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ORIGINAL ARTICLE

# Minimum wood density of conifers portrays changes in early season precipitation at dry and cold Eurasian regions

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## Abstract

***Key message*** **Minimum wood density exhibits strong responses to precipitation and, thus, it is a robust proxy of early season water availability.**

*Abstract* Tracheids fulfil most wood functions in conifers (mechanical support and water transport) and earlywood tracheids account for most hydraulic conductivity within the annual tree ring. Dry conditions during the early growing season, when earlywood is formed, could lead to the formation of narrow tracheid lumens and a dense earlywood. Here, we assessed if there is a negative association between minimum wood density and early growing-season (spring) precipitation. Using dendrochronology, we studied growth and density data at nine forest stands of three Pinaceae species (*Larix sibirica*, *Pinus nigra*, and *Pinus sylvestris*) widely distributed in three cool–dry Eurasian regions from the forest-steppe (Russia, Mongolia) and Mediterranean (Spain) biomes. We measured for each annual tree ring and the common 1950–2002 period the following variables: earlywood and latewood width, and minimum and maximum wood density. As expected, dry early growing season (spring) conditions were associated with low earlywood production but, most importantly, to high minimum density in the three conifer species. The associations between minimum density and spring precipitation were stronger ($r = -0.65$) than those observed with earlywood width ($r = 0.57$). We interpret the relationship between spring water availability and high minimum density as a drought-induced reduction in lumen diameter, hydraulic conductivity, and growth. Consequently, forecasted growing-season drier conditions would translate into increased minimum wood density and reflect a reduction in hydraulic conductivity, radial growth, and wood formation. Given the case-study-like nature of this work, more research on other cold–dry sites with additional conifer species is needed to test if minimum wood density is a robust proxy of early season water availability.

**Keywords** Black pine · Scots pine · Siberian larch · Dendroecology · Water availability · Wood density

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## Introduction

In trees, wood fulfils multiple functions including mechanical support, transport, storage, and defense against biotic agents (Zobel and van Buijtenen 1989). The balances between these functions are reflected in changes of wood density between (Muller-Landau 2004) and within tree species (Martínez-Vilalta et al. 2009; Fajardo 2016). Trade-offs determining wood density result from the conflict between xylem filling with carbon-rich walls and parenchyma vs. leaving open conduit spaces (Carlquist 1975). A higher wood density provides greater strength but also entails higher construction costs (Niklas 1992). It is common that tree species forming narrow conduits and having high wood density show low growth rates (Chave et al. 2009). Conversely, conduit diameter increases in tree species with softer wood (Hacke and Sperry 2001; Bouche et al. 2014), thus providing a high hydraulic conductivity. However, presumed conflicts in wood functions may reflect evolutionary paths of co-varying traits, and caution must be taken to interpret such assumed trade-offs (Larjavaara and Muller-Landau 2010). In addition, wood density is a very conservative trait showing low variation along climatic gradients (Zhang et al. 2011). Nevertheless, since both radial growth and density determine forest carbon uptake, assessments of their responses to climate together with a better characterization of climate-growth-wood density associations are required (Bouriaud et al. 2015).

Conifers subjected to double stress during seasonal wood formation (i.e., growing under cold and dry conditions) are particularly suited to perform such assessments, because wood functions are mostly carried out by tracheids which are formed during a short growing season (Larson 1994). In conifers, wood density may be defined as the ratio of cell-wall thickness to transversal lumen diameter, which is a proxy of absolute wood density (Yasue et al. 2000). This thickness–span ratio is considered a surrogate of xylem hydraulic functions, since a large tracheid lumen (low thickness–span ratio) provides more hydraulic conductivity but increases the risk of frost- or drought-induced embolism (Hacke et al. 2001, 2015). Under dry conditions during the early growing season, conifers produce narrow earlywood tracheid lumens, which account for most hydraulic conductivity within the annual tree ring (Domec et al. 2009) and, therefore, a dense earlywood. However, large tracheid lumens have also been reported in Scots pine (*Pinus sylvestris*) provenances from dry sites (Martín et al. 2010) or in trees subjected to imposed dry conditions (Eilmann et al. 2011). These contradictory patterns require a better interpretation. Therefore, more research is needed to ascertain how density responds to changes in water availability during the growing season in conifers thriving in cold and seasonally dry climates.

A negative association between minimum wood density and early growing-season (spring) precipitation was already observed in the Cupressaceae Spanish juniper (*Juniperus thurifera* L.) subjected to cool–dry conditions (Camarero et al. 2014). Nevertheless, this relationship has to be investigated in other species as pines and larches which are widely distributed in cool–dry regions and form the world's largest conifer forests (Richardson 1998). A reduction in hydraulic conductivity would be linked to narrower tracheid lumens and higher minimum density values (Pittermann et al. 2006). Thus, we hypothesize that dry spring conditions would increase minimum wood density. Specifically, we aim to: (1) analyse how seasonal growth (earlywood and latewood widths) and wood density components (minimum and maximum density) respond to climate (mean monthly and seasonal temperatures, and total precipitation); and (2) assess whether minimum wood density is consistently (negatively) associated with spring precipitation in Pinaceae species of two genera (*Larix* and *Pinus*) across a broad range of environmental conditions in Eurasia.

## Materials and methods

### Study sites and species

Sampling regions were selected to include Pinaceae species whose radial growth and wood formation were constrained by two stress types, namely low temperatures shortening the growing-season length and drought reducing the growth rates during the growing season. We selected four Eurasian regions from three countries subjected to cold and dry climatic conditions: southern Siberia and southern Urals in Russia, Khangai in Mongolia, and Sierra de Gúdar in eastern Spain (Table 1; Supporting Information, Fig. S1). Continental climate conditions (cold winters, ample temperature range) and warm conditions and low precipitation during the growing season constrain tree radial growth in all the study areas (Block et al. 2004, Dulamsuren et al. 2009, Velisevich and Kozlov 2006, Devi et al. 2008, Knorre et al. 2010, Camarero et al. 2015). In southern Siberia and Mongolia, we sampled Siberian larch (*Larix sibirica* Ledeb.), whilst Scots pine (*Pinus sylvestris* L.) was sampled in the Urals and Spain. In Spain, we also sampled Black pine (*Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco), a typical Mediterranean tree species (Richardson 1998).

The northernmost study region is located in southern Siberian forest-steppe zone where open larch forests are

**Table 1** Characteristics of the study sites

| Region (country) | Species (code) | Site (code) | Latitude(N) | Longitude | Elevation (m.a.s.l.) | No. trees | Age at 1.3 m (years) | Timespan with > 5 trees |
|---|---|---|---|---|---|---|---|---|
| Southern Siberia (Russia) | *Larix sibirica* (Ls) | Efremkino (EF) | 54°29′ | 89°28′E | 520 | 17 | 194 ± 49 | 1766–2002 |
| | | Shira (KH) | 54°24′ | 89°58′E | 590 | 24 | 142 ± 40 | 1877–2005 |
| Southern Urals (Russia) | *Pinus sylvestris* (Ps) | Aldanskoye (CA) | 52°11′ | 59°44′E | 740 | 16 | 80 ± 9 | 1902–2005 |
| Khangai (Mongolia) | *Larix sibirica* (Ls) | Khangai 2 (M7) | 47°24′ | 100°43′E | 1920 | 24 | 137 ± 75 | 1838–2002 |
| | | Khangai 1 (M0) | 46°44′ | 102°40′E | 1870 | 30 | 228 ± 80 | 1695–2002 |
| Sierra de Gúdar (Spain) | *Pinus sylvestris* (Ps) | Peñarroya (PN) | 42°23′ | 0°39′W | 2020 | 16 | 79 ± 19 | 1906–2011 |
| | | Las Roquetas (LR) | 40°19′ | 0°43′W | 1615 | 15 | 103 ± 20 | 1875–2011 |
| | *Pinus nigra* (Pn) | Las Roquetas (LR) | 40°19′ | 0°43′W | 1615 | 15 | 131 ± 33 | 1847–2011 |
| | | Alto de Cabra (AC) | 40°20′ | 0°48′W | 1090 | 16 | 120 ± 21 | 1859–2011 |

Age values are mean ± SD

typical (Dylis 1961, Knorre et al., 2010). The forest sampled in the Urals is situated in the Aldan plateau where open conifer forests predominate up to 1250 m (Devi et al. 2008). In Mongolian lowlands, sampled trees formed forest-steppe ecotones which constitute the lower treeline (Treter 2000, Dulamsuren et al. 2010). The southernmost study region is located in Sierra de Gúdar (southern Iberian Range, eastern Spain) and includes two Scots pine stands and two Black pine stands. In this region, the study sites were distributed along an altitudinal gradient, because Scots pine dominates at cold sub-Mediterranean sites situated at higher elevation, whereas Black pine is dominant at mid-elevation sites experiencing Mediterranean climate (Camarero et al. 2015). We sampled one site (LR in Table 1) where the two species co-occur. The selected study stands were not impacted by local anthropogenic disturbances (grazing, fires, and logging) since the 1960s. The understory is dominated by shrubs in most of the study sites (e.g., *Juniperus communis* L.). Soils are brown in the Russian and Mongolian sites, whereas basic and clayey soils appear in Spain.

## Field sampling

We randomly selected and sampled 15–30 dominant trees per site in ca. 1-ha large sampling areas (Table 1). A 10-mm wide core per tree was extracted at 1.3 m for densitometry analyses using Pressler increment borers. We took special care for sampling this last core perpendicular to the main stem so as to capture the main fibre direction. We also measured diameter at 1.3 m and total height of each tree using tapes and clinometers, respectively. Trees selected for sampling had diameters ranging between 39.0 and 47.0 cm, heights between 9.3 and 10.5 m, and ages (estimated at 1.3 m) between 79 and 318 years (Table 1). Stands are relatively open, with basal area values ranging between 12 and 38 $m^2$ $ha^{-1}$.

We took two additional 5-mm wide cores from each tree for obtaining tree-ring width data so as to cross-date the densitometry samples. These cores were glued onto wooden mounts, sanded, visually cross-dated, and checked for dating accuracy using dendrochronology (Fritts 2001).

## Width and density measurements

One radial X-ray density profile was obtained from each tree using indirect X-ray densitometry. Prior to further treatment, resin was extracted from the wood samples with alcohol in a Soxhlet extractor. Then, each core was cut carefully using a double-bladed saw to obtain ca. 1.5-mm-thick laths. These samples were air dried to moisture equilibrium and then subjected to X-ray exposure. The resulting X-ray films were scanned with a resolution of

10 µm using a microdensitometer DENDRO-2003 (Walesch Electronics Ltd., Switzerland).

The measured grey levels of the X-ray films were transferred to density values by comparing them to a standard of known physical and optical density also exposed on the same film. For each annual ring, the following variables were obtained from the tree-ring density profiles: earlywood (EW hereafter) and latewood widths (LW hereafter), and minimum (MN hereafter) and maximum wood densities (MX hereafter). Note that MN and MX are tightly related to earlywood and latewood mean densities, so we only analysed the former two variables, because they are easier to define and show a stronger response to climate variables (Camarero et al. 2014). To define the earlywood–latewood transition, we used the 50% level between the MN and MX values of each ring following Polge (1978), and confirmed this separation with a visual checking of the tree rings (Mäkinen and Hynynen 2014).

## Chronology building

The accurately dated tree-ring series produced in the previous step (EW, LW, MN, and MX) were individually detrended to remove non-climatic biological growth trends (Cook and Kairiukstis 1990). Prior to trend removal, however, a power transformation was applied to the raw density data. A 2/3 cubic smoothing spline with 50% frequency–response cutoff was fitted to the individual records and indexed values were calculated. Then, indexed tree-ring series were subjected to autoregressive modelling to remove the first-order autocorrelation and produce residual indices. This autoregressive (pre-whitening) method was applied, because instrumental target data may reflect white noise behaviour (Büntgen et al. 2010). Finally, site chronologies for each species and variable were obtained by averaging the residual indices on a yearly basis using a bi-weight robust mean. These procedures were performed using the library dplR in the R platform (Bunn 2008, Bunn et al. 2016).

To compare the resulting chronologies, several statistics were calculated for the common period 1950–2002 considering either the raw site chronologies (mean; SD, standard deviation; AR1, first-order autocorrelation) or the residual chronologies ($r_{bt}$, mean inter-series correlation; MSx, mean sensitivity, a measure of the relative variability between consecutive years; cf. Fritts 2011).

## Climate data

Local climate data (monthly total precipitation and mean temperature) were retrieved from the nearest meteorological stations for all study sites (Table 2; Supporting Information, Fig. S2), excepting Mongolian sites which are located far away from climate stations with long and homogeneous precipitation records. There, precipitation was obtained from the nearest 0.5° grid box to each sampling site of the high-resolution gridded climate data set (Climatic Research Unit, CRU TS 3.22; Harris et al. 2014). In Spain, local data from ten stations situated in the study area were converted into a regional climate series and elevation differences were corrected by calculating regressions between the station elevation and mean annual temperature or total annual precipitation. To take into account the elevation difference between climate stations and sampling sites, we corrected the regional mean temperature and precipitation data considering a mean lapse rate of $-7.8$ °C km$^{-1}$ and $+420$ mm km$^{-1}$, respectively (see more details in Sangüesa-Barreda et al. 2014). Climate data were obtained for the common period 1950–2002 when tree-ring data were available for all sites (Table 1).

**Table 2** Climatic characterization of the study sites calculated for the common period 1950–2002

| Region (country) | Study sites (species) | Closest meteorological station (coordinates) | Mean annual temperature (°C) | Annual precipitation (mm) | Annual water balance (mm) | Continentality index (type) |
|---|---|---|---|---|---|---|
| C. Siberia (Russia) | EF (Ls), KH (Ls) | Shira (54°29′N, 89°58′E, 448 m.a.s.l.) | −1.9° | 316 | −161 | 63 (continental) |
| S. Urals (Russia) | CA (Ps) | Bredy (52°25′N, 60°20′ E, 305 m.a.s.l.) | 2.4° | 352 | −240 | 60 (continental) |
| Khangai (Mongolia) | M7 (Ls), M0 (Ls) | Tsetserleg (47°24′N, 101°01′E, 1691 m.a.s.l.) | 0.4° | 331 | −124 | 50 (sub-continental) |
| Gúdar (Spain) | PN (Ps), LR (Ps), LR (Pn), AC (Pn) | Mora de Rubielos (40°15′N, 0°45′W, 1038 m.a.s.l.) | 9.5 | 533 | −849 | 26 (oceanic) |

Sites' and species' codes are as in Table 1. In climate–growth analyses, CRU gridded climate data (0.5° resolution) were used for Mongolian sites

To estimate the water balance at each study site, we calculated the potential evapotranspiration (PET) following the Hargreaves–Samani method (Hargreaves and Samani 1982). Then, we calculated the annual water balance as the sum of the monthly differences between precipitation and PET. We also calculated the Conrad continentality index to characterize the temperature range at each site (Tuhkanen 1980).

### Statistical analyses

To compare tree-ring statistics (means, $r_{\mathrm{bt}}$, MSx) of width and density variables, we performed one-way analysis of variance (ANOVA) in cases when data were normal (means, $r_{\mathrm{bt}}$) or Kruskal–Wallis test when normality could not be assumed (MSx). These comparisons were followed by Tukey's Honest Significant Difference test for normally distributed data or Mann–Whitney *U* test otherwise.

To evaluate how tree-ring variables were related, we calculated Pearson correlation coefficients between site chronologies for each species considering the common 1950–2002 period. We also performed separate Principal Component Analysis (PCA) on variance–covariance matrices of width and density chronologies to summarize their variability into a few principal components (Jolliffe 2002). Then, we used Pearson correlations to characterize climate–growth associations by relating either tree-ring width or density variables or the first (PC1) and second (PC2) principal components of their corresponding PCAs (summarizing their variability) with monthly climate data (mean temperature and precipitation). The first two PCA axes were retained as they accounted for at least 50% of the total variance (Jolliffe 2002). Climate-growth relationships were analysed from September prior to tree-ring formation to October of the growth year based on previous studies in the study regions (Kirdyanov et al. 2007, Camarero et al. 2010, 2015). Partial correlation analyses were calculated to discern if some variables (EW and MN) were more related to early season precipitation than to temperature data in sites where significant ($P < 0.05$) correlations were found for those variables. Analyses were done using the vegan package (Oksanen et al. 2013) in the R environment (R Development Core Team, 2015).

## Results

### General features of width and density site chronologies

Overall, Scots pine showed higher EW and LW, followed by Siberian larch and Black pine (Table 3). Conversely, Black pine presented the highest MN values, whereas larch showed the highest MX values. On average, MN showed the lowest mean autocorrelation (0.35), whilst EW showed the highest one (0.64). The coherence between trees ($r_{\mathrm{bt}}$) was significantly ($F = 2.53$, $P = 0.03$) higher in the case of seasonal width variables (EW 0.49; LW 0.51) than in the case of density variables (MN, 0.31; MX, 0.36). Note that the highest $\mathrm{r}_{\mathrm{bt}}$ values for MN were observed for the Mediterranean Black pine. Finally, the year-to-year variability (MSx) was significantly ($K = 0.99$, $P < 0.001$) higher in the case of width variables (EW 0.44; LW 0.55) as compared with density variables (MN 0.14; MX 0.13).

### Associations between tree-ring variables

EW and LW records were positively associated for all species and sites, being stronger in the case of larch ($r = 0.70$–$0.87$), followed by Black pine ($r = 0.45$–$0.60$) and Scots pine ($r = 0.28$–$0.39$) (Table 4). In contrast, EW and MN records were negatively related with stronger associations found for Black pine ($r = -0.73$ to $-0.81$), followed by larch ($r = -0.66$ to $-0.75$) and Scots pine ($r = -0.38$ to $-0.71$) (Table 4). More latewood production (higher LW) was also related to heavy latewood (higher MX), but this association was again particularly strong for larch and Black pine, which explains the strong positive EW-MX and the negative LW-MN associations observed for these species. MN and MX records were negatively associated, with this relationship being significant in all larch forests and one Black pine (AC site) and one Scots pine (CA site) sites (Table 4).

### Common patterns in width and density data between sites and species

According to the Principal Component Analyses (PCA), the variance captured by the first two axes was about the same for width and density variables, with the first principal component (PC1) accounting for about 35% of the total variance (Fig. 1). The second principal component (PC2) accounted for more variance in width than in density variables (21 vs. 15%; Fig. 1). The loadings of EW and LW data of the same species and sites were grouped together in the PCA diagram with maximum loadings on the PC1 corresponding to LW data from the low-elevation Spanish sites (Fig. 1a). In turn, EW-LW data for the larch sites had the highest loadings on the PC2 (Fig. 1a). Considering density data, larch MX and MN chronologies showed the highest and lowest PC1 loadings, respectively (Fig. 1b). The minimum and maximum PC2 loadings were observed for MN chronologies from the Black pine in AC site and Siberian larch in M7 site, respectively.

**Table 3** Comparison of the dendrochronological statistics calculated for the standard (mean, SD, and AR1) and residual site chronologies ($r_{bt}$ and MSx) of the three tree species considering four variables (*EW* earlywood width; *LW* latewood width; *MN* minimum wood density; *MX* maximum wood density)

| Species | Site | EW | | | | LW | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean ± SD (mm) | AR1 | $r_{bt}$ | MSx | Mean ± SD (mm) | AR1 | $r_{bt}$ | MSx |
| *Pinus sylvestris* | CA | 0.97 ± 0.17 b | 0.52 | 0.41 | 0.39 | 0.22 ± 0.08 ab | 0.32 | 0.49 | 0.62 |
| | LR | 0.80 ± 0.16 ab | 0.65 | 0.46 | 0.35 | 0.20 ± 0.06 ab | 0.41 | 0.54 | 0.58 |
| | PN | 1.05 ± 0.18 b | 0.58 | 0.62 | 0.48 | 0.26 ± 0.08 b | 0.60 | 0.46 | 0.46 |
| *Pinus nigra* | AC | 0.47 ± 0.07 a | 0.62 | 0.55 | 0.52 | 0.15 ± 0.04 a | 0.50 | 0.48 | 0.55 |
| | LR | 0.56 ± 0.13 a | 0.69 | 0.48 | 0.38 | 0.18 ± 0.06 a | 0.39 | 0.55 | 0.60 |
| *Larix sibirica* | EF | 0.58 ± 0.15 a | 0.71 | 0.63 | 0.54 | 0.24 ± 0.09 ab | 0.63 | 0.52 | 0.59 |
| | KH | 0.36 ± 0.17 a | 0.54 | 0.66 | 0.63 | 0.10 ± 0.02 a | 0.51 | 0.51 | 0.60 |
| | M7 | 0.37 ± 0.06 a | 0.78 | 0.33 | 0.26 | 0.13 ± 0.03 a | 0.41 | 0.48 | 0.54 |
| | M0 | 0.78 ± 0.15 ab | 0.68 | 0.45 | 0.38 | 0.21 ± 0.05 ab | 0.61 | 0.36 | 0.42 |

| | | MN | | | | MX | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean ± SD (g cm$^{-3}$) | AR1 | $r_{bt}$ | MSx | Mean ± SD (g cm$^{-3}$) | AR1 | $r_{bt}$ | MSx |
| *Pinus sylvestris* | CA | 0.28 ± 0.01 a | 0.39 | 0.31 | 0.27 | 0.82 ± 0.03 a | 0.41 | 0.26 | 0.14 |
| | LR | 0.33 ± 0.02 ab | 0.30 | 0.34 | 0.11 | 0.89 ± 0.05 ab | 0.36 | 0.35 | 0.11 |
| | PN | 0.30 ± 0.02 ab | 0.41 | 0.25 | 0.09 | 0.82 ± 0.03 a | 0.39 | 0.32 | 0.12 |
| *Pinus nigra* | AC | 0.39 ± 0.02 b | 0.22 | 0.40 | 0.16 | 0.88 ± 0.04 ab | 0.32 | 0.39 | 0.13 |
| | LR | 0.35 ± 0.01 ab | 0.35 | 0.38 | 0.11 | 0.85 ± 0.04 a | 0.43 | 0.38 | 0.10 |
| *Larix sibirica* | EF | 0.28 ± 0.02 a | 0.37 | 0.31 | 0.15 | 0.93 ± 0.04 b | 0.40 | 0.37 | 0.17 |
| | KH | 0.32 ± 0.02 ab | 0.34 | 0.32 | 0.15 | 0.90 ± 0.03 ab | 0.34 | 0.43 | 0.18 |
| | M7 | 0.27 ± 0.01 a | 0.46 | 0.25 | 0.10 | 0.93 ± 0.05 b | 0.51 | 0.34 | 0.10 |
| | M0 | 0.28 ± 0.01 a | 0.35 | 0.26 | 0.14 | 0.94 ± 0.06 b | 0.41 | 0.37 | 0.13 |

Values were calculated for the common period 1950–2002

Statistics abbreviations: *AR1* first-order autocorrelation; $r_{bt}$ mean inter-series correlation; *MSx* mean sensitivity

Significant ($P < 0.05$) differences between sites and species are indicated by different letters according to Tukey's Honest Significant Difference (means) or Mann–Whitney *U* tests (MSx). Sites' codes are as in Table 1

**Table 4** Pearson correlations calculated between tree-ring variables (*EW* earlywood width; *LW* latewood width; *MN* minimum wood density; *MX* maximum wood density) for each site-species combination

| Species | Site | EW-LW | EW-MN | EW-MX | LW-MN | LW-MX | MN-MX |
|---|---|---|---|---|---|---|---|
| *Pinus sylvestris* | CA | **0.39** | **−0.41** | **0.55** | **−0.32** | **0.43** | **−0.36** |
| | LR | **0.34** | **−0.71** | 0.22 | −0.23 | **0.55** | −0.14 |
| | PN | **0.28** | **−0.38** | 0.02 | −0.19 | **0.28** | −0.04 |
| *Pinus nigra* | AC | **0.60** | **−0.81** | **0.65** | **−0.34** | **0.64** | **−0.49** |
| | LR | **0.45** | **−0.73** | **0.44** | **−0.34** | **0.53** | −0.19 |
| *Larix sibirica* | EF | **0.70** | **−0.75** | **0.81** | **−0.45** | **0.72** | **−0.73** |
| | KH | **0.75** | **−0.70** | **0.76** | **−0.41** | **0.80** | **−0.45** |
| | M7 | **0.81** | **−0.69** | **0.31** | **−0.45** | **0.68** | **−0.34** |
| | M0 | **0.87** | **−0.66** | **0.80** | **−0.52** | **0.74** | **−0.68** |

Correlations were calculated based on residual tree-ring chronologies for the common period 1950–2002 and values with $P < 0.05$ are in bold. Sites' codes are as in Table 1

Regarding the width chronologies, low EW and LW values of the driest Black pine site (the low-elevation AC site) correspond to severe droughts (e.g., 1986 and 1994; Fig. 2). Low EW and LW values were also observed during the 1980s in Russian and Mongolian sites (Fig. 2). Regarding density data, high MN was found during dry years (e.g., 1994 in Spain, 1979–1980 in Russia and Mongolia, 1986–1987 in Mongolia), and

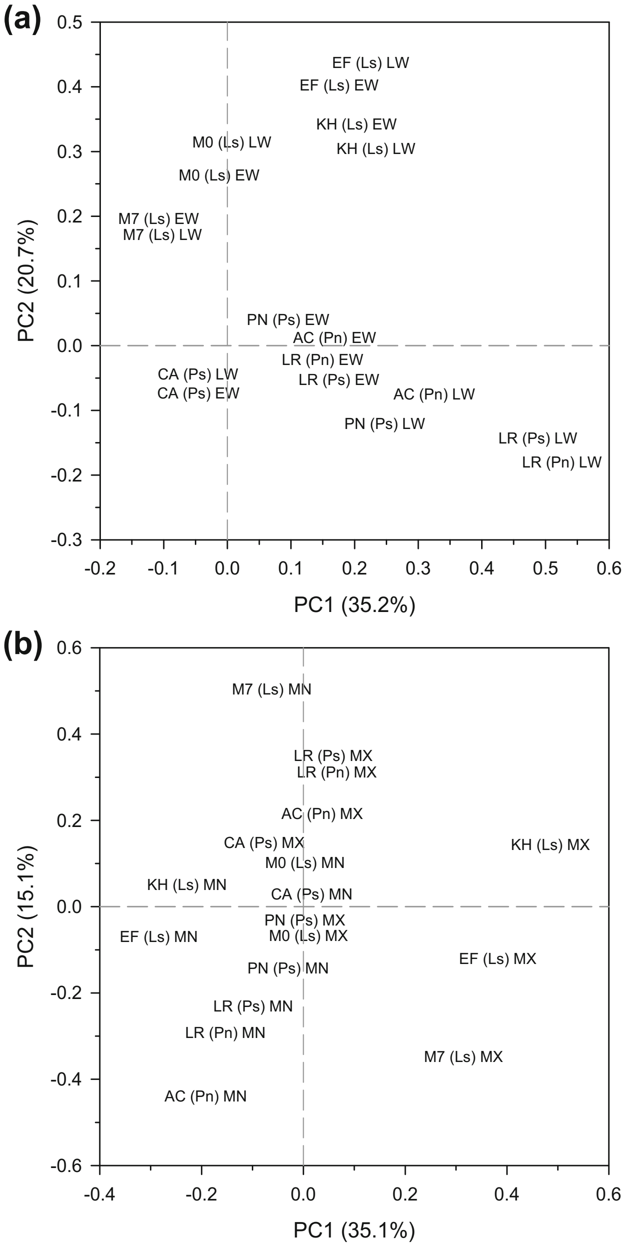


**Fig. 1** Scatter plots showing the loadings of the first (PC1) and second (PC2) principal components obtained by calculating Principal Component Analyses on the variance–covariance matrices of residual **a** width and **b** density site chronologies. **a** Earlywood and latewood widths are abbreviated as EW and LW, respectively. **b** Minimum and maximum wood densities are abbreviated as MN and MX, respectively. Sites are abbreviated as in Table 1. Tree species are abbreviated by the codes written between parentheses (Ls, *Larix sibirica*; Pn, *Pinus nigra*; Ps, *Pinus sylvestris*)

this pattern was most evident in dry sites as the Spanish AC site (Fig. 3a). Low MX values were observed during cool summers in cold sites (e.g., 1972 in the high-elevation PN Scots pine site; 1976 in Russian and Mongolian sites; Fig. 3b).

## Relationships between climate, width, and density variables

The first axis of the PCA based on climate–growth or climate–density relationships accounted for a high common variance in the case of LW (50%) and MN (46%) (see Supporting Information, Fig. S3). In both cases, Spanish sites grouped together and showed the highest PC1 scores, albeit the high-elevation PN Scots pine site showed a low PC1 score in the case of MN. Mongolian and Russian larch sites also grouped together and showed high PC2 loadings in the LW and MN. In the PCAs based on EW and MX data, the PC1 separated the PN site from the rest of Spanish sites suggesting a different impact of climate on the determination of EW and MX at this high-elevation location. Similarly, Siberian larch chronologies showed higher PC2 loadings compared to Mongolian sites.

Wet and cool spring (May to June) conditions enhanced EW formation but lead to low MN values, i.e., dry spring conditions were associated with low EW and high MN across sites and species (Fig. 4; see also Supporting Information, Table S1). LW formation was enhanced by wet–cool conditions during the growing season (May–September), particularly in Spanish pinewoods (excluding the high-elevation PN site) and Mongolian larch sites. MX increased in response to high May–June precipitation values and low June–July temperatures (Fig. 4; Table S1).

The strongest associations between climate and width or density variables were found for May or June precipitation and MN (Supporting Information, Table S1). The negative precipitation–MN relationship was consistently observed across species and countries. The strongest correlations were detected either in May (Spain, Black pine AC site; Russia, Scots pine CA site) or in June (e.g., Mongolia Siberian larch M7 site) (Fig. 5). May or June precipitation explained ca. 32–42% of the MN variance in these drought-prone sites (Fig. 5). Finally, partial correlation analyses confirmed that EW and MN responded more strongly to May–June precipitation than to temperatures. Partial correlations of EW and MN with May–June precipitation remained significant at the 0.01 significance after controlling for temperature effects (Supporting Information, Table S2), whilst partial correlations with May–June temperatures after controlling for precipitation effects were not significant ($P > 0.05$).

## Discussion

In agreement with our hypothesis, dry spring conditions were associated with high MN values and, consequently, to a dense earlywood across species and sites in Eurasia. Such strong response of MN to precipitation indicates that it is a

**Fig. 2** Residual earlywood (*upper panels*) and latewood chronologies (*lower panels*) for the study sites abbreviated as in Table 1. Graphs are plotted for each country. Tree species are abbreviated by the codes written between parentheses (Ls, *Larix sibirica*; Pn, *Pinus nigra*; Ps, *Pinus sylvestris*)

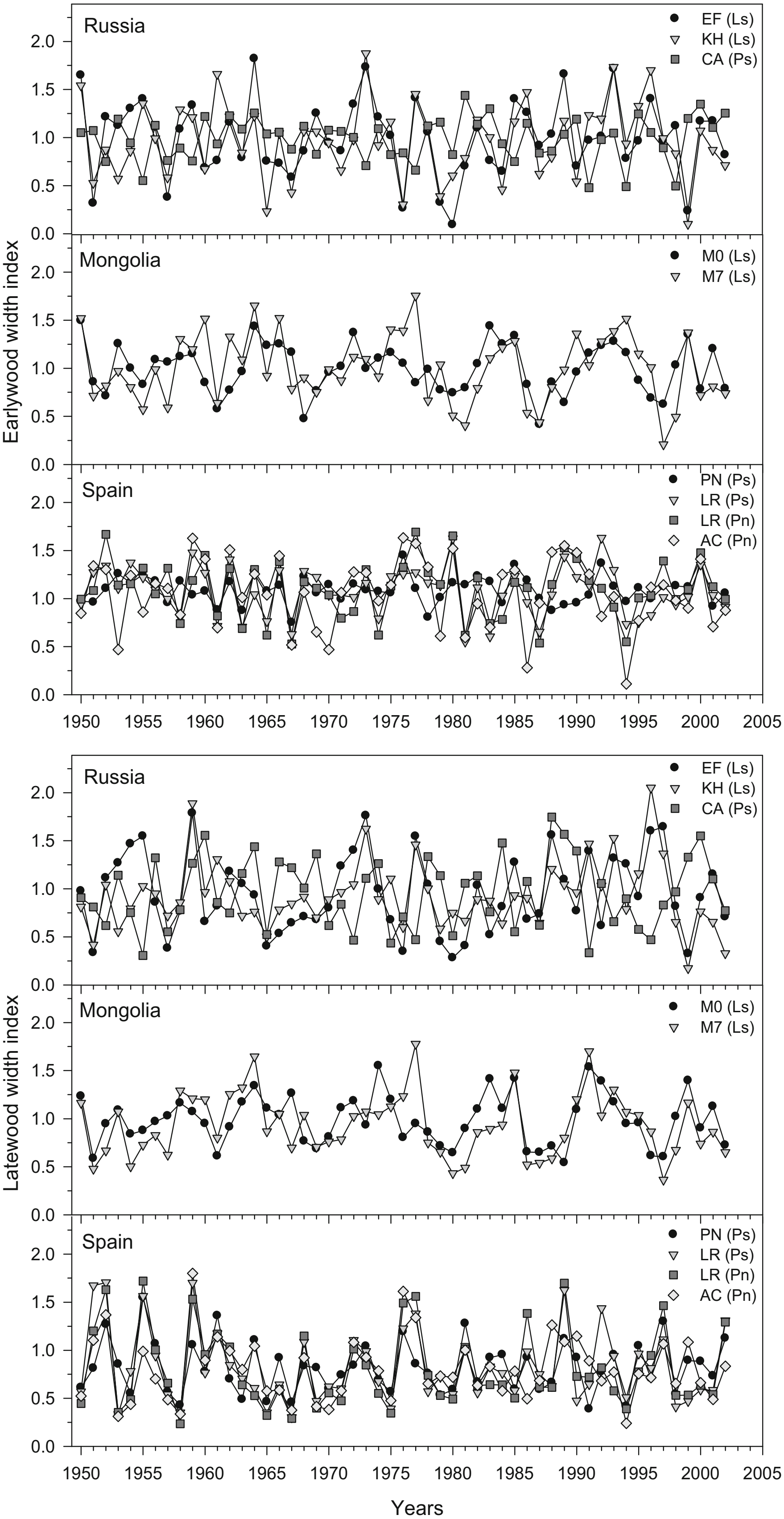
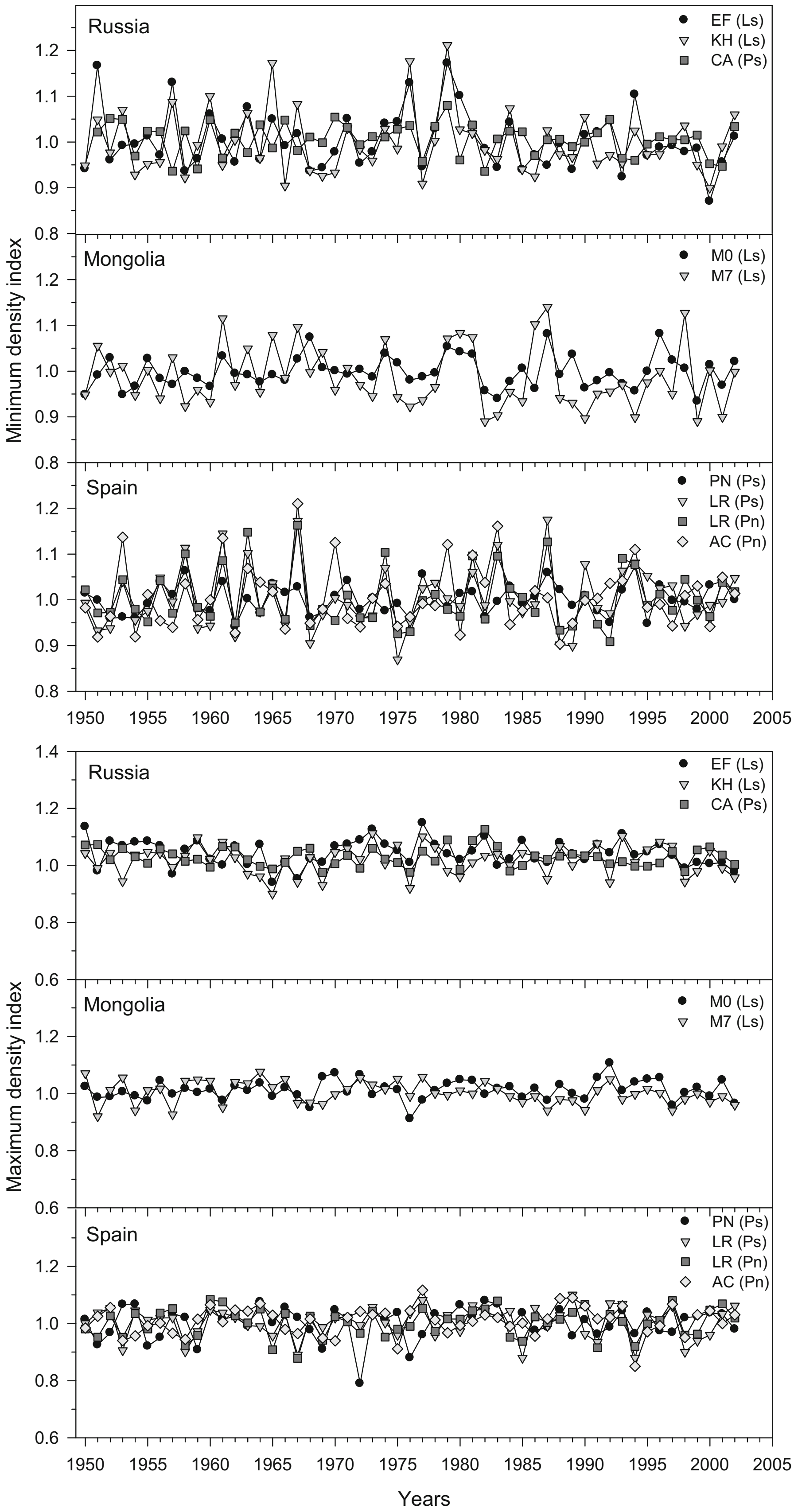


**Fig. 3** Residual minimum (*upper panels*) and maximum density chronologies (*lower panels*) for the study sites abbreviated as in Table 1. More details are shown in Fig. 2



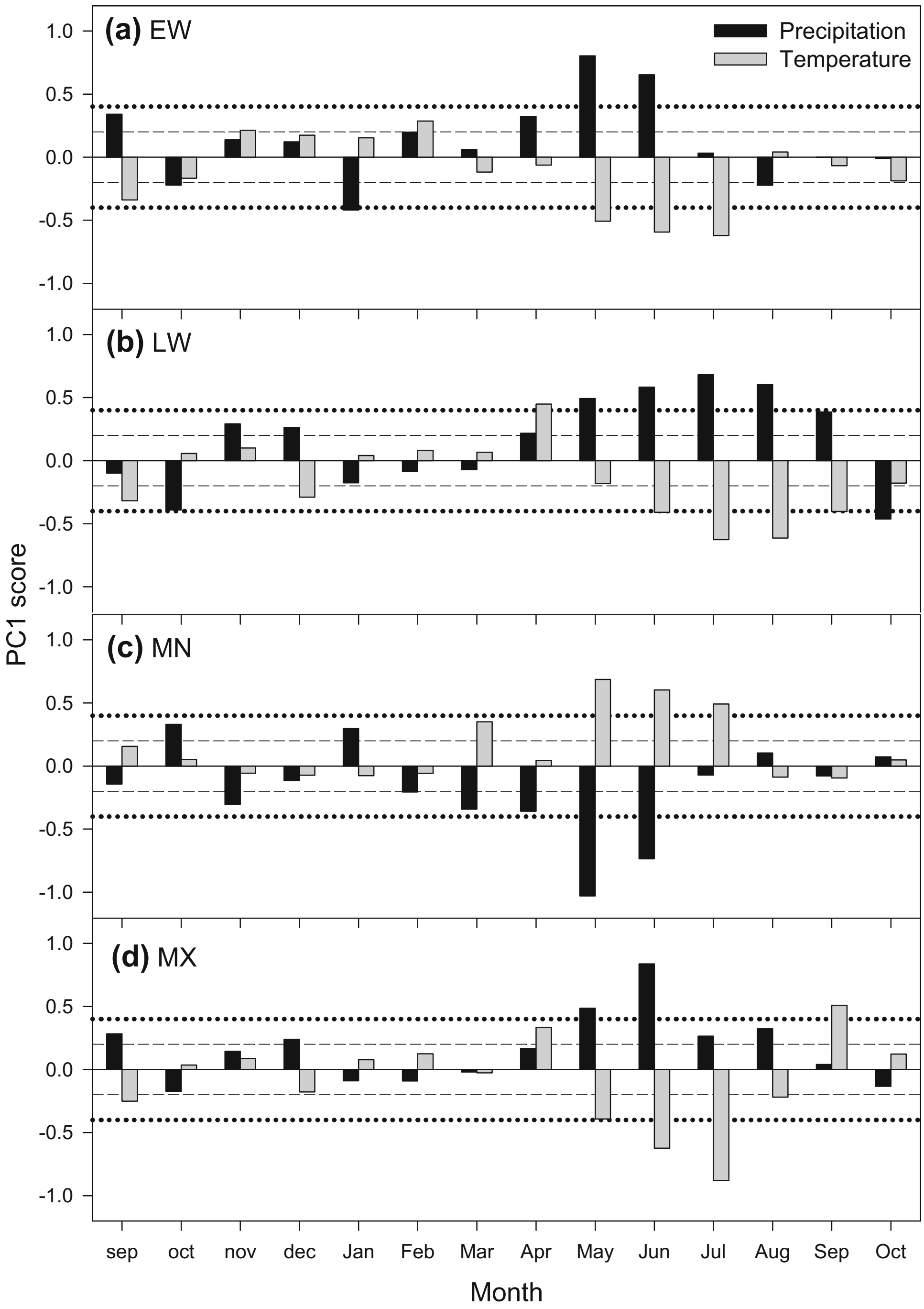


**Fig. 4** Associations between climate variables and scores of the first principal component (PC1) of Principal Component Analyses calculated on the indices of earlywood (EW; **a**) and latewood width (LW; **b**) data and minimum (MN; **c**) and maximum (MX; **d**) wood density data. Bars correspond to the correlations of summarized tree-ring variables (PC1 and PC2 scores) with monthly precipitation (*black bars*) and temperature (*grey bars*) data from September prior to tree-ring formation to October of the growth year (previous- and current-year months are abbreviated by *lowercase* and *uppercase letters*, respectively)

robust proxy of early season water availability Water deficit at the beginning of the growing season, when the earlywood is formed, leads to a dense earlywood (Vaganov et al. 2009). Such dense earlywood is characterized by tracheids with narrow lumens and a decreased hydraulic conductivity (Domec et al. 2009).

Our results confirm the previous studies showing that: (1) seasonal density data better reflect the moisture status of conifer species during the growing season than width variables, and (2) this difference is noticeable in drought-prone sites (Cleaveland 1986). Such precipitation-density coupling, possibly mediated by adjustments in hydraulic conductivity, could also explain the decrease in earlywood production observed in response to water deficit in drought-prone sites as showed for forest-steppe and Mediterranean biomes (e.g., Dulamsuren et al. 2010; Camarero et al. 2015). According to ecophysiological studies, photosynthesis rates decrease in both winter and summer in these cool–dry regions, and growing-season drought stress caused by elevated

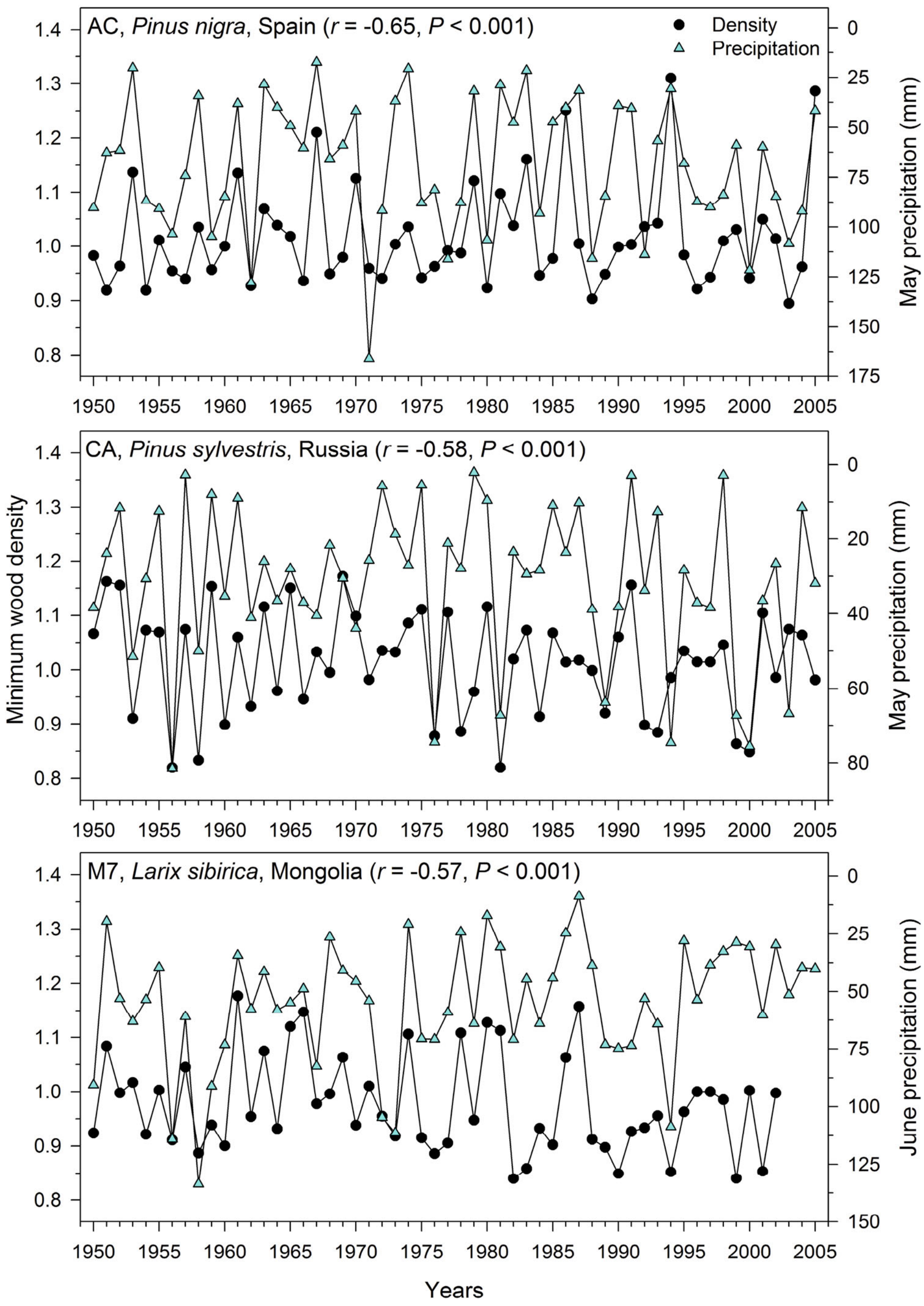


**Fig. 5** Main relationships observed between climate variables (May and June precipitation) and the residual chronologies of minimum wood density in each country. In each plot, the Pearson correlation (*r*) between precipitation and wood density values is shown with its corresponding significance levels (*P*). Note the reverse precipitation scales. Sites' codes are as in Table 1

atmospheric vapour pressure deficit and low soil water availability leads to radial growth reduction (Dulamsuren et al. 2009; Gimeno et al. 2012). Nevertheless, the correlations between spring precipitation and MN were always stronger, in absolute terms, than those detected between precipitation and EW (Fig. 4; Table S1). Consequently, MN exhibits strong response to precipitation and, thus, it is a robust proxy of early season water availability. This agrees with empirical approaches demonstrating that an improved water status is linked to a lower density in Norway spruce (*Picea abies*) (Lundgren 2004).

The correlations found between MN and spring precipitation in pine and larch (Fig. 5) were similar to those observed in Spanish juniper (*Juniperus thurifera*) (Camarero et al. 2014), explaining on average 37% of variability in minimum density. Indeed, further investigations should explore the nature of climate–MN associations in more detail. This research could explicitly consider wood anatomy to disentangle whether MN changes are mainly due to lumen modifications, as we assumed here, or to changes in cell-wall thickness. For instance, in drought-exposed Norway spruce trees, wood density augmented as a consequence of the formation of thicker cell walls (Jyske et al. 2010), whilst increased tracheid lignin content was observed in drought-prone Austrian Black pine forests (*Pinus nigra*) (Gindl 2001). Climate–MN associations could also reflect the extent of plastic responses to drought stress. For instance, Douglas fir (*Pseudotsuga menziesii*) trees showing high resistance to xylem cavitation and lower drought-induced mortality also presented the highest minimum wood density values (Dalla-Salda et al. 2009; Ruiz Diaz Britez et al. 2014), which could reflect narrower tracheid lumens. Nevertheless, other parameters affecting cavitation and hydraulic conductivity should be also considered, including conduit length, pit size, and the numbers of tracheids per unit area (Carlquist 1975).

Tree-ring width and density data often provide redundant information (Kirdyanov et al. 2007; Büntgen et al. 2010; Vaganov and Kirdyanov 2010, Galván et al. 2015). This redundancy could apply to MN, which is negatively related to EW (Tables 4) and, in turn, both variables show opposite associations with precipitation (Fig. 4). Note that we opted for analysing residual growth and density chronologies without removing dependences between them (e.g., EW–MN and LW–MX relationships), since our purpose was to assess how climate distinctively influenced seasonal growth and density data. A pro of analysing MN is that it offers indirect clues on wood phenology. For example, the shift in the strongest precipitation–MN association from May (Spanish and Russian sites) to June (Mongolian sites; Table S1) could be caused by a late peak of earlywood formation in Mongolian sites. This agrees with our knowledge of xylogenesis, with, e.g., maximum rates of tracheid production occurring from May to July (Antonova and Stasova 1993; Vaganov et al. 2006; Camarero et al. 2010).

In cold northern Siberian larch forests, width and density variables mainly respond to temperature changes during the short growing season (June–July) (Esper et al. 2010), and indirectly to winter precipitation which affects the length of snow melt season and soil temperatures (Vaganov et al. 1999; Kirdyanov et al. 2003). Our results also evidenced that MN was negatively related to spring precipitation in southern Siberia sites subjected to water shortage during that season (Fig. 4), suggesting that earlywood tracheid expansion is constrained by water availability. Low soil temperature can increase water viscosity leading to a high root hydraulic resistance, decreasing water flow from the soil to the tree and reducing stomatal conductance (Wan et al. 2001). Spring cold conditions could therefore constrain the radial enlargement of earlywood tracheids. Despite variables as EW and MN showed significant correlations with May–June temperatures, the associations between them and precipitation were stronger in absolute terms suggesting a secondary role of thermal factors (Fig. 4, Supporting Information, Table S1). Partial correlation analyses and the aforementioned arguments on xylogenesis confirm that temperature does not influence EW and MN in the study sites as much as precipitation does.

In cool–arid inner Asian forests, wet conditions during the growing season enhance radial growth (Poulter et al. 2013). However, Mongolian forest-steppe ecotones are experiencing warmer and drier conditions since the 1940s, causing growth decline and the retreat of larch forests (Dulamsuren et al. 2010). Increased aridity and drought stress are major restrictions of tree growth and functioning in these biomes where larches show low shoot water potentials and high stomatal conductance (Dulamsuren et al. 2009). This agrees with our findings and emphasizes the key role of sufficient moisture availability for tree growth and wood formation.

In Mediterranean pine forests, wet conditions during the previous winter and the current spring are associated with improved earlywood production (De Luis et al. 2007; Martín-Benito et al. 2008; Pasho et al. 2012) and a decrease in minimum density (Olivar et al. 2015). Wet conditions favour tracheid division which results in low minimum density (Bouriaud et al. 2005), as we found in the low-elevation Spanish sites (Fig. 5a; Table S1). Under more continental and colder conditions, cambial resumption is delayed and summer conditions become more relevant as drivers of Scots pine growth (Sánchez-Salguero et al. 2015). This explains why earlywood density may not be related to spring precipitation in some Mediterranean Scots pine stands (Olivar et al. 2015). In contrast, the positive association between summer temperatures and maximum density found in high-elevation Scots pine stands (PN site) (Table S1) is in agreement with other studies of cold biomes such as boreal and subalpine forests (e.g., Briffa et al. 1998). This relationship has previously been reported for pine species in Mediterranean environments (Olivar et al. 2015), and it is due to an improved thickening and lignification of latewood cell walls in response to warm summer and fall conditions (Gindl et al. 2000; Yasue et al. 2000).

Contrary to most previous studies at cold sites which found that summer temperatures and maximum latewood density are positively associated (e.g., Briffa et al. 2004), we found significant and negative correlations of MX with May-to-July temperatures (Fig. 4). We assume that such negative relationships are driven by water shortage caused by warm spring-to-summer temperatures. This is a typical climate effect observed in Mediterranean forests such as the Spanish study sites, but we also found such effect in other drought-prone sites from Russia (Scots pine CA site) and Mongolia (Siberian larch M7 site). We interpret this negative association as a drought-related reduction in the thickening and lignifications rates of latewood tracheids. This is confirmed by the positive effect of wet June conditions on MX observed in most of those sites, whilst MX was mainly negatively related to July temperatures, because water deficit usually peaks during that month.

An increasing influence of climate warming on temporal coherence in ring width records (spatial synchrony) has been observed across some of the studied Eurasian regions (i.e., Iberian Peninsula and Siberia; Shestakova et al. 2016). It could be tested if this enhanced synchrony holds too for density records at similar sub-continental scales, since wood density seasonal components (MN and MX) respond to different climate variables, and wood density is a fundamental variable to estimate forest carbon uptake and woody biomass pools (Bouriaud et al. 2015). It is expected that growing-season precipitation would drive earlywood density and hydraulic conductivity (Pacheco et al. 2016). Consequently, we predict that warmer and drier conditions during the most active phase of the growing season would reduce earlywood production, but increase earlywood density. These predictions must be taken with caution because of the case-study-like nature of this investigation. It should be underlined that much more research is needed to prove the validity and generality of our findings. If they turn to be true for other cold–dry sites where other Pinaceae species dominate, this would imply that minimum wood density could be a valuable proxy of early season precipitation.

To conclude, minimum wood density of three conifer species (*L. sibirica, P. nigra,* and *P. sylvestris*) reflects changes in growing-season (spring) precipitation in cool–dry Eurasian regions. An increase in minimum wood density in response to dry spring conditions was observed in drought-prone sites from the forest-steppe and Mediterranean biomes. The associations between minimum wood density and precipitation were stronger than those observed with seasonal width variables. Future drier conditions during the growing season may increase minimum wood density and reduce radial growth of Eurasian conifer forests, negatively affecting their potential to fix and store carbon pools as stem wood.

**Author contribution statement** JJC conceived the study and lead the writing. LFP, TAS, AVK, and VVK carried out wood densitometry and statistical analyses. JV, AAK, and JJC collected data in the field. All authors contributed to the discussion and the writing of the manuscript.

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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