19.3.4??Obligate seeders and resprouters: perennial plants that seed or resprout after ?re

Obligate seeders consist of plants which are either killed out-right by ?re and recruit thereafter from banks of seed buried in soil or encapsulated in woody fruits in the above-ground canopy (Figures 19.2b and 19.8C). Resprouters employ a sharply contrasting strategy whereby rootstocks (e.g. eucalypts in Figure 19.4 and banksias in Figure 19.5), thick trunks (Figure 19.6) and branches (e.g. casuarinas in Figure 19.8D) survive ?re and replace entire shoot canopies by sprouting from heat-resistant buds. These illustrations show that such heat-resistant buds can be below ground or in trunks and branches.

Table 19.2 Differences in growth, shoot : root dry mass ratio, starch levels and reproductive performances of naturally recruiting seeder and resprouter species of the northern sandplains of southwestern Australia. Means are given ± standard errors

	Mean for seeder species	Mean for resprouter species
Dry mass at 2–3 years (g plant^{-1})	10.7 ± 2.2	3.8 ± 0.9
Shoot : root dry mass ratio (g g^{-1})	5.0 ± 0.6	1.2 ± 0.1
Starch storage in shoots (mg g^{-1} (dry mass))	5 ± 2.1	15 ± 3.1
Starch storage in roots (mg g^{-1} (dry mass))	8 ± 0.7	55 ± 10.3
Time to first flowering (range in years)	2–4	5–11
Proportion of ovules giving rise to seeds (seed : ovule ratio)	0.5–0.8	0.04–0.4

(Based on Pate *et al.* 1990 and J. S. Pate, unpublished data)

[1]

Table 19.2

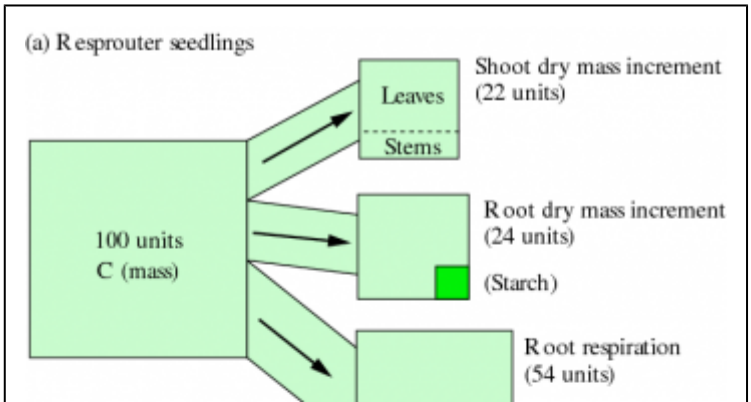


Figure 19.9 Scheme showing the relative sinks for assimilated carbon in seedlings of (a) resprouter and (b) seeder species from the family Proteaceae over an 18-month period after recruiting from seed germinated following a fire at Yanchep, Western Australia. Percentage allocation (units) of carbon to leaf, stem and root biomass is shown and carbon lost in root respiration indicated for each plant type. Note much larger allocation of carbon to starch storage (square in dark green) in roots of the resprouters than the seeders. (Based on Bowen and Pate 1991)

Seeders and resprouters are likely to be encountered in the same habitat but resprouters are normally predominant in habitats that are frequently burnt whereas seeders flourish where ?res are rarer events. Often a seeder and resprouter species of the same genus coexist in more or less equal densities at the same site, such 'congeneric' partners providing useful comparisons of how closely related species with contrasting ?re responses perform when sharing the same climate and ?re regime. Moreover, since new recruits to these seeder and resprouter populations are likely to germinate and establish proli?cally in the season following a ?re, comparisons can be made between cohorts of the same age over a number of subsequent seasons to compare biomass production, time to flowering and attributes such as longevity. For example, recruits of the seeder species in Table 19.2 were three times larger two to three years after germination than their resprouter counter-parts. By this time, shoots of a typical seeder are likely to weigh ?ve times more than the roots, while shoots and roots of a recruiting resprouter of the same age would weigh about the same (Table 19.2).

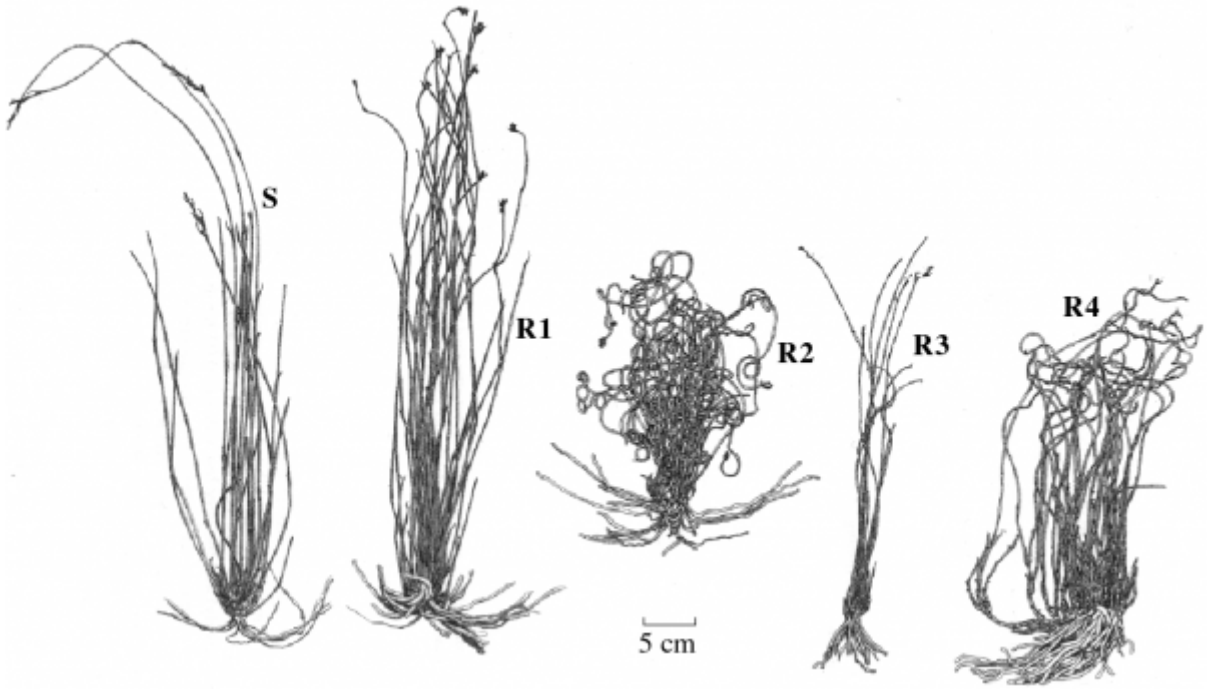
Disparities in distribution of dry matter between shoot and root indicate radically different patterns of allocation of photoassimilates and nutrient resources in the two ?re response types. Resprouters partition approximately three-quarters of new photoassimilates to roots (Figure 19.9a). Two-thirds of this carbon directed below ground is respired CO_2 with the remainder committed to establishing a starch-rich tap root or lignotuber capable of subsequently resisting ?re. With only a small proportion being invested into new leaf area, aerial growth of resprouter species proceeds slowly, as shown in Table 19.2. Seeders, on the other hand, commit less than half of new photoassimilates to roots and proportionately more to developing a leafy canopy (Figure 19.9b).

A major difference between seeders and resprouters relates to storage of starch, sugars and other carbon-based energy stores. While starch levels in shoots are lower than those in roots, signi?cantly more starch is invariably present in tissues of the resprouter species than in those of the seeder (Table 19.2), thereby reflecting the role of starch as a carbohydrate store for new growth. Starch deposits can be seen histo-chemically in stems of resprouters as darkly stained tissues comprising broad rays, abundant xylem parenchyma and thick cortical cell layers in roots (Figure 19.8E). Dense granules of starch within these resprouter roots account for the staining intensity. Seeders have almost none of the dark stain characteristic of starch (Figure 19.8F).

Similar measurements of levels of essential nutrients (e.g. nitrogen, phosphorus and potassium) in root dry matter show that nutrients are not accumulated in particular cell types in the manner observed for starch in resprouter species. Resprouters exploit stored carbon reserves to refoliate and produce new feeding roots immediately after ?re. Resumption of photosynthesis, transpiration and nutrient uptake follow, sustaining a new period of nutrient acquisition and storage. In this manner, established individuals of a resprouter species can generate biomass in a post-?re ecosystem well in advance of adjacent obligate seeders.

Recruiting individuals of seeders and resprouters also exhibit contrasting reproductive capacities (Table 19.2). Obligate seeders commence reproduction in the second or third season after germination, and seed production escalates annually thereafter for several years. By the time of the next ?re a large replacement seed bank is likely to have been accumulated. By contrast seedling recruits of resprouters might not start flowering for six to eight years and typically produce fewer flowers and smaller seed:ovule ratios (Table 19.2) than corresponding seeder species. That is, resprouters invest little in reproductive organs relative to the storage functions that help them re-establish quickly after ?re.

Congeneric partners, reflecting a balance between seeding and resprouting individuals, can thus be considered as alternative and more or less equally successful end points to evolutionary processes shaping responses of species to ?re. In evolutionary terms, intermediate types between seeders and resprouters would clearly embody an uneasy compromise between the two contrasting strategies, and, as might be expected, are not commonly encountered in present-day ecosystems. However, in certain exceptional taxa a continuum of response types can be discerned, as shown, for example, in the morphotypes of *Lyginia barbata* (Bell and Pate 1993), illustrated in Figure 19.10. Morphotypes range from a proli?c seed-producing, short-lived tufted seeder to resprouter forms that are long lived and produce few seeds. The resprouter forms reproduce vegetatively with clones arising from rhizomes of the parent plant. This spectrum of responses within *L. barbata* provides an ideal tool for study of evolutionary responses to ?re within a single taxon.



[3]

Figure 19.10 Fifth-year juveniles of morphotypes of *Lyginia barbata* R. Br. (Restionaceae) showing five contrasting growth forms of the same species. One is an obligate seeder (S) while the others are all resprouter forms (R1-R4). S is densely tufted and produces prolific seeds that germinate after fire has killed the parent plant. R1 and R2 are tufted resprouters but are short lived like S and able to recruit some new individuals from seed. R3 and R4 are long lived and strongly clonal, resprouting from adult rhizomes after fire to produce new juveniles vegetatively. (Reproduced courtesy Bell and Pate 1993)

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