

THE COMPARISON OF THE POTENTIAL EFFECT OF CLIMATE CHANGE ON THE SEGMENT GROWTH OF *FRAXINUS ORNUS*, *PINUS NIGRA* AND *AILANTHUS ALTISSIMA* ON SHALLOW, CALCAREOUS SOILS

TRÁJER, A.^{1,2*} – HAMMER, T.¹ – BEDE-FAZEKAS, Á.^{3,4} – SCHOFFHAUZER, J.⁵ – PADISÁK, J.^{1,2}

¹*University of Pannonia, Department of Limnology
H-8200, Veszprém, Egyetem utca 10.
(phone: +36-88-624-747)
e-mail address: atrajer@gmail.com*

²*MTA-PE Limnoecology Research Group
H-8200, Veszprém, Egyetem utca 10.
(phone: +36-88-624-747)*

³*Hungarian Academy of Sciences, Centre for Ecological Research,
Institute of Ecology and Botany
H-2163, Vácrátót, Alkomány u. 2-4.
(phone: +36-28-360-122 / 133)*

⁴*Corvinus University of Budapest, Faculty of Landscape Architecture and Urbanism,
Department of Garden and Open Space Design
H-1118, Budapest, Villányi út 29-43.
(phone: +36-1-482-6308)*

⁵*Independent author
H-8227, Felsőörs, József Attila utca 14.
(phone: +36-20-988-5971)*

**Corresponding author
e-mail: atrajer@gmail.com*

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Abstract. Growth patterns of different plant species are primarily determined by edaphic factors, climate conditions and their species-specific adaptation properties. Changing sub-regional aridity trends due to the projected climate change like soil erosion and the invasion of alien plant species threaten the ligneous vegetation of karst areas. We aimed to study and model the potential effect of aridity on the growth rate of young individuals of the native *Fraxinus ornus* and its two important competitors, the exotic *Pinus nigra* and the aggressive invader *Ailanthus altissima* in a karstic forest-steppe of the Veszprém plateau, Hungary on different soil depths. Mean soil depth and the Thornthwaite agrometeorological index were used as covariates. Climate data were gained from the E-OBS gridded dataset for the period of 1950 to 2013 and from the MPI Echam5 climate model for the period of 2081 to 2100. We found significant correlation between the soil depth values and the measured heights and the average of monthly Thornthwaite agrometeorological indices. In conclusion, aridity and soil-depth have significant, but different effect on the growth patterns of the studied species. While the annual growth season of *Pinus nigra* and *Fraxinus ornus* are determined by the aridity of the months of January to May, and from February to June, respectively, the growth of *Ailanthus altissima* is mainly determined by the period of March to August. The climate prediction-based growth model predicts the decline of the growth patterns of each species for the 2081-2100 period in Hungary due to climate change.

Keywords: *Fraxinus ornus*, *Pinus nigra*, *Ailanthus altissima*, climate change, Thornthwaite agrometeorological index, aridity

Abbreviations: The used tree and stand abbreviations were based on the symbols of International Union of Forest Research Organizations (IUFRO) standardization (van Soest, 1965) except the values which were given in cm^{-2} based values adjusting to the young age of the stands and some new value was introduced: the standardized annual stem segment growth (hs), the the annual segment height (ha), the calculated total height of the same age trees (hc) and the measured total height of trees of similar age (hm). The following abbreviations were used in the text: ha: annual stem offshoots growth, hs: standardized annual stem segment growth, hc: the calculated total stem height, hm: the measured total stem height, t: age from individual [years], Sm: mean soil dept, P: monthly sum of precipitation [mm], T: monthly mean temperature [$^{\circ}\text{C}$], r: the growth-soil depth coefficient, TAI: Thornthwaite agrometeorological index [$\text{mm } ^{\circ}\text{C}^{-1}$].

Introduction

The protection of the natural karst vegetation against the alien plant species is one of the most important elements of the conservation for preserving integrity of the soil cover on carbonate bedrocks and the karst aquifer systems. Recently, the native vegetation is threatened by invasive species like the tree of heaven, *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae). Some methods have been developed to control of the invasive *A. altissima* recommending the use of pathogens as weevils, insects, fungi or webworms (Ding et al., 2006). The substitutability of the tree-of-heaven during the changing climate with other plant species as e.g. *Fraxinus ornus* L. (Oleaceae) has not been numerically analyzed. *F. ornus* is a characteristic, widespread native ash species of the natural vegetation on dolomite and limestone karst of the South-Central Europe and the Mediterranean (Kostova, 2001). Due to their significant drought and fire tolerance (Chiatante et al., 2006), *F. ornus* is an important species and codominate the low canopy with *Quercus pubescens* Willd. (Fagaceae) in the *Cotino-Quercetum pubescentis* association (Csontos et al., 2001) which is common in the studied karstland area of Veszprém. *Pinus nigra* Arnold (Pinaceae) is an exotic tree on the dolomite rocks of the Transdanubian hills and the closest natural occurrence is in the Vienna Basin, Austria, representing the northernmost occurrence of the species in Europe (Leal et al., 2008). The dolomite terrains of the Transdanubian Mountains were intensively afforested with *P. nigra* in the 20th century (Csontos et al., 1996). Occupying large areas on diverse dolomite rock grasslands, *P. nigra* plantations resulted in the local extinction of the original flora and fauna (Cseresznyés et al., 2006; Udvardy, 1998a) and is also known as a transformer species (Winkler and Tóth, 2012; Bódis, 1993). *Ailanthus altissima*, which is also a worldwide established transformer plant species (Udvardy, 1998b) is native to China, Taiwan and Northern Vietnam (Kowarik and Samuel, 2007; Ding et al., 2006). Although the members of the family of Simarubaceae are mostly tropical woody plants, *A. altissima* grows under several climatic conditions from humid or dry temperate to sub-tropical areas (Miller, 1990). As an invasive species, *A. altissima* occur in different habitats in the Mediterranean coniferous and broadleaved associations (Kowarik, 1983) and is a typical early-successional species in forest ecosystems (Robinson and Handel, 1993). Producing allopathic materials, *A. altissima* can suppress the growth of other angiosperms in their vicinity (Ding et al., 2006; Heisey, 1990). Although the fossil members of the *Ailanthus* genera are known from the Tertiary sediments of Hungary e.g. the *A. confucii* Unger form the Middle Miocene (Hably, 2001) and the *A. tardensis* Hably form Lower Oligocene (Corbett, 2004; Hably, 2001), the first specimens of *A. altissima* were planted in Europe only in the 1751 in France (Hu, 1979). *A. altissima* might have been introduced in Hungary in the late 18th or the early 19th century. According to Sárospataki (2014), the first individuals were

planted in 1807 in Western Hungary, Keszthely then in 1814 in the archduke park of Sárvár. *A. altissima* has become the most important invasive species in the semi-natural forests, urban areas and dry deciduous woodlands in Hungary (Mihály and Botta-Dukát, 2004; Török et al., 2003; Udvardy, 1998b) as in many other areas of the world (Constán-Nava, 2010). *A. altissima* is a successful ligneous invader species on rock grasslands e.g. on the Szársomlyó Hill in the Duna-Dráva National Park in Southwestern Hungary (Erdős et al., 2005) and in the Aggtelek National Park in Northeastern Hungary (Vácz, 2001). It appears that *Pinus nigra* and *Ailanthus altissima* are the most important competitors of *Fraxinus ornus* in the natural rock grasslands and dry deciduous woodland habitats of Hungary. The rapid, anthropogenic climate change has the potential to change the fitness of the native plant populations, and can trigger the area expansion of certain species (Huntley, 1991) dramatically altering their compositions (Jump and Peñuelas, 2005), and the degradation of the fragmented flora and fauna results in poor plant associations dominated by alien species (Gibbons et al., 2000). It is widely agreed that climate change will result expansion of many invasive species (Hellmann et al., 2008; Gritti et al., 2006; Beerling et al., 1995) as a consequence of elongation of the vegetation period, increasing winter temperatures and the increasing aridity. The process will restructure the natural vegetation with replacing natural elements by more warm-resistant, partly Mediterranean species.

Regional climate models predict an increasing aridity of the Carpathian Basin by the end of the 21st century particularly in the vegetation period (Piecicka et al., 2011; Bartholy and Gelybó, 2007; Bartholy et al., 2009). The studied Veszprém karstland has a continental climate with warm, dry summers and mild winters. The zonal vegetation is the transition of the forest and forest steppe zones. The average annual precipitation was 650 mm, the annual mean temperature was 9.4°C in the period of 1902-1950 (Ádám et al., 1987). During 1980-2009 the annual mean temperature increased by 1.3 to 1.4°C in the area. In 1960-2009 the annual precipitation decreased by -5- to -15 % (Bartholy et al., 2007). In the last three decades the number of days of mean temperature higher than 25°C increased by 6-8 days/year (Bartholy et al., 2007). Summer precipitation is very likely to decrease for the period of 2071-2100 by -25 to -30% according to IPCC SRES emission scenario A2 or -10 to -15% according to scenario B2 (Strenger et al., 2004). On the other hand, winter precipitation is likely to increase by 35% (A2) or 20% (B2) (Bartholy and Gelybó, 2007).

Model results showed that the rising decay frequency of *Pinus nigra* individuals in the last decades was a parallel change to the decreasing growth rate of pines due to the increasing aridity trend in the Veszprém karst plateau (Trájer et al. 2015). As drought inhibits growth (Chiatante *et al.*, 2006; Kramer and Turner 1980), in this paper, we investigate the effect of the sub-regional drought trends and the foreseen change of precipitation and temperature on the stem growth of young individuals of *Fraxinus ornus* and its two most important competitors: *Pinus nigra* and *Ailanthus altissima*. Our specific aims were: (1) to describe the temporal patterns of temperature and precipitation on the annual vertical growth of young individuals of the three species and (2) to model the past and predict their future vertical growth. We hypothesized that aridity in the growing period may have a great influence on the annual segment growth in the future. Since the more noticeable phase of the anthropogenic climate change started in the 1950's (King and Harangozó, 1998), we intended to model the whole period of the last six decades as well as the predicted future effect of climate change of the last two decades of the 21st century.

Materials and methods

Study site and soil thickness measurements

The study was performed in the central part of the Transdanubian Highland in Hungary (Fig.1A). The bulk of the area built up mainly of Triassic carbonates which were formed on a tropical shallow carbonate platform (Balog *et al.*, 1997). The Triassic rocks of the Transdanubian Range belong to the Alpine Triassic type (Haas, 1992) which means that the analogies of the bedrock and the calcareous soils formed on the carbonates can be found in the entire Mediterranean Basin and the members of the Alpine orogeny as in the Alps (Goldhammer *et al.*, 1990), in the Betic Cordillera in Spain (Martin *et al.*, 1987). Genetically the karstic area of Veszprém belongs to the Transdanubian type which can be characterized by the significant affection of repeated tectonic movements and the faulting of the limestone and dolomite rocks into blocks (Bárány-Kevei, 2005). Due to the tectonic history, carbonate- and dolomite rubble-rich skeletal soils are characteristic to the area (Fodor *et al.*, 2005; Márton and Fodor, 2003). The bedrock of the shallow soils is hard, cemented dolomite and limestone breccias (Fig.1B). The thickness of the shallow, dolomite bedrock soil of the plant individuals were estimated by the averaging of four manual, perpendicular soil sounding measurements with an iron sounder from 30 cm of the basis of the stems in each case. The thickness of the soil was defined by the depths where the probe reached the firm bedrock carbonate rock. The soil thickness data were averaged in each case. Each of the studied tree individuals grows on well-lit, open area.



Figure 1. The studied karst region of the Carpathian Basin (yellow spot marks the place of Veszprém in the 'A' panel) and a typical section of a dolomite-based skeletal soil ('B' panel). The satellite picture was gained from the Google EarthTM landscape visualization (Sheppard and Cizek, 2009).

Measurement of the annual vertical growth of the species

The study was based on the measurement of 491 plant individuals. A total of 205 individuals of *Pinus nigra*, 140 of *Fraxinus ornus* and 146 of *Ailanthus altissima* were involved in the study. We measured the stem height and the corresponding soil thickness values of 81 individuals of *Pinus nigra*, the 40 of *Fraxinus ornus* and 63 of *Ailanthus altissima* and the annual stem segment heights of 124 individuals of *Pinus nigra*, 100 of *Fraxinus ornus* and 83 of *Ailanthus altissima*. The stem heights of the

individuals were measured from the soil level to the top of the stem. The reliably measurable number of the years varies by species, according to our observations this number is more than 11 years in *Pinus nigra*, about 9 years for *Ailanthus altissima* and 7 for *Fraxinus ornus*. We determined the ‘segment’ as the annual vertical and radial internodes between the branching levels of two adjacent years in case of *Pinus nigra* and the vertical dimension of a segment was measured between the two adjacent levels of the last 11 years (2004-2013). In cases of *Fraxinus ornus* and *Ailanthus altissima* the conception of the annual segments were based on the annual internodes of the plants. Seven years (2007 to 2014) were determined in case of *Fraxinus ornus* and nine (2005 to 2013) in case of *Ailanthus altissima*. The measurements in case of *A. altissima* were partly based on root sprout clones. We measured the individuals on well-illuminated, open areas (Fig.2A and 2B).

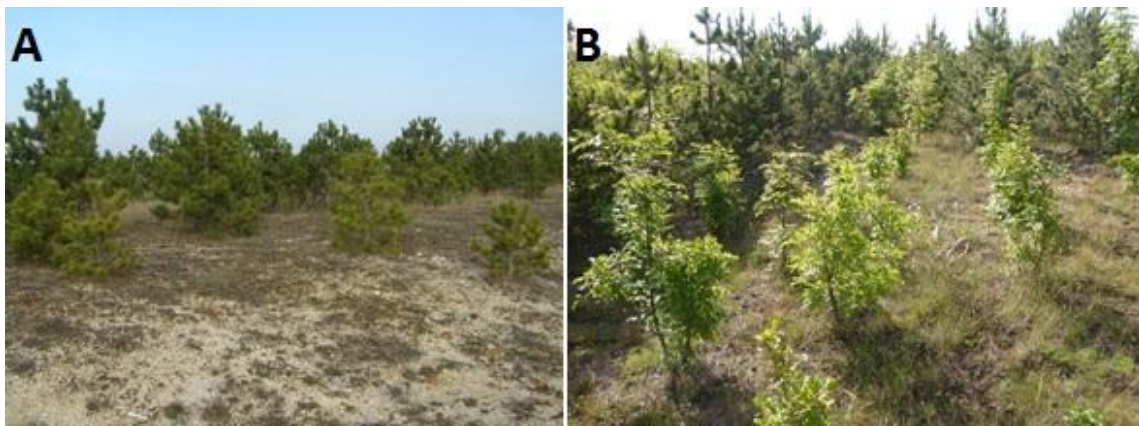


Figure 2. Characteristic landscape of the *Pinus nigra* (a) and *Pinus nigra*-*Fraxinus ornus* mixed plantations (b) in the studied sites.

We standardized the annual segment growth values of the plants to eliminate the individual differences e.g. due to the different soil thickness, the age of the trees as the segment lengths were linearly regressed in case of each specimen and then the yearly residuals were averaged. The standardized annual stem segment growth (h_s) was defined as the difference from the growth trend of the annual stem segments of the specimens (Fig.3A and 3B).

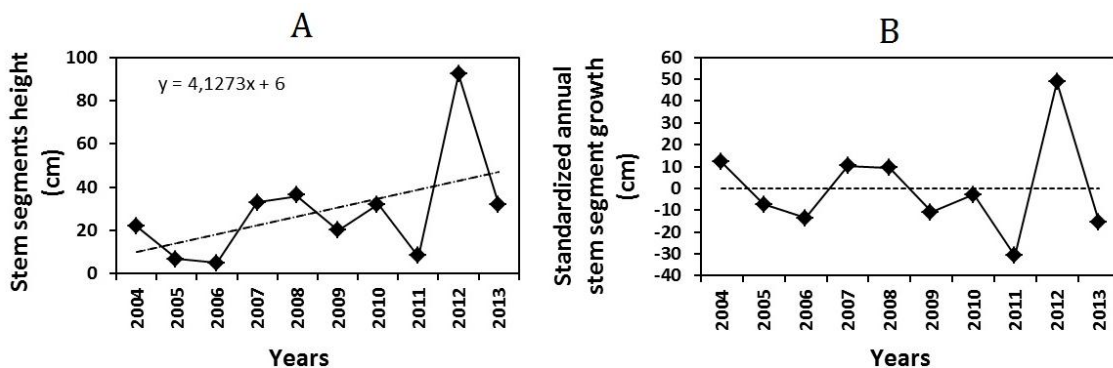


Figure 3. Example for the calculation of the used standardized annual stem segment growth (h_s): the annual stem segment height of a *Pinus nigra* individual with the equation of the growing trend (3A) and the differences from the trend (3B).

Climate data and data processing

The monthly mean daily surface air temperature and the monthly sum of daily precipitation data of the observed period were acquired from the E-OBS gridded dataset (source: E-OBS database 2014) for 0.25° grid resolution. The latitudinal expansion was 47.00°-47.50° N, and the longitudinal was 17.755°-18.25° E. The MPI Echam5 climate model was used (Jungclaus *et al.*, 2006) which was based on the SRES A1B scenario of the period January 2081 to December 2100 (Gaffin *et al.*, 2004). The latitudinal expansion was 46.632°-48.496° N, and the longitudinal was 17.813°-19.688° E. The slight difference of the grids was not arbitrary, originated from the differences between the databases of the observed and modelled climate. We aimed to find the most resemble grids which overlap the studied area. According to regional climate models the sum of the annual precipitation is not expected to change significantly for 2081-2100 in the region, but the modelled values of the seasonal precipitation sums show the significant redistribution of the annual precipitation patterns (*Fig.4A* and *4B*).

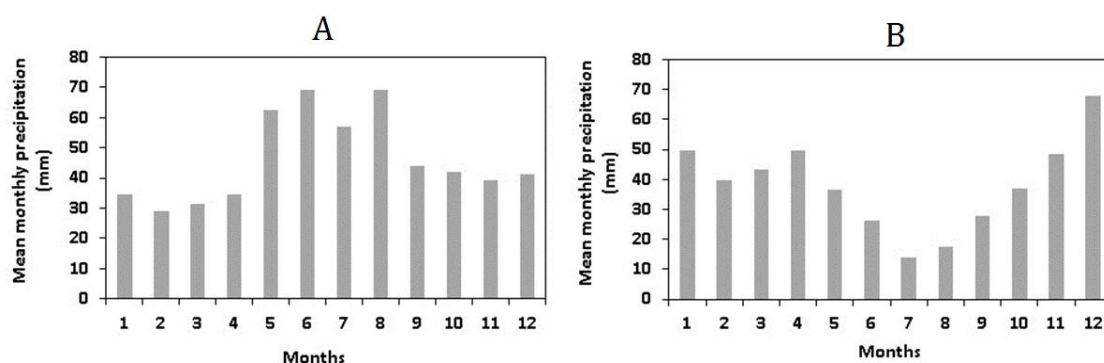


Figure 4. The mean annual distribution of the precipitation for the period of 2004-2013 (A) and the projected mean annual distribution of the precipitation for the modelled period of 2081-2100 according to the used MPI Echam5 climate model (B).

The Thornthwaite agrometeorological index (TAI) was employed as aridity index (Kemp, 1990). We averaged the monthly values during the correlations and the modeling steps.

$$TAI = 1.65 \cdot \left(\frac{P}{T + 12.2} \right)^{\frac{10}{9}} \quad (\text{Eq. 1})$$

Correlation between the aridity index and standardized annual stem segment growth, modelling

We studied the association between of the mean of the TAI of the months for continuous periods within the vegetation season of the year and the standardized annual stem segment growth. Continuous periods of the aridity indices of 9th, 10th, 11th and 12th months of the previous year also were involved to the study. The correlation with the best fitted significance value and R² of the options was chosen. We used this simple method to avoid the collinearity due to the few numbers (7, 9 and 11) of the testable years and the relatively large number of the variables (12-14). Equation of the best fit

linear regression correlation was used as the model of the aridity-based annual growth of the species. The years of 2004 to 2013 were used as the reference periods.

We used the associations between soil thickness and the total stem heights of the same year's old individuals (h) as the main factor which determines the absolute stem height. Due to the permanency of the soil thickness, in case of young individuals the soil thickness has no influence on the deviation of the individual trends. The estimation of the growth model provided a so-called "ideal" total vertical stem height according to the aridity values of the studied period starting from the height of 10 cm in case of *Fraxinus ornus* and *Pinus nigra*. Due to its clonal growth, in case of *Ailanthus altissima* we used the oldest 3 annual stem segment of the plants. Displaying the above described equations to the plantation of same aged individuals we calculated the correlation between the proportion of the measured (h_m) and the calculated (h_c) annual vertical growth values and the identical soil depth values.

$$r = \frac{h_m}{h_c} \quad (\text{Eq. 2})$$

The total annual vertical growth was calculated in different soil depths according to the Eq.3. Ten years of growth were modelled according to the projected monthly climate values for the soil depth of 5 to 20 cm.

$$h = r * h_c \quad (\text{Eq. 3})$$

Linear Correlation and Regression were performed by the online, free statistical program pack of VassarStats website (Lowry, 2012). The Fig.11 was prepared in ArcGIS 10.1 software (Longley *et al.*, 2001). For Fig.11-13, the different growth values of the years were sorted into attribute table. Values of the spatial data were interpolated by the IDW interpolation function of the Spatial Analyst Tool of ArcGIS.

Results

Young stems of the studied species showed rather different segment growths (Fig.5). The length of the annual stem offshoots of *Fraxinus ornus* showed a permanent growth (number of years=7, $R^2=0.05$, $p=0.625$).

$$h_a = -0.0894 \cdot t + 23.689 \quad (\text{Eq. 4})$$

In *Pinus nigra* a continuous growing trend was found (number of years=11, $R^2=0.76$, $p<0.001$).

$$h_a = 1.925 \cdot t + 12.567 \quad (\text{Eq. 5})$$

The length of the stem offshoots of *Ailanthus altissima* showed an exponentially decreasing trend (number of years=9, $R^2=0.84$, $p<0.001$).

$$h_a = 1.925 \cdot t + 12.567 \quad (\text{Eq. 6})$$

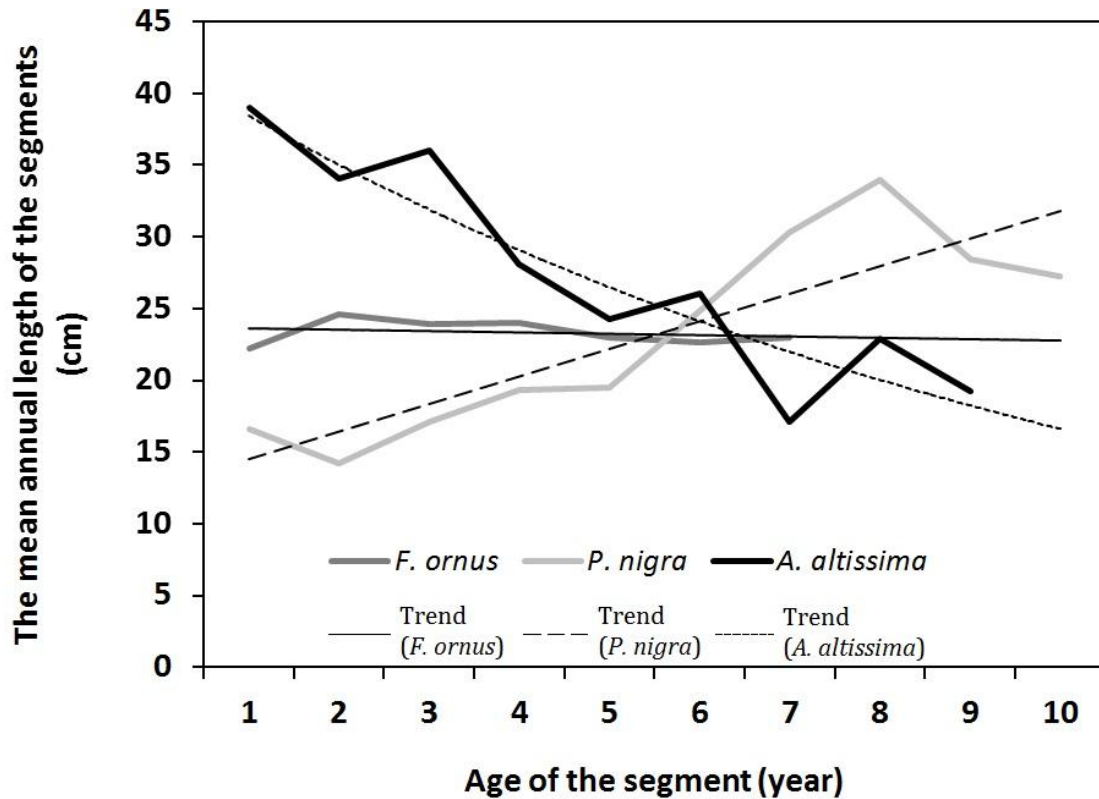


Figure 5. The trend of the length of the same years old annual segments of *Fraxinus ornus*, *Pinus nigra* and *Ailanthus altissima*

The averaged TAI of the following months were most significantly correlated to the standardized annual stem segment growth (h_s) in the period of 2007 to 2013: January to June ($R^2=0.75$, $p=0.002$), January to July ($R^2=0.73$, $p=0.014$) and February to July ($R^2=0.70$, $p=0.018$) in case of *Fraxinus ornus*; February to May ($R^2=0.70$, $p=0.002$, Fig.7), January to May ($R^2=0.69$, $p=0.005$) and March to May ($R^2=0.62$, $p=0.011$) in case of *Pinus nigra* and March to August ($R^2=0.62$, $p=0.011$), January to May ($R^2=0.69$, $p=0.005$) and March to May ($R^2=0.62$, $p=0.011$) in case of *Ailanthus altissima*. The following equations were used in the growth models: Eq.7 (*Fraxinus ornus*, Fig.6A), Eq.8 (*Pinus nigra*, Fig.6B) and Eq.9 (*Ailanthus altissima*, Fig.6C).

$$h_s = 1.4451 \cdot \text{TAI}_{\text{avg}(1,2,3,4,5,6,7)} - 5.7542 \quad (\text{Eq. 7})$$

$$h_s = 1.0579 \cdot \text{TAI}_{\text{avg}(2,3,4,5)} - 3.7276 \quad (\text{Eq. 8})$$

$$h_s = 1.0579 \cdot \text{TAI}_{\text{avg}(3,4,5,6,7,8)} - 3.7276 \quad (\text{Eq. 9})$$

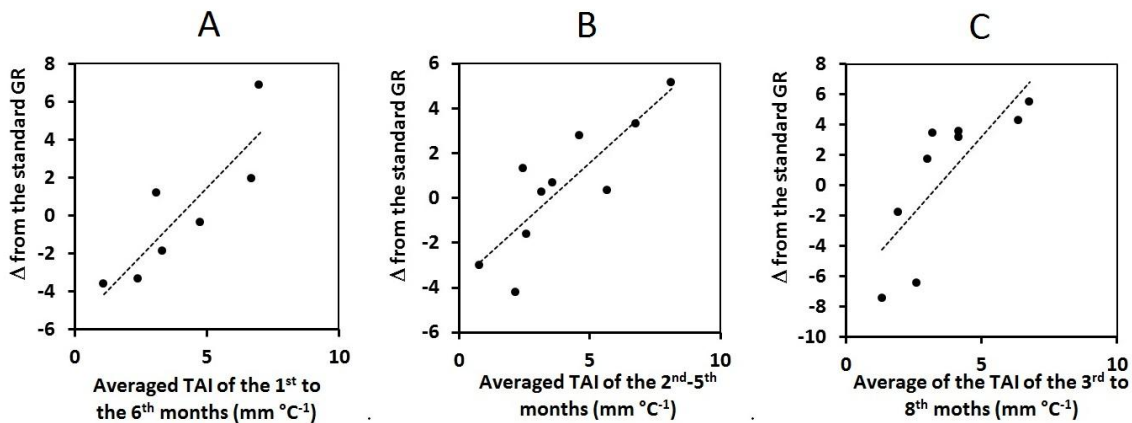


Figure 6. The association between the difference from the h_s and the averaged TAI in case of *Fraxinus ornus* (1st to the 6th months; 6A), *Pinus nigra* (2nd to the 5th; 6B), *Ailanthus altissima* (3rd to the 8th months; 6C).

Significant linear correlation was found between the mean soil depth and height of 7 years-old plantations of *Fraxinus ornus* ($R^2=0.46$, $p<0.001$, Eq. 10) and *Pinus nigra* ($R^2=0.54$, $p<0.001$, Eq.11). In case of *Ailanthus altissima* significant linear correlation was found between the mean soil depth and height of the oldest three annual segments ($R^2=0.21$, $p=0.001$, Eq.12; Fig. 7).

$$h_a = 7.1568 \cdot S_m - 53.8385 \quad (\text{Eq. 10})$$

$$h = 20.0345 \cdot S_m - 24.3157 \quad (\text{Eq. 11})$$

$$h = 5.2715 \cdot S_m - 40.727 \quad (\text{Eq. 12})$$

We calculated the ratio between the measured and calculated height of individuals of each species of the same age (*hence: ratio*) according to the segment growth trend and the TAI-based growth model equations. The gained ratios were regressed with the correspondent soil depth values. Significant correlation ($R^2=0.54$, $p<0.001$) were found between the ratios of 11 years old *Pinus nigra* individuals according to the Eq.4 and Eq.7 using the TAI values of 2004-2013 and soil depth values. We also found significant correlation ($R^2=0.47$, $p<0.001$) between the ratio of 7 years old *Fraxinus ornus* individuals according to the Eq.5 and Eq.8 using the TAI values of 2005-2013 and soil depth values. Lastly, significant correlation ($R^2=0.21$, $p<0.001$) was found between the ratio of the 3 years old *Ailanthus altissima* individuals according to the Eq.6 and Eq.9 using the TAI values of 2011-2013 and soil depth values (Fig.8).

$$\textit{Ailanthus altissima}: r = 0.0719 \cdot S_m + 0.5552 \quad (\text{Eq. 13})$$

$$\textit{Pinus nigra}: r = 0.0746 \cdot S_m - 0.0905 \quad (\text{Eq. 14})$$

$$\textit{Fraxinus ornus}: r=0.0452 \cdot S_m - 0.3403 \quad (\text{Eq. 15})$$

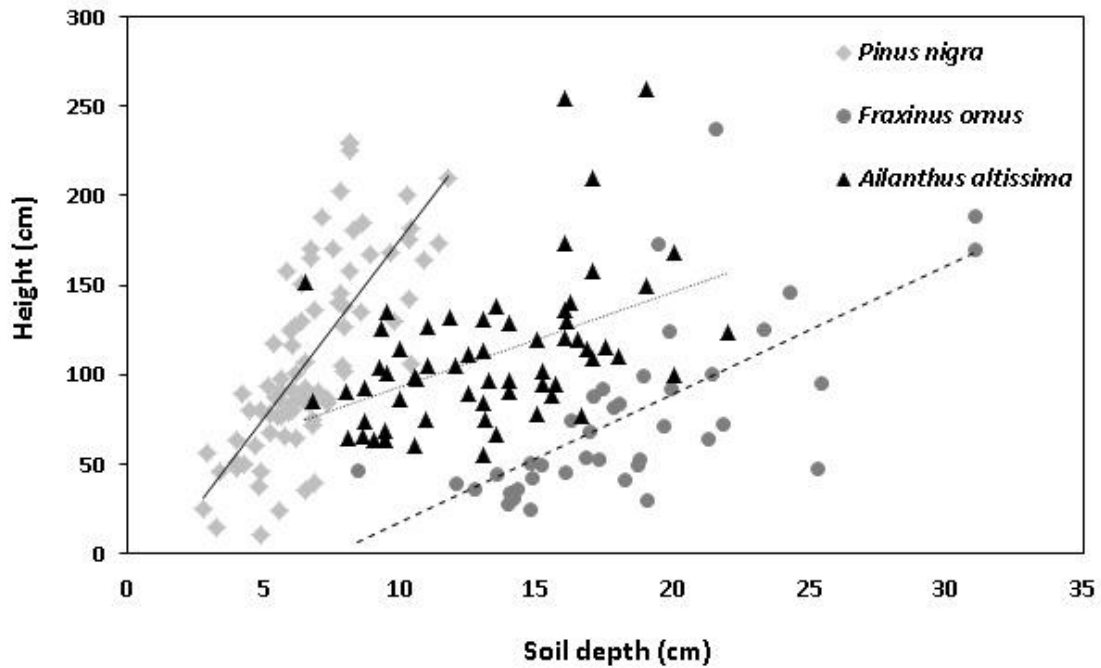


Figure 7. The correlation between the mean soil depths and the heights of 9 years old *Pinus nigra* (light gray rhombus), *Fraxinus ornus* (dark gray circles) and the summarized length of the 3 years old *Ailanthus altissima* individuals (black triangles) to determine the growth-soil depth coefficient (r)

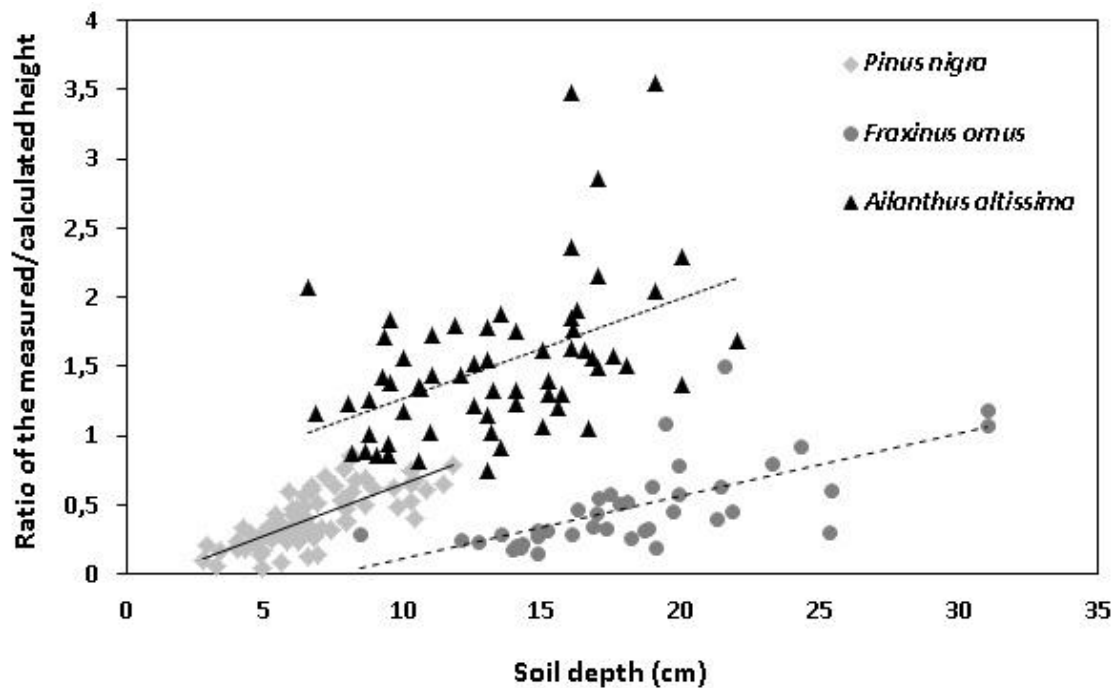


Figure 8. The correlation between the mean soil depths and the calculated per measured ratio of *Pinus nigra*, *Fraxinus ornus* and *Ailanthus altissima* individuals

The model predicts the significant decrease of standardized annual stem segment growth in case of *Fraxinus ornus* and *Ailanthus altissima* during the last five decades (1950-1999): [$R^2=0.17$, $p=0.001$; differences from the standardized stem segment growth: -0.99 (1950-1959), -1.27 (1960-1969), -1.76 (1970-1979), -1.93 (1980-1989), -2.89 (1990-1999)], [$R^2=0.07$, $p=0.045$; differences from the standardized stem segment growth: -2.09 (1950-1959), -2.05 (1960-1969), -2.33 (1970-1979), -2.56 (1980-1989), -2.97 (1990-1999)]. In case of *Pinus nigra* a barely significant decrease of the standardized annual stem segment growth was found during the last six decades (1950-2010): [$R^2=0.07$, $p=0.055$; differences from the standardized stem segment growth: -0.45 (1950-1959), -0.8 (1960-1969), -1.16 (1970-1979), -1.28 (1980-1989), -1.43 (1990-1999)]. Fig.9 shows the modelled standardized annual stem segment growth of the species for the period of 1950 to 2003.

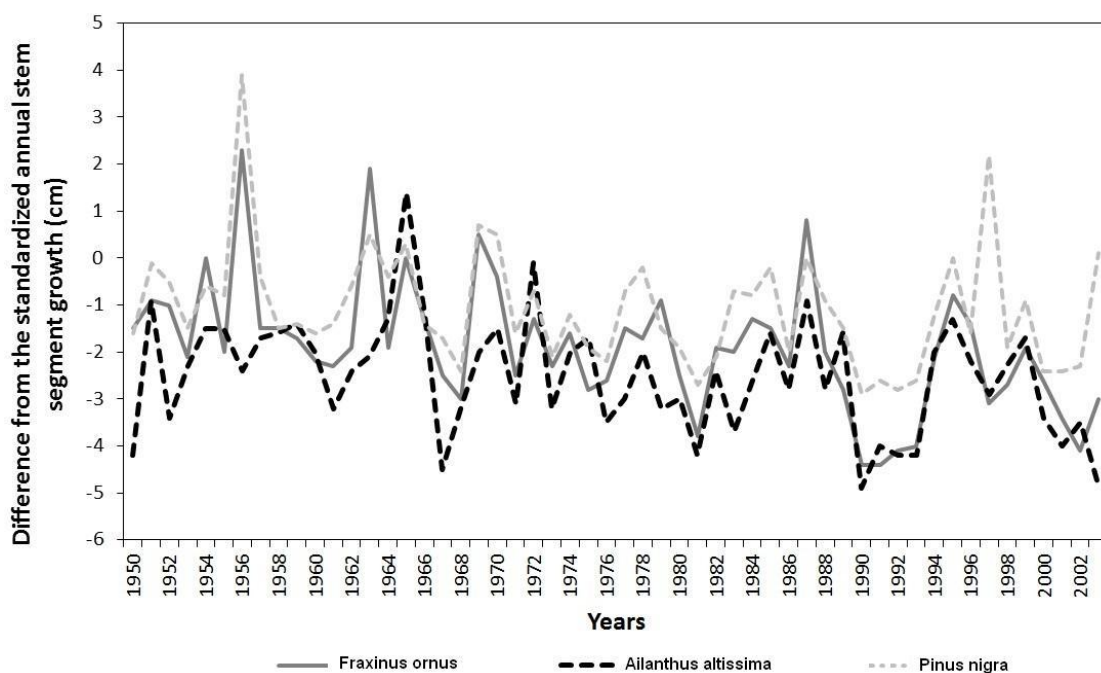


Figure 9. The modelled difference values of the standardized annual stem segment growth of *Fraxinus ornus*, *Pinus nigra* and *Ailanthus altissima* in cm from 1950 to 2003

The model predicts the decrease of standardized annual stem segment growth compared to the decades of the period for the future periods of 2081-2089 and 2090-2100: -2.54 and -2.54 (*Fraxinus ornus*), -4.29 and -4.64 (*Ailanthus altissima*), -1.55 and -1.50 (*Pinus nigra*; Fig.10).

The model predicts the highest decrease of the standardized annual stem segment growth in case of *Ailanthus altissima* in 1950-2010, including the future period of 2081-2100. In case of *Pinus nigra* the changing climate patterns will cause a relatively low decrease of the standardized annual stem segment growth, while the change in case of *Fraxinus ornus* can be moderate (Fig.11).

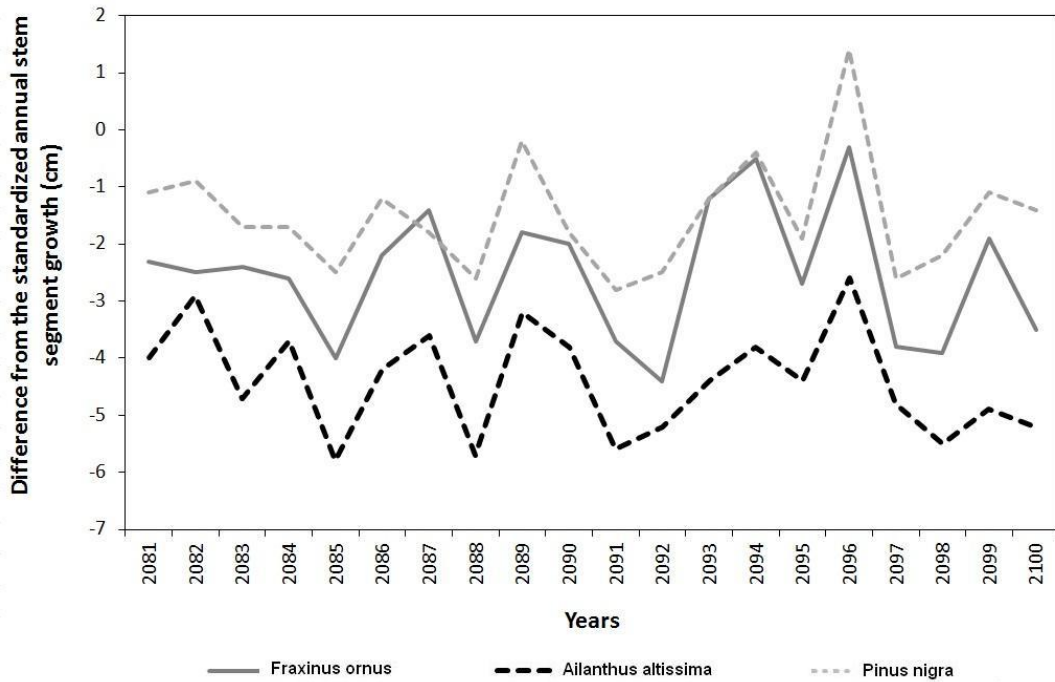


Figure 10. The modelled difference values of the standardized annual stem segment growth of *Fraxinus ornus*, *Pinus nigra* and *Ailanthus altissima* in cm from 2081 to 2100

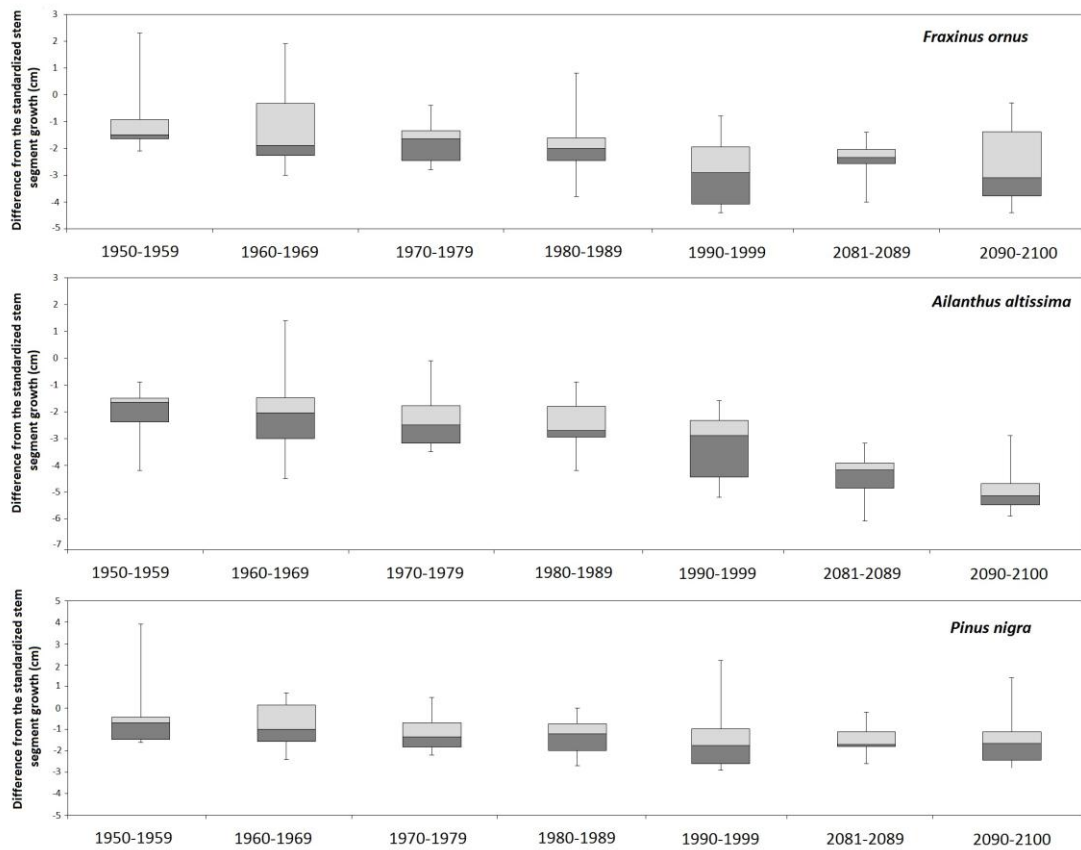


Figure 11. The box and whisker plots of the change of the modelled standardized annual stem segment growth.

Fraxinus ornus shows the lowest absolute stem segment growth for each modelled soil depths in the period of 2091-2100 (Fig.12).

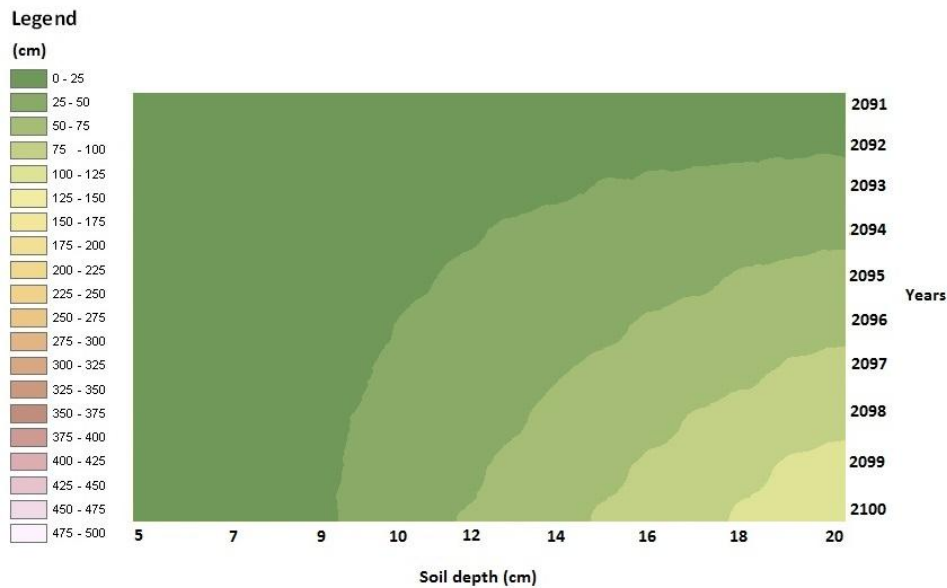


Figure 12. The modeled future (2081-2100) growth of *Fraxinus ornus* on soils of different depth

The model predicts an intermediate segment growth of *Pinus nigra* (Fig.13).

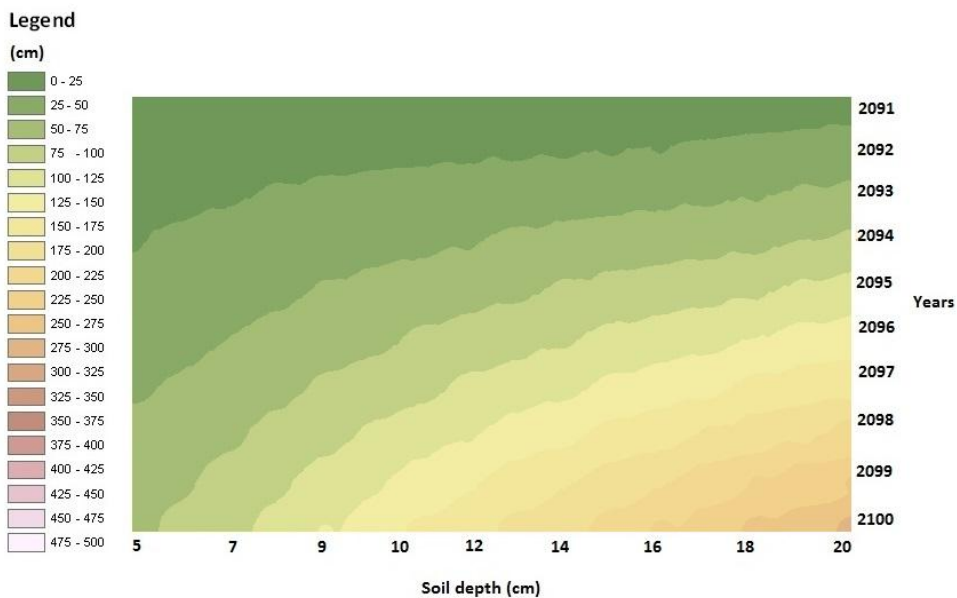


Figure 13. The modeled future (2081-2100) growth of *Pinus nigra* on soils of different depth

Ailanthus altissima seems to be the most rapidly growing tree species at same soil depths (Fig.14).

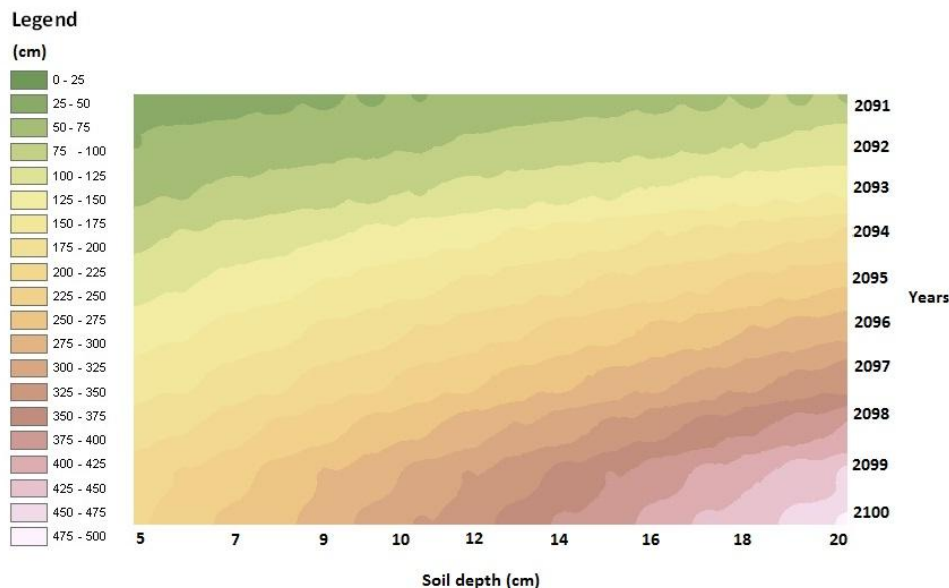


Figure 14. The modeled future (2081-2100) growth of *Ailanthus altissima* on soils of different depth

Discussion

Significant differences were demonstrated between the aridity and soil-depth based growth patterns of the young specimens of *Fraxinus ornus*, *Pinus nigra* and *Ailanthus altissima* on the dolomite karst area of the Transdanubian Range, Hungary. While the annual growth season of the primarily South-Central European and Mediterranean *Pinus nigra* and *Fraxinus ornus* are determined by the aridity of the months of January to May or from February to June, the growth of *Ailanthus altissima* is mainly determined by the period of March to August. The obtained results showed similar seasonal association between the annual stem segment growth of *Pinus nigra* and the precipitation patterns to the ring-based study of Martín-Benito et al. (2008). Martín-Benito et al. (2000) described that the early offshoots of *Pinus nigra* is mostly influenced by climatic conditions prior to the growing season. Wimmer et al. (2000) found a very similar association between the false rings and the precipitation of May.

It is important to note, that our model is valid only for the 1 to 10 old plants since e.g. in case of *Ailanthus altissima* after 10–15 years the initially branching growth pattern turns into dichasial or monochasial (Kowarik and Säumel, 2007). The model results showed that the increasing summer-spring aridity will enhance more the difference between the growth capability of *Fraxinus ornus* and *Ailanthus altissima* than in case of *Fraxinus ornus* and *Pinus nigra* therefore; *Pinus nigra* may overgrow the individuals of *Fraxinus ornus*. Although we tried to study different, non-clonal specimens of *Ailanthus altissima* it is possible that this aim was not totally fulfilled and hence complicates modeling and the comparison since the root sprouting plays an important role in the establishment of *Ailanthus altissima* in new areas (Kowarik, 1995; Rabe, 1985). It is likely that the found initial rapid segment growth of the young *Ailanthus altissima* clones are in accordance with the specific canopy and light gap filling strategy of the species (Knapp and Canham, 2000; Espenschied-Reilly and Runkle, 2008; Gómez-Aparicio and Canham, 2008; Call and Nilsen, 2003;

Espenschied-Reilly and Runkle, 2008). Nevertheless, the present observations correspond to the fact that both root sprouts and seedlings can exceed a very rapid, even 1-2 m segment growth in their first year (Hunter, 1995; Miller, 1990).

The measured segment growth partly reflects the height of the species at their maturity: the average mature height of *Pinus nigra* ranges from 20 to 50 m in the natural occurrence of the species (Krugman and Jenkinson, 1974), *Ailanthus altissima* can reach the 18 to 21 m in height (Vines, 1960) and the maximum height of *Fraxinus ornus* is about 20 m on humid and rich soils (Oxford Herbaria, 2014), but it rarely exceeds 10-15 m (Kwantlen Plant Database, 2015). Although *Pinus nigra* reaches its mature size by approximately 80 years of age (Van Haverbeke and David, 1990), the life span of the *Ailanthus altissima* individuals ranges only from 30 to 70 years (Espenschied-Reilly and Runkle, 2008; Miller and James, 1990). The ramet bank of *A.s altissima* may explain the fast initial grow of the species in contrast to *Pinus nigra* and *Fraxinus ornus* (Kowarik, 1995). The allopathic compounds (Heisey, 1996; McFeeters, 1977) of the leaves and the barks might explain the successful colonization of the species during the decreased segment growth in later years. Kowarik (1983) described that while the distribution of *Ailanthus altissima* is mainly affected by site fertility in the Mediterranean, in Central Europe climate is the major factor that affects occurrence.

We found that aridity is a secondary factor of growing and soil depth is a much more important factor of absolute growth in case of all species. These results indicate that considering the climate/aridity requirements of the species, the climate of the studied area is closer to the Mediterranean climate than to the typical continental what corresponds to the sub-Mediterranean character of the Transdanubian Mountains (Németh, 2011; Bartha and Nagy, 2005). *A. altissima* is able to survive severe droughts on dry, rocky soils using an effective water-saving mechanism that includes decreasing the water loss by leaves and reducing the root hydraulic conductance (Trifilò *et al.*, 2004). Vertical growth of *A. altissima* is also sensitive to aridity, but *A. altissima* has advantage in the absolute annual growth against *Pinus nigra* and *Fraxinus ornus* due to its rapid growth in the first years. *A. altissima* showed the greatest growth on shallow soils which is in accordance with the observations that its seedlings often occupy the pavement cracks and other dry sites (Graves *et al.*, 1989), e.g. wall cracks and flat concrete roofs, moreover can tolerate compacted soils (Miller, 1990; Pan and Bassuk, 1985). *Pinus nigra* also showed great tolerance against the shallow, calcareous soil. Similar to *Ailanthus altissima*, *Pinus nigra* in their natural occurrence lives in various soil types and is able to live near the sea tolerating dry, shallow soils, sands, chalks, and limestone soils (Haverbeke, 2014). *P. nigra* is characterized by a relatively rapid, cca 15 to 34 cm annual growth which, moreover, showed an accelerating trend in the first 11 years. The maximum of the measured segment growth is very close to the growth of the *P. nigra* individuals of the Great Plain where approximately a 30 cm yearly segment growth was measured on “average sites” in the first 20 years after planting (Sander, 1963). The modeled 300 cm stem length of the 10-years old *P. nigra* individuals on 20 cm deep soils is comparable to the 5.3 m height of the same year’s individuals which was measured in the Secret Arboretum at Ohio State University on deep, rich soils (Aughanbaugh, 1958).

A. altissima is able to become a dominant species on disturbed calcareous vegetation (Patterson, 2008). Although *Fraxinus ornus* in Central and Eastern Europe also lives mainly on dry chalk and dolomite rocks soils (Oxford Herbaria, 2014) we found slightly slower segment growth on shallow soils than for *Pinus nigra* and *Ailanthus altissima*

which can be a consequence the extensive root system of the *Fraxinus ornus* requiring deeper soils (Oxford Herbaria, 2014). Our findings confirm the importance of the effective treatment of re-naturalized areas at least in the first decades since the segment growth of the native *Fraxinus ornus* is significantly slower than that of the offshoots of *Ailanthus altissima*.

Emission models suggest the increase of the atmospheric carbon-dioxide concentration which may have beneficial effects on plant growth. For example, Kaushal et al. (1989) found that the height of the seedlings of *Pinus nigra* in their 2nd growth year was 10% more at 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ carbon-dioxide atmosphere than under the 'normal' 350 $\mu\text{mol}\cdot\text{mol}^{-1}$. Several further studies investigated the effects of elevated CO₂ level on tree growth (Kilpeläinen et al., 2003; Broadmeadow et al., 2000; Kaushal et al., 1989), but these studies in general agreed that other factors (like low soil nutrient availability, decreasing precipitation, unbalanced water supply, increasing atmospheric ozone concentration (Broadmeadow et al., 2000; Curtis, 1996; Lal, 2004; Nearing et al., 2004), can reduce or reverse the proposed positive effect of the increasing CO₂ concentration on plant growth. This effect can be particularly relevant for dry deciduous woodland vegetation which *a priori* grows on shallow soils. Due to the inconsistent, complex influence and the lacking experimental data of the studied species, the effect of the elevating atmospheric carbon-dioxide concentration was omitted from the model presented in this paper. Additionally, climate change may increase the risk of forest fires in the Mediterranean areas (Moriondo et al., 2006) and the fitness of *Pinus nigra* individuals can be considerably influenced by fungal infections during severe droughts in Hungary (Koltay et al., 2005).

Since climate models predict the Mediterranean-like rearrangement of the annual precipitation patterns in the Carpathian Basin (Bartholy et al., 2009, 2007), the native *Fraxinus ornus* may have a slight long-term advantage in contrast to *Ailanthus altissima* since *Fraxinus ornus* also has the ability of rapid invasion (Thebaud and Debussche, 1991) what can be supported by the continuous growth strategy of the species. In long term, replacement of *Pinus nigra* by *Fraxinus ornus* may be successful. Although conifers can successfully occupy canopy gaps from the seed bank (Daskalakou and Thanos, 1996), the seedling density strongly decreases with stand age (Augusto et al., 2001) and some of the species of the original dolomite grassland and dry deciduous woodland vegetation have a long-term persistent seed bank under *Pinus nigra* plantations (Csontos et al., 1996). The models predict that *F. ornus* will be a useful candidate of re-naturalizations if the necessary treatments will also be performed combined with the removal of *Pinus nigra* and *Ailanthus altissima*. Since *Fraxinus ornus* generally grows in mixed forests with oak and pine (Gratani and Foti, 1998) there is chance that the *F. ornus* will replace the *Pinus nigra* plantations because the invasion of *Ailanthus* is partly prohibited by the high light demand of the species in closed associations (Botta-Dukát, 2008; Kowarik and Sämel, 2007). It should be emphasized that we did not study the effect of the increasing shading on growth rates. The subsequent treatment is also important since *Ailanthus altissima* can survive in poorly lit environments while may be shrubby if suppressed beneath the canopy (Váczi, 2011). Our results showed that the reconstruction of the native dry deciduous woodland associations with *Fraxinus ornus* can be executed only with the continuous parallel removal of *Ailanthus altissima* due to the similar aridity tolerance and soil requirements of the species. The model predicts the similar affection of the annual growth of the species in the future due to the increasing aridity. Although *Pinus nigra* also threaten

the re-naturalization of the dolomite grasslands, the removal of the pine species may be more easily executed than the eradication of *Ailanthus altissima*.

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