

Fitness and evolution of resprouters in relation to fire

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Abstract There are many ways that plants may recover vegetatively from dieback caused by fires. Compared with fire-killed species, the presence of woody resprouters in fire-prone floras increases with fire frequency, though this is affected by site productivity that may have opposing correlates along different gradients. Population recovery is enhanced by resprouting when fecundity is low and/or seedling recruitment is not guaranteed. There is resource cycling between vegetative growth and storage but no clear trade-off between fecundity and storage, and more attention needs to be given to the role of somatic mutations in reducing fecundity. Seven fitness benefits of post-fire resprouting are noted that centre around the rapid return to adult growth rates and early flowering and seed set without the risks of recruitment failure. The extent of resprouting at

the individual, population, and species levels varies greatly but it is under genetic control. Recent studies on the evolution of resprouting in fire-prone systems have shown that types of resprouting (clonality, rootstocks, epicormic bud strands) are derived from surrounding parent lineages lacking these traits and confined to non-fire-prone environments. The oldest lineages with fire-related resprouting date to at least 61 million years ago, indicating that seed plants have had a long evolutionary relationship with fire. Various genetic mechanisms, including beneficial somatic mutations, have been invoked to explain how speciation of resprouters may keep pace with non-sprouters.

Keywords Vegetative resprouting · Fire regime · Phylogeny · Adaptation · Banksia

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Introduction

In fire-prone regions throughout the world, many woody plants recover after fire by resprouting from insulated aerial or subterranean buds. Depending on the severity of the fire, plants resprout from buds located in the leaf axils of twigs (axillary buds, Cremer 1972) or sunken accessory buds on main stems (epicormic strands/buds, Burrows 2002) or rootstocks (lignotuberous buds, Chattaway 1958). Resprouting may also occur from primary axillary buds on rhizomes (Witkowski and Lamont 1997) or adventitious buds on lateral roots (Lamont and Barrett 1988) or swollen

stems (Klimešomá and Klimeš 2007). Grass-trees (e.g. *Xanthorrhoea* spp.) and other plants with a palm-like growth habit are unusual in that the apical bud is not killed by fire. It is insulated from the heat, which may reach $>1,000^{\circ}\text{C}$, by dense immature foliage, so that the flush of new growth occurs from enhanced activity of the existing apical bud (Lamont et al. 2004). There are many species that survive light pruning, for example, from insect herbivory, that do not survive fires. Such species do not store accessory buds on old stems, lack lignotubers, or the cambium is killed through inadequate bark insulation.

Thus, two ecomorphological properties are required for successful resprouting after fire: (a) presence of buds or prebud meristems that are (b) located in plant parts that are sufficiently insulated to escape death from the heat of fire (Lawes et al. 2011). Resprouters, other than those with apical bud survival, have a large bud ‘bank’ often associated with many short stems, possibly as a ‘failsafe’ system following damage. Even so, their production may sometimes be spontaneous (Mesléard and Lepart 1989; López-Soria and Castell 1992; Vesk et al. 2004; *Banksia attenuata*, B. Lamont pers. obs.) suggesting that stem renewal is not just a way of recovering from fire but enhances growth and fecundity as well (Groom and Lamont 2011). As an additional requirement, López-Soria and Castell (1992) emphasise the need for resprouter genets to be able to survive/avoid post-fire drought and herbivory to persist.

Here, we consider the geographical spread of resprouting and the extent to which it is uniquely associated with fire in an attempt to derive a general relationship between fire frequency and presence of resprouters in woody floras. We review the fitness benefits of resprouting and present a case against a necessary trade-off between resource allocation to vegetative and reproductive growth. Factors affecting rates of recovery from fire point to the limitations of resprouting as a fire response. Finally, new insights on the paleontological and genetic origins and evolution of resprouting in relation to fire are summarized to help our understanding of why this trait is so well represented among fire-prone floras.

Occurrence of resprouting

There is a strong overall correlation between relative abundance of resprouting among and within woody

plant species and fire frequency (Bellingham and Sparrow 2000 for disturbance generally; Clarke and Knox 2002; Vesk and Westoby 2004b; Fig. 1 based on this review). Species that resprout in response to fire are seldom present in floras that rarely burn, such as *Nothofagus* forests, tropical rainforests, alpine heaths, and desert and endemic rock-outcrop floras (Williams 2000; Clarke and Knox 2002; Bond and Midgley 2003; Nzunda et al. 2007). Some floras cannot be ignited, such as succulent vegetation, whereas others do not experience crown fires or at best woody species are only partly scorched (testing for fire recovery requires that all foliage be burnt). Manual removal of the crown has been used as an alternative approach to test for the ability to resprout (Negreros-Castillo and Hall 2000; Parrotta et al. 2002) but, critically in the context of this review, it lacks the heat component. Burrows (2002) has shown how the stored buds in some rainforest trees are near the stem surface compared with their fire-prone counterparts, whereas burnt plants are more likely to die than pruned ones (Lloret et al. 1999; Vesk et al. 2004). Nevertheless, some systems burn strongly under special circumstances and this does enable fire-resprouters to be detected; e.g., large desert fires in central Australia have been recorded following occasional heavy rainfall events that provide temporary grassy fuel continuity (Luke and McArthur 1978; Nano and Clarke 2011).

Fire-prone shrublands, woodlands and forests characterised by intermediate fire intervals (i.e. 5–25 years) have more resprouters (50–85% of species) than non-sprouters (Le Maitre and Midgley 1992), with lowest percentages on more fertile substrates of similar fire regime in some systems (Enright et al. 2007) but the reverse in others (Clarke et al. 2005). Pausas et al. (2006) noted higher levels of resprouting in the Californian flora compared with that of the Mediterranean Basin, and attributed this to the greater incidence of fire in California. With fires in savanna grasslands at 1–5-year intervals, the limited number of shrubs and trees present there are all resprouters (Rebelo 2001; Williams et al. 2002). Thus, a monotonic relationship between percentage resprouters and mean fire interval is clear (Fig. 1), but the trend along individual productivity gradients as discussed below is highly variable and sometimes opposing.

Resprouting *Banksia* species are more abundant in the northern than the southern sandplains of SW

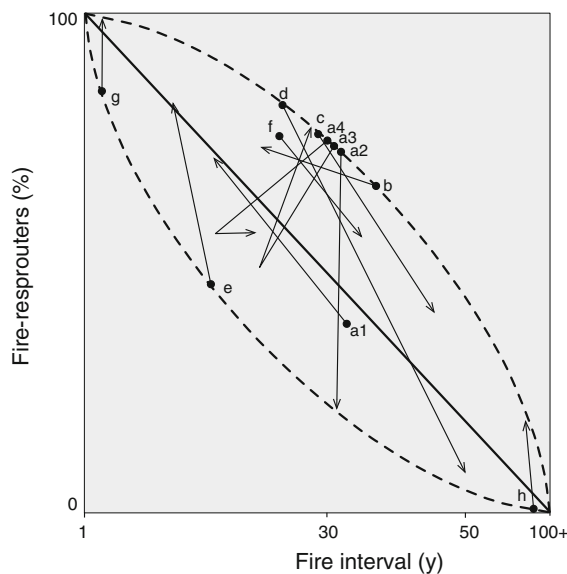


Fig. 1 Relationship between percentage fire-resprouters in the flora (omitting annuals and other fire avoiders, including tall trees that escape crown fire) and mean fire interval based on data reviewed in the text. Arrows are loosely based on gradient data and set the bounds within which the relationship may fluctuate, with the *tail of the arrow (spot)* representing highly productive sites and the *tip* representing poorly productive sites: *a1–4* from Lamont and Markey (1995), *b* Burrows et al. (2008), *c* Pausas and Bradstock (2007), *d* Clarke and Knox (2002), *e* Enright et al. (2007), *f* Pausas et al. (2006), *g* Williams et al. (2002), and *h* Bond and Midgley (2003). Note that both upper and lower bounds and longer or shorter fire intervals may correspond to more productive sites along different gradients. This pattern does not necessarily apply to the absolute number of species present

Australia where non-sprouters dominate, even though the rainfall is the same (Lamont and Markey 1995). The summer drought is much more intense in the north and crown-reaching fires are more frequent (Cowling and Lamont 1985; Wooller et al. 2002). It is not clear if resprouting improves fitness in relation to the greater risk of adult death through severe drought and reduced opportunities for seedling recruitment there (equivalent to lower productivity), or whether it is because fires are more prevalent (Fig. 1). Certainly, *Banksia menziesii* allocates more of its resources to reproduction in the more stressful environment and is more likely to be killed by fire there (Groom and Lamont 2011).

In SW Australian forests, as rainfall (productivity) increases from 750 to 1,250 mm year⁻¹ and fire frequency decreases, the number of resprouter species doubles but their contribution to the flora declines

slightly from 72 to 66% (Burrows et al. 2008). For percentage resprouting among banksias in the same region, the pattern depends on which compass direction is taken as length of the growing season declines from 8 months in the SW corner to 2 months in a N, NE, or E direction (Lamont and Markey 1995, Fig. 1). For central-southern Australia, Pausas and Bradstock (2007) showed that fire frequency rose as annual rainfall (productivity) increased from 250 to 650 mm year⁻¹ and, at the same time, the absolute number and percentage of resprouters doubled. However, they were undecided if this increase was a response to greater fire frequency or to the greater risk of recruitment failure in the more competitive (productive) environment. For SE Australian forests, Clarke and Knox (2002) and Clarke et al. (2005) concluded that the absolute number and fraction of resprouters were higher in habitats where fire was more frequent and fuel less patchy, but especially if they were more productive (higher soil fertility and moisture). The latter is partly because resprouters are more likely to recover from fire when growing more vigorously (López-Soria and Castell 1992; Knox and Clarke 2005) as well as avoiding the risk of recruitment failure in the face of greater competition. Thus, the percentage of resprouters is sometimes higher in more productive environments and sometimes lower, independent of, or confounded with, fire interval (Fig. 1).

Vegetative recovery and fitness benefits

While there are many alternatives to fire in causing the loss of above-ground parts (Bond and Midgley 2001), no other environmental factor produces such a sudden and complete loss of crown mass nor is responded to by such prolific growth rates, as occurs among resprouters following fire (Lamont et al. 2004; Chalwell and Ladd 2005). Vesik and Westoby (2004b) found that resprouting species in the most fire-prone systems were least likely to be killed by fire. However, the act of recovery is unrelated to any possible stimulatory heat effect of fire as pruning always initiates the resprouting response (Zammit and Westoby 1987), and there are no examples of plants recovering from fire damage but not from pruning (Vesik et al. 2004). In fact, for species with <100% survival from clipping, they are less likely to survive

when burnt: the difference is inversely related to the depth that buds are buried, and is clearly subject to selection pressure.

Fire creates an ideal opportunity for vegetative recovery as interplant competition is reduced and resource availability (water, nutrients, light, and space) is enhanced (Gill 1981). Resprouting has two fitness advantages over seedling recruitment in this regard—the growth response can be almost immediate and flowering can occur sooner. Nevertheless, the secondary juvenile period may last longer under lower rainfall (poorer growing conditions) even when the vegetation is considered more fire-prone (Burrows et al. 2008). Both these advantages still occur in the instance of individual-level shoot loss in the absence of fire. Recovery, however, would be at a much slower rate, as the level of competition would remain and there would be little resource enhancement. Furthermore, resprouting species tend to have greater drought resistance (Lamont and Markey 1995), wider geographic tolerances (Lamont and Markey 1995), and stronger resistance to diseases (Moore et al. 2007).

Resprouting improves fitness in fire-prone environments only if so few seeds are produced/stored that self-replacement is unlikely should the parent die; or if post-fire conditions for seedling recruitment are unfavourable or unpredictable (Enright et al. 1998a). Under such circumstances, population survival is enhanced by the parent recovering in response to fire rather than relying on seedlings. This enhancement applies to species that produce few seeds because of breeding system restrictions or congenital factors, prolonged time to reach maturity, recurrently high florivory/granivory, and/or particularly resource-demanding seeds, fruits, or infructescences relative to supply (Lamont 1988; Lamont and Wiens 2003; Groom and Lamont 2010). For example, among resprouting banksias, up to 70% of flower heads may be damaged or removed by larvae/nectar-seeking birds, up to 80% of barren cones may be infested by insect larvae, and up to 40% of stored seeds destroyed (Lamont et al. 2007).

Another reason for low seed availability among perennial species in fire-prone environments is short fire intervals. Resprouting buffers populations against their rapid decline or even local extinction (storage effect *sensu* Chesson 1986) by avoiding the risk of poor recruitment following short-interval fire (Groeneveld et al. 2002). Thus, resprouters should

have a fitness advantage over non-sprouters in frequently burnt vegetation (Enright et al. 1998a; Bellingham and Sparrow 2000; Wright and Clarke 2007a). However, resprouters are slower growing than fire-killed species and can take many years to become fire-tolerant (Abbott 1985; Lamont and van Leeuwen 1988; Enright and Lamont 1992), so the fitness advantage of resprouters applies to variable fire regimes within which short fire intervals are common rather than to recurrent short intervals per se (Enright et al. 1998b; Groeneveld et al. 2002).

The extent of resprouting also varies greatly between species (Vesk et al. 2004; Vesk and Westoby 2004b; Clarke et al. 2005) and within species (Lamont et al. 1994; Lamont 1996; Bellingham and Sparrow 2000). López-Soria and Castell (1992) argued that high variation in survival of genets after severe fire between populations and co-occurring species indicates that fire has not been the primary selective agent for resprouting, as levels should be the same. However, this argument neglects the fact that seeds are an alternative method of surviving disturbance, and this needs to be taken into account as it also greatly varies between species. Ignoring variations in seed production, resprouting will be maladaptive at mean fire intervals less than the period required to become fire-tolerant and adaptive where the mean fire intervals exceed the period required to become fire-tolerant but shorter than plant longevity, which greatly exceeds that of non-sprouters (Enright et al. 1998a).

In addition, fires themselves may decrease plant longevity depending on their frequency and intensity and life stage of the species. Short-interval fires, and/or frequent pruning to simulate the effect of fire, can lead to premature death (Grano 1970; Zammit and Westoby 1987; Watson and Wardell-Johnson 2004; Wright and Clarke 2007a; Enright et al. 2011). However, Wright and Clarke (2007a) report a rare instance, in central Australian spinifex-mulga vegetation, where a 2-year-interval fire resulted in an increase in resprouter abundance compared with longer intervals. Some species appear to reach a peak in their fire tolerance with young and old plants most likely to die (Burrows 1985; Hodgkinson 1998; Vesk et al. 2004; Enright et al. 2011). Season of burn as it affects fire intensity, post-fire water availability and starch reserves may also be important (Wright and Clarke 2007b). All these point to the limitations of resprouting as an adaptation to fire, but in none of

these situations is non-sprouting/obligate seeding a more viable option.

Whether the long-term fitness of resprouters exceeds that of non-sprouters depends on their level of genet recovery compared with the level of seedling recruitment under the same fire regime (Enright et al. 1998a, b; Higgins et al. 2008). Superior fitness ultimately lies with those resprouters that have high levels of vegetative recovery, and retain the ability to produce seeds, as this gives greater adaptive flexibility. In fact, asexual resprouters are extremely rare, restricted to a few clonal species with nonviable pollen (Lamont 1988), consistent with the somatic mutation view discussed in the following section. However, Vallejo-Marín et al. (2010) have argued that, as investment in sexual reproduction is logarithmically (rather than linearly) related to fitness (because of increasing risk of inbreeding), whereas ramet production is linearly related to fitness, there is a strong selective pressure towards sterility among clonal species. This ignores both the dispersal and genetic-novelty roles of seeds among resprouters that replace their population-persistence function among fire-killed species.

Reasons for low fecundity among resprouters

There is a general trend for the level of post-fire resprouting to be inversely related to fecundity (Vesk and Westoby 2004a). This has been interpreted as a resource trade-off between reproductive effort and structures that support resprouting, such as thick stems and starch accumulated by rootstocks (Bellingham and Sparrow 2000; Knox and Clarke 2005). However, such trade-off is only clearly established between the resource demands of vegetative growth and storage organs (Pate et al. 1990; Schutz et al. 2009). Stored starch is used for post-fire root and shoot recovery (Bowen and Pate 1993; Langley et al. 2002; Korczynskyj and Lamont 2005; Schutz et al. 2009), but can also be used for supporting inflorescence production in the case of grasstrees (Lamont et al. 2004) and some geophytes that flower before foliating (Ruiters et al. 1993; Lamont and Downes 2011).

Thus, it is best to view much of the carbon, even here, as the subject of exchange, cycling to and from storage organs at different times, rather than strictly as a trade-off with growth. Resources for flowering and fruiting are provided locally (remobilisation and

retranslocation from the supporting branches and current nutrient uptake) and it would be necessary to show that levels there are lower in resprouters to support the prevailing storage/fecundity hypothesis. However, there is no empirical support for a resource trade-off at the reproductive or physiological levels (Zammit and Westoby 1987; Cruz and Moreno 2001; Lamont and Wiens 2003; Enright et al. 2007). For example, it cannot explain the lower viability of intact seeds in congeneric co-occurring resprouters as this postdates resource expenditure in their development (Lamont and Wiens 2003).

For co-occurring *Ceanothus*, resprouters have a better water supply than non-sprouters (Davis et al. 1999), whereas for adult *Banksia* species, there is no difference in water status (Lamont and Bergl 1991). Seed set is limited by nutrient supply under field conditions for both fire-response types among *Banksia* and other Proteaceae (Stock et al. 1989; Lamont et al. 1994; Vaughton and Ramsey 1998; Groom and Lamont 2010, 2011). For *Erica*, root starch concentration in resprouters is 20 times that in non-sprouters but shoot levels are erratic in both and not significantly different overall (Bell and Ojeda 1999). For *Erica australis*, there is no biomass trade-off between reproductive effort and starch storage in the lignotuber, indicating that carbohydrate supply is not limiting fecundity (Cruz and Moreno 2001). A similar pattern applies among Restionaceae (Pate et al. 1991), where relatively high shoot starch and sugar concentrations in resprouters are actually associated with low seed set for four of the five generic pairs examined. In addition, seed set among resprouters is sometimes pollen rather than resource-limited (Copland and Whelan 1989; Anderson and Hill 2002).

Thus, while stored carbohydrates serve to support vegetative regrowth after fire, there is no evidence that this is at the expense of seed production. Furthermore, resprouting structures are neither a preferential sink for mineral nutrients compared with seeds nor are stored mineral nutrients important in resprouting (Witkowski and Lamont 1996; Cruz et al. 2003). Leaf concentration of highly mobile phosphorus on a mass basis, but not nitrogen, potassium, or sodium, was higher among non-sprouters than resprouters in a comprehensive study of Mediterranean Basin shrubs (Saura-Mas and Lloret 2009). The study was not done in the context of flowering or fruit set and, as carbon content of the resprouter leaves was also higher, this

method underestimates the amount of nutrient actually available for retranslocation. In addition, many resprouters show fire-stimulated flowering when resources are at a maximum for both sexual reproduction and vegetative recovery (Lamont and Downes 2011), a case of resource matching rather than resource switching (Monks and Kelly 2006).

In trying to explain low seed set among many resprouters, it has also been postulated that they are outbreeders that abort most zygotes; but evidence shows that many congeneric non-sprouters are also outbreeders (Lamont and Wiens 2003). Another possible cause is the presence of deleterious somatic mutations because resprouters are slow to mature and survive many fire cycles. As the accumulation of mutant alleles and chromosomal aberrations is simply a time-dependent process, they will be best expressed among resprouters, which typically survive an order of magnitude longer than non-sprouters (Enright and Lamont 1992; Lamont and Wiens 2003). Deleterious mutants are only purged at the time of fertilization, especially where selfing occurs, or where weakened seedlings fail to recruit. This interpretation requires

that the percentage flowering and/or fruit set, seed set/viability, or seedling vigour (a) be lower than matched non-sprouters, (b) decline with age of resprouters, (c) become more variable in different parts of the same plant with time because of the random nature of mutations, and (d) that evidence for somatic mutations is not only obtained but also that their incidence increases with time. The first is strongly supported for all indices of fecundity by the meta-analysis of Lamont and Wiens (2003) for a wide range of species pairs. Another example is the occasional albino seedlings produced by the clonal *Nuytsia floribunda* (B. Lamont unpublished) that is the largest and possibly oldest resprouter that shows fire-stimulated flowering (Lamont and Downes 2011).

The second requirement is supported by the strong negative relationship between plant size (as a surrogate for age) and relative fruit set in *Ceanothus tomentosus*, *Adenostoma fasciculatum*, *Banksia goodii*, *B. menziesii* (Lamont and Wiens 2003), and *B. attenuata* (Fig. 2). The previously unpublished data for the last species are especially useful for it shows that as lignotuber circumference increases from 10 to

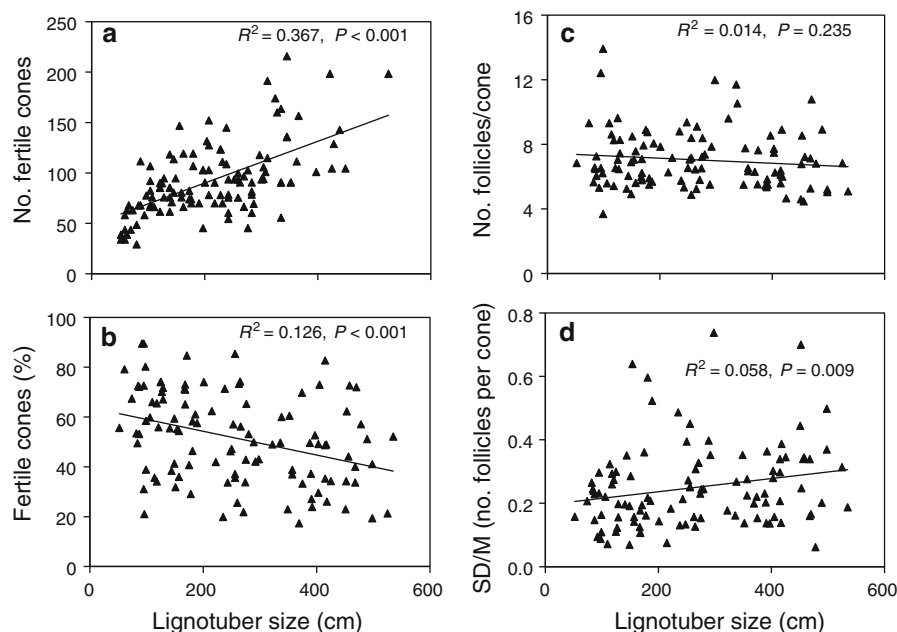


Fig. 2 Relationship between lignotuber size (circumference, as a surrogate for age) and (a) number of fertile (seed-bearing) cones per plant, (b) fraction of fertile cones, (c) number of follicles (seed-bearing fruits) per fertile cone, and (d) mean for five branches of the ratio of standard deviation (SD) to mean (M) per branch for number of follicles per cone per plant of

Banksia attenuata. A total of 125 plants were chosen in a random walk (provided they possessed at least five flower heads or cones) at a single population burnt 12 years ago. Best-fit lines are given plus their coefficient of determination (R^2) and probability (P)

535 cm (=maximum diameter of 130 cm), crown biovolume rises steadily and the number of major stems (all the same age since fire and size) produced by the lignotuber increased from 1 to 60, i.e., there is no progressive senescence to explain the results. Furthermore, the coefficient of variation between 5 or 6 main branches on the same plant for most indices of fecundity rose with the increase in lignotuber size, supporting (c) above. Analysis of 11 microsatellite loci as described in He et al. (2007) on 5–6 branches of 54 plants, mean circumference 383 cm, showed that 4 (7.4%) possessed non-identical heterozygous alleles in different branches on the same plant (Xiaofang Deng, He and Lamont, unpublished) in support of (d) though the sample size is too small to show any relationship with lignotuber size.

As clonal species live the longest among resprouters and sometimes fail to set any seeds despite prolific flowering (Lamont and Barrett 1988), they are ideal candidates to explore this alternative hypothesis further (provided individuals can be distinguished). With this view, low seed set may be an inevitable consequence of the longevity of resprouters rather than central to understanding their fitness benefits, and allows for the many instances of resprouters with high fecundity (Lamont 1985, Bellingham and Sparrow 2000; Enright et al. 2007) as well as the lack of trade-offs noted above.

Trait evolution

Measures that prevent heat death of the meristems or sunken buds, such as thick non-combustible bark (Gill and Ashton 1968; Lawes et al. 2011) and leaf bases (Lamont et al. 2004), might be considered as fire adaptations if it can be shown that they are an evolutionary response to fire, rather than, for example, deterring stem borers in a pre-fire environment. In American *Pinus*, resprouting is rare, derived, and linked to fire (Keeley and Zedler 1998). By contrast, in South African *Erica*, resprouting is rare, ancestral and its loss may be linked to fire (Verdaguer and Ojeda 2005). Certainly, resprouting is heritable and can even operate at the population and subregional scales (Lamont and Connell 1996; van der Bank et al. 1999). The ability to form lignotubers, for example, is genetically controlled (Mullette and Bamber 1978; Whittock et al. 2003; Verdaguer and Ojeda 2005).

Morphological and physiological differences between resprouter and non-sprouter populations of the Californian *Ceanothus tomentosus* (Rhamnaceae) are maintained in a common environment (Schwilk and Ackerly 2005). But their expression may depend on growing conditions: there is evidence that pruning and dieback (as occurs during fire) may promote lignotuber and multiple-branch development in species that otherwise resprout epicormically from a single stem (Mullette 1978; *Banksia menziesii* at Eneabba, personal observation) and resource availability also may be important in lignotuber formation (Beadle 1968).

Lloret et al. (1999) found that most shrubs in non-fire-prone shrublands in Mexico were resprouters. Species with relatives in fire-prone chaparral shrublands showed high levels of resprouting when the plants were clipped and subjected to flame temperatures of 300–400°C for 3 min, and they concluded that resprouting evolved before the appearance of chaparral. However, neotropical species, with no relatives in chaparral shrublands, recovered less vigorously and were less likely to survive and thus this group was excluded from fire-prone environments, i.e., they were subjected to selection by fire without the ability to adapt.

In an influential paper, Wells (1969) considered that resprouting was an ancestral trait hampering speciation, whereas non-sprouters were favoured with their short generation times and therefore greater opportunities for fitness selection and speciation. Yet resprouting species, for example, may account for 60–90% of species in fire-prone shrublands of SW Australia (Bell 2001; Enright et al. 2007) and 10–100% of the major families and of genera in the Cape shrublands (Le Maitre and Midgley 1992). Resprouting has evolved and been lost repeatedly within lineages of genera well represented in Mediterranean-type regions (Bond and Midgley 2003; Pausas and Verdú 2005). Among 45 genera examined in Australia and South Africa, Verdú et al. (2007) obtained no evidence that molecular evolutionary or speciation rates were different between resprouters and non-sprouters. However, these phylogenetic analyses have been at the level of qualitative fire responses rather than examining the evolution of specific mechanisms, such as sunken accessory buds covered by thick bark, or soil that would enable survival from increasingly more intense and frequent fires, such as occurred during the late

Cenozoic. It is the particular environmental context of the renewal buds that must be searched for specific fire adaptations rather than viewing resprouting as a single universal mechanism that succeeds under all fire regimes (Clarke et al. 2010).

In this regard, He et al. (2011) have recently shown that clonal lineages (resprouting from rhizomes or root suckers) in *Banksia* arose 6–15.6 million years ago (possibly only 14 Ma as root suckering appears to be a recent trait in the 15.6-My old *B. elegans*) in a genus that has been fire-prone for 61 My (Fig. 3). Resprouting arose at least 14–21.5 million years ago in four lineages, so clonality is a derived trait in this group and clearly linked ('fine-tuned') to intensifying fire during the mid-late Neogene. Non-sprouting, from 19 to

26.5 Ma, appears to be represented in even older lineages but accurate comparative dating is confounded by the equal probability of being non-sprouting or resprouting in lineages older than 25 My. Certainly, the immediate rainforest (non-fire-prone) ancestors of *Banksia* are non-sprouters, so resprouting may be interpreted as a derived trait and linked to fire.

Simon et al. (2009) highlighted how the evolution of a variety of resprouting mechanisms (xylopodia, rhizomes, thick bark) enabled four genera and one family to invade South American savannas from the surrounding non-fire-prone regions from 10 Ma, peaking at 1–4 Ma. Of 26 species with such mechanisms, 23 are restricted to savannas. At the other

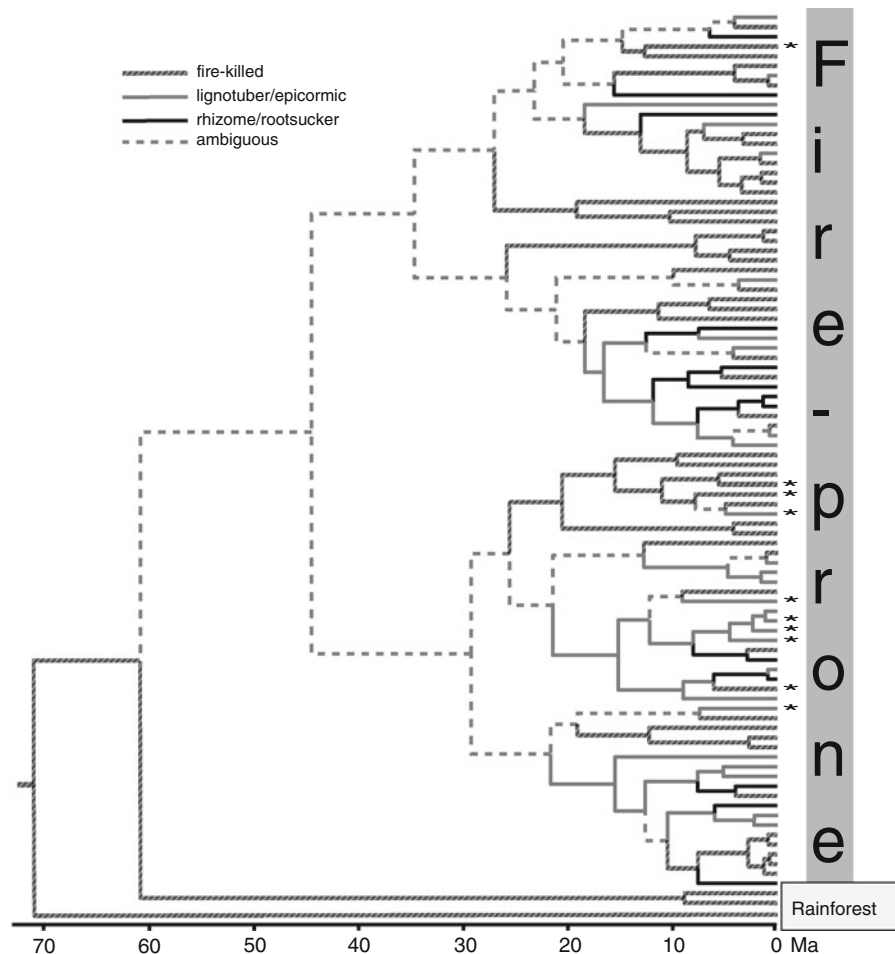


Fig. 3 Ancestral state reconstruction for resprouting in Banksiinae (84 *Banksia* + 5 *Dryandra* taxa, the latter at the top of the chronogram) and related taxa. *Non-serotinous species, indicating that they do not rely on fire for seedling recruitment and

are less fire-prone than the other species. Analysis adapted from He et al. (2011). A colour version with species names is available as Supplementary Material Figure S1

extreme, the rhizomatous/epicormic tree mistletoe, *Nuytsia floribunda*, originating in a fire-prone environment 45 Ma (Vidal-Russell and Nickrent 2008), stands as the oldest resprouting species known, though there is an equal probability this ability might even have evolved along its stem that originated 82 Ma (Lamont and Downes 2011).

Burrows (2002) noted that the epicormic, bud-bearing meristematic strands in *Eucalyptus* (Myrtaceae) are associated with the outer wood and vascular cambium whereas in the related rainforest *Lophostemon* and other trees in non-fire-prone systems they are located in the outer bark, but the analysis was non-phylogenetic. This has now been addressed by Crisp et al. (2011) who show that the epicormic strands in many members of the Myrtaceae are an ancient trait that can be traced back to 60 Ma and is uniquely associated with fire-prone environments that can be traced to 62 Ma from non-sprouting rainforest ancestors. While they suggest that epicormic strands are unique to the eucalypt lineage, similar simultaneous proliferation of branchlets at old nodes in the *Melaleuca* lineage, Proteaceae and Casuarinaceae (B. Lamont, pers. obs.) post-fire indicates that this phenomenon deserves wider study.

Speciation mechanisms

Imputing fire as a strong agent of natural selection does not offer any genetic mechanism for explaining a speciation rate among resprouters that in many taxonomic groups has kept pace with that of non-sprouters. In plants, somatic mutations and chromosomal re-arrangements have long been considered a significant source of new genetic variation, both within and between individuals (Whitham and Slobodchikoff 1981). Although most mutations are thought to be deleterious, Peck (1994) showed that abundant deleterious alleles do not deter the expression of a single beneficial mutant provided most reproduction is sexual, which is the case for the great majority of resprouters. Despite an overall reduction in fecundity for *Banksia attenuata*, the mean number of follicles per cone per branch does not change as plants age (greater lignotuber size) but the coefficient of variation between branches in the same plant increases significantly (Fig. 2c,d). This means that the increasing beneficial effects of somatic mutations on fruit set

in some branches balance out the increasing deleterious effects of other mutant alleles in other branches.

Since somatic mutation is a stochastic process, mutant alleles will build up in resprouters over time as potentially novel and beneficial genetic combinations are stored in meristematic tissues such as dormant rhizomatous and epicormic buds. Adaptation is therefore likely to be faster from these pre-existing novel genotypes than from novel genotypes among seedlings because they occur at a faster rate than via meiosis and (dominant) beneficial alleles may be immediately expressed (Pineda-Krch and Lehtila 2004; Barrett and Schulter 2008). Resprouters also tend to be outbreeders, enhancing their ability to carry a high mutational load (Lamont and Wiens 2003; Vallejo-Marín et al. 2010). Thus xenogamy-longevity in association with frequent axillary branching (induced by recurrent fire) via copious stored buds will favour the accumulation and expression respectively of occasional beneficial somatic mutations present in the meristematic tissues of resprouters. This leads rapidly to ecotypic differentiation among seeds produced from those branches, with eventual genetic isolation and speciation.

The best known example of the scope for this phenomenon among resprouters is *Eucalyptus melliodora* that normally is highly susceptible to the herbivorous beetle, *Anoplognathus montanus*. Edwards et al. (1990) noted that branches in some trees were avoided by the beetle and showed that damaged and undamaged leaves possessed different essential oils, attributed to genetic mosaics arising from somatic mutations within meristems producing those branches. Should these branches produce seeds (they would grow at the expense of the rest of the crown) they will have a fitness advantage over the parent genotype. Another example are yellow (mutant) and red blooms produced on the same plant of *Banksia menziesii* (Collins et al. 2008) though it is unknown under what circumstances yellow flowers might have a fitness advantage over red.

Verdú et al. (2007) pointed to the existence of resprouter and non-sprouter populations among Mediterranean-climate species (e.g. Lamont and Connell 1996) and suggested that the switch may occur very late in the evolution of the species, masking any differences in evolutionary rates between them. Certainly fire-response type is highly labile in banksias, switching in either direction, and occurring at the fastest rates among the five fire-adapted traits

examined by He et al. (2011), though it is much more unidirectional among proteas (Lamont, He and K. Downes, unpubl.). Second, molecular evolutionary rates are unrelated to the rate of generation turnover as plants do not undergo determinate germline replication (Whittle and Johnston 2003). Third, species diversification rate is not a constant function of mutation rate (Barracough and Savolainen 2001). Fourth, newly segregating non-sprouter species are more prone to local extinction from short fire intervals while evolving resprouter populations remain stable and multigenerational (Groeneveld et al. 2002) representing a greater range of genotypes and giving greater flexibility for adaptive responses to fire. The genetic mosaic view offers a mechanism for novel variation while the last ('storage' effect) provides the environmental context for selection by fire. All lack solid empirical support at present.

Conclusions

Generally, habitats that experience more frequent and stochastic fires favour a greater contribution of resprouters to woody floras. More productive (competitive) environments may have opposing effects on fire frequency and incidence of resprouters within the envelope of possible responses, so that their effect cannot simply be 'scaled'. There is little evidence to support the assumption that resource expenditure on resprouting structures and storage is at the expense of the resource requirements for sexual reproduction. While carbon may be stored to assist post-fire recovery instead of supporting current growth, seed production is more likely to be nutrient-limited. The current paradigm of vegetative/reproductive trade-offs between fire-response types needs to be re-assessed (Cruz and Moreno 2001). Evidence of a role for somatic mutations in accounting for low seed set in many long-lived resprouters is increasing but remains poorly explored.

Combinations of traits that enable survival through the most intense fires, such as accessory buds sunken beneath thick non-combustible bark or adventitious buds on lateral roots insulated by soil, are starting to be studied in an evolutionary context to determine when they arose and if they are uniquely associated with fire. Already, the association revealed between the evolution of types of resprouting and presence in a fire-prone

environment is startling in both its strength and antiquity. It seems that fire has influenced the direction of evolution of many fire-related traits for at least 60 My in some currently fire-prone regions (Crisp et al. 2011; He et al. 2011). While resprouting may occur after any extensive damage to the plant crown and will always enhance fitness where seed production and seedling recruitment are curtailed, its predominant association with fire currently and in the past is only now beginning to be appreciated.

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