



## Review

## 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<sup>☆</sup>



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## ABSTRACT

Climate change is increasing temperatures globally and drought in many regions. If climate change continues at its current rate, the resilience of many ecosystems will likely be exceeded, altering their structure and function. A consistent understanding of the impacts, however, remains elusive due to the difficulty of obtaining data of field studies at different scales from local to regional. We review the impacts of climate change on terrestrial ecosystems of the Mediterranean region based mostly on long-term field experiments of climatic manipulation and monitored field sites in Catalonia (NE Spain). These studies provide diverse experimental and observational field evidences that rising temperatures, new patterns of precipitation and other climatic changes are already affecting ecosystems in this Mediterranean region. Rapid genetic, epigenetic and metabolomics changes in plants have been described. They have resulted in changes in morphology, physiology, growth, reproduction, and mortality. Some species are more vulnerable to these changes than others are, which has altered their competitive ability and thereby changed microbial, plant and animal community composition. Many other impacts have been observed in response to climate change, for example an increase in the emission of biogenic volatile organic compounds or an increased risk of fire and a decrease in the absorption of CO<sub>2</sub> in periods of drought. A reduction of the capacity to retain nutrients and C in vegetation is accompanied, in the short term, by an increase in soil C and nutrient contents due to a decrease in the enzymatic capacity and mineralization of soil. The projected increase of torrential rainfalls introduces a scenario of uncertain changes in nutrient cycles, soil fertility and nutrient fluxes at medium and long terms. All these changes in water and nutrient availability suggest, though, net losses in the capacity of Mediterranean forests and shrublands to act as C sinks. Future research should quantify C in above- and belowground biomasses and soils under drought and warming, because this necessary information is lacking. Future studies should also investigate the losses of soil nutrients by leaching and erosion, and the possible feedbacks of land cover changes on water availability and regional climate. Policies of environmental and forestry management should take into account these impacts of the environmental and climatic conditions projected for the coming years and decades.

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## 1. Introduction

The Mediterranean region, as most regions in the world, is warming and becoming increasingly arid (Peñuelas et al., 2005; IPCC, 2013). Precipitation in the Mediterranean region has begun to either decrease in the long term, mainly in the dry season (Esteban-Parra et al., 1998), or not change significantly (Peñuelas et al., 2005; Piñol et al., 1998). In all cases, though, an increase in potential evapotranspiration has led to increased aridity (Peñuelas et al., 2005; Piñol et al., 1998) since temperatures have also increased in Mediterranean region (Peñuelas et al., 2005, 2002; Peñuelas and Boada, 2003). This increase of aridity comes together with associated disturbances such as floods, extreme heat and drought events and forest fires all them having strong impacts on many ecosystems (Peñuelas et al., 2013). Mediterranean plant communities are generally dominated by sclerophyllous woody plants with an herbaceous or shrubby understory (Specht, 1981; Orshan, 1983). The most specific structural characteristics of Mediterranean plants are those related to conservative mechanisms linked to the avoidance of water stress but frequently also to the scarcity of soil nutrients (Specht, 1981; Sardans and Peñuelas, 2013). But, despite the great array of physiological and morphological adaptations of Mediterranean plants to cope with drought and nutrient scarcity (Gulías et al., 2002; Fiochetto et al., 2003; Padilla and Pugnaire, 2007; Vilagrosa et al., 2010; Sardans and Peñuelas, 2013) a cascade of feed-back effects among increased aridity, more frequent torrential rainfalls and fires, and land-use changes have exceeded the capacity of Mediterranean plants to cope with drought, for instance in several areas of central and south Spain (Moreno-de las Heras et al., 2011; Ruiz-Sinoga et al., 2011, 2012). Most studies suggest a significant positive and rapid feedback between soil properties linked to fertility (water-storing capacity, permeability, nutrient availability, depth) and plant cover (Gallardo et al., 2000; Johnson-Maynard et al., 2002; Castaldi et al., 2009; Ochoa-Hueso et al., 2011). All these processes have further impacts on soil fertility and stability linked to less organic matter inputs, increased photodegradation of litter when plant cover decreases and more erosion associated to torrential rainfalls (Riera et al., 2007; González-Hidalgo et al., 2007; Moreno-de las Heras et al., 2011; Barnes et al., 2012).

All these processes which are temperature- and water-dependent are thus very likely to be altered by climate change. We here have reviewed the available data for the impacts of climate change at different spatial and temporal scales in the Mediterranean region from the long-term monitoring of field studies in Catalonia (NE Spain) highly representative of the terrestrial ecosystems of the Mediterranean region. These long-term field studies include experiments of climatic manipulation (Prades and Garraf), long-term monitored field gradients (e.g. in Montseny) and the Catalan Forest Inventory, all in Mediterranean woodlands (Fig. 1). Some of these data were collected by the authors to report the effects of climate change on the terrestrial ecosystems of Catalonia (Peñuelas et al., 2016). The two experimental sites represent two of the most typical terrestrial Mediterranean ecosystems, the semi-arid shrubland and the evergreen forest. The Garraf site has a typical calcareous shrubland representative of the Mediterranean communities with semi-arid conditions with widely distributed Mediterranean shrubs such as *Erica multiflora* or *Globularia alypum*, as dominant species. The evergreen-*Quercus ilex* forest of Prades mountains represents the Mediterranean mesic climatic ecosystem with *Quercus ilex* as dominant tree. The long-term monitored field gradients of Montseny range from the Mediterranean *Quercus ilex* forest at low altitudinal level to the European wet temperate *Fagus sylvatica* forest in high altitudinal levels.

This study focuses on the reported effects of climate change on the genetics, epigenetics, morphology, physiology and phenology of living organisms; interactions between species; changes in species composition; the structure and functioning of ecosystems; and finally the effects of biological changes on the C and nutrient cycles.

## 2. Field sites

The Garraf experimental site is a dry shrubland (Rosmarino-Ericion) in Garraf Natural Park, Barcelona, northeastern Spain (41°18'N, 1°49'E), at 210 m a.s.l. and on a south-south-eastern slope (13°). The climate is typically Mediterranean, with a mean annual precipitation of 455 mm and a mean annual temperature of 15.1 °C (Beier et al., 2004). The site, which is located on terraces of abandoned vineyards, was burned in the summers of 1982 and 1994. The soil is a petrocalcic calcixercept, thin (12–37 cm), with a loamy texture and abundant calcareous nodules. The regenerating vegetation currently covers 50–60% and has a maximum height of 70 cm. The dominant species, *Erica multiflora* L. (*Ericaceae*) and *Globularia alypum* L. (*Globulariaceae*), are evergreen, sclerophyllous shrubs that typically occur on basic soils of the western Mediterranean Basin, where they are common components of the coastal shrubland. Nine 20-m<sup>2</sup> (4 × 5 m) plots were established: three untreated control, three warming and three drought plots. The plots were organized in three blocks (each block with one control, one drought and one warming plot). Control plots had scaffolding similar to the warming and drought plots, but with no curtains to exclude rain or retain heat (see below). All plots were open around their edges. The outer 0.5 m of each plot was considered a buffer zone, and all measurements were conducted in the central 12 m<sup>2</sup>.

We established two types of climatic manipulation using automatically sliding curtains (approx. 20 cm above the maximum height of the vegetation). (1) Extended summer drought was induced by covering the natural vegetation and soil with transparent and water-proof plastic curtains during all rains over two growing seasons, from March–April to July–August and from September–October to December–January. Rain sensors closed the curtains in the drought treatment to cover the plants and soil during a rain and opened them when the rain stopped. (2) Passive night-time warming was achieved by covering the vegetation and soil at night with aluminum curtains. Solar energy accumulates in the ecosystem during the day, and a fraction of the energy is re-radiated back to the atmosphere at night as long-wave infrared radiation. The covering of the ecosystem with the curtains at night reduced the loss of infrared radiation, simulating the mechanism of global warming from the accumulation of greenhouse gases. The coverage of the plots was activated automatically by a preset light level (< 5 μmol m<sup>-2</sup> s<sup>-1</sup>). This treatment began on 16 March 1999 and continued throughout the study, except during three periods (August 1999, January 2000 and September–October 2001), when the treatment was stopped for calibration of the system effects or due to mechanical problems. The curtains were automatically opened during night-time rains to avoid excluding precipitation. For more detailed information, see (Beier et al., 2004).

The Prades experimental site was established in 1998 at the Prades holm-oak forest in southern Catalonia (northeastern Iberian Peninsula) (41°21'N, 1°20'E) at 930 m a.s.l. on a south-facing slope (25% slope). The forest is dominated by holm oak (*Quercus ilex*) and the tall shrubs *Phillyrea latifolia* and *Arbutus unedo*. The forest has a very dense multi-stem crown (18 366 stems ha<sup>-1</sup>), with 3850 stems ha<sup>-1</sup> and 50 Mg ha<sup>-1</sup>, 12 683 stems ha<sup>-1</sup> and 29 Mg ha<sup>-1</sup> and 667 stems ha<sup>-1</sup> and 9 Mg ha<sup>-1</sup> of *Q. ilex*, *P. latifolia* and *A. unedo*, respectively. These three species are accompanied by other Mediterranean woody species that do not reach the upper canopy (e.g. *Erica arborea* L., *Juniperus oxycedrus* L. and *Cistus albidus* L.) and the occasional isolated deciduous tree (e.g. *Sorbus torminalis* L. Crantz and *Acer monspessulanum* L.). This forest has been managed as a coppice for centuries but has not been substantially disturbed in the last 70 years. The climate is typically Mediterranean. The site has had a mean annual precipitation of 610 mm and a mean annual temperature of 12.2 °C since the beginning of 1998. The annual and seasonal distribution of precipitation is irregular, with annual precipitation ranging from 376 to 926 mm in the 12 years of the experiment described below. Spring and autumn are the wettest seasons, and summer droughts usually last three months, during which

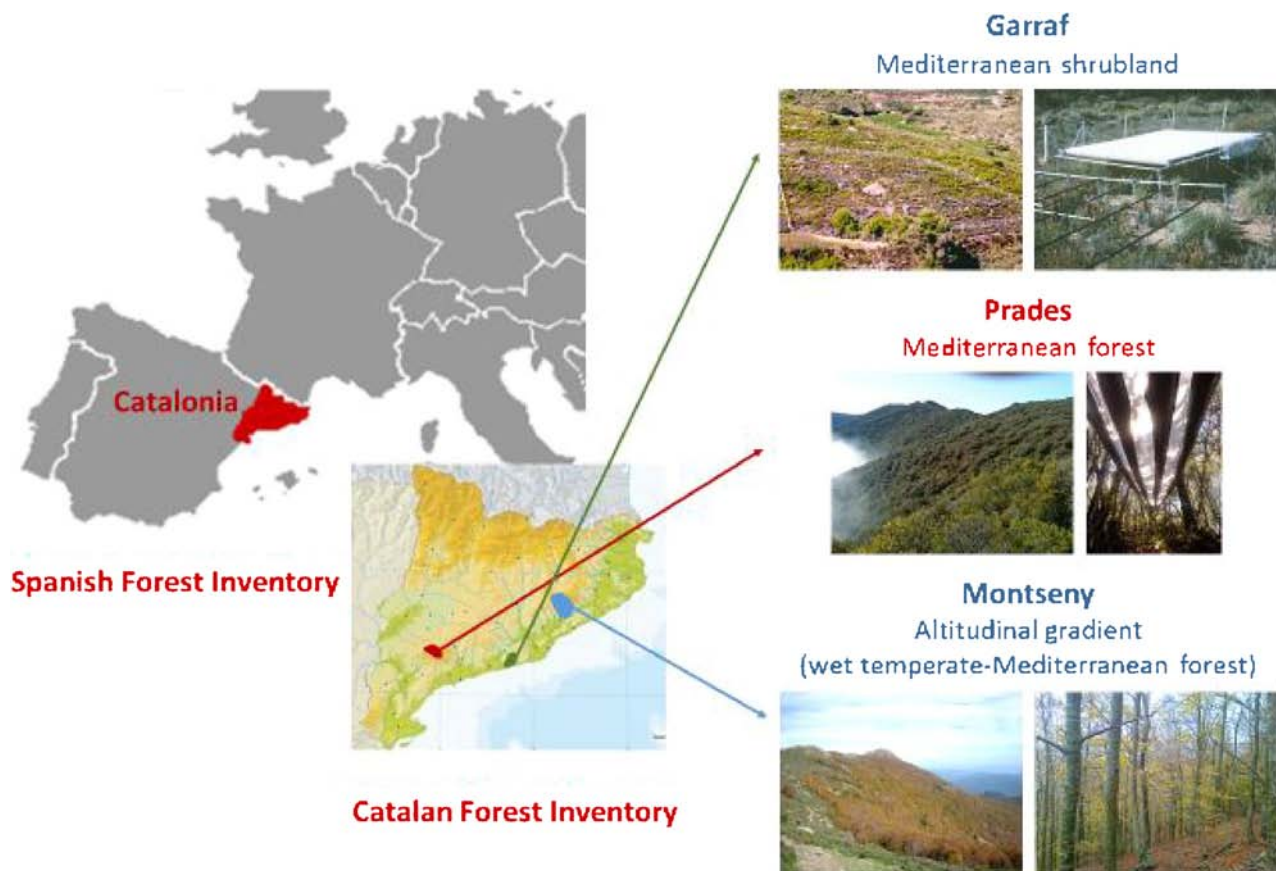


Fig. 1. Catalan experimental and long-term monitoring field sites of the study. Spanish and Catalan Forest Inventories were also used in this study.

precipitation is ~10% of the annual total and coincides with the highest temperatures. Winters are relatively cold. January is the coldest month (mean temperature of 4.4 °C), and the mean daily temperature is < 0 °C an average of eight days per winter. The soil is a Dystric Cambisol over Paleozoic schist and has a mean depth of ~35 cm. The mean annual precipitation is higher than that in the driest distributional limit of *Q. ilex*, but the topographic characteristics of the study site represent drier conditions due to the shallow soils and steep terrain.

The experimental system consisted of eight 150-m<sup>2</sup> plots delimited at the same altitude along the slope. Half the plots (randomly selected) received a drought treatment, and the other half faced natural conditions. Precipitation was partially excluded from the plots of the drought treatment by PVC strips suspended 0.5–0.8 m above the soil and covering approximately 30% of the plot surfaces. A ditch 0.8 m in depth was excavated along the entire top edge of the plots to intercept runoff water. The water intercepted by the strips and ditches was conducted around the plots, below their bottom edges. The strips were installed below the canopy and thus did not intercept direct sunlight. Litter falling on the plastic strips was regularly transferred below them to ensure that differences in the content of soil nutrients among treatments and control plots were attributable only to the availability of water for the decomposition of this litter. For more details, see Ogaya and Peñuelas, (2004).

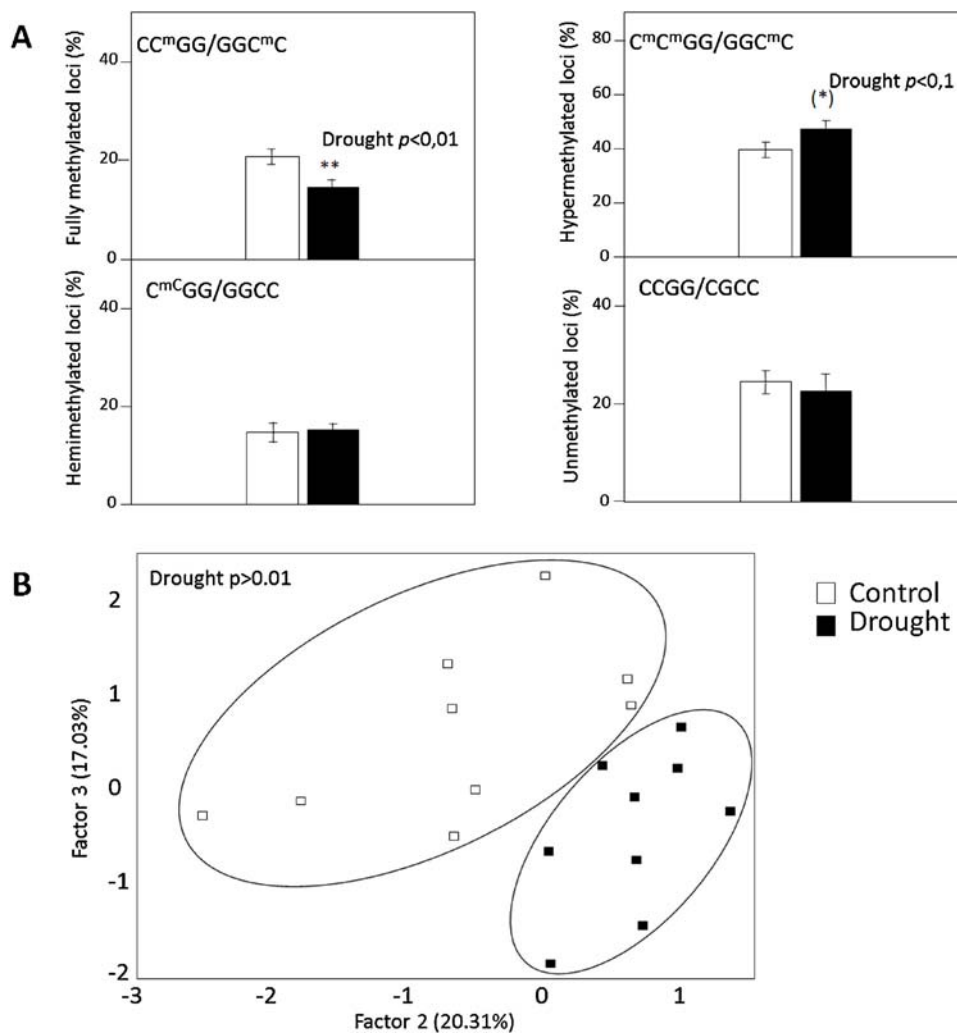
The holm-oak and beech forests in Montseny Natural Park have been monitored since 2002. The studies were conducted in the northeast of the Iberian Peninsula, at the southern edge of the distribution of *Fagus sylvatica* in Europe (Jump et al., 2006a,b; Peñuelas and Boada, 2003; Peñuelas et al., 2007). The holm oak and beech forests in the park are 50 km northeast of Barcelona (Catalonia) (41°42′–41°52′N, 2°16′–2°33′E). Beech colonized the Montseny Mountains more than 4000 years ago (Comps et al., 2001). The northeastern ridge of the Montseny Mountains rises to 1712 m a.s.l. and includes 2380 ha of nearly

continuous beech forest (Jump et al., 2006a). The southwestern ridge rises to 1344 m a.s.l. and is mainly dominated by pastures that occupy the top of a high plain, and fragments of beech forest are restricted to the steeper surrounding areas. Individual fragments cover an area of up to 52 ha (Jump and Peñuelas, 2006) (Fig. 1). The two ridges are separated by a valley, so the fragments and continuous forests are separated by 1.5–5.5 km. Beech forests occur above 1000 m a.s.l. and form the tree line on the highest peaks of the region (Turó de l'Home and Les Agudes, 1712 and 1706 m, respectively). The vegetation below the beech forest in all areas of these mountains is Mediterranean, dominated by *Q. ilex* (Peñuelas et al., 2007). The bedrock consists mostly of metamorphic phyllites and schists (Ávila et al., 2002; Comps et al., 2001), with some areas of granodiorites on the northeastern ridge.

We have also used the data from the inventory of the Catalan National Forest (Gracia et al., 2004) to analyze the relationships of the climatic gradients of this region with forest traits and to test different scenarios using the program GOTILWA (Gracia et al., 1999; Keenan et al., 2009; Nadal-Sala et al., 2014, 2017) to project future conditions for Mediterranean forests.

### 3. Responses at the molecular level and the use of elements: genetics, epigenetics, metabolomics and stoichiometry

The interaction of genetic variability in natural populations with climate induces the emergence of adaptive and evolutionary responses to new climatic conditions. The application of various techniques of molecular biology to the study of natural forest populations has allowed the identification of loci associated with these responses to climate, quantifying their frequency in the population and determining the role of genetic modifications in a fast adaptive response. Field studies of altitudinal gradients in the Montseny Mountains (Jump et al., 2006a,b; Jump and Peñuelas, 2006) and field-warming and drought-



**Fig. 2.** Epigenetic study of natural populations of *Quercus ilex* under control and drought conditions. A) Patterns of methylation of spot samples showing the percentages (mean ± SE) of each state of methylation of the GGCC sequence analyzed. The differences were analyzed by an ANOVA. \*,  $P < 0.1$ ; \*\*,  $P < 0.01$ . B) Principal component analysis of methylation at each type of locus in populations of *Q. ilex*. The percentages indicate the proportion of variance explained by each factor. The effect of the drought on factors 2 and 3 have been calculated using an ANOVA. For more details, see Rico et al. (2014).

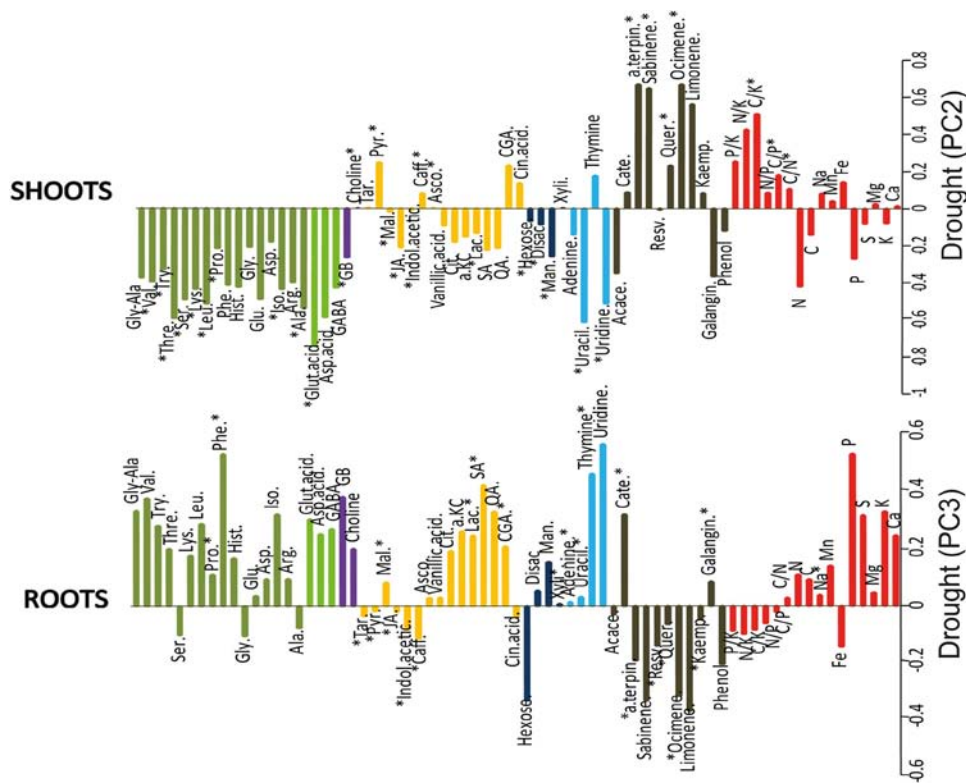
manipulation experiments in typical Mediterranean shrubland in the Garraf Mountains (Jump et al., 2008) have demonstrated rapid responses for the acclimation and adaptation (evolution) of species to climate change by taking advantage of the existing genetic variability in natural populations.

Genetic changes have thus been detected in the response of plants to progressive drought and warming, but alterations in gene expression not attributable to variations in DNA sequences have also been detected. These epigenetic changes can occur in complex and interrelated molecular processes, such as DNA methylation, histone modification and RNA regulation. DNA methylation is stable over time at the individual level, has varying degrees of heritability and may be influenced by the environment. The ability of tree species to respond quickly in natural conditions by epigenetic changes, such as those observed in *Q. ilex* subjected to experimentally induced drought, were determined using specific molecular markers sensitive to DNA methylation (Rico et al., 2014) (Fig. 2).

Metabolomic analyses of wild plants have identified decreases in the activity of the metabolic pathways associated with the accumulation of energy and growth and increases in the activity of secondary metabolic pathways associated with anti-stress mechanisms in response to drought in dominant species of Mediterranean shrubs and trees (Rivas-Ubach et al., 2016, 2014, 2012). Field experiments of climate manipulation have shown changes in elemental composition (Sardans et al., 2013). Moreover, the changes in elemental composition are linked with the functional shifts of plants under higher levels of drought and warming as observed in metabolomic studies (Rivas-Ubach et al., 2016,

2012). These effects of climate change on leaf elemental composition have shown to be associated with the level of herbivore pressure suggesting shifts in leaf palatability (Rivas-Ubach et al., 2014). Differences in soil depth are also directly associated with the metabolomic structure of trees, indicating that droughts can more significantly affect trees in shallower soils (Rivas-Ubach et al., 2016). Moreover, warming and drought can affect chemical composition of aerial plant organs differently and even oppositely than roots (Gargallo-Garriga et al., 2015, 2014) (Fig. 3). A decrease in activity of the metabolic pathways in primary metabolism associated with growth and decreases in N, P and K concentrations have been observed in the aerial organs. In contrast, higher concentrations of N, P and K and of primary metabolites involved in protein synthesis and energy production, such as amino acids and sugars, have been found in roots. These asymmetrical effects on above- versus belowground chemical composition can also have asymmetrical and/or different consequences in above- versus belowground trophic webs.

Field experiments of warming and drought have been thus associated to changes in elemental composition (Sardans et al., 2013, 2012b). Changes in elemental composition and stoichiometry are linked to shifts in the flow of matter and nutrients through the trophic chain and therefore modifications of the biogeochemical cycles of the plant-soil system (Sardans et al., 2012c; Sterner and Elser, 2002). Foliar C/N/P/K stoichiometric ratios of the main forest species in studies of climatic gradients were largely due to weather conditions, especially rainfall (Sardans et al., 2016, 2015, 2011; Sardans and Peñuelas, 2014, 2013a,b). This relationship has also been observed in the same species



**Fig. 3.** Metabolome of shoots and roots in response to drought. Shoots are metabolically deactivated during drought to reduce the consumption of water and nutrients, whereas roots are metabolically activated to enhance the uptake of water and nutrients, together buffering the effects of drought, at least at the short term. The experiment was conducted with a common grass species, *Holcus lanatus* L., submitted to drought conditions in the field. The various metabolomic families are represented by colors: blue, sugars; green, amino acids; dark green, amino-acid derivatives; yellow, compounds associated with amino-acid and sugar metabolism; cyan, nucleotides; violet, osmolytes and brown and brown and phenols. Metabolites: glycine-alanine (Gly-Ala), valine (Val), tryptophan (Try), threonine (Thr), serine (Ser), lysine (Lys), leucine (Leu), proline (Pro), phenylalanine (Phe), histidine (Hys), glycine (Gly), glutamine (Gln), asparagine (Asn), isoleucine (Ile), arginine (Arg), alanine (Ala), glutamic acid (Glu), aspartic acid (Asp), gamma-aminobutyric acid (GABA), glycine betaine (GB), choline (Choline), tartaric acid (Tar), pyruvate (Pyr), malic acid (Mal), jasmonic acid (JA), indol acetic acid (Indol.acetic), caffeic acid (Caff), ascorbic acid (Asco), vanillic acid (Vanillic.acid), citric acid (Cit),  $\alpha$ -ketoglutaric acid ( $\alpha$ KC), lactic acid (Lac), shikimic acid (SA), quinic acid (QA), chlorogenic acid (CGA), chnic acid (Cin.acid), xylose (Xyli), hexose (Hexose), mannose (Man), disaccharides (Disac), adenine (Adenine), uracil (Uracil), thymine (Thymine), uridine (Uridine), acacetin (Acace), catechin (Cate),  $\alpha$ -terpinene ( $\alpha$ Terpin.), sabinene (Sabinene), resveratrol (Resv), quercetin (Quer), ocimene (Ocimene), limonene (Limonene), galangin (Galangin), kaempferol (Kamp) and phenolic groups (Phenol). For more details, see Gargallo-Garriga et al. (2014).

across its distributional area rainfall (Sardans et al., 2016). Decreases in water availability are therefore associated with shifts in nutrient concentrations and their allocation to different organs (Sardans and Penuelas, 2013a,b), the stoichiometric relationships among the main nutrients (Sardans et al., 2008a,c; Sardans and Penuelas, 2013a,b) and the distribution of nutrients between plants and soils (Sardans et al., 2008a,c,d).

#### 4. Morphological, physiological, phenological and growth changes in plants

All metabolic responses mentioned above have a strong effect on the growth and development of organisms in the medium and long term. For example, a small reduction in soil moisture in Prades has significantly reduced the biomass increases in holm oaks (Barbeta et al., 2013; Liu et al., 2015; Ogaya and Penuelas, 2007a). This strong decrease in the growth of trees has been produced by both a slight decrease in net photosynthetic rates and an increase in defoliation (Ogaya and Penuelas, 2004). High mortality rates have also been observed in the last two decades due to periods of extreme drought (Ogaya et al., 2015). These negative effects, however, have progressively decreased, probably due to epigenetic adaptation, a decrease in foliar biomass and/or unknown reasons (Liu et al., 2015). The effect of drought, however, can finally increase over time by the exhaustion of deep soil water (Barbeta et al., 2015).

Our field study sites at Prades and Garraf have allowed us to observe the sensitivity of Mediterranean species to severe warming and drought conditions despite their strong ability to acclimate to warm and dry conditions (Llorens et al., 2004; Munné-Bosch et al., 2004; Munné-Bosch and Penuelas, 2004; Sardans and Penuelas, 2013b; Serrano et al., 2005). The experimentally induced drought in Prades delayed the phenophases of leaf shedding and flushing, flowering and fruit growth, manipulation and abscission in *A. unedo* but not those of the two other dominant species, *Q. ilex* and *P. latifolia* (Ogaya and Penuelas, 2004). It

decreased the growth and increased the mortality of *Q. ilex* and *A. unedo* (Barbeta and Penuelas, 2016; Barbeta et al., 2013; Ogaya and Penuelas, 2007a). These results thus showed that a drought-resistant species such as *P. latifolia* could have a greater ability to grow and produce reproductive structures than less resistant species such as *Q. ilex* or *A. unedo* in a drier environment, as predicted for Mediterranean areas in the near future by models of global circulation. The Garraf experiment produced similar results; drought and warming had negative effects on flower production in some shrub species but not others (del Cacho et al., 2013b). In contrast, flower production was reduced in the drought and warming treatments in the spring-flowering species *Dorycnium pentaphyllum* and *Helianthemum syriacum* but not in the autumn/winter-flowering species *E. multiflora*, which increased flowering in the warming treatment (del Cacho et al., 2013b). Seedling emergence in two of the dominant species in these shrublands, *E. multiflora* and *G. alypum*, decreased significantly in the drought treatment, and the decrease was larger in open areas than below vegetation cover. Seedling survival for both species decreased closer to competing neighbors, and survival in *G. alypum* was higher with lower mean annual temperatures and higher annual rainfall, but survival was also higher in the drought treatment, where vegetation cover decreased (del Cacho et al., 2013a). This study supports the prediction that the increasing aridity in Mediterranean ecosystems would constrain the early stages of development in typical co-occurring shrubs. Both field studies thus suggested that these different responses among species for some variables contributing to reproductive success could produce changes in seedling recruitment and resprouting ability and, in the longer term, in species distribution.

Drought increases terpene emissions of holm oak forests in Prades mountains, specially in more biologically active seasons, spring and autumn (Llusia et al., 2006; Llusia and Penuelas, 2000), with large differences among species (Llusia et al., 2008, 2006). Terpene emissions have also increased in three of the four species in the drought treatment at the Garraf experimental site (Llusia et al., 2008). These shifts in plant terpene contents and emissions have a great significance for the fire

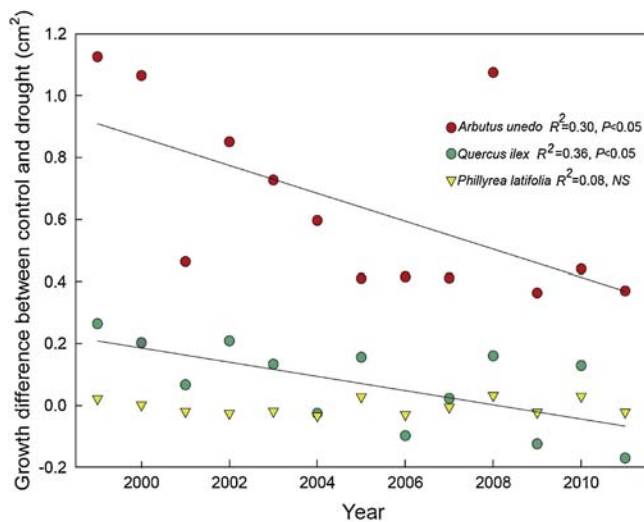


Fig. 4. Differences in basal-area growth between the control and droughted plots in the field experiment in the Prades Mountains for three species (*Arbutus unedo*, *Quercus ilex* and *Phillyrea latifolia*). The coefficient of determination and the significance level of the temporal trend of the dependent variable for each species are indicated. [For more details, see Liu et al. (2015) and Barbata et al. (2013)].

patterns due to the great importance of terpenes in the flammability of forests (Alessio et al., 2008a,b).

## 5. Changes in populations and communities

Our climatic-manipulation field experiments have demonstrated that prolonged drought drives asymmetrical changes in species populations, with some species more negatively affected than others (Barbata et al., 2013; Prieto et al., 2009). These results highlight the variable vulnerability of Mediterranean species to more frequent and intense droughts, which may lead to partial species substitution and changes in forest structure and thus C uptake. The response to drought, however, changed over time. Decreased intra- and interspecific competition after extreme droughts with high mortality, together with probable morphological and physiological acclimation to drought during the study period, may buffer forests against drier conditions, at least in the short term. The species-specific responses to drought may eventually lead to a partial communal shift favoring the more drought-resistant species. The effect of the drought treatment, however, was dampened for the two drought-sensitive species after 13 years in the Prades experiment, which may indicate a potential adaptation to drier conditions at the ecosystemic or populational level (Barbata et al., 2013). The effect of drought treatment also differed among species in the post-fire Mediterranean shrubland in the Garraf experiment. The drought and warming treatment reduced the competitive ability of the obligate seeder tree *Pinus halepensis* against native resprouter shrubs, which slowed the transformation of the dominant vegetation from shrubs to pine trees. Conversely, the strategy of water use by *G. alypum* may have allowed this species to maintain a dominant position in the drought plots (Prieto et al., 2009).

A metadata analysis found that the different responses of each individual and species to climate change generated both demographic changes and changes in the composition and functioning of the communities, consistent with the results at the experimental field sites (Carnicer et al., 2013a,b). Gymnosperms are currently being replaced by *Quercus* sp. in several areas of the Iberian Peninsula due to their different roles during succession and basic traits (Carnicer et al., 2014). On the other hand, the most representative *Quercus* tree species in Mediterranean basin, *Q. ilex*, is suffering decreases of growth and increased of mortality and defoliation (Peñuelas et al., 2000, 1998). Moreover, in the same areas tall shrubs better adapted to arid environment than trees

are minimally affected by drought (Liu et al., 2015; Peñuelas et al., 2000, 1998), suggesting that if climate becomes drier the in Mediterranean Basin the trend towards a replacement of trees by tall shrubs could become stronger.

## 6. Disturbed communities and young ecosystems are the most sensitive

Changes in the abundance and dominance of species were monitored by Kröel-Dulay et al. (2015) in a long-term experiment (14 years) simulating warming and drought growing conditions in seven shrubland ecosystems geographically distributed throughout Europe. The study included sites that had not been disturbed for a long time and others that had suffered recent fire or pests, as was the case of the fire in the Garraf Mountains (Barcelona) in 1994. The ecosystems that had been altered, either by natural causes or human activity, were most vulnerable to climate change (Kröel-Dulay et al., 2015). The association between human activity and the frequency and severity of disturbances that disturb ecosystems suggest that disturbed ecosystems will respond more strongly to climate change. These studies demonstrate the need to know the history and successional state of ecosystems for accurately predicting their responses to climate change, paying special attention to recently degraded ecosystems currently in early successional stages.

## 7. Biogeochemistry and ecosystemic functioning

### 7.1. Responses of the holm-oak forests to long-term drought

The drought experiments in the forests indicated that an increase in the intensity, frequency and duration of droughts can negatively affect Mediterranean ecosystems, such as those of *Q. ilex* forests (Carnicer et al., 2011). If water availability decreases, trees transpire less, assimilate less C and thus grow less. In addition, an increase in mortality in the species more vulnerable to drought could favor the more resistant species, thereby changing the structure and composition of ecosystems and the environmental services they offer. Differences in the rates of growth recorded between drought and control plots at the beginning of an experiment in Prades between 1999 and 2011, however, eventually decreased or disappeared (Fig. 4) (Barbata et al., 2013; Liu et al., 2015). The causes of the dampening effect of drought are several but could be partly result of the reduction in competition for water resources between individuals due to the death of more individuals in the drought than the control plots. This compensation of the effect of drought treatment was also accelerated by episodes of extreme drought, such as the drought during 2005 and 2006 that dramatically increased mortality. Adjustments in the morphology, allometry and physiology of trees from epigenetic modifications may have also contributed to the acclimation of the forest to drier environmental conditions (Barbata et al., 2013).

The drought treatment in the Prades experiment reduced flower and fruit production in *Q. ilex* by 30 and 45%, respectively, whereas these variables did not change significantly in the other two dominant species, *P. latifolia* and *A. unedo* (Ogaya and Peñuelas, 2007b). The decreases in growth and fruit production in some species, despite being asymmetrical among species, was nevertheless accompanied by a global decrease of biomass in the plant community.

Mushrooms have also decreased production in response to drought (Ogaya and Peñuelas, 2005), all of which strongly suggest a slow shift from a mesic evergreen oak forest to a drier forest with increasing relative dominance of the tall shrubland *P. latifolia*, the species that has generally been damaged less by the 17 years of experimental drought in the Prades Mountains.

The use of stable isotopes indicated that the deep soil water was the preferred usage during summers, and water from surface horizons was preferentially used in wet seasons. The drought treatment plots in our drought-manipulation field studies, however, did not follow this

pattern; the trees took up more deep water in the wet seasons (Barbata et al., 2015). This difference may have been due to differences in the distribution of fine roots, which extended to greater depths in the drought plots to avoid summer desiccation. The experimentally induced drought instead decreased the use of this deeper water in the summer, probably due to the depletion of the water trapped in rock fractures (Barbata et al., 2015).

These studies mainly indicated that the resilience of holm-oak forests to an increase in drought is more important than initially thought, so these ecosystems may adapt to a progressive increase of arid conditions. The mechanisms of resistance and resilience to drought at the tree level, however, may not be sufficient to mitigate the effects of extreme episodes of drought and warming (Penuelas et al., 2001). Studies that directly evaluate the consequences of these episodes to the structure and function of ecosystems and to the subsequent recovery and accumulated effect of more than one episode are thus clearly warranted.

### 7.2. Alterations in the use of nutrients

Recent studies based on data from the Catalan Forest Inventory found that nutrient contents and allocation to different organs (leaves and wood) were significantly correlated with weather conditions and especially with annual precipitation, with higher contents with higher precipitation, especially in the leaves (Sardans et al., 2012a, 2011; Sardans and Penuelas, 2014, 2013a). These results also indicate the importance of the availability of water in our forest ecosystems and how small decreases in the availability of water can have disproportionately large impacts on the ability of forests to retain and accumulate nutrients.

Our experimental studies of climate change simulated under field conditions found that a moderate increase in drought (15–20% decrease in the availability of soil water) generally decreased the concentrations and contents of N, P and micronutrients in the forests (Sardans et al., 2008a; Sardans and Penuelas, 2007). The total content of nutrients in aboveground biomass thus decreased with these levels of drought (Sardans et al., 2006, 2008a,b,d), except for K that increased in the aerial organs of some species (Sardans and Penuelas, 2007). Aridity increased the C:N and C:P ratios of our fields and forests, associated with conservative strategies to adapt to the lower availability of water, with a corresponding increase in sclerophylly (Sardans et al., 2006). Similarly, drought also changed the allocation of nutrients to the organs, increasing the allocation of N to the roots, probably to help fulfil the increased need for water (Sardans et al., 2008b).

Some of the dominant species at our experimental sites in Prades and Garraf had higher foliar K concentrations and K:P ratios and lower C:K and N:K ratios after 11 years of continuous drought (Egilla et al., 2005; Laus et al., 2011; Sardans et al., 2012a). These results are consistent with the tissue concentrations of K for controlling the loss of water from leaves (Babita et al., 2010) by their positive effects on stomatal function (Khosravifar et al., 2008) and the control of osmosis (Babita et al., 2010; Laus et al., 2011). K is especially important in dry environments due to its role in the control of water retention. K can have a significantly positive effect on plant drought resistance in both natural ecosystems (Egilla et al., 2005) and crops (Stone and Moreira, 1996). The use and remobilization of K in Mediterranean plants is associated with the requirements of osmotic control (Milla et al., 2005). A reduction in the availability of K in *Pinus pinaster* in natural ecosystems in the Iberian Peninsula led to an increase in stomatal conductance and consequently a reduction in water-use efficiency (Fernández et al., 2006). Rivas-Ubach et al. (2012) reported increases in foliar K concentrations in *E. multiflora* in summer (the driest period) due to metabolomic shifts toward increasing concentrations of metabolites associated with osmotic control. Analyses of the Catalan Forest Inventory have provided evidence that Mediterranean forests have higher foliar K concentrations in summer, coinciding with drought periods (Sardans

et al., 2012a). The changes in plant K concentrations and ratios with N and P in response to drought merits further research for obtaining a better understanding of the relationships between terrestrial plant stoichiometry and environmental changes.

Increases in drought also strongly affect soils, which is critical because soils are main C sinks. Our experiments simulating climate change at a field scale have indicated that the mineralization of organic matter in Mediterranean soils is strongly affected by changes in water availability (Sardans et al., 2012b, 2006; Sardans and Penuelas, 2010, 2005). Soil respiration and the activities of soil and rhizospheric enzymes have decreased in response to moderate levels of increased drought. The decrease in enzymatic activity was directly correlated with the reduction in water content of the soil (e.g. (Sardans and Penuelas, 2010)). The impact of drought on the growth and ability of plants to accumulate nutrients in biomass, along with the decrease in soil mineralization, would promote the accumulation of nutrients in the soil, which would increase the flow of nutrients to water. The experimental drought treatments in the forests of the Prades Mountains thus decreased the ecosystemic N content because they decreased the total biomass content and increased the loss of N by leaching (Penuelas et al., 2013, 2000).

### 7.3. The effects of climate change on the C balance

C and N accumulation decreased in the aboveground plant communities at our experimental sites after six years of drought treatment, whereas soil organic C and total N increased, indicating slower rates of C and N mineralization and lower N uptake and C fixation together with a slower turnover of soil C and N (Sardans et al., 2008a,c). These results suggest a slowdown in the turnover of ecosystemic C and a decrease in aboveground C accumulation, but the effect of drier conditions on soil at medium and long terms is not clear. The short-term accumulation of soil organic C could therefore decrease because of the successive reduction in aboveground biomass reducing the input of organic matter to the soil, the increase in leaching due to the reduced plant cover and density and the higher frequency and intensity of torrential rains. Moreover, net photosynthetic rate, stomatal conductance and leaf-water potential decreased with increases in vapor-pressure deficits and decreases in soil moisture in *Q. ilex* and *P. latifolia*, the two co-dominant species of the climatic-manipulation field experiment in the Prades Mountain evergreen forest.

A future drier climate may decrease the C stock of Mediterranean species, and some shrub species highly resistant to drought could gain a competitive advantage over *Q. ilex*, currently the dominant species in this forest (Ogaya et al., 2014). This negative impact of drought on the capacity of Mediterranean ecosystems to accumulate C could be even larger if warming is combined with drought.

## 8. The future: impact of climate change on mediterranean terrestrial ecosystems predicted for the coming decades. GOTILWA + simulations

We here used the Spanish Forest Inventory to evaluate the response of these various types of Mediterranean forests to climate change by using the GOTILWA model of forest growth (Gracia et al., 1999; Keenan et al., 2009; Nadal-Sala et al., 2014, 2017; [www.creaf.uab.cat/gotilwa/](http://www.creaf.uab.cat/gotilwa/)). We used the general circulation model ECHAM4 and the A2 socioeconomic scenario (850 ppm of atmospheric CO<sub>2</sub> by 2100). Fig. 5A shows the projected GPP and net primary production (NPP) for four periods of the 21st century. GPP progressively increases throughout the century as a result of the expected fertilization effect of the progressive increase in atmospheric CO<sub>2</sub>, which is manifested mainly in the forests of northern and northeastern Iberian Peninsula. In contrast, NPP widely tends to decrease. The increase in autotrophic maintenance respiration and the progressive increase in the temperature can deplete carbohydrates and progressively decrease forest biomass (Nadal-Sala et al., in

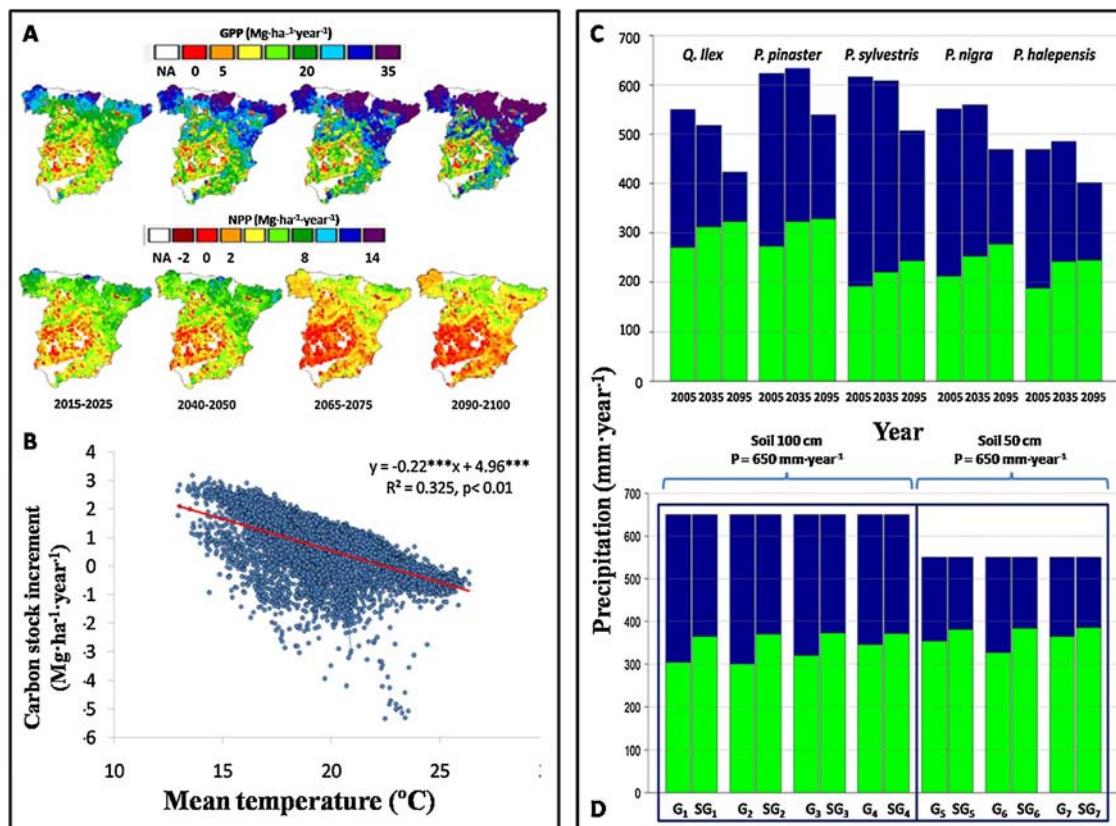


Fig. 5. A) Productivity of mono-specific forests in Spain for socioeconomic scenario A2 (850 ppm of atmospheric CO<sub>2</sub> by 2100) and the general circulation model ECHAM4. The number of plots from the Spanish Forest Inventory (IFN) database used in the simulation was 34 000. Upper panels show gross primary production (GPP) and lower panels show net primary production (NPP) by the same stage during four periods of the 21st century. White areas represent where no data were available. B) Increase in forest carbon budget during 2076–2100 period relative to mean annual temperature for the same period. C) Changes in the distribution of blue water (drainage and runoff, blue in the figure) and green water (evapotranspiration, green in the figure) during 21st century. 500 randomly chosen IFN plots in mainland Spain were simulated for the five species noted in the figure. Mean simulated 2000–2010 (2005), 2030–2040 (2035) and 2090–2100 (2095) periods values are represented. Climate change scenario considered was A2 (850 ppm of atmospheric CO<sub>2</sub> by 2100) in a ECHAM4 general circulation model (Roeckner et al., 1996). D) GOTILWA + (Nadal-Sala et al., 2017) simulations of the effects of forest management upon a *Pinus halepensis* forest water balances in the Montmell Reserve (Catalonia). We analyzed Generalitat de Catalunya's standardized forest management procedures (Beltrán et al., 2011) at increasing turn lengths (turn length G(n) < turn length G(n + 1), minimum turn equals to 47 years, maximum turn equals to 120 years) in two different plot quality conditions (from G1 to G4 correspond to a precipitation of 650 mm y<sup>-1</sup> and 1 m soil depth forest, and from G5 to G7 correspond to a precipitation of 550 mm y<sup>-1</sup> and 0.5 m soil depth forest). Each management (Gn) was compared to the corresponding case SG (unmanaged). As in C, D also shows the changes in the distribution of blue water (drainage and runoff, blue in the figure) and green water (evapotranspiration, green in the figure).

press). The loss of biomass is illustrated in Fig. 5B, which shows the negative correlation between the increase in C stocks and air temperature.

The projected increase in temperature and decrease in precipitation simulated by climate-change scenarios also involve a redistribution of green water (evapotranspired water) and blue water (drainage and surface runoff) in the forest types in Fig. 5C. The scenarios predict an increase in evapotranspiration or green water, probably due to the increase in evaporative demand that accompanies higher temperatures. The decrease in precipitation and increase in evapotranspiration, however, would decrease the movement of blue water from the forests to downstream ecosystems. An overall increased water limitation is therefore expected in Mediterranean forests. A decrease in the proportion of the precipitation available for downstream water systems is also expected. Practices of forest management focused on water such as thinning could help to mitigate the growing impact of forests on the green-water fraction. Fig. 5D illustrates various itineraries of forest management, proposed for a *P. halepensis* forest in the Mediterranean region. Forest management could reduce the amount of “green” water, leaving more “blue” water. A decrease in precipitation would decrease the amount of “blue” but not “green” water, which is strictly correlated with evaporative demand in water-stressed environments, such as the simulated *P. halepensis* forests.

## 9. Final remarks

1. This summary of several studies mainly focused on woody Mediterranean ecosystems, indicates that the projected level of drought and aridity in the next decades may have important effects on the functioning and structure of Mediterranean plants, forests and shrublands. New experimental studies that reproduce natural conditions, including cases of extreme and sudden changes, are needed for better understanding and thus better managing these changes.
2. The experiments at our field sites have provided extensive evidence of the effect of further projected drought increase reducing growth and increasing mortality and defoliation, being this effect asymmetrical between species, thus suggesting a future dominance replacement of trees by tall shrubs.
3. Despite the negative relation between drought and growth, and photosynthesis capacity, Mediterranean species have shown a notable capacity to adapt at short term being this capacity even greater than previously supposed. Epigenetic and genetic processes may have had a key role in this fast capacity of adaptation in some studied species.
4. Drought has a disproportionate effect on nutrient cycle in the plant-soil system. Moderate decreases of soil water availability are in general associated to a shift of nutrient from aboveground biomass



to soil, and decrease of mineralization and enzyme activity capacity in soils. The study of the losses of soil nutrients by leaching and erosion should be incorporated into long-term experiments of climatic manipulation in Mediterranean forests. Our studies have provided solid evidence of a trend toward the reduction of above-ground cover and the accumulation of recalcitrant nutrient compounds in soil, suggesting a potential increase in nutrient losses at a higher frequency and/or intensity of torrential rains.

5. Drought has several other impacts such as increases in terpene emissions or accumulation of litter and recalcitrant soil organic matter in soil that can further interact with drought and disturbances such as fire and erosion.
6. Future research should quantify accurately the impacts of increasing aridity on the capacity of Mediterranean woodlands to store C in above- and below-ground biomasses and soils, because this necessary information is currently lacking. As it is also lacking the knowledge on the feedbacks of land cover changes on water availability and regional climate.
7. The available experimental and observational data provide useful information to improve the Mediterranean forest management in the coming decades. To prevent the increases in mortality, an adequate reduction of the stem density should help to adapt to the aridity rise.

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## References

- Àvila, A., Rodrigo, A., Rodà, F., 2002. Nitrogen circulation in a Mediterranean holm oak forest, La Castanya Montseny, northeastern Spain. *Hydrol. Earth Syst. Sci.* 6, 551–557. <http://dx.doi.org/10.5194/hess-6-551-2002>.
- Alessio, G.A., Penuelas, J., De Lillis, M., Llusà, J., 2008a. Implications of foliar terpene content and hydration on leaf flammability of *Quercus ilex* and *Pinus halepensis*. *Plant Biol.* 10, 123–128. <http://dx.doi.org/10.1111/j.1438-8677.2007.00011.x>.
- Alessio, G.A., Penuelas, J., Llusà, J., Ogaya, R., Estiarte, M., De Lillis, M., 2008b. Influence of water and terpenes on flammability in some dominant Mediterranean species. *Int. J. Wildl. Fire* 17, 274–286. <http://dx.doi.org/10.1071/WF07038>.
- Babita, M., Maheswari, M., Rao, L.M., Shanker, A.K., Rao, D.G., 2010. Osmotic adjustment, drought tolerance and yield in castor (*Ricinus communis* L.) hybrids. *Environ. Exp. Bot.* 69, 243–249. <http://dx.doi.org/10.1016/j.envexpbot.2010.05.006>.
- Barbeta, A., Penuelas, J., 2016. Sequence of plant responses to droughts of different timescales: lessons from holm oak (*Quercus ilex*) forests. *Plant Ecol. Diver.* 9 (4), 321–338. <http://dx.doi.org/10.1080/17550874.2016.1212288>.
- Barbeta, A., Ogaya, R., Penuelas, J., 2013. Dampening effects of long-term experimental drought on growth and mortality rates of a Holm oak forest. *Glob. Change Biol.* 19, 3133–3144. <http://dx.doi.org/10.1111/gcb.12269>.
- Barbeta, A., Mejía-Chang, M., Ogaya, R., Voltas, J., Dawson, T.E., Penuelas, J., 2015. The combined effects of a long-term experimental drought and an extreme drought on the use of plant-water sources in a Mediterranean forest. *Glob. Change Biol.* 21, 1213–1225. <http://dx.doi.org/10.1111/gcb.12785>.
- Barnes, P.W., Throop, H.L., Hewins, D.B., Abbene, M.L., Archer, S.R., 2012. Soil coverage reduces photodegradation and promotes the development of soil-microbial films on dryland leaf litter. *Ecosystems* 15, 311–321. <http://dx.doi.org/10.1007/s10021-011-9511-1>.
- Beier, C., Emmett, B., Gundersen, P., Tietema, A., Penuelas, J., Estiarte, M., Gordon, C., Gorissen, A., Llorens, L., Roda, F., Williams, D., 2004. Novel approaches to study climate change effects on terrestrial ecosystems in the field: drought and passive nighttime warming. *Ecosystems* 7, 583–597. <http://dx.doi.org/10.1007/s10021-004-0178-8>.
- Beltrán, M., Piqué, M., Vericat, P., Cervera, T., 2011. Models de gestió per als boscos de pi blanc (*Pinus halepensis* L.): producció de fusta i prevenció d'incendis forestals. *Sèrie: Orientacions de Gestió Forestal Sostenible per a Catalunya (ORGEST)*. Centre de la Propietat Forestal. Departament d'Agricultura, Ramaderia, Pesca, Alimentació i Medi Natural, Generalitat de Catalunya.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., Penuelas, 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. <http://dx.doi.org/10.1073/pnas.1010070108>.
- Carnicer, J., Barbeta, A., Sperlrich, D., Coll, M., Penuelas, J., 2013a. Contrasting trait syndromes in angiosperms and conifers are associated with different responses of tree growth to temperature on a large scale. *Front. Plant Sci.* 4, 409. <http://dx.doi.org/10.3389/fpls.2013.00409>.
- Carnicer, J., Stefanescu, C., Vila, R., Dinçá, V., Font, X., Penuelas, J., 2013b. A unified framework for diversity gradients: the adaptive trait continuum. *Glob. Ecol. Biogeogr.* 22, 6–18. <http://dx.doi.org/10.1111/j.1466-8238.2012.00762.x>.
- Carnicer, J., Coll, M., Pons, X., Ninyerola, M., Vayreda, J., Penuelas, J., 2014. Large-scale recruitment limitation in Mediterranean pines: the role of *Quercus ilex* and forest successional advance as key regional drivers. *Glob. Ecol. Biogeogr.* 23, 371–384. <http://dx.doi.org/10.1111/geb.12111>.
- Castaldi, S., Carfora, A., Natale, A., Messere, A., Miglieta, F., Cotrufo, M.F., 2009. Inhibition of net nitrification activity in a Mediterranean woodland: possible role of chemicals produced by *Arbutus unedo*. *Plant Soil* 315, 273–283. <http://dx.doi.org/10.1007/s11104-008-9750-x>.
- Comps, B., Gómory, D., Letouzey, J., Thiébaud, B., Petit, R.J., 2001. Diverging trends between heterozygosity and allelic richness during postglacial colonization in the European beech. *Genetics* 157, 389–397. <http://dx.doi.org/10.1016/j.foreco.2007.04.018>.
- del Cacho, M., Estiarte, M., Penuelas, J., Lloret, F., 2013a. Inter-annual variability of seed rain and seedling establishment of two woody Mediterranean species under field-induced drought and warming. *Popul. Ecol.* 55, 277–289. <http://dx.doi.org/10.1007/s10144-013-0365-6>.
- del Cacho, M., Penuelas, J., Lloret, F., 2013b. Reproductive output in Mediterranean shrubs under climate change experimentally induced by drought and warming. *Perspect. Plant Ecol. Evol. Syst.* 15, 319–327. <http://dx.doi.org/10.1016/j.ppees.2013.07.001>.
- Egilla, J.N., Davies, F.T., Boutton, T.W., 2005. Drought stress influences leaf water content, photosynthesis, and water-use efficiency of *Hibiscus rosa-sinensis* at three potassium concentrations. *Photosynthetica* 43, 135–140. <http://dx.doi.org/10.1007/s11099-005-5140-2>.
- Esteban-Parra, M.J., Rodrigo, F.S., Castro-Diez, Y., 1998. Spatial and temporal patterns of precipitation in Spain for the period 1880–1992. *Int. J. Climatol.* 18, 1557–1574. [http://dx.doi.org/10.1002/\(SICI\)1097-0088\(19981130\)18:14<1557:AID-JOC328>3.3.CO;2-A](http://dx.doi.org/10.1002/(SICI)1097-0088(19981130)18:14<1557:AID-JOC328>3.3.CO;2-A).
- Fernández, M., Novillo, C., Pardos, J.A., 2006. Effects of water and nutrient availability in *Pinus pinaster* Ait. open pollinated families at an early age: growth, gas exchange and water relations. *New For.* 31, 321–342. <http://dx.doi.org/10.1007/s11056-005-8196-8>.
- Fiorotto, A., Papa, S., Fuggi, A., 2003. Litter-fall and litter decomposition in a low Mediterranean shrubland. *Bio Fert Soils* 39, 37–44. <http://dx.doi.org/10.1007/s00374-003-0675-5>.
- Gallardo, A., Rodríguez-Saucedo, J.J., Covelo, F., Fernández-Alés, R., 2000. Soil nitrogen heterogeneity in a Dehesa ecosystem. *Plant Soil* 222, 71–82. <http://dx.doi.org/10.1023/A:1004725927358>.
- Gargallo-Garriga, A., Sardans, J., Perez-Trujillo, M., Rivas-Ubach, A., Oravec, M., Vecerova, K., Urban, O., Jentsch, A., Kreyling, J., Beierkuhnlein, C., Parella, T., Penuelas, J., 2014. Opposite metabolic responses of shoots and roots to drought. *Sci. Rep.* 4, 1–7. <http://dx.doi.org/10.1038/srep06829>.
- Gargallo-Garriga, A., Sardans, J., Oravec, M., Urban, O., Jentsch, A., Kreyling, J., Beierkuhnlein, C., Parella, T., Penuelas, J., 2015. Warming differentially influences the effects of drought on stoichiometry and metabolomics in shoots and roots. *New Phytol.* 207, 591–603. <http://dx.doi.org/10.1111/nph.13377>.
- González-Hidalgo, J.C., Peña-Monné, J.L., de Luis, M., 2007. A review of daily soil erosion in Western Mediterranean areas. *Catena* 71, 193–199. <http://dx.doi.org/10.1016/j.catena.2007.03.005>.
- Gracia, C.A., Tello, E., Sabaté, S., Bellot, J., 1999. GOTILWA: an integrated model of water dynamics and forest growth. In: Rodà, F., Retana, J., Bellot, J., Gracia, C.A. (Eds.), *Ecology of Mediterranean Evergreen Oak Forests*. Springer, Berlin, pp. 163–178.
- Gracia, C., Burriel, J.A., Ibáñez, J.J., Mata, T., Vayreda, J., 2004. *Inventari Ecològic i Forestal de Catalunya*, vol. 9 CREA, Bellaterra, Mètodes ISBN: 84-932860-2-8.
- Gulías, J., Flexas, J., Abadía, A., Medrano, H., 2002. Photosynthetic responses to water deficit in six Mediterranean sclerophyll species: possible factors explaining the declining distribution of *Rhamnus ludovici-salvatoris*, an endemic Balearic species. *Tree Physiol.* 22, 687–697.
- IPCC, 2013. Summary for Policymakers. In: *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M., Tignor, S.K., Allen, J.] 10.1017/CBO9781107415324.
- Johnson-Maynard, J.L., Graham, R.C., Wu, L., Shouse, P.J., 2002. Modification of soil structural and hydraulic properties after 50 years of imposed chaparral and pine vegetation. *Geoderma* 110, 227–240. [http://dx.doi.org/10.1016/S0016-7061\(02\)00232-X](http://dx.doi.org/10.1016/S0016-7061(02)00232-X).
- Jump, A.S., Penuelas, J., 2006. Genetic effects of chronic habitat fragmentation in a wind-pollinated tree. *Proc. Natl. Acad. Sci. U. S. A.* 103, 8096–8100. <http://dx.doi.org/10.1073/pnas.0510127103>.
- Jump, A.S., Hunt, J.M., Martínez-Izquierdo, J.A., Penuelas, J., 2006a. Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Mol. Ecol.* 15, 3469–3480. <http://dx.doi.org/10.1111/j.1365-294X.2006.03027.x>.
- Jump, A.S., Hunt, J.M., Penuelas, J., 2006b. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob. Change Biol.* 12, 2163–2174. <http://dx.doi.org/10.1111/j.1365-2486.2006.01250.x>.
- Jump, A.S., Penuelas, J., Rico, L., Ramallo, E., Estiarte, M., Martínez-Izquierdo, J.A., Lloret, F., 2008. Simulated climate change provokes rapid genetic change in the Mediterranean shrub *Fumana thymifolia*. *Glob. Change Biol.* 14, 637–643. <http://dx.doi.org/10.1111/j.1365-2486.2007.01521.x>.
- Keenan, T., García, R., Friend, A.D., Zaehle, S., Gracia, C., Sabate, S., 2009. Improved understanding of drought controls on seasonal variation in Mediterranean forest

- canopy CO<sub>2</sub> and water fluxes through combined in situ measurements and ecosystem modelling. *Biogeosciences* 6, 1423–1444. <http://dx.doi.org/10.5194/bg-6-1423-2009>.
- Khosravifar, S., Yarnia, M., Khorshidi Benam, M.B., Hosseinzadeh Moghbeli, A.H., 2008. Effect of potassium on drought tolerance in potato cv. Agria. *J. Food Agric. Environ.* 6 (3&4), 236–241.
- Kröel-Dulay, G., Ransijn, J., Schmidt, I.K., Beier, C., De Angelis, P., de Dato, G., Dukes, J.S., Emmett, B., Estiarte, M., Garadnai, J., Kongstad, J., Kovács-Láng, E., Larsen, K.S., Liberati, D., Ogaya, R., Riis-Nielsen, T., Smith, A.R., Sowerby, A., Tietema, A., Penuelas, J., 2015. Increased sensitivity to climate change in disturbed ecosystems. *Nat. Commun.* 6, 6682. <http://dx.doi.org/10.1038/ncomms7682>.
- Laus, M.N., Soccio, M., Trono, D., Liberatore, M.T., Pastore, D., 2011. Activation of the plant mitochondrial potassium channel by free fatty acids and acyl-CoA esters: a possible defence mechanism in the response to hyperosmotic stress. *J. Exp. Bot.* 62, 141–154. <http://dx.doi.org/10.1093/jxb/erq256>.
- Liu, D., Ogaya, R., Barbeta, A., Yang, X., Penuelas, J., 2015. Contrasting impacts of continuous moderate drought and episodic severe droughts on the aboveground-biomass increment and litterfall of three coexisting Mediterranean woody species. *Glob. Change Biol.* 21, 4196–4209. <http://dx.doi.org/10.1111/gcb.13029>.
- Llorens, L., Penuelas, J., Estiarte, M., Bruna, P., 2004. Contrasting growth changes in two dominant species of a Mediterranean shrubland submitted to experimental drought and warming. *Ann. Bot.* 94, 843–853. <http://dx.doi.org/10.1093/aob/mch211>.
- Llusà, J., Penuelas, J., Alessio, G., Estiarte, M., 2006. Seasonal contrasting changes of foliar concentrations of terpenes and other volatile organic compound in four dominant species of a Mediterranean shrubland submitted to a field experimental drought and warming. *Physiol. Plant.* 127, 632–649. <http://dx.doi.org/10.1111/j.1399-3054.2006.00693.x>.
- Llusà, J., Penuelas, J., Alessio, G., Estiarte, M., 2008. Contrasting species-specific, compound-specific, seasonal, and interannual responses of foliar isoprenoid emissions to experimental drought in a Mediterranean shrubland. *Int. J. Plant Sci.* 169 (5), 637–645.
- Llusà, J., Penuelas, J., 2000. Seasonal patterns of terpene content and emission from seven Mediterranean woody species in field conditions. *Am. J. Bot.* 87 (1), 133–140.
- Milla, R., Castro-Díez, P., Maestro-Martínez, M., Montserrat-Martí, G., 2005. Relationships between phenology and the remobilization of nitrogen, phosphorus and potassium in branches of eight Mediterranean evergreens. *New Phytol.* 168, 167–178. <http://dx.doi.org/10.1111/j.1469-8137.2005.01477.x>.
- Moreno-de las Heras, M., Espigares, T., Merino-Martín, L., Nicolau, J.M., 2011. Water-related ecological impacts of rill erosion processes in Mediterranean-dry reclaimed slopes. *Catena* 84, 114–124. <http://dx.doi.org/10.1016/j.catena.2010.10.010>.
- Munné-Bosch, S., Penuelas, J., 2004. Drought-induced oxidative stress in strawberry tree (*Arbutus unedo* L.) growing in Mediterranean field conditions. *Plant Sci.* 166, 1105–1110. <http://dx.doi.org/10.1016/j.plantsci.2003.12.034>.
- Munné-Bosch, S., Penuelas, J., Asensio, D., Llusà, J., 2004. Airborne ethylene may alter antioxidant protection and reduce tolerance of holm oak to heat and drought stress. *Plant Physiol.* 136, 2937–2947. <http://dx.doi.org/10.1104/pp.104.050005>. discussion 3002.
- Nadal-Sala, D., Sabaté, S., Gracia, C., 2014. GOTILWA+: una herramienta para optimizar la gestión forestal adaptada al cambio climático. *Ambienta* 106–120.
- Nadal-Sala, D., Sabaté, S., Gracia, C., 2016. The relative importance of soil depth for Aleppo pine (*Pinus halepensis* Mill.) resilience in face of the increasing aridity promoted by climate change. *Ecosistemas* (in press).
- Nadal-Sala, D., Keenan, T.F., Sabaté, S., Gracia, C., 2017. Forest eco-physiological models: water use and carbon sequestration. *Managing Forest Ecosystems: The Challenge of Climate Change*. Springer International Publishingpp. 81–102.
- Ochoa-Hueso, R., Hernandez, R.R., Pueyo, J.J., Manrique, E., 2011. Spatial distribution and physiology of biological soil crust from semi-arid central Spain are related to soil chemistry and shrub cover. *Soil Biol. Biochem.* 43, 1894–1901. <http://dx.doi.org/10.1016/j.soilbio.2011.05.010>.
- Ogaya, R., Penuelas, J., 2004. Phenological patterns of *Quercus ilex*; *Phillyrea latifolia*; and *Arbutus unedo* growing under a field experimental drought. *Ecoscience* 11, 263–270.
- Ogaya, R., Penuelas, J., 2005. Decreased mushroom production in a holm oak forest in response to an experimental drought. *Forestry* 78, 279–283. <http://dx.doi.org/10.1093/forestry/cpi025>.
- Ogaya, R., Penuelas, J., 2007a. Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought. *Plant Ecol.* 189, 291–299. <http://dx.doi.org/10.1007/s11258-006-9184-6>.
- Ogaya, R., Penuelas, J., 2007b. Species-specific drought effects on flower and fruit production in a Mediterranean holm oak forest. *Forestry* 80 (3), 351–357. <http://dx.doi.org/10.1093/forestry/cpm009>.
- Ogaya, R., Llusà, J., Barbeta, A., Asensio, D., Liu, D., Alessio, G.A., Penuelas, J., 2014. Foliar CO<sub>2</sub> in a holm oak forest subjected to 15 years of climate change simulation. *Plant Sci.* 226, 101–107. <http://dx.doi.org/10.1016/j.plantsci.2014.06.010>.
- Ogaya, R., Barbeta, A., Bañou, C., Penuelas, J., 2015. Satellite data as indicators of tree biomass growth and forest dieback in a Mediterranean holm oak forest. *Ann. For. Sci.* 72, 135–144. <http://dx.doi.org/10.1007/s13595-014-0408-y>.
- Orshan, G., 1983. Approaches to the definition of Mediterranean growth forms. *Ecol. Stud.* 43, 86–100. [http://dx.doi.org/10.1007/978-3-642-68935-2\\_5](http://dx.doi.org/10.1007/978-3-642-68935-2_5).
- Padilla, F.M., Pugnaire, F.I., 2007. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Funct. Ecol.* 21, 489–495. <http://dx.doi.org/10.1111/j.1365-2435.2007.01267.x>.
- Penuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob. Change Biol.* 9, 131–140. <http://dx.doi.org/10.1046/j.1365-2486.2003.00566.x>.
- Penuelas, J., Filella, I., Llusà, J., Siscart, D., Pinol, 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. <http://dx.doi.org/10.1093/jxb/49.319.229>.
- Penuelas, J., Filella, I., Lloret, F., Piñol, J., Siscart, D., 2000. Effects of severe drought on water and nitrogen use by *Quercus ilex* and *Phillyrea latifolia*. *Biol. Plant.* 43 (1), 47–53.
- Penuelas, J., Lloret, F., Montoya, R., 2001. Severe drought effects on mediterranean woody flora in Spain. *For. Sci.* 47 (2), 214–218.
- Penuelas, J., Filella, I., Comas, P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Glob. Change Biol.* 8, 531–544. <http://dx.doi.org/10.1046/j.1365-2486.2002.00489.x>.
- Penuelas, J., Filella, I., Sabate, S., Gracia, C., 2005. Natural systems: terrestrial ecosystems. In: Llebot, J.E. (Ed.), *Rep. Clim. Chang. Catalonia. Inst. d'Estudis Catalans*, pp. 517–553.
- Penuelas, J., Ogaya, R., Boada, M., Jump, A.S., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography (Cop.)* 30, 829–837. <http://dx.doi.org/10.1111/j.2007.0906-7590.05247.x>.
- Penuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., Barbeta, A., Rivas-Ubach, A., Llusà, J., Garbulsky, M., Filella, I., Jump, A.S., 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Glob. Change Biol.* 19, 2303–2338. <http://dx.doi.org/10.1111/gcb.12143>.
- Penuelas, J., Sardans, J., Filella, I., Estiarte, M., Llusà, J., Ogaya, R., Carnicer, J., Bartrons, M., Rivas-Ubach, A., Grau, O., Peguero, G., Margalef, O., Pla, S., Stefanescu, C., Asensio, D., Preece, C., Liu, L., Verger, A., Rico, L., Barbeta, A., Sperlich, D.A.-C.A.-G.-A., Farré-Armengol, G., Fernández-Martínez, M., Liu, D., Zhang, C., Urbina, I., Camino, M., Ubach, A., Wheat, C., Nadal, D., Sabaté, S., Gracia, C., Vives, M., Terradas, J., 2016. Impactes del canvi climàtic sobre els ecosistemes terrestres catalans. A: Martín Vide, J. (Coord.). *Tercer Informe sobre el canvi climàtic de Catalunya*. Generalitat de Catalunya: Barcelona ISBN 9788499653174 (IEC). ISBN 9788439394488 (Generalitat de Catalunya).
- Piñol, J., Terradas, J., Lloret, F., 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Int. J. Wildl. fire* 11, 95–106. <http://dx.doi.org/10.1023/A:1005316632105>.
- Prieto, P., Penuelas, J., Lloret, F., Llorens, L., Estiarte, M., 2009. Experimental drought and warming decrease diversity and slow down post-fire succession in a Mediterranean shrubland. *Ecography (Cop.)* 32, 623–636. <http://dx.doi.org/10.1111/j.1600-0587.2009.05738.x>.
- Rico, L., Ogaya, R., Barbeta, A., Penuelas, J., 2014. Changes in DNA methylation fingerprint of *Quercus ilex* trees in response to experimental field drought simulating projected climate change. *Plant Biol.* 16, 419–427. <http://dx.doi.org/10.1111/plb.12049>.
- Riera, P., Penuelas, J., Farreras, V., Estiarte, M., 2007. Valuation of climate-change effects on Mediterranean shrublands. *Ecol. Appl.* 17, 91–100. [http://dx.doi.org/10.1890/1051-0761\(2007\)017\[0091:VOCEOM\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2007)017[0091:VOCEOM]2.0.CO;2).
- Rivas-Ubach, A., Sardans, J., Perez-Trujillo, M., Estiarte, M., Penuelas, J., 2012. Strong relationship between elemental stoichiometry and metabolome in plants. *Proc. Natl. Acad. Sci. U. S. A.* 109, 4181–4186. <http://dx.doi.org/10.1073/pnas.1116092109>.
- Rivas-Ubach, A., Gargallo-Garriga, A., Sardans, J., Oravec, M., Mateu-Castell, L., Pérez-Trujillo, M., Parella, T., Ogaya, R., Urban, O., Penuelas, J., 2014. Drought enhances folivory by shifting foliar metabolomes of *Quercus ilex* trees. *New Phytol.* 202, 874–885. <http://dx.doi.org/10.1111/nph.12687>.
- Rivas-Ubach, A., Barbeta, A., Sardans, J., Guenther, A., Ogaya, R., Oravec, M., Urban, O., Penuelas, J., 2016. Topsoil depth substantially influences the responses to drought of the foliar metabolomes of Mediterranean forests. *Perspect. Plant Ecol. Evol. Syst.* 21, 41–54. <http://dx.doi.org/10.1016/j.ppees.2016.06.001>.
- Roeckner, E.K., Arpe, L., Bengtsson, M., Christoph, M., Claussen, L., Dümenil, M., Esch, M., Giorgetta, U., Schlese, U., Schulzweida, 1996. The atmospheric general circulation model ECHAM4: Model description and simulation of present-day climate. *Max Planck Institut für Meteorologie, Report No. 218*, Hamburg, Germany, 90 pp.
- Ruiz-Sinoga, J.D., Gabarón Galeote, M.A., Martínez Murillo, J.F., García Marín, R., 2011. Vegetation strategies for soil consumption along a pluviometric gradient in southern Spain. *Catena* 84 (1–2), 12–20. <http://dx.doi.org/10.1016/j.catena.2010.08.011>.
- Ruiz-Sinoga, J.D., Pariente, S., Romero Díaz, A., Martínez Murillo, J.F., 2012. Variability of relationships between soil organic carbon and some soil properties in Mediterranean rangelands under different climatic conditions (South of Spain). *Catena* 94, 17–25. <http://dx.doi.org/10.1016/j.catena.2011.06.004>.
- Sardans, J., Penuelas, J., 2005. Drought decreases soil enzyme activity in a Mediterranean *Quercus ilex* L. forest. *Soil Biol. Biochem.* 37, 455–461. <http://dx.doi.org/10.1016/j.soilbio.2004.08.004>.
- Sardans, J., Penuelas, J., 2007. Drought changes the dynamics of trace element accumulation in a Mediterranean *Quercus ilex* forest. *Environ. Pollut.* 147, 567–583. <http://dx.doi.org/10.1016/j.envpol.2006.10.008>.
- Sardans, J., Penuelas, J., 2010. Soil enzyme activity in a Mediterranean forest after six years of drought. *Soil Sci. Soc. Am. J.* 74, 838. <http://dx.doi.org/10.2136/sssaj2009.0225>.
- Sardans, J., Penuelas, J., 2013a. Tree growth changes with climate and forest type are associated with relative allocation of nutrients, especially phosphorus, to leaves and wood. *Glob. Ecol. Biogeogr.* 22, 494–507. <http://dx.doi.org/10.1111/geb.12015>.
- Sardans, J., Penuelas, J., 2013b. Plant-soil interactions in Mediterranean forest and shrublands: impacts of climatic change. *Plant Soil* 365, 1–33. <http://dx.doi.org/10.1007/s11104-013-1591-6>.
- Sardans, J., Penuelas, J., 2014. Climate and taxonomy underlie different elemental concentrations and stoichiometries of forest species: the optimum biogeochemical niche. *Plant Ecol.* 215, 441–455. <http://dx.doi.org/10.1007/s11258-014-0314-2>.
- Sardans, J., Penuelas, J., Rodà, F., 2006. Plasticity of leaf morphological traits, leaf

- nutrient content, and water capture in the Mediterranean evergreen oak *Quercus ilex* subsp. *ballota* in response to fertilization and changes in competitive conditions. *Ecoscience* 13 (2), 258–270. <http://dx.doi.org/10.2980/i1195-6860-13-2-258.1>.
- Sardans, J., Penuelas, J., Estiarte, M., Prieto, P., 2008a. Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland. *Glob. Change Biol.* 14, 2304–2316. <http://dx.doi.org/10.1111/j.1365-2486.2008.01656.x>.
- Sardans, J., Penuelas, J., Ogaya, R., 2008b. Drought-induced changes in C and N stoichiometry in a *Quercus ilex* Mediterranean forest. *For. Sci.* 54, 513–522.
- Sardans, J., Penuelas, J., Prieto, P., Estiarte, M., 2008c. Drought and warming induced changes in P and K concentration and accumulation in plant biomass and soil in a Mediterranean shrubland. *Plant Soil* 306, 261–271. <http://dx.doi.org/10.1007/s11104-008-9583-7>.
- Sardans, J., Penuelas, J., Prieto, P., Estiarte, M., 2008d. Changes in Ca, Fe, Mg, Mo Na, and S content in a Mediterranean shrubland under warming and drought. *J. Geophys. Res. Biogeosci.* 113, 1–11. <http://dx.doi.org/10.1029/2008JG000795>.
- Sardans, J., Rivas-Ubach, A., Penuelas, J., 2011. Factors affecting nutrient concentration and stoichiometry of forest trees in Catalonia (NE Spain). *For. Ecol. Manage.* 262, 2024–2034. <http://dx.doi.org/10.1016/j.foreco.2011.08.019>.
- Sardans, J., Penuelas, J., Coll, M., Vayreda, J., Rivas-Ubach, A., 2012a. Stoichiometry of potassium is largely determined by water availability and growth in Catalanian forests. *Funct. Ecol.* 26, 1077–1089. <http://dx.doi.org/10.1111/j.1365-2435.2012.02023.x>.
- Sardans, J., Rivas-Ubach, A., Penuelas, J., 2012b. The C:N:P stoichiometry of organisms and ecosystems in a changing world: a review and perspectives. *Perspect. Plant Ecol. Evol. Syst.* 14, 33–47. <http://dx.doi.org/10.1016/j.ppees.2011.08.002>.
- Sardans, J., Rivas-Ubach, A., Penuelas, J., 2012c. The elemental stoichiometry of aquatic and terrestrial ecosystems and its relationships with organismic lifestyle and ecosystem structure and function: a review and perspectives. *Biogeochemistry* 111, 1–39. <http://dx.doi.org/10.1007/s10533-011-9640-9>.
- Sardans, J., Rivas-Ubach, A., Estiarte, M., Ogaya, R., Penuelas, J., 2013. Field-simulated droughts affect elemental leaf stoichiometry in Mediterranean forests and shrublands. *Acta Oecol.* 50, 20–31. <http://dx.doi.org/10.1016/j.actao.2013.04.002>.
- Sardans, J., Janssens, I.A., Alonso, R., Veresoglou, S.D., Rilling, M.C., Sanders, T., Carnicer, J., Filella, I., Farré-Armengol, G., Penuelas, J., 2015. Elemental composition of European forest tree species results from evolutionary traits and the present environmental and competitive conditions. *Glob. Ecol. Biogeogr.* 24, 240–255. <http://dx.doi.org/10.1111/geb.12253>.
- Sardans, J., Alonso, R., Janssens, I.A., Carnicer, J., Veresoglou, S., Rilling, M.C., Fernandez-Martinez, M., Sanders, T.G.M., Penuelas, J., 2016. Foliar and soil concentrations and stoichiometry of nitrogen and phosphorous across European *Pinus sylvestris* forests: relationships with climate, N deposition and tree growth. *Funct. Ecol.* 30 (5), 676–689. <http://dx.doi.org/10.1111/1365-2435.12541>.
- Serrano, L., Penuelas, J., Ogaya, R., Savé, R., 2005. Tissue-water relations of two co-occurring evergreen Mediterranean species in response to seasonal and experimental drought conditions. *J. Plant Res.* 118, 263–269. <http://dx.doi.org/10.1007/s10265-005-0220-8>.
- Specht, R.L., 1981. Primary production in Mediterranean-climate ecosystems re-generating after fire. In: Di Castri, F., Goodwall, D.W., Specht, R.L. (Eds.), *Mediterranean-Type Ecosystems*. Elsevier, Amsterdam, The Netherlands, pp. 257–268.
- Sterner, R., Elser, J., 2002. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, NJ.
- Stone, L.F., Moreira, J.A., 1996. Response of upland rice ploughing depth, potassium fertilization, and soil water status. *Pesq. Agrop. Bras.* 31, 885–895.
- Vilagrosa, A., Morales, F., Abadía, A., Bellot, J., Cochard, H., Gil-Pelegrín, E., 2010. Are symplast tolerant to intense drought conditions and xylem vulnerability to cavitation coordinated? An integrated analysis of photosynthetic, hydraulic and leaf level processes in two Mediterranean drought-resistant species. *Environ. Exp. Bot.* 69, 233–242. <http://dx.doi.org/10.1016/j.envexpbot.2010.04.013>.