Science of the Total Environment 534 (2015) 31–42

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

A synthesis of postfire recovery traits of woody plants in Australian ecosystems

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HIGHLIGHTS

- We examined postfire resprouting (R+) and seeding (S+) in Australian ecosystems.
- More tree (>84%) than shrub (~50%) taxa resprouted, mostly basally (71%).
- Basal R+ was prevalent in rainforest taxa (91%), and epicormic R+ in savanna (59%).
- S+ was uncommon in ecosystems that burnt infrequently at low intensity.
- R+ was positively associated with ecosystem productivity.

ARTICLE INFO

Article history:
Received 19 August 2014
Received in revised form 20 March 2015
Accepted 1 April 2015
Available online 15 April 2015

Keywords:
Basal resprouting
Crown-fire
Ecosystem assembly
Epicormic resprouting
Fire-cued seeding
Persistence niche
Plant resilience traits

ABSTRACT

Postfire resprouting and recruitment from seed are key plant life-history traits that influence population dynamics, community composition and ecosystem function. Species can have one or both of these mechanisms. They confer resilience, which may determine community composition through differential species persistence after fire. To predict ecosystem level responses to changes in climate and fire conditions, we examined the proportions of these plant fire-adaptive traits among woody growth forms of 2880 taxa, in eight fire-prone ecosystems comprising ~87% of Australia's land area. Shrubs comprised 64% of the taxa. More tree (>84%) than shrub (~50%) taxa resprouted. Basal, epicormic and apical resprouting occurred in 71%, 22% and 3% of the taxa, respectively. Most rainforest taxa (91%) were basal resprouters. Many trees (59%) in frequently-burnt eucalypt forest and savanna resprouted epicormically. Although crown fire killed many mallee (62%) and heathland (48%) taxa, fire-cued seeding was common in these systems. Postfire seeding was uncommon in rainforest and in arid *Acacia* communities that burnt infrequently at low intensity. Resprouting was positively associated with ecosystem productivity, but resprouting type (e.g. basal or epicormic) was associated with local scale fire activity, especially fire frequency. Although rainforest trees can resprout they cannot recruit after intense fires and may decline under future fires. Semi-arid *Acacia* communities would be susceptible to increasing fire frequencies because they contain few postfire seeders. Ecosystems dominated by obligate seeders (mallee, heath) are also susceptible because predicted shorter inter-fire intervals will prevent seed bank accumulation. Savanna may be resilient to future fires because of the adaptive advantage of epicormic resprouting among the eucalypts. The substantial non-resprouting shrub component of shrublands may decline, but resilient *Eucalyptus* spp. will continue to dominate

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http://dx.doi.org/10.1016/j.scitotenv.2015.04.002

under future fire regimes. These patterns of resprouting and postfire seeding provide new insights to ecosystem assembly, resilience and vulnerability to changing fire regimes on this fire-prone continent.

Abbreviations

R+	postfire resprouting — generation of new shoots from dormant buds after stem has been fully scorched by fire
R−	no postfire resprouting
S+	postfire seeding — generation of a fire-resistant seed bank with postfire seed germination and seedling recruitment
S−	no postfire seeding

Combinations of R and S yield the following plant fire functional groups:

R+ S+	Facultative resprouters
R+ S−	Obligate resprouters
R− S+	Obligate seeders
R− S−	Fire-avoiders

1. Introduction

Fire is a pervasive disturbance that influences the evolution, distribution and abundance of woody plants worldwide (Bond and Van Wilgen, 1996; Bowman et al., 2009; Bradstock et al., 2012; Murphy et al., 2013; Whelan, 1995). The resprouting response to fire is a key life-history trait that has profound effects on species' postfire persistence and population dynamics and hence community composition (Bellingham and Sparrow, 2000; Bond and Midgley, 2001). Fire-cued recruitment from seed is similarly a key fire-history trait that promotes population growth and genetic variability within fire regime thresholds. As arguably the most fire-prone of continents (Chuvieco et al., 2008), the responses of plants to fire have been well documented in Australia (see Appendix 1; e.g. Bell, 2001; Nano and Clarke, 2011; Russell-Smith et al., 2012). Schemes to classify fire response strategies are mostly based on whether a plant is killed by or resprouts after fire, whether seeds are stored in the canopy or soil, and whether seed germination is fire-cued (e.g. Gill and Bradstock, 1992; Pausas et al., 2004). While many factors such as fire season and intensity, plant physiological status and intraspecific genetic variation can contribute to variable postfire responses (e.g. P.J. Clarke et al., 2013; Lamont et al., 2011; Morrison and Renwick, 2000; Wright and Clarke, 2007), the typical response of a species to a crown-scorching fire can be useful in classifying species' persistence under different fire regimes among ecosystems (Fig. 1). Indeed, even surface-fire systems experience at least some degree of crown-fire (Archibald et al., 2013; Moritz et al., 2012).

Resprouting is the initiation of new shoots from surviving buds and/or the meristem after fire, and can arise from insulated aerial, basal or underground buds, or combinations of these (P.J. Clarke et al., 2013). For example, palms and palm-like plants (cycads and tree ferns) often resprout after fire from a terminal bud protected by leaf bases. Trees may also resprout epicormically from pre-bud meristems that are protected by thick bark, whereas shrubs mostly resprout basally or from underground storage organs (P.J. Clarke et al., 2013). Combinations of these different resprouting responses affect species composition and competitive dominance, and consequently the stand-level rates of carbon (biomass) retention and of biomass recovery after fire (Fig. 1). For example, ecosystems dominated by stem-killed species are subject to large losses of live above-ground biomass, whereas those that resprout epicormically experience little loss after fire (P.J. Clarke et al., 2013; Lawes et al., 2011a).

Recovery after fire can also occur by recruitment from seed (Fig. 1). Germination in the immediate postfire period (≤1 year), as opposed to in the longer intervals between fires, is well known in many crown-fire ecosystems such as heath and shrubland (Keeley et al., 2012), but appears to be rare among woody species in surface-fire systems such as savanna and grassland. Species with canopy-held, serotinous seed banks are particularly well represented in crown-fire systems because their seeds survive fire, and are released synchronously in profusion after fire into an environment where competition for resources is reduced (Buma et al., 2013; Keeley et al., 2012). Despite the importance of delayed seed germination in determining postfire community composition, landscape, ecosystem and continental patterns of fire-cued 'seeding' have not been

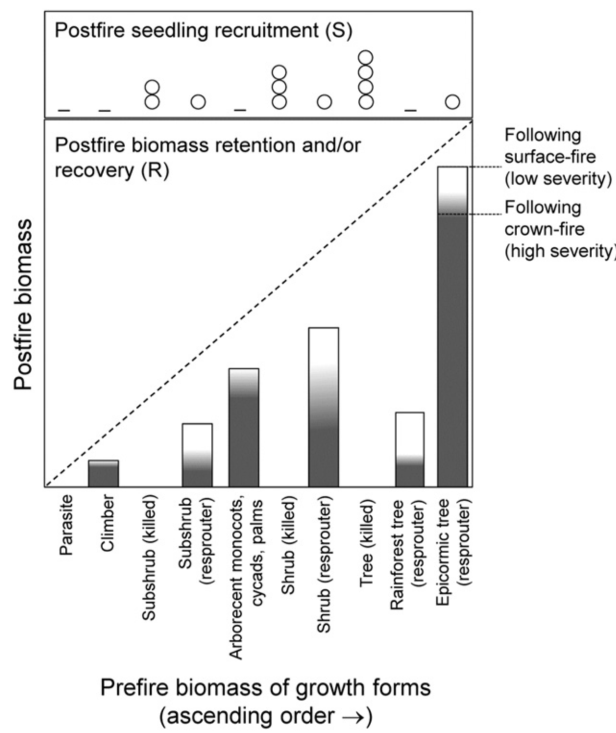

Fig. 1. Conceptual framework showing postfire seeding (S, upper panel) and resprouting (R, lower panel) responses one year after fire across growth forms. The dashed-line indicates the point at which postfire and prefire biomass are equal. Bars that reach this line indicate growth forms that either fully retain or recover biomass soon after fire. Fire-killed growth forms exhibit total loss of biomass after fire, but often have seed banks in the soil or in their canopies that are cued by fire and cause fire 'event' dependent recruitment (S+) (shown as open circles, in the upper panel, whose number represents the relative size of the seed bank). Most parasites, climbers, arborescent monocots, cycads and tree ferns, and rainforest trees do not recruit from seed after fire (S−). In growth forms that resprout, postfire biomass is strongly dependent on fire severity (greater loss of biomass in high-severity crown-fire systems). Taller growth forms are predicted to retain and recover biomass to a greater extent after high-severity fire because of (1) greater bud protection from thick bark in trees, and (2) increasing height of escape from fire effects among palms, cycads, and tree ferns because their buds are on terminal apices. Ecosystems can comprise one or more of these growth forms. Thus, combinations of R and S will vary among ecosystems, which will determine overall ecosystem resilience to future fire conditions and regimes. Ecosystems dominated by growth forms that have low resilience to fire may experience state shifts, while those dominated by growth forms with high resilience will likely remain stable under worsening fire conditions (Bowman et al., 2013).