frontiers in Forests and Global Change

ORIGINAL RESEARCH
published: 14 November 2019
doi: 10.3389/ffgc.2019.00074

Widespread Crown Defoliation After a Drought and Heat Wave in the Forests of Tuscany (Central Italy) and Their Recovery—A Case Study From Summer 2017

Martina Pollastrini[1]*, *Nicola Puletti*[2], *Federico Selvi*[1], *Giovanni Iacopetti*[1] and *Filippo Bussotti*[1]

[1] Department of Agriculture, Food, Environment and Forestry (DAGRI), University of Florence, Florence, Italy, [2] Research Centre for Forestry and Wood, Council for Agricultural Research and Economics (CREA), Trento, Italy

An anomalous event of drought and heat occurred in central Italy during the summer of 2017. Based on the SPI (Standardized Precipitation Index) and data from the European Space Agency, this event started in November 2016 and was characterized by a strong reduction of precipitation and soil moisture, especially in lowland areas with Mediterranean climate. The aim of this case report were to describe the impact of this event on representative forest communities in central Italy, to analyze the different responses of deciduous and evergreen tree and shrub species in contrasting environmental conditions and to assess their subsequent capacity of recovery or, if not, mortality. Trees suffered severe impacts consisting of widespread crown defoliation, leaf desiccation, crown dieback and whole tree mortality. Deciduous tree species (*Fagus sylvatica*, *Quercus pubescens*, *Quercus cerris*) shed their leaves during the summer, but apical buds and twigs were preserved. This allowed these species to produce new shoots in the following year (2018) and to restore the canopy closure of the stands. Mediterranean evergreen broadleaves, such as *Quercus ilex* and *Phillyrea latifolia* suffered of total or partial crown desiccation with wilting leaves and branch dieback. These species partially resprouted in 2018 from axillary and latent buds. The case presented here is discussed within the wider context of the impacts of climate change on Mediterranean forests. Future research directions should include an effective forest monitoring system that combines terrestrial and remote sensing surveys, *ad hoc* field climate change experiments and silvicultural trials from the perspective of proactive management for the adaptation of forests to future climatic conditions.

Keywords: defoliation, drought, heatwave, extreme event, Mediterranean forests, resilience, tree mortality

OPEN ACCESS

Edited by:
Adrià Barbeta,
INRA Centre
Bordeaux-Aquitaine, France

Reviewed by:
Dominik Sperlich,
University of Freiburg, Germany
Cate Macinnis-Ng,
The University of Auckland,
New Zealand

***Correspondence:**
Martina Pollastrini
martina.pollastrini@unifi.it

Specialty section:
This article was submitted to Forest Hydrology, a section of the journal Frontiers in Forests and Global Change

Received: *19 July 2019*
Accepted: *30 October 2019*
Published: *14 November 2019*

Citation:
Pollastrini M, Puletti N, Selvi F, Iacopetti G and Bussotti F (2019) Widespread Crown Defoliation After a Drought and Heat Wave in the Forests of Tuscany (Central Italy) and Their Recovery—A Case Study From Summer 2017. Front. For. Glob. Change 2:74. doi: 10.3389/ffgc.2019.00074

BACKGROUND

Events of extensive tree dieback and mortality related to drought have been detected across the world and described in several papers (Gitlin et al., 2006; Allen et al., 2010, 2015; Anderegg et al., 2013, 2015; Choat et al., 2018). Increasing drought conditions, together with rising temperatures, weaken trees making them prone to insect and pathogen attacks that in some cases are the

ultimate cause of tree death (Dobbertin et al., 2007; Wermelinger et al., 2007; Anderegg et al., 2015; McDowell et al., 2019). In Europe, a large body of literature deals with the dieback of Scots pine (*Pinus sylvestris* L.) at the southernmost portion of its range (see Bussotti et al., 2014, 2015 for review), especially in Valais, Switzerland (Rigling et al., 2013) and Spain (Vilà-Cabrera et al., 2011). Concerning the broadleaf tree species, the so-called "oak decline" is an issue addressed in Europe (Thomas et al., 2002) from the 80s of the twentieth century and is considered the result of the interactive action of drought stress and weakness parasites.

Evergreen sclerophyllous tree and shrub species of the Mediterranean areas in Southern Europe are commonly considered resistant to drought and other environmental stressors typical of this region, such as high temperatures, high solar irradiation, UV radiations etc. (Bussotti et al., 2014). In recent years, however, these forests were subject to both continuous increase of drought and temperature and to recurrent extreme episodes with waves of heat and dry spells, as reported from the Iberian peninsula (Lloret et al., 2004; Carnicer et al., 2011; Camarero et al., 2015a,b; Peñuelas et al., 2018). The Mediterranean sclerophyllous forests can restore the "before event" conditions (resilience) by regenerating the crowns due to the resprouting ability of axillary and suppressed buds at the stump and branches (Del Tredici, 2001). This ability evolved in plants subjected to recurrent environmental disturbances, like fire and severe drought (Pausas and Keeley, 2014) and represents a strategy to rapidly restore the closure of the canopies. Recent research underlines the role of non-structural carbohydrates in plant growth (Mason et al., 2014): after the loss of the shoot tip, sugars are rapidly redistributed over large distances between different parts and organs of the plant and accumulated in axillary buds within a timeframe compatible with the resumption of their activity. Causing the depletion of non-structural carbohydrates in plant tissues, however, recurrent drought episodes can dramatically reduce the resprouting ability and the resilience of the whole plant (Barbeta and Peñuelas, 2016). In turn, this is likely to result in a shift from forest to Mediterranean steppe if severe drought will persist in the long-term (Jacobsen and Pratt, 2018).

In Italy, cases of severe tree decline and mortality induced by long periods of drought stress have been documented on oak and pine species (Ragazzi et al., 1989; Castagneri et al., 2015; Colangelo et al., 2017; Gentilesca et al., 2017), but until now there were no reports about the impacts of drought at ecosystem level, affecting contemporaneously a large number of woody and herbaceous species coexisting in a forest communities. No similar event had been previously documented for Italy. The 2017 summer drought impact was observed in the Italian ICP Forests Level I survey (Iacopetti et al., 2019), although the structure of this monitoring network fails to capture and describe in detail events at spatial local scale (Bussotti and Pollastrini, 2017). With the present report, we give original information about this case of tree dieback and mortality in central Italy to contribute to a more comprehensive understanding of the consequences of recurring extreme heat and drought waves in the Mediterranean region. Resilience processes, such as those allowing the restoration of the conditions before the event, were also considered. Finally, indications for the future direction of research are provided.

CASE DESCRIPTION

Forest Types, Climate and Drought Conditions

Half of the surface of Tuscany is covered by forests (1 M ha, data from Forest Inventory of Tuscany, Hoffman et al., 1998). The main forest types are distributed along an altitudinal (from low to high altitude) and a geographic (from southwest to northeast) gradient. These are (a) evergreen Mediterranean forests with *Quercus ilex* L. (holm oak) as the dominant species in coastal and sub-coastal areas (240,000 ha); (b) supra-Mediterranean thermophilous deciduous forests with deciduous oaks (*Quercus cerris* L., Turkey oak, covering 240,000 ha; *Quercus pubescens* Willd., downy oak, 127,000 ha) and *Castanea sativa* Mill. (sweet chestnut, 177,000 ha) as the dominant tree species in the hilly areas in central Tuscany, from 300 to 800 m a.s.l.; and (c) mesophilous deciduous forests with *Fagus sylvatica* L. (beech) as the dominant species (76,000 ha) at the highest altitudes in the mountain areas (800–1,200 m a.s.l.). Along this altitudinal gradient, there is a strong variation from Mediterranean to montane climate type (Rapetti and Vittorini, 2012). Average annual precipitation and annual temperature range from 1,500 to 2,500 mm and from 7°C to 10°C, respectively, in the mountain areas and from 600 to 850 mm and 13°C to 17°C, respectively, in the Mediterranean areas.

Temperatures and summer heatwaves have increased in recent decades, and severe drought episodes are recurring every 4–5 years; the last ones occurred in the years 2011–2012 and 2016–2017 (Magno et al., 2018). This latter event was characterized by strong decline in soil moisture, documented by the European Space Agency (https://phys.org/news/2017-09-italy-drought-space.html). Soil water deficit began during spring, and partially in the preceding winter (Magno et al., 2018). **Figures 1A–C** show the patterns of monthly precipitation and temperatures (average of maximum) during 2017, compared with the means of the last 30 years, in three localities of Tuscany representative of coastal areas (Follonica, Lat. 47.54 N., Long. 16.44 E; Alt. 15 m a.s.l.), hilly areas (Gaiole in Chianti, Lat. 48.14 N., Long. 16.95 E; Alt. 360 m a.s.l.) and mountain areas (Vallombrosa, Lat. 48.45, Long. 17.05; Alt. 980 m a.s.l.). Increase of temperatures and drop of precipitation are evident in spring and summer months in all sites. Frequent temperature peaks over 40°C were also registered. Drought conditions were characterized using the Standardized Precipitation Index (SPI; Guttman, 1998, 1999). This index uses historical precipitation data at a given location to develop a probability of precipitation that can be computed at different timescales. SPI is calculated on a time series of 30 years of data and has an intensity scale (0 to 3), in which both positive and negative values correspond, respectively, to wet and dry events. Whereas the value 0 indicates no anomalies, drought conditions occur when SPI $= -1$ (moderate drought). The

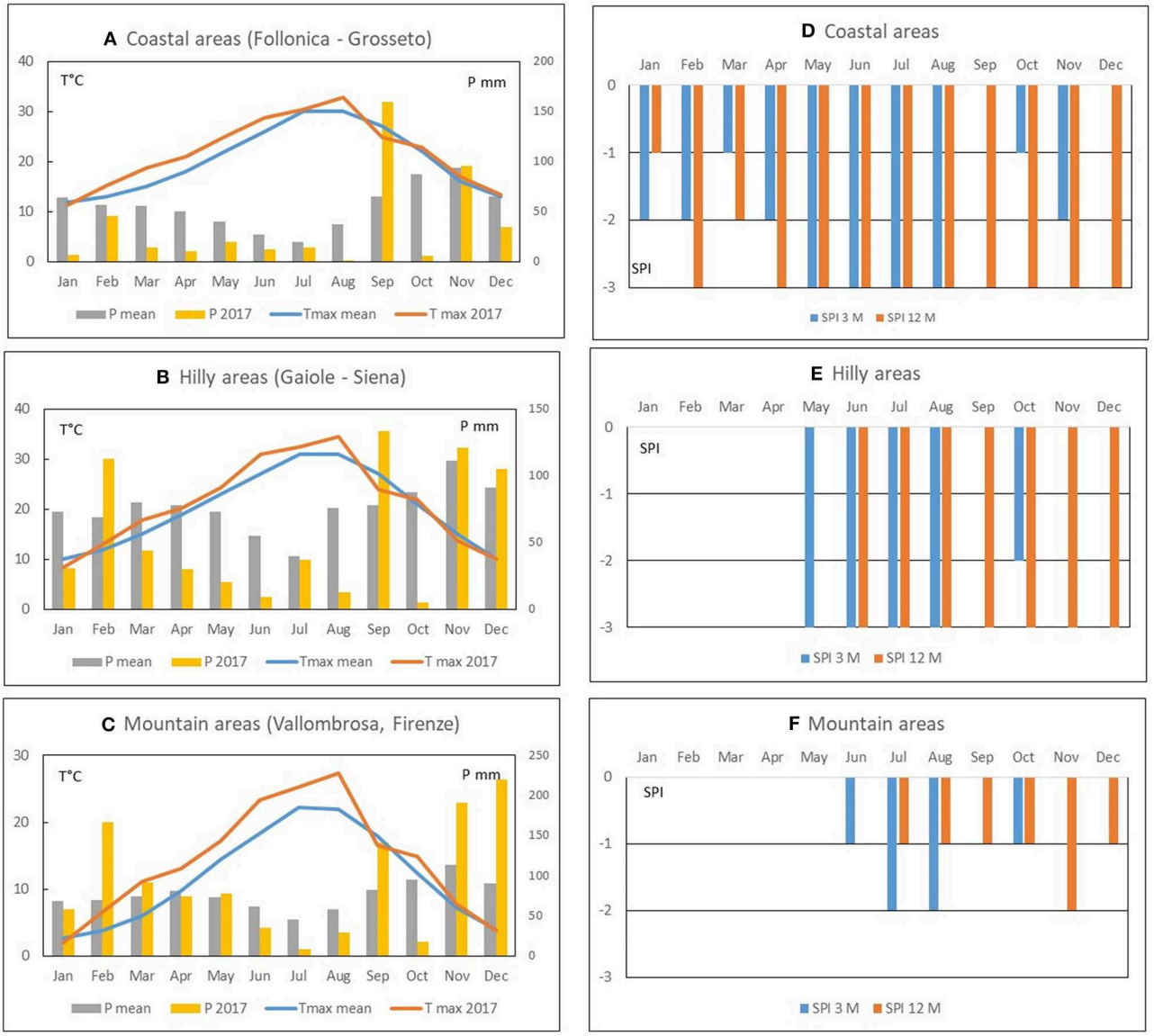

FIGURE 1 | Left: Annual pattern of monthly precipitations (Pmm, total monthly, columns) and temperatures (T°C, mean of daily maximum, lines) in coastal **(A)**, hilly **(B)**, and mountain **(C)** areas of Tuscany. P and T are presented as average of the last 30 years (mean) and as values of the critical year (2017). The data were collected from http://www.sir.toscana.it/ricerca-dati. Right: Annual pattern (2017) of SPI (Standardized Precipitation Index) in coastal **(D)**, hilly **(E)**, and mountain **(F)** areas of Tuscany. SPI is reported for short (3 months) and long (12 months) periods. Negative values indicate drought conditions. The scale indicates moderate (−1), severe (−2), and extreme (−3) drought. Absence of anomalies is indicated with 0 (no bar). The data were collected from: http://www.lamma.rete.toscana.it/archivio-bollettini-siccit.

values −2 and −3 indicate, respectively, severe and extreme drought. The SPI values reported in **Figures 1D–F**, presented for short (3 months) and long (12 months) periods, are an elaboration of the data reported in the "drought bulletins" for Tuscany available online (http://www.lamma.rete.toscana.it/archivio-bollettini-siccit). Coastal areas suffered long-term (12 months) and short-term (3 months) drought stress from the very beginning of 2017, whereas stress conditions started between the late spring and early summer in hilly and mountain areas.

Description of the Impact of Drought on Forests

Preliminary visual field observations were carried out from mid-August to October 2017 on 118 observation points randomly selected between drought-damaged and non-damaged forest stands on the mountain, supra-Mediterranean and Mediterranean forests to obtain a first description of the impacts. In each point we carried out a summary description of the plant species (trees, shrubs and perennial herbs) affected by leaf loss, discoloration and desiccation, as well crown dieback, branch

desiccation, and the possible presence of fungal and pest attacks. Physical site features such as altitude, bedrock, aspect and slope were included in such description. Deciduous broadleaved trees (beech dominated forests in the mountain and deciduous oaks dominated forests in hilly areas) were affected by leaf desiccation and defoliation starting from the second half of July. *Fagus sylvatica* trees were subjected to a leaf early senescence and shedding across the mountain areas of Tuscany. *Q. pubescens* was strongly defoliated, especially on the hills with calcareous soil in central Tuscany, where this species was prone to water depletion and high soil temperature. In the shrub layer, we found desiccation on *Spartium junceum* L. Severe impacts were also observed on the Mediterranean evergreen vegetation, especially on *Q. ilex* coppices (**Figures 2A,B**) growing in the southern coastal areas. All the evergreen Mediterranean shrub species (*Phillyrea latifolia* L., *Arbutus unedo* L., *Juniperus oxycedrus* L., *Myrtus communis* L.., *Erica* sp. pl.) with the only exception of *Pistacia lentiscus* L., were affected by drought. In *Q. ilex*, high forest desiccation occurred on individual trees depending on local micro-environmental conditions. No fungal infections or pest attacks connected to such dieback were detected. The subsequent autumn and winter months (2017–2018) were wet and rainy (**Figure 1**), favoring a substantial recovery from drought. In June 2018, the foliar mass of *F. sylvatica* forests appeared almost completely restored (data confirmed by airborne observations, Puletti et al., 2019). *Quercus pubescens* showed a similar pattern. After the 2017 drought, the organs (stem and branches) of *F. sylvatica* and *Q. pubescens* remained alive and were able to resprout from the apical buds in spring 2018. The severe dieback of branches and twigs, as well the persistence of dead leaves on the crowns, made visible the impact of the 2017 drought in *Q. ilex* dominated forests also 1 year after the event.

A more accurate analysis of the effects of extreme summer events on the vegetation was carried out on Mediterranean evergreen forests since they were subjected to stronger and long-term drought stress with respect to the deciduous forests (**Figures 1A–C**). The purpose of this analysis was to provide baseline data and to start following the subsequent phases of recovery or decline in the long-term. Four permanent plots, from 100 to 200 m^2 depending on the structure of the forests, were established in October 2017 in unmanaged stands (latest interventions date back to the half of the past century) within the nature reserves of Caselli (Pisa, Lat. 43.23, Long. 10.68, Alt. 55 m a.s.l.) and Casole Val d'Elsa (Pisa, Lat. 43.37, Long. 11.01, Alt. 60 m a.s.l.), both with Mediterranean climates (see **Figure 1A**). Plots were selected in high forests and old coppices (70–80 years old), where *Q. ilex* and *Phillyrea latifolia* were the dominant species and *Arbutus unedo*, *Erica arborea*, *Viburnum tinus* L. were the most common associated species. The number of plants per ha ranges from 575 to 3,475, and the basal area ranges from 12 to 31 m^2 ha^{-1}, which is common in Mediterranean forests in Italy. In each plot, all woody plants with DBH (diameter at breast height) >3 cm were numbered and measured (DBH and height). Then, defoliation (i.e., loss of leaves as compared to a reference tree with a completely foliated crown) and damaged and dead leaves (partially and completely dry leaves, respectively) were visually evaluated for each plant by well-trained crews, in classes of severity of 20% (ICP Forests guidelines, Eichhorn et al., 2016 modified). In June 2018, a second measurement on the same plants was carried out focusing on the amount of new shoots by suppressed and adventitious buds (i.e., resprouting capacity) on the distinct parts of plant (crown, stem and stump). The same scoring system to the previous one was used. Data analysis includes the calculation of mean and standard deviation of all the measured attributes, as well their correlations by using the non-parametric test of Spearmann *r*. All the analyses were performed with Statistica 7.0 (Statsoft, Tulsa, OK, USA) and R (R Core Team, 2016). The intensity of defoliation of *P. latifolia* and *Q. ilex* were similar across sites (30–40%). The amount of dead leaves was significantly higher in *Q. ilex* in both sites (**Table 1**), whereas partially damaged leaves were more abundant at Casole d'Elsa than Caselli in both species. The resprouting capacity from the different parts of the plant (crown, stem, stump, and total)

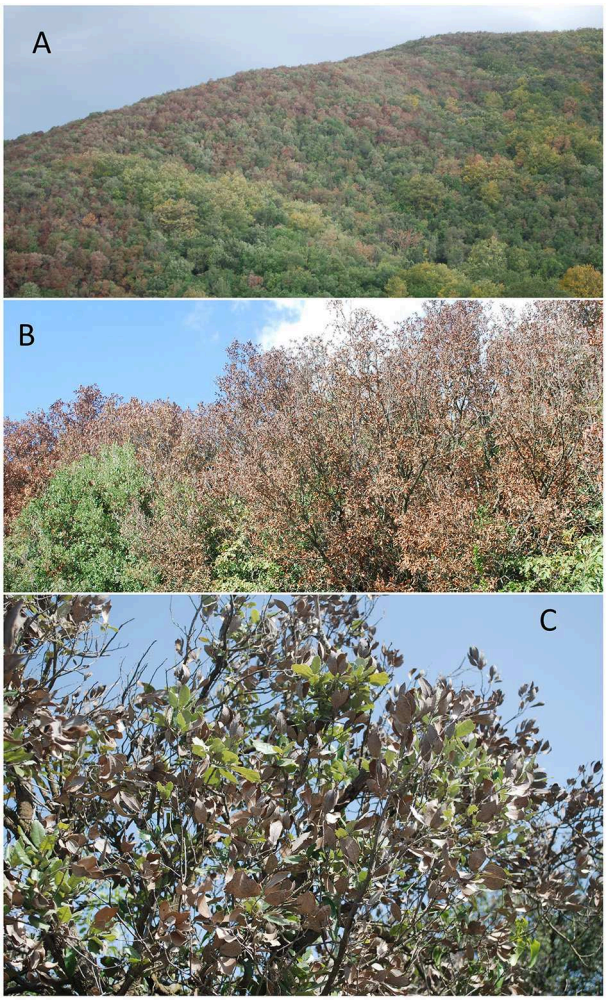

FIGURE 2 | Images of drought impact and recovery on Mediterranean vegetation in Tuscany (Italy) after the drought and heat event of summer 2017. **(A)** Impact at landscape level (November 2017). **(B)** Crown dieback on *Quercus ilex* (November 2017); **(C)** Partial crown recovery on *Quercus ilex* (July 2018).

TABLE 1 | Drought-induced damage and recovery parameters of the most abundant plant species *Phillyrea latifolia* and *Quercus ilex* in 2018 in the permanent plots at Caselli and Casole d'Elsa (*n* = number of the assessed trees at each site).

	Phillyrea latifolia				*Quercus ilex*			
	(Caselli *n* = 23)		(Casole *n* = 56)		(Caselli *n* = 29)		(Casole *n* = 32)	
	Mean	**St.dev.**	**Mean**	**St.dev.**	**Mean**	**St.dev.**	**Mean**	**St.dev.**
N/Ha	575		3,457		725		1,975	
DBH (cm)	6.17	±2.32 B	5.45	±1.56 B	10.91	±3.25 A	10.74	±3.68 A
H (m)	4.22	±1.42 B	4.40	±1.03	7.17	±2.00 aA	5.51	±0.78 b
Defoliation (%)	39	±15	32	±21	35	±15	40	±19
Dead leaves (%)	11	±12 B	4	±9 B	43	±28 A	32	±26 A
Damaged leaves (%)	5	±9 b	15	±9 a	2	±6 b	11	±15 a
Crown resp. (%)	14	±17	7	±11	6	±11	16	±17
Stump resp. (%)	3	±8 bB	6	±10 aB	12	±14 A	18	±15 A
Stem resp. (%)	2	±7 bB	11	±16 aB	10	±13 A	16	±12 A
Total resp. (%)	34	±43	38	±41 B	43	±37 b	77	±42 aA

DBH, Diameter at Breast Height; H, Height; Defoliation, loss of leaves. Dead leaves, completely dry leaves. Damaged leaves, partially dry leaves. Crown, Stump, Stem and Total resp., resprouting from dormant and adventitious buds in the crown, stump, stem and in total, respectively. Different letters indicate significant differences (P < 0.05). Capital letters indicate differences between species at the same site; lower cases indicate the differences on the same species between different sites (P < 0.05).

was in general higher in *Q. ilex* than in *P. latifolia*. Overall, the amount of dead leaves showed significantly positive correlations ($P < 0.05$) with tree size parameters (diameter and height, **Figure 3**), whereas the partially damaged leaves showed the opposite behavior. Tree diameter was positively related ($P < 0.05$) to resprouting from the stem (epicormic shoots) and stump.

DISCUSSION AND CONCLUSIONS

The drought and heatwave in 2017 had a different impact on deciduous and evergreen forest tree species. Deciduous species (namely the *F. sylvatica* and *Q. pubescens* dominated forests) lose their leaves early in the summer to avoid water loss and desiccation of branches, whereas evergreen sclerophyllous species (*Q. ilex* dominated forests) maintain their leaves so enhancing water loss and branch desiccation. These different behaviors may be partially determined by intrinsic characteristics of the species, but also by the level of drought experienced in the summer, that was higher in the Mediterranean areas.

In deciduous tree species at intermediate (hilly) and high (mountain) elevation, twigs and buds remained alive and the crowns were fully regenerated by the activity of the terminal buds in the following year (2018). The loss of leaves during the growing season, however, may harm the budget and dynamics of the stored carbohydrates (D'Andrea et al., 2019), making trees more sensitive to additional stress factors (Hartmann and Trumbore, 2016). In sclerophyllous species at the Mediterranean areas, subjected to branch desiccation, the crowns are restored with of the activity of the adventitious buds. In this case the recovery processes are slow, and the evidences of the drought impact were detected in the year 2018 with a remote sensing survey (Puletti et al., 2019).

In the first months after the drought event, evergreen trees retain the dead leaves, so, at least in the short period, the amount of dry leaves on the plant is a better indicator of drought impact than defoliation. Defoliation levels were close to those observed in previous surveys carried out on Mediterranean forests in Tuscany, on forests not affected by drought (Pollastrini et al.,

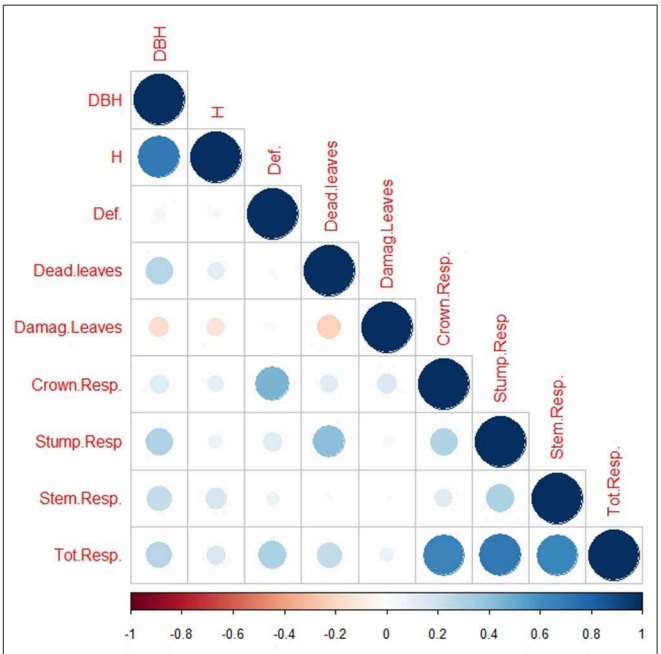

FIGURE 3 | Correlation matrix (non-parametric test, Spearman *r*) between the variables assessed in the permanent plots for *Quercus ilex* and *Phillyrea latifolia* together. DBH, Diameter at Breast Height; H, Height; Def., defoliation; Dead.leaves, dead leaves (completely dry leaves); Damag.Leaves, damaged leaves (partially dry leaves); Crown.Resp., Stump.Resp., Stem.Resp., Tot.Resp., resprouting from dormant and adventitious buds from the crown, stump, stem and in total. Bar indicates the *r* values.

2016). The results presented in **Table 1** suggest therefore that *Q. ilex*, with a significantly higher amount of dead leaves, is more drought sensitive than *P. latifolia*, in line with a large body of evidence on the comparative behavior of these two species under stress conditions (Peñuelas et al., 1998, 2000; Ogaya and Peñuelas, 2003; Ogaya et al., 2003; Barbeta et al., 2013; Rosas et al., 2013; Sperlich et al., 2015). Drought impact was greater on the largest trees (Grote et al., 2016). The resprouting capacity of defoliated trees is higher in trees with high DBH (Matula et al., 2019), but it declines with age (Clarke et al., 2013). According to Crouchet et al. (2019), the impact of the drought is higher on the dense stands and affects the less competitive trees, including smaller and older plants. Mediterranean coppices are very complex and dynamic systems (Fabbio, 2016) rich in diversity, in which increasing drought conditions may affect competition processes with changes in structure and composition. Rapidly changing climatic conditions can, therefore, lead to reaching new ecological equilibriums.

The extreme heat and drought wave that occurred in Tuscany in summer 2017 was an occurrence within the wider context of the fate of the South European forest vegetation under climate change (Bussotti et al., 2014). Cumulative episodes of extreme drought may compromise the resilience of the ecosystems (Lloret et al., 2011) and may damage the long-term performance and survival of Mediterranean evergreen forests (Galiano et al., 2012; Peguero-Pina et al., 2018). Extreme climatic events, rather than trends (Jentsch et al., 2007), drive forest dieback and mortality and can result in dramatic changes at the landscape level. On the contrary, a gradual shift of climate parameters is supposed to promote the acclimation of tree species within the limits of their phenotypic plasticity (Nicotra et al., 2010).

The event described in this report invites us to pay more attention to the impact of climate change on the forests of the Mediterranean region. We underline the importance to pursue long-term monitoring with terrestrial and remote sensing techniques, experimental studies in the field and silvicultural trials (Giuggiola et al., 2015; Vilà-Cabrera et al., 2018). The questions to be addressed in future research should concern: (a) the geographic extent and intensity of the climate impacts and the identification of the most fragile forest structures and species assemblages; (b) the re-organization of the current forest monitoring networks (Bussotti et al., 2018) to make them able to capture drought impacts on forests at regional levels; (c) the establishment of permanent study areas along to vegetational and ecological gradients, to assess the impacts of drought at stand level and the subsequent ecological dynamics; and (d) the most effective silvicultural strategies to be adopted in forests subject to drought risks, before and after drought events.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

MP was responsible for the general design of the research, field assessment and data analysis. NP carried out the remote sensing analyses. FS contributed to the design of the research and field assessment. GI collaborated to field activities. FB participated to the design of the research and wrote the manuscript. All the authors contributed to the discussion of the results, read and approved the manuscript.

FUNDING

This research was funded and carried out within SMART4Action LIFE+ project Sustainable Monitoring and Reporting to Inform Forest and Environmental Awareness and Protection LIFE13 ENV/IT/000813. The work was supported also by a grant of the Research Doctorate in Agricultural and Environmental Science, XXXII course, University of Firenze.

ACKNOWLEDGMENTS

We would like to thank Dr. Davide Bettini (Unione Comuni Alta Val di Cecina, Pisa) and Leonardo Tonveronachi (Research Centre for Forestry and Wood, Council for Agricultural Research and Economics, CREA) for his helpful support in field surveys. We also thank Dr. Henrik Hartmann (Max Planck Institute for Biogeochemistry, Jena, Germany) for his encouragement and suggestions.

REFERENCES

Allen, C. D., Breshears, D. D., and McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6, 129, 1–55. doi: 10.1890/ES15-00203.1

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., et al. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 259, 660–684. doi: 10.1016/j.foreco.2009.09.001

Anderegg, W. R., Hicke, J. A., Fisher, R. A., Allen, C. D., Aukema, J., Bentz, B., et al. (2015). Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol.* 208, 674–683. doi: 10.1111/nph.13477

Anderegg, W. R. L., Kane, J. M., and Anderegg, L. D. L. (2013). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Chang.* 3, 30–36. doi: 10.1038/nclimate1635

Barbeta, A., Ogaya, R., and Peñuelas, J. (2013). Dampening effects of long-term experimental drought on growth and mortality rates of a Holm oak forest. *Glob. Change Biol.* 19, 1–12. doi: 10.1111/gcb.12269

Barbeta, A., and Peñuelas, J. (2016). Sequence of plant responses to droughts of different timescales: lessons from holm oak (*Quercus ilex*) forests. *Plant Ecol. Div.* 9, 321–338. doi: 10.1080/17550874.2016.1212288

Bussotti, F., Ferrini, F., Pollastrini, M., and Fini, A. (2014). The challenge of Mediterranean sclerophyllous vegetation under climate change: from acclimation to adaptation. *Environ. Exp. Bot.* 103, 80–98. doi: 10.1016/j.envexpbot.2013.09.013

Bussotti, F., and Pollastrini, M. (2017). Observing climate change impacts on European forests: what works and what does not in ongoing long-term monitoring networks. *Front. Plant Sci.* 8:629. doi: 10.3389/fpls.2017.00629

Bussotti, F., Pollastrini, M., and Gessler, A., Luo Z.-B. (2018). Experiments with trees: from seedlings to ecosystems. *Environ. Exp. Bot.* 152, 1–6. doi: 10.1016/j.envexpbot.2018.04.012

Bussotti, F., Pollastrini, M., Holland, V., and Brüggemann, W. (2015). Functional traits and adaptive capacity of European forests to climate change. *Environ. Exp. Bot.* 111, 91–113. doi: 10.1016/j.envexpbot.2014.11.006

Camarero, J. J., Franquesa, M., and Sangüesa-Barreda, G. (2015a). Timing of drought triggers distinct growth responses in holm oak: implications to predict warming-induced forest defoliation and growth decline. *Forests* 6, 1576–1597. doi: 10.3390/f6051576

Camarero, J. J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., and Vicente-Serrano, S. M. (2015b). To die or not to die: early-warning signals of dieback in response to a severe drought. *J. Ecol.* 103, 44–57. doi: 10.1111/1365-2745.12295

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., and Peñuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* 108, 1474–1478. doi: 10.1073/pnas.1010070108

Castagneri, D., Bottero, A., Motta, R., and Vacchiano, G. (2015). Repeated spring precipitation shortage alters individual growth patterns in Scots pine forests in the Western Alps. *Trees* 29, 1699–1712. doi: 10.1007/s00468-015-1250-z

Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., and Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature* 558, 531–539. doi: 10.1038/s41586-018-0240-x

Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., et al. (2013). Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytol.* 197, 19–35. doi: 10.1111/nph.12001

Colangelo, M., Camarero, J. J., Battipaglia, G., Borghetti, M., De Micco, V., Gentilesca, T., et al. (2017). A multi-proxy assessment of dieback causes in a Mediterranean oak. *Tree Physiol.* 37, 617–631. doi: 10.1093/treephys/tpx002

Crouchet, S. E., Jensen, J., Schwartz, B. F., and Schwinning, S. (2019). Tree mortality after a hot drought: distinguishing density-dependent and -independent drivers and why it matters. *Front. For. Glob. Change* 2:21. doi: 10.3389/ffgc.2019.00021

D'Andrea, E., Rezaie, N., Battistelli, A., Gavrichkova, O., Kuhlmann, I., Matteucci, G., et al. (2019). Winter's bite: beech trees survive complete defoliation due to spring late-frost damage by mobilizing old C reserves. *New Phytol.* 224, 625–631. doi: 10.1111/nph.16047

Del Tredici, P. (2001). Sprouting in temperate trees: a morphological and ecological review. *Bot. Rev.* 67, 121–140. doi: 10.1007/BF02858075

Dobbertin, M., Wermelinger, B., Bigler, C., Bürgi, M., Carron, M., Forster, B., et al. (2007). Linking increasing drought stress to Scots pine mortality and bark beetle infestations. *Sci. World J.* 7, 231–239. doi: 10.1100/tsw.2007.58

Eichhorn, J., Roskams, P., Potocic, N., Timermann, V., Ferretti, M., Mues, V., et al. (2016). "Part IV: visual assessment of crown condition and damaging agents". In *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*, ed UNECE ICP Forests Programme Coordinating Centre (Eberswalde: Thünen Institute of Forest Ecosystems), 54. Available online at: http://www.icp-forests.org/Manual.htm]. ISBN: 978-3-86576-162-0

Fabbio, G. (2016). Coppice forests, or the changeable aspect of things, a review. *Ann. Silv. Res.* 40, 108–132. doi: 10.12899/asr-1286

Galiano, L., Martinez-Vilalta, J., Sabat,é, S., and Lloret, F. (2012). Determinants of drought induced effects on crown condition and their relationship with depletion of carbon reserve in a Mediterranean holm oak forest. *Tree Physiol.* 32, 478–489. doi: 10.1093/treephys/tps025

Gentilesca, T., Camarero, J. J., Colangelo, M., Nolè, A., and Ripullone, F. (2017). Drought induced oak decline in the western Mediterranean region: an overview on current evidences, mechanisms and management options to improve forest resilience. *iForest* 10, 796–806. doi: 10.3832/ifor2317-010

Gitlin, A. R., Sthultz, C. M., Bowker, M. A., Stumpf, S., Paxton, K. L., Kennedy, K., et al. (2006). Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conserv. Biol.* 20, 1477–1486. doi: 10.1111/j.1523-1739.2006.00424.x

Giuggiola, A., Ogée, J., Rigling, A., Gessler, A., Bugmann, H., and Treydte, K. (2015). Improvement of water and light availability after thinning at a xeric site: which matters more? A dual isotope approach. *New Phytol.* 210, 108–121. doi: 10.1111/nph.13748

Grote, R., Gessler, A., Hommel, R., Poschenrieder, W., and Priesack, E. (2016). Importance of tree height and social position for drought-related stress on tree growth and mortality. *Trees* 30:1467. doi: 10.1007/s00468-016-1446-x

Guttman, N. B. (1998). Comparing the palmer drought index and the standardized precipitation index. *J. Am. Wat. Res. Ass.* 34, 113–121. doi: 10.1111/j.1752-1688.1998.tb05964.x

Guttman, N. B. (1999). Accepting the standardized precipitation index: a calculation algorithm. *J. Am. Wat. Res. Ass.* 35, 311–322. doi: 10.1111/j.1752-1688.1999.tb03592.x

Hartmann, H., and Trumbore, S. (2016). Understanding the roles of nonstructural carbohydrates in forest trees - from what we can measure to what we want to know. *New Phytol.* 211, 386–403. doi: 10.1111/nph.13955

Hoffman, A., Goretti, D., Merendi, A., Tabacchi, G., Vignoli, M., and Bernetti, G. (eds.). (1998). *L'Inventario Forestale. Serie: Boschi e Macchie della Toscana*. Regione Toscana – Giunta Regionale, 220.

Iacopetti, G., Bussotti, F., Selvi, F., Maggino, F., and Pollastrini, M. (2019). Forest ecological heterogeneity determines contrasting relationships between crown defoliation and tree diversity. *For. Ecol. Manage.* 448, 321–329. doi: 10.1016/j.foreco.2019.06.017

Jacobsen, A. L., and Pratt, R. B. (2018). Extensive drought-associated plant mortality as an agent of type-conversion in chaparral shrublands. *New Phytol.* 219, 498–504. doi: 10.1111/nph.15186

Jentsch, A., Kreyling, J., and Beierkuhnlein, C. (2007). A new generation of climate change experiments: events, not trends. *Front. Ecol. Environ.* 5, 315–324. doi: 10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2

Lloret, F., Keeling, E. G., and Sala, A. (2011). Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120, 1909–1920. doi: 10.1111/j.1600-0706.2011.19372.x

Lloret, F., Siscart, D., and Dalmases, C. (2004). Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Glob. Chang. Biol.* 10, 2092–2099. doi: 10.1111/j.1365-2486.2004.00870.x

Magno, R., De Filippis, T., Di Giuseppe, E., Pasqui, M., Rocchi, L., and Gozzini, B. (2018). Semi-automatic operational service for drought monitoring and forecasting in the tuscany region. *Geosciences* 8:49. doi: 10.3390/geosciences8020049

Mason, M. G., Ross, J. J., Babst, B. A., Wienclaw, B. N., and Beveridge, C. A. (2014) Sugar demand, not auxin, is the initial regulator of apical dominance. *Proc. Natl. Acad. Sci. U.S.A.* 111, 6092–6097. doi: 10.1073/pnas.1322045111

Matula, R., Šrámek, M., Kvasnica, J., Uherková, B., Slepička, J., Matoušková, M., et al. (2019). Pre-disturbance tree size, sprouting vigour and competition drive the survival and growth of resprouting trees. *Forest Ecol. Manag.* 446, 71–79. doi: 10.1016/j.foreco.2019.05.012

McDowell, N. G., Grossiord, C., Adams, H. D., Pinzón-Navarro, S., Mackay, D. S., Breshears, D. D., et al. (2019). Mechanisms of a coniferous woodland persistence under drought and heat. *Environ. Res. Lett.* 14:045014. doi: 10.1088/1748-9326/ab0921

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., et al. (2010). Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* 15, 684–692. doi: 10.1016/j.tplants.2010.09.008

Ogaya, R., and Peñuelas, J. (2003). Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: photosynthetic response to experimental drought conditions. *Environ. Exp. Bot.* 50, 137–148. doi: 10.1016/S0098-8472(03)00019-4

Ogaya, R., Peñuelas, J., Martínez-Vilalta, J., and Mangirón, M. (2003). Effect of drought on diameter increment of *Quercus ilex*, *Phillyrea latifolia*, and *Arbutus unedo* in a holm oak forest of NE Spain. *For. Ecol. Manage.* 180, 176–184. doi: 10.1016/S0378-1127(02)00598-4

Pausas, J. G., and Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytol.* 204, 55–65. doi: 10.1111/nph.12921

Peguero-Pina, J. J., Mendoza-Herrer, Ó., Gil-Pelegrín, E., and Sancho-Knapik, D. (2018). Cavitation limits the recovery of gas exchange after severe drought stress in holm oak (*Quercus ilex* L.). *Forests* 9, 443. doi: 10.3390/f9080443

Peñuelas, J., Filella, I., Lloret, F., Siscart, D., and Piñol, J. (1998). Comparative field study of spring and summer leaf gas exchange and photobiology of the Mediterranean trees *Quercus ilex* and *Phillyrea latifolia*. *J. Exp. Bot*. 49, 229–238. doi: 10.1093/jxb/49.319.229

Peñuelas, J., Filella, I., Llusi,à, J., Piñol, J., and Siscart, D. (2000). Effects of a severe drought on water and nitrogen use by *Quercus ilex* and *Phillyrea latifolia*. *Biol. Plant*. 43, 47–53. doi: 10.1023/A:1026546828466

Peñuelas, J., Sardans, J., Filella, I., Estiarte, M., Llusi,à, J., Ogaya, R., et al. (2018). Assessment of the impacts of climate change on Mediterranean terrestrial ecosystems based on data from field experiments and long-term monitored field gradients in Catalonia. *Environ. Exp. Bot*. 152, 49–59. doi: 10.1016/j.envexpbot.2017.05.012

Pollastrini, M., Feducci, M., Bonal, D., Fotelli, M., Gessler, A., Gossiord, C., et al. (2016). Physiological significance of forest tree defoliation: results from a survey in a mixed forest in Tuscany (central Italy). *For. Ecol. Manage*. 361, 170–178. doi: 10.1016/j.foreco.2015.11.018

Puletti, N., Mattioli, W., Bussotti, F., and Pollastrini, M. (2019). Monitoring the effects of extreme drought events on forest health by Sentinel-2 imagery. *J. App. Rem. Sens*. 13:020501, doi: 10.1117/1.JRS.13.020501

R Core Team (2016). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available online at: https://www.R-project.org/

Ragazzi, A., Fedi, I. D., and Mesturino, L. (1989). The oak decline: a new problem in Italy. *Eur. J. For. Path*. 19, 105–110. doi: 10.1111/j.1439-0329.1989.tb00240.x

Rapetti, F., and Vittorini, S. (2012). Note illustrative della carta climatica della Toscana. *Atti Soc. Tosc. Sci. Nat. Mem. Serie A*. 117–119, 41–74. doi: 10.2424/ASTSN.M.2012.27

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., et al. (2013). Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Glob. Chang. Biol*. 19, 229–240. doi: 10.1111/gcb.12038

Rosas, T., Galiano, L., Ogaya, R., Peñuelas, J., and Martinez-Vilalta, R. (2013). Dynamics of non-structural carbohydrate in three Mediterranean woody species Following long-term experimental drought. *Front Plant Sci*. 4:400. doi: 10.3389/fpls.2013.00400

Sperlich, D., Chang, C. T., Peñuelas, J., Gracia, C., and Sabaté, S. (2015). Seasonal variability of foliar photosynthetic and morphological traits and drought impacts in a Mediterranean mixed forest. *Tree Physiol*. 35, 501–520. doi: 10.1093/treephys/tpv017

Thomas, F. M., Blank, R., and Hartmann, G. (2002). Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *For. Path*. 32, 277–307. doi: 10.1046/j.1439-0329.2002.00291.x

Vilà-Cabrera, A., Collb, L., Martínez-Vilalta, J., and Retana, J. (2018). Forest management for adaptation to climate change in the Mediterranean basin: a synthesis of evidence. *Forest Ecol. Manag*. 407, 16–22. doi: 10.1016/j.foreco.2017.10.021

Vilà-Cabrera, A., Martínez-Vilalta, J., Vayreda, J., and Retana, J. (2011). Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula. *Ecol. Appl*. 21, 1162–72. doi: 10.1890/10-0647.1

Wermelinger, B., Rigling, A., Schneider Mathis, D., and Dobbertin, M. (2007). Assessing the role of bark- and wood-boring insects in the decline of Scots pine (*Pinus sylvestris*) in the Swiss Rhone valley. *Ecol. Entomol*. 33, 239–249. doi: 10.1111/j.1365-2311.2007.00960.x

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.