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SEASONAL DEVELOPMENT OF CAMBIUM AND SECONDARY XYLEM IN *POPULUS×EURAMERICANA CV. '74 /76'* DURING THE 2010 GROWING SEASON

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ABSTRACT

This study describes characteristics of cambium and the accumulation of xylem cells of fast-growing *Populus×euramericana cv. '74 /76'* during the active phase. Wood samples were collected periodically, and phenology and climate data was recorded weekly in the same period in 2010. The relationship between seasonal cambial activity, xylem development, and phenology are discussed. Results showed that the cambium presented a seasonal cyclical pattern of activity and dormancy. The accumulation of xylem cells was closely related to the features of cambium, in particular to the layers of cambium. The seasonal characteristics of cambium and the formation of xylem cells were not only decided by their own internal condition, but also affected by the climatic conditions of the outside environment. The higher cambial activity correlated to the temperature rang. In xylem cells, a larger development region was observed in June, when the trees were in full foliage.

KEYWORDS: *Populus×euramericana cv. '74 /76'*, active phase, cambial activity, xylem development, phenology.

INTRODUCTION

The cambium of trees in the temperate zone presents a seasonal cyclical pattern of activity and dormancy (Chen et al. 2010). During this periodicity, cambial cells and secondary xylem reveal changes in structure (Barnett 1973, Catesson 1994). Many researchers have focused on studies related to cambial activity and have researched the anatomical, cytological, and histochemical changes that occur in the cambium (Catesson 1994, Larson 1994). Many studies have dealt with the cellular changes associated with cambium periodicity, especially changes in the cytoplasm (Larson 1994, Iqbal 1995, Farrar and Evert 1997, Rensing and Samuels 2004). Numerous experiments have also demonstrated that studies on the cambial activity, especially in xylem formation, provide not only data about the age of trees, but also clues about the possible factors that control the growth of the trees. This kind of data is also useful in dendrochronology, in forecasting timber and biomass yield, and in determining forest dynamics (Jacoby 1989, Kozlowski et al. 1991, Eckstein et al. 1995, Priya and Bhat 1999). Studies about the seasonal development of secondary xylem and phloem in tropical trees, mainly Indian species, have been published (Rao and Rajput 1999, 2000, 2001, Rajput and Rao 2001, Venugopal and Liangkuwang 2007). Marcati et al. (2006) studied the cambial activity and annual rhythm of xylem production of *Cedrela fissilis* (Meliaceae) from the standpoint of phenology and climatic factors. The relationship between seasonal cambial activity, xylem and phloem development, and phenology in schizolobium parahyba, is that they all describe a fast growing tree from southeastern Brazil (Marcati et al. 2008).

Populus is presented as a model system for the study of wood formation (xylogenesis). The formation of wood (secondary xylem) is an ordered developmental process involving cell division, cell expansion, secondary wall deposition, lignification, and programmed cell death. Because wood is formed in a variable environment and subject to developmental control, xylem cells are produced that differ in size, shape, cell wall structure, texture, and composition (Mellerowicz et al. 2001). *Populus* is one of the fastest growing tree species, which is why it is used extensively in reforestation projects.

It is evident that the ability to improve wood properties depends on a fundamental understanding of the processes of xylem cell production and differentiation (Whetten and Sederoff 1991). The morphology of secondary xylem cells is determined in part by the dimensions of the cambial initials from which they are derived, and in part by the developmental changes that occur during differentiation (Ridoutt and Sands 1983). Changes in cambial anatomy are reported to occur with stem diameter, height, and season (Iqbal and Ghouse 1990). Previous studies have focused mainly on mature wood (secondary xylem) variation in cell morphology (Fahn and Werker 1990), but such features are not involved with the quantity changes during the active phase. In this study, cambial activity of *Populus×euramericana cv. '74 /76'* and the relationship of this activity with phenology and annual climatic variations were examined.

MATERIAL AND METHODS

Healthy plants of two-year old fast-growing *Populus×euramericana cv.'74/76'* grown in a plantation of Xiaotangshan in Beijing's Changping district (40°17″N, 116°39″E; Beijing, China) with the same diameter at breast height were chosen and marked. Two plant materials were collected 1.3 m above the trunk and sampled once a week from April to October in 2010. A month was divided into four periods, the first stage was 7th of each month, the second one was 15th of each month, the third one was 22nd of each month, and the fourth one was 30th of each month. The following figures are the same. On each occasion, blocks of about 10 mm^3 including phloem, cambium, and xylem cells were immediately immersed in fixative formalin–acetic acid–alcohol. Upon returning to the laboratory, they were placed in the same fresh fixative under a slight vacuum for 30 min. Following vacuum, these pieces were fixed in fresh fixative and preserved at 4°C.

Cross slices with a thickness of 10 μm, including phloem, cambium, and xylem, were cut on a sliding microtome, and then stained with 1 % safranine of alcohol solution for 2 hours. In the next stage, the slices were dehydrated with gradient alcohol, from 50, 70, 85, 95, 100 % into xylene, and then cemented with neutral gum. After that, an image analysis system and a research microscope (Olympus BH-2) were used to make measurements of cambium number, radial and tangential diameter of cambium, number of immature xylem and wood fiber, and number of mature xylem and wood fiber, according to quantitative anatomy conventional methods of wood. The data were analyzed by analysis of variance (ANOVA) and the correlations were made by One-way linear correlation with Pearson's analysis method.

With reference to the method that Cui et al. (1993) described, the numbers of three kinds of cells were counted, respectively, in accordance with the following morphology standard, and then variance analysis and drawings were made for better analyzing.

(1) Cambium cells, or cambial zone, radial rows of fusiform and ray initials, including phloem and xylem mother cells, which are located between xylem and phloem, that have a radial diameter that is two times less than or equal to the smallest cell along the radial direction.

(2) Immature xylem cells, secondary xylem suffering/underdifferentiation, which are located inside of cambium, that have a radial diameter that is greater than that of the biggest cambium cell, less than or equal to that of the mature xylem cells, and have a cell wall that is thinner than that of mature xylem without secondary wall.

(3) Mature xylem cells, which have the largest radial diameter with the thickest secondary wall and deeper colors.

The climatic data (minimum temperature, maximum temperature, barometric pressure, relative humidity, and total rainfall) were collected from April to October in 2010 at one-week intervals during the sampling (Tab. 1).

Tab. 1: Meteorological data during the sampling in 2010.

Sampling time	Maximum temperature	Minimum temperature	Barometric pressure	Relative humidity	Precipitation
	(°C)		(hPa)	(%)	(mm)
Apr.7, 2009/2010	17	5	1018	34	0.8
Apr.15, 2009/2010	14	6	1019	43	1.3
Apr. 22, 2009/2010	16	9	1019	65	4.2
Apr.30, 2009/2010	18	17	1012	34	10
May 7, 2009/2010	28	14	1004	39	13
May 15, 2009/2010	25	14	1013	40	0.8
May 22, 2009/2010	27	16	1004	54	12.3
May 30, 2009/2010	30	20	1009	47	6.5
Jun. 7, 2009/2010	28	18	1014	58	40
Jun. 15, 2009/2010	29	20	1008	62	21.6
Jun. 22, 2009/ 2010	29	20	1003	66	20
Jun. 30, 2009/2010	31	22	1005	56	0
Jul. 7, 2009/2010	35	24	1000	49	0
Jul. 15, 2009/2010	28	23	1006	74	19.6
Jul. 22, 2009/2010	32	24	1005	69	14.3
Jul. 30, 2009/2010	35	27	1003	67	0
Aug. 7, 2009/2010	31	23	1007	55	27.2
Aug. 15, 2009/ 2010	32	24	1003	67	3.2

Aug. 22, 2009/2010	30	22	1010	71	126.5
Aug. 30, 2009/2010	30	21	1011	63	28
Sep. 7, 2009/2010	28	21	1012	68	6.5
Sep. 15, 2009/2010	32	21	1011	54	0
Sep. 22, 2009/2010	21	14	1013	80	56.4
Sep. 30, 2009/2010	23	11	1020	48	0
Oct. 7, 2009/2010	23	11	1018	59	0
Oct. 15, 2009/2010	21	12	1016	56	25.4
Oct. 22, 2009/2010	13	8	1024	68	4
Oct.30, 2009/2010	15	4	1028	50	8.6

RESULTS AND DISCUSSION

Seasonal changes of cambial activity and characteristics of the cambial zone

The changes of cambium and the formation of xylem have a close relationship with the changes of phenology characteristics during the active phase of *Populus×euramericana cv. '74/76'*. Phonological data (anthotaxy elongation, leaf growth, full foliage, yellow leaf, partial defoliation, and defoliation) were collected at one-week intervals during the reproductive period in 2010 (Tab. 2). As it can be seen in Tab. 2, the range of cambium cells number was from 5 to 12 layers during the seasonal cycle. The trend of cambial cells number first increased then decreased, and the number reached to a peak (11-12 layers) in June and July. The diameter of trees grew from 27.73 to 36.25 mm during the active phase. The active phase of *Populus×euramericana cv. '74/76'* was from early April to late September in 2010. On April 7th, the cambium was beginning its activity, and the trees were in the budding phenophase. The highest cambial activity was observed between April 30th and September 22nd, when the trees had mature leaves. The beginning of the reduction of cambial activity to a minimum was on September 30th, when the trees underwent partial leaf fall.

Tab. 2: Relationship of cambium activity with phenology.

Sampling time	Cambial cell number	Diameter at breast height (mm)	Tissue differentiation	Phenological features	Different phase of cambial activity
Apr.7, 2010	5.38	27.73±0.17	Phloem	Anthotaxy elongation	Active phase
Apr.15, 2010	6.38	27.78±0.30	Phloem	Leaf growth	Active phase
Apr. 22, 2010	6.67	28.32±0.25	Xylem+Phloem	Leaf growth	Active phase
Apr.30 2010	7.10	28.82±0.36	Xylem+Phloem	Full foliage	Active phase
May 7, 2010	9.60	29.10±0.11	Xylem+Phloem	Full foliage	Active phase
May 15, 2010	10.78	29.78±0.27	Xylem+Phloem	Full foliage	Active phase
May 22, 2010	10.17	29.60±0.36	Xylem+Phloem	Full foliage	Active phase
May 30, 2010	10.02	30.59±0.20	Xylem+Phloem	Full foliage	Active phase
Jun. 7, 2010	9.78	30.66±0.22	Xylem+Phloem	Full foliage	Active phase
Jun. 15, 2010	11.12	31.66±0.31	Xylem+Phloem	Full foliage	Active phase
Jun. 22, 2010	10.47	31.73±0.29	Xylem+Phloem	Full foliage	Active phase
Jun. 30, 2010	11.52	31.83±0.40	Xylem+Phloem	Full foliage	Active phase

Jul. 7, 2010	10.51	32.08±0.25	Xylem+Phloem	Full foliage	Active phase
Jul. 15, 2010	9.20	32.04±0.49	Xylem+Phloem	Full foliage	Active phase
Jul. 22, 2010	8.53	32.51±0.41	Xylem+Phloem	Full foliage	Active phase
Jul. 30, 2010	11.56	32.67±0.27	Xylem+Phloem	Full foliage	Active phase
Aug. 7, 2010	8.53	33.28±0.30	Xylem+Phloem	Full foliage	Active phase
Aug. 15, 2010	9.51	33.63±0.13	Xylem+Phloem	Full foliage	Active phase
Aug. 22, 2010	8.27	33.97±0.15	Xylem+Phloem	Full foliage	Active phase
Aug. 30, 2010	11.61	34.16±0.43	Xylem+Phloem	Full foliage	Active phase
Sep. 7, 2010	10.22	34.16±0.32	Xylem+Phloem	Full foliage	Active phase
Sep. 15, 2010	9.09	34.66±0.37	Xylem	Full foliage	Active phase
Sep. 22, 2010	7.10	35.18±0.33	Xylem	Full foliage	Active phase
Sep. 30, 2010	9.06	35.40±0.40	Xylem	Yellow leaf	Dormant phase
Oct. 7, 2010	9.34	35.51±0.18	-	Partial defoliation	Dormant phase
Oct. 15, 2010	6.61	35.95±0.13	-	Partial defoliation	Dormant phase
Oct. 22, 2010	5.56	36.20±0.25	-	Defoliation	Dormant phase
Oct.30, 2010	5.71	36.25±0.44	-	Defoliation	Dormant phase

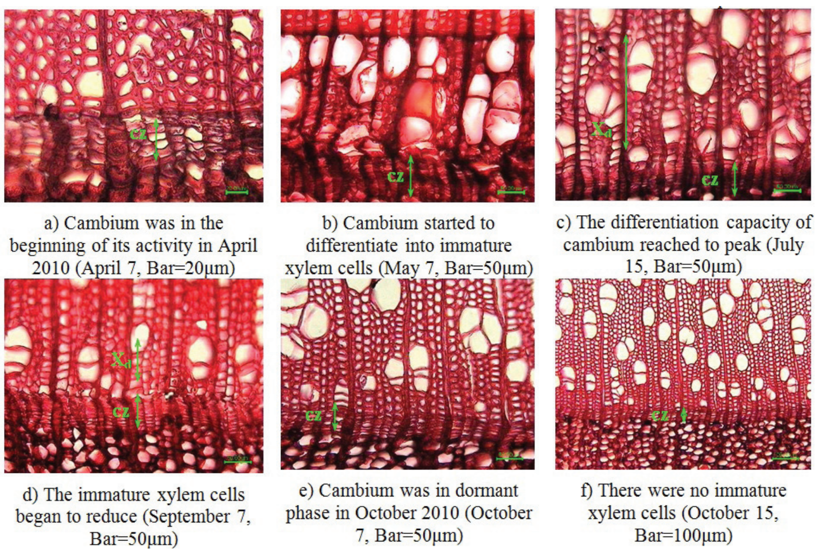

Fig. 1: Microstructure of cross section of Populus×euramericana cv. '74/76'.

According to Figs. 1, on April 7th (Fig. 1a), the cambial cells (5-7 layers of fusiform cells) were swelling and showed few periclinal divisions, indicating the beginning of cambium activity. When the cambium was active, there were a large number of immature xylem cells differentiating. On May 7th, cambial activity was just beginning, and approximately 4-10 layers of xylem immature cells and 6-11 layers of cells in the cambial zone were visible (Fig. 1b). On July 15th, the cambium had 7-15 layers of fusiform cells and many layers (10-25) of immature xylem cells, indicating high cambial activity (Fig. 1c). On September 7th, the cambium was reducing its activity to a minimum, with 5 to 10 layers of cells in cambium and 7-12 layers of immature xylem cells (Fig. 1d). When the cambium was entered in dormant phase, the cambial zone was narrow, with relatively thick radial walls and surrounded by no layers or only a few (1-2) layers of immature secondary xylem. Dormant cambium is shown in Fig. 5. On October 7th (Fig. 1e) and October 15th (Fig. 1f), the cambium was dormant and contained 5-7 cells in the radial rows. During this period, there were 0-2 immature xylem cells.

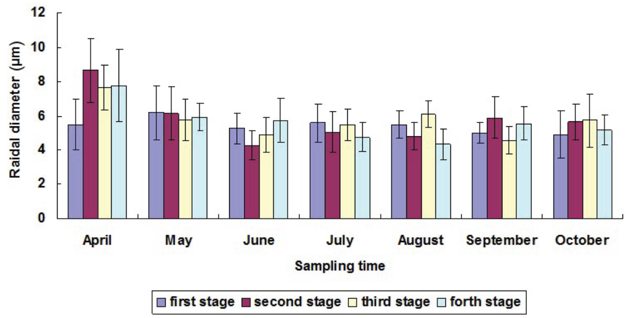

Fig. 2: The changes of radial diameter of cambium cells.

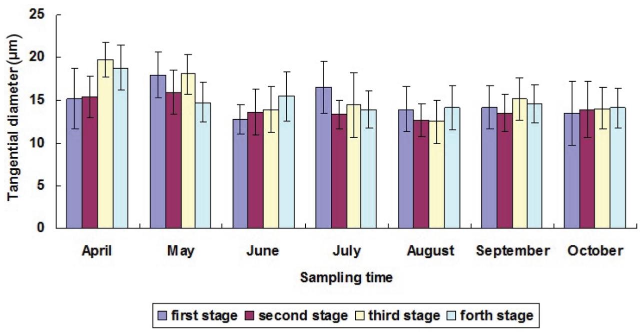

Fig. 3: The changes of tangential diameter of cambium cells.

The radial and tangential diameters of cambial cells in different stages during the active phase were measured and analyzed. The results of mean and standard deviation are shown in Figs. 2 and 3. According to the figures, the radial diameter of cambial cells reached the maximum of 8.68 μm on April 15th. The cambial cell division was in the active period in April, during the time that the radial extension of cambial cells was more remarkable. It decreased gradually from May and then remained stable. The tangential diameter of cambial cells achieved the maximum of 19.8 μm on April 22nd. The tangential diameter was greater in the period from April to May. It tended to decrease in June, and then was kept in a steady state. Changes of radial diameter and tangential diameter were basically the same.

According to the ANOVA, three characters of cambial cells were significantly correlated at the 0.01 levels. This indicates that the cambial cells are largely impacted by growth time during the active phase.

Seasonal formation of the xylem

Xylem cells were produced in mid-April, but until April 21st, one week after the growth of leaves, only 2 layers immature xylem cells appeared (including the expanding vessel elements and wood fibers). Larger vessel elements and thin-walled wood fibers (early wood) were formed during the cambium's higher activity (May 7th) (Fig. 1b). Small differentiated vessel elements and thick-walled and flattened fibers (latewood) were visible adjacent to the cambium when its activity was at its lowest (October 7th and October 15th) (Figs. 1e and f).

The seasonal changes of the xylem cells during the active phase can be seen in Figs. 4-7. The layers of immature xylem cells (vessel elements and wood fibers) increased rapidly in May, and reached their maximum (about 20 layers) in mid-June, followed by a decline (Figs. 4 and 6). The cell wall of differentiated immature xylem cells in mid-August was thicker than that of the previous months. The immature xylem cells were not been found on September 30th (Figs. 4 and 6), indicating that the cambium has stopped differentiating the xylem cells. In late-May (Figs. 5 and 7), it began to show the mature xylem cells which had multi-level thickened secondary wall, therefore, it can be speculated that the maturity of xylem cells need 30-40 days to complete. From May to September, the total number (about 170-180 layers) of xylem cells increased significantly and it was maintained until September 30th (Figs. 5 and 7), until the leaves started to turn yellow (Tab. 2).

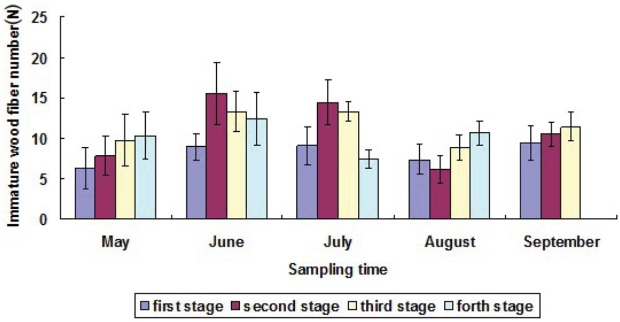

Fig. 4: The changes of immature wood fiber number.

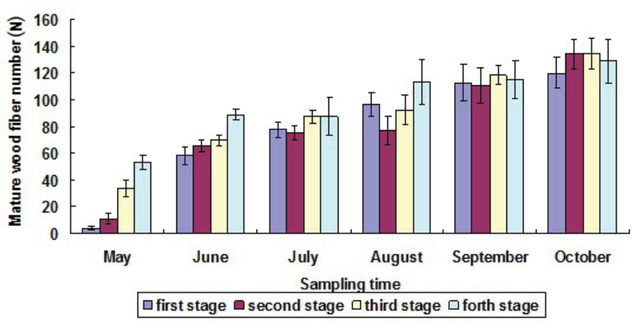

Fig. 5: The changes of mature wood fiber number.

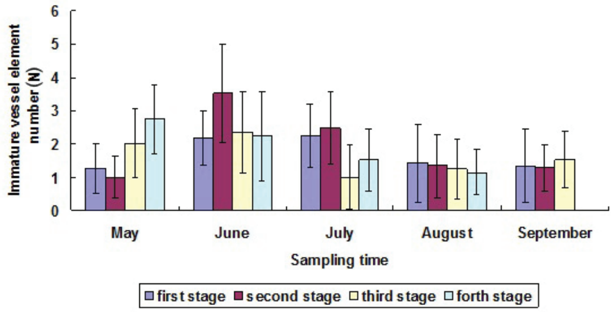

Fig. 6: The changes of immature vessel element number.

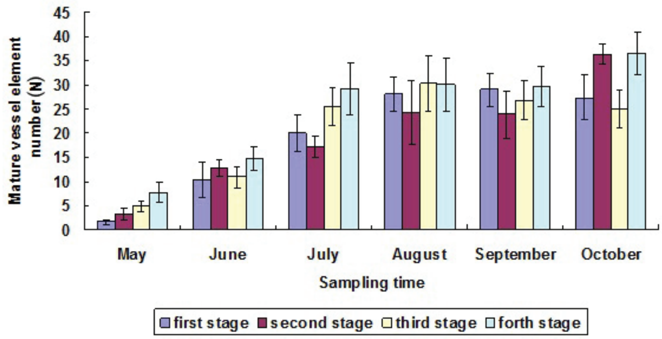

Fig. 7: The changes of mature vessel element number.

It can be seen from the ANOVA that the number of xylem cells in different stages were significantly correlated at the 0.01 levels. This indicates that the cambial cells are largely impacted by growth time during the active phase.

Correlation between cambium and xylem

Linear relationship analysis was made between the cambial characteristics and the xylem anatomical features. The measured data was taken in comparison. The most significant relations are highlighted in Tab. 3. According to the Pearson's analysis method, the coefficient of correlation between the cambium cell number and the number of immature wood fiber and immature vessel element were 0.321 and 0.233, respectively. The results showed that the cambium cell number had a highly significant positive correlation with the number of immature wood fiber and immature vessel element. It also can be seen from the results that the number of mature vessel element had an extremely significant negative correlation with the radial diameter of the cambium cell and the tangential diameter of the cambium cell, and the correlation coefficients were -0.121 and -0.192, respectively. The number of mature wood fibers had a significant negative correlation with the tangential diameter of the cambium cells and the coefficient was -0.098. There was a significant negative correlation between the cambium cell number and the number of mature vessel element, and the coefficient was -0.181.

Tab. 3: Linear correlation analysis between cambium and xylem.

	Number of immature wood fiber	**Number of mature wood fiber**	**Number of immature vessel element**	**Number of mature vessel element**
Cambium cell number	0.321**	-0.054	0.233**	-0.181*
Cambium cell R-diameter	-0.080	-0.063	-0.046	-0.121**
Cambium cell T-diameter	-0.042	-0.098*	-0.008	-0.192**

** Correlation is significant at the 0.01 levels (2-tailed);
* correlation is significant at the 0.05 levels (2-tailed).

The periodicity of cambium activity of deciduous trees in the temperate region was usually apparent. A complete cycle of seasonal changes of vascular cambium ultrastructure of *Populus×euramericana cv. '74/76'* was studied. The cambial cells reactivated before bud swelling. However, initiation of cambial activity with cell proliferation and increase of immature xylem cells took place about a week later than bud sprouting in 2010. The cambial cells shape, division, and arrangement in trees are commonly considered to be indirectly controlled by indole acetic acid (IAA) streams produced from buds and new leaves (Sachs 1981, Little 1981, Wodzicki and Wodzicki 1981). The results in the present study are coincident with this assertion. Furthermore, the phenomenon of new xylem production after new leaves appear evidently supported the assumption that growth substances from growing leaves are necessary for continuous normal formation of xylem. It was also suggested that the differentiation of xylem tracheary elements was induced by the polar transport of auxin streams from developing leaves (Wodzicki and Wodzicki 1981, Sachs 1993).

The TEM observations showed clearly that cambial cells division and the formation of new phloem cells started before the production of xylem (Yin et al. 2002). More details about the changes of cambial cells at the onset of cambial activity have been reported (Zhang et al. 1982, Cui et al. 1993, Luo et al. 1995, Yin et al. 2002). It has been shown (Fan et al. 1999) that when the fusiform initial cells and their derived cells grow to be the tubular cells, they would be necessarily subject to certain factors. The environment near or within a cell determines its differentiation and development, and this internal environment is mainly composed of plant hormones with different capacity and proportion (Savidge 1994). In addition, seasonal external factors such as sunlight, moisture, nutrients, and temperature will be significantly modified the xylem phenotype (Walsel and Fahn 1965). Therefore, the morphology of xylem cell is a unified reflection of its own genetic characteristics and variable regularity influenced by the environment.

Cambial activity and xylem formation in relation to phenology and climatic factors

The characteristics of cambium and the formation of xylem cells are not only decided by its own internal condition, but also closely related to the climatic features of the outside environment during the growth active phase. Tab. 2 indicates the relationship between the cambium activity and the phenological characteristics. It can be seen from the table that the cambium began into the active stage in April and the young leaves started to grow. Cambium cell layers were with a gradual increase in early April. It was in a vigorous division period during May and June. After September, It was started into the period of dormancy, and the cambium stopped differentiating the xylem cells. It can be seen from Tab.1 that the maximum difference in temperature (about 10°C) appeared in May and June. Corresponding to this period, the quantity accumulation of cambium layers was clearly at a peak of 11~12 layers.

The overall trends of atmospheric pressure were first reduced and then increased and the lowest value was 1003.30 hPa in July. On the contrary, the relative humidity reached a larger value of 72.71 % and maximum 76.29 %, appeared in September. The total rainfall volume was 126.50 mm in late August. Under certain lighting conditions, changing of air humidity can cause changes in plant phenology, such as in a 24 hour-light condition, increase of air humidity can slightly promote crop flowering, when in the less than 24 hour-light condition, the increase of air humidity can slightly delay flowering.

In order to make clear of climatic factors on seasonal development of *Populus×euramericana cv. '74/76',* linear relationship analysis was made between anatomical characteristics and climatic factors. The measured data were taken in comparison. The most significant relations are highlighted in Tab. 4. According to the table, the maximum and minimum temperatures had significant correlations with cambium cell number, cambium cell R-diameter, cambium cell T-diameter, immature wood fiber number, and immature vessel element number. The air pressure had significant negative correlations with cambium cell number, immature wood fiber number, and immature vessel element number. The relative humidity had significant negative correlations with cambium cell R-diameter and T-diameter, and significant positive correlation with immature wood fiber number, mature wood fiber number, and mature vessel element number.

Tab. 4: Linear correlation analysis between anatomical features and climatic factors.

	Maximum temperature	**Minimum temperature**	**Barometric pressure**	**Relative humidity**	**Precipitation**
Cambium cell number	0.827**	0.752**	-0.716**	0.163	-0.055
Cambium cell R-diameter	-0.492**	-0.486**	0.256	-0.501**	-0.116
Cambium cell T-diameter	-0.314	-0.400**	-0.027	-0.457**	-0.307
Immature wood fiber number	0.749**	0.796**	-0.715**	0.457**	0.255
Mature wood fiber number	0.190	0.268	0.157	0.570**	0.180
Immature vessel element number	0.712**	0.723**	-0.712**	0.296	0.163
Mature vessel element number	0.234	0.301	0.122	0.533**	0.257

** Correlation is significant at the 0.01 levels (2-tailed).

The trees begin to grow only when they are at a certain temperature range. Temperature for growth has a comprehensive effect. It can, through affecting photosynthesis, respiration, transpiration, and other metabolic processes, affect the synthesis and transport of organic matter and other metabolic processes to affect plant growth, but also it can, through direct affecting soil temperature, air temperature and the absorption and transporting of water and fertilizer, influence plant growth (Hannien 1995). The activity of the enzymes involved in metabolic activity has different performance at different temperatures; therefore, the effect of temperature on tree growth also has three basis points: minimum temperature, optimum temperature, and maximum temperature. Trees can grow only in the range of minimum temperature and maximum temperature (Snyder et al. 2001).

Although each type of xylem cells is differentiated by the cambium, and cells may maintain some relationships to a certain extent, the formation of the wood is a complicated process. The study showed that the accumulation of xylem cells was related to the cambium character, especially to the cambium number. Furthermore, the anatomical features of cambium and secondary xylem are affected partially by the environmental conditions, especially by temperature. From an ecological standpoint, this study will provide important data for research into dynamic growth.

CONCLUSIONS

The cambium presented a seasonal cyclical pattern of activity and dormancy. The active phase of *Populus×euramericana cv. '74/76'* was from early April to late September in 2010. The highest cambial activity was observed on April 30th to September 22nd, when the trees had mature leaves. The beginning of the reduction of cambial activity to a minimum was on September 30th, when the trees underwent partial leaf fall. From May to September, the total number (about 170~180 layers) of xylem cells increased significantly, and it was maintained until September 30th, when the leaves started to turn yellow. The accumulation of xylem cells was closely related to the features of cambium, in particular to the layers of cambium. The seasonal characteristics of cambium and the formation of xylem cells were not only decided by their own internal condition, but also affected by the climatic conditions of the outside environment. The higher cambial activity correlated to the temperature rang.

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