

Chapter 8

Mediterranean Pine Root Systems Under Drought



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8.1 Mediterranean Pines' Root Structure and Function

Plant survival during drought requires not only aboveground water conservation strategies, but also utilization of all possible moisture sources available underground to sustain plant cell turgor. Roots are the vital organ permitting such functioning.

The genus *Pinus* in the Mediterranean includes drought-adapted species such as *P. halepensis* Mill., *P. brutia* Ten., *P. pinaster* Aiton., *P. pinea* L. and *P. nigra* J.F. Arnold (Barbéro et al. 1998), although drought-resistance varies from one species to the other, with *P. halepensis* and *P. brutia* capable of colonizing the most arid of the habitats that the genus inhabits in the Mediterranean (Dorman et al. 2015a; Mauri et al. 2016). Aboveground adjustments to drought in conifers include flexibility in their seasonality of cambial activity (Liphshitz and Lev-Yadun 1984; Sarris et al. 2013), whereas after severe and frequent droughts, conifers can produce shorter needles and shoots (Vennetier et al. 2013) and reduce green biomass through shedding needles, resulting in changes in tree architecture. Nonetheless, this mechanism has its limitations since not all needles can be shed to prevent conifer desiccation (Körner et al. 2005; Sarris et al. 2007; Allen et al. 2010). Drought-adapted tree species tend to invest more biomass in longer-lasting root organs, as well as minimizing water loss from transpiration (Brunner et al. 2015). These patterns have contributed to the hypotheses that trees respond to water deficit by increasing

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root-to-shoot ratios and rooting depth. Indeed, species adapted to dry climatic regimes generally have higher root-to-shoot ratios and deeper root systems than species that are more suited to mesic climatic conditions (see Brunner et al. 2015 and references therein).

If deep roots are indeed the most vital organs that pines possess to deal with drought, understanding the responses of pines under moisture stress presents a serious challenge. Deep roots are their less-studied organs, as is the general case for tree roots (Brunner et al. 2015; Fan et al. 2017). This is because the biomass of root systems is difficult to measure in any forest ecosystem, in contrast to the several established methods for estimating the biomass of aboveground tree components (Sanford and Cuevas 1996). Roots remain hidden belowground, giving little access for direct scientific measurements, particularly under field conditions (Brunner et al. 2015). This difficulty is even greater when it comes to deep roots.

According to Guo et al. (2013), direct measurement of coarse roots is conducted using destructive methods (e.g., excavation, uprooting, soil block, and profile wall technique), which are laborious and time consuming, thus restricting the manageability of sampling numbers and the repeatability of measurements (Oliveira et al. 2000; Van Noordwijk et al. 2000; Polomski and Kuhn 2002; Reubens et al. 2007). Guo et al. (2013) agree that such methods are not always appropriate for studying roots as they introduce external disturbance to the rhizosphere environment and/or destroy root systems if not done appropriately, making long-term repeated measurements inaccurate or impossible (Van Noordwijk et al. 2000; Nadezhdina and Čermák 2003; Reubens et al. 2007; Danjon and Reubens 2008). Consequently, significant efforts (e.g., Berntson et al. 1995; Hruška et al. 1999; Čermák et al. 2008; Zenone et al. 2008; Leucci 2010) have been made to develop non-destructive coarse root analysis methods in recent decades, including labeling methods (e.g., radioisotope and stable isotope labeling), sap flow approaches, and geophysical imaging techniques (e.g., electrical resistivity tomography, seismic refraction tomography, and ground penetrating radar; Guo et al. 2013). Among these techniques, stable isotopes (Rose et al. 2003; Sarris et al. 2013) can provide considerable information about how deep pine roots function under drought. Other methods include tree-ring stem analysis. By correlating tree-ring width with precipitation variables that determine groundwater availability it is possible to indirectly assess whether pines are deep rooted and what is the origin of the moisture sources their roots have access to. This can provide an inexpensive and easily reproduced, non-destructive method for assessing *in situ* groundwater utilization variability over the course of a pine's entire life span (Sarris et al. 2007; Dorman et al. 2015b; Mazza et al. 2018). Information offered using the above methods suggests that deep pine roots and their rapid growth indeed hold some of the key traits that have enabled the genus to successfully colonize the semiarid habitats of the Mediterranean (Andivia et al. 2018) and beyond.

8.1.1 *Pine Roots and Genetic Adaptations to Drought*

Xerophytic plants have roots characterized by their superficial and horizontal dispersal starting from 5–10 cm. A part of the roots penetrates to the depth to which rainwater penetrates (Fahn 1964; Gindel 1973). In phreatophytes this depth can reach tens of meters belowground as an evolutionary adaptation of tree and shrub species for surviving throughout the dry season in arid and semiarid habitats (Thomas 2014; Fan et al. 2017). Pine species of the semi-arid Mediterranean environment, having developed the genetic potential for lateral and tap roots (Sarris et al. 2013), should be considered as “facultative” or “temporary” phreatophytes. Their tap roots have the potential to access the water table, although this is not necessary for their successful growth. Nonetheless, they are usually not considered to be phreatophytes (Thomas 2014).

Most pine populations around the world grow in low-temperature biomes; thus, the mean rooting depth of this genus has been considered to be ca. 2.5–6.5 m. Compared to phreatophytic genera present mostly in warm climates this may not be too impressive. For example, *Eucalyptus* is considered to have a mean rooting depth of ca. 9–18 m, while *Acacia* appears to be even more deep-rooted (ca. 13–31 m mean rooting depth; Fan et al. 2017). Nevertheless, pine species in warm, semiarid climates, unlike their cold-adapted relatives, can develop a deep taproot which can explore water sources many meters belowground reaching water tables up to 20 m deep (Fan et al. 2017) or even deeper (24 m taproot for *P. ponderosa*; Cannon 1960 in Stone and Kalisz 1991). This may very well also be the case for some typical lower-elevation Mediterranean pine species, such as *P. halepensis* or *P. brutia*, although deep rooting is a trait that higher-elevation pine species such as *P. nigra* may also possess (Fig. 8.1).

Long lateral roots may also assist in expanding the range of topsoil moisture acquisition under drought before it evaporates or before it is utilized by competing species. Some Mediterranean pines that are not known to produce very deep roots, such as *P. pinea*, can grow lateral roots up to 38 m long (Fratteggiani et al. 1994) or even longer, as recorded for *P. pinaster* (44 m; Sudmeyer et al. 2004).

8.1.2 *Pine Root Functioning and Its Environmental Drivers*

In addition to genetics, topography and hydrology regulate plant rooting depth (Fan et al. 2017). Therefore, root architecture in pines is determined by the combined effect of species’ genetics and environmental factors such as moisture availability, water infiltration and oxygen availability.

Pine species such as *P. halepensis* or *P. brutia*, which can access deep moisture sources, appear to be able to grow deep roots only where wet season rainfall is sufficient to penetrate deep into the soil. In such cases, these drought-tolerant pine species can utilize moisture from deeper soil/bedrock layers that has accumulated



Fig. 8.1 The dimorphic root structure of *Pinus brutia* (left) and *P. nigra* subsp. *pallasiana* (right), with surface (S) and deeper roots (D) uncovered after land/rockslides on Mt. Ambelos (Samos Island), Greece. The deeper roots are visible down to 4 m for *P. brutia* and to 10 m for *P. nigra*. Note that they exceed black pine's height. Photos Sarris & Christodoulakis

from rainfall events that have occurred over the course of up to 5–6 years (Sarris et al. 2007; Dorman et al. 2015b). Such root functioning permits drought-adapted pines not only to overcome the lack of topsoil moisture during the dry season, but also to deal with the effects of several consecutive drought years (Sarris et al. 2013). Other pine species such as *P. nigra* (Mazza et al. 2018) or even *P. pinea* (Mazza and Manetti 2013) have been shown to demonstrate similar performance. Pines, however, do not appear to grow deep roots when rainfall is not sufficient to penetrate deep into the soil, and/or evapotranspiration rates are too strong to permit sufficient rainfall to infiltrate deep into the soil (Dorman et al. 2015b). This is not unexpected, as not only the deepest, but also the shallowest roots in the world can be found in biomes adapted to arid regions (Fahn 1964; Kleidon and Heimann 1998; Fan et al. 2017).

Where deep pine roots exist in semiarid habitats with sufficient rainwater infiltration or with access to the water table, species such as *P. halepensis* are considered to perform hydraulic lift (Filella and Peñuelas 2003). This occurs when surface soils dry up during the dry season, but deep water is still available to roots. Hydraulic lift can support water and nutrient uptake during prolonged dry periods (Breda et al. 2006) in a similar way that hydraulic redistribution may permit fine roots to retain their life span under drought at levels similar to roots under conditions without water stress (Bauerle et al. 2008; Prieto et al. 2012).

Plants growing close to hydraulic-lifting plants may use such water (Prieto et al. 2010) to improve their moisture content and growth rates compared to those that do

not have access to this source of water (Filella and Peñuelas 2003; Zou et al. 2005), especially during long periods of drought (Caldwell and Richards 1989; Dawson 1993; Horton and Hart 1998; Filella and Peñuelas 2003). Pine roots are known for their symbiosis with mycorrhizal fungi (Gardes and Bruns 1996; Ashkannejhad and Horton 2006). The uplifted water that reaches surface pine roots in dry season soil may also be valuable for sustaining the vitality of such microbial communities. It is believed that when surface soils are very dry, water is redirected, by water potential gradients, from tree shoots to fine roots, and then into mycorrhizal fungal hyphae, whereas hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying (Querejeta et al. 2003, 2007). In contrast, common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants (Egerton-Warburton et al. 2007). Thus, pines' deep-rooting potential may assist ecosystem productivity under drought by sustaining the vitality of soil microbiota as well as understory vegetation, although such an ecological trait may not only be limited to pines, but rather, it may be typical of many tree species adapted to semiarid conditions.

Apart from mycorrhizal networks trees may transport water, minerals and organic compounds by natural grafting of surface roots, a phenomenon that has been observed in many pine species and received various explanations for its occurrence (Graham and Bormann 1966; Lipschitz and Bonnef 1987; Lev-Yadun 2011; Tarroux and DesRochers 2011). The extent of this phenomenon in Mediterranean pine forests and its ecological impact is difficult to assess as it has not well been investigated. Nonetheless, its potentials effects may be stronger the closer pines grow together and the longer their lateral roots. Thus, its existence may be less frequent in open dry habitat pine stands or in pines that invest in deep rather than surface roots (Loehle and Jones 1990).

Time is an additional factor to consider. Water utilization by pine roots may considerably change as aridity varies within the growing season, but also as climate changes over longer climatic periods.

In semiarid conditions pines absorb moisture from the topsoil during the wet season. As these reservoirs dry up, roots of some, but not all plants, track water depletion down the soil/bedrock moisture profile (Bledsoe et al. 2014). Pines in Mediterranean climates have been known to track water (Fig. 8.2). As the seasonal climate becomes drier and the overlying substrate is depleted of moisture, progressively deeper water sources, including weathered bedrock can be exploited to a depth of several meters, enabling trees to escape desiccation (Rose et al. 2003 for *P. jeffreyi*; Sarris et al. 2013 for *P. brutia*). Water uptake by roots shifts back to topsoil moisture once the wet season resumes (Sarris et al. 2013). Not only roots, but mycorrhizal fungi also extend into the bedrock and/or search out suspended pockets of water (Hubbert et al. 2001; Querejeta et al. 2007; Estrada-Medina et al. 2013; Bledsoe et al. 2014). Mycorrhizal fungal hyphae can also track roots through fractures in the rock and then extend from root tips penetrating the bedrock for water extraction (Allen 2006; Bledsoe et al. 2014). Thus, we must ask whether shifts from top to deeper moisture utilization, under increasing drought stress, involve or are driven by changes in the growth characteristics and/or the community structure of

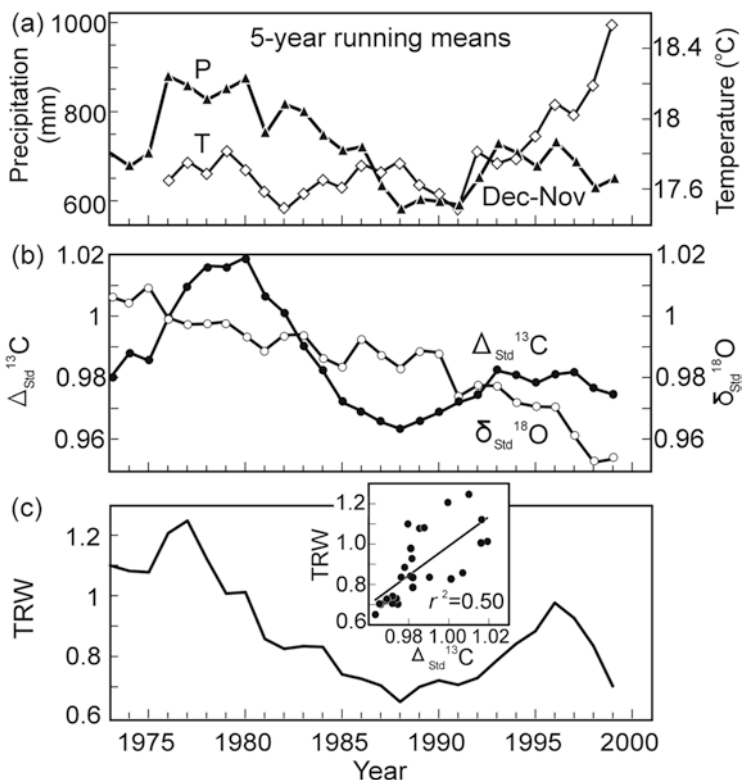


Fig. 8.2 (a) Full-year (Dec–Nov) precipitation (P) and temperature (T) for Samos Island, Greece; (b) $\Delta_{\text{std}}^{13}\text{C}$ and $\delta_{\text{std}}^{18}\text{O}$ tree-ring signatures from *Pinus brutia* ($S_n = 3$ trees); and (c) corresponding tree-ring width (TRW). The insert shows the linear regression ($r^2 = 0.50$, $p < 0.001$) between the $\Delta_{\text{std}}^{13}\text{C}$ tree-ring signals and corresponding TRW ($S_n = 3$ trees) appearing in (b) and (c). As long-term drought intensifies (a), drought stress increases as displayed by a decline in $\Delta_{\text{std}}^{13}\text{C}$ (b), and growth declines as displayed by a decline in TRW (c). Moreover, deep roots in *P. brutia* become more important, as indicated by the gradual utilization of deeper moisture pools, displayed by the decline in $\delta_{\text{std}}^{18}\text{O}$ (b). (See Sarris et al. 2013 for details)

pine root mycorrhiza, since changes in soil moisture have been found to have a strong impact on mycorrhiza (Jarvis et al. 2013 for *P. sylvestris*).

A shift in the utilization of water from different soil horizons is typical of plants with dimorphic roots in Mediterranean-type ecosystems (Dawson and Pate 1996). The phenomenon can also be observed from one decade to another, with a series of wet years permitting pines to rely more on topsoil moisture, whereas a series of dry years can force pines such as *P. brutia* and *P. halepensis* into lower productivity driven by deeper moisture uptake (Sarris et al. 2007; Dorman et al. 2015b). Nevertheless, when a series of dry years causes deeper moisture pools to become depleted, these pines shift their water uptake back to surface moisture inputs (Dorman et al. 2015b; Fig. 8.3). In such a case, soil depth, by affecting rooting depth, together with the degree of exposure to the sun's radiation, are among the

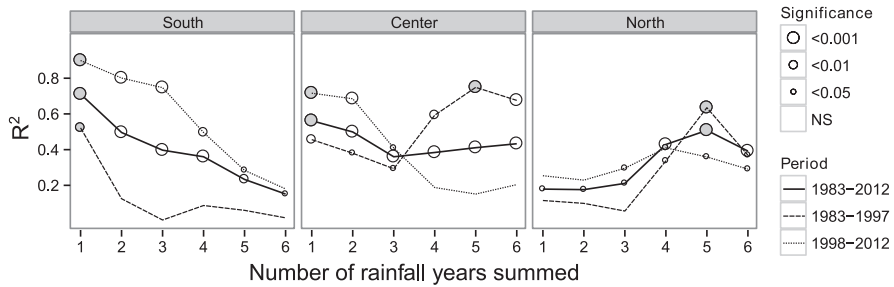


Fig. 8.3 Linear regression of *Pinus halepensis* growth (BAI) and different rainfall integration timescales (1–6 years) for three periods (1983–1997 wet climate, 1998–2012 dry climate, and 1983–2012) in three regions of Israel. The integration period that produced the highest r^2 in each region and period is marked with a filled circle. Under a wetter climate, deep-rooted *P. halepensis* trees were identified, utilizing moisture from deeper soil supplied by the last 5 years of rainfall (North). Under an extremely dry climate, coinciding with pine desiccation, shallow-rooted pines that depended on current year’s rainfall were identified (South). Under intermediate moisture, pines depended on deeper moisture supplies in rainy years (Central). However, after severe drought, deeper moisture pools most likely became depleted, and pines in Central Israel shifted their water uptake to surface moisture inputs. (See Dorman et al. 2015b for details)

prime factors that determine the fate of pine desiccation or survival (Dorman et al. 2015c). Deep soils may affect tree architecture, prohibiting deep rooting into the bedrock, which in turn can lead to elevated tree vulnerability in times of drought on south-facing slopes with sparse pines, particularly when the entire soil profile dries out, while water stored in rock layers is beyond the reach of tree roots (Fensham and Fairfax 2007; Dorman et al. 2015c).

A similar response can be observed for pine species adapted to sandy habitats with a shallow water table, such as *P. pinea*. *Pinus pinea* roots reach toward the capillary rise of the water table under normal climatic conditions. Under drought, when the water table declines below 4 m, the deepest rooting depth observed for the species (Stone and Kalisz 1991), *P. pinea* can only rely on surface moisture inputs for survival (Mazza and Sarris, pers comm). Losing contact with the water table likely reduces these pines’ productivity and makes them more vulnerable to drought stress, which may further intensify due to competition from better drought-adapted species with deeper root system capacity (e.g., *P. halepensis*).

8.2 Pine Roots and Forest Management Under Climatic Change

Management of Mediterranean pine forests for resistance to drought intensification should aim at increasing moisture availability within tree stands. Thinning has been widely applied and is still considered an important tool for achieving this goal, although it has its limitations (Dorman et al. 2015b, c). The effect of such practices

on the structure and function of pine roots is important; however, it has been given little attention to date. Thus, successful management practices to increase pine stand resilience to drought should aim at both increasing root depth, where deeper moisture pools do exist, and removing pines that have low productivity and shallow root systems. However, the chances of increasing erosion and heat stress on soil due to thinning (Dorman et al. 2015b, c) should also be considered.

After thinning, trees may develop more extensive individual root systems over time, hence, increasing their capacity to extract water from the soil during and after drought periods, compared to trees in unthinned stands (Whitehead et al. 1984; Aussenac and Granier 1988; Misson et al. 2003). Comparing two *P. pinaster* stands with different thinning intensity under decreasing precipitation revealed significant differences in groundwater utilization. The stand with the lower tree density, unlike its denser counterpart, utilized deeper moisture supplies from past rainy years, especially for earlywood formation (Mazza et al. 2014). As the upper soil layers dry up faster in open woodland than in dense forested stands (Raz-Yaseef et al. 2010), pines in low-density stands created by thinning may explore deeper soil horizons, thus reaching water resources stored from past years' precipitation, particularly during periods of drought.

In turn, understanding rooting functioning can assist forest thinning. Based on an intra-stand dendroecological approach using tree rings, Mazza et al. (2018) discovered that in wet years most *P. nigra* subsp. *laricio* trees utilized not only surface but also deeper moisture pools at a Calabrian site within the pines' mesic to xeric distribution range. In contrast, under a drier climate, approximately one-third of the trees within the stand significantly reduced their capacity to utilize deeper soil/bedrock moisture (Fig. 8.4). The survival of these trees, apparently reliant on surface roots during drought, depended mostly on any surface rainfall input provided by summer rainfall. This suggests that they are the most vulnerable to summer drought within the stand.

The intra-stand dendroecological approach could also prove useful in supporting the management of mixed stands (e.g., pine-oak forests). The management of mixed stands is one of the great challenges for increasing forest resilience to climate change; understanding root structure and functioning may hold one of the keys for their successful management. In the Mediterranean, most of the pine stands planted for the purpose of reforesting degraded lands are at the end of their pioneering role, as the chain of ecological succession continues towards more resilient ecosystems characterized by native broadleaved species and higher levels of biodiversity (Pausas et al. 2004). The root systems of oaks, such as *Quercus cerris*, may allow them to explore a more extensive surface soil layer than pines, especially in mixed stands with *P. nigra* trees. In turn, *P. nigra* trees appear to have deeper roots that utilize deeper moisture pools to avoid competition with *Q. cerris* trees in the upper soil layers (Mazza et al. 2021).

Therefore, where deep rooting permits higher resilience to drought, identifying and quantifying the shallow-rooted pines more vulnerable to drought stress is vital for applying appropriate site-specific silvicultural treatments (e.g., selective thinning or modulating thinning intensity; Mazza et al. 2018). Such an approach may

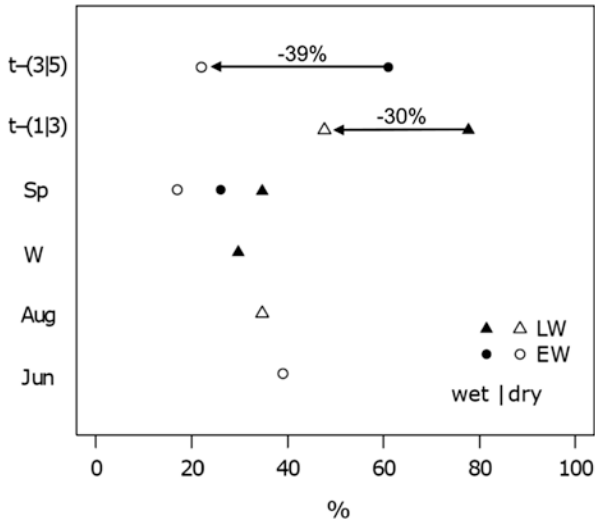


Fig. 8.4 Percentage of *Pinus nigra* subsp. *laricio* trees from Southern Italy producing significant correlations with three precipitation integration time-scales (monthly, seasonal 1–3 and 3–5 past years) for earlywood (EW) and latewood (LW) formation during wet and dry climatic periods. Only the best climate drivers are shown. Arrows indicate the percentage of trees that depleted deeper moisture pools during dry climate and shifted their water uptake from multiple year precipitation to summer rainfall using surface roots. These trees were considered to exhibit higher vulnerability to future drought events. (See Mazza et al. 2018 for details)

increase the resilience of single stands or mixed pine stands to drought, which is expected to affect large areas of the Mediterranean region under climate change.

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