

Intra-annual Secondary Growth Rate-Climate Relations of *Fagus orientalis* Lipsky in the Center of Hyrcanian Forests

Reza OLADI*, Kambiz POURTAHMASI

University of Tehran, Faculty of Natural Resources, Karaj, Iran; oladi@ut.ac.ir (*corresponding author)

Abstract

Weekly rate of Beech tree ring increment were related to the changes of climatic factors in weekly intervals. In order to do so, small samples were extracted from 5 Oriental beech trees located in Nowshahr educational forest in the central part of the Hyrcanian forests of Iran during 2008 growing season. Microscopic sections were prepared and average increases in tree ring width were measured, standardized and modeled using Gompertz equation. The results showed that the minimum air temperature and water evaporation had the strongest and positive effect on the secondary growth rate while the role of precipitation was minor and negative. Air temperature and evaporation variations during growing season were assumed to remain in their optimum level; increasing xylem formation by accelerating carbohydrate production and carbon uptake of trees, respectively. Since the studied site had warm and humid climate receiving sufficient amount of rainfall before and during growing season, water availability was not a limiting factor of radial growth and its minor negative relation was interpreted according to its small hampering effect on the air temperature and sunlight absorption of trees. It was concluded that meteorological factors affecting secondary growth rate of trees should be interpreted as a package rather than analyzed disconnectedly.

Keywords: evaporation, Oriental beech, precipitation, temperature, wood formation

Introduction

In woody gymnosperms and dicotyledon angiosperms i.e. softwoods and hardwoods with distinct growth rings, xylem is formed each year as a result of cambium reactivation and its divisional activity. The beginning and the rate of wood formation during growing season is controlled by internal and external factors (Begum *et al.*, 2012; Vaganov *et al.*, 2006). Climatic factors are among the main external ones which have been extendedly studied especially in cold and temperate regions of Europe and North America. However, most of these studies have been focused on the long term relations of climate-growth based on inter-annual tree ring researches but results of such studies could derive from the intra-annual climate/growth analysis (Seo *et al.*, 2011). There are few dendroclimatological studies in the northern Iran but fully understanding of climate-growth relation in that area needs further, high resolution approaches (Pourtahmasi *et al.*, 2011). Hence, short term studies are necessary to understand the link between climate and growth rate (Gruber *et al.*, 2009).

Temperature and precipitation are generally the most important regulators of biological growth and development (Antonova and Stasova, 1997; Begum *et al.*, 2012; Oliveira *et al.*, 2009; Vaganov *et al.*, 1999). However, the long lists of other climate variables are influencing xylem production (Gruber *et al.*, 2009) and the effects of these environmental regulators can be quite subtle (Barlow and Powers, 2005). It is generally accepted that the onset of cambium activity is strongly affected by the environment

(Schweingruber, 1988; Seo *et al.*, 2011) and the timing of maximum growth rate is controlled by either photoperiod (Rossi *et al.*, 2006b) or temperature (Mäkinen *et al.*, 2003) but the studies on the relation between the growth rate and environment during the growing period is less frequent (Downes *et al.*, 2009) and this relation is still not fully understood. It should be added that the nature of this relation is reported to differ greatly according to site conditions and species. In addition to the important climatic factors like temperature and precipitation, the mean growth rate could be a function of other less-known factors like the extension of the crown (Bräuning *et al.*, 2008) or cardinal directions of stem (Mäkinen *et al.*, 2003). These great variations and complexity deserve more ecological investigations.

The Hyrcanian forests in Iran are located in a narrow strip between the Caspian Sea and Alborz Mountains which experience different climates from eastern to its western parts. Due to its diverse ecological condition (Mohadjer, 2005), it is a perfect area to study the effect of climate on tree growth. Since Oriental beech (*F. orientalis* Lipsky) is well distributed in these forests; studying these trees can provide useful information on the response of trees to different climate and climatic factors.

The objectives of this investigation is to study the influence of different climatic factors on growth rate during a growing season in high resolution intervals and finding the most associated environmental parameter affecting growth rate.

Materials and methods

Study site

The study was conducted in an Instructional Forest in the central part of the Hyrcanian region. The study site (650 m a.s.l) is placed in a mixed *Parrotio carpinetum* forest with some beech stands in moist valleys and its distance to Alborz Mountains is less than 2 km. The area has humid temperate to subtropical climate with a mild and wet winters and hot and humid summers (Fig. 1).

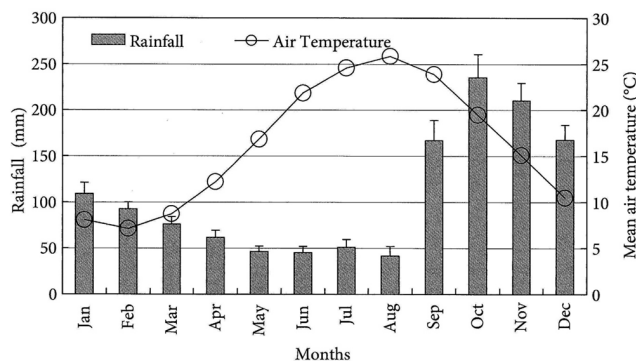


Fig. 1. Monthly mean rainfall and air temperature recorded during 23 years (1985-2008) by the Nowshahr synoptic weather station located in the airport. Error bars show the standard error of monthly rainfall during the recorded period (from Ahmadi *et al.*, 2009)

Meteorological data (daily mean, maximum and minimum temperature, sum of daily precipitation and water evaporation) were obtained from a well equipped meteorological station placed in Nowshahr airport for the year 2008. This station (36°39' N, 51°30' E) is about 5 km away from the study site and belongs to Iranian Meteorological organization (IMO).

Sampling

Five intact and upright beech trees (*Fagus orientalis* Lipsky) with diameters of 45-50 cm were selected and marked. It was tried to avoid choosing trees grown on steep slopes since these kind of trees are susceptible to form reaction wood. In 2008, from mid-March up to the time when the trees had completely lost their leaves (early December), micro-cores were extracted from two opposite directions of each tree, using a specially designed tool for long-term sampling named Trephor (Rossi *et al.*, 2006a). The micro-cores (2 mm in diameter and 10 mm in length) contained phloem, cambium, newly formed tree ring and 1-2 previous rings. The micro-coring from two opposite sides of the tree may have helped to study and take into account the effect of uneven growth or tree eccentricity around the stem. To avoid wound effects, a spiral pattern of sampling around the trunk were followed. The sampling was done at 10-day intervals during the first month and 20-day intervals throughout the rest of the growing season.

Tree ring increment measurement and standardization and its relation to the meteorological factors

Eighteen μm thickness sections were prepared from micro-cores using sledge microtome and stained with 1% water solution of safranin-astar blue (Oladi *et al.*, 2011). The sections were pictured under a Nikon YS 100 light microscope and the developing and last year tree-ring widths were measured along three radial files using Image J software (Fig. 2).

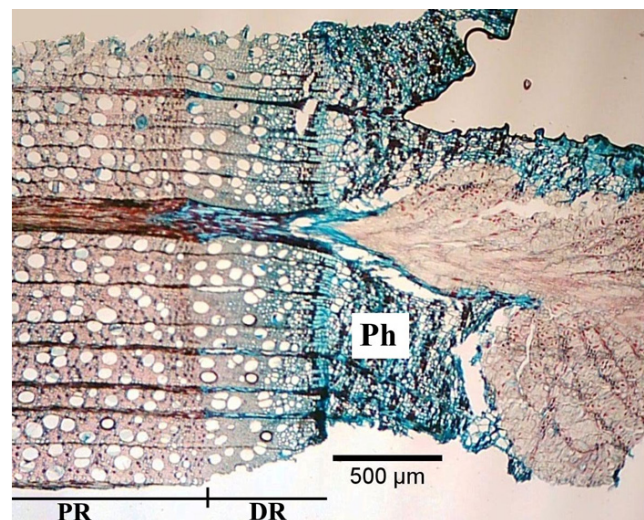


Fig. 2. A microscopic section from a sample taken in the beginning of May. Phloem (Ph), developing tree ring (DR) and a part of previous tree ring (PR) have been labeled in the photograph

The cambial activity around the stem circumference may differ at short tangential distances (Van der Werf *et al.*, 2007). As a result, even at the same tree height, the width of tree ring may not be identical at different positions around a stem. Hence, the two-step standardization was conducted in order to correct the tree-ring width measurements (Oladi *et al.*, 2011). The pattern of tree-ring loop is repetitive in the next year i.e. a point or side of a tree which produced a narrower ring will almost always do so and *vice versa*. This fact has been used to standardize the tree ring width data at the first step (Rossi *et al.*, 2003). In the second step, the corrected tree ring width of two samples taken from opposite sides of a tree in each field campaign was averaged. This value was used to calculate the mean ring width of trees at each sampling date.

In order to obtain the weekly increment of tree ring during the growing season, the mean growth pattern of trees was modeled using Gompertz function. The three parameter Gompertz function belongs to the exponential decline family of growth equations which is widely used to present relative growth rates in biological studies (Zeide, 1993). This equation is defined as:

$$y = A \exp[-e^{(\beta - kt)}] \quad (1)$$

were:

y = cumulative ring width at time t

t = Julian day

A = final asymptotic size, representing the maximum ring width

β = x-axis placement parameter

k = rate of change parameter

In order to do so, first, Gompertz parameters (A , β and k) were obtained by SAS[®] software using actual cumulative ring widths. Then by inserting t values (time) as Julian days into the equation, the corresponding y (ring width) were calculated.

Mean weekly increment of trees were assessed simply by subtracting the mean cumulative tree ring width of trees in a Julian day (y_t) from the corresponding value of the next week (y_{t+7}):

$$\Delta y = y_{t+7} - y_t \quad (2)$$

For the same intervals weekly mean, maximum and minimum air temperature, precipitation sums and water evaporation sums were calculated. Pearson product-moment correlation analysis (r) was applied to identify the climatic factors most closely associated with xylem production (Gruber *et al.*, 2009). Multiple (partial) regression analysis was done and “parameter estimate” were calculated to determine the influence of particular climatic factor on xylem production rate (Venugopal and Liangkuwang, 2007). The “parameter estimates” are the partial regression coefficients that show which factor had the greatest contribution to the model.

Results

Cambium reactivation and formation of new tree ring started at the beginning of April and lasted up to the end of September. The weekly changes in climatic factors (mean, maximum and minimum air temperature, precipitation sums and water evaporation sums) and weekly increase in tree ring during this period is plotted in Fig. 3a to c.

Pearson correlations coefficients (r) between mean tree ring increment in weekly intervals and climate parameters during 2008 growing season are summarized in Tab. 1. Besides, in this table the “parameter estimate” for each factor is listed. The strongest correlation coefficient was found with water evaporation sum ($r = +0.67$, $p < 0.01$), followed by minimum temperature ($r = +0.56$, $p < 0.01$), mean temperature ($r = +0.52$, $p < 0.01$), maximum temperature ($r = +0.46$, $p < 0.01$) and precipitation ($r = -0.33$, $p < 0.05$), respectively. All the climatic factors had positive relation with tree ring growth except precipitation.

The multiple (partial) regression analysis has shown that minimum temperature had the greatest contribution to the model. However, the only statistically significant parameter estimate was calculated for water evaporation sum.

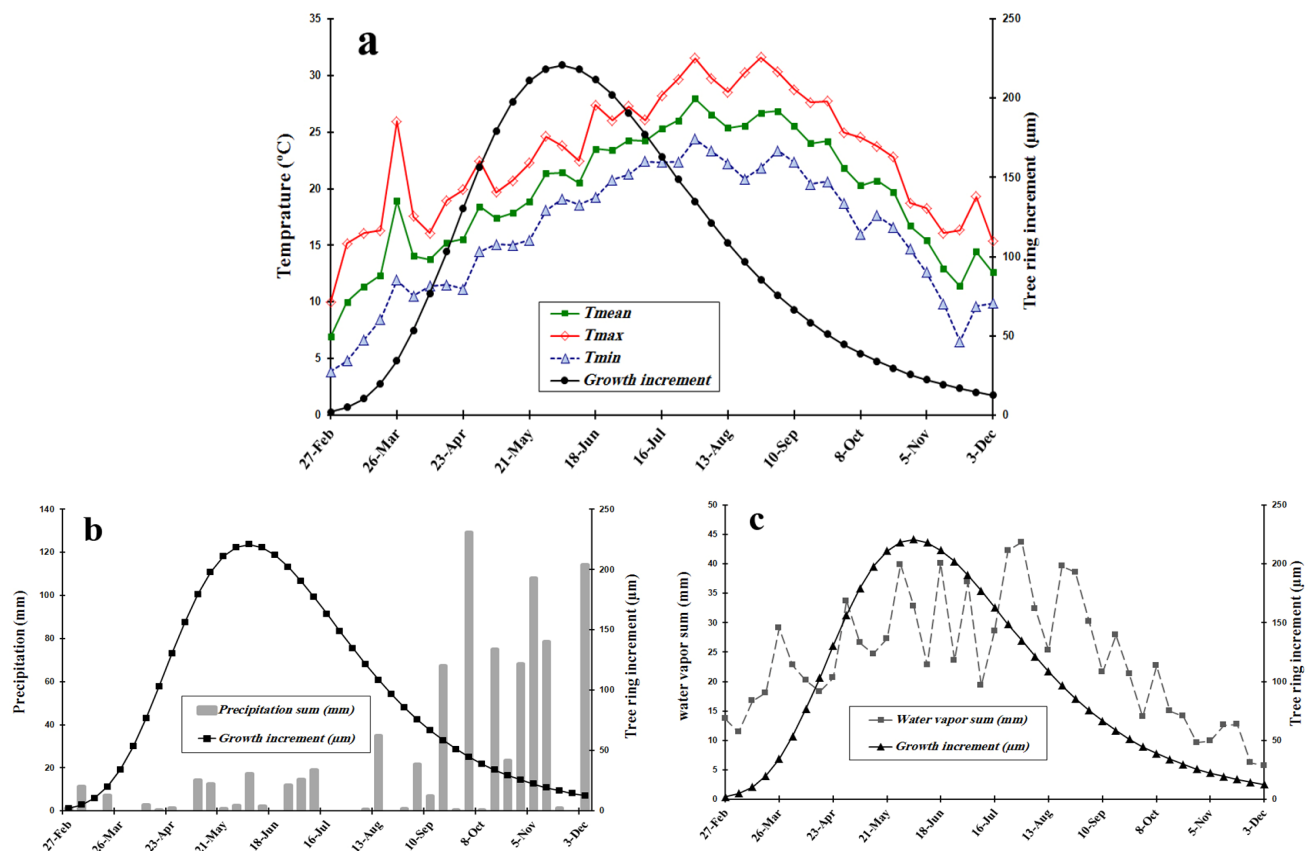


Fig. 3. Weekly changes in mean, maximum and minimum air temperature (a), precipitation sums (b) and water evaporation sums (c) and weekly increase in average ring width of trees during 2008 growing season. Interval between tick markers in horizontal axis is 4 weeks

Tab. 1. Correlation coefficient (r) and “parameter estimate”-values of weekly tree ring increment versus different climatic factors

	Climatic factors									
	Weekly mean temperature (°C)		Weekly mean maximum temperature (°C)		Weekly mean minimum temperature (°C)		Weekly sum precipitation (mm)		Weekly sum water evaporation (mm)	
	r	Parameter estimate	r	Parameter estimate	r	Parameter estimate	r	Parameter estimate	r	Parameter estimate
Weekly tree ring increment (μm)	0.52	-11	0.46	-13.4	0.56	23.8	-0.33	-0.5	0.67	4.5*

Note: All r-values are significant at $p < 0.05$; *parameter estimate-values are significant at $p < 0.05$

Discussion

According to the statistical analyses, it can be concluded that the minimum air temperature and water evaporation had the most important effect on the rate of xylem formation while precipitation role was minor and negative. Similarly, Venugopal and Liangkuwang (2007) reported that the peak activity of xylem production was generally favoured by the mean minimum temperature in a species grown in subtropical area of India but mean rainfall was less important. In some conifers of alpine forests, rate of tracheid production was related to the air temperature but no significant correlations were found between wood formation and precipitation or soil temperature (Gruber *et al.*, 2009).

Although almost all researchers have confirmed the role of temperature in activation of cambium and rate of xylem formation especially in temperate regions (Moser *et al.*, 2009) but it's not generally accepted which form of temperature (Max and Min air temperature, stem and soil temperature, the mean number of degree days, etc) has the main contribution on tree radial growth. Adding to this complexity, different species may respond differently to this environmental factor (e.g. Begum *et al.*, 2010). An increase in temperature might accelerate the conversion of storage starch to sucrose which is used for cell production (Begum *et al.*, 2007; Oribe *et al.*, 2003) and hence increase the growth rate. Besides, it seems that temperature has a positive effect on the rate of photosynthesis up to a certain point (Hoshino *et al.*, 2008; Woledge and Parsons, 1986) and if it exceeds an optimum level, it may impose limiting effect on radial growth. That may be the reason why Min temperature showed stronger relation with growth than Max and Mean temperature (Deslauriers and Morin, 2005).

There are several reports about the importance of precipitation on wood formation in arid and semi-arid regions (Pumijumnon and Wanyaphet, 2006) but in temperate and cold areas, its role diminishes and there may be no relation between annual growth and precipitation in these areas (Gruber *et al.*, 2009; Hoshino *et al.*, 2008). Although, water status of tree is highly related to the rate of wood formation (Larson, 1994) but rainfall probably is an important factor only in the regions where the soil moisture content is dependent on rainfall (Eilmann *et al.*, 2011; Rao and Rajput, 2001). In this study, water availability was not a limiting factor of growth since the study site is gener-

ally very humid and large amount of precipitation in the growing season and previous autumn and winter (data not shown) presented enough water resources for the trees. The minor negative relation of rainfall on growth could be interpreted according to its indirect effect on temperature and solar radiation. On rainy days, air temperature and light absorption of plant slightly drops; mostly because of clouds. Therefore, the rate of wood formation somewhat decreased in rainy weeks.

The relation between evaporation and tree growth has not been studied comprehensively, so far. It can be suggested that an increase in water evaporation leads to a higher rate of stomata transpiration in tree leaves which in turn increase the carbon uptake and rate of xylem formation. It should be mentioned that Stomata usually close when the leaves are in danger of losing too much water (Thomas, 2004) and under high temperature and low soil moisture, drought could be amplified by increasing evapotranspiration (Eilmann *et al.*, 2011) but since water was not in short supply and weather didn't get too hot in studied area, evaporation probably remained mostly in the optimum level for the growth of trees.

Conclusions

In order to interpret the effect of different meteorological factors on the rate of wood formation, the mutual dependence of these factors should be considered rather than considering them separately (Seo *et al.*, 2011). Since the studied trees received abundant amount of precipitation before and during growing season and weather was not too hot, the evaporation and minimum temperature had the main positive influence on xylem formation of beech trees.

References

- Ahmadi MT, Attarod P, Marvi-Mohadjer MR, Rahmani R, Fathi J (2009). Partitioning rainfall into throughfall, stemflow, and interception loss in an oriental beech (*Fagus orientalis* Lipsky) forest during the growing season. *Turk J Agric For* 33:557-568.
- Antonova GF, Stasova VV (1997). Effects of environmental factors on wood formation in larch. (*Larix decidua* Ldb.) stems. *Trees* 11:462-468.
- Barlow PW, Powers SJ (2005). Predicting the environmental thresholds for cambial and secondary vascular tissue

- development in stems of hybrid aspen. *Ann For Sci* 62:565-573.
- Begum S, Nakaba S, Oribe Y, Kubo T, Funada R (2007). Induction of cambial reactivation by localized heating in a deciduous hardwood hybrid poplar (*Populus sieboldii* x *P. grandidentata*). *Ann Bot* 100:439-447.
- Begum S, Nakaba S, Oribe Y, Kubo T, Funada R (2010). Cambial sensitivity to rising temperatures by natural condition and artificial heating from late winter to early spring in the evergreen conifer *Cryptomeria japonica*. *Trees* 24:43-52.
- Begum S, Nakaba S, Islam MdA, Yamagishi Y, Funada R (2012). Effects of low temperature in reactivated cambial cells induced by localized heating during winter dormancy in conifers. *American J Plant Physiol* 7(1):30-40.
- Bräuning A, Homeier J, Cueva E, Beck E, Günter S (2008). Growth dynamics of trees in tropical mountain ecosystems. *Ecol Stud* 198:291-302.
- Deslauriers A, Morin H (2005). Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables. *Trees* 19:402-408.
- Downes GM, Drew DM, Battaglia M, Schulze D (2009). Measuring and modelling stem growth and wood formation: an overview. *Dendrochronologia* 27:147-157.
- Eilmann B, Zweifel R, Buchmann N, Graf Pannatier E, Rigling A (2011). Drought alters timing, quantity, and quality of wood formation in Scots pine. *J Experiment Bot* 62(8):2763-2771.
- Gruber A, Baumgartner D, Zimmermann J, Oberhuber W (2009). Temporal dynamic of wood formation in *Pinus cembra* along the alpine treeline ecotone and the effect of climate variables. *Trees* 23:623-635.
- Hoshino Y, Yonenobu H, Yasue K, Nobori Y, Mitsutani T (2008). On the radial-growth variations of Japanese beech (*Fagus crenata*) on the northernmost part of Honshu Island, Japan. *J Wood Sci* 54:183-188.
- Larson PR (1994). The vascular cambium: development and structure. Springer, Berlin, 725 p.
- Mäkinen H, Nöjd P, Saranpää P (2003). Seasonal changes in stem radius and production of new tracheids in Norway spruce. *Tree Physiol* 23:959-968.
- Mohadjer MMR (2005). Silviculture. University of Tehran Press, Tehran, 387 p.
- Moser L, Fonti P, Büntgen U, Esper J, Luterbacher J, Franzen J, Frank D (2009). Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. *Tree Physiol* 30:225-233.
- Oladi R, Pourtahmasi K, Eckstein D, Bräuning A (2011). Seasonal dynamics of wood formation in Oriental beech (*Fagus orientalis* Lipsky) along an altitudinal gradient in the Hyrcanian forest, Iran. *Trees* 25:425-433.
- Oliveira JM, Santarosa E, Pillar VD, Roig FA (2009). Seasonal cambium activity in the subtropical rain forest tree *Araucaria angustifolia*. *Trees* 23:107-115.
- Oribe Y, Funada R, Kubo T (2003). Relationships between cambial activity, cell differentiation and the localization of starch in storage tissues around the cambium in locally heated stems of *Abies sachalinensis* (Schmidt) Masters. *Trees* 17(3):185-192.
- Pourtahmasi K, Lotfi N, Bräuning A, Parsapajouh D (2011). Tree-ring width and vessel characteristics of oriental beech (*Fagus orientalis*) along an altitudinal gradient in the Caspian forests, northern Iran. *IAWA J* 32 (4): 461-473
- Pumijumnong N, Wanyaphet T (2006). Seasonal cambial activity and tree-ring formation of *Pinus merkusii* and *Pinus kesiya* in Northern Thailand in dependence on climate. *For Ecol Manage* 226:279-289.
- Rao KS, Rajput KS (2001). Xylem structure and annual rhythm of development in the twigs of *Acacia nilotica* (L.) Del. growing in different forest of Gujarat State (India). *Phyton* 41(1):1-12.
- Rossi S, Deslauriers A, Morin H (2003). Application of the Gompertz equation for the study of xylem cell development. *Dendrochronologia* 21:33-39.
- Rossi S, Anfodillo T, Menardi R (2006a). Trephor: a new tool for sampling microcores from tree stems. *IAWA J* 27:89-97.
- Rossi S, Deslauriers A, Anfodillo T, Morin H, Saracino A, Motta R, Borghetti M (2006b). Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *New Phytol* 170:301-310.
- Schweingruber FH (1988). Tree rings: basics and applications of dendrochronology. D. Reidel Publishing Company, Dordrecht, 276 p.
- Seo JW, Eckstein D, Jalkanen R, Schmitt U (2011). Climatic control of intra- and inter-annual wood-formation dynamics of Scots pine in northern Finland. *Environ Experiment Bot* 72:422-431.
- Thomas P (2004). Trees: Their Natural History, 2nd Ed. Cambridge University Press, UK, 286 p.
- Vaganov EA, Hughes MK, Kirdyanov AV, Schweingruber FH, Silkin PP (1999). Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature* 400:149-151.
- Vaganov EA, Hughes MK, Shashkin AV (2006). Growth dynamics of conifer tree rings: image of past and future environments. Springer, Germany, 354 p.
- Van Der Werf GW, Sass-Klaassen UGW, Mohren GMJ (2007). The impact of the 2003 summer drought on the intra-annual growth pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) on a dry site in the Netherlands. *Dendrochronologia* 25:103-112.
- Venugopal N, Liangkuwang MG (2007). Cambial activity and annual rhythm of xylem production of elephant apple tree (*Dillenia indica* Linn.) in relation to phenology and climatic factor growing in sub-tropical wet forest of northeast India. *Trees* 21:101-110.
- Woledge J, Parsons AJ (1986). The Effect of Temperature on the Photosynthesis of Ryegrass Canopies. *Ann Bot* 57(4):487-497.
- Zeide B (1993). Analysis of growth equations. *Forest Sci* 39:591-616.