WOOD FORMATION IN *JUNIPERUS EXCELSA* SSP. *POLYCARPOS* IN THE HIGH MOUNTAINS OF NORTH-EAST IRAN

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SADERI SM, POURTAHMASI K, OLADI R & RATHGEBER CBK. 2013. Wood formation in *Juniperus excelsa* ssp. *polycarpos* in the high mountains of north-east Iran. Cambial activity and of xylem formation in Persian juniper (*Juniperus polycarpos*) were studied during the 2010 growth season in the high mountains of Chaharbagh, Gorgan, north-east Iran. Wood microcores were collected weekly from March till May and biweekly from June till September from four trees. Thin sections were cut and anatomical features of the developing and mature tracheids were observed, counted and measured along three radial files of the growing xylem. Monthly tree-ring increments were correlated with monthly mean temperature and total rainfall. The dormant cambium contained 2–3 cell layers adjacent to the last formed phloem fibres in the previous year. Cambial cell division began on the second week of April and terminated at the end of August. The maximum number of cambium cells (8–9) and the maximum daily growth rates of all trees were achieved around mid-June. Rainfall and temperature showed a strong positive and negative relation respectively with monthly tree-ring increment. As the study area is cool and semi-arid, cambial reactivation is controlled by temperature. However during the growing period, water availability is the main limiting factor for growth.

Keywords: Cambial activity, xylem formation, wood anatomy, Persian juniper

SADERI SM, POURTAHMASI K, OLADI R & RATHGEBER CBK. 2013. Pembentukan kayu dalam *Juniperus excelsa* ssp. *polycarpos* di kawasan pergunungan di timur laut Iran. Aktiviti kambium dan pembentukan xilem dalam *Juniperus polycarpos* dikaji di kawasan pergunungan Chaharbagh, Gorgan di timur laut Iran semasa musim pertumbuhan tahun 2010. Mikrokor kayu diambil daripada empat batang pokok setiap minggu dari bulan Mac hingga Mei dan setiap dua minggu dari bulan Jun hingga September. Keratan nipis dibuat dan ciri anatomi trakeid yang membesar serta yang matang diperhati, dikira dan diukur sepanjang tiga baris jejari xilem yang membesar. Pertambahan gelang pokok bulanan dikorelasikan dengan purata suhu bulanan serta jumlah hujan bulanan. Kambium yang dorman mengandungi 2–3 lapisan sel bersebelahan dengan gentian floem terakhir yang terbentuk pada tahun sebelumnya. Pembahagian sel kambium bermula pada minggu kedua bulan April dan berakhir pada akhir bulan Ogos. Bilangan maksimum sel kambium (8–9 sel) dan kadar pertumbuhan harian yang maksimum bagi kesemua pokok dicapai sekitar pertengahan bulan Jun. Hujan dan suhu masing-masing menunjukkan perhubungan positif dan negatif yang kuat dengan pertambahan gelang pokok bulanan. Memandangkan kawasan kajian ini dingin dan separa kontang, pengaktifan semula kambium adalah dikawal oleh suhu. Namun semasa tempoh pertumbuhan, air merupakan faktor pengehad yang utama.

INTRODUCTION

Juniperus excelsa ssp. *polycarpos* known as Persian juniper is a dioecious tree up to 6–7 m tall or a low shrub with dense head (Emami et al. 2011). It is one of the dominant species of the Junipero-Pistacietea steppe forest in the interior basins of Iran (Liphschitz et al. 1979). It is also widely distributed in other areas such as south-east Arabia, Iran, Caucasus, Baluchistan, Afghanistan, north-west Himalaya (Townsend & Guest 1966), Armenia, India, Uzbekistan and Pakistan (Franco 1964) .

In Iran, Persian juniper is distributed on the southern slopes of the high mountains of Alborz, in the northern parts of Khorassan and Arassbaran and also in some central mountains (Diavanshir 1974). However, juniper forests are mostly located in the north-east of Iran, at an elevation of 1500 to 2500 m above sea level (asl)

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(Fadaei et al. 2009) but have been seen as far south as Bandar Abbas close to the Persian Gulf. The significant role of the Persian juniper in soil protection and its ability to grow in very adverse climatic condition make it an important species in Iran. Its high resistance to frost enables it to grow in areas where the minimum temperature is -35 °C (Diavanshir 1974).

Monitoring cambial phenology and intra-annual growth dynamics is a useful approach in characterising tree growth response to climate change (Michelot et al. 2012). The distinct annual growth rings of Persian junipers and high sensitivity of this species to climatic factors (Wigley et al. 1984, Pourtahmasi et al. 2007) make this coniferous species suitable for intra-annual and dendroclimatological studies. There is high potential for dendroclimatological investigation in Iran, especially in the western and central parts of the country, an area situated in the most eastern district of the Middle East and Asia Minor where little information about past climate is available (Pourtahmasi et al. 2007). Although there are increasing inter-annual tree ring studies in north-east Iran, the results are sometimes difficult to interpret since detailed studies on tree physiology and exact growth period are still missing from this region (Pourtahmasi et al. 2007, 2009). The aim of our study was, therefore, to investigate the cambium phenology and intra-annual wood formation of Persian juniper with respect to climatic factors.

Temperature seems to be the strongest factor limiting the growth of juniper as has been shown in other high-elevation conifers (Deslauriers et al. 2008). However, this hypothesis has not been validated for semi-arid mountainous areas such as the eastern Alborz where rainfall deficit may also play an important role in controlling tree growth. In this study, we reported the timing of the cambial activity and different phases of xylem development of Persian juniper in order to understand the seasonal climatic factors influencing local tree growth and the ecological behaviour of this regionally important tree species.

MATERIALS AND METHODS

The study was carried out in a Juniper forest (36° 40.2' N, 54° 31.4' E, 2300 m asl) in the mountains of Chaharbagh, Gorgan, north-east Iran, at the east edge of Jahannama protected area (Figure 1). These open forests have very low tree density and experience dry and cold climatic conditions. Annual precipitation and mean annual temperature are 395 mm and 8.3 °C respectively (Nadi et al. 2010). Monthly mean temperature drops below zero from January till March (Figure 1c). The study site is covered in snow for almost the whole winter. The meteorological data were obtained from Nadi et al. (2010). They interpolated the monthly rainfalls and temperatures of the studied area based on 20 nearby stations located at heights greater than 400 m.

Four healthy Juniper trees with a diameter of 20–30 cm were randomly selected for the study. The sampling of wood samples for analysing cambial activity was done using a Trephor corer (Rossi et al. 2006a), taking microcores around the stems at breast height (1.3 m) from two opposite sides of each tree. Collection of samples was carried out weekly from March till May and biweekly from June till September 2010. The distance between sample positions on stems was at least 3 cm to avoid any wound effect (Gričar et al. 2007). The microcores were immediately transferred in FEA (formalin, ethanol, acetic acid) solution.

In the laboratory, samples were immersed in distilled water for 2–3 days, moulded with paraffin and immediately sectioned using a sledge microtome. Sections of 18 μm thick were cut and double-stained with 1% water solution of safranin-astra blue, then dehydrated in a graded series of ethanol (50, 75 and 100%) and mounted on glass slides for observation under a light microscope.

A digital camera attached to a polarising microscope was used to photograph the thin sections using normal and polarised light. The cambium was considered active when the first periclinal cell division was observed within the cambial zone (Frankenstein et al. 2005). The number of cambium cells is an indicator of cambial activity, i.e. the higher the number of cells, the higher is the activity of the cambium. The number of cambium cells and cells in three xylem differentiation phases (cell enlargement, secondary wall deposition and lignification) was counted along three radial files in each microsection. Different xylem differentiation phases were distinguished; cells in the enlarging

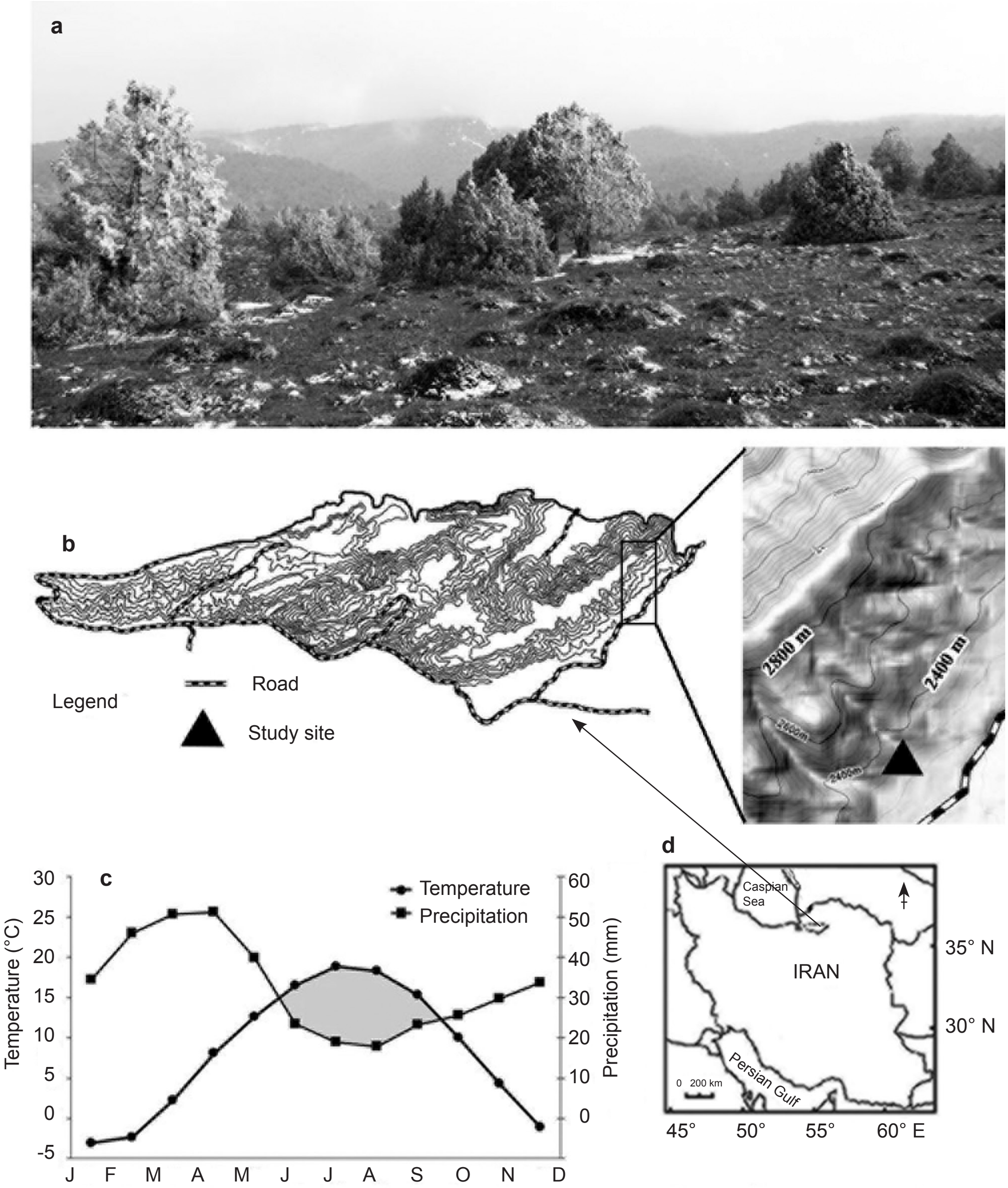

Figure 1 Study site in Chaharbagh, northern Iran: (a) view of the forest interior at the end of March, (b) topographic map of the Jahannama protected area, (c) ombrothermic climatic diagram for the study site from 1985–2010; shaded area shows the xerothermic period and (d) location of the study site in Iran

phase were larger than cambium cells and had non-lignified thin walls. The beginning of secondary wall deposition was determined using polarised light microscope. Polarised light does not pass through the irregularly arranged fibrils of primary cell walls so that tracheids containing only primary wall appear dark whereas cells with secondary walls shine under polarised light (Schweingruber 2007). The lignification phase was characterised by a change in colour of cell walls from pure blue to reddish purple and red. The average number of cells in each of these phases was standardised to minimise the effect of the relative position of sampling on the stem (Rossi et al. 2003). The standardised cell number calculated for each of the two opposite sides of a tree was then averaged and referred to in further analyses.

Finally, the total number of cells for each sampling date was modelled using Gompertz function (Rossi et al. 2003):

$$y = A\exp\left[- e^{(\beta - kt)}\right]$$

where y = weekly sum of cells, t = time computed as days of the year, A = upper asymptote and the maximum growth expressed as cell number, β = the x-axis placement parameter and k = rate of changes of the shape. First, the Gompertz parameters (A, β and k) were estimated by applying the Gauss–Newton method with Proc NLIN of SAS® software using the actual cumulative tree-ring cell numbers. By inserting t values (time) as days of the year into the equation, the corresponding y values (predicted tree-ring cell numbers) were then calculated. Finally, the cumulative and daily growth rates of the trees were calculated.

To identify the climatic factors most closely associated with xylem formation, Pearson correlation coefficients (r) were computed between mean monthly growth rates and mean monthly temperatures and sums of monthly rainfall during the growing season (May–August) (Gruber et al. 2009). To distinguish any significant growth difference between trees, the ANOVA_GLM test was applied in SAS® software.

RESULTS

Distinguishing the cambium from the adjacent phloem cells was challenging since both cell types were similar in size and shape. However, a tangential row of phloem fibres with slightly thicker and partly lignified walls was used as a guide (Figure 2a). The contrast between these fibres and cambium cells was best recognised under polarised light where the secondary fibre walls exhibited bi-refringency (Figure 2b). Since the cambial layer composed only of cambium initials, xylem and phloem mother cells, the appearance of phloem fibres adjacent to cambium cells could be considered as an end point to phloem cells and the beginning of the cambial zone. At the end of the growing season, the last formed phloem fibres had thickened but not yet lignified walls (Figure 2d).

During winter, the dormant cambium reduced to 2–3 layers. The onset of cambial activity in spring and its recession in autumn occurred at almost the same time in all trees: starting at the beginning of April (a week after snow had completely melted) and finishing at the end of August. During the early growing season, the number of cambium cell layers increased and reached its peak with 6–8 cells from 14 June till 6 July. Then, the activity of the cambial zone declined gradually until the end of the growing season. The cambium cells had thinner walls when they were active.

The number of cell layers in the enlarging phase was 1–6, showing no significant trend throughout the growing season. Cell enlargement started on average 1 week after cambial activation and ended 10 days after the cessation of the cambium cell division. Cell-wall thickening was first observed on April 20 (more than 1 week after the previous phase) and continued till early August. Lignification started on May 5 (around 2 weeks after secondary cell-wall thickening) and lasted less than 2 weeks after the end of the growth season. This phase of cell development started from the corners and outer parts of the cell walls to the tracheid lumens (Figures 2c and e). In total, the duration of cambial activity and wood formation lasted about 5 months.

The GLM test in SAS did not show any significant difference between trees ($p > 0.01$). The fitting of the intra-annual growth dynamics by the Gompertz function (Figure 3a) resulted in pseudo-r^2 values above 0.96 for all trees. Based on the Gompertz model, the maximum daily growth rate occurred in mid-June (Figure 3b). The sum of monthly rainfall and monthly average temperature showed strong positive ($r = 0.61$, $p < 0.05$) and negative ($r = -0.53$, $p < 0.05$) correlations respectively with monthly tree-ring increments (results not shown).

DISCUSSION

Cambial reactivation at the beginning of the growing season is highly related to temperature in early spring (Gričar et al. 2007, Lupi et al. 2010). This relation also has significant effect on the cell production of conifer species in boreal and high-altitude forests (Deslauriers & Morin 2005). Several studies revealed that there was delay in the onset of cambial activity and shorter length of the growing season in species growing at high latitudes such as *Pinus cembra* and *Larix decidua* (Rossi et al. 2006a), *Picea abies* (Mäkinen et al. 2003), *Abies balsama* and *Picea mariana* (Thibeault-Martel et al. 2008), *Abies alba* and *Pinus sylvestris*

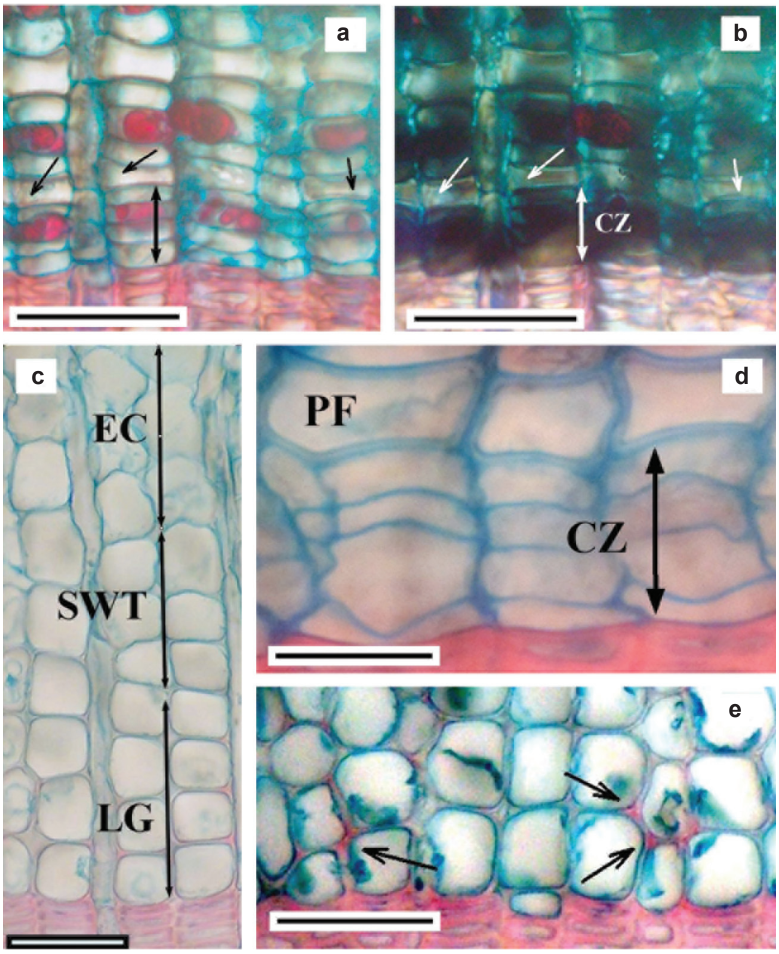

Figure 2 Microscopic transverse sections of *J. polycarpos*: (a) cambial area just before beginning of the growing season, phloem fibres (black arrows) are hard to recognise under visible light; (b) under polarised light, cambial zone (CZ) is considered as cells between the first row of these fibres (white arrows) and the previous year's xylem tracheids, sample taken on March 22; (c) newly-formed xylem cells in different phases of xylem development, i.e. radial enlargement (EC), secondary wall thickening (SWT) and lignification (LG), sample taken on May 25; (d) cambium area at the end of the growing season, phloem fibres (PF) have distinctly thicker walls than cambium cells but their lignification has not started yet, sample taken on August 10; (e) lignification started from cell corners (arrows), sample taken on May 25; scale bars for a, b, c and e = 50 µm, d = 20 µm

(Rathgeber et al. 2011) compared with species growing at lower latitudes such as *Pinus halepensis* (De Luis et al. 2007). Temperature seemed to play an important role in the activation of juniper cambium too since xylogenesis began soon after the complete melting of snow (Rossi et al. 2011).

The intervals between the onset of different xylogenetic phases, i.e. cambium reactivation, cell enlargement, cell-wall thickening and lignification in Persian junipers were almost the same as those previously reported for some hardwood and softwood grown in different locations and climates, e.g. oriental beech (Oladi et al. 2011), European beech (Čufar et al. 2008) and stone pine (Rossi et al. 2007, Gruber et al. 2009). It seems that once the cambium is activated, climatic factors have low effect on the timing of these intervals and affect only the duration of each phase (Rossi et al. 2006a).

Lignification continues after cambial activity has stopped (De Luis et al. 2007, Čufar et al. 2008, Levanič et al. 2009). In this study, the time necessary for the last formed tracheids to become fully lignified was less than 2 weeks which was fairly short compared with 6–9 weeks delay in other mountainous conifers (Rossi et al. 2007, Gričar & Čufar 2008). It has been reported that the time for xylem cell maturation increases during the course of the growing season (Lupi et al. 2010). In our case, however,

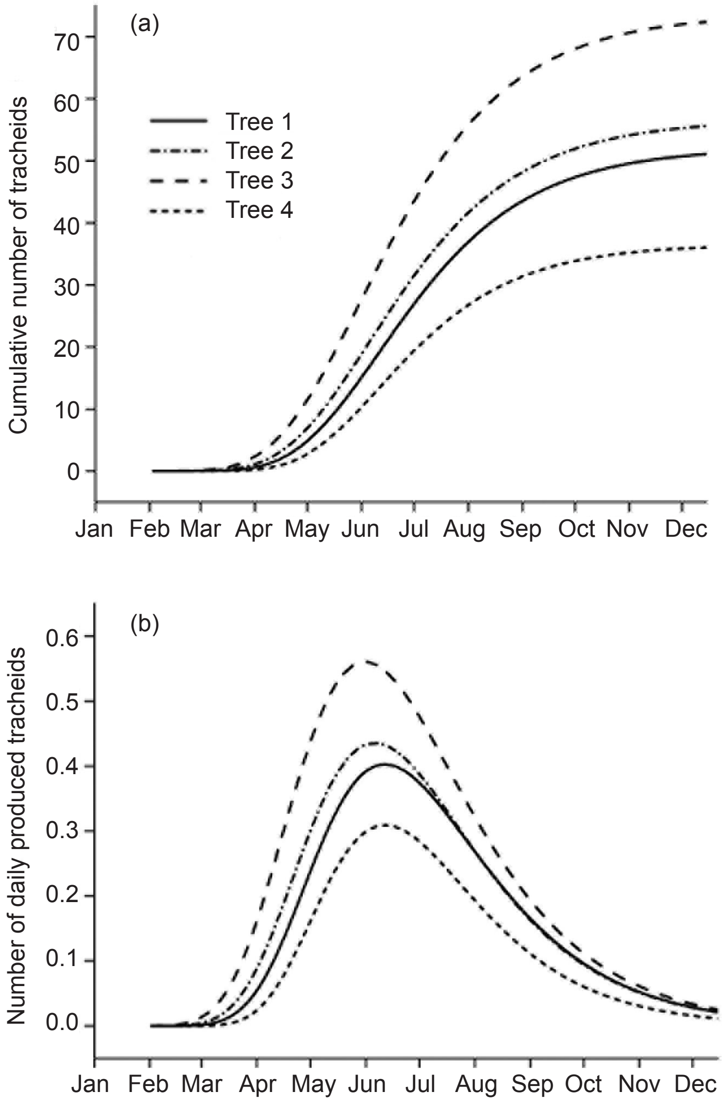

Figure 3 Persian juniper tree growth modelled by the Gompertz function: (a) cumulative and (b) daily increments of tree-ring width during the 2010 growth season

secondary cell-wall thickening and lignification at the end of the growing season were as fast as its beginning. Temperature (Čufar et al. 2008), growth rate (Grünwald et al. 2002) and some internal factors are the main factors controlling the duration of lignification. At higher elevation, temperature is an important determinant and there is direct relationship between temperature and lignification, especially at the end of summer (Gindl et al. 2000). It has been shown that lignification terminates earlier in trees growing at higher/colder sites (Gindl et al. 2000, Gruber et al. 2009). The trees completed the differentiation of the last formed tracheids early enough to avoid encountering a sudden temperature drop in late autumn (Rossi et al. 2008).

The most intense period of cambial division activity and maximum daily growth rates of trees occurred in the second half of June. Several studies reported the simultaneous time of maximum increment for different species at different latitudes around the summer solstice (21 June) (Mäkinen et al. 2003, Gričar et al. 2007, Oladi et al. 2011, Seo et al. 2011). This has been related to the effect of the photoperiod in timing of maximum radial growth (Rossi et al. 2006b).

In cold and high elevation ecosystems, precipitation usually is the second major environmental factor affecting tree growth rate and timing. It has been reported that after cambial reactivation the role of temperature declines and the influence of precipitation increases towards the end of the growing season (Sass & Eckstein 1995). This relation is more pronounced in areas where water availability is a limiting factor for growth, i.e. drought-subjected parts of cold and temperate ecosystems (Bräuning 2000, Gričar & Čufar 2008, Lupi et al. 2010, De Luis et al. 2011) and trees growing in Mediterranean climates (Martin-Benito et al. 2011) or in tropical dry forest (Marcati et al. 2008). However, the mutual dependence of temperature and precipitation, rather than considering them separately (Seo et al. 2011), could be the key concept in interpreting their roles in cell production and radial growth, especially when trees experience water stress during growth. The high positive and negative correlations respectively of monthly rainfall and air temperature with monthly tree-ring increments of Persian junipers can be interpreted in this way. Total annual rainfall in the region is low and a xerothermic period begins around mid-May and lasts up till mid-September. Thus, water availability may become a limiting factor for growth at our study site. Our finding was consistent with results of an inter-annual study on Persian juniper where total ring width was positively influenced by high spring and early summer (May–June) rainfall (Pourtahmasi et al. 2007). Since the most intense period of xylem formation occurred in May and June, it could be concluded that radial growth was highly promoted by rainfall in these months and vice versa. Trees in hot and dry conditions usually close their stomata in the hottest hours of the day in order to prevent water loss through transpiration (Thomas 2004) which in turn reduces the photosynthetic activity and plant productivity (Woodruff et al. 2009, Meinzer et al. 2011). Hence, the photosynthates available for xylem formation (and therefore, growth rate and final tree-ring width) decline with increasing temperature and decreasing rainfall. This oppositional correlation between temperature and growth versus rainfall and growth was in agreement with the findings by Mäkinen et al. (2003), Čufar et al. (2008) and Seo et al. (2011) but deviated from observations by Deslauriers and Morin (2005) and Gruber et al. (2009) who found no significant intra-annual correlations between wood formation and precipitation and/or temperature. However, a long-term dendroclimatological study on juniper and oak in the studied region confirms that rainfall during the growth season is the most important factor determining juniper ring width but having minor effect on oak (Pourtahmasi et al. 2009). Summer temperature is generally negatively correlated with tree growth of junipers, although not always significant (Pourtahmasi et al. 2007). It seems that winter temperature prior to the growth season plays a more important role (Pourtahmasi et al. 2007) and its influence during the growth is partly the mirror effect of rainfall. Since our study is only based on 1-year observation, on-going measurements of wood formation during climatologically varying years may reveal the sensitivity of juniper growth to water availability during different phases of the growing season.

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