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Research paper

Diameters of phloem sieve elements can predict stem growth rates of woody plants

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Understanding forest dynamics is crucial to addressing climate change and reforestation challenges. Plant anatomy can help predict growth rates of woody plants, contributing key information on forest dynamics. Although features of the water-transport system (xylem) have long been used to predict plant growth, the potential contribution of carbon-transporting tissue (phloem) remains virtually unexplored. Here, we use data from 347 woody plant species to investigate whether species-specific stem diameter growth rates can be predicted by the diameter of both the xylem and phloem conducting cells when corrected for phylogenetic relatedness. We found positive correlations between growth rate, phloem sieve element diameter and xylem vessel diameter in liana species sampled in the field. Moreover, we obtained similar results for data extracted from the Xylem Database, an online repository of functional, anatomical and image data for woody plant species. Information from this database confirmed the correlation of sieve element diameter and growth rate across woody plants of various growth forms. Furthermore, we used data subsets to explore potential influences of biomes, growth forms and botanical family association. Subsequently, we combined anatomical and geoclimatic data to train an artificial neural network to predict growth rates. Our results demonstrate that sugar transport architecture is associated with growth rate to a similar degree as water-transport architecture. Furthermore, our results illustrate the potential value of artificial neural networks for modeling plant growth under future climatic scenarios.

***Keywords*:** carbon allocation, forest ecology, machine learning, plant anatomy, sugar transport, tree physiology, xylem.

Introduction

Understanding the mechanisms underlying variation in plant growth rates is vital to crop selection (Nunes-Nesi et al. 2016) and contributes important information for the accurate prediction of forest performance, especially in the face of global climate change (Li et al. 2015). Functional traits determine the range of individual growth rates under different environmental conditions and plant developmental stages (Flores-Moreno et al. 2019). Traits that predict variation in growth rates have been used in large-scale ecological studies to define the global spectrum of plant form and function (Díaz et al. 2016) and characterize global plant competition patterns (Kunstler et al. 2016). Previous studies reported that traits related to photosynthetic capacity (e.g., specific leaf area; Gibert et al. 2016) and water-transport efficacy (e.g., wood density and xylem vessel diameter, Carrasco et al. 2014, Hietz et al. 2017) are correlated with species-specific growth rates under a wide range of environmental conditions.

This study tests the hypothesis that functional traits related to carbon (sugar) transport can predict part of the observed variation in plant growth rates (Savage et al. 2016). Photosynthesis in leaves uses the carbon from CO_2 to produce sugars that are transported in the vascular phloem tissue to carbon-consuming and -storing organs, such as roots, fruits, flowers and stems. Like xylem vessels, the phloem harbors highly specialized transport cells, the sieve elements, which form a low resistance pathway for mass-flow of the sugar-rich phloem sap (Liesche and Patrick 2017). Unlike vessels, mature sieve elements are living cells. Since they lose their nucleus and most other organelles during cell differentiation, their function depends on the molecular exchange with companion cells (van Bel et al. 2002). A series of stacked sieve elements are axially connected by wide plasmodesmata. In carbon source tissues, sugars are loaded into the sieve element–companion cell complex, whereas they are unloaded in sink tissues. Because sugar concentration influences a cell's osmotic water uptake or efflux, the difference between sieve elements in source and sink tissues translates into a hydrostatic pressure potential that drives mass flow (Liesche and Patrick 2017). Despite the large carbon reserves typically found in woody plants, especially in the stems, species-specific variation in sieve element anatomy might affect growth rates if these features—rather than the amount of stored sugar—scale with the rate of sugar supply to growing tissues (Carbone et al. 2013, Palacio et al. 2014). Accordingly, we hypothesize that sieve element anatomy is correlated with plant growth in woody plants.

Sieve element diameter is the key variable of phloem conductivity (Liesche et al. 2015, Savage et al. 2017), just like vessel diameter is the main factor in xylem conductivity (Poorter et al. 2010). Here, we first tested if phloem sieve element diameter is associated with the growth rate in 25 liana species, using the association of xylem vessel diameter with growth rate as reference. Then, we extended our analysis to a wide range of woody plants by collecting data from the Xylem Database (Schweingruber and Landolt 2010). We trained and applied an artificial neural network to determine the value of sieve element diameter data for growth rate prediction compared with other variables. The usefulness of neural network-based models in this context was recently indicated by the accurate prediction of *Ficus benjamina* stem growth rates (Alhnaity et al. 2019). One advantage of this approach is that a neural network is not bound to linear associations but can also utilize non-linear associations. Moreover, nearly unlimited variables can be added to neural networks to test their relative value and improve prediction accuracy. Because of this ability to integrate highly complex data, artificial neural networks are instrumental for predicting forest performance under future climates (Ashraf et al. 2015, Rocha et al. 2018).

Materials and methods

Growth rates

We obtained growth rates from stem diameter increments of 25 liana species growing on 30 1-ha permanent plots in a Central Amazonian undisturbed old-growth rainforest (Ducke Forest Reserve, Amazonas, Brazil; −2.94708, −59.975221). In total, 80 individuals were sampled, meaning that three or four individuals per species were analyzed. The first census was carried out between 2004 and 2005 (Nogueira et al. 2011) and the second in 2014 (Gerolamo et al. 2018). Mean diameter increment ($DI_{diameter =}$ cm $year^{-1}$) was calculated using the equation: $DI_{diameter} = (D_f - D_i)/\Delta t$, where D_f = final diameter in 2014, D_i = initial diameter in 2004–2005 and Δt = timeframe. The liana stems were measured at a distance of 1.30 m from the rooting point (for details see Gerolamo et al. 2018). Raw data of the censuses are available on the forestplot website (https://www.forestplots.net/en).

Growth rates of plants listed in the Xylem Database were taken from the sample descriptions (Schweingruber and Landolt 2010). Growth rate values were determined on samples taken at the transition zone between root and stem from healthy individuals of average height growing on 'typical' sites. As detailed by Schweingruber et al. (2011), samples were conserved in 40% ethanol until they were sectioned using a microtome. Cross-sections were stained with Astrablue and Safranin to highlight lignin and cellulose in cell walls and imaged on a wide-field light microscope. Growth rates could be measured for species with visible growth rings. In cases where growth rings were not clearly demarcated, differences in vessel size between earlywood and latewood or zones of cells with thick fiber-rich walls were used to estimate ring width. The values of annual growth rates given in the Xylem Database represent the average width of growth rings and were calculated by dividing the longest radius of the xylem by the number of growth rings (Schweingruber and Landolt 2010).

The datasets included plant species with varying growth forms: trees, shrubs, dwarf shrubs and lianas. Samples were collected in each species' native biome, which were defined as arctic, arid, boreal, hill, Mediterranean, mountain and subtropical (Schweingruber and Landolt 2010) following the classification of Walter and Lieth (1967). A primary dataset compiled from the Xylem Database comprised 242 species. Species represented by samples from plants below 6 years of age were excluded, because of the high intra-species variability of vascular anatomy previously observed in young woody plants (Kiorapostolou and Petit 2018). A secondary dataset with 322 species with plants older than 2 years was used exclusively for the artificial neural network analysis described below.

Sieve element and vessel anatomy

Sampling and analysis of sieve element and xylem vessel diameter of lianas mostly followed previous protocols (Pace et al. 2015, Liesche et al. 2017). A 1 × 1 × 2 cm (width, length and height) piece of stem with bark and xylem was cut from the plant at breast height (1.3 m) using a sharp knife, immediately fixed in 70% formalin acetic acid:ethanol and subsequently stored in 70% ethanol. Samples were embedded either in historesin (Leica Microsystems, Mannheim, Wetzlar, Germany) or polyethylene glycol (PEG) 1500 (Rupp 1964) and sectioned with permanent microtome knives sharpened with sandpaper. To perform historesin embeddings, 2-mm cubes containing xylem, cambium and contiguous phloem were placed for about 1 month in pre-embedding solution, followed by 1 month in embedding solution in a refrigerated vacuum chamber. Samples were subsequently placed into casting molds, later sectioned with the aid of a rotary microtome and finally stained in 0.05% toluidine blue O in glacial acetic buffer at pH 4.7. For samples embedded in PEG 1500, sections of entire stems were prepared with the aid of a sliding microtome (Leica Biosystems, Wetzlar, Germany), using a Styrofoam resin to prevent the samples from tearing apart and preserving, as well as possible, the fragile phloem (Barbosa et al. 2010). Images of samples were obtained by bright-field light microscopy (Leica Microsystems, Wetzlar, Germany), and the measurements were carried out in the software ImageJ (Schindelin et al. 2012). At least three samples per species were analyzed, and measurements conducted on 10–27 sieve elements and xylem vessels per sample.

Phloem sieve element diameter of species included in the Xylem Database was determined on phloem cross-section images downloaded from the Xylem Database (Schweingruber and Landolt 2010). On these images, we measured the diameter of at least 30 sieve elements to obtain mean values for each species. Xylem vessel diameter values were extracted from the sample descriptions in the Xylem Database (Schweingruber and Landolt 2010). For ∼10% of species, for which no explicit value is given in the descriptions, diameters were measured using the database's images of stem wood cross-sections.

Statistical analyses and artificial neural network

Pairwise Pearson Product Moment correlations between the growth rate and sieve element and vessel diameters were performed in SigmaPlot 12.5 (Systat Software). Partial Mantel tests were conducted in FStat 2.9.4 (Goudet 2003) with growth rate coded as dependent variables and sieve element diameters, vessel diameters and evolutionary distances as independent variables. Prior to the analyses, growth rate, sieve element diameter and vessel diameter were transformed to Euclidian distance matrices. For the liana species, we calculate the evolutionary distance matrix using the package *Ape* (Paradis et al. 2004) implemented in R based on two molecular markers (*ndh*F and *pep*C; see Lohmann 2006) and the Kimura80 substitution model. For all other species, we aligned sequence data of the marker *rbc*L obtained from the Barcode of Life Data System (Ratnasingham and Herbert 2007) and calculated the evolutionary distance matrices in MEGA X (Kumar et al. 2018). We also analyzed the correlation coefficients of the relationship between sieve element diameter and growth rate (and vessel diameter and growth rate) from alternative subsets of the 242 species aged above 5 years old to investigate differences across growth forms (dwarf shrubs, lianas, shrubs and trees), biomes (arid, hill, Mediterranean, mountain and subtropical) and the botanical families with representation by at least 20 species (Ericaceae, 25 species; Fabaceae, 27 species and Rosaceae, 31 species).

The artificial neural network was implemented using Python 3 in the Orange environment (Demsar et al. 2013). The training data were pre-processed by imputing missing values with averages. This procedure was only relevant for ∼10% of species that lacked data for some climate-related variables. Normalization did not improve prediction accuracy and was, therefore, not employed. The artificial network consisted of two layers with 10 neurons each, activated via a rectified linear unit (ReLU). As solver, we used Adam, a stochastic gradient-based optimizer with a maximal number of iterations of 200. The dataset used for training and evaluation contained 242 (plants above 5 years) or 322 (plants above 2 years) samples. Each sample corresponded to one species for which data on the relevant variables was extracted from the Xylem Database. The stem diameter growth rate served as the target variable. Other variables that were considered included sieve element and vessel diameters, age, altitude, growth form, latitude, longitude, mean annual precipitation, mean annual temperature, mean temperature in July, mean temperature in January, soil water content and vegetation type.

Training efficiency was evaluated after 20 train/test cycles. In each cycle, the samples were randomly assigned to the training or testing dataset. The training set size was 80% of samples, and the test set size was 20%. Prediction accuracy was evaluated according to the proportion of the variance in the target variable that was predictable from the independent variables, which is indicated by the R^2 value.

Linear regressions were implemented in Excel (Version 2016; Microsoft, Redmond, WA, USA).

Results

Growth rate associations in lianas

Sieve element and vessel diameter of 25 liana species of the tribe Bignonieae (Figure 1a) were found to positively correlate with growth rate (Figure 1b and Table 1). We evaluated the relative contributions of sieve element and vessel diameter to growth rate using a partial Mantel test (Omelka and Hudecova 2013) while correcting for phylogenetic relatedness.

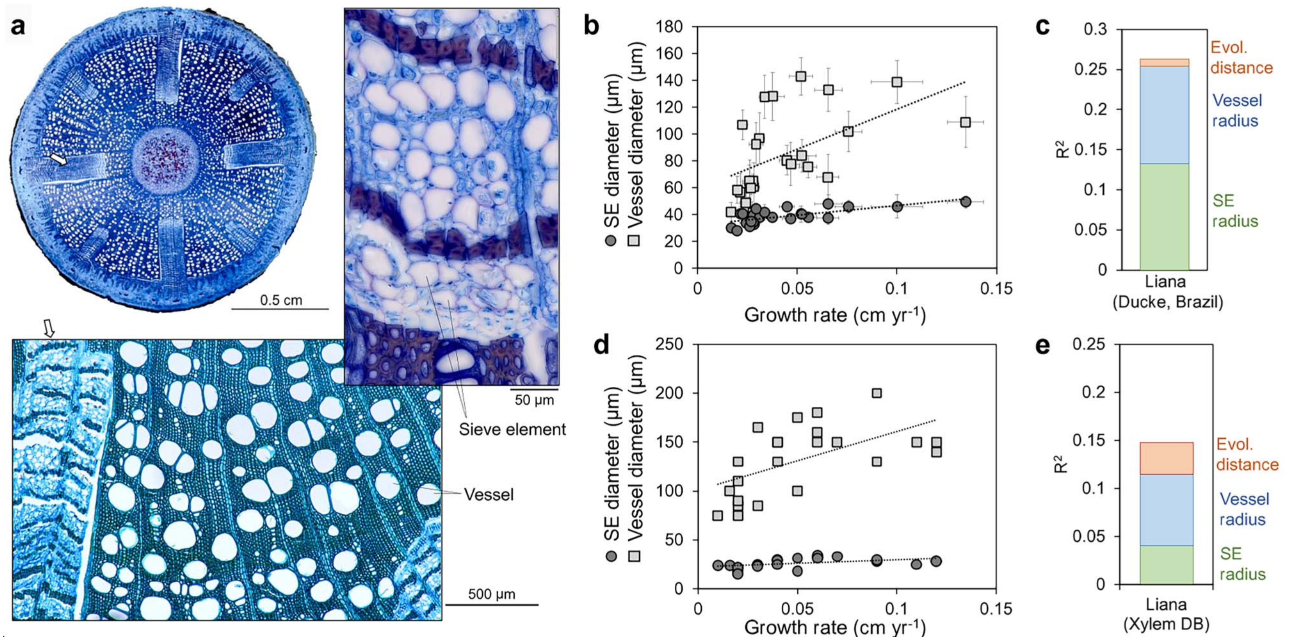

Figure 1. Relationship between sieve element and vessel diameters with stem growth rates in lianas. (a) *Anemopaegma robustum* stem cross-section showing magnifications of the wood (lower image) and inner bark tissues (right image). Images like these were used to determine sieve element and vessel diameters. Arrows indicate phloem wedges typical of Bignonieae (Bignoniaceae) lianas. (b) Sieve element (SE) and vessel diameters plotted against stem diameter growth rates of lianas growing at the Ducke Forest Reserve (Amazonas, Brazil). (c) Cumulative percentage of explained variance in growth rates based on three predictor variables (i.e., sieve element diameter, vessel diameter and phylogenetic relatedness), inferred from R^2-values of model terms in partial Mantel tests for lianas sampled at the Ducke Forest Reserve. (d) Sieve element (SE) and vessel diameters plotted against growth rates with data obtained through the Xylem Database. (e) Cumulative percentage of explained variance in growth rates based on sieve element diameter, vessel diameter and phylogenetic relatedness of lianas available from the Xylem Database (Xylem DB). Regression lines in (b) and (d) indicate significant correlation ($P < 0.05$). $N = 25$ (b, c) and 23 (d, e). Relevant statistics are provided in Tables 1 and 2.

Our approach allowed us to tease apart the effect of phloem and xylem conducting cell anatomy to species-specific variation in growth rate. The three variables (i.e., sieve element diameter, vessel diameter and phylogenetic relatedness) explained ~26% of the growth rate variation (see R^2-value in Figure 1c). We detected positive associations with similar explanatory power between the growth rate and both the sieve element and vessel diameter (Figure 1c and Table 2).

We compiled a second dataset for 23 liana species belonging to various plant families from the Xylem Database (Schweingruber and Landolt 2010). In this case, growth rates represented the average growth ring width. We detected a positive correlation of sieve element and vessel diameter with growth rate (Figure 1d and Table 1). The partial Mantel test also showed significant associations (Table 2), but with lower explanatory power than for the results from the Amazonian rainforest reserve (Figure 1e). Our results show a significant association of vessel and sieve element diameters with growth rate across liana species, independent of how the growth rate data were gathered.

Growth rate association across woody plants

We expanded our focus from lianas to woody plants of various growth forms and from different biomes by utilizing the Xylem Database (Figure 2a). The primary dataset (plants above 5 years of age) contained 242 woody plant species. Like for the liana species (Figure 1), sieve element diameter and vessel diameter positively correlated with growth rates for woody plants in general (Figure 2b, c and Table 1). The partial Mantel test indicated an explanatory power of growth rate variations to ~20% (Figure 2d), with positive associations of both vessel and sieve element diameter with growth rate (Table 2).

Climate- and growth type-dependence of associations

To further test if the association between sieve element diameter and growth rate is as strong as between vessel diameter and growth rate among different growth forms, biomes and families, we analyzed the relationship of correlation coefficients obtained in alternative subsets of the 242 species of the primary dataset. Generally, growth rate correlations of similar strength were observed for sieve element and vessel diameters (Figure 3 and Table 1).

Among growth forms, notable differences were observed for dwarf shrubs. In this case, no significant correlation was found between growth rate and vessel diameter, although the growth rate was strongly correlated with sieve element diameter (Figure 3 and Table 1). Interestingly, the opposite pattern was observed for trees (Figure 3 and Table 1). Shrubs and

Table 1. Pearson correlation statistics of the relationship between diameter growth rate and different variables (sieve element (SE) diameter, vessel diameter or predicted growth rate). *P*-values < 0.05 are highlighted in bold.

Variable	Characteristic	*R*	*P*	*n*	Graphical representation
SE diameter	Lianas	0.69	**0.0008**	25	Figure 1b
Vessel diameter	Lianas	0.74	**0.0002**	25	Figure 1b
SE diameter	Lianas	0.493	**0.019**	23	Figure 1d
Vessel diameter	Lianas	0.571	**0.005**	23	Figure 1d
SE diameter	—	0.381	**0.0001**	242	Figure 2b
Vessel diameter	—	0.399	**0.0001**	242	Figure 2c
SE diameter	Dwarf shrubs	0.423	**0.00019**	74	Figure 3
Vessel diameter	Dwarf shrubs	0.224	0.0567	74	Figure 3
SE diameter	Shrubs	0.32	**0.00041**	119	Figure 3
Vessel diameter	Shrubs	0.531	<**0.00001**	119	Figure 3
SE diameter	Trees	0.273	0.119	35	Figure 3
Vessel diameter	Trees	0.461	**0.006**	35	Figure 3
SE diameter	Lianas	0.494	**0.019**	22	Figure 3
Vessel diameter	Lianas	0.571	**0.005**	22	Figure 3
SE diameter	Mountain	0.599	<**0.00001**	55	Figure 3
Vessel diameter	Mountain	0.465	**0.00039**	55	Figure 3
SE diameter	Hill	0.48	**0.00003**	69	Figure 3
Vessel diameter	Hill	0.35	**0.00346**	69	Figure 3
SE diameter	Arid	0.522	**0.0152**	22	Figure 3
Vessel diameter	Arid	0.496	**0.0222**	22	Figure 3
SE diameter	Mediterranean	0.389	**0.0021**	61	Figure 3
Vessel diameter	Mediterranean	0.428	**0.0006**	61	Figure 3
SE diameter	Subtropical	0.321	0.156	22	Figure 3
Vessel diameter	Subtropical	0.472	**0.031**	22	Figure 3
SE diameter	Rosaceae	0.609	**0.000351**	31	Figure 3
Vessel diameter	Rosaceae	0.473	**0.0083**	31	Figure 3
SE diameter	Fabaceae	0.543	**0.0041**	27	Figure 3
Vessel diameter	Fabaceae	0.589	**0.0015**	27	Figure 3
SE diameter	Ericaceae	0.502	**0.0125**	25	Figure 3
Vessel diameter	Ericaceae	0.681	**0.00025**	25	Figure 3
Predicted growth rate	—	0.77	<**0.00001**	322	Figure 4c

Table 2. Results of partial Mantel tests using stem diameter growth rate as the dependent variable and sieve element (SE) diameter, vessel diameter and evolutionary distances as independent predictive variables. *P*-values < 0.05 are highlighted in bold. Xylem DB, Xylem Database.

Dataset	Independent variable	*R* (partial)	*P* (SS)	*n*	Graphical representation
Lianas (Ducke, Brazil)	SE diameter	0.341	**0.0015**	25	
	Vessel diameter	0.321	**0.016**	25	Figure 1c
	Phylo. relatedness	0.056	0.734	25	
Lianas (XylemDB)	SE diameter	0.199	**0.045**	23	
	Vessel diameter	0.282	**0.017**	23	Figure 1e
	Phylo. relatedness	0.174	0.075	23	
All growth forms (XylemDB)	SE diameter	0.278	**0.002**	242	
	Vessel diameter	0.201	**0.0085**	242	Figure 2d
	Phylo. relatedness	0.157	0.077	242	

lianas showed correlations of similar strength for both variables (Figure 3 and Table 1).

The comparison of correlation coefficients between different biomes indicated a stronger association of growth rate and vessel diameter in the warm, arid, subtropical and Mediterranean biomes, than in cooler mountain and hill biomes (Figure 3 and Table 1). In contrast, sieve element diameter showed stronger associations with growth rate for plants from the mountain and hill biomes than for plants from the Mediterranean and subtropical biomes (Figure 3 and Table 1).

All three families that were well-represented in the dataset, the Ericaceae, Fabaceae and Rosaceae, showed significant

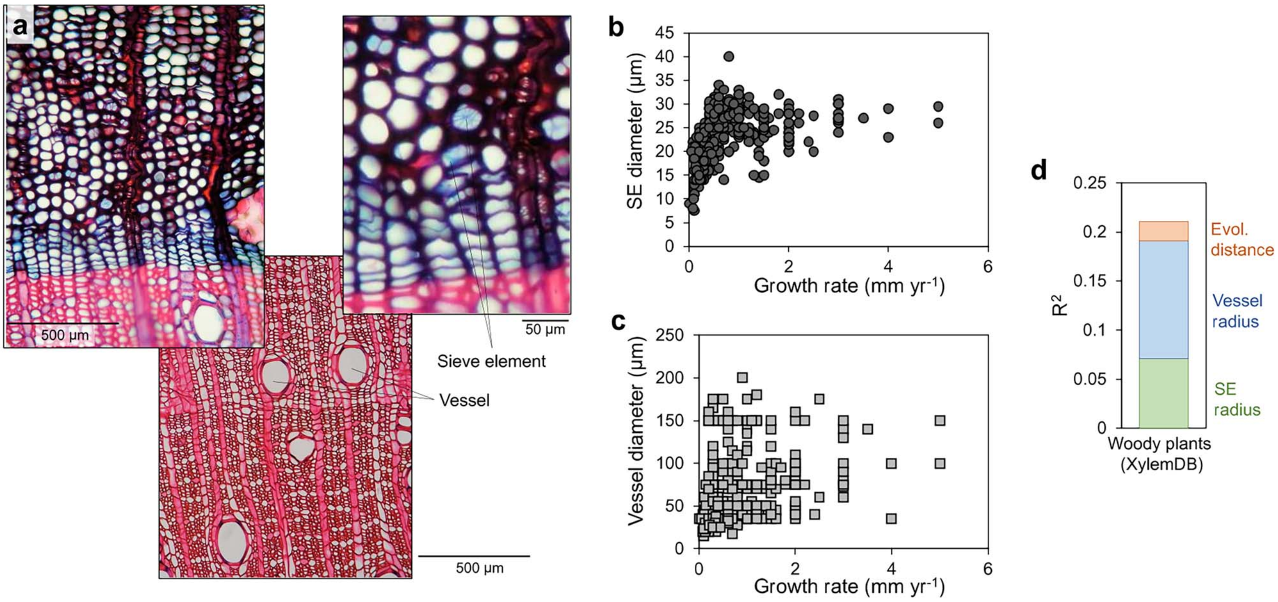

Figure 2. Relationship of sieve element and vessel diameters with stem growth rates across growth forms. (a) *Diospyros kaki* stem cross-sections. The right image shows a magnified view of the cambium and phloem. The lower image shows the xylem. Such images were used to determine the sieve element and vessel diameters. (b, c) Sieve element (SE) (b) and vessel (c) diameter plotted against stem diameter growth rates of 242 mature herbaceous plants, shrubs, lianas and trees. (d) Explained variance in growth rate for the 242 plants aged above 5 years old. Relevant statistics are provided in Tables 1 and 2. Xylem DB, Xylem Database. Images are reproduced with permission from F. Schweingruber and W. Landolt, Swiss Federal Institute for Forest, Snow and Landscape Research WSL.

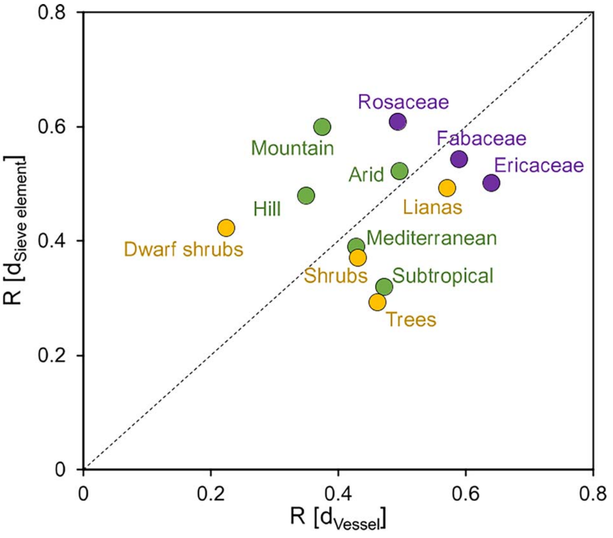

Figure 3. Pearson correlation coefficients describing the standardized covariance between growth rate and sieve element diameter ($d_{\text{Sieve element}}$) and vessel diameter (d_{vessel}). Different subsets of data were defined according to specific growth forms (yellow), biomes (green) and three well-represented families (purple). The respective values of *R*, *P* and *n* are provided in Table 1.

correlations between conducting cell diameters and growth rates (Figure 3 and Table 1). However, the Rosaceae differed from the Ericaceae in the relative strength of associations of sieve element and vessel diameters (Figure 3 and Table 1). This difference is not aligned with differences between the dwarf shrub and tree growth forms and between the mountain/hill and subtropical biomes described above. The prevailing growth form in our Ericaceae species was dwarf shrub (60% of species, no trees). However, although the combined species of all families of this growth form showed a stronger growth rate association with sieve element diameter, the Ericaceae showed a stronger association with vessel diameter (Figure 3 and Table 1). Similarly, the Rosaceae showed a stronger association with sieve element diameter even though most of its species are trees (48%, only 3% dwarf shrubs), which was more strongly associated with vessel diameter when considering species from all families (Figure 3 and Table 1). Differences between the subtropical and hill/mountain biomes did not influence the difference between Rosaceae and Ericaceae, as both families contain similar proportions of species in these biomes (Rosaceae: 74% hill/mountain, 13% subtropical and Ericaceae: 68% hill/mountain, 8% subtropical).

An artificial neural network to predict growth rates

After establishing the link between vessel and sieve element diameters and stem diameter growth rates, we aimed to harness the association's potential to predict growth rates by combining the variables in an artificial neural network. The highest prediction accuracy was achieved with a neural network consisting of two hidden layers with 10 neurons each and all variables except soil water content and mean temperature in July (Table 3). The prediction accuracy increased when the sample number was increased to 322 by including plants with ages between 2 and 5 years (Table 3), reaching an R^2 value of 0.36 (Figure 4a). The

Table 3. Parameters indicating the results of artificial neural network training. MSE, means square error; RMSE, root mean square error; MAE, mean absolute error; R^2, coefficient of determination.

Data	MSE	RMSE	MAE	R^2	*n*	Graphical representation
>5 years	0.348	0.590	0.397	0.338	242	
All	0.431	0.657	0.455	0.359	322	Figure 4a

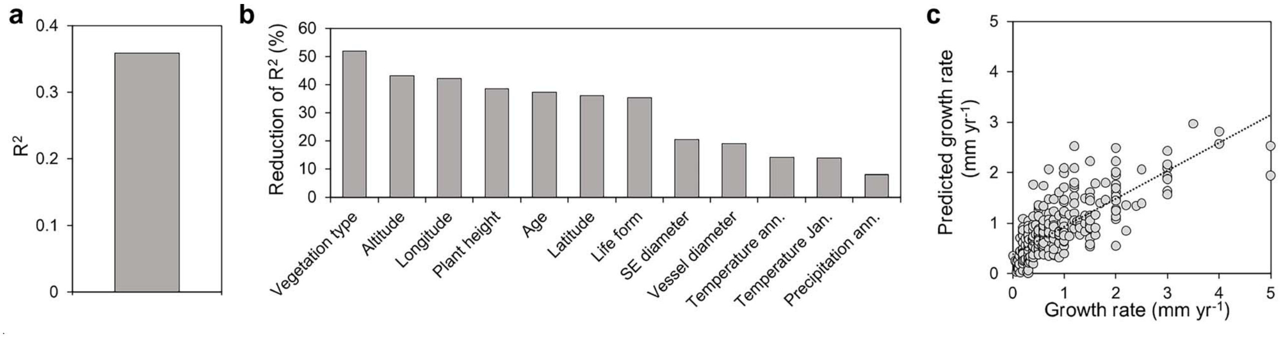

Figure 4. Employment of an artificial neural network to predict stem diameter growth rates. (a) The prediction coefficient R^2 indicates neural network prediction accuracy. (b) Importance of input variables for the neural network's prediction accuracy is shown as the reduction of R^2 when the respective variable is removed from the model. (c) Growth rates predicted by the artificial neural network for the samples of the training data set composed of 322 samples plotted against experimentally determined growth rates. Regression lines were fitted for significantly correlated variables ($P < 0.05$). Statistical parameters are provided in Tables 1 and 3.

reasoning behind the inclusion of younger plants was that the non-linearity of the artificial neural network approach enables range-dependent associations of variables.

To evaluate the relative importance of variables for prediction accuracy, we observed the effect of removing a single variable. Vegetation type was the variable whose removal had the strongest negative effect on prediction accuracy, followed by altitude and longitude (Figure 4b). We observed a strong positive correlation when plotting predicted growth rates against measured growth rates for the 322 plants ($R = 0.77$; Figure 4c and Table 1).

Discussion

Our results identified an association between conducting cell diameters of both phloem and xylem with growth rates of woody plant species. The Mantel tests indicated a similar explanatory power of stem diameter growth rates for sieve element and vessel diameters. As indicated by R^2 values in the partial Mantel tests, the total explanatory power of vessel and sieve element diameters was relatively low, which is presumably because parts of the growth rate variance reflect variation in photosynthetic traits (e.g., specific leaf areas) or leaf nitrogen content (Díaz et al. 2016).

Vessel diameter has long been recognized as a key indicator of woody plant performance (Poorter et al. 2010, Carrasco et al. 2014, Hietz et al. 2017). Phloem sieve element anatomy in leaves has previously been linked to the carbohydrate export capacity in some herbaceous and tree species (Cohu et al. 2013, Liesche et al. 2021). Moreover, sieve element diameter was shown to correlate with tree height (Liesche et al. 2017, Savage et al. 2017). The association with stem growth rates shown here strengthens the view of phloem conductivity being relevant for woody plant growth. This view is supported by experiments in which sieve element conductivity was artificially reduced, as this resulted in reduced stem diameter growth (De Schepper et al. 2011, Lopez et al. 2015). Even without detailed mechanistic insight, our results show a potential value of using measurements of phloem anatomy (sieve element diameters) to guide tree breeding efforts (Franklin et al. 2014).

We detected differences in the strength of association between vascular anatomy and growth rates between the liana, tree and dwarf shrub growth forms (see Figure 3). Accordingly, measurements of sieve element diameters might improve ecological models by widening the considered trait space and helping to capture a wider range of plant growth strategies (Li et al. 2015, Díaz et al. 2016). A robust association between growth and xylem anatomy, and tight scaling of xylem and phloem architectures has been reported for lianas (Carlquist 1988, Angyalossy et al. 2012). The potential influence of phylogenetic history could not be conclusively evaluated with our data from only three well-represented families. The relevance of phylogeny cannot be excluded as inter-family differences in scaling relationships were not explained by other factors such as growth type or biome.

Recent years have seen increasing applications of artificial neural network-based approaches, for example, for predicting crop yield (Silva et al. 2019, van Dijk et al. 2020). A first promising attempt to use artificial neural networks to predict growth rates has been made for greenhouse-grown *Ficus benjamina* trees (Alhnaity et al. 2019). Our results highlight that artificial neural networks can greatly contribute to predicting growth rates in woody plants. The inclusion of sieve element diameter, as well as xylem vessel diameter, increased the prediction accuracy. Both variables were not among the ones with the highest relative value. However, the differences between variables were generally small. Thereby, our analysis illustrates the importance of including a wide range of variables to improve prediction accuracy.

Our study raises new interesting questions that should be addressed in subsequent investigations. To understand the physiological link between sieve element conductivity and growth dynamics, future studies are needed to explore the contributions of the structure and abundance of pores connecting consecutive sieve elements, phloem sap viscosity, carbohydrate content, the cross-sectional area of active sieve elements and hydrostatic pressure gradients, all of which can affect rates of phloem transport (Jensen et al. 2016). Moreover, measurements of phloem anatomy and stem diameter growth during plant development might help answer the question whether sieve element size is a reason for a certain growth rate or its consequence. Further research is also needed to identify the tradeoff associated with larger sieve elements. The working hypothesis could be that the nature of sieve elements as living cells that have to be maintained by their neighboring companion cells (van Bel et al. 2002) causes costs that rise with increasing sieve element size. The transport of proteins, lipids and energy carriers across the sieve element companion cell interface might become a limiting factor (van Bel and Koblauch 2000). This hypothesis is corroborated by the observation of two companion cells accompanying especially long and wide sieve elements (Pace et al. 2015).

To a certain degree, sieve element dimensions might also be related to xylem vessel dimensions because of their shared developmental program. The same signals, such as the hormone cytokinine, can influence the development of both cell types (Nieminen et al. 2015). However, cases of independent development, for example in response to different environmental conditions, are well known (e.g., Blagitz et al. 2021).

Verifying the hypothesis that the association of vessel and sieve element diameters with growth rates is stronger in certain growth forms requires collecting data on all relevant variables for species with different growth forms at the same site. Such a study would help to define principal differences in resource allocation between plant functional types (Wyka et al. 2013). The inclusion of additional variables could further improve the artificial neural network for growth rate predictions. These could be variables that were previously shown to correlate with diameter growth rates, such as a tree's rank in a forest stand and variables related to tree biomass (Ishihara et al. 2016), as well as variables related to leaf architecture and photosynthesis (Qi et al. 2021). The accuracy of the artificial neural network would also benefit from a larger training dataset covering a wider range of biomes.

In conclusion, we showed that phloem sieve element diameter in the stems of woody plants is associated with plant growth rate, similar to the previously known association of xylem vessel diameter and growth rate. Including sieve element and xylem vessel diameters among other variables in an artificial neural network showcases the potential of such an approach for the accurate prediction of woody plant growth.

Authors' contributions

J.L. conceived the project. Y.T., S.Y. and J.L. assembled the dataset and conducted the association analysis. M.R.P., C.S.G. and A.N. collected samples and made anatomical measurements. C.S.G. and A.N. measured growth rates. A.Z., L.G.L. and S.Y. constructed the phylogenetic trees. M.P. devised statistical tests. Y.T. and J.L. conducted the artificial neural network training and analysis. All authors contributed to the writing of the manuscript.

Data availability statement

All processed data will be published as part of this study. Relevant raw data can be obtained from public databases (Schweingruber and Landolt 2010) or will be provided by the corresponding author upon request.

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Conflict of interest statement

The authors declare no competing interests.

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