ISSN 1995-4255, Contemporary Problems of Ecology, 2020, Vol. 13, No. 7, pp. 780–787. © Pleiades Publishing, Ltd., 2020.
Russian Text © The Author(s), 2019, published in Lesovedenie, 2019, No. 5, pp. 375–384.

Response of Forest Phyllophagous Insects to Climate Change

V. V. Rubtsov[a], * and I. A. Utkina[a]

[a] Institute of Forest Science, Russian Academy of Sciences, Uspenskoe, Moscow oblast, 143030 Russia

*e-mail: VRubtsov@mail.ru

Received March 29, 2019; revised April 28, 2019; accepted June 5, 2019

Abstract—Modern climate characteristics have a strong impact on plants, insects, and biogeocoenotic relations among them. This is unambiguously supported by multiple studies worldwide, the reports of which are briefly reviewed in the present article. Most of the authors agree that air temperature is the most important factor directly affecting the development and population level of insects. Ranges of plant and insect species are shifting northwards and to higher altitudes. Phenological phases come ahead of time in spring and later in fall, which results in longer growth season. Time-series analysis and trends in five major weather elements in the southern forest-steppe zone in Voronezh oblast have revealed the weakening of climate continentality, increased precipitation over the growth period, and a higher frequency of extreme weather events. Additionally, the study detected changes in the population-level dynamics of insects, specifically, the gypsy moth, the green oak leaf roller, and the winter moth, which commonly occur on this plot, and the disturbance in their relations with host plants. The harmfulness of some species declines, while that of other species rises. Modeling allows one to predict some consequences of the direct effects of climate change on relationships between phyllophagous insects and their host plants. Delayed consequences associated with indirect climatic forcing are hard to predict. They will depend on the character of climate change and on response of plants and insects driven by their adaptation mechanisms.

Keywords: phyllophagous insects, host plants, climate changes, oak forests of the forest steppe, English oak

DOI: 10.1134/S1995425520070094

The ongoing climate changes, which have a significant effect on natural systems, have become apparent over the recent decades, both at the end of the last century and the beginning of this one. One of the frequently cited reviews on the topic generalizes data from 228 publications with respect to the fact that natural terrestrial communities experience changes in the phenology of plants and animals—the ranges of both shift northward or upward in elevation; predator–pray and plant–phytophage interactions are disrupted due to different responses of species to warming; the evolutionary adaptation of species to new conditions occurs inside the shifting ranges; and new food resources enter usage (Parmesan, 2006).

The effects of the occurring climate changes on interactions between phytophagous insects and their host wood species have been reported by multiple studies. Reviews that appeared at the turn of the century (Hudges, 2000; McCarty, 2001; Harrington et al., 1999; Root et al., 2003; etc.) are added with new ones (Jaworski and Hilszczański, 2013; Musolin and Saulich, 2012; Heimonen et al., 2015; Kolb et al., 2016; Pureswaran et al., 2018; etc.).

Previously, we wrote about the main conclusions made by these reviews (Utkina and Rubtsov, 2017; Rubtsov and Utkina, 2008, 2010; etc.). Here it may be just noted that recent publications support the conclusions drawn earlier, present evidences that support the complexity, and point out that insect species from different functional groups are differently affected by the occurring changes (Jaworski and Hilszczański, 2013); it still remains unclear what the effect of the predicted change will be in the amount and frequency of precipitation and its redistribution against a rising temperature on the forest insects and pathogenic outbreaks (Kolb et al., 2016). Even more difficult to predict under the changing environmental conditions is the behavior of invasive species capable of substantially damaging the natural communities they colonize (Ramsfield et al., 2016).

A large body of evidence has been also accumulated with respect to significant ecological implications due to disturbance of phenological synchrony between insects and their host trees as a result of the warming. In the temperate and boreal zone forests, the start time of the spring growth of plants and phyllophages (folivores) has been shown to play a major role using an example of English oak and winter moth (Buse and Good, 1996) and the quaking aspen, paper birch, and forest tent caterpillar (Schwartzberg et al., 2014).

Much attention was devoted by A.S. Isaev to the problem of a change in the relationships between various phytophagous species of insects and their host trees under climate change. Among others, they include the pine looper in the Siberian pine forests (Isaev et al., 1997, 1999) and gypsy moth in the oak and mixed forests of European Russia (Lyamtsev and Isaev, 2005; Lyamtsev et al., 2000). "Future climatic changes can appreciably change the nature of interactions within the forest–insect system and result in more frequent mass outbreaks of pests and worsen the damage caused by them. The threat of a significant increase in forest damage level in relation to the climate warming necessitates the assessment of the extent to which these changes will impact the population level dynamics of insects and the scale of the impact on the forest ecosystems" (Isaev et al., 1999, p. 39).

A.S. Isaev attached great importance to one technique of mathematically modeling such relationships, notwithstanding its limitations, with a view to predict the likely consequences: "Models describing the tree–insect interaction do not appear to generate an unambiguous answer to the question of what will happen to plants and insect populations under the possible global climate change. The climate change can both increase a level of damage caused to forests by insects and reduce the effect of the latter on forest ecosystems. A more accurate evaluation of consequences generated by the possible climate change requires more detailed information about the parameters of tree–insect interaction, in particular pest species and their host trees, as well as knowledge of the ecological and physiological reactions of the insects and trees in response to variations in temperature and humidity" (Isaev et al., 1999, p. 43).

The same conclusion was made 20 years later using two phyllophagous species with similar characteristics as an example, namely, winter moth and mottled umber moth, distributed across oak tree stands in Germany (Hittenbeck et al., 2019). Verifying the model built by the authors for both species in combination showed that it was necessary to collect supplementary data and design models for each species separately.

The goal of the present work is to present the current status of research on the matter of interactions between the forest phyllophagous insects and host plants under the observed climatic changes using oak tree stands and phyllophagous insects in the south of the forest-steppe zone as an example (Voronezh oblast, Tellerman oak forest), make a general quantitative assessment of changes in the main meteorological parameters of the study region, and demonstrate the effect of the modern climate situation on the cyclicity of mass outbreaks of phyllophages over the recent decades.

MATERIALS AND METHODS

Experimental data on the population-level dynamics of the main phyllophages, namely, green oak leaf roller (*Tortrix viridana* L.), winter moth (*Operophtera brumata* L.), and gypsy moth (*Lymantria dispar* L.), were derived from the long-term yearly observations in various types of oak woodlands across the territory of the Tellermanovskoe Experimental Forest Division (TEFD), which is located in the eastern part of Voronezh oblast and is a branch of the Institute of Forest Science of the Russian Academy of Sciences.

All stands in the TEFD were annually surveyed to identify centers of damage to foliage. Defoliation levels were determined by eye using the binocular for crowns and by calculations for trees that had been inventoried for caterpillars and examined for characteristics of foliage regeneration after defoliation. The state of the trees and their crowns were determined using enumeration on permanent and temporary sample plots, as well as model trees (approximately 900) of the various phenological forms of English oak marked beforehand and model trees additionally selected in the centers of severe damage to foliage. Egg masses of the green oak leaf roller were counted using a combined technique after N.N. Egorov et al. (1953) and V.A. Efremova (1969). Gypsy moth was counted annually based on egg masses by scrutinizing the bottom parts of tree trunks in the main types of forest. Winter moth at a caterpillar stage were counted in crowns together with other phyllophages, as well as using grease bands during butterfly flight periods; female fecundity was determined by opening and counting eggs in them (Rubtsov and Utkina, 2011).

An analysis of the long-term weather (meteorological) elements dynamics and detection of their trends were performed using the regression models and time series analysis. Periods of abnormal weather conditions were determined using Walter–Gossen climate charts (Rubtsov and Utkina, 2008). The effects of the weather conditions on green oak leaf roller interaction with foliage were assessed in simulation experiments using the mathematical model built by us earlier (Rubtsov and Rubtsova, 1984). The model is based on three common nonlinear differential equations solved by the numerical method using a computer.

RESULTS AND DISCUSSION

Species in the genus *Quercus* L. are the preferred choice for many insects. Specifically, the English oak (*Q. robur* L.), which is among the forest-forming wood species of European Russia, is home to more than 700 insect species. Various oak species and phyllophages consuming their foliage (folivores) are commonly employed by national and foreign researchers as materials for the study of universal mechanisms of the mutual adaptation of plants and insects in various terrestrial ecosystems (Utkina and Rubtsov, 2019; Rubtsov and Utkina, 2008).

Climate factors can have both direct and indirect effects on ecosystems. As was noted by A.I. Vorontsov (1978), with the direct effect, the prevailing weather conditions promote or delay insect development, growth, and feeding, as well as other biological processes. The same conditions determine the mortality due to the environmental physical factors (kill caused by low temperatures, excess rainfall/heavy rains, drought, etc.). More often than not, different needs of species for physical factors give rise to asynchrony in the development of pest and its entomophages. Indirect effects are delivered via the food and habitat of particular developmental stages, entomophages, and diseases. Inasmuch as the climate change is nonuniform in space and time, its impact on ecosystem varies, which was brought into sharp focus by works of A.S. Isaev (Lyamtsev and Isaev, 2005; Isaev et al., 1999).

The regular monitoring of mass propagation outbreaks of the main phyllophagous insect species has been practiced across the TEFD since the day the forest district was created in 1944 and since 1975 by the authors of the present communication. Four outbreaks of gypsy moth and five outbreaks of winter moth were recorded during this time interval. The reproduction of the green roller displayed a permanent pattern accompanied by five well-defined peaks in the population level.

In this region, a trend toward weakening of the climate continentality was detected by the long-term series analysis of the main weather elements in the proximal areas of the forest-steppe zone south, that is, in the Khoper (Biryukov and Marchenko, 2001) and Voronezh (Vengerov et al., 2001) nature reserves and the Tellerman oak forest (Rubtsov and Utkina, 2008). We analyzed the time series of some of the climatic parameters based on data from the weather station at Borisoglebsk (Voronezh oblast) located 8 km of the TEFD. The annual average temperature was established to have risen nearly by 2°C since 1927 to date. The average temperature of the growing season fell slightly. This was accompanied by a strong increase in the amount of precipitation during the growth season, that is, by 99 mm since 1949. There was no single year with a total amount of precipitation of more than 300 mm over the growth season from 1949 to 1975; such seasons numbered 11 from 1976 to 2009, including four seasons with the amount of precipitation over the growth season of more than 400 mm. An analysis of the Gossen–Walter climate charts revealed a trend toward a significant increase over the recent decades in the number of growth seasons without drought, which is beneficial for the humidity deficit zone.

The observed climate changes had a significant impact on interactions of many forest phyllophagous species with their host trees, as already have been reported by us (Utkina and Rubrsov, 2017; Rubtsov and Utkina, 2008, 2010). This is primarily associated with a difference in responses to the ongoing climate changes among different species of plants and phyllophages. In the TEFD, considerable variations have been recorded in the population dynamics of the abovementioned phyllophagous species over the recent decades; the level of damage caused by them to foliage has considerably decreased in oak woodlands. The well-defined cyclicity of outbreaks, persisting for many decades, has been disturbed; specifically, no mass reproduction of gypsy moth has occurred since 1990 to date (the previously typical outbreak time interval constituted 10–12 years); for more than 20 years now, a major depression has been experienced by the green oak leaf roller (prior to that, the population density was characterized by undulating ups and downs). The next-to-last outbreak of winter moth in the TEFD was prolonged (1997–2004). As early as in 2009, 5 years later, a new outbreak began (before that, inter-outbreak intervals constituted 10–11 years), which proved to have become short-term, lasting from 2009 to 2011, including two periods with extreme weather conditions, that is, the exceptionally hot summer of 2010 during pupation and the winter of 2011/2012, with a prolonged period of extremely low temperatures, which resulted in a nearly complete death of egg masses and attenuation of the outbreak in 2012. During this short-term outbreak, the flight period of the winter moth began three weeks later than normal, which is directly related to weather conditions (Fig. 1).

At the same time, the uncommonly large outbreak of the leaf blotch miner moth (brown oak slender) (*Acrocercops brongniardella* L.) was observed across the TEFD, which was described for Voronezh oblast by V.B. Golub et al. (2009, 2011). It has been more than 20 years in a row that this species damages up to 60–70% of the oak foliage surface area by mining the tree leaves, both of the early and late phenological forms, regardless of their age. The damage level of each of the forms depends on the weather conditions and the occurrence of other folivores (Rubtsov and Utkina, 2008). Over time, the leaves dry up and roll (Fig. 2).

All of the works known to us point out that temperature is among the most important external factors that affect the development and state of phyllophagous insect populations. In the context of ongoing climate changes, this is clearly demonstrated in the review by J.S. Bale et al. (2002). Based on the analysis of data from 134 sources, the authors state that temperature is the dominant abiotic factor, directly affecting herbivorous insects, while the effect of CO_2 concentration and increasing UVB is much weaker. Temperature directly affects the development, survival, range, and population level. Species with a more extensive range tend to be less affected (Isaev et al., 1999; Bale et al., 2002; etc.).

Response of insects to climate change, however, is not always linear. Thus, the developmental stages of insects experience the effects of changes in different ways; that is, the growth can accelerate with the rise in temperature, while a diapause can last longer. Additionally, the major effect of temperature is its influence

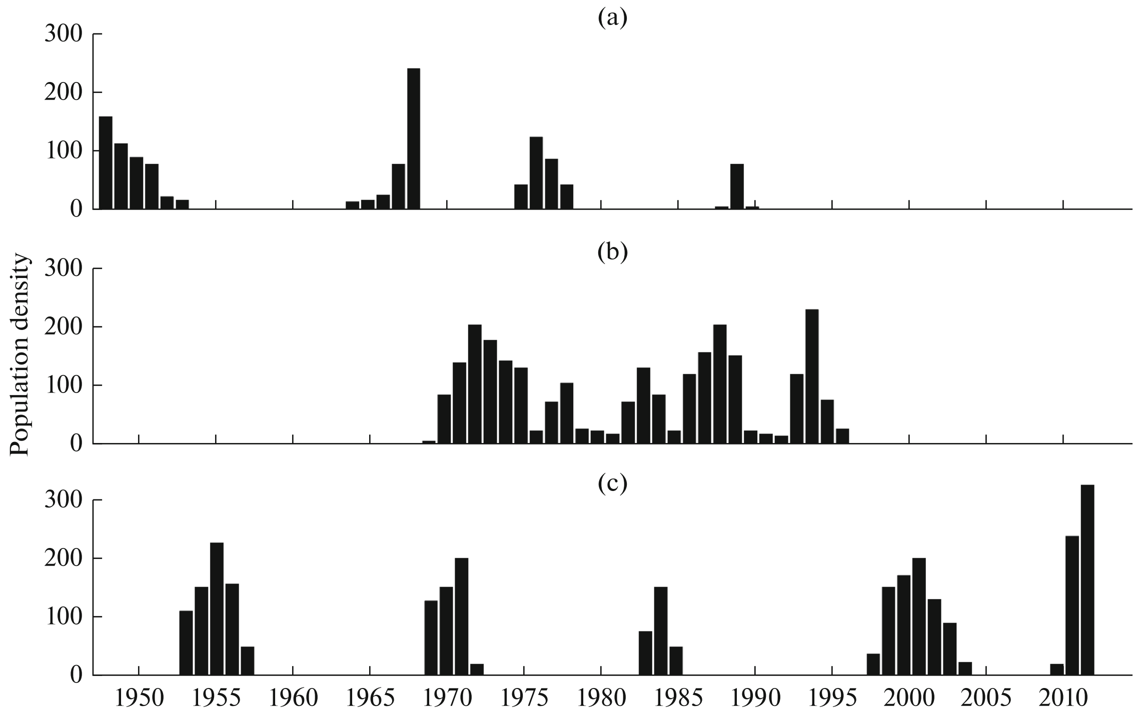

Fig. 1. Population level dynamics in some phyllophagous insects that had outbreaks in Tellermanovskaya oak woodland over the past 60 years: (a) Gypsy moth, number of egg masses per 50 trees; (b) green oak leaf roller, number of egg masses per five linear meters of twig length; and (c) winter moth, number of female butterflies per one tree.

Fig. 2. Damage caused to the oak foliage by the leaf blotch miner moth.

on winter survival in the middle (temperate) latitudes; in the northerly latitudes, a rise in temperature prolongs the growth season, which results in a higher sum of temperatures available for growth and reproduction.

The various life strategies available to phyllophagous insects allow them to use the plants of various life forms and different strategies, which are affected by the ongoing climate change in different ways, in their diet. In the abovementioned works, Isaev et al. employ as their methodological foundation statistical techniques and simulation modeling to predict the effect of climate change on the dynamics of the population level of phyllophages, their ranges, and the damage to tree stands (Lyamtsev and Isaev, 2005; Isaev et al., 1997; etc.).

Using this modeling, the authors thoroughly analyzed the effects of 100 various climatic scenarios on the population dynamics of the pine looper (*Bupalus piniarius* L.). They determined critical values of climatic parameters causing the regular outbreaks of its mass reproduction. According to the available global climate scenarios, the rise in the average annual temperature by 2–4°C has been established to possibly pose a potential threat for pine forests in Central Siberia due to the outbreak dispersal of the pine looper. In the opinion of the authors, an analysis of the impact of global climate change should take into account not only midyear climate shifts, but also climate changes for the full year, inasmuch as the population development during the season depends on various climate factors. The general conclusion of the authors is that, with climate warming, the likelihood of occurrence of injurious insect outbreaks may increase, while the zone of their potential distribution is likely to expand. Along with this, it is stated that currently it does not appear possible to elucidate an unambiguous answer with respect to the consequences of the global climate change for insect population-level dynamics and degree of damage caused by them to forests. Deeper insight is required into the tree–insect relationships for individual insect species and their host trees (Isaev et al., 1997, 1999).

As was noted above, the oak tree commonly hosts a multispecies set of phyllophages, featuring a complex set of relationships. During the periods of mass pest outbreaks, the population level of other species is depressed. The interspecific and, later, intraspecific competition occurs with a spike in population level of any of the species. The major role in outcompeting is played by the development rate of insects during the feeding period, which is closely associated with the weather conditions and the air thermal regime in particular.

Based on our observations, the development of caterpillars of the green oak leaf roller and winter moth unfolds rapidly under TEFD conditions, in 3 weeks on average. This offers them benefits compared with many other competing insect species (Rubtsov and Rubtsova, 1984; Rubtsov and Utkina, 2008).

Waves in the leaf roller population occur under the influence of a great number of diverse modifying and regulating factors. The latter fail to form an efficient and flexible mechanism of negative feedback loop and, thus, predetermine the duration of outbreaks of this species, which commonly acquire a permanent character. The main factors affecting the population level dynamics in leaf roller include the following:

modifying factors, the direct and indirect effects of which on the leaf roller population are manifested in the forms of (1) severe winter frosts with a temperature below the values equal to absolute minimums average, which causes the death of leaf roller eggs and affects survival of its entomophages; (2) warm dry weather during the caterpillar phase, which promotes an improvement in the feeding value of the foliage, rapid caterpillar development, enhanced survival, and butterfly fecundity; (3) the pattern (numerical values and distribution peculiarities) of temperature in winter and early spring, which determines the course of embryogenesis in leaf roller and oak buds and occasionally has a strong effect on caterpillar survival; (4) spring frosts, killing the buds and foliage and increasing the mortality of leaf roller caterpillars;

regulating factors associated with intraspecific competition, which feature a high level of activity threshold and have an appreciable regulating effect under overpopulation. In the context of the oak leaf roller, this entails decreased fecundity and infertility of the female butterflies, as well as migrations, increasing mortality among individuals and flattening the population density. Biocenotic regulating mechanisms are characterized by a lower level of activity threshold. The center stage here is taken by entomophages featuring the rich species composition in the Tellerman oak forest. A certain regulating role is played by birds and, occasionally, diseases.

The process of regulation of the leaf roller population density is frequently managed to be satisfactorily simulated and predicted using this mathematical model. Prediction of the density modification, however, is commonly a very complex task due to its probabilistic and intrinsically nonstationary nature.

Simulation experiments involving the mathematical models built for studying the direct effects of weather factors and air thermal regime in particular on relationships between green oak leaf roller and oak, demonstrated that, under high levels of leaf roller population density, the mean weight of its caterpillar at the end of feeding on foliage before the pupation proves to be equal or lower under weather conditions beneficial for the caterpillar development than with moderate or bad levels (Rubtsov and Rubtsova, 1984). Our explanation lies in the intraspecific competition of caterpillars for food. Favorable weather conditions promote the feeding and migration rates of caterpillar; the latter rapidly and completely damage the foliage on trees, while their average weight is low. Some of the caterpillars are unable to pupate due to underfeeding and die; the newly formed pupae are very small, while the emerged butterflies are not fecund. At the same time, their feeding rate is lower, while mortality is generally higher under weather conditions more detrimental for the development of leaf roller caterpillars. Foliage mass accretion outstrips level of its destruction; competition for food subsides; the surviving portion of caterpillars has higher weight. This contributes to the preservation of the population under the conditions of overpopulation.

The extent of defoliation of tree crowns by the time of pupation of phyllophages is determined by mass and growth rate of foliage during the caterpillar feeding period, feeding rate, and population level dynamics of caterpillars. Using modeling, weather conditions were shown to affect the extent of crown defoliation to a greater degree under a low population level of phyllophages and to an appreciably lesser degree under the high population level. In other words, as the pest population attains sufficiently high level, the regulating role of the weather factor weakens. As the population level of phyllophages continues to rise, the importance of the weather factor increases again under conditions of overpopulation, as was stated above. These examples clearly demonstrate relativeness of "beneficial weather conditions" for the specific phase of development in particular insect species.

The foregoing modeling outcomes reveal a rather complex and mixed effect of weather factors on relationships between the population of phyllophage and host plants. Our conclusions are consistent with the findings of other studies (Lyamtsev and Isaev, 2005; Isaev et al., 1999; Ramsfield et al., 2016; Kolb et al., 2016; etc.).

The amount and time period for regenerative foliage formation (refoliation level) is a critical factor affecting the future state of trees after the intense defoliation. The potential ability of plants for compensating the leaf area to replace the lost foliage characterizes the tolerance of plants to phyllophages. The conclusions of researchers with respect to the effect of refoliation (regenerative shoot and leaf formation) on the tree state differ, which can be largely attributed to the complex nature of the relationship between regenerative shoot formation and defoliation, as well as other biotic and abiotic factors.

In addition to abiotic factors and characteristics of insects, the study of relationships between phyllophages and their host trees should take into account the ecophysiological characteristics of this particular wood species (type of shoot formation, growth rate of shoots and leaves, crown and root system formation characteristics, etc.), as well as individual characteristics of this trees, that is, growth conditions, position in the tree stand, etc. The most important parameters of species strategy include how and what type of shoots form the tree. Thus, English oak and other oak species feature determinate shoot growth (during one or a number of short periods), while in birch it is indeterminate (continues throughout the growth season). Of major importance is the time point of foliage damage, whether the latter occurs in the beginning, middle, or at the end of the growth season, and, undoubtedly, a level of damage, i.e., defoliation. Processes of regenerative shoot and leaf formation in English oak after complete or partial defoliation were considered by us earlier (Rubtsov and Utkina, 2008).

Curious facts supporting the data obtained by us for English oak are reported in a study concerned with defenses of various oak species (Pearse and Hipp, 2012). Using methods of phylogenetic regression, the authors analyzed various characteristics of 56 oak species growing in Europe, Asia, and North America. In their opinion, climate has a deciding impact on both the chemical and physical defense responses. In response to the attack of folivorous insects and miners, the latter in leaves of one and the same oak species were stronger in habitats from lower absolute latitudes, which is interpreted by the authors as indirect climate action. A comparison between different species revealed that defensive traits were at a higher level in those oak species that grow in the regions featuring low temperatures, mild winters, and low minimum precipitation. The relationship between oak leaf traits and abiotic environment were consistent with a combination of climate parameters, "which may relate to different herbivore pressure," and the resource-availability theory, according to which the more limited the host plants are in resources, the stronger the pressure exerted on them by phytophages carrying out natural selection.

CONCLUSIONS

This study employed an analysis of time series and revealed trends of basic weather elements in the southern forest steppe. It showed a weakening of climate continentality in the region, a significant increase in the amount of precipitation over growth, and an increased frequency in periods with abnormal weather events. The modern climate characteristics have a great impact on plants and insects and their biocenotic relationships. This has been unambiguously supported by works worldwide, the reports on which are reviewed in the present article. Most of the authors note that temperature is the most significant factor, directly affecting the development and population level of insects. They report changes in the ranges of multiple species of plants and insects in the form of shifts northwards and to higher altitudes; the earlier arrival of spring phenological phases; and the later arrival of the fall phases, resulting in the prolongation of the growth season.

In Tellerman oak forest, the observations revealed that the modern climate characteristics cause appreciable changes in the currently prevailing cycles of the insect population level dynamics and disturb the equilibrium in their interactions with host plants. Particularly, this concerns the populations of some economically important phyllophages, such as gypsy moth, green oak leaf roller, and winter moth. The harmfulness of some species declines, while that of other species rises.

Currently, modeling makes it possible to predict some consequences of the direct effects of climate change on the relationship between phyllophagous insects and their host plants. The long-term (delayed) consequences associated with the climate effect are hardly predictable at the moment. They will depend, on the one hand, on the character of climate change and, on the other hand, on the response of plants and animals, which is determined by their adaptation mechanisms.

FUNDING

The study was carried out within the framework of the State Assignment of the Institute of Forest Science, Russian Academy of Sciences for 2019, project no. AAAA-A19-1190530900754.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. This article does not contain any studies involving animals performed by any of the authors.

REFERENCES

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K, Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., et al., Herbivory in global climate change research: direct effects of rising temperature on insect herbivores, *Global Change Biol.*, 2002, vol. 8, no. 1, pp. 1–16.

Biryukov, V.I. and Marchenko, N.F., Characteristics of weather and climate parameters of the territory of Khopyor Nature Reserve and their changes in 1939–2000, in *Vliyanie izmeneniya klimata na ekosistemy. Okhranyaemye prirodnye territorii Rossii: Analiz mnogoletnikh nablyudenii* (Impact of Climate Change on Ecosystems. Protected Natural Territories of Russia: Analysis of Long-Term Observations), Moscow: Russkii Universitet, 2001, pp. 82–86.

Buse, A. and Good, J.E.G., Synchronization of larval emergence in winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur* L.) under simulated climate change, *Ecol. Entomol.*, 1996, vol. 21, no. 4, pp. 335–343.

Efremova, V.A., Estimation of moves in population number of the green oak tortrix, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Moscow: Moscow Forest Tech. Acad., 1973.

Egorov, N.N., Rubtsova, N.N., and Solozhenikina, T.N., Assessment of green oak leaf roller from egg masses, *Lesn. Khoz.*, 1953, no. 10, pp. 47–49.

Golub, V.B., Berezhnova, O.N., and Kornev, I.I., Outbreak of widely-mining moth *Acrocercops brongniardella* F. (Lepidoptera, Gracillariidae) in Voronezh oblast, *Izv. S.-Peterb. Lesotekh. Akad.*, 2009, no. 187, pp. 96–102.

Golub, V.B., Prostakov, N.I., and Khitsova, L.N., The dynamics of damage of oak crowns by the leaf blotch miner moth *Acrocercops brongniardella* F. (Lepidoptera, Gracillariidae) in Usmanskii Oak Forest (Voronezh oblast), *Izv. S.-Peterb. Lesotekh. Akad.*, 2011, no. 196, pp. 29–36.

Harrington, R., Woiwod, I., and Sparks, T., Climate change and trophic interactions, *Trends Ecol. Evol.*, 1999, vol. 14, no. 4, pp. 146–150.

Heimonen, K., Valtonen, A., Kontunen-Soppela, S., Keski-Saari, S., Rousi, M., Oksanen, E., and Roininen, H., Colonization of a host tree by herbivorous insects under a changing climate, *Oikos*, 2015, vol. 124, no. 8, pp. 1013–1022.

Hittenbeck, A., Bialozyt, R., and Schmidt, M., Modeling the population fluctuation of winter moth and mottled umber moth in Central and Northern Germany, *For. Ecosyst.*, 2019, vol. 6, no. 4.

Hudges, L., Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.*, 2000, vol. 15, no. 2, pp. 56–61.

Isaev, A.S., Ovchinnikova, T.M., Pal'nikova, E.N., and Sukhovol'skii, V.G., Simulation of population dynamics of the pine looper under various climatic scenarios, *Lesovedenie*, 1997, no. 4, pp. 40–48.

Isaev, A.S., Ovchinnikova, T.M., Pal'nikova, E.N., Sukhovol'skii, V.G., and Tarasova, O.V., Assessment of forest–insect relations in forests of boreal zone under probable climatic changes, *Lesovedenie*, 1999, no. 6, pp. 39–44.

Jaworski, T. and Hilszczański, J., The effect of temperature and humidity changes on insects development and their impact on forest ecosystems in the expected climate change, *For. Res. Pap.*, 2013, vol. 74, no. 4, pp. 345–355.

Kolb, T.E., Fettig, C.J., Ayres, M.P., Bentz, B.J., Hicke, J.A., Mathiasen, R., Stewart, J.E., and Weed, A.S., Observed and anticipated impacts of drought on forest insects and diseases in the United States, *For. Ecol. Manage.*, 2016, vol. 380, pp. 321–334.

Lyamtsev, N.I. and Isaev, A.S., Modification of types of mass outbreaks of the gypsy moth depending on the ecological and climatic conditions, *Lesovedenie*, 2005, no. 5, pp. 3–9.

Lyamtsev, N.I., Isaev, A.S., and Zukert, N.V., The influence of climate and weather on the dynamics of the gypsy moth population in European part of Russia, *Lesovedenie*, 2000, no. 1, pp. 62–67.

McCarty, J.P., Ecological consequences of recent climate change, *Conserv. Biol.*, 2001, vol. 15, no. 2, pp. 320–331.

Musolin, D.L. and Saulich, A.Kh., Responses of insects to the current climate changes: from physiology and behavior to range shifts, *Entomol. Rev.*, 2012, vol. 92, no. 7, pp. 715–740.

Parmesan, C., Ecological and evolutionary responses to recent climate change, *Annu. Rev. Ecol., Evol., Syst.*, 2006, vol. 37, no. 1, pp. 637–669.

Pearse, I.S. and Hipp, A.L. Global patterns of leaf defenses in oak species, *Evolution*, 2012, vol. 66, no. 7, pp. 2272–2286.

Pureswaran, D.S., Roques, A., and Battisti, A., Forest insects and climate change, *Curr. For. Rep.*, 2018, vol. 4, no. 2, pp. 35–50.

Ramsfield, T.D., Bentz, B.J., Faccoli, M., Jactel, H., and Brockerhoff, E.G., Forest health in a changing world: effects of globalization and climate change on forest insect and pathogen impacts, *Forestry*, 2016, vol. 89, no. 3, pp. 245–252.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A., Fingerprints of global warming on wild animals and plants, *Nature*, 2003, vol. 421, no. 6918, pp. 57–60.

Rubtsov, V.V. and Rubtsova, N.N., *Analiz vzaimodeistviya listogryzushchikh nasekomykh s dubom* (Analysis of Interaction of Leaf-Eating Pests and Oak), Moscow: Nauka, 1984.

Rubtsov, V.V. and Utkina, I.A., *Adaptatsionnye reaktsii duba na defoliatsiyu* (Adaptive Reaction of Oak on Defoliation), Moscow: Grif i K, 2008.

Rubtsov, V.V. and Utkina, I.A., Phylophages of forest ecosystems under changing climate, *Vestn. Mariisk. Gos. Tekhn. Univ., Ser.: Les. Ekol., Prirodopol'z.*, 2010, no. 3, pp. 3–15.

Rubtsov, V.V. and Utkina, I.A., Long-term dynamics of *Operophtera brumata* L. in the oak stands of forest-steppe, *Contemp. Probl. Ecol.*, 2011, vol. 4, no. 7, pp. 777–783.

Schwartzberg, E.G., Jamieson, M.A., Raffa, K.F., Reich, P.B., Montgomery, R.A., and Lindroth, R.L., Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees, *Oecologia*, 2014, vol. 175, no. 3, pp. 1041–1049.

Utkina, I.A. and Rubtsov, V.V., Modern ideas about the impact of climate change on interactions of forest trees and phytophagous insects, *Lesn. Vestn.*, 2017, vol. 21, no. 6, pp. 5–12.

Utkina, I.A. and Rubtsov, V.V., General patterns and species differences in the reaction of representatives of the genus *Quercus* to defoliation, *Materialy Vtoroi Vserossiiskoi konferentsii s mezhdunarodnym uchastiem "Monitoring i biologicheskie metody kontrolya vreditelei i patogenov drevesnykh rastenii: ot teorii k praktike," Moskva, 22–26 aprelya 2019 g.* (Proc. Second All-Russ. Conf. with Int. Participation "Monitoring and Biological Control of Pests and Pathogens of Wood Plants: From Theory to Practice," Moscow, April 22–26, 2019), Krasnoyarsk: Inst. Lesa, Sib. Otd., Ross. Akad. Nauk, 2019, pp. 178–179.

Vengerov, P.D., Sapel'nikova, I.I., Bazil'skaya, I.V., and Masalykin, A.I., Climate change direct and indirect effects in the Voronezh Nature Reserve, in *Vliyanie izmeneniya klimata na ekosistemy. Okhranyaemye prirodnye territorii Rossii: Analiz mnogoletnikh nablyudenii* (Impact of Climate Change on Ecosystems. Protected Natural Territories of Russia: Analysis of Long-Term Observations), Moscow: Russkii Universitet, 2001, pp. 39–47.

Vorontsov, A.I., *Patologiya lesa* (Forest Pathology), Moscow: Lesnaya Prom-st', 1978.

Translated by E. Kuznetsova