Sancho, the oldest known Iberian shrub

J. Julio Camarero[a,*], Miguel Ortega-Martínez[b]

[a] Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, 50192, Zaragoza, Spain
[b] Centro de Interpretación Espacio Salto de Roldán, Ctra. Sabayés s/n, 22150, Huesca, Spain

ARTICLE INFO

ABSTRACT

Cliffs are refuges for old trees and shrubs. In the Mediterranean Basin most dendroclimatic reconstructions have focused on high-elevation forests where tree radial growth is constrained by low temperatures in addition to drought stress. Old shrubs may provide longer ring-width series of hydroclimate proxies in low-elevation, drought-prone Mediterranean ecosystems where old trees are rare. To fill this research gap we investigated the maximum age and climate sensitivity of young, old, and recently dead Phoenician junipers (*Juniperus phoenicea* L.), growing on calcareous cliffs and nearby plains, in the Guara Natural Park (northeast Spain). The oldest living juniper was ^{14}C-dated to be 927 years old, and it was named "Sancho" after Don Quixote's squire. Based on ring counts, the maximum age was 655 years. The difference in age estimates between the ^{14}C-dates and ring counts was 39 years indicating that ring counts underestimate age. This was due to missing and wedging rings making the cross-dating of old junipers unfeasible. Cool and wet conditions from May to July enhanced radial growth of young junipers. Old shrubs have a high dendroecological potential in Mediterranean sites where their growth is constrained by warm-dry conditions during the growing-season. Further techniques combining dendrochronological and wiggle-match ^{14}C dating may allow reconstructing long-term hydroclimate in low-elevation Mediterranean areas.

1. Introduction

Dendroecologists have shown interest in the research and conservation of old trees given their multiple and unique ecological values (Lindenmayer, 2016), including their pivotal role as carbon sinks (Luyssaert et al., 2008). Old-growth forests enhance carbon storage because of their long carbon residence times (Körner, 2017). Since the residence time of carbon depends on longevity it is critical to investigate and conserve old populations of woody plants including trees but also shrubs (Keith et al., 2009). However, longevity is inversely related to the rate of radial growth (LaMarche, 1969; Loehle, 1988; Bigler and Veblen, 2009) and the stem metabolic rates (Issartel and Coiffard, 2011). But it still remains unclear if the tradeoff between longevity and growth rate described for trees also holds for shrubs, and if it is modified by environmental conditions (Larson, 2001; Lanner, 2002; Rosbakh and Poschlod, 2018).

Similar to trees, shrubs are also long-living woody perennials. Shrubs are the dominant woody forms in cold tundra and semi-arid regions, and they are expected to become more important due to climate warming and land-use changes (Myers-Smith and Hik, 2017). In drought-prone biomes, warmer and drier conditions are forecasted to be detrimental for the largest trees (Bennett et al., 2015), which could be replaced by shrubs. In cold biomes, shrubs will benefit from rising temperatures and show improved encroachment and growth rates across the tundra (Büntgen et al., 2018) or invade formerly grazed pasture lands (García-Cervigón et al., 2012).

Slow growing trees get older, but what about shrubs? For instance, slow-growing *Juniperus communis* individuals live longer than fast growing conspecifics in Britain (Ward, 1982). These data suggest that harsh environmental conditions, leading to slow growth rates and long life-spans, also apply to shrubs. Such conditions are found in unproductive rocky outcrops and cliffs from North America and Europe, where old trees and shrubs over 1000 years in age are found and grow very slowly under unique microclimate conditions, being protected from disturbances including fire, logging or herbivory (Larson et al., 1999, 2000a; Mathaux et al., 2016). Here we quantify the age of old juniper (*Juniperus phoenicea*) shrubs growing on cliffs in northeast Spain by combining dendrochronological techniques and ^{14}C measurements. We also assess the responsiveness of young junipers to recent climate conditions by relating ring-width to mean temperature and precipitation data.
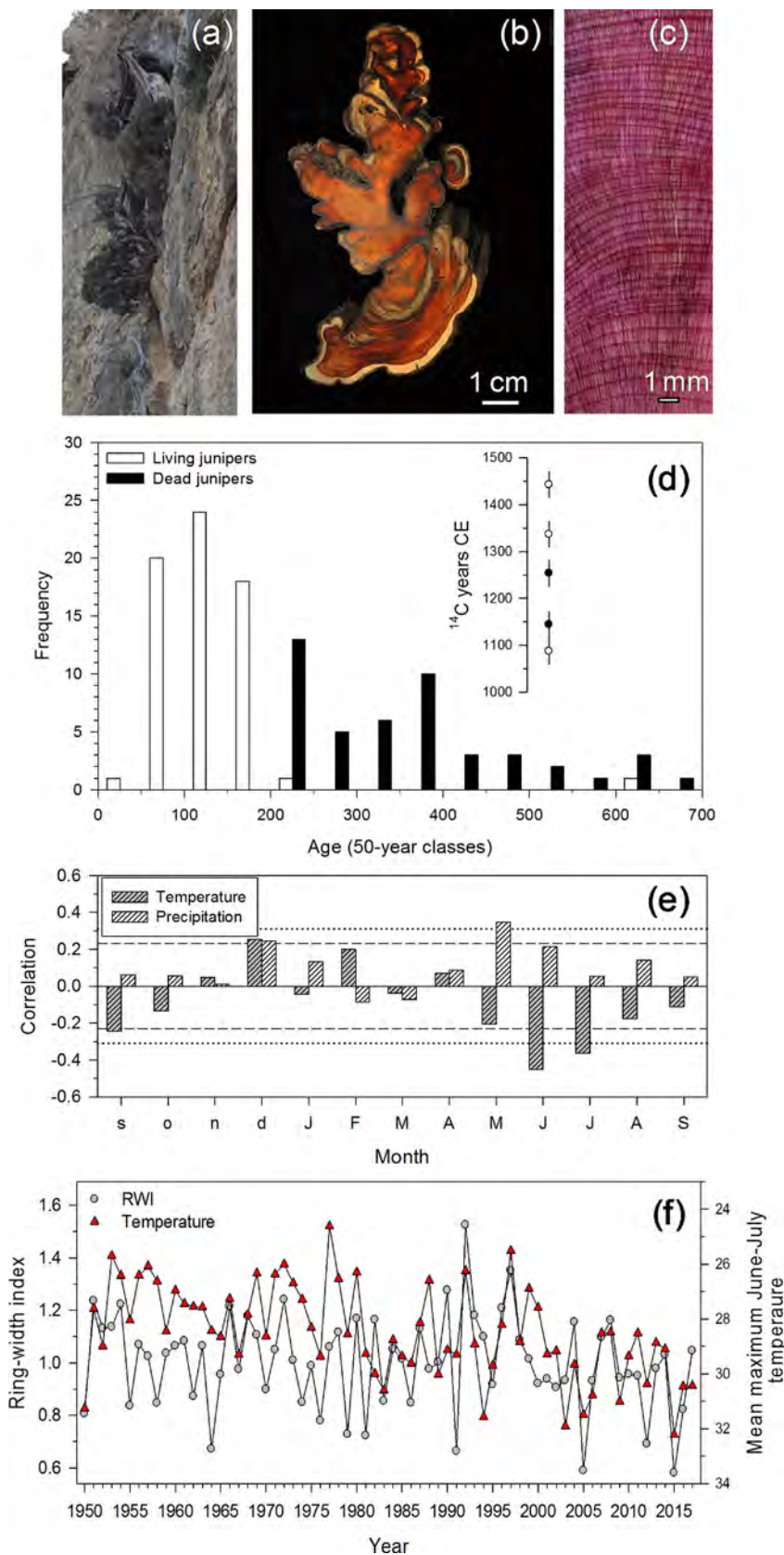
Fig. 1. View of an old, living Phoenician juniper growing on a cliff (a), transversal section of an old individual showing lobed shape (b), micro-section showing narrow and wedging rings (c), histogram (bins are 50-year classes) of age frequency of old junipers with ages estimated by ring counting and inset showing ^{14}C-dated ages (error bars are standard deviations) (d), climate-growth associations of cored young junipers (e), and coherence through time between radial growth (RWI, ring-width indices) of cored young junipers sampled in plains and mean maximum June-July temperatures (note the reverse scale of temperature, in °C) (f). The histogram (d) summarizes the ages of living ($n = 65$) and dead ($n = 47$) junipers sampled in cliffs, and empty and filled bars and symbols correspond to living and dead junipers, respectively. In plot (e) bars are correlations calculated between RWIs and monthly mean temperature and total precipitation from the previous up to the current September (previous and current months are abbreviated by lowercase and uppercase letters, respectively) over the best-replicated period (1950–2017); and horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

2. Material and methods

The Phoenician juniper (*Juniperus phoenicea* L., Cupressaceae; hereafter juniper) is a pioneer species which grows up to 10 m high; it is found around the Mediterranean Basin, but may reach Arabia and the Canary Islands (Farjon, 2005). The species has dendrochronological potential and its ring widths were used to reconstruct precipitation in the Middle East (Waisel and Liphschitz, 1968; Touchan et al., 1999).

Sampling was conducted in the cliffs of the "Parque Natural de la Sierra y Cañones de Guara" (42.25 °N, 0.28 °W, Huesca province, north east Spain) (Fig. 1a). The elevations of sampled cliffs varied from 90 to 700 m a.s.l. The size of all sampled individuals was determined by measuring the basal diameter using tapes. Cross-sections from seemingly old junipers (n = 112) were cut down for the study using a hand-saw. Old individuals were selected based on their external features such as twisted and leaning (often inverted) stems, strong taper (high basal diameter to height ratio), crown dieback, reduced canopy, exposed roots, strip-bark and moderate to large size (Swetnam and Brown, 1992; Matthes et al., 2008). Sampled individuals displayed a stunted growth form (height between 0.70 and 1.75 m) and were multistemmed. In the case of old dead individuals, sections were taken at the base of the largest and main stem, whereas in the case of old living individuals, sections were taken from the base of the thickest stem to avoid killing the shrub. This sampling was reduced to the minimum so as to preserve most old-growth shrubs. In addition, 12 living junipers growing in a nearby flat site (located 12 km apart) were cored at 1.3 m using a 5-mm wide increment borer. Cross-sections and cores were carefully sanded using 300, 600 and 1200 grit sandpapers and a belt sander. Cores were visually cross-dated, and their ring width series measured to the nearest 0.001 mm using a LINTAB-TSAP measuring device (Rinntech, Heidelberg, Germany). Cross-dating was then checked with the software COFECHA (Holmes, 1983).

To assess climate-growth relationships in young, living junipers we obtained a mean series of indexed ring-width values. Ring-width series were detrended by fitting negative exponential functions and dividing the observed by the fitted indices (Fritts, 1976). The resulting indices (RWI) were subjected to autoregressive modelling to remove the first-order autocorrelation (Cook, 1985). Finally, these dimensionless indices were averaged using a biweight robust estimation of the mean to obtain a mean site series or chronology. Chronology building was done using the ARSTAN software (https://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software). The chronology was characterized using several statistics (cf. Briffa and Jones, 1990) showing the year-to-year RWI variability (mean sensitivity) and the coherence between cross-dated series (mean correlation of individual series with the chronology; Rbar, mean correlation among ring-width series; EPS, Expressed Population Signal).

Finally, the residual chronology was correlated with monthly climate data (mean maximum and minimum temperatures, precipitation) obtained from the 0.25°-grid (42.00–42.25 N, 0.00–0.25 W) in the EOBS dataset (Haylock et al., 2008). Pearson correlations (r) were calculated from previous to current September over the best-replicated period (1950–2017).

In the case of cross-sections from old trees, cross-dating was not possible due to the abundant missing, narrow and wedging rings, intra-annual density fluctuations, and the frequent eccentric growth (Figs. 1b and c). From the disk samples, ring counting was performed along three different radii from the bark to the pith, albeit four radii are recommended when cross-dating is the main objective (Buras and Wilmking, 2014). Plant age is considered as the highest number of rings counted in any of the three radii. These estimates provide a rough approximations of juniper age (cf. Mathaux et al., 2016).

Three wood samples (approximately 10 mg in weight) were taken from the piths of the five oldest junipers according to ring counting (two living individuals plus three recently dead individuals which still had bark and fine branches). Pith-^{14}C dating was performed at the Laboratory of Ion Beam Physics (ETH Zurich). A base-acid-base-acid-bleaching method was applied to clean the wood samples and extract cellulose (Wacker et al., 2014). Samples were graphitized and analyzed in comparison to standards and reference samples (Wacker et al., 2014). The dating precision of these analyses is ± 28 years.

3. Results and discussion

The mean diameter of old junipers, both living and dead, was 16.0 ± 4.0 cm (mean ± SD), whereas the mean diameter of cored young junipers was 7.6 ± 2.6 cm. Based on ring counting, the maximum ages of old dead and living junipers is 655 and 623 years, respectively (Fig. 1d). The young junipers showed a mean age of 76 ± 15 years (range 64–103 years). The maximum length of measured series was 1915–2017, but the best-replicated period was 1950–2017 (n = 20 series). These young junipers presented a growth rate of 0.678 ± 0.247 mm yr^{-1}, and their mean sensitivity was 0.40 ± 0.07, the Rbar was 0.35 ± 0.17, and the EPS was 0.86. The mean correlation of the individual series with the chronology was 0.52 ± 0.14.

Based on ^{14}C-dating, the mean age of old junipers was 731 ± 28 years, the oldest dead juniper was 874 ± 28 years old, and the oldest living juniper was 927 ± 28 years old. The latter juniper was named "Sancho" in homage to Don Quixote's short-stature squire. The difference in age estimates of old junipers between their ^{14}C-dates and ring counts was 69 ± 32 years (range 5–305 years) which concurs with the previous observation that ring counting underestimates the actual age (Mathaux et al., 2016). The difference in ring counts between the three different radii measured in each juniper was 27 ± 11 years. Since we sampled basal disks from recently dead trees, and not decaying individuals (snags) with eroded trunks, this underestimation can be explained by the frequency of missing and double rings which are common in junipers (Pacheco et al., 2016).

In southern France (Ardèche canyon), Mandin (2005) discovered a 1500-year old juniper. Mathaux et al. (2016) sampled some of those old junipers and counted 1225 rings in one and ^{14}C-dated the pith of another to 2520 ± 35 years BP. According to these authors, this species could provide some of the longest tree-ring series in the Mediterranean Basin. In addition, the decay-resistant juniper wood prevents trunk collapse (Larson, 2001). Consequently, old juniper stems are not hollow as usually happens with old trees. However, the cross-dating of these eccentric cross-sections, which usually have lobate form, is generally unfeasible as already noted by Mathaux et al. (2016).

Old ages are not unusual in juniper species. For instance, *J. communis* may reach maximum life spans of 840 years in the Polar Urals (Schweingruber and Poschlod, 2005). *Juniperus occidentalis* and *Juniperus turkestanica* have been dated using dendrochronology to be 2675 and 1437 years old, respectively (Miles and Worthington, 1998; Esper et al., 2007). In the Iberian Peninsula, the oldest living trees are black pines (*Pinus nigra* subsp. *salzmannii*) and Mountain pines (*Pinus uncinata*) which have been crossdated to be ca. 850–1100 years old (Creus Novau, 1998, Camarero et al., 2015). However, these old Iberian pines are located at elevations between 1700 and 2200 m, where climate conditions are cool and wet, and in those mountain sites meteorological stations are scarce or have short records. Therefore, Mediterranean junipers may be better long-term monitors of low-elevation, drought-prone conditions.

Cool and wet conditions during the growing season (May-June) enhanced radial growth of young junipers (Fig. 1e). Warm and wet conditions during the prior December and cool conditions during the previous September and the current July also enhanced radial growth. The correlation between RWI with mean maximum June-July temperatures was r = −0.50 (P < 0.0001), and with May precipitation was r = 0.35 (P = 0.004) (Fig. 1f). The studied juniper species forms a shallow root system and is considered a drought-tolerant species (Baquedano and Castillo, 2007). This explains why warm summer conditions, enhancing evaporation, reduce radial growth and enhance the water-use efficiency of this species (Altieri et al., 2015). In extreme cases, like dry spells and heat waves, dieback and widespread mortality of juniper occurs despite the species' drought tolerance (Gazol et al., 2017).

The age-related deterioration of several physiological functions, related to water and nutrient uptake, has been attributed to the increase

in size of aging trees (Mencuccini et al., 2005), but this idea may not apply for short-stature shrubs. Old trees may show enhanced growth in response to favorable environmental conditions (Granda et al., 2017) because senescence does not necessarily impair cambial meristems (Lanner and Connor, 2001). In the case of old shrubby junipers, small size, sectoriality and partial cambial mortality (strip-bark growth habit) are linked to long life-spans (Mandin, 2006). These traits would allow old woody individuals inhabiting cliffs to survive rockfall but also drought (Larson et al., 1994; Matthes et al., 2008). The very low growth rates of old junipers agree with the harsh conditions of cliffs, because old individuals could thrive on more stable ground but are competitively excluded to these escarpment ecosystems (Kelly et al., 1992), and agrees with the preferential investment in dense wood with abundant metabolites, and resistant to fungal decay (Loehle, 1988; Klötzli, 1991).

Old junipers represent a valuable proxy of paleoecological information because such old specimens are very rare at low elevations in the Mediterranean Basin where most dendroclimatic reconstructions are based on high-elevation forests of pine, fir and cedar species (Cook et al., 2015, and references therein). These drought reconstructions may be biased in some cases because cold conditions prevail in mountains where the climate-growth relationships may be overridden by thermal constraints that differ from those experienced at lower elevation where water shortage is actually constraining tree or shrub growth (Sánchez-Salguero et al., 2015). Climatic reconstructions based on very old Mediterranean junipers, which are very sensitive to growing-season hydroclimate variability (Camarero et al., 2014; Esper et al., 2015) but may not always be cross-dated, would benefit from complementary dating techniques such as wiggle-matching ^{14}C dating (Biondi et al., 2007; Piovesan et al., 2018), and sampling of archaeological material with known provenance and historical documentation. The combination of several dendrochronological proxies (wood anatomy, microdensity, isotopes) would help to cross-date old junipers, thus advancing a better understanding of the speceis' long-term growth functions, and how senescence progresses on harsh cliff environments. For instance, we could investigate how these old junipers are responding to rising air temperatures in comparison with their young conspecifics since in the study area mean maximum June-July temperatures have significantly risen since 1950 ($r = 0.50$, $P = 0.0001$) at a mean rate of $+0.04°C$ yr^{-1} (Fig. 1e). Cliffs provide a refugia for many endemic rock-crevice plants. Their unique microclimate conditions may be more favorable for the long-term survival of shrubs than nearby Mediterranean sites. Finally, further exploration of calcareous cliffs, steep slopes and canyons, with the help of naturalists and rock climbers, would help to locate older juniper populations as has been done with *Thuja occidentalis* in North America (see Larson et al., 2000b). This exploration could also include individuals of Mediterranean shrub species forming annual rings but still understudied (e.g. *Juniperus* and *Pistacia* species). The finding of old shrubs in Iberia and southern France is not only a research of local interest because it may foster the discovery of other old-shrub populations across the Mediterranean Basin.

4. Conclusions

The oldest living Phoenician juniper was ^{14}C-dated to be 927 years old and named "Sancho". Ring counting underestimates the age of old junipers which form missing, double and wedging rings, and show eccentric growth. Cool and wet conditions during the growing season enhance radial growth of young Phoenician junipers. These old junipers, usually inhabiting calcareous cliffs and similar escarpment ecosystems, represent unique remnants of old-growth shrub populations in low-elevation areas across the circum Mediterranean area where old trees are rare.

Acknowledgements

References

Altieri, S., Mereu, S., Cherubini, P., Castaldi, S., Sirignano, C., Lubritto, C., Battipaglia, G., 2015. Tree-ring carbon and oxygen isotopes indicate different water use strategies in three Mediterranean shrubs at Capo Caccia (Sardinia, Italy). Trees 5, 1593–1603.

Baquedano, F.J., Castillo, F.J., 2007. Drought tolerance in the Mediterranean species *Quercus coccifera, Quercus ilex, Pinus halepensis,* and *Juniperus phoenicea.* Photosynthetica 45, 229–238.

Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. Nat. Plants 1, 15139.

Bigler, C., Veblen, T.T., 2009. Increased early growth rates decrease longevities of conifers in subalpine forests. Oikos 118, 1130–1138.

Biondi, F., Strachan, S.D.J., Mensing, S., Piovesan, G., 2007. Radiocarbon analysis confirms the annual nature of sagebursh growth rings. Radiocarbon 49, 1231–1240.

Briffa, K.R., Jones, P.D., 1990. Basic chronology statistics and assessment. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology: Applications in the Environmental Sciences. Kluwer, Dordrecht, pp. 137–152.

Büntgen, U., Bolze, N., Hellmann, L., Sittler, B., Frauenberger, B., Piermattei, A., Kirdyanov, A., Schweingruber, F.H., Ludemann, T., Krusic, P.J., 2018. Long-term recruitment dynamics of arctic dwarf shrub communities in coastal east Greenland. Dendrochronologia 50, 70–80.

Buras, A., Wilmking, M., 2014. Straight lines or eccentric eggs? A comparison of radial and spatial ring width measurements and its implications for climate transfer functions. Dendrochronologia 32, 313–326.

Camarero, J.J., Rozas, V., Olano, J.M., 2014. Minimum wood density of *Juniperus thurifera* is a robust proxy of spring water availability in a continental Mediterranean climate. J. Biogeogr. 41, 1105–1114.

Camarero, J.J., Gazol, A., Galván, J.D., Sangüesa-Barreda, G., Gutiérrez, E., 2015. Disparate effects of global-change drivers on mountain conifer forests: warming-induced growth enhancement in young trees vs. CO_2 fertilization in old trees from wet sites. Glob. Ch. Biol. 21, 738–749.

Cook, E.R., 1985. A Time Series Analysis Approach to Tree Ring Standardization. PhD. Dissertation. The University of Arizona, Tucson, USA, pp. 171.

Cook, E.R., et al., 2015. Old World megadroughts and pluvials during the Common Era. Sci. Adv. 1e e1500561.

Creus Novau, J., 1998. A propósito de los árboles más viejos de la España peninsular: los*Pinus nigra* Arn. ssp. *salzmannii* (Dunal) Franco de Puertollano-Cabañas sierra de Cazorla, Jaén. Montes 54, 68–76.

Esper, J., Frank, D.C., Wilson, R.J.S., Büntgen, U., Treydte, K., 2007. Uniform growth trends among central Asian low and high elevation juniper tree sites. Trees 21, 141–150.

Esper, J., Grossjean, J., Camarero, J.J., García-Cervigón, A.I., Olano, J.M., González-Rouco, J.F., Domínguez-Castro, F., Büntgen, U., 2015. Atlantic and Mediterranean synoptic drivers of central Spanish juniper growth. Theoret. Appl. Climatol. 12, 571–579.

Farjon, A., 2005. CupressaceaeSciadopitys. Royal Botanic Gardens, Kew, UK.

Fritts, H.C., 1976. Tree Rings and Climate. Academic Press.

García-Cervigón, A.I., Olano, J.M., Eugenio, M., Camarero, J.J., 2012. Arboreal and prostrate conifers coexisting in Mediterranean high mountains differ in their climatic responses. Dendrochronologia 30, 279–286.

Gazol, A., Sangüesa-Barreda, G., Granda, E., Camarero, J.J., 2017. Tracking the impact of drought on functionally different woody plants in a Mediterranean scrubland ecosystem. Plant Ecol. 218, 1009–1020.

Granda, E., Camarero, J.J., Galván, J.D., Sangüesa-Barreda, G., Alla, A.Q., Gutiérrez, E., Dorado-Liñán, I., Andreu-Hayles, L., Labuhn, I., Grudd, H., Voltas, J., 2017. Aged but withstanding: maintenance of growth rates in old pines is not related to enhanced water-use efficiency. Agric. For. Meteorol. 243, 43–54.

Haylock, M.R., Hofstra, N., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M.A., 2008. European daily high–resolution gridded data set of surface temperature and precipitation for 1950–2006. J. Geophys. Res. Atmos. 113 D20119.

Holmes, R.L., 1983. Program COFECHA user's manual. Laboratory of Tree–Ring Research. The University of Arizona, Tucson, USA.

Issartel, J., Coiffard, C., 2011. Extreme longevity in trees: live slow, die old? Oecologia 165, 1–5.

Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. Proc. Natl. Acad. Sci. U. S. A. 106, 11635–11640.

Kelly, P.E., Cook, E.R., Larson, W.L., 1992. Constrained growth, cambial mortality, and dendrochronology of ancient *Thuja occidentalis* on cliffs of the Niagara Escarpment:

an eastern version of bristlecone pine? Int. J. Plant Sci. 153, 117–127.

Klötzli, F.A., 1991. Niches of longevity and stress. In: Esser, G., Overdieck, D. (Eds.), Modern Ecology. Elsevier, Amsterdam, pp. 97–110.

Körner, C., 2017. A matter of tree longevity. Science 355, 130–131.

LaMarche Jr., V.C., 1969. Environment in relation to age of bristlecone pines. Ecology 50, 53–59.

Lanner, R.M., 2002. Why do trees live so long? Ageing Res. Rev. 1, 653–671.

Lanner, R., Connor, K.F., 2001. Does bristlecone pine senesce? Exp. Gerontol. 36, 675–685.

Larson, D.W., 2001. The paradox of great longevity in a short-lived tree species. Exp. Gerontol. 36, 651–673.

Larson, D.W., Doubt, J., Matthes-Sears, U., 1994. Radially sectored hydraulic pathways in the xylem of *Thuja occidentalis* as revealed by the use of dyes. Int. J. Plant Sci. 155, 569–582.

Larson, D.W., Matthes, U., Gerrath, J.A., Gerrath, J.M., Nekola, J.C., Walker, G.L., Porembski, S., Charlton, A., Larson, N.W.K., 1999. Ancient stunted trees on cliffs. Nature 398, 382–383.

Larson, D.W., Matthes, U., Gerrath, J.A., Larson, N.W.K., Gerrath, J.M., Nekola, J.C., Walker, G.L., Porembski, S., Charlton, A., 2000a. Evidence for the widespread occurrence of ancient forests on cliffs. J. Biogeogr. 27, 319–331.

Larson, D.W., Matthes, U., Kelly, P.E., 2000b. Cliff Ecology: Pattern and Process in Cliff Ecosystems. Cambridge University Press, New York.

Lindenmayer, D.B., 2016. Conserving large old trees as small natural features. Biol. Conserv. 211, 51–59.

Loehle, C., 1988. Tree life history strategies: the role of defenses. Can. J. For. Res. 18, 209–222.

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. Nature 455, 213–215.

Mandin, J.P., 2005. Découverte de très vieux genévriers de Phénicie (*Juniperus phoenicea* L.) dans les gorges de l'Ardèche (France). J. Bot. 29, 53–62.

Mandin, J.P., 2006. Morphologie des très vieux genévriers de Phénicie (Juniperusphoenicea L.) en parois rocheuses (gorges de l'Ardèche, France). III Coloquio Internacional sobre los Sabinares y Enebrales (Género Juniperus): Ecología y Gestión Forestal Sostenible, Soria (Spain), 24–26 May 2006, vol. 1, 303–310.

Mathaux, C., Mandin, J.-P., Oberlin, C., Edouard, J.-L., Gauquelin, T., Guibal, F., 2016. Ancient juniper trees growing on cliffs: toward a long Mediterranean tree-ring chronology. Dendrochronologia 37, 79–88.

Matthes, U., Kelly, P.E., Larson, D.W., 2008. Predicting the age of ancient *Thuja occidentalis* on cliffs. Can. J. For. Res. 38, 2923–2931.

Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S., Michiels, B., 2005. Size-mediated aging reduces vigour in trees. Ecol. Lett. 8, 1183–1190.

Miles, D.H., Worthington, M.J., 1998. Sonora Pass junipers from California USA: construction of a 3,500-year chronology. Stravinskiene, V., Juknys, R. (Eds.), Dendrochronology and Environmental Trends - Proceedings of the International Conference 17-21 June 1998.

Myers-Smith, I.H., Hik, D.S., 2017. Climate warming as a driver of tundra shrubline advance. J. Ecol. 106, 547–560.

Pacheco, A., Camarero, J.J., Carrer, M., 2016. Linking wood anatomy and xylogenesis allows pinpointing of climate and drought influences on growth of coexisting conifers in continental Mediterranean climate. Tree Physiol. 36, 502–512.

Piovesan, G., Biondi, F., Baliva, M., Calcagnile, L., Quarta, G., Di Filippo, A., 2018. Dating old hollow trees by applying a multistep tree-ring and radiocarbon procedure to trunk and exposed roots. MethodsX 5, 495–502.

Rosbakh, S., Poschlod, P., 2018. Killing me slowly: harsh environment extends plant maximum life span. Basic Appl. Ecol. 28, 17–26.

Sánchez-Salguero, R., Camarero, J.J., Hevia, A., Madrigal-González, J., Linares, J.C., Ballesteros-Canovas, J.A., Sánchez-Miranda, A., Alfaro-Sánchez, R., Sangüesa-Barreda, S., Galván, J.D., Gutiérrez, E., Génova, M., Rigling, A., 2015. What drives growth of Scots pine in continental Mediterranean climates: drought, low temperatures or both? Agric. For. Meteorol. 206, 151–162.

Schweingruber, F.H., Poschlod, P., 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. Forest Snow Landsc. Res. 79, 195–415.

Swetnam, T.W., Brown, P.M., 1992. Oldest known conifers in the southwestern United States: temporal and spatial patterns of maximum age. Pp. 24-38 in M.R. Kaufmann, W.H. Moir, and R.L. Bassett, tech. coords., Old-growth forests in the Southwest and Rocky Mountain regions: the Status of our knowledge. Proceedings of a Workshop, Portal, Ariz., 9-13 March 1992. General Tech. Rep. RM-213.

Touchan, R., Meko, D.M., Hughes, H., 1999. A 396-year reconstruction of precipitation in southern Jordan. J. Am. Water Res. Assoc. 35, 45–55.

Wacker, L., Güttler, D., Goll, J., Hurni, J.P., Synal, H.-A., Walti, N., 2014. Radiocarbon dating to a single year by means of rapid atmospheric ^{14}C changes. Radiocarbon 56, 573–579.

Waisel, Y., Liphschitz, N., 1968. Dendrochronological studies in Israel II. Juniperus phoenicea of north and central Sinai. La Yaaran 18, 67–69.

Ward, L.K., 1982. The conservation of juniper: longevity and old age. J. Appl. Ecol. 19, 917–928.