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Short communication

Small does not mean young: Age estimation of severely browsed trees in anthropogenic Mediterranean landscapes

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ABSTRACT

The knowledge of the age of individual trees and of population age structure is of great importance for conservation purposes. In Mediterranean areas, however, trees are rarely used for dendroecological studies as ring growth is strongly perturbed by browsing and other disturbances. This study focused on the Tertiary relict tree species *Zelkova abelicea* (Ulmaceae) endemic to the mountains of Crete (Greece) and searched for new approaches to estimate the age of threatened trees in severely browsed populations. Our results demonstrate that dwarfed *Z. abelicea* trees can attain ages >500 yr and that such individuals often surpass normally growing trees of the same population in number and age. These findings significantly change the perception of population age structure in forest remnants of Mediterranean landscapes. Additionally, we show that tree age is well correlated (64%) with trunk circumference, for severely browsed dwarfed trees, however not so much (11%) for normally developed, large trees. Thus, our results can be used directly for age estimations of severely dwarfed *Z. abelicea* individuals in the field and the new approach can be easily reproduced for other threatened tree species affected by strong browsing pressure. Future conservation efforts and management strategies should, therefore, take into account not only normally developed trees but also severely browsed individuals and their populations.

1. Introduction

On the Mediterranean island of Crete, agriculture and livestock breeding have existed for the past 10,000 yr (Cowling et al., 1996). However, browsing has occurred in this environment since the Pleistocene due to several large herbivores, and numerous plants have developed adaptations such as spines or cushion growth (Rackham and Moody, 1996). In combination with a drier climate and human pressure during the last millennia, a drastic reduction of the once widespread wooded areas and the formation of maquis or garigue can be observed, where trees often have dwarfed and bushy forms (Fielding and Turland, 2005).

Nevertheless, the Mediterranean contains several refugial regions and is rich in relict plant species (Quézel and Médail, 2003). Among these, the Tertiary relict trees are of special interest, as they have been able to cope with changing environmental conditions for millions of years. However, modern-day representatives of genera such as *Liquidambar, Platanus, Juglans, Pterocarya, Aesculus*, and *Zelkova*, have only few natural and well-functioning populations, mainly in the eastern Mediterranean region – they should therefore be a conservation priority (Fineschi et al., 2002; Quézel and Médail, 2003).

The knowledge of the age of individual trees and of population age structure is of great importance for conservation purposes (Valladares and Sánchez-Gómez, 2006). Data on tree ages and ring-growth rates can be obtained with dendroecological methods. The most accurate results are usually obtained by destructive sampling (i.e. cutting down trees to count their increment rings), and are therefore not appropriate for threatened relict trees. Moreover, tree-ring analyses are not frequently performed on Mediterranean trees (Cherubini et al., 2003), primarily because browsing, along

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with other perturbations, often results in blurred environmental signals in the tree-ring record and disturbed ring formation (i.e. irregular growth, narrow or missing rings).

In this study, we used the Tertiary relict tree *Zelkova abelicea* (Ulmaceae), endemic to the mountains of Crete, Greece (Søndergaard and Egli, 2006), as a model organism to search for an approach to improve age estimates of threatened trees in heavily browsed populations with dwarfed individuals. The specific goals were (1) to determine the age of *Z. abelicea* individuals, including both normally growing and browsed, dwarfed trees; (2) to assess the relationship between tree age and circumference, and thus (3) to be able to predict the age of individual trees and the age structure of natural populations without using invasive sampling methods.

2. Materials and methods

2.1. Study area and species information

Crete is one of the major Mediterranean islands with a total area of 8729 km^2 and has a landscape dominated by karstic mountain ranges (from west to east: Levka Ori, Ida Mountains, Dhikti Mountains and Thripiti Mountains; Supplementary Fig. S1) (Jahn and Schönfelder, 1995). Crete has a Mediterranean climate with hot and dry summers and cool and wet winters. Westerlies transport 1000–2000 mm of annual precipitation to the mountains, resulting in a precipitation gradient with larger total precipitation in the Levka Ori (west) than in the Thripiti Mountains (east) (Egli, 1997). Snowfall is not unusual in the mountains but only accumulates above 1400 m a.s.l., where it may persist until May (Rackham and Moody, 1996). Moisture from winter precipitation is partially stored in the soil throughout the summer (Egli, 1997). Over 1735 native plant species have been described on Crete, of which ~10% are endemic to the island (Fielding and Turland, 2005).

Zelkova abelicea (Lam.) Boissier is a monoecious, broadleaved, ring-porous tree belonging to the elm family (Ulmaceae) (Denk and Grimm, 2005; Kozlowski et al., 2012). *Z. abelicea* was presumably widespread and likely formed a forest belt in the Cretan mountains in the past (Søndergaard and Egli, 2006). Nowadays, it occurs in scattered populations in the four mountain regions (Fig. S1) and is found growing between 900 and 1800 m a.s.l. *Z. abelicea* often grows in mixed stands with *Acer sempervirens*, *Quercus coccifera* and occasionally *Cupressus sempervirens*, on north-facing slopes, as well as in or around sinkholes where the water supply is most adequate and relatively constant and where soil conditions are most favorable (Egli, 1997; Søndergaard and Egli, 2006). *Z. abelicea* also grows in or around rocky river beds or gullies which are dry during summer but where humidity tends to remain in the subsurface and at high elevations (>1500 m a.s.l.) on south-facing slopes.

The species is widely distributed in the Levka Ori Mountains and well represented in the Dhikti Mountains. In the Ida Mountains, only two populations occur nowadays: a large (>2000 dwarfed and normally growing trees) and scattered one (>20,500 m^2) on Mt. Kedros and a small (<800 dwarfed and normally growing trees) and restricted one (~6670 m^2) on Mt. Psiloritis. A single population is known from the Thripiti Mountains (Fig. S1) (Egli, 1997).

Z. abelicea can be found as flowering, normally growing individuals with a crown, producing leaves 1.5–6 cm long as well as fruit. Shrubby, dwarfed individuals are also found, often with multiple stems, dense growth and leaves <2 cm, mainly due to browsing and presumably also water stress in some areas. Shrubby, dwarfed individuals are much more common than normally growing individuals and can form dense thickets in some areas. Seedlings are scarce and young plants have been reported to suffer from low survival rates (Egli, 1997). A precise description of the morphology and biology of the species can be found in Egli (1995, 1997) and Sarlis (1987).

Browsing represents a major threat to the sexual reproduction of the species as seedlings have little survival chances and browsed shrubs do not produce fruit. Fire also affects *Z. abelicea*, but shrubs have been seen to regenerate by suckering after fire disturbance (Søndergaard and Egli, 2006). In addition, altered water regimes resulting from the construction of reservoirs, land-use changes, road construction, and climatic changes, further affect the species populations. Soil erosion prevents seedlings from growing but aids the species' asexual perpetuation by exposing roots (*personal observation*).

2.2. Sampling sites and dendroecological analyses

The four mountain areas with *Z. abelicea* occurrences were sampled at 14 different sites so as to cover the entire distribution range of the species (Fig. S1 and Table S1). Samples were taken from 99 trees. In total, 186 increment cores and five cross-sections were taken and sampled individuals were divided into three categories (Figs. S2–S4): (1) large, normally growing trees with a fully developed crown, with (potential) fruit production and having escaped browsing apart for the lowest branches; (2) an intermediate transitional category, grouping trees that could not be clearly categorized in one of the two other categories; and (3) small trees with a shrubby, dwarfed habit producing no fruit and being heavily browsed. Categories were called large, intermediate and small, respectively, and will be referred to as such from this point. The number of sampled trees per category and per sampling site is given in Table S1.

Ring widths were measured using a digital LINTAB 5 (resolution 1 μm) positioning table and TSAP-Win software (Rinntech, 2011). A mean annual ring-growth rate was calculated for each tree with the annual ring-width values of the cores.

2.3. Age determination and statistical analyses

Each tree was aged by dividing its trunk radius by its mean annual radial growth rate at breast height for large and intermediate trees and at the root collar (i.e. germination age) for small trees. Linear regressions were done and coefficients of determination (R^2) were calculated to show the proportion of the age that is explained by the circumference. Moreover, Kruskal–Wallis and Mann–Whitney U tests were performed to check similarity and significant differences, respectively, between the mean growth rates of large, intermediate and small trees.

3. Results

Tree-ring counting in large trees was usually straightforward and ring boundaries were easy to distinguish. This was not the case for intermediate nor, in particular, for small trees, in which very narrow and compact rings (<0.2 mm) were found, often reduced to one single row of vessels with intermitting tracheids, fibers and parenchyma cells. Annual ring growth rates could be determined successfully for 96 of the 99 trees selected for analysis (Tables 1 and S2). Growth rates differed greatly from one category to another and annual ring widths varied strongly in individuals with annual growth rates ranging from <0.5 to >3 mm for some trees.

A few small and intermediate trees showed multiple piths (i.e. joining of several trunks) when observed under the microscope (Table S2) and their age might therefore have been overestimated in some cases. Trunk circumferences, radii, tree heights, mean