CONTRIBUTION OF LOCAL HABITAT CONDITIONS AND INDIVIDUAL VARIABILITY TO THE CLIMATIC RESPONSE OF CONIFERS IN THE FOREST-STEPPES OF SOUTH SIBERIA

Liliana V. Belokopytova

Advisor: Dr Elena A. Babushkina

Khakass Technical Institute Siberian Federal University Abakan, Russia 2017

ABSTRACT

Dendroclimatic studies in the forest-steppe regions of South Siberia and, in particular, in the territory of Khakassia, date back to the mid-1980s; however, they were mostly sporadic and non-systemic. The organization of the laboratory "Dendroecology and Ecological Monitoring" in the Khakass Technical Institute, Siberian Federal University, allowed collecting wood samples and developing long-term tree-ring chronologies throughout the distribution area of the most widespread conifer species of Khakassia (pine, larch, spruce) from the driest conditions of the steppe boundary to the mountains up to heights of 2000 m. a.s.l.

This thesis consistently shows the results of a dendroclimatic analysis of two main forest species occupying the semiarid zone of the region. It was important to identify the main climatic factors limiting radial growth. To consider it in detail, possible methodological approaches to analyzing the growth-climate relationships were compared, including paired and partial correlations and various duration of the climatic factor generalization. The general outline of climatic response for the study area, and its details depending on particular conifer species physiology and spatial climatic gradients were investigated.

South Siberia is characterized by a high diversity of landscape, soil and hydrology, and in the semiarid climatic conditions the habitat has a substantial influence on plant growth. Thus the next step of the study was demonstrating the differences in the conifers radial growth and its response to the climatic factors in forest-steppes due to the local habitat conditions. Particularly, tree-ring chronologies from pairs of sites with contrast soil moisture were compared for both pine and larch.

Responses of trees of different growth rates to general climatic factors were investigated at the next stage. To estimate growth rate, a sample of about 200 individual pine trees from Minusinsk forests was classified into clusters with similar characteristics of the age trend functions using an original approach. Dependences of tree sensitivity to climatic factors and timing of the climatic response to their growth rate were considered. As a result, the most sensitive to climate variation clusters in the stand were identified, which are clusters of medium growth rate. This appears promising for increasing the quality of the tree-ring based reconstructions of climatic factors.

The final part of the work was devoted to testing the hypothesis about the possible contribution of genetic components to the variability of radial growth and its sensitivity to climatic changes. Testing was carried out on the sample of 100 trees of the Siberian larch from two sites. For this purpose, heterosis of individual trees was estimated by the proportion of heterozygous alleles in a set of 8 highly polymorphic microsatellite loci common for larch genera in the initial study, in a set of 11 new species-specific loci and in a combined set in a later study. Various characteristics of the radial growth series were tested to estimate homeostasis (growth stability) of each individual tree or a group of trees, including the mean value and variation of radial growth, its autocorrelation and strength of the common signal, growth rates of individual trees and details of climatic response. Unfortunately, most of the approaches did not reveal any significant relationships between genetic traits and the radial growth of trees. The only result confirming the hypothesis was a slightly increased climatic response of the more heterozygous tree groups probably due to their faster recovery after stress.

LIST OF PUBLISHED PAPERS

1. Babushkina EA, **Belokopytova. LV** (2014) Climatic signal in radial increment of conifers in forest steppe of Southern Siberia and its dependence on local growing conditions. *Russian Journal of Ecology*, 45(5): 325-332. doi: 10.1134/S1067413614050038

2. Babushkina EA, Vaganov EA, **Belokopytova LV**, Shishov VV, Grachev AM (2015) Competitive strength effect in the climate response of Scots pine radial growth in south-central Siberia forest-steppe. *Tree Ring Research*, 71(2): 106-117. doi: 10.3959/1536-1098-71.2.106

3. Babushkina EA, Vaganov EA, Grachev AM, Oreshkova NV, **Belokopytova LV**, Kostyakova TV, Krutovsky KV (2016) The effect of individual genetic heterozygosity on general homeostasis, heterosis and resilience in Siberian larch (*Larix sibirica* Ledeb.) using dendrochronology and microsatellite loci genotyping. *Dendrochronologia*, 38: 26-37. doi: 10.1016/j.dendro.2016.02.005

4. **Belokopytova LV**, Babushkina EA, Zhirnova DF, Panyushkina IP, Vaganov EA (Submitted) Climatic response of the conifers radial growth in the forest-steppes of South Siberia: comparison of the three approaches. *Contemporary Problems of Ecology*

Other relevant papers

5. Shah SK, Touchan R, Babushkina EA, Shishov VV, Meko DM, Abramenko OV, **Belokopytova LV**, Hordo M, Jevsenak J, Kędziora W, Kostyakova TV, Moskwa A, Oleksiak Z, Omurova G, Ovchinnikov S, Sadeghpour M, Saikia A, Sidenko T, Strantsov A, Tamkeviciute M, Tomusiak R, Tychkov I, Sewastynowicz L (2015) August-July precipitation from tree rings in forest-steppe zone of Central Siberia (Russia). *Tree Ring Research*, 71(1): 37-44. doi: 10.3959/1536-1098-71.1.37

6. Babushkina EA, **Belokopytova LV** (2015) Cambial zone is the main target of external factors influence on the conifers tree-ring formation. *Lesnoy Zhurnal* [Forestry Journal], 6: 35-45. doi: 10.17238/issn0536-1036.2015.6.35 [In Russian]

7. Babushkina EA, **Belokopytova LV**, Grachev AM, Meko DM, Vaganov EA (2017) Variation of the hydrological regime of Bele-Shira closed basin in Southern Siberia and its reflection in the radial growth of *Larix sibirica*. *Regional Environmental Change*, 17(6): 1725-1737. doi: 10.1007/s10113-017-1137-1

8. Demina AV, **Belokopytova LV**, Andreev SG, Kostyakova TV, Babushkina EA (In print) Radial growth dynamics of Scots pine (*Pinus sylvestris* L.) as an indicator of the hydrothermal regime of the Western Transbaikalia forest-steppe. *Contemporary Problems of Ecology*

9. Babushkina EA, **Belokopytova LV**, Kostyakova TV, Kokova VI (In print) Characteristics of earlywood and latewood of *Pinus sylvestris* in semiarid natural zones of South Siberia. *Russian Journal of Ecology*

PREFACE

This work was performed in the Dendroecology and Ecological Monitoring Laboratory, Khakass Technical Institute, Siberian Federal University, Abakan, Russia. In regards to the contribution to the research papers, I was responsible for processing and analysis of the dendroclimatic data and graphical representation of the results. In addition, I contributed to writing and translating the text of the manuscripts, as well as conducting them through the submission and peer-review process.

I express my gratitude, first and foremost, to my advisor, Dr Elena A. Babushkina, and SFU Rector, Professor Eugene A. Vaganov, who devoted their time to working with me for many years and constantly urged me to do my best. I would like to thank all my co-authors and colleagues from the laboratory for their useful discussions, suggestions and advice that helped to improve methodology of analysis and obtain interesting and novel results in the aforementioned papers. I also appreciated the comments of reviewers and editors that helped to make papers more clear and improve their quality.

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Chapter 1. INTRODUCTION (THEORETICAL BACKGROUND)

1.1. Tree rings as archives of information about environment and adaptation of plants to unfavorable conditions

Current climatic long-term trends of global warming do not only involve temperature increase, but also changes of water balance and frequency/severity of unfavorable events, such as droughts (Easterling et al. 2000; Rosenzweig et al. 2002, 2014; Lobell et al. 2011; Mueller, Seneviratne 2012; Porter et al. 2014; Roshydromet 2014; IPCC 2015). Its impact on terrestrial ecosystems has certain patterns on a global scale. In low and medium latitudes, warming leads to more frequent droughts and increases the vulnerability of plants to moisture shortage (IPCC 2013; Jones et al. 2016). In high latitudes with sufficient moisture level and a short vegetative season, warming intensifies growth and development of plants. Overall, geographic ranges of most plant species shift to higher latitudes (Bindi, Olesen 2011; Peltonen-Sainio et al. 2016; Wang et al. 2016). The same can be said about altitudinal transects in mountains, as they have similar climatic gradients and thus zonality of ecosystems with their warming-induced shift to the higher altitudes.

In light of global climatic change problem of growth stability and the response to environmental stress should receive special attention. Long-term changes in climate as well as its short-term fluctuations are of special concern for trees. In contrast to freely moving animals they cannot purposefully search more favorable habitat and move there. And unlike annual plants, trees have to withstand environmental stresses and changes during their lifetime as long as, for instance, 300–400 years on average and up to 750 years for Siberian larch (Vaganov et al. 2006). Other traits of trees as long-living organisms are relatively slow changes at the level of the population, which can be substantially lower than rates of climatic changes (Savolainen et al. 2004, 2007; Petit, Hampe 2006; Aitken et al. 2008; Kuparinen et al. 2010; compare with Hetem et al. 2014 study of animals). Therefore trees need to have a high level of phenotypic plasticity to adapt successfully to the changing environment.

Conifer trees, such as pine, larch and spruce, are the keystone species of boreal forest ecosystems. They can be significantly affected by global climate change and at the same time play a very important role in the mitigation of climate change effects due to their ability of mass carbon deposition (Kasischke, Stocks 2000; Soja et al. 2007; Nelson et al. 2007; Chen, Luo 2015; Gauthier et al. 2015). Conifers have a substantial adaptive capacity at the individual tree level due to high phenotypic plasticity and at the population level due to high genetic variation (Hamrick 2004; Santos-del-Blanco et al. 2013). However, mechanisms of this high adaptability at both levels are not completely understood.

It is well-known that each annual layer of wood (tree-ring) registers conditions during and before its development (Hughes, 2011). We can list some advantages of tree-rings before other proxy records of the past environments (Cook, Kairiukstis 1990; Fonti et al. 2010):

- quantitative parameters of variability;
- widespread distribution of tree species in terrestrial ecosystems;
- high temporal resolution of the record (from year down to month and even shorter time periods);

- possibility to precisely find a calendar year of each ring in a record;
- life-span of some centuries (with addition of the dead wood and samples from buildings and fossils, combined chronology can cover periods up to millennia).

The most commonly used parameter of the annual tree growth is tree-ring width (TRW), or radial growth (Fritts, 1976). In fact, TRW integrates the impact of external factors on the tree growth processes during the development of a current ring, and often during preceding months, up to the end of the previous ring development. Its measurement is relatively fast and easy, and there are classical techniques and computer programs for cross-dating and processing TRW series (e.g., Holmes, 1983; Cook, 1985; Grissino-Mayer 2001; Cook, Krusic 2005).

Long-term tree-ring chronologies can be used in different research fields: reconstruction of past climatic factors beyond instrumental and historical data (Cook et al. 2007; Touchan et al. 2007; Yang et al. 2014; DeRose et al. 2015); modeling of the growth and development processes in woody plants (Fule 2010; Vaganov et al. 2011); estimation of the health state of vegetation (Cortina et al. 2006; Laughlin, Grace 2006); prediction of the dynamics of climatic factors and forest ecosystems in future (Pan, Raynal 1995; Tessier et al. 1998; Goldblum, Rigg 2005).

Revealing an environmental signal in wood is simple when the growth and development of plants are limited by a single extreme factor. Thus, detailed data have been obtained on the effect of temperatures in the first half of the growing season at the upper and northern forest limits and of precipitation in highly arid regions (Naurzbaev et al. 2003; Briffa et al. 2004; Sidorova et al. 2007; Esper et al. 2010). However, most of forest ecosystems are located in the areas with less stressful conditions, where the effects of several factors are overlapping (Fritts 1976; Schweingruber 1996; Panyushkina et al. 2005; Moser et al. 2010; Seim et al. 2016). On the other hand, even when plant growth is limited by one factor, the analysis of its influence can be hindered by the lack of instrumental data related to this factor. This pattern is typical for arid regions, where plant growth is limited by soil moisture. However, in the absence of long series of soil moisture measurements, the analysis is usually carried out for the combination of other environmental factors that affect it in one way or another and where we have long-term instrumental data. This combination may include temperatures as a regulator of evapotranspiration, precipitation as the primary water source and / or other environmental variables related to water availability, e.g. various drought indices, discharge or water levels of close water bodies, snow depth, etc. (Pederson et al. 2001; Meko et al. 2013; Belmecheri et al. 2016; Hou et al. 2016). Anyway, to estimate significant effects of some external factors on tree growth more accurately we can compare TRW series with a difference in local conditions and / or tree species, because these differences modify climatic signal in tree growth.

The methodological apparatus of dendroecological analysis has undergone significant development during its history. The classical and most widely used analysis tool is Pearson paired correlation coefficients between tree-ring chronologies and monthly series of climatic or other factors (Pederson et al. 2001; Slimani et al. 2014; Maxwell 2016; Opala et al. 2016; Restaino et al. 2016; Cavin, Jump 2017; Rozas, Olano 2017). To take into account the impact of several factors on the tree growth, various changes and additions have been made to this method over time. For example, the averaged or summed series for longer periods (season, year, etc.) are calculated from the monthly climate data. Most often, only specific periods are chosen (Wang et al. 2016; Cai, Liu 2017; Opala et al. 2017). However, this selection of periods is not always obvious from the results of monthly series analysis, a more complete and accurate picture can be

obtained from the complete enumeration of periods with different lengths, from one month to a year or even more (Kurz-Besson et al. 2016; Tejedor et al. 2017). In the regions characterized by a combination of two interrelated limiting factors (e.g., temperature and precipitation) dendroclimatic analysis often starts from the ranking of these factors on the strength of their impact. Then the response to the secondary factor is calculated by partial correlation coefficients, i.e. taking into account the effect of the primary factor for which paired correlation coefficients are used (Meko et al. 2013; Touchan et al. 2014; Shah et al. 2015; Coulthard, Smith 2016). Recently, moving short (5-15 days) periods for averaging or summarizing of climatic factors from daily series have also been used in dendroclimatic analysis (Panyushkina et al. 2003; Babushkina et al. 2010; Liang et al. 2013; Carrer et al. 2017). Thus, one of the primary tasks in dendroclimatology is the selection of an analysis algorithm, depending on the specific purpose and the regional peculiarities of natural conditions.

1.2. Non-climatic factors of local and individual scale: contribution in the tree growth and development

Several studies have been dedicated to the problem of identifying and quantifying the influence of various non-climatic factors affecting tree-growth. Important non-climatic factors are tree age, position in the stand (competitiveness), and local conditions, such as soil and landscape. For example, it was shown that the proportion of the non-climate related variability of the tree-ring chronologies of pine and larch in the Alps is reducing with age. This leads to the reduction of noise and an increase of the TRW sensitivity to climate (Carrer, Urbinati 2004). Esper et al. (2008) noted similar influence of age on the climatic response of pine in the Alps with the same magnitude as one of the influence of local conditions. The change of the climatic response of the tree-ring width with age also was observed for pine in Spain (Dorado Linan et al. 2012).

It should be noted that the sensitivity of a tree to climatic influence depends on its size. There are data from the Alps showing that the response of spruce growth rate to rainfall in May to June depends on the trunk diameter and the height of the tree, which determine the competitiveness of trees (Schuster, Oberhuber 2013). Studies of the differences in climatic response of the trees separated into groups based on the diameter of the trunk (Campelo at al. 2013) and the class of the crown (Martin-Benito et al. 2008) also showed the dependence of the level of the individual tree adaptation to extreme precipitation and temperatures, based on these parameters of the tree size.

One may ask an obvious question of interrelations between the size and age of the tree, and which of these factors in fact contributes in the sensitivity / stability of the tree growth and development against external extremes. The rate of change of the tree size with age is called "growth rate" and "growth energy" in different sources, or serves as an estimation of the tree competitive strength (Lebedenko 1969; Nicault et al. 2010; Babushkina et al. 2015). Mathematically, growth rate can be expressed through the parameters of the function of the age trend in TRW. However, most of the studies measuring these parameters did not specifically investigate the direct influence of the growth rate on the tree climate response. Rather the aim has been to improve the methods of standardization of the chronologies used in dendroclimatological reconstructions. For example, in using regional curve standardization,

Esper et al. (2002) separated the individual age curves into two groups based on their linearity, whereas Melvin (2004) and Briffa and Melvin (2011) made a distinction between groups of fast growing and slow growing trees.

Tree growth depends on many factors in addition to regional climate, including habitat conditions. For example, recent studies performed in Siberian taiga ecosystems relate to the effects of the pattern of permafrost (Nikolaev et al. 2011), soil moisture (Velisevich, Khutornoi 2009), and landscape heterogeneity (Kuznetsova, Kozlov 2011; Tabakova et al. 2011) on treering width. Some publications are available on dendroclimatic analysis of conifers from different habitats in the forest-steppes of the Altai–Sayan mountain region (Magda, Zelenova 2002; Magda, Vaganov et al. 2006; Babushkina et al. 2010, 2011; Knorre et al. 2010). The results of these studies have confirmed that the influence of external factors on the TRW in semiarid conditions strongly depends on local habitat conditions.

A local landscape includes the form of the land surface per se (flat / slope / depression etc.), altitude, direction and steepness of the slope. On the one hand, these parameters influence the regime of insolation and thus local air temperatures and microclimate as a whole (e.g. Gruber et al. 2009; Moser et al. 2010). On the other hand, a relief defines the layout of the underground and surface waters, therefore impacting the availability of soil moisture. The next component of local conditions is the physic and chemical properties of the soil as a result of the interaction between the landscape and the living matter of the ecosystem. It can also play a substantial role in the processes of the tree adaptation to the extreme climatic fluctuations as a moisture container and a source of the necessary nutrients. Dendroecological research tends to combine it with the landscape into one complex factor if influence of soil is taken into account.

Even within the boundaries of the site with homogenous habitat conditions there are always trees with various growth rates. It is partially explained by the long-term dynamics of the competitive relationships between trees. For example, after the death of the large tree, the growth rate of its neighbors increases abruptly with a gradual decrease afterwards (Blasing et al. 1983). As forest management studies have shown, tree growth rate depends negatively on the stand density (Tappeiner et al. 1997; Franklin et al. 2009).

In addition, it should be considered that the reaction of woody plants to environmental conditions is species-specific, especially when there are more than one limiting factor (Wilson, Elling 2003; Vaganov et al 2006; Friedrichs et al. 2009). First and foremost, it is the result of inter-species genetic differences, leading to the different mechanisms of tree adaptation to extremes and thus to different intervals of their ecological plasticity. A clear example of such a pattern is the difference in the timing and intensity of the wood development processes between deciduous and evergreen conifers in the same conditions (e.g. Babushkina et al. 2010). However genetic heterogeneity is also manifested on smaller scales. Within the boundaries of one species it leads to the differences in the adaptability to various factors between ecotypes / climatypes due to the long-term processes of natural selection. However, this selection is carried out through the survival of the fittest, so the influence of a genotype is also manifested on the individual level, where trees with certain genetic combinations have better adaptability.

1.3. The concepts of individual homeostasis and heterosis as genetic reasoning of the trees adaptability to climatic factors

The concept of individual homeostasis in a heterogeneous environment as indicated by the low impact of environmental factors (temperature, precipitation, etc.) on individual development was first introduced by Cannon (1929). It was further developed into the concept of developmental homeostasis (Dobzhansky, Wallace 1953), genetic homeostasis (Lerner 1954), developmental stability (Mather 1953; Thoday 1955) and phenotypic stability (Lewis 1954). The concept was based on the observation that individuals with higher individual heterozygosity (IndHet) were characterized by a more stable growth pattern and less impacted by environmental factors, such as, for instance, temperature and precipitation (see Livshits, Kobyliansky 1985 for early review). The concept was revisited and reevaluated multiple times, but still needs additional studies and experimental data to improve our understanding of the molecular basis and genetic mechanisms underlying individual homeostasis and heterosis (for recent reviews, see Woolf, Markow 2003; Hochholdinger, Hoecker 2007; Fridman 2015; Lippman, Zamir 2007; Nicoglou 2015; Peirson 2015).

The two main hypotheses of the genetic mechanisms that may explain why individuals with higher IndHet could be less impacted by environmental factors and demonstrate higher heterosis are: (1) overdominance (see review by Hansson, Westerberg 2002), and (2) dominance, because highly heterozygous individuals by definition have lower levels of inbreeding and less inbreeding depression (e.g., David 1999; Reed et al. 2012; Gonzalez-Varo et al. 2012; Abrahamsson et al. 2013). Both these genetic mechanisms could be responsible for the stable growth of individual trees with higher IndHet and their resistance to fluctuations in the environment, i.e., homeostasis can be associated with heterosis due to either the higher fitness of heterozygotes because of dominance (when the detrimental or less favorable recessive alleles that weaken the individual adaptability in homozygotes are masked and do not affect the individual fitness in heterozygotes) and/or overdominance (when heterozygotes have higher fitness than any of homozygotes). Either case would lead to the natural selection of trees with higher IndHet, and one can expect that trees that are more resistant to (and more independent from) the environmental stress would have both a more stable development and a higher IndHet. Maladaptive seedlings and trees would occur in the population, however, as a genetic segregation load that could be a heavy price that a population would need to pay to maintain a high level of heterozygosity (Altukhov 1991). Therefore, an optimal level of IndHet is expected to be observed. Exceeding this optimal level may lead to an increase of the segregation load and thus IndHet can be regulated by selection making extremely heterozygous trees less adaptive and less stable.

In addition, several variants of certain multimeric enzymes can be formed in heterozygotes, which acting together may be more efficient than the single form of the enzyme found in homozygotes (Berger 1976). In this case, heterosis and homeostasis can be due to overdominance of heterozygotes. More heterozygous individuals are better adapted according to the theory of balancing selection in favor of heterozygotes. The mechanisms of heterosis and homeostasis are poorly understood, however, and available data are very contradictory.

Both heterosis and homeostasis have been studied in different organisms, including tree species and using different traits and genetic markers, such as allozymes (e.g., Ledig et al. 1983;

Mitton and Grant 1984; Strauss 1986; Bush et al. 1987; Strauss, Libby 1987; Zouros et al. 1988; Jelinski 1993; Gonzalez-Varo et al. 2012), microsatellites or so-called simple sequence repeats— SSRs (e.g., Abrahamsson et al. 2013; Zgaga et al. 2013), as well as single nucleotide polymorphisms – SNPs (e.g., Govindaraju et al. 2009; Chelo, Teotonio 2013). Correlation of IndHet with various physiological, morphological and biochemical traits of heterosis and homeostasis (stable development) was estimated in these studies. Traits used included bilateral asymmetry (see Livshits, Kobyliansky 1991; Parsons 1992; Leung et al. 2000 for early reviews and more recent Kurbalija et al. 2011; Weisensee 2013), growth rate (Ledig et al. 1983; Mitton, Grant 1984; Strauss 1986; Bush et al. 1987; Strauss, Libby 1987; Zouros et al. 1988; Jelinski 1993), and skeletal meristic traits (Zink et al. 1985).

In the previous genetic studies some evidence was obtained suggesting that IndHet is positively associated with heterosis – a higher viability and stronger adaptive traits were observed in hybrids obtained from crossing parents that were genetically different and distant from each other. It was expressed as higher resistance to environment change or stress, increased growth rate and biomass growth, etc. (Schnable, Swanson-Wagner 2009; Schnable, Springer 2013; Feng et al. 2015). Of course, there is interesting question – if tree ring parameters and various statistical characteristics of their series can be used in research of heterosis and homeostasis.

1.4. Dendroecological researches in the forest-steppes of Minusinsk depression

Necessity of the dendroecological research throughout the territory of the Asian part of Russia was substantiated in the end of the 20th century (Shiyatov, Vaganov 1998). The first studies of the TRW and cell anatomical parameters of pine and larch in the South of Central Siberia were carried out by Vaganov (1990) with application of Vaganov-Shashkin imitation model (Vaganov et al. 2006, 2011). It was shown that in forest-steppe zone growth of conifer tree rings have strong reactions to the soil moisture seasonal variation. Soil moisture in its turn depends on temperature and precipitation not only during a vegetative season, but also in the period from the previous autumn, when initial water supply is formed for the beginning of growth.

Dendroclimatic research in Khakassia and adjacent areas was continued by Magda and co-authors (Magda, Zelenova 2002; Magda, Vaganov et al. 2006; Magda et al. 2011). They confirmed complex and relatively weak response to temperature and precipitation of conifers in steppes, flatland and mountain forest-steppes in comparison to the timberline of Altai-Sayan mountain region. A negative reaction of the pine and larch TRW to temperature was observed in May-June of the current year and previous August-September. The response of TRW to the precipitation is positive and strongest for similar time periods. It was shown that the climatic response of conifer growth is less stable in mountain forest-steppes, and its strength fluctuates in synchronicity with air temperatures of a warm season.

Knorre et al. (2010) further analyzed how climatic changes were reflected in the tree-ring chronologies of Siberian larch in Shira district of Khakassia. They investigated a wide set of the wood structure parameters: tree-ring width, earlywood and latewood widths, maximal density, mean density of earlywood and latewood, and the concentration of δ^{13} C and δ^{18} O isotopes in

wood as a whole and in cellulose, in particular. It was found that all parameters have complex climatic response and depend on both temperature and precipitation.

In 2008, dendroecological studies in the Minusinsk depression were started by Babushkina with co-authors (Babushkina et al. 2010, 2011). The first dendrochronological station was established in the forest-steppe zone of the Shira district. It included two habitats with contrasting landscapes and soil moisture regimes: 1) steep southern slope; 2) the bottom of a slope with a creek. Studies on Scots pine, Siberian larch, and Siberian spruce TRW and cell parameters at this station have shown that they depend on precipitation and temperature in the first half of the growing season, but the effect of these factors is species-specific and strongly differs depending on local conditions. The investigation of the cell anatomical structure allowed specifying the periods of climatic impact on the tree ring formation, and offering some hypotheses about the interrelations between cell parameters, and internal and external factors. These studies were expanded in 2012, when Dendroecology and Ecological Monitoring Laboratory was organized at Khakass Technical Institute, Siberian Federal University. There were about 20 sites established in the study area. The main field of research in the laboratory is investigating climatic response in TRW and anatomical cell structure of wood (Babushkina, Belokopytova 2015; Shah et al. 2015; Fonti, Babushkina 2016) and its dependence on other factors (Babushkina, Belokopytova 2014; Babushkina et al. 2015, 2016, In print). In addition, there are other research projects in adjacent fields being performed by the laboratory team. For example, it was revealed that the water level of the Lake Shira changes (annual differences) are recorded in the regional chronology of Siberian larch TRW, obtained within Bele-Shira closed basin (Babushkina et al. 2017). Pine and larch TRW chronologies were also compared with the yield of the main crops (wheat, barley and crops) in Khakassia, and TRW-based estimation of crops yield was constructed for the most of agricultural development period in the region (unpublished). Some of results obtained in the Dendroecology and Ecological Monitoring Laboratory are presented in this work.

1.5. Study aim and objectives

The primary aim of this study is the investigation of the factors determining the differences between trees on the individual and local scales, and their impact on the radial growth and structure of wood, and on their reaction to climatic conditions. Within the framework of this aim, the tasks were set to research the following relationships:

- 1) climatic response of TRW and its dependence on the local landscape-soil complex;
- 2) dependence of the TRW climatic response on the individual growth rate;

3) relationships of IndHet with individual growth rates, statistical characteristics of individual TRW series and climatic response of the tree radial growth.

Scots pine (*Pinus sylvestris* L.) and Siberian larch (*Larix sibirica* Ledeb.) were used as typical representatives of deciduous and evergreen conifers, so we could compare their mechanisms of adaptation to the extremal conditions. The forest-steppe zone of the Minusinsk depression was chosen as a study area due to the following reasons: significant response of the tree growth to temperatures and precipitation; a substantial contribution of the non-climatic variation in the tree growth induced by local and individual factors; widespread and overlapping distributions of larch and pine as forest-forming conifer species.

To estimate IndHet as a measure of the heterosis level, we used genome wide genetic markers: random (and, therefore, likely intergenic) microsatellite loci (SSRs). Microsatellite loci were chosen because they are highly informative and relatively inexpensive for measuring genome-wide individual heterozygosity (but see Väli et al. 2008). They have a high mutation rate, high levels of polymorphism, a relatively uniform distribution across the genome, broad representation, and are relatively simple to detect and to genotype (e.g., Schlötterer 2000). Using tree ring data to estimate stability and homeostasis in comparison with genetic traits was proposed in this study for the first time.

Chapter 2. MATERIALS AND METHODS

2.1. Study area

The Minusinsk Depression is situated in the South of the Central Siberia, in the middle reaches of Yenisei river. Minusinsk Depression is a wide valley open towards the North and surrounded by ranges of the Altai-Sayan mountain system from other three sides: Kuznetsk Alatau from the West, Western Sayan from the South, and Eastern Sayan from the East. Altitudes in the plains of the valley are 200-700 m a.s.l. (including foothills). Region is situated in the middle of continent far from the ocean, but has broad Yenisei River with its two reservoirs (Chlebovich, Bufal 1976). Climate is moderately cold continental (Fig. 1a-c) with considerable seasonal and daily variations of temperature (Alisov 1956; Grigoryev, Budyko 1960). The temperature during warm season on plains increases along a latitudinal gradient from North to South. The precipitation decreases along the altitudes from the mountain ranges towards the bottom of valley.



climatic diagram of the Shira (a), Minusinsk (b), and Tashtyp (c) stations; comparison of the summer precipitation sum (d) and the summer mean temperature (e) time series from different datasets: geographic grid data for the areas of BER and EFR sites, and data from the closest to these sites Shira station

The average annual temperature on plains is about $0...+1^{\circ}$ C. In spring rapidly increasing temperature has high daily variation (15°C and more). It causes delay of the frost-free period about 30-35 days after date of mean daily temperature crossing +5°C threshold (end of May and end of April respectively). As a result spring frosts often inhibit plant growth. The period of temperatures above +10°C start around mid May and lasts 110-120 days. Maximal temperatures are observed in July (mean daily temperature is up to +30°C). Winter starts in the end of October – beginning of November and characterizes by temperature inversion, i.e. temperatures in the bottom of valley are 4-5°C lower than in mountains (Nikolskaya 1968). The period of negative temperatures lasts 170-190 days.

The average annual amount of precipitation is 300-350 mm. Precipitation has pronounced maximum in July (70 \pm 30 mm) whereas winter precipitation is scarce with minimum in February (7 \pm 5 mm). Typical snow depth in the end of winter is about 20 sm in steppes. Its interannual variation is very high, for monthly data it attains 45-57% of mean value in summer and 56-90% of mean value in winter. The first half of the growing season is characterized by more pronounced deficit of precipitation than second half. Main reason of precipitation shortage in the Minusinsk Depression is its location in the rain-shadow of western mountain ranges (Lysanova 2000). Due to this fact and spatio-temporally uneven precipitation the drought indices on the plains are unstable with temporal variation from sub-humid to arid conditions. It should be noted that the regional climate fluctuations are characterized by the typical continental counter course of temperature and precipitation during the warm season (Table 1), i.e. the alternation of contrasting hot dry and cool wet years (Bazhenova, Tyumentseva 2010).

Station		Month										
Station	Ι	II	III	IV	V	VI	VII	VIII	IX	Х	XI	XII
Shira	-0.19	-0.07	0.10	-0.22*	-0.27	-0.22	-0.32	-0.26	-0.41	-0.32	-0.19	-0.16
Minusinsk	-0.11	-0.02	-0.04	-0.05	-0.24	-0.24	-0.41	-0.22	-0.28	-0.02	-0.23	-0.03
Tashtyp	-0.02	0.24	0.05	-0.13	-0.23	-0.31	-0.33	-0.28	-0.28	-0.13	0.01	0.25

Table 1. Correlation coefficients between mean temperatures and precipitation

^{*} Correlation coefficients significant on the level p < 0.05 are bold

In this study monthly data of average air temperature and total amount of precipitation from Shira (1937–2012, 54°30' N 89°56' E), Minusinsk (1936-2012, 53°41' N 91°40' E), and Tashtyp (1936-2012, 52°48' N 89°53' E) meteorological stations were procured and analyzed (Fig. 1a-c). For estimation of the moisture regime Selyaninov Hydrothermal Coefficient (HTC, Selyaninov 1958) was computed from May to August on the base of temperature and precipitation data. Additionally temperature, precipitation (Fig. 1de) and Palmer Drought Severity Index (PDSI, Palmer 1965) were obtained from open monthly Climatic Research Unit (CRU) database (1901-2014, Harris et al. 2014; van der Schrier et al. 2013) for areas of the two sampling sites.

Regional hydrographic network is also uneven. Most of the water bodies are concentrated in the mountain part of territory; northern half of Minusinsk Depression has the least density of hydrographic network, it includes some closed basins of lakes with both salt and fresh water. Water bodies are mainly fed by underground and surface inflow, thus their discharge depends on climatic conditions. Most of the rivers including the second largest Abakan River belong to the Yenisei basin. There are two large reservoirs on the Yenisei River: Sayano-Shushenskoe reservoir to the South, and Krasnoyarsk Reservoir partially within boundaries of the valley. In the southern part of valley large rivers and their many tributaries form the base of developed irrigational network (Territorial planning scheme 2015).

Vertical differentiation of soil and vegetation is clearly manifested in the study area (Kuminova 1982; Chytry et al. 2008). Bottom of the valley is represented for the most part by steppes on chernozems in the North, and on chestnut soils in the South. Forest-steppes on dark gray soils are situated primarily in the foothills of mountain ranges. The most widespread conifer species in the forest-steppes are Scots pine and Siberian larch, with small amount of Siberian spruce by water bodies. There are also dry forest areas on the sandy soils in the East-South of the Minusinsk Depression, mainly confined to the hydrological objects. Conifers there are represented primarily by Scots pine. The main foliage tree species of forest-steppes belt and dry forests are silver birch and common aspen, with basket willow by water bodies. The higher parts of the mountain slopes are covered by taiga forest with wider variety of conifers, including Siberian pine and Siberian fir besides aforementioned species.

2.2. Measurement and processing of tree-ring width

The tree samples (cores) from healthy living trees of Scots pine (*Pinus sylvestris* – PS) and Siberian larch (*Larix sibirica* – LS) were collected during 2008-2014. Sites were chosen in the forest-steppes of the Batenevsky and Abakansky Ridges foothills (Kuznetsky Alatau), and in the insular dry forests in steppes near Yenisei. Information about sites used in this study is shown in the Table 2.

SiteCoord.Site descriptionYearSp.Publ.*Efremkino $54^{\circ}29^{\circ}$ NSteep western slope, light grass-herb larch forest, mountain gray forest soil2014LS3Berenzhak $54^{\circ}24^{\circ}$ NMedium southeastern slope, grass-herb larch forest with pine and birch, mountain gray forest soil2014LS3Berenzhak 1 (BER) $89^{\circ}57^{\circ}$ Ewith pine and birch, mountain gray forest soil2014LS3Berenzhak 1 (BER1) $54^{\circ}20^{\circ}$ NSteep southern slope, grass-herb pine-larch forest with birch, mountain gray forest soil2008LS1Berenzhak 2 (BER2) $89^{\circ}44^{\circ}$ EFloodplain, sedge-moss streamside spruce forest with larch and birch, meadow chernozem soil2008LS1Bidgha $54^{\circ}00^{\circ}$ NMedium southern slope, grass-herb pine-larch forest, with larch and birch, meadow chernozem soil2012PS4Minor Minusa (MIN) $53^{\circ}45^{\circ}$ NAeolian-humus chernozem soil2012-2013PS1-2Taraska (SCH) $91^{\circ}56^{\circ}$ ESteep southern slope, grass-herb birch-pine forest, aeolian-humus chernozem soil2012-2013PS1-2Zeleniy Shum (SCH) $53^{\circ}37^{\circ}$ NFlatland near Yenisei, grass-herb birch-pine forest, aeolian-humus chernozem soil2012-2013PS2Minor Nichka (NIC) $53^{\circ}37^{\circ}$ NFlatland adjacent to swamp, herb pine forest, aeolian-humus chernozem soil2012-2013PS2Minor Nichka (NIC) $53^{\circ}37^{\circ}$ NFlatland adjacent to swam											
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	(KAZ)	90°05' E	rocky mountain gray forest soil	2013-2014	LS	+					

 Table 2. Sampling sites

* No. of paper in this study

Sampling, transport and preprocessing of cores for the TRW measurement were determined by standard techniques accepted in dendrochronology (Cook, Kairiukstis 1990). Measurements of TRW were performed on semiautomatic measuring system LINTAB 5 with specialized software package TSAP Win (accuracy 0.01 mm) (Rinn, 2011). Dating of samples (definition of the calendar year of each ring) was confirmed by the cross-correlation analysis in the specialized program COFECHA (Holmes 1983). During the standardization of individual chronologies in the first stage age trend was removed, to describe age trend A negative exponential and linear functions were used:

$$A(t) = a \cdot e^{-b \cdot (t+p)} + d, \tag{1}$$

$$A(t) = c \cdot (t+p) + d, \qquad (2)$$

where t – age of tree estimated from individual series, a, b, c, d – numeric parameters of the functions, identified separately for each individual series to fit age trend into them; p – pith offset to account for missing inner rings, which is estimated from the curvature and width of the innermost rings of core (Duncan 1989; Esper et al. 2009). Other approach to standardization in this study was estimation of the age trend by cubic smoothing spline having the length equal to 67% of the length of the series (Cook and Peters 1981).

Measured ring widths were then divided by the value of the fitted spline curve to obtain dimensionless indices. Indexed series after the first stage of standardization are called "standard" (*std*). In the second stage of standardization autocorrelation dependence of the first order was removed, and "residual" (*res*) series obtained as a result. Both *std* and *res* individual TRW indices were averaged by bi-weight robust mean to obtain generalized chronologies (Cook, Kairiukstis 1990). Standardization procedure was performed by specialized program ARSTAN (Cook, Krusic 2005).

2.3. Genotyping with nuclear microsatellite loci

Samples of the needles (100 to 200 mg per tree) were collected from the same trees as cores and used as material for genotyping. To estimate genetic polymorphism of the larch population and individual tree heterozygosity, we used 19 best performing and the most polymorphic nuclear microsatellite loci (SSRs), first 8 of which were previously developed for Japanese larch (L. kaempferi Sarg.) – loci bcLK, alpine larch (L. lyallii Parl.) and western larch (L. occidentalis Nutt.) - loci UAKly and UBCLX, and then adapted for the Siberian larch (Oreshkova et al. 2013). Later 11 new loci were developed specifically for Siberian Larch by Krutovsky KV and his colleagues (in the framework of RFBR 14-04-01462 project) and used as the second set. The characteristics of all these markers and the PCR conditions of their amplification are presented in Table 3. Individual samples of the total DNA were extracted from needles. These extractions were performed according to the standard protocol for plant tissues using cetyltrimethylammonium bromide, CTAB (Devey et al. 1996). The fragment analysis and sizing of the amplified individual alleles of the microsatellite loci and their genotyping were done using 6% polyacrylamide gel electrophoresis (PAGE) in Tris-EDTA-borate electrode buffer. Polymorphism of new loci was analyzed using capillary electrophoresis on the sequencer ABI PRISM 3730. Gels were stained in ethidium bromide solution and visualized using the

system of gel documentation. The fragment lengths were determined by comparison with the standard DNA ladder (plasmid pB*R*322 DNA digested by the HpaII restriction enzyme) using the Photo-Capt software. To more precisely determine the lengths of the PCR fragments (microsatellite alleles) multiple comparisons of variants of each locus were performed by running them on the same gel. Genotyping of the new loci was carried out with the help of the GeneMapper program. Genetic diversity parameters were estimated using the GenAlEx 6.41 software (Peakall, Smouse 2006). Individual heterozygosity was calculated as ratio of heterozygous loci number to the total number of loci used for each particular study.

Loope	Locus Motif		Number of	Fragment
Locus			alleles	size, bp
	First	set		
bcLK056	(AG) ₂₀		10	140-200
bcLK066	(TG) ₁₂	Tauahdaum	4	140-172
bcLK224	(AG) ₁₇	63 53°C	4	130-168
bcLK260	(TG) ₁₄ (AG) ₉	05-55 C	5	80-126
bcLK232	(AG) ₁₉		4	135-178
bcLK235	(TC)9(AC)2AG(AC)14		15	168-220
UBCLXtet-1-22	(TATC)9(TA)12	58°C	3	175-250
UAKLly6	UAKLly6 (GT) ₁₇		9	212-264
	Second	l set		
Ls_1106920_AG	(AG) ₂₁		18	145-263
Ls_796783_CT	(CT) ₂₁		13	151-177
Ls_955052_CT	(CT) ₂₁		20	225-347
Ls_19333_TC	(TC) ₂₀		13	223-255
Ls_440296_TC	(TC) ₂₀	Touchdown	13	169-243
Ls_621673_TC	(TC) ₂₃	fouchdown	16	184-218
Ls_1089834_AG	1089834_AG (AG) ₂₁		26	187-235
Ls_1274831_CT	(CT) ₂₀		14	203-229
Ls_66831_CA	(CA) ₂₁		14	207-231
Ls_915025_AT	(AT) ₂₁		16	132-186
Ls_12590_TG	(TG) ₂₄		23	151-201

2.4. Statistical analysis

Following statistical characteristics were used for tree-ring series and chronologies:

- mean value (*mean*);
- minimal / maximal values (*min / max*);
- standard deviation (*stdev*)
- variation coefficient (*var* = *mean* / *stdev*);
- coefficient of sensitivity (sens = mean $(2 \cdot |X_t X_{t-1}| / (X_t + X_{t-1})))$

(Shiyatov 1986);

- expressed population signal (*EPS*) (Wigley et al. 1984);
- individual (for one series) or average (for generalized chronology) inter-series correlation coefficient (*rbar*) (Cook 1985);

- signal-to-noise ratio ($SNR = N \cdot rbar/(1 rbar)$) (Cook, Kairiukstis 1990);
- average coefficient of series correlation with generalized chronology (*R*);

• individual (for one series with generalized chronology) or average (for all series in chronology) synchronicity (*S*) (Huber 1943; Shiyatov 1986);

• first-order autocorrelation (*ar*-1).

Correlation analysis was performed using paired and partial Pearson correlation coefficients between considered series (Pearson 1895; Wilks 1995; Meko et al. 2011). Reason of the partial correlations using is the significant interrelations between climatic factors (Lavergne et al. 2015). In practice, to calculate the partial correlation coefficient $r_{x_2,x_3|x_1}$ between the variables x_2 and x_3 , taking into account the influence of the variable x_1 , simple linear regressions $x_2(x_1)$ and $x_3(x_1)$ are calculated, and then paired correlations of their residuals, i.e. the results of subtracting the regression function from the original variable (Mardia et al. 1979). In dendroclimatic analysis, the variable x_1 is the primary climatic factor, x_2 is the secondary climatic factor, and x_3 is the TRW chronology.

In order to select groups of trees with similar growth rate or other characteristics of TRW series, two types of cluster analysis were used: 1) hierarchical classification with complete linkage as linkage criteria and Euclidean distance as metric; 2) method of K-means with different cluster numbers (Wilmking et al. 2004, 2005). Factor analysis was carried out for TRW series statistical characteristics to obtain lesser number of significant individual tree traits.

Calculations and analysis were performed with software COFECHA, ARSTAN, Seascorr (Meko et al. 2011), STATISTICA (Hill, Lewicki 2007) and Microsoft Excel.

Chapter 3. RADIAL GROWTH OF CONIFERS IN THE SEMIARID CONDITIONS AND ITS CLIMATIC RESPONSE

3.1. Influence of climate on the TRW of pine and larch in the forest-steppe

To evaluate climatic response of the conifers radial growth, *res* chronologies of Scots pine and Siberian larch from two sites were chosen: BID and KAZ (Table 2, Fig. 2). Both sites have similar local conditions. Statistical characteristics of raw and *res* chronologies for 1936-2012 (period of instrumental climatic data) are shown in the Table 4. All statistical characteristics of chronologies are high enough for use in dendroclimatic analysis. The *mean* TRW is 1-1.7 mm with the lowest value for KAZ PS. The same chronology has the smallest *stdev* and autocorrelation. Chronologies are more sensitive on KAZ than on BID site. Within each site correlations between chronologies of different species are r = 0.66-0.67 over the same period, between sites but for within same species r = 0.28-0.45 (p < 0.01). The smallest similarity (r = 0.17, p = 0.096) is observed between BID PS and KAZ LS.



Fig. 2. The TRW chronologies of conifers and their sample depth

Characteristics	KAZ LS	KAZ PS	BID LS	BID PS
N	20	21	16	15
	raw chr	onologies		
<i>mean</i> , mm	1.632	1.061	1.593	1.696
stdev, mm	0.809	0.418	0.678	0.598
<i>ar</i> -1	0.531	0.295	0.722	0.685
	res chro	onologies		
stdev	0.467	0.353	0.239	0.252
rbar	0.712	0.589	0.526	0.606
EPS	0.948	0.959	0.918	0.946
sens	0.514	0.447	0.295	0.308

 Table 4. Statistical characteristics of the chronologies

In the forest-steppe, the main limiting factor for tree growth is soil moisture (Fritts 1976). However, the absence of long instrumental data leads to the need to assess moisture indirectly, through environmental factors that determine its dynamics. A frequently used variant of this combination of factors is the average air temperature and the total amount of precipitation. The joint use of the three discussed approaches to dendroclimatic analysis allowed us to consider how in the forest-steppes of the South Siberia the conifers radial growth is regulated by temperature and precipitation variation during different seasons (Andreev et al. 2001; Agafonov, Kukarskih 2008; Magda et al. 2011).

Classical approach to dendroclimatic analysis showed the following results (Fig. 3). Typical for semiarid regions combination of a positive response to precipitation and a negative response to temperature is observed for previous July-September and current April-June at the KAZ site, at the BID site it is ending in July. For the month when a stable snow cover is formed (November), there is a slight positive effect of both temperatures and precipitation on the larch growth, but the level of significance of these correlation coefficients is at the limit $p \approx 0.05$. However, only the precipitation of this period is significant for the pine growth.

Insufficient moisture leads to a positive response of growth to the precipitation, as the main source of water, during the entire growing season. After the end of vegetation as the temperature decreases, precipitation accumulates in the soil. Later it forms a snow cover, which serves as protection from freezing for soil and as additional moisture accumulator that slows the soil drying in the spring (Vaganov et al. 1999). The least influence is exerted by the precipitation in the second half of the cold season, when its amount is minimal (in January-March, an average precipitation amount is less than 10 mm/month), and the snow cover is already formed.

The negative influence of the temperature in the growing season is determined by the fact that it regulates potential evapotranspiration, i.e. the rate of moisture loss from soil and plants (Fritts 1976; Rossi et al. 2008b; Bjorklund et al. 2017). In June-July, when temperatures reach a maximum, its impact on plants can also be exacerbated by the occurrence of heat stress. In March-April, the temperature increase sufficient for trees to leave the resting phase can be replaced by spring frosts, which leads to tissue damage and growth inhibition (Schulze et al. 2005).



Fig. 3. Paired correlations of TRW chronologies with monthly temperatures and precipitation Months of the previous year are marked with asterisk (*)

When using in the classical approach periods of the climatic factors generalization of 2-12 months (Fig. 4), very similar patterns are noticeable for both species, but sufficient differences between sites. On the BID site, the negative growth response to the temperature is most clearly pronounced in the April-July or April-August of the current year, August-September and August-December of the previous year. The response to precipitation has a pronounced maximum for the annual period August-July. But adjacent period July-June has almost the same intensity, i.e. we can speak about July-July period of the precipitation influence. At the KAZ site, the reaction to the temperature is weaker, the maxima are observed in previous August-September and current May-June or May-July. On the contrary, the response on precipitation is more pronounced with maxima for the July-June and February-June periods.



Fig. 4. Paired correlations of TRW chronologies with temperatures and precipitation for periods with length of 2-12 months

Length of period is showed on the vertical axis, last month of period is showed on the horizontal axis. Months of the previous year are marked with asterisk (*). Values of correlation coefficients exceeding 0.214 are significant on level p < 0.05



Fig. 5. Seascorr analysis of TRW chronologies with precipitation (primary factor) and temperatures (secondary factor) for periods with length of 1, 4, 8, and 12 months Last month of period is showed on the horizontal axis. Months of the previous year are marked with asterisk (*). Correlations significant on levels *p* < 0.05 and *p* < 0.01 are marked with light and dark shades respectively</p>

Seacorr analysis was used to take into account possible interactions between temperature and precipitation (Meko et al. 2011). Precipitation has been selected as primary climatic factor, since in the study area it has more pronounced and persistent effect on the growth of conifers. Calculations of the climatic response for periods of different lengths have shown that in both regions the response to temperature is the most pronounced for the period of 4 months, and the response to precipitation is the most pronounced for the period of 12 months (Fig. 5). The pattern of the response to precipitation almost completely coincides with the results of the classical approach, since Seascorr calculates paired correlation coefficients for the main factor. The use of partial correlation coefficients for response on temperature leads to decreasing of correlation values and a smaller number of significant relationships.

An approach using 15-day moving climatic series provides a more accurate determination of the time limits of the positive and negative effects of temperature and precipitation on the conifers radial growth (Fig. 6). For example, for KAZ larch precipitation is important from April and almost until the end of June. Negative influence by high temperatures is exerted from the end of April to June inclusive, with the most pronounced correlations in May and the first half of June. For the growth of pine in the same area precipitation effect is the most significant from mid-May to June inclusive, in April and the first half of May it is less pronounced. In the negative influence of temperatures, two small intervals in the first decade of May and the first decade of June are allocated, when it is maximal.

For larch at the BID site, the highest temperature influence is in the middle of April and the end of June, and the positive influence of precipitation is evident from mid-May to mid-July. For pine at this site three separate intervals (second half of April, the third decade of May – the first decade of June and the middle of July) are distinguished during which the positive influence of precipitation and the negative influence of temperature are most pronounced, while in the climatic response of larch these three intervals are observed only for the influence of temperatures. At both sites, the periods of significant influence of climatic factors on growth finish for larch earlier on about 5-10 days than for pine, at the same time at the KAZ site this moment arrives more than two decades earlier than at the BID site.



Fig. 6. Paired correlations of TRW chronologies with moving series of temperatures and precipitation (window 15 days, step 1 day) for the current and previous vegetative periods Months of the previous year are marked with asterisk (*). Cold period is not shown

Comparison of the results obtained using different approaches showed the following. The classical correlation analysis of the monthly climatic series allows to identify and evaluate the significance of the growth response to the monthly climatic series. Thereby, it can be used for a preliminary assessment of the factors that are significant for the tree growth. However, the complex structure of the climatic response leads to the fact that each individual factor determines a small fraction of the growth variability, which often implies low correlation coefficients. Therefore, the next step is to generalize the climatic series throughout the time intervals for which their influence is of the same type. This generalization integrates the climatic influence throughout all season or even year, which leads to the identification of the most pronounced relationships and to the lessening of interspecies differences in the climatic response caused by the discrepancy in the timing of the pine and larch phenophases. On the other hand, differences between sites persist, since the natural-climatic conditions themselves differ. For example, the shift in the main annual period of precipitation influence and the spring-summer period of temperature influence is related to the later end of the annual ring formation at the BID site, where higher summer temperatures are observed.

The rationale for applying the second approach – the use of partial correlation coefficients - is the presence in the region of significant negative correlations between temperatures and precipitation, as well as their divergent influence on the soil moisture dynamics. The results of Seascorr analysis showed that the effect of temperature and precipitation on conifers growth is indeed interrelated, since the partial temperature correlations with growth are lower than the paired ones. Nevertheless, the presence of significant partial temperature-growth correlations indicates that the climatic response of trees in the forest-steppe zone cannot be described solely by the influence of precipitation, in contrast to the extremely dry regions such as the Southwest USA (Meko et al. 2013). In this respect, the forest-steppes of the South Siberia can be compared with the semiarid Mediterranean regions, where the growth of woody plants is also under the divergent influence of precipitation and temperatures, although in other seasonal intervals (e.g., Touchan et al. 2016). The main advantage of this approach is the identification of the most critical limiting factor and the interval of its maximal impact. In the study area it is the annual July-June (KAZ) or August-July (BID) precipitation. Thereby, Seascorr analysis is most applicable in such a direction as the long-term reconstruction of climatic and other environmental factors (e.g., Meko et al. 2013; Touchan et al. 2014, 2016; Shah et al. 2015; Coulthard, Smith 2016). However, this approach does not allow for a more detailed time analysis of the climate response.

More detailed results are obtained by using the third approach – the use of climatic series calculated for moving 15-day periods with step of 1 day (Vaganov et al. 1999; Panyushkina et al. 2003; Babushkina et al. 2010; Carrer et al. 2017). It is more often used to analyze the climatic response of the tree-ring structure, e.g., of the histometric parameters or maximal density. This is due to the fact that such parameters are formed in a relatively short period of time. Nevertheless, this approach is also applicable to dendroclimatic analysis of radial growth. There is no doubt that the seasonal growth of trees is not confined to the calendar, and monthly climate data may not correspond to the actual beginning or end of the growth season. In addition, the species-specific nature of the climatic response and its dependence on the local growth conditions and climatic gradients are evident (Friedrichs et al. 2009; Velisevich, Khutorornoy 2009; Kuznetsova, Kozlov 2011). The significant difference between KAZ and BID sites can be caused

by higher summer temperatures and less precipitation at the BID site, while the main cause of interspecies differences in the details of the climate response is the physiological characteristics of evergreen (pine) and deciduous (larch) conifers. Therefore, the third approach helps to identify the periods of significance of the climatic factors influence, not necessarily tied to monthly series. That is, its use allows to more accurately specify those critical periods of the season, when the influence of climatic factors is most significant for the seasonal growth of theerings.

Thus, the third approach, in spite of its limitation on the availability of daily climate data, can be useful for such research fields as the physiology of plant growth and development. This is especially important for regions with a high diversity of terrain, climate and natural areas, where local differences lead to a significant spatial variation in the climatic response of plants. It is also notable that this approach seems very promising in analyzing the changes in dates and intensity of seasonal growth of woody plants in the case of regional climate changes. This is confirmed by a number of studies in which such directed changes in the timing of the beginning of the vegetative season are revealed in the growth of tree-rings, in phenology of woody plants or in remote data (Bunn et al. 2013; Yang et al. 2017).

3.2. Habitat-induced differences in the TRW chronologies of pine and larch and its climatic response

For the comparison of different local conditions two pairs of sites were investigated, where each pair consists of two close habitats with same tree species available but contrasting soil moisture content: steep slope and floodplain at its base with close water stream. We investigated four raw (before standardization) and *res* local chronologies (Fig. 7ab): two for larch on the sites BER1 (slope – LS1) and BER2 (floodplain – LS2), and two for pine on the sites TAR (slope – PS1) and MIN (floodplain –PS2). Approximate gradient of the soil moisture estimated from the landscape, soil and vegetation cover (Table 2) is shown on the Fig. 7c.

Analysis of the chronologies statistical parameters has shown that the radial growth of both species is hither in habitats with higher soil moisture, as follows from both maximum and average TRW values (Table 5). Thus, the significance of this factor for the processes of wood formation is obvious. Tree rings in pine are wider than in larch, which is explained by younger age of pine trees and by longer period of xylem formation for pine as evergreen conifer (see Babushkina et al. 2010). Higher standard deviations and variation coefficients recorded in floodplain sites are indicative of a wider range of variation in TRW, but the effect of external factors is stronger on the slopes (were the coefficient of sensitivity is higher); i.e., variation in the floodplain is mainly caused by internal and phytocenotic factors. Coefficients of correlation of individual chronologies with the local chronology, signal-to-noise ratio, and expressed population signal are traditionally used to reveal the presence of an external signal and determine if a chronology is suitable for dendrochronological research (Cook 1985). In our case, the values of all these parameters are sufficiently high for both raw and *res* chronologies.



Fig. 7. Pine and larch radial growth in the contrasting local conditions Local raw (a) and *res* (b) TRW chronologies (vertical grid step is 1 mm for raw and 1 for *res*; chronologies are shown with vertical shift, and zero values are indicated for each one); scheme of the soil moisture gradient (c)

CharacteristicLS1LS2PS1PS2Duration, years27216589105Period, years1737-20081844-20081924-20121911-2012Number of trees14101217Total number of tree rings213813317931319raw chronologiesmin, mm0.1300.1690.8501.216max, mm1.8302.8804.8756.349mean, mm0.7210.7812.0763.252stdev, mm0.3300.4760.7691.372var0.4580.6100.3700.422sens0.2960.2340.2020.169R0.7270.7130.6490.698SNR20.458.925.6712.64EPS0.9530.8990.8500.927res chronologiesres chronologies12.64EPS0.9530.2840.198SNR20.458.925.67Stdev0.2810.2280.198SNR0.3250.2520.228R0.7390.6340.704SNR14.084.9810.93SNR14.084.9810.93SNR14.084.9810.93SNR14.084.9810.93SNR14.084.9810.93SNR14.084.9810.93SNR14.084.9810.93SNR14.08 </th <th></th> <th></th> <th></th> <th>e</th> <th></th>				e	
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Period, years1737-20081844-20081924-20121911-2012Number of trees14101217Total number of tree rings213813317931319raw chronologiesmin, mm0.1300.1690.8501.216max, mm1.8302.8804.8756.349mean, mm0.7210.7812.0763.252stdev, mm0.3300.4760.7691.372var0.4580.6100.3700.422sens0.2960.2340.2020.169R0.7270.7130.6490.698SNR20.458.925.6712.64EPS0.9530.8990.8500.927res chronologiesres chronologies0.3250.2280.229R0.2810.2280.1980.374SNR14.084.9810.9310.65EPS0.9340.8330.9160.914	Duration, years	272	165	89	105
Number of trees14101217Total number of tree rings213813317931319raw chronologiesmin, mm0.1300.1690.8501.216max, mm1.8302.8804.8756.349mean, mm0.7210.7812.0763.252stdev, mm0.3300.4760.7691.372var0.4580.6100.3700.422sens0.2960.2340.2020.169R0.7270.7130.6490.698SNR20.458.925.6712.64EPS0.9530.8990.8500.927res chronologiessens0.3250.2280.198 \mathcal{SNR} 20.458.925.6712.64EPS0.9530.8990.8500.927res chronologies \mathcal{R} 0.7390.6340.7040.630SNR14.084.9810.9310.65EPS0.9340.8330.9160.914	Period, years	1737-2008	1844-2008	1924-2012	1911-2012
Total number of tree rings 2138 1331 793 1319 raw chronologiesmin, mm 0.130 0.169 0.850 1.216 max, mm 1.830 2.880 4.875 6.349 mean, mm 0.721 0.781 2.076 3.252 stdev, mm 0.330 0.476 0.769 1.372 var 0.458 0.610 0.370 0.422 sens 0.296 0.234 0.202 0.169 R 0.727 0.713 0.649 0.698 SNR 20.45 8.92 5.67 12.64 EPS 0.953 0.899 0.850 0.927 res chronologiessens 0.325 0.228 0.198 0.374 SNR 20.41 0.228 0.198 0.374 SNR 0.325 0.228 0.198 0.374 SNR 0.325 0.228 0.198 0.374 SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914	Number of trees	14	10	12	17
raw chronologiesmin, mm0.1300.1690.8501.216max, mm1.8302.8804.8756.349mean, mm0.7210.7812.0763.252stdev, mm0.3300.4760.7691.372var0.4580.6100.3700.422sens0.2960.2340.2020.169R0.7270.7130.6490.698SNR20.458.925.6712.64EPS0.9530.8990.8500.927res chronologiessens0.3250.2520.2280.229R0.7390.6340.7040.630SNR14.084.9810.9310.65EPS0.9340.8330.9160.914	Total number of tree rings	2138	1331	793	1319
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mean, mm 0.721 0.781 2.076 3.252 stdev, mm 0.330 0.476 0.769 1.372 var 0.458 0.610 0.370 0.422 sens 0.296 0.234 0.202 0.169 R 0.727 0.713 0.649 0.698 SNR 20.45 8.92 5.67 12.64 EPS 0.953 0.899 0.850 0.927 res chronologiesstdev 0.281 0.228 0.198 0.374 sens 0.325 0.252 0.228 0.229 R 0.739 0.634 0.704 0.630 SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914	<i>max</i> , mm	1.830	2.880	4.875	6.349
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sens 0.296 0.234 0.202 0.169 R 0.727 0.713 0.649 0.698 SNR 20.45 8.92 5.67 12.64 EPS 0.953 0.899 0.850 0.927 res chronologies stdev 0.281 0.228 0.198 0.374 sens 0.325 0.252 0.228 0.229 R 0.739 0.634 0.704 0.630 SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914	var	0.458	0.610	0.370	0.422
R 0.727 0.713 0.649 0.698 SNR 20.45 8.92 5.67 12.64 EPS 0.953 0.899 0.850 0.927 res chronologies stdev 0.281 0.228 0.198 0.374 sens 0.325 0.252 0.228 0.229 R 0.739 0.634 0.704 0.630 SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914	sens	0.296 0.234		0.202	0.169
SNR 20.45 8.92 5.67 12.64 EPS 0.953 0.899 0.850 0.927 res chronologies stdev 0.281 0.228 0.198 0.374 sens 0.325 0.252 0.228 0.229 R 0.739 0.634 0.704 0.630 SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914	R	0.727	0.727 0.713		0.698
EPS0.9530.8990.8500.927res chronologiesstdev0.2810.2280.1980.374sens0.3250.2520.2280.229R0.7390.6340.7040.630SNR14.084.9810.9310.65EPS0.9340.8330.9160.914	SNR	20.45	20.45 8.92		12.64
res chronologies stdev 0.281 0.228 0.198 0.374 sens 0.325 0.252 0.228 0.229 R 0.739 0.634 0.704 0.630 SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914	EPS	0.953	0.899	0.850	0.927
stdev 0.281 0.228 0.198 0.374 sens 0.325 0.252 0.228 0.229 R 0.739 0.634 0.704 0.630 SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914		res chronolog	gies		
sens 0.325 0.252 0.228 0.229 R 0.739 0.634 0.704 0.630 SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914	stdev	0.281	0.228	0.198	0.374
R 0.739 0.634 0.704 0.630 SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914	sens	0.325	0.252	0.228	0.229
SNR 14.08 4.98 10.93 10.65 EPS 0.934 0.833 0.916 0.914	R	0.739	0.634	0.704	0.630
<i>EPS</i> 0.934 0.833 0.916 0.914	SNR	14.08	4.98	10.93	10.65
	EPS	0.934	0.833	0.916	0.914

Table 5. Statistical characteristics of the TRW chronologies

Characteristic	LS1/LS2	PS1/LS1	PS1/LS2	PS2/LS1	PS2/LS2	PS1/PS2
Correlation coefficient	0.186	0.205	-0.048	0.009	-0.078	0.674
Duration of the comparison period, years	165	85	85	101	101	89
Significance level	0.017	0.060	0.665	0.928	0.441	0.000

Table 6. Correlations between TRW chronologies

Analysis of similarity between *res* chronologies with regard to the significance level of correlation coefficients have shown that the strongest correlations exist between chronologies from the neighbor sites, especially between pine chronologies from MIN and TAR (p < 0.0005), where habitat conditions are less contrasting (Table 6). A positive correlation is also observed between pine and larch chronologies from the slopes, but it is less significant because of species-specific differences in climatic response and spatial separation of the sites. However, such a correlation is absent under higher soil moisture, which is evidence for local conditions closer to optimal and consequent attenuation of common signal (Fritts 1976; Shiyatov 1986; Vaganov et al. 2006). Chronologies from different tree species growing in the contrast habitats are not correlated with each other, despite uniformity of climatic conditions; i.e., the TRW response to climate in the forest-steppe zone is very strongly dependent on local conditions and species-specific features of trees.

Climatic response was evaluated primarily by correlation analysis of chronologies with monthly values of temperature and precipitation from the close meteostations (Fig. 8). The climatic signal in pine chronologies from Minusinsk forest is generally similar, but correlations with temperature and precipitation are stronger on the slope, where the groundwater lies deep beneath the surface and the sole source of moisture is precipitation, which has a significant effect on the radial growth in the first half of the growing season, especially in May. At the same time, the rise of temperature during the greater part of the season enhances evaporation from the soil surface and transpiration, which leads to water stress and consequent inhibition of xylem formation. The hydrological regime at the base of the slope is different due to precipitation runoff from the slope both on the surface and drainage through well-drained sandy soil, relatively shallow groundwater table, and proximity to the Minusinka River. Hence, the effect of precipitation and temperature is weaker than on the slope in the first half of the growing season but becomes stronger in July, upon natural drop of the groundwater table and water level in the river. The amount of precipitation in previous October-November has an effect as a factor determining the depth of snow cover, which insulates tree root systems in winter and serves as a source of moisture at the beginning of the growing season. A positive, although not highly significant (0.071) correlation is observed between TRW in pine growing on the slope and the average temperature in February. A probable explanation is that snow depth on the slopes is relatively low due to it being blown off by winds, and the root system of pine can suffer frost damage in severe frost.



Fig. 8. Correlation coefficients of the *res* local TRW chronologies with monthly average temperature (T) and precipitation (P) over the common to all chronologies period 1924-2008 Coefficients significant at p < 0.10 are indicated with dark bars and markers; values are shown for coefficients significant at p < 0.05

An important factor for trees on relatively dry and less fertile soil on the slopes is accumulation of assimilates, which continues until the end of September. Its results largely determine the rate of growth processes at the beginning of the next season, which explains a positive correlation of the pine TRW with precipitation in September. The rise of temperature in this period, as well as in summer, has a desiccating effect. A similar but weaker correlation is also observed for the larch TRW from the slope. The absence of significant correlations with autumn precipitation in this case may be explained by higher climate continentality (i.e., smaller amount of autumn precipitation) in Berenzhak, compared to Minusinsk forest, which leads to earlier cessation of assimilate accumulation. The positive response of TRW to precipitation during the first half of the growing season and its negative response to May temperatures for larch growing on the slope are attributable to the same factors as for pine, and a relatively low degree of their expression may be explained by plasticity of larch adaptation to semiarid ecological conditions (Dylis 1961; Sudachkova 1977). Under sufficient soil moisture conditions, TRW of larch shows no significant correlation with precipitation but have positive correlation with temperature in June, which stimulates photosynthesis and, therefore, growth processes. In April, long-term thaws often occur in the study region, promoting premature onset of vegetative

growth. In the floodplain site, where soil moisture is high, subsequent frosts may result in damage to the shallow root system of larch (Vaganov et al. 2006), which explains negative correlation of TRW with temperature in April (p = 0.052).

Since simultaneous positive correlation with precipitation and negative correlation with temperatures in May–July were observed in three out of the four chronologies, it was of interest to consider one of drought indices as an ecological factor, e.g. Selyaninov HTC. However, correlation analysis revealed no significant relationships, thus it was decided to use a different approach. Calculations of HTC were performed for the period from 1915 to 2012. Then so-called pointer years were selected, when rings in the most of trees are either the narrowest (negative pointer year) or the widest (positive pointer year) (Cook, Kairiukstis 1990). It should be noted that the sets of pointer years for each pair of neighbor sites were practically identical, so differences in the response to HTC between sites variation were not evaluated. Next, for every month three sets of HTC values were compared: 1) all years; 2) positive pointer years; and 3) negative pointer years. Statistically significant differences between *mean* values of each set provided evidence for the dependence of radial growth on HTC in May and June for pine and only in May for larch (Table 7). Thus, the hydrothermal regime in May and, to a lesser extent, in June proved to be the most significant factors for the growth and development of conifers in the forest-steppe of Minusinsk depression.

6									
Mean value	HTC _{May}	HTC _{May} HTC _{June}		HTC _{Aug}					
	Minusinsk station								
over entire period	over entire period 1.003 1.082 1.094								
over pagetive pointer veers	0.679	0.942	0.821	1.049					
over negative pointer years	p = 0.054	p = 0.648	p = 0.118	p = 0.813					
	1.439	1.527	1.206	1.172					
over positive pointer years	p = 0.031	p = 0.023	p = 0.427	p = 0.801					
	S	Shira station							
over entire period	0.935	1.065	1.236	1.184					
over pegetive pointer veers	0.704	0.871	1.031	1.223					
over negative pointer years	p = 0.178	p = 0.307	p = 0.504	p = 0.749					
over positive pointer veers	1.446	1.162	1.012	0.911					
over positive politier years	p = 0.043	p = 0.611	p = 0.606	p = 0.326					

Table 7. Differences between mean values of HTC for pointer years

 from the long-term mean value of HTS

Chapter 4. DEPENDENCE OF THE CLIMATE RESPONSE IN TREE-RING WIDTH ON THE INDIVIDUAL TREES GROWTH RATE

4.1. TRW chronologies of pine in the Minusinsk forest

Large amount (~200 trees) of individual TRW series from the four sites in the Minusinsk pine forest (ZSH, MIN, TAR and NIC, Table 2) was used for the research of the growth rate impact on the climatic response of conifers TRW.

To analyze range of the input of local habitats in the tree growth local and regional (ALL) *res* chronologies were developed and compared. For these chronologies statistical characteristics were obtained, which are presented in Table 8. For all of the chronologies *EPS* exceeds the threshold value of 0.85. *Rbar* values are significant at p <0.005, but they are lower than those typically observed in regions where there is only one dominant limiting factor (Shiyatov 1973). This may be due to the presence of several climatic factors in the forest-steppe zone that significantly affect TRW. Another contribution may be due to the strong influence of non-climatic external factors, such as local conditions, competition, etc. (Magda, Vaganov 2006, Babushkina et al. 2011). Nevertheless, the sample replication was in all cases sufficient for dendroclimatological analysis, as pointed out by the values of *EPS*.

The correlation coefficients between local chronologies are sufficiently high (Table 9) with the maximum correlation between MIN and TAR, whereas chronology ZSH is correlated with others to a lesser extent. At each site, the sample is represented by trees of different ages – from 21 to 167 years in the whole area. The age structure of the sample is similar for all sites except TAR, where no trees older than 100 years are present (Fig. 9a).

			U	U	
Characteristics	MIN	TAR	NIC	ZSH	ALL
Length of the chronology, years	167	100	142	133	167
Number of trees	36	34	29	95	194
Age of the trees, years	21-167	40-96	39-142	31-133	21-167
Stdev	0.19	0.19	0.20	0.28	0.20
Sens	0.22	0.23	0.24	0.33	0.23
EPS^*	0.88-0.98	0.96-0.97	0.92-0.96	0.99	0.97-0.99
<i>R-bar</i> *	0.44-0.51	0.44	0.40-0.48	0.56-0.62	0.41-0.47

Table 8. Statistical characteristics of *res* local and regional chronologies

* Characteristics were measured for window length of 50 years with step 25 years

Table 9. Correlation coefficients between regional and local chronologies (1915-2012)

	MIN	TAR	NIC	ALL
ZSH	0.633	0.589	0.656	0.952
MIN		0.895	0.776	0.819
TAR			0.700	0.767
NIC				0.810



Fig. 9. The age structure of the samples: local samples (a) and clusters (b) of trees

4.2. Classification of the individual trees into groups by their growth rate

In order to select groups of trees with similar growth rate individual functions of the age trend were calculated for the first 100 years of the tree life (when the difference between the individual trees is the greatest): actual annual values of functions were taken from file of age curves created in ARSTAN during the standardization, values missing in this file were calculated by formulas (1) or (2) with parameters also obtained from ARSTAN. Then moving average values of the age trends were calculated using 10 years window and step, so to 10 values were calculated for each tree.

Subsequently two types of cluster analysis were conducted for the entire regional sample of trees using these average age trend values. Initially, in order to assess the possibility for such a division the hierarchical classification were used with complete linkage as linkage criteria and Euclidean distance as metric (Fig. 10a). The dendrogram indicates that the data can be separated into distinct groups. However, the possible number of groups remained unspecified. Therefore further cluster analysis was conducted using the method of K-means with the cluster number varying from 3 to 8. Discriminant analysis of clusters showed that for 3 and 4 clusters, the quality of classification is not sufficiently high (Fig. 10b). For 5 cluster quality of classification is sufficient, and as the number of clusters is increased from 5 to 8 the quality further increases, but more gradually. On the other hand, increasing of the clusters number reduces volume of the cluster samples; therefore 5 was selected as the optimal number of clusters for the available sample. Results of these two methods of clusterization are almost the same (about 98% of trees went into the same clusters). Earlier a similar method, i.e. a combination of hierarchical classification method and the method of K-means, was used in dendroclimatology for the separation of trees at the local level by the type of climate response into three groups with positive, negative and insignificant response (Wilmking et al. 2004, 2005). To verify the results of the classification, calculation of the average exponential function for each cluster was carried out by formula (1) without pith offset of the age trend for each cluster sub-set of trees from individual annual values of the age trend functions. The resulting graphs and functions are shown in Fig. 11, and it is evident that each cluster really contains trees with similar growth rate. Clearly apparent are the differences between the clusters in all numeric parameters of average

age functions. Resulting clusters than were numbered in the order of decreasing of all these parameters, i.e. from the highest (I) to the lowest (V) growth rate. In cluster I a few trees are grouped that are characterized by the maximum growth rate for the region, sharply differing from other clusters, whereas the differences between other adjacent clusters are much smaller. Trees with the lowest competitive strength enter in cluster V. For these trees a significant contribution to the external signal is provided by the phytocenotic influence (competition) and peculiarities of microrelief. So our classification based on the parameters of age trend functions reflects the competitive relationships between trees and their social position in the stand. Our findings are consistent with the results of research of thinning and stand density effects on the growth rate of individual trees (Blasing et al. 1983; Franklin et al. 2009).



Fig. 10. Classification of the chronologies by the parameters of age curves:(a) a hierarchical classification; (b) quality indicators (F-test and the Wilks Lambda) of individual age curves classification using the K-Means method as a function of the clusters number



Fig. 11. Classification results: individual age curves and cluster average age trend functions

In the each site samples include trees from different clusters and the distribution is close to normal, because the Shapiro-Wilks criterion is significant at p < 0.005 (Table 10). The deviations of these distributions from normal depend on the sample size: the Shapiro-Wilks' criteria of normality is more significant for large (ZSH and ALL) samples than for small ones. However, at sites NIC and TAR no trees were assigned to cluster I. Moreover, at the site TAR the distribution is shifted towards IV-V clusters. On the site MIN there is an increased proportion of the extreme (I and V) clusters. It means that the shift of the distribution towards low growth rates is observed for sites with more extreme local conditions, i.e. smaller amount of soil moisture due to the greater distance from water bodies (MIN) or the location of the site on the steep slope (TAR). Thus, the characteristics of the distribution of local samples by clusters are correlated with habitat conditions, but its common regional pattern represents competitive relationships between individual trees.

Sample	Ι	II	Ш	IV	V	Total	Shapiro-Wilks' W test
ZSH	3	28	39	18	7	95	W=0.8913, <i>p</i> =0.0000
MIN	4	9	10	5	8	36	W=0.8963, <i>p</i> =0.0027
TAR	0	3	8	13	10	34	W=0.8627, <i>p</i> =0.0005
NIC	0	6	11	8	4	29	W=0.8804, <i>p</i> =0.0034
ALL	7	46	68	44	29	194	W=0.9039, <i>p</i> =0.0000

Table 10. Distribution of individual trees by clusters / sites, and criterion of its normality

Statistical characteristics of the cluster chronologies are shown in Table 11. Relatively low values of the *sens* may be caused by the pooling into one sample of trees from different local habitat conditions, significance of which influence in the forest-steppe zone has been shown earlier (Babushkina et al. 2011; Babushkina, Belokopytova 2014). The *stdev*, *sens* and *EPS* in extreme clusters I and V are slightly lower than in the medium clusters II-IV. It can be associated with a smaller sample size, as well as with the interaction of climatic and phytocenotic (competitive) factors. The strongest, dominant and fast-growing trees, for which the effect of competition is minimal, are more resistant to the influence of climatic variables, which leads to the weakening of the climatic signal (van den Brakel, Visser 1996). For weak and suppressed low-growing trees the influence of phytocenotic factors becomes comparable in strength to the climatic. It brings noise in common signal, which leads to the lower sensitivity of chronologies, as pointed out, for example, in Martin-Benito et al. (2008). Therefore the climatic response is the most stable for intermediate clusters II-IV. Nevertheless, for all cluster chronologies *EPS* exceeds the threshold value of 0.85, *rbar* values are significant at the level p <0.005. Sample sizes are uneven, as clusters V and especially I are represented by a lower number of trees.

Comparison of the correlations of the cluster chronologies between each other (Table 12) shows that clusters II-IV are most similar to each other; cluster V is correlated with others to a lesser degree; the greatest difference is present for cluster I. In general, the differences increase with increasing "distance" between clusters. Each cluster is represented by trees of different ages. Differences in age structure between the clusters, except cluster I, are virtually absent (Fig. 9b).

				U	
Characteristics	Ι	II	III	IV	V
Length of the chronology, years	101	142	126	142	167
Number of trees	7	46	68	44	29
Age of the trees, years	32-100	39-142	21-126	50-142	37-167
Stdev	0.18	0.22	0.22	0.21	0.20
Sens	0.21	0.24	0.25	0.25	0.23
EPS^*	0.87	0.92-0.98	0.97-0.98	0.96-0.98	0.85-0.95
<i>R-bar</i> *	0.52	0.39-0.52	0.40-0.44	0.42-0.52	0.35-0.46

Table 11. Statistical characteristics of res cluster chronologies

* Characteristics were measured for window length of 50 years with step 25 years

	II	III	IV	V	ALL
Ι	0.736	0.715	0.733	0.724	0.759
II		0.969	0.935	0.846	0.977
III			0.960	0.882	0.987
IV				0.927	0.983
V					0.921

Table 12. Correlation coefficients between regional and cluster chronologies (1915-2012)

4.3. Climatic response of pine TRW: the main pattern and variations due to local and individual differences

Analysis of the correlation coefficients of the regional and local chronologies with climate variables shows (Fig. 12) that climate response in the pine radial growth is complex, typical for the forest-steppes of Central Asia (Magda, Zelenova 2002; Knorre et al. 2010 etc.). Precipitation induces a direct positive impact on the growth of annual ring as the water source. It is significant in autumn of the previous season (September, November), February and May-July. November is the period of the first frosts and setting of the snow cover, i.e. precipitation of this period mainly plays a protective role and is highly significant at the regional scale. Presence of a significant correlation of the chronology ZSH with precipitation in April and its reduced response in July allows us to hypothesize that an earlier activation of growth in pine can be possible, causing shift of the growing season in this site.



Fig. 12. Correlation coefficients of local and regional TRW chronologies with climatic variables: temperature (a); precipitation (b) for the period 1915-2012

Negative influence of temperature of the end of the previous growing season (September of the previous year) and most part of the current season (May-August). In February the temperature, on the contrary, is positively correlated with the variability of growth. The negative effect of temperature in May-July is indirect since warming leads to increased transpiration and evaporation from the soil surface, resulting in a water stress for the plants. Local peculiarities of this response are associated with groundwater table location for each site, and with the water regime of the nearest water objects (Yenisei river near ZCH, Minusinka River not far from MIN, and small water bodies in the NIC site), which serve as an additional source of moisture when their water level is at maximum. The significance of temperature and precipitation of September of the previous year (i.e., after the completion of growth processes) is explained by the accumulating precipitation in the soil and its subsequent use in the spring, as well as processes of storing additional assimilates by trees in the end of the warm season.

In order to identify the dependence of climate response on the growth rate dendroclimatological analysis of cluster chronologies was performed (Fig. 13). In general, the climatic signal of the cluster chronologies is similar to the regional, however there are some differences. The negative effect of temperature of the previous September and of current May and June increases as the growth rate is reducing from cluster I to cluster V. In July, on the contrary, the correlation with temperature is largest for the fast-growing trees of cluster I. Strengthening the climate signal in slow-growing trees is observed for the precipitation of the previous September. It may be noted that there is a reduction in the impact of precipitation in February and May on the growth of trees belonging to the extreme clusters (I, V). In July as the hottest month strong reaction of growth to precipitation stands out for cluster I.





Previously the differences in climate response were shown for other growth conditions for trees classified by the class of the crown or by the trunk diameter, i.e. by the volume of the living space and respectively by the availability of resources (Martin-Benito et al. 2008; Campelo et al. 2013). Similar differences are observed in the forest-steppes of South Siberia too: strengthening of the temperature negative impact in the first half of the season and of the climate in the previous September for slow-growing trees is related to the decrease in the availability of soil moisture due to the smaller volume, branching and depth of the root system. It is observed in July that there is a reduction of the influence of temperature and precipitation associated to a decrease in the growth rate of the trees. This is related to the differences in the timing of cambial activity (Rossi et al. 2008a). For example, for study area the cell division ends approximately at the end of July (Babushkina et al. 2010), however for slower growing trees this process ends earlier. Since the cambial zone accepts most of climatic signal (Vaganov et al. 2011; Babushkina, Belokopytova 2015), the dominant trees show a more significant climatic response in this period. Nevertheless, it is observed for all the clusters that there is a general pattern of regional climate signal.

Thus, in the conditions of the forest-steppe zone the complex climatic signal is most fully expressed in the intermediate clusters II-IV, but for some climate variables it is more appropriate to consider the response of the extreme cluster chronologies: the fastest-growing trees (cluster I) have a stronger response to precipitation in July, the slowest-growing trees (cluster V) have a stronger response to the climate of the previous September. Therefore, for a detailed study of the climatic signal and for dendroclimatological reconstructions separate sub-samples of the trees can be used, classified by the growth rate and position in the stand – fast-growing dominant trees (I), slow-growing suppressed (V), and trees of in-between positions in medium clusters with gradually decreasing growth rates from II to IV.

Chapter 5. RELATIONSHIPS AMONG TREES' INDIVIDUAL HETEROZYGOSITY, THEIR GROWTH TRAITS AND CLIMATIC RESPONSE IN RADIAL GROWTH

5.1. Initial study: genetic traits and radial growth series of the Siberian larch

To investigate heterosis and homeostasis in the Siberian larch, two populations (different forest stands) were chosen: BER and EFR sites (Table 2). On each site samples from 50 trees were collected for measurement of TRW series and genotyping. Heterosis was estimated by individual heterozygosity calculated from set of 8 microsatellite loci (Table 3). Genetic diversity parameters for these loci are shown in Table 13. Genetic variation was high in both populations across all loci, varying from 3 to 15 alleles per locus. Observed heterozygosity (H_0) varied from 0.040 to 0.560 per locus and was 0.315 and 0.260 on average for all loci in BER and EFR populations, respectively.

Population	Para- meter	bcLK 056	bcLK 224	bcLK 066	bcLK 260	bcLK 235	UBC- 1-22	UAKL İy6	bcLK 232	Mean ±SE
	N_a	10	4	4	5	15	3	9	4	6.8±1.5
	N_e	6.2	2.8	1.4	2.1	8.8	1.2	5.6	1.7	3.7±1.0
BER	H_o	0.340	0.180	0.260	0.340	0.560	0.040	0.380	0.420	0.315±0.056
	H_{e}	0.839	0.637	0.270	0.517	0.886	0.185	0.821	0.407	0.570 ± 0.095
	F	0.595	0.717	0.037	0.343	0.368	0.784	0.537	-0.032	0.419±0.106
	Na	9	3	4	5	9	3	7	3	5.4±0.9
	N_e	5.4	1.8	1.2	1.4	4.3	1.4	4.3	1.2	2.6±0.6
EFR	H_o	0.420	0.200	0.180	0.120	0.440	0.260	0.320	0.140	0.260±0.043
	H_{e}	0.816	0.455	0.168	0.287	0.768	0.295	0.767	0.165	0.465 ± 0.099
	F	0.486	0.561	-0.073	0.582	0.427	0.120	0.583	0.154	0.355 ± 0.089
	N_a	9.5±0.5	3.5±0.5	4.0 ± 0.0	5.0±0.0	12.0±3.0	3.0±0.0	8.0±1.0	3.5±0.5	6.1±0.9
	N_e	5.8±0.4	2.3±0.5	1.3±0.1	1.7±0.3	6.5±2.2	1.3±0.1	4.9±0.7	1.4±0.2	3.2±0.6
Mean \pm standard error (SE)	H_o	0.380 ± 0.040	0.190± 0.010	0.220 ± 0.040	$\begin{array}{c} 0.230 \pm \\ 0.110 \end{array}$	0.500 ± 0.060	0.150 ± 0.110	0.350 ± 0.030	0.280 ± 0.140	0.288±0.035
error (SE), BER & EFR	H_{e}	0.828± 0.011	0.546 ± 0.091	0.219± 0.051	0.402± 0.115	$\begin{array}{c} 0.827 \pm \\ 0.059 \end{array}$	0.240 ± 0.055	0.794± 0.027	0.286± 0.121	0.518±0.068
	F	0.540 ± 0.055	$\begin{array}{c} 0.639 \pm \\ 0.078 \end{array}$	-0.018± 0.055	$\begin{array}{c} 0.463 \pm \\ 0.120 \end{array}$	0.398 ± 0.030	$\begin{array}{c} 0.452 \pm \\ 0.332 \end{array}$	0.560± 0.023	0.061± 0.093	0.387±0.067

Table 13. Genetic variation of 8 microsatellite loci in two Siberian larch populations

 N_a – number of different alleles; $N_e = \frac{1}{\sum_{i=1}^n p_i^2}$ – number of effective alleles; $H_o = \frac{\text{number of heterozygotes}}{N}$ – observed heterozygosity; $H_e = 1 - \sum_{i=1}^n p_i^2$ –expected heterozygosity; $F = (H_e - H_o)/H_e = 1 - (H_o/H_e)$ – fixation index; where *N* is number of trees genotyped, and p_i is the frequency of the *i*-th allele in the population

The homeostasis on the scale of individual tree was estimated by traits of the tree radial growth, in the first hand the average tree ring width (AvTRW, i.e. *mean* of the individual raw TRW series) and the variance of tree ring width (VarTRW, i.e. *stdev* of the individual raw TRW series). There were also used other statistical characteristics of the individual TRW series.

Both parameters AvTRW and VarTRW had positive, but weak and statistically nonsignificant correlations with IndHet (Table 14, Fig. 14a). At the same time, AvTRW and VarTRW were positively correlated at a highly significant level. This phenomenon can be explained if under unfavorable conditions most (if not all) trees grow slower regardless of their genotype, but under favorable conditions some trees may respond better via increased radial growth. It is difficult to draw a conclusion about the relationships of AvTRW and VarTRW parameters with IndHet based on the data presented here. Although the correlations were nonsignificant, they were nonlinear. Therefore, the effect of individual heterozygosity could be very complex, and there may be an optimal intermediate level, when low IndHet could be as detrimental as a very high value (Altukhov et al. 1986; Altukhov 1996, 1998, 1999; Altukhov, Sheremeteva 2000; Altukhov, Moskaleichik 2006; Olano-Marin et al. 2011;Thoß et al. 2011).

Population	Parameter*	AvTRW /	IndHet /	IndHet /
		VarTRW	AvTRW	VarTRW
BER	r	0.805	0.215	0.265
	р	0.000	0.134	0.063
EFR	r	0.660	0.203	0.203
	р	0.000	0.156	0.158
BER&EFR	r	0.726	0.146	0.122
	p	0.000	0.147	0.225

Table 14. Correlations between AvTRW, VarTRW and IndHet of trees

* r is correlation coefficient, p is its significance level

Relationships of IndHet with the tree radial growth were also estimated using various statistical characteristics of the measured (raw) individual series of the TRW absolute values, as well as of the two types of standardized (std and res) series of the TRW indices (Table 15, Fig. 14b). All correlation coefficients were close to zero and nonsignificant. The lack of correlation between IndHet and characteristics of radial growth can be explained by the ascertainment bias caused by typically selecting only the most polymorphic microsatellite markers in the genome, which may lead to reduced sensitivity for judging genome-wide levels of genetic diversity. Väli et al. (2008) tested this potential limitation of microsatellite-based approaches by correlating nucleotide diversity in noncoding regions of eight different carnivore populations assessed by sequencing 10 introns (5.4–5.7 Kb) in 20 individuals of each population with mean multilocus heterozygosities based on microsatellite genotyping (10-27 markers) of the same animals. Although there was a positive correlation between microsatellite marker heterozygosity and nucleotide diversity at the population level, no significant correlation was found at the individual level. These results imply that the variability of microsatellite marker sets typically used in population studies may not accurately reflect the underlying genomic diversity. This suggests that researchers should consider using resequencing-based approaches for assessing genetic diversity when accurate inference is critical, as it may be in our case.

Another problem could be associated with a relatively high frequency of null-alleles that can mask heterozygotes. The high *F*-values observed in several loci in both populations (Table 12) can be a signature of null-allele presence. Inbreeding can also inflate *F*-values, and self-pollination seems higher in larch compared to other conifers (Knowles et al. 1987; Oreshkova et al. 2013), but it cannot explain uneven distribution of *F*-values across loci.



Fig. 14. Relationships between IndHet and the radial growth series characteristics: relationships between IndHet, AvTRW and VarTRW (a); relationships of IndHet with various characteristics of raw, *std* and *res* TRW series (b)

	Parame		raw							res	
Population	tor*	mean	stdev	sens	ac1	R	stdev	sens	ac1	stdev	sens
	ter	(AvTRW)	(VarTRW)								
BER	r	0.215	0.222	0.109	-0.142	-0.173	0.045	0.088	-0.117	0.047	0.050
	р	0.134	0.122	0.449	0.325	0.231	0.757	0.542	0.420	0.744	0.732
EED	r	0.172	0.202	0.119	-0.035	0.190	0.017	0.115	-0.068	0.059	0.006
EFK	p	0.234	0.159	0.412	0.809	0.186	0.907	0.426	0.637	0.684	0.969
BER&EFR	r	0.126	0.111	0.054	-0.062	0.024	0.023	0.048	-0.038	0.005	0.002
	p	0.213	0.272	0.597	0.540	0.814	0.822	0.635	0.710	0.964	0.985

Table 15. Correlations of IndHet with the radial growth series statistics

* *r* is correlation coefficient, *p* is its significance level

5.2. Growth rate of the individual trees and its possible relationship to IndHet

Since the radial growth largely depends on the tree age, a phenomenon referred to as the age trend, the possible impact of IndHet on the growth rate of tree was estimated for one of the populations (BER). To classify trees on their growth rate we used their functions of age trends. There were two variants of these functions used: 1) smoothing spline; and 2) exponential or

linear functions (see section 2.2). The calculation of the distances between the age curves A(t) was carried out for the age interval from 6 to 127 years, where 6 is the median of the pith offset *PO*, and 127 is the median of the tree cambial age *T*. The distances Δ_{ij} were calculated for each pair of *i*-th and *j*-th trees using the formula:

$$\Delta_{ij} = \frac{1}{t_2 - t_1 + 1} \sum_{t=t_1}^{t_2} |A_i(t) - A_j(t)|, \qquad (3)$$

where $t_1 = \max(PO_i, PO_i, 6)$ and $t_2 = \min(T_i, T_i, 127)$ are the borders of the particular age interval for pair of *i*-th and *j*-th trees, taking into account the aforementioned restrictions. The resulting table of the distances was employed to perform hierarchical cluster analysis of the local set of trees. The clustering at each step was performed using the method of complete linkage. Optimal number of clusters was determined in the same way as in section 4.2, and four clusters were found to be optimal classification for both types of used age curves. The hierarchical dendrograms of classification are shown in Fig. 15, and the cluster subsets of age curves are shown in Fig. 16. Different methods of calculating the age curves yielded significantly different results of classification, although certain common patterns were found: 37 trees were in the same cluster in both cases, and 13 trees were in adjacent clusters (e.g. II and III), more pronounced differences were not observed at all. Nevertheless, no common patterns in the distribution of trees with different IndHet were found in either case, as differences between clusters on the IndHet values estimated by Discriminant analysis are not significant. It means that genetic traits (or at least heterozygosity of the investigated loci) have much less prominent impact on the growth rate of the tree than external factors (such as micro-differences in landscape-soil complex and phytocenotic interactions).



Fig. 15. Hierarchical dendrograms of trees classification by growth rate for BER dataset: age curves calculated as exponential / linear functions (a), or as smoothing cubic spline (b)



Fig. 16. Age curves for each of cluster subsets: age curves calculated as exponential / linear functions (a), or as smoothing cubic spline (b)

5.3. Chronologies of subsamples of trees with high and low IndHet and their climatic response

Each population (BER and EFR) was partitioned into two subsets after removing trees younger than 50 years from the analysis. The first subset "low IndHet" included trees with individual heterozygosity in the range of 0-0.25, and the second subset "high IndHet" included trees with IndHet in the range of 0.375-0.75. For each subset standard dendrochronological procedures were then performed, and the generalized *std* and *res* chronologies were obtained. The statistical characteristics of these chronologies are shown in Table 16. The most significant and stable differences were found for *EPS*, which was higher for more heterozygous chronologies at all stages of standardization. The same but less significant regularity was observed for the *R* and *sens* coefficients.

Table 16. The statistic characteristics (in form of $mean \pm stdev$) of raw, std, and res chronologiesfor tree groups with low and high IndHet from BER and EFR

Type of	Statistics	В	ER	E	FR						
chronology	Statistics	low IndHet	high IndHet	low IndHet	high IndHet						
	mean (AvTRW)	1.42±0.63	1.37±0.68	0.80±0.72***	1.85±0.77***						
	stdev (VarTRW)	0.74 ± 0.26	0.75 ± 0.34	1.13 ± 0.45	1.11 ± 0.45						
raw	sens	$0.36{\pm}0.07^{**}$	$0.39{\pm}0.07^{**}$	$0.44{\pm}0.11$	0.47 ± 0.10						
	ac1	0.66±0.14	0.65±0.15	$0.67{\pm}0.14^{**}$	0.59±0.12**						
	rbar	$0.57{\pm}0.12^{*}$	$0.62{\pm}0.15^{*}$	0.56±0.10	$0.59{\pm}0.08$						
	eps	$0.94{\pm}0.05^{***}$	$0.96 \pm 0.02^{***}$	$0.94{\pm}0.04^{***}$	$0.97{\pm}0.01^{***}$						
	R	$0.74{\pm}0.10$	0.75±0.10	$0.69{\pm}0.14^{***}$	$0.76 \pm 0.08^{***}$						
	stdev	$0.48{\pm}0.09^{*}$	$0.51 \pm 0.12^{*}$	0.53±0.11	0.51±0.10						
	sens	$0.36{\pm}0.07^{**}$	$0.39{\pm}0.07^{**}$	0.43±0.11	$0.46{\pm}0.10$						
std	ac1	0.57±0.14	0.56±0.17	0.54±0.11***	$0.43 \pm 0.14^{***}$						
	rbar	0.56±0.13**	0.62±0.15**	$0.57{\pm}0.09^{**}$	$0.62{\pm}0.09^{**}$						
	eps	$0.93{\pm}0.05^{***}$	0.96±0.02***	0.94±0.03***	$0.97 \pm 0.01^{***}$						
	stdev	$0.37{\pm}0.06^{*}$	$0.39{\pm}0.07^{*}$	0.43±0.09	0.45±0.09						
	sens	$0.43{\pm}0.08^*$	$0.46{\pm}0.08^{*}$	$0.48{\pm}0.12$	$0.49{\pm}0.10$						
res	rbar	$0.62{\pm}0.09$	0.65±0.10	$0.60{\pm}0.07$	$0.62{\pm}0.09$						
	eps	$0.94{\pm}0.06^{*}$	$0.96{\pm}0.03^{*}$	0.95±0.03**	$0.97 \pm 0.01^{**}$						
Number of cores		41	54	55	27						

Significance level of differences between low and high IndHet: p < 0.10, p < 0.05, p < 0.01

These patterns suggest a trend towards more pronounced common external signals in trees with higher heterozygosity because both R and EPS are measures of common variation of individual growth series in the chronology, especially since EPS can be interpreted as a measure of closeness between individual series and theoretical chronology of entire population (Wigley et al. 1984). As common environmental factors become more extreme, the populations exhibit a higher synchrony in growth patterns of individual trees and thus the common signal (Cook 1985; Briffa, Jones 1990). In the same environment, a common signal also depends on tolerance of plants to local conditions (Merian, Lebourgeois 2011). Autocorrelation in the heterozygous chronologies, on the contrary, was lower (although this difference was significant in only one population): that is, the radial growth in the current year was less dependent on growth in the previous year. Therefore, on the basis of identified trends, we can assume that for trees with

higher heterozygosity there was slightly more pronounced effect of factors common for the entire population (climate, general characteristics of the landscape and the soil), especially climatic variables with their high-frequency variation. For less heterozygous trees, the impact of individual stress factors (microenvironment, competitive relationship, etc.) was more important, which can be cautiously interpreted as their individual development is less stable.

For each subset, classical correlation dendroclimatological analysis was carried out. Paired correlation coefficients of the chronologies with the monthly total precipitation, average temperature and the PDSI from geographic grid dataset were found to be significant for some months (Fig. 17). Climatic response of low IndHet and high IndHet chronologies (both std and res) varied, but most of differences were subtle and not highly significant Table 17. There was a stronger negative response to the warm season temperatures for the data subsets with high IndHet in both populations and a stronger positive response to the spring-summer precipitation and PDSI as factors decreasing water deficit stress in plants of the BER population. On the contrary, in the more humid and thus less extreme environmental conditions of the EFR population, the positive effect of increased moisture factors (precipitation and PDSI) was more pronounced for the data subset with low IndHet. The dendroclimatic analysis, however, generally confirmed an expected pattern of positive relationship between heterozygosity and common signal strength in moderately extreme conditions of water availability. It can be assumed that radial growth of trees with high IndHet responded more strongly to the climatic changes because of their faster recovery after extreme stress. On the contrary, radial growth of trees with low IndHet is more affected by continuously acting stress factors, as it is more autoregressive.

Climatic	Chronology		Month										
variable	type	IX-1	X-1	XI-1	XII-1	Ι	II	III	IV	V	VI	VII	VIII
	BER												
Temp.	std	0.77	0.73	0.73	0.84	0.72	0.72	0.76	0.95	0.74	0.73	0.70	0.82
	res	0.79	0.98	0.81	0.95	0.92	0.85	0.98	0.98	0.81	0.86	0.93	0.75
Prec.	std	0.91	0.71	0.91	0.99	0.79	0.85	0.88	0.87	0.69	0.88	0.92	0.96
	res	0.81	0.78	0.95	1.00	0.98	0.86	0.92	0.95	0.70	0.91	0.75	0.88
DDGI	std	0.87	0.77	0.74	0.73	0.72	0.71	0.73	0.86	0.63	0.63	0.68	0.75
FDSI	res	0.95	0.94	0.87	0.86	0.87	0.86	0.85	0.93	0.76	0.74	0.70	0.73
					EF	^r R							
Temn	std	0.62	0.50	0.66	0.89	0.99	0.83	0.70	0.72	0.93	0.67	0.34	0.50
remp.	res	0.69	0.69	0.56	0.75	0.75	0.80	0.70	0.51	0.93	0.66	0.48	0.68
Prec	std	0.47	0.73	0.50	0.53	0.63	0.97	0.71	0.27	0.95	0.45	0.18	0.84
1100.	res	0.74	0.94	0.61	0.60	0.64	0.87	0.57	0.46	0.76	0.83	0.35	0.89
PDSI	std	0.43	0.40	0.36	0.37	0.35	0.38	0.33	0.60	0.30	0.27	0.14	0.18
	res	0.88	0.95	0 99	0.95	0 99	0.98	0 99	0 78	073	0 79	0 53	0.64

 Table 17. Significance level of differences in the climatic response between low and high IndHet chronologies



Fig. 17. The climatic response of the low and high IndHet chronologies of BER and EFR sites dotted line indicates the significance threshold for p < 0.05

5.4. Further studies: does addition of 11 new loci matter?

Distributions of the heterozygous trees for two sets microsatellite loci ("old" set of 8 loci non-specific for Siberian larch, and "new" set of 8 loci developed special for this species, Table 3) were compared. A new set reveals more polymorphic genes: the distribution of IndHet for 8 old loci is shifted towards a lower level compared to the distribution for 11 new loci (Fig. 18). This is probably due to the fact that for loci which are amplified by the same primers in different species, loci are selected with unchanged annealing sites, i.e. the most conservative loci. The new set is species-specific and was selected directly by the Siberian larch sequences. Such selection is not related to the conservatism of the annealing sites and loci, and thus presents more random sample of loci, the variability of which is almost three times higher (Table 18). IndHet values were calculated for old (IndHet8) and new (IndHet11) loci sets separately, as well as for the combined set of 19 loci (IndHet19).

Distributions of the heterozygous trees for each locus are independent, as correlations between them are in range from -0.286 to +0.286, and 96% of them are not significant on the

level p < 0.05. Correlation between IndHet8 and IndHet11 is -0.189 and not significant on the level p < 0.05 too.



Fig. 18. Distribution of the experimental sample (100 trees) on number of the heterozygous loci: old set of 8 loci (a); new set of 11 loci (b); and combined set of 19 loci (c)

Locus	H_o	Locus	H_o			
Old set		New set				
bcLK056	0.380	Ls_1106920_AG	0.590			
bcLK224	0.190	Ls_796783_CT	0.670			
bcLK066	0.220	Ls_955052_CT	0.880			
bcLK260	0.230	Ls_19333_TC	0.890			
bcLK235	0.500	Ls_440296_TC	0.620			
UBCLXtet-1-22	0.150	Ls_621673_TC	0.710			
UAKLly6	0.350	Ls_1089834_AG	0.850			
bcLK232	0.280	Ls_1274831_CT	0.667			
Mean	0.288	Ls_66831_CA	0.827			
		Ls_915025_AT	0.630			
		Ls_12590_TG	0.847			
		Mean	0.744			

Table 18. The observed heterozygosity for each locus

There are no substantial relationships of IndHet11 and IndHet19 with AvTRW and VarTRW, as their correlations are nonsignificant on the level p < 0.05, similarly to results for IndHet8 (Table 19). The same pattern is observed for other statistical characteristics of the radial growth: their correlations with IndHet11 and IndHet19 are in range from -0.192 to 0.091; correlations with observed heterozygosity of each one locus are in range from -0.271 to 0.242.

Population	Parameter*	old –I	ndHet8	new – Iı	ndHet11	combined -	– IndHet19
		AvTRW	VarTRW	AvTRW	VarTRW	AvTRW	VarTRW
BER	r	0.215	0.265	-0.140	-0.181	0.031	0.030
	р	0.134	0.063	0.332	0.209	0.829	0.837
EFR	r	0.203	0.203	0.169	-0.115	0.266	0.071
	р	0.156	0.158	0.241	0.425	0.062	0.624
BER&EFR	r	0.146	0.122	0.016	-0.053	0.122	0.046
	р	0.147	0.225	0.878	0.598	0.225	0.648

Table 19. Correlations of IndHet of trees for different sets of loci with AvTRW and VarTRW

* r is correlation coefficient, p is its significance level

To evaluate possible impact of the IndHet on the patterns of the radial growth the following statistical characteristics of the individual TRW series were chosen: mean (AvTRW), stdev (VarTRW), ar-1, R, S and sens of the raw series; stdev, ar-1, R, S and sens of the std series calculated with using of cubic smoothing splines as estimation of age trends; and additionally Rand S of the first differences of the raw series (Δraw). These first differences are interesting to investigate, because they highlight year-to-year variation of growth. Example of the individual series on the each step of processing is shown on the Fig. 19. Both R and S characteristics estimate degree of similarity between individual TRW series and local chronology as average pattern of the growth of larch in the same local and climatic conditions, because R is correlation between individual and local series by definition, and S is proportion of the year-to-year differences of the same directions in them (i.e. concurrent increasing of growth or, vice versa, concurrent depression). Thus they can be used for evaluation of the common signal contribution in the tree radial growth, i.e. impact of external factors common for all population, such as main features of local habitat, climatic and hydrological factors, etc. If an individual tree has stronger homeostasis then most of population and thus more stable growth, then low proportion of common signal will be combined with high growth rate (and thus high AvTRW). And in the opposite case an individual tree have not enough strength to increase growth substantially even in fortunate circumstances, so such a tree should have low growth rate and perhaps low sensitivity.



Fig. 19. Individual TRW series and respective local chronology on the each step of processing Raw series (a), first differences of the raw series (b), and standard series (c) for the period 1901-2013. Local chronology (BER) is thick red line; individual series (on examples of BER LS_13 and BER LS_15) are solid and dashed thin black lines

Relationships of these characteristics with IndHet obtained from the full set of loci are shown on the Fig. 20. It is evident that addition of 11 new species-specific loci did not change main pattern of the absence of significant correlations. Moreover, analysis IndHet calculated only from new loci and heterozygosity of each separate locus did not revealed any significant correlations too.



Fig. 20. Relationships between IndHet obtained from the full set of loci and the radial growth series characteristics

Some of chosen statistical characteristics correlate with each other. Therefore it was interesting to perform factor analysis on the set of these characteristics, which will allow to form much shorter list of variables describing the most important traits of the radial growth. Results of the factor analysis are shown in the Table 20. Factor 1 is describes year-to-year variation of the radial growth, as it has high loadings on sensitivity and standard deviation of the TRW indices. Factor 2 describes presence of common pattern in the radial growth, i.e. its coherence to the growth of other trees, as it has high loadings on series' synchronicity and correlation with local chronology. Factor 3 clearly is autocorrelation component of growth. Factor 4 represents growth rate as it has high loadings on the both AvTRW and VarTRW, and both characteristics positively related to the growth rate of tree. All four factors are independent by default (have zero correlation between each other).

		Factor loa	Factor loadings [*] (Varimax normalized)						
Type of series	Sstatistics	Extrac	tion: Princ	ipal comp	onents				
		Factor 1	Factor 2	Factor 3	Factor 4				
	mean	-0.507	-0.147	-0.201	0.777				
	stdev	-0.077	-0.154	0.117	0.933				
row	ar-1	-0.165	-0.235	0.806	0.286				
Idw	R	-0.106	0.519	0.378	0.358				
	S	0.273	0.797	-0.012	-0.164				
	sens	0.958	0.166	-0.190	-0.078				
	stdev	0.905	0.120	0.261	-0.239				
	ar-1	-0.007	0.076	0.912	-0.173				
std	R	0.110	0.797	0.043	-0.036				
	S	0.269	0.779	-0.109	-0.191				
	sens	0.955	0.175	-0.189	-0.090				
Arow	R	0.189	0.733	-0.076	-0.144				
Liaw	S	0.236	0.660	-0.100	-0.265				
Explained	Explained variation		3.298	1.848	1.941				
Proportion from	n total variation	0.246	0.254	0.142	0.149				

Table 20. Factor analysis of the statistical characteristics of the individual TRW series

* Maximal loading for each variable is marked with bold font

Investigated sample of 100 trees was classified into groups on base of these four factors with k-means method. Minimal value of Wilks' lambda in interval from 2 to 6 clusters was observed for 3 clusters (0.113), so it was chosen as optimal number of clusters. Mean values and standard deviations of the factors for obtained clusters I-III are shown on the Fig. 21, and analysis of variance is shown in the Table 21. Results of classification have sensible, if complex interpretation: I cluster is represented by trees with high growth rate and stable growth (low year-to-year variation); II cluster – by trees with medium-to-high growth rate, high sensitivity and low autocorrelation; and III cluster include trees with low growth rate and the highest common signal.



Fig. 21. Mean values and standard deviations of the main growth traits (factors 1-4) for clusters

		5				
	Between SS	df	Within SS	df	F	р
Factor 1	49.35	2	48.65	96	48.68	0.0000
Factor 2	8.52	2	89.48	96	4.57	0.0127
Factor 3	10.79	2	87.21	96	5.94	0.0037
Factor 4	59.50	2	38.50	96	74.18	0.0000

Table 21. Analysis of variance for clusters I-III

Possible relationships between heterozygosity and these obtained factors of the individual tree radial growth were examined with several approaches. Correlations between factors 1-4 and IndHet for all sets of loci and for each locus separately are close to zero and nonsignificant on the level p < 0.05. Discriminant analysis also showed no genetic differences between clusters with using of IndHet for any set of loci, as well as with using separate loci. Thus it can be said with sufficient certainty that examined genetic variables and classification by growth traits are independent. Though, results of factor analysis – cluster analysis combination are quite interesting and can be used in further dendroecological research.

In the end, proposed hypothesis of possible relationships between the heterosis estimated from 8 and later from 19 microsatellite loci, and homeostasis (growth stability) estimated by various characteristics of TRW series, because chosen for the study methods of analysis did not shown any clear positive results. It can be related to different reasons, for example, too low total amount of investigated genes and thus too little influence of these loci heterozygosity on the individual tree homeostasis in comparison of its genome as a whole (this reason is partially confirmed by absence of significant correlations between IndHet of different sets of loci). Other possible reason is little influence of these particular loci on the tree growth in the conditions of the study area or at all. Possible solution in both cases is investigating much larger set of different genes, and then repeating of search for the possible relationships. The third possible reason is more complex nature of interrelations between tree genome and impact of other internal and external factors then it was suggested. In such case complexity can be reduced by repeating of this search work in the different study area with simple limiting of tree growth by single factor, e.g. on the northern or upper tree-line.

CONCLUSIONS

1. For the semiarid forest-steppe zone of Khakassia, the leading climatic factor determining the variability of the conifers radial growth is the moisture regime. In May-July of the current year, the increase in precipitation influences it positively, whereas the temperature increase depresses growth indirectly through the increase of evapotranspiration. The positive influence of precipitation of the previous September-November is also clearly manifested, which increases the stock of moisture in the soil at the beginning of the current growth season.

2. Traditional dendroclimatic analysis estimates the significance of monthly climatic series for the formation of radial growth, thereby highlighting the positive or negative effects of the conditions of individual months. This assessment shows differences, both between tree species and between habitats. When integrating climate variables over several months, the common pattern of the climate-growth response for different species in the same conditions is more clearly distinguished. It shows positive influence of precipitation throughout the year, and negative influence of temperature of a warm season.

3. The use of partial correlations in Seascorr ranks the climatic factors for their significance for the variability of radial growth in specific growth conditions, reinforces and clarifies the important time interval of the influence of the leading factor. Its results are potentially most suitable for reconstructing the leading factor (annual precipitation) from the past variability of radial growth.

4. An approach using short moving time intervals for the generalization of climatic factors makes it possible to establish more precisely the critical intervals in a season when the influence of these factors is most significant. These intervals do not coincide with the calendar months, so this approach also partially explains weakness of the correlation between conifers growth and monthly climatic series. It also shows the differences in timing of these critical intervals beginning and termination due to species physiological characteristics and spatial diversity of habitat & climatic conditions.

5. Classification of individual TRW series according to the characteristics of the age trend curve allows grouping trees with similar growth rate as estimation of their competitive strength into clusters. This reflects phytocenotic relations in the tree stand, as trees growth rate estimates their competitive strength. Statistical characteristics of the cluster generalized chronologies depend on their habitat and sensitivity to external factors.

6. Climate response varies depending on the trees growth rate. The moisture-reducing influence of summer temperatures is more strongly expressed in the variability of growth of the lowest tree clusters, the root system of which has a smaller volume and is more sensitive to the lack of moisture. In July, the timing of the cambial activity period, which is also under the impact of the growth rate, influences the climate response.

7. The differences of the climatic response caused by local habitat conditions and by growth rate have the same scale. Therefore, they both can be considered in improving the quality of dendroclimatological reconstructions. In order to account for the growth rate, it can be useful to choose clusters with its medium range that have the most stable climatic response for physiological reasons and competition.

8. Dependence of some radial growth characteristics of Siberian larch trees on their individual heterozygosity was investigated. Application of different approaches demonstrated that partitioning the populations into two groups (subsets) with low and high individual heterozygosity, respectively, and the subsequent comparison of their chronologies provided additional valuable information. It can be assumed that radial growth of trees with high IndHet responded slightly more strongly to the climatic changes because of their faster recovery after extreme stress. On the contrary, radial growth of trees with low IndHet is more autoregressive and is more affected by continuously acting stress factors. Other approaches have not shown any differences in the radial growth characteristics, including growth rate, due to different sets of investigated loci, as well as from a combined set.

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