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REGULAR PAPER

Intervessel connectivity and relationship with patterns of lateral water exchange within and between xylem sectors in seven xeric shrubs from the great Sahara desert

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Abstract The main objective of this study was to evaluate the role of intervessel contacts in determining the patterns of hydraulic integration both within and between xylem sectors. The degree of intervessel contacts and the lateral exchange capability within and between sectors were examined and correlated in different xeric shrubs. A dye injection method was used to detect the connections between vessels; an apoplastic dye was sucked through a known number of vessels and its distribution in the xylem network was followed. Hydraulic techniques were used to measure axial and tangential conductivity both within and between xylem sectors. The intra- and inter-sector integration indexes were then determined as the ratio of tangential to axial conductance. Species differed significantly in the degree of intervessel contacts, intra- and inter-sector integration index. In all cases, hydraulic integration was observed to be higher within sector than between sectors. From the correlation analyses, the intervessel contacts showed a very weak relationship with inter-sector integration index and a strong positive relationship with intra-sector integration index. Results suggested that (1) the factors affecting patterns of lateral flow within xylem sectors might be relatively different from those between sectors. (2) The degree of intervessel contacts was a major determinant of hydraulic integration within the same xylem sector. (3) Intervessel connectivity alone was a poor predictor of hydraulic integration between different sectors, implying a significant contribution of other anatomical, physiological and environmental factors in determining the patterns of integrated–sectored transport within woody stems.

Keywords Desert shrubs · Integration · Intervessel contacts · Lateral flow · Sectoriality · Xylem sectors · Water transport

Introduction

Usually, secondary vessels in stems of woody species are laterally interconnected by bordered pits, providing lateral apoplastic continuity for water exchanges within the xylem network (Burggraaf 1972; Fujii et al. 2001; Tyree and Zimmermann 2002; Kitin et al. 2004). Lateral flow is important for rapid and sustainable water movement both within and between plant organs (Tyree and Ewers 1991; Tyree et al. 1994; Tyree and Zimmermann 2002; Schulte and Brooks 2003, Schulte 2006). It is also important for vital processes such as the growth of cambium and differentiating wood (Kitin et al. 2009). However, because of the hydraulic sectoriality often found in the xylem of plant stems (Tyree and Zimmermann 2002), lateral flow within one xylem sector may differ considerably from that between different sectors. While water in one sector travels

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a short distance between neighboring vessels, water has to travel a long distance between vessels of different sectors passing through a range of xylem structures, such as membranes of bordered pits, vessel lumens and xylem rays.

The transport and distribution of materials within the whole organism largely depend on the pattern of lateral water exchanges both within and between xylem sectors. Lateral exchange capability of the xylem is one of the plant strategies for adaptation to various ecological conditions (Orians and Jones 2001; Zanne et al. 2010). Numerous studies have noted a correlation between hydraulic sectoriality and species' ecological tolerances (Waisel et al. 1972; Orians et al. 2004, 2005; Ellmore et al. 2006; Zanne et al. 2006; Gloser et al. 2008; Schenk et al. 2008; Taneda and Tateno 2007; Thorn and Orians 2011). Specifically, it has been shown that plants with higher tolerance to drought conditions, such as desert shrubs, tend to have sectored water transport (reviewed by Schenk 1999). Some authors have suggested that the restricted transport in sectored wood could be attributed to low degree of interconnectedness between vessels (i.e. low intervessel transfer capacity). Indeed, in their study on 18 temperate tree and shrub species, Zanne et al. (2006) have noted a correlation between intervessel connectivity and hydraulic sectoriality. They have shown that sectored transport tends to increase with anatomical features leading to low lateral connectivity between vessels, while integrated transport increases with increasing lateral connectivity. Although a number of other studies have supported such a relationship between intervessel contact and xylem sectoriality (Orians et al. 2004; Ellmore et al. 2006), it seems too early to generalize this trend. Further researches on large number of species from different habitats are badly needed to determine the functional relationship between the extent of intervessel connections and lateral exchanges between xylem sectors of the stem wood.

In the present study, the capacity of lateral flow between vessels and the degree of hydraulic integration within and between xylem sectors were examined in different xeric shrubs common in the Sahara desert. The purpose was to test how patterns of water exchanges within and between sectors are related to intervessel connectivity in the xylem network. Here the capacity of lateral flow between vessels (intervessel transfer capacity) was used, instead of anatomical analyses, as an indicator for the presence and extent of functional intervessel contacts. This is because anatomical traits such as pitting, vessel size and distribution, and vessel density are incomplete predictor of the capacity of lateral connectivity between vessels (Ellmore et al. 2006). The dye injection method of Taneda and Tateno (2007) was used to evaluate the intervessel transfer capacity. An apoplastic dye, toluidine blue O (Shane et al. 2000), was directly sucked through a known number of vessels and its distribution in the xylem network was followed. Since any transfer of tension from the selected vessels to other conducting vessels must be through lateral contacts, the distribution of dye, in this case, should reflect the extent of functional intervessel contacts in the xylem network. On the other hand, the hydraulic technique of Ellmore et al. (2006) was primary developed as a rapid tool for comparing patterns of integration–sectoriality among woody species. The principle of this technique is to evaluate the relative ease of tangential spread in the sapwood of isolated stem segments. Since this technique was very reliable and applicable to evaluate the pattern of lateral flow between different xylem sectors, we used this technique to determine an index of hydraulic integration between different sectors. However, to reach our objectives and to better understand the role of intervessel connectivity in water-conducting mechanism of highly drought stress-adapted xylem, it would be interesting to evaluate the ease of tangential spread within a single xylem sectors. Therefore, the method of Ellmore et al. (2006) was somewhat modified to determine an intra-sector integration index. The relationship of intervessel transfer capacity with inter-sector and intra-sector integration indexes was analyzed to determine the role of intervessel connectivity in the patterns of lateral water exchange within and between xylem sectors.

Materials and methods

Samples

Twigwood samples were collected from seven common shrub species growing at the region of Touggourt located in the northeastern Sahara desert (Low Sahara basin) of Algeria. The climate along this area is arid to hyperarid, characterized by low rainfall and high rates of evapotranspiration. Daily mean temperatures vary between 10 °C in the winter to 32 °C in the summer with August being the hottest month. Rainfall is generally low and tends to fall between November and March. The average annual rainfall is approximately 58 mm. The species tested in this study were *Calligonum comosum* L'her. (Polygonaceae), *Genista saharae* Cosson et Dur. (Fabaceae), *Limoniastrum guyonianum* Dur. (Plumbaginaceae), *Nitraria Retusa* (forssk) Asch. (Zygophyllaceae), *Retama retam* Webb. (Fabaceae), *Tamarix gallica* L. (Tamaricaceae), *Zizyphus lotus* (L.)Desf. (Rhamnaceae). Samples were collected in autumn 2011 at the end of the vegetative growth. Five mature plants per each species were sampled: per plant, five twigs of >1 year old were harvested. For all laboratory analyses, branch samples were 0.7–1.2 cm in diameter.

Intervessel transfer capacity

The method of Taneda and Tateno (2007) was used to determine the magnitude of lateral flow between xylem vessels (i.e., the degree of intervessel connectivity). The dye solution was directly pulled through a known number of vessels and its distribution in the xylem network was followed. 7-cm-long segments were cut from stems >1 year old. 16-gauge needle, commonly used for blood donations, was used to pull the dye through a small number of xylem vessels. The metal needle was carefully cut to eliminate the piquant end (Fig. 1). Under a stereomicroscope and using a fast-setting, water-insoluble epoxy glue (Kafuter Epoxy AB Glue Adhesive, Guangdong Hongda New Materials Technology Co., Ltd, Guangdong, China), the cut needle was placed and fixed in a sapwood area on the cut distal end. The cut distal surface of the stem segment was then entirely sealed with glue, so only the small circle delimited by the syringe needle, remained unsealed (Fig. 1). Usually, the unsealed circle contained about 9–27 open vessels. A plastic tubing of suction pump was connected to the syringe needle while the basal end of the segment was immersed in filtered (0.2 µm) toluidine blue O (1 % w/v aqueous solution). By using a relatively high suction force of −150 kPa, the dye solution was directly pulled, for 5 min, through the open vessels that delimited by the syringe needle. To check for the presence of dye in the xylem network, free-hand cross-sections were taken every 1 cm starting from the outflow point. Slides were then viewed under optical microscope, and the number of stained vessels was counted. Xylem vessels were easily distinguished in cross sections because of their larger lumen diameters and their thin walls. The lignified cells with smaller diameters were either tracheids or fibers and were excluded from our analyses. However, xylem vessels near the dye injection site might take the dye by capillarity and diffusion under laboratory conditions (Umebayashi et al. 2007). To take these artifacts into consideration, 7-cm-long segments were similarly collected from our tested species and, at atmospheric pressure, the basal end of each segment was immersed in the dye solution for a period of 5 min. Segments were then examined in the same manner as above to follow the simple passive infusion of dye. All material was examined with a Zeiss KF2 compound light microscope (Carl Zeiss, West Germany). The photomicrographic images were captured using Motic Digital Microscope (DMB1-2MP, Motic Instruments Inc., Xiamen, China).

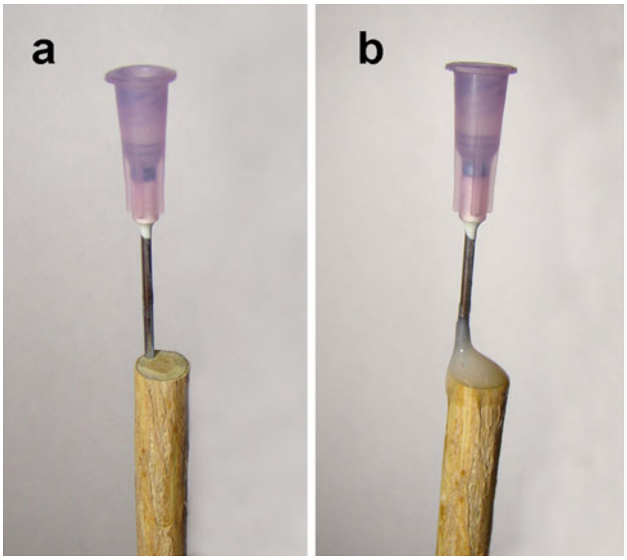


Fig. 1 **a** Showing how 16-gauge needle was fixed on the cut surface of the tested segment to delimit a small area of sapwood. **b** Epoxy glue was used to seal the entire cut surface and to mechanically stabilize the needle. Through the needle, a positive or negative pressure could be applied to a smaller number of vessels. This technique was used to examine the capacity of lateral flow and also to determine the hydraulic integration within a single xylem sector

Inter-sector integration index

Using the hydraulic technique of Ellmore et al. (2006), an index of lateral integrity between sectors, ranging from 0 to 1, was calculated for each species. This index has the advantage that variables in the degree of lateral exchange between different xylem sectors can be directly compared. The xylem sector tested by this method does not represent the real area of one xylem sector, but simply a limited part of sapwood (about 60° section of the sapwood) where vessels were assumed to be closely adjoining. This is because of the difficulty in delineating the boundary of one unit xylem sector within the vascular cylinder. Therefore, the inter-sector integration index would reflect the capability for long distance lateral water movement in the stem xylem, which in turn would reflect the degree of hydraulic integration between different sectors.

On 5 cm long woody segments and under a stereomicroscope, the proximal inflow end of each segment was sealed with fast-setting, epoxy glue except for a 60° section of the sapwood that was left unsealed (Fig. 2). This inflow end was then connected to rubber tubing and filtered toluidine blue dye was forced at low pressure of 50 kPa into the segment for a few seconds to map axial pathways. After flushing any residual stain, filtered 20 mM KCl (Zwieniecki et al. 2001) was pushed at 100 kPa pressure through the inflow section until a steady flow was observed (Fig. 2). To calculate axial conductance (K_{axial}), the outflow from the unglued distal surface was absorbed into lab tissue and weighed after 3 min of collection using electronic balance (model 210, Sartorius). Hydraulic conductance (K) was determined as, K = flow rate/pressure (g MPa − 1s − 1).

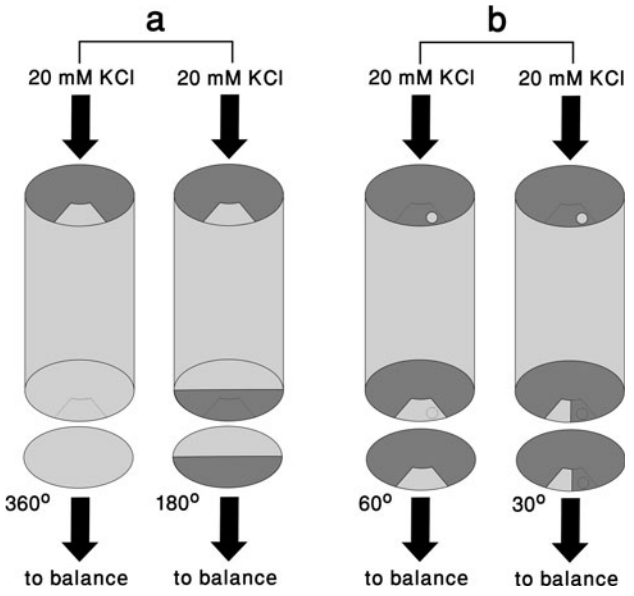


Fig. 2 Schematic presentation of the methods used to measure the hydraulic integration both within and between xylem sectors: *dark grey*, glue; *light grey*, sapwood. *Circles* below the branch segments represent the distal outflow end. **a** for integration between sectors, 20 mM KCl was pushed through 60° inlet in the proximal end and the flow rate from the distal outflow was measured before and after sealing the half of the outflow including the area of direct flow from the unsealed inflow section. **b** for integration within sector, a syringe needle was used to push 20 mM KCl through a smaller area at one side of the selected 60° section, while the flow rate from the distal unsealed section was measured before and after sealing the half of the outflow section including the area of direct flow

To determine tangential conductance ($K_{tangential}$), axial flow path was completely blocked by sealing a 180° section of the distal outflow surface such that the stained area denoting axial flow was blocked and centred in the middle of the 180° glued section (Fig. 2). The 20 mM KCl was again pushed through the inflow section and the tangential conductance was measured as above. Integration index for water exchange between different xylem sectors was calculated using the following equation: Inter-sector integration index $= 2(K_{tangential})/K_{axial}$.

Intra-sector integration index

We quantified here the relative ease of tangential spread within a single xylem sector (represented by 60° section of the sapwood). Intra-sector integration index was obtained as a ratio of lateral conductance to axial conductance within one xylem sector. This index, which reflected the short distance lateral flow, was considered as an indicator for the hydraulic integration within sector. The proximal surface of the 5 cm long segment was sealed with epoxy glue except for a 60° section of the sapwood. After determining the same section at the distal surface by using dye flow, the distal surface was also sealed except the determined section. At the proximal end, a 16-gauge hypodermic needle was prepared as above and gently connected with glue to a sapwood area at one side of the unsealed section (Fig. 2), and then all the rest of section was completely sealed. After the glue hardened, a pressure source was attached to the needle and a filtered 20 mM KCl was pushed at 100 kPa. After a steady flow was attained, the rate of outflow from the unglued section of the distal surface was measured for 3 min to calculate axial conductance (K_{axial}).

To determine tangential conductance ($K_{tangential}$), axial flow path was completely blocked. To do this, the half of the unsealed section at the distal outflow including the area of direct flow from the needle was carefully sealed using a droplet of glue (Fig. 2). Then, the filtered 20 mM KCl was again pushed through the needle until a steady flow was reached. Tangential conductance was measured for 3 min, and the integration index for water exchange within the same xylem sector was calculated as follows: Intra-sector integration index $= 2(K_{tangential})/K_{axial}$.

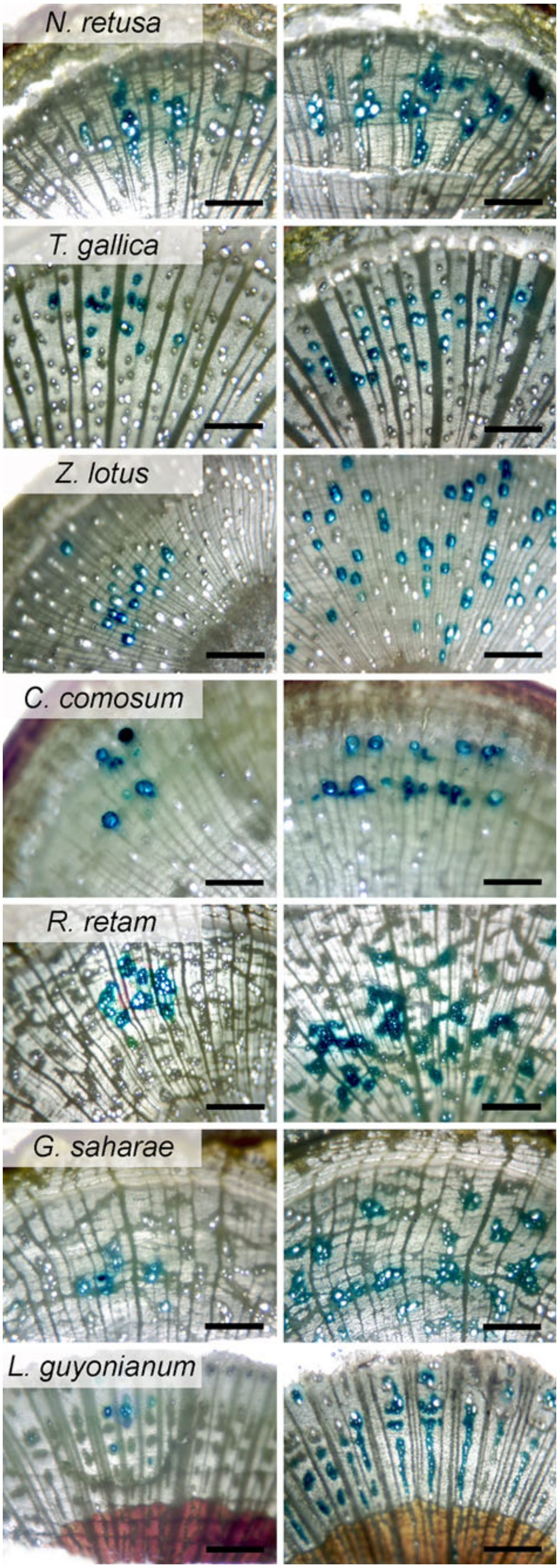
Statistical analysis

The data were analyzed using SPSS software package (SPSS Ver. 15.0, SPSS Inc., Chicago, IL, USA), and the variables were given as mean ± standard deviation. Different experimental groups were compared either with the Student's *t* test or with the one-way ANOVA followed by Bonferroni's test for comparisons post hoc. The relationship between intervessel transfer capacity and (1) lateral integration between sectors, and (2) lateral integration within a sector, were tested using two-tailed simple linear correlation (Pearson's correlation coefficient). Only the *P* values of less than 0.05 could be accepted as a significant level.

Results

Intervessel transfer capacity

The magnitude of lateral flow between vessels was evaluated and considered as a direct and immediate indicator of the degree of intervessel connectivity in the sapwood of drought-adapted plants. The movement of toluidine blue dye was followed when the tension occurred only in a small number of vessels. Firstly, when the dye solution was allowed to flow passively under laboratory conditions, stained vessels were observed only in the basal portion of segments. No dye was observed beyond a distance of 1.5 cm above the loading site. Results were different when the dye was pulled through the syringe needle at the distal



◀**Fig. 3** Microphotographs showing the results of dye injection experiments for the capacity of lateral flow. The suction force was applied to a small area of sapwood at the distal end of 7-cm-long segments, while the proximal end was immersed in the dye solution. *Left panels* show freehand cross sections through the tested segments at 1 cm from the suction point. The stained vessels presented in these panels reflect the small number of vessels where the tension was applied. The right panels show the cross sections at 5 cm from the suction point. The increased number of stained vessels reflects the degree of lateral transfer of tension, which in turn reflects the extent of functional lateral contacts between vessels. Note that the dye is distributed only in one side of the stem sections. Species are ranked in order of ascending value of intervessel transfer capacity. *Scale bars* = 200 μm

end. Dye stain was observed not only in the few vessels delimited by the syringe needle, but also in other neighboring vessels. In all cases, the number of sapwood vessels stained by the dye increased gradually with increasing distance from the outflow surface. At a few millimeters below the suction point, the dye distribution in the sapwood was so limited and was observed only in a small number of vessels which reflected the number of unsealed vessels delimited by the hypodermic needle (Fig. 3). At 2–3 cm behind the distal cut end, additional stained vessels started to appear around those observed at the outflow surface. At a distance of >4 cm below the distal outflow, the dye was observed to distribute further within the sapwood and, in most samples, the number of stained vessels was more than 2 times greater than that at the outflow cut end (Figs. 3, 4a). It must be noted that the dye distribution was restricted to one side of the tested segments, where the suction was applied. Very little or no stained vessels were observed in the opposite side (Fig. 3).

To facilitate comparisons between species, intervessel transfer capacity was expressed as the number of stained vessels at 5 cm normalized by that observed at the outflow surface. Species differed significantly in the capacity of lateral flow (Fig. 4a; $F = 18.95$, $P < 0.0001$; one-way ANOVA), with *Limoniastrum guyonianum* exhibited the highest values (8.73 ± 1.36; mean ± SD) while *Nitraria retusa* had the lowest values (1.68 ± 0.62). Also, it must be noted that the dye distribution pattern varied among species and had no obvious trend. In some cases (e.g., *Calligonum comosum* and *Tamarix gallica*; Fig. 3), lateral flow of dye extended in the tangential direction, but in others (e.g., *Limoniastrum guyonianum* and *Genista saharae*; Fig. 3), lateral flow extended in the radial direction or randomly distributed within the sapwood.

Inter-sector integration index

Generally, all samples showed a low degree of lateral spread between xylem sectors, and this resulted in low

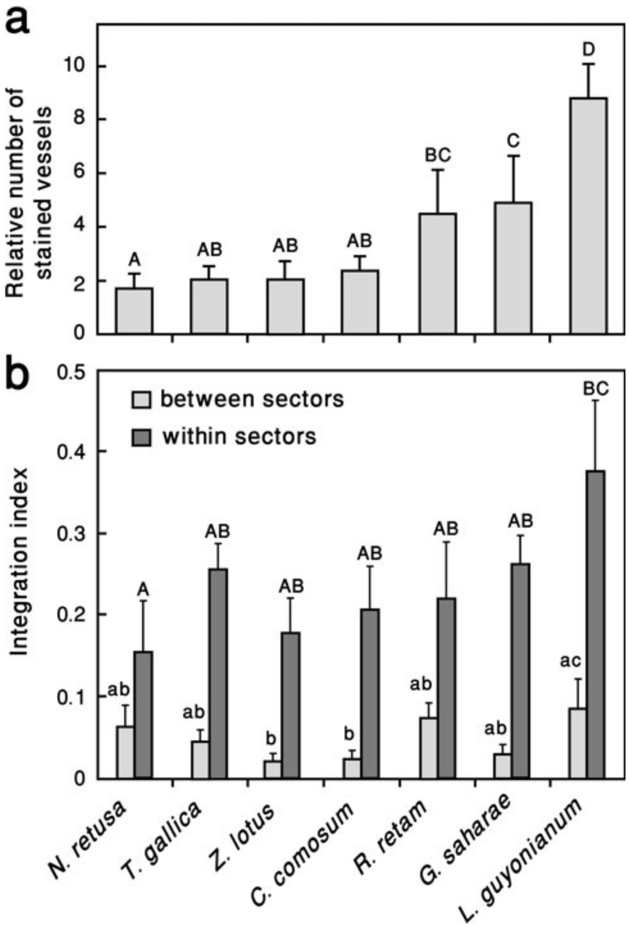


Fig. 4 **a** Differences in the intervessel transfer capacity between the seven desert shrubs, expressed as the number of stained vessels at 5 cm normalized by that observed at the outflow surface. Species are ranked in order of ascending value of lateral flow capacity. **b** Lateral exchange capability within and between xylem sectors. *Bars* topped by different letters are significantly different at $P < 0.05$ (Bonferroni's test). Values are mean ± SD ($n = 6$ stem segments)

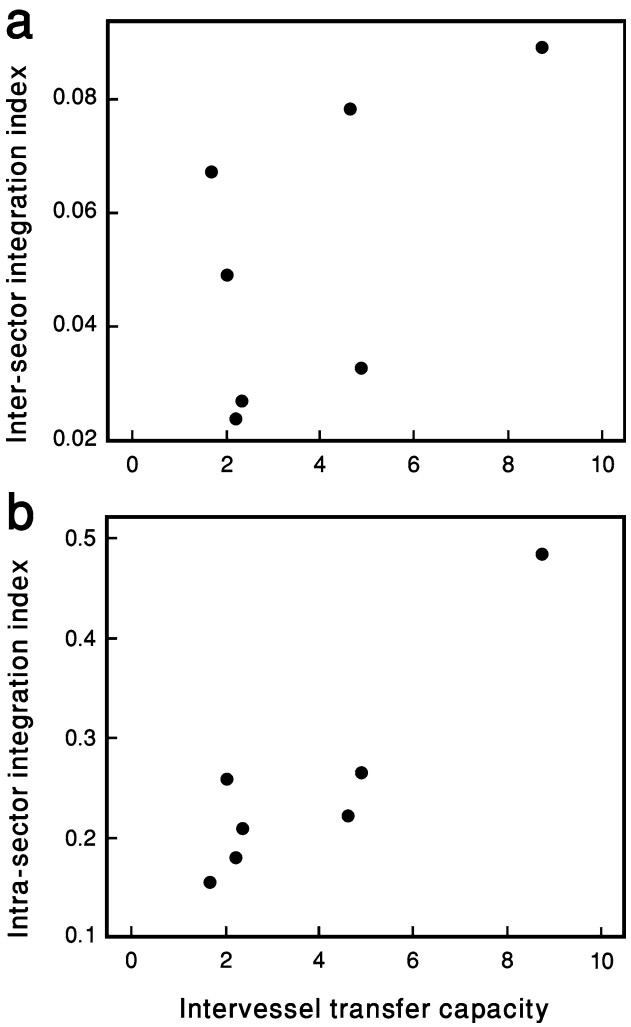


Fig. 5 The relationship between intervessel transfer capacity and **a** lateral integration between sectors, and **b** lateral integration within a sector

values of inter-sector integration index, which ranged from 0.024 ± 0.01 to 0.089 ± 0.02. However, the differences between species in this index were statistically significant (Fig. 4b; $F = 4.97$, $P = 0.003$; one-way ANOVA). *Limoniastrum guyonianum* showed the highest index of integration between sectors, while the lowest integration index was observed in *Zizyphus lotus*. Pearson product moment correlation analysis showed that the degree of integration between sectors was only weakly correlated with intervessel transfer capacity (Fig. 5a; $r = 0.61$, $P = 0.151 > 0.05$).

Intra-sector integration index

Compared to the lateral flow between different sectors, water moved much more easily between vessels within the same sector, and consequently the values of intra-sector integration index were significantly higher than those of the inter-sector integration index (Fig. 4b; Student t test, paired; $P < 0.05$). The index of integration within sector ranged from 0.18 ± 0.1 to 0.38 ± 0.16, and the differences observed between species in this index were statistically significant ($F = 2.79$, $P = 0.037$; one-way ANOVA). The highest capacity for intra-sector transfer occurred in *Limoniastrum guyonianum*, whereas the lowest capacity was observed in *Nitraria retusa* (Fig. 4b). The correlation analysis showed a significant positive relationship between the degree of integration within a sector and the intervessel transfer capacity (Fig. 5b; $r = 0.89$, $P = 0.008$). Species with higher intra-sector integration index had high capacity of intervessel flow and vice versa.

Discussion

The presence and extent of functional connections between sapwood vessels was clearly shown by the distribution of the toluidine blue in the dye-injection experiments. Although the suction force was applied only to a limited number of vessels, the dye could be clearly observed in other neighboring vessels (Fig. 3). This implied that the tension was transmitted via intervessel pitting from the selected vessels to others. Artifacts arising from capillarity and diffusion were excluded because, in the absence of tension, dye solution did not extend beyond 1.5 cm from the injection site, while all results reported in this study were taken beyond 2 cm from the injection site.

The lateral flow between vessels was observed to occur within a distance of <5 cm, indicating that vessel-to-vessel contacts were frequently distributed along the xylem pathway of these seven examined species. Furthermore, all the tested segments showed a gradual increase in stained vessels towards the proximal end, and this was consistent with the fact that the intervessel connections increase with increasing distance of water transport, i.e., longer xylem pathway provides more chance for intervessel connections (Taneda and Tateno 2007; Halis et al. 2012). On the other hand, the differences observed in the patterns of lateral dye distribution within the sapwood could be attributed to the differences in anatomical arrangement of xylem components. For example, the tangential distribution of dye was associated with the tangential arrangement of large vessels in *Calligonum comosum,* while the radial extent of dye was clearly observed in the sapwood that characterized by thick and frequent xylem rays such as in *Limoniastrum guyonianum.*

However, the stained patterns provided by the dye-injection technique appeared to be a better predictor of intervessel connectivity than anatomical features of xylem network and conduits. Although we could not precisely determine the number and position of lateral connections between vessels, and although we did not examine separately the inter-sector and intra-sector dye flow, the distribution of dye allowed for direct comparison between species in their ability to laterally distribute water in the stem sapwood and consequently, comparing the degree of intervessel connectivity. The stained patterns suggested that the xeric shrubs examined in this study differed considerably in their capacity of intervessel transfer and this, in turn, indicated that the degree of intervessel connections differed significantly between these species. Additionally, it is worth to mention that the dye technique (intervessel transfer capacity) could also be used to evaluate lateral water movement within and between sectors, and this by determining and sealing xylem sectors and by increasing both the time of application of the pressure and the length of stem segments. Of course, this needs to take into account the differences between solute (dye) and water movement within the xylem network. However, this was not the objective of our analyses, because intervessel transfer capacity was used in this study only to evaluate the degree of intervessel connectivity.

Based on the values of inter-sector integration index, all of the species studied could be classified as sectored plants. But this was not surprising because hydraulic sectoriality is a very common phenomenon in plants from arid and semi-arid environments (Waisel et al. 1972; Watson 1986; Schenk 1999; Zanne et al. 2006; Schenk et al. 2008). However, some authors (e.g. Orians and Jones 2001; Orians et al. 2004; Schenk et al. 2008) have considered the hydraulic sectoriality as being very important, as the restricted transport between different sectors would prevent affected xylem parts from negatively affecting other parts, such as the spread embolisms and vascular pathogens.

At the level of single xylem sector, although relatively high values of intra-sector integration index were observed (Fig. 4b), this does not necessarily reflect a high lateral integrity within sectors than between sectors. Integration index was much higher within sectors because water presumably moves much more easily between adjacent vessels within one xylem sector. Whereas in the long distance lateral movement between sectors, water has to pass many vessel lumen and intervessel pitting that are the resistances. It cannot be ignored that both inter-sector and intra-sector integration index should be compared by its lateral distance quantitatively. However, it is intuitively clear that the desert shrubs could also benefit from advantage of the relative ease of short-distance lateral flow within sectors, if this exists. Unrestricted transport within a single sector would allow for the effective transport of water along the xylem sector even in the presence of vessel occlusions, as water can easily bypass these occlusions by lateral spread to other functioning vessels within the sector (Tyree et al. 1994).

However, the remarkable finding of this study was that the relationship between intervessel transfer capacity and the inter-sector integration index was apparently weak (Fig. 5a). This might support the view that the patterns of integrated–sectored transport in woody species depend not only on the degree of vessel-to-vessel connections but also on other structural, physiological and even environmental factors. In this context, Sprugel et al. (1991) and Tyree and Ewers (1991) suggested that hydraulic integration is a function of the vascular architecture of the xylem, and consistently, many reports in the literature indicated that integrated–sectored transport depend on composite characteristics involving the size and frequency of vessels, inter-vessel pitting and pit membrane features, vessel wall and perforation plate structure, cross-grained drift of vessels, and relationships between vessels, fibres and tracheids (Jones and Lord 1982; Whalen 1987; Kitin et al. 2004; McCulloh and sperry 2005; Sperry et al. 2006; Pratt et al. 2007; De Micco and Aronne 2008; Nadezhdina 2010).

Physiologically, plants could regulate their degree of integration through enrichment of xylem sap with cations, as pit membrane porosity changes in response to ion concentration (Zwieniecki et al. 2001). Beyond these internal factors, other external factors such as water limitation, heterogeneity of soil conditions and pressure gradients brought about by transpiration may also play a role (Schenk 1999; Orians et al. 2004; Thorn and Orians 2011).

On the other hand, vessel-to-vessel connections appeared to be the major determinant of the degree of hydraulic integration within the same xylem sector. This is because the intervessel transfer capacity exhibited a strong positive correlation with the intra-sector integration index (Fig. 5b). The simple explanation for this was that the water presumably moved much more easily between nearby conduits within the sector than among sectors. Another possible explanation was that there were frequent connections between vessels within the same sector, whereas connections between vessels of different sectors were infrequent. Indeed, several anatomical and developmental sequences could lead to within-xylem heterogeneity in intervessel connections, and thus sectoring the vascular cylinder of woody stems. For example, it is well known that the stem xylem of most dicotyledons species is split up into radial blocks of secondary tissue by the broad and tall primary and secondary rays (Larson 1994). This, together with the presence of larger nonconducting pith area, would of course restrict the lateral continuity among the xylem network.

To conclude, intervessel transfer capacity was used in this study as a direct indicator to evaluate the differences in vessel-to-vessel connections between seven desert shrubs, and this was related to the differences in the intra- and inter-sector exchange capability to clarify the role of intervessel contacts in determining the patterns of integrated–sectored transport. The strong correlation of intervessel connections with intra-sector integration index and its weak correlation with inter-sector integration index suggested that the degree of intervessel contacts could be considered as a pertinent and useful parameter only to predict lateral integration within a single xylem sector, while for lateral integration between different sectors, intervessel contacts alone was not necessarily a reliable predictor. This confirms the idea that the patterns of integrated–sectored transport are a function of the complex relationship between anatomical features, vascular architecture of xylem network and other physiological and environmental factors. All of these considerations suggested that the factors affecting patterns of lateral flow within xylem sectors might be relatively different from those between sectors. Therefore, to model water exchanges in strongly sectored xylem, it is not reasonable to consider this system only as a restricted pathway. Rather, it should be considered as a combination of hydraulic units (sectors) and should thus distinguish the lateral continuity within sector from that between sectors. Finally, this study is only the ground for further investigation, as it does not provide final answers to all questions regarding the impact of intervessel connections. Additional data and further research are needed to form a more complete understanding of the topic, and to resolve a number of related questions.

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