



Tansley review

Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire

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Summary

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Resprouting as a response to disturbance is now widely recognized as a key functional trait among woody plants and as the basis for the persistence niche. However, the underlying mechanisms that define resprouting responses to disturbance are poorly conceptualized. Resprouting ability is constrained by the interaction of the disturbance regime that depletes the buds and resources needed to fund resprouting, and the environment that drives growth and resource allocation. We develop a buds-protection-resources (BPR) framework for understanding resprouting in fire-prone ecosystems, based on bud bank location, bud protection, and how buds are resourced. Using this framework we go beyond earlier emphases on basal resprouting and highlight the importance of apical, epicormic and below-ground resprouting to the persistence niche. The BPR framework provides insights into: resprouting typologies that include both fire resisters (i.e. survive fire but do not resprout) and fire resprouters; the methods by which buds escape fire effects, such as thick bark; and the predictability of community assembly of resprouting types in relation to site productivity, disturbance regime and competition. Furthermore, predicting the consequences of global change is enhanced by the BPR framework because it potentially forecasts the retention or loss of above-ground biomass.

I. Introduction

Disturbance and resource availability interact to drive plant responses (Westoby, 1998), resulting in plant functional traits that underpin the mechanisms of community assembly (Ackerly, 2003). Resprouting is a tolerance trait that confers persistence at the plant level, enabling it to survive diverse disturbance regimes. At the community level, this gives rise to biomes that are resilient to severe (biomass depleting) disturbance (e.g. fire in savanna). Resprouting ability is determined by the development, protection and resourcing of a viable bud bank. Despite the early recognition of resprouting as a functional trait by Noble & Slatyer (1980), only relatively recently has the resprouting trait been incorporated in models of plant dynamics (e.g. Loehle, 2000; Hoffmann *et al.*, 2009), but it is still neglected as a source of variation in reviews of biomass allocation (Poorter *et al.*, 2012). Strong empirical evidence is now emerging of the central importance of resprouting across contrasting biomes, from rainforest (Poorter *et al.*, 2010) and conifer forests (Dietze & Clarke, 2008) to desert shrublands (Nano & Clarke, 2011), savanna (Higgins *et al.*, 2000; Lawes *et al.*, 2011a) and Mediterranean-type ecosystems (Keeley *et al.*, 2012).

Previous reviews (Bellingham & Sparrow, 2000; Bond & Midgley, 2001, 2003) of resprouting ecology were based on models of how trees escape fire effects, concentrating on the role of fire frequency and severity and their interaction with basal sprouting only. However, it is clear that in some ecosystems, many

resprouting species sprout not only from the rootstock, but also from the stem (Meier *et al.*, 2012). In this review we expand on current resprouting theory by redefining the ecological scope of resprouting and emphasizing the need to understand the underlying mechanisms responsible for different resprouting responses to disturbance. We link the three basic types of resprouting – aerial, basal, and below-ground – to resprouting response and examine evolutionary and proximal influences (Figs 1, 2). In addition, we consider hypotheses that predict constraints on resprouting and scale up these issues to the community level by developing a model that predicts vegetation assembly.

Resprouting is an active field with > 500 peer-reviewed research papers published since 2000 (ISI Web of Science). We advance the field by proposing a new conceptual framework for resprouting theory, the buds-protection-resources (BPR) scheme, for understanding resprouting as a plant functional trait based on bud location, their protection, and resourcing of regrowth, in response to disturbance (Clarke *et al.*, 2010; Lawes & Clarke, 2011; Hoffmann *et al.*, 2012; Fig. 1). We review recent findings on resprouting, adding greater precision to the ‘persistence niche’ concept that was developed with a focus on basal resprouting by Bond & Midgley (2001, 2003). We focus on resprouting in woody plants as a response to fire regimes, as fire is a pervasive disturbance (Chuvieco *et al.*, 2008) that has been integral to the evolution of the angiosperms (Bond & Scott, 2010; Bond & Midgley, 2012b), and the evolutionary ecology of major biomes (Sankaran *et al.*, 2005; Bond, 2008).

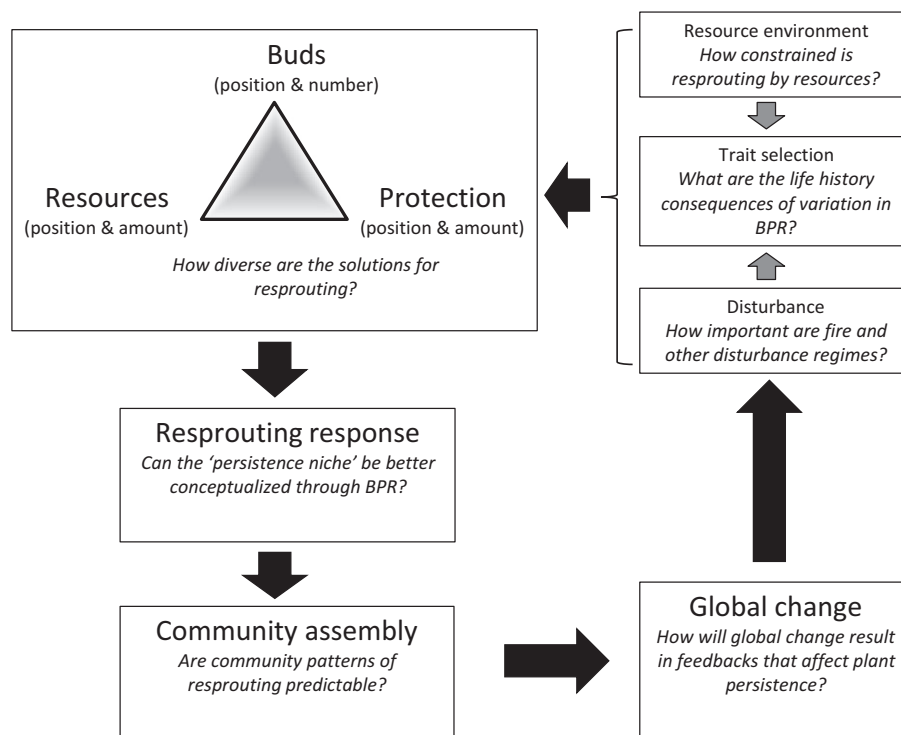


Fig. 1 The influences and consequences (arrows) of resprouting from individuals to communities. The bud-protection-resources (BPR) scheme is a conceptual framework around which critical evolutionary and proximal questions can be posed (boxed questions). The BPR scheme defines how plants resprout (Sections II and III in this review). Consequently, the influence of trait selection (Section IV), environment and disturbance (Section V) on resprouting ability can be predicted. The BPR scheme also enables prediction of community assembly after disturbance (Section VI) and of global change (Section VII).

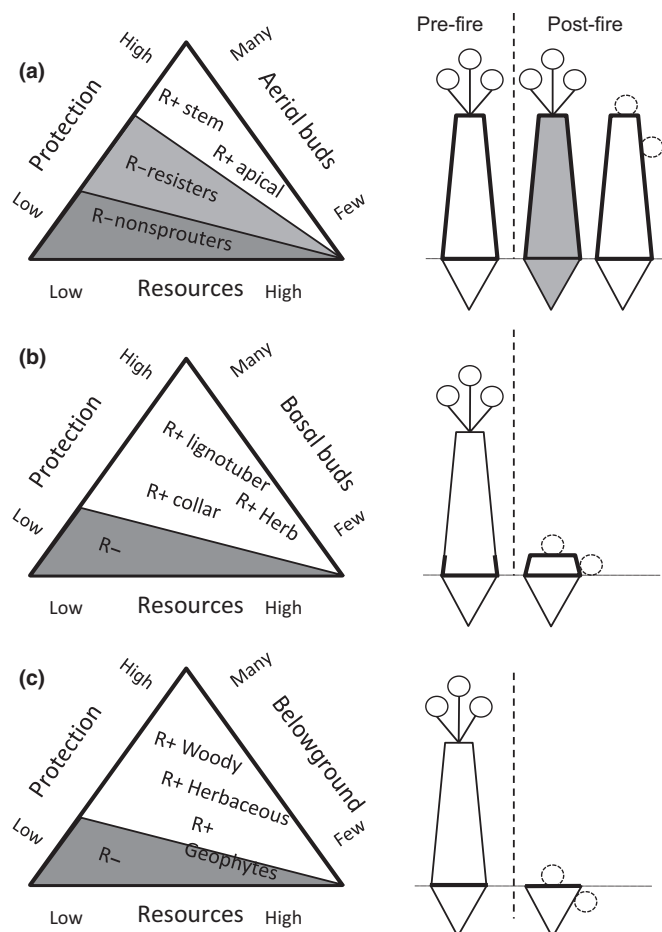


Fig. 2 Three axes of variation drive resprouting ability: location and number of buds, protection of buds and hydraulics, together with nutrient and carbohydrate resources to fund resprouting. These axes represent coordinated tradeoffs that vary depending on position of resprouting. (a) Aerial buds are protected by bark (thicker line) and leaves that allow for fire resisters (stem shaded) or aerial resprouting by either apical or axillary buds (dashed circles); (b) basal buds are protected mainly by bark, resulting in basal resprouting mostly from axillary buds, often from swollen lignotubers; (c) underground buds are mainly protected by soil and may result in horizontal spread, and clonality, as plants resprout from axillary and apical buds. The range of resprouting subtypes is defined by position along axes of protection, number of buds and amount of resources (mainly nonstructural carbohydrates). Nonsprouters (R–; darkest shading) are killed by disturbance and lack sufficient buds, protection and/or stored carbohydrates to resprout. R+, resprouters.

II. Resprouters rather than ‘sprouters’

Fire and other severe disturbances have a binary effect on individual plants – they either die, or resprout from buds. The terms ‘sprouting’ and ‘resprouting’ have been used interchangeably to define the production of new vegetative growth induced by injury or a marked change in growing conditions (del Tredici, 2001). Botanically, sprouting is the initiation of growth from buds and is not necessarily a disturbance response, whereas resprouting is used in the context of a response to disturbance, as it implies the potential for repeated vegetative regeneration from a source of ‘protected’ buds and meristems. The position of buds and the location of

resprouting shoots after fire are extremely varied and are key criteria that define resprouting ability because bud location is a primary constraint (Table 1, Figs 2, 3).

The dichotomous classification of species as resprouters (R+) or nonsprouters (R–) simplifies the continuum of population responses to fire (Pausas *et al.*, 2004). While this classification has proved useful (Bond & Midgley, 2001), the variation in resprouting response to fire is not well reflected in current typologies (R+, R–) because bud position is ignored (e.g. Bellingham & Sparrow, 2000; Vesik & Westoby, 2004a). Resprouting typologies have focused mainly on disturbance severity (Bellingham & Sparrow, 2000) or bud bank location in shrub and tree species (del Tredici, 2001; Klimešová & Klimeš, 2007) and herbs (Klimešová & Klimeš, 2003). Since the 1970s, a popular approach to classifying the response of plants to fire was based on the response to 100% leaf scorch (Gill, 1981). Here we develop this approach under the framework of bud origins/number, their protection and resource location, because these factors characterize the ecological outcome. Three broad classes of R+ response are presented – aerial, basal, and below-ground – within which there are classes that reflect the origins of buds and the source of resources to fund regrowth (Table 1, Fig. 2). While this approach adequately summarizes the response of individuals and species at the adult life stage, the effect of plant developmental stage should also be considered in classifications (Vesik, 2006; Fig. 4).

How does resprouting ability change with age? Resprouting ability after felling or decapitation (coppicing) decreases with the stage of tree development in production (del Tredici, 2001; Sands & Abrams, 2009) and natural forest ecosystems (Bellingham & Sparrow, 2000, 2009; Dietze & Clarke, 2008). Why this occurs is unknown, but it is thought to arise from a combination of genetic, physiological and related anatomical changes (del Tredici, 2001; Waters *et al.*, 2010). In the context of fire, Vesik (2006) demonstrated that ground-dwelling species maintained considerable resprouting ability regardless of age, while shrubs increased and trees decreased their resprouting ability with age (see also Bond & Van Wilgen, 1996). The relationship between growth form and ontogeny suggests that age-related resprouting ability is linked to bud senescence (Bond & Van Wilgen, 1996; Vesik, 2006; Waters *et al.*, 2010) and is adaptive because juvenile plants cannot escape fire (Keeley *et al.*, 2012). In nonsprouter (R–) species, bud senescence at an early ontogenetic stage appears to explain their inability to persist through fire (Hodgkinson, 1998; Verdaguer & Ojeda, 2005; Gignoux *et al.*, 2009). Our review links the concept of age-based bud senescence with the position and number of buds in a model of resprouting types (Fig. 4).

III. How do plants resprout?

Understanding postfire resprouting responses requires an understanding of what tissues survive fire and other severe disturbances. The most important are the meristematic tissues, in particular the buds or bud-forming tissues and, for woody plants, the vascular and cork cambia. Buds are protected by soil (below-ground tissues) and/or by bark or leaf bases (for above-ground tissues; Table 1). Resource allocation to resprouting is reflected in the degree of

Table 1 Classifying resprouters: how buds, protection and resources drive different types of fire persistence (this classification assumes that the crowns of plants have been scorched or combusted by fire; this classification may also be useful for other disturbance, such as wind damage)

Bud location/type	Resprouter type	Protection	Resource location	Postfire shoots	Examples
Aerial stem survives	I Aerial				
Terminal	Ia Aerial apical sprouter	Leaf bases, overlapping leaf primordia, leaf scales, woolly indumentum	Primary stem	Original bud and single stem(s) retained	Grasstrees (Asparagales), palmettos, cycads, tree ferns, pandans, Aloe, aralioids
Axillary	Ib Aerial axillary resprouter	Leaf bases, bud scales, bark	Branches	Original stems retained	Many shrubs and trees only receiving light disturbance
Accessory	Ic Epicormic resprouter	Bark	Primary stem, branches	Original trunk retained	Casuarinaceae, Fagaceae, Myrtaceae, Oliniaceae, Proteaceae, rare in conifers and oaks (<i>Pinus</i> , <i>Pseudotsuga</i> , <i>Quercus</i>)
Aerial stem killed	II. Basal				
Axillary (herbaceous)	IIa Basal herbaceous resprouter	Leaf sheaths, bud scales, clumped stems, rhizomes	Stem bases, stolons, rhizomes	Multiple new stems. Potential for clonality.	Bunch grasses, sedges, restioids, forbs, lilioids
Accessory (swollen stem base)	IIb Lignotuberous resprouter	Bark, stem bases, soil	Lignotuber	Multiple new stems, thinning to many stems	Many Myrtaceae (<i>Eucalyptus</i>), Asteraceae, Bruniaceae, Elaeocarpaceae, Ericaceae, Fagaceae, Oleaceae, Proteaceae, Rhamnaceae, Rosaceae
Accessory (no swollen base)	IIc Collar resprouter	Bark	Stem base	Multiple new stems, thinning to few stems	Many Eudicot trees and shrubs. Some conifers (Cupressaceae, Taxaceae, Taxodiaceae)
Underground	III Below-ground				
aerial stem killed if present					
Terminal (herbaceous)	IIIa Geophyte	Soil, leaf bases, bud scales	Corms, bulbs, short rhizomes, tubers	Usually single new stem, rarely multiple. Potential for clonality	Terrestrial orchids, Amaryllidaceae, Iridaceae, Lilioids <i>sensu lato</i> , Haemodoraceae
Axillary (herbaceous)	IIIb Herbaceous rhizomatous resprouter	Soil, leaf bases, bud scales	Long rhizomes	Multiple new stems, thinning to many stems. Often clonal	Perennial grasses, forbs, sedges, restioids
Axillary (woody)	IIIc Woody rhizomatous resprouter	Soil, bark	Underground stem	Multiple new stems, thinning to many stems. Potential for clonality.	Rare in gymnosperms (<i>Actinostrobus</i> , <i>Podocarpus</i>), some woody angiosperms (e.g. <i>Banksia</i> , <i>Dryandra</i> , <i>Grevillea</i> , <i>Protea</i> , <i>Quercus</i>)
Axillary (swollen rootstock)	IIId Xylopodial root resprouters*	Soil, bark	Swollen vertical roots or rhizophores	Limited initial stems. Limited potential for clonality	Common in angiosperm forbs, fewer among Eudicot shrubs and trees. Rare in gymnosperms
Adventitious buds (horizontal roots)	IIle Root-suckering resprouter	Soil, bark	Lateral roots	Multiple new stems, thinning to many stems. Potential for clonality	Common in angiosperm forbs, some shrubs (e.g. <i>Acacia</i> , <i>Hakea</i> , <i>Isopogon</i>) and trees (<i>Banksia</i>). Rare in gymnosperms

*Terminology widespread in South America – see, for example, Alonso & Machado (2007).

protection given to the meristems, allocation and location of storage reserves, and the relative proportions of vegetative and reproductive growth. The BPR scheme, shown in Fig. 2, contextualizes these various dimensions to resprouting and provides a framework for predicting resprouting responses to disturbance.

1. Buds

Fire resisters vs resprouters Some plants, mostly trees, resist ground fire effects by having a tall, well-insulated (thick-barked) bole, with the buds in the crown usually subjected to only a mild heat pulse (leaf scorch not leaf combustion; Fig. 2a). For example, fire-resistant European pines have large, protected buds (shielded by scales and relatively thick/long needles), crown structure favorable to heat dissipation, and tall stems that are self-pruning (Fernandes *et al.*, 2008; Table 1). Such 'fire resisters' are rare in crown fire systems, but in South African fynbos (Midgley *et al.*, 2011) and Australian woodlands there are fire resisters in crown fire systems, for example, some *Callitris* species that suppress fuel loads (Bradstock & Cohn, 2002). Fire resisters depend on thick bark to protect their hydraulics and vascular cambium from fire damage (Midgley *et al.*, 2011). While fire resistance may confer persistence,

these species are not necessarily resprouters because their aerial buds are not protected from extreme crown fires that may kill them (Fig. 2a).

Apical sprouters A specialized subset of aerial sprouters survive fire by protecting the apical bud and do not resprout *per se* (Fig. 2a). These include arborescent monocots (grasstrees, palms, pandans, Velloziaceae), tree ferns, cycads and some pachycaul shrubs (Fig. 3a). They protect the apical meristem with tightly clustered leaf primordia and leaf bases of the mature leaves (Table 1; Lamont *et al.*, 2004). In addition, most do not possess a vascular cambium and their 'scattered' primary vascular tissues (i.e. no peripheral vascular cambium) are protected by leaf bases. Such aerial sprouters are represented by relatively few species, but their biomass can dominate the understory of fire-prone savanna and some Mediterranean-type woodlands (e.g. *Livistona*, *Macrozamia* and *Xanthorrhoea* in Australia, *Chamaerops humilis* in the western Mediterranean Basin, and *Mimosa* in the Cerrado) and some conifer forests (Fernandes *et al.*, 2008). Apical sprouters are shorter than fire resisters (except for some palms), but their hydraulics and apical bud are well protected and consequently they have high probabilities of surviving fire (Fig. 4).

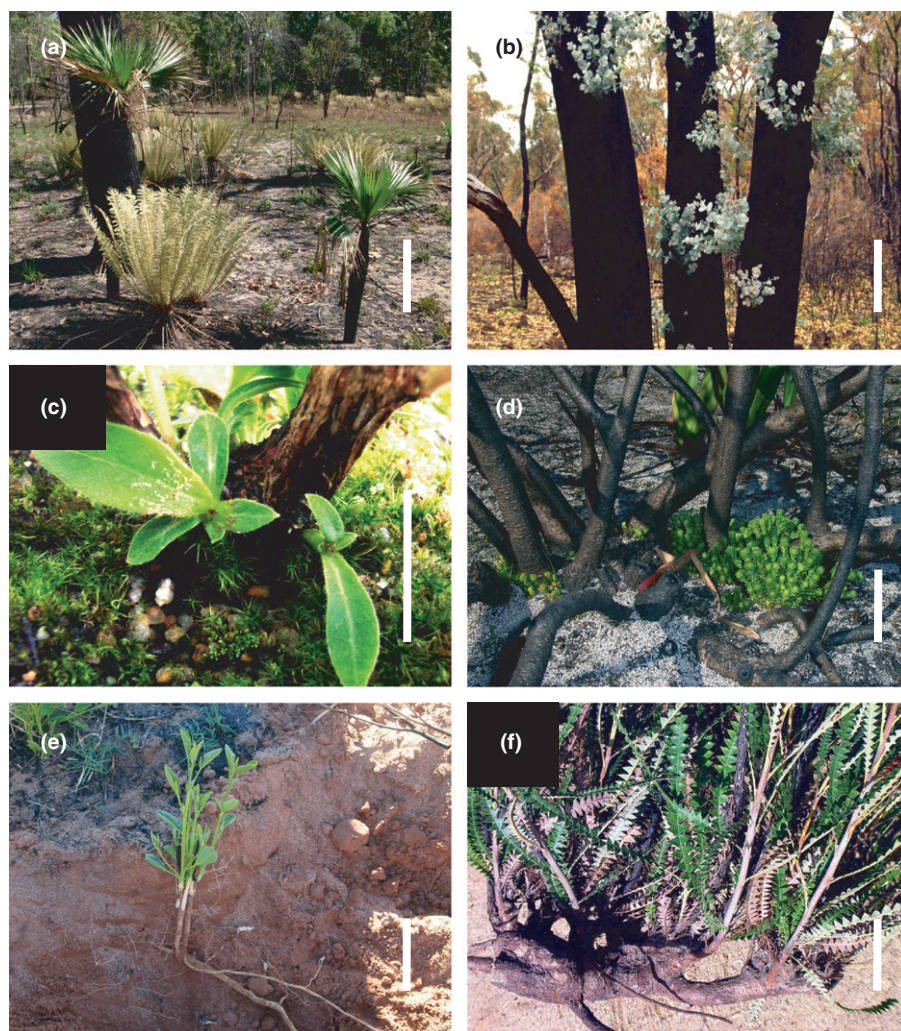


Fig. 3 Common forms of resprouting after crown fire: (a) apical sprouting from an aerial terminal bud in a cycad (*Cycas armstrongii*) and a palm (*Livistona humilis*); common understory components of Australian tropical savannas; (b) epicormic resprouting typical of many eucalypt species (*Eucalyptus banksii*) after crown fire; (c) basal resprouting from a stem collar after ground fire in a rainforest (*Hibbertia* sp.); (d) basal resprouting from a lignotuber after crown fire in fynbos (*Leucadendron* sp.); (e) below-ground resprouting from lateral roots after ground fire in an Australian desert (*Crotalaria* sp.); and (f) underground resprouting from a woody rhizome after crown fire in kwongan (*Banksia candolleana*). (Photographs by Peter Clarke, Michael Lawes, and Byron Lamont). Bars: 1 m on stem (a, b); 5 cm (c–f).

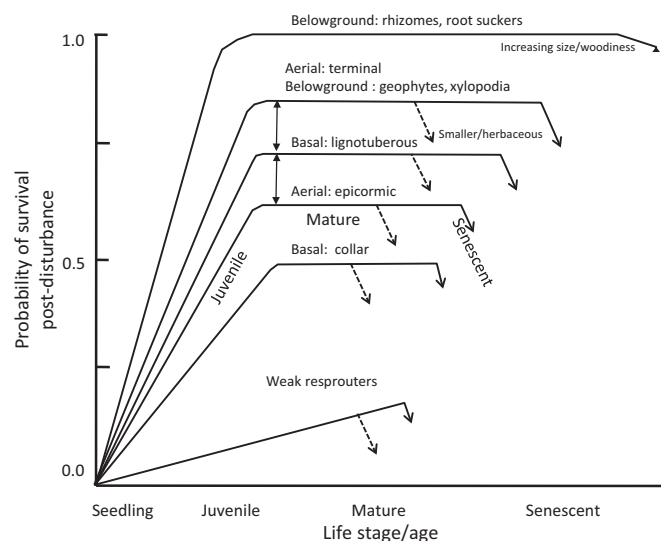


Fig. 4 A conceptual model of the relationship between survival after severe disturbance and life stage/age for resprouter types (see Table 1). Smaller growth forms will mature more rapidly and decline sooner than longer-lived woody plants (broken lines). Many woody resprouters have both basal and epicormic resprouting, and local circumstances will influence alternative probabilities of survival (indicated by double arrow heads). Life stage/age is distributed on a semilogarithmic scale. Examples of supporting fitted models are given in Gignoux *et al.* (2009) and Hodgkinson (1998).

Epicormic resprouters While structural modifications may protect the crown buds of a mature tree during a surface fire, greater protection and a different arrangement of bud-forming tissues are needed for above-ground resprouting after a crown fire, because these are usually more intense. Many angiosperm species are capable of epicormic resprouting, although these are only prominent in a few, but biome-important, angiosperm families (Meier *et al.*, 2012). After high-intensity fire, aerial resprouters produce large numbers of epicormic (aerial) shoots, not only on boles but also on branchlets (Figs 3b, 5). By contrast with angiosperms, epicormic resprouting in gymnosperms is limited to a few species (e.g. *Pinus canariensis*), which may reflect the lack of axillary meristems and hydraulic limitations of gymnosperms.

Worldwide, the most successful epicormic resprouters are in the Australian Myrtaceae, (especially *Eucalyptus* and its allies) so that overstory species in forests, woodlands and savannas there display remarkable resilience to crown fire (Fig. 3b). McArthur (1968) estimated that 7000 accessory strands were present in the trunk and main branches of a typical eucalypt tree, 21 m tall (one accessory strand per leaf), making this group the quintessential fire resprouter. While there are eucalypts that are killed by severe fires, most can produce epicormic, basal and/or below-ground sprouts (Nicolle, 2006). Each epicormic strand has several narrow strips of cells of meristematic appearance that traverse the bark and the

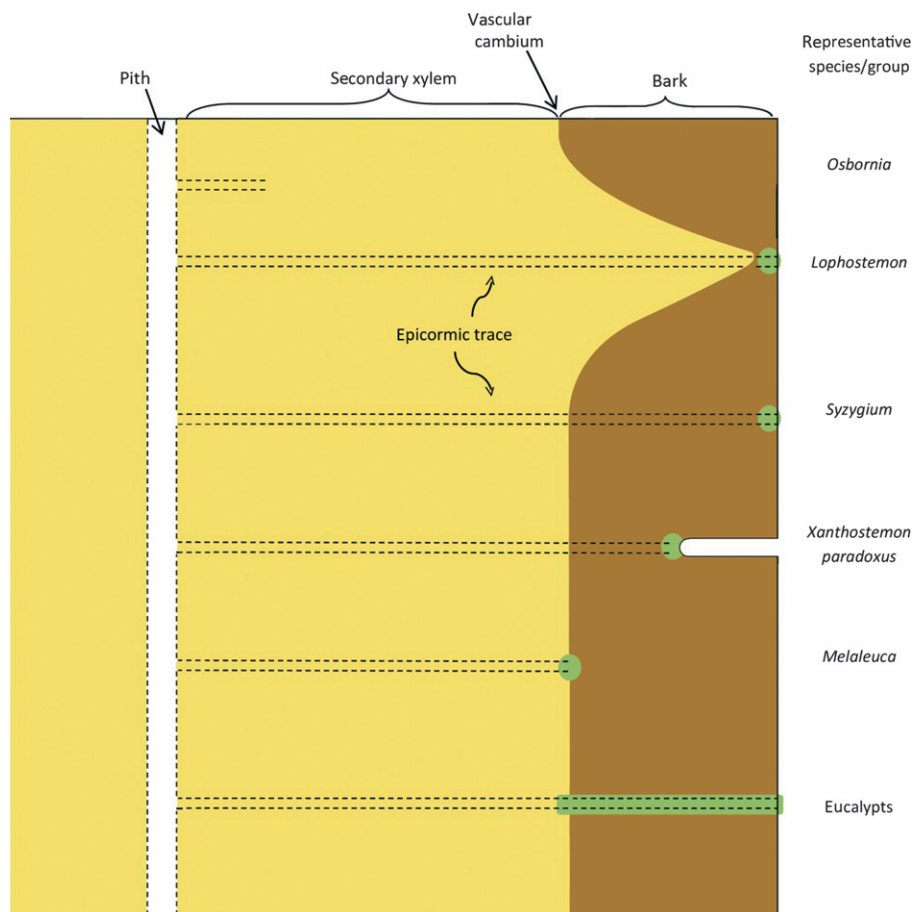


Fig. 5 Position of epicormic traces and bud origin (green) across major groups of the Myrtaceae. Note the deep location in the eucalypt (*Angophora*, *Corymbia*, *Eucalyptus*) and *Melaleuca* groups, which are dominated by woodland epicormic resprouters, in contrast to the mangrove *Osbornia*, which occurs in an environment that rarely, if ever, burns. Note that the *Osbornia* epicormic trace only extends a small distance from the pith, as the axillary and accessory buds do not develop into epicormic structures. *Lophostemon*, *Syzygium* and *Xanthostemon* all occur in rainforests that rarely burn. Based on Burrows (2000), Burrows (2002), Burrows *et al.* (2010). Relative proportions of bark and secondary xylem are not to scale.

outermost secondary xylem (Fig. 5; Burrows, 2002; Burrows *et al.*, 2010). After fire, numerous bud primordia are initiated along these meristem strips. Consequently, at least some bud-forming cells are protected by the maximum available bark thickness. Phylogenetic analyses suggest a very early evolution (60–62 million yr ago (Ma)) of such bud traits among eucalypts in response to fire (Crisp *et al.*, 2011).

In contrast to *Eucalyptus*, other Myrtaceae genera display a wide range of epicormic strand structures that are correlated with fire regime (Burrows *et al.*, 2010; Fig. 5). *Osbornia*, the only mangrove in the Myrtaceae, has no epicormic resprouting potential, and *Syzygium* species (generally trees of rainforest) have buds at the surface level (Fig. 5) and are topkilled by fire. The apparent lack of specialized bud strands in the Myrtaceae of frequently burnt savannas of the Cerrado suggests that either the bud architecture of *Eucalyptus* is a biogeographic artefact or that savanna fire intensities have selected for thick bark rather than specialized buds.

Basal buds After moderate to highly intense fires and especially after crown fires, many woody resprouters regenerate from buds at or below ground level (Figs 2b, 3c,d; Table 1; Hoffmann, 1998; Bond & Midgley, 2001; Moreira *et al.*, 2009), but their resprouting ability varies among species, with fire regime (e.g. Gignoux *et al.*, 2009) and also biogeographically (Vesk & Westoby, 2004b). Like stem resprouting, continental comparisons are emerging with the African savannas dominated by woody basal resprouters, while other savannas have more of a mix of stem and basal resprouting (e.g. Cerrado; Hoffmann *et al.*, 2003). Similarly, some heathlands are dominated by lignotuberous basal resprouter shrubs (chaparral and kwongan), while others have a large component of nonsprouting species (e.g. fynbos; Keeley *et al.*, 2012).

Below-ground bud banks Because soil is an excellent insulator, below-ground bud banks are widely sourced from axillary buds in woody (e.g. xylopodia) and herbaceous plants (e.g. rhizomes), in addition to adventitious root buds (Figs 2c, 3e,f; Table 1). Consequently, the diversity of underground storage organs that give rise to sprouts is broad in both woody (Lacey & Johnston, 1990) and herbaceous species (such as many geophytes) and may lead to clonality (Klimešová & Klimeš, 2007). While the source of axillary buds on rhizomes is well known, the anatomical origins of 'basal' buds for many woody and herbaceous plants are often obscure. Buried buds can arise from a number of ontogenetic mechanisms, including buried seeds with hypogeal germination, as well as seeds that germinate on the soil surface but subsequently bury their cotyledonary nodes (Fisher, 2008). Rhizophores can originate from such cotyledonary nodes and develop into swollen, root-like 'xylopodia' in the fire-prone Cerrado (Hayashi & Appezzato-da-Glória, 2005) and many other surface-fire ecosystems. However, xylopodia are more characteristically formed from swollen, vertically aligned primary, and occasionally lateral, roots (Alonso & Machado, 2007). In addition, contractile roots and plumule burying (cryptogeal germination) can be important mechanisms for protecting the seedling shoot apex in fire-prone systems (Jackson, 1974; Fisher, 2008). Among resprouting lineages in *Banksia*, lignotuberous/epicormic species can be traced to mid-

late Miocene, while rhizomatous and root-suckering species (clonal) represent the derived condition, having arisen 6–16 Ma (mid-early Miocene; He *et al.*, 2011).

2. Protection

Protecting aerial buds from fire Plants that resprout from above-ground and/or basal stems protect their aerial and/or basal bud bank from fire in several ways: by growing rapidly and tall (so reaching escape height), which allows buds in the crown to escape being scorched (Higgins *et al.*, 2000; Balfour & Midgley, 2006; Bond, 2008; Burrows *et al.*, 2008); by producing a thicker stem and thus buffering the xylem against hydraulic failure (Midgley *et al.*, 2011; Michaletz *et al.*, 2012); and by having thick bark (bark thickness) that protects the phloem and cambium and/or other bud protection mechanisms such as deeply embedded meristems (Gignoux *et al.*, 1997; Hoffmann *et al.*, 2009; Burrows *et al.*, 2010; Midgley *et al.*, 2010; Waters *et al.*, 2010; Table 1). By contrast, in forest systems where fire is less selective, bark thickness may actually inhibit resprouting because it may hinder epicormic bud emergence; hence the higher failure rate of resprouting in older oak trees with thick bark (Johnson *et al.*, 2002).

Fire damage to the stem, rather than the crown, kills most trees (Gignoux *et al.*, 1997; Balfour & Midgley, 2006; Midgley *et al.*, 2010), although how fire kills the stem is poorly understood (see Midgley *et al.*, 2010). Topkill may be caused by cambium necrosis (Bond & Van Wilgen, 1996; Dickinson & Johnson, 2004; Michaletz & Johnson, 2007), but a case has also been made for the effects of fire on the xylem (Balfour & Midgley, 2006; Michaletz *et al.*, 2012), phloem and crown death (Midgley *et al.*, 2010). Whatever mechanism is responsible, the probability of topkill scales with bark thickness (McArthur, 1968; Gignoux *et al.*, 1997; Hoffmann *et al.*, 2003; Lawes *et al.*, 2011a). Stem thickness *per se* is insufficient protection from fire for forest trees that suffer higher degrees of mortality compared with savanna trees for the same stem thickness (e.g. Hoffmann *et al.*, 2009). Thus, unless the stem is protected, rapid height or diameter growth on their own are unlikely to allow an individual to escape the fire trap. Lawes *et al.* (2011a) showed that increasing probabilities of tree survival were correlated exclusively with bark thickness rather than stem height or diameter. They concluded that, in fire-prone savannas, height and width growth are essentially mechanisms for achieving thicker bark and resilience to topkill (Fig. 6).

Thick bark protect buds Variation in the insulating properties of different bark types may confound the utility of absolute bark thickness as a measure of the degree of bud protection conferred by bark. However, the rate at which heat is transferred through the bark is independent of bark density and, to a lesser extent, moisture content, but is strongly dependent on (inverse function) absolute bark thickness (Pinard & Huffman, 1997; Lawes *et al.*, 2011c; Brando *et al.*, 2012). Thus, bark thickness appears to have evolved in direct response to the degree and type of protection demanded by a particular disturbance regime. Perhaps the most striking difference in bark thickness is observed between eucalypt and

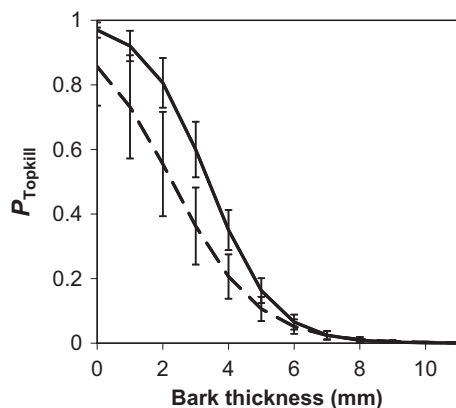


Fig. 6 Predicted probability (\pm SE) of stem death or 'topkill' in relation to bark thickness for eucalypts (dashed line) vs noneucalypts (species not in the Myrtaceae, solid line) in Australian tropical savanna. (Redrawn from Lawes *et al.*, 2011a.)

noneucalypt species in Australian fire-prone savannas (Lawes *et al.*, 2011a,c; Fig. 6). Here, bark is relatively thin in eucalypts compared with noneucalypts, yet eucalypts are less likely to be topkilled by fire (Fig. 6). This is because deeply embedded epicormic meristems (see Fig. 5) make thick bark less critical in the eucalypts. Thus eucalypts can allocate resources that would have been required for thick bark to height growth, overtopping noneucalypts that employ diameter growth to achieve thick bark. The latter offers a proximate explanation for the dominance of eucalypts in Australia in spite of their relatively thin bark compared with noneucalypts, whereas the persistence of trees in other systems such as the Cerrado may be more related to thick bark. These continental differences highlight the need to take into account both bark thickness and bud location in characterizing the resprouting capability of plants (Fig. 2).

Buds insulated by soil Buds positioned at or below ground level during fires have the advantage of being protected not only by plant traits such as bark, leaf sheaths and scale leaves (e.g. cataphylls, storage leaves) but also by the soil, because of its low thermal conductivity (Table 1; Figs 2c, 3e,f). Soil insulates resprouting organs from the effects of fire, influencing the distribution of buds in the soil temperature profile and thus the proportion of buds exposed to lethal temperatures (Choczynska & Johnson, 2009). Short fire residence times in grassland systems reduce lethal soil heating to a few cm and account for the high resilience of grasses to fire regimes (Scott *et al.*, 2010), but in more sclerophyllous systems, much deeper and prolonged soil heating has been measured (Wright & Clarke, 2007). Nevertheless, basal or below-ground resprouting occurs widely in all fire-prone ecosystems, but the costs and tradeoffs associated with maintaining buds at depth are not well known.

3. Resource limitations

Biomass allocation patterns and related storage of nonstructural carbohydrates (NSC) fundamentally drive the resources available for plants to resprout after severe disturbance. Allocation to stems (stem mass fraction (SMF)) and roots (root mass fraction (RMF))

are potential sources for funding resprouting and are under moderate environmental control, but it is clear there are systematic allocation differences among functional groups and biomes (Poorter *et al.*, 2012), which we suggest reflect selection not only by climate-type but also by disturbance regime.

Stem survival guarantees resources for resprouting Producing and protecting buds ensures an adaptive response by a plant to damage, but such a response is not possible without sufficient resources to fund formation and growth of buds, protection of the buds, and any subsequent sprouting (Table 1). Resprouting woody plants rely on NSC reserves to fund respiration and regrowth until the plant has recovered photosynthetic capacity to support these costs (Chapin *et al.*, 1990). When aerial stems are not consumed or killed by disturbance, such as fire, NSC resources for resprouting are derived from substantial storage in their xylem parenchyma tissues (Kozłowski, 1992; Lamont *et al.*, 2004), or from current photosynthesis if leaves are not damaged (Sakai & Sakai, 1998). The former is confirmed in trees whose root connections were severed by wind damage and in which epicormic resprouting is necessarily supported from stem reserves (Franklin *et al.*, 2010). While the resource demand by resprouting stems has received considerable research (see next section), the resources required to repair damaged bark for protection have rarely been examined, especially in the context of fire (Vesk & Westoby, 2004a). The carbon costs of bark protection from fire may be substantial, as the costs of bark replacement can be high (e.g. cork oak bark; Oliveira & Costa, 2012) and variation in SMF among species and biomes may reflect the cost of stem defense.

Stem reserves are important in tropical forest trees and their seedlings (Hoffmann *et al.*, 2003; Myers & Kitajima, 2007; Poorter & Kitajima, 2007; Nzunda *et al.*, 2008), as wind damage selects for stem storage rather than below-ground storage because stems are retained after storms. In drier tropical forests, however, both roots and stems have similar NSC concentrations (Hoffmann *et al.*, 2003) and lower SMF (Poorter *et al.*, 2012), reflecting the combined risk of fire and wind disturbance on the need to have both storage reserves. Stem (rather than root) reserves are also high in vines (Mooney *et al.*, 1992), which reflects their need to resprout from stems should they fall from the canopy (Clarke *et al.*, 2009). In systems where stem browsing occurs, stem resprouting shrubs also have greater relative allocation of NSC to stems than those that lack stem resprouting (Palacio *et al.*, 2007).

Whole-plant models of reserve mobilization are needed for woody resprouters to better predict the role of biomass allocation and reserves in resprouting. Although there is a broad conceptual understanding of the role of NSC in epicormic and basal stem resprouting in trees, fire-driven reserve mobilization has not been described at the whole-tree level. This is critical for whole-plant estimates of the amount of NSC available for regrowth. Measures of NSC pools for temperate and tropical forest trees show that leaf flushing does not draw heavily upon NSC pools (Barbaroux *et al.*, 2003; Hoch *et al.*, 2003; Würth *et al.*, 2005); additionally, the starch pools are sufficient to replace the total leaf crown several times over in deciduous trees (Hoch *et al.*, 2003). Importantly, the three evergreen trees reported in Hoch *et al.* (2003) were conifers

that had much lower amounts of NSC in the sapwood than other species. Combined with a lack of axillary meristems, lower NSC content may explain why few tree conifers resprout despite having a higher SMF than angiosperms.

Do lignotubers or roots fund resprouting? In fire-prone biomes, biomass allocation to leaves is relatively constant, but allocation to roots increases as systems become drier and more fire-prone (Poorter *et al.*, 2012). For basal resprouters, organs such as lignotubers are obvious sites for NSC storage (Wildy & Pate, 2002), but they are not necessarily the preferential site of NSC storage, with some lignotuberous shrubs and trees showing higher starch content in their roots (Cruz & Moreno, 2001; Wildy & Pate, 2002). Furthermore, the development of lignotubers may be unrelated to nutrient or water availability (Walters *et al.*, 2005). Root traits are associated with differing abilities to acquire resources for storage vs growth, with R− species having finer roots concentrated in the upper soil layer while R+ have thicker roots that permit both carbon storage and deep soil penetration (Paula & Pausas, 2010). The role of the lignotuber as a specialized organ for starch storage has been questioned by some authors (Cruz *et al.*, 2003b), its selective advantage being mainly attributed to the enlargement of the bud bank (Carrodus & Blake, 1970; Kummerow, 1989). By contrast, numerous studies have highlighted the xylem parenchyma of woody roots as the main site of below-ground NSC storage in lignotuberous plants (Carrodus & Blake, 1970; Loescher *et al.*, 1990; Bell *et al.*, 1996). In a comparative study of nonsprouter and resprouter *Erica* spp., Bell & Ojeda (1999) showed thicker parenchymatous rays and much higher concentrations of starch in roots of lignotuberous resprouters than in nonsprouters (lacking a lignotuber). If the lignotuber is a specialized structure for starch storage, such differences in root starch would not be expected (see also Verdaguer & Ojeda, 2002). Overall, lignotubers appear to be multifunctional, having a large bud storage capacity linked with roots that supply stores of NSC.

Resourcing basal buds and growth: carbohydrates vs mineral nutrients Below-ground resprouting, in contrast to aerial resprouting, depends on remobilization of below-ground reserves – often starch in woody plants and C₄ grasses or water-soluble carbohydrates in C₃ grasses, or both, as in geophytes (Smouter & Simpson, 1989; Tertuliano & Figueiredo-Ribeiro, 1993; Ranwala & Miller, 2008). For clonal plants, it is likely that only small amounts of NSC are needed because ramets are able to quickly develop new roots and shoots needed for carbon and nutrient gain. The resources needed for nonclonal resprouting are reflected in the large NSC reserves present in the below-ground organs of savanna trees (Miyanishi & Kellerman, 1986; Hoffmann *et al.*, 2004; Schutz *et al.*, 2009), temperate trees (Langley *et al.*, 2002), tropical trees (Würth *et al.*, 2005), tropical vines (Mooney *et al.*, 1992), Mediterranean shrubs (Pate *et al.*, 1990; Canadell & López-Soria, 1998; Bell & Ojeda, 1999; Palacio *et al.*, 2007), temperate sclerophyllous shrubs (Knox & Clarke, 2005), semiarid shrubs (Van der Heyden & Stock, 1996) and herbaceous species (White, 1973; Pate *et al.*, 1991; Ranwala & Miller, 2008). Whether mineral nutrients such as N and P are remobilized from storage organs and

limit resprouting has been little explored, but N does not appear to be preferentially accumulated in R+ species (Pate *et al.*, 1990; Cruz *et al.*, 2003a; Palacio *et al.*, 2007).

Does resprouting vigour scale with increasing below-ground carbohydrate concentration? The ability of woody and herbaceous species to resprout from their base is common in fire-prone biomes and depends on remobilization of accumulated reserves that are replenished between fires (Canadell & López-Soria, 1998; Schutz *et al.*, 2009). Hence, we expect resprouting ability to scale with increasing resource concentration. Strong evidence has emerged from fire-prone environments that nonsprouters (R−) have lower amounts of NSC in their roots (generally < 10 mg g^{−1}) than their (R+) congeners (often > 20 mg g^{−1}; Bell & Ojeda, 1999; Bell, 2001; Knox & Clarke, 2005). However, the NSC concentrations span orders of magnitude (5–200 mg g^{−1}) and they are not strongly related to resprouting vigour (Richards & Caldwell, 1985; Erdmann *et al.*, 1993; Sparks & Oechel, 1993; Cruz *et al.*, 2003a,b).

Bud vs resource limitation: an ongoing debate While some experiments comparing the effects of clipping with that of fire suggest that basal bud limitation is more important than NSC limitation to the resprouting response of shrubs (Bell & Pate, 1996; Cruz *et al.*, 2003b), the bud vs resource debate is ongoing (Paula & Ojeda, 2009, 2011). It is likely that both factors are limiting, depending on the environmental context. For example, herbaceous plants rapidly re-establish reserves for regrowth after severe defoliation such as by fire (Scott *et al.*, 2010; Tolsma *et al.*, 2010), but the likelihood of subsequent defoliation by herbivores (leading to depletion of reserves) is higher than in woody plants (Tolsma *et al.*, 2010). Hence reserve thresholds (< 5% NSC DW), rather than loss of meristems, are thought to be an important driver of differences in persistence of grasses in grasslands where fire and grazing defoliation are frequent (Danckwerts, 1993; Tolsma *et al.*, 2007).

In fire-prone systems, basal bud limitation does not appear to restrict resprouting ability, as repeated removal of emerging buds in lignotuberous species does not exhaust the bud bank of mature plants (Canadell & López-Soria, 1998; Wildy & Pate, 2002). Seedlings of lignotuberous species are known to rapidly develop bud banks. Fidelis *et al.* (2010) in the Brazilian Campos showed bud numbers of below-ground organs in excess of that required for multiple resprouting events. Similarly, 2-yr-old seedlings of a mallee eucalypt can develop hundreds of bud primordia while 4-yr-old saplings can have > 1000 buds (Wildy & Pate, 2002), suggesting that buds do not limit resprouting capacity during the juvenile phases. Nevertheless, bud availability can interact with fire regime to influence resprouting vigour (Keeley *et al.*, 2012).

IV. Life-history consequences of resprouting

Tradeoffs in resource allocation to growth and maintenance vs reproduction are predicted to occur among congeners with alternative (R− vs R+) life histories (Bellingham & Sparrow, 2000; Bond & Midgley, 2001, 2003; Vesk & Westoby, 2004a). These tradeoffs ultimately account for the contrasting demography

between R+ and R− species (Bond & Van Wilgen, 1996; Ojeda *et al.*, 2005; Keeley *et al.*, 2012). In fire-prone ecosystems, compared with nonsprouters, resprouters allocate more biomass to roots; have lower seed output; have lower seedling recruitment rates; and take longer to reach sexual maturity (Bell & Ojeda, 1999; Lamont & Wiens, 2003), giving rise to the notion of a persistence vs recruitment tradeoff in fire-prone systems (Bond & Midgley, 2001).

There are several nonmutually exclusive reasons why reproduction may be compromised by resprouting. First, allocation to buds, their protection and resource storage to fund growth after disturbance potentially diverts resources from sexual reproduction (Bellingham & Sparrow, 2000; Bond & Midgley, 2001; Vesik & Westoby, 2004a; Vallejo-Marín *et al.*, 2010). Evidence for this comes from seed mass differences where R− species generally have larger seed mass than their congeners (Knox & Clarke, 2005; Lasso *et al.*, 2009; Nzunda & Lawes, 2011). Secondly, field observations of seedling development show that maturation rates of congeners are invariably faster for R− species (Bell, 2001; Lamont & Wiens, 2003; Clarke *et al.*, 2005); additionally, in common-garden comparisons, R− species mature more quickly (Knox & Clarke, 2005; Schwilk & Ackerly, 2005), although this could also be an expression of the storage-growth tradeoff.

While lower per-capita seed and seedling production in resprouters (Clarke & Dorji, 2008; Clarke & Knox, 2009; Nzunda & Lawes, 2011) are also cited as evidence for tradeoffs, these attributes could be explained by other mechanisms, especially in clonal plants (Lamont & Wiens, 2003). Reduced reproductive performance may be a result of sublethal somatic mutations accumulating over successive disturbance events (Lamont & Wiens, 2003; Lamont *et al.*, 2011). Nevertheless, complete loss of sex is rare in resprouting plants, because they are less likely to be exposed to selection events and opportunities for purging deleterious alleles (Lamont & Wiens, 2003; Vallejo-Marín *et al.*, 2010).

Traditionally, a number of plant growth traits are associated with resprouting. For example, basal resprouters are shorter, have higher RMF, higher seed mass lower leaf mass area (LMA), and lower water stress tolerance for seedlings than nonsprouters (Kruger *et al.*, 1997; Bell, 2001; Knox & Clarke, 2005; Schwilk & Ackerly, 2005; Paula & Pausas, 2006; Pratt *et al.*, 2007; Saura-Mas & Lloret, 2007). However, epicormic and apical resprouters may be as tall as nonsprouters because height is not constrained by stem death and the need to resprout from the base. Remarkably, growth rates of some congener R− and R+ shrub seedlings do not appear to differ in common-garden experiments (Knox & Clarke, 2005), suggesting some leaf level adjustment where carbon assimilation rates may be enhanced to meet the demands of storage for resprouting (Paula & Pausas, 2006).

Resprouting may impose life-history constraints but it does not appear to constrain speciation. The notion that speciation is limited in resprouters compared with nonsprouters, because of shorter generation times and lack of generation overlap in the latter (Wells, 1969; Bond & Midgley, 2003; Verdú *et al.*, 2007), is not supported by phytogeographic analyses (Lamont & Wiens, 2003), or by tests for higher rates of molecular evolution (Verdú *et al.*, 2007). However, at a microevolutionary scale, higher degrees of genetic

diversification occur in nonsprouter populations than in resprouter ones in the dimorphic species *Erica coccinea* (Segarra-Moragues & Ojeda, 2010).

V. Environmental constraints on resprouting

1. Environment regulates resprouting

All resprouters are able to allocate resources to where they are needed for recovery from disturbance, but types of resprouting reflect both resource availability and disturbance type (Fig. 7). Biomass, nutrient and NSC allocations vary with environment (availability and seasonality of light, nutrients, water) and disturbance regime (fire, grazing, wind, freezing; Chapin *et al.*, 1990; Kabeya & Sakai, 2005; Groom & Lamont, 2011; Lawes & Clarke, 2011; Poorter *et al.*, 2012).

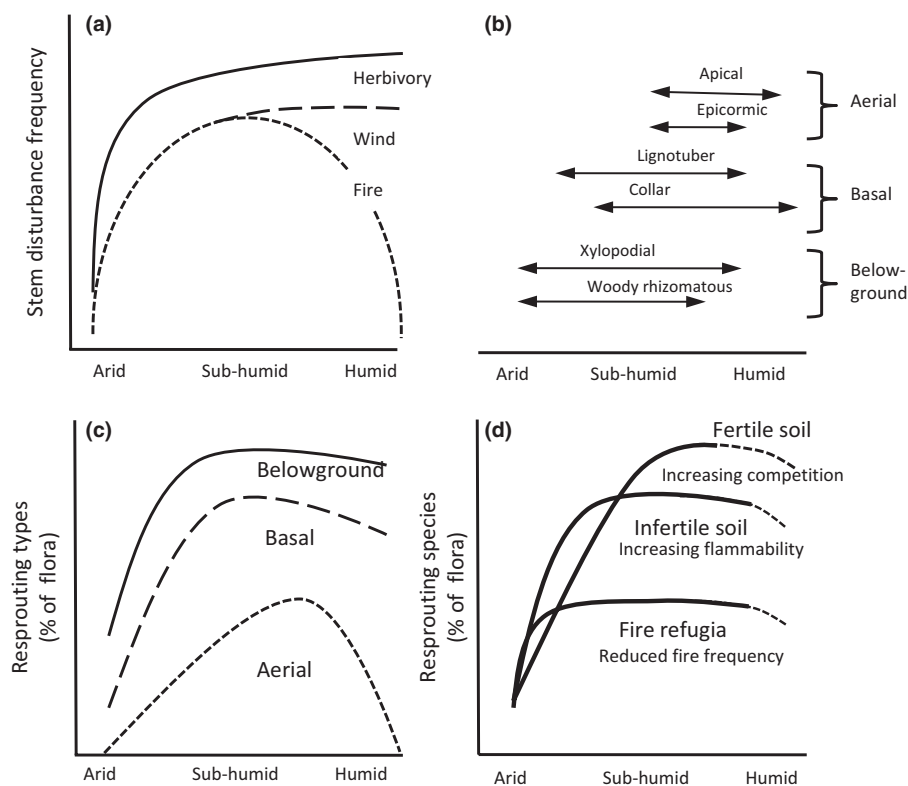
Olano *et al.* (2006) demonstrated long-term depletion of NSC in understory resprouter species of pine savanna in Florida as the overstory develops with time-since-fire, consistent with the general decrease in RMF under low light (Poorter *et al.*, 2012). This may partly explain the pattern in tropical savannas of replacement of epicormic resprouters (eucalypts) by noneucalypt and forest elements where fire disturbance is excluded (Russell-Smith *et al.*, 2003; Lawes *et al.*, 2011b). In contrast to savannas, Poorter & Kitajima (2007) showed that species regenerating in shady evergreen rainforest habitats have higher stem carbohydrate concentrations and survival than more light-demanding species. Additionally, when they snapped the stems of rainforest species, nearly all resprouted but shade-tolerant species had greater resprouting vigor (Poorter *et al.*, 2010). Interestingly, when fires burn into subtropical and temperate evergreen forests, saplings often resprout, which could be a consequence of rapid reserve accumulation before canopy closure between disturbances (Knox & Clarke, 2011). Similarly, Falster & Westoby (2005) emphasize postfire height growth as important for survival where shorter multistemmed shrubs have more rapid growth before they are shaded by taller single-stemmed species.

Low nutrient availability is well known to increase RMF (Poorter *et al.*, 2012). Hence the expectation is that fire-prone communities with low nutrient status should be dominated by basally resprouting species. Nevertheless R+ and R− species often coexist in nutrient-poor ecosystems (Clarke *et al.*, 2005). This is probably because competitive interactions between resprouting and nonsprouting species are reduced in nutrient-poor environments, but as nutrient concentrations increase, competition favors growth and persistence of resprouters (Clarke & Knox, 2009).

2. Disturbance regimes and stem persistence

The ability of mature R+ individuals to recover biomass following disturbance is strongly influenced by the disturbance regime within the broader abiotic constraints of rainfall and soil fertility (Fig. 7). This individual persistence, or ability to recover biomass, declines with increasing frequency, severity and variability of the disturbance type by decreasing bud availability, their protection and the resources to fund regrowth (Enright *et al.*, 2011). Nevertheless, for

Fig. 7 Conceptual relationships between stem disturbance frequency, resprouter type and resprouting community assembly of woody plants: (a) fire frequency, wind disturbance (increasing with height) and herbivory scaled to increasing rainfall; (b) distribution of major woody resprouter types across disturbance and rainfall gradients; (c) relative proportions of resprouter types across disturbance and rainfall gradients; and (d) relative proportions of woody resprouters in communities across disturbance, rainfall and soil fertility environments (dashed line indicates uncertainty). Fire refugia and low productive environments allow nonsprouters to coexist with resprouters. Winter rainfall seasonality also allows nonsprouters to coexist with resprouters in higher rainfall regions.



species with adaptive traits shaped by disturbance the consequences of decreasing disturbances, such as fire, may also have negative effects on the ability to recover from a disturbance event (Enright *et al.*, 2011). Hence the composition of resprouter-dominated communities is unlikely to have a simple linear relationship with disturbance (Enright *et al.*, 2011), because disturbance regimes are not linearly related to climate (Fig. 7a; see section VI. Resprouting community patterns and assembly).

The consequences of increasing severity and frequency of disturbance are to deplete above-ground biomass and to shift the location of resprouting from axillary and epicormic to basal and ultimately below-ground resprouting (Bellingham & Sparrow, 2000; Morrison & Renwick, 2000; Keeley, 2006). Thus, aerial resprouting peaks under subhumid conditions where trees abound but fires are not severe (e.g. the Cerrado), while basal resprouting peaks under less humid climates where trees are scarce and crown fires occur (e.g. Mediterranean heathlands; Fig. 7c). Convergence on basal resprouting, however, does not occur in either crown or ground fire biomes because of apical and stem resprouting (e.g. eucalypt forests and Cerrado). Consequently, global vegetation/carbon models need to align disturbance/climate regimes with bud position traits rather than simply the probability of resprouting (Higgins & Scheiter, 2012; Fig. 7b–d).

If severe depletion of above-ground biomass occurs, root concentrations of NSC decrease (Canadell & López-Soria, 1998; Cruz *et al.*, 2003b; Tolsma *et al.*, 2007; Schutz *et al.*, 2009), demonstrating reserve mobilization to fund resprouting. Epicormic and many basally resprouting woody plants, as well as apical sprouters, store reserves in excess of their needs for a single resprouting episode (Canadell & López-Soria, 1998; Cruz *et al.*,

2003b; Lamont *et al.*, 2004; Wright & Clarke, 2007) and these may be rapidly replenished in the inter-fire interval (Paula & Ojeda, 2009; Schutz *et al.*, 2009). Nevertheless, repeated disturbance is more likely to limit resprouting from basal than epicormic buds because of massive stem storage in the latter. For example, Knox & Morrison (2005) show that frequent fires reduced postfire reproductive output in basal but not in epicormic resprouters. Numerous studies have also shown that short intervals between fires reduce the capacity of basal resprouters to recover (Moreno & Oechel, 1991; Cruz *et al.*, 2003b; Paula & Ojeda, 2009, 2011; Enright *et al.*, 2011; Schutz *et al.*, 2011).

Even when the intervals between fires are long enough for the costs of resprouting to be recovered, herbivory of resprouts may thwart this recovery (Paula & Ojeda, 2011; Schutz *et al.*, 2011). Defense of resprouts from herbivores is an important, but neglected, component of understanding resprouter reserve economics. This is highlighted in a comparison of resprouter *Erica* spp. that differed in their leaf herbivory defense traits. The congener with defended leaves was slower to recover starch and was less resilient to repeated disturbance than the species with low leaf defense (Paula & Ojeda, 2011).

VI. Resprouting, community patterns and assembly

1. Community patterns of resprouting are predictable

While most communities comprise both resprouters and nonsprouters, there is increasing evidence that the type and proportion of resprouting species vary spatially in predictable, but nonlinear, ways along productivity and disturbance gradients (Ojeda, 1998;

Bellingham & Sparrow, 2000; Lamont *et al.*, 2011; Russell-Smith *et al.*, 2012; Fig. 7b–d). At the community level, resprouting is predicted to increase with disturbance frequency (Fig. 7d) but decreases when productivity is low, as this restricts the ability of resprouters to reoccupy a site (Bellingham & Sparrow, 2000; Hoffmann *et al.*, 2012; Fig. 7d). This basic framework applies to all forms of severe disturbance—for example, storms in tropical forest, fire in flammable shrublands, herbivory in palatable grassland, frost in temperate forest and stochastic drought in arid biomes (Bellingham & Sparrow, 2000). Initial global syntheses of species responses across disturbance types showed an increase in resprouting ability with disturbance severity (Vesk & Westoby, 2004b). For example, <20% of shrub species on rocky outcrops (less frequently burned fire refugia) resprout following crown fire, but in adjacent heaths (more frequently burned) 78% of shrub species are resprouters (Clarke & Knox, 2002). Are these persistence patterns in fire-prone ecosystems mirrored in other disturbance-prone environments? Evidence for this is emerging, with multitemming more common close to and at the base of avalanche tracks (Stokes *et al.*, 2012) and in wind-disturbed forests (Bellingham *et al.*, 1994, 1995; Nzunda *et al.*, 2007).

Separating the effect of disturbance frequency and resource availability across landscapes is problematic because productivity and fire frequency interact (Pausas & Bradstock, 2007; Nano & Clarke, 2011; Hoffmann *et al.*, 2012; Fig. 7a). For example, the proportion of basal resprouters decreases in some Mediterranean-type systems in drier, less productive habitats (Keeley *et al.*, 2012). However, their relative contribution is greater under warmer, drier, more variable rainfall conditions among banksias (Lamont & Markey, 1995), although basal resprouters are more common in less variable climates among other systems (Lloret *et al.*, 2005; Nano & Clarke, 2011). Clarke *et al.* (2005) attempted to separate these factors by comparing resprouting across five vegetation types in a humid climate zone. They found that resprouters were better represented in vegetation types on higher nutrient soils where canopy closure or ground cover closure occurs rapidly after fire (Fig. 7d), thus excluding seedling recruitment by nonsprouting species. This pattern is repeated in subhumid communities where decreasing aridity and increasing fire frequency correspond to increasing proportions of resprouter species (Pausas & Bradstock, 2007; Nano & Clarke, 2011; Russell-Smith *et al.*, 2012; Fig. 7d). Overall there appears to be a tight coupling of fire frequency and basal resprouters on infertile soils, but on more fertile soils this coupling with fire is not as strong (Fig. 7a,d). Higher productivity and competition appear to restrict site occupancy, resulting in more resprouters in humid sites where wind rather than fire may also be a factor (Fig. 7a,d).

2. Resprouting, seed banks and site occupancy

Communities dominated by basal resprouters are more seedbank-limited than those dominated by nonsprouters because of the apparent tradeoff in allocation to reproduction vs persistence (Odion & Davis, 2000; Clarke & Dorji, 2008). Consequently, seedling densities also differ, with communities dominated by resprouters having fewer postfire recruits, whereas nonsprouters

recruit prolifically if competition is not strong (Falster & Westoby, 2005; Higgins *et al.*, 2008; Clarke & Knox, 2009; Keeley *et al.*, 2012). However, resprouters must, at some stage, recruit to replace adult mortality and, in these instances, they appear to be more tolerant of competition as seedlings than are nonsprouter seedlings (Chew & Bonser, 2009; Clarke & Knox, 2009), so that differences in fecundity are the key to differences in recruitment rates (Enright *et al.*, 2007).

3. Disturbance, structural assembly and dynamic global vegetation models (DGVMs)

Predicted plant height in communities represents a balance between resources that drive height growth potential (nutrients and moisture) and those that restrict height (disturbance and costs of height; Falster & Westoby, 2005). Therefore, in disturbance-prone forests, accessing light is likely to be partitioned temporally via tradeoffs in resprouting ability, growth and shade tolerance (Huston & Smith, 1987; Falster & Westoby, 2005). Shorter woody species, especially those that resprout, are expected to grow more rapidly after disturbance than taller species; their growth rates should be faster because they need to store NSC before they are shaded by taller species. Consequently, their stem (low wood density) and leaf traits (low LMA; Falster & Westoby, 2005) restrict these species to basal resprouting (Knox & Clarke, 2011) and their storage capacity should decrease over time as a result of shade limitation (Olano *et al.*, 2006). Taller forest species will therefore be particularly susceptible to repeated fires because they may not have the ability to rapidly accumulate resources to resprout if they have not been able to develop thick bark (see Hoffmann *et al.*, 2012) or do not have specialized epicormic buds. Such models explain alternative community states where forests are replaced by grasslands in systems where trees resprout basally (Staver *et al.*, 2009). They also explain the dominance of trees and shrubs in some savannas despite frequent burning, because of epicormic resprouting (unique buds + bark protection; Lawes *et al.*, 2011a). While current DGVMs include probabilistic basal resprouting response to changes in [CO₂] (Higgins & Scheiter, 2012), they do not include probabilities of stem resprouting. Also DGVMs have, at present, not included how increasing [CO₂] may increase the resprouting response because of better resourcing for buds and bark from bigger NSC stores. The BPR scheme may improve DGVMs by providing data on how global change may influence protection; for instance, warmer conditions may lead to more intense fires and less resprouting and may drive selection for thicker bark.

VII. Global change, carbon storage and resprouting

Climate change will affect canopy disturbance regimes and carbon sequestration in resprouting woody plants (Bradley & Pregitzer, 2007). In particular, over the past decade there has been an increase in large fires on most vegetated continents, with predictions of climate-related increases in the frequency and severity of fires (Chuvieco *et al.*, 2008; Bowman *et al.*, 2009) and changes as a result of invasive species. Therefore, the interaction of changing rainfall, fire regime and resprouting ability will be critical in influencing the

carbon cycle and global change feedbacks because of the carbon-rich status of woody plants (Bradley & Pregitzer, 2007). Although the ability to resprout repeatedly is a key conceptual component of models of woody persistence (Higgins *et al.*, 2000), resprouting behavior (i.e. whether from epicormic, basal or below-ground bud banks), the costs of protecting buds (bark), and resource (NSC) storage, which determine the capacity for individual resprouting and vegetative recovery, have not been incorporated into functional models of carbon dynamics (Higgins & Scheiter, 2012). For example, the most highly cited model of savanna dynamics (Higgins *et al.*, 2000) only considers stem death where resprouting occurs from basal buds in response to fires. However, in various savannas and forests (Australia and the Cerrado), stems are not killed but resprout epicormically in response to canopy fires. The consequences of these two responses are stark: stem kill results in large losses of carbon, whereas stem persistence and epicormic sprouting promote the rapid recovery of the full canopy and sequester more carbon (Crisp *et al.*, 2011). Unless we couple predictions of persistence through a BPR approach with the CO₂ fertilization effect, global models of carbon-carrying capacity, and hence the carbon sequestration potential of ecosystems, will be imprecise. One of the outstanding issues in predicting resprouting is the interactive effect of increased concentration of atmospheric CO₂ on bud formation, protection and resource allocation, and disturbance (Bond & Midgley, 2012a).

VIII. Conclusions

The BPR scheme provides a unifying framework for understanding and predicting the wide array of resprouting responses and the role of the persistence niche under present and changing climate and disturbance regimes. This scheme emphasizes important differences in plant responses to disturbances, such as the ability to resprout after repeated disturbances, and how differences in bud protection and resourcing mechanisms define resprouting responses and the nature of the persistence niche.

Much previous research in fire-driven ecosystems has focused on lignotuberous resprouters and resprouting from basal buds. However, immense forest and savanna ecosystems are dominated by apical and epicormic resprouters that rapidly recover from fire and/or other disturbances. The BPR scheme emphasizes the importance of epicormic resprouting to the maintenance of disturbance-prone ecosystems and renders much of the previous theory on resprouting incomplete. For example, where post-disturbance plant recovery is not from the base, plant dynamics do not depend on a significant disturbance-free period to reach escape height. By recognizing that plant response to disturbance is optimized by rapid recovery of photosynthetic potential from protected buds on the stem, BPR extends resprouting models beyond the binary patterns (topkilled or not) of prevailing basal resprouting models.

Central to theoretical advances in resprouting ecology is a greatly improved understanding of the role of bud protection mechanisms, especially bark thickness, in the evolution of resprouting responses and the competitive advantage this confers on individuals in disturbance-driven environments. Predictions of woody plant recovery and persistence after fire have been widely based on

whether saplings can grow tall enough to escape fire injury. However, in systems dominated by apical and epicormic resprouters, it is not clear that height growth *per se* determines 'escape'. BPR argues that escape height is not the height of the plant crown above the flame zone, but is, in fact, the height on the stem to which the buds are protected from fire – that is, it does not matter how tall a sapling grows if the buds are not protected, as is highlighted by the dominance of apical sprouters in the understory of some savannas.

Missing from current perspectives on resprouting (including this review) is detailed knowledge of the floristic and taxonomic spread of resprouting trait types (apical, epicormic, basal, below-ground), leading eventually to a pyrogeography of the globe. We applaud the fact that the mechanisms by which plants respond to physical damage, especially by fire, is increasingly being noted in local floras. Phylogenetic time-based trait analysis requires a thorough knowledge of resprouting bud types and fire-resistance traits within clades and has recently begun (Crisp *et al.*, 2011; He *et al.*, 2011, 2012; Lamont *et al.*, 2011). Although epicormic resprouting is an important trait, particularly among the Myrtaceae, its prevalence among other plant groups is less well known (Meier *et al.*, 2012).

The capacity to resprout is not only determined by the availability of buds and their level of protection but also critically by the availability of resources. Separating the relative contribution of site productivity and disturbance to landscape patterns of resprouting (Bellingham & Sparrow, 2000) remains elusive despite the better understanding of biomass allocation (Poorter *et al.*, 2012). This review has focused on fire disturbance but there is a need to revisit productivity models of resprouting responses in relation to other disturbance types. In particular, the theory that resprouter shrubs and trees are more likely to occur at low resource sites (Hoffmann *et al.*, 2012), regardless of disturbance type and degree (see Lamont *et al.*, 2011), needs global analysis.

It is now relatively well established that resprouter lineages do not have lower rates of molecular evolution and diversification than nonsprouters (Lamont & Wiens, 2003; Verdú *et al.*, 2007). Hence their diversity has enabled them to dominate plant communities affected by large-scale disturbances such as fire. The global consequences of plant persistence are important and need to be better known, especially given the enormous area of vegetation that is regularly disturbed by fire and other severe disturbances. Whether resprouter-dominated ecosystems can be carbon sinks under even moderate rates of disturbance is unknown. Furthermore, the response of resprouters, especially epicormic resprouters, to rising [CO₂], to contingent changes in climate and disturbance regimes and increases in the distribution of invasive species, is an important future research challenge.

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