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Effects of climate change on leaf litter decomposition across post-fire plant regenerative groups

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ABSTRACT

Decomposition is a determining factor for the functioning of ecosystems because litter dynamics (litter fall and litter decomposition) constitute a key process in the regulation of the recycling of carbon and nutrients. We studied the litter decomposition properties of a set of 19 Mediterranean-basin woody species with different post-fire regenerative strategies (resprouters and non-resprouters), under experimental climate manipulation (simulating warming and drought) over a 2-year period. We show that climate change modifies litter decomposition of these Mediterranean woody species as litter contributions to the soil (g/year) were lower under drought experimental conditions. Species with different post-fire regeneration performance showed different leaf decomposition patterns, though these patterns were influenced by the taxonomical affiliation of the species. As expected, the mass loss of the non-resprouter litter, after 2 years, was higher than in resprouters. Non-resprouters showed higher nutrient concentration per mass of leaf litter after 2 years of experiment than resprouters, possibly because they have lost more C-rich biomass, allowing high nutrients concentration in the remaining litter. That would apply particularly to P as litter N:P ratio was lower in non-resprouters than in resprouters. This study suggests that, in Mediterranean ecosystems, nutrients' return from leaf litter to the soil will be slower under the projected future drier conditions. Furthermore, changes in fire regimes that lead to modifications in the abundance of post-fire regenerative groups are likely to affect ecosystem's functional properties. Thus, if new fire regimes enhance non-resprouters' abundance, we can expect a greater return of organic matter contributions to the soil and a lower litter N:P.

1. Introduction

Shrublands occupy extensive areas of the Mediterranean region (Moreno and Oechel, 1995; Riera et al., 2007), where the availability of water is a key factor determining vegetation composition and patterns of plant distribution. A trend to progressive aridification has been seen over the last few decades in many of these areas, as a result of increased evapotranspiration (caused by approximately 1 °C average warming), without any parallel increase in rainfall (Piñol et al., 1998; Peñuelas et al., 2002; Peñuelas and Boada, 2003). Furthermore, climatic projections anticipate further warming and aridification over the coming decades in the Mediterranean region (Peñuelas et al., 2005; IPCC, 2007).

Apart from aridity, drought and warming, it also increases the risk of wildfires. In fact, the frequency of wildfires in some areas of the Mediterranean basin has increased over the last few decades as a result of climate change and changes in land use and human socioeconomic activities (Piñol et al., 1998; Pausas, 2004). Evolution and dynamics of most Mediterranean-type ecosystems are linked to wildfires (Hanes, 1971; Whelan, 1995; Lloret et al., 2002; Keeley et al., 2011; Bradshaw et al., 2011) and most Mediterranean woody species present regeneration mechanisms after this type of disturbances, determining several post-fire regeneration types. Obligate seeders germinate abundantly after fire from soil or canopy banks, counterbalancing fire-induced mortality. Obligate resprouters diminish fire-induced mortality thanks to vegetative organs with some kind of protection against high temperatures that are able to resprout after wildfires. Seeder–resprouters (or facultative seeders) exhibit both mechanisms, and finally a few species – at least in Mediterranean ecosystems – are not able regenerate well after wildfire. The combination of these responses results on four groups of species (sensu Pausas and Verdú, 2005): seeders (S+ R−), resprouters (S− R+), seeders–resprouters (S+ R+) and those that do not regenerate after wildfire (S− R−). The proportion of these types of species in plant community depends, among other factors, on fire regime and climatic gradients. In the Mediterranean

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basin there is a trend toward an increased proportion of short-lived seeders under moderately high fire frequencies (Lloret et al., 2005; Vila-Cabrera et al., 2008). Also in this region, non-resprouters (S+ R−) have a shorter life cycle and a higher recruitment rate after disturbances such as fire or drought (Verdaguer and Ojeda, 2002; Pausas and Verdú, 2005). In contrast, the group of resprouters (S− R+, S+ R+) is mostly constituted by long-lived species, typically those found in late successional shrublands, in which a high percentage of individuals survive and resprout after fire but do not present any significant short-term recruitment of new individuals. So, long-lived resprouters are expected to show a higher resource allocation to underground organs in order to sustain plant re-growth (Pate et al., 1990; Knox and Clarke, 2005; Schwilk and Ackerley, 2005), while short-lived non-resprouters would have a shorter leaf lifespan and higher photosynthetic rates (Bell, 2001; Ackerly, 2004), similar to early successional species of mesic forests (Bazzaz, 1979). These traits are expected to be reflected in the leaf litter decomposition of these groups of species. These differences could be heightened by differences in leaf properties, such as lower leaf dry-matter content and higher seasonal re-hydration capacity in seeders versus resprouters (Saura-Mas and Lloret, 2007).

Decomposition is a key to better understanding of the effects of climate change, particularly those involving growth as well as carbon and nutrient cycles. It is thus a determining factor for ecosystem production and there is a significant positive lineal relationship between the decomposition rate and relative growth rate for different types of communities, including shrublands (Cebrián and Duarte, 1994, 1995; McTiernan et al., 1997; Maisto et al., 2011). Moreover, the balance between net primary production and decomposition strongly influences carbon and nutrient cycling at ecosystem scale (Chapin et al., 2002). Litter dynamics (litter fall and litter decomposition) constitute a key process in the functioning of ecosystems, as they exert a decisive effect on the recycling of carbon and nutrients. Litter fall represents an output of nutrients from the aerial parts of the plants, and also an input of nutrients to the soil. Subsequent decomposition is the route by which some of the carbon fixed by plants and nutrients is partially incorporated into the decomposing biomass, as inorganic nutrients in the soil or returned to the atmosphere as CO_2. So, this process releases carbon into the atmosphere, as well as nutrients in forms that can be used for plant and microbial production (Chapin et al., 2002; Gartner and Cardon, 2004). This conversion of dead organic matter (leaf litter) occurs by means of a leaching action (removing soluble materials from decomposing organic matter), fragmentation (by soil-dwelling animals that break large pieces of organic matter into smaller ones and mix the decomposing organic matter into the soil) and chemical alteration (primarily through the activity of bacteria and fungi). The decomposition rate is therefore regulated by a set of factors that affect soil biota activity: physical environment (mainly the climate), litter composition and substrate nutrients (Kang et al., 2010; Prescott, 2010).

In this study our main objective was to explore the differences in litter decomposition between species of Mediterranean basin shrublands with different post-fire regeneration under an experimental climatic manipulation of temperature and rainfall. Beyond this, our objective was to establish a link between ecosystem functioning and community composition defined by species attributes related to post-disturbance regeneration, according to their sensitivity to current trends of climate change (i.e. decrease in water availability, increase of temperatures and increase in fire occurrence). More specifically, we tested two main hypotheses. First of all, we hypothesized that since resprouter species have higher leaf dry-matter content (Saura-Mas and Lloret, 2007) than non-resprouters, then, leaf litter of these species would present a lower leaf litter decomposition likely promoting a slower flux of carbon to the soil. The second hypothesis was that higher temperatures and drought could alter soil biota species composition and metabolic activity, affecting litter decomposition rate. However these effects may be complex because in the meantime that temperature and soil humidity are related, higher temperatures tend to increase metabolic activity, while low soil humidity should deplete microbial functioning. In these assessments, we also considered the taxonomical affiliation of species, as differences between the functional properties of post-fire regenerative groups could be linked to their evolutionary history (Verdú, 2000; Pausas and Verdú, 2005; Saura-Mas and Lloret, 2009b; Verdú et al., 2007).

2. Materials and methods

2.1. Species sampling

The study was carried out on a subset of 19 woody plant species growing on limestone in coastal shrublands of Catalonia (northeast of the Iberian peninsula). They were representative of a community that is widely distributed in the region and belonged to as many different families, life-form types and post-fire regenerative groups as possible (Table 1). Depending on their post-fire regenerative strategy (Cucó, 1987; Papió, 1988; Lloret and Vilà, 1997; Verdú, 2000; Alberdi and Cavero, 2003; Lloret et al., 2003; Paula et al., 2009), and after direct field observations in a nearby area that was burnt in September 2004, species were classified into two post-fire regenerative groups: resprouters (R: S− R+, S+ R+) and non-resprouters (S+ R−). Freshly, senescent leaves were collected from the plants of the different species from March 2003 to March 2004. The precise time of collection depended on their phenology (Floret et al., 1989).

Leaf litter was collected in the Montgrí Massís (except for *Arbutus unedo* and *Globularia alypum*, which were collected in Garraf), a protected coastal area located in the NE of Catalonia (northeast Iberian Peninsula, 42.16°N, 3.24°W).

Vegetation is mainly constituted by open *Pinus halepensis* forests and shrublands, dominated by *Quercus coccifera*, *Cistus albidus*, *Cistus monspeliensis*, and *Rosmarinus officinalis* (Polo and Masip, 1987). The annual precipitation is 655 mm, with cool winters and warm summers (mean annual temperature: 14.8 °C) (Ninyerola et al., 2000, 2003). Sampling was conducted in mature shrubland (1–2 m high) that had been untouched by wildfire for over 10 years.

The Montgrí community has been sampled for the characterization of different leaf attributes (Saura-Mas and Lloret, 2007) of the main species, while Garraf was the nearest site with the same type of ecosystem (coastal shrubland on limestone) and an established experimental setting of climate manipulation (Peñuelas et al., 2004). The experiment was therefore located in Garraf, a protected coastal area located in the NE of Catalonia (41.19°N, 1.49°W). The vegetation is similar to the Montgrí shrubland and is mainly dominated by *Q. coccifera*, *Globularia alypum*, *Erica multiflora* and *R. officinalis*. The annual precipitation is 455 mm, with cool winters and warm summers (mean annual temperature: 15.1 °C). The study area soil type is described as a petrocalcic calcixerept soil (pH 8.2), with low quantities of organic matter in the upper soil horizons (3.5%).

2.2. Experimental design

2.2.1. Climate treatments

Nine experimental plots (5 m × 4 m) were established in relatively homogeneous areas within the Garraf study area. Three treatments were allocated: control (C), warming (W), and prolonged drought during the growing season (D). A light scaffolding structure was built around each plot, comprising galvanized steel tubes covered by thin plastic sleeves to prevent contaminants from