Chapter 4

TREE GROWTH DECLINE ON RELICT WESTERN-MEDITERRANEAN MOUNTAIN FORESTS: CAUSES AND IMPACTS

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ABSTRACT

Climate variability and land-use modifications are among the main components of global change, but their combined effects on forests have rarely been addressed. Relict tree species from the Mediterranean Basin are appropriate experimental models to investigate these effects since they grow in climatically-stressed areas, which have undergone intensive land-use changes. We hypothesize that intense logging and overgrazing could be related to forests decline, but also the abandonment of traditional land-use practices and subsequent enhancement of density-dependent factors acted as a predisposing stressor that modified the response of several tree species from the Mediterranean Basin to recent climate change. We summarize results from current forest structure and mortality patterns, as well as relationships between tree radial-growth and regional climatic trends in four tree species from western Mediterranean Mountains: Silver fir (*Abies alba*) from the North of Spain, Pinsapo fir (*Abies pinsapo*) from south

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Spain, European black pine (*Pinus nigra* ssp. *salzmannii*) from south-east Spain, and Atlas cedar (*Cedrus atlantica*) from north Morocco. Regional warming and a long-term decrease in precipitation were recorded over the second half of the 20th century. Moreover, an increase in the variability of local year-to-year precipitation patterns was recorded in the study area, beginning in the 1980s. At the low-elevation sites tree mortality were higher than in the high-elevation sites. Radial growth began to decline in the early 1980s in the four studied species. A sharp growth reduction occurred in extreme drought events but less growth decline was observed at the highest/moister sites. Climatic variability showed a significant effect in the four tree species, however it could not fully account for this growth decline. Our results suggest that human use may enhance (or mitigate) the vulnerability of relict Mediterranean tree species to climate change.

1. INTRODUCTION

There is a general recognition from scientists that climatic warming and land-use modifications, two of the most conspicuous components of current global change (Vitousek 1994), have the potential to profoundly change the distribution and growth of tree populations (Brubaker 1986; Parmesan 2006). In most situations, these two components are likely to operate as concomitant stressors on forest ecosystems, making it difficult to disentangle their separate impacts. Both components influence the distribution of mountain forests in the Mediterranean Basin, since secular land-use has shaped forest structure and climatic warming is severely affecting the growth of tree species, especially those that are highly sensitive to water stress (Grove and Rackham 2001). Many studies reporting on species, and even biome, distribution shifts in Mediterranean mountains attribute the majority of observed changes to either climate change or land-use alterations, or are unable to provide a quantitative separation of their relative contributions (Peñuelas and Boada 2003). Recent findings, however, suggest that the shift of Mediterranean tree species to higher elevations may be linked to both regional warming and land-use changes (Peñuelas *et al.* 2007).

An important consideration in the analysis of the interactions between climate and historical land-use is that many species' ranges are not in equilibrium with the climate because their current distribution was shaped by additional factors such as historical disturbances (Svenning and Skov 2004). Disturbances include land-use modification which may alter density-dependent factors at the stand level, which in turn could impact the responses of trees to climatic stress (Linares *et al.* 2010). For instance, Atlas cedar (*Cedrus atlantica*) stands in intensively logged and overgrazed areas from north Morocco are leading to their replacement by species more resistant to water deficit and human disturbances. However, a decrease in logging activities, as recorded in Pinsapo fir (*Abies pinsapo*) forests from south Spain, may lead to an increase in tree density and basal area, thus reducing soil-water availability and predisposing trees to subsequent drought-induced decline (Linares *et al.* 2009a). Between the strict protection of pinsapo fir and the intensive perturbation regime observer in Atlas cedar, we have the study cases of silver fir (*Abies alba*) and black pine (*Pinus nigra*), which have been harvested following management plans. Furthermore, the potential of past land-use changes to modify the functional limit of a tree species might be greater at the edge of its natural range. Therefore, marginal tree populations may be particularly well-suited to assess the modulating effects of density-dependent factors on climatic stress.

Relict tree species are a model case for this type of assessment. They usually form isolated and small populations, and are regarded as very vulnerable in the face of climatic oscillations and stochastic extinction phenomena (Davis and Shaw 2001). On the other hand, they are often selected as target species in conservation politics, and their ranges are being increasingly preserved within protected areas. In the case of Mediterranean tree species, this conservation effort has resulted in an elimination of traditional uses (e.g., logging, grazing) with subsequent increases in tree density. In spite of the importance of endemic tree species as palaeo-genetic reservoirs, many uncertainties still remain about how the synergistic effects of climatic warming and habitat modification affect their conservation.

Phylogeographic data indicate that Mediterranean mountains are very important for the conservation of many relict tree species and the maintenance of biodiversity (Medail and Diadema 2009). Mediterranean firs, pines and cedars exemplify plant diversification related to long-term climatic, geological, and evolutionary changes. On the other hand, the current relict status of these species constitutes an example of endangered ecosystems, highly vulnerable to global change. Indeed, based on modeling results, Mediterranean regions might be some of the most vulnerable areas for the loss of tree species due to climatic warming (IPCC 2007). Events of regional-scale vegetation mortality appear to be increasing in a variety of biomes throughout the Earth and are frequently associated with increased temperatures, droughts, and often (but not always) with outbreaks of biotic agents such as insects and pathogens (Allen *et al.* 2010). Atmospheric warming recorded over the western Mediterranean during the 20th century was ca. +1.6ºC, with years like 1994 and 1995 being among the warmest of the past century (Giorgi 2002). In addition, a 20% reduction in total precipitation has been observed in the western Mediterranean Basin during the last 50 years (Piervitali *et al.* 1997). Rodrigo *et al.* (1999) reported an overall trend of decreasing precipitation in southern Spain from 1980 to present. In this area, the last 25 years have been characterized by severe droughts, which caused several forest-dieback episodes (Peñuelas *et al.* 2001). Extreme climate events such as successive and intense droughts may cause sudden growth declines and pulses of elevated tree mortality (Linares *et al.* 2009a). This increase in year-to-year precipitation variability might be expected to more severely affect populations of relict trees growing near the species' climatic tolerance limit.

2. STUDY SPECIES AND SITES

2.1. Silver Fir (*Abies alba*) Forest from the Aragón Pyrenees (North Spain)

The Pyrenees constitute a transitional area from the more humid northern margin to the drier southern one, where Mediterranean vegetation becomes dominant. Several *Abies alba* Mill. populations have been studied by Camarero et al. (2002, 2011) in the Aragón Pyrenees, NE Spain (Figure 1), where silver fir stands are usually found at wet sites on north-facing slopes forming pure or mixed stands with *Fagus sylvatica* or *Pinus sylvestris*. Most studied stands are located on marls and limestones, which generate basic soils, or on moraine deposits with rocky but deep soils. The most used method for timber harvesting in the study area was the diameter limit cutting, which mostly affected fast-growing and big trees. During the 20th

century, logging intensity in the Pyrenees was greater in the 1950s, but no data are available on how widespread it was in the region (Cabrera 2001).

In the Aragón Pyrenees, silver fir decline was characterized by defoliation and high mortality rates mostly affecting low-elevation sites since the 1980s (Camarero *et al.* 2000, 2002). Extensive field surveys have been performed where silver fir formed forests across the Aragón Pyrenees. Camarero *et al.* (2011) sampled at least one site in each 10-km^2 grid with silver fir forest in the Aragón Pyrenees (Figure 1). At each site, 10-15 dominant trees were selected for sampling, giving a total of 378 sampled trees. Several topographical variables have been obtained for each site and tree, as the size of each tree, or its vigor (percentage of crown defoliation). Declining trees were considered as those with crown defoliation greater than 50%, and declining sites were regarded as those with more than 25% trees with such a degree of defoliation decline.
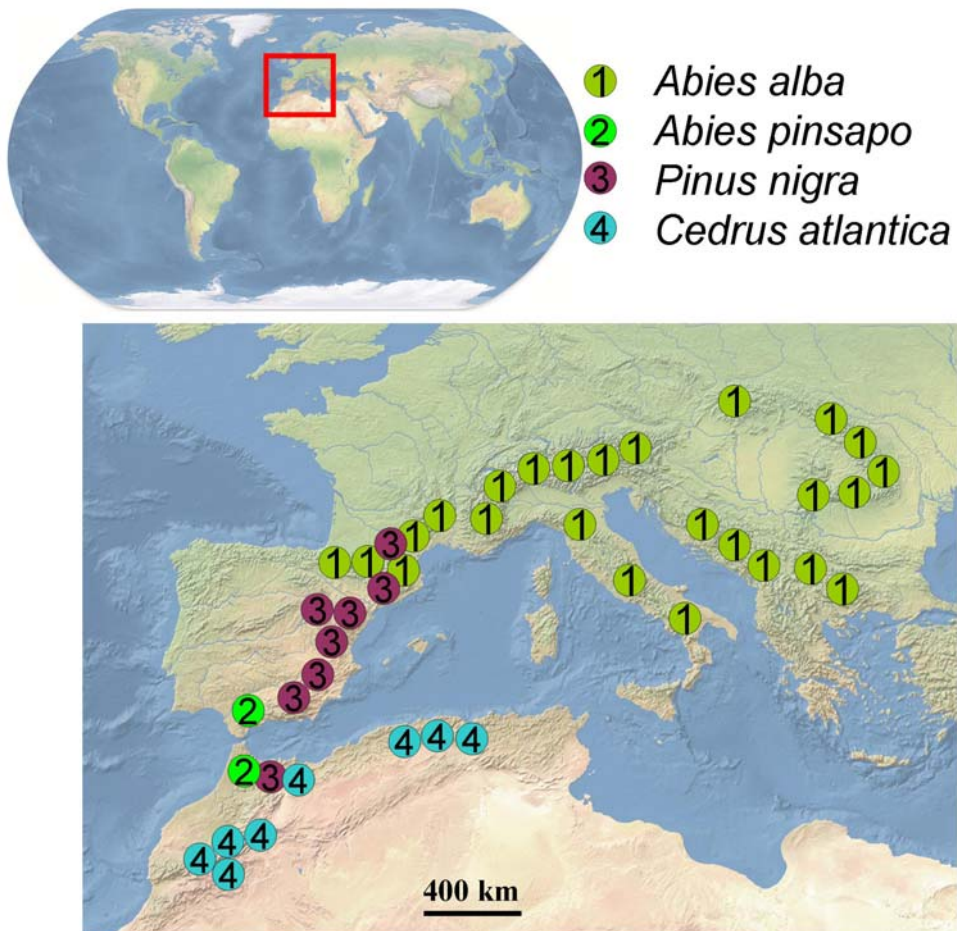

Figure 1. Study area (inset) and geographical distribution of the studied tree species: *Abies alba* (1), *Abies pinsapo* (2), *Pinus nigra* ssp. s*alzmannii* (3), and *Cedrus atlantica* (4).

2.2. Pinsapo Fir (*Abies pinsapo*) Forest from the Sierra de las Nieves (South Spain)

As we have noted above, relict tree species and isolated populations are commonly found in the mountains of the Mediterranean Basin. This is the case for *Abies pinsapo* Boiss., a relict fir species which is endemic to south Spain and north Morocco (Linares and Carreira 2009). It belongs to the group of the circum-Mediterranean fir species, most of which are restricted to small and isolated populations located in coastal mountain ranges within the Mediterranean Basin (Figure 1). Currently, *A. pinsapo* is found only in about 3600 ha in south Spain, mainly on north-facing slopes, 1000 m a.s.l. and higher. Fragmented populations of *A. pinsapo* experienced an expansion and densification of the remaining stands following the implementation of conservation measures in the 1950s, such as the cessation of logging and grazing by domestic animals (Linares and Carreira 2009). For example, in our study area (see below) *A. pinsapo* occupied ca. 724 ha in 1936, ca. 1500 ha in 1957, 3027 ha in 1993, and 3956 ha in 2002 (Linares *et al.* 2009a).

The study area for *A. pinsapo* is located in its eastern distribution limit (Sierra de las Nieves Natural Park), near the Mediterranean coast (36º 40'- 36º 44' N, 4º 55'- 5º 01' W; Figure 1). This area was chosen because most of the current *A. pinsapo* populations are located in this area and several episodes of fir decline have been observed here since 1994 (Linares *et al.* 2009a). In the study area, the mean annual temperature is 14.7ºC and the annual precipitation ranges from 800 mm in the lower sites to approximately 2000 mm in the upper study sites. Rainfall patterns are distinctly Mediterranean, with ca. 80% of all the precipitation falling between October and May, while summers are dry and long.

2.3. European Black Pine (*Pinus nigra*) Forest from the Sierra de Cazorla (South-East Spain)

European black pine (*Pinus nigra* Arnold) is a circum-Mediterranean pine species. Its natural range extends from Spain and north Morocco to Austria, Turkey and Cyprus. Most forests occur in mountainous areas between 1000 and 1500 m a.s.l. As a result, its populations are fragmented and exhibit high morphological, physiological and ecological variability. Numerous subspecies, varieties, and forms have been named following that diversity; five subspecies are currently recognized: *nigra*, *salzmannii*, *dalmatica*, *pallasiana* and *laricio* (Alejano and Martínez 1996).

Pinus nigra ssp. *salzmannii* Dunal (Franco) (*Pinus nigra* or Black pine hereafter) is native to the calcareous mountains of southeast France, eastern Spain and northern Morocco. French and Moroccan populations cover no more than 4000 ha, but *Pinus nigra* is the dominant tree species in 544.286 ha of Spanish forests (Figure 1).

In southeast Spain (our study area), *Pinus nigra* is found in ten separate mountain ranges (Cazorla-Segura-Castril, Mágina, Sagra, Huétor, Baza, Nevada, Almijara, María, Lúcar and Filabres) all of which are part of the Baetic Mountain Range (Figure 1). The ecology and management of *Pinus nigra* forests from the Cazorla-Segura area (ca. 60.000 ha) have been extensively studied during the last decade; all the studies and results we report here were carried out in this mountain range, unless otherwise stated.

Cazorla-Segura mountain range has a Mediterranean type climate. Snowfalls and frost are common during the winter, but summers are dry and hot. At the core of Cazorla-Segura forests, the average rainfall is 1075 mm, of which 55 mm occur during the summer, and mean monthly temperatures range from 5.1ºC in February to 22.3ºC in August. *Pinus pinaster, P. halepensis*, *Juniperus oxycedrus*, *Quercus ilex* and *Q. faginea* are possible companions of Black pine in those localities where it mixes with other tree species, but *Pinus nigra* stands are mostly monospecific in the study area. Shrub species such as *Juniperus communis*, *Crataegus monogyna*, *Rosa* sp., *Amelanchier ovalis*, *Berberis hispanica* and *Satureja montana* are frequent across the natural distribution area of *Pinus nigra* in the Baetic Mountain Range. Most forests from Cazorla-Segura have been harvested following management plans since the late 19th Century. At that time, *Pinus nigra* forests were put under the shelterwood method, with a shelter-phase of 20 years and a rotation period of 120 years. This silvicultural method changed to an uneven-aged system some decades later, due to the difficulties in achieving successful natural regeneration. Since 1986, Cazorla-Segura mountain range forms part of a Natural Park, well known for its biological richness which includes an important number of endemic species.

2.4. Atlas Cedar (*Cedrus atlantica*) Forest from North Morocco.

The genus Cedrus may once have been present in coastal mountains of the former Tethys Sea from north-western Africa and southern Europe to western Asia, including the rising Himalayas (Cheddadi *et al.* 2009). During the Pleistocene, ice ages and emerging deserts isolated the western, central, and eastern populations, leading to speciation and caused the extinction of the genus in Europe. Currently, this genus includes three extant species native from the Mediterranean mountains and one species from the Himalaya: *Cedrus atlantica* (Endl.) Manetti ex Carrière, in Algeria and Morocco; *Cedrus libani* Rich., in Asia Minor; *Cedrus brevifolia* (Hooker fil.) Henry, in Cyprus; and *Cedrus deodara* Don, in the Himalaya.

The Atlas cedar forests cover an area of over 130,000 ha (Cheddadi *et al.* 2009; Figure 1) distributed in Morocco (Rif, Middle Atlas, and north-eastern High Atlas) and Algeria (Aurès, Belezma, Hodna, Djbel Babor, Djurdjura, Blida and Ouarsenis). *C. atlantica* occurs at elevations of 1300 to 2600 m a.s.l., where the amount of annual rainfall ranges from 500 to 2000 mm and the minimum temperature of the coldest month ranges between -1 and -8ºC (Benabid 1994; Mhirit 1994). The Middle Atlas in northern Morocco is home of about the 80% of the Atlas cedar forest area (ca. 100,000 ha; Benabid, 1994). We summarize here results from stands of *C. atlantica* located at the Ifrane-Azrou forests (Ifrane National Park, northern Morocco). The Atlas cedar has relatively wide tolerances with regard to climate and soil type. Middle Atlas cedar forests contain several evergreen (holm oak, *Quercus rotundifolia*; prickly juniper, *Juniperus oxycedrus*; European holly, *Ilex aquifolium*) and deciduous (*Acer opalus*, *Crataegus laciniata*) tree and shrub species. The most abundant tree species in the stands studied was *Q. rotundifolia*, mostly regenerated as sprouts.

3. CLIMATIC TRENDS AND TREE GROWTH DECLINE IN RELICT WESTERN MEDITERRANEAN FORESTS

Multiproxy reconstructions of seasonal temperature show that the late 20th- and early 21st-century European climate was very likely warmer than that at any time during the past 500 years (Luterbacher *et al.* 2004). This agrees with findings from our analysis of the 19th-20th centuries on a regional scale. Spring and winter showed the greatest temperature increases, while summer temperature exhibited a milder increase since 1970 (see for instance results from Ifrane, north Morocco, at Figure 2). Winter average temperatures during the period from 1500 to 1900 were lower ~0.5°C (0.25°C for annual mean temperatures) compared to the 20th century, while summer temperatures did not show systematic lower values at century-scale, relative to present conditions (Luterbacher *et al.* 2004; Xoplaki *et al.* 2004; Xoplaki *et al.* 2005). On the other hand, successive and severe droughts may cause abrupt growth declines and pulses of elevated tree mortality and are expected to most severely affect tree populations growing near the species' climatic tolerance limit. Annual precipitation showed a significant negative trend. In addition, the greatest precipitation decrease was found in the spring; this was strongly related to the 20th century tree growth decline in the four studied species (see below).

Warming-related tree growth decline and associated increased mortality risk are recurrent phenomena that have been reported in a variety of forest communities around the world (Allen *et al.* 2010). Drought-induced growth decline has been recently noted in forests subjected to water deficit, such as most of those located in the Mediterranean Basin (Peñuelas *et al.* 2001). These observations raise the possibility that such growth reduction may be occurring in response to ongoing climate warming. For instance, in the past 25 years, severe drought events characterized by high temperatures and low precipitation caused intense forest-dieback episodes throughout Europe (Peñuelas *et al.* 2001; Bigler *et al.* 2004; Dobbertin 2005) and North America (van Mantgem and Stephenson 2007; McDowell *et al.* 2008). Results reported here link growth decline with increasing dryness in the Mediterranean Basin.

Warming-induced drought may intensify physiological stress on long-lived woody vegetation, leading to sudden tree growth reduction. Moreover, growth decline in response to severe droughts may trigger widespread mortality which can transform forested landscapes at regional to local scales (Galiano *et al.* 2010). Currently, no consistent mechanism exists to explain why some trees die during drought, but the general consensus is that mortality depends on the whole-tree water status and carbon budget (McDowell *et al.* 2008). Several studies have reported low relative growth, negative growth trends, higher variation in growth, and greater sensitivity to climate as the characteristic growth patterns of declining and dying trees. Therefore, to the extent that secondary growth is correlated with the whole-tree carbon budget, wood growth would be expected to be a reliable indicator of tree decline. On summary, reduced wood formation occurs before visual symptoms of decline and tree death appear, highlighting the usefulness of dendrochronological analyses to investigate the ecological implications of climate-driven changes in forest dynamics and to forecast the impending tree decline (Bigler *et al.* 2004; Linares *et al.* 2009a, 2011). In addition, contrasting growth responses to water stress among different age-class trees might help us to understand their vulnerability to climatic change (see Atlas cedar study case below).
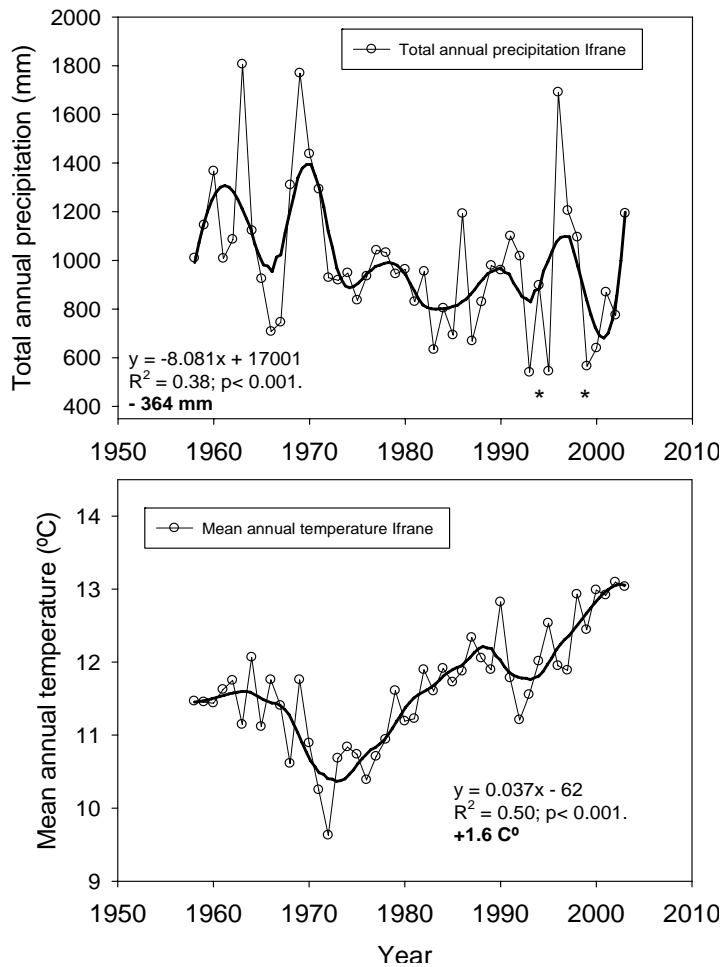
Figure 2. Local data for annual mean temperature and annual total precipitation spanning 1958-2003 from the Ifrane meteorological station (33° 32'N, 5° 07' W, 1630 m; ~14 km apart from the studied Atlas cedar forest). Smoothed lines indicate the long-term trends according to polynomial regression, and weights computed from the Gaussian density function (LOESS, see Zuur *et al.* 2007). The linear regression performed over the long-term trends and the average slopes are also noted; * indicates drought events registered in 1993 and 1995.

It is well established that *A. alba* stem growth is negatively effected by high temperature conditions during the growing season and in years prior to it (Carrer *et al.* 2010; Macias *et al.* 2006; Camarero *et al.* 2011). Recent results obtained by Camarero *et al.* suggest that *A. alba* growth decline is more likely related to temperature-induced drought stress than to low-precipitation events pattern, since no significant extreme low-precipitation events were recently recorded in our study area and rainy years prevailed since 1960 (excepting 1965 and to less extent 1989). By opposite, mean annual temperature has been systematically above average values since 1981 onwards.

Rising temperatures increase the atmospheric vapour-pressure deficit and the soil water evaporation, resulting in greater water loss. Moreover, temperature rises may affect

negatively the *A. alba* trees carbon storage, because the rate of carbohydrate consumption required to maintain cell metabolism (respiration) is strongly linked to temperature (Atkin *et al.* 2005). This hypothesis could be supported by the marked growth decline (Figure 3), and subsequent *A. alba* mortality, observed after 1986-1990 and 1997-1998 extreme hot events (Camarero *et al.* 2011), compared to growth decline and mortality induced by 1965 drought event, when lower mean temperatures could have prevented or alleviate water stress.
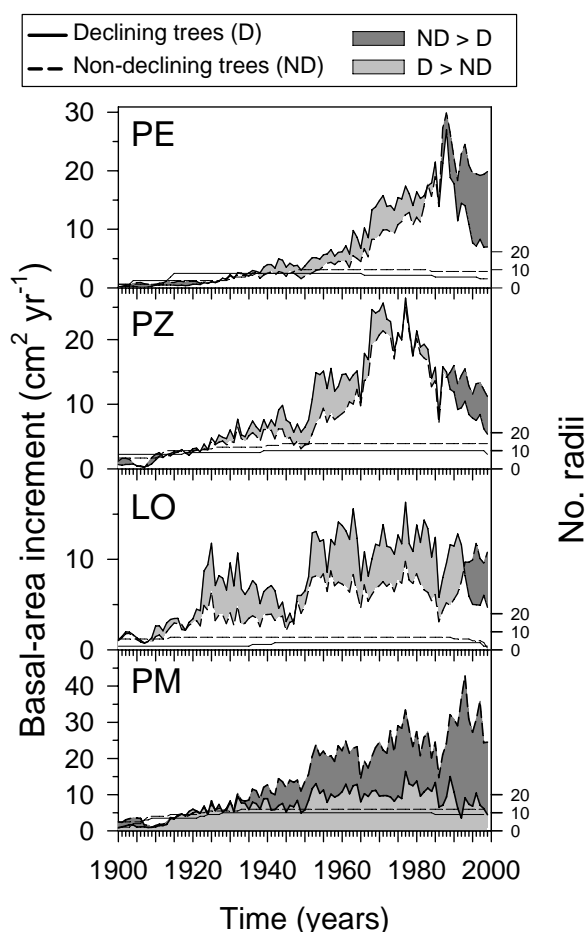

Figure 3. Trends in basal-area increment of silver fir (*Abies alba*) individuals from the Spanish Pyrenees. The continuous line and dashed lines correspond to declining and non-declining trees, respectively. Sample size (right axes) is displayed with the same symbols in the lower parts of each graph. Codes (PE, LZ, LO, PM) refer to different populations (see also Camarero *et al.* 2011).

Analysis of *A. pinsapo* ring-width chronologies show that, on average, recent radial growth has been the highest in the uppermost *A. pinsapo* stands (1700 m a.s.l., Linares *et al.* 2009a). The lower-elevation site (1200 m) has the highest year-to-year variability in growth and a higher mean correlation of all series with the master chronology, which suggests *A. pinsapo* growth, at the lower-elevation, is more subjected to external forces such as climate-related stress. However, the proportion of growth variance explained by climate was in some

cases higher in the mid- and high-elevation sites (1550 and 1700 m, see Linares *et al.* 2009a), suggesting that additional factors, such as human perturbations, may be playing a major role in *A. pinsapo* growth rates at the lowest elevation (see also Linares and Carreira 2009).
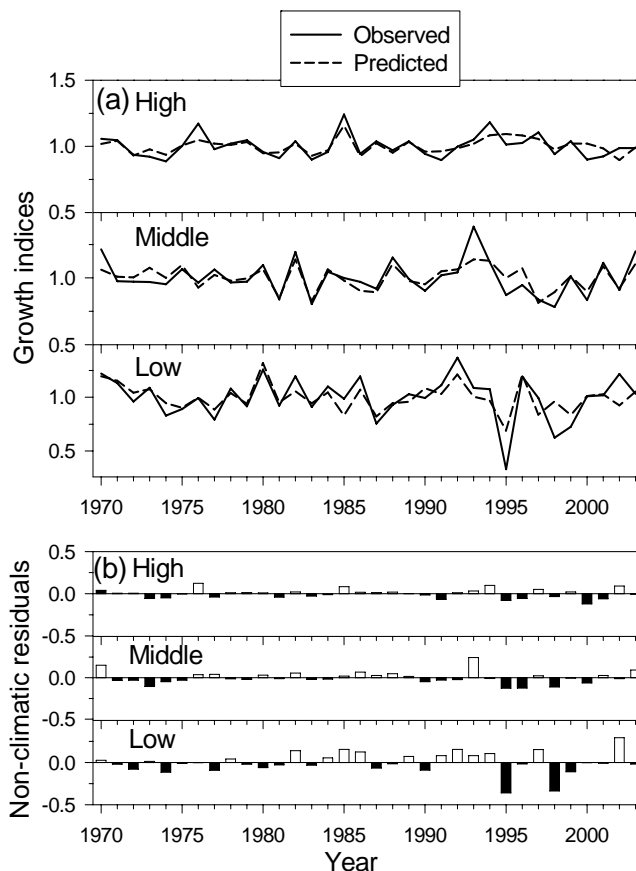

Figure 4. Comparison between the observed and predicted *A. pinsapo* growth indices (a) and residuals after extracting the climatic information (b). The non-climatic growth residuals (b) were obtained after subtracting the predicted growth indices based on the response function from the observed indices. In (b), open bars are positive residuals and solid bars are negative residuals. Low, Middle and High refer to contrasting elevations (1200, 1550 and 1700 m a.s.l.) along the distribution area of *A pinsapo*.

In the low- and mid-elevation sites, we identified a positive relationship between *A. pinsapo* growth and previous October and current June precipitation. In addition, previous December temperature showed a positive relationship with *A. pinsapo* tree-ring width at the mid-elevation site. A positive relationship was identified at the high-elevation site between late-winter and early-spring temperature and growth. The observed *A. pinsapo* radial-growth indices (Figure 4a) indicated negative departures from the climate-predicted indices in 1995 and 1998 in all sites, but these non-climatic residuals were more negative at the low-elevation site (Figure 4b).

Findings obtained by Linares and Tíscar in *Pinus nigra* forests suggest that growth response to rising temperatures varies among study sites following sub-regional geographic

and climatic ranges, as has been suggested by previous studies of Quaternary climatic changes (Linares and Tíscar 2010, 2011). Climate conditions in the autumn prior to active growth and in the current spring were consistently and significantly correlated with *Pinus nigra* growth. However, winter temperatures may be also important for assessing the potential impacts of climate change on stands at higher elevations.
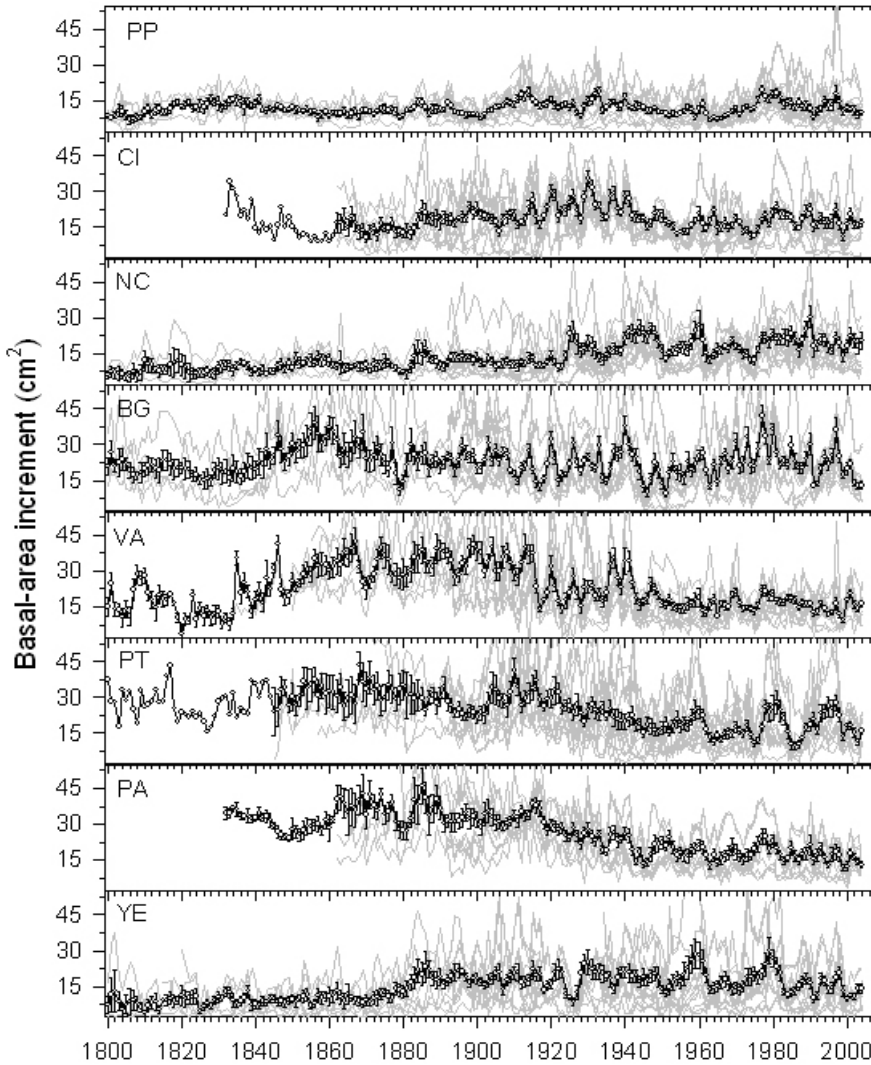

Figure 5. Mean radial growth during the period 1799-2004 in *Pinus nigra* ssp. *salzmannii* expressed as basal-area increment. Gray lines represent the individual series. Error bars represent the standard error. Codes (letters) refer to different populations of *Pinus nigra* ssp. *salzmannii*.

The studied populations of *Pinus nigra* showed different patterns in basal area increment across the sampled sites (Figure 5). Linares and Tíscar (2010, 2011) observed that long-term growth responses to climatic change are linked to local mean precipitation and, therefore, that the capacity to adapt to climate change will likely vary across climatic gradients. These

results suggest that *Pinus nigra* growth is largely influenced by autumn (both prior and current) as well as by spring drought in water-limited stands, with differences in growth responses between warmer sites and cooler sites. Conversely, results also suggest that warmer winters in cold sites and warmer springs in mild sites may enhance tree radial growth in stands with higher precipitation.

Dendroclimatic reconstructions of drought in the north of Africa confirm that during the early 2000s this area underwent some of the most severe droughts since at least the middle of the 15th century (Till and Guiot 1999; Luterbacher *et al.* 2004; Esper *et al.* 2007; Touchan *et al.* 2008). Such retrospective assessment based on a proximate proxy (tree-ring width of Atlas cedar chronologies) is also consistent with climate data and model projections which respectively indicate and forecast a trend of increasing aridity in the Mediterranean Basin for the current century (Xoplaki *et al.* 2004; Luterbacher *et al.* 2004; Norrant and Douguédroit 2006). Results support the contention that rising spring-to-summer temperatures and decreasing rainfall from winter to early summer will magnify Atlas cedar drought stress and growth decline (Figure 6; see also Aussenac and Finkelstein 1983; Till 1987; Mokrim 2009).

Sudden growth reductions of Atlas cedar have mainly occurred since 1978, and have been related to severe drought events and temperature rise as reflected in the available local climatic records (Figure 2; see also Mokrim, 2009). Precipitation showed a significant positive correlation with Atlas cedar growth from November of the year prior to the growing season to the current July, which agrees with previous climate-growth analyses, illustrating how precipitation is the main limiting factor for the growth of this cedar species (Aussenac and Finkelstein, 1983; Till, 1987; Mokrim, 2009); as well as for *Cedrus libani* in Turkey (Selik *et al.* 1990; Hughes *et al.* 2001; Touchan *et al.* 2005), *Cedrus brevifolia* in Cyprus (Touchan *et al.* 2005), and *Cedrus deodara* in the Himalayas (Borgaonkar *et al.* 1999).

However, recent findings by Linares *et al.* (in prep.) of correlations between Atlas cedar basal area increment and temperature contrast with those of Till (1987), who reported a positive effect of January mean temperature (and to less extent August mean temperature) on Atlas cedar secondary growth, while all correlations reported by Linares *et al.* (in prep.) for BAI and temperature were negative. It should be noted that correlation analysis performed by Linares *et al.* was restricted to the second half of the 20th century (1958-2003), for which the temperature trend was characterized by a steep increase (Figure 2). In addition, this study focused on Atlas cedar forests near the low elevation limit of the species distribution in the Middle Atlas (Benabid 1994), and a positive effect of winter-to-spring temperatures on Atlas cedar growth should be expected at higher elevation stands. Finally, recent investigations suggest that climatic stress may influence the physiological status of Atlas cedar and determine whether trees withstand, for instance, severe defoliations or bark stripping by Barbary Macaques. In turn, climate change appears to exert a significant effect on herbivore behavior (Camperio Ciani *et al.* 2001; Camperio Ciani and Mouna 2006).

On summary, decreasing growth curves are, as we pointed above, among the most obvious growth-related characteristics of declining trees (Waring 1987). The process of dying often takes decades driven by a sequence of multiple stress factors (Manion 1991; Franklin *et al.* 1987). For instance, for Norway spruce (*Picea abies*) growing in sub-alpine forests of the Swiss Alps, growth declines generally started several years up to more than 100 years prior to death, on average spanning 50–70 years (see Bigler and Bugmann 2004). The results reported here for black pine illustrate that BAI trend of old *Pinus nigra* trees, subjected to drier

conditions within the species distribution area in south-east Spain, were on average negative over the 20th century (Linares and Tíscar, 2010, 2011; Figure 5).
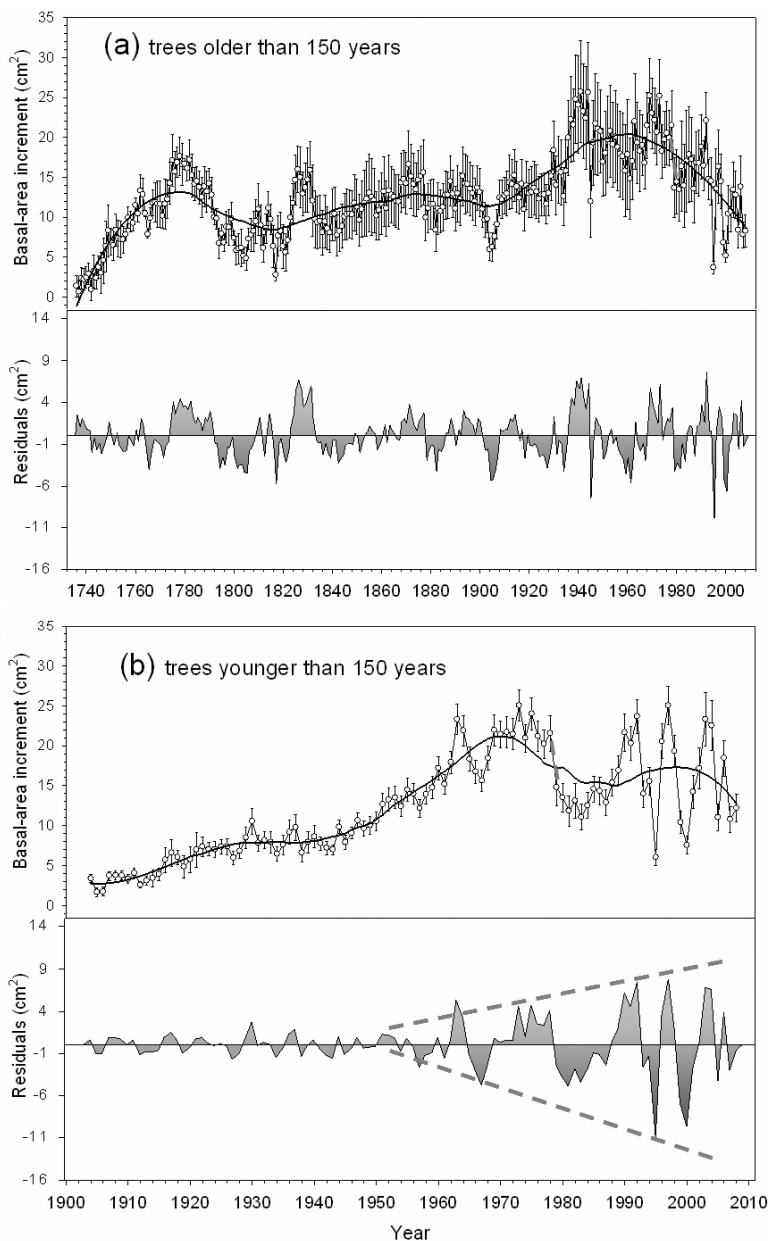

Figure 6. Basal area increment for Atlas cedar older (a) and younger (b) than 150 years. Linares *et al.* (in prep.) have separated the secondary growth on two components: low frequency and a high frequency, by a smoothing of the data and thereafter by obtaining the high frequency signal as the difference between the observed and the smoothed predicted values (residuals). Atlas cedar growth shows an average decline since the middle of the twenty century and sudden growth decline at the onset of the eighties.

Silver fir from Slovenia showed that tree growth from declining stands decreased for about 50 years (Bigler *et al.* 2004; Torelli *et al.* 1999). The growth curves of dead and living Scots pine trees at three different sites in the Valais (Switzerland) started to diverge on average between 10 and nearly 20 years prior to death (Bigler *et al.* 2006). Similar results were obtained here for *A. alba* (Figure 3), *Abies pinsapo* (Figure 4), and *Cedrus atlantica* (Figure 6).

4. POTENTIAL GLOBAL CHANGE-INDUCED VEGETATION SHIFTS

Mountain tree populations are expected to track the changing climate with an upslope shift, if other factors play a minor role, which is not usually the case. Biotic interactions or dispersal may be as significant as climate in forecasting how the range of different tree species may shift in response to climatic warming. Linares *et al.* (2009a, 2010) have shown that land-use changes may also modulate the response of tree populations to warming in Mediterranean mountains. The recent overprotection of forests and the absence of perturbations that could control stand density appear to be major drivers in the decline and retreat of *A. pinsapo* populations due to increasing stress. Mortality of mature trees may promote a succession of species, leading to dominance by plants that are typical of more arid conditions.
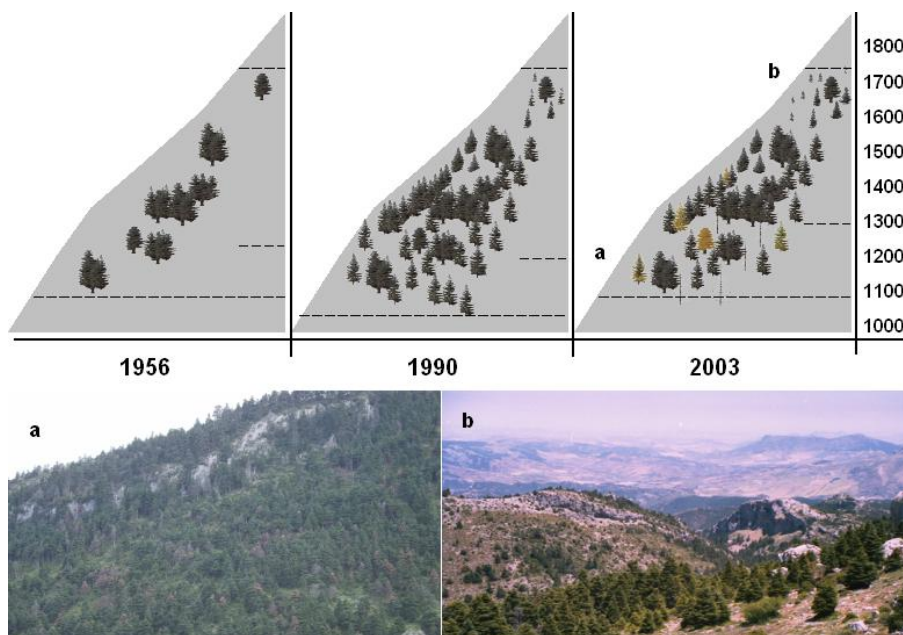

Figure 7. Schematic representation of the historical changes in density, distribution and vigour of *A. pinsapo* along the altitudinal gradient of Sierra de las Nieves (S Spain). Changes in traditional land-use regimes and conservation measures adopted since the 1950s led to increases in cover and density of *A. pinsapo* forests. Regional climatic changes recorded since the 1980s (e.g., droughts in 1994-1995) caused growth reduction, decline episodes and frequent mortality events at the low-elevation sites (mainly below 1300 m, photograph a), whereas the high-elevation sites (above 1700 m, photograph b) showed growth enhancement despite the density increase (see also Linares *et al.* 2009a).

Colonization and subsequent replacement of *A. pinsapo* by *Pinus halepensis* has already been observed in the low-elevation sites (Linares *et al.* 2009a). Similarly, a replacement of cold-temperate forests by Mediterranean communities has been reported in NE Spain (Peñuelas and Boada 2003). Therefore, it is expected that warmer conditions and land-use changes in Mediterranean mountains will promote mortality and an overall population decline of species that are poorly adapted to the more arid conditions that occur near the low altitude limit of their range. Results emphasize that land-use and climatic changes may have acted synergistically to alter the physiological thresholds of endangered relic trees as *A. pinsapo* through greater competition for soil water and the promotion of severe short-term growth reductions, respectively (Linares *et al.* 2009a). A similar hypothesis could explain the current decline of marginal *A. alba* forests (Camarero *et al.* 2011).

The upslope shift of drought-sensitive relic species in the Mediterranean mountains may be explained, at least in part, by reduced drought stress and stand density at the higher elevations. By opposite, forest decline at lower elevations might occur following a tree-density increase, related to historical land-use changes, which led to greater competition among individuals occupying the arid, low-altitude landscapes. Historical land-use and density changes in these forests were, therefore, more important in the lower than in the upper sites (Figure 7).

Figure 8. Recent extreme drought in North Africa could be linked to severe mortality of Atlas cedar.

The opposite side of this complex interaction between human perturbation regime and forest dynamics could be found in the Atlas cedar (Figure 8). In north Morocco, human demographic pressure and livestock grazing have widely disturbed the main forest ecosystems which show a continual regression in terms of surface area in the most xeric areas (Barbero *et al.* 1990). The Atlas cedar forests of the Middle Atlas in Morocco have been severely affected by drought, by overgrazing involving mixed herds of goat and sheep, as well as by excessive logging for timber, firewood, and livestock fodder. Human disturbances have strongly altered Atlas cedar-forest structures and holm-oak stands, formerly coppiced through frequent cutting cycles, and the resulting open areas serve for grazing. Ongoing decline of open Atlas cedar stands in intensively logged and overgrazed areas are leading to their replacement by holm oak (*Quercus rotundifolia*) and prickly juniper (*Juniperus oxycedrus*). High-frequency cutting and worsening drought could be encouraging the extension of high-density holm oak coppices and decline of the Atlas cedar overstory (Figure 8). Further exclusion of cedar regeneration by more competitive oak seedlings and other angiosperm species with a more efficient hydraulic system might accelerate the postulated vegetation shift.

Decline symptoms in Atlas cedar have attracted attention recently, mainly in 2001, but records of sudden BAI reductions go back to 1945 (Figure 6) when a severe drought caused the death of cedars, presumably, with a comparable dieback extent (Chenchouni *et al.* 2008; Et-tobi *et al.* 2009). In the Middle Atlas (north Morocco), an estimated 23% of the forest surface area (3,400 of 15,000 hectares) showed some symptom of decline after the 1999-2000 drought event. Mainly old trees were affected (Figure 8). However, the pattern of mortality was highly heterogeneous, showing both clumped and scattered spatial patterns, and trees located near declining individuals frequently exhibited no symptoms (Linares *et al.* in prep.).

5. CONCLUDING REMARKS

Forest decline summarised here could affect both carbon and water cycles at a regional scale. Successive replacement of drought-sensitive tree species by better drought-adapted evergreen species could cause a reduction in net primary production, because firs, pines and cedars are the species that currently reach the greatest biomass in the studied forests. Decline and mortality imply a net input of organic carbon to the soil, which could enhance the soil heterotrophic respiration and the decomposition of organic matter, thus increasing carbon emissions.

Forest vulnerability to climate change is still uncertain because different growth responses may differentially alter species dynamics and competitive interactions. Given drought sensitivity and temperature-induced stress of water-limited populations, the role of temperature rise in shaping communities and affecting selection pressures in the Mediterranean mountain forests, as well as other drought-prone systems, will likely become even more important in a global-warming scenario. Recently, several studies have linked tree-growth decline with increasing dryness in the Mediterranean Basin, suggesting a widespread climate-change-related growth decline in several forests. These findings bear implications for growth and persistence of relict Mediterranean trees species. Dense stands of protected *A. pinsapo* forests seem to be more vulnerable to drought stress, while ongoing decline of open

Atlas cedar stands in intensively logged and overgrazed areas are favoring their replacement by *Quercus rotundifolia* and *Juniperus oxycedrus*.

Several relic Mediterranean mountain trees have become increasingly vulnerable to drought, as reflected in the low secondary growth values during drier periods. Temperature-induced stress appears to become increasingly limiting as tree ages, leading to higher climate sensitivity in older individuals. Long-term temperature increases could impose further challenges to trees recuperating after severe drought events, such as a requirement for a superior carbon balance when challenged to recover from drought-induced defoliation or after pest outbreaks. Increasing sensitivity to climate may have a significant impact on predictions of future carbon uptake and forest dynamics at regional scales in the Mediterranean Basin, since both a precipitation decline and a temperature rise have been confirmed from 20th-century climate data and this tendency is expected to follow in the current century based on model predictions.

REFERENCES

Alejano R. and Martínez E. 1996 Distribución de Pinus nigra Arn. ssp. Salzmannii en las Sierras Béticas. *Ecología*, 10, 231-241.

Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., Mcdowell N., Vennetier M., Kitzberger T., Rigling A., Breshears D.D., Hogg E.H., Gonzalez P., Fensham R., Zhang Z., Castro J., Demidova N., Lim J.-H., Allard G., Running S.W., Semerci A., and Cobb N. 2010 A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660-684.

Aussenac G. and Finkelstein D. 1983 Influence de la sécheresse sur la croissance et la photosynthèses du Cèdre. *Ann. Sci. For*, 40, 67-77.

Barbero M., Bonin G., Loisel R., And Quezel P. 1990 Changes and disturbances of forest ecosystems caused by human activities in the western part of the mediterranean basin. *Vegetatio*, 87, 151-173.

Benabid A. 1994 Biogéographie phytosociologie et phytodynamique des cédraies de l'Atlas Cedrus atlantica (Manetti). Le cèdre de l'Atlas. Actes du séminaire international sur le cèdre de l'Atlas. *Annales de la Recherche Forestière au Maroc*, 27, 62-76.

Bigler C.J., Bräker O.U., Bugmann H., Dobbertin M., And Rigling D. 2006 Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems*, 9, 330-343.

Bigler C.J. and Bugmann H. 2004 Assessing the performance of theoretical and empirical tree mortality models using tree-ring series of Norway spruce. *Ecological Modelling*, 174, 225-239.

Bigler C.J., Gricar J., Bugmann H., and Cufar K. 2004 Growth patterns as indicators of impending tree death in silver fir. *Forest Ecology and Management*, 199, 183-190.

Borgaonkar H.P., Pant G.B., and Kumar K.R. 1999 Tree-ring chronologies from western Himalaya and their dendroclimatic potential. *IAWA J.*, 20, 295-309.

Brubaker L.B. 1986 Responses of tree populations to climatic change . *Plant Ecology*, 67, 119-130.

Cabrera M. 2001 Evolución de abetares del Pirineo aragonés. *Cuadernos de la Sociedad Española de Ciencias Forestales*, 11, 43-52.

Camarero J.J. 2000 El decaimiento del abeto en los Pirineos. *Medio Ambiente Aragón*, 4, 18-20.

Camarero J.J., Padró A., Martín-Bernal E., and Gil-Pelegrín E. 2002 Aproximación dendroecológica al decaimiento del abeto (*Abies alba* Mill.) en el pirineo Aragonés. *Montes*, 70, 26-33.

Camarero J.J., Bigler C., Linares J.C., and Gil-Pelegrín E. 2011 Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. *Forest Ecology and Management*, doi:10.1016/j.foreco.2011.05.009.

Camperio Ciani A., Martinoli C., Capiluppi C., Arahou M., and Mouna M. 2001 Effects of Water Availability and Habitat Quality on Bark-Stripping Behavior in Barbary Macaques. *Conservation Biology*, 15, 259-265

Camperio Ciani A. and Mouna M. 2006 Human and environmental causes of the rapid decline of the Barbary macaque in the Middle Atlas of Morocco. In: Hodges,J.K., Cortes,J. (eds) *The Barbary Macaque: Biology, Management & Conservation*. Nottingham University Press, Nottingham, UK.

Carrer M., Nola P., Motta R., and Urbinati C. 2010 Contrasting tree-ring growth to climate responses of *Abies alba* toward the southern limit of its distribution area. *Oikos*, 119, 1515-1525.

Cheddadi R., Fady B., François L., Hajar L., Suc J.-P., Huang K., Demateau M., Vendramin G., and Ortu E. 2009 Putative glacial refugia of *Cedrus atlantica* deduced from Quaternary pollen records and modern genetic diversity. *J. Biogeogr*, 36, 1361-1371.

Chenchouni H., Abdelkrim S.B., and Athmane B. 2008 The deterioration of the Atlas Cedar (*Cedrus atlantica*) in Algeria. Oral presentation at: International Conference "Adaptation of Forests and Forest Management to Changing Climate with Emphasis on Forest Health: A Review of Science, Policies, and Practices", Umeå, Sweden: FAO/IUFRO, 25-28 August 2008.

Davis M.B. and Shaw R.G. 2001 Range shifts and adaptive responses to Quaternary climate change. *Science*, 292, 673-679.

Dobbertin M. 2005 Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *Eur. J. Forest Res*, 124, 319-333.

Esper J., Frank D.C., Büntgen U., Verstege A., Luterbacher J., and Xoplaki E. 2007 Long-term drought severity variations in Morocco. *Geophysical Research Letters*, 34, L17702.

ET-Tobi M., Mhirit O., and Benzyane M. 2009 Changements climatiques, dégradations et dépérissements: Arguments et nouveaux outils pour une réforme de la sylviculture des cédraies au Maroc. *Annales de la Recherche Forestière au Maroc*, 41, 27-47.

Franklin J.F., Shugart H.H., and Harmon M.E. 1987 Tree death as an ecological process. *BioScience*, 37, 550-556.

Galiano, L., Martinez-Vilalta, J., Lloret, F., 2010. Drought-induced multifactor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. Ecosystems, 13, 978-991.

Giorgi F. 2002 Variability and trends of sub-continental scale surface climate in the twentieth century. Part I: observations. *Climate Dynamics*, 18, 675-791.

Grove A.T. and Rackham O. 2001 *The Nature of Mediterranean Europe: an Ecological History*. New Haven: Yale University Press.

Hughes M.K., Kuniholm P.I., Eischeid J., Garfin G., Griggs C.B., and Latini C.E. 2001 Aegean tree-ring signature years explained. *Tree-Ring Research*, 51, 67-74.

IPCC 2007 *Climate change, fourth assessment report*. London, UK: Cambridge University Press.

Linares J.C., Camarero J.J., and Carreira J.A. 2009a Interacting effects of climate and forest-cover changes on mortality and growth of the southernmost European fir forests. *Glob. Ecol. Biogeogr.*, 18, 485-497.

Linares J.C. and Carreira J.A. 2009 Temperate-like stand dynamics in relict Mediterranean-fir (*Abies pinsapo*, Boiss.) forests from Southern Spain. *Ann. For. Sci.*, 66.

Linares J.C., Carreira J.A., and Ochoa V. 2010 Human impacts drive forest structure and diversity. Insights from Mediterranean mountain forest dominated by *Abies pinsapo* (Boiss.). *European Journal of Forest Research*, DOI: 10.1007/s10342-010-0441-9.

Linares J.C., Delgado-Huertas A., Camarero J.J., Merino J., and Carreira J.A. 2009b Competition and drought limit the water-use efficiency response to rising atmospheric CO_2 in the Mediterranean fir *Abies pinsapo*. *Oecologia*, 161, 611-624.

Linares J.C. and Tíscar P.A. 2010 Climate change impacts and vulnerability of the southern populations of *Pinus nigra* ssp. *salzmannii*. *Tree Physiology*, 30, 795-806.

Linares J.C. and Tíscar P.A. 2011 Buffered climate change effects in a Mediterranean pine species: range limit implications from a tree-ring study. *Oecologia*, DOI 10.1007/s00442-011-2012-2.

Luterbacher J., Dietrich D., Xoplaki E., Grosjean M., and Wanner H. 2004 European seasonal and annual temperature variability, trends and extremes since 1500. *Science*, 303, 1499-1503.

Macias M., Andreu L., Bosch O., Camarero J.J., and Gutiérrez E. 2006 Increasing aridity is enhancing silver fir *Abies alba* (Mill.) water stress in its south-western distribution limit. *Clim.Change*, 79, 289-313.

Manion P.D. 1991 *Tree Disease Concepts*. Englewood Cliffs, NJ, EUA.: Prentice-Hall.

Mcdowell N., Pockman W.T., Allen C.D., Breshears D.D., Cobb N., Kolb T., Sperry J., West A., Williams D., and Yepez E.A. 2008 Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719-739.

Medail F. and Diadema K. 2009 Glacial refugia infuence plant diversity patterns in the Mediterranean Basin. *J. Biogeogr.*, 36, 1333-1345.

Mhirit O. 1994 Le cèdre de l'Atlas (*Cedrus atlantica* Manetti). Présentation générale et état des connaissances à travers le reseau Silva Mediterranea 'Le Cèdre'. Le cèdre de l'Atlas. Actes du séminaire international sur le cèdre de l'Atlas. *Annales de la Recherche Forestière au Maroc*, 27, 4-21.

Mokrim A. 2009 Dépérisement du cèdre de l' Atlas: Ambiance climatique et bilan de la croissance radiale. *Annales de la Recherche Forestière au Maroc*, 41, 48-68.

Norrant C. and Douguédroit A. 2006 Monthly and daily precipitation trends in the Mediterranean (1950-2000). *Theor.Appl.Climatol.*, 88, 89-106.

Parmesan C. 2006 Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolutionand Systematics*, 37, 637-669.

Peñuelas J. and Boada M. 2003 A global change-induced biome shift in the Montseny mountains (NE Spain). *Glob.Change Biol.*, 9, 131-140.

Peñuelas J., Lloret F., and Montoya R. 2001 Severe drought effects on mediterranean woody flora in Spain. *Forest Science*, 47, 214-218.

Peñuelas J., Ogaya R., Boada M., and 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*, 30, 830-838.

Piervitali E., Colacino M., and Conte M. 1997 Signals of climatic change in the Central-Western Mediterranean Basin. *Theor. Appl. Climatol.*, 58, 211-219.

Rodrigo F.S., Esteban-Parra M.J., Pozo-Vázquez D., and Castro-Diez Y. 1999 A 500-year precipitation record in Southern Spain. *Int. J. Climatol.*, 19, 1233-1253.

Sarris D., Christodoulakis D., and Körner C. 2007 Recent decline in precipitation and tree growth in the eastern Mediterranean. *Glob. Change Biol.*, 13, 1-14.

Selik M., Eckstein D., and Wrobel S. 1990 Dendrochronological investigations on cedar of Lebenon, *Cedrus libani. Proc. International Cedar Symposium, 22-27 Oct. 1990, Antalya, Turkey*. pp. 990-992.

Svenning J.-C. And Skov F. 2004 Limited filling of the potential range in European tree species. *Ecology Letters*, 7, 565-573.

Till C. 1987 The summary response function of Cedrus atlantica (Endl.) Carriere in Morocco. *Tree-Ring Bull.*, 47, 23-36.

Till C. and Guiot J. 1999 Reconstruction of precipitation in Morocco since 1100 AD based on Cedrus atlantica tree-ring widths. *Quaternary Res.*, 33, 337-351.

Torelli N., Shortle W.C., Cufar K., Ferlin F., and Smith K.T. 1999 Detecting changes in tree health and productivity of silver fir in Slovenia. *Eur. J. For. Pathol.*, 29, 189-197.

Touchan R., Anchukaitis K.J., Meko D.M., Attalah S., Baisan C., and Aloui A. 2008 Long term context for recent drought in northwestern Africa. *Geophysical Research Letters*, 35, L13705.

Touchan R., Xoplaki E., Funkhouser G., Luterbacher J., Hughes M.K., Erkan N., Akkemik U., and Stephan J. 2005 Reconstructions of spring/summer precipitation for the Eastern Mediterranean from tree-ring widths and its connection to large-scale atmospheric circulation. *Climate Dynamics*, 25, 75-98.

Van Mantgem P.J. and Stephenson N.L. 2007 Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters*, 10, 909-916.

Vitousek P.M. 1994 Beyond global warming: ecology and global change. *Ecology*, 75, 1861-1876.

Waring R.H. 1987 Characteristics of Trees Predisposed to Die. *BioScience*, 37, 569-574.

Xoplaki E., González-Rouco J.F., Luterbacher J., and Wanner H. 2004 Wet season Mediterranean precipitation variability: influence of large-scale dynamics and trends. *Climate Dynamics*, 23, 63-78.

Xoplaki E., Luterbacher J., Paeth H., Dietrich D., Steiner N., Grosjean M., and Wanner H. 2005 European spring and autumn temperature variability and change of extremes over the last half millennium. *Geophys.Res.Lett.*, 32.

Zuur A.F., Ieno E.N., and Smith G.M. 2007 *Analysing Ecological Data*. Springer. 680 p.