Acta Oecologica 36 (2010) 202–210

Contents lists available at ScienceDirect

Acta Oecologica

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

Original article

Soil seed banks confer resilience to savanna grass-layer plants during seasonal disturbance

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ARTICLE INFO

Article history:
Received 17 September 2009
Accepted 28 December 2009
Published online 27 January 2010

Keywords:
Seed bank
Grass-layer
Germination
Northern Australia
Smoke
Fire

ABSTRACT

An understanding of soil seed bank processes is crucial for understanding vegetation dynamics, particularly in ecosystems experiencing frequent disturbance. This paper examines seed bank dynamics in a tropical savanna in northern Australia, an environment characterised by frequent fire and highly seasonal rainfall. In particular, we examine the contribution of seed bank processes to the high level of resilience shown by grass-layer vegetation in relation to fire. We assess the spatial congruence between seed bank composition and extant vegetation, document temporal variation in the germinable seed bank over the annual dry season, test the effects of laboratory-applied heat and smoke treatments on seed germinability, and determine the effect of experimental fires on seed bank composition. Although dominant species were shared, the composition of the germinable seed bank was significantly different to that of extant vegetation, with approximately half the extant species not being detected in the seed bank. The density and species richness of germinable seeds was significantly greater in the late dry season than the early dry season, with annual grasses showing particularly high levels of seed dormancy in the early dry season. The density and species richness of germinable seeds in the seed bank was significantly enhanced by laboratory-applied treatments of smoke and especially heat, driven by the response of legumes. However, fire had no significant effect on the density or species richness of germinable seeds in the field, indicating soil temperatures during fire were too low to overcome physical dormancy, or burial was too deep to experience adequate heating or smoke exposure. Our results provide a mechanistic understanding of the persistence of annual grasses and forbs in an environment subject to frequent fire and highly seasonal rainfall, and, together with the sprouting capacity of perennial grasses, explain the high resilience of savanna grass-layer plants in relation to fire.

1. Introduction

Tropical savannas cover approximately 20% of the world's land surface, including extensive areas of sub-Saharan Africa, South America and northern Australia (Mistry, 2000). Rainfall in these environments is highly seasonal (Nix, 1983); an annual cycle of grass fuel accumulation and desiccation results in a fire regime typified by very short return intervals (e.g. 1–4 years; Russell-Smith et al., 1997; Scholes and Walker, 1993; van Wilgen et al., 2000). The structure and composition of savanna vegetation is highly resilient in relation to fire, with the majority of plants exhibiting adaptive traits (e.g. sprouting) or life-history strategies that enable them to persist in the face of frequent environmental stress and disturbance (Sarmiento, 1992). Grass-layer plants (grasses, sedges and other herbs) are particularly resilient to disturbance, with abundance tending to fluctuate largely as a result of rainfall variability rather than fire regime (Russell-Smith et al., 2003; Scholes and Walker, 1993; Williams et al., 2003).

The resilience of grass-layer plant populations in relation to fire can be interpreted mechanistically through an examination of life-cycle processes. Whelan et al. (2003) proposed key life-cycle processes to account for population change in fire-prone environments, including failure of seed production, failure of seed release or germination, failure of seedling establishment, interruption of

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URL: http://www.bushfirecrc.com

1146-609X/$ – see front matter
doi:10.1016/j.actao.2009.12.007

growth or maturation, and death of standing plants or seeds. Perennial grasses often sprout vigorously following disturbance, and so exhibit low mortality during fire (Mott and Andrew, 1985; Sarmiento, 1992). However, annuals must rely on effective seed bank processes – a bank of viable seeds in the soil that germinate to become the next generation of plants, in order to persist (Fenner and Thompson, 2005; Thompson and Grime, 1979). Seed banks therefore have great importance for grass-layer plants in tropical savannas, where fire is frequent and rainfall highly seasonal: they provide an important means of persistence during the annual winter dry season, and a source of regeneration in the subsequent growing season after fire (O'Connor and Pickett, 1992; Skoglund, 1992; Snyman, 2004; Williams et al., 2005).

Seed bank composition is determined primarily by seed rain from extant plants directly above, and so above- and below-ground compositions are often very similar (Fenner and Thompson, 2005; Hopfensperger, 2007). However, significant dissimilarity between the composition of seed bank and extant vegetation has been noted in a variety of ecosystems, including savannas (Solomon et al., 2006). The differential importance of seed banks to annual and perennial life forms can contribute to this. Such dissimilarity could also be influenced by seed dispersal from outside the community, where species are detected within the seed bank but not in the extant vegetation (Thompson and Grime, 1979). Finally, such dissimilarity can be caused by species differences in the longevity of seeds in the seed bank, determined by temporal patterns in seed dormancy and germination (Baskin and Baskin, 1998). The seeds of most grass-layer plants in tropical savannas are dormant following seed fall in the late wet season, but overcome this dormancy during the late dry season when soil temperatures increase (McIvor and Howden, 2000; Mott, 1978; O'Connor and Everson, 1998). Despite a loss of dormancy during the dry season, germination is usually prevented by a lack of soil moisture. Then, in response to the first rainfall events of the wet season, seeds germinate in a series of cohorts until no viable seeds remain in the soil (Andrew and Mott, 1983; Veenendaal et al., 1996); long term seed dormancy and persistent seed banks are uncommon (Gardener et al., 2001; O'Connor and Everson, 1998). There are notable exceptions to this pattern. For example, seeds of *Alloteropsis semialata* (R.Br.) Hitchc. (Crowley and Garnett, 2001) and *Cynodon dactylon* (L.) Pers. (Veenendaal and Ernst, 1991) are not dormant at seed fall, and are therefore not maintained in a dry season seed bank.

Exposure to heat during fire can break the dormancy of grasses (Clarke and French, 2005) and hard-seeded species (e.g. legumes), for the latter by fracturing the outer impermeable palisade cell layer (Bell and Williams, 1998). Williams et al. (2003b) demonstrated the promotive effect of heat (85 °C for either 5 or 45 min) on the germination of five native legumes from a savanna in north-eastern Australia. Smoke can also promote seed germination in tropical grasses (Clarke and French 2005; Read and Bellairs 1999; Williams et al., 2003b).

The vertical distribution of seeds in the soil profile is critical to the response of soil-stored seeds to fire, given that soil temperatures decrease rapidly with depth (Bradstock and Auld, 1995; Williams et al., 2004). For seeds to respond positively to soil heating, they must be located in the soil profile where dormancy can be overcome but without causing mortality, and at a depth suitable for emergence (Laterra et al., 2006; Williams et al., 2004). In the savannas of northern Australia, late dry season fires are usually more intense than early dry season fires as a result of both drier fuels and more severe fire weather conditions. As such, higher intensity fires in the late dry season extend elevated soil temperatures deeper into the soil profile and can break the dormancy of more hard-seeded species, depending on their depth (Williams et al., 2004). Different fire regimes may therefore cause differences in the composition of extant vegetation by altering seed bank dynamics. For example, the abundance of forbs and grasses in the standing vegetation in a perennial grass-dominated Australian savanna was significantly higher in the first wet season after fire, especially after late dry season fire (Williams et al. 2003a). This was directly related to the promotive effect of fire-related cues on the germination of the seed bank (Williams et al. 2003b, 2004, 2005).

This paper describes a comprehensive investigation of seed bank dynamics in relation to fire and seasonality in a tropical savanna of north-western monsoonal Australia. Its primary objective is to interpret the high level of resilience of extant grass-layer vegetation through an examination of seed bank processes. The work progresses current understanding of the field by examining seasonal differences in the size of the germinable seed bank in a mixed annual-perennial grass savanna, and the causes of these differences, within a one-year period. The specific aims of the study are to: (1) assess the extent of spatial congruence between seed bank composition and extant vegetation; (2) document temporal variation in the germinable seed bank over the annual dry season; (3) test the effects of laboratory-applied heat and smoke treatments on germinability; and (4) determine the effect of experimental fires on seed bank composition.

2. Methods

2.1. Study site

Soil seed banks were examined in an ungrazed savanna woodland with lateritic red earth soils at the Territory Wildlife Park, 30 km southeast of Darwin, Northern Territory, Australia (12° 41′ 42.25″ S, 130° 58′ 50.36″ E). The region experiences a monsoonal tropical climate (mean annual rainfall of 1399.1 mm), with a hot summer wet season between November and April, and a mild winter dry season between May and October (see Scott et al., 2009 for further information on climate, soils and vegetation). The site consisted of 18 contiguous 1 ha (125 m × 80 m) compartments that had experienced one of six experimental fire regime treatments since 2004, with each treatment replicated three times in a complete randomised block design. There was significant environmental variability inherent between the three blocks (North, Centre and South), due to an environmental gradient where canopy cover and woody plant density are significantly higher in the southern block (Scott et al., 2009).

2.2. Soil seed bank composition

Soil was taken from 12 (of the 18) experimental compartments to examine the density, species richness and composition of seeds of grass-layer plants in the germinable seed bank. Sampling took place in 2006 within each of the three compartments in four experimental fire regime treatments (12 compartments). Compartments representing two of these regimes remained unburnt during the study year, one was burnt in the early dry season (June), and one burnt in the late dry season (October). Samples were collected in June and October at the time of burning (including unburnt regimes). For regimes that experienced fire in the month of collection, sampling was undertaken both before and <1 week after fire. On each sampling occasion, 30 soil samples were collected using a circular core (9 cm diameter and 5 cm depth), in each of three randomly located replicate patches (approximately 400 m^2) per compartment. Samples were bulked, then sieved (10 mm mesh) in the laboratory to remove rocks and litter. A 1500 g sub-sample was obtained from each replicate and transferred to black plastic germination trays (35 cm × 25 cm × 10 cm) filled with a 5 cm layer of 50–50% sand-coco peat potting medium. Trays were