applied sciences

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Review

Opportunities and Threats of Mediterranean Evergreen Sclerophyllous Woody Species Subjected to Extreme Drought Events

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Received: 5 November 2020; Accepted: 25 November 2020; Published: 27 November 2020

Abstract: Climate change and extreme drought and heat events impact the Mediterranean evergreen sclerophyllous vegetation in South Europe, especially in Iberian and Italian peninsula, where widespread crown defoliation and dieback have been observed since the 90s of the XX century. Field observations and long-term experiments showed different sensitivity of the various woody species, *Quercus ilex* and *Arbutus unedo* being prone to drought, whereas *Phillyrea latifolia* and *Pistacia lentiscus* appeared to be resistant. The present review aims at exploring the phylogenetic and evolutionary basis of the resistance (or susceptibility) to drought of Mediterranean vegetation and its possible mechanisms of resilience. The main findings are summarized as follows: (1) Mediterranean regions in the world are refuge areas for several plant evolutive lineages and migratory routes. Evergreen sclerophyllous species, currently presented in Mediterranean basin, evolved under different climatic conditions; (2) the evergreen habitus represents an adaptation to mild drought conditions. Deciduous (specially summer deciduous) species are better performing under severe drought and low air relative humidity than evergreen species; (3) severe drought events acts selectively by favouring the species evolved in the Quaternary era and those originated in drier regions; (4) the evergreen trees and shrubs are resilient to the severe drought events and can restore the pre-event condition by resprouting from dormant buds in the cambium tissue. This ability is related to the non-structural carbohydrate content in the parenchyma-rays in woody stems. The amount and availability of these strategic reserve can be compromised by frequent drought events; (5) plant seed regeneration can be affected by drought and seedling establishment may be limited by soil dryness and microenvironment conditions; (6) the role of phenotypic plasticity of the species and epigenetic responses in Mediterranean-type ecosystems, although discussed in few papers, is still poorly known. We hypothesize that instead of latitudinal (South to North) or altitudinal (lowland to upland) plant migrations, Mediterranean forest ecosystems may respond to climate change by modulating their species composition and community structure with genetic resources (i.e., taxonomic diversity) already present in loco. Changes in vegetation assemblages and community structure may lead changes in ecological and landscape ecosystem values, with changes in related ecosystem services. A redefinition of management criteria of natural resources and a pro-active silviculture to make forest ecosystems more resilient are required.

Keywords: climate change; drought resistance; evergreeness; sclerophylly; resilience; resprouting capacity; severe drought events; species origin; vegetation changes

1. Introduction

Widespread forest tree mortality and dieback caused by drought and temperature stress (i.e., warm winters and hot summers), often followed by insect and pathogen attacks, is a worldwide problem connected to climate change [1–7]. In the last decades, European temperate forests were subjected to recurrent heat and drought waves, such as in 2003 and 2018 [8,9].

Mediterranean evergreen forests and shrublands, although considered well adapted and resistant to summer drought [10], were severely impacted in the Iberian Peninsula and in Italy, as reported by several papers [11–16]. Extreme climate events, including severe drought and heat waves, as described in these papers, affected selectively evergreen sclerophyllous species, both trees and shrubs. *Quercus ilex* L. and *Arbutus unedo* L. were the most sensitive species with severe crown dieback and high mortality rates, whereas *Phillyrea latifolia* L. and *Pistacia lentiscus* L. resulted in being resistant, with no or little crown damage (i.e., defoliation, branch and leaf desiccation). These findings were then confirmed in a long-term experiment of drought imposed in Catalunya [17].

We hypothesize that in ecosystems that are species-rich and have complex structures, such as the Mediterranean evergreen forests and shrubland, the worsening of climatic conditions, with increasing drought and extreme event frequency, will act as a factor triggering vegetational dynamics, modifying plant species composition, individual interactions in resource use and structure of the stands [18].

2. Is Sclerophylly Related to Drought Resistance?

The dominance of evergreen sclerophyllous trees and shrubs in forest ecosystems is a common trait that characterizes the Mediterranean-type vegetation in different regions of the world [19]. It is generally accepted that sclerophylly and evergreeness are adaptive strategies to cope with several environmental factors [20,21], such as the lack of nutrients in the soils [22,23], and to optimize the metabolic costs for the construction of leaves by means of longer lifespan and economy of nutrients [23].

The different strategies of evergreen sclerophyllous and deciduous species to cope with severe summer drought have been largely debated [21,22]. Drought-deciduous species, dropping leaves in late summer or even earlier under extreme water stress, can avoid the most severe physiological consequences [24]. Differently, evergreen sclerophylls do not lose their leaves, perhaps because of the greater metabolic cost for the plant to build the photosynthetic apparatus, than in a deciduous species. Mediterranean deciduous species are built to recover nutrients from leaves prior to their abscission [25]; once the deciduous species has lost its leaves, they have more of a physiological advantage to deal with drought than the evergreens. Where strong water stress is common in summer, growing conditions for plants, generally, occur in late spring; later environmental conditions become progressively harsher, until soil moisture reaches the minimum level at the end of summer. In evergreen species, autumn and winter photosynthesis can be limited by low light availability and soil moisture; consequently, a positive carbon budget may not always be possible. Therefore, early leaf loss in deciduous species may be more efficient than evergreeness [22].

Deciduous trees and shrubs have more rapid maximum photosynthetic rates and can annually grow quickly than evergreens, [26,27]. Evergreen sclerophylls have a lower rate of photosynthesis at that time, although they maintain a relatively stable rate of net photosynthesis throughout the year thanks to the winter photosynthesis. Evergreen Mediterranean species compensate their lower mesophyll CO_2 conductance with high carboxylation rate, reaching a photosynthesis level similar to deciduous plants [28]. Evergreen species manage to do this thanks to their larger leaf mass per area.

Some studies compared the relative behavior of co-occurring deciduous and evergreen species in Mediterranean environments. According to [29,30], *Quercus pubescens* Willd. (deciduous) has a lower construction cost (per leaf area, i.e., metabolic investment to assemblate the photosynthetic apparatus) than *Q. ilex* (evergreen), without difference in carbon assimilation rate. Despite different leaf biochemical composition, size and mass per unit area, the two oak species have similar responses to water shortage. Tognetti et al. [31], comparing the physiological behaviour of *Q. pubescens* and *Q. ilex* in natural stands under summer water stress, concluded that although highly tolerant to severe water stress and tissue dehydration, both species operate at the limits of hydraulic safety. Prolonged climate stress might predispose these *Quercus* species to physiological decline and dieback because their limits of hydraulic safety can be surpassed with frequent and repeated stress occurrence.

Vulnerability or resistance to extreme drought is rather related to the xylem characteristics than to leaf sclerophylly and phenology, and the recovery capacity from xylem embolism plays a crucial role [32] in sclerophyllous trees' responses to drought stress. Xylem vulnerability and recovery capacity are related to wood anatomy, including wood density; vessel diameter; pith size; mechanical elements, like fibers; and non-structural carbohydrates (NSC) storage in the parenchyma [33–36]. Sclerophyll species skillfully manage the water stress recovery, with a complete resolution of xylem cavitation, by means of simultaneous rehydration of the leaf apoplast and symplast [32].

The great elasticity of xylem cavitation strain of sclerophyll species depicts tree response to a large drop in stem water potential during the day, followed by night recovery [32]. This usually occurs in Mediterranean sclerophylls, because they grow with high irradiance and air temperature during the day and with high air humidity condensing on the soil surface at night. Differently, where air relative humidity is low, it is advanced the presence of drought deciduous species, such as *Phlomis fruticosa* L., [37].

3. Does Evolutionary History Explicate the Resistance or Sensitivity to Climate Change?

Some authors [21,38] suggest that evergreen species react better to mild temperature seasonal fluctuations and to the absence of pronounced drought periods. In other words, evergreens are better adapted to semi-arid conditions in which dry spells are relatively short, while deciduous taxa may be better adapted to long (i.e., seasonal) droughts. The sclerophylly of Mediterranean species is hypothesized to originate from a similarity in leaf anatomical structure between species formerly adapted to humid environments, like tropical *taxa*, which later migrated to arid zones [39]. Indeed, the Mediterranean climate originated in the Quaternary [40–42], and the morpho-anatomical characteristics of plants that sign the evolutionary convergence between genera and species were evolved in Tertiary [39]. The current trait similarities among Mediterranean and tropical taxa may be due to phylogenetic constraints rather than evolutionary convergence [39–41]. These Authors argue that the current sclerophyllous Mediterranean vegetation derive from different evolutive lineages and migration routes and evolved partly from pre-adapted taxa from the Mediterranean basin, Macaronesia, and the tropics. Table 1 reports the era of origin of some relevant Mediterranean evergreen woody species.

Table 1. Mediterranean evergreen woody species listed on the basis of the era of origin.

Tertiary (Pre-Mediterranean *)	Quaternary (Mediterranean *)
Abies cephalonica Loudon	*Cistus albidus* L.
Abies numidica de Lannoy ex Carrière	*Cistus creticus* L.
Arbutus unedo L.	*Cistus monspeliensis* L.
Buxus sempervirens L.	*Cistus salviifolius* L.
Cedrus libani A. Rich.	*Lavandula* spp.
Ceratonia siliqua L.	*Erica* spp.
Coryaria mirtifolia L.	*Genista* spp.
Cupressus sempervirens L.	*Rosmarinus officinalis* L.
Daphne laureola L.	
Ephedra fragilis Desf.	
Ilex aquifolium L.	
Juniperus excelsa M. Bieb.	

Table 1. *Cont.*

Tertiary (Pre-Mediterranean *)	Quaternary (Mediterranean *)
Juniperus macrocarpa Sm.	
Juniperus phoenicea L.	
Juniperus oxycedrus L.	
Juniperus thurifera L.	
Laurus nobilis L.	
Myrtus communis L.	
Nerium oleander L.	
Pinus brutia Ten.	
Pinus halepensis Mill.	
Pinus nigra J. F. Arnold	
Pinus pinaster Ait.	
Pinus peuce Griseb	
Pinus sylvestris L.	
Pistacia lentiscus L.	
Pistacia terebinthus L.	
Pyracantha coccinea M. Roem.	
Phillyrea angustifolia L.	
Phillyrea latifolia L.	
Punica granatum L.	
Olea europaea L.	
Quercus coccifera L.	
Quercus ilex L.	
Quercus faginea Lam.	
Quercus suber L.	
Rhamnus alaternus L.	
Ruscus aculeatus L.	
Smilax aspera L.	
Tetraclinis articulata (Vahl) Mast.	
Viburnum tinus L.	

* Pre-Mediterranean and * Mediterranean according to Palamarev 1987; Penuelas et al., 2000; Valiente-Banuet et al., 2006.

Today, Mediterranean sclerophyll species are widely distributed outside the Mediterranean basin, according to their evolutionary history. Therefore, their occurrence is not primarily related to the typical Mediterranean climate with winter-wet and summer-dry conditions. Species belonging to the Oleaceae family, such as *Olea europaea* L. and *P. latifolia,* spread from North Africa to Middle East in non-Mediterranean climates; the genus *Pistacia* (family of Anacardiaceae) evolved in Central Asia under semi-arid climate [43]; while the distribution *A. unedo* (Ericaceae) is connected to oceanic climatic conditions and it can be found also in the British Islands [43]. Evergreen sclerophyllous oaks of the section *Ilex* (*sensu* [44], family of Fagaceae) originated from East Asia in a subtropical wet climate and migrated to western Eurasia (Europe), through the Himalayan corridor [45,46] during the Pliocene era. In the Mediterranean basin, evergreen oaks followed ecological adaptation to the prevalent climatic conditions, i.e., level of dryness [47]. *Quercus ilex* subsp. *ballota* and *Quercus coccifera* L. subsp. *calliprinos* are the most drought-adapted *taxa* of trees, respectively, in western and eastern Mediterranean basin. Overall, *Q. ilex* can be found in quite different climatic conditions [48] and local evolution patterns have been described as adaptations to varying ecological conditions within the distribution range of this species [49,50].

In a field study [51], after a severe summer drought event in Spain, the responses of species evolved under pre-Mediterranean (mostly trees) and Mediterranean (mostly shrubs) climate conditions, where the first were more damaged by drought stress than the latter. According to [52], the vulnerability or resistance to drought is better explicated by ecological and climatic conditions where a species evolved, than its phylogenetic history.

4. Winners and Losers of Mediterranean Species under Climate Change

The relative behaviour (i.e., physiological performances, growth, reproduction) and resistance of different Mediterranean species under increasing drought and temperature has been compared in researches by means of long-term field experiments [53]. Many papers explored the physiological drivers of the greater resistance of *P. latifolia* and *P. lentiscus* in comparison with *Q. ilex* and *A. unedo*, as reported in field observations [51,54] (Figure 1), and the ecological consequences of such differences in terms of species competitiveness, community composition and vegetational dynamics.

Figure 1. *Quercus ilex* L. (holm oak) forest stands in the Regional Park of Maremma (Tuscany, Central Italy). Trees of holm oak are completed defoliated, while *Phillyrea latifolia* L. trees show green canopy (photo by M. Pollastrini, 20 January 2020).

From a physiological point of view, *P. latifolia* and *P. lentiscus* showed higher photosynthetic rates and lower stomatal conductance than *Q. ilex* in water stress conditions, thus exhibiting higher instantaneous plant water use efficiencies [55]. *Phillyrea latifolia* survived under severe short-term drought events, whereas *Q. ilex* did not [55–57]. These findings were confirmed by [58] by comparing the behavior of *P. latifolia* and *Q. ilex* in field and experimental conditions. These authors found that *P. latifolia* can take advantage on *Q. ilex* by maintaining higher sap flow rates during dry periods. *Phillyrea latifolia*, moreover, is better performing than *Q. ilex* in drier soils: whereas *Q. ilex* assimilation rates increased with soil humidity; in *P. latifolia,* assimilation rates did not increase above 17% of soil humidity, showing no water availability response above such threshold [59]. Under severe drought stress, the optimal temperature for photosynthesis is 20–30% lower than in wetter conditions. This condition can overpass the high acclimatory capacity of Mediterranean trees to high air temperatures, which could provoke growth reduction rise in leaf shedding and, for some species such as *A. unedo*, increase mortality risk [60].

Lower water potentials in *P. latifolia* were not clearly associated with higher risk of hydraulic failure. Differently, hydraulic failure remains the most likely cause of death in *Q. ilex* under extreme drought [61]. The vulnerability to xylem embolism has been assessed by [62,63] in a number of Mediterranean species and a pattern was proposed from the most to the lesser vulnerable: *Quercus ilex* = *Acer monspessulanum* L. = *Arbutus unedo* = *Sorbus torminalis* L. = *Cistus laurifolius* L. > *Cistus albidus* L. = *Ilex aquifolium* L. > *Phillyrea latifolia* > *Juniperus oxycedrus* L.

Concerning the reproductive processes [64], reporting the results of an experimental drought suggest that in a drier environment drought-resistant species such as *P. latifolia* could present greater ability to produce reproductive structures than less-resistant species, such as *Q. ilex* or *A. unedo*. In *Q. ilex* and *A. unedo*, flower and specifically fruit production were strongly correlated with annual rainfall, but not in *P. latifolia*. Experimental drought, tested by [65], reduced flower and fruit production in *Q. ilex* by 30% and 45%, respectively, whereas they were not significant in *A. unedo* and *P. latifolia*.

Overall results induced [66–68] speculation that in the drier conditions predicted in Mediterranean area, a relevant reduction of tree growth rates can be expected, combined with an increase of diffusion of drought-tolerant species, such as *P. latifolia*, in detriment of more mesic species, such as *Q. ilex*. In a 14-year-long field experiment, [69,70] observed that *A. unedo* was the only species showing a significant reduction in basal area increment (BAI) under drought. By contrast, *Q. ilex* reduced stem growth only during the first 4 years of treatment and *P. latifolia* remained unaffected over the whole study period. Moreover, [69] found a clear association between the concentrations of NSC and defoliation in *Q. ilex*, with lower total concentrations of NSC and a lower proportion of starch in defoliated individuals. Finally, *P. latifolia* was more able to retain nutrient stocks (C and N) under drought conditions [71].

Different responses among species could produce different patterns in tree mortality, changes in seedling recruitment, resprouting ability (by suppressed and latent buds) and, in the longer term, in species distribution. It is highly likely that mesic species such as *Q. ilex* lose competitive advantage in the drier environment forecasted for next decades than the more xeric *P. latifolia* and *P. lentiscus* [64].

5. Impacts and Recovery in Mediterranean Vegetation

The maintenance of the community structure and plant species composition of the Mediterranean ecosystems is connected to their ability to recover after the impacts of repeated environmental stress and disturbances (i.e., drought, fire). Evergreen sclerophyllous species have a strong capacity of vegetative regeneration (resprouting) and can restore the stand before the disturbance in relatively short time. Evidences suggest that plant communities dominated by resprouter species (RS) recover from disturbance more quickly than those composed by non-resprouters (NRS). The ability of resprouter species to resist drought and avoid mortality, combined with their ability to restore, totally or partially, defoliated crowns, prompts that the impact of increased drought stress in communities dominated by these species may be smaller [72] than in those of non-resprouters. It is necessary, however, in RS to preserve the vitality of the cambium tissue, to allow the production of adventitious buds. Extraordinarily strong drought events may lead to the shrinkage of cambium [73], thus reducing the recovery ability of woody species. In addition, the ability to produce adventitious buds declines with the age of trees and stem size [74,75].

Although resprouting capacity is advantageous in stressful conditions, there are some metabolic costs to sustain, as lower seed production, higher allocation of biomass to roots than to stem and crown, and longer time to reach sexual maturity [72]. Resprouting species, moreover, need greater allocation resources to roots than shoots and greater non-structural carbohydrate (NSC) stores to support the growth of shoots [72]. Drought, as well many other stress factors, implies the consumption of NSC reserves [76]. In a meta-analysis study, [77] compare responses of woody species to drought intensity and duration, in terms of soluble sugars, starch, and total non-structural carbohydrates (TNSC), in leaf, stem, and root. Starch decreased in all organs, while soluble sugars increased in leaf with prolonged experiment time. The changes in soluble sugars in all organs were stronger under severe drought than under slight-to-moderate drought. Under slight-to-moderate drought, trees increased carbon storage, by means of physiological regulation processes, in order to reduce the risks of carbon starvation. In contrast, long-term severe drought could lead to NSC depletion in the whole plant, so reducing the ability to recover after stress. Barbeta and Peñuelas [78] found this process in *Q. ilex*, which can vigorously resprout after drought episodes, but its resilience (i.e., the ability to cope with further stressful events) may be reduced. In the future, the higher frequency of recurrence of extreme droughts will be a challenge for plant communities, and thus, the capacity of these forests to recover.

The time occurring for a (more or less) complete recovery of NSC reserves is therefore crucial for the resilience of Mediterranean vegetation subjected to dry spell events. Research focused on evaluating the development of crown conditions and NSC stored in lignotubers 7 years after a drought event [79] showed that crown dieback was associated with a depletion of the carbon reserves in lignotubers. López et al. [80] found that, 10 years after a drought event, starch stocks in the lignotubers have recovered to half the former amount. In a study [80], it was pointed out that more frequent droughts may provoke a progressive depletion of carbon reserves and a loss of resilience in Mediterranean resprouter species.

Concerning the recovery by sexual reproduction processes (i.e., by seeds), increased drought reduces acorn production in *Q. ilex* [81]. The effects of drought on seed production and germinative ability may be different according to the sensitivity of each species to water stress [64]. Drought, moreover, can modify the local conditions of the soil by affecting the mycorrhizal status and thus the establishment of seedlings [82].

The combination of sexual and vegetative regeneration, together with individual and species competition processes, drives the dynamic of vegetation after a climatic impact. An analysis of the situation 6 years after a severe drought event in the Iberian peninsula [14] evidenced that the loss of canopy cover, mainly composed by *Q. ilex,* was not still recovered, and the more drought-tolerant species *P. latifolia* tended to increase its relative abundance in the upper vegetation canopy. In addition, early successional shrubs, such as *Cistus* sp.pl., increased their abundance in the understorey.

6. Which Future for Mediterranean Vegetation?

The analysis of literature, together with our surveys and field observations, evidenced that severe drought events selectively impact the Mediterranean woody species. The Mediterranean basin is considered a “biodiversity hotspot” [83], characterized by forests and shrublands with many species with different phylogeny and evolutionary history. The different sensitivity of the current Mediterranean species to drought may depend on the region of species origin and subsequently from the adaptation to the climatic evolution [52]. In the Mediterranean region, the genetic richness of the plant communities is an essential resource that makes possible the evolution of ecosystems in different ways, in accordance with the change of the main environmental drivers. Increasing dryness may favor the best adapted species, which originated in drier regions, or under typical Mediterranean climate, namely in the Quaternary period [42]. For these reasons, we can hypothesize that instead of latitudinal (South to North) or altitudinal (lowland to upland) migrations [84], Mediterranean forest ecosystems may respond to climate change by modulating their composition and structure with the genetic resources already present in loco. Possible interventions of “assisted migration” [85], to assure land cover and soil protection, should take into consideration taxa and provenances that originated from the driest regions of Mediterranean and summer deciduous species.

Experimental evidences [86] suggest that *Q. ilex* seedlings that originated from mother trees of different provenances show distinct behaviors and sensitivity to drought stress in relation to the ecology of the origin population. These findings indicate a local evolution with differentiation of distinct ecotypes, or the triggering of mechanisms of epigenetic responses and trans-generational memory [87–89]. Epigenetic regulation is an important mechanism for plant adaptation to changing environment without DNA alteration. Plants cannot adapt their behavior or migrate instantly, so phenotypic plasticity and epigenetic responses are crucial for the survival of plants [90].

7. Conclusions

The impact of climate change, including extreme heat and drought waves, on Mediterranean evergreen forest vegetation and the subsequent recovery or changes in composition, structure and ecosystem functioning, is a current environmental issue that can potentially interest wider areas. It is essential, therefore, to address researches on Mediterranean ecosystems' vulnerability to environmental impacts and to catch the attention of forest managers and stakeholders on what is happening and the future risks. Below we list the most relevant points to be addressed in future researches.

First, we need to better understand the physiological processes of the vegetative regeneration, the role of NSC and the resilience of trees severely damaged by drought. The relevant question is how many years after the stress event and which climatic and environmental conditions are needed to restore the NSC reserves and the full functionality of plants. According to [91], from the beginning of the 21st century, severe drought events have been recurrent every 4–5 years in Central Italy.

Secondly, the sexual regeneration poses further problems, concerning the quantity and quality of seed produced by damaged plants. A specific question is connected to a possible memory of the stress [92] as a factor that improves the epigenetic adaptation to the new environment.

Then, it is necessary to investigate the different sensitivities to drought of a wider range of Mediterranean woody species, to define the limits of the stress that can be tolerated even by the most resistant species, and the distinct mechanisms to withstand with drought [93,94].

Finally, extreme drought events bring the vegetational dynamics back to the initial stages. The natural processes of forest reconstruction must be observed in long term permanent areas, by developing and integrating the forest monitoring networks already existing [6,95]. Changes in vegetational assemblages and structure may lead to changes in ecological and landscape characteristics and values, with corresponding ecosystem services, including bio-economic aspects and touristic fruition. That requires a redefinition of management criteria and a pro-active silviculture to make the ecosystems more resilient.

Author Contributions: F.B. wrote the first draft; M.P. wrote, reviewed and editing the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Conflicts of Interest: The Authors declare no conflict of interest.

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