**How *Rhododendron* shrubs respond to climate on the southeastern
Tibetan Plateau: prospects for shrub-based dendrochronology**

XIAOMING LU, J. JULIO CAMARERO, YAFENG WANG, ERYUAN LIANG,
DIETER ECKSTEIN

*Xiaoming Lu, Yafeng Wang, Eryuan Liang (liangey@itpcas.ac.cn), Key Laboratory of Tibetan
Environment Changes and Land Surface Processes, Key Laboratory of Alpine Ecology and
Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, 100101 Beijing,
China; Eryuan Liang, CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing
100101, China; J. Julio Camarero, Instituto Pirenaico de Ecología (IPE-CSIC), Avda.
Montañana, 1005, 50059 Zaragoza, Spain; Dieter Eckstein, Section Wood Biology, Centre of
Wood Sciences, University of Hamburg, Leuschnerstrasse 91, 21031 Hamburg, Germany.*

Corresponding author:

Dr. Eryuan Liang

Email: liangey@itpcas.ac.cn

Abstract

In harsh and treeless environments, shrubs constitute the dominant growth form of woody plants. However, shrub-based dendrochronology has produced few long and climate-responsive ring-width chronologies on such stressful sites. Along the highest tree lines and shrub lines of the world, located on the Tibetan Plateau, alpine shrubs offer a unique opportunity to apply dendrochronology beyond the uppermost distribution limit of trees. Previous studies on *Rhododendron* shrubs resulted in the assembly of several but short ring-width chronologies. Now, we considerably extend these chronologies in space and time by collecting and cross-dating cross-sections of *Rhododendron aganniphum* stems from six sites located at elevations from 4000 to 4500 m a.s.l. The ring widths were measured and correlated with time-series of monthly climate data. A principal component analysis (PCA) was used to convert the total variability of indexed ring-width chronologies into PCs. An up to 400-year long *Rhododendron* ring-width chronology was built. The year-to-year variability in the ring-width indices positively correlated with July temperature. We concluded that shrub ring-width chronologies can be used as reliable climatic proxies in treeless environments of the Tibetan Plateau and elsewhere.

Introduction

Shrubs and dwarf shrubs (chamaephytes) inhabit treeless areas with harsh environmental conditions (e.g. tundra, steppe) and unlike trees provide the possibility to address questions on how primary and secondary growth are related to each other at the whole-plant level (Bernal *et al.* 2011; Camarero *et al.* 2013). Moreover, shrubs offer a unique opportunity to extend the existing dendrochronological networks to extremely cold or dry areas beyond the survival limits of trees, i.e. beyond the cold and/or dry tree lines. In addition, they also allow a better understanding on how the secondary lateral cambium in the shoots, responsible for annual ring formation, responds to climate as compared to other meristems, e.g. in roots or leaves (Körner 2012; Camarero *et al.* 2013).

In spite of an early attempt for dendrochronological analysis of shrub species in the 1950s (Ferguson 1959), actual progress has only been made in the recent two decades (e.g. Rayback & Henry 2005; Bär *et al.* 2006; Au & Tardif 2007; Xiao *et al.* 2007; Battipaglia *et al.* 2010). Most of the studies on shrub dendrochronology disclosed difficulties in cross-dating the extremely narrow, sometimes wavy or wedging growth rings of shrubs (e.g. Woodcock & Bradley, 1994; Schweingruber & Dietz 2001). But such difficulties did not hinder further efforts from exploring the dendrochronological potential of several new shrub species (e.g. Srur & Villalba 2009; Hallinger *et al.* 2010; García-Cervigón *et al.* 2012; Gazol & Camarero 2012; Liang *et al.* 2012; Schweingruber *et al.* 2013). However, few long (>150 years) shrub ring-width chronologies have been developed to the best of our knowledge with one exception (see Weijers *et al.* 2010).

In the case of the highest observed tree lines and shrub lines located on the Tibetan Plateau, most dendrochronological studies were indeed applied on trees (e.g. Zhang *et al.* 2003; Shao *et al.* 2005; Liu *et al.* 2005; Liu *et al.* 2006; Gou *et al.* 2008; Liang *et al.* 2008; Zhu *et al.* 2008; Chen *et al.* 2013; Yang *et al.* 2014). But beyond the tree line, alpine shrubs as several *Rhododendron* species are widely distributed. A recent study confirmed their dendrochronological potential (e.g. Liang & Eckstein 2009). However, it is not clear yet whether it is possible to find older individuals so as to build ring-width chronologies longer than 200 years (Li Z *et al.* 2013). Therefore, the objectives of this study were: (i) to find old *Rhododendron* individuals and (ii) to evaluate their dendroclimatic potential by cross-dating and assembling long ring-width chronologies series and by analyzing their relationships with climatic variables. We focused on *Rhododendron aganniphum* var. *schizopeplum* Balf. f. & Kingdon-Ward (hereafter called *Rhododendron*), a shrub species dominant above tree line, and we investigated its growth variations and its response to climate along two altitudinal transects. Based on a similar research on trees along an altitudinal gradient in the same area (Liang *et al.* 2010), we hypothesize that the radial growth of *Rhododendron* would mainly respond to summer temperature and that the strength of that response will change with elevation.

Materials and methods

Study area and climate

The Sygera Mountains (29°10'-30°15' N, 93°12'-95°35' E, maximum elevation of 5200 m a.s.l.) are located in a transitional area between humid and semi-humid conditions on the SE Tibetan Plateau. In summer, due to the barrier formed by the Himalayas, the south-west Asian monsoon flows northward along the Yarlung Zangbo Grand Canyon, bringing abundant rainfall to Southeast Tibet. In winter, the region is mainly influenced by westerly winds bringing about sunny and dry weather. The sampling sites were located from 4000-4500 m a.s.l. (Fig. 1a).

According to the nearby meteorological station at Nyingchi (29°34' N, 94°28' E, 3000 m a.s.l.), located on the valley bottom, the annual average sum of precipitation from 1960-2013 was 672 mm. Most precipitation was recorded from June to September and accounted for 71.5% of the annual amount. The annual average temperature was $8.9 \pm 0.6^\circ\text{C}$; January and July were the coldest and warmest months with mean temperatures of 0.6 and 15.9°C , respectively (Fig. 1b). Due to the abundant water supply in summer, low temperatures during the growing season may be the major constraint of secondary growth at these high-elevation areas (Li X *et al.* 2013).

In the study area, an automatic meteorological station was installed in November 2006 near the tree line (29°39' N, 94°42' E, 4390 m a.s.l.). From 2007-2013, the mean annual temperature ranged from -0.2 to 0.8°C and the annual total precipitation was 957 mm (Liu *et al.* 2011). The daily, 5-day, 10-day and monthly records of mean temperature and the sum of precipitation between the automatic and the Nyingchi meteorological stations correlated significantly ($p < 0.001$ in all cases) to each other over the 7-year common period ($r = 0.96, 0.98, 0.98$ and 0.99 for daily, 5-day, 10-day and monthly mean temperature; $r = 0.57, 0.73, 0.85$ and 0.86 for daily, 5-day, 10-day and monthly total precipitation), so that the long climate record from the Nyingchi meteorological station were used in this study (see also Liang *et al.* 2011).

Shrub sampling and cross-dating

In September 2011, six study sites were selected along a north-facing (4000-4500 m a.s.l.) and a southeast-facing (4400-4500 m a.s.l.) slope, 59 km north-east from Nyingchi. *Rhododendron* is one of the most widely distributed shrubs in this area. It is an evergreen and clonal species, forming 1-3 m tall mats, and it flowers from May to June bringing about a spectacular view in these mountains (Fig. 2). On the north-facing slope, we set four well-drained sites at 4000, 4200, 4400, 4500 m a.s.l., hereafter abbreviated as N40, N42, N44 and N45. On the southeast-facing slope, we set one site at 4400 m (abbreviated as SE44) at the tree line and another site at 4500 m (abbreviated as SE45) above the tree line. On each site, 20 to 25 *Rhododendron* individuals were randomly selected located apart from each other by at least 10 m to avoid sampling the same individual twice. About 130, 3-4 cm thick, stem disks, many of them from dead individuals, were taken near the soil level. All samples were air-dried before further analysis.

After sanding and polishing the cross-sections of these disks, the ring-width patterns were visually cross-dated among each other by using the skeleton-plot technique (Stokes & Smiley 1968). Two radii of each cross-section were measured with a precision of 0.01 mm using a LINTAB measuring system (Rinntech, Heidelberg, Germany). Then, the cross-dating and the measurements were checked using the COFECHA program (Holmes, 1983). The two ring-width series per disk were averaged. These ring-width series showed age-size related trends, i.e. decreasing ring width with increasing age and shoot diameter. Therefore, we used the ARSTAN program to detrend and standardize the individual ring-width series by a 32-year long cubic smoothing spline and to average the resulting indices into a site chronology using a bi-weight robust mean (Cook & Kairiukstis 1990). The first-order autocorrelation of these series was also modeled and partially removed to obtain residual or pre-whitened ring-width indices. These so-called ‘residual’ site chronologies have preserved the high-frequency variability (yearly to decadal) of radial growth, which presumably reflects climate variability, whereas the longer-term trends (decadal to centennial) were eliminated.

As Wilmking *et al.* (2012), based on Kolishchuk’s approach (1990), found that the

cambium at lower stem sections of trees and shrubs under severe stress conditions
'may be inactive, yet functional, for up to 18 years', we selected two individuals for
within-shrub cross-dating ('serial sectioning'). For this, cross-sections were sampled
along the stems every 20 cm to check the completeness of the shrub rings, in
particular in the lower stem sections.

Data analyses

We calculated three statistical descriptors to characterize the six site chronologies:
mean sensitivity (MS), expressed population signal (EPS) and mean series
intercorrelation (R_{bar}). The MS is a measure for the year-to-year changes of the ring-
width indices (Fritts 1976). The EPS assesses the degree to which a chronology
represents a hypothetical chronology of an infinite number of samples; a value of
EPS > 0.85 is usually accepted for a sufficiently reliable ring-width chronology
(Wigley *et al.* 1984). Lastly, the R_{bar} is the mean correlation among the individual
ring-width series of a site, and it is used to characterize how growth responds to
abiotic factors such as climate (Briffa & Jones 1990).

To assess how shrub growth responds to climate, Pearson's correlations were
calculated by relating the site tree-ring index chronologies and local climate variables
(monthly minimum, maximum and mean temperature and monthly total
precipitation). The analysis period included 15 months from July of the previous year
to September of the year of shrub-ring formation. A principal component analysis
(PCA) was calculated on the covariance matrix of the six residual chronologies and
used to describe their common patterns during the common period 1810-2011. The
first three principle components (PC1, PC2 and PC3) with eigenvalues greater than 1
were selected following the Kaiser criterion (Cook & Kairiukstis 1990). Finally, the
chronologies' loadings on these three PCs were used to compare the site chronologies
as related to their different slope aspects and elevations.

Results

Serial sectioning

The two shrubs selected for serial sectioning were about 150 and 250 years old. We found no consistently missing rings along the two stems. Pearson's correlations of ring-width indices, averaged over 11 (shrub N1) and 14 cross-sections (shrub N2), were 0.63 ($p < 0.001$) and 0.53 ($p < 0.001$), respectively. Thus, the ring-width series along these two shrubs cross-dated well from the root collar to the top of the stems, meaning that basal cross-sections are suitable for developing reliable shrub-ring chronologies (Fig. 3).

Rhododendron site chronologies and statistical descriptors

A microscopic cross-section through one of the shoots exemplarily revealed the clarity of the *Rhododendron* tree rings and their diffuse-porous/semi-ring-porous wood structure (Fig. 4). The tree-ring borders become distinctly visible by one or two rows of radially flattened, thick-walled fibers.

Six ring-width site chronologies were successfully established. The longest one spans 400 years and encompasses the period 1611-2011 (Fig. 5), being well replicated from 1670 to 2011, thus making it the longest shrub chronology. At least 7 shrubs were needed to achieve an EPS > 0.85 . With increasing altitude, the mean ring width decreased from 0.33 mm at 4000 m (site N40) to 0.18 mm at 4500 m (site SE45). The percentage of missing rings also increased upwards from 0.25 to 0.52% (Tab. 1). The mean shrub age per site ranged from 99 to 220 years. The sample sizes varied from 13 (site SE45) to 23 shoots (site N40). The MS and R_{bar} of the chronologies were relatively low at all sites, ranging from 0.14-0.19 and 0.24-0.31, respectively. All chronologies were highly correlated with each other, indicating that the growth of *Rhododendron* is limited by similar regional climatic constraints.

Climate-growth relationships along the elevation gradient

The PCA of site chronologies produced three first PCs which accounted for 65.9%, 15.7% and 6.2% of the total variance in ring-width indices, respectively (Fig. 6). PC1 had positive loadings on all six chronologies but yielded higher loadings at high-elevation sites (N44, N45, SE44 and SE45), whereas PC2 was characterized by

negative loadings at low-elevation sites (N40 and N42). The climate-growth relationships produced a similar grouping as the PCA regarding the groups of sites with similar responses (Fig. 7). Growth of *Rhododendron* individuals on the four high-elevation sites responded positively to temperature and negatively to rainfall in August (and September) in the prior year as well as positively to temperature in June-July and negatively to rainfall in June of the current year, irrespective of the slope aspect. We also found positive growth responses at high-elevation sites (e.g. N44) to current January mean minimum temperature and February precipitation. Conversely, at low-elevation sites (N40, N42) *Rhododendron* responded negatively to temperature in late autumn (October, November) and positively to October precipitation (in most cases fallen as snow) before the growing season. During summer, *Rhododendron* on these sites also benefitted from wet conditions in June and warmth in July.

Discussion and conclusions

We developed a network of six *Rhododendron* tree-ring site chronologies, thereof one covering 400 years which is longer than all hitherto assembled shrub chronologies worldwide (Weijers *et al.* 2010). This was possible due to successful cross-dating taking locally or totally missing rings into account. Our starting hypothesis saying that the year-to-year growth variability of *Rhododendron* is associated to July temperature similarly to nearby trees (Liang *et al.* 2010) was confirmed. The mean ring-width of *Rhododendron* was wider than of the alpine shrub *Empetrum hermaphroditum* in Norway (Bär *et al.* 2007), *Betula nana* in Northeastern Siberia (Blok *et al.* 2011) and *Salix arctica* in the High Arctic (Woodcock & Bradley 1994), but narrower than in *Proustia cuneifolia* and *Fabiana imbricata* in the Chilean Andes (Barichivich *et al.* 2009) and in *Artemisia tridentata* in the US Great Basin (Biondi *et al.* 2007). The MS of the *Rhododendron* chronologies was lower than of the majority of other shrub chronologies (e.g. Srur & Villalba 2009; Zalatan & Gajewski 2006) suggesting that the weather conditions in the Sygera Mountains were not varying from year to year as much as in arid or semi-arid and subarctic shrublands. However, a low

mean sensitivity does not necessarily mean that there is no climatic signal reflected by the ring-width variability (Wilson & Topham 2004). Similar to other stressful environments (Villalba *et al.* 1997; Splechna *et al.* 2000; Frank *et al.* 2005; Leal *et al.* 2007; Bär *et al.* 2007; Liang & Eckstein 2009; Hallinger *et al.* 2010; Blok *et al.* 2011; Weijers *et al.* 2012), summer temperature played an important role in controlling wood formation of *Rhododendron*, irrespective of slope aspects and elevations. Interestingly, the correlation between July mean minimum temperature and radial growth increased with rising elevation and became significant at 4500 m a.s.l. (sites N45 and SE45). No altitude-dependent effects of climatic signals are recorded in Smith fir tree-ring $\delta^{18}\text{O}$ from the same study areas (Zeng *et al.* 2014). It is uncommon that the radial growth of *Rhododendron* also benefited from above-average January minimum temperature. However, a winter-temperature effect promoting the growth of woody plants at cold sites has already been reported in recent decades for several woody species (D'Arrigo *et al.* 1997; Pan *et al.* 1997; Tardif *et al.* 2001; Cullen *et al.* 2001; Pederson *et al.* 2004; Hallinger *et al.* 2010). In the Sygera Mountains, there is snow until early May (Li X *et al.* 2013). Above-average warm winters combined with a high snow pack might reduce root mortality and promote microbial life activity in the soil underneath (Pederson *et al.* 2004; Sturm *et al.* 2005), resulting in an increased photosynthetic rate, carbohydrate formation and nutrient supply in the following growing season (Marchand 1980; Mack *et al.* 2004; Chapin *et al.* 2005). However, a high snowpack in spring can even delay the onset of the growing season (Vaganov *et al.* 1999; Kirilyanov *et al.* 2003; Seo *et al.* 2011). In conclusion, *Rhododendron* shrubs can be used to develop up to 400-year long tree-ring-width chronologies as reliable proxies for summer temperature variability in treeless areas. However, this issue deserves further studies on how *Rhododendron* growth is linked to changes in snow depth and whether an upward shift of *Rhododendron* can be expected in response to climate warming.

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492 *Table 1.* Statistics of the shrubring-width data and indices considering the six site
 493 chronologies. Abbreviations of variables are as follows: MS, mean sensitivity; R_{bar} ,
 494 average correlation within sites; EPS, expressed population signal.

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					Raw measurements		Residual indices		
Site code	No. shoots/radii	Time span	Mean age (years)	Missing rings (%)	Mean ring width (mm)	First-order auto-correlation	MS	R_{bar}	EPS>0.85 since
N40	23/46	1750-2011	99	0.25	0.33	0.76	0.19	0.24	1860
N42	19/38	1692-2011	141	0.26	0.25	0.77	0.17	0.31	1775
N44	17/28	1611-2011	191	0.27	0.2	0.82	0.16	0.26	1670
N45	20/38	1687-2011	220	0.52	0.2	0.84	0.14	0.28	1740
SE44	19/38	1629-2011	215	0.45	0.21	0.83	0.14	0.27	1730
SE45	13/24	1713-2011	146	0.52	0.18	0.76	0.16	0.27	1895

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507 **Figure legends**

508 *Figure 1.* (a) Location of the study area in the south-eastern Himalayas (inset) and of
509 the six study sites located in the Sygera Mountains at elevations from 4000 to 4500 m
510 a.s.l. (b) Variations of the monthly mean air temperature and total precipitation from
511 1960 to 2013 at Nyingchi, southeastern Tibet.

512 *Figure 2.* Flowering *Rhododendron* shrubs above the tree line in early summer in
513 4400 m a.s.l.

514 *Figure 3.* Within-shrub cross-dating based on serial sectioning of 11 disks taken in 20
515 cm distances along the shoot of the *Rhododendron* individual N1 (r , mean correlation
516 between the 11 ring-width series from N1-1 at the base up to N1-11 at the apex,
517 calculated for the common period 1965-2011).

518 *Figure 4.* Microscopic cross-section through a *Rhododendron* shoot; bark side to the
519 left, pith side to the right. [Scale bar=](#)

520 *Figure 5.* Year-to-year variability of six site chronologies of *Rhododendron* with ten-
521 year running averages superimposed; dotted lines indicate the sample depths (number
522 of measured shoots); vertical arrows show the year beyond which the $EPS > 0.85$ and
523 the chronology is reliable.

524 *Figure 6.* Loading for the first three principal components (PC1, PC2 and PC3), based
525 on a Principal Component Analysis of the variance of tree-ring indices of six
526 *Rhododendron* site chronologies.

Figure 7. Correlation between the six *Rhododendron* site chronologies and the monthly mean, maximum and minimum temperatures as well as monthly sum of precipitation; sites responding similarly to climate variables are framed by dotted-line boxes; horizontal dashed lines show the 0.05 significance levels.

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554 *Figure 1.*

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584 *Figure. 4.*

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Figure. 5.

Figure. 6.

Figure. 7.