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Using a functional ecology approach to assist plant selection for restoration of Mediterranean woodlands

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ABSTRACT

Drought is likely to increase in intensity and frequency across most of the Mediterranean areas due to climate change. There is thus an urgent need to assess differences in the ability of plants to withstand water stress, especially when selecting appropriate species for ecological intervention. This study focuses on Mediterranean-type ecosystems (MTEs) and identifies plant traits associated with drought resistance that are key in differentiating plant functional types in relation to water use. We further discuss how this knowledge can be used by restoration practitioners. The study was conducted in the *Banksia* woodlands, Southwestern Australia, and six areas across a gradient of water availability were selected. We measured twelve functional traits associated with water use in fifteen plant species. Next, we applied multivariate analyses to examine how traits varied in relation to each other, grouping species based on these traits and investigating similarities within and between functional groups and sites. Functional trait correlations were consistent with the worldwide leaf and wood economic spectra. Among the twelve traits measured, six explained most trait variation: mean xylem vessel diameter (D_{ave}), number of xylem vessels per mm^{-2} (D_s), leaf mass per area (LMA), stem density (WD), foliar carbon isotope composition ($\delta^{13}C$), and leaf water potential at turgor loss point (π_{TLP}). Species were clustered into five different functional groups. Differences within and between functional groups and sites are reported through their Euclidean distances. Analyses of these traits provided insights into the water-use strategies of native plants, revealing those species with greatest potential to resist water deficits. Such knowledge enables the formation of a more functionally diverse assembly of species bearing complementary traits, which in turn can be used to strengthen resistance to invasion in restored communities. This functional ecological approach is transferable to other and for application by restoration practitioners since the traits selected are relatively easy and cheap to measure and require only simple analytical approaches.

1. Introduction

Mediterranean-type ecosystems (MTEs) experience seasonal drought characterized by hot-dry summers followed by mild-wet winters (Aschmann, 1973). Soil water availability during the dry summer is a major environmental limitation under Mediterranean conditions (Castri, 1973), and can lead to water deficits within leaf tissue and xylem vessels critically affecting physiological processes and overall plant performance and survival (Hsiao, 1973). Such ecosystems also support a high diversity of uniquely-adapted plant species (Cowling et al., 1996) that present a wide range of functional responses to water use and carbon assimilation (Mitchell et al., 2008; Vilagrosa et al., 2010; West et al., 2012). Such responses include use of deep water, efficient stomatal conductance, robust hydraulic architecture, and adaptations in leaf physiology and phenology.

The high diversity of MTEs, however, is under threat as they represent some of the most highly altered ecosystems on the planet (Hobbs et al., 1995). In addition, climate change predictions suggest that temperature and rainfall variability will increase significantly, resulting in most MTEs becoming drier in the future (Klausmeyer and Shaw, 2009; IPCC 2014). Within this context, there is a need to restore degraded and abandoned lands to maintain biodiversity and critical ecosystem functions. In MTEs, however, water deficit stress is the principal cause of failure of many restoration projects (Mendoza et al., 2009; Vallejo et al., 2012); and this scenario is expected to be exacerbated by the drier conditions projected for the future. Designing

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and implementing ecological intervention plans based on historical information can be inappropriate since species currently live under already modified environmental conditions with predictions of "no-analogue futures" due to climatic changes (Fox, 2007; Seastedt et al. 2008). New approaches are required in ecological intervention to improve the success of future efforts within drying MTEs. To facilitate these new approaches, a better understanding of how plants function is needed, particularly the species traits likely to become critical for persistence in a drier future (Hobbs, 2007; Hobbs et al., 2011).

Ecological filtering of local biotic and abiotic variables (such as water, nutrients, temperature, competition, parasites and herbivores) determine which functional traits or trait values will facilitate survival under prevailing environmental conditions (Díaz Barradas et al., 1999; Hobbs and Norton, 2004). Over time, changes in climate variables will likely alter ecological filters and consequently plant communities will be represented by species with physiological traits that enable them to persist and reproduce under the new conditions (Kraft et al., 2015). Understanding the interactions between the species pool and ecological filters, particularly water deficits, is becoming extremely important for biodiversity conservation in the face of climate change (Funk et al., 2008; Myers and Harms, 2009). Plant functional traits are attributes relevant to the life history and resource use of a species and can be used to define its ecological role or function (Díaz et al., 1999; Lavorel and Garnier, 2002) and its response to environment change (Kimball et al., 2016; Lavorel et al., 1997). Consequently, there is increasing interest in using traits (Cadotte et al., 2011; Gondard et al., 2003; Pywell et al., 2003; Sandel et al., 2011) as well as the genetic diversity and adaptability of species (Sejian et al., 2015) to guide ecological intervention. The potential for success of an intervention project can be increased by ensuring the maintenance or enhancement of diversity of functional types, particularly if there is uncertainty about future environmental states (Funk et al., 2008).

Functional traits are classified as "response traits", those that determine how organisms respond to environmental conditions; or "effect traits", those that determine the effect of organisms on ecosystem functions (Laughlin, 2014). Response traits are often subjected to ecological filters and play an important role in community assembly and species interactions (Laughlin, 2014), whereas effect traits influence ecosystem processes through nutrient recycling and storage, modifications of soil water holding capacity, grazer efficiency, litter decomposition and primary production (Eviner and Chapin I, 2003). The community assembly comprising individuals with appropriate response traits, however, can determine effects on ecosystem properties (Grime, 2006). To be efficient, the use of response traits as a basis for planning and monitoring ecological intervention of biodiverse MTEs would necessitate a focus on a small number of traits that also allows for uncomplicated and inexpensive measurement of multiple species. Therefore the selected response traits must be directly associated to plant water use strategies, efficient to measure, and which methodologies are applied to the wide range of plant morphology of Mediterranean species (Mooney et al., 1973).

In MTEs, where ecological intervention is increasingly necessary in the context of a future scenario of severe climate changes, there is an urgent requirement to use plant functional traits as the basis for species selection. A diverse field of reproductive, life-history and morphological traits have been used in ecological intervention (Ostertag et al., 2015; Pywell et al., 2003; Weiher et al., 1999). In a study in Southwest Australia, Mitchell et al., (2008) found that minimum leaf water potential and leaf mass per area appeared to be key in differentiating plant functional types in relation to water use. However, to our knowledge, there has been no synthesis of water stress-related physiological and anatomical traits associated with tolerance of seasonal drought in MTEs that are also efficient to measure. Such approach is highly relevant for ecological intervention of MTEs, where large species sets need to be assessed in an efficient and cost-effective way. Therefore, the aims of this study were to (1) identify the physiological and anatomical functional traits that can be used to efficiently measure and screening species in MTEs under threat of climate change; (2) test whether they can be used to characterize Mediterranean plant species in relation to water use; and (3) use these and other findings to devise a theoretical approach that can be generally used by restoration practitioners to select suitable species in the face of climate and other environmental changes.

2. Materials and methods

2.1. Traits selection

From the literature, the selection of the principal response traits for MTEs was based on the following three criteria: (1) measured traits that reflect responses to the key factors, i.e. water deficit stress rather than other abiotic/biotic factors; (2) traits which offer efficacy of measurement across multiple species; and (3) traits which are measured using methodologies that can be applied to the wide range of leaf types, stem characteristics and plant habits of MTEs plant species. These traits are described below.

2.2. Study site and species selection

The study was conducted in Southwest Australia, a region characterized by a Mediterranean-type climate (Aschmann, 1973; Gentilli, 1972). Six sample sites were randomly selected on the Swan Coastal Plain (SCP) with four on the Bassendean dunes at Gnangara (GN) and two on the Eneabba Sandplain (ES). The Swan Coastal Plain has a very low water-holding capacity but varies widely in soil water availability (McArthur and Bettenay, 1960; McArthur, 1991; Table 1). At each study site, the five most dominant plant species (by percentage cover) were determined within three randomly selected replicate 10 x 10 m quadrats and selected for sampling. A total of fifteen species from three taxonomic families were selected, with five plants used as replicates for each species. The species selected were: *Adenanthos cygnorum* Diels., *Banksia attenuata* R.Br., *B. carlinoides* (Meisn.) A.R.Mast & K.R.Thiele, *B. hookeriana* Meisn., *B. ilicifolia* R.Br., *B. menziesii* R.Br., *Beaufortia elegans* Schauer, *Eremaea beaufortioides* Benth., *E. pauciflora* (Endl.) Druce, *Hibbertia subvaginata* (Steud.) F.Muell., *Melaleuca leuropoma* Craven, *Regelia inops* (Schauer) Schauer., *Scholtzia laxiflora* Benth., *S. involucrata Endl* and *Verticordia nitens* (Lindl.) Endl.. Further information on these species are outlined in the Supplementary Information including species' rooting depths which were obtained from Dodd et al., (1984) and Sommer and Froend, (2011) (Supplementary information 1). Samples were collected in March, which corresponds to the period of the year with the lowest available soil water.

2.3. Plant material collection and preparation

Branches (20–40 cm) were collected in the evening, between 1600 and 1700 h, and immediately sealed in humidified plastic bags to minimize water loss. Upon arrival at the laboratory, branches used for osmometer measurements were recut under water and kept in a dark cool place overnight. These samples were rehydrated following a standard method (Bartlett et al., 2012a; Sack et al., 2003; Sack and Pasquet-Kok, 2010), all samples were kept in humidified plastic bags and refrigerated at 4–5 °C for a maximum of two days prior to analysis.

2.4. Osmometer measurements

For each branch, leaves were rapidly picked, wrapped in aluminium foil, placed in liquid nitrogen for 2 min and let to thaw for one hour before the extraction of leaf sap. A leaf press (Markhart leaf press LP-27, Wescor) was used to extract cell sap straight to a filter paper disc that matches the diameter of the Wescor vapor pressure osmometer (VAPRO 5600) 10 µl chamber well. The saturated filter paper was then sealed in