# Final report

# **NKFI SNN 125652** Effects of climatic and defoliation stresses on the growth and vitality of trees in mixed oak forests: dendroecological and ecophysiological approaches

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## 1. Introduction and background of cooperation between the partner institutions

Climate change-related changes in oak forests are in the focus of the Hungarian and Slovenian partner institutions participated in the present bilateral project. The two research groups started a cooperation in the framework of a COST STReESS FP1106 sub-project on prediction of stress-induced radial growth change before tree mortality by using tree ring signatures (Cailleret et al. 2016).
Then the joint work has continued in an informal way with introduction of dual stable isotope analysis technics developed in the Slovenian partner laboratory according to ISO rules into ecophysiological monitoring project on stress responses of oak species coordinated by the Hungarian partner institute**.** The two groups cooperating in the present project are mostly using different research approaches and time-scales in studying tree responses to stress factors, but this mutually reinforced the work in the project. The project is partly connected to EU COST Action CA15226 *Climate-Smart Forestry in Mountain Regions* that we could join in 2016.

## 2. Objectives of the proposed project

In this project, we aimed to study the relationship between temporal variability of radial growth rate and individual vitality of sessile oak across different sites. Specific focus was put on understanding the potentially contributing physiological processes leading to reduction of radial growth under changing climate and variable tree vitality by using multiproxy analysis including tree-ring size traits and $\delta^{13}$C and $\delta^{18}$O stable isotope signatures.

## 3. Study sites and selection of sample trees

We selected four mixed oak forest sites for the current project work in the North Hungarian Central Range, 2 sites in Mátra Mountains (MA and MF) and 2 sites in Bükk Mountains (SIK and BZS). Table 1 summarizes the main characteristics of the sites. SIK site (in the proposal Site 1) is the Sikfőkút LTER-Europe Site (LTER_EU_HU_004; https://deims.org/632895f6-b954-4fd9-90bb-b427b22585ac). This site is an intense ecological site of University of Debrecen since 1972, located in the Bükk Mountains at a mean elevation of 320 m. This represented the core site of this project, due to the long-term forest monitoring database and research facilities. MA and MF sites are more humid and higher elevation sites compared to SIK and BZS sites. SIK site represents the most xeric site for *Q. petraea* and the mixed oak forest of *Q. petraea* and *Q. cerris*, due to the transitional location between closed forest and forest-steppe zones.

We applied vitality approach in selection of *Q. petraea* trees for sampling. We distinguished three tree vitality classes according to the crown status of trees (defoliation, dead branches) as suggested by Drobyshev et al. (2007) and the ICP Forests Manual: Class 1, the high vitality class: visibly healthy trees with crown defoliation less than 25%, very few dead thin branches; Class 2, medium vitality class: moderately declining trees with crown defoliation between 25% and 60%, relatively high number of dead branches; Class 3, low vitality class: severely declining trees with crown defoliation above 60%, typically with a large number of thick dead branches in the top of tree crown. After the health status survey in all sites, sample sessile oak trees were selected randomly and marked for representation of different vitality classes: 20-20 trees were sampled from the three vitality class with the exception of MF site where sessile oak trees have outstanding vigour and trees for vitality class 3 could not be selected.

**Table 1** Location and basic characteristics of study sites and forest stands. Mean annual precipitation and mean annual air temperature values were calculated using the monthly data from CRU TS 4.03 dataset with a 0.5 × 0.5° spatial resolution database for 1990-2019 period.

| **Site** | **Location** | **Lat./Lon.** | **Elevation (a.m.s.l.)** | **soil** | **Annual P mm** | **Annual mean T oC** | **Stand age in 2019 (years)** | **Dominant canopy species** | **Mean tree height (m)** | **Mean DBH (cm)** |
|---|---|---|---|---|---|---|---|---|---|---|
| **MA** | Mátra; Gyönyössolymos 85A sub-compartment | 47°51'13"N<br>19°57'53"E | 620 | Ranker | 591 | 10.2 | 80 | *Q. petreaa* 91%, *Q. cerris* 2%, *Carpinus betulus* 7% | 21 | 25 |
| **MF** | Mátra; Gyöngyössolymos 66C sub-compartment | 47°51'44"N<br>19°57'54"E | 660 | Ranker | 591 | 10.2 | 85 | *Q. petreaa* 91%, *Q. cerris* 2%, *Carpinus betulus* 7% | 25 | 30 |
| **SIK** | Bükk; LTER-Europe Site (LTER_ET_HU_004) | 47°55'N<br>20°26'E | 320 | brown forest soil | 557 | 10.7 | 115 | *Q. petraea* 42%, *Q. cerris* 22%, *Acer campestre* 36% | 18 | 34 |
| **BZS** | Bükk - Bükkzsérc 47D sub-compartment | 47°59'17"N<br>20°29'57"E | 450 | brown forest soil | 549 | 11.0 | 122 | *Q. petraea* 93%, *Q. cerris* 7% | 18 | 35 |

## 4. Dendrochronological and dendroclimatological investigations

### 4.1 Field sampling for tree-ring measurements and stable isotope composition analysis

We performed increment core sampling of *Q. petraea* trees for dendrochrological and dendroclimatological investigation during winter period (January/February) in years 2018 (MA and MF sites, 2019 (SIK site) and 2020 (BZS site). We used the same standard dendrochrological protocols for sampling increment cores and measurement of tree-ring size parameters in this project. Briefly: We collected two wood cores per tree were from opposite sides of the stem at breast height (1.3m) using a 0.5cm diameter increment borer (Haglöf Sweden AB, Sweden). The diameter at breast height (DBH) and height of trees were also registered for each tree. We sampled in total 225 *Q. petraea* trees and collected 450 cores for set up tree-ring size chronologies.

In the laboratory, these increment cores were air-dried, then glued onto wooden mounts and sanded to a high polish using sanding paper of progressively finer grit. Then the cores were scanned using the ATRICS system (Levanič, 2007). CooRecorder and CDendro software (www.cybis.se) were used for quantification of full tree-ring width (TRW), earlywood width (EW) and latewood width (LW) in the scanned pictures to the nearest 0.01mm. The EW-LW transition within the annual ring was abrupt in most samples, which facilitated visual identification of the two zones. We used the same software for quality control of the measured tree-ring width sequences. We average the data from the two cores to obtain the mean TRW, EW and LW time series of individual trees.

We used the raw TRW time series for calculation of basal area increment (BAI cm$^2$ yr$^{-1}$) of individual trees.

## 4.2 Analysis of time series of tree-ring size parameters (TRW, LW and EW)

After crosschecking the tree time series, we were able to set up the mean raw TRW, EW and LW chronologies of *Q. petraea* separately for vitality classes in the study sites.
We standardized the individual raw TRW, LW and EW series in order to remove the age-trends from the tree-ring chronologies using the R programme (R Core Team 2016) and the dplR package (Bunn, 2008) and to set up indexed (TRWI, LWI, EWI) chronologies.
Tree-ring sequences were detrended using the Modified Negative Exponential function ("ModNegExp" detrending method in *dplR*) with an option for linear regression in case curve-fitting fails. Tree-ring width indices were calculated by dividing each tree-ring width sequence by the corresponding growth trend. The indexed series were combined by means of a bi-weight robust estimation of the mean to get the standard and residual chronologies after a pre-whitening process using an autoregressive model selected by the Akaike information criterion. Two indexed chronologies can be obtained from *dplR*, namely standardized and residual chronologies. We used the residual chronologies (TRWI, LWI, EWI) for analyses of climate-growth relationships Parallel to the dendrochronological analysis in this project we applied the same methods in a study of growth of young co-existing oak species in West-Hungary (Móricz et al. 2021), our experience contributed to the successful work in that study.

We tested the chronologies of tree-ring size parameter for accuracy using descriptive statistics. We calculated mean, median, standard deviation (SD), mean sensitivity (MS**),** GINI parameter, skewness (SKEW), first order autocorrelation (AC1), expressed population signal (EPS) and mean inter-series correlation (Rbar) to assess the quality of raw TRW, EW and LW chronologies of *Q. petraea* in the three vitality classes.

## 4.3 Additional sampling and dendrochronological measurements on Turkey oak (*Q. cerris)*

Although our main focus is on the sessile oak in this project, we have extended the dendrochronological work to Turkey oak (only with dominant trees), which is co-existing with sessile oak in the forest canopy layer in all study sites. Using the same standard procedure for sampling and analysis of sampled cores, we established TRW, EW and LW chronologies (raw and indexed ones) of Turkey oak in SIK site (61 trees, 122 cores) with ending year of 2019, while in the additional three sites (12 trees/site, 2 cores/tree, 24 cores/site) with ending year 2020. We used a part of dataset in comparative analysis on radial growth and climate-growth responses of *Q. petraea* and *Q. cerris* (Mészáros et al. 2022).

## 4.4 Updating the dataset of existing tree-ring chronologies available for SIK site with differentiated measurements of EW and LW

We also performed a "re-analysis" of the increment core samples collected from visibly healthy *Q. petraea* and *Q. cerris* trees in SIK site, the intensive forest monitoring site, in winter 2011 by means of the same dendrochronological protocols worked out in this project. This increment core sample bank consists of core samples extracted from 80-80 trees (2 cores/tree) for *Q. petraea* and *Q. cerris* separately. The updating work involved the separate measurement of EW and LW section of tree-ring.
We were able to demonstrate that setting up differentiated chronologies of EW and LW, (for the first time in Hungary), which contribute to better understanding the climate responses of radial growth of the two species co-existing in the same site (Mészáros et al. 2022).

### 4.5 Important results of dendrochronological work

The full tree-ring width data from our dataset available for SIK site have been integrated in the international TRY database (Kattge et al. 2020) available electronically and open access as the result of significant international collaboration. Our paper describes the TRY plant trait database (created by 730 co-authors) and evaluates the extent of the trait data compiled in TRY and analyses the emerging patterns of data coverage and representativeness.

We also analysed the potential use of the TRW time series for assessing potential indicators for predicting tree mortality of main forest species including *Q. petraea* in comparative study (Cailleret et al. 2019). From the dataset of SIK site we selected tree-ring data of sessile oak (living and dead trees that were implemented into a pan-continental database. We used this database for testing whether annual radial growth data can be considered as universal indicators, and represent early warning signals of tree mortality. The published results are very consistent with those observed in the current comparative analysis of TRW time series in different vitality groups of sessile oak and support that tree vitality loss may start even decades ago and may be induced by extreme drought event (negative pointer year) such as in SIK site.

We established in total 11 mean raw and residual chronologies of TRW, LW and EW representing 3 vitality classes of *Q. petraea* in 4 sites. Using descriptive statistics, we revealed significant variability of chronologies among the sites and among the vitality categories within a given site. Concerning the three tree-ring traits the smallest variation was found for EW in each site.

We found mean length of tree-ring chronologies for sites as MA 71-72yr, MF 76-80yr, SIK 106-109yr, BZS 110-114yr. The long-term median of TRW extracted from chronologies varied across the vitality classes (Table 2). We found no change or a slight TRW decrease (max 7%) with declining vitality in SIK site. In MA, MF and BZS sites, the TRW was smaller by 26-35% in vitality class 2, and 38-42% in vitality class 3 than in vitality class 1.

**Table 2** Descriptive statistics of raw TRW chronologies. The number after the sign of site denote the vitality class 1, 2 and 3.

| TRW raw | mean length of chronology | mean | median | SDv | SKEW | GINI | AR1 |
|---|---|---|---|---|---|---|---|
| MA_1 | 71 | 1.804 | 1.748 | 0.597 | 0.342 | 0.191 | 0.552 |
| MA_2 | 72 | 1.380 | 1.289 | 0.571 | 0.414 | 0.230 | 0.675 |
| MA_3 | 72 | 1.124 | 1.017 | 0.647 | 0.537 | 0.321 | 0.785 |
| | | | | | | | |
| MF_1 | 76 | 1.966 | 1.899 | 0.641 | 0.551 | 0.180 | 0.568 |
| MF_2 | 80 | 1.312 | 1.236 | 0.559 | 0.619 | 0.242 | 0.674 |
| | | | | | | | |
| SIK_1 | 106 | 1.113 | 1.026 | 0.533 | 1.153 | 0.247 | 0.228 |
| SIK_2 | 105 | 1.131 | 1.029 | 0.548 | 1.203 | 0.246 | 0.300 |
| SIK_3 | 109 | 1.123 | 0.957 | 0.698 | 1.764 | 0.307 | 0.549 |
| | | | | | | | |
| BZS_1 | 110 | 1.474 | 1.400 | 0.585 | 1.008 | 0.213 | 0.558 |
| BZS_2 | 114 | 1.047 | 0.903 | 0.614 | 1.725 | 0.295 | 0.738 |
| BZS_3 | 112 | 1.012 | 0.870 | 0.664 | 1.582 | 0.342 | 0.745 |

We observed increasing divergence among the TRW chronologies of different vitality classes in all sites after 1970 due to the enhanced growth suppression of trees in vitality class 2 and 3. Similar trends were found for BAI derived from TRW data. These results suggest that the current vigour status can be tracked back to the presence of growth influencing factors as we found in our mortality paper (Cailleret et al. 2019).

We have performed pointer year sensitivity analysis based on the raw TRW chronologies. We used three indices to describe the responses of tree growth to extreme events: resistance, recover and resilience. We observed significant temporal change in resilience of radial growth over the study period presumably due to the effect of age and growth history of trees and the weakening resilience of growth with the loss of tree vitality.

Pointer year analysis has revealed negative event years during the common period of chronologies (1940-2020) for the study sites when trees produced narrow tree-rings. For SIK site we identified a negative pointer year which had a long-lasting effects on radial growth of *Q. petraea* and also for the co-existing species, *Q. cerris*. This event year was 1968 that appeared as severe drought year in agreement with climate data (PDSI -3.1) when most of the sampled sessile oak trees showed low TRW. This drought event affected the subsequent growth responses of currently dominant/co-dominant trees sessile oak that needed a long period to recover completely and showed reduced growth rate compared to the expected level until 1999. We also assume that high mortality of *Q. petraea* trees observed in this site between late 1970ies and early 1990ies. However, growth of coexisting Turkey oak was able to recover rapidly.

## 5. Tree-ring stable carbon (δ13C) and oxygen (δ18O) composition

### 5.1 Increment core sampling and analysis of tree-ring stable carbon and oxygen isotope analysis

We took increment cores from 7 individuals in each vitality class of sessile oak at breast height (1.3 m) using Pressler 4.3 mm diameter increment borer. After air-drying, the single rings were separated into earlywood and latewood section with an annual resolution. We used the latewood section of tree-rings for carbon and oxygen isotope analysis since formation of earlywood in oaks relies significantly on the organic substances accumulated previous growing season. We used a pooled-ring approach, we cut the latewood section of respective years from the seven cores of a given vitality class and pooled them. The pooled sample of vitality classes were used for laboratory analysis performed in yearly resolution for the period 1940-2020.

Isotope composition ($\delta^{13}C$‰ and $\delta^{18}O$‰) was measured in cellulose extracted from pooled latewood samples by the method adopted in the Slovenian partner laboratory. In total, we could establish 11 time series of δ13C and δ18O for *Q. petraea*, respectively, for the four study sites.
Regarding $\delta^{13}C$ signatures, we corrected the raw $\delta^{13}C$ of latewood for the Suess Effect (decrease in $\delta^{13}C$ of atmospheric $CO_2$ since the beginning of industrialization) and used the corrected latewood $\delta^{13}C$ of series for calculation of $^{13}C$ discrimination ($\Delta^{13}C$) and intrinsic water use efficiency (iWUE). The corrected $\delta^{13}C$ was used these values for calculation of $^{13}C$ discrimination ($\Delta^{13}C$) and intrinsic water use efficiency (iWUE). For these calculation we used the air $\delta^{13}C$ and air $CO_2$ concentration (ca) compiled by Cernusak and Ubierna (2022).

### 5.2 Important results of tree-ring stable carbon and oxygen isotope analysis

In cooperation with the Slovenian partner institution, we were able to establish in total 11 time series of $\delta^{13}C$, $\delta^{18}O$, $\Delta^{13}C$ and iWUE for *Q. petraea*, respectively, for the four study sites. This is the first dataset of these tree ring proxies for *Q. petraea* in Hungary, which can be integrated into international data networks and will contribute to the better understanding the physiological background processes of the highly variable radial growth of *Q. petraea* within the distribution area.

The corrected $\delta^{13}C$ of latewood showed high temporal variability in all sites and in all vitality classes and a decreasing trend in MA, and MF and SIK sites over the study period, but with not significant trend or even a decreasing one in BZS site. The mean $\delta^{13}C$ (‰) of the study period ranged between -22.7‰ and 24.0‰ in Bükk sites and between 23.1‰ and 23.8‰ in Mátra sites.
The $\delta^{18}O$ (‰) was relatively stable and showed no significant trend over the study period in all sites. The mean $\delta^{18}O$ of latewood ranged between 24.2‰ and 26.0‰ in Bükk sites and between 25.3 and 26.2 in Mátra sites.

iWUE derived from $\delta^{13}C$, it basically exhibited a strong increasing trend during the study period (r2=0.799-0.867) but with a decreasing slope with declining tree vitality in each site. Our results indicate that the increasing air $CO_2$ concentration since 1960 resulted in higher intrinsic water use efficiency (iWUE) but most synchronously in trees of high vitality class in all sites. We also showed decreasing slope of the fitted linear trend line with declining tree vitality: in MA from 0.5267 to 0.364, in MF from 0.5626 to 0.4109, in SIK from 0.9005 to 0.6066, in BZS from 0.7331 to 0.561, and among them the lowest was for trees in vitality class 3 in each sites. iWUE positively correlated with BAI, but the strength of iWUE-BAI relationships varied across vitality classes and sites being significantly strong for high vitality class (r2=0.320-0.405 $p < 0.05$) with a declining order of sites MF> MA > BZS. We observed weak iWUE - BAI correlations for SIK site. These results indicate that the translation of increasing intrinsic water use efficiency (iWUE) of *Q. petraea* into enhanced tree radial growth depends on the tree vigour and the site conditions.

We observed strong positive correlations between iWUE and $\delta^{18}O$ in trees with higher vitality (vitality class 1 in MA, MF and BZS sites, and class 2 in SIK site), but declining strength of these correlations in trees with low vigour. Positive correlations of iWUE and $\delta^{18}O$ indicate a relatively strong coupling between the leaf-level processes and oxygen isotope ratios in tree-rings. Our results confirm that δ18O is a good indicator of the change in relative contribution of A and $g_s$ to carbon isotope signatures in latewood of *Q. petraea*. In addition, the relationships of iWUE - $\delta^{18}O$ pointed to the decrease of coupling between leaf-level processes and oxygen isotope ratios in tree-rings with declining tree vitality of this species.

## 6. Inter-site correlations of chronologies of tree-ring proxies

We observed variable strength of correlations between the respective tree-ring trait chronologies of different sites and vitality classes. Most of the inter-site correlation coefficients were significant at least at $p < 0.05$, with the highest values for iWUE (r=0.835-0.923) and BAI (r=0.620-0.949) in vitality class 1, even between more remote sites. We found surprisingly very low inter-site correlation coefficient for $\delta^{13}C$ and intermediate r-values for TRW and $\delta^{18}O$. The r-values indicated that there is also a substantial component of variance in the time series of tree-ring proxies which is not common for the sites and vitality classes. Moving correlation analysis (21-yr window) revealed a temporary reduction in the correlation of site-specific chronologies between 1970 and 2000, compared to the preceding (1940-1969) and following (2000-2019) periods.

## 7. Analysis of relationships between climate and tree-ring variables

### 7.1 Climate data used for the analysis and

Monthly T (min, max, mean), P and scPDSI and SPEI data for the study sites from the CRU TS 4.03 dataset with 0.5 × 0.5◦ spatial resolution web pages http://climexp.knmi.nl and https://spei.csic.es/spei_database, E-OBS and OMSZ. We also obtained values of the Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) based on the CRU TS v. 4.03 dataset in the same 0.5 grid, including the study site, from the https://spei.csic.es/spei_database (Vicente-Serrano et al., 2010) for the study period. We analyzed the climate-growth correlations with monthly and seasonally averaged climate data of the current spring (March-May; MAM), current summer (June-August; JJA), previous late summer (August-September; pAS), previous autumn (October-November; pON) and previous winter (December-February; DJF). The 0.05 significance level of coefficients was established using the bootstrap method (1000 iterations) by means of DENDROCLIM2002.

We showed that the collected mean annual and seasonal values of climate data indicate a clear significant increasing trends for temperature after the 1970s, accompanied with a decreasing trend of PDSI and SPEI drought indices indicating serious or extreme droughts in 1973, 1984, 1990, 1993, 2002, 2003, 2007, 2008, 2012, 2015, 2019, 2020 in the study sites. The time-series precipitation data analysed in the project showed variation of annual precipitation but it showed no significant trend. These trends are consistent with the reports for Hungary by National Meteorological Service and Europe (Hosseinzadehtalaei et al. 2020).

### 7.2 Important results of climate-growth analysis on different tree-ring proxies

*Relationship between climate and radial growth*

We found that the tree-ring growth of sessile oak in the study sites showed significant dependence on climate conditions of both the current year (the growth year) and the preceding year. We observed differences in climate sensitivity among the studied tree-ring traits and significant variation of climate-growth correlations across the sites. However, we observed similar responses of vitality classes to climate factors in a given site. Among the tree-ring size parameters, LW and TRW exhibited significantly larger sensitivity to monthly climate variables of the current spring-summer period in every site. In contrast, EW responded more sensitively to the climate conditions of the previous late summer-autumn period (August-September).

We found differences in **the number of significant correlations between studied climate variables** and tree-ring growth and these results confirmed the lowest sensitivity of *Q. petraea* radial growth to climate in MF site, while the highest sensitivity in SIK site.

In all sites, precipitation was the major growth-limiting factor for *Q. petraea*, having positive influence particularly during the early growing season (March-June, with a peak in June) of the growth year, on EW in the previous late summer (August-September) and in the current early spring (March). Winter (December) precipitation also positively influenced the next year growth, but with different intensity, it has particularly strong importance in SIK site. In contrast to precipitation, temperature proved to have a secondary influential role. However, we found significant negative effect of temperature on radial growth in current spring (May) and late summer (August) of both current and previous years.

We have also shown that growth of sessile oak exhibits high sensitivity to climate conditions of previous late summer-autumn accelerating water deficit, lack of precipitation and high temperature. We have presumed that the lagged effects of these conditions on the next year' radial growth rate of sessile oak might be due to the influence on the accumulation of non-structural carbohydrates (NSC including starch and soluble sugars). Our carbohydrate analysis confirmed that during this period there is an increase in TNSC content of sapwood and inner bark of tree stem.

*Relationships between climate and $\delta^{13}C$, $\delta^{18}O$ and iWUE*

We observed positive relationships between $\delta^{18}O$ of latewood and monthly air temperature ($T_{max}$) before the radial growth started (Jan-Febr), during the early phase of tree growth (March-May) and in late summer of current year, but the strength of correlations varied significantly across the sites and vitality classes: the highest number of significant correlation values was found for the SIK site and the lowest one for the MF site. With the exception of MF site, $\delta^{18}O$ of trees with lower vigour (tree vitality class 2 and 3) was more strongly correlated with temperature. The analysis revealed negative correlations between $\delta^{18}O$ and precipitation in current summer (May-June) and previous winter (Nov-Febr), which were particularly strong for SIK and BZS sites. This indicates that the radial growth is associated with the water availability in shallow water sources influenced by high temperature induced increase of evapotranspiration, since these are less depleted in $^{18}O$ utilization of water source.

We observed that the intrinsic water efficiency (iWUE) derived from $\delta^{13}C$ was more sensitive to temperature than TRW. We found strong positive correlations between iWUE and temperature of both the current and previous growing seasons in all sites. In addition, iWUE in all vitality classes showed the strongest reaction to temperature in August of both current and previous years. The analysis revealed that iWUE in trees of high vitality class responded more sensitively to temperature than trees with less vigor. We found strong negative correlation between iWUE and precipitation in current June and previous winter (November-December), particularly in SIK site. In addition, iWUE showed positive correlation with precipitation in September.

### 7.3 Responses of tree-ring proxies to drought

In synchronicity with increasing trends for temperature, we observed decreasing trends of drought indices indicating serious or extreme droughts in the growing season of 1968, 1973, 1984, 1990, 1993, 2002, 2003, 2007, 2008, 2012, 2015, 2019, 2020 in the study sites. Most of the negative event years in TRW chronologies appeared as the growth reduction in association with these drought events, identified by means of pointer year analysis.

We investigated the responses of BAI and iWUE to droughts in these years compared to wet years (1965, 1966, 1967, 1970, 1999, 2006, 2010). In wet years the mean values of iWUE ranged from 98.6-133.8 $cm^2$ $y^{-1,}$ while BAI ranged between 5.2 and 20.3 $cm^2$ $y^{-1}$, decreasing values were found with declining tree vigour. Droughts induced in average a 10-30% increase of iWUE with a simultaneous 10-55% decrease of BAI, depending on the vitality class. The lowest BAI reduction was found for vitality class 1 and 2 in Mátra sites.

In this analysis, *Q. petraea* proved to be the most vulnerable to drought in SIK site in all vitality classes and showed 52-55% decrease of BAI. Interestingly trees in SIK site showed the highest increase of iWUE (27-35%) during drought, but this iWUE increase was not translated into enhanced radial growth.

## 8. Non-structural carbohydrates (NSC) in sapwood and inner bark

### 8.1. Field sampling and analysis

We studied the seasonal course of non-structural carbohydrates (NSC) in sapwood (the last 10-yr segment) and inner bark of trees selected from every vitality classes in 3 sites (SIK, MA and MF) during the project years. We excluded BZS site from this work due to the difficult accessibility to the site. Samples were taken at 1.3 m height to a depth of 4-6cm by means of a standard increment borer and frozen in liquid $N_2$ in field. In the laboratory, samples are stored at -80°C until analysis. For the sample preparation and NSC analysis we have selected and followed the protocols suggested in a large scale comparative study on forest tree species (Quentin et al. 2015). Basically, we used spectrophotometric methods for measuring soluble carbohydrates and starch in sapwood segments and inner bark.

### 8.2 Important results of NSC investigation

Most of these results of these measurements have already been summarized in progress reports.
Our results have reflected significant variation of total NSC pool and the two NSC fractions -soluble sugars (SS) and starch- between the sapwood and inner bark samples of sessile oak and during the season.
Total NSC content pool was similar in the inner bark and sapwood (100-150 mg $g^{-1}$ (d.m.) but the soluble sugar (SS) and starch contents were different. In general, inner bark contained 2-3 times higher SS content (60-100 mg $g^{-1}$) compared to starch. SS/starch ratio in the inner bark showed maximum in July with a parallel decrease of starch. We measured high SS concentration in the inner bark in late winter before bud-burst and a strong decrease during time of leaf emergence in April. The SS/starch ratio varied with weakening of tree vitality reaching low values in the low vitality class.
Contrastingly, in the sapwood the SS/starch ratio was low (0.2-1.3) in spring and early summer and showed increases during summer till autumn (0.4-1) and remained relatively high till late winter. These results seem to confirm the observation on the importance of climatic conditions in previous late summer-autumn in formation of next year' EW of sessile oak. In summer, we observed a significant decrease of starch content reflecting mobilisation processes. Trees with low vitality had lower SS concentration in the inner bark while higher SS concentration in the xylem compared to other trees.

## 9. Intra-seasonal tree growth pattern

### 9.1 Monitoring of growth and analysis of recorded data

Seasonal pattern of tree radial growth has been monitored by means of fine time-resolution point-dendrometers (DR type, Ecomatik with time resolution of 15 min) installed at the trunk of selected trees (number of trees: 23 in the intense growth monitoring network of SIK site; 4 in MF site 2 (since 2018) and 4 in Site 3 (since 2019) at height of 1 m. In SIK site a part of these trees are also supplied with sapflow sensors, thus the records of the two type physiological measurements can be used for assessing the water status of trees.
Analysis of raw dendrometer data revealed that the daily mean and maximum values calculated from the raw data series are usable parameters for establishing raw cumulative radial growth curves for the sampled trees as well as for obtaining averaged cumulative growth curves for vitality categories. We used 3-parameter Gompertz function to describe the cumulative seasonal growth. Growth curves obtained by Gompertz model and the raw growth curves were used to estimate the phases and duration of growth: the points in time corresponding the 5 and 95% of the total radial increment were identified and set as growth onset and growth cessation, respectively.

### 9.2 Results of dendrometer measurements

The fitted model of dendrometer raw data showed significant variation both in growth maximum value and duration of growth across the sites. Our results indicated lower maximum growth values and shorter growth period for trees in SIK (Bükk), compared to MA and MF (Mátra). The duration of radial growth was in average 30 days longer, but started two weeks later in MF and MA sites in Mátra than in the SIK site in Bükk.
Since the records of fine-time resolution dendrometers also reflect water storage fluctuations of trees, based on our former experience we have extracted data from the raw dendrometer signal series to estimate maximum daily shrinkage (MDS) values of stem and the tree water deficit (DW). These data together with the sapflow data have been used for identification of periods critical for the tree water budget.

## 10. Publications and presentations

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## 11. Difficulties in research work

The COVID-19 pandemic caused many problems in organisation of the planned research. We could not work in the partner laboratory because of the regulation and illnesses in both partner groups. Thus, we had to extend the project period.

## 12. Continuation of the research

We plan to continue the dendrochronological and dendroclimatological investigations with involvement of other forest species coexisting with *Q. petraea* in same localities. We proposed a new bilateral NKFIH project with the Slovenian partner group, and the funding would provide opportunity broadened the scope of our forest ecophysiological research.

## 13. Potential usage of the results in practice

The project results contribute to understand the responses of *Q. petraea* and forest stands to the climatic and other stresses. In addition, the results can be used for more accurate and reliable prediction on the future status of the sessile oak in Hungary. The results can be used in silvicultural management planning and deforestation since change of currently existing tree species will be necessary in climate-sensitive transitional habitats in the near future.

## 14. References

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