Quantifying Above- and Below-ground Growth Responses of the Western Australian Oil Mallee, *Eucalyptus kochii* subsp. *plenissima*, to Contrasting Decapitation Regimes

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Resprouting in the oil mallee, *Eucalyptus kochii* Maiden & Blakely subsp. *plenissima* Gardner (Brooker), involves generation of new shoots from preformed meristematic foci on the lignotuber. Numbers of such foci escalated from 200 per lignotuber in trees aged 1 year to 3000 on 4- to 5-year-old trees. Removal of shoot biomass by decapitation 5 cm above ground in summer (February) or spring (October) resulted in initiation of 140–170 new shoots, but approx. 400 shoots were induced to form if crops of new shoots were successively removed until sprouting ceased and rootstocks senesced. Initially, the new shoot biomass of regenerating coppices increased slowly and the root biomass failed to increase appreciably until 1·7–2·5 years after cutting. Newly cut trees showed loss of fine root biomass, and structural roots failed to secondarily thicken to the extent shown by uncut trees. After 2 years, the biomass of shoots of coppiced plants was only one-third that of uncut control trees and shoot : root dry mass ratios of coppiced plants were still low (1·5–2·0) compared with those of the controls (average ratio of 3·1). Spring cutting promoted quicker and greater biomass recovery than summer cutting. Starch in below-ground biomass fell quickly following decapitation and remained low for a 12–18 month period. Utilization of starch reserves in naturally regenerating coppices was estimated to provide only a small proportion of the dry matter accumulated in new shoots. Results are discussed in relation to their impact on coppicing ability of the species under natural conditions or when successively coppiced for shoot biomass production.   © 2002 Annals of Botany Company

Key words: Coppice, short-rotation forestry, shoot growth, root growth, starch utilization, shading, rootstock decline, oil mallee, *Eucalyptus kochii* Maiden & Blakely subsp. *plenissima* Gardner (Brooker).

INTRODUCTION

The ability of herbaceous and woody species to generate new shoots from older basal regions of their shoots is well displayed throughout the plant kingdom and is prominent amongst both shrub and tree components of temperate ecosystems (Blake, 1983; Bell *et al.*, 1984; Del Tredici, 2001). Plants with this ability are commonly referred to as 'sprouter', 'resprouter' or 'coppicing' species. They collectively exhibit a broad range of morphological and physiological characteristics conducive to rapid regeneration of new shoots. In most cases, resprouting is initiated only after part or all of the original shoot system has been damaged, stressed or killed by natural agencies, or following deliberate removal of shoot biomass by man in harvesting for fodder, timber, paper pulp, firewood or biomass for generation of electricity.

Regardless of life form and sprouting morphology, early growth of shoot sprouts is associated with some degree of mobilization of previously accumulated reserves of nutrients, starch, sugars and other soluble and insoluble energy reserves (Woods *et al.*, 1959; Zimmerman, 1971; Canadell and López-Soria, 1998; Garcia *et al.*, 2001). Where comparisons have been made between cohabiting groups

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of shrubby species of resprouting capacity (sprouters) or those killed by fire (obligate seeders) within Western Australian fire-prone ecosystems, root reserves of starch occur in consistently greater amount in the sprouters (Pate *et al.*, 1990; Bell *et al.*, 1996). Sprouters are also typically slow growing, slow to commence reproduction and much longer lived than counterpart obligate seeders (Bell *et al.*, 1984).

'Mallee' eucalypts are characterized by multiple woody stems arising from an underground lignotuber (Kerr, 1925; James, 1984). The latter houses a large store of potential bud-forming sites carrying the capacity for rapid regeneration of a canopy after decapitation. A lignotuber typically contains several thousand of such 'meristematic foci' (Noble, 2001), each of which is capable of producing several individual shoots (Noble, 1989; Burrows, 2000, 2002). Opinions differ as to whether the lignotuber is also important as a major storage site of non-structural carbohydrate reserves (Carrodus and Blake, 1970; Bamber and Mullette, 1978; Del Tredici, 2001; Noble, 2001).

Mallees are very long lived, with some species (e.g. the Meelup mallee, *Eucalyptus phylacis*) reaching ages possibly exceeding 6000 years (Rosetto *et al.*, 1999). With the death of central parts and peripheral fragmentation of the plate-like lignotuber, close groupings of genetically identical individuals may be formed around a single parent tree. Such

clones are likely to have experienced numerous cycles of shoot destruction and replacement and accordingly carry a continued capacity to implement coppicing processes at fairly frequent intervals during their life (Mullette, 1978; Tyson *et al*., 1998; Rosetto *et al*., 1999; Noble, 2001).

Regularly coppiced plantings of mallee eucalypts are being trialled in the Western Australian wheatbelt for the generation of bio-electricity, extraction of essential leaf oils and production of activated carbon from shoot biomass (Enecon Pty Ltd, 2001). Suitable 'oil mallee' species such as *E. kochii* subsp. *plenissima*, *E. horistes* and *E. loxophleba* subsp. *lissophloia* (Wildy *et al*., 2000*b*) are typically established in narrow belts across conventional cereal and grazing land where they benefit from the 'edge effect' of greater access to soil moisture, nutrients and light than would occur if they were competing in plantation layout. The incorporation of a deep-rooted, summer-active component into farming systems such as one based on oil mallee is also viewed as being importance in restoring the hydrological balance in situations where continued use of inadequately transpiring annual crop and pasture species has led to dangerous rises in water tables and resulting dryland salinization of cleared landscapes (State Salinity Council, 2000). High yielding biomass production on a continuous basis is important for the economic viability of an integrated bio-energy production industry (Enecon Pty Ltd, 2001).

Rates of regenerative growth of coppicing species are generally influenced by both the original vigour of the uncut plant (Jacobs, 1955; Hillis and Brown, 1984; Sims *et al*., 1999) and the season of cutting. In Mediterranean climates, it is well established that autumn cuts result in poorer eucalypt regeneration than winter or early spring cuts (Milthorpe *et al*., 1994; Wirthensohn and Sedgley, 1998; Wildy *et al*., 2000*b*; Noble, 2001). As described generally for the closely-related *Melaleuca* genus (Murtagh, 1996), the optimal cutting time in temperate mallee eucalypts is one in which production of new shoot biomass coincides with the natural seasonal flush growth of intact plants of the species. In Mediterranean climates, this generally corresponds to the late spring and early summer period when temperatures are warm and soil moisture has been replenished by winter rains (Noble, 1989; Specht, 1996; Wildy *et al*., 2000*a*).

Previous cutting history also appears to affect productivity and survival. When first cut at ages of 1–3 years and then repeatedly on 1–2 year rotations, plantation-grown mallees can exhibit progressively reduced yields (Milthorpe *et al*., 1998) and increased mortality (Eastham *et al*., 1993; Wildy *et al*., 2000*b*). This parallels what has been experienced in non-mallee eucalypts grown on 6–10 year rotations (Reidacker, 1973; Schönau, 1991; Barros and Novais, 1996; Nambiar, 1999) and in other temperate woody species (Ceulemans and Deraedt, 1999; Mitchell *et al*., 1999; Hytönen and Issakainen, 2001). Early research attempted to explain such declines through depletion of stored carbohydrate and nutrient reserves, but this may be only part of a complex set of interacting factors that are not well understood (Chapin *et al*., 1990; Sennerby-Forsse *et al*., 1992). It is possible that, in part, too-frequent cutting of slowly regenerating plants may not allow below-ground

reserves to be replenished. Similarly, root systems may cease to grow or partly senesce while regenerating plants are preferentially directing photosynthates to new shoots (Hodgkinson and Becking, 1977; Steinbeck and Nwoboshi, 1980; Dickmann *et al*., 1996). In addition, a disrupted shoot : root ratio may cause a large proportional burden in root respiration relative to meagre photosynthate returns from coppiced shoots (Noble, 2001), and regularly cut stumps are also likely to be more susceptible to disease (Christersson *et al*., 1992).

To further understand the coppicing ability of an oil mallee species [*E. kochii* Maiden & Blakely subsp. *plenissima* Gardner (Brooker)], which has been widely planted over the past 8 years in the drier zones of the wheatbelt of south-west Western Australia, we first examined the morphology of lignotuber development in planted stands differing in age. Then, using a 4–5-year-old stand for detailed investigation, we studied coppicing responses in terms of recovery of shoot biomass, changes in root biomass and quantification of below-ground starch contents under contrasting cutting regimes in comparison with uncut trees. The overall aim was to describe the general biology of coppicing in the species and thereby provide a basis for the design of management practices to enable continual production of shoot biomass from short-rotation coppicing stands.

MATERIALS AND METHODS

Principal site for studying coppicing under different cutting regimes

At the principal trial site (30°09′S, 117°12′E) (Fig. 1A and B) near Kalannie, in the central wheatbelt of Western Australia, alley plantings of *E. kochii* subsp. *plenissima* had been established as seedlings in July 1994 immediately after ripping and scalping of topsoil to remove weeds. Fertilizer was not applied since the soil was relatively fertile through continuous use of fertilized crops of wheat and nitrogen-fixing lupins (*Lupinus* spp.). Each belt of trees consisted of two rows 2 m apart, with an average of 1·8 m spacings between trees within rows. The average alley width available for crop/pasture between belts of trees was 90 m. Planting density was 2820 trees per hectare in that part of the land surface devoted to trees, or the equivalent of 121 trees ha^{-1} across the whole ecosystem at the time of planting. Since only 85 % of seedlings survived the dry year of establishment (238 mm rainfall in 1994), the effective density at the start of the study was reduced to 103 trees ha^{-1}. Measurements were made between February 1999 (when trees were 4·6 years old) and October 2001 (trees aged 7·2 years).

The extra-dry Mediterranean climate (Beard, 1984) of the Kalannie region of the wheatbelt (Table 1) typically features hot, dry summers (December–February) and cool, wet winters (June–August). The long-term (74 year) annual average rainfall at Kalannie is 319 mm (Bureau of Meteorology, Australia). However, 1999 was an exceptionally wet year (504 mm falling at the principal study site) and unusually heavy summer rain fell in 1999–2000 and again in

FIG. 1. A, General view of study site showing hedges of decapitated (arrows) and intact 4·6-year-old *Eucalyptus kochii* trees at the time of first cutting in February 1999. B, Close-up of adjacent uncut and coppicing trees in February 2001 (note 3 m high marking pole dividing quadrats). C, Six-month-old seedling showing swellings on and above hypocotyl region. D, Older (2·6 year) seedling showing greater enlargement of swellings especially in the hypocotyl region. E, Sapling aged 4·6 years showing fusion of swellings into a lignotuber completely enveloping the lower base of the shoot. F, Surface of cambial face of one of the composite swellings on a lignotuber with bark removed showing 'pimple-like' meristematic foci, any of which can generate new shoots. Bar = 10 mm. G, Remains of lignotuber and lateral and sinker roots of an old *E. kochii* plant removed during clearing of the land prior to the current study.

TABLE 1. *Monthly rainfall and temperature data for Kalannie, Western Australia*

	J	F	M	A	M	J	J	A	S	O	N	D
Rainfall (mm)												
1999	25	4	113	11	147	49	40	22	29	18	20	26
2000	56	0	156	4	3	15	40	19	17	0	0	11
2001	72	22	7	0	24	2	51	18	19	7	11	0
Long-term average rainfall (mm)	14	16	24	24	44	57	50	38	19	14	9	10
Mean max. daily temp. (°C)	33	33	29	26	21	18	16	17	21	25	29	34
Mean min. daily temp. (°C)	19	19	16	14	9	5	6	5	7	10	13	18

Rainfall data for 1999–2001 (recorded at the principal trial site) and mean daily temperatures (the average of data recorded at Kalannie between 1999 and 2001) were provided by Agriculture WA. The long-term (74-year) average monthly rainfall for Kalannie was supplied by the Bureau of Meteorology, Perth.

2000–2001 (see Table 1). The soil at the principal study site was a gradational yellow sand (Gn 2·21: Northcote, 1979) overlying a siliceous hardpan of 'silcrete' at varying (1–8 m) depths across the study site. Roots of planted and native mallees in the region were found to have penetrated through weak zones in the silcrete, thereby possibly gaining access to groundwater below this layer.

Lignotuber development and increases in potential resprouting capacity with age

Lignotuber development was studied in February 1999 by random sampling across a range of differently aged (0·6–4·6 years) plantings of as yet uncut saplings selected in the Kalannie area. All sites involved deep yellow sands similar to those at the principal site. Five trees of each age class were excavated, including one set of 4·6-year-old trees from the principal study site referred to above. Residual soil and the rough outer bark around the shoot : root junction were removed, thus enabling counts to be made of the number and size (outer diameter) of the distinct swellings present on the lignotuber and adjacent lower shoots (Fig. 1C–E). All bark down to cambium level was peeled off the lignotuber, surrounding stem and upper root to expose the closely spaced groups of pimple-like 'meristematic foci' (approx. 1 mm diameter) typically encountered within each swollen region on or in the vicinity of the lignotuber (Fig. 1F).

Decapitation and shading regimes

At the principal study site, a random series of 100 m long quadrats of tree belt was selected (Fig. 1A and B show the junction of coppicing and uncut trees) and stems of all trees were cut with a chainsaw to 5 cm above ground level. The quadrats designated for cutting were sited within a fully randomized block design comprising 16 quadrats cut in late summer (February), a further 16 cut the following spring (October) of 1999 and a matching set of 16 quadrats of uncut saplings incorporated as controls. Following initial

cutting, mortality was only 2·0 and 0·5 % for trees cut in February and October, respectively.

In each of the 16 coppice quadrats used for the two seasons of cutting, most trees were allowed to regenerate naturally for the duration of the study (C_N treatment, Table 2), while two in each quadrat were subjected to additional decapitations on a 3-monthly basis (C_R treatment). To further test the resprouting ability of rootstocks, another three tree stumps (C_S treatment) in each quadrat were left to regenerate while caged in multiple layered shade cloth (permitting penetration of approx. 25 % of ambient light and designed to maintain young shoots at or near their CO_2 compensation point), and, finally, two trees were subjected to both shading and repeated 3-monthly decapitation (C_{SR} treatment, Table 2).

Counts of resprouting shoots

Numbers of shoot sprouts [equivalent to the fascicles of Noble (2001)] arising from lignotubers were counted at 3-monthly intervals after decapitation (see Table 2). Counting was carried out non-destructively for C_N plants while for C_R and C_{SR} plants, shoots were counted at the time of each 3-monthly decapitation.

Measurement of shoot and root biomass

Shoot biomass of control uncut trees and trees regenerating naturally from cutting in February or October 1999 (C_N) was measured at ten sampling dates between February 1999 and February 2001 (Table 2). At each sampling date, 42 randomly selected trees of these treatments were cut to 5 cm above ground level and weighed fresh in the field. Subsamples of leaf, twig and larger stems were collected, weighed fresh and then oven-dried at 70 °C to constant weight for fresh : dry weight conversions.

For C_R and C_{SR} trees, shoot biomass produced after initial decapitation was measured at each further 3-monthly decapitation event. Shoot biomass of C_S plants was

Table 2. *Experimentation, general treatment codes, sampling frequency and numbers of replicates in the study of coppicing in* Eucalyptus kochii *subsp.* plenissima *at Kalannie, Western Australia*

Code	Treatment	Measurements Shoot biomass	Shoot number	Below-ground biomass	Below-ground starch
	Uncut saplings (control)	2- to 5-monthly (42)	–	2- to 5-monthly (10)	2- to 5-monthly (10)
	Decapitated trees				
C_N	No further intervention	2- to 5-monthly (42 × 2 seasons)	3-monthly (16 × 2 seasons)	2- to 5-monthly (10 × 2 seasons)	2- to 5-monthly (10 × 2 seasons)
C_S	Shading	Final (48 × 2 seasons)	–	Final (10 × 2 seasons)	Final (10 × 2 seasons)
C_R	Repeated 3-monthly decapitation	3-monthly (32 × 2 seasons)	3-monthly (32 × 2 seasons)	Final (10 × 2 seasons)	Final (10 × 2 seasons)
C_{SR}	Shading + repeated decapitation	3-monthly (32 × 2 seasons)	3-monthly (32 × 2 seasons)	Final (10 × 2 seasons)	Final (10 × 2 seasons)

All measurements on decapitated trees were carried out both for plants first cut in February 1999 or in October 1999. Sampling frequency is indicated as 'final' for C_S, C_R and C_{SR} where a single measurement was made at the end of the experiments (when approx. 15 % of plants had died, after approx. 12 months). These final measurements were then made on the remaining plants. For all treatments, the number of trees (replicates) sampled at each date is shown in parentheses. Note that below-ground starch measurements were made between July 1999 and February 2001 only.

measured 1 year after decapitation. Shoots were oven-dried at 70 °C to constant weight before weighing.

Below-ground biomass was excavated to assess root and lignotuber biomass using a bobcat which progressively transferred soil plus root material onto a mobile mechanical sifting device. The readily recognizable lignotuber was removed with a chainsaw at the point of root proliferation and weighed fresh. Root biomass was separated visually into lateral (flaking bark, straight) and sinker (non-shedding bark, contorted shape) roots. These were then weighed fresh, fed through a garden chipper, and a small sub-sample frozen immediately pending oven-drying for fresh : dry weight conversions and starch analysis (see below). A section taken through the lignotuber using a chainsaw was also frozen for starch analysis and fresh : dry weight conversions. For control saplings and C_N plants, the average ratio of lignotuber weight : rest-of-shoot weight for each treatment at each root harvest was used to estimate total shoot biomass (i.e. shoot including lignotuber) of the corresponding 42 trees from a treatment and sampling date (described above).

Root and lignotuber biomass was harvested for control saplings and C_N trees from ten plants per treatment at each sampling date and at 2–5 month intervals during the study period. Root biomass of C_R, C_S and C_{SR} plants was sampled for ten plants from each treatment at one final sampling date 12 months after the initial decapitation of the plants (February or October 2000) (Table 2).

The regularly employed root harvesting procedure involved a 'standard' excavation 1 m deep and extending 1 m out from the tree stump into the alley (with no trees) and similarly out to the midpoint between neighbouring trees (Fig. 2). To estimate the proportions of lateral and sinker root biomass not likely to be recovered by the 'standard' procedure, selected trees were subjected to a series of more 'extensive' excavations executed in 1 m stages to a depth of 4 m and 5 m out into alleys (see Fig. 2). These were carried out on three trees (including both uncut and coppiced plants) at five sampling occasions throughout the study period. Such excavations were found to harvest virtually all lateral root biomass and all but the lowermost parts of deeply penetrating sinker roots. By following the attenuation in recovery of sinker root biomass for each successive 1 m level of excavation, it was estimated that unrecovered root biomass extending below the 4 m depth limit would be equivalent to only 4–8 % of the total root biomass of trees of the age class under study. Comparisons of data from these 'standard' and occasional 'extensive' excavations indicated that the standard (incomplete) excavation would typically recover 80 % of the lateral root biomass and 50 % of that of sinker roots.

Shoot : root dry weight ratios were determined for the excavated C_N and intact trees at each sampling date. Throughout the text, the term 'root' refers to the full extent of the root system, excluding lignotuber biomass, while 'shoot' includes both the aerial canopy removed in a normal harvest procedure (leaf + stem) plus the shoot stump remaining above ground and the lignotuber. Conversely, the term 'below-ground biomass' refers to the calculated full extent of roots + lignotuber (i.e. that remaining after shoot harvest).

Study of the effect of coppicing on secondary growth of roots

An anatomically based technique for evaluating possible inhibitory effects of cutting on root growth of coppiced (C_N
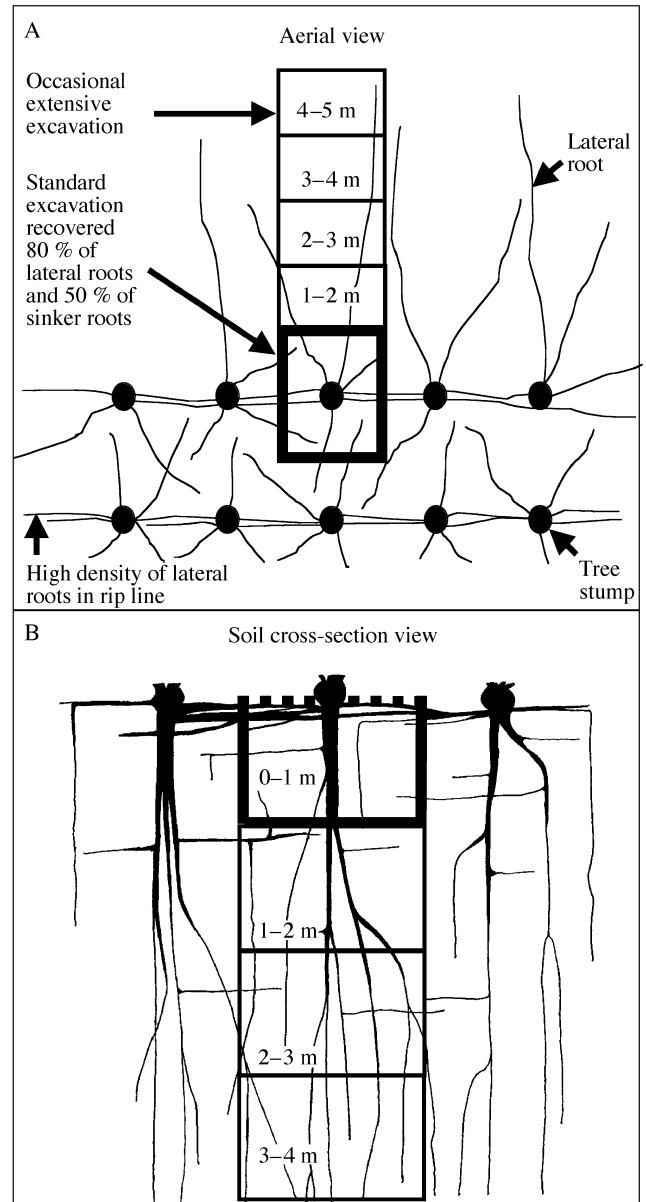

FIG. 2. Stylized root systems and dimensions of excavations used in sampling root biomass for mallees grown in twin-row hedges, as shown by an aerial view (A) and a cross-sectional view through the soil profile (B). The 'standard' excavation (bold lines) was 1 m deep and extended from to midpoint between neighbours and 1 m out into the alley (with no trees). Occasional 'extensive' excavations (non-bold lines) allowed regular standard excavations to be scaled-up to include all root biomass, which included the estimated 4–8 % of deeply penetrating sinkers that were not recovered in the extensive excavation.

trees) compared with uncut trees was initiated 3 months after setting up the summer or spring coppice treatments (May 1999 or January 2000, respectively). It involved non-destructive exposure of one or two major sinker and lateral roots of each of 16 randomly selected coppicing or uncut trees and removal of a small 0·5 cm² window of bark down to the cambium to expose the outer layer of xylem. The portion removed in each case involved less than 12 % of the root circumference and was therefore unlikely to have a major deleterious effect on subsequent secondary growth of the root. Treated roots were re-covered with soil and left for 21 months (until February or October 2001). A 10 cm length of root including the 'window' was then harvested and transversely sectioned to assess the extent of increase in root stele diameter in undamaged radial sections of the root to that of the non-growing exposed portion underlying the window. Comparative estimates were thus made of the proportional extents to which secondary growth of roots of coppicing trees had been reduced over the 21-month period relative to that exhibited by uncut trees.

Starch concentrations and total starch reserves of below-ground biomass

For each tree excavated for root biomass between July 1999 and February 2001, starch concentrations were determined separately for lignotubers, lateral roots and sinker roots. Dried sub-samples of material of each plant part were finely ground to pass through a final mesh width of 0·5 mm. Starch was extracted from a 0·1 g sub-sample using the perchloric acid method (Pucher *et al.*, 1948) and then assayed using the phenol method (Dubois *et al.*, 1956; Pate *et al.*, 1990) giving reproducible recoveries of starch, including both amylose and amylopectin. Starch concentrations in roots and lignotubers are given on a weight for weight basis (g starch per g organ dry matter) and are expressed as percentages.

Since determinations of starch in root biomass collected from standard excavations required extrapolations based on more extensive excavations, it was necessary to test whether the starch concentration in outer-lying root biomass differed appreciably from that obtained from more proximally located roots recovered in standard excavations. Three uncut saplings and coppicing C_N trees from both seasons of initial cutting were sampled in this way in July 2000 and February 2001. The resulting data (Table 3) showed general

trends towards an increased concentration of starch in root biomass with distance out along a lateral or down a sinker root (e.g. see Kolb and McCormick, 1991). An appropriate correction factor was therefore applied when scaling up starch contents of both lateral and sinker roots from a standard excavation to provide a more accurate assessment of total starch concentration (and consequently total starch storage) within the entire below-ground biomass of each tree investigated.

RESULTS

Development of lignotuber and resprouting potential with age

Distinct opposing and usually paired sets of swellings developed at, or above, the cotyledonary node of juvenile trees during their first season of growth (Fig. 1C). Further swellings then arose at various positions close to the initial pair (Fig. 1D and E) until some 15–20 such structures were typically present on rootstocks of second and third year trees (Fig. 3A). As the swellings enlarged further, they fused laterally with others to form an aggregate collar-like lignotuber of greater diameter than that of adjacent parts of stem and root (Fig. 1E), and the mean number of distinctly separate swellings began to decrease (Fig. 3A). Remnant rootstocks of very old trees of *E. kochii* removed during clearing of virgin bush for agriculture possessed lignotubers of truly massive proportions, with a complex complement of thick lateral and tap roots arising at various positions below the lignotuber (Fig. 1G).

Counts of meristematic bud foci on debarked stumps (Fig. 1F) showed 2-year-old trees to possess approx. 500 foci per lignotuber, rising to 1000 in 3-year-old trees and then to 3000 per lignotuber for 5-year-old trees (Fig. 3A). When cut at age 4·6 (February cutting) or 5·2 (October cutting) years, stumps coppicing unhindered (C_N treatment) showed similar intensities of coppice shoot production, viz. 140–170 per lignotuber (Fig. 3B).

Resprouting of repeatedly decapitated and/or shaded stumps (C_R, C_S and C_{SR} treatments)

Repeated 3-monthly shoot removal after initial cuts in either February or October 1999 [treatments C_R (repeated decapitation) and C_{SR} (shading + repeated decapitation); see Table 2] resulted in eventual death of the plants. Each

Table 3. *Starch concentrations (± s.e.) in* Eucalyptus kochii *roots in the 'standard' excavation zone (see Fig. 2) and in the remainder of roots collected in 'extensive' excavations beyond the standard excavation zone*

	Uncut saplings (% of dry mass)	February-cut coppice (% of dry mass)	October-cut coppice (% of dry mass)
Lateral roots			
In standard excavation	2·1 (± 1·0)	1·4 (± 0·4)	1·7 (± 0·4)
Beyond standard excavation	3·8 (± 0·9)	2·6 (± 0·9)	3·5 (± 2·0)
Sinker roots			
In standard excavation	1·6 (± 0·7)	1·6 (± 0·7)	1·3 (± 0·2)
Beyond standard excavation	3·8 (± 1·6)	1·2 (± 0·5)	2·9 (± 0·7)

successive regeneration event released between 40 and 170 accessory shoots per plant (Fig. 4A) to give cumulative numbers over the four regeneration intervals of approx. 400 shoots per tree. There were no significant differences in shoot numbers produced by matching pairs of shaded (C_{SR}) and unshaded (C_R) trees at any sampling date, thus data for shaded and unshaded trees were combined. Significantly more shoots ($P < 0.05$) were produced at the initial resprouting event than in the final decapitation event for trees cut originally either in February or October. The new shoot biomass produced at successive harvests for the same treatments (Fig. 4B) showed greatest amounts of coppice shoot biomass produced during the natural period of shoot extension of the species, regardless of the number of previous coppice crops that had been removed.

Table 4 summarizes data for the end of the 1-year period following initial decapitation of saplings in either February or October. Shaded trees (C_S and C_{SR} together) produced significantly less new shoot biomass over this period (0·11–0·29 kg d. wt per plant) than repeatedly cut, unshaded plants (C_R) (0·27–0·47 kg d. wt per plant) ($P < 0.001$).

Shoot biomass of uncut trees and C_N coppice from a summer or spring cut

Coppice shoots recovering naturally from a single decapitation event in February or the following October

(C_N) showed slow recovery in the first year after cutting, and this was especially apparent for plants cut in February (Fig. 5A). After 2·0 years of coppice regrowth, February-cut plants had restored only 53 % of their original shoot biomass, compared with 76 % for October-cut trees (Fig. 5A). Increments in shoot biomass production over the 2·7-year study period were greatest for uncut saplings ageing from 4·6–7·2 years (20 kg d. wt per plant) (Fig. 5A).

Excavations of root biomass

Excavations showed that all trees had developed a number of deeply penetrating sinker roots, originating directly below the stem (see Fig. 1E), and also from shallow lateral roots that radiated out to 5 m at most from the stem base. Most trees also possessed horizontally extending lateral roots that developed from sinker roots at depths down to 2–3 m. Lignotubers were calculated to comprise on average 17 % of total below-ground biomass compared with 41 % for lateral roots and 42 % for sinker roots.

Observations on excavated root systems of all decapitated plants showed that large amounts of fine roots (<2 mm) had
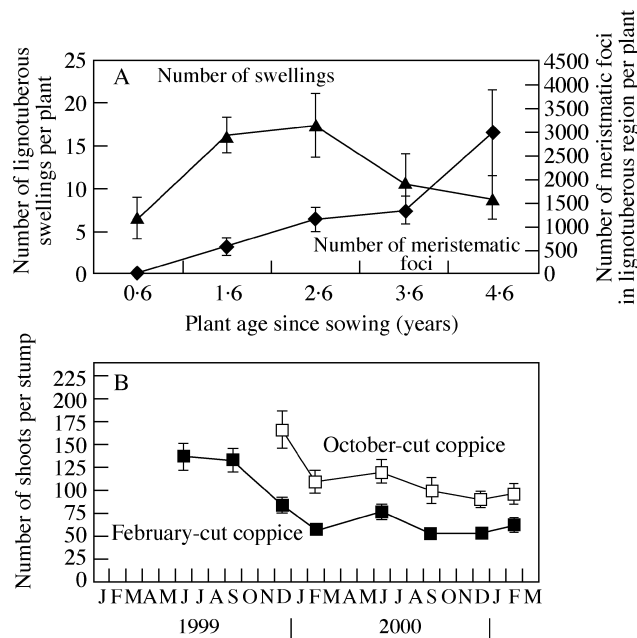

Fig. 3. A, Number of swellings on the hypocotyl region and lower stem of uncut saplings of *Eucalyptus kochii* of various ages showing an initial increase and then coalescence of the swellings (see Fig. 1C–E) as trees aged, and the overall increase with plant age in the number of meristematic foci (see Fig. 1F) of the lignotuber. B, Number of new shoot sprouts arising from stumps of 4- to 5-year-old trees decapitated in summer (February 1999) or the following spring (October 1999) (C_N treatment). Note that the original complement of shoots was reduced through senescence of smaller shoots. Vertical bars represent 2 s.e.
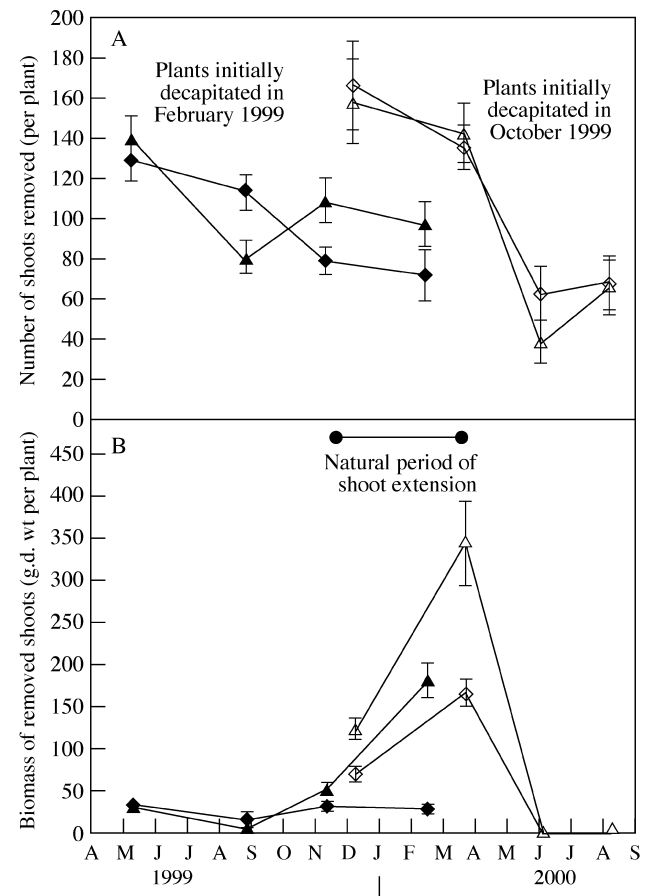

Fig. 4. Number of new coppice sprouts (A) and new sprout biomass (B) produced per tree by shaded (diamonds) and non-shaded (triangles) *Eucalyptus kochii* stumps subjected to repeated decapitation following initial cutting in February 1999 (closed symbols) or October 1999 (open symbols). Vertical bars represent 2 s.e.

senesced. Root biomass of plants subjected to repeated decapitation and/or shading was consistently lower than the original root biomass measured at the time of cutting (Table 4). Occasionally, the root system of these plants had also been attacked by fungi and borer insects. Net increases in root biomass of C_N trees ceased over a period of 1·7 years for October-cut trees and 2·5 years for February-cut trees (Fig. 5B). By contrast, root biomass increased three-fold for uncut saplings over the study period (Fig. 5B). For the treatments sampled temporally, root biomass varied significantly with time ($P < 0.001$, uncut saplings; $P = 0.001$, February-cut C_N trees; $P = 0.046$, October-cut C_N trees).

Root secondary thickening following decapitation

As shown in Table 5, marked depressions in secondary growth of major roots of cut (C_N) plants relative to uncut plants were also recorded for roots that had been partly debarked and left to grow for 21 months. Combining data for lateral and sinker roots (separately for the two 21 month periods) showed significantly greater increases ($P < 0.001$ for both) in root secondary thickening in uncut control trees (75–130 %) compared with February-cut trees (14–26 %) or October-cut trees (23–30 %).

Shoot : root ratios

Shoot : root dry matter ratios for uncut saplings ranged from 2·5 to 3·5 (Fig. 5C). This variation resulted from the different phenologies of root and shoot growth (e.g. Specht,

1996). In contrast, shoot : root dry matter ratios of decapitated C_N trees increased continuously until July 2001, but failed to reach the values of uncut plants.

Starch concentrations and below-ground starch reserves

Concentrations of starch measured in regularly excavated portions of below-ground biomass were significantly higher in uncut saplings (mean of all starch samples 2·9 %) than in coppices regenerating unhindered from a single decapitation in either February or October (1·4 and 1·7 %, respectively; $P < 0.001$). Lignotubers had significantly lower ($P < 0.05$) concentrations of starch (generally less than 1 %) than either lateral or sinker roots in all of the above treatments (Table 6).

Combining dry weight values for the full extent of below-ground biomass with the starch concentration data above (appropriately corrected for higher starch concentrations in outlying roots as shown in Table 3) gave calculated values for mean below-ground starch concentrations in the range of 2–6 % of dry mass for uncut saplings and 1–5 % for regenerating C_N coppice (Fig. 6A). Below-ground starch concentrations varied significantly with season ($P < 0.001$ combining C_N and uncut treatments), with uncut saplings showing peak starch concentrations just prior to the period of main shoot extension growth in spring of 1999 and 2000, followed by a decline in starch content in summer. Fluctuations in the total below-ground starch reserve pools (Fig. 6B) followed similar patterns, except that the smaller root biomass of coppiced plants (see Fig. 5B) resulted in total starch reserves in below-ground parts remaining

TABLE 4. *Summary of changes in above- and below-ground pool sizes following contrasting decapitation regimes in* Eucalyptus kochii *growing at Kalannie, Western Australia, over a 1-year period for 4- to 5-year-old plants cut initially in either February or October 1999*

	Total shoot biomass produced over period (kg d.wt per plant)	Change in root biomass (kg d.wt per plant)	Change in lignotuber biomass (kg d.wt per plant)	Final below-ground starch conc. (% of d.wt)	Calculated change in below-ground starch store (kg per plant)
Between February 1999 and February 2000 (February-cut trees)					
Uncut controls	6·56*	+1·64*	+0·31	4·7[†a]	+0·03[‡]
C_N	0·88*	−0·40*	−0·01	2·1[†b]	−0·18[‡]
C_R	0·27	−0·57	−0·00	0·5[c]	−0·24[‡]
C_S	0·14	−0·54	−0·10	0·9[bc]	−0·11[‡]
C_{SR}	0·11	−0·28	−0·10	0·7[c]	−0·23[‡]
Between October 1999 and October 2000 (October-cut trees)					
Uncut controls	6·83*	+1·58*	+0·31	5·7[†a]	+0·13[†]
C_N	2·46*	−0·50*	+0·02	4·6[†a]	−0·09[†]
C_R	0·47	−0·64	−0·21	1·0[b]	−0·29
C_S	0·29	−1·27	−0·16	0·4[b]	−0·31
C_{SR}	0·24	−1·10	−0·16	0·9[b]	−0·28

Coppice treatments were C_N (regenerating naturally after the initial cut), C_R (repeated 3-monthly decapitation), C_S (shaded) and C_{SR} (shaded + repeated decapitation) and are compared with control saplings left uncut. Significant differences ($P < 0.05$) in starch concentrations in total below-ground biomass are shown by different superscript letters separately for both of the year-long periods.
  * Data calculated from Fig. 5.
  [†] Data taken from Fig. 6.
  [‡] Original starch concentration at time of cutting estimated as 250 g per plant from extrapolation of Fig. 6B since comprehensive starch analyses were not carried out until July 1999.

significantly lower ($P < 0.05$) than those of uncut saplings until February 2001. October-cut trees possessed a significantly greater total below-ground starch store than the February-cut trees ($P = 0.003$) despite starch concentrations not varying significantly between the two (see Fig. 6A).
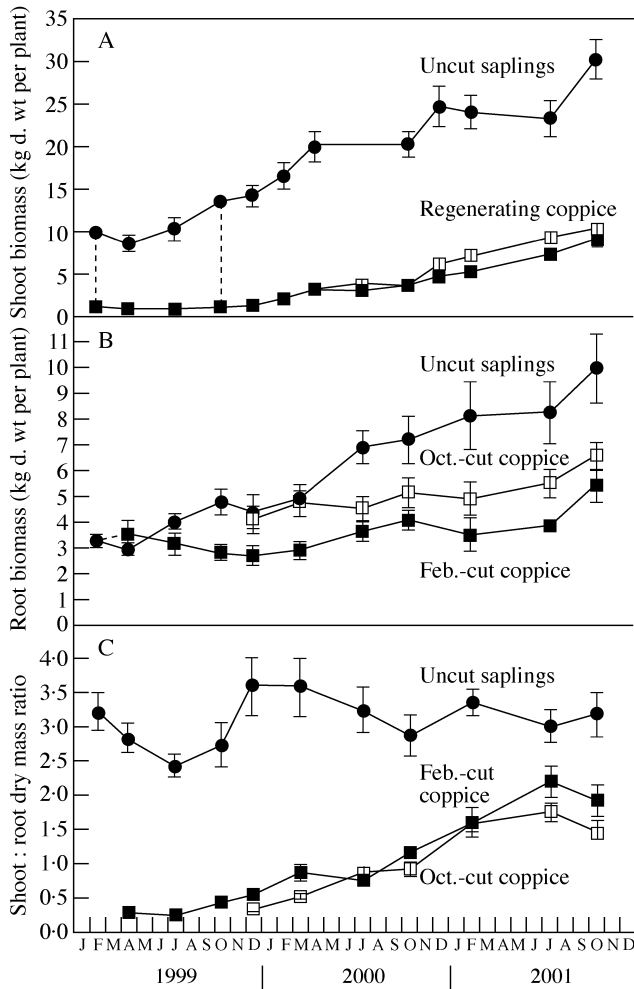

FIG. 5. Comparisons of shoot biomass (A), root biomass (B) and shoot : root dry weight ratio (C) of 4- to 7-year-old trees of *Eucalyptus kochii* left intact (uncut saplings, closed circles) or coppiced (C_N treatment) in summer (February 1999 cut, closed squares) or the following spring (October 1999 cut, open squares). Dashed lines indicate time of cutting. Vertical bars represent 2 s.e.

DISCUSSION

Lignotuber development in the mallee eucalypt, *Eucalyptus kochii* subsp. *plenissima*, showed a similar pattern to that recorded for a wide range of eucalypts (Chattaway, 1958; Carrodus and Blake, 1970; Graham *et al.*, 1998). Meristematic foci from which shoot buds can arise increased markedly in number as lignotubers aged, with several hundred present on 2-year-old seedlings and over 1000 on 4-year-old saplings. Once the shoot system of 4- to 5-year-old *E. kochii* was removed, in excess of 100 new shoots developed from each lignotuber. Subsequently, a large proportion of the smaller of these new shoots senesced within the first year (Fig. 3B). With further attrition over subsequent years, coppice shoot numbers would be expected to reduce much further until only 12 or so shoots remain (see scheme of Noble, 1989), as is typically observed during resprouting of naturally occurring, fire-decapitated populations of the species at sites close to the plantings at Kalannie.

A greater number of meristematic foci could be induced to commence growth if each crop of new growth was removed (e.g. see Zammit, 1988; Canadell and López-Soria, 1998). However, the 400 shoots produced by such repeatedly decapitated plants was far fewer than the potential 3000 or so discernible on 5-year-old lignotubers. Regardless of the fact that lignotuber size and potential bud number would be unlikely to increase further for more than a year after cutting (Table 4), the large store of remaining foci available for new growth would still be expected to allow coppicing to take place even if young trees were repeatedly cut on rotations of less than 1 year.

Lignotubers of *E. kochii* appear less important as starch storage organs than they are as providers of replacement shoot meristems after decapitation (c.f. Bamber and Mullette, 1978; Del Tredici, 2001). Lignotubers in this study possessed consistently lower starch concentrations than roots (see Table 6), which may be attributed to a lack of suitable storage tissue (Carrodus and Blake, 1970; Noble, 2001). Combined with the fact that the lignotuber contributed on average only 17 % of the below-ground biomass, this organ would have contributed just 5–10 % of the starch reserves of the recently decapitated *E. kochii* plants in this study.

The variations in above-ground coppicing performance between trees of *E. kochii* from contrasting decapitation treatments (see Table 4) did not appear to be explained by

TABLE 5. *Secondary root thickening over a 21-month period in control* Eucalyptus kochii *trees compared with trees decapitated once*

	Comparison 1		Comparison 2	
	February-cut coppice	Uncut sapling	October-cut coppice	Uncut sapling
Stem	–	88 ($\pm$ 9)	–	213 ($\pm$ 36)
Lateral roots	26 ($\pm$ 10)	86 ($\pm$ 17)	23 ($\pm$ 9)	129 ($\pm$ 23)
Sinker roots	14 ($\pm$ 8)	74 ($\pm$ 9)	30 ($\pm$ 7)	70 ($\pm$ 17)

Data are expressed as mean percentage increase ($\pm$ s.e.) in wood cross-sectional area.

TABLE 6. *Starch concentrations measured in excavated portions of below-ground organs of uncut and naturally regenerating coppice of* Eucalyptus kochii *at Kalannie, Western Australia*

	Mean of all samples (% of dry mass)	Range of all means across harvests (% of dry mass)
Uncut saplings		
Lignotuber	0·77[c]	0·5–1·5
Lateral roots	3·59[a]	1·7–5·4
Sinker roots	4·07[a]	1·2–6·2
February-cut coppice		
Lignotuber	0·41[c]	0·1–1·5
Lateral roots	1·81[b]	0·9–3·9
Sinker roots	1·85[b]	0·7–3·8
October-cut coppice		
Lignotuber	0·37[c]	0·3–0·4
Lateral roots	2·21[b]	1·2–4·6
Sinker roots	2·29[b]	1·5–3·8

Different superscript letters indicate significant differences ($P < 0.05$) between organs across all treatments using Tukey's pairwise comparison.
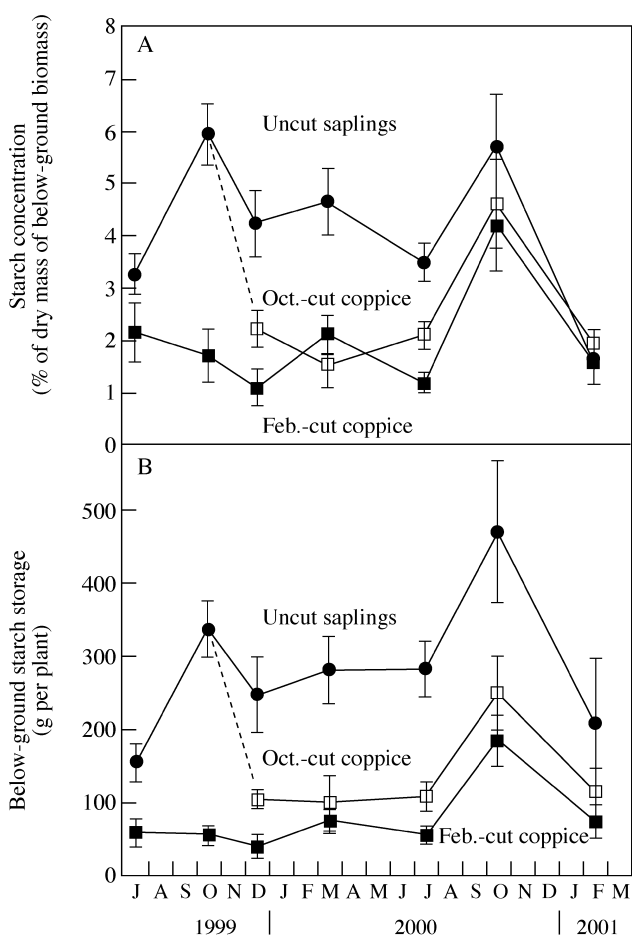

FIG. 6. Changes in concentration (A) and total below-ground reserves (B) of starch in total below-ground biomass of 4- to 7-year-old trees of *Eucalyptus kochii* left intact (uncut saplings, closed circles) or coppiced (C_N treatment) in summer (February 1999 cut, closed squares) or the following spring (October 1999 cut, open squares). Dashed lines indicate time of cutting. Vertical bars represent 2 s.e.

event. For example, similar numbers of shoots were produced after decapitation treatments in February or October (Fig. 3B), but trees of the latter treatment restored their new canopies more rapidly (Table 4). Similarly, despite a slowly declining number of shoots produced successively by repeatedly decapitated (unshaded) plants following an initial cutting in February, the biomass of new shoots produced after each harvest was actually significantly greater at the final decapitation event. Thus, once initiated, shoot growth was clearly more related to climatic conditions than to the actual number of sprouts produced in this case. Indeed, poor correlations between sprout number and survival or productivity are generally found in coppicing tree species (Sennerby-Forsse *et al.*, 1992).

This study clearly showed that removal of shoots resulted in greatly inhibited production and secondary thickening of root biomass during the first 1·7–2·5 years of shoot regeneration, compared with continual unimpeded increases in root biomass of uncut trees. In other woody species, reports of reductions in root growth following shoot removal are common (Kny, 1894; Hodgkinson and Becking, 1977; Schroth and Zech, 1995; Crombie, 1997; Ruess *et al.*, 1998) but not universal (Dickmann *et al.*, 1996; Kosola *et al.*, 2001).

Interpreting the literature pertaining to the wide variety of root responses following shoot removal in other species, and evidence from this study, suggest that *E. kochii* sheds fine root biomass while the superstructure of the root system is retained. Soon after reformation of the canopy, fine roots may start being produced again in balance with the regenerating shoot, but further investment in structural roots or lignotubers remains slow until the functional shoot : root ratio nears restoration (Reidacker, 1973; Hodgkinson and Becking, 1977; Steinbeck and Nwoboshi, 1980; Reis and Kimmins, 1986; Kummerow *et al.*, 1990; Fownes and Anderson, 1991; Dickmann and Pregitzer, 1992; Schroth, 1995; Ruess *et al.*, 1998; Farrar and Jones, 2000). Indeed, the apparent slowing of the dry mass-based shoot : root ratio at a level below that of uncut plants towards the end of this study (see Fig. 5C) may belie a functionally restored shoot : root ratio (Thornley, 1977;

the size of the lignotuber reserve of meristematic foci nor by the number of shoots emerging after each decapitation

Wilson, 1988; Farrar and Jones, 2000) given the approx. 50 % greater photosynthetic activity of coppice shoots measured over the study period (D. T. Wildy and J. S. Pate, unpubl. res.).

Root respiration would, of course, place a large burden on the reserves of recently decapitated trees, especially in species with naturally low shoot : root ratios such as *E. kochii*. While the carbon cost of root systems of coppiced *E. kochii* plants showing reduced rates of fine root production could be lower than that of an actively expanding root system (e.g. see Nobel *et al.*, 1992; Ryan *et al.*, 1996; Keith *et al.*, 1997), it is possible that below-ground maintenance would still comprise a sink of equal or greater magnitude to that of the new shoot (Smith *et al.*, 1992; Farrar and Jones, 2000; Noble, 2001). Much of the observed loss of starch from root systems might then be committed to respiration rather than contributing to dry matter gain of new coppice shoots. However, it is possible that translocation of organic compounds and carbohydrates, such as sugars and wall-based polysaccharides, from senescing roots might partially offset this cost. Since these potential sources and sinks of carbon were not examined in this study, it is not possible to evaluate their impact on the early carbon economy of a coppicing tree. Nevertheless, as suggested by Noble (2001), this potentially large respiratory tax on coppicing trees may be a major factor in the relatively slow regeneration of *E. kochii* after coppicing, particularly when canopy restoration coincides with winter months of low photosynthetically active radiation.

Greater below-ground starch concentrations available for coppicing in spring-cut plants (Fig. 6A) could, in part, explain the superior coppice shoot production of October-cut trees (see Cremer, 1972). However, most evidence points to only a small contribution by starch reserves to the development of new canopies in *E. kochii* (Deans and Ford, 1986; Garcia *et al.*, 2001). For example, the minimal difference in new shoot growth between shaded and unshaded trees after repeated decapitation in winter months might suggest a similar role for starch in the development of shoots at this time in both treatments. This would indicate that the magnitude of such a contribution is less than 40 g per plant (Fig. 4B), though this may also be confounded by generally slow growth in winter months. In the case of naturally regenerating plants, the 0·1–0·2 kg lost from the below-ground starch stores would probably only account for a small fraction of the 0·9–2·5 kg of shoot biomass produced after 1 year if starch was the only source of carbon for both root respiration and development of a new shoot. Possible further evidence for the importance of starch only in the very early stages of canopy regeneration was the rapid decline of root starch contents after decapitation followed by a constant low level (Fig. 6).

Thus, the importance of such reserves in the decline of poorly managed coppice stands is debatable in *E. kochii* (c.f. Woods *et al.*, 1959; Canadell and López-Soria, 1998; Latt *et al.*, 2000). Although the final low starch levels could constitute a simple explanation for the eventual death of the repeatedly harvested and/or shaded trees in this study, we believe that in this case it is more probable that these are symptoms associated with the general decline of these

plants (Taylor *et al.*, 1982; Chapin *et al.*, 1990; Kosola *et al.*, 2001). For example, the analyses showed that a significant fraction of starch remained in plants just prior to their death (Table 4), and, though low, these were only marginally below values shown by naturally regenerating coppice (Fig. 6A) (see Chapin *et al.*, 1990). It was also apparent that such presumed low levels of starch in February-cut plants subjected to their fourth consecutive 3-monthly shoot removal (Fig. 4A) did not stop these trees producing their largest coppice crop, coinciding with the regular season for shoot growth. Finally, despite starch concentrations of naturally regenerating trees having returned to those of uncut trees by 1–1·5 years after decapitation (Fig. 6A), other studies on the same species still recorded declining yields and increasing mortality when harvested repeatedly at similar, or slightly longer, intervals (Eastham *et al.*, 1993; Milthorpe *et al.*, 1998).

The results from this study suggest that management of *E. kochii* for long-term productivity over repeated decapitation events would firstly need to take account of the greater biomass produced by less frequently cut plants (see Table 4). In addition, cutting on 2- or 3-year intervals, or more (depending on season), may avoid gradual rootstock decline by allowing active secondary growth between harvests.

ACKNOWLEDGEMENTS

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