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Original article

The effects of nutrient availability and removal of competing vegetation on resprouter capacity and nutrient accumulation in the shrub *Erica multiflora*

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ABSTRACT

Nutrient availability is increasing in the Mediterranean Basin due to the great number and intensity of fires and higher levels of anthropomorphic pollution. In the experiment described in this paper, we aimed to determine the effects of N and P availability and of the removal of competing vegetation on resprouter capacity, biomass, and nutrient accumulation in *Erica multiflora*. Plants of the resprouter species *E. multiflora* were clipped to 0% of aerial biomass in a post-fire Mediterranean shrubland and fertilisation experiments and removal of competing vegetation were established in a factorial design. The resprouting of clipped plants was monitored during the first year after clipping and at the end of the year, all plant resprout populations were harvested and their resprout structure, biomass and N and P content measured. N fertilisation had no significant effect on leaf biomass either at plant level or on the total aerial biomass per stump unit area; however N concentration in resprout biomass did increased. P fertilisation slightly increased resprouting vigour and had a significant effect on P content of the leaf biomass. The removal of competing vegetation increased the ratio between leaf biomass and stem biomass, the lateral expansion of resprout, the hierarchy of resprouts branching, and the P content of stems, above all when P fertilisation was applied. These results show that as a response to decreased competition *E. multiflora* has the capacity to modify the relative proportions of the nutrients in the aerial biomass. All these characteristics allow *E. multiflora* to persist in increasingly disturbed Mediterranean ecosystems and contribute to the retention of nutrients in the ecosystem during early resprouting phases.

1. Introduction

In Mediterranean ecosystems, the high cost of biomass production together with the considerable levels of natural damage (recurrent fires, severe dry periods, and herbivore pressure) are proposed as general explanations for resprouting capacity (Mooney and Dunn, 1970; Lloret et al., 1999). This reproductive strategy enables plants to immediately recover lost ground and has even been considered in ecological theory auto-succession (Hanes. 1971).

In general, Mediterranean ecosystems are considered to be poor in nutrients (Mooney and Dunn, 1970; Ellis and Kummerow, 1989). On the other hand, there is evidence of the role played by nutrients in limiting resprouting capacity (Prevost,

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1994; Cruz and Moreno, 2001). Resprouting capacity should be especially important in nutrient-poor environments and in environments such as Mediterranean ecosystems where there is a great risk of post-fire nutrient losses caused by torrential rainfalls.

Some experiments have demonstrated that resprouting vigour is strongly reduced by the presence of competing vegetation. Resprouting should be stronger when a perturbation has destroyed not only the biomass of a single plant but also that of its neighbours (Vilà and Terradas, 1995a, 1998; Vilà et al., 1998). Less is known about the interaction between nutrient availability and the presence of competing vegetation on patterns of resprouting intensity, on the nutrient capture during resprouting and on the structure of sprouts population of each plant.

In some studies, competition has been considered to have a more relevant role in nutrient-rich than in nutrient-poor environments (Grime, 1977; Reader, 1990); in others, however, competition has been reported to be equally important in rich and poor environments (Tilman, 1982; Wilson and Tilman, 1993). The idea that the intensity of competition depends on resource availability in ecosystems remains controversial (Welden and Slauson, 1988; Peltzen and Kochy, 2001). Most experiments carried out on the interaction between competition and nutrient supply levels have been conducted by removal of competing vegetation. These experiments have been conducted mostly in grassland communities (see Tilman, 1990) and less often in Mediterranean shrublands (Vilà and Terradas, 1995a). Furthermore, two different structural levels can be distinguished in a context of plant competition. The first level is represented by genetic individuals in the population that are the result of sexual reproduction; the second level is found within individual plants and is the result of their modulated growth pattern. At this second level, competition exists between different modules within the same plant (Berstson and Weiner, 1991).

During the last century, the temperature in the Mediterranean Basin showed an overall trend towards warming (Piñol et al., 1998; Peñuelas et al., 2002; Peñuelas and Boada, 2003) and precipitation levels are currently experiencing a long-term downward trend in some Mediterranean areas (Kutiel et al., 1996; Esteban-Parra et al., 1998). This change in climate is occurring simultaneously with changes in nutrient availability in many areas of the Mediterranean Basin. Fire frequency has increased in the eastern part of the Iberian Peninsula in recent decades (Pausas, 2004). Frequent fires may result in cumulative nutrient loss through volatilisation, smoke particles, windblown ashes, soil leaching, and erosion, thereby magnifying the possible limiting role of nutrients. Fire can increase N and P availability in the initial period after fire (Carreira et al., 1996; Gimeno-García et al., 2000). However, this sudden increase in P availability only last for a short time due to the fact that such increases principally occur in soluble P in inorganic soil (Kutiel and Kutiel, 1989; Thomas et al., 1999). Moreover, P losses caused by volatilisation (Soto et al., 1997) or rainfall erosion (Thomas et al., 1999) can often be higher after fire. The capacity of quick absorption of nutrients after a fire event has been suggested as one of the benefits of a resprouting strategy (Specht, 1973; Romanya et al., 2001) and, in this way, the liberated nutrients can easily be retained by the resprouting species following a disturbance. Another driver of change in nutrient availability is the alteration of global biogeochemical cycles by human activities. The global N cycle has now reached the point in which more N is fixed annually by human-driven processes (fertilisers, combustion of fossil fuels, and waste from stock-raising) than by natural processes (Vitousek et al., 1997). Nitrogen inputs and N and P foliar concentrations seem to have increased in some Mediterranean species in the last few decades (Peñuelas and Filella, 2001).

The capacity to capture nutrients may become a vital part of the ecological strategies of Mediterranean plants in context of a global change, in which a decrease of water availability, more erratic and torrential rainfalls, greater erosion, and increased fires and nutrient deposition may lead to steeper gradients in nutrient supply and thus affect the regenerative capacity of the Mediterranean sclerophyllous ecosystems. This new environmental scenario may challenge the capacity of sprouting strategies and their role in the maintenance of the structure of present-day Mediterranean ecosystems. The capacity to capture nutrients under different levels of competition and nutrient availability may be the key for Mediterranean resprouters to maintain their current areas of distribution and retain nutrients in the ecosystem in the near future.

Erica multiflora is a common evergreen shrub that typically occurs in coastal shrublands on calcareous soils in the western Mediterranean Basin (Orshan, 1989). Its resprout vigour has been studied in light of a number of different disturbances (Lloret and López-Soria, 1993); water stress (Vilà and Terradas, 1998; Llorens et al., 2003), warming (Llorens et al., 2004), competing vegetation (Vilà, 1997) and herbivores (Vilà and Lloret, 1996; Vilà et al., 1998). The current coincidence between climate change and increase in nutrient supplies warrants an investigation of the capacity of dominant Mediterranean shrubs to change their sprout structure and to capture and retain nutrients in their biomass in response to nutrient pulses originating from forest fires or pollution.

In a post-fire shrubland with a history and a structure typical of widespread zones of the Mediterranean Basin, we conducted a factorial design experiment involving nutrient fertilisation and the removal of competing vegetation as way of studying to study the effects of disturbance on *E. multiflora*, a typical Mediterranean resprouting shrub species. Our aims were to investigate the effects of a sudden increase in N and P supplies and different densities of competing vegetation on (i) resprouting vigour and structure (biomass, number, size, and branching distribution of resprouts at genet level), and (ii) the nutrient content of the resprouts.

2. Materials and methods

2.1. *Experimental site*

The experiment was conducted in a naturally regenerated post-fire shrubland that was burnt three times in the period 1965–1985. The last fire occurred in summer 1985, 5 years before the experiment started. The study site was located on a