

IncrementR: Analysing height growth of trees and shrubs in R

Jakub Kašpar^{a,b}, Jan Tumajer^{a,*}, Václav Trembl^a

^a Charles University, Faculty of Science, Department of Physical Geography and Geoecology, Albertov 6, 12843 Prague, Czech Republic

^b The Silva Tarouca Research Institute for Landscape & Ornamental Gardening, Department of Forest Ecology, Lidická 25-27, 60200 Brno, Czech Republic



ARTICLE INFO

Keywords:

Apical growth
Dendrochronology
Eccentricity
Primary growth
Serial sectioning
Stem taper

ABSTRACT

Dendrochronology mostly deals with secondary (radial) growth and attention to primary (height) growth has so far been limited. However, tree-ring widths might not adequately represent stem volume increments, net primary productivity and the size of the tree stem carbon sink. The main reason for the prevailing focus on radial growth is that establishing height growth chronologies requires time-consuming and destructive methods. However, for certain ecological applications, less laboriously acquired data on height growth averaged over several successive years are satisfactory. Here we present an R package that contains a set of tools for the analysis of height growth. The tools have been developed for input data of tree-ring widths extracted from series of successive stem height levels. Tree-ring widths ideally represent four directions in each cross section to capture potential changes in stem eccentricity between various height levels. The main computed parameters provided by the package include height growth along the stem, changes of stem eccentricity and stem taper. Accurate determination of average height growth depends on the correct estimation of the number of tree rings at different stem height levels, which might be complicated by missing rings in off-pith cores. The presented package therefore also contains functions implementing common procedures for the estimation of the number of missing tree rings near to the pith. Most outputs can be visualized graphically. The package is useful for estimating height growth in ecological and dendrogeomorphological studies, especially in situations where both primary and secondary growth is influenced by different environmental factors. It is also useful for analysing tree-ring chronologies assembled using serial sectioning, which typically applies to shrubs.

1. Introduction

Dendrochronology traditionally deals with radial (secondary) growth as a sensitive environmental archive with annual resolution (Speer, 2010). Whereas radial growth is extremely important for the development of conductive and supportive wood elements, primary (height or apical) growth is important too, since it provides trees with a competitive advantage against surrounding vegetation. Chronologies of height growth have proved to be well correlated with climatic variables (Salminen and Jalkanen, 2005; Salminen et al., 2009; Lindholm et al., 2009), in some cases even better than chronologies of tree-ring widths (McCarroll et al., 2003). From an ecological perspective, height growth is highly important in temperature-limited environments, where it determines whether a woody plant attains a tree stature or not (Paulsen et al., 2000; Körner, 2012). Height growth can also be limited by environmental variables other than radial growth (Gamache and Payette, 2004). Compared to radial growth, height growth is usually more affected by weather in the season preceding the tree-ring formation year because the shoot growth structure is established during bud formation

in the previous summer whereas radial growth is mostly affected by conditions in the year of ring formation (Pallardy, 2008). Moreover, precise information on stem allometry, acquired through coupled radial and height growth analysis, can improve the estimation of stem biomass and can be useful for estimating the plant carbon budget (Babst et al., 2014; Klesse et al., 2016).

Just as in trees, height or apical growth in shrubs is considered an important variable indicative of growth dynamics (Myers-Smith et al., 2015; Weijers et al., 2018). The recent expansion of shrubs in the Arctic was related to infilling of existing patches by increased lateral (= apical) growth of prostrate and decumbent shrubs (Myers-Smith et al., 2011). Chronologies of shrub height growth are therefore able to reveal the factors which limit the expansion of shrubs (Pajunen, 2009; Buchwal et al., 2013; Paradis et al., 2016).

In comparison with radial growth, however, height growth is less investigated by dendrochronologists. The main reasons for the scarcity of height growth studies are the more laborious techniques necessary for the construction of a height increment chronology. Annually resolved height growth chronologies can be based on measuring distances

* Corresponding author.

E-mail address: tumajerj@natur.cuni.cz (J. Tumajer).

<https://doi.org/10.1016/j.dendro.2018.11.001>

Received 29 March 2018; Received in revised form 3 October 2018; Accepted 2 November 2018

Available online 03 November 2018

1125-7865/ © 2018 Elsevier GmbH. All rights reserved.

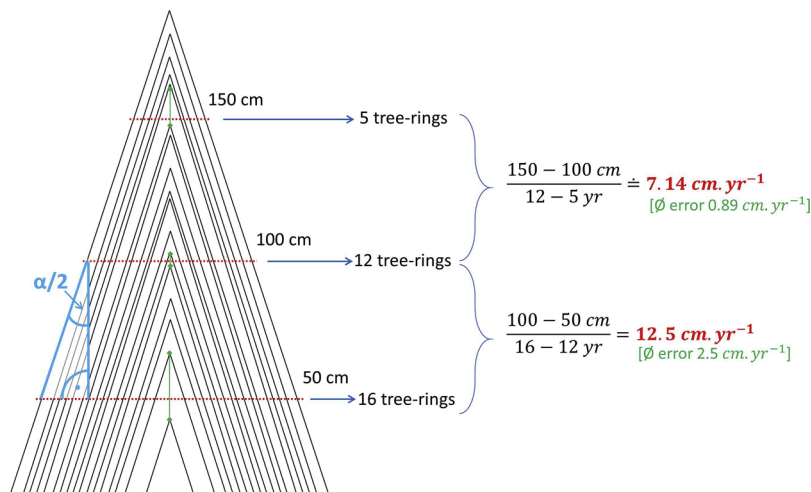


Fig. 1. Constructing an interpolated height growth time series by coring the tree stem at different height levels (red dotted lines) and counting the number of their tree rings. Errors in estimates (overestimates) of mean height growth between coring levels originate from the unknown position of the coring levels between two consecutive whorls (green vertical lines). α - stem taper angle (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

between successive well-detectable whorls of some species (e.g. *Pinus sylvestris*, Pensa et al., 2005; Lindholm et al., 2009; Jansons et al., 2013) or on tangential sections through stems, which are laborious to obtain (Pensa et al., 2005; Salminen et al., 2009). For many applications employing height growth as a parameter of tree vitality and tree response to environmental factors, the height growth time series with annual resolution are not necessary and coarser temporal resolution is satisfactory (Ivancich et al., 2012; Šenfeldr et al., 2014; Kašpar et al., 2017). Such series can be created by coring stems at (regular) height intervals and counting tree rings at each height level (Fig. 1). A similar approach, called ‘serial sectioning’, is commonly used when studying the growth of shrubs (Myers-Smith et al., 2015).

Computation of height growth by the means of serial sections or cores taken at regular intervals along a stem is suitable mainly for trees and shrubs with low height increments to minimize the overestimation of height growth (Fig. 1). For instance, the true velocity of height growth between the first and second coring level in Fig. 1 is lower than estimated, mainly because the tree reached the height of 50 cm not at the age of 2 years, but already at approx. 1.4 years; put differently, the tree took 0.6 of a year longer to grow from 50 to 100 cm in height. This overestimation is caused by the unknown position of both lower and higher coring levels between whorls; it could therefore take up to two years longer to grow from one level to the next.

Besides height growth determination, ring-width data sampled from successive sections along the stem are also useful in revealing the full range of environmental conditions influencing stem growth from the base to the apex (Chhin et al., 2010; van der Maaten-Theunissen and Bouriaud, 2012). Various external conditions (e.g. mass movement, wind action or grazing) may cause stem inclination in trees (Łuszczynska et al., 2017) or deflection of prostrate stems in shrub ramets (Pajunen, 2009). Subsequent production of reaction wood (Groover, 2016) in the most stressed stem segment results in variation of tree-ring widths and tree-ring shapes along the stem (presence of elliptical or egg-shaped tree rings; Schweingruber, 1996), which might affect the climatic signal provided by a limited number of cores around the stem or branch circumference (Buras and Wilmking, 2014). Reduced height and retaining (or even increasing) of radial growth leads to greater stem taper of mechanically influenced parts of the stem (Bonnesoeur et al., 2016; Kašpar et al., 2017).

Here we present the “IncrementR” R package (R Core Team, 2017), which has been developed to automate the analysis of average height growth and eccentricity of tree rings along the stem. This package is designed for the evaluation of samples (cores, cross sections) taken at different height levels along the tree stems or serially-sectioned shrubs. However, some of the functions may be applicable also to the “traditional” sampling scheme, i.e. coring multiple samples at one coring

level around the stem circumference. The key features of this package are: (i) functions for the calculation of height growth of trees or elongation of shrub ramets based on counts of tree rings representing different height levels along the stem, (ii) a function for estimating the number of missing rings at the beginning of the tree-ring series and (iii) other functions for the visualization of cross-sections and calculation of their parameters (such as basal area increment or eccentricity indices according to Schweingruber, 1996; Alestalo, 1971 and Braam et al., 1987).

2. Description of the “IncrementR” package

The “IncrementR” package is written in the R open-source language and environment for statistical analysis (R Core Team, 2017). The package is designed mainly for applications in dendroecological studies dealing with height growth of trees, ramet elongation of shrubs and partly for other dendrochronological subdisciplines such as dendrogeomorphology. We have developed several new functions and, in addition, revised some commonly used functions to make them applicable to height growth analysis (e.g. replacement of missing rings near to the pith). The package with its full documentation is available for download in a GitHub repository (github.com/jantumajer/IncrementR). The easiest way to install and launch “IncrementR” in the R environment is via the “devtools” package (Wickham et al., 2018):

```
> install.packages("devtools")
> library(devtools)
> install_github("jantumajer/IncrementR")
> library(IncrementR)
```

With the installation of “IncrementR” package, several other packages are automatically installed, specifically “dplR” (for reading tree-ring data and BAI calculation; Bunn, 2008), “ggplot2” (for most of the graphics; Wickham, 2009) and “cowplot” (for additional graphics; Wilke, 2017).

2.1. Input data

Three different input files are required for the proper functioning of all algorithms in the “IncrementR” package (Fig. 2). The first file contains tree-ring width series obtained for different coring levels along the stem and different orientations around its circumference (‘trw.series’ file in Fig. 2; see Table 1 for its structure). Tree-ring width series should be cross-dated before running any analysis with “IncrementR”. The algorithms were designed for four perpendicularly oriented cores per sampling level; however, most of the functions are applicable also to one or two cores per level. Nevertheless, all tree-ring data (from different plots, trees and sampling levels) should be stored in a single data

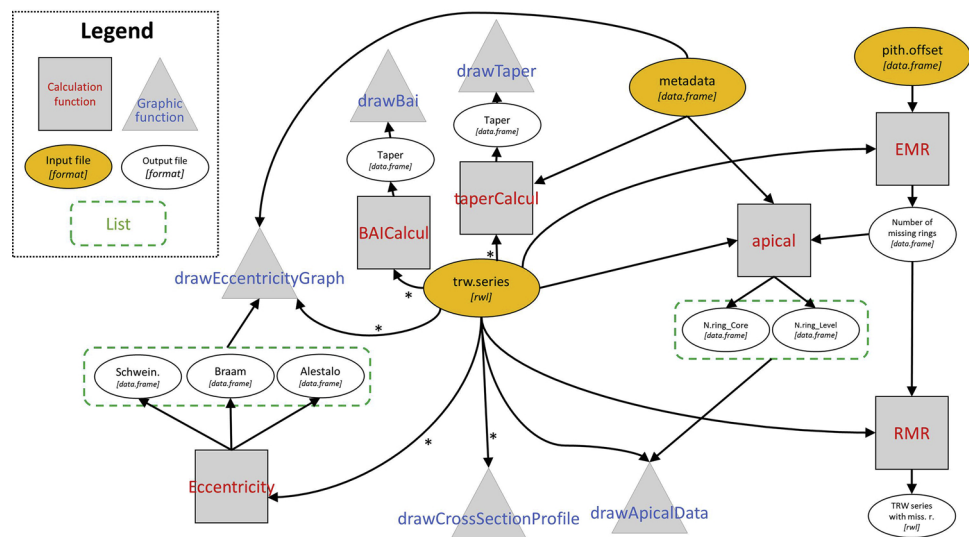


Fig. 2. Workflow chart for the “IncrementR” package. Asterisks indicate input steps where the original file containing tree-ring widths can be replaced with one containing “virtual” rings replacing rings missing near the pith (output of the RMR function).

frame. Each core needs to have its unique name indicating the sampling plot, tree and position along the stem (delimited by the underscore character) with a suffix describing its orientation (aspect). For the latter, the predefined suffixes are N (north), S (south), E (east) and W (west). As an example, code 2_8_5N is the valid identifier of a core from sampling plot no. 2 and tree no. 8, which was extracted from the northern side of the 5th consecutive level from the stem base.

The second input file required for the proper functioning of the “IncrementR” package’s functions contains metadata on the distance of individual coring levels from the stem base (‘metadata’ in Fig. 2; see Table 2 for structure). This data frame must contain at least two columns. The first one (“ID”) serves as a sampling level identifier and is in the format “PlotID_TreeID_LevelID”, where “LevelID” indicates the sampling level and should be numbered consecutively from the sampling level closest to the stem base (LevelID = 1) upwards. If total tree height was measured in the field, its level should be coded as 999. The other column “Level_cm” stores the height of each coring level from the ground in cm.

The last input data frame should contain information about pith offset (i.e. the estimated distance between the first measured tree ring and the pith) for each core sampled (‘pith.offset’ in Fig. 2; see Table 3 for its structure). There are two required columns of this input table, “ID” being the full identifier of each core (e.g. 5_7_1N) and the “P.OFFSET” column storing the estimated distance from the last

Table 2
Structure of metadata input file.

ID	Level_cm	Type of the sample (optional column)
8_2_1	57	core
8_2_2	104	core
⋮	⋮	⋮
8_2_7	354	cross-section
8_2_999	394	apex

Table 3
Structure of pith offset input file.

ID	P.OFFSET
8_2_1S	7.844444
8_2_1N	7.844444
8_2_1E	3.3125
8_2_1W	3.3125
⋮	⋮
8_2_7S	0
8_2_7N	0
8_2_7E	0
8_2_7W	0

Table 1
Structure of tree-ring width input file.

Calendar year (rownames)	8_2_1S	8_2_1N	8_2_1E	8_2_1W	...	8_2_7S	8_2_7N	8_2_7E	8_2_7W
1971	1.58	1.08	0.62	0.56	...	NA	NA	NA	NA
1972	1.76	1.55	0.92	0.56	...	NA	NA	NA	NA
1973	1.38	0.89	0.50	0.99	...	NA	NA	NA	NA
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
2014	2.04	1.18	1.73	1.53	...	2.18	4.14	3.33	3.35
2015	1.84	0.56	1.99	1.34	...	1.06	2.86	1.63	1.68
2016	1.05	0.98	1.87	1.42	...	2.17	3.58	3.13	3.21

measured tree ring to the pith (in mm). For the pith offset and metadata input data frames, it is important to use column names as described above.

The file ‘trw.series’ is an essential input of all functions included in the “IncrementR” package; however, ‘metadata’ and ‘pith.offset’ are required only for some functions, and the package can be run in limited mode if they are not available (see Fig. 2 for the detailed workflow of the “IncrementR” package).

2.2. Main functions

The package “IncrementR” contains several calculation functions and graphical functions for visualizing output data (Fig. 2). Calculation functions include *apical*, *taperCalcul*, *BAICalcul*, *Eccentricity*, *EMR* and *RMR*. Graphical functions are represented by *drawEccentricityGraph*, *drawCrossSectionProfile*, *drawTaper*, *drawApicalData* and *drawBai*. In addition, several private functions, containing parts of scripts dealing mainly with dataset formatting and pre-processing, are also part of the package. These functions are not directly accessible to the user but are automatically invoked by graphical or calculation functions.

Here we present an elementary description of each graphic and calculation function of the package. Their detailed syntax is included together with the list of input files and the structure of output files in the Supplementary material of this article and GitHub documentation (github.com/jantumajer/IncrementR/blob/master/README.md).

Height growth is calculated by the function *apical*. This function extracts the number of measured tree rings from each series and adds the estimated number of missing tree rings (see the description of the *EMR* function below) to calculate the calendar year in which the stem reached a specific height. If discrepancies in the total number of tree rings exist between different coring orientations at the same level and none of the cores includes pith, the median of the estimated number of tree rings is used. In addition to the total number of tree rings at each level, mean height growth velocity between two consecutive levels is calculated (as their distance divided by the difference in the count of tree rings). To deal with the uncertainty attributed to the unknown position of the core between two successive whorls when the whorls are not visible, the average uncertainty in average height growth is computed (Fig. 1). The mean height growth error (plotted in green in Fig. 1 and returned by the *apical* function) is based on the assumption that difference in the number of tree rings between two consecutive levels is on average greater by one than the value estimated by counting tree rings. The uncertainty reported by the *apical* function thus reflects one missing whorl between two successive sampling positions.

The taper (gradual thinning of the stem diameter with distance from the base) between two sampling levels is computed using the function *taperCalcul*. Stem taper from the base towards the apex can be expressed as a ratio (cm of stem diameter thinning per cm of stem length), in relative numbers (magnitude of change per unit of distance) or as the angle between stem taper and the stem longitudinal axis (Fig. 1). Due to stem eccentricity, the first values to be calculated are the girths of ellipses defined by cores sampled at two consecutive coring levels; these values are then entered into the formula for the calculation of circle diameter. Taper is defined as the difference in the diameter of the stem between two sampling points, divided by their distance. The output of the *taperCalcul* function is a list containing values of taper and taper angle for each tree and stem segment.

The function *BAICalcul* was designed to simplify the calculation of area increment at different sampling levels. *BAICalcul* averages tree-ring width series from the same tree and coring level and, subsequently, applies the function *bai.in* from the “dplR” package (Bunn, 2008) to obtain a series of basal area increment.

The function *Eccentricity* calculates three eccentricity indices according to Alestalo (1971), Braam et al. (1987) and Schweingruber (1996) for each sampling level and each tree ring and returns a list containing three data frames (one per eccentricity index). The

eccentricity indices are based on comparison of widths of the same tree ring around the stem circumference.

The function *EMR* estimates the number of missing tree rings between the last known tree ring and the pith. Three different approaches are implemented (Altman et al., 2016). The first is based on dividing pith offset by the mean tree-ring width of the innermost measured tree rings. The number of considered innermost tree rings is user-defined. The second is based on dividing the circle area with a radius equal to the pith offset by mean BAI of the innermost tree rings. The last option is the intermediate between the two previous approaches and, according to Altman et al. (2016), is the most accurate. The output of the *EMR* function is a data frame containing the number of missing rings close to the pith of each core.

In the next step after invoking the *EMR* function, it is possible to add missing rings to each core using the *RMR* function. The *RMR* function returns a new data frame containing tree-ring sequences with “virtual” tree rings added to replace missing rings around the pith. The number of “virtual” tree rings is given by the output of the *EMR* function and their width is computed by dividing pith offset by the number of “virtual” tree rings. If this manipulation results in a different number of tree rings in samples from the same coring level, the respective series are trimmed by their median length (the same approach as in the *apical* function). This function was designed specifically to be used in conjunction with the following functions of the “IncrementR” package, where it is desirable to also consider tree-rings not present in the sample core (e.g. *drawCrossSectionProfile*, *taperCalcul*, *BAICalcul*). Furthermore, it may be useful in studies focused on dating of tree or shrub establishment. Anyhow, “virtual” tree rings appended to series are artificial and should be used with caution.

The function *drawApicalData* is implemented for the visualization of height growth. It plots (1) the number of tree rings for different sampling levels and (2) mean velocity of height growth in individual stem segments together with its potential error. The function *drawEccentricityGraph* creates a graph of the stem profile, optionally with eccentricity indices of individual sampling levels. This function is a graphical representation of the *Eccentricity* function and enables visual comparison of tree-ring shape along the length of the stem. This may be useful, for instance, in studies on the effects of different factors influencing the basal and upper parts of the stem (e.g. sliding snow in the lower and wind flow in the upper part) or to identify the distribution of growth zones along and around stems of prostrate or decumbent shrubs. The visual representation of a cross-section profile can be drawn for individual sampling levels using the function *drawCrossSectionProfile*. This creates an elliptical model of the cross section by modelling tree rings in quarters of the Cartesian coordinate system. The final shape of the tree ring is then approximated as a combination of four ellipses with different eccentricity. Neighbouring ellipses share common values on the x- and the y-axis (i.e. common coring positions), which ensures their smooth connection at common points. If an ellipse is defined by four perpendicularly oriented cores, then its area equals the area of the circle with the mean radius of the cores. The output of *taperCalcul* and *BAICalcul* can be visualized as line charts using the function *drawTaper* and *drawBai*, respectively.

3. Illustrative example

A subsample of previously assembled dataset of tree-ring cores from Norway spruce (*Picea abies* L. Karst) collected in the treeline ecotone of the Hrubý Jeseník Mts (N 50.08°, E 17.23°, 1350–1450 m a.s.l., Czech Republic) was chosen to illustrate the use of the “IncrementR” package. We were interested in temporal dynamics of height growth and in the variable effects of environmental factors on stem eccentricity with tree ontogeny. Our research questions included: (i) How did height growth velocity change in the past? (ii) How did the cross-section profile change along the stem and over time? and (iii) Is there any height-related trend in stem taper?

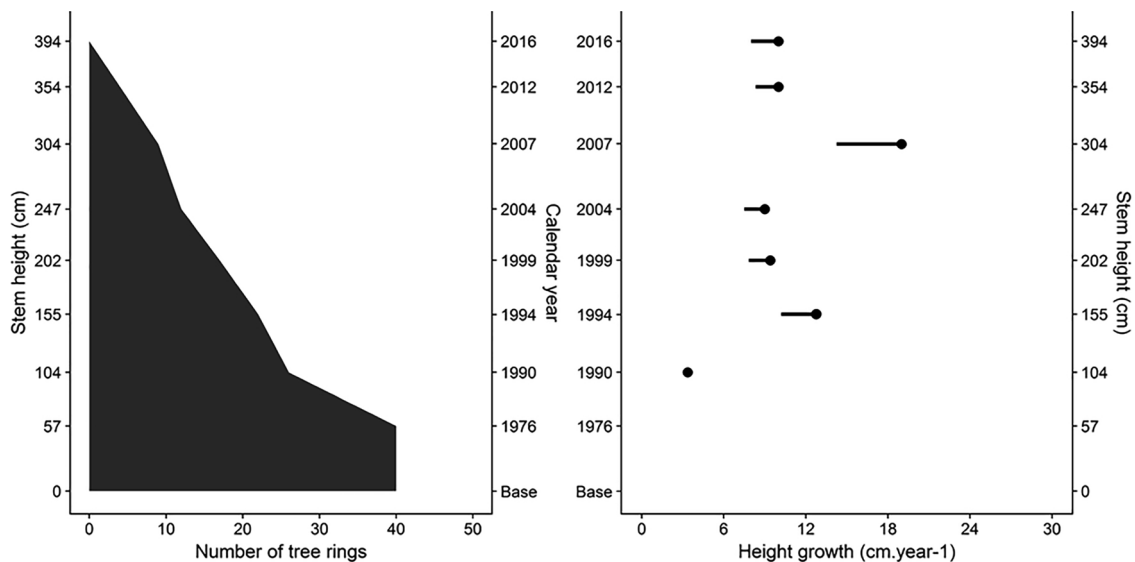


Fig. 3. Number of tree-rings and height growth velocity at different coring levels along the stem (dots). Error bars indicate the range of possibly lower height growth rates when accounting for the possibility that growth whorls were not sampled by the cores (output of *drawApicalData*).

From each tree we took four perpendicularly oriented cores from each height level along the stem. The first height level was situated approx. 50 cm above ground and each successive level was approx. 50 cm higher than the previous one. The exact height of the sampling position was determined. In total, 40 trees were sampled in this way; however, in this illustrative example of using the “IncrementR” package, only one specimen is presented – tree number 8.2 (i.e. plot no. 8, tree no. 2 in our notes). The height of the tree was 394 cm and the sampling was performed at seven successive levels between 57 cm and 354 cm.

Tree-ring widths of all cores were measured and pith offset was estimated for cores with missing pith using the graphical method (Applequist, 1958). We prepared three input files: (1) an *.rwl file with tree-ring widths (referred to as ‘trw’ in examples below), (2) a metadata file with heights of individual coring levels (‘meta’), and (3) a metadata file with pith offsets of individual cores (‘po’). For the structure of these files, refer to Tables 1–3. Input data frames of tree 8.2 are included in the installation of the “IncrementR” package and may be accessed using the following script:

```
> data(IncrementR_data)
> View(trw);View(meta);View(po)
```

After estimating the number of missing rings for each core (EMR), it is possible to derive the total number of tree rings at each level along the stem and the velocity of height growth between two consecutive coring levels (apical), and finally, to plot the results (*drawApicalData*):

```
> miss.ring <- EMR(trw.series=trw, p.off=po,
nyrs=5, method="Both")
> apical.series <- apical(trw.series=trw, meta
=meta, mr.estimate=miss.ring)
> drawApicalData(trw.series=trw,
apicalData=apical.series, plot=8, tree=2)
```

The results (Fig. 3) indicate that the velocity of height growth varied around $10 \text{ cm} \cdot \text{yr}^{-1}$ (average $10.5 \text{ cm} \cdot \text{yr}^{-1}$) for most of the tree’s life. This does not apply to parts of the stem between 57–104 cm from the ground, which exhibit very slow growth ($3.4 \text{ cm} \cdot \text{yr}^{-1}$) and, on the other hand, increased height growth between 247–304 cm ($19 \text{ cm} \cdot \text{yr}^{-1}$). The slow height growth in lower parts of the stem might be related to the effect of competition with an adjacent *Pinus mugo* Turra. shrub (current height 170 cm). The accelerated height growth between 2004 and 2007 (i.e. between 247–304 cm) might be a consequence of mild growing seasons of 2005–2007, when seasonal average temperatures were substantially above the long-term mean, with 2006 being among the

warmest growing seasons since the beginning of the 20th century (Ponocná et al., 2018). The uncertainty in the estimation of height growth is in this case relatively high due to a small difference in tree-ring counts (Fig. 3).

After correcting tree-ring width series for missing rings near to the pith (RMR), the shape of the stem is modelled by combining the functions *Eccentricity* and *drawEccentricityGraph*. This returns a stem profile visualization from the base to the top (Fig. 4a). In addition, the shape of stem sections between two adjacent coring levels may be quantified and viewed using taper functions (Fig. 4b):

```
> trw.cor <- RMR(trw.series=trw, mr.estimate=
miss.ring, nyrs=5, nsph=4)
> eccent <- Eccentricity(trw.series=trw.cor)
> drawEccentricityGraph(trw=trw.cor, ecc=
eccent, meta=meta, plot=8, tree=2, withEccentricity
=F, method="Schweingruber")
> taper <- taperCalcul(trw.series=trw.cor,
meta=meta)
> drawTaper(taperFile=taper, plot=8, tree=2,
variant="Angle")
```

Our results indicate that anomalies in the stem profile and taper are located mainly at levels between 150 and 200 cm above ground. The tree was located on the windy side of a mountain in the upper margin of the treeline ecotone; therefore, the bending effect of wind on the terminal part of the stem was strongest when the tree overgrew an adjacent *P. mugo* shrub and lost its protection.

To get a more detailed view of the shape of tree rings at specific coring levels along the stem, the function *drawCrossSectionProfile* may be used. The function plots the tree rings of one specific tree and sampling level approximated using ellipses:

```
> drawCrossSectionProfile(trw=trw.cor, plot=8,
tree=2, level=3, show.legend=T)
```

When plotting cross-section profiles at different coring levels (modifying argument level) for tree 8.2, the different orientation of tree-ring eccentricity along the stem becomes apparent. Tree rings in lower parts of the stem (i.e. 2nd–4th level – 104–202 cm) are slightly elongated in the E–W direction (Fig. 5a), becoming almost circular at the 5th level (247 cm; Fig. 5b), while strong N–S eccentricity dominates near the tree top (6th and 7th level, 304–354 cm; Fig. 5c). This may indicate that different forces influence tree shape in lower (snow creep) and higher (wind) parts of the stem.

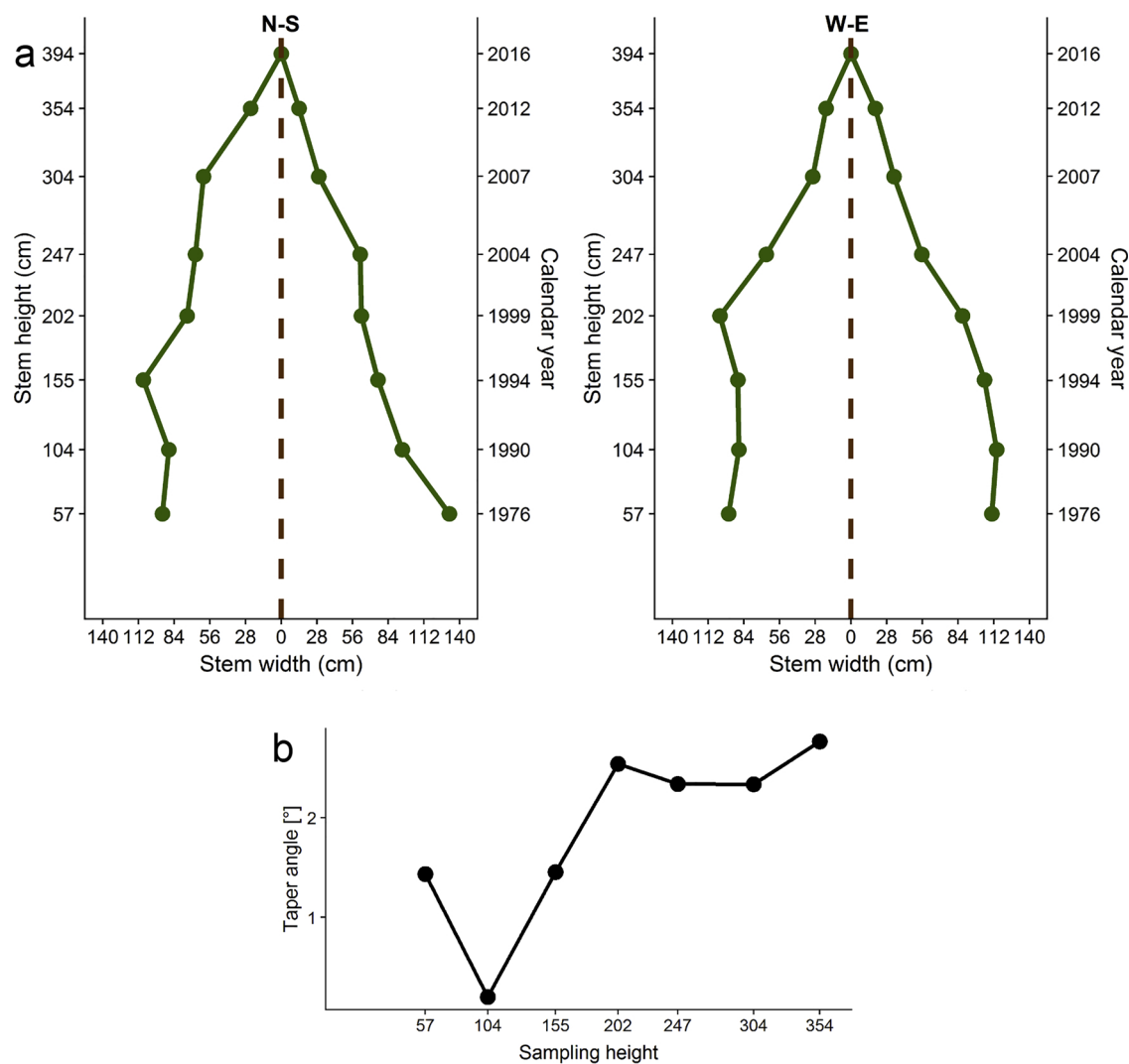


Fig. 4. Stem eccentricity (a) and stem taper angle between subsequent coring levels (b) (outputs of *drawEccentricityGraph* and *drawTaper*).

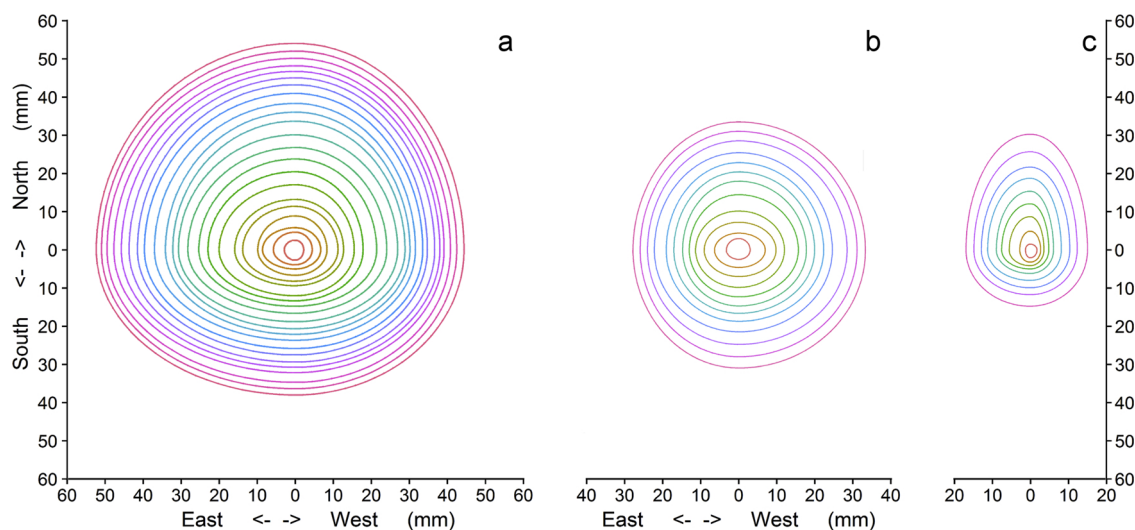


Fig. 5. Model of a cross-section profile from the 3rd coring level (a), the 5th coring level (b) and the 6th coring level (c) of tree 8.2 (output of *drawCrossSectionProfile*).

4. Conclusions

The presented package “IncrementR” is useful when working with average height growth data in dendroecology and dendrogeomorphology. This tool enables the evaluation of average height growth series, which are indicative of changes in the competition status of trees and the intensity of factors limiting height growth. Determination of radial and height growth is further suitable for measuring stem biomass. “IncrementR” also allows to quantify the elongation of shrub ramets when serial sectioning is applied. In addition, the package is suited for the analysis of changes in stem eccentricity at different stem height levels in conjunction with functions designed to discern the effects of different environmental factors mechanically affecting basal and upper parts of the stem.

Declarations of interest

None.

Acknowledgements

The study was supported by Grant Agency of Charles University [GAUK 996216] and the Ministry of Education, Youth and Sports of the Czech Republic [SVV 260438]. Authors acknowledge the help of D. Krause in the field. We thank F. Rooks for improving the English language. We are grateful to two reviewers and associated editor for constructive comments.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.dendro.2018.11.001>.

References

- Alestalo, J., 1971. Dendrochronological interpretation of geomorphic processes. *Fennia* 105, 1–140.
- Altman, J., Doležal, J., Čížek, L., 2016. Age estimation of large trees: new method based on partial increment core tested on an example of veteran oaks. *For. Ecol. Manage.* 380, 82–89. <https://doi.org/10.1016/j.foreco.2016.08.033>.
- Applequist, M.B., 1958. A simple pith locator for use with off-center increment cores. *J. For.* 56, 141.
- Babst, F., Bouriaud, O., Alexander, R., Trouet, V., Frank, D., 2014. Toward consistent measurements of carbon accumulation: a multi-site assessment of biomass and basal area increment across Europe. *Dendrochronologia* 32, 153–161. <https://doi.org/10.1016/j.dendro.2014.01.002>.
- Bonnesoeur, V., Constant, T., Moulia, B., Fournier, M., 2016. Forest trees filter chronic wind-signals to acclimate to high winds. *New Phytol.* 210, 850–860. <https://doi.org/10.1111/nph.13836>.
- Braam, R.R., Weiss, E.E.J., Burrough, P.A., 1987. Spatial and temporal analysis of mass movement using dendrochronology. *Catena* 14, 573–584. [https://doi.org/10.1016/0341-8162\(87\)90007-5](https://doi.org/10.1016/0341-8162(87)90007-5).
- Buchwal, A., Rachlewicz, G., Fonti, P., Cherubini, P., Gärtner, H., 2013. Temperature modulates intra-plant growth of *Salix polaris* from a high Arctic site (Svalbard). *Polar Biol.* 36, 1305–1318. <https://doi.org/10.1007/s00300-013-1349-x>.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124. <https://doi.org/10.1016/j.dendro.2008.01.002>.
- Buras, A., Wilmking, M., 2014. Straight lines or eccentric eggs? A comparison of radial and spatial ring width measurements and its implications for climate transfer functions. *Dendrochronologia* 32, 313–326. <https://doi.org/10.1016/j.dendro.2014.07.002>.
- Chhin, S., Hogg, E.H., Lieffers, V.J., Huang, S., 2010. Growth-climate relationships vary with height along the stem in lodgepole pine. *Tree Physiol.* 30, 335–345. <https://doi.org/10.1093/treephys/tpq120>.
- Gamache, I., Payette, S., 2004. Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada. *J. Ecol.* 92, 835–845. <https://doi.org/10.1111/j.0022-0477.2004.00913.x>.
- Groover, A., 2016. Gravitropisms and reaction woods of forest trees - evolution, functions and mechanisms. *New Phytol.* 211, 790–802. <https://doi.org/10.1111/nph.13968>.
- Ivancich, H.S., Martínez Pastur, G.J., Roig, F.A., Barrera, M.D., Pulido, F., 2012. Changes in height growth patterns in the upper tree-line forests of Tierra del Fuego in relation to climate change. *Bosque (Valdivia)* 33, 11–12. <https://doi.org/10.4067/S0717-92002012000300006>.
- Jansons, A., Matisons, R., Libiete-Zalite, Z., Baders, E., Riekstis-Riekstīņš, R., 2013. Relationships of height growth of lodgepole pine (*Pinus contorta* var. *latifolia*) and scots pine (*Pinus sylvestris*) with climatic factors in Zvirgzde, Latvia. *Balt. For.* 19, 236–244.
- Kašpar, J., Hošek, J., Tremel, V., 2017. How wind affects growth in treeline *Picea abies*. *Alp. Bot.* 127, 109–120. <https://doi.org/10.1007/s00035-017-0186-x>.
- Klesse, S., Etzold, S., Frank, D., 2016. Integrating tree-ring and inventory-based measurements of aboveground biomass growth: research opportunities and carbon cycle consequences from a large snow breakage event in the Swiss Alps. *Eur. J. For. Res.* 135, 297–311. <https://doi.org/10.1007/s10342-015-0936-5>.
- Körner, C., 2012. *Alpine Treelines*. Springer, Basel, Basel. <https://doi.org/10.1007/978-3-0348-0396-0>.
- Lindholm, M., Ogurtsov, M., Aalto, T., Jalkanen, R., Salminen, H., 2009. A summer temperature proxy from height increment of Scots pine since 1561 at the northern timberline in Fennoscandia. *Holocene* 19, 1131–1138. <https://doi.org/10.1177/0959683609345078>.
- Łuszczynska, K., Wistuba, M., Malik, I., 2017. Dendrochronology as a source of data for landslide activity maps – an example from Beskid Żywiecki Mountains (Western Carpathians, Poland). *Environ. Soc.-Econ. Stud.* 5, 40–46. <https://doi.org/10.1515/enviro-2017-0015>.
- McCarroll, D., Jalkanen, R., Hicks, S., Tuovinen, M., Gagen, M., Pawellek, F., Eckstein, D., Schmitt, U., Autio, J., Heikkinen, O., 2003. Multiproxy dendroclimatology: a pilot study in northern Finland. *Holocene* 13, 831–841. <https://doi.org/10.1191/0959683603hl668rp>.
- Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., MacIsaac-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., Hik, D.S., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ. Res. Lett.* 6. <https://doi.org/10.1088/1748-9326/6/4/045509>.
- Myers-Smith, I.H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S.A., Weijers, S.J., Trant, A., Tape, K.D., Naito, A.T., Wipf, S., Rixen, C., Daves, M.A.A., Wheeler, J., Buchwal, A., Baittinger, C., MacIsaac-Fauria, M., Forbes, B.C., Lévesque, E., Boulanger-Lapointe, N., Beil, I., Ravolainen, V., Wilmking, M., 2015. Methods for measuring arctic and alpine shrub growth: a review. *Earth-Sci. Rev.* 140, 1–13. <https://doi.org/10.1016/j.earscirev.2014.10.004>.
- Pallardy, S.G., 2008. *Physiology of Woody Plants*. Elsevier.
- Pajunen, A.M., 2009. Environmental and biotic determinants of growth and height of arctic willow shrubs along a latitudinal gradient. *Arctic, Antarct. Alp. Res.* 41, 478–485. <https://doi.org/10.1657/1938-4246-41.4.478>.
- Paradis, M., Lévesque, E., Boudreau, S., 2016. Greater effect of increasing shrub height on winter versus summer soil temperature. *Environ. Res. Lett.* 11, 085005. <https://doi.org/10.1088/1748-9326/11/8/085005>.
- Paulsen, J., Weber, U.M., Körner, C., 2000. Tree growth near treeline: abrupt or gradual reduction with altitude? *Arctic Antarct. Alp. Res.* 32, 14–20.
- Pensa, M., Salminen, H., Jalkanen, R., 2005. A 250-year-long height-increment chronology for *Pinus sylvestris* at the northern coniferous timberline: A novel tool for reconstructing past summer temperatures? *Dendrochronologia* 22, 75–81. <https://doi.org/10.1016/j.dendro.2005.02.005>.
- Ponocná, T., Chuman, T., Rydval, M., Urban, G., Migala, K., Tremel, V., 2018. Deviations of treeline Norway spruce radial growth from summer temperatures in East-Central Europe. *Agric. For. Meteorol.* 253–254, 62–70. <https://doi.org/10.1016/j.agrformet.2018.02.001>.
- R Core Team, 2017. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Salminen, H., Jalkanen, R., 2005. Modelling the effect of temperature on height increment of Scots pine at high latitudes. *Silva Fenn.* 39, 497–508. <https://doi.org/10.14214/sf.362>.
- Salminen, H., Jalkanen, R., Lindholm, M., 2009. Summer temperature affects the ratio of radial and height growth of Scots pine in northern Finland. *Ann. For. Sci.* 66, 810. <https://doi.org/10.1051/forest/2009074>.
- Schweingruber, F.H., 1996. *Tree-rings and Environment*. Dendroecology. Swiss Federal Institute for Forest, Snow and Landscape Research, Berner, Stuttgart, Vienna, Haupt.
- Speer, J.H., 2010. *Fundamentals of Tree-ring Research*. The University of Arizona Press, Tucson, Arizona.
- Šenfeldr, M., Tremel, V., Maděra, P., Volařík, D., 2014. Effects of prostrate dwarf pine on Norway spruce clonal groups in the treeline ecotone of the Hrubý Jeseník Mountains, Czech Republic. *Arctic, Antarct. Alp. Res.* 46, 430–440. <https://doi.org/10.1657/1938-4246-46.2.430>.
- van der Maaten-Theunissen, M., Bouriaud, O., 2012. Climate-growth relationships at different stem heights in silver fir and Norway spruce. *Can. J. For. Res.* 42, 958–969. <https://doi.org/10.1139/x2012-046>.
- Weijers, S., Myers-Smith, I.H., Löffler, J., 2018. A warmer and greener cold world: summer warming increases shrub growth in the alpine and high Arctic tundra. *Erdkunde* 72, 63–85. <https://doi.org/10.3112/erdkunde.2018.01.04>.
- Wickham, H., 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer, Verlag-New York.
- Wickham, H., Hester, J., Chang, W., 2018. *devtools: Tools to Make Developing R Packages Easier*. R package version 1.13.5.
- Wilke, C.O., 2017. *cowplot: Streamlined Plot Theme and Plot Annotations for “ggplot2”*. R package version 0.9.2.