

The Significance of Root Starch in Post-fire Shoot Recovery of the Resprouter *Stirlingia latifolia* R. Br. (Proteaceae)

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Stirlingia latifolia, a common shrub of *Banksia* woodlands of SW Australia, is a highly successful resprouter species recovering from fire by multiple sprouting of new shoots from its upper root stock. In comparison with the congeneric fire-sensitive (obligate seeder) species *Stirlingia tenuifolia* it exhibits a low shoot:root dry weight ratio and high concentrations of stored starch in the cortical tissue of its roots. The relationship between root reserves of starch and development of newly sprouting shoot material following fire is examined in *S. latifolia* after spring and summer burns. During the initial 2–5 month period after fire, levels of stored starch in the roots fall by 50–75%, followed by a slow increase as plants reproduce and the attainment of pre-fire starch levels by 1.5–2 years after the fire. Starch reserves of roots can be further reduced by shading the regenerating shoots to limit their input of photosynthates and almost totally eliminated by monthly removal of successive flushes of new shoots over a 10–12 month period. New shoots continue to sprout until all the starch is eliminated. The data are discussed in relation to the fire-induced reproduction of *S. latifolia* and its ability to thrive in very frequently burnt habitats.

Key words: Fire response, Proteaceae, resprouter, shoot:root ratio, starch storage, *Stirlingia latifolia*.

INTRODUCTION

The widespread occurrence of fire in Australia and other Mediterranean climate regions of the world is considered a major influence shaping the structure, composition and dynamics of natural plant communities and has prompted the evolution of a range of adaptations relevant to plant survival after fire (Gill, 1977, 1981; Kemp, 1978; Recher and Christensen, 1981; Frost, 1984; Keeley, 1986). As with taxa of many plant families, members of the Proteaceae subscribe to one or other of two categories of response to fire, namely recovery of the shoot by sprouting (resprouters) or death followed by re-establishment from seed (obligate seeders). In a study comparing species of south-west Australian plants displaying these alternative modes of response, Pate *et al.* (1990) demonstrated that resprouter species generally showed slower growth rates, lower shoot to root dry weight ratios, and devoted proportionally larger areas of their root tissues to storage of starch than did seeder species. Mean concentrations of root starch in resprouter species were four times greater than in seeders and many of the latter contained negligible levels of detectable root starch. Further comprehensive studies on seeder and resprouter representatives of the families Proteaceae, Fabaceae, Mimosaceae and the Restionaceae (Bowen, 1991; Hansen, 1991; Hansen, Pate and Hansen, 1991; Pate, Meney and Dixon, 1991) have fully substantiated these generalizations.

It is clearly of biological advantage to any species which has survived fire to have immediate access to a sufficiently large store of readily available energy to maintain what remains of the plant body, initiate further root growth and establish a sufficiently large new photosynthetic surface to

implement the shoot recovery process. While starch and other forms of carbohydrate have been clearly shown to be present in and consumed during the recovery process of certain woody species (for example, see Woods, Harris and Caldwell, 1959; Jones and Laude, 1960; Bamber and Humphreys, 1965), quantitative relationships between amounts utilized and growth initiated, or between growth and photosynthesis of new shoots and subsequent establishment of a new set of root reserves, have not been studied in detail in native taxa of natural ecosystems. The present investigation follows such relationships in *S. latifolia*, a long-lived shrubby member of the Proteaceae already noted for its large root reserves of starch (Pate *et al.*, 1990). The species regenerates from its root stock after fire and then flowers prolifically. The species is proving to be notably persistent in habitats subject to prescribed burns on a 5–7 year cycle. Its inflorescences comprise an important component of the cut flower industry of W Australia so understanding the biology of its response to fire is of economic significance.

MATERIALS AND METHODS

The study species

S. latifolia R. Br. (Fig. 1A), a 0.5–1.5 m tall resprouter shrub of the tribe Proteoideae of the Proteaceae (Johnson and Briggs, 1975) is widespread in the South-West Botanical Province of Western Australia, occurring most commonly in the deep sands and lateritic soils of heaths and woodlands extending from Kalbarri (27° 43' S, 114° 10' E) to Albany (35° 02' S, 117° 53' E) (George, 1984; Marchant *et al.*, 1987). It typically develops a stout tap-root, from the crown

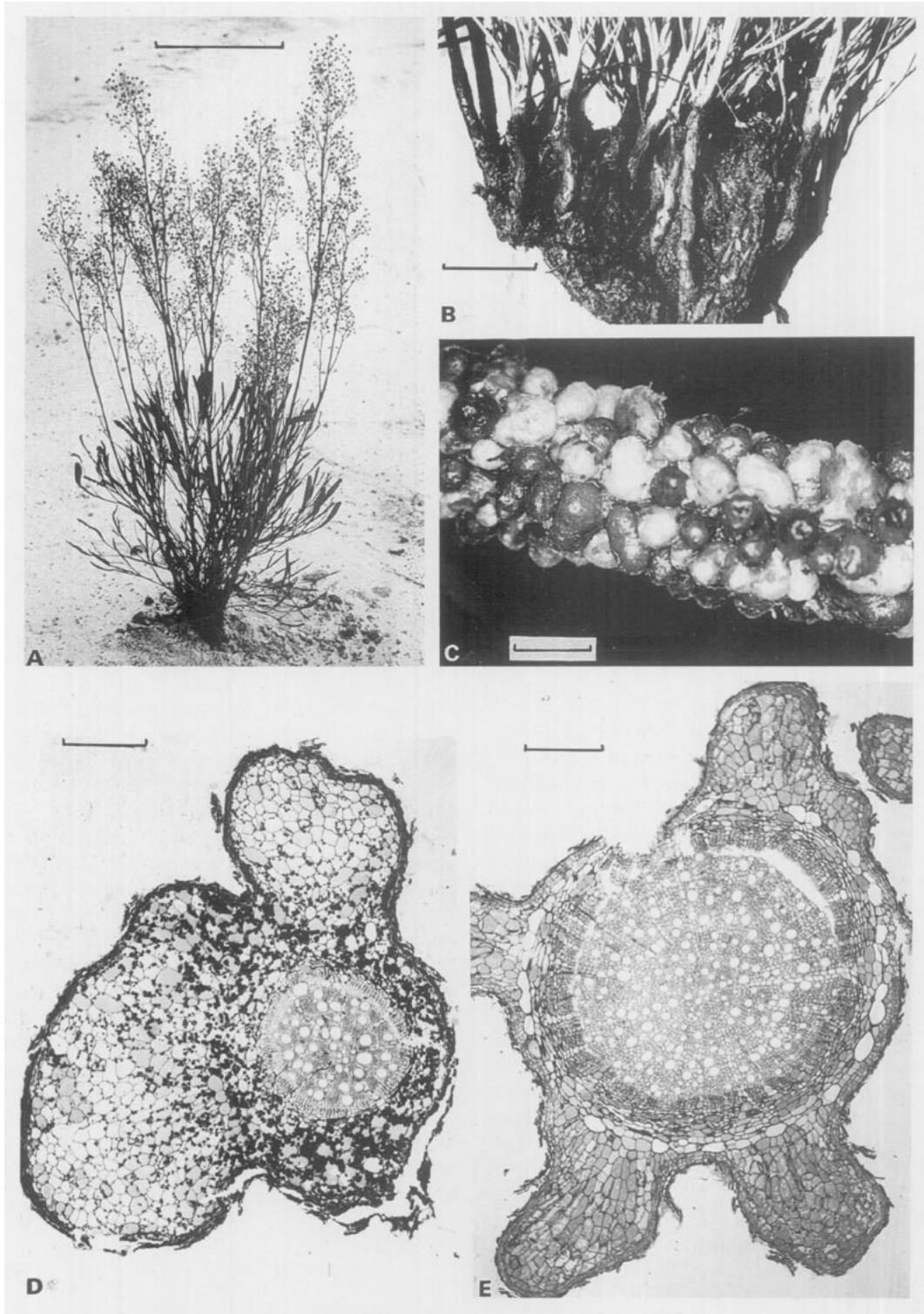


FIG. 1. Features of *Stirlingia* spp relevant to response to fire. A, Flowering adult of the resprouter *S. latifolia*. Bar = 0.25 m. B, Root crown of *S. latifolia* with emergent shoots following recovery after fire. Bar = 0.05 m. C, Root surface of *S. latifolia* showing the development of outgrowths (tubercles) of the secondary cortex. The tubercles of this portion of root are of varying ages, new tubercles are pale while older tubercles become dark brown. Bar = 3 mm. D, E, Photomicrographs of cross sections of roots of *S. latifolia* with prominent starch grains in broadened tuberculate cortex (D) and *S. tenuifolia* with cortical tubercles but absence of starch grains (E). Material embedded in glycolmethacrylate and sections treated with PAS reagent and Toluidine Blue. Starch grains appear as dense black dots on the micrographs. Bar = 1 mm.

of which multiple shoot sprouts arise (Fig. 1B) following destruction of above ground parts by fire. The leaves are glaucous, 20–30 cm long and divided into many flat linear lobes, each about 0.25–1.5 cm wide and 5–12 cm long. The inflorescence comprises a large panicle which greatly exceeds the leaves in length (Fig. 1A). The root system of *S. latifolia* can extend over 3 m in depth and is accordingly able to tap ground water where the latter is, say, 2–5 m below the ground surface (Dodd *et al.*, 1984). All but the finest roots are invested with a secondary cortex of small closely-spaced spherical tubercles (Fig. 1C) (see Pate and Dixon, 1982) which persist for several seasons and consist of highly-vacuolate storage parenchyma (Fig. 1D) containing large quantities of starch (Pate *et al.*, 1990; Bowen, 1991).

Flowering of *S. latifolia* occurs synchronously in populations in the second year after a burn (Baird, 1977) but small numbers of individuals may also flower asynchronously during long fire-free intervals (George, 1984). The panicles (Fig. 1A) develop in the mid-summer following a fire, flowers do not open until the following spring and dispersal of seeds occurs during the following January (i.e. a full 2 years after a mid summer fire).

Study sites and collection of plants

S. latifolia was studied at three principal locations in natural *Banksia* woodlands within an area bordered by Wanneroo, Guilderton and Gingin approximately 40–75 km north of Perth (31° 57' S, 115° 51' E), Western Australia. Sites were characterized by dense stands of *Banksia attenuata* and *Banksia menziesii* accompanied less commonly by *Banksia ilicifolia*, *Banksia prionotes*, *Eucalyptus todtiana*, *Nuytsia floribunda*, and *Casuarina fraseriana*. The understory of the sites comprised a sclerophyllous, species-rich stratum of shrubs mostly from the Proteaceae, Myrtaceae, Papilionaceae and Epacridaceae and a range of perennial herbs (see Dodd and Griffin, 1989 for examples of species). The deep leached sands supporting *Banksia* woodland generally have an extremely low water holding capacity (Dodd, 1985) and are extremely infertile (see McArthur and Bettaney, 1960; Pate and Dell, 1984; Jeffrey, 1989).

The climate of the study region is Mediterranean with hot dry summers and with 86% of the annual rainfall (approx. 660 mm) falling in the winter months between May and Oct. (Beard, 1989; Bureau of Meteorology, Perth, Western Australia). Accumulation of highly flammable plant litter makes this region prone to episodic wildfires during summer.

Site 1 consisted of a shallow sandy depression with a water table at an average depth of 2.7 m (bore site FWP3, Water Authority of Western Australia). This site had been burnt in Jan. 1986 by a wild-fire and seedling recruitment of the uniformly distributed population of *S. latifolia* took place from pre-fire seed banks the following winter. Excavations of mature plants to determine shoot:root dry weight ratios and distribution of roots with depth were made during flowering in Nov. 1987 and again in Jan. 1990 when plants had completed fruiting. Juvenile plants were excavated at the site every 6–12 months, the first collection in May 1987 when seedlings were approximately 10 months

old, the final collection in Aug. 1989 when these recruits were 3 years old.

Plants of *S. latifolia* collected from Sites 2 and 3 were used to evaluate changes in concentration of root starch during natural shoot recovery following fire. Site 2 contained an evenly-distributed dense population of the species which had been exposed to a fire in early spring (Sep. 1987). Site 3 contained a population which had been exposed to a summer fire (Jan. 1989). Samples from both these sites were collected before each fire and then at regular intervals up to 2 years thereafter.

Shoot:root dry weight measurements and assays for starch in roots were also made on a congeneric seeder species, *S. tenuifolia*, studied in Dec. 1987 in populations approximately 4, 16, 28 and 40 months old from sites, 20–25 km east of Denmark, Western Australia (34° 57' S, 117° 21' E). Road side populations of this species had established as a result of fire or other disturbances and flowered profusely each year after their second year of establishment from seed. Populations of the species in adjacent bushland failed to survive a burn in 1989 whereas co-habiting plants of *S. latifolia* resprouted and behaved thereafter essentially as those at the major study sites 500 km to the north. The roots of *S. tenuifolia* bear tubercles but do not contain starch (Fig. 1E).

Sampling of plants for shoot:root dry weight ratios

Roots and corresponding shoots of *S. latifolia* were harvested using either of two methods. The first, employed for relatively small plants 6–24 months of age, involved the construction of deep pits (approximately 2.5 m long by 1.5 m wide and 2–2.5 m deep) alongside the plants in question. Intact root systems with shoots still attached were then carefully prised away from the sand at the pit face. The second technique, utilized for large uniform stands of older juveniles (≥ 30 months) and mature plants, first involved removal and careful recovery of all shoot material from a series of large plots each of 3 m² area, followed by progressive harvesting of root material at 200 mm intervals downwards below this area until the water table was reached (at approx. 2.5 m). It was assumed that any portions of lateral roots missed from plants within the pit area were balanced by lateral roots invading the excavation area from neighbouring plants outside the area of the excavation pit. Samples of 15–20 plants of *S. latifolia* of each age group were collected from each plot.

Roots of *S. tenuifolia* were smaller and did not extend laterally or in depth to any great extent, so that roots of these species could be completely excavated using a spade. Approximately 20 plants of *S. tenuifolia* of each age group were collected.

Individual shoots were dried to a constant weight over a 2-d period at 80 °C and their dry weights determined. Individual roots (unburnt *S. latifolia* and *S. tenuifolia*), or bulked roots at 200-mm intervals of depth (resprouted *S. latifolia*), were washed, dried and weighed. The shoot:root ratio derived for each species at each sampling age was assessed from the dry weight of all harvested shoot material

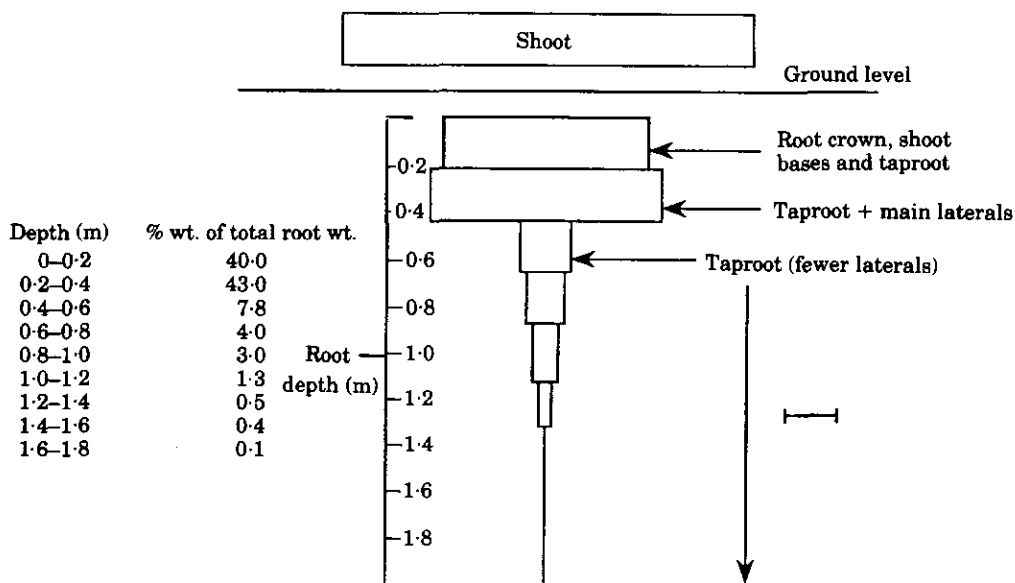


FIG. 2. Diagrammatic representation showing the relative distribution of biomass (dry matter) between shoots and roots and the percentage distribution of below-ground biomass with depth in naturally growing adult plants of *Stirlingia latifolia* at Yanchep, Western Australia. Mean d. wt. ratio of shoot:root biomass = 0.80. Bar = proportion of 0.1.

divided by the combined weight of all excavated root material.

Sampling for shoot biomass

This was conducted at site 2 (spring burn) and site 3 (late summer burn) and involved a series of harvests of the complete shoots of 15–30 plants selected at random in the habitats. A first harvest conducted a month before each prescribed burn estimated pre-fire shoot biomass. Subsequent harvests examining time courses of recovery of shoot biomass were then carried out at monthly intervals for the first 6 months and then every 2 or 3 months until the new shoot systems had completed fruiting and were approximately 2 years old. Dry weights of all material were determined.

Sampling of root biomass for starch

Using the same sampling times as for shoot biomass, sets of ten unburnt plants from each burnt site and from bushland closely adjacent to each burn were progressively excavated to 0.4-m depth and all main and lateral root material harvested and dry weights determined. This depth zone was shown in preliminary investigations to contain over 80% of the total root biomass. Further sets of ten burnt plants at sites 2 and 3 were selected for shading experiments aimed at determining the effect of reduced photosynthetic input on utilization of root reserves of starch in resprouting plants. Recovering shoots were caged in layered shade cloth immediately after both the spring (1987) and summer (1989) fires for a period of 6 months, resulting in the reduction of internal illumination to 30% of ambient. The roots of these plants were sampled at 200-mm depth intervals down to 1 m to determine whether utilization of

starch during resprouting occurred evenly or unevenly with depth. A set of ten unshaded, unburnt plants was excavated similarly to follow normal variations in root starch in the absence of fire.

A detailed study of the relationship between declining root starch and progressive capacity to form shoots was conducted on 30 plants at site 3 (summer burn). Once resprouting had commenced (approximately 2 months after the fire) new shoots of these plants were removed and all further shoots harvested at monthly intervals until production of new shoots had ceased. Complete roots were then excavated for analysis of starch. Numbers of new shoots formed by the plants each month were counted and their dry weights determined. Over half of the plants were still producing shoots after a period of 10 months and these were then covered in cages of shade-cloth for a further 4-month period until all had ceased producing new shoots. The roots of these plants were then harvested and dried.

Analysis of root material for starch and sugars

Anatomical investigation showed starch reserves to be restricted to the tubercular cortical tissues outside the root stele (Fig. 1D and see Pate *et al.*, 1990; Bowen, 1991) so all analyses were conducted on these tissues. The cortex was stripped off the root, washed, dried at 80 °C, finely ground (0.1-mm mesh) and starch concentrations determined by extracting 0.1-g aliquots of dry matter in perchloric acid and precipitating the solubilized starch with iodine (Pucher, Leavenworth and Vickery, 1948). The starch was then redissolved in dilute perchloric acid and assayed by the phenol method (Dubois *et al.*, 1956). Concentrations were measured at a wavelength of 490 nm. Each determination was conducted in replicate and each batch of determinations was calibrated against a new set of starch standards (potato

starch, Sigma Chemical Company, U.S.A.). Samples of fresh root material of burnt and unburnt plants were extracted in 80% ethanol and assayed for free sugars and fructans using the HPLC techniques recently described by Pate *et al.* (1991).

RESULTS

Distribution of total biomass between shoots and roots

The mean shoot:root dry weight ratio of a fully representative size range of 20 mature resprouted individuals 2 years after the fire was 0.8 (Fig. 2). Due to the predominance of laterals in upper layers and the strongly tapering nature of the main root, by far the greater proportion (80% or more) of root biomass of *S. latifolia* was regularly encountered in the top 400 mm and approximately 95% in the upper 1 m of the rooting profile (Fig. 2).

The shoot:root ratios of unburnt juveniles between 1.5 and 3 years of age proved to be closely similar to that attained by resprouted mature individuals of *S. latifolia* by 2 or 3 years after fire (Fig. 3). Both age groups maintained ratios in the range 0.8–1.0. By contrast, plants of varying age of the obligate seeder *S. tenuifolia* showed shoot:root ratios ranging from 4–6 times greater than those of *S. latifolia* (*t*-test, $P < 0.001$, Fig. 3).

Concentrations of root starch and sugars in relation to shoot recovery after a spring or summer fire

Emergence and growth of shoot sprouts commenced from burnt root stocks approximately 2 months after both the spring (Sep. 1987) and summer (Jan. 1989) burns and progressed so rapidly that, by 6–10 months after the respective fires, shoot biomass (d. wt per plant) already exceeded that present before the fire (Figs 4 and 5). For

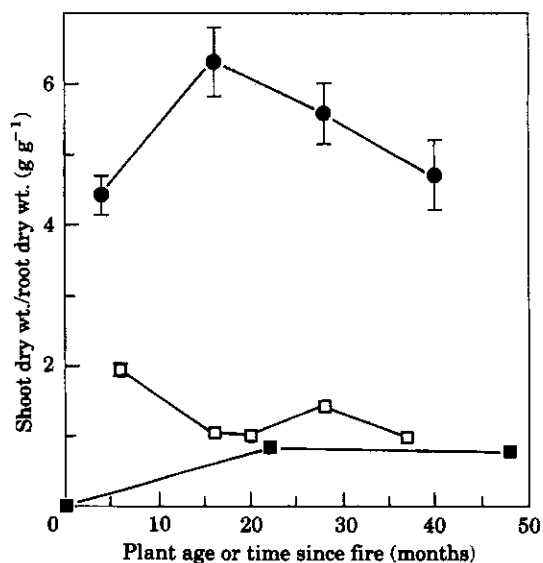


FIG. 3. Shoot:root d. wt ratios of unburnt plants of *S. latifolia* (□) and *S. tenuifolia* (●) of known age after recruitment from seed and of mature resprouted specimens of *S. latifolia* (■) at known times after a fire. Standard errors are indicated for harvests where individuals were excavated separately.

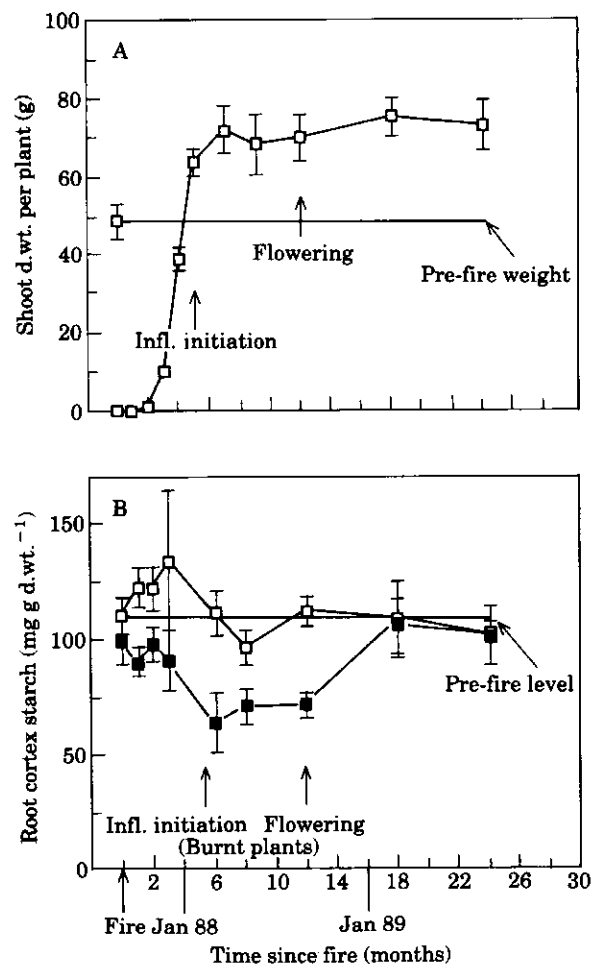


FIG. 4. Recovery of *S. latifolia* after a spring burn (Sep. 1987). A, Pre- and post-fire shoot biomass expressed as g d. wt per plant (\pm s.e.). B, Pre- and post-fire concentrations of starch in the cortex of the roots of unburnt (control, □) and burnt (■) plants expressed as mg g d. wt⁻¹ (\pm s.e.). Times of inflorescence initiation and flowering are indicated.

plants recovering after the spring burn (Fig. 4A) inflorescence initiation began at 5 months and flowering took place the next spring i.e. 12 months after the fire. By contrast summer-burnt plants (Fig. 5A) did not initiate their inflorescence until 13 months after the fire and then flowered 7 months later. Both sets of plants achieved peak shoot biomass at flowering but average shoot biomass was greater after the summer burn (compare Fig. 4A with 5A).

The average concentration of starch in the root cortex of the unburnt control plants was similar for the spring-burn plants (113 ± 4 mg g d. wt⁻¹) and summer-burnt plants (100 ± 4 mg g d. wt⁻¹) (Figs 4B and 5B). Small seasonal fluctuations in root starch levels were apparent, with both sets of control plants recording a slight decline in starch levels at the end of summer (Mar.).

Concentrations of starch in the cortex of roots of burnt plants declined markedly in the first few months after fire coincident with the production of resprout shoots (Figs 4 and 5). In spring-burnt plants this initial reduction in starch was approximately 50 mg g d. wt⁻¹ and subsequent recovery of starch concentrations to pre-fire levels by the plants had occurred by 18 months after the fire (Fig. 4B). For summer-

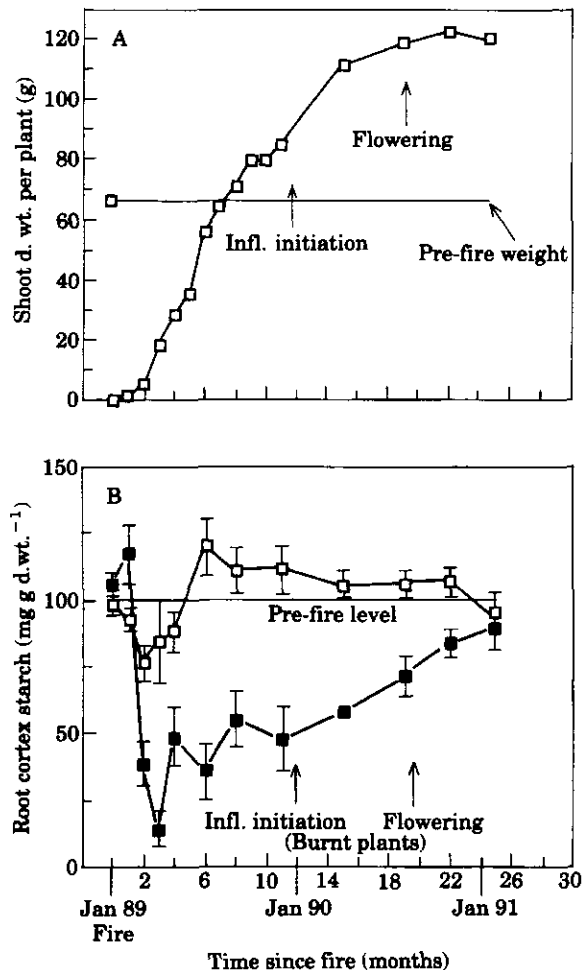


FIG. 5. Recovery of *S. latifolia* after a summer burn (Jan. 1989). A, Pre- and post-fire shoot biomass expressed as g d. wt per plant. B, Pre- and post-fire concentrations of starch in the cortex of the roots of unburnt (control, \square) and burnt (\blacksquare) plants expressed as mg g d. wt⁻¹ (\pm s.e.). Times of inflorescence initiation and flowering are indicated.

burnt plants the corresponding reduction in starch level was 70 mg g d. wt⁻¹ and the recovery period to pre-fire levels of starch was 24 months (Fig. 5B). In both cases starch began

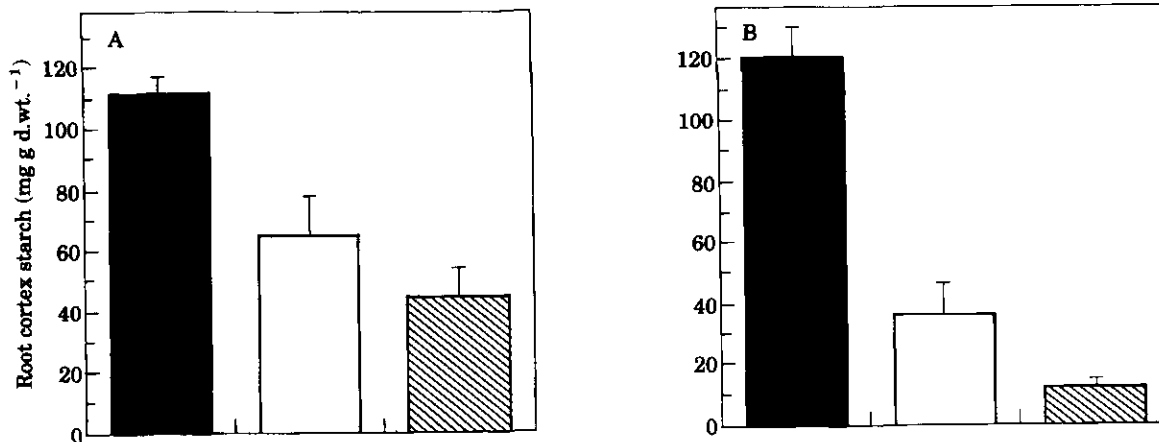


FIG. 6. The concentration of starch in cortex of the roots of *S. latifolia* in unburnt (control, \blacksquare) and burnt plants (\square) and in plants recovering under shade-cloth (\square) 6 months after being burnt in spring (Sep. 1987) (A) or summer (Jan. 1989) (B). The light intensity for shaded plants was approximately 30% that of ambient. All data expressed as mg g d. wt⁻¹ (\pm s.e.).

TABLE 1. Measurements of starch concentrations (mg g d. wt⁻¹ \pm s.e.) in the root cortex of *S. latifolia* at 200-mm depth intervals down to 1 m for control (unburnt) plants and for burnt plants regenerating under shade* for a period of 6 months (shaded). Yanchep, Western Australia, 1989

Depth (mm)	Control starch (mg g d. wt ⁻¹)	Burnt + shaded starch (mg g d. wt ⁻¹)
100-200	122.4 \pm 10.1	11.6 \pm 2.7
200-400	134.2 \pm 12.8	8.4 \pm 2.5
400-600	147.5 \pm 2.2	7.5 \pm 3.1
600-800	142.5 \pm 7.5	6.7 \pm 2.2
800-1000	134.0 \pm 10.3	10.8 \pm 2.7

* Whole regenerating shoots caged in shade cloth which reduced light intensity to approximately 30% of ambient levels.

to increase as shoots were initiating inflorescences, although final replenishment to pre-fire levels did not take place until shoot biomass had stabilized (Figs 4 and 5).

Reductions equivalent to a further 20 mg of starch g d. wt⁻¹ were induced in spring or summer-burnt plants subjected to shading for 6 months (Fig. 6). The respective differences from the unshaded unburnt and burnt plants were significant (Fisher's l.s.d. $P < 0.05$).

The average concentration of starch in the root cortex of shaded plants did not vary significantly with depth (Table 1). Unburnt plants (controls) also showed no significant difference in concentration of starch in the zone 0.1-0.4 m when compared with that between 0.4 and 1 m (Table 1).

Analyses of ethanolic extracts of root cortex of recently burnt and unburnt plants for soluble carbohydrates showed sucrose and lesser amounts of fructose and glucose to be the only sugars present in appreciable amounts. Fructan-type compounds were absent. Total sugar levels ranged from 5 to 20 mg g d. wt⁻¹ and were usually less than 7 mg g d. wt⁻¹. They were in all cases of considerably lesser magnitude than the current starch level of a tissue sample. Sugars were therefore regarded as a less important source of carbohydrate storage than starch.

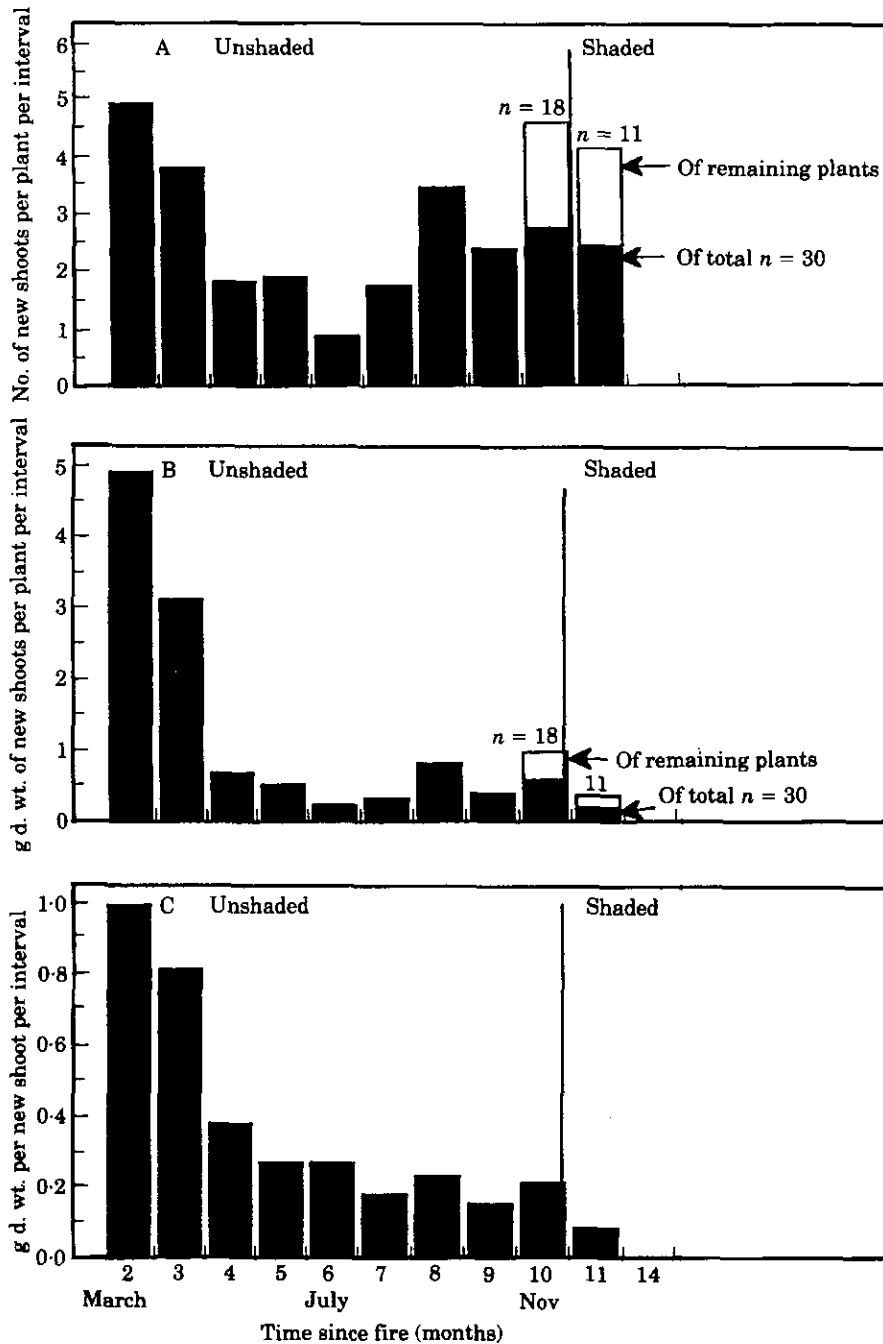


FIG. 7. Histograms showing the effects of progressive (monthly) removal of resprouting shoots of burnt mature plants of *S. latifolia* on: A, the average number of resprout shoots emerging each month; B, the average total dry weight of new shoots produced each month; and C, the average dry weight of each resprouted shoot. Plants were shaded after the 10th month to reduce the ambient light intensity received by resprouting shoots to approximately 30%.

The effect of repeated removal of resprouted shoots on generation of new shoots and levels of starch in roots

The summer-burnt plants at site 3 produced on average an initial set of five resprout shoots (see Mar. values Fig. 7). Following removal of these, and monthly removal of further shoots thereafter, a cumulative total of 29.5 ± 2.7 shoots were produced per plant over the 12-month period following the fire. Shoot production per month varied greatly with time elapsed since the fire (Fig. 7A), com-

mencing with four–five shoots per plant per month over the first 2–3 months after fire, declining markedly to one–two shoots per month during winter (May to Aug.), and then increasing again to about four shoots per month during spring and summer (Sep. to Dec.). By this stage, however, some plants had ceased producing new shoots, so average numbers of shoots for the total group of plants ($n = 30$) was low, despite relatively high numbers for those plants which were still continuing to sprout in Nov. ($n = 18$) or Dec. ($n = 11$). Plants still initiating buds in Nov. were then

subjected to shading and, although some continued to produce shoots for a further month, all shoot production ceased after the Dec. harvest (Fig. 7A).

The average total weight of shoots produced by the plants each month showed a similar pattern of changes to that in shoot number but, due to progressively smaller resprout size, the decline in the new shoot dry weight per month during winter was greater and the subsequent recovery during spring months less than that evident on a numerical basis (compare Fig. 7B, C).

By the time of cessation of bud initiation the roots of continuously disbudded and shaded plants had become virtually devoid of starch (mean levels of only 1.6 ± 1.0 mg of starch g d. wt⁻¹). This was in marked contrast to concurrent levels of starch in roots of unburnt control plants (111.7 ± 8.7 mg of starch g d. wt⁻¹) and plants which had been burnt and allowed to recover without disbudding or shading (48.4 ± 11.9 mg of starch g d. wt⁻¹).

DISCUSSION

Mature individuals of *S. latifolia* possess features already shown (Bowen, 1991) to be typical of resprouters of the family Proteaceae, namely low shoot:root ratios and high levels of starch in their roots. In these respects the species differs radically from its seeder counterpart *S. tenuifolia* which—while admittedly growing in a distant location—is shown here to exhibit a five-fold higher shoot:root ratio than *S. latifolia* and negligible levels of starch in its roots. Although the concentration of starch per unit dry weight of cortical tissue is uniform throughout the deeply penetrating root system of *S. latifolia*, a very high proportion of the total starch reserve is located superficially since 95% of the root biomass is found in the uppermost metre of rooting profile.

Evidence is presented in this paper that the depletion of starch in the roots of *S. latifolia* is strategically related to the process of shoot recovery and that during the initial few months of the regrowth phase after fire from 50–75% of the pre-fire store of starch is consumed. An average-sized mature plant is estimated to lose starch from its root biomass equivalent to about 3–6 g of total dry matter, an amount rated comparable with the amount of dry matter which the plant invests in shoot resprouts during the first 2–2.5 months after fire. Levels of starch in roots can be reduced by a further 20% when naturally recovering shoots are covered by shade cloth and starch is virtually eliminated from roots of plants whose resprouts are continuously removed until further shoot production has ceased. On this evidence the initial magnitude of the root starch reserve may be regarded as a primary limitant of a plant's capacity to produce new shoot biomass. Moreover, the mean weight of the final flush of new shoots which a de-sprouted plant forms is very much lower than those formed in earlier flushes, suggesting progressive limitation of shoot growth rate due to dwindling reserves. All of the above mentioned decreases in starch levels following stress of fire, shading and shoot removal are of several fold magnitude greater than those occurring seasonally in roots of plants growing normally in an unburnt environment.

Starch reserves of roots of plants which have been burnt and allowed to recover unimpaired fall to low levels in the initial stages of shoot recovery and begin to increase slowly only after shoot biomass has attained a value similar to, or greater than that before fire. A final return of the starch pool to levels typical of unburnt control plants is then delayed until inflorescence growth has been completed and flowering commenced. This latter effect suggests that photosynthates produced initially by new shoots are diverted preferentially into further shoot growth and inflorescence production, and that no priority is given at this time to replenishment of root reserves. Flowering coincides with the beginning of the second growing season after the fire and the photosynthates produced after this time are likely to be more than adequate to meet the relatively modest demands of fruiting and further shoot growth. As a result ever increasing proportions of photosynthate become directed to root storage. Finally, by 1.5–2 years after fire the plants have successfully completed their reproduction, attained their pre-fire shoot size and shoot:root ratio and have increased the starch reserves of their roots to levels of those exhibited before the plants were burnt. The rapidity with which these events are achieved may be a major fact in the ability of the species to survive and, in many situations, become noticeably dominant in the understorey of very frequently burnt woodland.

The sequence of shoot regrowth, flowering and establishment of root starch reserves in *S. latifolia* follows a time course markedly dependent on when the fire occurred, suggesting a highly intricate interactive relationship between seasonal production of photosynthates and shoot growth, reproduction and storage of starch. A plant burnt in summer has a complete year of vegetative growth before initiating inflorescences, whereas one burnt in spring has only 5 months of vegetative growth before commencement of reproduction (see Figs 4 and 5). So, although initial rates of shoot regrowth are higher during the summer following a spring burn than in the autumn and winter after a summer burn, shoot biomass 2 years after fire is over 1.5 times greater after a summer burn than a spring burn. Conversely, the immediate post-fire decline in root starch of a summer-burnt plant is proportionally much greater than in a spring-burnt plant, apparently because resprouting in the former occurs during times when plants would normally experience a seasonal drop (Feb. to Apr.) in their starch reserves. Similar seasonal declines in starch levels associated with the growing season have also been observed in juvenile plants of *S. latifolia* (Bowen, 1991) as well as in other starch-storing herbaceous and woody species (Woods *et al.*, 1959; Jones and Laude, 1960; Larcher and Thomaser-Thin, 1988; Diamantoglou *et al.*, 1989).

It is clear that utilisation of starch is a vital element of the process of resprouting in *S. latifolia*. Nevertheless, the overt regenerative success and exceptional rapid initial growth of this species after fire stand in marked contrast to the much poorer regenerating capacity of many cohabiting shrubs, some of which may possess equally concentrated reserves of root starch (see Pate *et al.*, 1990). Such differences between species may be due to a whole series of attributes amongst which the magnitude of root starch reserves may play a role only in the early stages of the regeneration syndrome. For

instance, regrowth of certain species might well be characterized by stimulation of photosynthetic rates in the new shoot regrowth, as has been shown elsewhere for chaparral resprouts (Radosevich, Conrad and Adams, 1977; Oechel and Hastings, 1983; DeSouza, Silka and Davis, 1986) and in regenerating oak forest species (Reich *et al.*, 1990). Effects of this kind might result from increased nutrient availability in the soil (Christensen and Muller, 1975; Oechel and Hastings, 1983; DeSouza *et al.*, 1986; Reich *et al.*, 1990), improved water relations (Radosevich *et al.*, 1977; Wellington, 1984) or merely reflect unusually high photosynthetic capacity in the juvenile type foliage which is characteristically produced in a large number of taxonomically unrelated species after fire. In these connections changes in chloroplast structure and an increase in the concentration of chlorophyll have also been recorded for resprouting leaves of plants from Mediterranean-type environments (Arianoutsou-Faraggitaki and Margaris, 1981; Christodoulakis, Arianoutsou-Faraggitaki and Psaris, 1986; Traubaud and Méthy, 1988), features both likely to increase the efficiency of photosynthesis of new foliage. Further comparative studies on resprouting in *S. latifolia* and other common species of its natural habitat would clearly be of value in determining which, if any, of the above factors are important in the relative success or otherwise of resprouting in different species.

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