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ORIGINAL ARTICLE

# Age-related drought sensitivity of Atlas cedar (*Cedrus atlantica*) in the Moroccan Middle Atlas forests

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ABSTRACT

Age-related tree responses to climate change are still poorly understood at the individual tree level. In this paper, we seek to disentangle the relative contribution of tree age to growth decline and growth–climate relationships in Atlas cedar (*Cedrus atlantica* Manetti) trees at the Middle Atlas Mountains, northern Morocco. Dendrochronological methods were applied to quantify growth–climate relationships using tree-ring width indices (TRWi) calculated for cedars of two contrasting age groups (old trees, age ≥150 years; young trees, age <150 years). TRWi–climate relationships were assessed at the site and tree levels by using response functions and linear mixed-effects models, respectively. Growth of the studied Atlas cedars was negatively affected by recurrent droughts and by the steep temperature rise since the 1970s. Response functions and mixed-effects models indicated that the decline in tree growth was mainly explained by diminishing precipitation. The negative association between cedar growth and temperature was stronger in old than in young trees. Vulnerability to temperature-induced drought stress in old cedar trees may lead to an impending growth decline. We argue that the age dependence of growth sensitivity to drought must be quantified and considered at the individual tree level when predicting the future dynamics and persistence of cedar forests in the Moroccan Middle Atlas.

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## Introduction

Drought-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 (e.g., Dobbertin, 2005; van Mantgem et al., 2009; Allen et al., 2010; Linares and Camarero, 2012). Drought may intensify physiological stress on long-lived woody vegetation, leading to sudden growth reduction (Bigler et al., 2004; McDowell et al., 2008; Lloret et al., 2011; Hereş et al., 2012). Growth decline in response to severe droughts may trigger widespread mortality which can transform drought-sensitive pine, fir or cedar landscapes to more open stands dominated by other woody species more resistant to drought, including oaks (*Quercus* sp.) and junipers (*Juniperus* sp.), at regional to local scales (Allen and Breshears, 1998; Galiano et al., 2010; Gonzalez et al., 2010; Linares et al., 2011).

Radial growth can be used as a surrogate of the whole-tree carbon budget (e.g., Litton et al., 2007; Zweifel et al., 2010; but see also Rocha et al., 2006). Such use implies that tree-ring data provide valuable information about the effects of environmental change on forest productivity. Dendrochronology has long used tree-rings to better understand climate–growth relationships in trees within a site or across a region, with tree age often considered to contribute unwanted noise to the signal (Cook, 1985; Osborn et al., 1997; Vaganov et al., 2006). Thus, age-dependent effects often have not been taken into account in investigations of the interactions between climate change and tree growth decline (Voelker, 2011).

The most common approach in dendroecological studies to deal with age growth trends, i.e. the tendency of tree rings to get narrower as trees get bigger and older, is to detrend tree-ring width series by calculating ratios or differences between the raw data and fitted curves (e.g., negative linear or exponential curves) to obtain site mean chronologies averaging the indexed values across trees and for each year (Cook and Peters, 1981, 1997). Therefore, such pooled tree-ring indices do not account for the variance in climate–growth responses among trees. Moreover if the age growth trends of some trees covary with a given climatic

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trend, detrending would also remove part of the environmental signal of interest. Here, we combined both standard detrending methods, widely used among dendrochronologists, with linear mixed-effects models and multi-model selection criteria, to model, at an individual tree scale, age-dependent growth responses to local temperature and precipitation. We provide a novel advance for analyzing the effects of both climatic stress and intrinsic age effects on growth, using linear mixed-effects models to reproduce changes in tree-ring width indices at the individual tree level.

We focused on Atlas cedar (*Cedrus atlantica* Manetti) because it is an endemic and long-lived tree species, which is considered to be highly vulnerable to climatic warming and the related decrease in soil-water availability (Cheddadi et al., 2009; Linares et al., 2011). Since the early 1980s, severe droughts have been related to Atlas cedar growth decline and mortality (Bentouati, 2008; Mokrim, 2009; Allen et al., 2010), mainly in the mountainous xeric areas near the Sahara Desert (Chenchouni et al., 2008). The Atlas cedar growth decline seems to affect mainly old dominant trees, which suggests age/size-dependent tree responses to long-term changes in water availability (Linares et al., 2011).

We hypothesized that: (i) growth response to drought increases is modulated by inherent age-dependent sensitivity to temperature, precipitation and drought and (ii) age affects the vulnerability of tree species to climate-induced stress. To test these hypotheses, we investigated local climatic trends (temperature and precipitation) for the 20th century, and we measured tree-ring width and calculated tree-ring width indices from *C. atlantica* trees sampled in the Middle Atlas, northern Morocco. Our specific aims were: (i) to quantify the extent to which temperature, precipitation and drought drive the *C. atlantica* climate–growth patterns in trees of different ages and (ii) to evaluate whether age-dependent responses to climate could explain recent Atlas cedar growth decline. The fulfillment of these aims may shed light on the nature of age-dependent links between climate change and growth in trees. Furthermore they could allow evaluation of whether variables such as tree age are appropriate to forecast drought-induced forest decline.

## Methods

### Study species

Currently, the genus *Cedrus* includes three extant species native to the Mediterranean mountains (*C. atlantica* from Algeria and Morocco; *Cedrus libani* Rich. in Asia Minor; *Cedrus brevifolia* (Hooker fil.) Henry in Cyprus) and another one in the Himalaya (*Cedrus deodara* Don; Farjon, 2008). The Atlas cedar forests cover an area of over 130,000 ha (Cheddadi et al., 2009) distributed over Morocco (Rif, Middle Atlas and north-eastern High Atlas) and Algeria (Ouarsenis, Aurès and Djurdjura; see Linares et al., 2011). *C. atlantica* occurs at elevations of 1300–2600 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 °C and −8 °C (Benabid, 1994; Mhirit, 1994). The Middle Atlas in northern Morocco contains about the 80% of the world's Atlas cedar forest area (ca. 100,000 ha; Benabid, 1994; Linares et al., 2011). 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* Lam.; prickly juniper *Juniperus oxycedrus* L.; European holly, *Ilex aquifolium* L.) and deciduous (*Acer opalus* Mill., *Crataegus laciniata* Ucria) tree and shrub species. The most abundant tree species, beside Atlas cedar, in the stands studied was *Q. rotundifolia* (Linares et al., 2011).

### Climate data

To quantify temperature and precipitation trends over the second half of the 20th century (period 1950–2006) we used local climatic data (monthly mean temperature and total precipitation) from the Ifrane meteorological station located about 14 km apart from the studied plots (33°32′N, 5°07′W, 1630 m, period 1958–2003 and estimated the other values through linear correlations using gridded regional data from the CRU TS 3.0 dataset produced by the Climate Research Unit (CRU, 2008). Although all correlations between local and regional data were highly significant, we only used the local dataset to model tree growth in further analyses (see Linares et al., 2011). The annual water budget was estimated by the Palmer drought severity index (PDSI) obtained from gridded regional data from the CRU TS 3.0 dataset (van der Schrier et al., 2006; CRU, 2008). Mean temperature and PDSI were standardized by subtracting the mean and dividing by the standard deviation:

$$Z_i = \frac{(x_i - \bar{x})}{\sigma}, \qquad (1)$$

where $Z_i$ expresses the $x_i$ score distance from the $x$ average ($\bar{x}$) in standard deviation units ($\sigma$).

To determine the severity and the rarity, in statistical terms, of extreme drought events, precipitation data were standardized by calculating the standardized precipitation index (SPI; McKee et al., 1993a). The SPI accounts for the frequency distribution of precipitation. Conceptually, the SPI also represents a z-score of an event, i.e. the number of standard deviations above or below the mean of that event, as has been defined in Eq. (1) for temperature and PDSI values. However, the SPI performs a pre-adjustment to this formulation because precipitation is usually positively skewed (Bordi et al., 2001). To adjust for this statistical bias in rainfall data, the precipitation data were transformed to a more normal distribution by applying the gamma function (see Appendix 1 for a detailed report about SPI computation).

### Dendrochronological methods

To quantify the growth patterns of *C. atlantica*, a total of 53 dominant and co-dominant trees were selected based on an extensive field survey within an area delimited by the following coordinates: latitude 33°24′40″–33°24′60″N and longitude 5°03′00″–5°08′40″W. The elevation varied from 1830 to 1890 m, i.e. near the lowermost elevation limit of the distribution of this species in the Middle Atlas (Benabid, 1994; see also Linares et al., 2011). All trees were located on limestone substrates. We selected and specifically sampled trees showing regular and straight boles, and we avoided those with asymmetrical or eccentric growth. We then extracted from two to four cores per tree at breast height (1.3 m) and always in a direction perpendicular to the terrain maximum slope using 40-cm or 60-cm long Pressler increment borers, depending on the diameter of the trees sampled. Bark and core length were measured in the field (as well as tree diameter). When the core did not reach the pith (ca. 10% of the cored trees), total tree age at coring height was thereafter estimated by linear regressions assuming an averaged growth rate for the missing innermost rings.

All cores were sanded with sandpapers of progressively finer grain until tree rings were clearly visible under a binocular microscope, and then were visually cross-dated. Tree-ring widths were measured to the nearest 0.001 mm using a LINTAB measuring device (Rinntech, Heidelberg, Germany), and cross-dating quality was checked using the COFECHA program (Holmes, 1983).

The trend due to the geometrical constraint of adding a volume of wood to a stem of increasing radius was corrected by

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