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Designing resilient and sustainable grasslands for a drier future: Adaptive strategies, functional traits and biotic interactions

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ABSTRACT

In many regions of the world, such as Southern Europe and most Mediterranean areas, the frequency and magnitude of droughts and heat waves are expected to increase under global warming and will challenge the sustainability of both native and sown grasslands. To analyze the adaptive strategies of species, genotypes and cultivars, we aim both (i) to understand the composition and functioning of natural grasslands and (ii) to propose ideotypes of cultivars and optimal composition for mixtures of species/genotypes under water deficit and high temperatures. This review presents a conceptual framework to analyze adaptive responses of perennial herbaceous species, starting from resistance to moderate drought with growth maintenance (dehydration avoidance and tolerance of lamina) to growth cessation and survival of plants under severe stress (dehydration avoidance and tolerance of meristems). The most discriminating functional traits vary according to these contrasting strategies because of a trade-off between resistance to moderate moisture deficit and survival of intense drought. Consequently it is crucial to measure the traits of interest in the right organs and as a function of soil water use, in order to avoid misleading interpretations of plant responses. Furthermore, collaboration between ecologists, eco-physiologists, and agronomists is required to study the combination of plant strategies in natural grasslands as only this will provide the necessary rules for species and cultivars or ecotypes assemblage. This 'agro-ecological' approach aims to identify and enhance functional complementarity and limit competition within the multi-specific or multi-genotypic material associated in mixtures since using plant biodiversity should contribute to improving grassland resistance and resilience.

Contents

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1. Introduction

Grasslands cover vast areas of the Earth's surface and other than producing forage provide a range of ecosystem services including carbon storage, soil protection and the preservation of biodiversity. In most rain-fed environments, the productivity and sustainability of both native and sown grasslands, depends mainly on temperature and precipitation (Boyer, 1982) and will be challenged by predicted warmer climates (IPCC, 2007). In Southern Europe, a decrease in summer precipitation accompanied by increased temperatures and solar radiation would inevitably lead to more frequent and more intense droughts (Supit et al., 2010; Trnka et al., 2011). Therefore the frequency of widespread mortality events is likely to increase along with long-term pasture degradation associated with the droughts (Ciais et al., 2005). To cope with the negative effects of climate change, short-term adaptations may include changes of species or populations with greater drought tolerance (Olesen et al., 2007). However, breeding efforts in 'cool season' forage plants have taken place mainly in temperate areas and very few cultivars adapted to severe drought are currently available in Europe (Lelièvre and Volaire, 2009). It is now known that forage persistence during severe drought is governed by mechanisms different than those conferring resistance to moderate droughts (Milbau et al., 2005; Volaire et al., 2009). The plant traits conferring relevant adaptive strategies should therefore be defined according to the targeted environments. It is also advocated increasingly to maximize genetic diversity in multi-specific and multi-genotypic grasslands as a possible adaptation strategy against climate change (Kreyling et al., 2012). Therefore, this review addresses the following questions: (1) what is a drought tolerant perennial forage genotype? (2) What are the traits associated with the different adaptive strategies to drought and how are these measured reliably? And (3) how do we combine strategies (genotypes) for persistent forage mixtures under drought? Our objective is to clarify concepts and methods for the study of drought resistance of perennial forage plants since they differ from those intensively studied in major annual crops (Sinclair, 2012; Tardieu, 2012). We aim to stress the inputs of functional and community ecology applied to native grasslands in order to understand (1) the nature of trade-offs between plant strategies that should have more implications in the design of breeding programs and (2) the elaboration of a framework to rationalize the association of genotypes in forage mixtures resilient under both current and future environmental conditions.

2. The differences between drought resistance & drought survival

2.1. Plant growth maintenance versus plant survival: a trade-off

Drought resistance in crop plants usually defines the ability of species or varieties to grow and yield satisfactorily under periodic drought (May and Milthorpe, 1962). This definition is generally assumed without much discussion and is applied to all cultivated species, whether annual of perennial, whether producing grains or biomass and irrespective of the types of drought and environmental constraints. We believe that for perennial herbaceous species, this definition is inadequate and needs modification. Forage crops and perennial grasslands are expected to produce over many years and their sustainability is associated with yield stability and long-term resilience. Their drought resistance should be therefore analyzed over the appropriate time scale and as a function of the magnitude of water deficit experienced by the plants. This drought intensity is estimated as a cumulative index of 'precipitation' minus or versus 'evapotranspiration' accumulated during the dry period (FAO, 2008; Tsakiris and Vangelis, 2005; Vicente-Serrano et al., 2012). Measurements of soil water reserve and rooting depth will also provide complementary information on water availability for plants (Vicca et al., 2012).

In the temperate and Mediterranean bioclimatic areas, we propose to make a clear distinction between *drought resistance* and *drought survival*, based in particular on recent experiments (Poirier et al., 2012). Under moderate water deficits (cumulative P-ETP lower than around −300 mm according to soil water reserve) and in temperate climates, most genotypes and cultivars of cool-season perennial forage species can be expected to grow. In this case, drought resistance complies with the general definition, i.e. the ability to maintain satisfactory aerial growth and production under a moderate water deficit. Conversely, under severe water deficits (cumulative P-ETP between −300 and −600 mm and according to soil water reserve), plants are expected 'to know when not to grow' (Bielenberg, 2011) in order to survive potential lethal conditions. In these environments, drought resistance combines the ability not to grow during the dry period albeit to survive drought and to regrow when drought is relieved. In this case 'drought survival' is a more suitable term than 'drought resistance'. This issue is exemplified by summer dormancy which confers to genotypes of some grass species the endogenous ability to cease aerial growth and senesce irrespective of the water supply in summer (Volaire and Norton, 2006). Summer dormancy has been correlated with superior survival after severe and repeated summer droughts (Norton et al., 2006, 2012), showing that the ability not to grow during the drought period is the most efficient response to maximize drought survival. This 'trade-off' between 'drought resistance' and 'drought survival' can be paralleled with plant responses under winter and low temperatures, when winter dormant plants (no growth) are those most able to survive the winter and regrow in spring (Castonguay et al., 2006). 'Drought survival' should not therefore, only be associated with marginal cereal crops under extreme environments (Sinclair, 2011) or with desiccation tolerant species none of which are of agricultural importance (Farrant and Moore, 2011). 'Drought survival' for perennial pasture species is instead, a valuable plant adaptation during part of the plant cycle which may enhance long term persistence and productivity under increasing drought (Lelievre et al., 2011).

2.2. Importance of intra-specific variability for drought resistance/survival

For plant breeders, agronomists and eco-physiologists, the importance of intra-specific variability which is one of the major sources of genetic improvement, is an undisputable fact. In plant ecology working on native plant species, the inter-specific variability of functional traits has been recently challenged by the increasingly recognized importance of intra-specific and ecotypic variability (Albert et al., 2011; Violle et al., 2012). Adaptation of