Changes in Climate Characteristics of Forest Altitudinal Zones within the Czech Republic and their Possible Consequences for Forest Species Composition

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Abstract

Forest altitudinal zones are important ecological units of forest classification within the Czech Republic. The aim of the present study was to evaluate the changes in climate characteristics of forest altitudinal zones (FAZ) during climatic seasons of 1961-1990 and 1991-2014 within the Czech Republic. Based on these changes, the risks in forestry are identified and it is evaluated whether the current concept of FAZ is still applicable to the differentiation of forest management in the face of climate change. The most important changes from the perspective of growth conditions occurred after 1990 from the 1st to 3rd FAZs, where temperatures increased significantly, spring precipitation decreased, and both the number of days with absolute maximum temperature above 30°C and reduced water availability in the soil increased. The detected changes in climate parameters of forest altitudinal zones are an important factor affecting the FAZs application in forest management used in the forestry practice.

Keywords: forest altitudinal zone, climate change, long-term planning, risk, forest management

Introduction

The global climate change strongly affects the vulnerability and adaptive capacity of forest tree species and ecosystems (e.g. Lindner et al. 2010, Olson et al. 2017). Current projections of climate change predict further increase in mean temperatures; for instance, in the Czech Republic in spring and summer from 2.3 °C to 3.2 °C, in autumn from 1.7 °C to 2.1°C and in winter from 1.5 °C to 2 C by the year 2050 (Ministry of Environment of the Czech Republic 2015). Seasonal changes in the rainfall distribution and more frequent extreme weather are also predicted (Christensen et al. 2007). The global effect of the humankind on ecosystems with all its consequences (including climate change) has gained a classification as a new geological period, the Anthropocene (Steffen et al. 2007, Anderson-Teixeira et al. 2014). The European forest ecosystems are also notably affected by the changes. It is clear that tree biomass production and all other goods and services provided by European forests will also be affected by climate change (Lindner et al. 2010) with important impacts on biodiversity and nature conservation (Milad et al. 2011, Thom et al. 2017). Zeppel et al. (2014) identified two basic social priorities related to climate change: water resources management and the impact of climate change on vegetation. Both priorities are closely related to forests whose management is traditionally conditioned by a proper ecological classification of forest ecosystems.

In the Czech Republic, such classifications (Czech Forest Ecosystem Classification – CFEC) ultimately affect the management methods at each specific site, for example, to a large extent it prescribes the species composition of the target stands. The forest altitudinal zone (FAZ) is the essential ecological unit of the CFEC, ‘forest-typology classification system’ in the Czech Republic (Viewegh et al. 2003). Forest altitudinal zones form the basic climate framework for the differentiation of sustainable management in forests. FAZ categorization is considered an important part of the ecological basis for developing sustainable management guidelines. Nowadays, the FAZ classification suggests the species composition of planted trees, forcing foresters to prefer native tree species defined by the FAZ classification. The forest site complexes (the main unit of CFEC), including the major climatic information on a relevant FAZ, and site information on a relevant edaphic category, are used for creation of the fundamental structure of forest management guidelines (Plíva 1987, 2000, Průša 2001) and forestry legislation in the Czech Republic (Kusbach et al. 2017).

The concept of altitudinal zones is based on the relationship between potential natural vegetation and climatic characteristics (Tüxen 1956, Zlatník 1976, Moravec 1998). The potential natural vegetation expressed by the dominant climax tree species is an indirect expression of the altitude climate (macroclimate) and the local topography affecting mesoclimate in each FAZ. The target tree species are arranged in order of increasing altitude as follows: *Quercus* spp., *Fagus sylvatica*, *Abies alba*, *Picea abies*, *Pinus mugo* (see Table 1). Therefore, forest altitudinal zones reflect natural communities formed by macroclimatic and mesoclimatic conditions (Randuška 1986, Zlatník 1976). In other words, the target tree species composition is driven by macroclimatic and mesoclimatic conditions via FAZs. These conditions are responsible for the cultivation of the target tree species.

Table 1. Forest altitudinal zone characteristics (Plíva, 1987; Viewegh et al., 2003) and number of grid points in 500 × 500 m grid

Name of Forest altitudinal zone*	Number of points
1 *Quercus*	5240
2 *Fagus–Quercus*	11531
3 *Quercus–Fagus*	27392
4 *Fagus*	21492
5 *Abies–Fagus*	21842
6 *Picea–Fagus*	11929
7 *Fagus–Picea*	4106
8 *Picea*	1069
9 *Pinus mugo*	180

* The second tree genus name is the main determinant, the first is codeterminant.

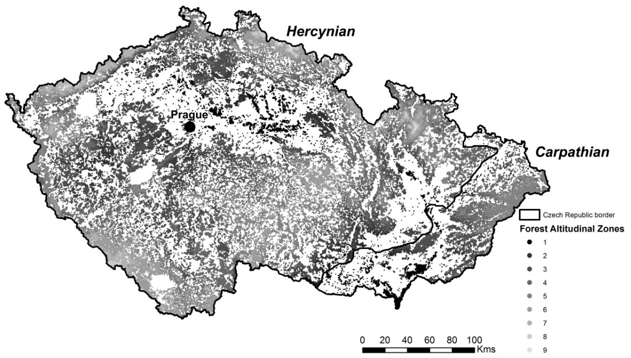

Figure 1. Forest altitudinal zones on regular grid 500 × 500 meters

The territory of the Czech Republic is divided into nine FAZs (Figure 1, Table 1).

If forest management is to effectively deal with the ongoing global change, it is necessary to identify the extent of the changes of climate parameters that determine the FAZs and also establish possible limits for the distribution of economically valuable tree species. The derivation of FAZ climate parameters is complicated by the existence of two phytoclimatic systems (Hercynian and Carpathian, see Figure 1), and several versions (chorological, ecological, and chorology-ecological) of altitudinal zonation (Zlatník 1976, Ambros 1992, Buček and Lacina 1999). Calculations of climate characteristics of altitudinal zones and predictions of their changes for the Czech Republic have been published by Hlásny et al. (2011), Macků (2014), and Machar et al. (2017). However, the studies had different aims and used methodologies different from our methods. Hlásny et al. (2011) predicted future climate conditions in four elevation zones which were defined specially for the study. Macků (2014) compared temperature and precipitation of FAZs in two periods 1961–1990 and 1991–2009 for 41 Czech Natural Forest Areas. Machar et al. (2017) discuss the biographical model of climate conditions as support for management strategies in European beech dominated forests.

The aims of the study were as follows: a) to evaluate changes in the basic and derived climate characteristics of FAZ for normal climate period 1961–1990 and period 1991–2014 for the Czech Republic; b) to evaluate whether the existing concept of FAZ is still applicable to derive recommendations for forest management in the face of climate change; and c) to define the ongoing and the expected changes in forest stands and forest management based on the changes of climate characteristics of the FAZs. Our underlying hypothesis was that a change in climate characteristics of ecological units is so great that the management recommendations based on them do not correspond with the current optimum conditions of the species which are currently being recommended for management of commercial forests.

Methods

Weather data

The meteorological database, produced from a joint effort between the Global Change Research Institute, Czech Hydrometeorological Institute and Mendel University in Brno as part of projects of National Agency for Agricultural Research, CzechAdapt and InterDrought was used in this study. The dataset included daily minimum and maximum temperatures, the sum of global radiation, precipitation totals, and mean wind speed and air humidity. These were then used to derive a set of climate variables. Special attention was paid to global radiation (i.e., incoming short-wave radiation), which was a key input parameter in evapotranspiration calculations. The value of global radiation was based partly on direct measurements through pyranometers (11 sites from 1983) and 122 sites using Campbell-Stokes heliographs determining sunshine duration hours for the whole 1961–2014 period. These data were homogenized, checked for consistency and gap-filled before being used by AnClim and ProClim software packages (Štěpánek et al. 2009) that were tested in detail by Brázdil et al. (2012). Local linear regression was applied to interpolate the daily weather data. For each grid, we included all stations within a diameter of 40 km for climatological stations (air temperature, global radiation, wind speed, and water vapour pressure) and 20 km for rain gauge stations (precipitation). As input for the interpolation, the so-called technical series of climate data variables (quality controlled, homogeneous and with filled gaps; for more details, see Štěpánek et al. 2011) were used and more details are provided in Trnka et al. (2015a).

Soil moisture modelling

This study is based on the analysis of root-zone soil moisture content (from the surface down to 1 m or less in shallow soils) using the modelling approach suggested by Allen et al. (1998), which was partially modified by Hlavinka et al. (2011) into a stand-alone SoilClim model. This is a robust two-layer soil moisture and evapotranspiration model, accounting not only for the vegetation dynamics (e.g. Trnka et al. 2015a) but also for the snow cover (Trnka et al. 2010) and other factors. SoilClim was applied for each grid and accounted not only for the soil water holding capacity but also for the type of vegetation cover; i.e. evergreen, mixed or deciduous one based on the forest type assigned to the grid by Corine land cover data (EEA 2000, CLC 2012), phenology development or snow cover accumulation/melting (Trnka et al. 2010). The module for actual evapotranspiration (ETa) and soil water content estimates considers two soil layers: the topsoil layer (from the ground surface to 0.4 m depth) and the subsoil layer (between 0.4 and 1.0 m). The cascading approach for transferring water from the topsoil to subsoil layers is used when the topsoil is less than 50% saturated which is assumed to represent the point of limited soil water availability (Novák and Havrila 2006). In the case of higher soil water content in the topsoil proportion of soil water in the topsoil is allowed to seep into the subsoil, mimicking the macropore and preferential water transport. SoilClim has dynamically simulated vegetation cover that allows for changing parameters of the canopy (e.g., leaf area index) during the growing season based on the thermal time. Therefore, the crop parameter Kc (Allen et al. 1998), as a single parameter in which all vegetation variables affected evapotranspiration are lumped, as well as root growth dynamics, vary for individual vegetation covers and through the year (or through the growing season).

Preparing of climatic predictors

We evaluated the shift in climatic predictors which are known to affect tree growth and vitality (Table 2). The predictors were defined in previous research (Rybníček et al. 2015, Kolář et al., 2015, 2017) or were taken from available research sources (Hlásny et al. 2011, Wilhite et al. 2016). In total, 21 predictors were evaluated: mean annual temperature; annual precipitation total; annual sum of global radiation; mean temperature of March-May, April-June, June-September; total precipitation of March-May, April-June, June-September; global radiation of March-May, April-June, June-September; mean annual relative soil water content at a depth of 0–40 cm (Available Water – Relative AWR1); mean annual relative soil water content at a depth of 0–100 cm (AWR); number of days of reduced water availability at a depth of 0–40 cm, AWR1<50; number of days with drought stress at a depth of 0–40 cm, AWR1<30; number of days with mean temperature above 10 °C; number of tropical days, T_{max} 30 °C, and higher; number of days with precipitation lower than 1 mm in a continuous period of at least ten days; effective global radiation – sum of the global radiation on frost – and snow-free days with mean daily temperatures above 5 °C and no water stress.

This paper only presents the predictors, in which a significant difference between the values of both periods has been statistically confirmed in at least one FAZ. As regards mean annual temperatures and precipitation totals, in addition to annual averages, values for three-month periods have also been compared. Here we only present values for the period from April to June, in which the greatest changes have been observed.

Climate change analysis

The basic step in the climate change analysis was to determine basic descriptive statistics parameters of defined climatic predictors for specific FAZs (Figure 1). The calculation was performed over regular 500 × 500 m grid (Table 1) generated over a layer of forest stands taken from digital forestry maps of the Czech Republic provided by the Forest Management Institute (FMI). A layer of FAZs determined by field survey was used as a GIS mask. The values of FAZs were extracted into points of the regular grid. The distance of the points was deliberately chosen so as to match the resolution of interpolated climatic data according to Štěpánek (2009, 2011). This point layer was assigned with a value of climate characteristics within the periods monitored: climate normal period of 1961–1990 and 1991–2014. The climate normal was traditionally defined as non-overlapping 30-year periods (1901–1930, 1931–1960, 1961–1990. The period from 1961 to 1990 has been retained as a standard reference period for long-term climate change assessments (WMO 2017). With this climate normal we than compared the second part of the record that constitute 80% of the next normal period 1991–2020. A number of points of each FAZ is mentioned in Table 1. To eliminate the effects of proxy variables we tested the relationships between all predictors using the Spearman correlation. The evaluation of the differences between the values of climate characteristics for the two periods was carried out in STATISTICA 10 (StatSoft 2013), graphically expressed in the form of box-and-whisker charts and tested by a paired *t*-test. Maps were processed in ArcGIS 10.3 (ESRI 2015).

Results

We observed changes in all compared climate parameters in the two periods, 1961–1990 and 1991–2014 (Table 2). In particular, mean annual temperature increased significantly, mostly in the 3rd FAZ, where the mean annual temperature increased by 1 °C; in contrast, the smallest increase (by 0.59 °C) has been observed in the 9th FAZ (mountains). The number of days with a mean temperature above 10 °C increased significantly in all FAZs as well as the number of tropical days ($T_{max} \geq 30$ °C) in the 1st–7th FAZs. The sum of annual precipitation increased slightly (a significant increase from the 4th FAZ up). However, the number of days with reduced water availability increased too (a significant increase except the 4th and 9th FAZs).

The temperature in spring (April–June) increased in all FAZs: the increase was significant in the 2nd–7th FAZs; at the same time, precipitation decreased: the decrease was significant in all FAZ except the 8th one. Detailed data for the FAZs with basic statistical parameters are presented in Figures 2–4 and the Appendix.

The differences found between the two periods show that the mean annual temperature and average temperatures per month or period increased in values which roughly correspond to a shift by one FAZ. The mean annual temperatures in the 2nd–5th FAZs in 1991–2014 were higher than the mean annual temperatures in lower FAZs (i.e., the 1st–4th ones) in the previous period. The temperatures of the 6th and the 7th FAZs approached the values of a lower FAZ considerably, to a difference of 0.10 °C and 0.12 °C, respectively. In the case of the 2nd, 3rd, 5th, and 6th FAZs, the mean temperatures for April-June in 1991–2014 are higher than the mean temperatures of lower FAZs in 1961–1990. In the case of the 4th FAZ, the mean temperature of April–June period in 1991–2014 is even equal to the mean temperature of the 2nd FAZ in the previous climate normal period (Appendix).

The period of 1991–2014 was nearly 1 °C warmer than the period of 1961–1990 as a whole; at the same time, precipitation increased slightly. In absolute terms, mean annual temperature after 1990 rose the most in the lowest FAZs; however, in relative terms (compared to mean temperature of the FAZ in the normal period), the rise in temperature increased with altitude. On the grounds of the observed changes of climate characteristics of FAZ, we described present forest-related risks and predicted future forest-related risks in all altitudinal zones in the Czech Republic (Table 3).

Drought and the associated biotic factors (above all bark beetles and other borers attacking on drought-stressed trees) are the main risks in the 1st–4th FAZs. The increasing temperature and its consequences as a better

Table 2. Overview of climate characteristics of forest altitudinal zones (FAZ) and the recorded mean differences between the periods of 1961–1990 and 1991–2014. Significance is reported for $\alpha = 0.05$ (Student's *t*-test)

Climate characteristics	Change between periods 1961–1990 and 1990–2014		Significance of the differences between the periods for FAZ									Fig. No.
	minimum	maximum	1	2	3	4	5	6	7	8	9	
Mean annual temperature	↑ 0.59°C (9th FAZ)	↑ 1.00°C (3rd FAZ)	*	*	*	*	*	*	*	*	*	Fig. 2
Mean temperature April-June	↑ 0.96 °C (8th FAZ)	↑ 1.15 °C (2nd FAZ)		*	*	*	*	*	*			A
Annual precipitation total	↑ 19.0 mm (1st FAZ)	↑ 136.4 mm (9th FAZ)				*	*	*	*	*	*	Fig. 3
Precipitation total April-June	↓ 14.9 mm (2nd FAZ)	↓ 20.3 mm (8th FAZ)	*	*	*	*	*	*	*		*	A
Number of days with mean temperature above 10 °C	↑ 11 days (1st FAZ)	↑ 17 days (9th FAZ)	*	*	*	*	*	*	*	*	*	A
Mean number of tropical days (T_{max} 30°C and higher)	↑ 0.9 (6th FAZ)	↑ 6.8 days (1st FAZ)	*	*	*	*	*	*				A
Number of days of reduced water availability at a depth of 0–40 cm (days with AWR1<50*)	↑ 0 days (9th FAZ)	↑ 8 days (1st FAZ)	*	*	*		*	*	*	*		Fig. 4
Number of days with precipitation lower than 1 mm in a continuous period of at least ten days	↓ 0.4 days (9th FAZ)	↓ 5.3 days (2nd FAZ)	*	*	*	*	*	*	*			A

A – Appendix

AWR1 = mean annual relative soil water content at a depth of 0-40 cm (AWR)

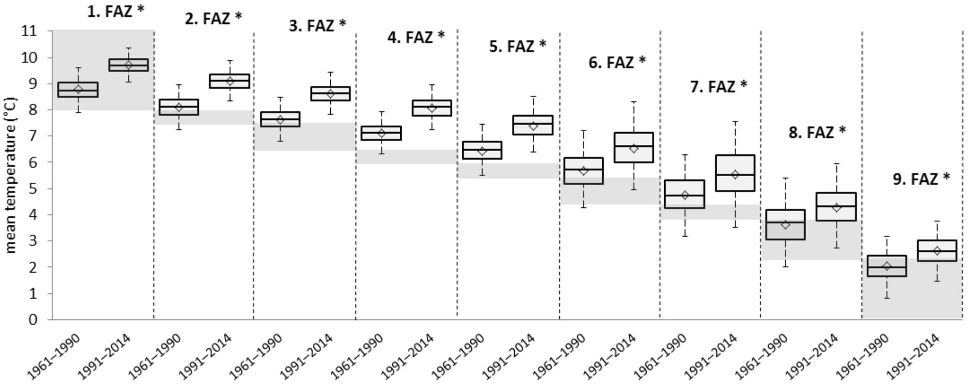

Figure 2. Mean annual temperatures for the forest altitudinal zones (FAZ) in 1961–1990 and 1991–2014. The box represents the spread of the 1st and the 3rd quartile with a line indicating the median, the point inside the boxes indicating the arithmetic mean, and the whiskers indicating the lowest figure 1.5 IQR of the lower quartile and the highest figure 1.5 IQR of the upper quartile. The difference between two periods is statistically significant at $\alpha = 0.05$ level (Student's *t*-test) in the FAZs marked with asterisk (*). The gray fields show the values for FAZs provided by Plíva (1987) for Hercynian part of the Czech Republic

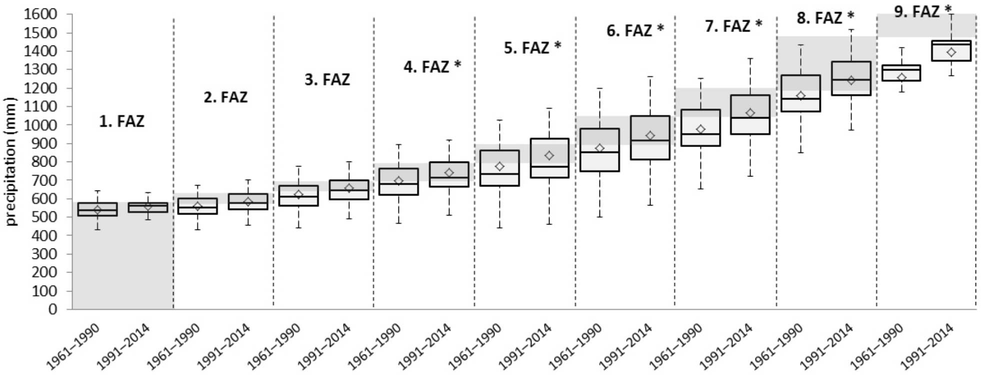

Figure 3. Annual precipitation totals for forest altitudinal zones (FAZ) in 1961–1990 and 1991–2014. The box represents the spread of the 1st and the 3rd quartile with a line indicating the median, the point inside the boxes indicating the arithmetic mean, and the whiskers indicating the lowest figure 1.5 IQR of the lower quartile and the highest figure 1.5 IQR of the upper quartile. The difference between two periods is statistically significant at $\alpha = 0.05$ level (Student's *t*-test) in the FAZs marked with asterisk (*). The gray fields show the values for FAZs provided by Plíva (1987) for Hercynian part of the Czech Republic

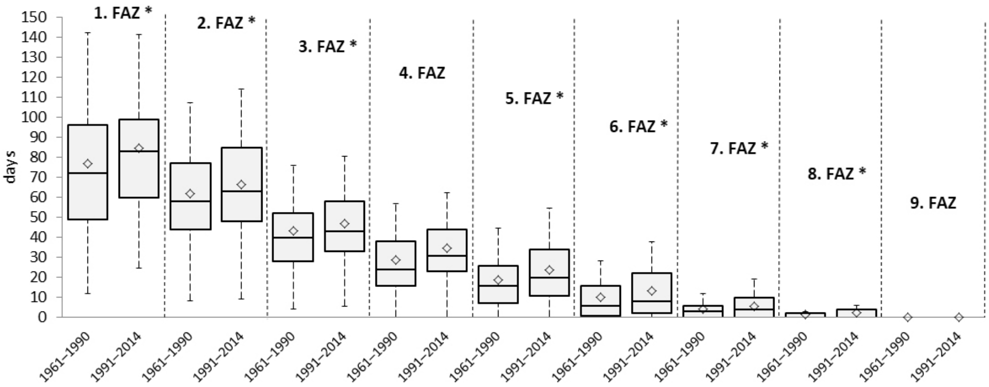

Figure 4. The mean number of days with reduced water availability at a depth of 0-40 cm, AWR1 lower than 50 for forest altitudinal zones (FAZ) in 1961–1990 and 1991–2014. The box represents the spread of the 1st and the 3rd quartile with a line indicating the median, the point inside the boxes indicating the arithmetic mean, and the whiskers indicating the lowest figure 1.5 IQR of the lower quartile and the highest figure 1.5 IQR of the upper quartile. The difference between two periods is statistically significant at $\alpha = 0.05$ level (Student's *t*-test) in the FAZs marked with asterisk (*)

condition for pest development (shorter generation time, increasing the overwintering survival), early frost damage risk, disturbances in existing Norway spruce monocultures and the increasing risk of pest attack will affect stands in the 5th–8th FAZs. The climate changes observed in the 3rd–5th FAZs are significant from the perspective of environmental claims of *P. abies*, which is the dominant tree species of economic forests in these FAZs. The climatic conditions in these FAZs have moved to the edge of the spruce ecological optimum or even outside due to the changes and Norway spruce silviculture will be very complicated or impossible on these sites (Table 3).

Table 3. Observed and predicted risks for forest altitudinal zones and forest management (outcomes of project FRAME ADAPT, www.frameadapt.cz/en/)

Name of FAZ	Risks	Recommended basic changes of species composition
1 *Quercus*	Drought – drought-induced forest decline, extremely bad condition for generative reproduction (difficult or even impossible reforestation with native species); increased biotic infestations (defoliators, fungi pathogens) for all tree species.	Higher proportion of thermophile and drought tolerant species – e.g. *Q. cerris*
2 *Fagus–Quercus*	Drought – drought-induced forest decline, bad condition for generative reproduction especially for *F. sylvatica* (high % of reforestation failure, difficult reforestation especially in xeric sites); increased biotic risks (defoliators, fungi pathogens) for all tree species; deterioration of growth conditions of *F. sylvatica*; *Quercus* spp. – increasing threat by defoliators.	Decreasing proportion of *F. sylvatica*, increasing proportion of *Q. petraea*, woody plant species diversity increase
3 *Quercus–Fagus*	Drought (for all tree species) – drought-induced forest decline, poorer condition for generative reproduction (elevated % of reforestation failure) and increased biotic risks (defoliators, bark beetles, fungi pathogens); inadequate planned species composition (presence of *P. abies* in planned composition); large disturbances in existing secondary *P. abies* dominant monocultures (windbreaks, bark beetle disasters, acute attacks by *Armillaria* sp., multifactorial disease);	Exclude *P. abies* from planned composition, increasing proportion of *Q. petraea*, woody plant species diversity increase
4 *Fagus*	Drought (for all tree species) – drought-induced forest decline, poorer condition for generative reproduction (elevated % of reforestation failure) and increased biotic risks (defoliators, bark beetles, fungi pathogens); inadequate planned species composition (too high % of *P. abies* leading to *P. abies* dominant stands); large disturbances in existing secondary *P. abies* monocultures (windbreaks, bark beetle disasters, acute attacks by *Armillaria* sp., multifactorial disease.	Considerable decreasing proportion of *P. abies,* increasing proportion of *Q. petraea*, increasing proportion of *F. sylvatica*, woody plant species diversity increase
5 *Abies–Fagus*	Increasing temperatures (for all tree species) – increased biotic risks (defoliators, bark beetles, fungi pathogens) due to better condition for pest development (higher % of successfully wintering individuals, increasing the number of generations of polyvoltine pests), longer vegetation period (early frost damage risk); inadequate planned species composition (too high % of *P. abies* leading to *P. abies* dominant stands), climate change enable silviculture of *Q. petraea*; large disturbances in existing secondary *Picea* -dominant monocultures (windbreaks, bark beetles disasters, acute attacks by *Armillaria* sp., multifactorial disease).	Decreasing proportion of *P. abies*, increasing proportion of *F. sylvatica*, increasing proportion of *A. alba*, inclusion of *Q. petraea*, woody plant species diversity increase
6 *Picea–Fagus*	Increasing temperatures (for all tree species) – increased biotic risks (defoliators, bark beetles, fungi pathogens) due to better condition for pest development (higher % of successfully wintering individuals, longer vegetation period (early frost damage risk); inadequate planned species composition (too high % of *P. abies*); large disturbances in existing secondary *P. abies* dominant monocultures (windbreaks, bark beetle disasters, acute attacks by *Armillaria* sp., multifactorial disease).	Decreasing proportion of *P. abies*, increasing proportion of *F.sylvatica*, increasing proportion of *A. alba*, introduce woody plant species diversity increase
7 *Fagus–Picea*	Increasing temperatures (for all tree species) – increased biotic risks (bark beetles, fungi pathogens) due to better condition for pest development (higher % of successfully wintering individuals, increasing the number of generations of polyvoltine pests); large disturbances in existing secondary *P. abies* dominant monocultures (windbreaks, bark beetle disasters, multifactorial disease);	Increasing proportion of *F. sylvatica*, woody plant species diversity increase including also increasing proportion of pioneer trees
8 *Picea*	Increasing temperature – better condition for pest development (higher % of successfully wintering individuals, increasing the number of generations of polyvoltine pests); large disturbances in existing secondary *P. abies* dominant monocultures (windbreaks, bark beetle disasters); increased biotic risks (bark beetles, fungi pathogens).	Woody plant species diversity increase including also increasing proportion of pioneer trees
9 *Pinus mugo*	Climate-induced shift of tree line.	

Discussion

The changes in climate characteristics of forest altitudinal zones

This study was conceived as an observational, country scale assessment aiming at obtaining available knowledge of the climatic characteristics of FAZs. Our results demonstrate that in the course of the last fifty years there has been a significant change in climate characteristics within the whole territory of the Czech Republic. These changes were caused by the global trend of temperature increase, changes in rainfall distribution, the increase in CO_2 as well as the onset of more extreme weathers (e.g. Milad et al. 2011). Forest managers should take the climate change into account of their decisions. They should respect autochthonous tree species composition together with the support of natural regeneration. Native tree species are less risky with respect to invasiveness, genetic depletion and sustainable forestry. The high genetic diversity within stands is a key prerequisite for forest trees to adapt and be resilient to the effects of climate change (Fady et al. 2016). A deeper insight into the future impacts of climate change along the altitudinal gradient requires an understanding of climate as a driving factor of the tree dominants distribution. Decisions about appropriate tree species will be especially difficult if climatic conditions at given site change rapidly (Milad et al. 2011). Regarding the sustainable forestry, we must accelerate revision of what might be defined as natural/target tree species at a particular FAZ.

Forest management in the Czech Republic is traditionally supported by the sustainable ecosystem principle (UHUL 2008), i.e. forest management should help maintain ecological balance and sustainable productivity. It should be done through the recognition of the site conditions via forest site complexes with based on FAZ categorization. The forest altitudinal zones in the Hercynian part were, contrary to Carpathian part, empirically defined by mean annual temperatures, annual precipitation totals and the length of the growing season (Plíva 1987) in the period when the climate data for 1961–1990 were not fully available.

In the period after 1990, the annual temperature increased significantly in the lower FAZs (the 3rd–5th ones). This increase was accompanied by lower spring precipitation, a higher number of tropical days, and a significantly higher number of days with reduced water availability in the soil (Table 2). The trend at middle altitudes (the 4th–6th FAZ) was similar: the spring and annual temperatures rose significantly as well as the number of tropical days and the number of days with reduced water availability in the soil. Although at the middle altitudes the interpolated precipitation increased, the amount of rainfall in spring decreased. Yet the rainfall amount and distribution in spring are crucial for ecological processes, e.g. regeneration, growth, mortality, and tree productivity (Zeppel et al. 2014). These findings correspond with the results of Trnka et al. (2015a, b), who pointed out the trend of AWR decline and an earlier onset of the dry season in the period from April to June for the territory of the Czech Republic.

The period from spring to early summer (April-June) is a key period affecting their radial growth as well as their health (Fritts 1976, Churakova et al. 2014). The significant effect of precipitation and AWR on the tree ring width in Europe has been proven for all of the main tree species of the species composition of the Czech Forests. As regards the oak, radial growth on the majority of sites at lower altitudes is affected by spring or early summer precipitation or soil water content (Doležal et al. 2010, Petráš and Mecko 2011, Rybníček et al. 2015, 2016). As for the beech (Dittmar et al. 2003, Rohner et al. 2016, Kolář et al. 2017) and the fir (van der Maaten-Theunissen 2012, Büntgen et al. 2011), there are studies with the similar findings from various altitudinal zones. As regards the spruce, it is affected by spring and early summer precipitation above all in extreme sites and sites outside its ecological optimum (e.g., Rybníček et al. 2012, Kolář et al. 2017), as well as the sites at mountain altitudinal zones (e.g. Pichler and Oberhuber 2007, Affolter et al. 2010, Kolář et al. 2015).

The environmental characteristics of FAZs are given by a combination of climate parameters corresponding with the altitude. The differences of climate parameters values between FAZs were various (Figure 2-4); there were not even statistically significant differences between some FAZs. For example, the values of the FAZs annual precipitation markedly overlapped: see intervals of Q1–Q3 (Figure 3). Especially the difference between annual precipitation totals of the 1st and the 2nd FAZ was not significant, in both periods (20.4 mm on average in 1961–1990 and 26.7 mm in 1991–2014).

These findings are important for differentiation of forest management since we use FAZs as units of the differentiation, even though some their important parameters can be the same or very similar, this may thus lead to incorrect management recommendations. The calculated ranges of model climate characteristics are mainly given by the macroclimatic nature of the interpolated climate data. Mesoclimatic conditions, which the FAZ concept must take into account due to the complexity of the terrain and local specifics, are neglected in our study (see Kusbach et al. 2017) because the information was not available in relevant spatial distribution. The range of climate characteristics is also affected by the data scale used. However, this resolution (500 × 500 m grid, see Figure 1) is the most detailed one that has been used for the analysis of ecological units so far.

Ongoing and predicted changes in forest stands and the related management

The temperature increase and the changes in rainfall distribution leading to the reduced AWR (Table 2) are reflected in the health of trees (Hlásny and Sitková 2010 and others, see below) and in their radial growth (productivity). These changes are also reflected in the altered nature and intensity of the impact of individual factors limiting radial growth, for example, the increased significance of the spring precipitation effect or the reduced impact of summer temperatures at higher altitudes (e.g., Kolář et al. 2017, Čermák et al. 2017). The fluctuations in soil water content and extreme precipitation may influence physiological responses and plant water relations, whereas changing seasonal precipitation may influence phenology including early/late wood development (Zeppel et al. 2014).

Many of the risks were identified for Norway spruce (Table 3), which is the prevailing forest tree species in the Czech Republic (50.5% of the forest area in 2016). Stands of *P. abies* are particularly susceptible to disturbances, e.g. drought and insect outbreaks (Lindner et al. 2010). Climate-conditioned episodes of Norway spruce decline in northern Moravia and Silesia in the 3rd up to the 5th FAZ in Vítkovsko and Libavá (Novák and Dušek 2014) or in the 3rd up to the 6th FAZ of the Beskydy (Grodzki 2007, Hlásny and Sitková 2010, Čermák and Holuša 2011) took place in tens of thousands of hectares. The decline started in the dry year 2003. Unspecific symptoms were observed: chlorosis, defoliation, radial growth decrease, and dieback of particular trees and groups. At first, the dieback affected mature trees; eventually, trees older than approximately 30 years were affected (Jeniš 2014). The main identified predisposing factors were the artificial origin of stands, growth out of ecological optimum (Plíva 2000), low content of the basic elements in the soil, and the drought episodes (Šrámek et al. 2015). Severe infestation by fungi *Armillaria sp.* was often an inciting factor for a subsequent attack of the bark beetles (*Ips typographus*, *Ips duplicatus* and *Pityogenes chalcographus*) as a contributing factor causing final mortality (Vakula et al. 2015). The consequences of the decline are evidenced by e.g. the increasing proportion of salvage logging, for example, in Libavá territory the salvage logging accounted for over 80% of the volume in most of the last fifteen years (Jeniš 2014).

The current proportion of *P. abies* is 50 % of the total timber land in the Czech Republic. It does not correspond to the potentially natural vegetation where their proportion would be only 11%. The decrease of the proportion and the increase of tree species diversity are key important aims for Czech forestry in the current situation when many studies report increasing unsuitability of *P. abies* for Central Europe (Milad et al. 2011). Therefore, forest management strategies must include altering tree species composition by targeted stand tending operations (to *Quercus* spp., *F. sylvatica*, *P. sylvestris*). *P. sylvestris* is more drought-tolerant than *P. abies,* has good commercial potential and is predicted to have superior adaptive capacity in mixed forests (Milad et al. 2011). Friedrichs et al. (2009) identified that the drought sensitivity of *P. sylvestris, F. sylvatica* and *Q. petraea* increase in Central-West Germany, i.e. in a condition similar of the Czech Republic. *F. sylvatica* is relatively tolerant to moderate drought periods (Grundmann et al. 2008); however, prolonged periods of severe droughts may negatively affect it. A loss in the competitive ability of *F. sylvatica* for the benefit of more drought tolerant tree species was identified by Fridrichs et al. (2009).

Studies dealing with climate characteristics in the Czech Republic in the period after 1990 and their impacts on vegetation (Brázdil et al. 2009, Hlavinka et al. 2009, Možný et al. 2009, Pretel 2012) showed that a combination of higher total radiation, higher temperatures, and water vapour pressure deficit increasing evapotranspiration, along with an earlier start of the growing season lead to faster depletion of water in the soil (Trnka et al. 2015b). The effect of the precipitation deficit on forest management in the Czech Republic can be evidenced by e.g. the proportion of area with repeated restoration (enforced by mortality of the first restoration) within the total forest restoration area. While in precipitation-normal or better than normal periods, the proportion of repeated restoration in the Czech Republic is within 14–20% in the long term, it is considerably higher in longer periods with precipitation deficits. The highest proportion was recorded in the dry period of 1991–1995, when it was over 30% in all the years, with the maximum amounting to 47% in the dry year 1994 (Ministry of Agriculture 2017).

Spring and summer drought episodes have been shown to be not only a factor limiting tree growth (Kolström et al. 2011) but also an important predisposing stressor (Zeppel et al. 2014). Our field campaign experience (Cermak pers. comm.) as well as scientific literature (McDowell et al. 2008, Kolb et al. 2016) shows that drought increases the sensitivity to some biotic diseases (in particular, a higher occurrence of vascular fungal infections and leaf and needle diseases can also be expected); additionally, drought increases the risk of pest attacks, in particular wood and bark borers, but in some cases also defoliators. Bark beetles are one of the dominant factors in the aforementioned episodes of Norway spruce decline in northern Moravia and Silesia, in full accordance with the concept of tree death by drought mechanisms (McDowell et al. 2008).

The applicability of forest altitudinal zones for forest management differentiation

Taking into account the predicted continuation of the changes of climate characteristics of forest altitudinal zones (Hlásny et al. 2011, Machar et al. 2017), our findings are an important factor affecting the use of ecological units conceived and mapped in this way for the general planning of forest management. In the case of a considerable change in FAZ climate characteristics in a relatively short period, the target species composition driven by macro- and mesoclimatic conditions, lower ecological units of CFEC (Viewegh et al. 2003), and the derived management series (Plíva 2000) do not correspond with the ecological optimum of the target species as regards the climate or correspond with it only in some parts of FAZ. Long-term forest management planning usually works with time horizons of 20 years or longer via Regional Plans of Forest Development, RPFD (Forest Management Institute 2005).

Our results showed that in the current conditions of climate change the discrepancy between recommendations included in the RPFD and the real conditions in the forests can be so large that the recommendations become inadequate in the course of the 20-year-long planning period, let alone during the lifespan of a tree or a forest stand. Furthermore, climate change will affect the functioning of the vast majority of forest ecosystems (Linder et al. 2010, Kolström et al. 2011, Milad et al. 2011, Hanewinkel 2012); we expect the greatest impacts on exposed, acidic, and nutrient sites, i.e., the sites that are not affected by stagnant or underground water where the risk of lack of soil moisture is the highest. The effect of macroclimate on tree growth is less predictable at water-affected sites (floodplain sites with alluvial soils, wet ravines, and gulleys, a site with Gleysols). For example, the current climatic conditions in the 3rd FAZ (see above) correspond to the conditions in the 2nd FAZ in the normal period; however, the planned species compositions of the 2nd and the 3rd FAZs are different (and thus their management differs fundamentally). Spruce is not present in the target tree species composition of nutrient sites of the 2nd FAZ, but it can be represented by up to 60% in the 3rd FAZ. In contrast, the oak is planned for the 2nd FAZ as the main tree species, but it only forms an admission in the 3rd FAZ. We recommend a reduction of the planned representation of the spruce in the 3rd–5th FAZs and increased representation of natural deciduous trees in the 3rd–8th FAZs (Table 3 and also see Kolström et al. 2011). In forest planning, the shortening of rotation period can also be an appropriate management response to accelerated growth in mountains (Kolström et al. 2011). Adaptation measures in precommercial thinning should support mixed stands of well-adapted tree species. These objectives should be adequately included in the long-term planning.

The calculated change and the significant overlap of climate characteristics for the adjacent FAZs call for a major revision of the way FAZs are used for long-term forest planning. However, differentiation of FAZ is not based on climate conditions only; therefore, the real prediction of the changes cannot be simply calculated (see Kusbach et al. 2017). Modelling any changes in the defined forest altitudinal zones can be facilitated e.g. by applying physiological and process models that are able to model the tree response to individual parameters and subsequent changes in the tree growth and distribution that would help better define the FAZs (Kupka 2002). The approach of natural vegetation, respectively target tree species, should identify suitable (temperature-dependent) indicators for possible changes caused by climate change, especially with regard to future monitoring (see Bässler et al. 2010) and long-term planning of forests (Šebesta et al. 2011).

Due to the significant changes in the climate characteristics of FAZs, and also because of a direct link of CFEC system units with forest management units (management series, Plíva 2000), forest management must respond to the dynamics of climate change by long-term planning and possibly a revision of typological forest classification (Kusbach 2012, Zouhar 2013). Long-term plans should fully integrate the principles of adaptive management, support operational decisions responding to the state of the stands, and take into account the need to convert forests managed under systems involving coupes to uneven-aged mixed forest silviculture (Temperli et al. 2012, the Ministry of Environment of the Czech Republic 2015). If the long-term plans are designed in this way, ecological units, such as FAZs, can be further used for the basic differentiation of management. The changing climate conditions may be taken into account by using the upgrade of FAZ climate parameters at 10-year intervals. For instance, under the changing climatic conditions, the site approach respecting the tree ecological claims is a suitable tool for holistic multi-criteria decision-making and adaptive forestry planning. The results indicate that, FAZ will be still applicable to derive recommendations for forest management if we change using of FAZ from a static (when the species composition is recommended according to past climate characteristics for 20 years or a longer period) to dynamic approach (when recommendations are evaluated and eventually revised during the feasible planning period of 10 years).

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Appendix

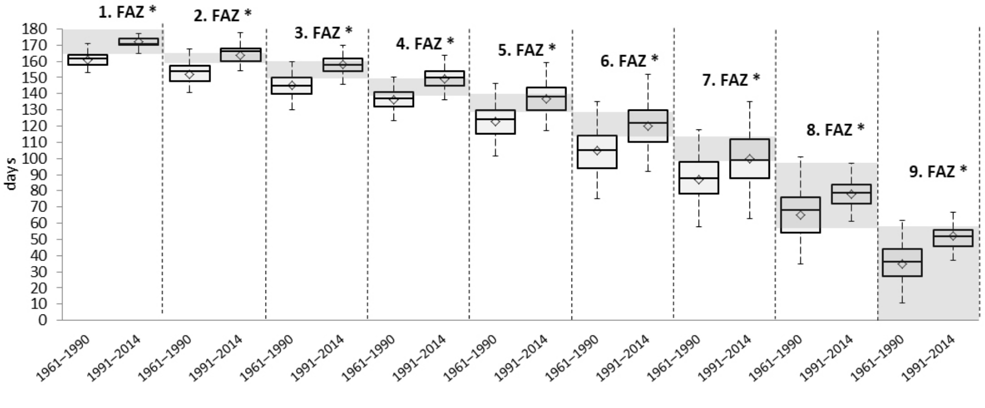

Figure 1. The mean number of days with an average temperature above 10 °C in a continuous period (growing season length) for forest altitudinal zones (FAZ) in 1961–1990 and 1991–2014. The box represents the spread of the 1st and the 3rd quartiles with a line indicating the median, the point inside the boxes indicating the arithmetic mean, and the whiskers indicating the lowest figure 1.5 IQR of the lower quartile and the highest figure 1.5 IQR of the upper quartile. The difference between two periods is statistically significant at α = 0.05 level (Student's *t*-test) in the FAZs marked with asterisk (*). The gray fields show the values for FAZs provided by Plíva (1987) for Hercynian part of the Czech Republic

Appendix (*Continued*)

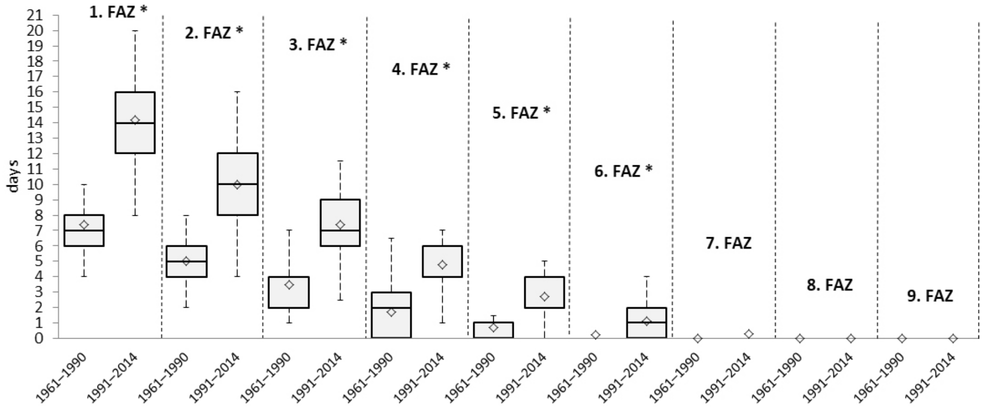

Figure 2. The mean number of days with a maximum temperature of 30 °C and more (tropical days) for forest altitudinal zones (FAZ) in 1961–1990 and 1991–2014. The box represents the spread of the 1st and the 3rd quartiles with a line indicating the median, the point inside the boxes indicating the arithmetic mean, and the whiskers indicating the lowest figure 1.5 IQR of the lower quartile and the highest figure 1.5 IQR of the upper quartile. The difference between two periods is statistically significant at $\alpha = 0.05$ level (Student's *t*-test) in the FAZs marked with asterisk (*)

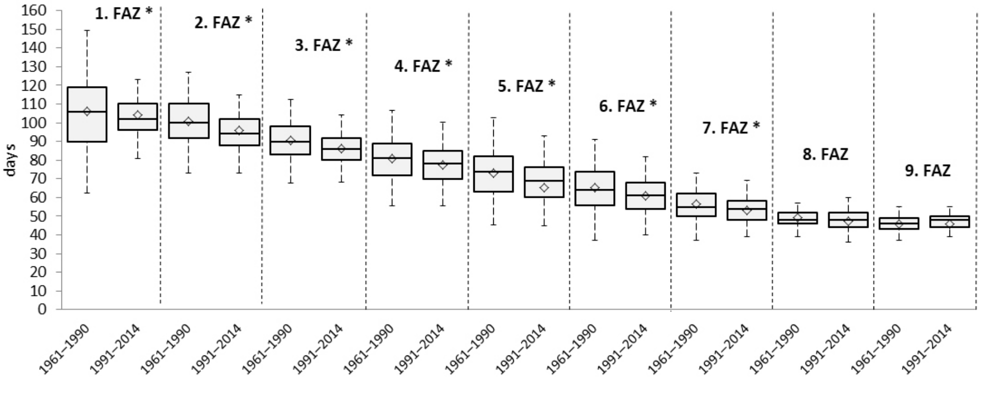

Figure 3. The mean number of days with precipitation lower than 1 mm in at least 10 day-periods for forest altitudinal zones (FAZ) in 1961-1990 and 1991-2014. The box represents the spread of the 1st and the 3rd quartiles with a line indicating the median, the point inside the boxes indicating the arithmetic mean, and the whiskers indicating the lowest figure 1.5 IQR of the lower quartile and the highest figure 1.5 IQR of the upper quartile. The difference between two periods is statistically significant at $\alpha = 0.05$ level (Student's *t*-test) in the FAZs marked with asterisk (*)

Appendix (*Continued*)

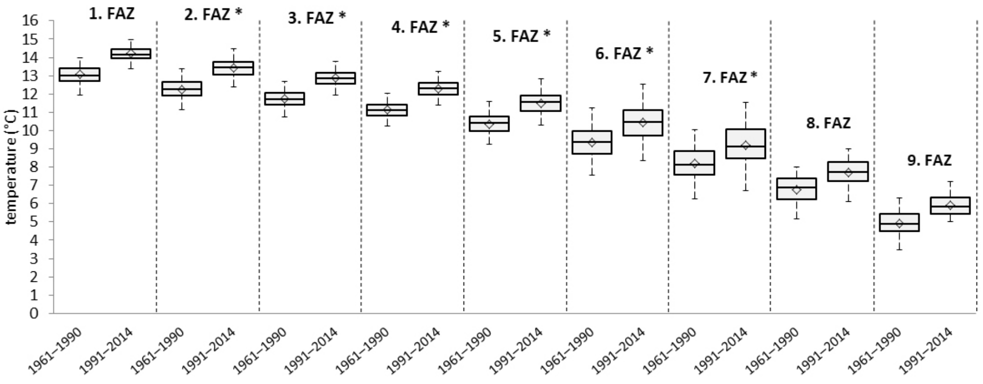

Figure 4. Mean annual temperatures in April-June for forest altitudinal zones (FAZ) in 1961-1990 and 1991-2014. The box represents the spread of the 1st and the 3rd quartiles with a line indicating the median, the point inside the boxes indicating the arithmetic mean, and the whiskers indicating the lowest figure 1.5 IQR of the lower quartile and the highest figure 1.5 IQR of the upper quartile. The difference between two periods is statistically significant at $\alpha = 0.05$ level (Student's *t*-test) in the FAZs marked with asterisk (*)

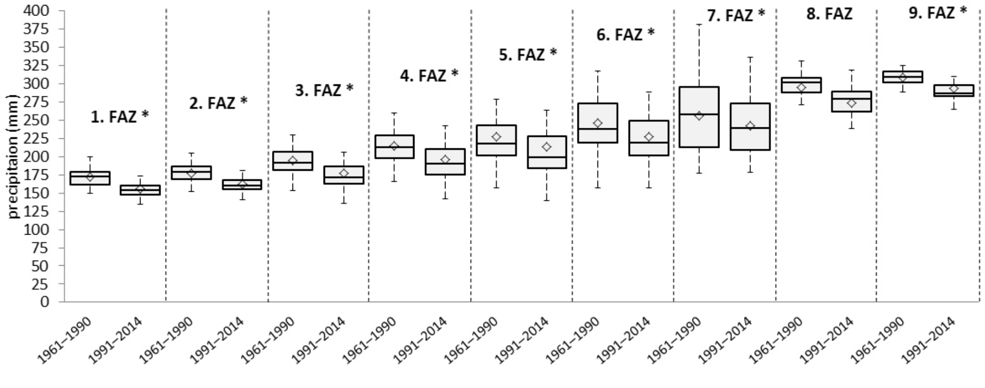

Figure 5. Mean precipitation totals in April-June for forest altitudinal zones (FAZ) in 1961-1990 and 1991-2014. The box represents the spread of the 1st and the 3rd quartiles with a line indicating the median, the point inside the boxes indicating the arithmetic mean, and the whiskers indicating the lowest figure 1.5 IQR of the lower quartile and the highest figure 1.5 IQR of the upper quartile. The difference between two periods is statistically significant at $\alpha = 0.05$ level (Student□s *t*-test) in the FAZs marked with asterisk (*)