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Analysis of cambial activity and formation of wood in *Quercus robur* L. under conditions of a floodplain forest

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ABSTRACT: The analyses of the activity of cambium and the study of the increment of wood during one growing season of pedunculate oak (*Quercus robur* L.) under conditions of a floodplain forest is provided. The following parameters were studied: the beginning and end of the cambial activity, differentiation of wood fibres (libriform) and vessels and analysis of the total increment of wood during vegetation in dominant (D), co-dominant (CD) and subdominant (SD) trees in relation to ecological factors of the environment. The course of wood formation corresponds to typical growth curves which are modified by factors of the environment (mean daily temperature, precipitation, soil water supply). The rate of growth is limited by factors of the environment and under the lack of some of them it is reduced resulting in the decrease in the total production of cells. Oak is a species sensitively responding to the period of drought which is particularly manifested in wood increment in subdominant trees. Sufficient supplies of water during spring months accelerate the formation of early wood including differentiation of spring vessels as corroborated by the results. The total formation of wood is dependent not only on the characteristics of the respective growing season but particularly on the social position of trees in the stand.

Keywords: wood formation; effect of environment; cell differentiation; radial growth; *Quercus robur* L.

The study is aimed at the explanation of the effect of environmental factors (seasonal character of climate) of a floodplain forest on the cambial activity and formation of wood in *Quercus robur* L. The objective of the paper was to characterize the activity of cambium and differentiation of xylem elements (libriform fibres, vessels) in the course of a growing season. The paper is considered as a preliminary outline (because the analysis was carried out for one growing season, i.e. 1998 only) of the effect of a site on the duration of cambial activity and the total increment of wood. Attention was paid to the meristematic activity of cambium because it effects to a certain extent the radial growth of plants (EVANS 1972; MATOVIČ 1975, 1990; HORÁČEK 1994b). The radial growth is characterized by the total width and density of annual rings. The number and size of cells is dependent on the environmental factors which can modify the structure of annual rings. Effects of the seasonal character of climate reflects on the anatomical structure of annual rings (FRITTS 1976, 1990; SCHWEINGRUBER 1990) influencing the growth parameters. Changes in growth (formation of wood) and differentiation of wood structural elements, i.e. cells occur in relation to particular ecological factors. The recorded changes in climate can thus be detected in the tree-ring structures (FRITTS 1976; HUGHES et al. 1982; BRUBAKER, COOK 1983; BRIFFA et al. 1990). Among the studies that deal with wood formation in relation to the environment there are few which observe differentiated phases of cell growth (WAREING 1958; SKENE 1969; WODZICKI 1971; WAISE, FAHN 1965; VAGANOV et al. 1990; FRITTS et al. 1991, 1992; ANTONOVA, STASOVA 1996).

The radial growth of plants in relation to ecological conditions as a set of measurable factors was analysed by HORÁČEK (1994a,b, 1995, 2003), HORÁČEK et al. (1999).

BRAUN (1970) ranks *Quercus robur* L. among structural types the basic tissue of which is formed by libriform fibres and tracheids (1:1). Tracheids with vessels proceed radially through late wood. A hydrosystem is concentrated in the region of vessels – tracheids. Our measurements concerning the differentiation of wood fibres was carried out on libriform fibres forming more or less radial strips along wide pith rays. Authors (WAGENFÜHR 1989; SCHWEINGRUBER 1990; GROSSER 1977) mention for wood of oak representing ring-porous broadleaved species the following anatomical structure: macro and micro vessels, thick-walled libriform fibres, vasicentric tracheids (fibrous tracheids), apotracheal wood parenchyma, viz.

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reticular or scalariform, homogenous single-layer pith rays and often also multi-layer ones. In wide annual rings only (more or less radially orientated groups of summer vessels), anatomical structure is characteristic. SCHWEINGRUBER (1990) mentions that particular species of the genus *Quercus* cannot be differentiated on the basis of their anatomical structure.

MATERIAL AND METHODS

Trial plot characteristics

Sampling was carried out on a trial plot (IBP) in a floodplain forest 2 km north of Lednice na Moravě (the Horní les locality, stand No. 623 a_2). The plot is situated at 165 m altitude. The geographic position is given by the following co-ordinates: 48°48´22´´N and 16°46´32´´E. Mean annual temperature amounts to 8.4°C and mean annual precipitation 524 mm. The soil type of the area is semi-gley developed on alluvial depositions of the Dyje river, forest type group *Ulmeto-Fraxinetum-carpineum. Quercus robur* L. is a dominant species (74%). The stand is 92–107 years old. Mean height of the trees is 27 m, max. height 34–35 m. Duration of the growing season is 172–183 days, solar radiation amounts to 1,800–2,000 hours. More detailed data on the area gives PENKA et al. (1985).

Sampling and methods of processing

In the trial plot, nine trees were selected of different diameter classes representing dominant (D), co-dominant (CD) and subdominant (SD) trees, three trees each. The dominant trees (D) reach a height over 29 m and age 102 years, the co-dominant trees (CD) 27–29 m and age 96 years and the subdominant (SD) trees less than 27 m and age 85 years. The samples were taken using a puncher auxanometer at breast height (1.3 m) in one-month intervals in the course of the 1998 growing season. By taking samples along the whole stem girth its possible eccentricity was eliminated. FAA (formaldehyde-aceto-ethanol) was used as a fixation medium for the samples. Samples for the microscopic analysis of cambial activity and differentiation of wood elements were cut using the Jung's slide microtome for making permanent preparations. Cross sections 30–40 µm in thickness were dyed by a combined dye, viz. light green – safranine (NĚMEC 1962; WODZICKI 1971) which colours non-lignified parts of wood green and lignified parts red. In each of the samples (preparations) representing particular trees, five parallel measurements were carried out by an ocular micrometer with 300× magnification. The following characteristics were studied: start and termination of cambial activity, mean width and mean number of cells in the cambial zone, mean increment of wood (in µm and the number of cells), mean width and mean number of cells in the layer of radially enlarging, maturing and mature wood, differentiation of vessels. Differentiation of libriform fibres in the course of the growing season was studied along wide pith rays where it forms more or less radial strips. Climatic data (mean daily temperatures at a height of 2 m above the ground, stand precipitation, soil water supply) were taken over from the staff of the Institute of Forest Ecology, Mendel University of Agriculture and Forestry, Brno (data on soil water reserves were not converted).

RESULTS

Characteristics of the cambial zone

The cambial zone variability (width, number of cells) is depicted in Fig. 1. With respect to warm April (temperatures > 8°C) and considerable supplies of physiologically available water, the activity of cambium was started already before the first sampling, i.e. 27 April. The start of cambial activity is related to the observation of the first differentiating cells. At the end of April, on average 6.66 radially enlarging cells were already observed. On 27 April 1998, mean number of cells in the cambial zone amounted to 4.36 (width 21.33 µm) gradually increasing both in terms of the number of cells and the cambial zone width. The number of cells reaches its maximum 5.57 at the end of August, maximum width 26.36 µm of the cambial zone was observed at the end of July. Then, a slight decrease follows down to values found in the spring period at the beginning of the cambial activity. At the end of October (27 October), 4.65 cells 21.49 µm in width occur in the cambial zone. The termination of cambial activity refers to a date when no wood increment was noticed. In our case, cambium finished its activity in the period from the end of September to October. With respect to monthly sampling, it is not possible to determine the time exactly (on 28 September, 0.4 maturing cells were found in CD and SD trees). The prolongation of cambial activity can be related to the rich supply of soil water under conditions of the floodplain forest. In the period of dormancy, mean number of cells in the cambial zone amounted to 4.2–4.6 (width 20.48 µm). The values given above are, however, subject to certain inaccuracies with respect to the often rupture of a preparation just in the region of a cambial zone.

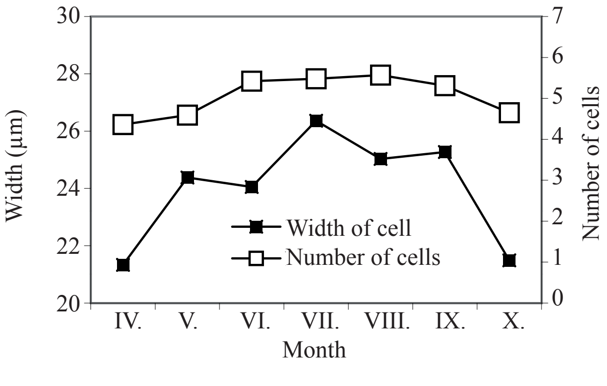

Fig. 1. Width and number of cells in the cambial zone during the growing season

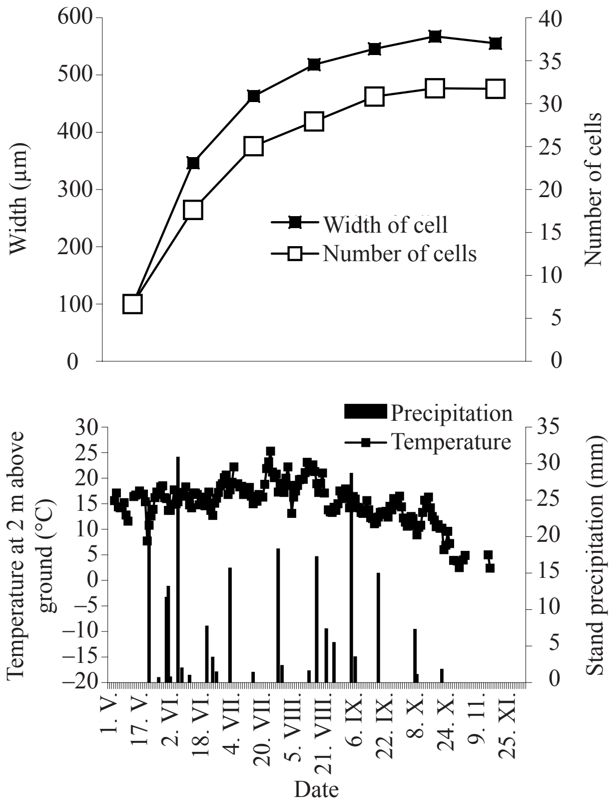

Fig. 2. Total increment of wood in relation to daily temperatures and monthly precipitation

Analysis of the radial increment of wood

The radial increment of wood is characterized by the total width of the wood layer or by the total number of differentiated elements at the end of the growing season. The course of wood formation during the growing season corresponds to growth curves. Fig. 2 shows the relationship between total wood increment and temperature and precipitation. The curve shape is modified according to growth conditions. The shape of curves in D, CD and SD trees is depicted by Fig. 3. Growth curves in SD trees are flatter than in CD and D trees. Decrease in values of climatic characteristics in a certain growing season results in the decrease in wood increment in the given time period. The maximum increment of wood was observed in the period from the end of May to the end of June (26 May–27 June). Mean values of the increment for the period amounted to 248.21 µm. The period was richest in precipitation, mean daily temperatures amounted to 16°C (max. 18.5°C, min. 12.7°C). Later on, wood increment was gradually lower which is related to increased transpiration and decreased intensity of photosynthesis during summer months. A marked difference in the total increment of wood occurred in D trees where the annual ring amounted to about 1 mm, in CD trees 746 µm and SD trees 267 µm. In SD trees, only a small percentage of late wood was formed (see Fig. 4). Narrow annual rings were, however, noticed also during previous three years. It is evident from a climogram (see Fig. 2) that a so-called precipitation deficit occurred from the end of July to the end of August. The fact reflected in the decreased increment of wood.

Results confirm that both temperature and precipitation (soil water supplies), and the social position of trees in the stand modify the growth curve shape and affect the total increment of wood.

Differentiation of wood fibres (libriform)

Numbers of cells and width of layers (µm) were studied in particular stages of the creating annual ring representing mean values in dominant, co-dominant and subdominant trees. The terminology is adopted from WODZICKI (1971) and MATOVIČ (1990). Analysis of the relationship between radial growth and environmental factors was focused on the phases of radial enlargement and maturation. In the process of enlargement and maturation, cells attain different size and exhibit variable wall thickness. At any moment of the growing season it is possible to specify the cell-growth phase in which any of the xylem elements occur. The average radial number of cells found in each of growth phases is presented in Fig. 5.

The first radially enlarging cells in the differentiation zone were formed at the end of April (27. 4.), on average 6.7 cells. At the end of May (26. 5.), on average

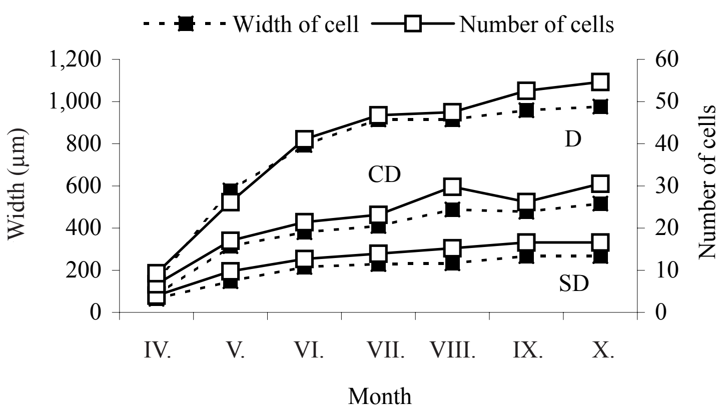

Fig. 3. Analysis of the radial increment of wood of dominant (D), co-dominant (CD) and subdominant (SD) trees

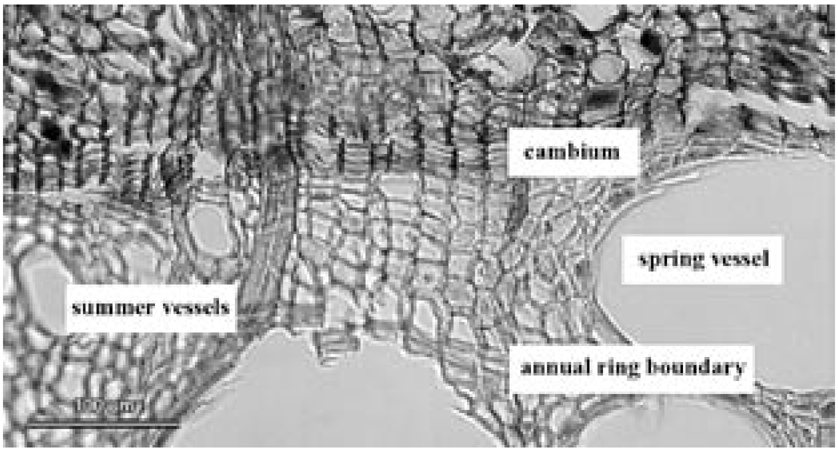

Fig. 4. The formation of xylem in subdominant trees – atypical microstructure

11 cells occur in the differentiation zone and in the zone of mature wood already 6.6 lignified cells (secondary cell wall formed, lysis of the cell content). On 28 June, 14.6 cells occur in the zone of mature wood. At the end of July (27. 7.), considerable decrease in the number of cells and in the differentiation zone width in favour of mature wood occurs. In the zone of mature wood, 23.4 cells occur measuring 458.3 µm from the total mean increment of 518.1 µm. At the end of August (26. 8.), 3.5 cells only occur in the differentiation zone, the zone of mature wood being formed on average by 27.3 cells. At the end of September (28. 9.), 0.3 cells occur in the differentiation zone, in the zone of mature wood being on average 31.8 cells. The end of September – the beginning of October can be considered to be the end of the differentiation of wood fibres.

Differentiation of vessels

The first non-lignified spring vessels were formed at the end of April (27. 4.) in D trees, a series of cells was formed. A typical circular grouping of spring vessels can be observed in all trees at the end of May. In D trees, the second series of partly lignified vessels was formed at the end of May. Sporadic summer vessels were formed in CD and SD trees at the end of June, in D trees the beginning of the radial grouping of summer vessels was observed. At the end of July, summer vessels remain individual in CD and SD trees, in SD trees being very sporadic. In D trees, characteristic radial grouping of mainly lignified summer vessels is finished. At the end of August, all summer vessels are already lignified. In SD trees, radial grouping of summer vessels typical of oak trees was not formed during the growing season. The fact can be attributed to the small increment of wood. Narrow annual rings without the radial grouping of vessels were also observed in previous three years in SD trees. Thus, it is possible to conclude that the wider the annual rings the more robust the radial grouping of summer vessels. At the end of the growing season, diameters were measured of spring vessels in D, CD and SD trees (n = 100, in each of the trees, evaluation by standard statistic methods, mean (x), standard deviation (s_x), variation coefficient (V)). The measurement was carried out in the radial and tangential direction. Dimensions of vessels markedly differed in D and SD trees. Dimensions of vessels in D and SD trees were 282.65 × 270.93 and 229.57 × 227.18 µm, respectively. Mean dimensions of spring vessels are: x = 253.51 × 252.36 µm, s_x = 3.86, V = 15.39%. Diameters of summer vessels were measured as well (n = 200), x = 43.20 µm, s_x = 0.74, V = 48.61%. WAGENFÜHR (1989) gives the following dimensions for spring vessels: 150–270–350 µm, for summer vessels: 37–70–140 µm.

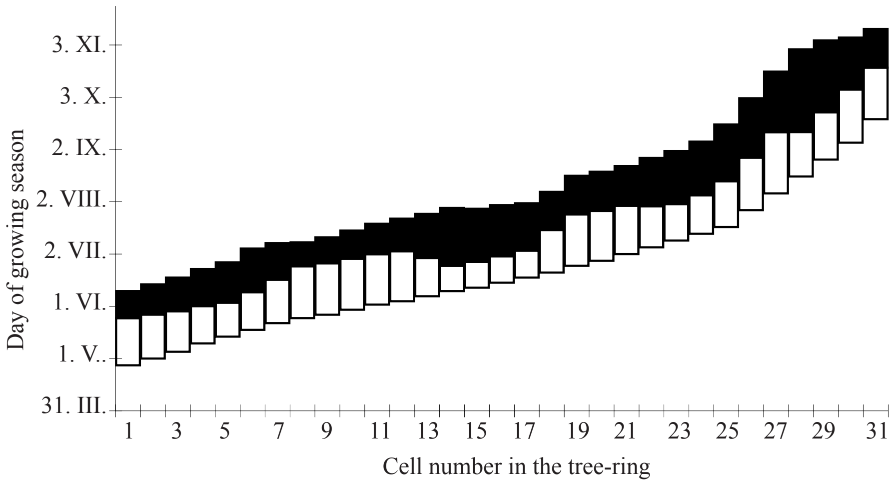

Fig. 5. The average duration of each differentiated cell in the zones of enlargement (light columns) and maturation (dark columns) formed during the season 1998

DISCUSSION AND CONCLUSION

In the paper, we endeavoured to analyse the activity of cambium and to study the increment of wood during the growing season of pedunculate oak (*Quercus robur* L.) under conditions of a floodplain forest. The following parameters were studied: the beginning and end of the cambial activity, differentiation of wood fibres (libriform) and vessels and analysis of the total increment of wood during vegetation in dominant, co-dominant and subdominant trees in relation to ecological factors of the environment. With respect to favourable temperature conditions and rich supplies of physiologically available water (total monthly precipitation at a depth of 40 cm, i.e. the physiologically active layer of soil, amounted to 168 mm in April) in soil at the beginning of the growing season, cambium was active as early as the end of April (27 April 1998). The onset of mitotic activity of cambium at the turn of April and May is related to the increase in mean daily air temperatures to a critical temperature.

MATOVIČ (1990) mentions that a sum of long-term active temperatures over 8°C is necessary for starting the cambial activity in ash. The end of cambial activity falls on the period end of September – beginning of October. With respect to monthly sampling it is not possible to determine an exact date as well as an exact date of the beginning of cambial activity. The activity of cambium in pedunculate oak in a floodplain forest takes about 6 months. Problems of cambial activity and wood formation were dealt with by a number of authors (PHILIPSON et al. 1971; WODZICKI 1971; KOZLOWSKI 1971; FRITTS 1976, 1990). Problems of the formation of wood in ash and spruce were studied by MATOVIČ (1975, 1977, 1990).

The course of wood formation corresponds to typical growth curves which are modified by factors of the environment (mean daily temperature, precipitation, soil water supply). The rate of growth is limited by factors of the environment and under the lack of some of them it is reduced resulting in the decrease in the total production of cells. The gradual decrease in radial growth is a response to the decrease in soil water supplies in the physiological depth (the locality in the floodplain forest is permanently well supplied by soil water). HORÁČEK (1994a,b) mentions in spruce (Rájec and Bílý Kříž localities) the termination of radial growth during the first half of September, i.e. one month earlier as compared with oaks in the floodplain forest. Increase in mean daily air temperatures accelerates the radial growth already in the first half of the growing season. Social position of SD trees considerably affect the total increment of wood through their small increments their microscopic structure being atypical as well (narrow annual rings, small percentage of late wood, sporadic vessels). Maximum increment was studied in the first half of the growing season, i.e. from the end of May to the end of June in all trees. Mean daily temperatures in the period amounted to 16°C (max. 18.5°C, min. 12.7°C), precipitation in the period can be considered to be richest. At the end of May, the onset of the formation of late wood and first lignified wood fibres were noticed in dominant trees. A period of the formation of early wood can be considered to be very short in all trees. The fact can be also attributed to favourable climatic conditions. At the end of June, late wood was formed already in all trees (SD, CD, D). In D trees, more than one half of the increment was formed by totally lignified mature cells of wood fibres. In trees only which formed wider annual rings during the growing season it was possible to notice the characteristic anatomical structure of oak, i.e. radial grouping of summer vessels as confirmed by SCHWEINGRUBER (1990). In the second half of the growing season, increments of wood are more gradual which can be ascribed to high daily temperatures accelerating transpiration and decreasing photosynthesis. The period end of July – end of August can be considered to be poor in precipitation (see the climogram in Fig. 2). The increment of wood is terminated at the end of September to the beginning of October. Oak is a species sensitively responding to the period of drought which is particularly manifested in wood increment in subdominant trees.

In general, sufficient supplies of water during spring months accelerate the formation of early wood including differentiation of spring vessels as corroborated by the results. In ring-porous broadleaved species, the process of differentiation of particular anatomical elements is more complex as compared with conifer species (MATOVIČ 1977, 1990). The analysis does not, however, confirm a general fact that the maximum formation of wood occurs from the second half of June. It is given by specific features of the floodplain forest locality (water reserves in the physiologically active layer of soil). The cambial activity shows positive correlation both with temperature and water provided, none of the factors is in stress condition. The radial growth can be affected by both factors during the whole growing season. The total formation of wood is dependent not only on the characteristics of the respective growing season but particularly on the social position of trees in the stand.

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Analýza kambiální aktivity a tvorby dřeva u *Quercus robur* L. v podmínkách lužního lesa

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ABSTRAKT: Byla analyzována činnost kambia a přírůst xylému v průběhu vegetačního období u dubu letního (*Quercus robur* L.). Byl sledován počátek a ukončení činnosti kambia, diferenciace dřevních vláken (libriformu), cév a analýza celkového přírůstu dřeva během vegetace u stromů nadúrovňových, úrovňových a podúrovňových ve vztahu k ekologickým faktorům prostředí. Průběh tvorby dřeva odpovídá typickým růstovým křivkám, které jsou modifikované faktory prostředí (průměrná denní teplota, srážky, zásoba půdní vody). Rychlost růstu je limitovaná faktory prostředí – při nedostatku některého z nich je redukována a vede ke snížení celkové produkce buněk. Dub je dřevinou citlivě reagující na suché období, což se projevuje zejména na přírůstu dřeva u podúrovňových stromů. Dobrá zásoba vody v jarních měsících urychluje tvorbu jarního dřeva včetně diferenciace jarních cév, což potvrzují výsledky. Celková tvorba dřeva je závislá nejen na charakteristice příslušného vegetačního období, ale zejména na sociálním postavení stromů v porostu.

Klíčová slova: tvorba dřeva; vliv faktorů prostředí; diferenciace xylému; radiální růst; dub letní (*Quercus robur* L.)

Práce je zaměřena na analýzu činnosti kambia a sledování přírůstu dřeva v průběhu vegetačního období 1998 u dubu letního (*Quercus robur* L.) v podmínkách lužního lesa. Odběr vzorků byl proveden na pokusné ploše (IBP) v lužním lese 2 km severně od Lednice na Moravě (oblast Horní les, č. porostu 623 a_2). Plocha se nachází v nadmořské výšce 165 m. Byl sledován počátek a ukončení činnosti kambia, diferenciace dřevních vláken (libriformu) a cév. Byl analyzován celkový radiální přírůst dřeva během vegetačního období u stromů nadúrovňových, úrovňových a podúrovňových ve vztahu k ekologickým faktorům prostředí.

Cílem práce bylo charakterizovat činnost kambia a diferenciaci xylémových elementů (libriformních vláken, cév) v průběhu vegetačního období. Pozornost byla věnována meristematické aktivitě kambia, neboť ovlivňuje do určité míry radiální růst rostlin. Radiální růst je charakterizován celkovou šířkou letokruhu, počtem a velikostí buněk (což je druhově dané) a jejich variabilita závisí na faktorech prostředí, které mohou pozměnit strukturu letokruhu. Vliv sezonního charakteru klimatu se odráží na anatomické struktuře letokruhů. Změny růstu (tvorby dřeva) a diferenciace jeho strukturálních elementů – buněk – probíhají v návaznosti na jednotlivých ekologických faktorech.

Obecně platí, že dobrá zásoba vody v jarních měsících urychluje tvorbu jarního dřeva včetně diferenciace jarních cév, což potvrzují výsledky. U kruhovitě pórovitých listnatých dřevin probíhá proces diferenciace jednotlivých anatomických elementů složitěji než u jehličnatých dřevin. Analýza nepotvrzuje obecně platný předpoklad, že maximální přírůst dřeva se tvoří od druhé poloviny června, což je dáno specifičností lokality lužního lesa (zásoba vody ve fyziologicky aktivní vrstvě půdy). Aktivita kambia vykazuje pozitivní korelaci jak s teplotou, tak i zásobou vody v půdě, pokud žádný z faktorů není stresující. Radiální růst může být oběma faktory ovlivňován po celou dobu růstového období. Celková tvorba dřeva je závislá nejen na charakteristice příslušného vegetačního období, ale zejména na sociálním postavení stromů v porostu. Dub je dřevinou citlivě reagující na suché období, což se zejména projevuje na přírůstu dřeva u podúrovňových stromů. Pouze u stromů, které vytvořily během vegetačního období širší letokruhy, lze pozorovat charakteristickou anatomickou stavbu dubu, tj. radiální seskupení letních cév. U podúrovňových stromů se nevytvořilo během vegetačního období pro duby typické radiální seskupení letních cév. Lze to přisuzovat malému přírůstu dřeva.

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