

The effect of temperature and humidity changes on insects development and their impact on forest ecosystems in the context of expected climate change

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Abstract. Ongoing climate change is mainly evident as increased in average temperature. It is expected to have a significant impact on world's biomes, with forest ecosystems especially vulnerable to these changes. The effect of climate change on forests is both indirect, through its impact on various tree species of different ecological requirements, and direct, through its impact on all living components of the forest ecosystem. Among the latter, insects are the group of the greatest importance, including species detrimental to forest health. The impact of climate change on forest insects may be reflected in their distribution, phenology, activity, number of generations and, indirectly, through impact on their natural enemies. Predicting the future direction and pace of the climate change, as well as direct and indirect consequences of its effect on forest insects is difficult and often subject to considerable inaccuracy. The paper presents a review of data from the published literature in this area of study. The influence of the basic climate parameters, temperature and humidity, on forest herbivore insects is discussed, particularly in the context of the most probable scenarios of climate change, i.e. the gradual increase in the average temperature. Observed and projected impacts of climate change in relation to the influence of herbivorous insects on forest ecosystems are characterised. We present some of the possible adaptation strategies of forest management to the expected climate changes.

Key words: global warming, forest insects, population dynamics, forest insects' outbreaks, range shift, phenology, forest management

1. Introduction

Climate changes have significant impact on natural environment, regardless of their primordial cause. They also influence forest ecosystems. On the one hand, alternated basic climate parameters affect individual tree species of different ecological requirements directly, on the other hand, it affects all other living components of the forest ecosystem. Among the latter, insects are the group of the greatest importance, including species detrimental to forest health with regard to forest management.

Insects belong to an ectothermic group of animals; thus, they are highly dependent on thermal conditions of the surrounding environment. Hence, besides food plants, climate conditions are basic factors that form

insect range. Any climate changes are not neutral for insects' assemblages. The impact of climate change on forest insects may be reflected, e.g. by affecting their range, phenology, activity, number of generations and winter survival. Among the present theories of climate changes, average temperature increase theory dominates (IPCC 2007). Most of the several dozens of predictive models indicate that average temperature can increase by 1.7–5.3°C, as a result of doubling CO₂ concentration within next 60–100 years. 2.3°C is a value most often mentioned what means an increase by 0.3°C a decade.

As opposed to temperature, humidity is characterised by higher variability. It is difficult to indicate a distinct trend within humidity as it is with regard to temperature. By average temperature increase, atmospheric precipitation increase in the middle and the northern

parts of the Northern Hemisphere is predicted. Apart from that, it is assumed that water shortage will intensify in the temperate zone in result of temperature increase that will cause increase in evaporation. Soil will dry up due to the result of varied factors: time reduction of the snow retention, high saturation of surface soil at the end of the winter and an accelerated surface water drainage (Sadowski 1996, Chmura et al. 2010).

In the opinion of many researchers, predicted climate changes will have an adverse influence on forests (Wigley 1993; Ayres, Lombardero 2000; Battisti 2008; Moore, Allard 2008). For instance, increase in fires and adverse weather phenomenon (i.a. floods and hurricanes) is predicted. In effect, a negative influence of secondary pests will accelerate (Sadowski 1996; Logan et al. 2003). Tree species of narrow ecological tolerance (for instance, spruce and fir) will retreat in Europe in favour of species of a broad ecological optima (for instance, poplar and alder) what involves a structural change in dominant herbivores (Ryszkowski et al. 1995). Northern and southern range shift is predicted with regard to many insect species towards higher altitude and elevation (Pawłowski 1995; Parmesan 1996; Walther et al. 2002; Parmesan, Yohe 2003; Menéndez 2007; Battisti 2008). It involves a risk of expansion and adjustment of new, sometimes dangerous pests. Many native herbivore species can increase the annual generations' number, as well as they can increase their chances to survive the winter, and in result, they can multiply the population number (Ayres, Lombardero 2000; Battisti 2008; Netherer, Schopf 2010). Climate changes can also affect the activity of native pests' species that previously had no significant role for forests (Tenow et al. 1999).

Future direction and pace of the climate change as well as its direct and indirect effects are difficult to predict. It is caused by time and space unpredictability and variability of climate parameters, as well as by varied ways of climate influence on individual functional groups of biocoenosis and, last but not least, by the complexity level of the biocoenosis. However, it is also essential to recognise the mechanism behind climate influence on individual ecosystem components and in case of forest environment – on insects that are ecological guilds of a great importance to forest ecosystem. This paper is a review on selected literature regarding the aforementioned problem. We discuss different ways of influence of the climate basic parameters – temperature and humidity – on phytophagous insects, regarding the most probable scenario of climate changes, i.e. successive increase in the average temperature on Earth.

We discuss humidity influence less, because of small number of research and difficulties with interpreting results. By giving examples, we also characterise predicted and observed effects of climate changes with regard to the influence of phytophagous insects on forest ecosystem. Finally, we present several bearings of forest management adaptation regarding predicted climate changes and phytophagous insect influence.

2. The influence of climate on insects

The basic climate parameters, i.e. temperature and humidity, influence insects both directly and indirectly. The direct influence can be observed through limiting and stimulating the activity of larvae and adults, insects dispersal in the environment, phenology and growing length, as well as through the possibility of surviving in adverse weather conditions population genetics, etc. Indirect influence includes a climate influence on environment where insects appear, such as influence on plant formations, plant phenology, food quality, predators, parasitoids and activity of entomopathogens.

It should be emphasised that the present review does not exhaust the subject and the list of all possible relations between climate changes and insects population dynamics. However, it is essential to present examples of basic interactions that occur between aforementioned elements.

2.1. Direct influence

2.1.1. Activity

Insects as poikilothermic animals change their activity visibly depending on the temperature of the surrounding environment (Bale et al. 2002; Menéndez 2007). Increasing the temperature to the thermal optima level causes acceleration of the insect metabolism. Hence, it directly influences their activity increase. In the temperate climate zone conditions, the average temperature increase is followed by i.a. more intensive and longer total day and night's activity of imago of majority phytophagous species in forest environment, implied as feeding and mating, as well as time spent on finding proper place for laying eggs (Moore, Allard 2008; Netherer, Schopf 2010). It can also result in insects dispersion increase in the forest environment, as well as more frequent oviposition and possibility of colonising larger number of host plants.

2.1.2. Length of insect growth

In higher temperature conditions, the development of egg, larva and pupa shortens, which is the characteristic phenomenon for large group of forest species (Szujecki 1998). Faster development of preimaginal stages implies shorter time of exposure to adverse environment conditions such as low temperature, too high or insufficient humidity, attacks of predators and parasitoids, and entomopathogen's activity. It can result in reproductive success of many insect species.

Temperature influence on a length of larval development has been observed under laboratorial conditions for two significant species of native foliophages: the nun moth, *Lymantria monacha* (L.) and the gypsy moth *Lymantria dispar* (L.) (Karolewski et al. 2007). In both cases, temperature increase has had an influence on reducing growth period, from egg phase to pupa. Different results have been obtained regarding larva survivability of both species. When the average environment temperature has increased, higher mortality has been observed for caterpillars of *L. monacha*. Whereas the survivability of *L. dispar* larvae has increased. These differences probably result from two different thermal optima for both species reflected in varied environmental preferences. The results of the described experiment present variety of climate parameters' influence on the insect development, even when closely related species are compared.

2.1.3. Phenology

Under the temperate climate zone conditions, periodicity of insect activity in the environment is influenced by a sequence of seasons. Temperature is particularly important as a factor that limits insects activity. Average temperature changes are interrelated with changes within insect phenology. It is one of the well-documented sign of a global warming. Earlier appearance of some species in spring and their longer activity are the most characteristic symptoms of a global warming (Walther et al. 2002; Logan et al. 2003; Parmesan, Yohe 2003; Menéndez 2007; Moore, Allard 2008). The described examples can have a significant influence with regard to herbivores that develop more than one generation during the year. Average temperature increase causes faster growth and can have an influence on generation number increase of these species. As a result, biological life cycle is shortened and the larva number on the one host plant, as well as outbreaks

frequency, increases. Negative influence of the average temperature increase on the forest management is observed with regard to European spruce bark beetle *Ips typographus* (L.), which is the most dangerous pests of this tree species in Europe, including Poland (Jönsson et al. 2007; Netherer, Schopf 2010).

Winter climate conditions are key importance for many insects of the temperate climate zone. Temperature increase in winter can cause survival increase, what occurs especially in northern and upper range borders, where extreme low temperature usually causes higher mortality within the population. However, many species is not able to finish the developmental cycle or to continue feeding in spring without sufficient number of low temperature days (Jönsson et al. 2007; Netherer, Schopf 2010). Decrease of snow retention as a result of average temperature and humidity increase can also have a negative influence on species that overwinter in forest bed and soil (Nupponen et al. 2010).

2.1.4. Population genetics

Climate changes can cause faster evolutionary adaptation than usually. Menéndez (2007), Moore and Allard (2008) and Régnière (2009) have presented a short review of researches on it regarding selected insect species. They have observed how European butterfly Brown Argus *Aricia agestis* (Den. & Schiff.) adapted to new thermal conditions in short period of time by shifting diapause-inducing temperature threshold. Another example of such phenomenon is the chrysomelid beetle *Chrysomela aeneicollis* (Schaeff.) for which an increase in allele frequency responsible for the synthesis of low-temperature proteins resistance has been observed. Hill et al. (1999) have presented results that show morphological changes in the population of the butterfly *Pararge aegeria* (L.). Individuals from the population that colonised new areas in Great Britain for 20 years before the studies have started had larger wing area surface as well as weight of the thorax in comparison with individuals from the settled populations. The increase in dispersal forms has also been observed on the British Isles for the two bush-cricket species *Conocephalus discolor* (F.) and *Metrioptera roeselii* (Hagenbach) that have extended their previous range (Thomas et al. 2001).

There are also examples of forest phytophages that show high adaptive capability to dynamically changing environmental conditions. Larvae of the Winter Moth *Operophtera brumata* (L.), which is the important

folivore of deciduous trees and shrubs, hatch in early spring, after overwintering in egg stadium on host plants' shoots. The time of hatching is crucial for the species. In case of too early hatching in relation to buds and leaves growth, mortality of caterpillars increases as a result of starvation. However, the recent research has showed that there is a natural selection in *O. brumata* populations that favours genotypes characterised by slower egg development (Asch 2007). As a result, hatch occurs few days later nowadays than it was previously and because of that a synchronisation of caterpillar hatching with bud burst is preserved.

2.2. Indirect influence

2.2.1. Influence on physiology and metabolism of host plants

Temperature and humidity change can influence insects indirectly by changes in host plants metabolism and physiology (Ayres, Lombardero 2000; Rouault et al. 2006; Moore, Allard 2008; Netherer, Schopf 2010).

In general, it is indicated that long and intense droughts, as one of the average temperature increase results, have negative impact on plants' condition, thus increasing their susceptibility to phytophagous insects. Dying of oak stands, as a result of water shortage followed by folivore, cambioophage, and xylophage attacks, is a current example of such interaction observed in Europe (Thomas 2008). Although a moderate temperature increase (as well as and CO₂ concentration) can cause a decrease in food quality for some foliophages, as a result of nitrogen level decrease in foliage, as well as an increase in the synthesis of secondary metabolites, e.g. tannins (Buse et al. 1998; Dury et al. 1998; Kuokkanen et al. 2001). It has an influence on deterioration of plant as food and may increase plant resistance.

Huberthy and Denno (2004) and Rouault et al. (2006) have conducted a result meta-analysis regarding the influence of plant humidity shortage on development, survivability and fertility of phytophagous insects. Their studies have been inspired by observed discrepancy between outbreaks number in natural environment that often occur after droughts, and results that have showed negative influence of water shortage on phytophagous insects. Analysis results have indicated that reactions of phytophagous insects to water level decrease in plants tissues depend on their affinity to ecological guilds, so to the group of species sharing similar feeding habit. Positive influence of drought (especially long-lasting

drought) has been observed with regard to insects developing in wood, whereas the decrease in water and turgor level in plant cells has had negative influence on species that suck out liquids from tissues (aphids) and on species that develop in galls. Analysis results of the influence on other phytophagous insects, external leaf feeders and leaf miners, have been ambiguous.

2.2.2. Host plant phenology

Development of many phytophagous insects is closely related with host plant phenology (Szujewski 1998; Bale et al. 2002) that is mainly regulated by temperature conditions in the environment. The same factor, such as average temperature increase, can influence differently on plants and phytophagous insects. Examples of negative influence of climate changes are described, e.g. resulting from disruption of synchronisation of important processes occurring at different trophic levels of the ecosystem. For instance, higher temperature in early spring can cause earlier development of oak leaves what results in disruption of synchronisation between the process and the hatching of winter moth larvae (Visser, Holleman 2001). Similar interrelation has been observed for the nun moth for which the development of the first-instar larvae is usually correlated with the formation of the flowers in Scots pine. Male flowers of pine trees are highly important food for the nun moth larvae, by increasing species survival and faster development, and any disturbance of the interrelation affects the species negatively (Laryšev 1968; Śliżyński 1970; Withers, Keena 2001). The tortricid moth *Zeiraphera griseana* (Hbn.) is another example of the similar interrelation. However, faster plant growth in spring and longer vegetation can be beneficial to these phytophagous species that develop inside plant organism. It applies to some European spruce bark beetle species that can have extra generation during the year (Netherer, Schopf 2010).

2.2.3. Activity of natural enemies

Natural enemies are another element of the ecosystem by which climate changes influence indirectly phytophagous insects. Enemies activity and effectiveness and the way of influencing phytophagous populations can be diverse. Furthermore, interrelation of both the elements (phytophages versus natural enemies) is complicated by indirect climate influence on host plants. For instance, lower food quality of

plants in result of drought causes longer development of phytophages (see Section 2.2.1) what determines higher probability of the attacks of natural enemies, such as predators and parasitoids (Coviella, Trumble 1999; Rouault et al. 2006). On the other hand, plant chemism change, caused by climate parameters influence, results in quality change (size and chemical contents) of phytophagous insects as hosts, for example, of parasitoid larvae. It influences elements as parasitoid effectiveness of the victim search, the egg number, the size and sex ratio (Coviella, Trumble 1999).

Higher temperature as the stimulating factor can cause activity increase of natural enemies and their faster development (Netherer, Schopf 2010). Temperature influence can also regard phytophagous insects itself and as such it can influence their susceptibility to enemy attacks. For instance, under higher temperature conditions, weaken reaction for alarm pheromones, produced in case of predator or parasitoid attack, has been observed for aphids (Awmack et al. 1997). On the other hand, faster development, induced by higher temperature, especially in instars exposed to parasitoid attacks, can result in higher survivability of some phytophages (Petzoldt, Seaman 2006).

3. Climate changes' effects observed in forest ecosystems in result of entomofauna influence

3.1. Range shift of phytophagous insects

The current distribution pattern of most insect species is an effect of climate. The phenomenon can be observed particularly on range borders where temperature is a main limiting factor. For instance, -16°C is the critical value for North American species of bark beetle *Dendroctonus frontalis* Zimm., one of the most dangerous pests for coniferous trees in the region. Nearly absolute mortality of the population occurs below this value. Such temperature is observed on the northern range border of the aforementioned species (Ayres, Lombardero 2000). It implies that average temperature increase can enable more termophilous species to expand in the northern direction and on higher altitudes. Simultaneously, southern and lower range borders can be shifted (Parmesan 1996; Walther et al. 2002; Parmesan, Yohe 2003; Menéndez 2007; Battisti 2008). With regard to many phytophagous insects, a range increase is probable also because species' ranges are smaller than areas where their host plants grow.

Many examples of insects' range shift were observed in recent years. In the 1990s, few leaf mining moths of the family Gracillariidae have occurred in the Central Europe, including Poland (Šefrová 2003). The horse-chestnut leaf miner *Cameraria ohridella* Deschka & Dimić that attacks horse chestnuts *Aesculus hippocastanum* was the most spectacular example among them. Apart from accidental introduction of the pest, shifting of the northern and eastern range borders, as a result of temperature increase, was the most probable cause of the species expansion to new areas.

Range shift of forest folivores in Europe has been well researched for two species of geometrid moths, Winter moth, *O. brumata*, and Autumnal moth, *Epirrita autumnata* (Borkh.), in forest stands of northern Scandinavia (Jepsen et al. 2008). Cyclic outbreaks have been observed for both species in the aforementioned area sometimes leading to substantial loss of foliage. For the last 15–20 years, areas of both defoliators' mass outbreaks have increased significantly. *Operophtera brumata*, a species less resistant to low temperature, has expanded to the north-east to areas where *E. autumnata* was the dominant species so far. The latter has increased range to areas located inland and characterised by cooler climate. According to authors range increase for both species results from increase of both average year temperature and minimum winter temperature. The Pine processionary moth *Thaumetopoea pityocampa* Den. & Schiff is another well-documented example of the species range shift with regard to the influence on forest management. The species is recognised to be one of the main foliophagous pests in the Mediterranean region. Temperature in winter, when caterpillars feed on needles of various pine species (rarely on other coniferous species), is the main factor that influences range limits of *T. pityocampa*. From the mid-1970s to 2004, the species enlarged its range in France to the north direction by almost 90 km. In the same period, its upper range border in Italian Alps moved up by over 200 m in some regions (Battisti 2008; Battisti et al. 2005). Same observations have been made for changes in an upper range border of the species in Spanish Sierra Nevada (Hódar, Zamora 2004). Average temperature increase enabled expansions to areas that have not been colonised before. Higher survivability of caterpillars in winter, during feeding time, was observed (Battisti et al. 2005, Buffo et al. 2007), whereas warmer nights in summer (with temperature over 14°C) influenced distance and altitude increase of female expansion (Battisti et al. 2006).

It has been often pointed at the necessity of constant monitoring of insects range shifts and of selecting either species or groups of insect species that would indicate changes in forest environment (for instance, Ayres, Lombardero 2000; Bale et al. 2002; Logan et al. 2003; Menéndez 2007). Attempts at predicting species range shift have also been made (for instance, Williams, Liebhold 1995 a, b; Jönsson et al. 2007; Régnière 2009). Apart from ecological requirements of indicator organisms, varied factors are included in the aforementioned research, such as typology (for instance, the type of habitats and plant formations) and climate parameters (average, minimum and maximum temperature/precipitation per month). The variability of the latter implies noticeable bias in any attempts to predict changes in insects range. Hence, such predictions can only be seen as possible scenarios. Results can be influenced by relatively small changes in parameters that with regard to climate unpredictability (even in few-year scale) can hinder from making any exact prognosis.

Williams and Liebhold (1995a, b) have conducted prognostic research on insect range shift. They have used data on defoliated forest stands in the states of Oregon and Pennsylvania that were previously exposed to attacks of tortricid moth *Choristoneura occidentalis* Free and of *L. dispar*. Alternative scenarios have been discussed that included: (a) average temperature increase by 2°C and unchanged precipitation level, (b) average temperature increase by 2°C and precipitation level decrease by 0.5 mm/day and (c) average increase in values of both parameters. Average temperature increase and unchanged precipitation level have been factors that caused *L. dispar* expansion increase, while predicted range of *Ch. occidentalis* has decreased. The assumed temperature increase and precipitation level decrease have caused range decrease of both defoliators, whereas increase of both parameters was positively correlated with the growth of the outbreaks areas.

Similar research has also been conducted in Finland (Vanhanen et al. 2007). Probable range shifts of *L. monachal* and *L. dispar* have been predicted on the basis of selected average temperature change scenarios that are included in Intergovernmental Panel on Climate Change (IPCC) report of 2001. Each simulation (i.e. temperature increase by 1.4, 3.6 and 5.8°C) has initiated range shift for both species. Northern and southern range borders of both species have shifted by 500–700 and 100–900 km, respectively, in the North Pole direction.

3.2. Activity of phytophagous insects and its harmful effects: outbreaks frequency

Many insect species belongs to the group of pests with regard to the forest management. Cyclic outbreaks of some phytophagous insects are connected with forest condition decrease, losses in forest production and with bearing high costs of controlling pest population. Therefore, it is essential to answer the question to what degree predicated climate change will interrelate with negative influence of insect species on forests.

American researchers have conducted interesting studies in this respect (Currano et al. 2008). They have analysed plant fossils dated for 59–52 million years (at the turn of the Paleocene and Eocene). One of the highest temperature increases was noted on Earth at this time (by about 6°C) in result of larger CO₂ concentration in the air. According to authors the then climate conditions on Earth can be compared to the current situation. They have observed that the average level of damages of leaf lamina made by folivores and the average temperature increase, as well as CO₂ concentration, were positively correlated. It was explained by the increase in CO₂ concentration in the air which interrelates with increase in carbon-to-nitrogen ratio in plant tissues resulting in decrease in the nutritive values of the foliage. Hence, losses from lower leaves nutritional value need to be compensated by higher consumption. Comparing the aforementioned results with the currently observed climate changes, increase in defoliation levels should be expected, followed by increased damage of forest stands (Rouault et al. 2006; Battisti 2008; Currano et al. 2008; DeLucia et al. 2008).

Changing thermal conditions and humidity both can have positive and negative influence on insects. Battisti (2008) has given an example of two forest phytophages on which temperature increase had significantly different influence. Between 1985 and 1992, an unexpected mass outbreak of web-spinning sawfly *Cephalcia arvensis* Panzer, an oligophagous hymenopteran species associated with spruce, was observed in Southern Alps. The species usually do not have a tendency to a mass outbreaks, which result from limited dispersal abilities and low female fertility, as well as from long (even up to few years) diapause followed by higher mortality in the population. According to authors, the outbreak of *C. arvensis* was caused by few-year-period of high average temperatures and drought in June and July, during larval feeding time. On the one hand, higher temperature and low humidity caused shorter

development of larvae of *C. arvensis*; on the other hand, enabled faster pupation and avoiding the longer diapause. In effect, the species has produced generation once a year for few years, which caused sudden eruption of population density.

The opposite phenomenon has also been observed in the region of Alps for another folivore species, Larch Tortrix *Zeiraphera griseana* (= *diniiana*). The species develops on few coniferous species; however, its main host plant in the discussed area is larch. The species is of great significance because of 8- to 10-year cycles of outbreaks; the history of which was estimated on the basis of dendrochronological research dating back over a thousand years (Esper et al. 2006). Caterpillars of *Z. griseana* hatch in spring and commence feeding on developing needles. Starting from 1989, a significant decrease in the number of larch tortrix has been observed for few seasons. In effect, the number of outbreaks has dropped as well. Meteorological analyses have showed that high temperature in winter and spring influenced higher mortality of eggs and disturbance of synchronisation between eggs 'hatch and needles' development.

Climate change can also cause higher activity of pest species that was not significant before for the forest management in the area. The outbreak frequency of the European pine sawfly, *Neodiprion sertifer* (Geoff.), regarding temperature increase and selected environmental elements, has been analysed in Finland (Virtanen et al. 1996). Research has showed that days with the temperature lower than -36°C in winter is the main factor limiting *N. sertifer* outbreaks in the Northern Finland because the high mortality of eggs is observed below this temperature. The same research has focused on scenario of the average winter temperature increase by 3.6°C to 2050. According to authors, the global warming can cause increase in the outbreaks frequency of the European pine sawfly in areas where the species does not occur or occurs sporadically.

Similar simulations regarding population dynamics of European spruce bark beetle have been performed in Southern Sweden (Jönsson et al. 2007). Currently, the species has only one generation during the year in the researched area. By predicted increase in yearly average temperature by $2\text{--}3^{\circ}\text{C}$, the second swarming of the beetles is possible and increase by $5\text{--}6^{\circ}\text{C}$ can cause development of the another generation. However, the authors have noticed that favourable thermal conditions for *I. typographus* can occur nor every year, even if the predicted scenario will be realised. Adequately

early time of spring swarming and shorter period of development preimaginal stages influence the possible development of the second generation of the species.

3.3. Invasive species

Insects belong to the group of animals where alien species are the most frequently represented for the area. Climate change can result in adaptation, population increase and expansion of alien species that are better adapted than native taxa (Capdevila-Argüelles, Zilletti 2008). Temperature increase can positively influence the population number of introduced species whose development and survivability were limited before by low temperature. Apart from climate change, human activity is the significant factor in the process, such as intentional or accidental introducing of exotic plants and phytophagous species.

In European forest ecosystem, two moths in the family Gracillariidae are claimed to be invasive: *Parectopa robiniella* Clem. and *Phyllonorycter robiniella* (Clem.) that arrived to Europe from North America (Šefrová 2003). Caterpillars of both species develop in leaf mines on the leaves of the black locust *Robinia pseudoacacia* L., a tree species introduced in Europe at the beginning of the 17th century. Even though the host plant has been present for the several centuries in Europe, both insect species were recorded for the first time in the second half of the 20th century in the Southern regions of the continent. Since then, the expansion process is observed in the Northern direction, and the phenomenon is usually explained to be caused by global warming.

3.4. Host shifts of phytophagous insects

Insect range shifts, resulting from changing climate parameters influence, can also cause insects adaptation to new host plants. The situation occurs especially when closely related species of the host plant exists in the new range of the phytophagous insect. Widening of host plants spectrum or even a change in feeding preferences by using available niches can occur. *Thaumetopoea pityocampa*, observed in Serra Nevada Mountains, in southeast Spain, is an example of such a phenomenon. The average temperature increase for the last several decades enabled species dispersion to the higher altitudes where it has not existed before. Range shift was accompanied by adaptation to the new host plant, i.e. a relict subspecies of Scots pine, *Pinus sylvestris* var. *nevadensis* (Hódar, Zamora 2004).

4. Forest management adaptation to climate change with regard to entomofauna influence

The contemporary forestry faces many challenges and predicted climate change is one of the most important among them. Climate parameters change will have both positive and negative influence on forest ecosystems. In the temperate zone, longer vegetation and faster photosynthesis are expected in result of higher CO₂ concentration. It can result in higher wood production. Stress factors, such as water shortage, adverse weather phenomenon and higher pathogen and phytophages activity, can cause deterioration of the forest condition. Therefore, changes in structure, productivity and functioning of the forest ecosystem can also be observed in result of predicted climate change, and it can influence forest management. Because of the aforementioned issues, it is crucial to adapt forest ecosystems and forest management to climate changes (Resolution H4 1993; Spittlehouse, Steward 2003; Moore, Allard 2008; Netherer, Schopf 2010).

Forestry adaptation to climate change can be discussed as:

- a spontaneous process, although limited and proceeding at too slow pace in comparison to change progression and
- a process of forest and forestry adaptation that should be proceeded by a sensible way of forest management; it should include current and predicted climate changes and secure complete productive, ecological and social role of the forest or at least, should minimise wastes within these roles.

The former definition of adaptation results from natural ability of forest ecosystem to adapt to new conditions; the latter also includes modification in current law and regulations.

The strategy of adaptation of forests (natural ecosystems) and forestry (practices and forest management) to climate change with regard to influence of insects should be considered in all its bearings. Part of the strategy will not differ from general directions that have been used in forestry for many years. Regarding stability and stress resistance of the forest stand, including insect attacks, adjusting species composition of the stand to habitat's conditions is important. It is hoped to use natural tree (species, populations, phenotypes) resistance against insect attack; however, these actions should be preceded by a research on resistance heredity. Including phenology of trees and

their pests in forest plans can prevent or limit defoliation, for example, in result of disturbing synchronisation between bud burst and leaf development and hatching of larvae. Introducing late-developing oak species forms could be a good example of such actions because it is more resisted against damages caused by frost and foliophages in the spring. Species of lower susceptibility to water shortage should be prioritised because it can limit the primary weakening of tree conditions and forest stands what is important in case of drought, and in results, can reduce the risk of the secondary attacks of phytophagous insects. The sessile oak *Quercus petraea* or the grey alder *Alnus incana* are examples of the tree type that have lower water requirements in relation to the common oak *Quercus robur* and black alder *Alnus glutinosa*, which are currently more popular. Water retention in forests should be introduced and maintained to limit the risk of stress related to water shortage and, indirectly, to secondary pests attacks.

Global warming is conducive to range shift of some organisms, including many pest species. The risk for invasive species occurrence and damage resulting from their influence on forest ecosystems can be sometimes estimated in advance on a basis of knowledge about ecological requirements of phytophages and host plants distribution. New, modern tools, geographic information system, simulation and prognostic models among others, can enable to achieve it (Williams, Liebhold 1995a, b; Jönsson et al. 2007; Vanhanen et al. 2007; Régnière 2009). It will be essential to include in a future management planning elements of variability and uncertainty, as well as risk analysis and decision support system in case of new pest species occurrence (Moore, Allard 2008; Chmura et al. 2010; Netherer, Schopf 2010). Together with the trade development, the amount of transported goods and new areas of their distribution, it is the increased risk of alien species that will be significant for the forestry. Therefore, wood trade control and quarantine regulations will have a significant role. It is also necessary to develop effective system of detecting, monitoring and controlling invasive species.

5. Conclusions

There are currently many evidences for climate change on Earth. The most popular hypothesis states that average temperature will increase in result of higher CO₂ concentration in the atmosphere, among others. Predicted changes will have a significant influence on forest ecosystems and on all elements of forest

biocenosis: both trees that are forest's basic component and other groups of organisms. Climate changes are important for phytophagous insect species, and basic climate parameters – temperature and humidity – influence it both directly and indirectly. Research, performed to estimate climate change influence on insect development and activity, often produced equivocal results. However, on the basis of the result synthesis, the following general conclusions can be made:

1. Global warming is conducive to polyphagous and eurytopic species. It results from higher ecological plasticity and adapting abilities of the organisms.

2. The general observations of the climate change influence on phytophagous insects suggest that the role of thermophilous species has currently increased. This results mainly from range shift to the northern direction and to higher altitudes.

3. In result of changing climate conditions, some phytophagous species status can change, the role some species can increase, while the other can decrease.

4. The number and the role of phytophagous species overwintering in egg stage have increased in comparison to species that overwinter in other development stages. It relates to average temperature increase in winter as larvae, pupae and the adults show higher mortality at that time, whereas eggs have probably higher resistance to low temperatures.

5. Stress, which results from water shortage, is one of the global warming consequences. It can have varied influence on phytophagous insects population dynamic. An effect of the influence is related not only to frequency and the level of water shortage but also to the trophic guild that a phytophagous species belongs. In general, species developing in wood present positive reactions to moderate decrease of humidity. Humidity shortage negatively influences species that suck sap from plants tissues as well as gall-makers. Research regarding typical foliophages as well as leaf-miners does not give unequivocal results.

6. Climate change together with constantly increasing trade can be conducive to invasive phytophagous insect species. Absence of effective natural enemies in new areas and higher plasticity of invasive species in comparison to native species can cause higher level of damage in forest ecosystem.

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