensitive to the prevailing D (Bréda et al., 1995), thereby increasing transpiration or conductance per unit leaf area without increasing assimilation, and resulting in a lower water-use efficiency (WUE; annual wood or biomass growth per unit transpiration). On the other hand, thinning may also increase the efficiency with which trees and stands use water. Higher resource acquisition or availabilities have been associated with higher WUE of trees and stands (Stape et al., 2004), which may be reinforced following thinning. Thinning effects on WUE have received little attention, but this information provides an important basis for linking silvicultural interventions to managing water resources (White et al., 2009).

Fertiliser application often increases leaf area, which can result in faster rates of stand transpiration (Hubbard et al., 2004), but in consequence, also reduces soil moisture availability, increases interception losses and increases self-shading within the canopy (Myers and Talsma, 1992; Pinkard et al., 2007), all of which may reduce transpiration. The effects of fertiliser or site quality on WUE appear to be species and site-specific with reports of increases (Stape et al., 2004) or no changes in WUE (Hubbard et al., 2004). It remains unclear whether these effects may also interact with pruning and thinning treatments.

Pruning can immediately reduce transpiration by removing part of the trees' leaf area as well as reducing A_l:A_s. These changes may improve soil moisture availability and the water status of the retained leaves, as indicated by increases in stomatal conductance (and photosynthetic rates) that often follow defoliation (Pinkard et al., 1998). These leaf-level compensatory responses to pruning or defoliation are often transitory, disappearing as the leaf area is rebuilt (Pinkard et al., 1998; Quentin et al., 2011). The influence of pruning on whole tree or stand transpiration and WUE has received little attention.

Different size classes within a stand of trees experience different canopy conditions and consequently may respond differently to a given treatment. For example, prior to thinning, larger trees experience higher levels of solar radiation, D and windspeed. They may also have higher rates of photosynthesis and stomatal conductance, as well as a different hydraulic architecture, compared with smaller trees that occupy a subordinate position in the lower canopy (O'Grady et al., 2008). Therefore it is useful to separate the direct effects of the treatments from those related to tree size by examining responses at the tree as well as the stand level. Since treatments such as thinning and pruning are focused on specific size classes, this information can show the implications of retaining or removing particular groups of trees and aid with the design of silvicultural systems to meet defined objectives.

The objective of this study was to simultaneously measure the effects of thinning, pruning and nitrogen fertiliser treatments at age 3.2 years in an *E. nitens* plantation on transpiration and water-use efficiency between ages 5.3 and 6.3 years, and to understand the basis of interactions between treatments. We hypothesised that (1) pruning would reduce tree and stand transpiration, and that the effect would be relatively lower in unthinned than thinned stands because the lower crown leaves transpire less in unthinned stands, so their removal has a smaller effect on transpiration; (2) pruning would increase WUE because the lower, less efficient section of the crown is removed, and light-saturated rates of photosynthesis in the remaining crown will increase; (3) the effect of pruning on WUE would be higher in unthinned than thinned stands, because in unthinned stands the difference in light-saturated rates of photosynthesis between the upper and lower crown is greater, thus removing the lower and less efficient foliage has a greater effect on the tree WUE; and (4) fertiliser application would increase tree and stand level transpiration but would not change WUE or interact with thinning or pruning.

2. Methods

The experiment was in an *E. nitens* (Deane and Maiden) plantation located 1.5 km south-west of Carrajung, Victoria, Australia (38°23′ S, 146°41′ E). Mean annual pan evaporation is 1039 mm; mean annual precipitation is 1124 mm with a spring maximum. The mean daily maximum temperature is 22.3 °C in January and the mean minimum temperature is 3.9 °C in July. The site has gradational soils with silty loam to clay loam A horizons and light clay to medium clay B horizons, which are classified as Humose-Acidic, Dystrophic, Red or Brown Dermosols (Isbell, 1998), Gn4.11 or Gn4.71 Primary Profile Form (Northcote, 1979). The trees were planted in June 2003 at a spacing of 2.5 × 4 m (1000 trees ha^{-1}). Measured plots were eight rows × about nine trees (0.07 ha), and were surrounded by a single row of buffer trees. Fertiliser was applied to individual trees 2 and 12 months after planting, a total equivalent to 170 N, 110 P and 50 K kg ha^{-1}. More detail about the site and establishment are provided in Forrester et al. (accepted for publication-a).

2.1. Experimental design

The trial was a 2 × 2 × 2 factorial of thinning, pruning and nitrogen fertiliser treatments in a complete randomised block design with three replicates. The two fertiliser treatments were no fertiliser after age 12 months (F0) and 300 kg N ha^{-1} at age 3.2 years (F1).

The thinning treatments were unthinned (T0) and thinned to 300 trees ha^{-1} at age 3.2 years (T1). An equivalent cohort of 300 trees ha^{-1} was selected in the T0 treatments for direct comparison with the same cohort retained in T1. The 200 largest-diameter trees ha^{-1} of the retained (T1) or selected (T0) 300 trees ha^{-1} are referred to as potential sawlog crop trees (SCT_{200}). In T1, the trees selected for retention, as well as for pruning (see below), were chosen based on form (single-stemmed, straight, vertical), size (larger diameters) and spacing (uniformity). Selection was immediately prior to the thinning and first pruning operations when trees were approximately 9 m tall. Initial stand stocking (trees ha^{-1}), basal area (m^2 ha^{-1}), volume (m^3 ha^{-1}), above-ground biomass (Mg ha^{-1}) and LAI at age 3.2 years were 903, 10.4, 38.9, 29.5 and 3.1, respectively (Forrester et al., accepted for publication-a). Thinning to 300 trees ha^{-1} resulted in the retention of 32% of the trees, 39% of the basal area, 41% of the volume, 44% of the above-ground biomass and 45% of the LAI.

The pruning treatments included unpruned (P0) or pruned to retain the upper 50% of the live-crown length, equivalent to 25% of the leaf area, at age 3.2 years (P1). The live-crown height (h_L; m) was defined as the point where the lowest main-crown live branch joined the stem. Mean h_L was 1 m when the trees were pruned and pruning was done to an average height of about 4.5 m. Pruned trees received a second pruning up to 6.5 m at age