

GDK 174.7 *Abies alba* Mill. : 48 - - 015

Prispelo / Arrived: 9. 1. 1997

Sprejeto / Accepted: 27. 2. 1997

UMIRANJA JELKE (*Abies alba* Mill.) V SLOVENIJI: PREGLED RAZISKAV KATEDRE ZA TEHNOLOGIJO LESA

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Izvleček

Predstavljamo pregled raziskav Katedre za tehnologijo lesa pod vodstvom Torellija o propadanju jelke (*Abies alba* Mill.) v Sloveniji. Raziskave v obdobju 1985-1996 so vključevale spremljanje stanja jelke s pomočjo merjenja električne upornosti (EU), anatomske in fiziološke interpretacije meritev EU, upadanje rasti in prirastka, študij fenologije, reproduktivne rasti, pojava sekundarne krošnje, ugotavljanje vlažnosti in kvalitete lesa, število sluznih celic v skorji in travmatskih smolnih kanalov v lesu ter odziv lesa in skorje na poškodovanje.

Ključne besede: *Abies alba*, propadanje, električna upornost, anatomija lesa in skorje, rast

SILVER FIR (*Abies alba* Mill.) DECLINE IN SLOVENIA: A REVIEW OF THE INVESTIGATIONS CARRIED OUT BY THE CHAIR OF WOOD SCIENCE

Abstract

Investigations on silver fir (Abies alba Mill.) decline in Slovenia conducted by the Chair of Wood Science directed by Torelli are reviewed. The investigations completed within 1985-1996 include the monitoring of tree condition using an electrical resistance (ER) measuring method with anatomical and physiological interpretation of the ER readings, studies on growth reduction, and phenology, reproductive growth, development of epicormic branches, wood moisture content and wood quality, the frequency of slime cells in the bark and traumatic resin canals in wood, and the responses of wood and bark to mechanical wounding.

Key words: Abies alba, decline, electrical resistance, wood and bark anatomy, growth

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The work was funded by the Ministry of Science of the Republic Slovenia; U.S. Department of Agriculture; and supported by the Forest Service of the Republic Slovenia, district units - Kočevje, Ljubljana, Maribor, and Postojna.

1 INTRODUCTION

Periodic silver fir decline has been observed in Europe for more than a century. In the 1970's it became a serious problem in Central Europe. Increased damage has also been observed in East and Southeast Europe and the survival of fir seemed to be endangered. The precise etiology of declining tree health was not known, but air pollution combined with drought, or other climatic changes, was considered to be part of the problem.

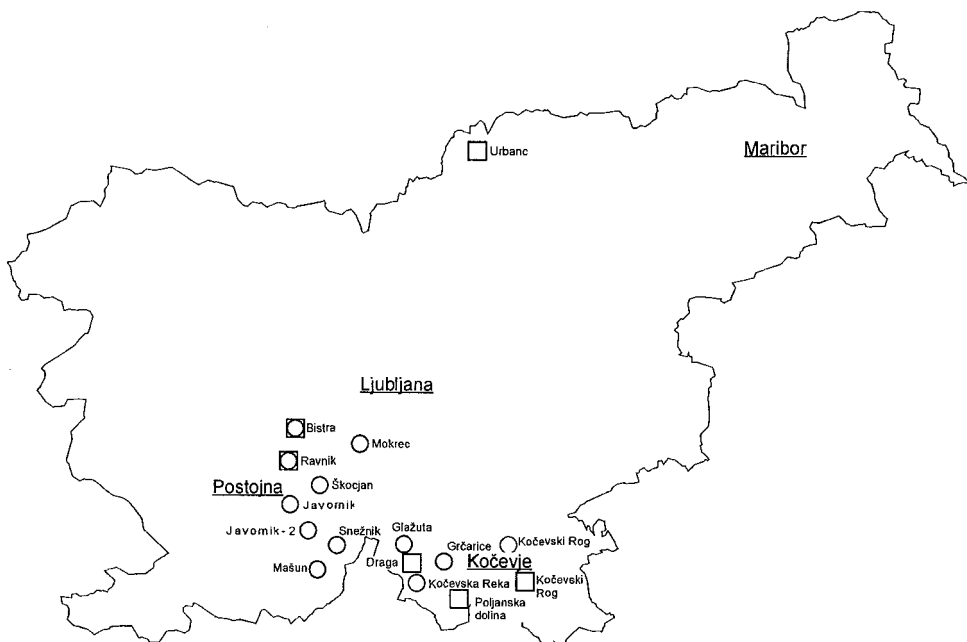
Generally Slovenia belongs to regions showing severe silver fir decline. In the last five decades the proportion of fir in Dinaric forest stands of Slovenia has steadily declined. The mortality especially increased in the early 1960's.

Due to high importance and damage of fir the Chair for Wood Science directed by Torelli investigated several aspects of fir decline. The objective of this paper is to review the results including: (a) monitoring tree condition using electrical resistance (ER) measuring method, (b) anatomical and physiological interpretation of ER readings, (c) reduction of growth, (d) study of phenology, (e) reproductive growth, (f) development of epicormic branches, (g) moisture content and quality of wood, (i) frequency of slime cells in bark and traumatic resin canals in wood, and (j) the response of wood and bark to mechanical wounding.

2 SAMPLING AREAS AND TEST TREES

The investigated forest stands belong to the Kočevje, Ljubljana, Maribor, and Postojna Forest Service district units. All of them, except Urbanc, are Dinaric silver fir - beech forest stands (*Abieti-Fagetum dinaricum*). The Figure 1 presents the sampling areas. Bistra and Ravnik were selected for long term observations of fir decline, periodical measuring of ER, anatomical and physiological interpretation of the readings, studies on growth reduction, phenology, reproductive growth, development of epicormic branches, as well as wood moisture content, wood quality, frequency of slime cells in the bark, traumatic resin canals in the wood, and the response of wood and bark to mechanical wounding. The sampling areas in Poljanska Dolina, Draga, Kočevski Rog and Urbanc were selected to measure the seasonal variation in ER as effected by

crown class and tree age. The sampling areas of Glažuta, Grčarice, Javornik, Kočevska Reka, Kočevski Rog, Mašun, Mokrec, Snežnik, and Škocjan were selected to study the growth depression and release, the relation between tree growth and climate, and to construct the tree-ring chronologies.



The investigations performed in areas labelled with marks:

Raziskave opravljene na različno označenih ploskvah:

- Long term observations of fir decline, seasonal and year variation in electrical resistance (ER), interpretation of ER, growth reduction, phenology, reproductive growth, epicormic branches, wood moisture content, wood quality, slime cells, traumatic resin canals, response of wood and bark to mechanical wounding;
Dolgotrajno spremljanje zdravstvenega stanja jelk, sezonske in medletne variacije električne upornosti (EU), interpretacija EU, rast in prirastek, fenologija, reproduktivna rast, sekundarna krošnja, vlažnost lesa, kvaliteta lesa, sluzne celice, travmatski smolni kanali, odziv lesa in skorje na mehansko poškodovanje;
- Seasonal variation in ER as effected by crown class and tree age;
Sezonska variacija EU kot posledica cenotskega statusa in starosti drevja;
- Growth depression and release, the relation between tree growth and climate, construction of tree-ring chronologies;
Upad in izboljšanje radialne rasti, zveza med rastjo drevja in klimo, sestava kronologij širin branik;

Figure 1: The location of sampling areas in Slovenia.

Slika 1: Lokacija vzorčnih ploskev v Sloveniji.

Mature, dominant or co-dominant trees ranging from healthy to severely damaged were selected. Their condition was assessed visually according to a three-class scale. The trees classified as 1 were assumed to be healthy, those classified as 2 were slightly affected and those classified as 3 were declining. The dying trees were not included in the sample.

3 ELECTRICAL RESISTANCE (ER) TO DETERMINE TREE CONDITIONS

Three types of measuring systems: the Shigometer, the Condiometer, and the Tree Tester were used to measure the ER. The Shigometer and the Condiometer are available commercially. The Tree Tester is microprocessor-based instrument to measure conductivity and temperature. It was devised by own experts (TORELLI *et al.* 1992a, BUČAR 1994). All instruments were equipped with moisture detection electrodes. The ER was measured at breast height. Pins were pushed through the bark and the vascular cambial zone and stopped at the most recent latewood. Since 1988, the measurements were taken periodically during the growing period.

The method proved to be essentially non-destructive. The wound caused by the electrode penetrating the living bark, cambial zone and recently formed wood, was relatively small (diameter 1 - 2 mm) and is compartmentalised within a short time (TORELLI *et al.* 1996).

The ER measuring proved to be a reliable method which could be used in addition to visual crown evaluation. The readings are easy to obtain but a lot of experience is needed to interpret the results.

3.1 ANATOMICAL AND PHYSIOLOGICAL INTERPRETATION OF ER READINGS

The ER in living trees generally depends on several factors like the thickness of vascular cambial zone (VCZ) and the living bark which are penetrated by the

electrodes (TORELLI *et al.* 1990d, TORELLI / ČUFAR 1994a), the number of living cells ruptured (OVEN 1993, OVEN *et al.* 1995), and the concentration of mobile ions, mainly potassium (KRIŽAJ *et al.* 1994). Seasonal variations of the ER is a consequence of variations in the thickness of the VCZ as well as ion concentration (KRIŽAJ / ŠTUPAR 1995b and 1996).

Generally, the mature unsuppressed healthy trees showed the lowest ER values (TORELLI *et al.* 1989b, 1990b). In declining trees the ER was higher due to reduced thickness of the VCZ (OVEN 1993, OVEN *et al.* 1995) and lower ion concentration (KRIŽAJ *et al.* 1994, KRIŽAJ / ŠTUPAR 1995b and 1996). Frequently, a pronounced decrease in ER in dying trees was linked to fungal decay (TORELLI *et al.* 1990d, TORELLI / ČUFAR 1994a).

During the year ER was lowest at the top of the growing season and highest in the dormant period. Younger healthy, unsuppressed trees with the thickest VCZ and thinnest living bark showed the most pronounced seasonal variations in the ER (TORELLI *et al.* 1992b, KRIŽAJ / ŠTUPAR 1995b and 1996). It can generally be stated that the ER increases during the drought periods.

A strong correlation was established between the ER at breast height and the crown class according to Kraft in even aged forests. ER values always increased with degree of suppression (ROBIČ *et al.* 1990, ROBIČ 1994).

3.2 MONITORING TREE CONDITION

At the maximum physiological activity in the growing season mature dominant and co-dominant silver firs were assessed as follows: ER 7-9 k Ω for healthy or slightly damaged trees, ER 10-11 k Ω for affected trees, where recovery is possible, ER 12-13 k Ω for irreversibly damaged trees, and ER 14 k Ω or above, for trees in which rapid dieback is expected (TORELLI *et al.* 1990d, TORELLI / KRIŽAJ 1991).

Almost 60% of trees showed slight year to year variation in the ER and their condition was considered stable (TORELLI *et al.* 1990d, TORELLI / ROBIČ

1992d). Healthy and less affected trees often showed an improvement, which was observed in those years with favourable hygrothermic conditions (e.g. 1989, 1990). Increased damage and mortality of declining trees was observed particularly after severe winters (e.g. 1985) or prolonged summer droughts (e.g. 1992, 1993), especially on dryer, rocky terrain.

In 1988, 32% of the trees from Bistra and 47% from the Ravnik were bioelectrically qualified as apparently healthy. In 1994 these values were 28% and 35% resp. By 1994, 25% of all trees in Bistra and 17% on the Ravnik died and were removed (TORELLI / ČUFAR 1994b, 1995b and 1996).

4 TREE RING ANALYSES

Tree ring analyses were performed in accordance with standard procedures. Either two cores per tree or stem discs were taken from breast height. In addition complete stem analyses were performed for 44 trees.

Tree rings in declining trees indicate that wood formation has been suppressed for at least for three decades. ČUFAR (1990) reported for 1985 that all trees from Bistra, including those classified apparently healthy, showed a declining tendency of tree-ring widths. The suppression of cambial mitotic activity and reduced wood formation usually began near tree base and proceeded acropetally. In declining trees we established up to 11 missing or incomplete rings (TORELLI *et al.* 1986a and 1986b, LEVANIČ 1996). The height growth was affected only in the most severely damaged trees (TORELLI *et al.* 1986a and 1986b, ČUFAR 1990). The growth depression increased with increasing stand destruction (ČUFAR *et al.* 1994).

Extended investigations of LEVANIČ (1996, 1997) in 12 sampling areas (indicated with circles in Fig. 1) showed that the ring widths of variously affected silver firs declined rapidly after 1960 and reached their minimum values in 1976. Later radial growth has gradually been recovering up to the present. The most notable growth release was observed in healthy trees.

Using response functions, the same author showed that warm spring months and moderately warm summer months with precipitation above the average were most favourable for the radial growth.

LEVANIČ (1996, 1997) also proved that the silver fir responded very sensitively to forest management treatments. The greatest growth reduction was observed after intense harvesting which coincided with unfavourable climatic conditions.

ČUFAR (1990) constructed the first local tree-ring chronology of fir. This work was continued by LEVANIČ and ČUFAR (1995a and 1995b). Based on seven local chronologies, LEVANIČ (1996) constructed the first regional Slovene Dinaric silver fir chronology which covered the period of 1790-1995. The standard chronologies were successfully used to detect and locate incomplete and missing rings as well as for improved understanding of the factors affecting radial growth of trees.

5 PHENOLOGY, OCCURRENCE OF EPICORMIC BRANCHES AND REPRODUCTIVE GROWTH

Five phenological phases determined as time of bud swelling, and of various phases of shoot growth were observed between 1988 - 1995. Among them, the time of bud bursting proved to be the most significantly correlated to tree conditions. Declining trees generally flushed at least one week earlier than apparently healthy ones. It remains unclear whether the earlier flushing is an inherited characteristic or a consequence of tree damage (ČUFAR *et al.* 1995 and 1996).

Epicormic branches formed a secondary crown. If present, they were always observed in declining trees. Their number along the bole increased with higher degrees of tree damage. Their occurrence generally retarded the dieback. In some rapidly declining trees epicormic branches did not occur. No correlation between their presence and the time of bud-bursting was established (ČUFAR *et al.* 1995 and 1996). The investigations of LEVANIČ (1996) showed that the presence of epicormic branches positively affected the radial growth at stem

base but also with lower proportions of late wood.

The quantity of male- (microstrobili) and female cones (megastrobili) was determined in late spring of the years 1988 - 1995. Their frequency generally decreased with increasing tree damage. Among declining trees those without cones predominated. Generally, abundant coning was only observed in healthy trees and the correlation between coning and tree damage was more significant for female cones (TORELLI *et al.* 1989c, ROBIČ *et al.* 1993, ČUFAR *et al.* 1994, 1995 and 1996).

6 WOOD QUALITY

Moisture content (MC) was recorded along radial profiles in the wood and the bark at various heights of the trees.

In healthy silver firs, the MC was generally the highest in sapwood (above 160%) and lowest in heartwood (around 40%). At the base of trees we usually found a normal wet-heart. The wet-heart always occurred at the location of an uncoloured heartwood. In declining trees an irregular wet-heart spread into the sapwood. It occurred at tree base and at higher stem levels. In the most damaged silver firs the wet-heart was dehydrated. It was normally surrounded by a 2-3 mm dry zone (ČUFAR 1990).

Because sapwood, wetwood, and the dry zone between them were found to coexist in living trees, it has been hypothesised that osmotic water transport may occur from sapwood to wetwood through the dry zone functioning as a semipermeable membrane (TORELLI *et al.* 1986a and 1986b).

No significant differences between healthy and declining trees were found for the moisture content of the bark.

The MC affects the quality of wood which can be separated into the following categories: sapwood, dehydrated non-coloured heartwood, normal wet-heart on the location of heartwood, and abnormal wet-heart radiating into the sapwood. Variability in MC of wood must be respected when choosing the kiln drying

schedules. Special care is advised when drying, gluing and finishing the wood.

Beside extremely narrow tree-rings and altered proportion of early- and late-wood (TORELLI *et al.* 1986a and b, LEVANIČ 1996) no changes in wood structure related to tree damage were observed. It is assumed that most physical and mechanical properties of wood remain unchanged.

In another experiment it has been shown that the magnetic resonance imaging (MRI) can be used successfully to determine the MC and the density of wood and their distribution, as well as to differentiate the tissues phloem, vascular cambial zone and wood (TORELLI *et al.* 1990a).

7 OCCURRENCE OF SLIME CELLS IN PHLOEM AND TRAUMATIC RESIN CANALS IN XYLEM

The occurrence of slime cells in the nonconducting phloem or traumatic resin canals in xylem was investigated according to the virus hypothesis but no correlation was found between their occurrence and the silver fir dieback. On the other hand, several indices showed that slime cells and traumatic resin canals might occur due to mechanical wounding (TORELLI *et al.* 1989a, 1992c, TORELLI *et al.* 1996).

8 RESPONSE OF WOOD AND BARK TO MECHANICAL WOUNDING

High variability was observed in the degree of discolouration associated with wounds in healthy or declining trees. In declining trees the discolourations coalesced with the presumably pre-existing wetwood (TORELLI *et al.* 1988, ČUFAR 1990).

After mechanical wounding cambium responded with the following disturbances in differentiation: the fusiform cambial initials and younger differentiating cells without secondary walls divided in transverse direction giving axial parenchyma. Older and less vital differentiating tracheids with protoplasts died and discoloured.

Tracheids formed after injury were shorter and smaller in cross-sections than the normal ones and were similar to juvenile tracheids. The rays often swelled, or uniseriate rays transformed to biseriate ones (TORELLI *et al.* 1990c, 1990e, 1990f, KRIŽAJ *et al.* 1995a).

Additionally, severe alteration of cell orientation was observed. In xylem formed after wounding, longitudinal sections resembled cross sections. The deorientation was ascribed to a partial release of growth stresses (TORELLI *et al.* 1990c, KRIŽAJ 1993). Based on experiments where we partly removed the strips of bark it has been suggested that the changed anatomy is the result of simultaneous response to the release of bark pressure and growth stresses in wood (TORELLI *et al.* 1990c).

With increasing radial and tangential distance from the wound, the anatomical characteristics of wood formed after wounding gradually approached normal adult wood. The dying-out of older tissues accelerated the radial growth of new tissues, which indirectly accelerated the restoration of cambium continuity and improved the mechanical strength.

The processes after wounding were discussed in the sense of the CODIT (Compartmentalisation Of Decay in Trees) conceptual model. Disordered callus, followed by the tangential lines of traumatic resin canals in the immediate vicinity of the wound could be interpreted as a wall 4 i.e. barrier zone (TORELLI *et al.* 1990c, 1990e, 1990f). Due to its limited extent (it ended after few centimetres), and variable structure, the function and the role of the barrier zone is under general discussion along with the model concept itself (TORELLI 1995a).

OVEN (1993) and OVEN / TORELLI (1994) showed the following changes and processes in wounded bark: (1) the outermost cells died out; (2) hypertrophy and hyperplasia of axial and ray parenchyma cells and formation of a parenchyma pad below dead tissues; (3) lignification of the outermost cells of the parenchyma pad; (4) suberization of the lignified cells; (5) division of the parenchyma cells and development of wound phellogen at the inner border of the ligno-suberized zone and (6) mitotic activity of newly formed phellogen and the development of

wound periderm; formation of ligno-suberized tissue seemed to be a prerequisite for its development. The formation of necrophyllactic periderms was considered as a type of bark compartmentalization. No significant differences in the responses to injury for healthy or declining trees were observed.

9 CONCLUDING REMARKS

Owing to its high economical importance, in the past silver fir has been increasingly extended over its natural range. Due to extensive cutting of beech, the fir often became a predominant species with much higher proportion than in natural mixed forests. The stands strongly affected by humans on atypical sites generally represent less stable ecosystems, where the fir presumably declines more rapidly. Visual, bioelectrical, and dendroecological observations of the silver fir in Slovenia have shown a sustained decline and mortality of mature trees, especially in the most man influenced, exposed, and extreme forest stands. Increased damage and mortality was commonly observed after severe winters or prolonged summer droughts, especially on dryer, rocky terrain. In the recent years healthy or only slightly damaged younger trees from less affected forest stands generally showed an improvement as indicated by a released growth. Growth release was especially observed in those years with favorable hygrothermic conditions. Measuring ER proved to be an objective and essentially non-destructive method to determine tree condition. Investigations to improve the method and to better interpret the results should continue.

The declining silver firs were characterized by loss of needles resulting in an increased crown transparency, occurrence of epicormic branches, earlier flushing, and decreased seed production. Additionally, the regeneration of young firs was often affected by increased roe and red deer populations. The natural regeneration of young trees was often possible only in fenced in areas to exclude animal populations.

Generally, the wood quality of affected trees was not reduced. The quality of wood originating from mechanically wounded forest trees was generally lowered. Special care is advised when processing the wood containing any kind of wet-heart.

10 SUMMARY

A review of the investigations on silver fir (*Abies alba* Mill.) decline in Slovenia, carried out by the Chair for Wood Science, directed by Torelli, are presented. The investigations comprised monitoring tree condition using electrical resistance (ER) measuring method, anatomical and physiological interpretation of ER readings, depression of cambial growth, study of phenology, reproductive growth, development of epicormic branches, moisture content and quality of wood, frequency of slime cells in bark and traumatic resin canals in wood, and the response of wood and bark to mechanical wounding.

Measuring ER proved to be an objective and essentially non-destructive method to determine the tree condition. It was influenced by the thickness and condition of the living tissues which were penetrated by the electrodes. The number of ruptured living cells and the concentration of mobile potassium ions affected the ER. The readings were lowest in mature unsuppressed, healthy trees at the top of the growing season. ER increased with degree of damage and suppression of trees and was highest in the dormant period.

The formation of wood was suppressed in declining trees for at least three decades. Growth declined rapidly after 1960 and reached its minimum in 1976. Later the radial growth gradually increased up to present. The most notable growth release was observed in healthy trees.

The declining trees were characterised by an earlier flushing, abundant occurrence of epicormic branches, reduced formation of male and female cones, reduced moisture content of the sapwood, and by the formation of irregular wet-wood. No correlation was found between tree damage and occurrence of slime cells in the nonconducting phloem or traumatic resin canals in xylem. Wood and bark tissues of healthy and declining trees responded similarly to mechanical wounding.

11 POVZETEK

Predstavljamo pregled raziskav Katedre za tehnologijo lesa pod vodstvom Torellija o propadanju jelke (*Abies alba* Mill.) v Sloveniji. Raziskave v obdobju 1985-1996 so vključevale spremljanje stanja jelke s pomočjo merjenja električne upornosti (EU), anatomske in fiziološke interpretacije meritev EU, upadanje rasti in prirastka, študij fenologije, reproduktivne rasti, pojava sekundarne krošnje, ugotavljanje vlažnosti in kvalitete lesa, števila sluznih celic v skorji in travmatskih smolnih kanalov v lesu ter odziv lesa in skorje na poškodovanje.

Raziskave so bile opravljene na območnih enotah Zavoda za gozdove Slovenije: Kočevje, Ljubljana, Maribor in Postojna. Vsi sestoji, razen tistih iz Urbanca, so pripadali dinarskemu jelovemu bukovju. Slika 1 prikazuje lokacijo vzorčnih ploskev. Ploskve kjer je bil opravljen isti tip raziskav so označene z enakim znakom. Drevesa so bila večinoma dominantna ali kodominantna in različno prizadeta. Zdravstveno stanje drevs smo ocenili kot: 1 navidezno zdrava, 2 - rahlo prizadeta in 3 - zelo prizadeta drevs. Umirajočih dreves nismo raziskovali.

Električno upornost (EU) smo merili s Shigometrom, Condiciometrom in lastnim Tree Tester-jem (TORELLI *et al.* 1992a, BUČAR 1994, TORELLI / ČUFAR 1994a). Merjenje smo opravili v prsni višini večkrat v sezoni od leta 1988. Elektrode so prebadale skorjo, kambijevo cono in les do najmlajšega kasnega lesa. Metoda je skoraj nedestruktivna. Pri prebadanju je nastala ranica s premerom 1-2 mm, ki jo je drevo omejilo v krajšem času (TORELLI *et al.* 1996). Izkazalo se je, da je merjenje enostavno, interpretacija meritev pa je težavna.

EU je v živih drevesih navadno odvsina od debeline kambijeve cone in žive skorje (TORELLI *et al.* 1990d, TORELLI / ČUFAR 1994a), števila prebodenih celic (OVEN 1993, OVEN *et al.* 1995) in koncentracije mobilnih ionov, predvsem kalija (KRIŽAJ *et al.* 1994). EU se je spreminjala s sezono zaradi spremenljive debeline kambijeve cone in koncentracije ionov (KRIŽAJ ŠTUPAR 1995b in 1996).

Vrednosti so bile najnižje pri vladajočih, zrelih in zdravih drevesih in najvišje pri prizadetih drevesih (TORELLI *et al.* 1989b, 1990b, 1990d, TORELLI / ČUFAR

1994a). Skozi leto so bile vrednosti EU najvišje v mirujočem obdobju in najnižje na višku vegetacijske dobe (TORELLI *et al.* 1992b, KRIŽAJ / ŠTUPAR 1995b in 1996). Dokazali smo značilno zvezo med EU in cenotskim statusom (ROBIČ *et al.* 1990, ROBIČ 1994). Vladajoča drevesa so pokazala najnižjo EU, obvladana pa najvišjo.

Na podlagi vrednosti EU smo drevesa razporedili v štiri razrede prizadetosti (TORELLI *et al.* 1990d, TORELLI / KRIŽAJ 1991). Med leti je bila EU pri približno 60% dreves stabilna, ostala drevesa pa so kazala variacije. Največ prehodov v boljši ali slabši razred prizadetosti so kazala srednje prizadeta drevesa. V letu 1988 je bilo zdravih v Bistri 32% in na Ravniku 47% dreves. V letu 1994 so bili deleži zdravih dreves 28% oz. 35%. Do leta 1994 jih je v Bistri odmrlo 28% na Ravniku pa 17%.

Ugotovili smo, da se širine branik manjšajo že najmanj 30 let. Leta 1985 so vsa drevesa na Bistri kazala zmanjšanje širin branik glede na preteklo obdobje. Zmanjšanje je bilo najbolj izrazito na bazi drevesa, kjer je bilo do 11 manjkajočih in nesklenjenih branik (ČUFAR 1990, LEVANIČ 1996, TORELLI *et al.* 1986a in 1986b). LEVANIČ (1996) je ugotovil, da so širine branik upadale hitreje po letu 1960 in dosegle minimum 1976. Po tem letu so se širine branik postopno povečevale predvsem pri zdravih drevesih.

Z odzivnimi funkcijami je LEVANIČ (1996) pojasnil vpliv klime na prirastek. Na prirastek ugodno vplivajo tople pomladi in zmerno topla poletja z nadpovprečnimi količinami padavin. Ugotovil je tudi, da premočno redčenje, posebno v kombinaciji z neugodnimi vremenskimi razmerami, neugodno vpliva na širine branik. Oblikovanih je bilo več lokalnih in regionalna dinarska jelova kronologija (ČUFAR 1990, LEVANIČ / ČUFAR 1995a in 1995b, LEVANIČ 1996). Kronologije so uporabne med drugim za datiranje izpada branik in za proučevanje vpliva različnih dejavnikov na radialno rast drevja.

Od petih faz rasti poganjkov je bilo nabrekanje popokov v najtesnejši zvezi s prizadetostjo drevja. Prizadeta drevesa so odganjala v splošnem vsaj en teden prej kot navidezno zdrava (ČUFAR *et al.* 1995 in 1996). Sekundarno krošnjo

smo navadno opazili pri prizadetih drevesih. Ta je nekoliko upočasnila umiranje. S prizadetostjo drevja je upadala količina moških in posebno ženskih socvetij (TORELLI *et al.* 1989c, ROBIČ *et al.* 1993, ČUFAR *et al.* 1994, 1995 in 1996).

Zdrave jelke so imele vlažno beljavo in suho jedrovino, na bazi drevesa pa normalno mokro srce na mestu jedrovine. Pri prizadetih drevesih smo na bazi in na višjih nivojih opazili anomalno mokro srce, ki je segalo tudi v beljavo in je imelo nižjo vlažnost kot normalno mokro srce (ČUFAR 1990, TORELLI *et al.* 1986a in 1986b).

Za potek sušenja, lepljenja in za površinsko obdelavo je pomembno ali les izvira iz beljave, suhe jedrovine, normalnega ali anomalnega mokrega srca. Večina fizikalnih in mehanskih lastnosti lesa prizadetih jelk je nespremenjenih, zato kvaliteta lesa v splošnem ni manjša. Kvaliteta lesa je pogosto zmanjšana v deblih, ki so bila mehansko poškodovana.

Slikanje z električno magnetno resonanco je pokazalo, da s to metodo lahko določimo vlažnost in kvalitativne razlike v tkivu lesa in skorje (TORELLI *et al.* 1990a).

Nismo uspeli dokazati zveze med prizadetostjo drevja in pojavom sluznih celic v prevodnem floemu ter travmatskih smolnih kanalov v lesu zaradi virusne hipoteze umiranja jelke (TORELLI *et al.* 1989a, 1992c, TORELLI *et al.* 1996).

Pri mehanskih poškodbah smo opazili razlike pri širjenju diskoloracij pri prizadetih in zdravih jelkah (TORELLI *et al.* 1988, ČUFAR 1990). Če je bil kambij mehansko poškodovan, se je odzval z nastankom aksialnega parenhima ter obarvanjem in odmrtnjem diferencirajočih se traheid. Traheide, nastale po poškodbi, so bile krajše in manjše, trakovi pa so pogosto nabrekli ali postali večredni (KRIŽAJ *et al.* 1995a, TORELLI *et al.* 1990c, 1990e, 1990f). Pogosto smo opazili deorientacijo tkiva. Z eksperimenti na skorjinih jeziki smo potrdili, da ta nastane zaradi zmanjšanja skorjinega tlaka in sprostitve notranjih napetosti v deblu. Z oddaljenostjo od poškodbe je postajala zgradba lesa vse bolj normalna. Naštete spremembe bi lahko interpretirali kot nastanek barierne cone (oz. stene

4) modelnega koncepta CODIT, vendar sklepamo, da je zaradi omejenega obsega in variabilne strukture dvomljiv obstoj barierne cone in univerzalnost modelnega koncepta CODIT (TORELLI *et al.* 1990c, 1990e, 1990f, TORELLI 1995a). OVEN (1993) ter OVEN / TORELLI (1994) sta razložila procese v skorji po mehanskih poškodbah, s poudarkom na suberizaciji tkiva. Odločilen za kompartmentalizacijo poškodbe v skorji je nastanek ranitvenega periderma. Na poškodovanje skorje so se podobno odzvale prizadete in navidezno zdrave jelke.

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