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Original article

Environmental gradients and grassland trait variation: Insight into the effects of climate change

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ABSTRACT

The research aim was to understand how variation of temperature and water availability drives trait assemblage of seminatural grasslands in sub-Mediterranean climate, where climate change is expected to intensify summer aridity. In the central Italy, we recorded species abundance and elevation, slope aspect and angle in 129 plots. The traits we analysed were life span, growth form, clonality, belowground organs, leaf traits, plant height, seed mass, and palatability. We used Ellenberg's indicators as a proxy to assess air temperature and soil moisture gradients. From productive to harsh conditions, we observed a shift from tolerance to avoidance strategies, and a change in resource allocation strategies to face competition and stress or that maximize exploitation of patchily distributed soil resource niches. In addition, we found that the increase of temperature and water scarcity leads to the establishment of regeneration strategies that enable plants to cope with the unpredictability of changes in stress intensity and duration. Since the dry habitats of higher elevations are also constrained by winter cold stress, we argue that, within the sub-Mediterranean bioclimate, climate change will likely lead to a variation in dominance inside plant communities rather than a shift upwards of species ranges. At higher elevations, drought-adaptive traits might become more abundant on south-facing slopes that are less stressed by winter low temperatures; traits related to productive conditions and cold stress would be replaced on north-facing slopes by those adapted to overcome both the drought and the cold stresses.

1. Introduction

Grime et al. (2000) argued that response to climate changes in grasslands depend strongly on the functional characteristics of the community. Indeed, plant traits reflect the trade-offs among different functions within a plant (Lavorel et al., 2007) and impact plant fitness via their effects on resource acquisition, growth, reproduction, and survival (McIntyre et al., 1999; Díaz and Cabido, 2001). Thus, assessment of species traits can be used in modelling vegetation changes (Noble and Gitay, 1996; Hobbs, 1997) and in managing grassland ecosystem services (Lavorel and Garnier, 2002). In particular, the study of trait variation along gradients may provide a useful space-for-time substitution to examine the capacity of plant traits to mediate responses to climate change (Michalet et al., 2014). In fact, variation in the occurrence of traits along environmental gradients reflects variation in the relative importance of adaptive mechanisms, and analysis of their trends provides a way of quantifying the relationship between environment and plant response (Barboni et al., 2004).

Globally, the trait-related response of plant communities to variation of temperatures and to gradients of moisture availability was associated with variations in life and growth form, clonality, belowground organs, leaf traits, plant height and seed mass (Mazer, 1989; Díaz and Cabido, 1997; Niinemets, 2001; Schenk and Jackson, 2002, 2005; Cornelissen et al., 2003; Lavorel et al., 2007). In addition, it was proved that productivity of grasslands with a high level of biodiversity is less affected by drought events (Isbell et al., 2015), recovering more quickly after drought (Tilman and Downing, 1996). However, Scocco et al. (2016) found different patterns of plant community response to drought events in Mediterranean mountains. Actually, species of Mediterranean-type grasslands developed a specific array of adaptations in response to dry climatic conditions, such as prostrate habit or pubescent/thorny dwarf shrub life forms, presence of storage organs, overwintering leaf persistence, and annual life span (Di Castri, 1981; Ehleringer and Mooney, 1982; Peco, 1989; Casado et al., 2004; Galmés et al.,

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2007; Tardella and Catorci, 2015). Other studies found a correlation between disturbance intensity (mowing and grazing), habitat productivity and the abundance of graminoids (Kramberger and Kaligaric, 2008; Peco et al., 2012; Catorci et al., 2013). Senescence of summer leaves, highly widespread in sub-Mediterranean grass species (Catorci et al., 2012b), is a mechanism of drought resistance as well (Volaire et al., 2014). Moreover, Acosta et al. (2008), indicated that perennial plants with deep roots, reserve organs (bulbs, rhizomes), horizontal growth and high palatability are typical of high elevations in Mediterranean mountains. Notwithstanding these knowledge, in order to forecast change due to climate change, we need to further deepen our understanding of the trait-environment patterns in Mediterranean grasslands, which are a biodiversity hot spot and priority habitats (Biondi et al., 2009) of the European Union (92/43/EEC Directive). Moreover, these grasslands are cultural landscapes, resulting from a long history of human management adapted to restrictive environmental conditions (Naveh and Lieberman, 1984). In spite of this, these ecosystems are threatened by abandonment (Sebastià et al., 2008) or by understocking conditions (Bagella et al., 2014; Catorci et al., 2012b; Ribeiro et al., 2014; Vitasović Kosić et al., 2011). Moreover, future threats to biodiversity due to climate change have been predicted (Casazza et al., 2014). Models indicate that areas characterized by substantial temperature increase and concomitant rainfall decrease will be particularly at risk of biodiversity loss (Engler et al., 2011), with a likely increase of drought resistant poorly palatable species (Sebastià et al., 2008). In this regard, forecasts for the sub-Mediterranean regions indicate a strong increase of summer dry conditions and a more marked inter-seasonal and inter-annual variability, with maximum changes in summer (about +3.0/5.5 °C temperature and - 20%/30% precipitation in the worst scenarios) and minimum ones in winter (about +2.0/3.5 °C temperature and −3/8% precipitation) (Giorgi and Lionello, 2008), making the Mediterranean grasslands particularly prone to climate change. Several studies have focused on the impact of climate change on plant physiology and phenology, on population dynamics of few species, or on change in species composition of plant communities; instead, little is known about changes in trait composition and abundance at the plant community scale, that is a key issue (see Walther, 2010). In fact, it was argued that biodiversity enhances the plant community resistance to extreme climate events (Isbell et al., 2015) and ecosystem stability (Hautier et al., 2015). However, species assemblage and diversity are a by-product of the species functional features (Mayfield et al., 2010), so that functional assessment of traits abundance variation along natural or anthropogenic gradients is a key tool and an essential understanding to model and predict species variation within the community in the face of environmental changes.

Air temperature and water availability are two of the main environmental variables affecting plant physiology and reproductive performances (Colin Prentice et al., 1992). While temperature is tied to the elevation gradient, moisture availability is not generally altitude specific, making it difficult to distinguish the effects of moisture from those of temperature on plant functional response along this gradient (Körner, 2003). Thus, data on trait trends should be collected not only along elevation gradients, but also across mountain regions contrasting in moisture regimes (Körner, 2003).

Our general aim was to understand how the variation of temperature and water availability, which reflects the drought and cold stress intensity experienced by plant communities, drives the trait-based species assemblage in Mediterranean-type grassland landscapes, considering different mountain ranges. In this regard, various authors have acknowledged that interpretation of plant distributions along complex gradients is problematic because traits associated with different factors, such as temperature, water and nutrient stress, can overlap or be independent (Cunningham et al., 1999; Dyer et al., 2001; Díaz et al., 2004; Lavorel et al., 2007). Consequently, in addition to air temperature and soil moisture, we considered soil nitrogen, to account for possible confounding effects on trait composition and because these factors, singly or in combination, might filter the trait abundance in different ways. We addressed the following questions: i) How do air temperature, soil moisture and nitrogen shape the trait-based assemblage of grassland communities? ii) What are the trait variation trends along air temperature and soil moisture gradients, and iii) what insight do they provide about the response of plant communities to climate change?

We hypothesized that high drought stress (linked to high air temperature and low water availability in the soil) fosters stress tolerance strategies that promote resource saving and retention, as well as avoidance strategies (*sensu* Briske, 1996), and that in conditions of low or absent drought stress, strategies linked to competitive ability, resource acquisition and re-growth capacity are prevalent. As annual life span, small plant size, low seed mass, prostrate habit, presence of storage organs, scleromorphic and succulent leaves, overwintering leaf persistence, senescence of summer leaves, are traits that allow plants to resist the dry climatic conditions of Mediterranean grasslands, as well as herbivory (Peco, 1989; Thompson, 2000; Casado et al., 2004; Galmés et al., 2007; Catorci et al., 2012b; Volaire et al., 2014; Tardella and Catorci, 2015), we predicted that these functional features would be associated to the most stressful end of the air temperature and soil moisture gradients. On the other hand, since tall plant size, rapid clonal propagation, re-growth capacity, and persistence of leaves are characteristics that allow plants to increase their competitive ability in productive environments (van Groenendael et al., 1996; Grime et al., 2000; Díaz et al., 2007; Klimeš, 2008), we predicted that these traits would be associated to the lowest levels of stress along the considered gradients.

As regards the possible response of the sub-Mediterranean mountain pastoral systems to the climate change, we expected that the presence of cold stress at the higher altitudes could play a significant role in species assemblage, preventing the shift upwards of species without traits that allow low temperature tolerance (Kelly and Goulden, 2008; Austin and Van Niel, 2011; Dobrowski, 2011; Suggitt et al., 2011).

2. Material and methods

2.1. Study area

The study area is located in the Central Apennines (Italy), along five parallel calcareous chains (Amerini, Martani-Sabini, Umbria-Marche, Marche, and Sibillini Mountains – Table 1), oriented NNW-SSE (Fig. 1), whose elevation increases from 800 to 1,600 m a.s.l. The Central Apennines have a marked climatic gradient from east to west (Pesaresi et al., 2014). In fact, the western side is highly characterized by Mediterranean climatic influences, while the eastern sectors are open to the cold wind and atmospheric disturbance coming from north-eastern Europe. Thus, climate becomes more arid from the north-east to the south-west of the study area and from the higher to the lower elevations (Table 1).

The study area belongs to the sub-Mediterranean bioclimate. It is a variant of the Temperate bioclimate, characterizing the border of the Temperate region, and that mostly includes mountain areas arranged around the Mediterranean basin (Rivas-Martínez et al., 2007). It is characterized by winter cold stress and summer drought stress, the intensity and duration of which depend on the elevation gradient and land form factors such as slope aspect and angle (Orsomando et al., 2000). Annual average temperature ranges