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"Plastic" and "static" behavior of vessel-anatomical features in Oriental beech (*Fagus orientalis* Lipsky) in view of xylem hydraulic conductivity

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Abstract

Key message **Xylem anatomical traits can be categorized into two groups: plastic properties which show a high inter-annual variability, and static characteristics which vary in a more conservative range.**

Abstract Water conduction in broad-leaved trees depends mainly on the size, number, and arrangement of vessels, which vary from year to year in response to varying exogenous factors, thus contributing to a safe and/or efficient water transport. However, the nature of such compensation is not clear; in particular, it is not obvious which traits act independently and which ones coincidentally. To better understand these inter-relations, tree-ring width (TRW), vessel-related anatomical traits, and the theoretical hydraulic conductivity were measured or modeled in the last 50 growth rings of mature Oriental beech trees growing at different altitudes in northern Iran. The study trees followed similar strategies compensating the effects of external factors by modifying their vessel-anatomical features. TRW and the number of vessels per unit of area were highly but negatively correlated and both were affected by exogenous factors. However, a decrease in vessel frequency (VF) is not a mirror effect of wider tree rings, but trees actively control the number of vessels produced. Principal component analysis revealed that the features VF, TRW and relative total conductivity were more plastic, whereas average vessel-lumen area, tree-ring porosity, and relative specific conductivity behaved more static. Moreover, we suggest that in theoretical approaches, total hydraulic conductivity rather than the specific hydraulic conductivity is a better indicator of a tree's hydraulic behavior in a given growing season.

Keywords Oriental beech · Hydraulic conductivity · Quantitative wood anatomy · Vascular characteristics · Tree-ring width · Phenotypic plasticity

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Introduction

In broad-leaved trees, water and dissolved minerals are transported through a capillary network (hydrosystem) of vessels from the roots throughout the stem to the leaves. In contrast to ring-porous trees where vessels are in two diverse size classes, in diffuse-porous trees such as beech, the vessels are of almost similar size and diffusely distributed (Thomas 2000). In response to short-term or long-term environmental changes, trees can modify their hydrosystem, particularly the size and frequency of the vessels, and thereby also their capability of water conductivity (Reyes-Santamaría et al. 2002; Bayramzadeh et al. 2008). However, these responses are restricted by a trade-off between three conflicting attributes, viz. the

efficiency and safety of water transport as well as a tree's mechanic strength (Gasson 1985; Hacke et al. 2006; Sperry et al. 2008).

Different tree species may follow different strategies to reduce the risk of hydraulic failure and/or to modify the flow of water (Umebayashi et al. 2010). However, it is not sufficiently known whether trees of the same species but growing in contrasting environments follow the same adaptation strategy (Fonti and Jansen 2012; Plavcová and Hacke 2012). Dissimilarity of tree's responses to environmental factors could be more severe in sites with fertile soil (Zubizarreta-Gerendiain et al. 2012) and/or when environmental conditions are not so harsh. Hence, it is not clear yet whether beech trees grown on fertile soil in northern Iran with subtropical climate use similar adaptation strategies in reacting to environmental conditions or not. For example, are wider tree rings always accompanied with bigger/smaller vessels or does this relationship vary in different microclimates? Moreover, according to Anfodillo et al. (2012), it is not yet fully explored how trees control the number and size of their water-conducting cells and which of the hydraulic-related cell traits have a higher potential for adapting to changing environmental conditions ("plastic") and which behave more conservatively and vary only within narrow ranges ("static").

Although wood anatomical traits like vessel diameter and frequency are easily accessible, ecological or climatological proxies for analyzing adaptation processes to environmental changes (Campelo et al. 2010; Crous et al. 2012), more exact knowledge on how much of the variability of these traits is genetically determined and how much is environmentally controlled (Leal et al. 2003; Fisher et al. 2007; Tixier et al. 2013) is needed. Although there are numerous studies about the association between tree-ring width (TRW), wood density and hydraulic conductivity for a wide range of species and environments (e.g., Preston et al. 2006; Poorter et al. 2010; Umebayashi et al. 2010; Fan et al. 2012), the approaches are based on the last-formed xylem (Schuldt et al. 2013) and do not take longer periods into account. Moreover, such studies often deal with saplings, comprising only juvenile wood (e.g., Reyes-Santamaría et al. 2002) while studies of trunks of adult trees are largely absent (Hao et al. 2013). A species-specific approach, using a higher number of old age study trees, may be able to back up the assumed links between wood anatomy and hydraulic conductivity by identifying statistical associations between hydro-physiological and vessel-anatomical variables.

The rationale of this study, therefore, was (a) to identify the intra-relationships between vessel-anatomical features in beech trees; (b) to investigate which vessel-related features of these trees are more static and which ones are more plastic. These ideas were discussed with respect to the main function of vessel elements, i.e., water conduction and the trade-off between hydraulic efficiency and safety; and (c) to see if these resulting behaviors and associations are the same at two different sites or if they are site-specific.

Materials and methods

Study sites and sample preparation

The study was conducted in the Caspian forest, Northern Iran. To evaluate the impact of environment on the variability of vessel-anatomical features, two sites, aligned along an altitudinal gradient were selected. The lower site (36° 35′ N; 51° 28′ E; 750 m a.s.l.) and the upper site (36° 31′ N; 51° 33′ E; 1,100 m a.s.l.) are named A and B, respectively. The closest climate station with long-term data series is located at Nowshar close to the shore of the Caspian Sea (36° N, 51° E; 21 m below global sea level), where a mean (1977–2003) annual precipitation of 1,297 mm and a mean annual temperatures of 16.1 °C indicate very humid and warm climatic conditions. From short-term climate data (2007–2008) recorded at a climate station at Kojour (1,550 m a.s.l.), a temperature lapse rate of 2.63 °C/km elevation can be derived, leading to estimates of ca. 0.68 °C cooler mean climatic conditions at site B (see also Oladi et al. 2011; Pourtahmasi et al. 2011). At each site, ten straight, intact and dominant trees with diameters of 37 ± 5 cm and ages of 103 ± 34 years were selected (Online Resource 1). One increment core per tree was extracted at breast height (1.3 m) perpendicular to the slope inclination to avoid a possible impact of reaction wood. The cores were fixed on wooden sample holders and their surfaces were smoothed using razor blades. To enhance the contrast between vessels and the surrounding tissue and to improve the visibility of tree-ring boundaries, a technique combining a black felt marker and white chalk was applied (Gärtner and Nievergelt 2010). The TRWs were measured at a precision of 0.01 mm with a LINTAB V measuring table (Rinntech, Heidelberg, Germany). Cross-sections of the last 50 growth rings (Fig. 1) of each tree were photographed under a stereo-microscope using a digital camera and edited and analyzed with WinCELL PRO (Régent Instruments, Canada). The vessel-anatomical variables were measured within a rectangle as wide as the TRW in radial direction and 1–2 mm long in tangential direction at a magnification of 6×. The analyzed area was usually selected between two extremely wide rays (Online Resource 2). An area of 500 μm^2 was set as a lower threshold for any object to be considered as a vessel. The number of vessels measured ranged from 250 to 1,100 per tree ring and tree. Due to unexpected technical difficulties
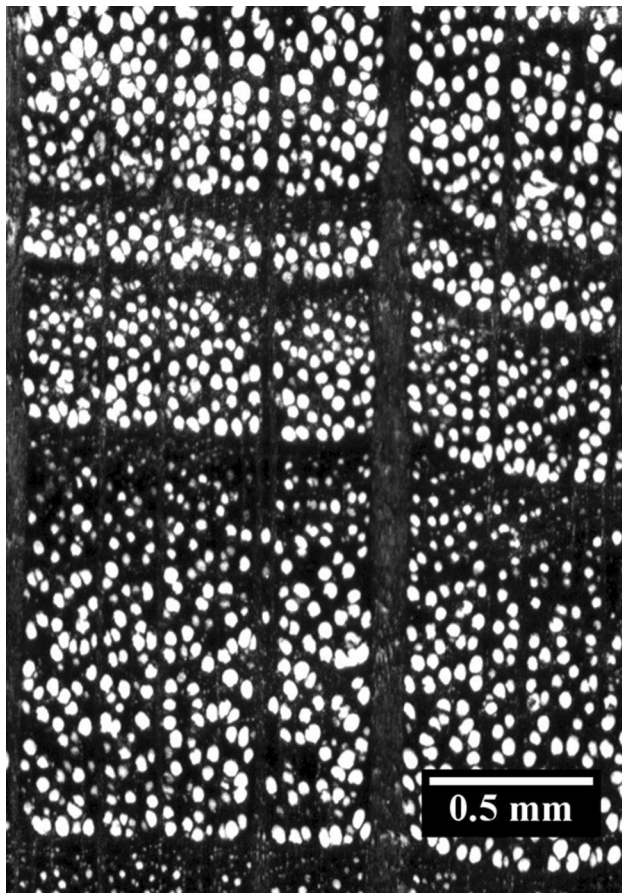
Fig. 1 Microphotograph of a cross-section through wide and narrow tree rings of an Oriental beech stem, collected at site A; vessels appear *white* in a *black* ground tissue

Table 1 Mean value $\pm$ standard deviation of all 11 variables measured/calculated from 450 and 400 tree rings of nine and eight beech trees for sites A and B, respectively

Variables	Unit	Site A	Site B
Tree-ring width (TRW)	mm	*2.25 ± 1.14*	*1.99 ± 0.80*
Tree-ring area (TRA)	mm^2	*1,581 ± 1,019*	*1,200 ± 681*
Vessel frequency (VF)	1/mm^2	109 ± 21	*127.5 ± 21.6*
Porosity	%	22.6 ± 4.6	22.0 ± 3.8
Tangential vessel diameter (TVD)	μm	*42 ± 3.9*	*38.9 ± 3.4*
Radial vessel diameter (RVD)	μm	*56.1 ± 6.2*	*50.9 ± 5.5*
Hagen–Poiseuille average vessel diameter (D_{HP})	μm	*54.7 ± 8.3*	*44.9 ± 4.3*
Average vessel-lumen area (AVLA)	μm^2	*2,087 ± 336*	*1,746 ± 309*
Vulnerability index (V_{Inx})	–	*0.53 ± 0.35*	*0.40 ± 0.09*
Relative specific conductivity (RSC)	–	*0.59 ± 0.26*	*0.49 ± 0.18*
Relative total conductivity (RTC)	–	*925 ± 711*	*616 ± 438*

Italic cells mark statistically significant differences for each variable at $p < 0.001$

and data loss, samples taken from one tree at the lower site and two trees from the upper site were omitted, so that 450 tree rings remained from the lower site and 400 tree rings from the upper site.

Variables measured/calculated

Altogether 11 variables were acquired (Table 1), six of them were directly measured and five of them were calculated:

- Tree-ring width (TRW);
- Vessel frequency (VF), i.e., number n of vessels per area (mm^2);
- Porosity (%), i.e., total vessel-lumen area/totally analyzed area $\times 100$;
- Average vessel-lumen area (AVLA);
- Average tangential vessel diameter (TVD);
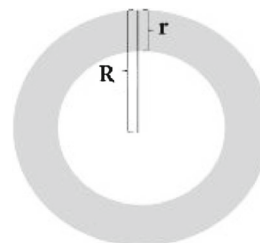- Average radial vessel diameter (RVD).

In addition to these directly measured variables, total tree-ring area (TRA) was calculated (shaded area, i.e., the area of a specific tree ring along the circumference of a tree):

$$TRA = \pi R^2 - \pi(R - r)^2$$

$$TRA = \pi r(2R - r)$$

Two tree rings of identical width may have different TRA values depending on their position in a cross-section, due to different tree circumference with age. Therefore, a tree ring with a higher TRA is capable of transporting more water than a tree ring with the same width but with a lower TRA. For the following calculations, we assumed a round shape of the stems and an even growth rate around the stems. This is a justified generalization for Oriental beech due to its straight and upright stem form (Pourtahmasi et al. 2011) (Online Resource 1).

Since most vessels in the studied beech trees had elliptic shapes and were radially flattened, radial and tangential diameters of each vessel were considered as major (a_i) and minor (b_i) vessel axis. This was statistically tested for 6,000 vessels of 15 randomly chosen tree rings using two analyzing parameters of ImageJ (v1.46, http://rsb.info.nih.

gov/ij); one measuring radial and tangential diameters of a given vessel (i.e., *Bounding Rectangle*) and the other measuring major and minor axes of the best-fitting ellipse to that vessel (i.e., *Fit Ellipse*). Hence, the Hagen–Poiseuille average vessel diameter for each tree ring (D_{HP}) was calculated as suggested by Steppe and Lemeur (2007) and Nobel (2009):

$$D_{HP} = \sqrt{4 \frac{1}{n} \sum_{i=1}^{n} \frac{2a_i^3 b_i^3}{a_i^2 + b_i^3}}$$

The derived vulnerability index (V_{Inx}) (Carlquist 1977) was calculated as follows:

$$V_{Inx} = \frac{D_{HP}}{VF}$$

A low index value indicates the capability of the hydrosystem to withstand water stress or freezing, whereas a high index value indicates a high susceptibility of the hydrosystem for being damaged during water conduction (Tyree and Zimmerman 2002). The relative specific conductivity (RSC) was calculated according to the modified Hagen–Poiseuille equation (Reyes-Santamaría et al. 2002; Verheyden et al. 2005; Arbellay et al. 2012):

$$RSC = r_{HP}^4 \times VF$$

where r_{HP} is the Hagen–Poiseuille average vessel radius (D_{HP}/2) and "VF" is the vessel frequency. RSC shows the potential capacity of a tree ring to transport water in a unit of its area; these values are relative units. The relative total conductivity (RTC) was calculated as

$$RTC = RSC \times TRA$$

where RSC is the relative specific conductivity and TRA is the total tree-ring area. RTC shows the potential water conductivity capacity of a whole tree ring independent of its width.

Relative and total hydraulic conductivity predicted from the Hagen–Poiseuille equation is theoretical and expected to be lower than the empirical hydraulic conductivity (Tyree and Zimmerman 2002; Schuldt et al. 2013). However, for intra-species comparisons, measured and theoretical conductivity show highly significant correlations (Martre et al. 2000, 2001; Tombesi et al. 2010; Schuldt et al. 2013; Tixier et al. 2013). Thus, theoretically derived estimates of the total hydraulic conductivity can confidently be used (Steppe and Lemeur 2007).

Statistical methods

A total of 450 tree rings from the lower site and 400 tree rings from the upper site were treated separately without distinguishing between trees in each site. The dataset of each variable was tested for normal distribution, both graphically and numerically (Shapiro–Wilk test); to meet the normality assumption, few extreme values had to be omitted as outliers. To determine whether the mean values of the measured or calculated variables are statistically different between two sites or not, a multivariate analysis of variance (MANOVA) was applied using the dataset of all tree rings in each site. To study the inter-relations between all 11 variables at each site, these were compared pairwise by Spearman's rank correlation. To characterize the correlations between the 11 variables and to discover possible multi-collinearities, a rotated principal component analysis (RPCA) was first applied for each site based on the raw data; then, due to the high similarity of the results from each study sites, another PCA was run including all data from both sites. All statistical analyses were done by SPSS version 20 (IBM® SPSS® Statistics, 2011).

Results

The results of MANOVA revealed a statistically significant difference between sites ($p < 0.0005$) for all 11 variables. Also, standard deviations were significantly ($p < 0.001$) larger at the low-elevation than at the high-elevation site, except for the number of vessels/mm^2 (VF), which was larger at 1,100 than at 750 m, and for Porosity, for which no difference between the sites was found (Table 1). In Fig. 2, we chose to show selective inter-relations between variables in a way to cover as many as possible correlation coefficients while avoiding presenting information which are redundant and/or less contributing to the aims of the study. Hence, inter-correlation coefficients between D_{HP}, TVD, RVD, and AVLA were not illustrated since they are easily and logically expected to have high positive correlations.

Except RSC, the sign and strength of correlation coefficients were the same for both sites (Fig. 2a–d). TRW showed high positive correlations with V_{Inx} and RTC. A strong negative relation was found between TRW and VF, whereas AVLA and porosity were poorly associated with TRW (Fig. 2a). In other words, wider tree rings had slightly larger, but considerably fewer vessels per mm^2, resulting in a negative correlation between TRW and porosity. It should be noticed that the strong negative relation between TRW and VF was not linear but followed a quadratic function at both sites (Fig. 3), i.e., with increasing TRW, VF sharply decreased. However, there was only a small difference in VF for moderately wide and very wide rings.

Porosity had the highest correlation with RSC, but was not or only poorly related to RTC and V_{Inx} (Fig. 2b). Besides, RSC increased with increasing vessel radius and related features (D_{HP}, AVLA and porosity), but its relation

Fig. 2 Spearman's correlation coefficients between various wood anatomical traits and tree-ring width [TRW (**a**)]; porosity (**b**); relative specific conductivity [RSC (**c**)]; relative total conductivity [RTC (**c**)] at sites A (*dark gray*) and B (*light gray*). The height of the *bar* shows the strength of the correlation. All coefficients are significant at the $p < 0.01$ level except for *bars* marked by one or two *asterisks* which are significant at $p < 0.05$ and non-significant ($p > 0.05$), respectively
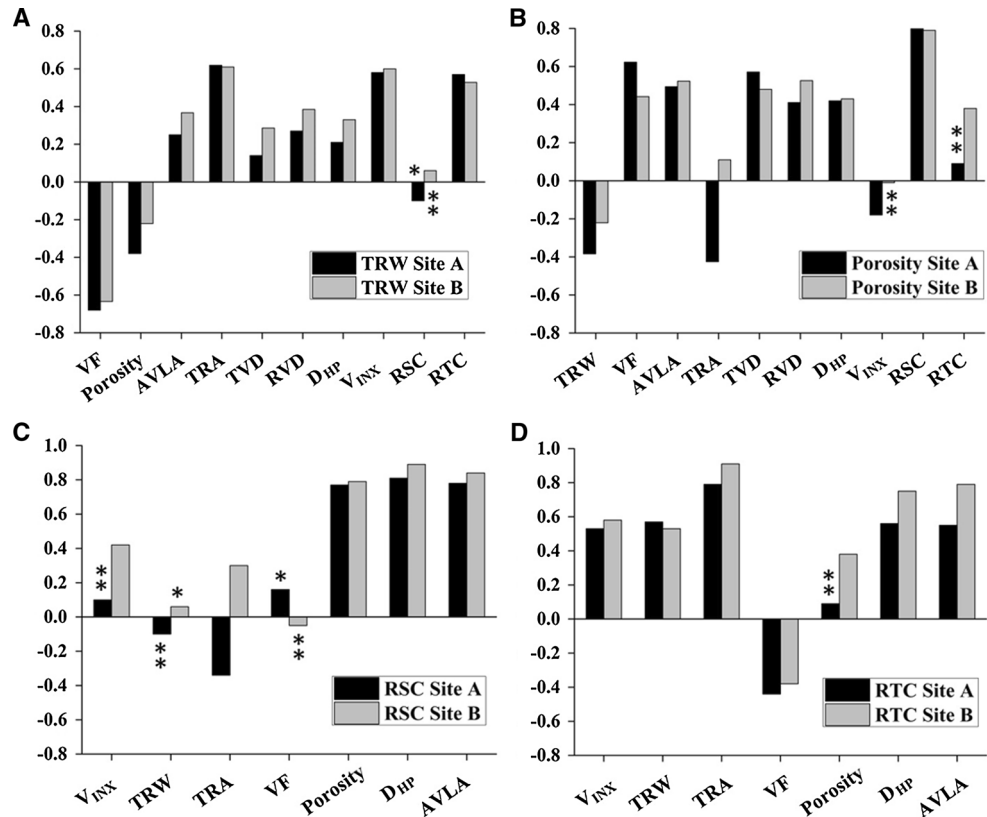
to other anatomical traits (TRW, TRA, VF and V_{Inx}) was very poor and/or of opposite sign (Fig. 2c). Unlike RSC, RTC showed homogenous positive correlations with all traits except with VF at both sites (Fig. 2d). Correlation coefficients between RSC and RTC were not very high (0.34 and 0.45 at sites A and B, respectively) (Online Resource 3).

The results of the RPCA were very similar for both sites (Online Resource 4). Therefore, we carried out another PCA considering all trees of both sites together (Fig. 4). The two first principal components accounted for 83 % of the total variance in the data. PC#1 explained 59 % of the variation among the 11 traits, and was strongly associated with RSC, Hagen–Poiseuille vessel diameter and vessel area (RVD, TVD, D_{HP} and AVLA) and porosity. PC#2 explained 24 % of the variation among the traits and was highly related with TRW, TRA, VF, vulnerability index (V_{Inx}) and total conductivity (RTC) (Fig. 4).

Discussion

In this study, patterns of adjustment in wood anatomical traits of Oriental beech trees were investigated at two elevations. Despite significant differences between the main anatomical properties, the quality of the inter-relations between these traits remained very stable among all

trees. Beech trees follow similar strategies to compensate the effects of external environmental factors by the way they change their anatomical features. In a similar study at three elevations in the Caspian forest (all higher than our study sites; 1,260, 2,000, 2,200 m a.s.l.), correlations between anatomical variables of beech trees (e.g., TRW, VF, AVLA and porosity) are mostly in accordance with our results, except for the site at 2,000 m where surprisingly no significant relations were found between most of the traits (Pourtahmasi et al. 2011). However, this minor discrepancy may result from different methodological approaches, since the latter study used standardized (age trend removed) tree-ring variables. Furthermore, values were averaged for all trees and since the number of studied trees was distinctly higher at the 2,000 m site, averaging may have had a stronger offsetting effect on anatomical traits. Furthermore, our study sites may be located too close together to impose significant climatic differences on trees; thus, stands from higher altitudes should be included to fully certify our conclusion.

Porosity was the only variable which showed no significant difference among the two study sites. Pourtahmasi et al. (2011) stated that in contrast to other anatomical traits, no environmental signal can be extracted from porosity variations of beech. Likewise, the vessel coverage remained rather constant for *Eucalyptus* trees within and across different clones grown at two sites in Portugal (Leal
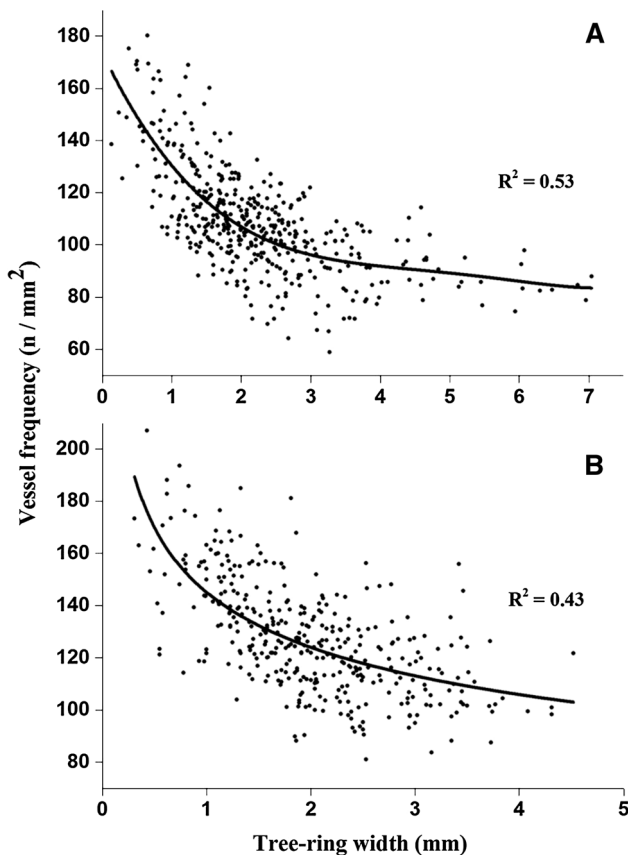
Fig. 3 Nonlinear relationship between tree-ring width vs. vessel frequency at the *lower* (**a**) and the *upper* (**b**) sites; superimposed *lines* are the curve best-fitting to the data
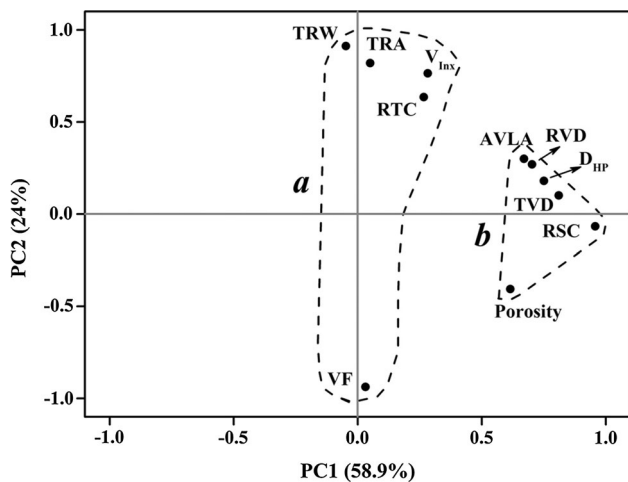

Fig. 4 Positions of the 11 variables along the first and second axes of a RPCA for all trees; two main groups are indicated with *dashed lines*. Group *a* which shows high loadings on RPC #1 contains the static features while group *b* which shows low loadings on RPC #1 but high positive or negative loading on RPC #2 includes plastic variables. For abbreviations, see Table 1

et al. 2003). Even considering different species, porosity only showed a moderate variation despite a wide range of other parameters (like VF) (Poorter et al. 2010; Fan et al. 2012). Since the mechanical strength of wood decreases with increasing porosity (Gasson 1985; Wagner et al. 1998), it seems that trees try to keep the total pore area within a safe range and control total hydraulic conductivity of a tree ring by changing other anatomical properties like VF, AVLA, and TRW. Hence, the way of distributing porosity throughout a tree ring shows much greater variance than its absolute value.

RSC, which had the most inconsistent and casual correlations with TRW and VF at both sites was closely associated with porosity and did not show high variability within and between trees (data not shown), and even between sites. Likewise, no differences of the relative hydraulic conductivity were found among diffuse-porous avocado stems, which were suggested to result from adjustment between the diameter of vessels and their frequency (Reyes-Santamaría et al. 2002). RSC variations along with tangential vessel diameter (TVD) loaded strongly on the first axis of the principal component biplot. Considering that the tangential expansion of vessels in angiosperms usually shows smaller variations than the radial diameter (e.g., Dodd 1984; Verheyden et al. 2005; Hass et al. 2010) and even may remain constant under varying environmental conditions (Schmitz et al. 2006), it is concluded that PC#1 represents an aggregation of factors which detain traits varying only within a strongly restricted range. These factors are probably more genetically determined than environmentally controlled. Consequently, PC#1 stands for "static" traits, although confidently relating these traits to internal regulators needs further investigation. This suggested classification is in agreement with findings by Hass et al. (2010), who illustrated that the construction plan of a beech tree follows the principle of keeping relative pore sizes and porosity more or less constant in different tree rings. Similarly, a strong genetic basis was found for vessel diameters of *Metrosideros polymorpha*, a Hawaiian diffuse-porous tree species (Fisher et al. 2007).

TRW and VF are strongly negatively correlated and variances of both traits are reflected by PC#2. In other words, the first anatomical feature changing with TRW is VF, and both are affected by the same set of environmental factors. Beech is a tree sensitive to environmental factors (Piovesan and Adams 2001; Köse and Güner 2012), and being in a mature state of growth, its TRW is known to be highly related to external factors (Eckstein and Frisse 1979; Sass and Eckstein 1995; García-Suárez et al. 2009; Pourtahmasi et al. 2011). VF also has shown to be more related

to exogenous factors like rainfall and temperature (Aguilar-Rodríguez et al. 2006) or groundwater level fluctuations (Schume et al. 2004). Hence, PC#2 may stand for "plastic" traits on which exogenous factors have a greater share in controlling their variability.

Reduction in VF could be a mirror effect of ring-width extension since the higher portion of latewood (with much fewer vessels) in wider tree rings may result in a lower number of vessels. However, the quadratic nature of this relationship challenges this idea: considering narrow or medium-wide tree rings, an increase in ring width will dramatically reduce VF, but when TRW shifts from mean values to extremely wide rings (containing a higher portion of latewood), the strength of this negative correlation becomes weaker. Thus, VF should be actively controlled by the tree but influenced by the same set of factors affecting ring width. Sass and Eckstein (1995) suggested that vessels are almost evenly distributed throughout a whole beech tree ring, but the results of their study are not directly comparable to ours because they were based on intra-tree ring comparisons of VF and size.

Total hydraulic conductivity is associated with TRW, VF and vessel diameters and area. TRC is more related to PC#1 than to PC#2. Since TRC is very important for tree growth and survival (Poorter et al. 2010; Crous et al. 2012) and can be considered as a pioneer variable to be adjusted, it can be deduced that in response to different annual conditions, beech trees control their hydraulic conductivity mainly by changing the number of vessels and tree growth rate, followed by vessel size. The lower sensitivity of vessel diameter to hydrological alterations in comparison to VF has previously been shown in hybrid poplar (Schume et al. 2004). However, these three main regulators are not controlled by the same environmental signals. In order to fully understand how trees manage their water-transport efficiency, intra-annul wood formation in space and time is to be envisaged. Strong hydraulic–photosynthetic coordination of trees has been demonstrated by Hubbard et al. (2001), Santiago et al. (2004), and Ishida et al. (2008): under suitable conditions, the rate of photosynthesis increases and the xylem production accelerates to accompany the high water and nutrient demand of the tree. Although the xylem produced in a specific time increases, the number of vessels produced in that interval remains constant or even decreases, resulting in fewer vessels per area. Instead, these vessels are bigger to increase water-transport capacity. Since vessel-lumen conductivity is related to the fourth power of lumen diameter (Tyree and Zimmerman 2002; Sperry et al. 2006), a minute increase in vessel dimension counterbalances the smaller number of vessels and total conductivity will increase (Cruiziat et al. 2002; Steppe and Lemeur 2007; Tombesi et al. 2010). This trade-off between size and number of vessels is not

controlled by identical environmental factor(s), which is supported by Carlquist and Hoekman (1985) and Fan et al. (2012), who suggested that VF changes more rapidly or is more evolutionarily labile than vessel area (AVLA). It was also suggested that despite of the strongly inverse relationship between VF and vessel diameter, these two features can vary independently to a large degree (Carlquist 2001). VF was found to be a promising environmental proxy, whereas vessel diameter (especially tangential diameter) was less sensitive to changes of exogenous factors (Schmitz et al. 2006).

RSC did not show great inter-annual variation and is considered to be a "static" variable. However, this does not imply that the potential of a tree ring to conduct water through its vascular system would almost be the same in different years. The total amount of water pulled from the roots to the leaves relies on the total TRA which is not only a function of ring width but also includes circumferential growth of the tree in a given year. Hence, considering only RSC to study the hydraulic architecture of diffuse-porous trees would be misleading: RTC was closely associated with exogenous factors and showed identical relations with other environmentally controlled traits (RW and VF), whereas weak and inconsistent relations of RSC with these properties makes it almost impossible to interpret a tree's hydraulic composition and response solely based on this variable. Considering total TRA and therefore RTC instead of RSC becomes even more convincing in ring-porous trees where water transport is mostly accomplished by the vessels of the outermost annual ring (Kramer and Boyer 1995); diffuse-porous trees, in contrast, may be transporting water through a dozen of rings or even more (Kramer and Boyer 1995; Thomas 2000). Hence, the circumferential position of a tree ring highly determines the total number of active conduits in a ring-porous tree.

In the principal component biplot (Fig. 4), the vulnerability index vector forms almost a straight angle with the VF vector, showing their intimate but reverse relation. Moreover, both variables have a strong loading on the second axis. Similar results were obtained for a diffuse-porous avocado tree (Reyes-Santamaría et al. 2002). Although the contribution of vessel diameter and frequency is equal in the vulnerability index equation, a higher variability of VF makes V_{Inx} more sensitive to the number of vessels rather than to their diameter. It means that while AVLA is more static in different years, an increase in VF will remarkably reduce the susceptibility of the vascular system for being dysfunctional or damaged during water conduction.

It should be noted that the general term "environmental factors" were intentionally used in this research because we don't know what they exactly are! Relating wood anatomical variables to commonly used environmental data

(like precipitation and temperature measurements) is not mostly satisfactory in the North of Iran. Reason for low correlations between climate data and tree-ring features are still under debate, but may include the distance of existing meteorological stations from study sites (usually up in the mountains) or the limited number of climatic variables available (usually only monthly precipitation and temperature). The present study is a first attempt to answer the vital question which xylem anatomical features can be more affected by exogenous factors. The next step in further studies will be to determine these exogenous factors which presumably are more complex integrative factors than just temperature, precipitation or soil type.

Besides the factors discussed, there are other anatomical variables which have not been considered in our study. Vessel length and percentage of vessels with scalariform perforation plates can theoretically limit the conducting efficiency in beech (Carlquist 1977; Sperry et al. 2006). However, the number of vessels with scalariform perforation plates in Japanese beech was shown to be unrelated to environmental factors (Bayramzadeh et al. 2011) and vessel element length was proved to be controlled by morphogenetic factors independent of those affecting the diameter of vessels and number of vessels per sq. mm (Carlquist 1977). The lateral water transportation in the xylem (Cruiziat et al. 2002) which can support the longitudinal conductivity is another important issue which should be considered in future. For example, with increasing TRW and consequently cross-sectional area, the number of vessel interconnections will probably increase which in turn will enlarge actual hydraulic conductivity of that tree ring (Patiño et al. 1995). Other xylem cells like imperforate tracheary elements and axial parenchyma are present in beech and may have a minor contribution to the hydraulic conductivity of a tree ring (Carlquist 2001; Sano et al. 2011). Hence, we suggest that further intra-species approaches could benefit from studying their frequency, distribution and morphology along with the vessel characteristics.

Conclusions

In diffuse-porous beech, water availability has a strong selective effect on wood anatomy like in many other species (e.g., Sperry et al. 2006; Crous et al. 2012). It changes some xylem anatomical features intensively and has few or no effect on others. This effect seems to be rather insensitive to local site conditions: total hydraulic conductivity of a tree ring is mainly adjusted by the positional TRW and VF rather than by other vessel-related traits. This behavior is different from ring-porous trees where abundant water supply was found to enhance the

formation of large vessels but has little or no effect on TRW (Campelo et al. 2010). Besides, the tight negative association between vessel size and frequency which regulate the hydraulic efficacy/safety of a tree is not aspired by the same controlling factor(s). VF is highly affected by "enviro-internal" factors which also govern TRW. On the other hand, vessel size and porosity are more static features, constrained within a smaller range of variation primarily controlled by genetic factors. The potential of xylem to pull up water in one unit of area (RSC) is also tightly controlled by the latter factor(s). However, total hydraulic conductivity of a tree ring is related to "enviro-internal" factors and therefore is a better criterion to study the effect of environment on the hydraulic architecture of diffuse-porous trees. Further studies considering different exogenous factors along with in situ tracing of xylem conduits formation (e.g., Oladi et al. 2011; Anfodillo et al. 2012) can help relating these proposed "plastic" and "static" traits to the applicable corresponding factors. It is especially interesting to study whether the way of alteration in anatomical features of beech xylem is species- and site-dependent or can be generalized to all diffuse-porous trees in different climates.

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