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Software note

Modelling seasonal dynamics of secondary growth in R

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The monitoring of seasonal radial growth of woody plants addresses the ultimate question of when, how and why trees grow. Assessing the growth dynamics is important to quantify the effect of environmental drivers and understand how woody species will deal with the ongoing climatic changes. One of the crucial steps in the analyses of seasonal radial growth is to model the dynamics of xylem and phloem formation based on increment measurements on samples taken at relatively short intervals during the growing season. The most common approach is the use of the Gompertz equation, while other approaches, such as general additive models (GAMs) and generalised linear models (GLMs), have also been tested in recent years. For the first time, we explored artificial neural networks with Bayesian regularisation algorithm (BRNNs) and show that this method is easy to use, resistant to overfitting, tends to yield s-shaped curves and is therefore suitable for deriving temporal dynamics of secondary tree growth. We propose two data processing algorithms that allow more flexible fits. The main result of our work is the *XPSgrowth()* function implemented in the radial Tree Growth (rTG) R package, that can be used to evaluate and compare three modelling approaches: BRNN, GAM and the Gompertz function. The newly developed function, tested on intra-seasonal xylem and phloem formation data, has potential applications in many ecological and environmental disciplines where growth is expressed as a function of time. Different approaches were evaluated in terms of prediction error, while fitted curves were visually compared to derive their main characteristics. Our results suggest that there is no single best fitting method, therefore we recommend testing different fitting methods and selection of the optimal one.

Keywords: artificial neural networks, cambium, generalized additive model, Gompertz function, growing season, intra-annual time series

Introduction

Growth of woody plants is related to various ontogenetic and environmental drivers (Babst et al. 2019), resulting in a cyclic increase in volume of roots, stem and branches

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(Lacointe 2000). The most common method to trace growth of woody species is by measuring the annual tree ring, commonly called secondary growth, produced by the vascular cambium (Nieminen et al. 2015). Monitoring the dynamics of secondary growth assesses carbon sequestration during the growing season (Rossi et al. 2014), elucidates the response of trees to environmental signals (De Micco et al. 2019), in particular allowing the assessment of vascular tissue adjustment that results from weather events during the growing season (Gričar et al. 2015, Ziaco et al. 2018). Changes in radial growth affect forest productivity, wood properties and timber quality, making intra-annual investigations of xylem and phloem formation a strategic tool in the forest sciences (Zhang et al. 2020). The radial growth of trees comprises xylem (wood) and phloem. The latter component is neglected or significantly less explored despite its importance in explaining the relationships between water, carbon and tree growth (Deslauriers et al. 2017). Xylem and phloem formation is asymmetric through the growing season. Increments in the xylem are the result of an accumulation of cambial cells produced within a growing season according to a well-known pattern: an initial positive exponential phase followed by gradual slowing in late summer (Cuny et al. 2013). The initial phloem consists of 1–2 overwintering cells formed by the cambium in the previous autumns, differentiating gradually in the following spring. As a result, initial phloem growth rates are greater than those of xylem (Prislan et al. 2013, 2018).

One of the major challenges in intra-annual studies is to derive smoothed temporal dynamics of secondary growth, describing the temporal accumulation of cells, including the onset and end of cambial division. To do so, we combine annual patterns and short-term events involving xylem and phloem formation based on measurements (cell counting or width measurements) performed on samples taken at weekly or biweekly intervals (Gričar et al. 2022). The measurements are taken at a microscopic level, where xylem and phloem are distinguished from the cambial derivatives based on their larger radial diameters (Supporting information).

Assessing the temporal dynamics of secondary growth remains a challenge, especially if sampling does not capture the onset and cessation of cambium activity. Moreover, radial growth around the circumference is usually heterogeneous (Lupi et al. 2014), which prevents a reliable estimation of the end of xylem and phloem formation. For modelling purposes, estimations should include winter cambium dormancy prior to growth reactivation in spring, and after the cambial cessation in late summer. During the growing season, the model should reliably describe the accretion of xylem and phloem cells. Accordingly, the derived function is expected to be strictly monotone, with constant values prior to and after the end of cambial cell production. In addition, the same function should be flexible enough to appropriately capture the bimodal xylem growth often observed in Mediterranean climates (De Luis et al. 2007, Camarero et al. 2010), although bimodal growth has also been observed in other climates, such as the oceanic temperate climate in France (Michelot et al. 2012). Therefore, the choice of the fitting

algorithm plays an important role in deriving the temporal dynamics of secondary growth.

The Gompertz function is one of the most used sigmoid models (Tjørve and Tjørve 2017) and also a common approach for modelling xylem and phloem formation (Rossi et al. 2003). The disadvantage of this function is the need to select initial parameters, which are often not straightforward to set, especially for phloem, while for xylem, Rossi et al. (2003) provided guidelines. Moreover, the function often exhibits convergence problems when observations are highly variable. The Gompertz function seems less suitable for the modelling of phloem growth due to the high growth rates at the beginning of the growing season. In addition, the Gompertz function is unable to model bimodal growth. In the last decade, general additive models (GAMs) have been implemented to overcome the cons of the Gompertz function (Cuny et al. 2013). GAM is a semi-parametric extension of generalised linear models (GLMs) (Hastie and Tibshirani 2017), which allows for non-linearity and non-constant variance structures in the data (Guisan et al. 2002). In GAMs, linear terms are replaced by flexible additive functions combined with smooth components (Hastie and Tibshirani 2017). While more flexible GAMs can better fit wood formation data, they often fail to meet the desired constant behaviour prior to and after the growing season. In this context, the final model could exhibit negative increments. In the present study, we have tested a new approach for the analysis of xylem and phloem data involving artificial neural networks (ANNs), which are flexible, nonlinear brain-like structures (Lek and Guégan 1999). Among the different types of ANNs, we used a multilayer perceptron consisting of an input, a hidden and an output layer, and a backpropagation learning algorithm (Park and Lek 2016). The latter refers to a process, where input–output pairs are presented to the network, and weights are adjusted to minimize the error between network output and actual value (Lenard et al. 1999). We selected the ANNs based on the Bayesian regularisation algorithm (BRNN) (Pérez-Rodríguez et al. 2013), which prevents overfitting and usually results in a sigmoid-shaped function, corresponding to the observed patterns of xylem and phloem formation. In a preliminary exploratory phase (Supporting information), we tested different ANN algorithms, which can be auto-tuned with the R package caret (Kuhn 2008). Among these, BRNN produced the most accurate outputs and always yielded a sigmoid-shaped function. The BRNN method generally performs well in comparative studies (Kayri 2016, Fikret Kurnaz and Kaya 2018, Peters et al. 2019) and has been shown to be suitable for many ecological and environmental applications, such as tree height modelling (Skudnik and Jevšenak 2022), estimation of corn biomass from remote sensing data (Geng et al. 2021) and interpolation of missing aerosol data (Chen et al. 2020).

A specific software addressing the above-mentioned requirements is still lacking. For this reason, we have developed a new tool in R (<www.r-project.org>), which will further leverage the existing wood-anatomical R tools, such as CAVIAR (Rathgeber et al. 2018) and RAPTOR (Peters et al.

2018). In this study, the functionality of rTG is demonstrated using data on xylem and phloem formation, but the algorithms can be applied to data sets where growth is expressed as a function of time. In Supporting information, we also show examples of inferring temporal growth dynamics from dendrometers (Deslauriers et al. 2007).

The main objective of this software note is therefore to present the radial Tree Growth (rTG) R package and the core function *XPSgrowth()*. It incorporates different fitting methods (Gompertz, GAM and BRNN) for modelling xylem and phloem formation data, estimates the optimal parameters of the Gompertz function, and applies two data processing algorithms. The latter were developed 1) to insert zero observations at the beginning of a growing season, and 2) to force constant behaviour after the end of cambial cell production. The derived growth curves allow to study time-dependent secondary growth of woody species.

Description of the rTG R package

The radial Tree Growth (rTG ver. 1.0.1) R package was developed for deriving temporal dynamics of secondary tree growth, obtained from seasonal xylem and phloem widths or cell numbers. It is freely available under the GPL 3.0 license from CRAN and can be installed using the standard command >*install.packages("rTG")*. Alternatively, the most recent version may be installed from GitHub using the command >*install_github("jernejjevsenak/rTG")*. Users should use R ver. 3.5 (<www.r-project.org>) or newer to ensure complete functionality. In addition to basic R functions, it currently relies on six other R packages, namely brnn (Pérez-Rodríguez et al. 2013), ggplot2 (Wickham 2016), mgcv (Wood 2011) and knitr (Xie 2017), dplyr (Wickham et al. 2020) and magrittr (Bache and Wickham 2020). The rTG R package is based on the core function *XPSgrowth()* and two generic S3 functions, i.e. *plot()* and *summary()*.

The *XPSgrowth()* function

The *XPSgrowth()* function can be used to compare and select fitting methods or to apply a fitting method on data sets expressing intra-annual growth. To compare different fitting methods, users should prepare two data frames, one representing seasonal growth (e.g. xylem and/or phloem formation data), the other including the selected parameters of the methods to be compared. Both tables are related through common ID variables. In these demonstration examples, the selected ID variables were species, tissue, site, year and tree (Table 1). The parameters can be defined manually for each subject, or alternatively, users can apply uniform parameter values across different trees and years by specifying the function arguments related to each parameter. The parameters gom_a, gom_b and gom_k are initial parameter values used to fit the Gompertz function, where gom_a represents asymptote or ultimate limiting value, and gom_c is growth constant, while gom_b represents displacement on the x axis (Richards 1959). The *XPSgrowth()* function has

Table 1. The organisation of two required tables: (A) *data_trees* with selected ID variables and two additional variables: 'doy' represents day of a year, and 'width' is the target variable which usually expresses growth, such as the number of radial cells (conifers) or radial width in µm (broadleaves). (B) Data frame *parameters* consist of selected ID variables and specified parameter values for the considered fitting methods.

Tissue	Species	Site	Year	Tree	doy	width
(A) *data_trees*						
PHLOEM	FASY	PAN	2011	1	76	6.2
PHLOEM	FASY	PAN	2011	1	97	14.2
PHLOEM	FASY	PAN	2011	1	102	40.2
PHLOEM	FASY	PAN	2011	1	109	60.2
PHLOEM	FASY	PAN	2011	1	116	97
PHLOEM	FASY	PAN	2011	1	123	73.1
PHLOEM	FASY	PAN	2011	1	128	59.6
PHLOEM	FASY	PAN	2011	1	136	69.8
PHLOEM	FASY	PAN	2011	1	143	85
PHLOEM	FASY	PAN	2011	1	150	96.5
…	…	…	…	…	…	…

Tissue	Species	Site	Year	Tree	gom_a	gom_b	gom_k	brnn_neurons	gam_k	gam_sp
(B) *parameters*										
PHLOEM	FASY	PAN	2011	1	3000	1534	1052	2	8	0.5
PHLOEM	FASY	PAN	2011	2	3000	472	375	2	11	0.5
PHLOEM	FASY	PAN	2011	3	3000	537	348	2	10	0.5
PHLOEM	FASY	PAN	2011	4	3000	166	118	2	10	0.5
PHLOEM	FASY	PAN	2011	5	3000	2019	856	2	10	0.5
PHLOEM	FASY	PAN	2011	6	3000	2025	1389	2	10	0.5
PHLOEM	PCAB	PAN	2011	1	3000	2017	1243	3	10	0.5
PHLOEM	PCAB	PAN	2011	2	3000	2017	1243	3	10	0.5
PHLOEM	PCAB	PAN	2011	3	3000	2017	1243	3	10	0.5
PHLOEM	PCAB	PAN	2011	4	3000	–	–	3	10	0.5
…	…	…	…	…	…	…	…	…	…	…

more than 5000 pre-defined combinations of a, b and k initial values, which are usually used with xylem and phloem formation data, so users do not need to provide initial values, but only set the argument *search_initial_gom* to TRUE. In the table named *parameters*, there are three additional columns: brnn_neurons, gam_k and gam_sp. These neurons represent the number of neurons used in the BRNN method, with a smaller number representing a less flexible fit, while a higher number of neurons allows for more flexible models. For the xylem and phloem formation data used in this study, the optimal number of neurons was between 2 and 3. Finally, the parameters gam_k and gam_sp are used to determine the flexibility of the GAM approach. Both GAM parameters define the smoothing flexibility, with the gam_k parameter representing the number of basis functions, and the gam_sp smoothing parameter calibrating the overall complexity of the bounds allowed by gam_k (Hastie and Tibshirani 2017).

Example of workflow

Example data

To demonstrate the functionality of *XPSgrowth()*, we used xylem and phloem formation data from European beech *Fagus sylvatica*, Norway spruce *Picea abies* and pubescent oak *Quercus pubescens*) from Slovenia (Table 2). Microcores 2.4 mm in diameter were collected at 7–10 day intervals from March to October with the Trephor tool (Rossi et al. 2006). The microcores, containing phloem, cambium and at least the three youngest xylem rings, were taken in stems at 0.7–1.7 m above the ground following a helical pattern and separated by 3–5 cm to avoid wound effects. The microcores were fixed in a solution of ethanol, formalin and acetic acid (FAA) for 1 week. In the laboratory, anatomical cross sections of developing xylem and phloem tissues were prepared and analysed following the protocol described by Prislan et al. (2013) and Gričar et al. (2014).

Below is an example of an R script to fit the Gompertz, GAM and BRNN models to the data used in our study. The full R scripts for reproducing our main results can be found in the Supporting information.

Table 2. Example of xylem and phloem data used in our study.

Tree species	n	Site coordinates	Elevation	Year	Reference
Norway spruce *Picea abies*	6	Panška reka 46°00′N, 14°40′E	400 m	2011	Gričar et al. 2015
European beech *Fagus sylvatica*	6	Panška reka 46°00′N, 14°40′E	400 m	2011	Prislan et al. 2019
Pubescent oak *Quercus pubescens*	6	Podgorski Kras 45°33′N, 13°55′E	430 m	2017	Gričar et al. 2019

```
> library(rTG)
> data(parameters); data(data_trees)
> simulation_1 <- XPSgrowth(data_trees, parameters,
        ID_vars = c("Species", "Tissue", "Site", "Year", "Tree"),
        fitting_method = c("brnn", "gam", "gompertz"),
        search_initial_gom = TRUE, fitted_save = TRUE,
        add_zeros = TRUE, add_zeros_before = "min",
        post_process = TRUE)
> plot(simulation_1)
> summary (simulation_1)
```

Method selection and adding zeros prior to radial tree growth

The *XPSgrowth()* function fits all three methods at once or the subset of methods specified with the argument *fitting_methods*. Users can supply the parameters for the methods to be compared. To save all individual fitted curves into the current working directory, set the parameter *fitted_save = TRUE*. It is often the case that the onset of cambial cell production is missed and therefore the first measurements are greater than 0. In this context, nonlinear regressions have difficulty estimating the x intercept, which represents the onset of cambial cell production. We have therefore implemented an option to manually add zeros to early DOYs, which helps all methods to estimate the onset of cambial cell production and predict the dormancy period prior to the onset of cambial cell production. For this aim, set the argument *add_zeros* to *TRUE* and use the argument *add_zeros_before* to specify the DOY prior to which zeros are added. If *add_zeros_before = "min"* zeros will be added prior to the first observation for each year.

Post-processing algorithm

More flexible curves, such as those of GAM and BRNN have the advantage of modelling short-term changes in intra-seasonal radial growth trends, while the Gompertz function usually fails to do so. This is particularly important in terms of developing predictive models to simulate intra-seasonal wood and phloem formation. The disadvantage of flexible curves is the potential for negative increments, which are biologically meaningless. Therefore, we have developed and implemented a post-processing algorithm which converts negative increments into constant values. However, users must be aware that such corrections might not always be justified and result in incorrect conclusions regarding the dynamics of secondary tree growth. Therefore, such modifications should be applied with caution.

The algorithm compares subsequent predictions and finds negative increments. All negative increments at the beginning of the growing season are converted to 0, while negative increments after the growing season are converted to the maximal predicted value. To apply the post processing algorithm, use *post_process = TRUE*. Examples of corrected and non-corrected curves are given in Fig. 1.
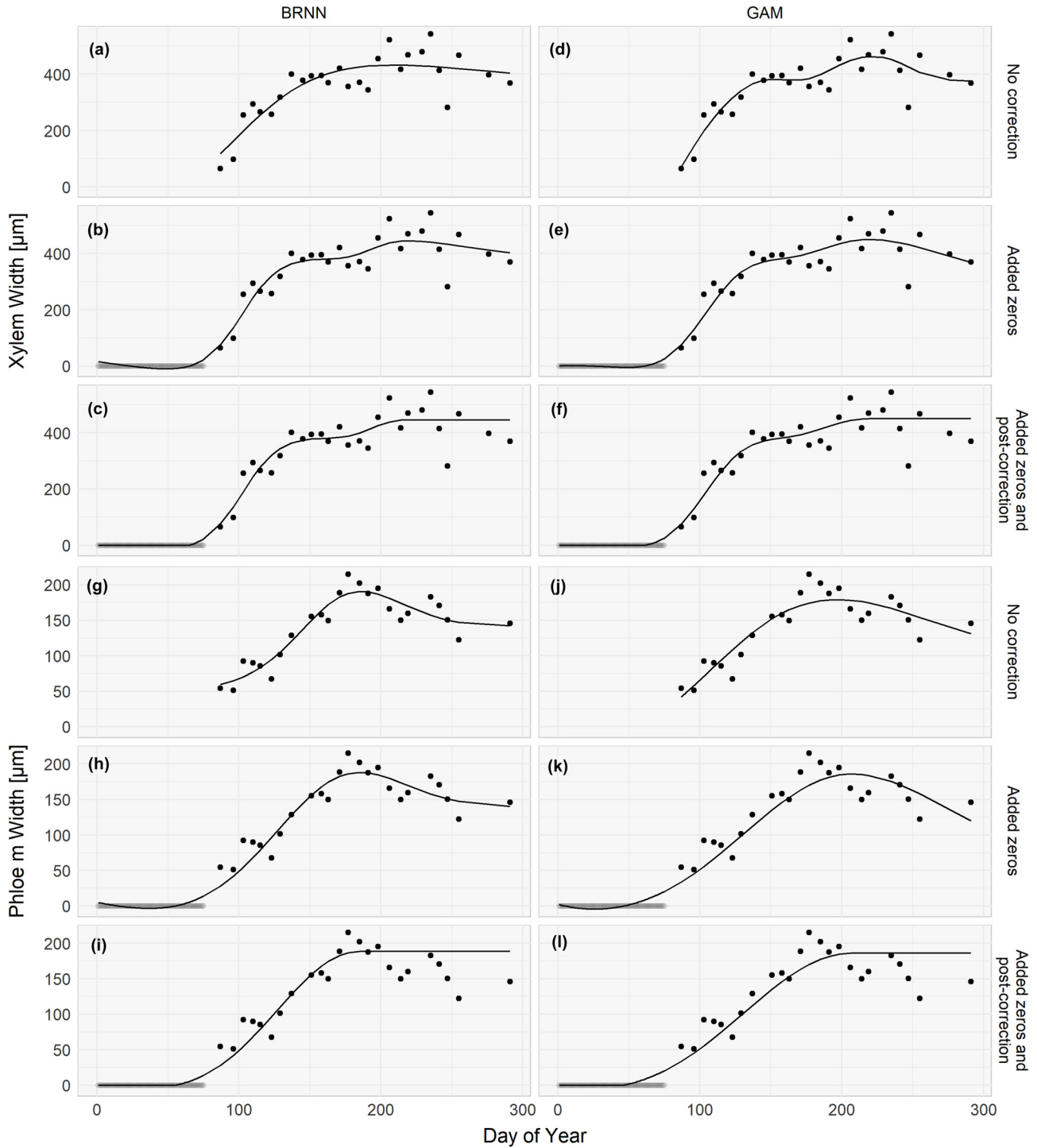
Figure 1. Comparison of modelling xylem (a–f) and phloem (g–l) seasonal growth using BRNN and GAM and different *XPSgrowth()* settings: no correction applied (a, d, g, j), added zeros at the beginning of the growing season (b, e, h, k) and added zeros and post correction of negative increments (c, f, i, l). Zero observations were added before day 75 and are depicted with less intensive colour.

Outputs of the *XPSgrowth()* function

A complete comparison of the three considered methods (Fig. 2) indicates that the differences between different approaches could be substantial. We have compared observed and predicted xylem and phloem width and calculated the root mean square error (RMSE), root relative mean square error (%RMSE) and coefficient of determination (R²) (equations are given in the Supporting information). On average, GAM and BRNN had lower errors than the Gompertz
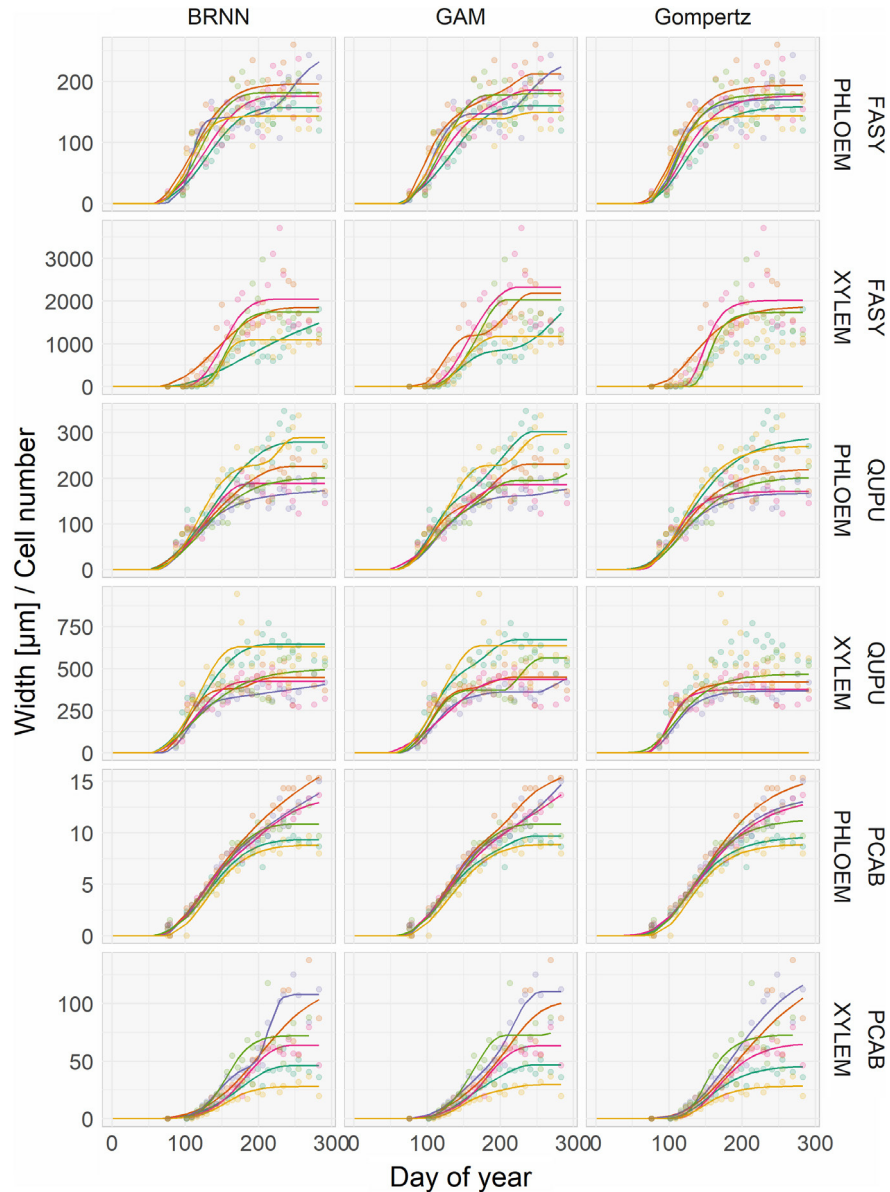
Figure 2. Fitted curves using the Gompertz, GAM and BRNN method. In some cases, we can observe unusual growth patterns, which are related to heterogeneous radial growth around the circumference or prolonged growing season and is not the result of wrong fitting.

function (Table 3). Finally, the output of *XPSgrowth()* is a list with three elements: 1) fitted and observed values of wood and phloem formation data for all trees, 2) results of the Gompertz function's initial values grid search and 3) a character vector of trees without successful grid search, if any.

Conclusions

We present the rTG R package, which was developed for deriving the temporal growth dynamics, and addresses some of the most common issues in ecology related to wood and phloem formation. The *XPSgrowth()* function can be used to compare three different fitting methods. In addition to

GAM and the Gompertz function, we have introduced a new approach based on the Bayesian regularised neural network (BRNN). Although Bayesian regularisation is one of the most effective methods to prevent overfitting (Burden and Winkler 2008, Okut 2016), too flexible parameters for BRNN (and also GAM) can lead to overfitting of the data. Therefore, users should always carefully evaluate the final fitted curves displayed using the generic *plot()* function. We have also introduced a post-processing algorithm, which corrects for the negative increments resulting from statistical errors that are biologically absurd in the process of wood formation. This algorithm can only be applied to the GAM and BRNN methods, because the Gompertz function is unable to provide negative increments. Our approach is not based on mathematical theory,

Table 3. The root mean square error (RMSE), relative root mean square error (%RMSE) and coefficient of determination (R^2) calculated for different fitting methods. See Supporting information for equation formulations.

Tissue	Species	Method	RMSE	%RMSE	R^2
PHLOEM	FASY	BRNN	25.02	18.53	0.75
PHLOEM	FASY	GAM	24.77	18.35	0.76
PHLOEM	FASY	GOMPERTZ	26.56	19.68	0.70
PHLOEM	PCAB	BRNN	0.66	8.86	0.97
PHLOEM	PCAB	GAM	0.64	8.55	0.97
PHLOEM	PCAB	GOMPERTZ	0.72	9.70	0.96
PHLOEM	QUPU	BRNN	27.62	16.90	0.84
PHLOEM	QUPU	GAM	26.77	16.38	0.86
PHLOEM	QUPU	GOMPERTZ	28.45	17.41	0.82
XYLEM	FASY	BRNN	364.38	36.88	0.72
XYLEM	FASY	GAM	373.85	37.84	0.76
XYLEM	FASY	GOMPERTZ	367.97	37.24	0.72
XYLEM	PIAB	BRNN	9.76	26.48	0.88
XYLEM	PIAB	GAM	9.81	26.60	0.89
XYLEM	PIAB	GOMPERTZ	10.39	28.20	0.87
XYLEM	QUPU	BRNN	81.72	20.65	0.72
XYLEM	QUPU	GAM	79.53	20.09	0.75
XYLEM	QUPU	GOMPERTZ	77.21	19.51	0.68

but is a pragmatic solution that converts negative increments to zero. The benefit of our approach is the possibility of using more flexible curves, which might better fit the data and capture the bimodal growth often observed under Mediterranean climates or growth limited conditions that occur during growing seasons (an example is given in the Supporting information). The derived relationships aim to better reflect the intra-annual dynamics of radial growth and can be used to investigate the timings of secondary growth, including the relative increments of trees, and compare individuals, sites and growing seasons. Further comparison of growth curves with daily climate may promote the development of new process-based or machine learning models that could simulate xylem and phloem formation at short time scales.

Our R package has potential applications in theoretical and applied ecology, where growth is monitored across time and space. These include seasonal height growth of woody plants (Dempewolf et al. 2017), radial growth obtained from other techniques (i.e. dendrometers) (Drew and Downes 2009), including applications in agriculture (i.e. monitoring temporal changes in fruit size) (Zadravec et al. 2014). We proposed reliable correction algorithms for deriving relative growth rates of nonlinear plant growth models (Paine et al. 2012).

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Author contributions

Jernej Jevšenak: Conceptualization (equal); Formal analysis (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Jožica Gričar**: Conceptualization (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal). **Sergio Rossi**: Supervision (equal); Validation (equal); Writing – review and editing (equal). **Peter Prislan**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fttdz08w4> (Jevšenak et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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