



## Full length article

Plant carbon pools and fluxes in coppice regrowth of *Eucalyptus globulus*Paul L. Drake<sup>a,b,c,\*</sup>, Daniel S. Mendham<sup>d,b</sup>, Gary N. Ogden<sup>c</sup><sup>a</sup> Natural Resources Branch, Department of Parks and Wildlife, 17 Dick Perry Avenue, Technology Park, Kensington, Western Australia, 6151, Australia<sup>b</sup> School of Plant Biology, University of Western Australia, 35 Stirling Highway, Crawley, Western Australia, 6009, Australia<sup>c</sup> CSIRO Sustainable Ecosystems, Centre for Environment and Life Sciences, Underwood Avenue, Floreat, Western Australia, 6014, Australia<sup>d</sup> CSIRO Sustainable Ecosystems, Private Bag 12, Hobart, Tasmania, 7001, Australia

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## ABSTRACT

Forestry systems frequently utilise coppice regrowth to establish 2nd and later rotations, partly because early growth in coppice is often faster than in seedlings. This rapid regrowth is to some extent attributable to translocation of below-ground reserves to support the development of new shoots. Translocation of below-ground carbon (C) from either the existing soluble pool or C mobilised from storage could require elevated respiration rates in roots. We studied changes in the rate of CO<sub>2</sub> efflux ( $R_{15}$ ) and total soluble sugar (TSS) concentration from different components of coppice and uncut trees in a *Eucalyptus globulus* (Labill.) plantation for 8 months after cutting. We also examined the impact of shading of the regrowth coppice as a means of increasing the dependence on carbohydrate reserves. The  $R_{15}$  of lateral roots declined soon after trees were felled but increased in uncut (control) trees. The TSS concentration decreased in the lateral roots of coppiced trees and also in the lateral roots of uncut trees. Early coppice regrowth was not associated with an elevated  $R_{15}$  or alteration to the TSS concentration of roots. A mass balance of C derived 8 months after trees were felled suggested that coppice maintained a significant amount of soluble C in roots, even though net C fixation was low, especially in the shaded treatment. One explanation for these observations is that mobilisation and/or transport of C in developing coppice is sink-limited, or alternatively, translocation of C from roots to shoots is constrained by vascular connections.

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## 1. Introduction

Respiration provides the energy and carbon (C) skeletons for solute exchange and the synthesis and maintenance of biomass. The balance between respiration and photosynthesis determines whether an ecosystem is a net source or sink of CO<sub>2</sub> and, globally, rising temperatures will likely increase the amount of C assimilated by photosynthesis and subsequently used by respiration up to a temperature optimum (Atkin and Tjoelker, 2003; Atkinson et al., 2007). In addition to temperature, it is known that both nutrient stress (Bottrill et al., 1970) and water stress (Brix, 1962) increase the allocation of assimilated C to respiration, although respiration rate ( $R$ ) will eventually decline under chronic stress conditions. Respiration is highly dependent on energy demand for the growth and maintenance of plant tissue (Noguchi et al., 2001) and this has relevance to managed forestry systems where the goal is to stimulate high growth rates to maximise economic return. One means of enhancing growth in short-rotation forestry

systems is to allow new rotations to regenerate as coppice regrowth. Using a short rotation *Eucalyptus globulus* Labill. plantation, we studied the patterns of change in  $R$  and total soluble sugar (TSS) concentration during the development of young coppice.

The above-ground growth rate of coppice is usually high (Blake, 1980; Tschaplinski and Blake, 1989; Antonio et al., 2007). This is partly because the coppice growth form has a high root to shoot ratio that can allow developing canopies access to large quantities of soil resources (Fleck et al., 1996; Poorter and Nagel, 2000) and potentially provide a source of carbohydrate to enhance early growth. In *E. globulus*, Drake et al. (2009) showed that the resource-availability benefits of a high root to shoot ratio in coppice (compared to seedlings) was not realised at the leaf level, but rather at a stand level, because foliar nutrient concentrations stayed approximately the same, whilst stand leaf area was markedly higher in early coppice regrowth compared to seedling stands for at least 12 months. At the stand-scale, the water-use efficiency (WUE) of wood production was found to be lower in young coppice compared to seedling *E. globulus* because much of the newly developed above-ground biomass of coppice is lost during reduction to a single stem – a forestry practice that optimises economic return during harvesting (Drake et al., 2012). Despite this research, there

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remains considerable uncertainty whether the energy demands of newly developed coppice shoots enhance  $R$  in the supporting root system and whether this is associated with an altered TSS content in roots due to the mobilisation and use of storage reserves. Resolving this uncertainty is particularly relevant in the context of carbon sequestration and energy production, topics that have arisen in response to the integration of forestry into CO<sub>2</sub> sequestration initiatives and bioenergy production.

While photosynthesis and respiration have been well studied in the canopy of short-rotation forestry systems (for example, O'Grady et al. (2008, 2010)), much less is known about respiration in roots and its interaction with management practices. In this study we investigate the changes in CO<sub>2</sub> efflux, the  $R$  of woody stems and roots, during coppice regrowth in an *E. globulus* plantation. We hypothesise that soon after felling, newly developing coppice will have elevated energy demands compared to uncut trees and that this will manifest as a higher CO<sub>2</sub> efflux and depletion of the TSS pool within root biomass in order to supply the developing canopy with the substrates for growth. Our aim was to quantify CO<sub>2</sub> efflux and the concentration of TSS in roots and stems of newly developed coppice in order to understand how removal of *E. globulus* above-ground biomass affects the plant carbon dynamics and balance. To help achieve this aim we compared the pools and fluxes of C in coppice and uncut trees in the same plantation.

## 2. Materials and methods

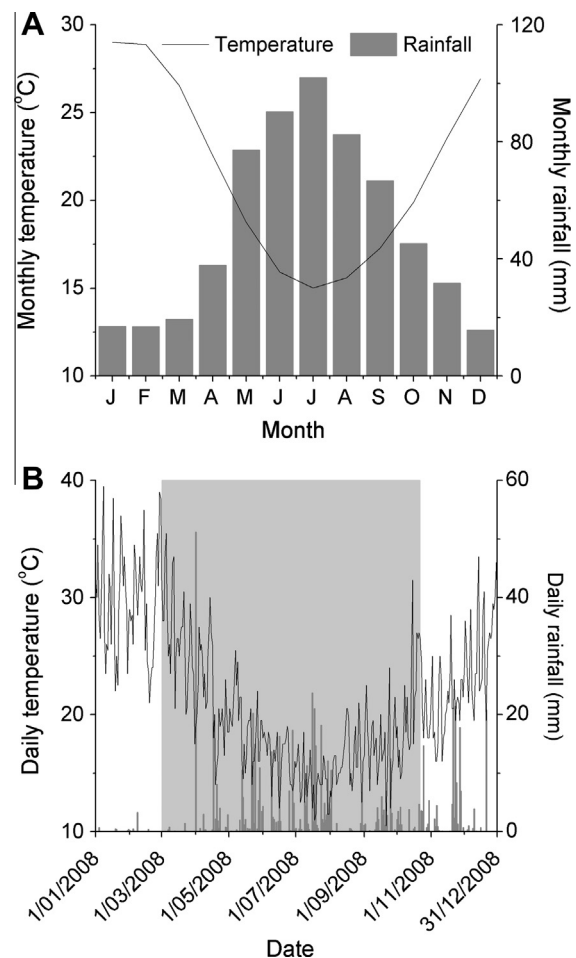
### 2.1. Experimental design

All measurements were carried out in an *E. globulus* plantation located in south western Australia (34.04°S, 116.69°E). Consistent with a Mediterranean climate, the plantation experiences hot dry summers and cool wet winters (Fig. 1A). Average annual rainfall between 1950 and 2011 was 610 mm with most rainfall occurring in winter (between May and September) (Australian Bureau of Meteorology, 2011). During summer, air temperature and vapour pressure deficit (VPD) can exceed 40 °C and 5 kPa respectively (Australian Bureau of Meteorology, 2011). Underlying the plantation is a deep soil profile composed of sand and gravel in the top 1 m grading to silty clay which occurs to a depth of around 8 m.

We established a fully randomised single tree plot experiment within a second-rotation *E. globulus* plantation. The trees were planted at a stocking density of 1000 stems per hectare and each tree received a starter fertiliser in the first rotation. We established three treatments within the measurement plot ( $n = 4$  randomly distributed trees per treatment): (1) control (uncut), (2) cut and allowed to coppice and (3) cut and allowed to coppice under shade. Control trees remained intact throughout the experiment whereas the coppice and shaded coppice treatments were felled approximately 1 month after the start of the experiment (March 2008). The unshaded coppice treatment was allowed to regenerate under natural conditions whereas the stool of the shaded coppice treatment was enclosed in shade cloth (Coolaroo, Braeside, Australia) made from high density polyethylene monofilament, which reduced light levels to 5% of ambient conditions. The shaded treatment was designed to encourage use of C held in storage reserves rather than photosynthate derived from new shoots. Parts of the root system of each tree were exposed around the base of the trunk to allow experimental access to tap roots and lateral roots. Whilst it was not being measured, this exposed area was covered with shade cloth. The shade cloth was the same type that was used in the shaded treatment. All of the felled trees produced a coppice resprout, but the shoots emerging from one stump in the unshaded coppice treatment died during the experiment. This individual was removed from analyses.

### 2.2. Biomass

At the start of the experiment height ( $h$ , m) and diameter at breast height (DBH, m) were recorded for each tree. The conical volume (Mendham et al., 2003) of each stem was calculated and was used to determine the amount of above-ground biomass according to the allometric functions derived by Rance et al. (2012). The ratio of below-ground biomass to above-ground biomass was estimated at 0.23 based on the study of Resh et al. (2003). For coppice, this meant that root biomass was estimated on the basis of the amount of above-ground biomass present prior to felling. We acknowledge that felling will have resulted in the partial loss of fine roots but it is likely that much of the coarse root fraction was retained during the development of coppice. At the conclusion of the experiment, the above-ground biomass emerging from each coppice stump was harvested and returned to a laboratory. In the laboratory all leaves were removed from stems and their area (m<sup>2</sup>) and dry weight (DW, g) measured. Leaf area was determined with a leaf area meter (model Li 3100C, Li-Cor Incorporated, Lincoln, USA). Leaf DW was measured after oven-drying at 70 °C for 48 h. Stems were also oven dried at 70 °C for 48 h and their dry weight determined.



**Fig. 1.** Climatic variables. (A) Average maximum monthly temperature and average monthly rainfall for the site. (B) Daily maximum temperature and daily rainfall during the calendar year of the experiment. The shaded area in B represents the period of the experiment. Data were obtained from Australian Bureau of Meteorology (2011).

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