

# Physiological and growth response of European larch (*Larix decidua* Mill.) and pedunculate oak (*Quercus robur* L.) to environmental changes

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## Introduction

Predictions of the long term consequences of the rise of greenhouse gasses in the atmosphere on changes in tree growth and forest species distribution have been confirmed by several studies in Europe (Spiecker 1996, 1999, Makkonen-Spiecker & Kotar 1999, IPCC 2001). It has been stated that in the last decades tree growth has been changed especially on poorer soil sites, such as in upper timberline and in lowlands where forests compete with agriculture (Morison & Morecroft, 2006). Apart from forest management and land use, forest ecosystems are affected mostly by increased ambient concentration of CO<sub>2</sub>, NO<sub>x</sub> emissions, air temperatures and precipitation distribution. Cumulative effect of climate changes should, according to the modelled estimates (Canell 1999), influence the growth especially on extreme sites.

Our study was oriented towards two forest ecosystems in Slovenia - in lowlands, where pedunculate oak forests are under severe agricultural pressure and where natural area of oak distribution is being reduced significantly by the different human activities (Wraber 1951), and at the upper timberline, where evident shift towards higher altitudes due to increased temperature and changed precipitation regime has been confirmed (Wieser et al. 2009). Recent studies suggest that reduction of natural area in lowland forests is in direct connection with agricultural activities and reduction of groundwater table (Levanič 1993, Čater & Levanič 2004). Changes in lowlands are reflected in decline of complete forest complexes, high mortality and uneven stand structure, accompanied by forest regeneration problems. Proportion of adult, vital forest stands is declining and sanitary cut increases due to physiological weakening and high mortality of oaks. Consequences are seen as an unbalance in the forest ecosystem and an increased susceptibility to weather extremes and pests. In the upper timberline growth conditions are, in comparison to lowlands, even more extreme and growing season shorter. Predicted temperature rise may affect the length of the growing season, vitality, regeneration and retention ability of the forest ecosystems at the upper timberline. Stability, survival and future existence of the upper timberline forest ecosystems may be in question.

Study and prediction of the tree response in disturbed forest ecosystems may significantly contribute to better guideline policies for the silvicultural and forest management practice in the changing environment in both stressed and stable forest ecosystems.

The objectives of our study were (1) to compare ecophysiological and growth response by adult trees of different vitality classes on marginal - extreme sites, and (2) to recognize and define tree response to rapidly changing growing conditions. In this paper we present preliminary results based on measurements from two research sites.

## Material and methods

Research areas were established at two different forest sites - pedunculate oak (*Quercus robur* L.) site in a floodplain area (156m ASL; 45. 8638<sup>0</sup>N, 15.4302<sup>0</sup> E) and European larch (*Larix decidua* Mill.) site (1600m ASL; 46.3582<sup>0</sup>N, 14.7053<sup>0</sup> E) at the upper timberline. At both locations, presence of both vital and declining adult trees was noticed on a small scale of a homogenous site. In our

research, six dominant vital and six declining trees per species according to the ICP methodology (tree status assessed by the crown condition) were selected (Anonymous 2006). All study plots have been fenced (50x50m). Ecophysiological response of trees has been recorded and compared with radial growth during three consequent vegetation periods (2007, 2008 and 2009). Photosynthesis measurements were performed at a constant temperature of the measurement block (20°C), a CO<sub>2</sub> concentration of 350 µmol/l, flow 500 µmol/s and different light intensities: 0, 50, 250, 600 and 1200 µmol/m<sup>2</sup>s, as described in Čater and Simončič (2009). The measurements started at ambient light conditions that were reduced to reach zero, then followed by a gradual increase toward maximum values, so that stomata could be adapted. A-Ci curves were established to compare and define assimilation response of trees (A) to different intercellular CO<sub>2</sub> concentrations (Ci): measurements were performed at constant light 600 µmol/m<sup>2</sup>s, humidity, constant block temperature 20°C and flow 500 µmol/s, while ambient CO<sub>2</sub> was varied as 0, 50, 100, 350, 700 and 1000 µmol/l. Maximal assimilation (A<sub>max</sub>) rates and calculated compensation points (CP) for the light saturation and A-Ci curves were used in comparisons of trees between different plots. Both types of responses were measured with the LI-6400 portable system on at least three sun canopy locations per tree, located in the upper third of the tree-crown height on every plot.

Pre-dawn water potential (PWP) was used as a measure of static water stress-estimate in every tree. Samples were taken from the upper part of the crown using a water pressure chamber (Plant Moisture Vessel SKPM 1400, Skye, UK) (Larcher 1995). At least five repetitions were made on each tree in order to obtain a representative average value of PWP. Measurements were done once in a vegetation period at the same height as other physiological measurements. Water use efficiency (WUE) was calculated and compared between both groups of trees (Larcher 1995, Lambers et al. 1998).

Cores were taken from all 24 studied trees (12 oaks and 12 larches). Each core was mounted and sanded to a high polish following standard dendrochronological procedures (Stokes & Smiley 1996). Cores were then digitized using ATRICS<sup>®</sup> system (Levanič 2007) and annual radial growth measured to the nearest 0.01 mm using WinDENDRO<sup>™</sup> software. Each tree ring series was then visually crossdated in PAST-4 using both visual comparisons and well established statistical parameters, including  $t_{BP}$  (Baillie & Pilcher 1973), GLK% (Eckstein & Bauch 1969), and Date Index - DI (Schmidt 1987). Values of  $t_{BP}$  greater than 6.0, GLK% values greater than 65% and DI values greater than 100 were considered significant. The ARSTAN programme (Cook, 1985; Cook and Holmes, 1999) was used to remove age trends in the ring width data and build site chronology. De-trending was achieved using a negative exponential or linear function. Indices were calculated as ratios between the actual and fitted values. Index values were then prewhitened using an autoregressive model selected on the basis of the minimum Akaike information criterion and combined across all series using bi-weight robust estimation of the mean to exclude the influence of the outliers (Cook 1985, Cook et al. 1990, Cook & Holmes 1999).

Indexed tree-ring widths were compared to meteorological data (mean monthly temperature and monthly sum of precipitation) from the nearby meteorological station.

## Results and discussion

### *Photosynthesis and water conditions*

Sensitivity of photosynthesis is similar for all C<sub>3</sub> plants and is in proportion with mesophyll CO<sub>2</sub> concentration (Farquhar et al. 1980). In view of climatic changes, numerous contradictory conclusions are being presented about the response of plants and future development to the environmental changes, especially due to temperature increase, decrease in the amount of precipitation and increase of atmospheric CO<sub>2</sub>.

In all measured years, significant differences in light response between declining and vital trees have been confirmed for both larch ( $p \leq 0.001$ ) and oak trees ( $p \leq 0.01$ ) (Figure 1); however,

differences in light compensation point, where production is balanced with consumption, were significant only between vital and declining oak trees ( $p \leq 0.001$ ). Smaller absolute response to same light intensity in larch may be connected with species better adapted to the higher light intensities during the whole vegetation period. Comparison of response by maximal assimilation rate ( $A_{\max}$ ) to different  $\text{CO}_2$  concentration between healthy and declining trees was also confirmed for both larch (declining:  $8.2 \pm 1.3 \mu\text{mol}/\text{m}^2\text{s}$ ; vital:  $11.7 \pm 0.9 \mu\text{mol}/\text{m}^2\text{s}$ ) ( $p \leq 0.01$ ) and oak (declining:  $7.8 \pm 1.2 \mu\text{mol}/\text{m}^2\text{s}$ ; vital:  $11.2 \pm 1.4 \mu\text{mol}/\text{m}^2\text{s}$ ) ( $p \leq 0.001$ ), while differences in  $\text{CO}_2$  compensation points between the groups proved yet again significant only for oak trees ( $p \leq 0.001$ ) (data not shown).

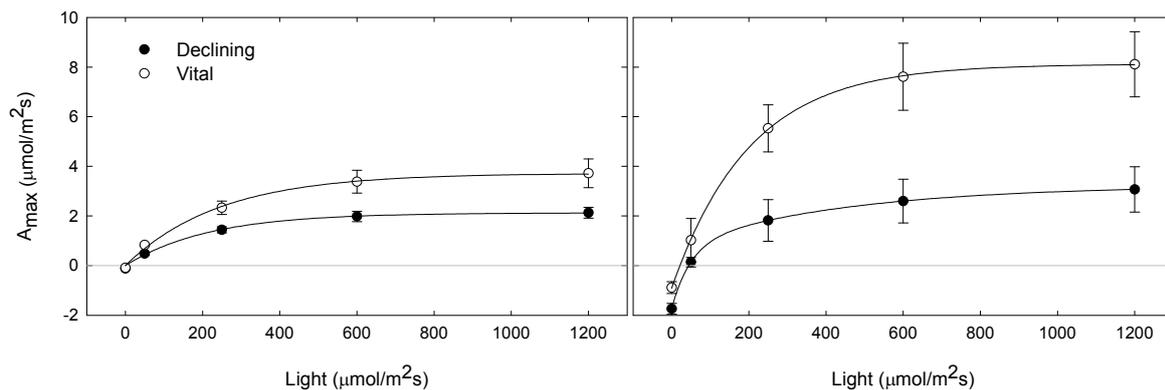


Figure 1: Average assimilation response with standard error of mean in dependence to light intensity for larch (left) and oak (right).

As part of the physiological measurements, pre-dawn water potential (PWP) was measured and water use efficiency (WUE) calculated. Both PWP (data not shown) and WUE were different for vital and declining trees in both species. WUE in vital larches was  $1.95 \pm 0.4$ , in declining larches  $3.12 \pm 0.7$ , in vital oaks  $1.74 \pm 0.8$ , and in declining oaks  $2.27 \pm 0.6$  [ $\mu\text{mol CO}_2/\text{m}^2\text{s}$ ]/( $\mu\text{mol H}_2\text{O}/\text{m}^2\text{s}$ ), indicating that less water was consumed in declining trees for the same amount of carbon gain. Plants tend to reduce stomatal opening under water stress, so that WUE is maximized (usually at the expense of PNUE, photosynthetic nitrogen-use efficiency).

The measurements of assimilation response and water status (PWP) confirmed differences between both groups in both species, but did not indicate severe stress conditions in the group of declining larch trees. Oaks, on the other hand, growing on rich floodplain sites, do not exhibit loss of nutrients, but are affected by the water stress more severely in both groups. Maximal assimilation rate in the vital oak group (approx.  $8\text{--}10 \mu\text{mol CO}_2/\text{m}^2\text{s}$ ) was also below the measured response of healthy oaks ( $10\text{--}15 \mu\text{mol CO}_2/\text{m}^2\text{s}$ ) on other comparable sites (Čater and Batič 2006), indicating that the vital oak group, too, is declared vital only in comparison with severely affected and almost dying oaks.

In spite of the relatively good insight into the carbon dynamics processes at the leaf level in changed  $\text{CO}_2$  environment, it is difficult to make a prognosis of the future response by the whole plant also because of a short-time interval of observations and numerous possible interactions that have not been recognized yet (increased WUE might stimulate development of foliar fungi (Thompson and Drake 1994), while more sugars in assimilation apparatus may stimulate development of pathogens and infections (Hibberd et al. 1996) etc.). Recent research quotes up to 30% growth increase in the ambient with twice higher  $\text{CO}_2$  environment (Medlyn et al. 2001). Smaller probability that such increase would reflect in long-term assimilation was confirmed in the study, where growth increased only at the beginning, and was later reduced in time (Batič 2007).

### Radial growth and climate response of studied trees

Both groups of the studied oak have been growing on the same site with same soil conditions differing only in groundwater table. On the site with declining oaks, groundwater level decreased after a road was built in 1938, which resulted in changed growing conditions (radial growth of oaks in vital and declining group) from that time on. Since 1938, vital oaks developed much wider tree-rings ( $2.70 \pm 0.48$  mm) than declining trees ( $1.14 \pm 0.25$  mm). Beside the differences in tree-ring widths, a significant difference in the year-to-year variability of tree-rings between both studied oak groups was also confirmed. Variability of the tree-ring width was much higher in vital trees than in declining trees. This indicates that the growing conditions for declining oaks were less favourable and that they were suppressed during the last 50-year period compared to the vital trees (Figure 2).

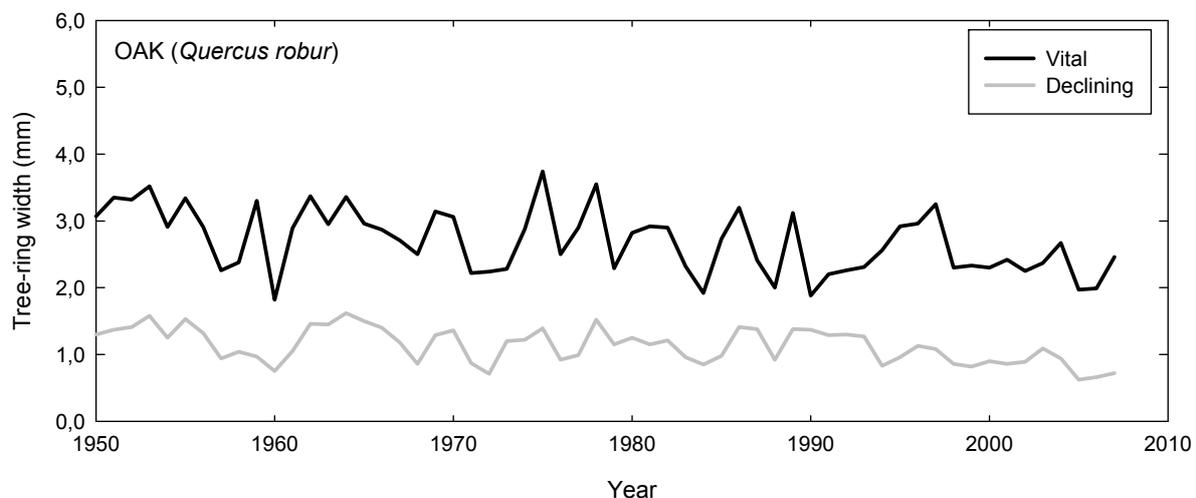


Figure 2: Tree-ring widths in the group of vital and declining pedunculate oak trees (*Quercus robur* L.).

Differences in radial growth in oak trees are more pronounced than in larch trees (Figure 3). We should expect tree growth on sites with soils consisting of high percentage of rocks and only organic horizons (larch site, upper timberline) more sensitive to the increasing temperature and also to water stress than on lowland oak sites. Vital larches had an average tree-ring width of  $0.77 \pm 0.14$  mm, and declining larches  $0.52 \pm 0.12$  mm, no significant changes in sensitivity or response to environmental factors were confirmed. According to the actual year by year growth, differences between the studied larch groups were small, which was also confirmed by ecophysiological studies.

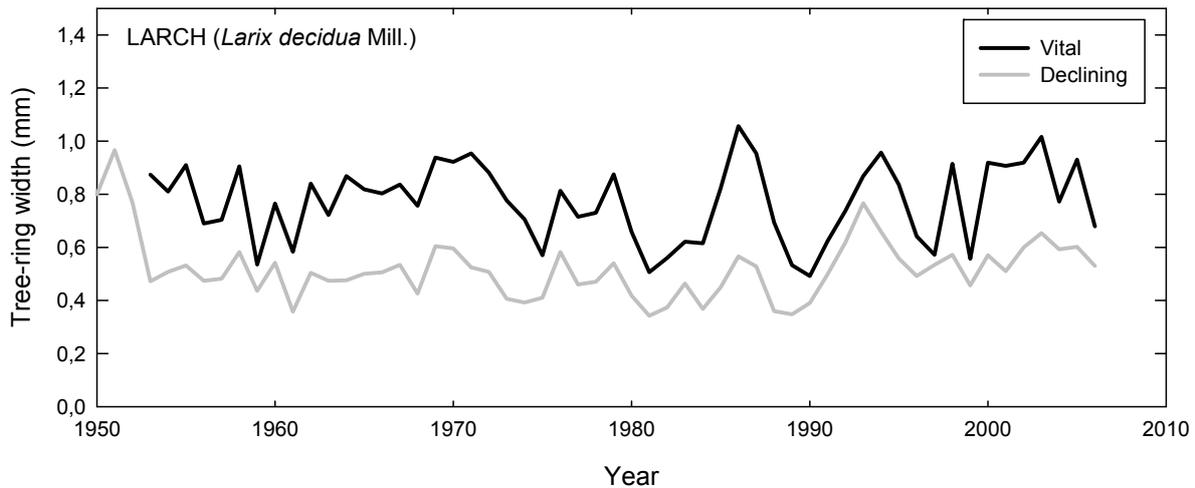


Figure 3: Tree-ring widths in the group of vital and declining European larch trees (*Larix decidua* Mill.)

Response of the studied trees to climate (Figure 4) differs significantly between sites and groups of trees. Growth of oaks in a floodplain forest depends mainly on the spatial and temporal distribution of the precipitation during the growing season. Vital oaks in floodplains responded positively to above average precipitation in May and June, while declining oaks with very narrow rings, usually consisting of only one row of vessels, responded negatively to above average temperature in March. Vital oaks show typical response of oaks in floodplain forests of Slovenia. In our case, the response of declining oaks was atypical, showing no response at all. Radial increment is too narrow to maintain the main role – conduction of water. Such trees are starving and are not able to respond to better growing conditions; their food reserves are limited and the only response to negative events is further decline of radial increment and even tree death (McDowell et al. 2008).

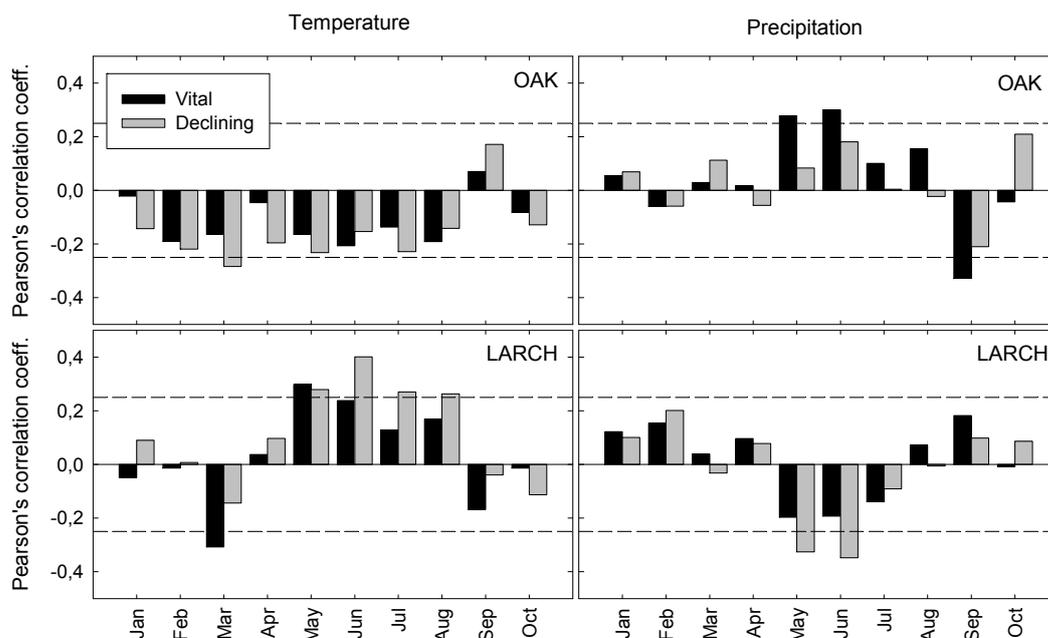


Figure 4: Response of studied oak trees (top) and larch trees (bottom) to the mean monthly temperature (left) and monthly sum of precipitation (right). Dashed lines represent 95% significance level for the correlation coefficients.

European larch at the upper timberline indicated a completely different response to climate than oak in the lowlands. Both groups of trees responded positively to above average temperature at the beginning of the growing season in May and June, which is in accordance with the findings of Frank and Esper for the European larch response to climate on the upper timber line (2005). Main difference between vital and declining trees is a short lag in their response. Vital trees start growing slightly earlier and are capable of taking advantage of the above average temperature in May, while declining trees start growing later. Above average temperatures in June have the most important influence on the formation of a wider tree ring in declining trees.

Precipitation has a more negative role at the upper timberline, since the greatest amount of precipitation in late spring falls as snow, which causes a considerable delay in the beginning of the growing season. It may also be connected with late frost events. Above average precipitation in May and June therefore negatively affects the growth on the upper timberline. Both groups of the studied trees respond similarly, with more intensive response to above average precipitation in declining group of trees than in vital trees.

## Conclusions

Oaks on plots with low water table are declining. Radial increments are small, responses to climate are evident only in the group of vital trees, while declining trees respond with a further growth decrease and finally die, as confirmed by our study. Declining trees are in more severe water stress and exhibit reduced transport function in xylem and roots; leaves lacking water transpire and assimilate less and the whole tree is subjected to a progressively physiological weakening. Responses of vital and declining trees at the upper timberline to microsite conditions are, contrary to lowland oaks, similar and in view of physiological response and radial increment very small. Weaker growing trees indicate a later response to above average temperatures during the vegetation period. Trees with bigger radial increment respond positively to above average temperatures in May and June (with emphasis on May); trees with narrower tree rings respond positively to above average temperatures during the same months as well, but with emphasis on June. Physiologically, the differences in assimilation rates are small and compensation points in both groups similar. Water stress is present, but not expressed as in the case of oak trees, where significant differences were confirmed in ecophysiological response regarding the maximal assimilation rates and compensation points for light and different CO<sub>2</sub> concentration. Pre-dawn water potential and water use efficiency were different for vital and declining trees in both species. In the case of larch, several positive pointer years were identified in hot and dry years (1960, 1976, 1988, 2003), showing that temperature at the upper timberline is one of the key limiting factors. Particularly dry and hot years, such as 1976 and 2003, had a significant positive effect on larch growth, while in lowlands their effect on oak growth was opposite. On the other hand, the cold and wet year 2005 had a positive influence on oaks and negative effects on larch tree growth. Despite the fact that a positive response of larch to temperature increase at the upper timber line was confirmed, such positive trends are questionable in the long term, because other environmental factors, such as mineral nutrition or amount and distribution of precipitation, may become limiting. Beside this, a rise of the upper timberline is only possible as long as soil conditions permit a shift upwards.

Oak forests in the lowlands are threatened mainly by the conversion of forest into agricultural land. Relatively small patches of the remaining forests are affected by the rapidly changing environmental factors. Oaks are stressed and physiologically weakened because climate change altered the relatively stable precipitation and flooding patterns. Radial growth of the studied trees has been declining since the late 1980's. Tree rings in vital oaks usually consist of 2-4 rows of early wood vessels and a significant proportion of latewood, normally more than 2 mm wide. The observed tree rings in declining oaks were very narrow, consisting of only 1-2 rows of vessels

without latewood. Such declining trees are too weak to respond to favourable growing conditions, so their only response is a decline and an increased mortality.

### Acknowledgement

This research was financially supported by the Slovenian Research Agency grant L4-9653 "Influence of climate change on growth response of Pedunculate oak (*Quercus robur* L.) and European Larch (*Larix decidua* Mill.)" and V4-0348 "Influence of climate change on growth and tree response on Slovenia's extreme sites" supported by the Slovenian Research Agency and the Ministry of Food, Agriculture and Forestry.

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