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Fine root growth of *Quercus pubescens* seedlings after drought stress and fire disturbance

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ABSTRACT

Post-fire resprouting is an important process in the Mediterranean climate regions of the world and involves considerable rearrangement of biomass allocation. We have investigated the morphological changes occurring in the fine root portion of *Quercus pubescens* seedlings growing in controlled conditions in which fire disturbance is superimposed on drought-stressed plants. We measured the absolute (length, number of apices) and relative (specific root length and root tissue density) morphometric traits of fine roots, and the biomass and water content of the main plant compartments (leaves, shoot, taproot and lateral fine roots). Initially, soil drying significantly increased the fine root standing mass and decreased the specific fine root length irrespective of the fire, but fine root biomass declined after a critical length of time. Fire significantly decreased the above-ground biomass and its water content notwithstanding the drought stress interruption. On the contrary, time, water supply and fire disturbance factors showed significant interaction effects for the plastic morphological traits, namely, length and number of apices. In fact, fire reduced and postponed the peak of root growth in terms of the thinnest fine root fraction (0.0–0.5 mm diameter) and number of apices. These findings indicate the advantages of shedding over maintaining the roots under a condition of severe drought. Indeed, shedding makes the overall reduction of the root system more functional, and induces a partial increase in water particularly in the thicker fraction of the fine roots (0.5–2.0 mm). Shoot removal by fire seems to lessen and prolong the acclimation process to drought, but the decrease in non structural carbohydrate reserves appears to impede the recovery process at least after persistent drought.

1. Introduction

Wildfires are strong unpredictable disturbance events that cause the partial or complete loss of the above-ground plant biomass. They are frequent in Mediterranean climate regions of the world, and plants have evolved a range of adaptations that enable them to survive fire (Keeley, 1991). At species scale, plant responses to disturbances have typically been classified dichotomously, separating species that survive and persist vegetatively (resprouters) from those that are killed and regenerate from seeds (seeders or non-sprouters) (Wells, 1968; Midgley, 1996). At community scale, the high resilience of Mediterranean plant communities after fire can be explained by the ability of plant species to recover by means of resistant structures, namely the bud bank (Malanson and Trabaud, 1988; Hodgkinson, 1998) and germination of fire-protected seeds stored in the soil or in the canopy bank (Noble and Slatyer, 1980; Lloret, 1998).

Growth resumption of resprouters appears to depend on a supply of stored non-structural carbohydrates (NSC) present both in stem-derived organs such as lignotubers, rhizomes, stolons, and in roots (Jones and Laude, 1960; Donart and Cook, 1970; White, 1973; Kays and Canham, 1991; Bowen and Pate, 1993; Van der Heyden and Stock, 1996; Canadell and Zedler, 1995; Canadell and Lopez-Soria, 1998). Resprouters allocate more biomass and NSC in their roots than non-root-sprouting congeners (Pate et al., 1990; Bowen and Pate, 1993; Langley et al., 2002; Palacio et al., 2007). Water shortage strongly affects the Mediterranean vegetation during summer, thereby disturbing plants that are already drought stressed (Trabaud, 1987). Therefore, it is the response of fine roots to the combined effect of increasing soil dehydration and fire disturbance rather than the two conditions separately that is crucial for plant survival.

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We investigated the combined effect of drought and fire at root system level in the resprouting process of Mediterranean species seedlings of *Quercus pubescens*, *Quercus ilex* and *Fraxinus ornus* (Chiatante et al., 2005, 2006). This study shows there is considerable re-arrangement of fine roots after the onset of soil drying in all the species studied, whereas our results concerning fine root growth rate in relation to fire disturbance are inconsistent. Stored NSC in *Quercus* congenera roots greatly affects damaged shoot recovery, and it was observed to decrease after resprouting (Kabeya and Sakai, 2005). Thus, assuming that root NSC availability decreases after fire disturbance, we expect root growth rate to decrease particularly during the period following the fire event.

Our general objective was to determine if, in controlled conditions, measurement of absolute morphometric traits (length and number of apices), relative traits (specific root length [SRL], root tissue density [RTD]), and biomass allocation in *Q. pubescens* seedlings confirms our previous findings of the bell-shaped fine root growth-response curve after the onset of soil drying, obtained under semi-natural condition (nursery) and the same water/fire treatment combinations. Our specific objective was to characterize the occurrence of different fine root growth rate, if any, between the unburnt and burnt drought-stressed plants.

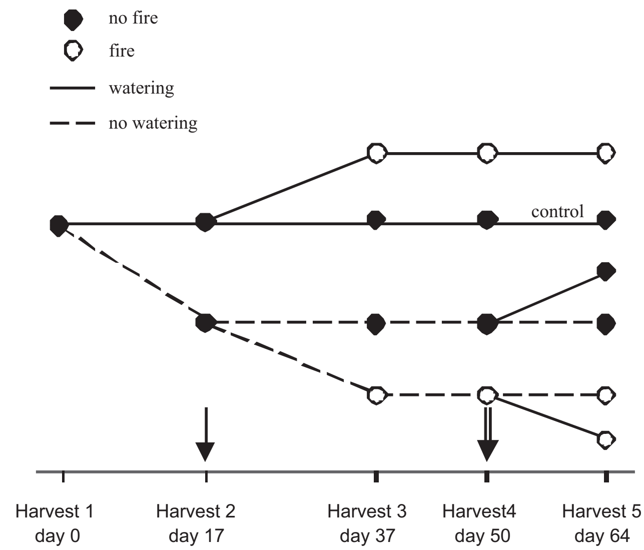

Fig. 1. Schedule and sequential connection among the four water/fire treatment combinations. Arrows indicate the experimental days of the fire event (left) and the beginning of the recovery period (right).

2. Materials and methods

2.1. Plant material

One-year-old dormant *Q. pubescens* Willd. seedlings (seeds from a local provenance, Central Apennine Ranges) of very narrow range of sizes (top bud 15–20 cm high) were transplanted in 5000 cm^3 pots filled with a 2:1:1 mixture of clayey loam soil:moist peat:vermiculite respectively. The plants were grown in a growth chamber under 25/18 °C day/night temperature, 300 $\mu mol\ m^{-2}\ s^{-1}$ PPFD, 16 h photoperiod and 45/70% relative humidity (RH) throughout the experiment. A typical watering regime for all potted seedlings consisted of 300 ml tap water every three days. All plants, 68 in total, were watered to field capacity for 40 days till all of them fully recovered from dormancy, then they were arranged for the experimental design.

2.2. Experimental design

The experiment lasted 64 days. The summer drought typical of the Mediterranean climate generally spans the months of June, July and August in the northern hemisphere. The experimental design is illustrated in Fig. 1. There were five harvests. Four water + fire treatment combinations (2 water levels × 2 fire levels) were applied in a completely randomized factorial design as follows: (1) watering – no fire (control): plants were watered once a day throughout the experiment; (2) watering plus fire (fire exposure): plants with the control watering regime were burnt on day 17; (3) no watering – no fire (drought stress): watering was stopped at the beginning of the experiment; (4) no watering plus fire (drought stress plus fire exposure): drought-stressed plants were burnt on day 17 and remained on a no watering regime. Stress interruption treatment, starting on day 50 and ending on day 64, was applied in the two drought-stressed conditions by resuming the original watering regime of 300 ml tap water every three days. At each harvest, four plants per treatment combination were collected. After the first harvest, 28 plants remained under the original watering regime and 36 plants were randomly selected for drought stress treatment applied by withholding water. After the second harvest, on day 17, 16 of the remaining 32 drought-stressed plants, and 12 of the-watered plants were burnt. To this end, a small amount of straw was placed around the stem to form a 3-cm thick mat on the pot surface, and set on fire. Plants were left to burn until all the leaves were destroyed. Thirty-three days after the fire event, and 50 days after withhold watering, a sub-sample of four plants that underwent drought stress and four that underwent drought stress plus fire stress were returned to a normal watering regime for 14 days.

2.3. Data collection

The seedlings were recovered from the growth chamber. The root system of each seedling was freed from soil by brushing, carefully washed by hand to minimize fine root loss and then scanned. A calibrated flatbed scanner LA1600+ (Epson America Inc., USA) coupled to a lighting system was used for image acquisition, with a setting of 400 dpi. This system is calibrated with the analytical software WhinRhizo 2003.b version (Regent Instruments Ltd., Canada). To measure fine-root (<2.0 mm) traits, we calibrated the WhinRhizo software with two fine root diameter classes: 0.0–0.5 mm and 0.5–2.0 mm, hereafter designated “thin-FR” and “thick-FR”, respectively. Image analysis showed that the 0.0–0.5-mm fine root diameter class grouped all the 2nd, 3rd and 4th (the greatest branching order observed) and the surface 1st order laterals. The 0.5–2.0-mm diameter class grouped all the remaining 1st order laterals, at least for most of their length. A single first-order lateral larger than 2 mm in diameter occurred only occasionally and only at the end of the bottom taproot. This root category was not considered because it substitutes the taproot tip damaged by the small nursery pots. We measured the following root morphological traits: fine root length (FRL), fine root apices (FRA) and fine root volume to determine root tissue density (RTD: see calculation method below). We did not include taproots in the measurements because taproots were not affected by drought and fire for the length of time considered in this study (Chiatante et al., 2005, 2006). After the image analysis, all fine roots were collected for the SRL and RTD measurements. Fine root samples were oven dried and the SRL estimated as the total fine root length divided by the total fine root dry mass (FRM) per plant. After oven drying, the RTD was obtained by dividing the total FRM by the total fine root volume. To evaluate biomass allocation and water content, we divided plants into taproot, laterals (>2 mm and <2 mm), shoot and leaves, and weighed them before (fresh weight, FW) and after (dry weight, DW) 24 h of drying in an oven at 105 °C. For fire-treated plants, only fully