EKOLOGIJA. 2011. T. 57. Nr. 1. P. 1–11

Modeling of temperate forest ecosystems' plasticity limits

Edmundas Lekevičius[1]*,

Remigijus Ozolinčius[2],

Arūnas Samas[1]

[1] *Centre for Ecology and*
Environmental Sciences,
Vilnius University,
Čiurlionio 21/27,
LT-07119 Vilnius, Lithuania

[2] *Lithuanian Forest Research Institute,*
Ecology Department,
Liepų 1, LT-53101 Girionys,
Kaunas distr., Lithuania

Data on the ability of forest plants and soil microorganisms to adjust their optimal and pessimal temperatures to environmental changes is discussed and modelled. Here we present also a conceptual model of an unusual heat wave impact on a temperate forest ecosystem – one of the most likely outcomes of climate warming. According to empirical data, optimal temperatures for plant growth differ from those favouring the growth of soil microorganisms, whereas differences between temperatures that are pessimal for both guilds are not significant. Therefore, if a heat wave strikes a temperate climate zone, the primary production of forests and local nutrient cycles are likely to suffer damage when air temperature reaches approximately the same limit, i. e. about 40 °C. The "plasticity margin" of several °C characteristics of temperate forests, most probably evidences that this climatic zone had been hit by warmings greater than the one observed presently. It is not unlikely, that the information on climate warmings that occurred in the comparatively recent past and that is similar to the predicted one, is still preserved in present-day populations of plants and not only. It has assumed the form of rare genes, genotypes (phenotypes) and species. Besides, it may have turned into silent loci and can be activated in the case of thermal stress.

Key words: plants, soil microorganisms, climate change, heat wave, adaptation

INTRODUCTION

Recent years have seen a marked increase in the number of publications dealing with natural ecosystems' response to the environmental changes. Attention is focused on the current and future changes that the fast climate change is likely to induce. According to expert- produced forecasts (IPCC, 2007), the climate in the 21st century is likely to warm up by 2–7 °C. For example, in his survey Huntley (2007) stressed: „...Europe can be expected to experience warming of a greater magnitude than the global mean. For general circulation model (GCM) scenarios giving the 21st century global mean warming of 2.3–2.6 °C for the SRES B2 scenario and 3.2–3.4 °C for the A2 scenario, annual mean temperatures across Europe increased by 2–4 °C and 2–6 °C, respectively (2071–2100 relative to 1961–1990). Seasonal temperatures showed even greater increases. JJA (June–July–August) mean temperature increased by 4–6 °C over large areas in most scenarios, and by as much as 10 °C in some scenarios and areas" (see also IPCC, 2007).

Although more accurate forecasts are lacking, according to the prevailing opinion, a more dramatic impact is expected to be exerted on terrestrial than on aquatic ecosystems, because the amplitude of air temperature fluctuations is always greater. Especially hazardous for natural ecosystems can be heat waves and oft-recurring droughts (Huntley, 2007; Jentsch et al., 2007). Unusual heat waves in separate years in the 21st century may last up to several weeks or more (IPCC, 2007).

Some of climate warming-produced outcomes are already recorded at present: the alpine taiga belt has shifted upwards, vegetation ranges in some lowland regions have moved northwards (in the northern hemisphere), forest dieback cases are becoming more common (Parmesan, 2006). The reason behind the above-mentioned changes is, undoubtedly, higher air temperatures recorded over the last decades. On the other hand, experts stress that cases of lowland forests, suffering climate change-induced damage, are not yet so numerous, shifts of vegetation ranges being not so frequent either (Jump et al., 2009).

The prevailing opinion is that organisms will migrate towards poles and mountaintops together with a shift of their

---

* Corresponding author. E-mail: edmundas.lekevicius@gf.vu.lt

climate zones. As plants can spread only by seeds or spores, their possibilities of dispersal are acknowledged to be slimmer than those of animals. Hence, it is plausible that plants, especially woody ones (Pearson, Dawson, 2003; Jump et al., 2009), will fail to migrate in synchronicity with their climatic zones. Thus, such a mode of adjustment to climate changes may be hardly feasible for plants. Another well-known adaptation mechanism is the ability of organisms to evolve *in situ.* It is widely acknowledged, though, that this mode of adaptation is hardly suitable for trees and shrubs due to their long generation time, which ranges from over a decade to several decades. Thus, it may take woody plants thousands of years to adapt to the environmental changes via evolution. It is not surprising, therefore, that many specialists (e. g. Huntley, 1991; Davis, Shaw, 2001; Rehfeldt et al., 2002; Jump, Penuelas, 2005) forecast catastrophic changes in forests by the end of this century.

Some authors maintain (e. g. Huntley, 2007; Thompson et al., 2009) that even with the climate changing, a forest community will retain the primary production at its previous or close to that level on condition that among indigenous species there emerge those that are preadapted to new changes in the environment. This approach is sometimes also based on investigations (e. g. Pretzsch, 2005), which have shown that the artificial thinning out or full elimination of some prevailing tree populations in temperate climate zones does not harm forest productivity at all. However, another opinion that is quite widespread among specialists is, that the existence of species preadapted to the environmental changes, not experienced in the most recent evolutionary past, is simply improbable (e. g. Huntley, 1991; Davis, Shaw, 2001; Jump, Penuelas, 2005). On the contrary, over the past millennia, natural selection and succession have managed to form such sets of species in every locality that are in balance with their environment. That means that the existence of any species, preadapted to unusual for that or another locality environmental conditions, is hardly presumable. It is on this opinion that the doctrine of „bioclimate envelope“ (Huntley et al., 1995), which is widely used in forecasting climate change impact on natural communities, is based.

Functional parameters of populations can be stabilized due to another component of the biodiversity, i. e. genotype diversity. An environmental change that is unfavourable to certain genotypes of the population may be favourable to others. Thus, some genotypes may compensate for activity losses in others. For instance, some experts (Mátyás, 1996; Davis, Shaw, 2001; Kelly et al., 2003; Hamrick, 2004; Jump et al., 2006; Thompson et al., 2009) maintain that populations of trees and shrubs possess quite a rich diversity of genotypes preadapted to climate warming or other environmental changes. It is very probable that in the case of global climate warming, the frequency of warmth-preferring genotypes will increase from one generation to another at the expense of cold-preferring genotype frequency.

Individual adaptation mechanisms are widespread among plants (e. g. Larcher, 2003) and may come in useful to plants when responding even to considerable environmental changes. Forest trees are normally considered to be rather plastic as during their lifetime, which is long enough, they are forced to adapt to a great many drastic changes in the environment, including periods of heat and drought. For instance, it has been found (Gunderson et al., 2010) that optimal for photosynthesis temperature, specific to separate trees, can fluctuate within several degrees °C depending on air temperature changes.

In this article we attempt to devise a conceptual model that would demonstrate the possible responses of trees and soil microorganisms to climate change and waves of unusual heat. For that purpose we invoked empirical data on optimal and pessimal temperatures and their shifting under the conditions of environmental temperature change. Normally, this shifting is regarded as an adaptive response. For modelling, some elements of the hierarchical adaptability theory (HAT – Conrad, 1983; Lekevičius, 1986, 1997) were used. This theory treats adaptation as a process of optima adjustment to the environment. Accordingly, there should exist in natural populations a great number of structures (genes, genotypes and species) pre-adapted to usual environmental changes. As a result of a routine change in the environment, some structures acquire an optimum while others lose it, which ensures optima fitting.

THE KEY TERMS AND CONCEPTS USED IN THE HIERARCHICAL ADAPTABILITY THEORY (HAT)

According to HAT authors, adaptation is a process in the course of which the environment change-induced decline in biological activity (growth, reproduction, etc.) is restored (Conrad, 1983; Lekevičius, 1986). In the ecological context especially, adaptation may be interpreted as a process during which individuals, populations and entire communities can adjust their optima to ever-changing environmental conditions. That is quite a broad treatment of the adaptation concept. It encompasses not only evolution, but also reversible rearrangements on the level of an individual, population or community (in case when these transformations are adaptive, so they ensure the survival and functional stability). This approach is close to the one taken by some other specialists (see Gunderson, 2000; Elmqvist et al., 2003; Norberg, 2004), although many of them are inclined to replace the concept of adaptability or adaptive capacity by the term "ecological resilience".

It is possible to distinguish the following mechanisms of adaptation (Conrad, 1983; Lekevičius, 1986): phenotypic plasticity (specific to an individual); adaptation due to preadapted genotypes (specific to a population); adaptation due to preadapted species (specific to an ecological community); evolutionary or genetic adaptation mechanisms (due to the newly emerged genetic information). These mechanisms form a hierarchy: individual mechanisms make up populational mechanisms and the latter are constituent parts of biocenotic ones. That means, first of all, that populations have a richer repertoire of responses (broader plasticity limits) at their disposal than separate individuals constituting them: they can resort not only to phenotypic plasticity but also to the possibility of changing the genotype frequency. Naturally, this proposition is valid only if there exists a genotype diversity in a population. An ecological community adapts to the environment using not only the phenotypic plasticity specific to organisms, genotype diversity typical of populations but also the possibilities offered by species diversity. Essential variables of an ecosystem (the total biomass, primary production, efficiency of nutrient cycling) should be considered to be the best buffered attributes of life or the most difficult to destabilize. HAT asserts that local nutrient cycles are the warrantor of long-term viability of the whole life including producers (Lekevičius, 2006).

The exceptional feature of this theory is that it foresees the existence of a considerable number of reserve structures (e. g. "silent" and weakly transcribable genes, rare genotypes and rare species). They can be viewed as a peculiar form of memory about the past events, as hidden information, part of which occasionally "comes to light", whenever the environmental conditions routinely recur. The gene pool of any natural population stores the whole or nearly the whole information on those environmental changes that the population has experienced in the past (Conrad, 1983; Lekevičius, 1986). Hence, any change in the environment within the usual range always provokes a corresponding response. The repertoire of these responses must have been built up by natural selection. This should explain the obvious fact that adaptation to ordinary changes in the environment, as a rule, does not call for any genetic changes, and new genetic information is dispensed with. It becomes indispensable only when extraordinary changes occur in the environment.

HAT urges that a differentiation should be made between the tolerance and plasticity curves. The tolerance curve can be produced by placing organisms in different environmental conditions and immediately measuring the biological activity, without waiting for a response to be evoked. In such a way we record the direct impact and not adaptation. Meanwhile, to produce the plasticity curve, changes in the environment should be brought about either slowly enough or, *in extremis*, the biological activity should be measured after a certain amount of time has elapsed since the occurrence of an abrupt change in the environment. The number of tolerance curves specific to an organism or a population is not finite, and they can move to one or another side in regard to the environment gradient. As plasticity curves are recorded in genetic material, they can shift only in the course of evolution. The same holds true for the limits of tolerance and plasticity. They represent the range of environmental conditions within which organisms can survive and reproduce themselves, the environment changing rapidly (limits of tolerance) or slowly (limits of plasticity). To be more exact, plasticity limits are the limits within which the pessimal points slide. They are, of course, always broader than the tolerance limits.

The idea that in the process of adaptation organisms attempt to adjust optima to the environment implies that an organism or a population may have an infinite number of optima. However, that does not mean that all of them are equal. Not only do tolerance curves shift, but their height can vary as well. The environmental conditions, ensuring the maximally possible biological activity (= degree of adaptation or adaptedness), can be referred to as the main or genetic optimum. All other optima that are actually observed are auxiliary, i. e. they are just the last resort.

The ability to adapt oneself or adaptability comprises two components: adaptation rate and plasticity limits (Lekevičius, 1986, 2007). Adaptation rate can be treated as a rate at which the tolerance curves slide along the axis of the environment gradient. It is clear that the faster adaptation rate is and the broader plasticity limits are, the greater is the adaptability of an individual, population or community. The set of adaptation mechanisms that life has ensures adaptation both to fast yet insignificant environmental changes and to slow but radical ones. Although the operation rate of individual mechanisms is the fastest, they are efficient only within the comparatively narrow range of environmental conditions. Thus, they ensure comparatively narrow plasticity limits. And on the contrary, although evolutionary mechanisms operate the slowest, these mechanisms make it possible to adapt to practically any conditions. In this respect, populational and biocenotic mechanisms occupy an in-between position. In short, there is some trade-off between the adaptation rate and plasticity limits: some adaptation mechanisms operate fast but they are efficient only within a comparatively narrow range of environmental conditions, while others, operating at a slow rate, are capable of ensuring much broader plasticity limits (Lekevičius, 1986). This could be explained by the fact that the rate of adaptive rearrangements on different organisational levels is restricted by different factors. The operation rate of individual mechanisms is controlled by the rates of molecule synthesis and cell multiplication (in a multicellular organism). In addition to that, the rate of populational and biocenotic rearrangements is also restricted by the generation time and fertility. As a matter of fact, the rate of evolution is restricted not only by the generation time and fertility, but also by the rate of mutagenesis and frequency of recombinations. Therefore, the process of evolution is extremely slow.

ECOSYSTEMS AND THEIR ENVIRONMENT ARE IN CONSTANT NON- EQUILIBRIUM EVEN UNDER THE USUAL CLIMATIC CONDITIONS

Forest organisms inhabit environments that have many dimensions (temperature, precipitation, etc.), each of which can vary temporally and / or spatially. For example, temporal fluctuations can occur over short or long timescales. Within these timescales, the variation can occur on a regular (e. g. diurnal and seasonal patterns of the environmental change, may be some multi-year oscillations), or on an irregular or random scale. The distribution of abiotic fluctuations is easily imagined as having a fixed mean and variance, at least in the short term.

There is a strong presumption that due to preadapted genes, the adaptation of a forest tree to seasonal changes in the environment takes approximately the same period of time as that of the co-existing community of soil microorganisms or that of small invertebrates. The above statement implies that the period of time needed for rare genotypes in populations of microorganisms and small invertebrates to turn into dominant ones is not much longer than that needed for the induction of enzyme synthesis in a plant cell, not to mention, the period needed for the multiplication of these cells or for the multiplication-induced morphological change in an organ to be produced (see Berry, Björkman, 1980; Hochachka, Somero, 2002; Larcher, 2003; Sage, Kubien, 2007).

Nonetheless, the ideal compatibility between the environment and forest organisms is hardly probable even if all of them are appropriately preadapted to periodical, i. e. easily predictable, environmental rhythms. The reason behind that is that besides the environmental rhythms mentioned above, there are occasional or irregular changes in the abiotic environment. As it is impossible to predict them in advance, the negative impact is, as a rule, unavoidable, especially if the environmental changes are abrupt and dramatic. In that case, a decline in adaptedness and an adaptation lag are observed. It takes time, and sometimes a long time, for adaptation to occur. Hence, as soon as an organism adjusts to one particular change in the environment, it is often exposed to another hardly predictable occurrence. For instance, when the sun is covered by a cloud, most forest plants respond to it, in all likelihood, (Barnes et al., 1998; Larcher, 2003, and references therein) by slightly lowering the points of light compensation and light saturation. In such a way, the efficiency of deficient solar energy assimilation is enhanced, i. e. adaptation to this environmental change takes place. However, this response lasts for at least several hours, and the sun may break through the clouds before the response period is over. It seems (Larcher, 2003; Valladares, Pearcy, 1997) that in the course of the day the curve of temperature vs. plant growth and that of ambient temperature vs. heat tolerance move also, although this response lasts an hour or even several hours. Plants seem to face a similar problem when seasonal temperature rhythms are disturbed, for instance when winter freeze starts earlier than usual, or unusual summer heat sets in. In the above-mentioned cases adaptation may lag behind, as there is no preadaptation to this change (it is unpredicted). What is more, such a change calls for rather radical physiological transformations. For instance, it takes *Betula, Quercus* and *Populus* trees up to 10 days to acclimate to abrupt and considerable air temperature fluctuations recorded in the course of a season (Gunderson et al., 2010).

The adaptation rate of soil microorganisms' community to diurnal and day-to-day changes is first of all limited by the generation time. In field conditions it may be as long as several days. Hence, the response itself can lag several weeks or even more behind. According to the data obtained from the experiment (Bárcenas-Moreno et al., 2009), the time needed for the accretion of populations that have gained advantage due to an abrupt change in soil temperature, is just the same. Processes of biochemical adaptation undoubtedly take place in cells, but they are much faster and therefore should not restrict the rate of community adaptation. These authors do not point out one more theoretically probable possibility, i. e. the genotype frequency fluctuation within a population, although it should not last longer than "species sorting".

The above mentioned speculations allow us to suggest that all forest organisms must be involved in the endless process of adaptation to the environment. No sooner has adaptation to particular environmental changes taken place than new changes emerge, and so on and so forth. Even the slightest change in the environment provokes an immediate response, and data on the possible sensitivity threshold are not available. However, adaptive rearrangements always take time, thus even comparatively fast individual adaptation mechanisms do not always manage to keep pace with the environmental changes. As it takes even more time for the frequency of preadapted genotypes to increase and "species sorting" to take place, a delay in these cases is consequently longer. Therefore populational and community mechanisms can prove handy only when an environmental change is comparatively slow. It should be pointed out therein that the notion of a "slow" change is relative: a "slow" change in the case of microorganisms is the one lasting weeks or months, whereas in the case of a forest tree guild a change of the same degree is "slow" if it lasts for hundreds or thousands of years. Also important is another conclusion, which follows from the above mentioned speculations: the slower changes in the environment are (even if they are unpredicted), the less incompatibility between organisms and the environment is to be expected (Fig. 1). This conclusion is drawn not only from HAT, it is also supported by empirical data (e. g. Law, Crafts-Brandner, 1999; Gunderson et al., 2010).

OPTIMAL AND CRITICAL TEMPERATURES FOR FOREST ORGANISMS

Optimal temperatures for forest tree growth and net photosynthesis are as follows: 15–25 °C for deciduous trees, 10–25 °C for coniferous trees, and 10–20 °C for cryptogams (Ellenberg, 1988; Kozlowski et al., 1991; Larcher, 2003). These are air temperatures at which growth rate and net photosynthesis reach maximally possible values, other conditions (e. g. lighting, water supply, difference between day and night temperatures) being favourable for species. It is difficult to say which optima, the main or the auxiliary ones, are implied therein as different authors used different

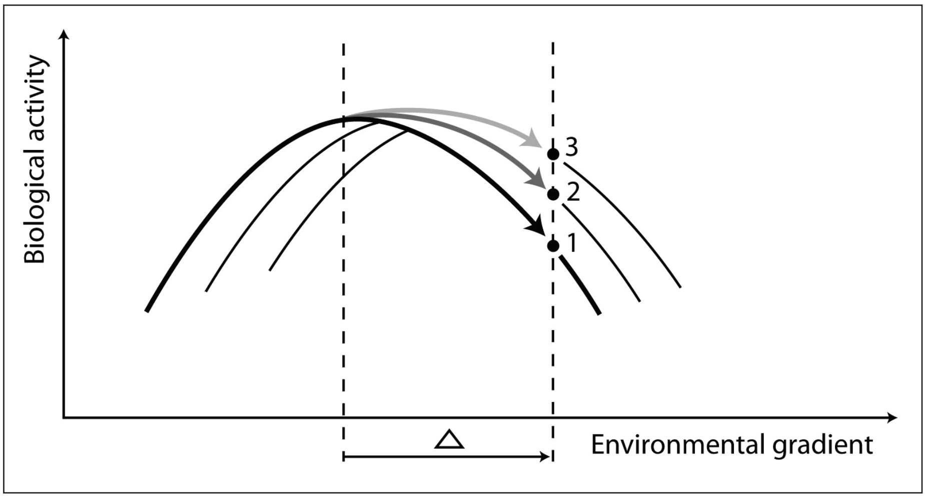

Fig. 1. A decline in biological activity or adaptedness observed under the conditions of unpredictable and abrupt environmental changes must be considerably greater than that recorded under the conditions of slow (2) or still slower (3) environmental changes, i. e. when adaptation mechanisms manage to realize all their potentials

experiment schemes yielding different results. Still, the examination of methods used, has revealed that most authors allowed plants to acclimate at a temperature at which net photosynthesis was recorded. Hence, it seems that the ranges mentioned above most often, although, perhaps, not in all cases, indicate the limits within which auxiliary optima shift.

Other data (Strain, Chase, 1966; Berry, Björkman, 1980; Ellenberg, 1988; Cunningham, Read, 2002; Kattge, Knorr, 2007; Gunderson et al., 2010) suggest that auxiliary optima for trees in temperate climate zones slide within a wider range, i. e. between 5 and 32 °C. On the basis of experiment findings, some authors (Gunderson et al., 2010) conclude that optimal temperature ranges for species sampled from geographical regions with markedly different climates (from ca. 28 °N to ca. 50 °N) overlap to a great extent, their optima can move within the range 17–34 °C due to acclimation. Higher plasticity limits were characteristic of the species that are exposed to a larger fluctuation in seasonal temperatures in their sampling locations (Cunningham, Read, 2002; Gunderson et al., 2010).

If the latter authors are right, the main or genetic optima for plant species are dispersed within a narrower range than the above-mentioned one (5–32 °C). In the case of trees, the main optima are most likely to be dispersed between 10 and 25 °C. We presume therein that one optimum point corresponds to one species, although in reality this point is rather difficult to determine (Barnes et al., 1998), the more so as temperature optimum is also most probably conditioned by the tree age, genotype and other factors. Undoubtedly, in field conditions the range within which air temperature varies during the vegetation period is much wider than that within which temperature optima can shift. Therefore during the greater part of the vegetation period plants have to grow in suboptimal conditions (Berry, Björkman, 1980; Larcher, 2003; Sage, Kubien, 2007). The scheme below summarizes all the above-given information (Fig. 2).

The knowledge of the upper temperature pessimum (heat tolerance) characteristic of plants of the temperate climate zone and its shifting caused by diurnal and day-to-day temperature fluctuations is considerable. Mechanisms of adaptation to heat are diverse: they vary from those that are triggered off comparatively fast to those which take several weeks to realize themselves. In summer, the upper lethal temperature, T_{max} (S) for trees of the temperate climate zone is 43–49 °C. However, it goes down by several degrees both after a sudden cooling in summer and in early autumn. It plummets still more in winter, although during thaw it can rebound for some trees again (see Ellenberg, 1988; Valladares, Pearcy, 1997; Barnes et al., 1998; Dreyer et al., 2001; Robakowski et al., 2002; Larcher, 2003; Froux et al., 2004; Hüve et al., 2006; Daas et al., 2008).

In winter, due to preadaptation, the lower pessimum for plants of our climatic zone, T_{min} (W), i. e. temperature causing death, slumps to minus 45–50 °C. Meanwhile, an unhardened tree can perish due to frosts at the beginning of summer: T_{min} (S) =–5–10 °C. In autumn the cold hardiness curve gradually glides towards low temperatures, while in spring it moves in the opposite direction (Ellenberg, 1988; Barnes et al., 1998; Guy, 1999; Larcher, 2003; Repo et al., 2006).

The optimal temperature for the growth of soil microorganisms seems to be slightly higher than that for plants (Fig. 2). Most data were obtained from soil investigations in South Sweden. The indicated optimal temperature is in the range 25–30 °C (Díaz-Raviña et al., 1994; Pietikäinen et al., 2005); Bárcenas-Moreno et al., 2009). Most probably these limits should be treated as the main optima zone, because in the course of acclimation a community of microorganisms is able to shift its optimum considerably, especially towards higher temperatures, even up to 45 °C (Bárcenas-Moreno et al., 2009). Thus in comparison with plants, species of soil bacteria and fungi in the temperate climatic zone

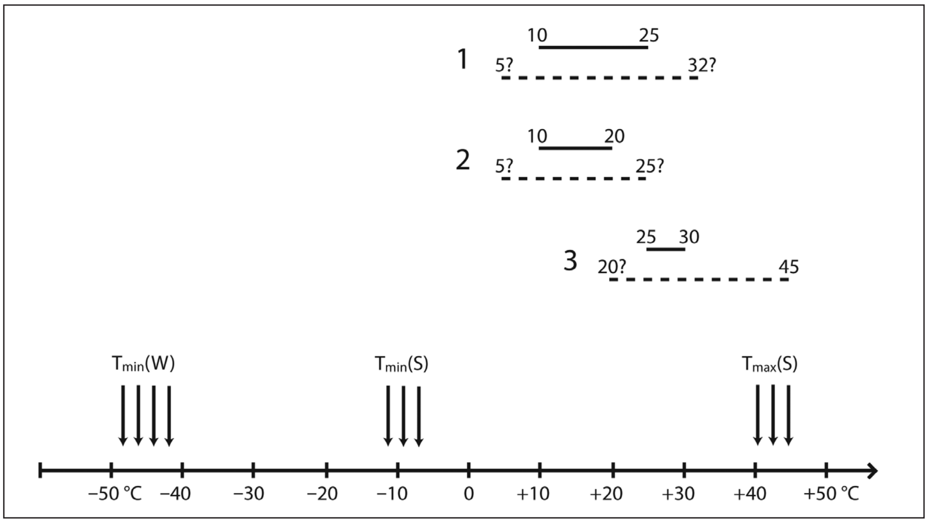

Fig. 2. Optimal and critical temperatures for trees and soil organisms of the temperate climate zone (rough model). T_{min} (W) – the lower pessimum for trees in winter, i. e. lethal temperature in winter; T_{min} (S) – the lower pessimum for trees and soil organisms in summer; T_{max} (S) – the upper pessimum or the upper lethal temperature for trees and soil organisms in summer. *1* – the range of the main or genetic optima for tree growth (solid line) and the probable shifting range of the auxiliary optima (dotted line); *2* – the same for cryptogams; *3* – the same for soil microorganisms

should be considered as more thermophylic. On the other hand, there is almost no difference between their pessimum points: T_{min} (S) for bacteria is minus 5–10 °C, for fungi – up to minus 15 °C (Díaz-Raviña et al., 1994; Pietikäinen et al., 2005), T_{max} (S) – 45–50 °C both for fungi and bacteria (Pietikäinen et al., 2005; Bárcenas-Moreno et al., 2009). We failed to clarify what maximally low temperatures spores of bacteria and fungi can endure. The long-term experience of microbiologists demonstrates that spores are highly resistant to all extreme factors; hence even severe winters can hardly harm them.

In summary, forest plants and soil organisms should show a quite good capacity to buffer the essential biotic parameters (primary productivity, plant and above-ground biomass, soil respiration and decomposition rates) against usual climate oscillations. Empirical studies seem to confirm such a prediction (Kreyling et al., 2008; Bárcenas-Moreno et al., 2009; but see Emmett et al., 2004).

CAN THE PREDICTED CLIMATE WARMING EXCEED PLASTICITY LIMITS OF TREES AND SOIL MICROORGANISMS?

Many authors forecast dramatic climate changes in the nearest future. There are no doubts that an increase in the mean annual temperature by several degrees, let's say from +6 °C that is characteristic of Lithuania to +9 or even +10 °C, should not create serious problems simply because in that case a gap between the mean temperature and optimal temperatures for growth would narrow (Fig. 2). In that case the number of days when plants and soil organisms vegetate in optimal or close to optimal conditions should increase. The vegetation period would most probably lengthen, and that, again, would have a positive rather than a negative impact.

As it has been already mentioned, extreme events can lead to more unwanted consequences. From the material presented in this article, it is not difficult to envisage the situation which may arise in forests of the temperate climate zone in the 21st century in the case of an extraordinary "heat wave" (Fig. 3). There is no universal definition of a heat wave. The definition recommended by the World Meteorological Organization is when the daily maximum temperature of more than five consecutive days exceeds the average maximum temperature by 5 °C, the normal period being 1961–1990. According to the American Meteorological Society glossary, a heat wave corresponds to a period of three consecutive days during which the maximum temperature is above the threshold of 32 °C (AMS, 2000). The U. S. National Service of Meteorology has proposed another definition: persistence for a period of at least 48 hours of daytime temperature above or equal to 40.6 °C, associated with nighttime temperature above or equal to 26.7 °C. As for French meteorologists, a heat wave is simply a period during which the maximum temperature goes beyond 30 °C (Poumadère et al., 2005).

For the sake of simplicity, optimal (T_{opt}) and lethal (T_{max}) temperatures are given therein only for two hypothetic tree species. Species 1 can be characterized as relatively cold-preferring, while species 2, on the contrary, as warmth-preferring. In Lithuania, Norway spruce and downy birch (*Betula pubescens* Ehrh.) may be regarded presumably as relatively cold–preferring trees. As an example of warm-preferring one, a small-leaved linden (*Tilia cordata* Mill.) may be mentioned. In Fig. 3, genotype diversity, which is

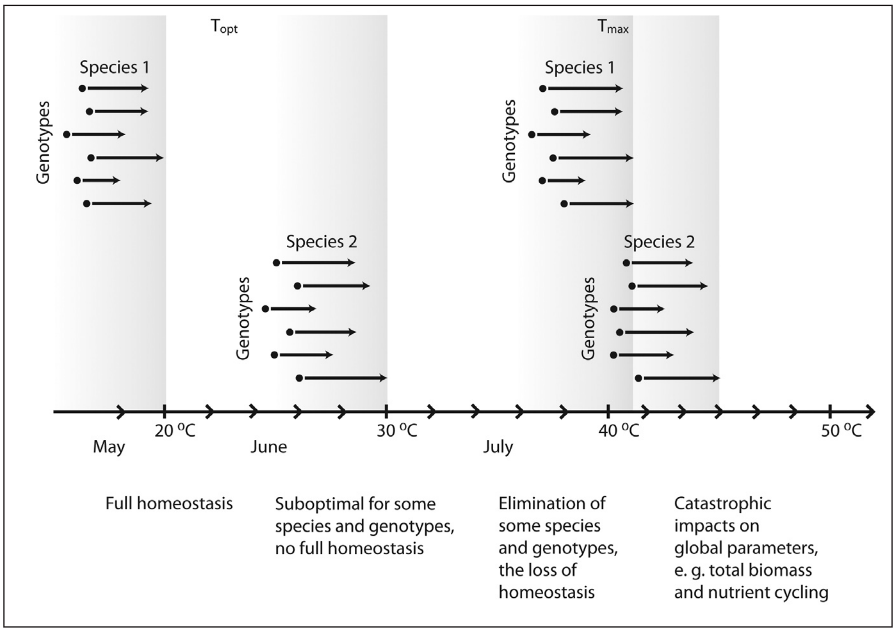

Fig. 3. The probable impact of an extraordinary heat wave on the forest tree guild. For the sake of simplicity, in the Figure the tree guild is represented by two hypothetic species: the relatively cold-preferring and relatively warmth-preferring one. The arrows indicate shifting limits of optimal (T_{opt}) and lethal (T_{max}) temperatures characteristic of separate genotypes

characteristic of populations of species 1 and 2, is reflected by a different positioning of optimal and critical points in regard to the temperature axis. The figure outlines the situation when from the end of spring to the end of July air temperature rises by approximately 0.4 °C per day reaching the high point of 45 °C by the end of the period.

Such a rate of the environmental change is rather usual for the temperate climate zone, and, at least initially, it is not likely to pose serious problems for biochemical and physiological mechanisms of adaptation, as they will manage to shift optima in the due direction. The temperature gradually rising, auxiliary optima will be shifting at the same rate to the right until reaching the indicated limits. As one can see from the figure, after exceeding approximately 20 °C, the temperature will become suboptimal for species 1. Meanwhile, for species 2, the temperature will become suboptimal after rising to approximately 30 °C. However, a part of genotypes of the same species will lose the optimum a little bit earlier, as there are both relatively cold-preferring and warmth-preferring genotypes among them, which is seen from the model. In any way, as it has been mentioned already earlier, in the case of mixed forests of the temperate climate zone, the 10–30 °C temperature band should be regarded as fairly well "buffered". It is the zone of a full or at least partial homeostasis on the guild level. Increased activity of some species and genotypes compensates for the growth deceleration in other species or genotypes, hence within this temperature range the primary production of the guild should not change considerably.

A distinctly suboptimal temperature band for the whole guild ranges between 30 and 40 °C (Fig. 3, see also Fig. 2). The situation is even more aggravated by the fact that the environmental changes in this case proceed too fast to trigger off other tree-specific adaptation mechanisms, such as change in genotype frequency and succession or "species sorting". Therefore optima and pessima shift towards higher temperatures insofar as individual adaptation mechanisms permit. As it is evident from Fig. 3, at approximately 41–42 °C the elimination of some cold-preferring genotypes should start in species 1. In case the temperature of 43 °C persists, all genotypes of the species will be eliminated which will lead to the species' death. This temperature has a drastic effect on relatively cold-preferring genotypes of species 2 as well. As the model shows, at the air temperature over 45–46 °C, this species together with all or nearly all forest tree guild is likely to become extinct.

The situation in the block of soil microorganisms (no illustration is provided) in analogous conditions should follow a different scenario due to short generation time characteristic to these organisms (Lekevičius, 2007). In all the temperature bands dealt with therein, adaptive rearrangements should proceed at all levels starting with the cellular one and ending with that of a guild. In this situation even seasonal selection and „species sorting" would be useful to them. The zone of a distinct suboptima for soil organisms should also differ from that predicted for trees – it should become evident only after the temperature has risen to 40 °C (see Fig. 2 and comments to it). The catastrophe is likely to strike this block only after the air temperature has exceeded 45 °C.

To sum up, the real danger for forests of Lithuania and other regions with a similar climate will arise only if the air temperature over 40 °C persists at least for several days, like happened some years ago in West Europe. The summer of 2003 was one of the hottest on record in Europe, especially in France. France does not commonly have very hot summers, particularly in the northern areas, but seven days with temperatures of more than 40 °C were recorded in Auxerre, Yonne. So far, the highest temperature recorded in Lithuania was 37.5 °C (http://www.meteo.lt/klim_rekordai.php). So, there exists a "plasticity margin" of at least 2–3 °C. In Central Europe, air temperature has reached 41–42 °C several times over the study period, although such heat used to last only for 1–2 days. What is the probability that similar heat will strike both Lithuania and neighbouring countries in the 21st century? Some meteorologist – produced scenarios for the second half of the 21st century (IPCC, 2007) really forecast such temperatures (exceeding 40 °C) not only for France but for all Central and Eastern Europe. However, such forecasts should not be taken for granted as expert opinions significantly vary. On the other hand, it should be taken into consideration that heat waves are often accompanied by droughts and attacks of insect pests and diseases (for survey see Johnston, 2010). Having this fact in mind, it is possible to presume that a catastrophe may occur even at slightly lower temperatures.

DISCUSSION

In our opinion, the main impediment to reaching more specific and grounded conclusions on the issues under consideration is the shortage of data on genotypes and species preadapted to the would-be climate warming. Researchers' opinions on that issue are divided: some of them (Kelly et al., 2003; Hamrick, 2004; Pretzsh, 2005; Jump et al., 2006; Huntley, 2007; Thompson et al., 2009) are inclined to believe that there will be no shortage of preadapted genotypes and species to ensure a successful adaptation, at least not until the middle of this century. However, other authors (e. g. Davis, Shaw, 2001; Rehfeldt et al., 2002) do not support this viewpoint and advance the following argument against it: genes and genotypes preadapted to prospective environmental conditions rather than to the previous ones can hardly be stored in gene pools. What is more, the traditional Darwinian logic contradicts that. Meanwhile, Kelly and his fellow researchers (Kelly et al., 2003) claim that the process of adaptation will be successful due to "warm year" genotypes which already exist in most plant populations: their frequency will increase, while that of "cold year" genotypes will, on the contrary, decrease. In our opinion, however, such a viewpoint is somewhat too optimistic, as Kelly and his fellow researchers have in mind genotypes which help populations to adapt to routine year-to-year fluctuations. These year-to-year differences in mean annual temperatures amount to just 1 °C, or even less, and are not related to the current climate warming altogether.

HAT suggests addressing this problem from a somewhat unusual standpoint. This theory holds (Lekevičius, 1986; 2007) that information on the environmental changes, previously experienced by populations, is stored in their gene pools. A routine recurrence of a change in the environment induces a retrieval of the stored information on the relevant change which is consequently used as an adaptive response. However, HAT says nothing about how far back the genetic memory goes. Nonetheless, this idea, in our opinion, may prove handy at that research stage when we rely on intuition as a guide rather than on precise data. It is just necessary to clarify whether periods of climate warming, similar to the predicted one, occurred several hundred or several thousand years ago, as the genetic memory should go that far back, at least in the case of trees. In our opinion, the "plasticity margin" of several °C characteristic of temperate forests most probably evidences that this climatic zone had been hit by warmings greater than the one observed presently.

In the northern hemisphere, periods of climate warming, similar to the currently observed one or that predicted in the first half of this century, must have occurred in the third decade of the last century (Alley et al., 2003), approximately 1 000 years ago as well as 7 000 years ago (Pielou, 1991; Bradley et al., 2003; Overpeck et al., 2003; Alley et al., 2003; Moberg et al., 2005). In general, according to these authors, in the historical period the climate has been changing unceasingly within rather wide limits and sometimes even faster than predicted for this century (Alley et al., 2003). Many of the trees that experienced the warming of the third decade of the 20th century are vegetating to the present day. Just a few individuals of those that experienced the warming of the Middle Ages have survived to this day, but, undoubtedly, there is still a great number of progeny of the 2nd–3rd generations in forests. We are separated from the pronounced warming that ended approximately 5 000 years ago by 10–100 tree generations, but from the standpoint of population genetics this figure is not big.

One of the possibilities to adapt is successful reactivation of silenced genes or "lost" development programs (Marshall et al., 1994; Mattick, 2004; Schlichting, 2008). These genes are sometimes called pseudogenes, and sometimes – genomic fossils, and the choice of such names seems to be grounded: these genes may preserve the potency of being activated for thousands and in separate cases maybe even for millions of years (Marshall et al., 1994). Hardly anyone today would dare to reject the idea that among these seeds and seedlings, millions of millions of which germinate every year in our forests and are discarded as genetic load by selection, there are no those, which in the future would become "wild" and would spread in populations in the course of several decades. Therefore it is quite probable that in the form of preadapted although rare species, genotypes and genes, the guild of forest trees stores till now the information on climatic oscillations that have occurred over the last 10–20 thousand years. In other words, the genes that proved to be useful for populations in those times, when there was a similar period of climate warming, should not be eliminated.

So, the preliminary analysis performed by us shows presumably that forest ecosystems in temperate climate zones will fairly well adapt to climate changes in the first half of the 21st century that we are anticipating with apprehension. Optimism arises from arguments that are dual in character. First of all, we hope that the information on climate warmings that occurred in the comparatively recent past and that are similar to the current one, is still preserved in present-day populations of plants and not only of them. It is quite probable that it has assumed the form of rare genotypes (phenotypes) or rare species. Besides, it may have turned into silent loci and can be activated in the case of stress. Some hopes may also rest on the current genetic load or maladapted genotypes – there may be a considerable number of such genotypes among them that in changed conditions will acquire the status of "wild" ones. Secondly, some hopes that seem to be quite realistic can be pinned on gene migration from warmer regions. Unfortunately, all the above mentioned conclusions are so far merely theoretical premises devoid of absolute certainty.

ACKNOWLEDGEMENTS

The authors acknowledge a very constructive contribution of anonymous reviewers. This study was made possible by the grant from the Research Council of Lithuania (project No. LEK-17/2010).

Received 3 March 2011
Accepted 21 April 2011

References

1. Alley R. B. et al. (11 authors). 2003. Abrupt climate change. *Science.* Vol. 299. P. 2005–2010.
2. AMS (American Meteorological Society). 2000. *Glossary of Meteorology*. Boston: American Meteorological Society.
3. Bárcenas-Moreno G., Gómez-Brandón M., Rousk J., Bååth E. 2009. Adaptation of soil microbial communities to temperature: comparison of fungi and bacteria in a laboratory experiment. *Global Change Biology*. Vol. 15. P. 2950–2957.
4. Barnes B. V., Zak D. R., Denton S. R., Spurr S. H. 1998. *Forest Ecology*. 4th ed. New York: John Wiley & Sons.
5. Berry J., Björkman O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology*. Vol. 31. P. 491–543.
6. Bradley R. S., Hughes M. K., Diaz H. F. 2003. Climate in medieval time. *Science*. Vol. 302. P. 404–405.
7. Conrad M. 1983. *Adaptability: The Significance of Variability from Molecule to Ecosystem*. New York–London: Plenum Press.
8. Cunningham S. C., Read J. 2002. Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature. *Oecologia*. Vol. 133. P. 112–119.
9. Daas C., Montpied P., Hanchi B., Dreyer E. 2008. Responses of photosynthesis to high temperatures in oak saplings assessed by chlorophyll-a-fluorescence: inter-specific diversity and temperature-induced plasticity. *Annals of Forest Science*. Vol. 65. P. 305.
10. Davis M. B., Shaw R. G. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science*. Vol. 292. P. 673–679.
11. Díaz-Raviña M., Frostegård ., Bååth E. 1994. Thymidine, leucine and acetate incorporation into bacterial assemblages at different temperatures. *FEMS Microbiology Ecology*. Vol. 14. P. 221–231.
12. Dreyer E., Le Roux X., Montpied P., Daudet F. A., Masson F. 2001. Temperature response of leaf photosynthetic capacity in seedlings from seven temperate tree species. *Tree Physiology*. Vol. 21. P. 223–232.
13. Ellenberg H. 1988. *Vegetation Ecology of Central Europe*. 4th ed. Cambridge: Cambridge univ. Press.
14. Elmqvist T., Folke C., Nyström M., Peterson G., Bengtsson J., Walker B., Norberg J. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*. Vol. 1. P. 488–494.
15. Emmett B.A., Beier C., Estiarte M., Tietema A., Kristensen H.L., Williams D., Peñuelas J., Schmidt I., Sowerby A. 2004. The response of soil processes to climate change: results from manipulation studies of shrublands across an environmental gradient. *Ecosystems*. Vol. 7. P. 625–637.
16. Froux F., Ducrey M., Epron D., Dreyer E. 2004. Seasonal variations and acclimation potential of the thermostability of photochemistry in four Mediterranean conifers. *Annals of Forest Science.* Vol. 61. P. 235–241.
17. Gunderson L. 2000. Ecological resilience: in theory and application. *Annual Review in Ecology and Systematics*. Vol. 31. P. 425–439.
18. Gunderson C. A., O'Hara K. H., Campion C. M., Walker A. V., Edwards N. T. 2010. Thermal plasticity of photosynthesis: the role of acclimation in forest responses to warming climate. *Global Change Biology*. Vol. 16. P. 2272–2286.
19. Guy C. 1999. Molecular responses of plants to cold shock and cold acclimation. *Journal of Molecular and Microbiological Biotechnology*. Vol. 1. P. 231–242.
20. Hamrick J. L. 2004. Response of forest trees to global environmental changes. *Forest Ecology and Management*. Vol. 197. P. 323–335.
21. Hochachka P. W., Somero G. N. 2002. *Biochemical Adaptation*. Oxford: Oxford University Press.
22. Huntley B. 1991. How plants respond to climate change – migration rates, individualism, and the consequences for plant communities. *Annals of Botany.* (Lond.) Vol. 67. P. 15–22.
23. Huntley B. 2007. Climatic change and the conservation of European biodiversity: Towards the development of adaptation strategies. In: *Convention on the Conservation of European wildlife and Natural Habitats.* 27th meeting Strasbourg, 26–29 November 2007, 59 p.

24. Huntley B., Berry P. M., Cramer W., Mcdonald A. P. 1995. Modeling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography*. Vol. 22. P. 967–1001.
25. Hüve K., Bichele I., Tobias M., Niinemets Ü. 2006. Heat sensitivity of photosynthetic electron transport varies during the day due to changes in sugars and osmotic potential. *Plant, Cell and Environment*. Vol. 29. P. 212–228.
26. IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate change 2007: the Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the IPCC. Online at: http://www.ipcc.ch/ipccreports/as4-wgl.htm
27. Jentsch A., Kreyling J., Beierkuhnlein C. 2007. A new generation of climate change
28. Johnston M. 2010. Tree Species Vulnerability and Adaptation to Climate Change: Final Technical Report. Saskatoon: Saskatchewan Research Council Publication No. 12416-1E10.
29. Jump A. S., Hunt J. M., Martinez-Izquierdo J. A., Penuelas J. 2006. Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica. Molecular Ecology*. Vol. 15. P. 3469–3480.
30. Jump A. S., Matyas C., Penuelas J. 2009. The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*. Vol. 24(12). P. 694–701.
31. Jump A. S., Penuelas J. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*. Vol. 8. P. 1010–1020.
32. Kattge J., Knorr W. 2007. Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant, Cell and Environment*. Vol. 30. P. 1176–1190.
33. Kelly C. K. Chase M. W., de Bruijn A., Fay M. F., Woodward F. I. 2003. Temperature-based population segregation in birch. *Ecology Letters.* Vol. 6. P. 1–3.
34. Kozlowski T., Kramer P. J., Pallardy S. G. 1991. *The Physiological Ecology of Woody Plants*. New York, etc: Academic Press.
35. Kreyling J., Beierkuhnlein C., Elmer M., Pritsch K., Radovski M., Schloter M., Wöllecke J., Jentsch A. 2008. Soil biotic processes remain remarkably stable after 100-year extreme weather events in experimental grassland and heath. *Plant and Soil*. Vol. 308. P. 175–188.
36. Larcher W. 2003. *Physiological Plant Ecology*. 4th ed. Springer, Berlin, etc.
37. Law R. D., Crafts-Brandner S. J. 1999. Inhibition and aclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase / oxygenase. *Plant Physiology*. Vol. 120. P. 173–181.
38. Lekevičius E. 1986. *Elements of a General Adaptation Theory*. Vilnius, Mokslas Publ. (in Russian).
39. Lekevičius E. 1997. *A Model of Adaptive Rearrangements on Community, Population and Organism Levels*. Thesis for Habilitation. Vilnius, Institute of Ecology.
40. Lekevičius E. 2006. The Russian paradigm in ecology and evolutionary biology: pro et contra. *Acta Zoologica Lithuanica*. Vol. 16(1). P. 3–19.
41. Lekevičius E. 2007. Gyvosios gamtos adaptyvumas ir jos prisitaikymo prie antropogeninių pokyčių galimybės (teorinė studija). In: M. Žalakevičius, V. Būda ir E. Lekevičius (eds.) *Biota ir globali kaita*. Vilnius: Institute of Ecology of Vilnius University. P. 8–78.
42. Marshall C. R., Raff E. C., Raff R. A. 1994. Dollo's law and the death and resurrection of genes. *Proceedings of the National Academy of Sciences of the USA* Vol. 91. P. 12283–12287.
43. Mattick J. S. 2004. The hidden genetic program of complex organisms. *Scientific American*. Vol. 291. P. 60–67.
44. Mátyás C. 1996. *Adaptation Processes in Forest Tree Populations*. Dr. Sci. Thesis, Sopron, 198 p. (in Hungarian).
45. Moberg A., Sonechkin D. M., Holmgren K., Datsenko N. M., Karlen W. 2005. Highly variable Northern Hemisphere temperatures reconstructed from low- and high-resolution proxy data. *Nature*. Vol. 433. P. 613–617.
46. Norberg J. 2004. Biodiversity and ecosystem functioning: a complex adaptive systems approach. *Limnology and Oceanography*. Vol. 49. P. 1269–1277.
47. Overpeck J., Whitlock C., Huntley B. 2003. Terrestrial biosphere dynamics in the climate system: past and future. In: K. D. Alverson, R. S. Bradley, T. F. Pederson (eds.). *Paleoclimate, Global Change and the Future*. Berlin: Springer-Verlag. P. 81–111.
48. Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*. Vol. 37. P. 637–669.
49. Pearson R. G., Dawson T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*. Vol. 12. P. 361–371.
50. Pielou E. C. 1991. After the Ice Age: *The Return of Life to Glaciated North America*. Chicago: Chicago Univ. Press.
51. Pietikäinen J., Pettersson M., Bååth E. 2005. Comparision of temperature effects on soil respiration and bacterial and fungal growth rates. *FEMS Microbiology Ecology.* Vol. 52. P. 49–58.
52. Poumadère M., Mays C., Le Mer S., Blong R. 2005. The 2003 heat wave in France: dangerous climate change here and now. *Risk Analysis*.Vol. 25. P. 1483–1494.
53. Pretzsch H. 2005. Diversity and productivity in forests: evidence from long-term experimental plots. In: Scherer-Lorenzen M., Korner C., Schulze E.-D. (eds.). *Forest Diversity and Function: Temperate and Boreal Systems*. Berlin: Springer. P. 41–64.
54. Rehfeldt G. E., Tchebakova N. M., Parfenova Y. I., Wykoff W. R., Kuzmina N. A., Milyutin L. I. 2002. Intraspecific responces to climate in *Pinus sylvestris. Global Change Biology*. Vol. 8. P. 912–929.
55. Repo T., Leinonen I., Wang K.-Y., Hänninen H. 2006. Relation between photosynthetic capacity and cold hardiness in Scots pine. *Physiologia Plantarum*. Vol. 126. P. 224–231.
56. Robakowski P., Montpied P., Dreyer E. 2002. Temperature response of photosynthesis in silver fir (*Abies alba*) seedlings. *Annals of Forest Science*. Vol. 59. P. 163–170.
57. Sage R. F., Kubien D. S. 2007. The temperature response of C_3 and C_4 photosynthesis. *Plant, Cell and Environment*. Vol. 30. P. 1086–1106.

58. Schlichting 2008. Hidden reaction norms, cryptic genetic variation, and evolvability. *Annals of the New York Academy of Sciences*. Vol. 1133. P. 187–203.
59. Strain B. R., Chase V. C. 1966. Effect of past and prevailing temperatures on the carbon dioxide Exchange capacities of some woody perennials. *Ecology.* Vol. 47. P. 1043–1045.
60. Thompson I., Mackey B., McNulty S., Mosseler A. 2009. *Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity / resilience / stability relationship in forest ecosystems.* Secretariat of the Convention on Biological Diversity, Montreal. Technical Series. No. 43, 67 p.
61. Valladares F., Pearcy R. 1997. Interactions between water stress, sun-shade acclimation, heat tolerance and photoinhibition in the sclerophyll *Heteromeles arbutifolia*. *Plant, Cell and Environment*. Vol. 20. P. 25–36.

Edmundas Lekevičius, Remigijus Ozolinčius, Arūnas Samas

VIDUTINIO KLIMATO MIŠKŲ PLASTIŠKUMO RIBŲ MODELIAVIMAS

Santrauka

Aptariami ir modeliuojami duomenys apie miško augalų ir dirvos mikroorganizmų gebėjimą priderinti prie aplinkos pokyčių optimalias ir pesimalias temperatūras. Pateikiamas konceptualus neįprastos karščio bangos, tikėtinos klimato atšilimo sąlygomis, poveikio miško ekosistemai modelis. Kaip rodo empiriniai duomenys, augalų ir dirvos mikroorganizmų augimui optimalios temperatūros skiriasi tarpusavyje, tuo tarpu skirtumai tarp vienai ir kitai gildijai pesimalių temperatūrų nėra dideli. Tikėtina, kad karščio bangos atveju vidutinio klimato sąlygomis miško pirminė produkcija ir vietiniai medžiagų ciklai nukentės, kai oro temperatūra pasieks apytikriai tą pačią ribą, maždaug 40 °C. Kelių °C „plastiškumo atsarga“, būdinga vidutinio klimato miškui, greičiausiai byloja apie tai, kad praeityje čia būta didesnių atšilimų už dabartinį. Antra vertus, dabartinėse augalų, ir ne tik jų, populiacijose iki šiol gali būti saugoma informacija apie palyginti netolimoje praeityje vykusius klimato atšilimus, panašius į dabartinį. Visai galimas dalykas, kad ji yra įgavusi retų genų, genotipų (fenotipų) ar tokių pat rūšių pavidalą. Taip pat tikėtina, kad ji yra virtusi tylinčiais lokusais ir gali būti aktyvuota šiluminio streso atveju.

Raktažodžiai: augalai, dirvos mikoorganizmai, klimato kaita, karščio banga, prisitaikymas