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Wide variation in post-emergence desiccation tolerance of seedlings of fynbos proteoid shrubs

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Abstract

Fynbos Proteaceae that are killed by fire and bear their seeds in serotinous cones (proteoids), are entirely dependent on seedling recruitment for persistence. Hence, the regeneration phase represents a vulnerable stage of the plant life cycle. In laboratory-based experiments we investigated the effect of desiccation on the survival of newly emerged seedlings of 23 proteoid species (*Leucadendron* and *Protea*) occurring in a wide variety of fynbos habitats. We tested the hypothesis that species of drier habitats would be more tolerant of desiccation than those from more moist areas. Results showed that with no desiccation treatment, or with desiccation prior to radicle emergence, all species germinated to high levels. However, with desiccation treatments imposed after radicle emergence, there were significant declines in seedling emergence after subsequent re-wetting. Furthermore, other than three species that grow in waterlogged habitats, germination responses could not be reliably modeled as a function of soil moisture variables. An important finding was that the species had highly individualistic responses to desiccation. In conclusion, early seedling emergence represents a species-specific stage that is highly sensitive to a decrease in soil moisture. Since species are killed by fire (non-sprouting), vulnerability to increasing aridity associated with anthropomorphic climate change would increase the odds of local and global extinction.

Keywords: Cape Proteaceae; Climate change; Regeneration niche; Seedling emergence; Soil moisture

1. Introduction

Many Cape fynbos plant communities have an overstorey of non-sprouting shrubs belonging to the Proteaceae genera *Leucadendron* and *Protea* (Cowling and Holmes, 1992). These shrubs store their large, protein-rich seeds in canopy-borne infructescences ("cones"), a seed ecology syndrome termed serotiny (Lamont et al., 1991). Commonly known as proteoids, these species are entirely dependent on seeds for persistence, since adult plants are killed by recurrent fires at roughly decadal frequencies (Le Maitre and Midgley, 1992). Seedling recruitment is confined to the immediate post-fire period (Bond, 1984) and germination is cued to the combination of high soil moisture and low soil temperatures that prevail in the cooler months (Bond, 1984; Brits, 1986; Mustart and Cowling, 1993a).

Like most other fynbos guilds, proteoids show high compositional turnover associated with soil nutrient and moisture regimes (Rebelo, 2001; Richards et al., 1995). It is feasible that edaphic specialization may be linked to aspects of the plants regeneration niche (Grubb, 1977; Harper et al., 1965). Specifically, newly emerged seedlings may be vulnerable to low soil moisture conditions associated with protracted bouts of dry weather. This sensitive phase of the plant cycle would be particularly vulnerable to any habitat aridification associated with anthropomorphic climate change (Latimer et al., 2009; Walck et al., 2010). Research has indicated that the emergence of seedlings of proteoids is indeed sensitive to soil moisture conditions: a field study which investigated emergence patterns of four species with restricted habitats showed lower levels of seedling emergence on a coarse-textured, sandier soil type than on a neighbouring soil with a finer-grained clay

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component (Mustart and Cowling, 1993a). This was attributed to the higher moisture capacity of the latter soil type, and was backed up by subsequent laboratory experiments where differences in the survival patterns of newly emerged seedlings of two proteoid species were found in soils with different moisture capacities (Mustart and Cowling, 1993b).

In this study we employ laboratory experiments to explore aspects of the desiccation sensitivity of early emergence stages of proteoids. Specifically we investigated the desiccation tolerance of newly emerged seedlings (radicle emergence of 1–2 mm) of 23 serotinous proteoid species that span a wide range of soil moisture regimes. We tested the hypothesis that species of drier habitats would be more tolerant of desiccation than those from more moist areas. We also investigated differences in tolerance to desiccation within two species (*P. neriifolia* and *P. repens*) that each occur in a wide range of moisture habitats as well as in both winter and bimodal rainfall zones.

2. Materials and methods

2.1. Study species and seed collection

We selected 12 *Leucadendron* and 11 *Protea* species (all proteoids) with distributions ranging over a wide variety of habitats and climatic conditions (Tables 1 and 2). Of these *P. neriifolia* and *P. repens* were collected from two localities each (eastern and western Cape with lower and higher rainfall, respectively, and with bimodal (equinoctial) and winter rain, respectively). Habitats varied from permanently moist situations near watercourses (e.g. *L. floridum*), moist mountain slopes (*P. coronata, P. mundii*), through to semi-arid conditions (*L. procerum, L. nobile*). Although most soils were typically sandy, those for some species had a relatively high fraction of fine particles (e.g. *L. teretifolium*).

We collected mature cones from approximately 10 plants within a single population of each species growing in their natural habitat (except *Protea punctata* which we obtained from Kirstenbosch Botanical Gardens) and dried these at 40^0 C in an oven until fruit were released. *Protea* fruits are achenes and those of *Leucadendron* are nutlets; hereafter we refer to both as seeds.

2.2. Germination experiments

We performed laboratory experiments that mimic conditions approximating natural post-fire soil surface conditions during the cool-season germination period (Brits, 1986; Mustart and Cowling, 1993a). Thus, we carried out experiments in a growth chamber with alternating temperatures 10 °C minimum and 20 °C maximum during a 14 h dark and 10 h light (PAR) regime, respectively. These conditions are optimum for the germination of proteoid species in the laboratory (Mustart and Cowling, 1991). We assessed seeds for their ability to germinate as judged by radicle emergence to at least 2 mm. In the case where seeds had germinated prior to desiccation treatments, we assessed for the ability of the radicles to expand and continue growing after re-wetting - in a strict sense this would be termed early post-germination survival; however, we refer to this as ability to germinate. We placed seeds on

Table 1
Identity, generalized habitat (Rebelo, 2001) and seed collecting locality of proteoid study species from the fynbos biome, South Africa.

Species	Habitat	Latitude (°S)	Longitude (°E)
Leucadendron coniferum (L.) Meisn.	Wind-blown sands	34.77	19.85
L. eucalyptifolium H. Beuk. ex Meisn.	Sandy soils	33.67	24.25
L. floridum R. Br.	Damp waterlogged soils and near streams	34.15	18.35
L. laureolum (Lam.) Fourc.	Deep sands	34.77	19.87
L. linifolium (Jacq.) R. br.	Waterlogged, sandy soils over clay	34.67	20.05
L. meridianum I. Williams	Shallow, limestone soils	34.73	20.03
L. nobile I. Williams	Gravelly or sandy soils	33.66	24.25
L. procerum (Salisb. ex Knight) I. Williams	Sandstone-derived sands	32.38	18.97
L. rubrum Burm. f.	Dry slopes on granite or sandstone	32.40	19.10
L. salicifolium (Salisb.) I. Williams	Sandstone-derived sands and seeps near streams	34.75	19.87
L. teretifolium (Andrews) I. Williams	Shale-derived soils	34.20	19.37
L. xanthoconus (Kuntze) K. Schum.	Sandstone-derived soils	34.75	19.92
Protea aristata E. Phillips	Rocky sandstone slopes	33.45	21.30
P. compacta R. Br.	Sandstone-derived soils	34.75	19.92
P. coronata Lam.	Heavy clay soils	33.98	18.42
P. laurifolia Thunb.	Dry sandy or granite soils	32.67	19.30
P. lepidocarpodendron (L.) L.	Sandstone, ferricrete or granite soils	34.05	18.43
P. mundii Klotzsch	Moist slopes and forest margins	33.98	23.90
P .neriifolia (East) R. Br.	Sandstone soils	33.85	24.90
P. neriifolia (West) R. Br.	Sandstone soils	33.97	18.92
P. obtusifolia H. Beuk. ex Meisn.	Shallow limestone soils	34.73	20.03
P. punctata Meisn.	Dry rocky or shale slopes	33.37	22.08
P. repens (East) (L.) L.	Extremely varied habitats	33.85	24.90
P. repens (West) (L.) L.	Extremely varied habitats	33.97	18.92
P. susannae E. Phillips	Calcareous and neutral sandy soils	34.77	19.85