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RIMVYDAS KAZIMIERAS KRIUKELIS

ANALYSIS OF *PINUS SYLVESTRIS* L. STEM AND ROOT RADIAL GROWTH FLUCTUATIONS AT THE LAKESIDE STANDS

Biology (Botany)

SYNOPSIS

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RIMVYDAS KAZIMIERAS KRIUKELIS

PINUS SYLVESTRIS L. STIEBO IR ŠAKNŲ RADIALINIO PRIEAUGIO FLUKTUACIJŲ ANALIZĖ PAEŽERIŲ MEDYNUOSE

Biologija (Botanika)

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SANTRAUKA

Požeminiai procesai - vis dar nepakankamai ištirta ekosistemų modelių dalis, tačiau yra tiesiogiai susiję su aplinkos ir išteklių naudojimo problemomis: produktyvumo didinimu, ekosistemų funkcionavimo nenutrūkstamumu, "šiltnamio efektu", biologinės įvairovės išsaugojimu, degraduotų ekosistemų atkūrimu (Vogt 1989). Dėl šių priežasčių labai svarbu gerai žinoti, kaip antropogeninės ir natūralios prigimties limituojantys faktoriai veikia ekosistemų funkcionavimą. Visapusiški ekosistemų funkcionavimo duomenys reikalingi, norint palyginti jas laiko ir aplinkos rodiklių atžvilgiu, taip pat nustatyti ekstremalias rūšies ekologinės amplitudės ribas.

Pagrindinė darbo hipotezė yra tokia: duomenų apie antžeminės ekosistemos dalies komponentus nepakanka siekiant nustatyti, kaip požeminėje jos dalyje vykstantys procesai atspindi aplinkos pasikeitimus. Požeminės dalies funkcinis vaidmuo skiriasi nuo antžeminės, todėl požeminės dalies arba visos ekosistemos reakcija į aplinkos pokyčius negali būti išsamiai išanalizuota tiriat tiktai kurią nors vieną ekosistemos dalį (Vogt K. A., Gordon, Vogt D. J. 1990).

Sumedėjusių augalų šaknų radialinį prieaugį yra tyrę tik keletas mokslininkų (Shulman 1945; LaMarche, Jr. 1963, 1968; Fayle 1968, 1983; Kalinin 1978; McCord 1986; Krause 1992; Krause, Eckstein 1992, 1993; Krause, Morin 1993). Tokio pobūdžio darbai, o ypač miško ekosistemų tyrimai yra labai sudėtingi, reikalaujantys daug fizinio darbo ir laiko sąnaudų.

Šis darbas yra mokslinių tyrimų, vykdytų Botanikos instituto Kraštovaizdžio ekologijos laboratorijoje, tąsa (Pakalnis 1970, 1971, 1972; Lapinskienė 1986; Lygis 1990) ir buvo atliktas pagal planinių tyrimų tematiką.

Medžiaga disertacijai buvo renkama 1987-1990 metais Aukštaitijos nacionaliniame parke esančiame Balčio ežero stacionare. Tyrimo aikštelės buvo parinktos Balčio ežerą supančiuose 90 ir 120-150 metų pušynuose (*Vaccinio-myrtillosum Pinetum)*.

Darbo tikslas - ištirti egzogeninių faktorių įtaką *Pinus sylvestris* L. paežerių medynų antžeminės ir požeminės dalies radialinio prieaugio dinamikai.

Tyrimų uždaviniai:

1. Parengti metodiką sumedėjusių augalų šaknų radialiniam prieaugiui matuoti.

2. Nustatyti *Pinus sylvestris* L. paežerių medynų antžeminės ir požeminės dalies prieaugio ilgalaikę dinamiką.

3. Nustatyti tyrimo objektų antžeminės ir požeminės dalių tarpusavio ryšius ir priklausomybę.

4. Išaiškinti egzogeninių faktorių, periodiškai sukeliančių ekstremalias aplinkos sąlygas, fluktuacijų išraiškos ypatumus radialinio prieaugio dinamikoje.

Darbo naujumas. Pirmą kartą Lietuvoje klasikinis plovimo metodas buvo pritaikytas suaugusių medžių šaknų sistemoms tirti. Sukurtas ir pritaikytas maksimalaus metinio šaknų radialinio prieaugio matavimo metodas. Pirmą kartą *Pinus sylvestris* L. stiebo ir horizontaliųjų šaknų radialinio prieaugio dinamikos, egzogeninių faktorių poveikio bei medžio antžeminės ir požeminės dalių tarpusavio ryšių ir priklausomybės analizė buvo atlikta panaudojant Tarptautinio medžių rievių duomenų banko (Arizonos universitetas, JAV) kompiuterinių programų biblioteką (Holmes 1983, 1994) bei formantinės analizės (Slivinskas ir kt. 1986; Slivinskas, Šimonyte 1990, 1992) metodą.

Pagrindiniai šio darbo rezultatai buvo svarstomi jungtinėje Lietuvos ir Gudijos jaunųjų mokslininkų konferencijoje (Beloveżskaja Pušča, Baltarusija, 1991), konferencijoje "Miško biogeocenologijos problemos ir jų sprendimo metodologiniai pagrindai" (Joškar-Ola, Rusija, 1992), Baltijos jūros regiono dendrochronologų pasitarime (Kopenhaga, Danija, 1993), Botanikos instituto ataskaitinėje mokslinėje konferencijoje (Vilnius, 1993), tarptautinėje konferencijoje "Medžių rievės, aplinka ir žmonija: tarpusavio ryšiai ir procesai" (Tucson, JAV, 1994), tarptautiniame pasitarime "Europos dendrochronologijos pasiekimai" (Travemünde, Vokietija, 1994).

Disertaciją sudaro 152 puslapiai (15 lentelių, 32 paveikslai, 315 šaltinių literatūros sąrašas).

SUMMARY

The processes occuring near and beneath the surface of the earth are the least investigated part of ecosystem models and bear directly on the major environmental and resource management problems now confronting us (Vogt 1989). Therefore, it is very important to know how the limiting factors of anthropogenic and natural origin affect the functioning of ecosystems. Exhaustive studies on ecosystem functioning are necessary in order to compare them across temporal and environmental gradients and to ascertain extremal limits of the species ecological amplitude.

The general testable hypothesis that has been pursued by this research is as follows: data obtained on the aboveground components are not sufficient to predict how the underground processes respond to environmental changes. Since underground functional roles do not mimic the aboveground, the underground or total ecosystem response to perturbations cannot be predicted in case only a part of ecosystem is examined (Vogt K. A., Gordon, Vogt D. J. 1990).

Only a few research works which include root radial growth studies are known (Shulman 1945; LaMarche, Jr. 1963, 1968; Fayle 1968,1983, Kalinin 1978; McCord 1986; Krause 1992; Krause, Eckstein 1992, 1993; Krause, Morin 1993, and some others), because such investigations, especially on forest communities, are very difficult and intricate.

The object of this research is to develop investigations carried out at the Laboratory of Landscape Ecology, Institute of Botany, Vilnius (Pakalnis 1970, 1972; Lapinskienė 1986; Lygis 1990). It has been accomplished due to the planned research of the Laboratory.

The main purpose of the research is to investigate impact of exogenous factors on dynamics of tree-ring growth of the aboveground and underground part of *Pinus sylvestris* L. at the lakeside stands.

Research goals:

1. To prepare methods for radial growth measuring of woody plant roots.
2. To determine growth dynamics of many years of the aboveground and underground part of lakeside pineries.
3. To ascertain interrelations and dependence of the aboveground and underground part of investigation objects.
4. To indicate fluctuation peculiarities of exogenous factors, periodically causing stress situations, in tree-ring growth dynamics.

Research results:

1. The original author's method on maximum annual root growth measuring was successfully applied. It enabled to use radial root growth in dendrochronology more widely.

2. Statistical analysis of *Pinus sylvestris* L. radial growth of individual series and chronologies from different sites is presented in this research.

3. Formant analysis of the tree-ring growth fluctuations as one of the ecosystem stability indicator's using ring-width series as well as chronologies was done.

4. Impact of exogenous factors (water level durations in the lake Baltys and precipitation) on radial growth of the aboveground and underground part of trees growing in different ecotopes, interrelations and dependence of growth of the aboveground and underground part of tree were investigated.

5. The carried out research confirms the general testable hypothesis that has been pursued by this research project - investigations on the underground part of tree as a part of complex research are necessary for the exhaustive dendroecological studies.

The research material was presented:

- at the Conference on Forest Biogeocenology and Methodological Ways of Problem Solving, 1992, Yoshkar-Ola, Russia;
- at the Conference of Young Scientists of Byelorus and Lithuania, 1991, Belovezhskaja Pushsha, Byelorus;
- at the Meeting of Dendrochronologists from around the Baltic Sea, 1993, The National Museum of Denmark, Denmark;
- at the Conference of Research Reports of the Institute of Botany, 1993, Vilnius, Lithuania;
- at the International Conference on Tree Rings, Environment, and Humanity: Relationships and Processes, 1994, The University of Arizona, Tucson, Arizona, U.S.A.;
- at the International Meeting on Advances in European Dendrochronology, 1994, Travemünde, Germany.

The dissertation consists of 152 pages including 15 tables, 32 figures and 315 references.

INTRODUCTION

The processes occuring near and beneath the surface of the earth are still not enough investigated part of ecosystem models and bear directly on the major environmental and resource management problems: enhancement of productivity, sustainability of ecosystem function, reduction of atmospheric greenhouse gasses, the preservation of biological diversity and the restoration of the degraded ecosystems (Vogt 1989).

The sphere of this research is a development of the research work of the Laboratory of Landscape Ecology, Institute of Botany, Vilnius (Pakalnis 1970, 1972; Lapinskienė 1986; Lygis 1990).

The general testable hypothesis that has been pursued by this research is as follows: data obtained on the aboveground components are not sufficient to predict how underground processes respond to environmental changes. Since underground functional roles do not mimic the aboveground, the underground or total ecosystem response to perturbations cannot be predicted in case only a part of the ecosystem is examined.

This research includes the analysis of tree-ring series both from the aboveground and underground parts of the lakeside pine stands. Only a few research works which include root radial growth studies are known (Shulman 1945; LaMarche, Jr. 1963, 1968; Fayle 1968,1983, Kalinin 1978; McCord 1986; Krause 1992; Krause, Eckstein 1992, 1993; Krause, Morin 1993, and some others), because such investigations, especially in forest communities, are very difficult and intricate.

1. ENVIRONMENTAL CONDITIONS AND DEVELOPMENT OF WOODY PLANTS

1.1. Character of the Environmental Factor Influence on Woody Plants

Species of trees or a tree itself is a complicated biological system, the constituent parts of which differ according to anatomical structure, physiological functions, etc., however, they are biologically closely related and that conditions their common existance and balanced evolution.

Tree growth intensity is conditioned by an integrated complex of factors (genetic peculiarities, hereditary characteristics) are equivalent with outer factors (nutritious matter, light, aeration, heat, humidity, etc.). The ratio of these factors in nature is accidental, but there is a lot of these factors. Every tree is characterised by a corresponding combination of factors conditioned by processes occuring at different time and on the different parts of a tree (Kalinin 1978).

1.2. Development and Radial Growth of Woody Plant Root Systems

Root is one of the main vegetative organs of higher plants which maintains a dynamical relation between the aboveground parts and soil and performs different vitaly important functions (Kramer, Kozlovskii 1983; Baitulin 1987). Root system development consists of three growth processes: growth lengthwise, formation of new side roots and root thickening (Krasovskaya 1955). The main quantities of root system elements sometimes vary individually, however, usually they change together under affect of biological, edaphic and biocenotic factors.

Interrelation of plant organs is characteristic to all stages of its ontogenesis (Chailakhian 1958; Voronova 1965). The functions of root system and aboveground organs are strictly differentiated and interdependent and they condition each other, while most stages of growth processes are synchronous (Fiodorova 1968; Baitulin 1987). Due to unfavourable environmental conditions or mechanical damages the slower growth in one part of the root system can cause a more intensive growth in another part or compensating growth (Baitulin 1987). Development and vitality of the root system defines activity of almost all processes taking part in the aboveground part (Kazarian 1969).

The zone of a rapid taper of the roots is caused by a number of different reasons:

- an exponential decrease in ring width and high frequency of long root branching near the stem;
- stem sway stimulates root thickening next to the stem;
- the exposed portion of the root near the base may be stimulated by light to produce thicker growth rings and "stem-like" wood;
- the fussion of adjacent horizontal roots may tend to block photosynthate transport to the bottom of the root (Wilson 1975).

The cross-section of young roots is rounded, however, the older the xylem, the more uneven its distribution around the root axis and it is more eccentric than in the stem (Fritts 1976; Kramer, Kozlovskii 1983). The side horizontal roots are more eccentric than vertical and those occuring behind the central part of the root system, however, a very high variety of annual tree-ring formations in different roots of the same tree is observed (Kramer, Kozlovskii 1983). Between root and stem tree-ring width chronologies we can observe a slight correlation, too. However, it might not be identified farther from the stem or with increasing root age (Fayle 1968).

1.3. Fluctuations of Tree-Ring Growth

Cyclic recurrence is the most significant factor of changeability of natural phenomena with respect to space and time. It is characteristic not only to inorganic and organic world of our planet, but also to cosmic phenomena occuring inside and outside the Solar system. It is supposed, that primary reasons of climatic changes are the Earth evolution, solar radiation, disorders in the cosmic space, the powers of the Moon and the Sun causing tides, the processes of deviations in the system of atmosphere-hydrosphere (Gorčakovskii, Shiyatov 1985).

Deviations with variable period, phase and amplitude but changing correspondingly in time and space are called cyclic or rhythmic (Shnitnikov 1968; Vozovik 1970; Maksimov 1976; Shiyatov 1986).

The annual tree-ring width is a sum of systematic regular and accidental component parts conditioned by supposed processes and some casual reasons (Stupneva 1984). An individual factor makes only a slight effect on the formation of annual tree-ring, however, its impact increases under simultaneous effect of other factors (Sabirov, Zheleznikov 1981).

Woody plat growth fluctuations do not distinguish themselves in strict periodicity. Every dendrochronological series consists of many cycles with different periods. The period phase and amplitude of these cycles are not constant and change in time and space (Douglass 1936; Siren 1963; Komin 1970; Bitvinskas 1974; Lovelius 1979; Shiyatov 1986; Shiyatov, Komin 1986), disappearing and reappearing from time to time (Shiyatov 1979, 1986). Investigations on cycles conditioned by the exogenous reasons are hampered by cycles which occur because of endogenous plant factors: structural changes in roots and stem, physiological state of a tree, etc. (Fritts 1976), as well as radial growth fluctuations caused by accidental reasons (Siren 1963).

2. MATERIALS AND METHODS

Sampling has been conducted in Aukstaitija National Park (Ignalina region, Lithuania). Mature 90-150 yr *Pinus sylvestris* L. trees growing near the self-contained 53.25 ha lake Baltys were considered for sampling. The lake has distinct 25-27 yr fluctuations of the waterlevel and periodically affects the lakeside pine stands as a limit factor (Pakalnis 1970, 1972). Water level fluctuations were documented during the period from 1959 to 1989.

To choose sites and to describe research objects we used the mapping and forest

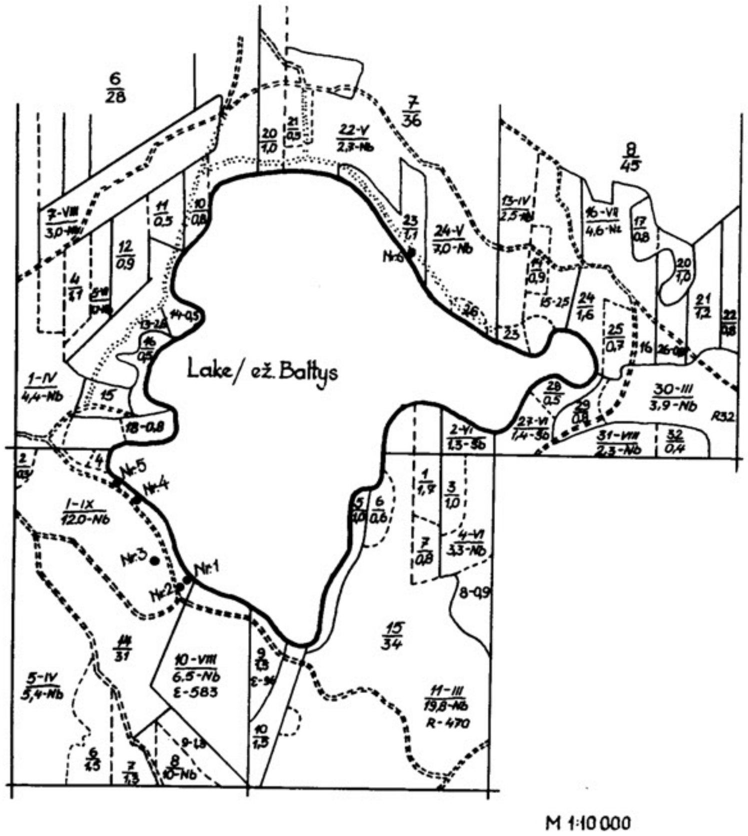


Figure 1. Site location near the flowless lake Baltys (NR 1, NR 4,NR 5 and NR 6 - lakeside sites, NR 2 and NR 3 - control sites).

valuation material prepared 1985. The surface of the sites was leveled every 1 m. To indicate absolute altitudes a ground reper T5974 with altitude of 146.352 m was used. The vegetative abundance and cover were estimated according to Braun-Blanquet scale (Natkevičaitė-Ivanauskienė 1983). Total 18 model *Pinus sylvestris* trees in 4 sites (NR 1, NR 4, NR 5, NR 6) in the nearest and lowest parts to the lake as well as 2 control sites (NR 2 and NR 3) at the higher places were investigated (Fig. 1). Site NR 3 was the highest to the lake, and site NR 2 took the middle height in this respect. The methods by N. P. Anuchin (1982) was used to describe research sites and model trees. Cross-sections were sawn off from the stem at breast height (1.3 m) of the tree and at the tree base.

The root systems of model trees were uncovered by the classical washing method (Böhm 1979; Guz 1981; Kriukelis 1989). In Lithuania the method for investigation of woody plants has not been applied before. After that we leveled and sawed off from each model tree 3 first-row horizontal roots growing in three different directions. For the dendrochronological analysis we used cross-section samples taken from the zone of the rapid taper of horizontal roots at the root base and at a distance of 20 cm from it (Fig. 2). Maximum annual root growth measuring method was used for roots (Kriukelis 1992). Total 54 cross-section series from 18 stems and 267 from different parts of roots were measured.

We used ITRDB Program Library -1.1 (April 1993) on IBM PC and VAX, Lab. of Tree-Ring Research, Univ. of Arizona. The computer program COFECHA was used for crossdating and measurement quality assessing (Holmes 1983, 1994). All cross-sections identified by COFECHA as having unusual measured values or significant ($P < 0.05$) lagged correlation with the master chronology were visually rechecked and corrected or eliminated from further analyses. The computer programs STATGRAPHICS-2.0 and PAGEPLOT (VAX version) successfully were used for such purpose. We used the ARSTAN program for detrending, chronology computation and statistical analysis (Holmes 1994). Three kinds of chronologies were produced by ARSTAN:

- site chronology contains 3 radial growth series with respect to different heights of the stem;
- site chronology contains 6 radial growth series from the both levels of the stem;
- site chronology includes all root radial growth series.

Low-frequency trends in growth related to age or stand dynamics were modelled by negative exponential curve-fitting technique

$$y=A * e ** (-B * t) + D$$

to each series using the ARSTAN procedure developed by Cook (1985). If the fitted curve had a negative constant (D) or a positive slope, it was rejected and a linear regression was fit to the data (Fritts et al. 1969). Dimensionless indices were formed by dividing the observed

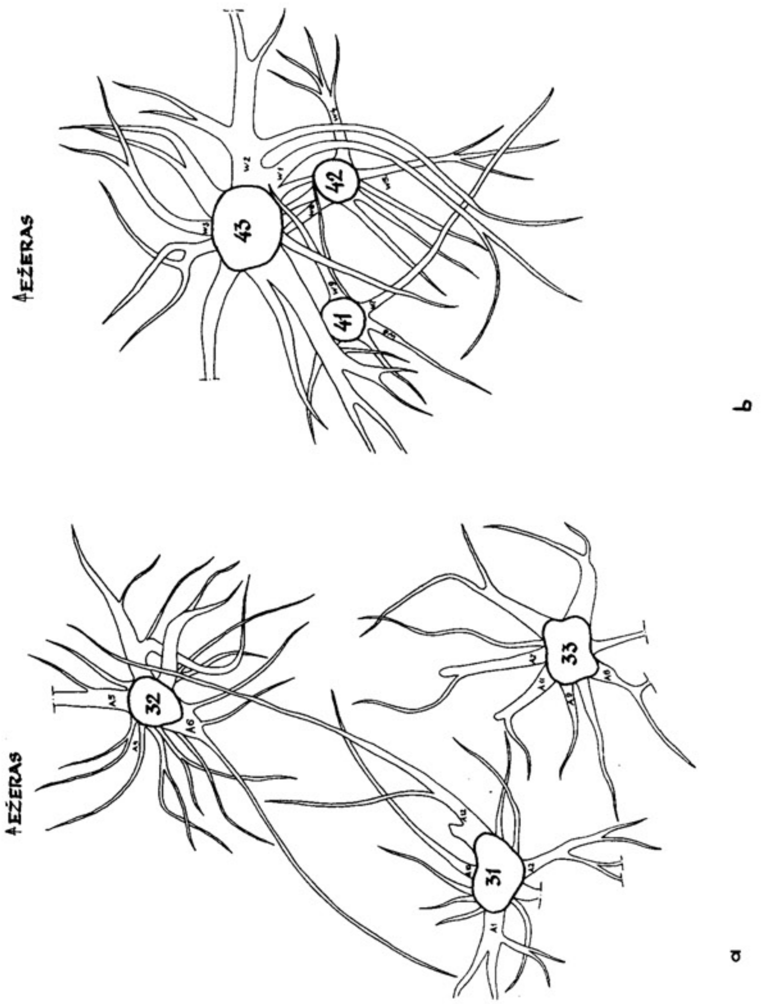


Figure 2. *Pinus sylvestris* L. horizontal root systems at the control site NR 3 (a) and the lakeside NR 4 (b).

ring-width value by the predicted ring-width value.

For statistical analysis (correlation, dispersive, regressive, etc.) we also used the program STATGRAPHICS-2.0.

We used the computer program Formant (version 1.0-PC) for the fluctuation analysis (Slivinskas et al. 1991). Formant is an interactive program to get mathematical models of signal data. The name Formant stands for a signal component which can be an exponent, pure sinusoid, polynomial, damped polynomial, quasipolynomial. The signal under investigation is assumed to be represented as the sum of formants:

$$s(t) = F_1(t) + \ldots + F_M(t).$$

The main goal of Formant is to express the data as the minimal sum of formants and to get the numerical values of their parameters. The data are considered to be a finite sequence of equidistant samples of investigated signal (Slivinskas, Šimonytė 1990). The approximation error of both interpolation curve of the singled out formants and the primary data had to be not higher than 25-30 % (Shiyatov, Mazepa 1987). In order to expose investigated climatic signal as well as to reduce unwanted formants, including age trend, the Norton editor was applied and new expression of mathematical model was obtained after the program run again.

3. DESCRIPTION OF SITES AND OBJECTS SAMPLED

3.1. Physical-Geographical Conditions

Lithuania is situated between 53^0 27' north latitude, and between 20^0 56' and 26^0 51' east longitude in the river Nemunas basin on the western border of the largest East European plain. Lithuania covers 65 303 km^2.

The Lithuanian climate is of a transitional (between sea and continental) nature. The relative air humidity ranges from 50 % in summer to 90 % in winter. An average annual air temperature in Lithuania is about $+6^0$C. Lithuania is in an excess humidity zone. An average amount of precipitation makes up from 520 to 901 mm per year. The hard precipitation comes to about 8-14 % of the total annual precipitation sum (Vaičys et al. 1979).

The present relief has been formed mainly by the last two glaciers. The highest place in Lithuania is 294 m above the sea level. 45.3 % of the area cover dernopodzolic soils, 4.2

% - podzols, 7.8 % - sod carbonate soils, 17.6 % - sod-gleyic and gley, 18.4 % - derno-podzolic gleyic and gleyed, 5 % - bog soils and 1.4 % - alliuvial soils (Buivydaitė 1994).

Redundancy of precipitation in Lithuania induced formation of a rather dense net of stable rivers and rivulets (on the average 0.4 km/km^2). An average abundance of lakes in Lithuania come to 1.3 % (Bieliukas 1958). Almost all largest lakes are flowing and of glacial origin while a lot of small lakes are flowless (Jablonskis 1969). The lakes cover 15.1 % of the Aukshtaitija Nacional Park's territory.

In Lithuania there are about 1.3 thousand plant species among which 25 autochthonous and 100 introduced woody plant species are found (Navasaitis A., Navasaitis M. 1979). Now the Lithuanian woodedness make up 30.0 %. Pine forests make up 43 %, spruce groves - 23 %, oak woods - 1.3 %, ash and hornbeam groves - 2.5 %, birch groves - 20.1 %, asp groves - 3.1 %, black alder groves - 50 %, white alder groves - 1.9 % of the total area of woods (Kenstavičius 1990). The main tree species forming woods or included into their composition are as follows: *Picea abies* (L.) Karst., *Pinus sylvestris* L., *Betula pendula* Roth, *Betula pubescens* Ehrh., *Populus tremula* L., Alnus glutinosa (L.) Gaertn., *Alnus incana* (L.) Moench., *Quercus robur* L., *Fraxinus excelsior* L., *Tilia cordata* Mill., *Ulmus glabra* Huds., *Ulmus laevis* Pall., *Acer platanoides* L. In Lithuanian forests grow over 40 species of shrubs which form a brush. The following shrub species can be mentioned: *Juniperus communis* L., *Sorbus aucuparia* L., *Rhamnus frangula* L., *Corylus avellana* L., *Rhamnus catharticus* L., *Padus avium* Mill., etc.

3.2. Description of the Objects Investigated

The investigations were carried out at the lakesides of the lake Baltys (Ignalina region, Aukshtaitija National Park, the forestry of Palushe, 6th, 7th, 8th, 14th and 15th sections) (Fig. 1).

The lake Baltys is a closed lake without tributaries and outlets. It is surrounded by Gruodishkiai, Baluoshas, Dringis, Asekas, Asalnai lakes and some small ones. The direct basin - the lake Asalnai, the main basin - the river Zheimena. The lake is surrounded by a 25 m height horseshoe-shaped hill with a sandy terraces overgrown with forest fragments. The investigation objects were studied in 90 yr old (sites NR 1-5) and 120-150 yr old (6th site) V*accinio-myrtillosum Pinetum*.

3.3. Scots Pine Biology and Ecology

Pinus sylvestris L. belongs to *Pinus* L. genus of *Pinaceae* family. Wide ecological amplitude of *Pinus sylvestris* conditioned its large areal which covers almost the whole

Western and Central Europe, Scandinavia and continue to the Verkhojansk mountain chain in Asia. Its areal covers the whole Lithuania (38.1 % of forest area) (Kapper 1954; Dendrologija 1963; Navasaitis A., Navasaitis M. 1979).

Scots pine is a light-demanding plant which does not need humid air, is resistant to extreme temperatures and sudden changes of temperature, windbreaks, it is a typical xerophyte. *Pinus sylvestris* does not demand ecological conditions and is physiologically labile to relief, soil, climate, humidity, but is a calciphobous species (Sinadskii 1983). The most suitable for growth is a slightly humid, deep, humic sand (Dendrologija 1963).

Pinus sylvestris has a very plastic root system which can change depending on the edaphic conditions. It endures overflowing of root system, which can last the whole vegetative period (Sinadskii 1983). In high humidity and marshy soils forms weakly developed surface root system unresistant to windbreaks. In a well-drained soil the root system grows wider and deeper (Dendrologija 1963; Javorskii 1988). In loamy, sandy and sand derno-podzolic soil the main root mass (about 75 %) is accumulated on the surface 20 cm soil layer (Rakhteenko 1952). The widely and deeply distributed roots are able to absorb water from a large soil area (Dendrologija 1963).

Pineries are important from the standpoint of sanitation and hygiene because of phytoncides. Scots pine is widely used for protective planting, it is valuable from the point of view of aesthetics, however, it is sensitive to the polluted air (Bulygin 1985; Drevesnye porody mira 1982).

Pinus sylvestris have a lot of morphological, ecological, geographical forms and varieties (Pravdin, 1978) as well as many ornamental forms (Krüssman, 1986). A genetic potencial of *Pinus* L. species is very high (Lyubavskaya 1982). Due to above mentioned characteristics scots pine is valuable for the research as an environmental indicator.

4. EXOGENIC CHANGES OF ECOTOPE

The fluctuations of lake water level are caused by the changes of climate. They are cyclic and can be short-term, seasonal, annual or perennial. Short-term fluctuatios are related with lake rough, water streams, heavy showers, droughts, and etc., they have a changeable frequency and low amplitude. Seasonal changes of lake water level are caused by yearly dynamics of precipitation evaporation (amplitude in Lithuania - less than 1 m), annual - by different environmental conditions in different years. The longer the period of fluctuations, the higher the amplitude, maximum amplitudes (< 4 m) are related with cycles of thousand years (Garunkštis 1988).

A. Shnitnikov (1969) affirms, that there are two kinds of water abundance periods observed at the shores of the Baltic Sea: minimum - in 1847-1863, about 1920, in 1941-1951 and in 1963-1972, and maximum - in 1828-1843, about 1900, in 1927-1935 and in 1952-1963.

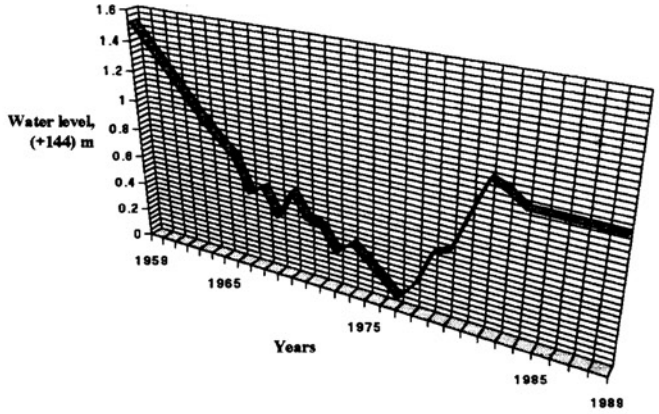
Perennial water level fluctuations of the Lithuanian lakes are based on the specific investigation data and usually cover the period of 3-11 yrs, because lake water level has been investigated for a rather short period (Garunkštis 1988).

In 1864-1967 four periods of high water level in the lake Baltys were singled out by R. Pakalnis (1970): 1878-1906, 1906-1911, 1930-1938 and 1959-1962. Radial growth chronology minimums of *Pinus sylvestris* trees growing near the lake Baltys conform with 25-27 yr period lake water level fluctuations and with the similar period precipitation cycle in Lithuania (Ščemeliovas 1964; Pakalnis 1970). V. Ščemeliovas (1964) singled out the following periods of increased precipitation: 1890-1906, 1920-1936 and 1945-1960. High water level periods in the lake Baltys usually start several years before the finishing of increased precipitation period and lasts from 3 to 9 yrs depending on precipitation amount and summer temperatures (Pakalnis 1970, 1971, 1972). According to E. Herbačiauskas (1968), an absolute average perennial water level and the lake Baltys water level in summer reaches 144.68 m. In 1958-1967 period the highest water level of the lake Baltys was registered in 1959. At that time there were flooded three isles and the lowest places of the lakeside stands (Pakalnis 1970).

In 1959-1976 the changes of lake Baltys water level in the course of a year were measured irregulary, in 1976-1983 - once in ten-day period. We had no data on the precipitation intensity in 1960-1965 and 1985-1988 periods, that's why they were extrapolated taking into account results of the adjacent years and a general tendency of the average annual water level change. In this way the curve of water level fluctuations (1959-1989) in the lake Baltys was established (Fig. 3).

Our research objects and Vilnius meteorological station belong to the same precipitation intensity zone. Hence, the longest known in Lithuania annual precipitation data (1887-1994) measured at Vilnius meteorological station was used in this research (Lithuanian Climate Reference Book 1991).

Figure 3. Lake Baltys annual water level dynamics in 1959-1989.



5. STATISTICAL ANALYSIS OF *PINUS SYLVESTRIS* L. RADIAL GROWTH DYNAMICS

The particular statistical analysis of individual tree-ring measurement data and standardized tree-ring index series as well as radial growth chronologies of *Pinus sylvestris* L. aboveground and underground parts in different sites was carried out using ARSTAN program.

Age trend of stem radial growth series was expressed mostly as a negative exponent, but in roots - as a linear regression of different kind.

Mean sensitivity (MS) measures the ring-width changes among adjacent rings and is influenced largely by the high-frequency variations in climate (Fritts 1971). MS values of tree-ring measurement as well as standardized tree-ring index series are rather similar. Mean sensitivity of stem radial growth series ranges from 0.17 to 0.33 in lakeside and from 0.14 to 0.31 - in control sites. MS of root ring-width series ranges between 0.25 and 0.51 in lakeside and between 0.16 and 0.47 - in control sites. MS ranges from 0.49 to 0.74 in stem

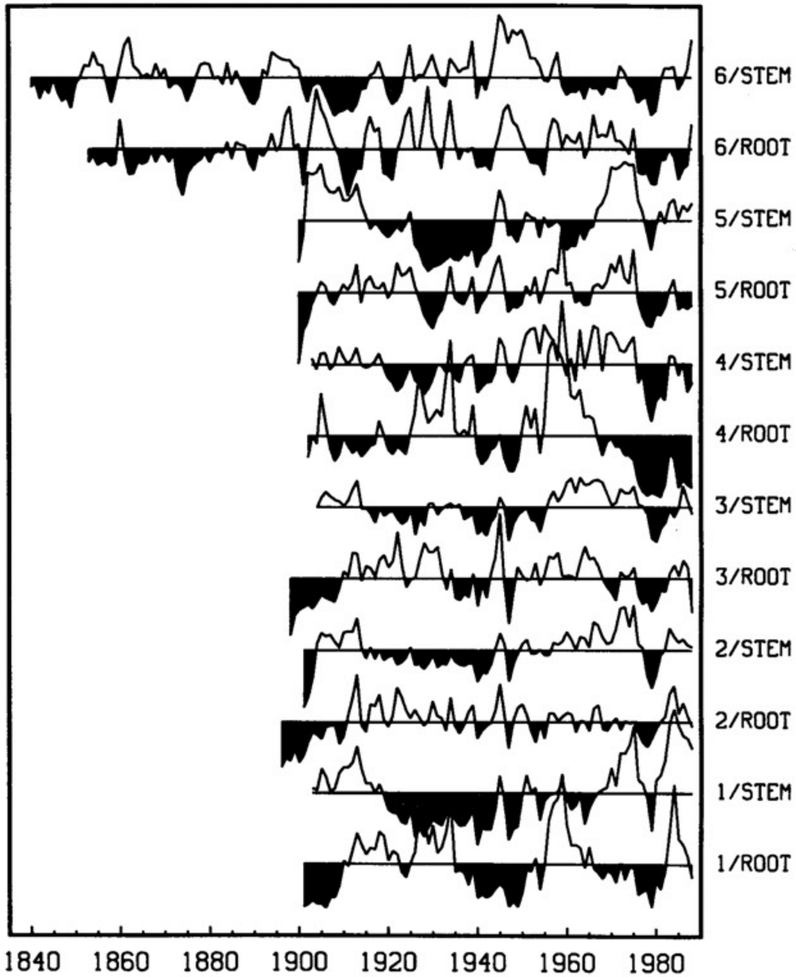


Figure 4. *Pinus sylvestris* L. radial growth Arstan type chronologijos (*/* - site NR / root or stem general chronology).

and from 0.55 to 0.78 - in root radial growth chronologies. Mean sensitivity is 25-38 % higher in roots to compare with stem individual radial series as well as chronologies ($P < 0.01$). MS values at breast height (1.3 m) of the tree and at the tree base are lower than in horizontal roots ($P < 0.05$). There is no significant difference in mean sensitivity at both stem heights ($P > 0.40$), between lakeside and control sites ($P > 0.13$).

Standard deviation (SD) and mean sensitivity are not equivalent measures because standard deviation is inflated more than mean sensitivity by long-term variations in climate (Fritts 1971). SD varies from 0.18 to 0.65 in stem and from 0.28 to 1.30 - in horizontal root radial growth series. Standard deviations are higher in lakeside than in control sites. Standard deviations vary from 0.20 to 0.32 in stem as well as from 0.27 to 0.53 in root chronologies (Fig. 5). SD values of the control site chronologies are always smaller with respect to other sites. There is no significant difference between SD values at the base or breast height of stem chronologies. Series with high SD frequently have high MS.

Trend in variance (%) ranges from -0.65 to 0.13 % in stem and from -0.43 to 0.65 % - in horizontal root tree-ring measurement data series and is mostly negative. After detrending it became mostly positive in stem but was the same - in roots. Trend in variance ranges from -0.06 to 1.09 % in stem, as well as, from -0.86 to 1.58 % in root standardized tree-ring index series. It is mostly positive in stem, as well as, in root radial growth chronologies.

Differences in autocorrelation structures may be attributed to differences in individual characteristics of trees, site conditions or stand influence (Fritts 1976). 1st order autocorrelation quantifies the association of ring widths with proceeding values, or the nonrandomness of the time series. Environmental factors causing long-term growth effects increase the autocorrelation value (Swetnam et al. 1988). 1st order autocorrelation coefficients range from 0.49 to 0.94 in *Pinus sylvestris* stem and from 0.37 to 0.94 - in root tree-ring measurement data series. After the detrending 1st order autocorrelation became lower because of excluding age trend influence. 1st order autocorrelation coefficient values range from 0.41 to 0.85 in individual standardized stem tree-ring index series and from 0.10 to 0.86 - in roots. First-order autocorrelation ranged from 0.49 to 0.74 across stem and from 0.55 to 0.78 across root chronologies (Fig. 5). There are no significant differences in 1st order autocorrelation between stem and horizontal root radial growth series, between lakeside and control sites.

Coefficients of variation range from 0.26 to 1.24 in aboveground and from 0.36 to 1.04 - in underground part of tree radial growth measurement data series. Variation coefficient values of stem tree-ring index series range from 0.23 to 0.63, as well as, root - from 0.33 to 0.98. Variation coefficients of root radial growth series are 24-48 % higher than in the aboveground part of *Pinus sylvestris* ($P < 0.01$). Coefficients of variation are

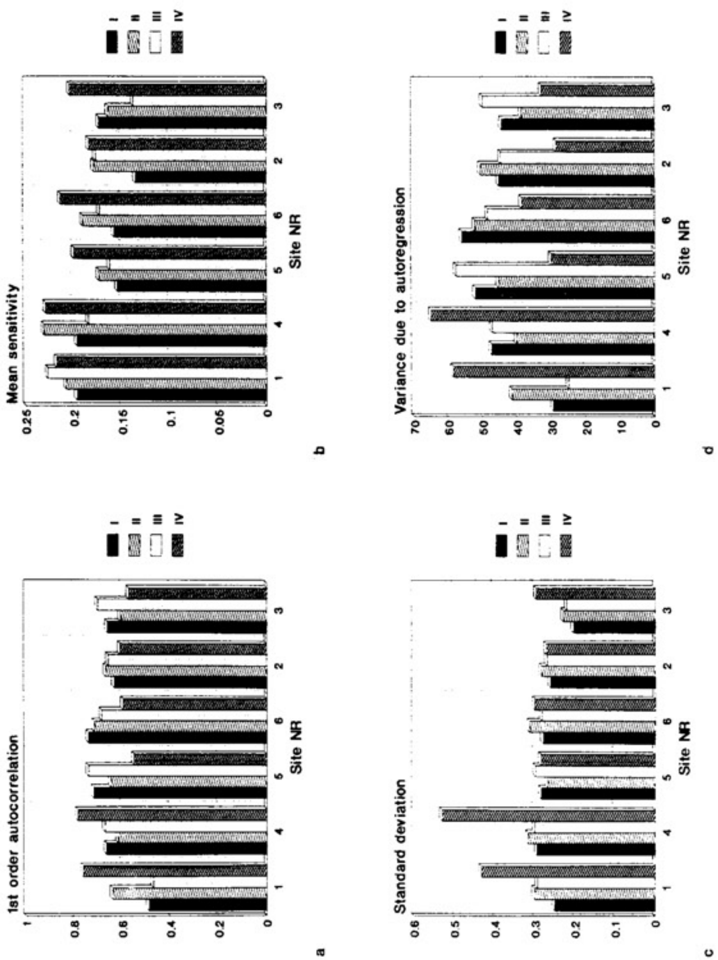


Figure 5. *Pinus sylvestris* L. radial growth Arstan type chronology statistics: 1st order autocorrelation (a), Mean sensitivity (b), Standard deviation (c), Variation due to autoregression (d). I - general stem chronology, II - ground level stem height chronology, III - 1.3 m stem height chronology, IV - horizontal root general chronology.

significantly higher (P < 0.01) in the lakeside sites than in control ones among root radial growth series. There is no significant difference between coefficients of variation at the base or breast height of stem.

Variance due to autoregression values range from 24.4 to 58.9 % in the aboveground and from 28.6 to 64.9 % in the underground chronologies (Fig. 5). It is rather similar in different stem height chronologies, in lakeside and control sites.

The variance in common can be relatively considered to represent the effects of macroclimate or the climate "signal" (S) because it seems to result primarily from large scale climatic variations limiting directly or indirectly the growth of all trees (Fritts 1976). The remaining more or less random error is considered as "noise" (N) which dilutes and perturbs the expression of the "signal" in the chronology for a given site. Chronology signal-to-noise ratio (SNR) in standartized ring-width chronology depends in part upon both limiting climatic factors and any other stand-wide conditions that influenced tree growth during the sampling years, and in part upon the number of cores and trees that were averaged to obtain the chronology for a site (Fritts, Swetnam 1989). SNR varies as a nonlinear function of sample size (Wigley et al. 1984). SNR ranges from 0.82 to 4.02 in stem radial growth standard chronologies, from 0.56 to 0.74 - in residual chronologies. SNR values at 1.3 m height of tree and at the tree base are rather similar. SNR ranges from 0.66 to 8.91 in root radial growth standard chronologies, from 1.13 to 6.17 - in residual chronologies. Common interval root radial growth chronologies were created using different amount of the roots (5-10) and radii (10-17) in different sites. Thus, it is clear that comparison of SNR's using different number of series for chronology development is rather problematic.

Mean correlations among all radii in site range from 0.28 to 0.58 in stem and from 0.14 to 0.58 in root radial growth series. Mean correlations within trees in site range from 0.53 to 0.73 in stem and from 0.54 to 0.77 in root radial growth series. Mean correlations among all radii series in site are 24-31 % higher in stems than in roots. Mean correlations between root and stem series in site range from 0.19 to 0.68, the lowest values were registered in the control sites. Correlations (P < 0.05) among *Pinus sylvestris* stem radial growth lakeside site chronologies range from 0.21 to 0.62, from 0.26 to 0.52 - in root chronologies. Correlation (P < 0.01) between control site stem radial growth chronologies is 0.57, between root - 0.56. Lakeside chronology correlations with lower control site range from 0.18 to 0.72 in the aboveground and from 0.15 to 0.47 in the belowground parts, with higher control site - from 0.18 to 0.50 in the aboveground and 0.19 in the belowground parts of *Pinus sylvestris*. Correlations (P < 0.01) between lakeside and control sites range from 0.18 to 0.72 in stem and from 0.15 to 0.47 - in root chronologies. Correlations (P < 0.05) between the aboveground and underground part chronologies of the same site range from 0.33 to 0.68 in the lakeside sites, in lower control site (NR 2) it is 0.27, in higher (NR 3) -

0.19. Correlations ($P < 0.01$) between lakeside site root chronologies and control site stem chronologies range from 0.24 to 0.62. *Pinus sylvestris* radial growth dynamics was more synchronous in the lakeside than in control sites due to periodically extreme ecological conditions (ground water level fluctuations).

6. EXPRESSION OF THE EXOGENIC FACTOR FLUCTUATIONS IN RADIAL GROWTH DYNAMICS

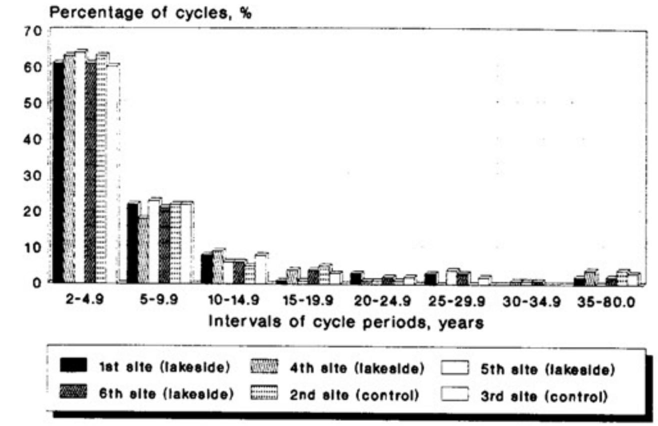
The regular perennial tree-ring radial growth fluctuations in dendrochronology are called cyclic (Shiyatov 1986). Tree-ring growth fluctuations are considered as the stability indicators. They correspond to the manner and selforganization of the biological processes occuring accross the temporal gradients. Such functions form the background of the ecosystem stability. The fluctuations express adaptability of the ecosystem to environmental changes, and fluctuation nature, at the same time, shows us the character of functional relations (Lygis 1990).

The fluctuations with the similar periodicity can be caused by different reasons. Therefore, it is necessary to have a more exhaustive information about the parameter fluctuations of various factors and their expression in radial growth dynamics. It is very complicated to identify nature of all determined fluctuations, that is why a possible origin of different periodicity cycles is analysed and discussed in this chapter.

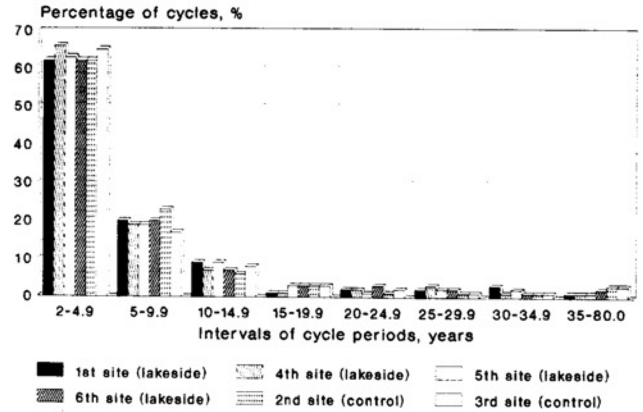
A *Pinus sylvestris* radial gowth fluctuation analysis of all tree-ring measurement data series as well as chronologies was done using the Formant analysis method. An average amount of formants (radial growth cycles), sum of which expresses radial growth dynamics, come to about 17. The determination of an individual radial growth cycle shows us the existence of the factor as well as amplitude, damping coefficient and phaze - its character.

The formant analysis of our dendrochronological data both from stems and horizontal roots shows a very similar structure of the radial growth cyclicity: the stable percentage of 2.0-14.9 yr period cycles (about 90 %) and the unstable varying percentage of all the rest 15.0-80.0 yr period fluctuations (Fig. 6). This phenomenon does not depend on the site conditions ($P > 0.41$) or part of tree investigated ($P > 0.15$) and let us come to the conclusion that the short-term 2.0-14.9 yr period fluctuations determine the stability of the tree-ring radial growth, and, at the same time, the remaining fluctuations as well as the nature of the age trend represent the radial growth changebility.

The percentage of *Pinus sylvestris* radial growth > 15.0 yr period cycles is similar in all tree-ring individual series and chronologies. Therefore, such kind of cyclicity was separated



a



b

Figure 6. Cyclicity structure of *Pinus sylvestris* L. tree-ring measurement data series in the aboveground (a) and the underground (b) parts of a tree.

from Pinus sylvestris radial growth dynamics using FORMANT program (Fig. 7). Then, only long-term periodicity dynamics was analysed. It was expressed in two forms: individual formants (cycles with > 15.0 yr period) and their sum - interpolation curve.

24-28, 30, 33-34 and 37 yr period cycles were determined in scots pine stem tree-ring growth series at the lakeside sites as well as 24-25 and 27-28 yr period cycles - at higher control site. 29 yr period cycle was determined at the lakeside site and 33 yr period - at the control site analysing stem radial growth chronologies. Formant analysis of the horizontal root tree-ring growth series shows 24-33 and 36 yr period cycles at the lakeside sites as well as 23, 25-27, 31-32, 34 and 37 yr period cyclicity at the control sites (Fig. 7). There is no similar periodicity cycles in lower control site stem radial growth series. 28 and 29 yr period cycles were determined in root radial growth chronologies at the lakeside sites. In lakeside sites, tree-ring growth cycles had higher amplitudes and lower damping coefficients than in the control ones. Diverse fluctuations are conditioned by different intensity of the expression of exogenous factors which impact in radial growth dynamics as well as individual characteristics of every tree (Pakalnis 1970), especially of the underground part of a plant. The impact of factors can manifest itself in transformations of tree-ring growth dynamics from several months to some years later (Fritts 1976). An intensive competition of trees growing in the stand, making use of both the underground and aboveground space, can decrease the total radial growth and suppress display of certain fluctuations, especially the long-term ones.

R. Pakalnis (1970, 1972), basing on wide tree-ring data analysis, affirms that 25-27 yr period cycle of the lake Baltys water level fluctuations tally with the same duration of precipitation cycle (Shnitnikov 1969), and, that these fluctuations are well-reflected on the stem radial growth of the lakeside scotch pine stands (periods of minimum growth). We also ascertained same phenomenon analysing *Pinus sylvestris* stem radial growth series or chronologies. Stem and root tree-ring growth dynamics was rather synchronous at the control sites. However, a positive reaction to high lake water level periods in the horizontal root radial growth dynamics at the lakeside sites is observed.

Formant analysis of the longest known in Lithuania precipitation data (1887-1990), obtained from the same climatic region as the research objects are, expose relatively stable 24, 28 and 76 yr period cycles. Minimum precipitation intensity according to 28 yr period cycle was registred in 1914, 1942 and 1970, and maximum - in 1900, 1928, 1956 and 1984. The minimums of 76 yr period cycle were in 1904 and 1980, maximum - in 1942 as well as minimums of 24 yr period cycle - in 1912, 1935, 1958 and 1981, maximums - in 1900, 1923, 1946 and 1969. The minimums of precipitation long-term dynamics (interpolation curve) are in 1914, 1939 and 1978, as well as, maximums - in 1899, 1927 and 1952. Maximum and minimum meanings of precipitation cyclicity conform with water abundance periods at the

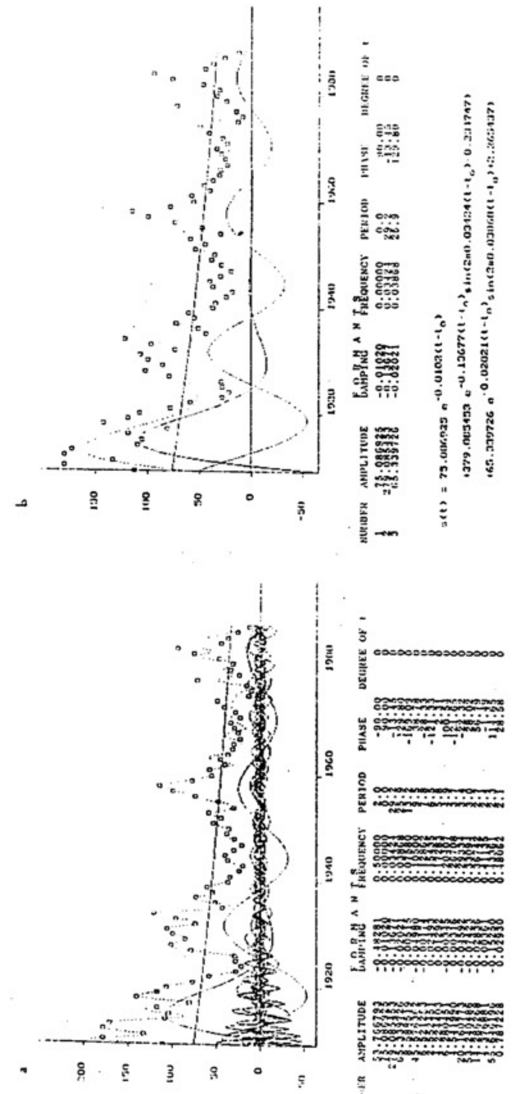


Figure 7. Formant analysis of the *Pinus sylvestris* L. individual horizontal root radial growth dynamics (a) and the long-term (formants with > 15.0 yr period) dynamics (b) at the lakeside site NR 1.

shores of the Baltic Sea (Shnitnikov 1969) and the periods of increased precipitation (Ščemeliovas 1964). High water level periods in the lake Baltys usually start several years before the end of increased precipitation period and lasts from 3 to 9 yrs (Pakalnis 1970, 1971, 1972). The amplitudes of periodically high Baltys lake water level are not the same in different years. Hence, the influence of lake water level on tree-ring radial growth at the lakeside scots pine stands is different. It was particularly high and clearly expressed in radial growth dynamics of lake water level in 1957-1963.

Due to our investigations 1930-1988 period *Pinus sylvestris* horizontal root radial growth series, decreased growth in long-term dynamics (interpolation curve of cycles with > 15.0 yr period) at the lakeside sites was ascertained mostly in 1939-1956 (low lake water level), in 1964-1979 (low water level, low precipitation), increased - in 1960-1963 (high lake water level, high precipitation) and in 1981-1985 (high lake water level, high precipitation). In some root radial growth series from lakeside sites an existence of the opposite reaction to lake water level fluctuations during the same periods was established. Minimums in long-term dynamics of stem radial growth series at the lakeside sites were in 1959-1963 (high Baltys lake water level) and maximums - in 1942-1954 (low lake water level) periods. In the control sites increased growth was determined in stem as well as in horizontal root radial growth long-term dynamics during the high lake water level and high precipitation periods. Analysing horizontal root radial growth chronologies of the lakeside sites, minimum growth in long-term dynamics was established in 1945 and 1973-1974, maximum - in 1959-1961 as well as in stem chronologies minimums were registered in 1962-1964 and maximums - in 1947-1949 and 1976-1980 periods. During the same periods the opposite reaction was ascertained in *Pinus sylvestris* stem radial growth chronologies of the control sites.

Coincidence of maximum and minimum radial increment periods in individual series or chronologies of the aboveground and underground part of trees growing under different ecological conditions sometimes occur due to water level fluctuations in Baltys lake and different intensity of precipitation as well as general effect of summer temperatures on dynamics of lakeside stand growth (Pakalnis 1972). A considerable increase of annual ring-width in a certain part of root system (e.g. horizontal roots) during high water level periods can be explained by the compensatory growth phenomenon (Fig. 7). Fluctuations of lake water levels periodically make up extreme growth conditions for the trees growing in the nearest to the lake and lowest places. However, passing by gradually from one critical water level to another, the zone affected by water level fluctuations result in favourable growth conditions, making growth more intensive than in soil with normal humidity.

The influence of exogenous factors (Baltys lake water level and long-term (> 15.0 yr) precipitation fluctuations) on long-term periodicity (> 15.0 yr) radial growth dynamics was analysed by means of a simple regression analysis, comparing its results and the reaction of

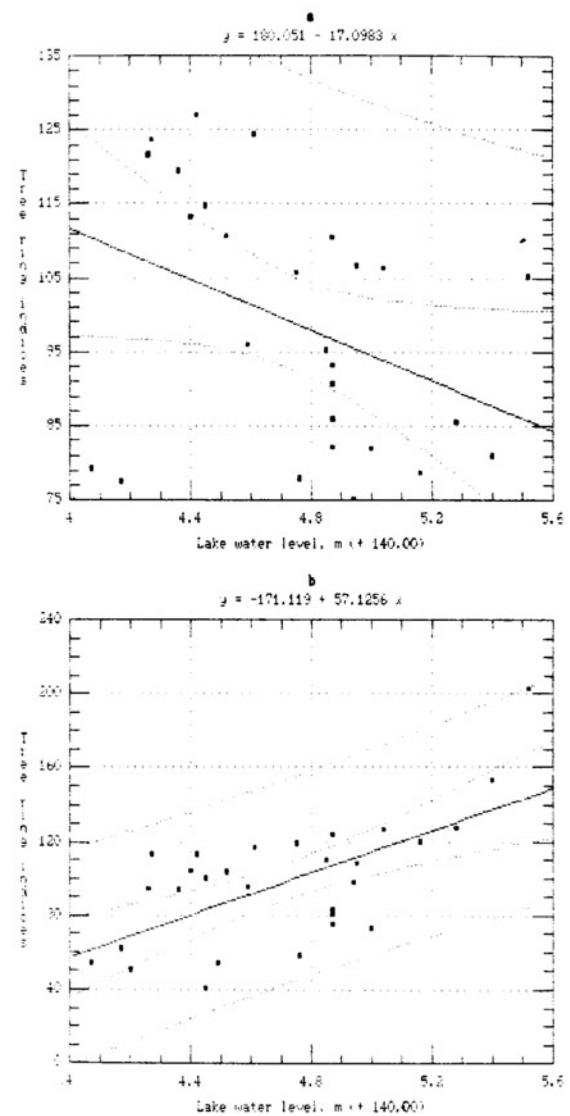


Figure 8. Regression of the radial growth between *Pinus sylvestris* L. radial chronologies of the lakeside sites and the changes of Baltys lake water level (a - stem radial growth, b - horizontal root radial growth).

Pinus sylvestris radial growth to particularly high water level of the lake Baltys in 1958-1960.

A negative line regression between precipitation dynamics and individual stem ring-width series as well as positive or negative - between precipitation and root radial growth series were determined in the lakeside sites. At the lower control site regression between precipitation and root radial growth series was negative, at higher - positive.

A positive line regression between *Pinus sylvestris* stem as well as root radial growth chronologies and precipitation intensity was determined only in the lakeside site NR 6. However, radial growth reaction in 1958-1960 was negative. Correlation ($P < 0.01$) between 1887-1988 period precipitation data and *Pinus sylvestris* radial growth chronology in the lakeside site NR 6 was the following: 0.47 - in the aboveground and 0.24 - in the underground parts of the tree.

Besides, common interval analysis (1958-1988) of Baltys lake water level, precipitation and *Pinus sylvestris* radial growth relationships doing simple regression and correlation analyses was carried out. The line regression between lake water level fluctuations and stem as well as root radial growth chronologies of the lakeside sites was determined. It was negative in the aboveground and positive - in the underground parts of the tree (Fig. 8). The line regression between 1958-1988 period *Pinus sylvestris* radial growth chronologies and precipitation was positive in the aboveground (lakeside site), negative - in the aboveground (higher control site) and the underground (lakeside site) parts. Radial growth reaction in 1958-1960 was negative in stem and positive - in roots of scots pine. Correlation ($P < 0.01$) between 30 yr lake water level dynamics and stem radial growth chronologies was only in the higher control site (0.28) and in the lakeside site (-0.44) as well as between lake water level fluctuations and root chronologies it was from 0.67 to 0.72 - in the lakeside sites and from 0.37 to 0.52 - in the control sites. 1958-1988 period cross-correlations among long-term dynamics of precipitation, radial growth chronologies and lake water level were not significant.

CONCLUSIONS

1. Application of standardized dendrochronological methods to investigations on root systems enables to compare different results of investigations on the aboveground and underground parts of woody plants, to give detailed analyses on the impact of different endogenous and exogenous factors. A maximum annual root radial growth measurement method, which has been developed and applied in this work, can be widely used for investigations on root systems of woody plants.

2. The formant analysis shows a very similar structure of the radial growth fluctuations which do not depend on the site conditions or part of tree investigated. The fluctuations of <15.0 yr period (about 90 %) determine the stability of the tree-ring radial growth cyclicity structure and, at the same time, the remaining fluctuations as well as the nature of the age trend represent the changebility. The age trend nature in *Pinus sylvestris* horizontal root maximum radial growth dynamics is more diverse than stem radial growth.

3. Formant analysis of the longest known in Lithuania precipitation data (1887-1990) expose relatively stable 24, 28 and 76 yr period cycles. Maximum and minimum meanings of precipitation cyclicity conform with water abundance periods at the shores of the Baltic Sea (Shnitnikov 1969) and the periods of increased precipitation (Ščemeliovas 1964). High water level periods in the lake Baltys (Pakalnis 1970) usually start several years before the end of 28 yr periodicity of increased precipitation period.

4. Diverse fluctuations are conditioned by different intensity of the expression of exogenous factors which impact on radial growth dynamics as well as individual characteristics of every tree, especially of the underground part of a plant. The amplitudes of periodical long-term lake water level fluctuations are unequal. They were especially high and well reflected on tree-ring growth in 1957-1963. *Pinus sylvestris* trees growing on lakesides are regularly influenced by 24-30 yr period lake water level fluctuations. These long-term fluctuations are invisible in the radial growth dynamics of the trees growing at the 2-3 m height from the average lake water level where a rather distinct influence of 24, 28 and 76 yr period precipitation changes is established. The tree-ring growth cyclicity of lakeside *Pinus sylvestris* trees was more clear and had higher amplitude as compared with the trees from higher locations.

5. 24-30, 33-34 and 37 yr period cycles were determined in scots pine stem tree-ring growth at the lakeside sites as well as 24-25, 27-28 and 33 yr period cycles - at the sites located on 2-3 m height from the average lake water level (control). Formant analysis of the horizontal root tree-ring growth series shows 24-33 and 36 yr period cycles at the lakeside sites as well as 23, 25-27, 31-32, 34 and 37 yr period cyclicity at the control sites.

6. Tree-ring radial growth reaction to lake water fluctuations of two kinds was established due to our investigations on 1930-1988 period of *Pinus sylvestris* horizontal root and stem radial growth dynamics: positive (mostly) or negative - in roots and negative - in stems. Decreased root radial growth in long-term dynamics at the lakeside sites was ascertained mostly in 1939-1956 (low lake water level), in 1964-1979 (low water level, low precipitation), increased - in 1960-1963 (high lake water level, high precipitation) and in 1981-1985 (high lake water level, high precipitation). In some root radial growth series from lakeside sites an existence of the opposite reaction to lake water level fluctuations during the same periods was established. Minimums in long-term dynamics of stem radial growth series

at the lakeside sites were registered in 1959-1963 and maximums - in 1942-1954 and 1976-1980 periods. In the control sites an increased growth was determined in stem as well as in horizontal root radial growth long-term dynamics during the high lake water level and high precipitation periods.

7. Coincidence of maximum and minimum radial increment periods in series of the aboveground and underground parts of trees growing under different ecological conditions sometimes occurs due to the influence of water level fluctuations in Baltys lake and different intensity of precipitation, general effect of summer temperatures on dynamics of lakeside *Pinus sylvestris* L. growth (Pakalnis 1972) as well as by the compensatory growth phenomenon (a considerable increase of annual ring-width in a certain part of root system during high water level periods).

8. The particular statistical analysis of different *Pinus sylvestris* L. tree-ring series and chronologies of the aboveground and underground parts in different ecotopes indicates, that root systems react to the changes of environment more sensitively, more diversely and not always synchronously. Variability in all frequency ranges (high-frequency and low high-frequency variations) in horizontal root radial growth dynamics of scots pine is significantly higher than in stems as well as at the lakeside sites - higher than in control ones. Mean correlations among all radii series in site are 24-31 % higher in stems than in roots. Correlation between the aboveground and underground part radial growth chronologies is higher in the lakeside than in control sites. *Pinus sylvestris* radial growth dynamics was more synchronous in the lakeside than in control sites due to periodically extreme ecological conditions.

9. At the lakeside *Pinus sylvestris* L. stands the belowground and the aboveground tree-ring growth fluctuations have close relationships with the changes of lake water level. According to our investigations on 1959-1989 period of radial growth dynamics and Baltys lake water level fluctuation data it was established that scots pine horizontal root radial growth increases up to 57 % as while stem radial growth decreases up to 17 % under increase of lake water level up to 1 m. Thus, it is possible to use them in forecasting of various natural phenomena and processes. Research results can be applied for prognoses and retrognoses of biological regime and water resources.

10. The general testable hypothesis was corroborated in this research: reaction of the underground part of stand components to the influence of environmental factors usually differs from that of the aboveground part. Thus, investigations on root growth dynamics, as a constituent part of complex investigations, may increase information to a considerable extent and help us reveal and explain functioning regularities of forest ecosystems.

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