Zbornik gozdarstva in lesarstva 80 (2006), s. 97 - 109

GDK: 56+111.8:174.7 *Picea abies*(497.12*02 Pokljuka)(045)=20
Prispelo / *Recived*: 24. 08. 2006 Izvirni znanstveni članek
Sprejeto / Accepted: 24. 10. 2006 *Original scientific paper*

USE OF DIFFERENT GROWTH PARAMATERS OF NORWAY SPRUCE (*Picea abies* (L.) KARST.) TO STUDY TREE RESPONSE TO CLIMATE

Tom LEVANIČ[1], R. JALKANEN[2], J. GRIČAR[3], M. GAGEN[4], Primož OVEN[5]

Abstract

In the paper, potential analysis of various growth parameters of Norway spruce are introduced at the macro and micro levels. Dendroecological measurements give information as to xylem growth ring widths, their density and content of stable isotopes in the xylem growth rings. Needle trace method of the terminal annual shoot allows retrospective view into needle density of the terminal annual shoot and consequently reconstruction of the several parameters linked to the needles and air pollution. Using pinning method, it is possible to follow intra-annual dynamics of the radial growth of trees at the cellular level and furthermore investigate the effect of climatic factors on cambial activity.

Key words: Norway spruce, *Picea abies*, multiproxy analysis, Pokljuka, Slovenia, dendroecology, pinning, needle trace method

UPORABNOST RAZLIČNIH RASTNIH PARAMETROV NAVADNE SMREKE (Picea abies (L.) KARST.) ZA ŠTUDIJ ODZIVA DREVES NA KLIMO

Izvleček

V prispevku so predstavljene možnosti analize različnih rastnih parametrov navadne smreke na makro in mikro nivoju. Dendroekološke meritve nam dajo informacijo o širinah branik, gostotah branik in vsebnosti stabilnih izotopov ogljika v njih na nivoju branike ter jih retrospektivno povezati z različnimi okoljskimi informacijami. Metoda preučevanja sledi iglic terminalnega poganjka nam omogoča rekonstrukcijo gostote iglic terminalnega poganjka in posledično analizo številnih parametrov, vezanih na iglice in zračno polucijo. Z metodo pinning je mogoče slediti intraanualno dinamiko debelinske rasti drevesa na celičnem nivoju in nadalje raziskati vpliv klimatskih dejavnikov na kambijevo aktivnost.

Ključne besede: navadna smreka, Picea abies, multiproksistična analiza, Pokljuka, dendroekologija, metoda pinning, metoda sledi iglic

INTRODUCTION
UVOD

Tree growth is limited to localized regions of specialized tissues, called meristems (e.g. KOZLOWSKI / PALLARDY 1997b). Their activity and hence growth is in temperate and boreal climatic zones restricted to the period of warm months (KOZLOWSKI 1971; LARSON 1994; KOZLOWSKI / PALLARDY 1997a; DESLAURIERS / MORIN 2005). Environmental conditions play an important role in controlling tree growth, but precise relationship between climate and beginning, culmination and termination of growth is only fragmentary understood. At the time of increasing threats of global climatic changes, which will not avoid forests, relevancy of this knowledge is increasing (KAJFEŽ-BOGATAJ / BERGANT 2005a, b). It is a tool for understanding past climatic and environmental events as a basis for prediction of development of forest ecosystems and forest-based industries in the future. Closely related goal of dendroclimatology is to identify the climate signal in tree-ring series and to use them to reconstruct past climate variation from several hundred to several

[1] doc.dr. T. L., Gozdarski inštitut Slovenije, Oddelek za rast in gojenje gozda, Večna pot 2, SI-1000 Ljubljana, SLO
[2] dr. R. J., METLA Rovaniemi Research Unit, Eteläranta 55, FIN-96300 Rovaniemi, FINLAND
[3] dr. J. G., ., Gozdarski inštitut Slovenije, Oddelek za rast in gojenje gozda, Večna pot 2, SI-1000 Ljubljana, SLO
[4] dr. M.G., University of Swansea, Department of Geography, Singleton park, Swansea, SA2 8PP United Kingdom
[5] prof.dr. P. O., Biotehniška fakulteta, Oddelek za lesarstvo, Rožna dolina c. VIII/34, SI-1001 Ljubljana, SLO

thousand-year-long tree-ring chronologies (FRITTS 1976; SCHWEINGRUBER 1989). As opposed to traditional definition, the number of tree-growth variables employed in contemporary dendroclimatological studies is increasing. Similarly, needle-related time series (JALKANEN / KURKELA / AALTO 2002) are very useful in climate reconstructions, and potentially useful in reconstruction of carbon storage. Tree-growth and needle-related parameters are referred to as proxies.

The seasonal dynamics of cambial activity and corresponding cell differentiation in trees can be followed by a variety of different methods, such as pinning, micro-coring, automatic dendrometers, sampling of intact blocks of tissues, etc. (WHITMORE / ZAHNER 1966; WOLTER 1968; WODZICKI 1971; SKENE 1972; ANTONOVA / STASOVA 1993, 1997; BÄUCKER / BUES / VOGEL 1998; FORSTER / SCHWEINGRUBER / DENNELER 2000; GINDL / GRABNER 2000; SCHMITT / MOLLER / ECKSTEIN 2000; DESLAURIERS et al. 2003; MÄKINEN / NÖJD / SARANPAA 2003; SCHMITT / JALKANEN / ECKSTEIN 2004; DESLAURIERS / MORIN 2005). The pinning method uses the ability of the cambium and its youngest derivatives to respond to a minute mechanical injury without affecting the physiological integrity of a tree (WOLTER 1968; SHIGO 1986). Pin insertion into the cambium causes minute wound reactions, which define the increment reached by the time of pinning. Therefore, precise knowledge of the species-related anatomical response to wounding is necessary when applying this technique (WOLTER 1968; YOSHIMURA / ITOH / SHIMAJI 1981; KURODA / SHIMAJI 1983, 1984b, a; KURODA / KIYONO 1997; SCHMITT / MOLLER / ECKSTEIN 2000; MÄKINEN / NÖJD / SARANPAA 2003; SCHMITT / JALKANEN / ECKSTEIN 2004). Apart from long chronologies, investigation of annual dynamics of wood formation received only little attention until last decade. Environmental factors, regulating wood formation in particular growing season are still not well understood and hence misleadingly interpreted in classical dendroclimatological studies.

As a part of an EU project (Predicting Impacts on Natural Ecotones, PINE, of the 5th framework program), multiproxy approach was applied at three sites of spruce forests in Slovenia and Austria in the years 2002–2005. This paper shortly introduces the applied methods and techniques in order to produce inter- and intra-annual chronologies of various stem-originated parameters of a single Norway spruce (*Picea abies* (L.) Karst.) tree from the experimental site Pokljuka, Slovenia. The purpose of the information gathered on only one tree was to demonstrate the possibilities of extracting different proxy data and use of them in further research. Results presented in this article are introductory rather than conclusive.

MATERIAL AND METHODS
MATERIAL IN METODE

EXPERIMENTAL SITE AND TREE

Five healthy Norway spruce (*Picea abies* (L.) Karst.) trees from Pokljuka (46º21'N, 13º59'E, elevation 1260-1290 m a.s.l.), northern Slovenia, were selected for multiproxy dendroclimatological studies in spring 2002 (Fig. 1). All trees were about 70 years old and approximately 35 m high. They were selected according to the following criteria: tree crown should be in the stand canopy and normally developed (social position 2 after Kraft's classification), stem should be without any visible mechanical damage, whereas root system should be more or less intact (at least 10m from any skidding trails). The site and the stand were considered to be moist, relatively cool in the summer and well suited for spruce growth. Soil on research plot is high in organic contents and shallow to medium deep (Rendzic Leptosol according to WRB 1998 soil classification). The experimental stand represented an average natural spruce forest of that age in stand density and silvicultural status including thinning. Ground vegetation of the site was scarce partly due to very dense crowns and partly due to the influence of the repeated cattle grazing. In May 2003, the sample trees were felled and sectioned for several purposes described below.

Examples of all the described proxies in the present study are illustrated and discussed based on one sample tree (tree No. 4). The test tree was 26.9 m tall and 26 cm in diameter at breast height.

PROXIES INVESTIGATED

Here, the introduced parameters of the tree No. 4 are: tree-ring width (TRW), maximum late-wood density (MxD), height increment (HI), stable carbon isotopes (ISO), summer needle retention (NRS), needle age (AGE), needle shed (SHED), needle production (PROD), needle pool (POOL), and needle density (DENS), and intra-annual wood formation (WF). Depending on the type of analysis, we sent samples to different laboratories: tree-ring width measurements were done at the Slovenian Forestry Institute, densitometry at WSL Birmensdorf, Switzerland and isotopic composition at the Department of Geography, University of Swansea, United Kingdom. Height increments and needle proxies were produced in Metla, Rovaniemi. The Department of Wood Science and Technology, University of Ljubljana analysed the intra-annual radial growth.

MEASUREMENTS OF TREE-RING WIDTHS

For tree ring studies, 5 mm thick cores and radial sections from stem discs were used. All samples were prepared according to the standard dendrochronological procedures well described in the literature (FRITTS 1976; SCHWEINGRUBER 1989). Tree-ring widths were measured on a measuring table LINTAB (www.rinntech.com), equipped with PAST-4 dendrochronological software (www.sciem.com). Tree-ring series were crosschecked, verified and synchronized against each other.

ANALYSIS OF WOOD DENSITY

For tree-ring density, WSL team used system provided by Walesch electronics (www.walesch.ch). Cores, 12 mm in thickness, or radial sections of stem discs were taken for this type of analysis. Samples were prepared on a double bladed saw and resin extracted with Soxlet apparatus (SCHWEINGRUBER et al. 1978a). X-ray images were processed according to the procedures developed at their own laboratory (see SCHWEINGRUBER et al. 1978b). Tree-ring density measurements gave a comprehensive set of different tree ring features – minimum density, maximum density, maximum latewood density, minimum earlywood density, average tree-ring density, proportion of early- and latewood and finally tree-ring width (see Figure 2). (SCHWEINGRUBER et al. 1978b)

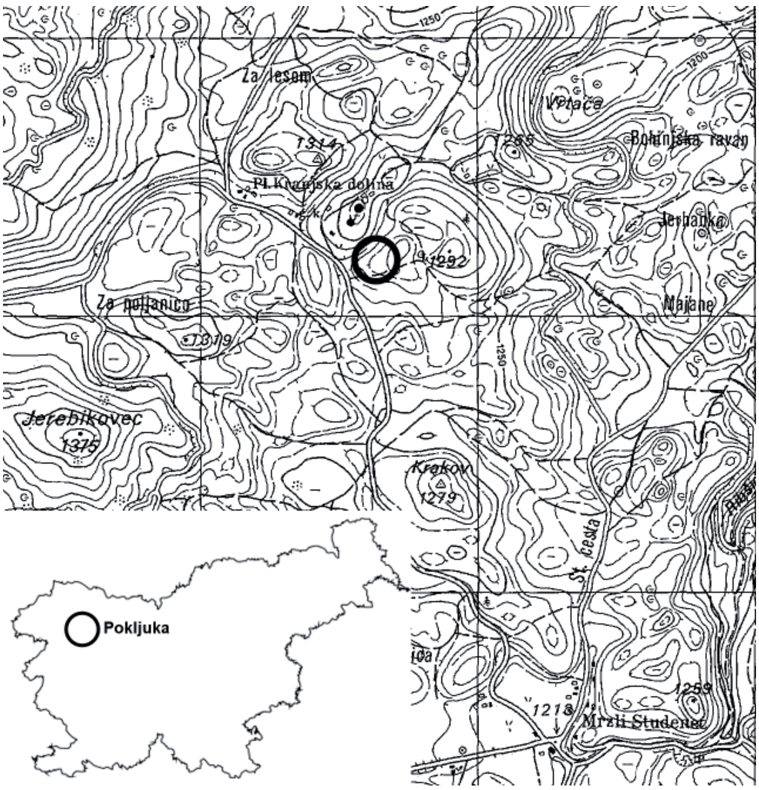


Fig. 1: Location of the plot on the Pokljuka plateau

Slika 1: Lokacija raziskovalne ploskve Pokljuka (Slovenija)

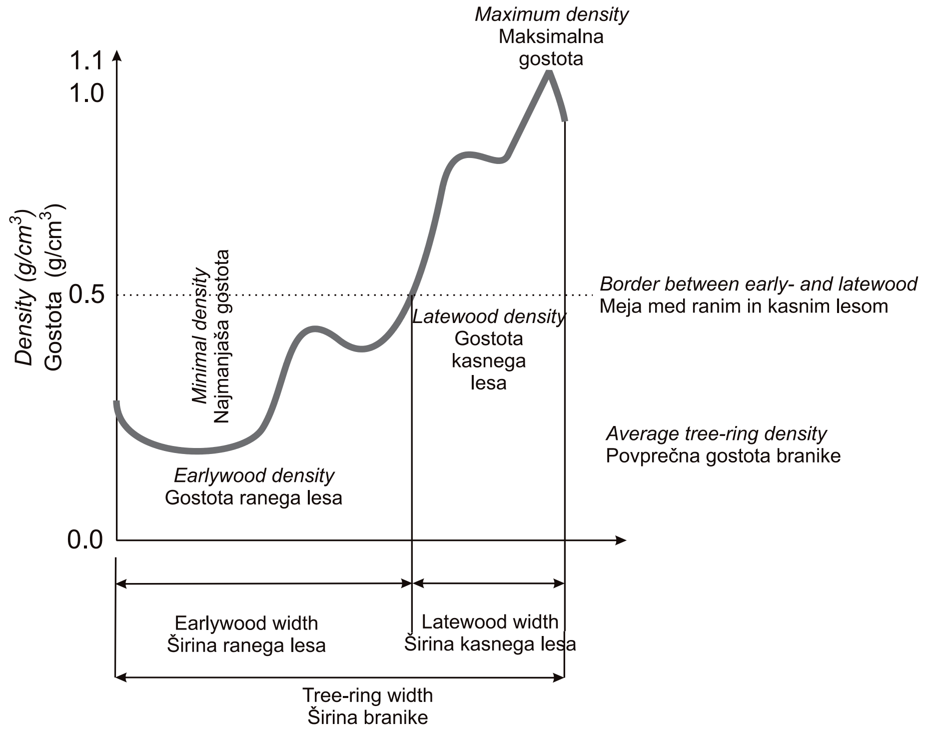


Fig. 2: Different parameters obtained in densitometric analysis (source: COOK / KAIRIUKSTIS 1989)

Slika 2: Nabor možnih spremenljivk, ki jih dobimo pri densitometrični analizi (vir: COOK / KAIRIUKSTIS 1989)

CARBON ISOTOPE COMPOSITION

Both cores and discs were sampled for stable carbon isotope analysis. The complete length (radius) of each core or disk was sampled. Each ring was located on the sample and separated using a very sharp chisel and razor blade. We did not separate earlywood from latewood considering that our objective was to quantify carbon isotope discrimination during the entire period of wood formation, therefore both early and latewood were used. We isolated α-cellulose from the slivers of wood through a series of chemical steps, using a modified Loader batch processing technique (see LOADER et al. 1997 for details).

Cellulose $\delta^{13}C$ was analysed using Europa 20/20 isotope ratio mass spectrometer coupled to an elemental analyser. Processing to cellulose and $\delta^{13}C$ analyses were carried out at the Department of Geography, University of Swansea, Britain. Nitrous oxide was removed by gas chromatography and corrections for ^{17}O (CRAIG 1954) were done for all runs. Precision calculation was done on a total of 303 tree ring samples at Pokljuka and overall precision for $\delta^{13}C$ was 0.01‰ (n=303). Stable carbon isotope ratio was calculated using equation 1.

$$\partial^{13}C(in‰) = \left(\frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{standard}} - 1 \right) \times 1000 \qquad (1)$$

The $^{13}C/^{12}C_{standard}$ used at University of Swansea is PDB standard (Pee Dee Belemnite from an internal calcite structure from a fossil *Belemnitella americana* from the Cretaceous Pee Dee Formation in South Carolina, USA).

HEIGHT INCREMENT AND NEEDLE TRACE ANALYSIS

Height increment was measured as the lengths of the annual length of the terminal shoot. The dating of the annual terminal shoots was controlled with the counting of tree rings in the discs originating in irregular distanced along the stem. Once the annual terminal shoots were determined, a 15-cm-long piece was sawn in each annual shoot for needle-trace analysis according to Aalto and Jalkanen (1998). The Needle Trace Method (NTM) (see KURKELA / JALKANEN 1990; JALKANEN / KURKELA / AALTO 2002) revealed retrospectively the needle and growth history of the analysed trees.

PINNING AND INTRA-ANNUAL ANALYSIS OF WOOD FORMATION

Selected tree was pinned weekly, from May 10th until September 13th in the year 2002, and experiment was made according to the procedure described below. Six pinning holes were set in a semi-helical pattern along the stem of the tree at the same experimental date, using a needle that was 1.75 mm at its thickest part. The holes were marked and numbered. After the 2002 growing season, the pinned tree was felled and samples containing wound tissues were removed, fixed in FEA (formalin-ethanol-acetic acid solution) and dehydrated in a graded series of ethanol (30%, 50% and 70%). Transverse sections of approximately 25 μm in thickness were prepared, using a Leica SM2000R microtome. They were stained with safranine and astra blue and mounted in Euparal. Microscopical observations and measurements were carried out with a Nikon Eclipse E800 light microscope and Lucia G 4.8 image analysis system. We counted the number of the cells and measured the width of the xylem increment reached from the time of pinning in at least three radial files of tracheids. In addition, we counted the number of cells and measured the width of the xylem growth rings formed during the 2002 season on the extreme sides of the cross-sections that were free of a wound response.

For description of the radial growth of tree No.4 at Pokljuka in the growing season 2002, the Gompertz function was used. Seasonal dynamics of wood formation follow S-shape of growth that show two different development phases: a positive exponential phase followed by a relative growth rate decrease (ROSSI / DESLAURIERS / MORIN 2003). Among different sigmoid growth models, the Gompertz equation seems the more appropriate for its asymmetrical shape. The inflection point in Gompertz equation is reached at a lower level, resulting in a shorter positive exponential phase (ROSSI / DESLAURIERS / MORIN 2003; KOTAR 2005). The Gompertz function can be written as growth function:

$$y = Ae^{\left[-e^{(\beta-\kappa t)}\right]}$$

where

y = cumulative of increment is expressed in cells/width, t = day of the year, A = upper asymptote of the maximum number of cells/width, β = x-axis placement parameter, κ = rate of change parameter

or increment function $y = A\beta\kappa e^{(-\kappa t)}e^{\left(-\beta e^{-\kappa t}\right)}$

where

y = weekly increment is expressed in cells/width

RESULTS AND DISCUSSION
REZULTATI IN DISKUSIJA

TREE-RING PROXIES (TRW, HI, MXD, ISO)

TRW and HI parameters are relatively easy and cost effective to measure. TRW measurements are based on cores and stem discs, while height increments are part of NTM analysis (explained later in this article) and tree need to be cut down to get this information.

In both parameters we can observe typical decreasing trend of both tree-ring widths and height increments in relation to tree age / calendar year. Correlation between TRW and HI is fairly high (r=0.78 ***), however, in some years we can observe disagreements (e.g. 1993, 2001). Since both proxies are correlated, one can be replaced by the other in studies that need multiple regression approach. Decreasing trend of both parameters can be removed with appropriate standardisation technique (Figure 3).

MxD is a parameter which correlates well with summer temperature and precipitation. It can also be observed that there is no age-related trend, however, troublesome with this parameter is in its weak sensitivity since its variation is usually very small. This parameter is more or less independent from tree-ring widths (r=-0.205 ^{NS}), height increment measurements (r=0.067 ^{NS}) and in weak correlation with measurement of stable carbon isotope content in tree rings (r=0.279*). Therefore, it can be used as one of the independent variables in multiple regressions (Figure 4).

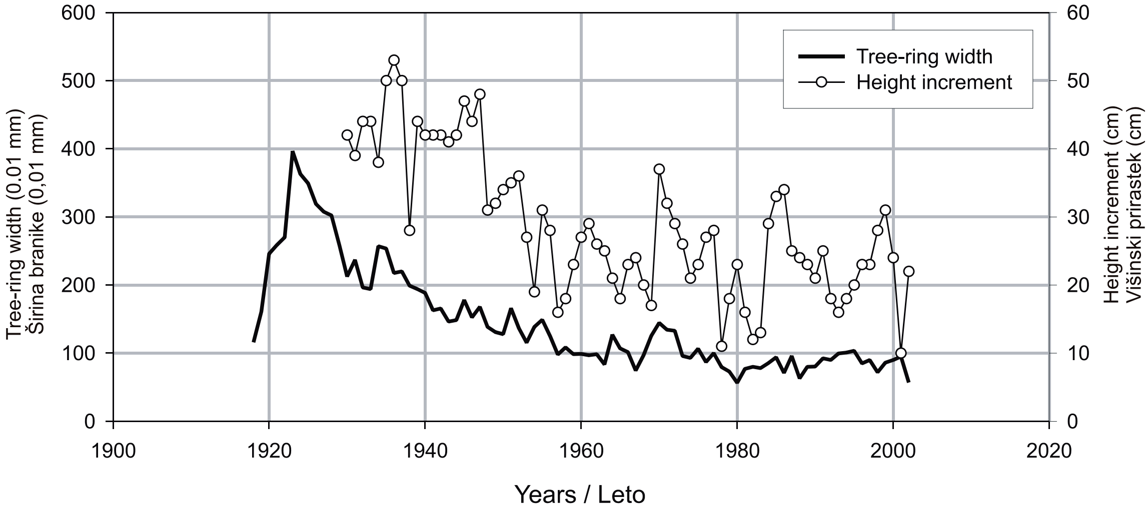


Fig. 3: Tree-ring widths and height increment, spruce No. 4, Pokljuka, Slovenia

Slika 3: Širine branik in višinski prirastki smreke št. 4 na Pokljuki, Slovenija

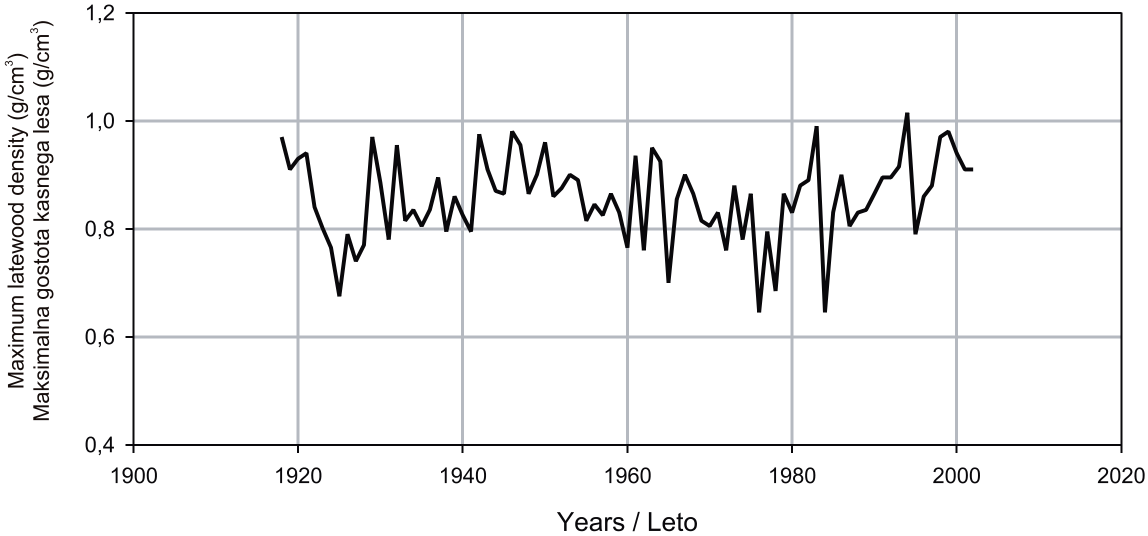


Fig. 4: Maximum late-wood density, spruce No. 4, Pokljuka, Slovenia

Slika 4: Maksimalna gostota kasnega lesa pri smreki št. 4 na Pokljuki, Slovenia

ISO is a parameter, with a very clear physiological background and is directly connected with transpiration, carbon storage and water stress (FARQUHAR / O'LEARY / BERRY 1982; FARQUHAR / EHLERINGER / HUBICK 1989). Generally we can expect that lower values are indicating less stress (less "heavier" $\delta^{13}C$ is stored in plant body), while higher values are connected with water stress. Expected value range is between -20‰ and -30‰ for C3 plants (all trees used in dendrochronology). Parameter does not correlate with tree-ring widths and height increments but slightly with maximum latewood density. Age trend is generally not present, so there is no need of standardisation. As such it can be used as an independent parameter in multiple regressions and also as an independent climate proxy (Figure 5).

THE NEEDLE PROXIES

Needle retention (Figure 6a), the Needle Trace Method (NTM) is able to produce needle-retention levels both for summer and winter. In this connection, summer needle-retention chronology (NRS) is introduced. Needle retention describes how many needle sets are present in the main stem at any

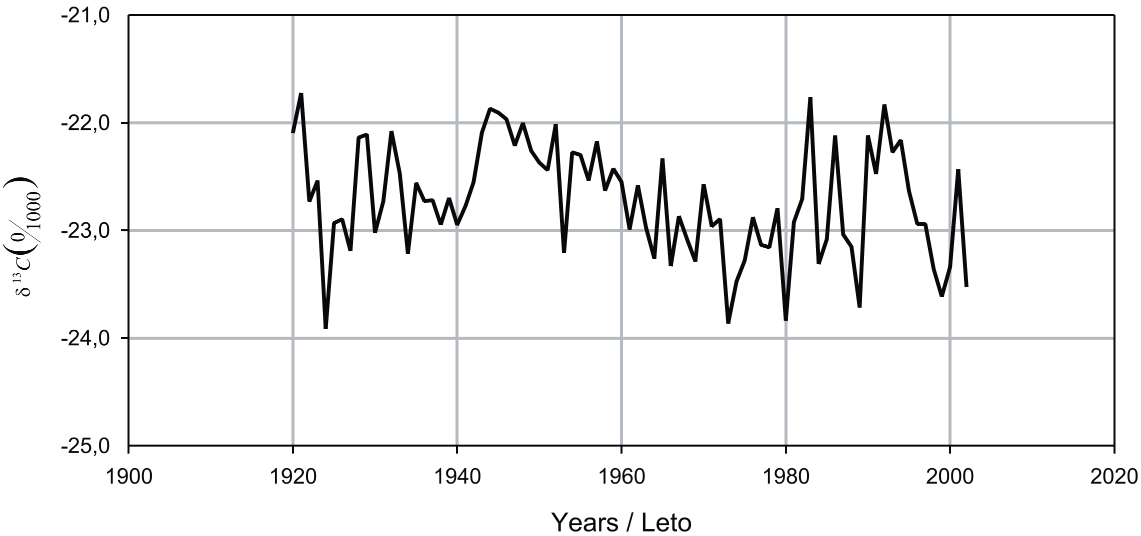


Fig. 5: Stable carbon isotopes in tree rings – early- and latewood were not separated. Spruce No. 4, Pokljuka, Slovenia.

Slika 5: Vsebnost stabilnega izotopa ogljika v braniko smreke št. 4 na Pokljuki, Slovenija – rani in kasni les nista bila analizirana ločeno.

time. This is the first time ever in unpolluted environments to launch a 65-year-long NRS chronology for spruce. Thus it is not known what the pattern should be. However, grown in more or less ‘normal’ conditions, this spruce may well indicate the normal NRS pattern for Norway spruce (for spruce in a polluted environment, see SANDER / ECKSTEIN 2001). In the first thirty years, NRS is increasing, then culminating and gradually declining. The pattern is similar to Scots pine (JALKANEN / AALTO / KURKELA 1995). Also the medium resolution variation seems to be the same in both species. Spruce indicates a 4 to 5-year period between the maximum within the whole-tree pattern. NRS pattern indicates some disturbances in spruce development in the early 1970s and at the end of 1980s. Highest mean NRS values up to 7.5 needle sets are met in the late 1960s. Long-term mean NRS for tree 4 was 6.5 needle sets.

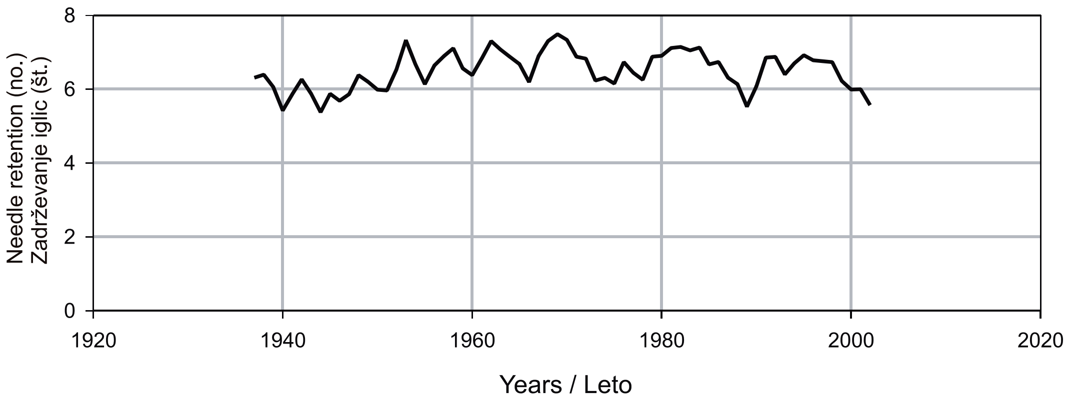
Needle age (Figure 6b) is able to produce chronologies for minimum, mean and maximum needle age of each needle-age class. Separately, the NTM calculates the average age of the attached needles at any time. In this connection, mean needle age (AGE) is introduced. Its general pattern of long-term variation is the same as for NRS; AGE is first increasing and then gradually decreasing. In fact, general patterns of AGE and NRS have to follow each other as needle age largely determines the number of attached needle sets. However, as AGE describes annual variation of each needle-age class, it has a different use in the description of the tree’s canopy or health history. As compared to NRS, mean AGE varies a lot. As the mean AGE of the entire tree number 4 was 6.0 years, annual maxima and minima were 7.4…7.3 in 1976, 1962 and 1951, and 4.3…5.2 in 1940, 1984 and 1960, respectively. Longest-living needle, born in 1954, was 11 years old. It is evident that AGE describes variations in growth conditions much better than NRS.

Needle shed (Figure 6c) - opposite to the previous parameters, the general pattern for needle shed (SHED) is first decreasing and in latest decades increasing. Logically, when needle age increases, dying of needles are delayed, thus resulting in lowered SHED values. Long-term average in ideal growing conditions should theoretically be one because on average one needle set is lost and one new is born every year. In tree No. 4 long-term mean SHED was 1.0, indicating that the tree is in balance and that no extra strong outside factor is influencing needle longevity. Minimum and maximum SHED, 0.2 and 1.6 needle sets, was met in 1952 and 1990, and in 1939, 1973, 1972 and 1988, respectively.

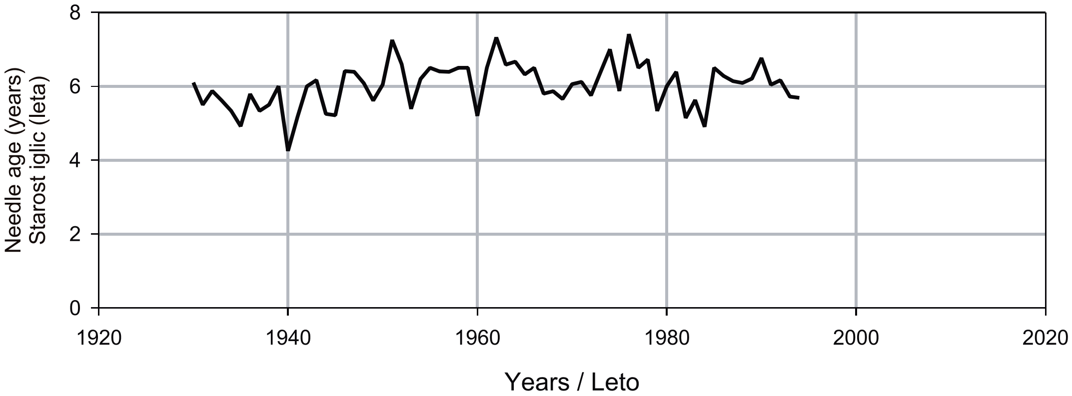
Needle production (Figure 6d) - annual needle production (PROD) reveals the number of needles produced in the leader shoot. As compared to pines with short shoots attached in the long shoot, needles are directly attached to the long shoot in spruce and firs. So the long-term mean PROD in the example tree, 441 needles, would result in a value of 220 short shoots in a 2-needle pine. At high latitudes PROD for Scots pine is below 100 to increase to over 200 in Estonia (PENSA / JALKANEN 2005), reaching nearly the 300-level in more southern latitudes with a vigorous growth (JALKANEN / LEVANIČ 2001). In spruce, needles are produced particularly in the early years of the tree and clearly less towards the middle age. Whether the slight increase in the pattern of PROD during the last 15 to 20 years is typical for spruce, is of silvicultural origin or is maybe related to climate warming, needs further studies.

Needle pool (Figure 6e) - as shown above, spruce needles are on average six years old when they die. This means that, on average, there are attached needles from at least six needle-age classes. The number of needles in different annual shoots is called needle pool (POOL). In the Pokljuka case, POOL decreases continuously and rather linearly in time. Pool values of above 4000 needles in the first decades were dropped to about half towards the 1990s. So far, no long-term POOL chronologies of any species in 'normal' conditions exist to indicate normal POOL behaviour.

Needle density (Figure 6f) - the number of needles of the long shoot per centimetre gives needle density (DENS). To produce DENS the NTM uses needle production and length of the sample, from which the needle traces are counted and which originates from the middle of the annual shoot (JALKANEN / AALTO / KURKELA 1998). Here DENS of spruce increases in time, starting from a level of 13 needles cm^{-1} in the 1930s and ending to a general level of 18 needles cm^{-1}. DENS is not the same from year to year, and in fact DENS is a very good parameter to describe disturbances in tree's history. Here the years of 1982–1983, and 2001 represent very well some unknown disturbances, during which DENS increases over to 30 needles cm^{-1}. However, the found disturbances can occur just in this tree, being e.g. a breakage of the leader shoot. Therefore, to get reliable density history at stand level, more trees are needed. Furthermore, annual leader shoot is much more vulnerable to disturbances than tree ring formation; however, they both react to short and long summers. Due to different structures of needle attachments in pines, Scots pine normally has between 6 to 8 short shoots per long shoot centimetre (JALKANEN / AALTO / KURKELA 1998; SAL-



a)



b)

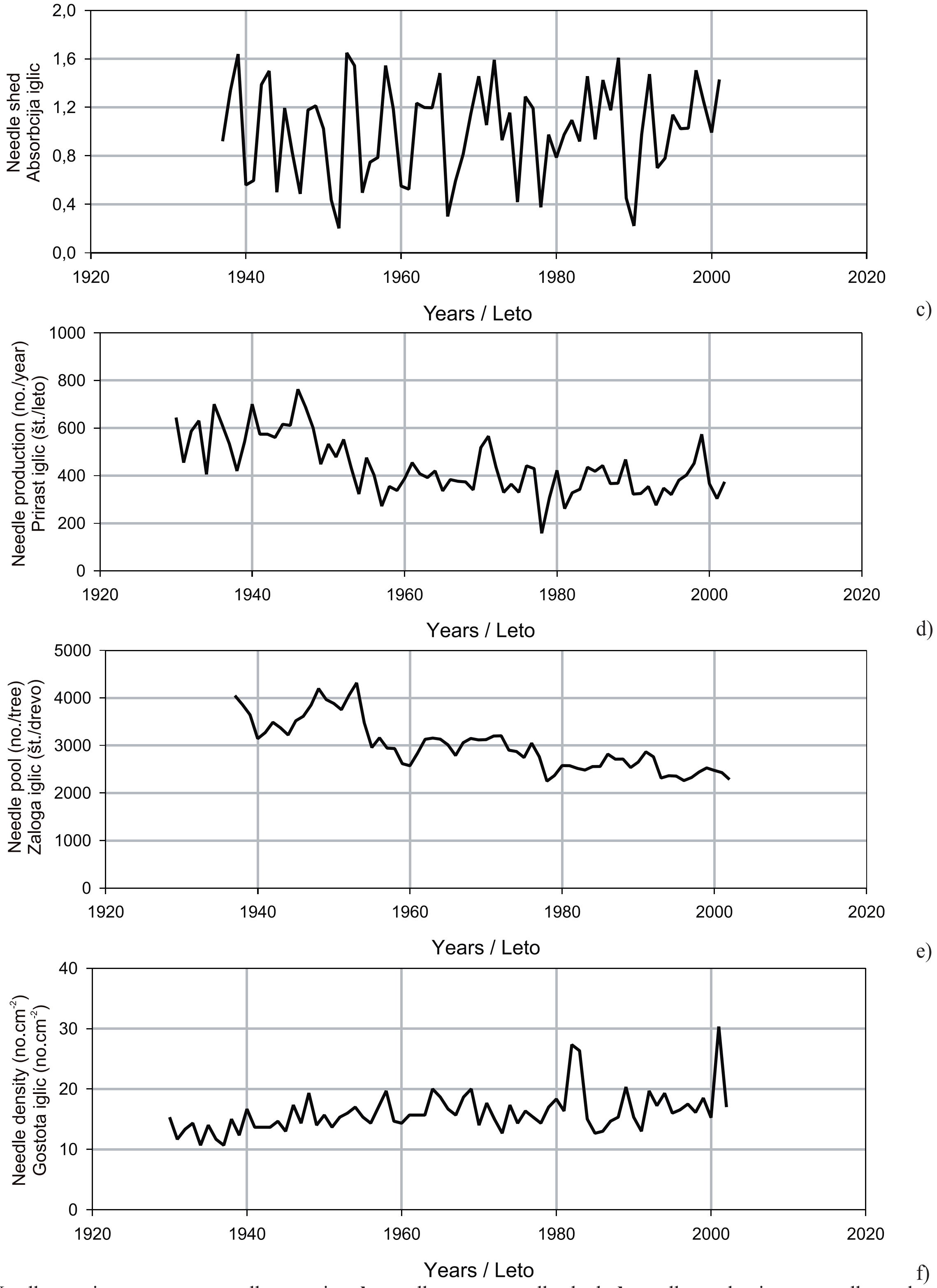


Fig. 6: Needle proxies **a**. summer needle retention, **b**. needle age, **c**. needle shed, **d**. needle production, **e**. needle pool, and **f**. needle density. Analysed spruce No. 4 at Pokljuka, Slovenia.

*Slika 6: Različne spremenljivke, vezane na sledove iglic glavnega poganjka, ki smo jih dobili s pomočjo NTM metode: **a**. poletno zadrževanje iglic, **b**. starost iglic, **c**. letni odmet iglic, **d**. prirast iglic, **e**. zaloga iglic in **f**. gostota iglic. Analizirano drevo št. 4 na Pokljuki.*

MINEN / JALKANEN 2006), disturbances resulting clearly higher values (FERRETTI et al. 2002)

INTRA-ANNUAL WOOD FORMATION

Investigated spruce No. 4 started with cambial activity between 17-24 May 2002. We defined the onset of the wood formation by distinguishing between cambial cells and radially expanding xylem cells in the callus that were found next to the xylem growth ring 2001. Radial dimensions of the cells in postcambial growth were larger compared to the cambial ones. Time for the beginning of late wood formation was defined qualitatively and corresponds to week 5-12 Jul 2002. At that time, the radial dimensions of the tracheids narrowed and thickness of the cell walls increased. Production of new cells in the cambium ended in the week between 26 Jul-2 Aug 2002. We determined the cessation of the regular cambial activity when the number of the cells of the current xylem increment 2002 coincided with the number of the cells in the intact part of the same growth ring aside the callus. Furthermore, the xylem cells in postcambial growth were not present in the callus and the latest formed late wood tracheids below the callus were in the final stages of differentiation (secondary wall formation and lignification).

Maximal weekly increment was detected in the 169th day of the year, irrespective if expressed in width or cell number increase. This is in accordance with Rossi et al. (2006), who reported a maximum growth rate for various tree species in temperate and boreal climatic zones around the summer solstice (172 day of the year) - the time of maximum day length, and not during the warmest period of the year, as previously suggested.

With measurements of the xylem increments and counting the number of cells, two types of information were obtained. Cell number gives information on cell production capacity of the cambium on the xylem side. On the other hand, increase of width of xylem increment contains the data of both; the number of xylem cells produced in the cambium, as well as the increase of radial diameter of cells during postcambial growth. In this context, wider earlywood cells formed in the first part of the growing season contribute more to the final width of the xylem growth increment. This could explain the differences in the shape of both growth functions (Figures 7, 8). It has to be stated that deposition of the multilayered secondary cell wall and lignification do not contribute to the increase of xylem increment, but only to the accumulation of the biomass into the cell walls.

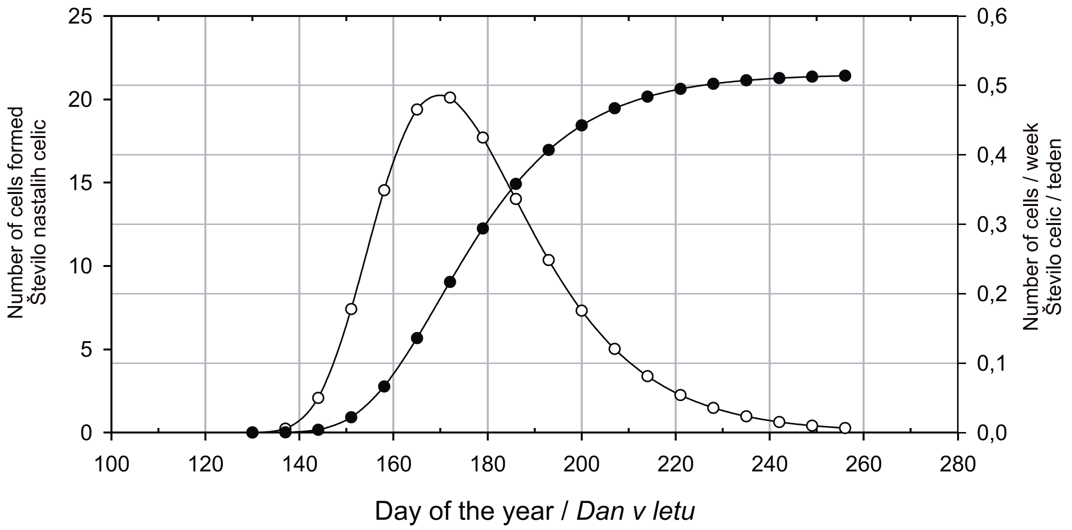


Fig. 7: Intra-annual dynamics of wood formation expressed in cell number formed by the pinning date in experimental tree No. 4 at Pokljuka in the season 2002.

Slika 7: Sezonska dinamika nastajanja ksilemske branike, izražena kot število celic, nastalih do dneva vboda z iglo pri drevesu št. 4 (Pokljuka) v rastni sezoni 2002.

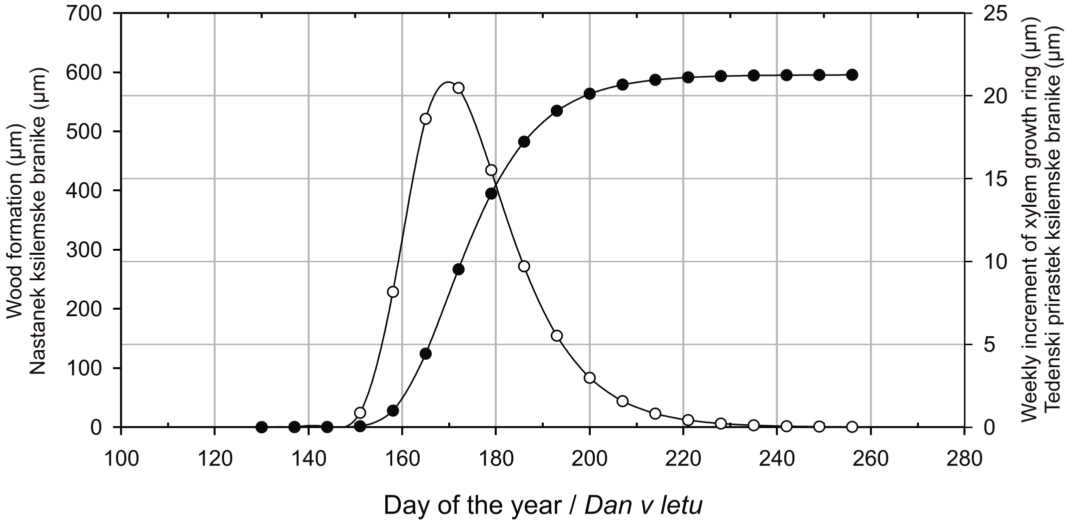


Fig. 8: Intra-annual dynamics of wood formation expressed as width formed by the pinning date in experimental tree No. 4 at Pokljuka in the season 2002.

Slika 8: Sezonska dinamika nastajanja ksilemske branike, izražena kot širina prirastka, ki je nastal do dneva vboda z iglo pri drevesu št. 4 (Pokljuka) v rastni sezoni 2002.

CONCLUSION

Different proxy data obtained from a single Norway spruce show that this kind of information is useful in ecological, physiological and climatological studies.

Tree ring widths, height increments, maximum latewood densities and stable carbon isotope contents are information directly connected with different environmental and climatic data. Therefore they can be used to analyse tree's response to climate and environment (including response to extreme events) and as a so called "proxy data" in reconstruction of past environmental and climatic events for the periods before instrumental data.

Different information regarding needles, their longevity and density could be obtained through the so called "Needle Trace Method". This method is using needle traces of terminal shoot to reconstruct various needle parameters and, further on, to reconstruct environmental or climatic factors that influence height growth, needle production, needle longevity, needle shed, etc. This is the only method that is capable to reconstruct any of the needle parameters back in time and it proved to be useful in all kind of ecological and climatological research dealing with conifers (especially pine and spruce). The method itself is more precisely presented in Kurkela and Jalkanen (1990) and in Jalkanen *et al.*(2002).

Intra-annual studies of cambial activity give data of wood formation at high resolution. This information is very useful in standard dendroclimatological studies. For correlations of temperatures of the current year and the widths of the xylem growth ring, the knowledge on the length of the growing season is crucial. Otherwise, high correlations of the September temperatures and the xylem ring widths are meaningless since trees from temperate and climatic boreal zone at this time of the year do not grow anymore.

POVZETEK

V pričujočem prispevku predstavljamo metode in tehnike, ki smo jih uporabili za sestavo dolgih časovnih vrst podatkov o rasti debla smreke (*Picea abies* (L.) Karst.). Tako pridobljene informacije lahko koristno uporabimo pri modeliranju odnosa med rastjo in klimo (še posebej v razmerah globalnega spreminjanja klime). Podatki, ki jih predstavljamo v tem prispevku, so bili zbrani za potrebe evropskega raziskovalnega projekta PINE – Predicting Impact on Natural Ecotone (5. okvirni program EU) na Pokljuki in na Sorškem polju v Sloveniji. V projektu PINE smo sicer zbirali podatke na večjem številu ploskev na transektu sever-jug od severa Finske do Slovenije na jugu.

TRW / ISO / HI / MxD

Spremenljivke o širini branike (TRW), maksimalni gostoti kasnega lesa (MxD), vsebnosti stabilnega izotopa ogljika (ISO) in višinskega prirastka (HI) so podatki, ki nam govorijo o odzivu drevesa na okoljske spremembe. Podatek o širini branike je izmed vseh štirih spremenljivk najlaže pridobiti, podatek o vsebnosti stabilnega izotopa ogljika pa najteže. V nasprotju z drugimi tremi podatki je podatek o višinskem prirastku, kjer merimo dejanske višinske prirastke glavnega poganjka, mogoče pridobiti samo s posekom drevesa in zatorej sodi med destruktivne vzorčne metode. Drugi trije podatki se lahko pridobijo iz debelih, 12 mm izvrtkov.

NTM

Podatke o iglicah smo izračunali s pomočjo t.i. metode NTM (ang. »Needle Trace Method«), to je metoda, ki uporablja sledi iglic glavnega poganjka za rekonstrukcijo oigličenosti glavnega poganjka. Iz tega osnovnega podatka pa lahko izračunamo množico različnih izvedenih spremenljivk, ki nam definirajo gostoto iglic na enoto mero, letno produkcijo in abscisijo iglic, kronološko spreminjanje števila iglic glavnega poganjka, ipd. Metoda NTM je edina, ki uporablja numerične podatke o iglicah glavnega poganjka in prek tega sklepa na klimatske / okoljske razmere, v katerih so iglice nastajale. Metoda je uporabna predvsem na smreki in boru ter je natančneje predstavljena v delu Kurkele in Jalkanena (1990) in Jalkanena s sodelavci (2002).

Sezonska dinamika rasti ksilemske branike (WF)

Z raziskavami sezonske dinamike kambijeve aktivnosti v teku enega leta dobimo visokoločljive podatke o nastajanju ksilemske branike. Z njimi je mogoče dopolniti in nadgraditi spoznanja o rasti drevesa, ki izvirajo iz klasičnih večletnih kronologij. Rezultati kažejo, da je poznavanje začetka in konca kambijeve aktivnosti za dendroklimatološke študije ključno. V tem smislu so npr. korelacije septembrskih temperatur tekočega leta in širine branik nesmiselne, četudi so korelacije visoko značilne, saj drevesa iz zmernega in borealnega klimatskega pasu največkrat v tem mesecu ne priraščajo več, ugodnim temperaturam navkljub. Kljub temu so takšne analize še vedno zelo pogoste v dendroklimatologiji in so predvsem posledica pomanjkanja znanja o dolžini rastne sezone posamezne drevesne vrste na različnih rastiščih.

ACKNOWLEDGEMENTS
ZAHVALA

We are grateful to Martin Zupančič and Peter Cunder from Department of Wood Science and Technology, Biotechnical Faculty and Pekka Narhi and Tarmo Aalto from METLA Rovaniemi research unit for their help in the field and laboratory. We are indebted to the Slovenian Forest Service, GGO Bled, GE Pokljuka for enabling us the experimental work in the field. The work was founded by the EU project PINE (EVK2-CT-2002-00136).

REFERENCES
VIRI

AALTO, T. / JALKANEN, R., 1998. Neulasjälkimenetelmä. The needle trace method.- Rovaniemi, Finnish Forest Research Institute, Research Papers 681,

ANTONOVA, G. F. / STASOVA, V. V., 1993. Effects of environmental factors on wood formation in Scots pine stems.- Trees - Structure and Function 7: 214-219.

ANTONOVA, G. F. / STASOVA, V. V., 1997. Effects of environmental factors on wood formation in larch (*Larix decidua* Ldb.) stems.- Trees - Structure and Function 11: 462-468.

BÄUCKER, E. / BUES, C. / VOGEL, M., 1998. Radial growth dynamics of spruce (*Picea abies*) measured by micro-cores.- IAWA Journal 3: 301-309.

COOK, E. R. / KAIRIUKSTIS, L. A., 1989. Methods of dendrochronology (applications in the environmental sciences).- Dordrecht, Boston, London, Kluwer academic publishers, 394 p.

CRAIG, H., 1954. Carbon-13 variations in Sequoia rings and the atmosphere.- Science, 119: 141-144.

DESLAURIERS, A. / MORIN, H., 2005. Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables.- Trees - Structure and Function 19, 4: 402-408.

DESLAURIERS, A. / MORIN, H. / URBINATI, C. / CARRER, M., 2003. Daily weather response of balsam fir (Abies balsamea (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Quebec (Canada).- Trees - Structure and Function 17, 6: 477-484.

FARQUHAR, G. D. / EHLERINGER, J. R. / HUBICK, K. T., 1989. Carbon Isotope Discrimination and Photosynthesis.- Annu. Rev. Plant Physio. Plant Mol. Biol. 40: 503-537.

FARQUHAR, G. D. / O'LEARY, M. H. / BERRY, J. A., 1982. On the Relationship between Carbon Isotope Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves.- Aust. J. Plant Physiology 9: 121-137.

FERRETTI, M. / INNES, J. L. / JALKANEN, R. / SAURER, M. / SCHÄFFER, J. / SPIECKER, H. / WILPERT, K. V., 2002. Air pollution and environmental chemistry - what role for tree-ring studies?- Dendrochronologia 20, 1-2: 159-174.

FORSTER, T. / SCHWEINGRUBER, F. H. / DENNELER, B., 2000. Increment puncher-a tool for extracting small cores of wood and bark from living trees.- IAWA Journal 21: 169-180.

FRITTS, H. C., 1976. Tree rings and climate.- London, New York, San Francisco, Academic Press, 567 p.

GINDL, W. / GRABNER, M., 2000. Characteristics of spruce (*Picea abies* (L.) Karst) latewood formed under abnormally low temperatures.- Holzforschung 54, 9-11.

JALKANEN, R. / AALTO, T. / KURKELA, T., 1995. Development of needle retention in Scots pine (Pinus sylvestris) in 1957-1991 in northern and southern Finland.- Trees - Structure and Function 10: 125-133.

JALKANEN, R. / AALTO, T. / KURKELA, T., 1998. Revealing past needle density in Pinus spp.- Scand. J. For. Res. 13: 292-296.

JALKANEN, R. / KURKELA, T. / AALTO, T., 2002. A review of the needle trace method.- Rovaniemi, Finnish Forest Research Institute, 110-117 p.

JALKANEN, R. / LEVANIČ, T., 2001. Growth and needle parameter responses of Pinus sylvestris after release from suppression.- Dendrochronologia 19, 2: 189-196.

KAJFEŽ-BOGATAJ, L. / BERGANT, K., 2005a. Kakšno bo podnebje v Sloveniji v tem stoletju? = What might the climate of Slovenia look like in this century?- Ujma, 19: 218-223.

KAJFEŽ-BOGATAJ, L. / BERGANT, K., 2005b. Podnebne spremembe v Sloveniji in suša = Climate change and drought in Slovenia.- Ujma, 19: 37-41.

KOTAR, M., 2005. Zdradba, rast in donos gozda na ekoloških in fizioloških osnovah.- Ljubljana, Zveza gozdarskih društev Slovenije, 500 p.

KOZLOWSKI, T. T., 1971. Physiological Ecology (Growth and Development of Trees - Cambial growth, Root growth and Reproductive growth).- New York, London, Academic Press, 514 p.

KOZLOWSKI, T. T. / PALLARDY, S. G., 1997a. Growth Control in Woody Plants.- New York, London, Academic Press, 641 p.

KOZLOWSKI, T. T. / PALLARDY, S. G., 1997b. Physiology of Woody Plants (2nd. edition).- London, Academic Press, 411 p.

KURKELA, T. / JALKANEN, R., 1990. Revealing past needle retention in Pinus spp.- Scand. J. For. Res. 5, 4: 481-485.

KURODA, K. / KIYONO, Y., 1997. Seasonal rhythms of xylem growth measured by the wounding method and with a band-dendrometer: an instance of *Chamaecyparis obtusa*.- IAWA Journal 18: 291-299.

KURODA, K. / SHIMAJI, K., 1983. Traumatic resin canal formation as a marker of xylem growth.- Forest Science 29: 653-659.

KURODA, K. / SHIMAJI, K., 1984a. The pinning method for marking xylem growth in hardwood species.- Forest Science 2: 548-554.

KURODA, K. / SHIMAJI, K., 1984b. Wound effects on xylem cell differentiation in a conifer.- IAWA Bulletin 5: 295-305.

LARSON, P. R., 1994. The Vascular Cambium - Development and Structure.- Berlin, Heidelberg, Springer Verlag, 725 p.

LOADER, N. J. / ROBERTSON, I. / BARKER, A. C. / SWITSUR, V. R. / WATERHOUSE, J. S., 1997. An improved technique for the batch processing of small wholewood samples to [alpha]-cellulose.- Chemical Geology 136, 3-4: 313-317.

MÄKINEN, H. / NÖJD, P. / SARANPAA, P., 2003. Seasonal changes in stem radius and production of new tracheids in Norway spruce.- Tree Physiology 23: 959-968.

PENSA, M. / JALKANEN, R., 2005. Variation in needle longevity is related to needle-fascicle production rate in Pinus sylvestris.- Tree Physiology 25, 1265-1271.

ROSSI, S. / DESLAURIERS, A. / ANFONDILLO, T. / MORIN, H. / SARACINO, A. / MOTTA, R. / BORGHETTI, M., 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length.- New Phytologist 170, 2: 301-310.

ROSSI, S. / DESLAURIERS, A. / MORIN, H., 2003. Application of the Gompertz equation for the study of xylem cell development.- Dendrochronologia 21, 1: 33-40.

SALMINEN, H. / JALKANEN, R., 2006. Modeling variation of needle density of Scots pine (Pinus sylvestris L.) at high latitudes.- Silva Fennica 40, 2: 183-194.

SANDER, C. / ECKSTEIN, D., 2001. Foliation of spruce in the Giant Mts. and its coherence with growth and climate over the last 100 years.- Ann. For.Sci. 58: 155-164.

SCHMITT, U. / JALKANEN, R. / ECKSTEIN, D., 2004. Cambium dynamics of *Pinus sylvestris* and *Betula* spp. in the Northern Boreal Forest in Finland.- Silva Fenica 38, 2: 167-178.

SCHMITT, U. / MOLLER, R. / ECKSTEIN, D., 2000. Seasonal wood formation dynamics of beech (*Fagus sylvatica* L.) and black locust (*Robinia pseudoacacia* L.) as determined by the "pinning" technique.- Angewandte Botanik 74, 1-2: 10-16.

SCHWEINGRUBER, F. H., 1989. Tree rings: basics and applications of dendrochronology.- Dordrecht, Boston, London, Kluwer Academic Publisher, 276 p.

SCHWEINGRUBER, F. H. / FRITTS, H. C. / BRAKER, O. U. / DREW, L. G. / SCHAR, E., 1978a. The X-ray technique as applied to dendrochronology.- Tree Ring Bulletin 38, 61-91; 12 ref.: 1 pl.

SCHWEINGRUBER, F. H. / FRITTS, H. C. / BRAKER, O. U. / DREW, L. G. / SCHAR, E., 1978b. The X-ray technique as applied to dendrochronology.- Tree Ring Bulletin 38: 61-91.

SHIGO, A. L., 1986. A New Tree Biology: Facts, Photos, and Philosophies on Trees and Their Problems and Proper Care/With Dictionary (2nd edition) -, Shigo & Trees, Associates, 132 p.

SKENE, D. S., 1972. The kinetics of tracheid development in *Tsuga canadensis* Carr. and its relation to tree vigour.- Annals of Botany 36: 179-187.

WHITMORE, F. W. / ZAHNER, R., 1966. Development of the xylem ring in stems of young red pine trees.- Forest Science 12: 198-210.

WODZICKI, T. J., 1971. Mechanism of xylem differentiation in *Pinus sylvestris* L.- Journal of Experimental Botany 22: 670-687.

WOLTER, E. K., 1968. A new method for marking xylem growth.- Forest Science 14: 102-104.

YOSHIMURA, K. / ITOH, T. / SHIMAJI, K., 1981. Studies on the improvement of the pinning method for marking xylem growth.- Mokuzai Gakkaishi 27: 755-760.