

Influence of climate on the total vessel lumen area in annual rings of teak (*Tectona grandis* L.f.) from Western Ghats of Central Karnataka, India

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Abstract: Total vessel lumen area (TVLA) of earlywood (EW) and latewood (LW) computed through image analysis has been analyzed to understand its relationship with the temporal variation of climate from dated tree-ring series of teak (*Tectona grandis* L.) from Western Ghats in Central Karnataka, India. The study showed that December rainfall of the previous year and May of the current year are the most important climatic variables in the development of large size EW vessel lumen area of an annual ring whereas rainfall of October and December (northeast monsoon) of previous year and June and September of current year played a significant role in the formation of small size LW vessel lumen area. Low temperature in December of previous year and low rainfall in February of succeeding year are important in the formation EW vessel lumen area while previous year's high temperature of November is important for the formation LW vessel lumen area. Pre-monsoon (April–May) high temperature also has significant role in the initiation of cambial activity and the formation of EW and LW vessel lumen area. It is recorded that total vessel lumen area (TVLA) of earlywood showed more climatic signal than TVLA of latewood.

Key words: Climate, teak, earlywood, latewood, total vessel lumen area.

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Introduction

Annual ring-width of a tree is traditionally used to analyze relationships between tree growth and climate (Fritts 1976) and to reconstruct past climates. However, many anatomical features of the annual rings contain much more climatic information than only that integrated in their ring-width (Fonti & Garcia-Gonzales 2004; Wimmer 2002). Among various anatomical features in hardwoods, vessel parameters are supposed to be the most promising proxy for dendroclimatic analysis (Corcuera *et al.* 2004;

Fonti *et al.* 2013; Gea-Izquierdo *et al.* 2012; Sass & Eckstein 1995). Vessel refers to a series of vessel elements which may be defined as xylem cells in which one or more pit like structures lack a pit membrane at maturity, thus forming perforations (Carlquist 1988). It is a constituent of secondary xylem, primarily meant for the conduction of water from soil to leaves especially in hardwood trees. Their size, number and distribution in tree ring, of both early wood (EW) and late wood (LW) portions, or in the entire ring have been recognized as significant parameters in ecology and environmental studies (Eckstein 2004; Fonti *et al.*

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2009). Application of vessel parameters in these aspects has been assessed mostly from temperate and Mediterranean hardwoods (Corcuera *et al.* 2004; Eckstein & Frisse 1982; Fonti & Garcia-Gonzales 2008; Fonti *et al.* 2013; Sass & Eckstein 1995).

Teak is a ring-porous tropical hardwood species having distinct annual rings (Chowdhury 1939). India is the known centre for genetic diversity and variability of teak, having its natural distribution zone concerted mainly in the peninsular region below 24°N latitude (Tewari 1992). Annual ring-width of teak has been widely analyzed for dendroclimatic analysis from peninsular India (Borgaonkar *et al.* 2007; Deepak *et al.* 2010; Kumar *et al.* 2014; Ram *et al.* 2008; Shah *et al.* 2007; Sinha *et al.* 2011; Sinha 2012). However, very limited studies have been carried out on the anatomical features of annual rings of teak in relation to climate. Among anatomical features of teak only vessel parameters like vessel area, vessel diameter and vessel density in a tree ring have been recognized as important variables and studied intensively in recent dendroclimatic analysis (Babu *et al.* 2015; Bhattacharyya *et al.* 2007; Pumijumnong & Park 1999; Sinha *et al.* 2009). Western Ghats of Karnataka is dominated by the tropical monsoon and it could form an important site for understanding dendroclimatic analysis of teak. Vessel variables like vessel density and vessel diameter together may give a better approximation of the water transporting capacity of wood (Ewers 1985; Fisher *et al.* 1997; Holbrook & Zwieniecki 1999; Verheyden *et al.* 2005; Zimmermann 1983). Using these two vessel variables, the total vessel lumen area of EW and LW was calculated in each annual ring of teak from Western Ghats of Central Karnataka and correlated with climatic variables.

The objective of the present investigation is to find the relationship between climatic variables *viz.*, monthly rainfall & temperature and total vessel lumen area (TVLA) of EW and LW in each annual ring of teak from Western Ghats of Central Karnataka.

Materials and methods

Study site and sample collection

One increment core sample (width 5 mm) per tree was extracted at breast height using increment borer from the trunk of ten teak trees at Shimoga in October 2007 (13°56'N latitude and

Table 1. Selected statistics of TVLA chronology of EW and LW of *Tectona grandis* L. at Shimoga.

	TVLA index of EW	TVLA index of LW
Chronology time span	1949 to 2007	1949 to 2007
Number of trees (radii)	10 (10)	10 (10)
Mean sensitivity	0.2189	0.2010
Standard deviation	0.2493	0.2383
Autocorrelation order 1	0.1862	0.1701
Common interval time span	1962 to 2007	1962 to 2007
Number of trees (radii)	8 (8)	8 (8)
Mean correlation among all radii	0.410	0.208
Mean correlation between trees	0.409	0.204
Signal-to-noise ratio	2.766	1.050
Expressed population signal	0.734	0.512
Variance explained	56.59%	40.86%

75°38'E longitude), located in the Western Ghats of Central Karnataka, India. Thus, totally 10 core samples were collected from ten teak trees for dendroclimatic analysis (Table 1).

Climatic description

In Shimoga district the SW monsoon generally starts from early June to September while October to December months experience scanty rain from N-E monsoon. Summer prevails between March to early June. The winter commences in mid-November and ends by middle of February. Based on the records of climatic data (1947–2007), the mean monthly temperature and rainfall data were collected from a meteorological station in the Shimoga district close to sampling site. The data showed that April–May (27.0 °C) and December–January (21.7 °C) are the hottest and coldest months, respectively. July receives the highest rainfall (1984 mm) and January–February is the driest months with only 17 mm of precipitation (Fig. 1).

Sample preparation and measurements

Each core sample collected from teak tree was mounted in a grooved wooden block with waterproof glue. The surface of cores was smoothed using a sanding machine with

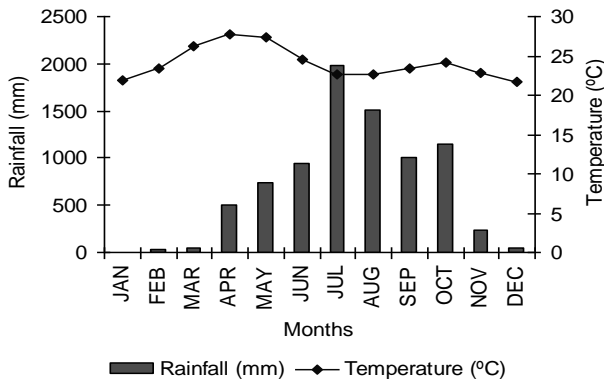


Fig. 1. Mean monthly precipitation and temperature at Shimoga based on the data from 1947–2007.

different grades of sand paper to expose the growth rings (Fig. 2a-c). Later, wood-dust from the vessel lumens or pores of all these smooth surfaces was removed by blowing with high-speed air, so that the outline and inside of the pores of each ring were clearly visible for analysis under a microscope. Later these pores were filled with white chalk powder by hand to obtain a contrast from the surrounding cells. Each ring of these cores was dated to the calendar year applying cross dating technique such as skeleton plotting (Stokes & Smiley 1968). Skeleton plotting involves the visual inspection of tree-ring samples to identify marker years (e.g. drought years) and plotting these years on an annually segmented piece of graph paper for comparison with other samples. Following visual cross-dating technique of skeleton plotting, the annual ring-width of each dated tree ring sample were measured along single radius to the nearest 0.01 mm under a Leica stereo-zoom microscope using a sliding linear measuring stage, interfaced with a computer system. The statistical accuracy of cross-dating is checked using a software program COFECHA (Holmes 1983) for any error in the measurement or dating of the samples.

For demarcating earlywood (EW) from latewood (LW), the former was identified with wider vessels and initial axial parenchyma (Fig. 3). The total vessel lumen area of EW and LW was calculated after the measurement of vessel density and tangential lumen diameter of EW and LW respectively from the dated tree ring sequences using an image analysis system (Leica Application Suite V3.3.0). The vessel tangential lumen diameter of EW and LW was measured directly on the polished core samples, along radial direction

from the bark to pith through a live measurement software and the vessel density of EW and LW was measured at an optical magnification of 12.5 times and the number of vessels per square millimeter was counted. At least 25 observations in each annual ring of core sample extracted from individual tree were taken for the measurement of tangential vessel lumen diameter and vessel density according to International Association of Wood Anatomists (IAWA) committee guidelines (Wheeler *et al.* 1989). The total vessel lumen area of EW and LW was calculated from the measured vessel density and diameters following the formula-vessel density multiplied by the mean vessel lumen area [$\pi \times (\text{mean tangential diameter})^2$] (Verheyden *et al.* 2005). The mean of total vessel lumen area (TVLA) of EW and LW is shown in Fig. 4.

The chronologies of the TVLA were worked following the same methods of detrending and filtering as known from ring-width analysis. In tree-ring-width analysis, we cannot use raw measurement data for our analysis because normal age related trend exists in all tree-ring data which need to be removed, some trees simply grow faster or slower despite living in the same location and despite careful tree selection, we may collect a tree that has aberrant growth pattern. Therefore, we cannot average all measurement for a single year. We must first transform all our raw measurement data to some common average by detrending or standardization technique. It is a common technique used in many fields when data need to be averaged but have different means or undesirable trends. All trends can be characterized by either a straight line or a curve. After fitting a suitable line or curve to raw measurement tree-ring series, we will then have an equation. We can use that equation to generate predicted values of tree growth for each year via regression analysis. For each year, we have an actual measured value and a predicted value derived from fitting a curve or line. To detrend or standardize the tree-ring series, we conduct a data transformation for each year using the formula, $\text{index} = \text{actual value}/\text{predicted value}$ or fitted value (Fritts 1976).

Standardization or detrending of raw measured value of TVLA series from EW and LW of teak has been done using the computer program ARSTAN (Holmes 1992). The program provides various options of detrending methods such as negative exponential, linear regression, cubic spline smoothing with detailed statistics of each series and

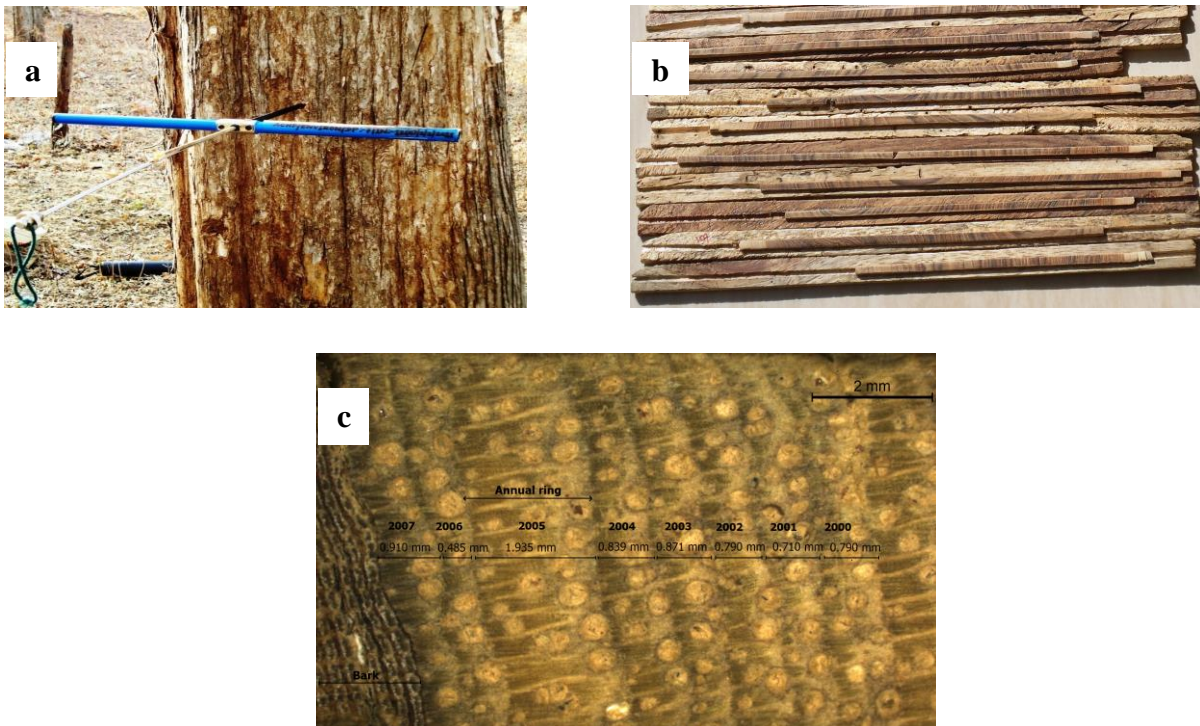


Fig. 2a-c. Extraction of core samples and variation of annual rings within and among teak trees. (a). Extraction of core sample from teak tree using increment borer, (b). Core samples mounted in grooved wooden blocks showing variation in annual rings within and between trees, (c). Variation of annual rings within a teak tree at 1.6 X objective under Leica stereo-zoom microscope.

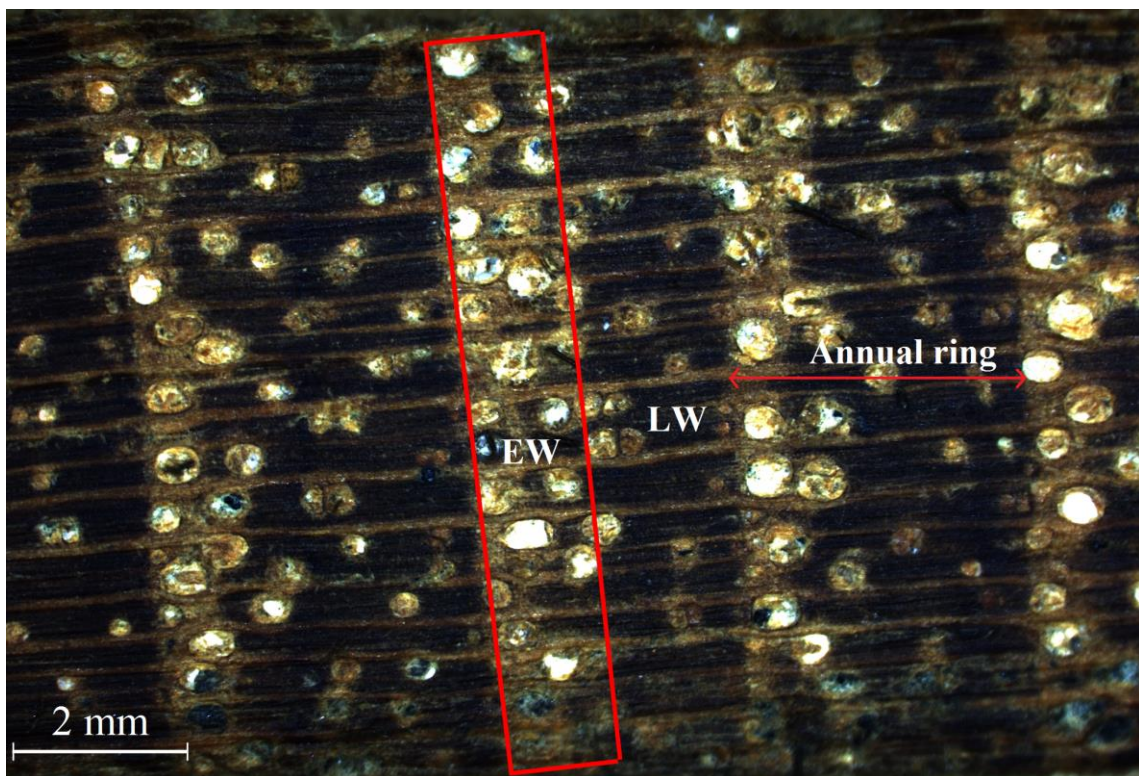


Fig. 3. Tree-ring of teak showing vessels in earlywood (EW) and latewood (LW) of annual rings.

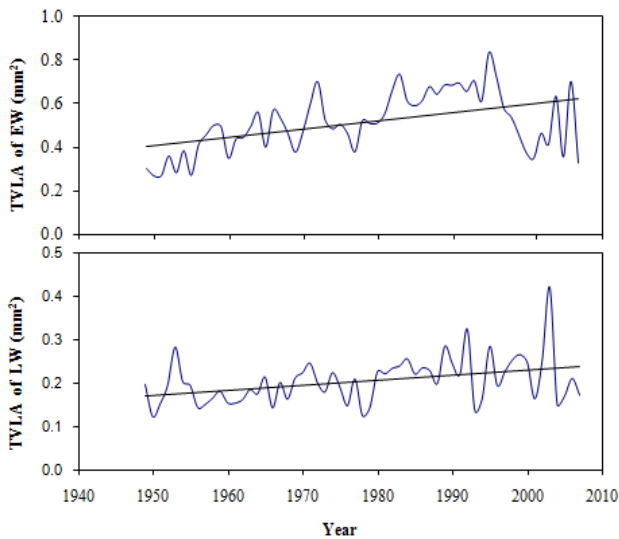


Fig. 4. Mean of raw TVLA of EW and LW of *Tectona grandis*.

chronology. In our analysis, a positive linear regression was found to be the most appropriate standardization option. Indices of each series were derived by dividing the raw measured value of TVLA by corresponding fitted or predicted value derived from linear regression equation for each year. Most of the TVLA series used in the analysis showed high auto-correlation. For this purpose auto-regressive modelling has been used which removes an auto-correlation structure in the series and enhance the common signal. All index series were averaged over the site and the TVLA index chronology of 59 years was prepared spanning AD 1949–2007. Fig. 5 indicates TVLA indices of EW and LW of teak (after auto-regression modeling) from the site.

Statistical analysis

Chronology statistics for the common period has been derived to understand its suitability for climatic analysis. The chronology suitable for dendroclimatic analysis is generally believed to have good correlation between trees, low autocorrelation, high mean sensitivity, high standard deviation, high value of common variance, high signal to noise ratio (SNR) and high expressed population signal (EPS). The statistical performance of TVLA index chronologies of EW and LW is given in Table 1. The auto-correlation is the association or linkage between ring-width for the year ($t-1$) and subsequently formed ring t , $t+1$, to $t+k$, which can disturb the casual relationship

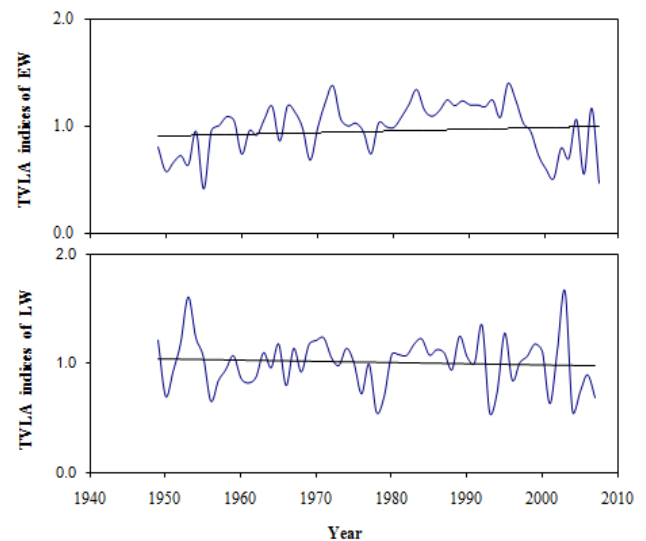


Fig. 5. Mean of TVLA indices of EW and LW of *Tectona grandis* after standardization.

between climate and tree growth (Shah *et al.* 2007). For example, a stressed tree may take a year or two to recover from a hard season. High autocorrelation is a problem in tree-ring analysis which can create more complex modeling. The mean sensitivity is a measure of relative difference in vessel lumen area between consecutive rings. Its value ranges from 0 to 2. The large value of auto-correlation and low value of mean sensitivity indicate the presence of more low frequency variance in the series. When the case is reverse, the high frequency variance is of more interest for dendroclimatic studies. Auto-regressive modeling removes an auto-correlation structure in the series and enhances the common climatic signal. In this chronology, moderately high value of standard deviation, mean sensitivity, EPS and common variance (mean correlation among all the tree samples) indicate the dendroclimatic potential of these two chronologies. Signal-to-noise ratio (SNR) >1 indicates the more common useful signal than the residual noise. In the present analysis, the value of SNR is greater than one for TVLA index chronology of EW and LW both which indicates the useful climatic signal in the vessel lumen area of teak.

Climate-tree-growth-associations can be assessed reliably by means of response function analysis (Fritts 1976). Similarly, association between climate and vessel area of EW and LW can also be assessed by means of response function analysis. This procedure is a multiple regression analysis in which monthly climatic parameters

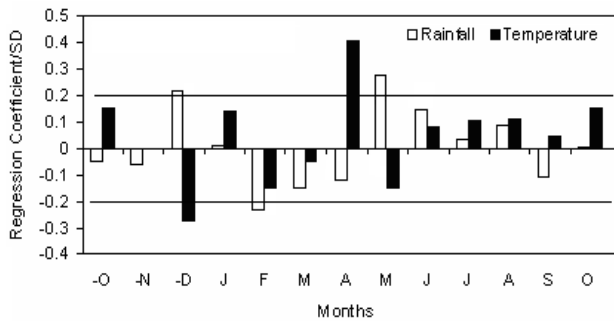


Fig. 6. Response function analysis of total vessel lumen area (TVLA) of earlywood (EW).

(temperature and rainfall) are predictors and TVLA indices are predictants. The resulting regression equation quantifies the response of the vessel lumen area to variations in the most important climatic variables. Monthly mean temperature and rainfall of Shimoga were entered as predictor variables and the TVLA indices as the predictant variables. The analyses were based on the time period 1949 to 2007 for Shimoga that were common to both meteorological and TVLA data respectively. In constructing the response functions, a total of 26 variables were used as predictor variables which means 13 for temperature and 13 for rainfall from previous October (end of previous growing season) to the current October (end of current growing season). Apparently, this time span corresponded to the interval just prior to initiation of cambial activity till maturation of vessel of EW and LW in teak. Thus selecting this time span, the role of climate of both the previous and current years on the development of vessel area could be assessed. Since many of the climatic variables are highly inter-correlated, principle components for 26 data series were obtained. TVLA index chronologies of EW and LW from Shimoga were regressed on the climate principal components to obtain response function coefficients. Fig. 6 and 7 show standardized regression coefficients for response functions on monthly scale for TVLA chronologies of EW and LW. The horizontal line in the figure indicates statistically significance level ($P \leq 0.05$) above and below.

Results and discussion

Response function analysis

The response function analysis for TVLA index chronology of EW showed that the TVLA of EW is

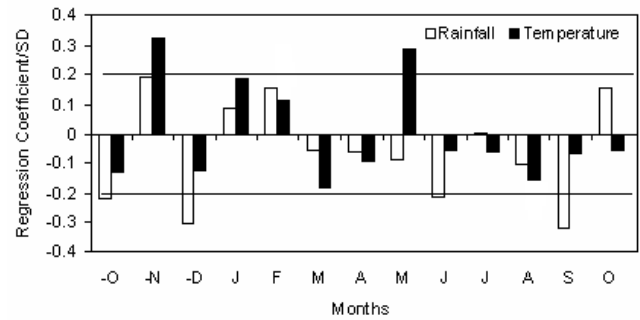


Fig. 7. Response function analysis of total vessel lumen area (TVLA) of latewood (LW).

positively correlated with previous year's December rainfall and current year's rainfall of May month (Fig. 6). Current year's April temperature is also positively associated with formation of EW vessel lumen area whereas, previous year's December temperature and current year's February rainfall have negative association with the formation of EW vessel lumen area. The amount of variance explained by climate has been 56.6%. Several attempts have been made to elucidate the possible role of climatic variables in limiting the development of vessel size considering available literatures related to ecology, phenology, local climate and site conditions of these trees from diversified geographical regions (Bhattacharyya *et al.* 2007; Chowdhury 1940; Priya & Bhat 1999; Rao & Rajput 1999). From these records, it shows that EW vessel development in teak starts around March and ceases during June, and by the first week of October there is no wood formation. Shedding of leaves starts by December and by first week of February, all trees remain leafless.

Positive correlation of TVLA of EW with previous year's December rainfall might be attributed to the effect of food storage and late NE monsoon. Increased precipitation during the later part of growing season might have enhanced photosynthetic rate when the trees continue to have active leaf area. Several studies clearly demonstrate that previous year's growth has a major role in growth of EW of subsequent years (Fritts 1976). Current year's May rainfall was positively correlated with the formation of TVLA of EW because rainfall plays an important role in development of EW vessel lumen area. Positive correlation of TVLA with current year's April temperature suggested that increased temperature during pre-monsoon month appears to have an important role in the initiation of cambial activity (Chowdhury 1940). Warm and dry conditions from

March to April (May) generally favour the formation of large vessels over the whole growing season (Pumijumng & Park 1999). Moreover, the influence of other physiological factors also seems to have a vital role in the formation of wider vessel lumen area in EW. These factors seem to be more effective at the beginning than the end of growing period. The development of wider vessel lumen area in the beginning of growing season helps in efficient water transportation to initiate the growth process, but subsequently the necessity of water seems to be non-critical to the vessel lumen area (Bhattacharyya *et al.* 2007). Negative correlation of TVLA of EW with the previous year's December temperature might be due to the fact that low temperature during December plays an important role in the formation wide vessel lumen area of EW. The inverse relationship with February rainfall might be due to the fact that during February, low rainfall favour respiration over photosynthesis as trees remain leafless and photosynthesis is almost nil at that time, affecting EW vessel lumen area.

The response function analysis of TVLA chronologies of LW showed that the TVLA of LW was negatively correlated with the rainfall of October and December of the previous year and June and September of current year whereas previous year's November temperature and May of current year were positively associated with formation of LW vessel lumen area. The amount of variance explained by climate is 40.9% (Fig. 7).

Negative correlation of TVLA of LW with previous year's rainfall of October and December reveals that post monsoon rainfall played an important role in the formation smaller vessel lumen area of LW. Positive correlation of TVLA with the temperature of May of the current year suggested that earlier increased temperature during pre-monsoon month affects the initiation of cambial activity as mentioned earlier and is also important in the formation of both EW and LW vessel lumen area. The negative correlation of TVLA of LW with the current rainfall of June and September might be due to the fact that lumen area of the latewood vessels depends more on cool conditions during summer and rainy seasons. This is supported by the study of Pumijumng & Park (1999), where it was mentioned that early wood vessels are more controlled by moisture availability and the lumen area of the latewood vessels is more dependent on cool summer conditions.

Conclusion

Response of monsoon rainfall and temperature on total vessel lumen area (TVLA) of both EW and LW at Shimoga of Western Ghats in Central Karnataka have great significance, since it adds novel information in understanding the chronological variability in total vessel lumen area of teak with climate. This study corroborates that total vessel lumen area of EW and LW in annual rings of teak is influenced by the temporal variation in the monthly rainfall and temperature of previous year and current year both. High temperature during pre-monsoon is important for the initiation of cambial activity and also in the formation of EW and LW vessel lumen area. It is investigated that TVLA of early wood retains more climatic signals than TVLA of latewood.

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