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Mean root trait more than root trait diversity determines drought resilience in native and cultivated Mediterranean grass mixtures

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ABSTRACT

Grasslands provide numerous ecosystem services but their sustainability is threatened by climate change. As plant functional diversity is expected to stabilize ecosystem functions, we tested whether mixing species with contrasting root systems could improve the resilience of Mediterranean grasslands under increasing aridity. We hypothesized that root functional identity (RFI) and diversity (RFD) respectively determines and improves soil water uptake capacity, aboveground biomass (AGB) production and resilience after drought stress (=post-stress AGB/pre-stress AGB). Monocultures, two- and three species mixtures of two groups of perennial grasses (cultivars and native species) were compared in a twin 3-years field experiment under two levels of summer drought in southern France. RFI and RFD were assessed as the mean and variance of multiple root traits (rooting depth, deep root mass fraction, root tissue density, root diameter and specific root length) measured in species monocultures. AGB and resilience were assessed from annual harvests; total transpirable soil water (TTSW) and evapotranspiration in summer (ET_sum) were assessed through the monitoring of soil water content. For both groups of species, RFI was a major predictor of TTSW and resilience, but not of AGB or ET_sum. Greater water uptake, especially from deep soil layers, increased resilience. Rooting depth distribution determined the potential depth of water uptake while root morphology influenced the precision of water uptake along the soil profile. However, RFD only marginally improved AGB production and resilience, although long-term effects of RFD should be tested. Designing artificial plant communities under water-limited conditions should therefore prioritize the maximization of rooting depth and root distribution along the soil profile. Diversifying root morphological traits associated with resource acquisition could also have a positive impact. The similarity of results between cultivars and native species suggests that agro-ecological guidelines for species assembly can be based on advances of functional ecology in natural ecosystems.

1. Introduction

Grasslands are the most important agro-ecosystems worldwide provisioning many ecosystem services including forage supply, carbon storage, soil and biodiversity preservation (Gaujour et al., 2012; Pilgrim et al., 2010). However, native or cultivated grasslands are threatened under the increasing impact of climate change (Tubiello et al., 2007). In Europe, reduced precipitation coupled with increased high temperatures already lead to more frequent and intense droughts (IPCC, 2014) with major continent-scale impacts on primary productivity and carbon sequestration (Bindi and Olesen, 2011; Ciais et al., 2005; Supit et al., 2010). Around the Mediterranean basin, the rate of warming may even lead to an additional month of summer conditions with greater water shortages (Giannakopoulos et al., 2009). There is thus an urgent need to enhance ecological stability of grasslands under increasing drought. To this end, a great challenge in agro-ecology is to use concepts from plant functional ecology and somehow mimic natural grasslands to design innovative and sustainable forage mixtures (Comas et al., 2011; Goslee et al., 2013; Volaire et al., 2014).

Plant functional structure, *i.e.* the value, range and distribution of functional traits of plants within a plant community, is increasingly recognized to have a major role in ecosystem

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functioning (Balvanera et al., 2006; Hooper et al., 2005). While plant functional identity, *i.e.* the mean value of trait distribution, was repeatedly shown to determine the average rate of most ecosystem functions such as biomass productivity (Falster et al., 2011; Vile et al., 2006), soil C storage (De Deyn et al., 2008; Garnier et al., 2004), soil microbial activity and nutrient cycling (de Vries et al., 2012; Orwin et al., 2010) and services (Díaz et al., 2007; Lavorel and Grigulis, 2012), plant functional diversity, *i.e.* the variance of trait distribution, is expected to improve both the performance and stability of ecosystem functions (Campbell et al., 2011; Proulx et al., 2010). According to the insurance hypothesis (Yachi and Loreau, 1999), plant functional diversity may insure grasslands against declines and loss of functions because mixing plant species with contrasting environmental sensitivities provides greater guarantees that some species will maintain ecosystem functioning even if others fail, hence buffering the impacts of environmental fluctuations. Furthermore, plant functional diversity is expected to increase the functional complementarity among plants resulting in greater temporal and spatial partitioning of resources and lower plant competition in the community (Hooper et al., 2005). Consequently, plant functional diversity can improve ecosystem productivity by making resource use more complete and hence benefits to stability of ecosystem functions (Bonin and Tracy, 2012; Hector et al., 2010). However, most studies on plant functional diversity and plant competition have been carried out to test resources such as light or soil nutrients and have been mainly focused on aboveground functional traits (Gross et al., 2007). The role of plant functional diversity on the outcome of plant competition for water and on ecosystem water-use is far less known, especially under water-limited conditions (Craine and Dybzinski, 2013).

To survive drought, plants developed adaptive strategies which combine multiple functional traits associated with dehydration avoidance and/or tolerance (Lambers et al., 2008; Ludlow, 1989). Among perennial herbaceous species, dehydration avoidance strategy is associated with both the efficient soil water acquisition and the reduction of water losses (Garwood and Sinclair, 1979; Volaire et al., 2009). In contrast, dehydration tolerance strategy is associated with the maintenance of viability in surviving organs under severe drought through osmotic adjustment (Volaire and Lelièvre, 2001; West et al., 1990). At the community level, enhancing dehydration avoidance appears to be the prime lever to enhancing grassland productivity and stability under drought (Skinner et al., 2006). However, despite increasing interest on belowground processes, only limited experimental data are available on the role of root traits in field conditions (Borman et al., 1992; Huang and Gao, 2000). Root functional traits such as rooting depth, deep root mass fraction, specific root length, root diameter and root tissue density are expected to be the cornerstone of dehydration avoidance because they altogether play a crucial role in water acquisition (Hernández et al., 2010; Pérez-Ramos et al., 2013). Rooting depth and deep root mass fraction are typically associated with the scale of belowground resource foraging, *i.e.* the numbers of soil layers and resource patches explored by roots, while root morphological traits may be associated with the precision of soil water exploitation within the explored soil layers and resources patches (Campbell et al., 1991; Kembel and Cahill, 2005). Therefore, mixing plant species with contrasting root traits, *i.e* increasing root functional diversity, could improve water uptake capacity over the entire soil profile, especially through a better use of deep soil water which remains available longer under drought.

In this study, we aimed to analyze the impact of mixing plant species with contrasting root functional traits (*e.g.* rooting depth distribution, root morphology) on ecosystem water use, biomass productivity and stability after two distinct Mediterranean drought events of varying intensities. The key stability component targeted was the resilience of ecosystem productivity, *i.e.* the recovery of productivity rates after drought (Lake, 2013). Since plant aboveground growth systematically ceases under severe drought (Volaire et al., 2014), improving the resistance of ecosystem productivity, which is usually assessed through the maintenance of green above-ground biomass during drought, appears hardly feasible in response to increasing summer drought in the Mediterranean. Improving the resilience of ecosystem productivity is therefore more relevant for agricultural purposes than resistance. We set up a 3-year field experiment combining six Mediterranean perennial graminoïd species divided in two groups of species, three cultivars and three native species, to assess whether the response to drought of mixed plant communities is more favorable than monocultures. The comparison between native species and cultivars was meant to ensure that the application of community ecology concepts is relevant for designing agricultural multi-species mixtures (Volaire et al., 2014) despite major differences between native species and cultivars in how plant functional traits have been selected (Lin et al., 2011).

We addressed the following question: can root functional diversity and functional identity enhance the resilience of grass mixtures after intense summer drought? We hypothesized that: (i) root functional identity (i.e. mean root traits) determines soil water uptake capacity and explains the differences in AGB production and resilience between plant communities under water-limited conditions; (ii) root functional diversity (i.e. root trait variance) increases soil water uptake capacity and hence improves AGB production as well as resilience of plant communities after drought; (iii) the contribution of root functional diversity to soil water uptake, AGB production and resilience of plant communities increases as the intensity of summer drought increases; and (iv) that patterns of response would be similar across plant communities based either on native species or agricultural cultivars.

2. Materials & methods

2.1. Plant material

Six Mediterranean perennial herbaceous species, three native species and three cultivars, were chosen according to their contrasting strategies for resource use and drought survival. The objective was to have a wide range of root functional trait values among the selected species. The three native species, *Bromus erectus* Huds. (Be), *Carex humilis* Leyss. (Ch) and *Festuca christianii-bernardii* Kerguélen (Fcb) were collected at La Fage INRA experimental site along a gradient of soil water availability (for site details see Bernard-Verdier et al., 2012; Pérez-Ramos et al., 2012). The three cultivars (cvs), *Dactylis glomerata* L. cv. Medly (Med), *Dactylis glomerata* L. cv. Kasbah (Kas) and *Festuca arundinacea* Schreb. cv. Centurion (Cen) were selected amongst Mediterranean forage cultivars known to be adapted to drought (Lelievre et al., 2011; Volaire, 2008). Previous characterization of the root systems under standardized conditions revealed that rooting depth distribution and root morphological traits differ among these species (Pérez-Ramos et al., 2013; Volaire, 2008). For example, amongst the native species, roots of Be were almost twice deeper than those of Ch, while specific root length of Fcb was more than twice as high as that of Be.

2.2. Experimental site and design

The study was performed in a field experiment located at the Centre d'Ecologie Fonctionnelle et Evolutive (CEFE-CNRS) in Montpellier (43°59′N, 3°51′E). The climate is Mediterranean sub-