ISSN 0013-8738, Entomological Review, 2017, Vol. 97, No. 2, pp. 143–157. © Pleiades Publishing, Inc., 2017.
Original Russian Text © A.Kh. Saulich, I.V. Sokolova, D.L. Musolin, 2017, published in Entomologicheskoe Obozrenie, 2017, Vol. 96, No. 1, pp. 3–24.

Seasonal Cycles of Noctuid Moths of the Subfamily Plusiinae (Lepidoptera, Noctuidae) of the Palaearctic: Diversity and Environmental Control

A. Kh. Saulich[a], I. V. Sokolova[b], and D. L. Musolin[c]

[a]*St. Petersburg State University, St. Petersburg, 199034 Russia*
e-mail: 325mik40@gmail.com

[b]*Astrakhan State Biosphere Reserve, Astrakhan, 414021 Russia*
e-mail: ilgas@mail.ru

[c]*St. Petersburg State Forest Technical University, St. Petersburg, 194021 Russia*
e-mail: musolin@gmail.com

Received June 4, 2016

Abstract—Analysis of data on seasonal development of noctuid moths of the subfamily Plusiinae shows that the control of their seasonal cycles is poorly understood. At the same time, the available data demonstrate considerable diversity of the seasonal patterns of Plusiinae species from different regions. The homodynamic type of seasonal development has been found in *Trichoplusia ni* and *Ctenoplusia agnata* of the tribe Argyrogrammatini and in *Autographa gamma* of the Plusiini. The seasonal development of these southern noctuids is accompanied by regular interzonal migrations of flying adults. When spreading northwards, they can produce a different number of annual generations, depending on the local climatic conditions, and establish temporary local populations whose longevity is limited by the available thermal resources. Adults of some species may fly back southwards, but it is more likely that individuals from temporary local populations cannot survive long winters and are destined to die. The heterodynamic type of seasonal cycles allows insects to survive in the regions with pronounced seasonality of climate. This type of seasonal development includes univoltine, multivoltine, and semivoltine seasonal cycles. Univoltine seasonal cycles with obligate diapause are known in *Autographa buraetica*, *A. excelsa*, and *Syngrapha ain* (Plusiini). Diapause provides tolerance to both low temperatures and a prolonged period when food is unavailable. In *Syngrapha ottolenguii* (Plusiini), the same result is achieved by inclusion of two photoperiodically controlled diapauses (winter larval and summer adult ones) into the life cycle. The semivoltine seasonal cycle has been reported in only one species of Plusiinae, namely *Syngrapha devergens*. Larvae of this moth overwinter twice before pupation. Multivoltinism is common in the tribe Plusiini. Depending on the latitude, different species of this tribe can produce up to four generations per year and overwinter as middle-instar larvae in the state of facultative diapause. However, the characteristics of diapause vary substantially between the species: diapause can be deep and stable (as in *Diachrysia chrysitis*, Plusiini) or unstable and thus not ensuring successful overwintering and steady population growth (as in *Macdunnoughia confusa*, Plusiini). The seasonal adaptations known in Plusiinae include migrations, winter and summer diapauses, photoperiodic control of larval growth rates, and seasonal polyphenism of larval body coloration. In general, seasonal adaptations of Plusiinae are determined by local environmental conditions and only loosely associated with the systematic position of particular taxa. Only the tribe Abrostolini stands apart from other taxa of Plusiinae: moths of this tribe differ not only in morphology but also in peculiarities of their seasonal development, because all the species of this tribe overwinter as pupae and their seasonal cycles are therefore different from those of the rest of Plusiinae.

DOI: 10.1134/S0013873817020014

The entire diversity of the schemes of seasonal development known in insects can be subdivided into two main types: homodynamic and heterodynamic. Insects inhabiting tropical and subtropical areas are usually characterized by homodynamic development, in which generations follow one another and the number of generations per year is solely determined by the environmental conditions. Such year-round activity may be interrupted by short periods of direct inhibition of development at any ontogenetic stage, when the environmental conditions become unfavorable for a relatively short time. By contrast, heterodynamic seasonal development is characterized by regular alternation of periods of activity and seasonal dormancy (Danilevsky, 1961; Tauber et al., 1986; Danks, 1987; Saulich and Musolin, 2017).

At present, seasonal adaptations and annual cycles of insects inhabiting tropical, subtropical, and adjacent warm regions have been studied less extensively than the adaptations of species living in the temperate climate (Denlinger, 1986; Danks, 2007). However, the recent years have seen clear progress in the studies of physiology and biochemistry of physiological dormancy in insects under the relatively constant conditions of the tropics (Navas and Carvalho, 2010; Storey and Storey, 2012). It is quite possible that new interesting seasonal patterns will soon be discovered in insects inhabiting these regions.

Insects can exist in regions with expressed climatic seasonality due to the presence of a special period of physiological dormancy in their annual cycle. This dormancy, which may be more or less pronounced, allows the insects not only to survive the periods unfavorable for active development, but also to synchronize different stages of their active life with the corresponding seasons of the year.

The best studied form of dormancy in insects is diapause, which occurs strictly at the species-specific stage (Danilevsky, 1961; Tauber et al., 1986; Danks, 1987; Saunders, 2002; Saulich and Volkovitsh, 2004; Košťál, 2006; Denlinger et al., 2012; Goto and Numata, 2015; Musolin and Saulich, 2017). Alternation of active development and diapause is the main feature of the heterodynamic seasonal cycle, which may be univoltine, multivoltine (including bivoltine), and semivoltine (or perennial). The diversity of the forms of diapause with regard to the ontogenetic stage involved (embryonic, larval, pupal, and adult), its timing in the season, duration, etc. together with other seasonal adaptations (such as migrations, polyphenism, and growth rate control) determine the specific pattern of the annual cycle that characterizes the given species or its population and differs from the seasonal cycles of other species and their populations (Saulich and Sokolova, 2002; Volkovitsh, 2007; Kipyatkov and Lopatina, 2007; Belozerov, 2012, 2013; Saulich and Musolin, 2014, 2017). Even representatives of relatively small taxa at the level of subfamilies or tribes quite often demonstrate a great variety of seasonal patterns. Of great interest in this respect is the subfamily of looper moths (Plusiinae), which reflects the entire diversity of life strategies of the family Noctuidae "like the ocean in a drop of water" (Goater et al., 2003).

The goal of this paper is to summarize the available literature data and our experimental results concerning the seasonal development of Plusiinae and to discuss the main eco-physiological adaptations that ensure synchronization of the seasonal development of these moths with the local climatic conditions. The literature devoted to noctuid moths is extensive, and data of different authors are often contradictory. The species' names are given herein according to Matov and coauthors (2008), and their ranges and host plants, according to Matov and Kononenko (2012).

Plusiinae is a relatively small but globally distributed subfamily of noctuid moths comprising about 400 species (Kitching, 1987). It includes four tribes: Argyrogrammatini, Plusiini, Abrostolini, and Omorphini (Speidel et al., 1996; Goater et al., 2003), which are overviewed below.

1. TRIBE ARGYROGRAMMATINI

This tribe unites mostly tropical and subtropical species characterized by the homodynamic type of seasonal development. They regularly appear in the Mediterranean but seldom overwinter even in that region. Their records in the geographic zones with expressed climatic seasonality result from occasional or regular and large-scale seasonal migrations. The tribe includes 15 genera that are rich in species and globally distributed (with the exception of the Antarctic). Its fauna is the least diverse in the temperate zone.

The cabbage looper ***Trichoplusia ni*** (Hübner, [1803]) is one of the best-known species with this life strategy. It has a cosmopolitan range and occurs in all the continents except the Antarctic. In the Palaearctic the species is distributed from Morocco to Japan. This is a broad polyphage, known to feed on 134 species of plants from 36 families (Sukhareva, 1999; Matov and Kononenko, 2012). The species is migratory, and its adults appear more or less regularly in the temperate latitudes. They can reproduce all the year round given favorable conditions, but successful overwintering at different development stages is unlikely even in the Mediterranean. In central and northern Europe different stages of the species can be found from May to October. Development is very fast, so that the entire life cycle from egg to adult takes about six weeks (Goater et al., 2003). *Trichoplusia ni* forms 2 generations a year in the steppe zone of European Russia, Kazakhstan, and the greatest part of Ukraine, and 3 or 4 generations a year in the Transcaucasia. As many as

13 generations a year can be obtained under laboratory conditions at the optimal temperature of 26°C (Sukhareva, 1999; Klyuchko, 2006).

Ctenoplusia agnata (Staudinger, 1892) has been recorded in the Palaearctic only in East Asia: in China, Korea, Japan, and the Russian Far East (the Chinese-Manchurian nemoral range, after Matov et al., 2008; Yamamura et al., 2008b; Li et al., 2014). The species is polyphagous, its larvae feeding on plants of seven families (Matov and Kononenko, 2012). Development is homodynamic, without diapause. In China the species is characterized by regular migrations over long distances, from the Yellow Sea coast to the north of the country (Li et al., 2014).

2. TRIBE PLUSIINI

This tribe unites the widespread species with Holarctic and Palaearctic ranges and also the species distributed in the north of the Oriental Region (India and Pakistan). Over 40 species have been recorded in the Palaearctic fauna (Goater et al., 2003). In the opinion of some authors (e.g., Lafontaine and Poole, 1991), the tribe Plusiini is a composite taxon uniting all the species that have not been placed in any of the remaining three tribes of Plusiinae.

The silver Y moth ***Autographa gamma*** (L., 1758) is one of the best studied migratory lepidopteran species. It has a trans-Palaearctic temperate range including North America and Eurasia and extending as far southwards as India, China, and Japan. The species was recorded in Greenland and Iceland, while in the south it occurs in the European part of the Mediterranean, North Africa, Asia Minor, and Central Asia (Yathom and Rivnay, 1968; Saito, 1988; Kaneko, 1993; Goater et al., 2003; Lafontaine and Schmidt, 2010). This moth is a broad polyphage feeding on over 180 plant species from nearly 40 families (Sukhareva, 1999; Honěk, 2002; Matov and Kononenko, 2012). The number of annual generations in European Russia varies from 1 in the north to 4 in the south (Sukhareva, 1999). In Belarus (Merzheevskaya, 1967), Ukraine (Klyuchko, 2006), and the south of Germany (Koch, 1958) the silver Y produces 2–3 overlapping generations. According to the observations made in Israel, frequent droughts and extreme high temperatures prevent the development of the summer generations, so that reproduction and development of the species takes place only in late autumn and winter when the mean monthly temperatures drop to 15–20°C (Yathom and Rivnay, 1968).

We have experimentally studied the silver Y moth populations from Belgorod Province (Belogorye Nature Reserve, 50° N, 36° E) and Krasnodar Territory (Slavyansk-na-Kubani, 45° N, 38° E). No diapausing individuals were recorded in the laboratory under any of the diapause-inducing regimes, even though we tested practically all the factors known to provoke diapause formation in insects (photoperiod, temperature, thermal rhythms, and population density). The possible influence of the parent generation on diapause induction in the offspring generation, described in the literature for some species, was also taken into account. However, development of the moth proceeded without interruption in all the laboratory regimes, and no signs of the overwintering state was observed at any ontogenetic stage. Thus, the absence of diapause was experimentally demonstrated, which characterized the silver Y moth as a species with the homodynamic type of development (Saulich, 1999).

In order to ascertain whether *A. gamma* could overwinter due to nonspecific resistance to low temperatures, we determined the cold tolerance of different developmental stages of this species by the thermoelectric method, and also studied its resistance to prolonged influence of low above-zero temperatures. The cold tolerance of the eggs and pupae was rather high (up to −30.0°C and −12.0°C, respectively), but prolonged overwintering was limited by the absence of dedicated energy reserves and by a high level of metabolism typical of non-diapausing insects. The young- and old-instar larvae had the same supercooling point (−4.4°C on average) while the adults could supercool only to −3.4°C. These experimental parameters of cold tolerance constituted the extreme values, which are not generally reached in the nature under the prolonged action of below-zero temperatures (Goryshin and Saulich, 1982). On the whole, it may be concluded that cold tolerance of the silver Y moth is not sufficient for overwintering in the temperate climate even under the cover of snow, but it is quite sufficient for surviving the mild subtropical winter in a state of low-temperature quiescence.

In experiments under quasi-natural conditions testing for the possible environmental factors of diapause induction, it was shown that the silver Y moth never formed diapause, both in the temperate zone of Russia and in the Ciscaucasia. Overwintering could start at any ontogenetic stage, and the existence of the population was naturally limited by the onset of below-zero temperatures at the end of the season (Goryshin and Saulich, 1982, 1983).

Local populations of the silver Y moth occur all the year round only in the Mediterranean. The appearance of adults in regions with pronounced climatic seasonality is determined by their seasonal migrations over long distances. It was earlier supposed that one of the reasons for migrations was seeking of blossoming plants, since nectar is the natural source of vitamin E needed for gonad development (Koch, 1965; Vojnits, 1966). According to this hypothesis, in the absence or shortage of vitamin E sources the moths have to migrate following the seasonal pattern of plant blossoming: to the north in spring and to the south in autumn.

Based on his long-term observations, Kaisila (1962) suggested that the silver Y moth population in Finland might be formed by two types of individuals: the scarce residents which have successfully acclimated in the region but never produce outbreaks, and migrants, i.e., moths and their offspring of southern origin, which cannot overwinter in the northern latitudes and either die or migrate back to the south with the onset of cold weather. The size of the resistant part of the population can be extremely small but still sufficient for its sustained existence, while the population growth occurs due to mass immigration of individuals from the central part of the range. This hypothesis was confirmed and further developed by observations of the local silver Y population in Czechia (Novák, 1968, 1972). The larvae collected in the nature in autumn formed three distinct groups with clearly different development strategies: some of them developed in the same way as the summer larvae, pupated, and molted into adults in October; other larvae grew very slowly and emerged as adults only in December; finally, larvae of the third group did not pupate but overwintered at the III instar. Experimental assessment of the cold tolerance of these larvae showed their supercooling temperature to be as low as −22.0°C.

Recent studies showed that the ecology and population dynamics of the silver Y moth was indeed largely determined by mass annual migrations of adults from the southern regions (mostly the Mediterranean) to the areas with a colder climate (Chapman et al., 2011, 2012). Insects usually migrate while their gametes are still immature, this phenomenon being known as the "oogenesis–flight syndrome" (Johnson, 1969; Dingle, 1996; Musolin and Saulich, 2017). The period from emergence to maturation of the adult was termed the pre-reproductive period (PRP) (Hill and Gatehouse, 1992a, 1992b, 1993). The cited authors suggested that the PRP duration could be used as a measure of migration potential, determined by both genetic and external ecological factors. They experimentally showed that the short day and lower temperatures promoted prolongation of the PRP. Moreover, the silver Y moths from Britain and Germany (50–53° N) were shown to have a longer PRP than the conspecific individuals collected in Morocco (34° N); correspondingly, the former could fly longer and reach more northern regions. Since the PRP is controlled by the same gene in both sexes, the long-distance migrants can successfully form temporary (seasonal) populations in new territories. Thus, the seasonal migrations of the silver Y moths are controlled both genetically and environmentally.

Interesting data were obtained in a study of *A. gamma* population from the north of Japan (Hokkaido Island, 43° N, 141° E), where three annual generations are formed and occasional overwintering of the IV instar larvae was recorded (Saito, 1988; Kaneko, 1993). Inhibition of development of the IV instar larvae was observed under experimental conditions with a short day (13 h of light) and a temperature close to the development threshold (13°C). The cited authors described this inhibition of larval development, controlled by the day length, as "diapause-like prolongation of larval duration," because overwintering larvae at this particular instar were found in the nature. The number of the III and IV instar larvae increased considerably by autumn. Besides, after acclimation in the laboratory (chilling for 1 day at 10°C and then for 5 days at 5°C), 1.4% of the 660 tested larvae survived at 0°C for 4 months (Kaneko, 1996; Saito, 2007). Considering these results, it is very likely that some larvae can indeed survive the severe conditions of Hokkaido Island where cold winter lasts for up to five months. Survival would be also facilitated by the snow cover which considerably reduces the effect of below-zero temperatures.

Inhibition of development at a specific larval instar in the silver Y moth may be not only a seasonal adaptation ensuring survival in winter but also a synchronizing photoperiodic mechanism. By arresting the development of conspecific individuals at the same stage, the diapause ensures uniform age composition after overwintering, thus facilitating mate seeking and reproduction.

Autographa buraetica (Staudinger, 1892) has a Holarctic boreal range (Matov and Kononenko, 2012). In Europe the species occurs in the central and northern parts of the continent while in Asia it reaches the north of China, North Korea, and Japan (Goater et al., 2003). This is a polyphagous moth whose larvae are known to feed on plants from four families (Matov and Kononenko, 2012). The species is univoltine over its entire range since it has an obligate larval diapause (Yamamura and Sasaki, 2006).

Autographa excelsa (Kretschmar, 1862) has a Eurasian boreal range the greatest part of which lies in Asia, extending from the eastern spurs of the Urals to South Siberia to the Russian Far East, the Korean Peninsula, and Japan. In Europe the species is distributed in the eastern and northeastern regions: Fennoscandia, the Baltic states, the northeast of European Russia, and was also recorded in the Polish part of the Tatra Mountains (Goater et al., 2003). This is a polyphagous moth whose larvae are known to feed on plants from seven families (Klyuchko, 2006; Matov and Kononenko, 2012). It has a univoltine seasonal cycle based on obligate larval diapause (Yamamura and Sasaki, 2006).

Autographa bractea ([Denis et Schiffermüller], 1775) has a Euro-Siberian temperate range covering most of Europe except its extreme south; in Asia the species is distributed only in the west of Siberia, as far eastwards as the Altai Mountains. In the mountains it occurs up to 2600 m above sea level. This is a polyphagous species whose larvae are known to feed on plants from nine families (Klyuchko, 2006; Matov and Kononenko, 2012). One annual generation is completed over the greatest part of the range, while partial development of the second generation was recorded in the south of the Alps (Goater et al., 2003); thus, the species may be regarded as potentially multivoltine.

Macdunnoughia confusa (Stephens, 1850) is a widespread migratory species with a trans-Eurasian temperate range. The species is polyphagous, its larvae feeding on plants from 16 families (Sukhareva, 1999; Klyuchko, 2006; Matov and Kononenko, 2012). The number of complete generations varies in different latitudes, depending on ecological conditions. Adults fly from April to November. Two complete generations usually develop in the temperate zone of Russia, in Belarus, Ukraine, and Germany, and up to four generations in the Transcaucasia (Koch, 1958; Merzheevskaya, 1971; Sukhareva, 1999; Klyuchko, 2006).

The population from Estonia (Tartu, 58° N, 26° E) was experimentally studied. Larvae diapaused at the IV instar but continued feeding (which is not typical of diapausing insects). They underwent additional molts, so that the number of instars increased from 5 (the normal number for non-diapause development) to 9, but did not pupate. The color of the diapausing larvae changed from pale green to black. Their oxygen consumption rate was 800–900 mm^3 O_2/g×h at 20°C at the beginning of diapause, and then decreased slightly, approximately to 500 mm^3 O_2/g×h. All these physiological data characterized the state of the overwintering *M. confusa* larvae as labile diapause. Despite the relatively high cold tolerance (with the supercooling temperature of overwintering larvae reaching −17°C in February), labile diapause did not ensure successful overwintering even in Estonia. Mortality of overwintering larvae was very high, and less than half of them survived to mid-January (Merivee, 1971).

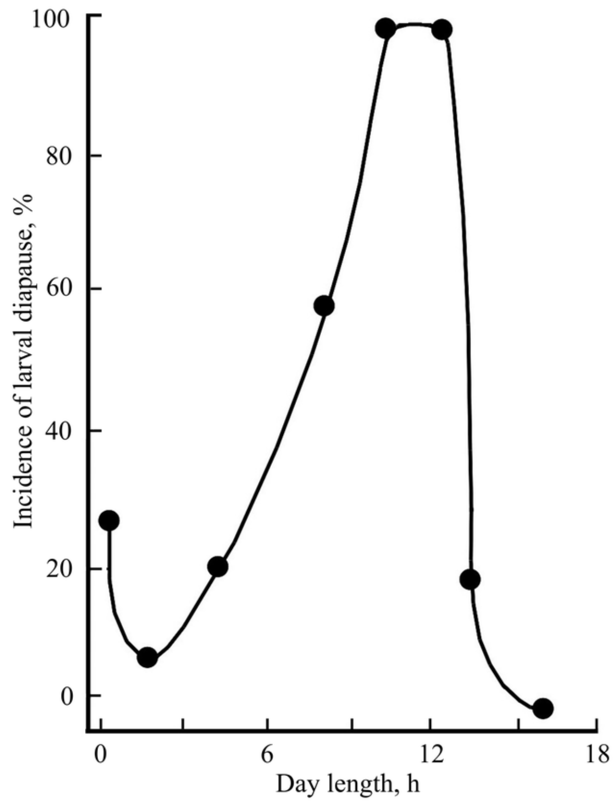

Fig. 1. Photoperiodic control of larval diapause induction in *Macdunnoughia confusa* (Stephens) at 21°C (population from Tartu, Estonia, 58° N, 26° E; after Merivee, 1971).

The formation of labile diapause in *M. confusa* was controlled by photoperiodic response (PhPR) of the long-day type with a narrow range of photoperiods capable of inducing diapause in the great majority of larvae (Fig. 1).

In the studied population from Estonia, the number of diapausing larvae reached 100% only under short-day conditions, at 10 and 12 h of light a day. The eco-

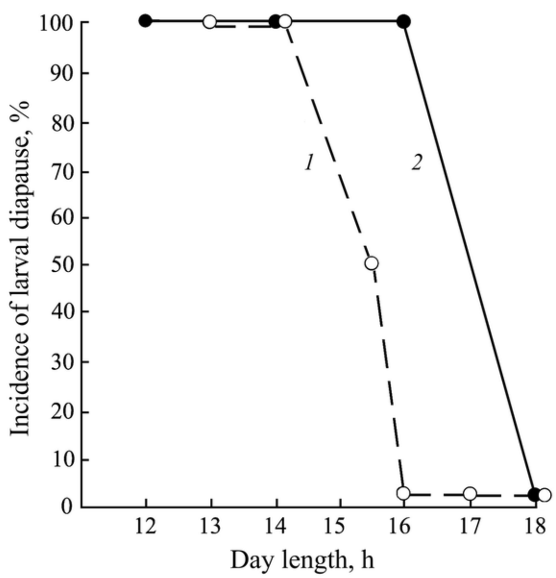

Fig. 2. Photoperiodic control of larval diapause induction in *Diachrysia chrysitis* (L.): (*1*) population from Belgorod Province (Belogorye Nature Reserve; 50° N, 36° E; our data), temperature 20°C; (*2*) population from Tartu, Estonia (58° N, 26° E; after Merivee, 1971), temperature 21°C.

logically significant critical day length, which induced diapause in 50% of the larvae in experiments, was about 13 h at 21°C. The upper thermal threshold of PhPR was between 21 and 26°C. An increase in the temperature considerably reduced the fraction of diapausing individuals, and at temperatures above 26°C all the larvae completed development without diapause and pupated (Merivee, 1971).

Photoperiodic sensitivity of the larvae was preserved during diapause. The diapausing larvae transferred into the long-day conditions rapidly reactivated and eventually pupated. Such characteristics of photoperiodic sensitivity, as well as the other physiological traits of the diapause of *M. confusa* considered above, are usually observed in southern species and populations of insects. Therefore, the studied Estonian population of *M. confusa* was also most probably of southern origin. The formation of this population in the region was probably related to the ability of these moths to migrate over long distances. Such migrations determine the existence of seasonal populations even in the north of Europe where *M. confusa* is quite abundant, especially in the second generation at the end of the summer season (Merivee, 1971).

Diachrysia chrysitis (Linnaeus, 1758) has a trans-Eurasian temperate range (Matov and Kononenko, 2012). The species can be found practically in the whole of Europe except Iceland, and in the whole of Asia except the tundra and subarctic zones. It is a polyphagous species whose larvae are known to feed on plants from 16 families (Klyuchko, 2006; Matov and Kononenko, 2012). Its seasonal cycle is multivoltine: the species has 1 generation a year in the north and 2 or 3 generations in more southern regions. The larvae overwinter and complete development in April–May of the following year (Goater et al., 2003).

Populations of this species from Estonia (Tartu; 58° N, 26° E: Merivee, 1971, 1978) and Russia (Belgorod Province, Belogorye Nature Reserve, 50° N, 36° E) were experimentally studied in the greatest detail. Facultative larval diapause occurred at the IV instar. The diapausing larvae stopped feeding completely, and their oxygen consumption rate dropped 4–5-fold during diapause as compared to the active period: from 800–900 mm^3 O_2/g×h at the beginning of diapause to 150–200 mm^3 O_2/g×h during the established diapause. The color of the diapausing larvae changed from pale green to velvety dark green. There were always six larval instars, regardless of the presence or absence of diapause. The mean supercooling temperature of diapausing larvae reached −25.0 ± 0.3°C (Merivee, 1971, 1978).

The onset of diapause was controlled by qualitative PhPR of the long-day type (Fig. 2). In the Estonian population the critical photoperiod was 17.5 h at 21°C. The upper temperature limit of PhPR was close to 26°C (Merivee, 1971). In Belgorod population of *D. chrysitis*, the threshold was considerably lower, about 15.5 h at almost the same temperature (20°C), while the upper temperature limit of PhPR was close to 24°C. Thus, the local populations demonstrated both geographic and temperature-dependent variation in the parameters of diapause-inducing PhPR under experimental conditions; therefore, these populations can be considered native.

Thus, *D. chrysitis* has a heterodynamic multivoltine seasonal cycle regulated by the long-day PhPR of diapause induction. Changes in the coloration are correlated with the physiological state of the larvae and also seem to be controlled by the day length.

Diachrysia stenochrysis (Warren, 1913) also has a trans-Eurasian temperate range (Matov and Kononenko, 2012) and occurs ubiquitously in Europe, from the Mediterranean coast to the subalpine belt. From 1 to 3 annual generations can be completed in different parts of Eurasia, depending on the climate (Goater et al., 2003). This species is polyphagous, its larvae feeding on plants from four families (Klyuchko, 2006; Matov and Kononenko, 2012). It prefers humid biotopes. The facultative larval diapause is controlled by the day length (Yamamura et al., 2008a).

Diachrysia chryson (Esper, 1789) is one more species with a trans-Eurasian temperate range (Matov and Kononenko, 2012). In Europe it is mainly distributed in the central and southern parts, and in Asia, in all the territories except the extreme north, from Turkey in the west to Japan in the east. The species is polyphagous, its larvae feeding on plants from four families (Klyuchko, 2006; Matov and Kononenko, 2012).

The population from Honshu Island (Japan, 36.1° N, 138.1° E), where *D. chryson* develops in two annual generations, was studied experimentally. The formation of facultative larval diapause in the species was controlled by PhPR with a threshold lying between 12 and 14 h (Fig. 3).

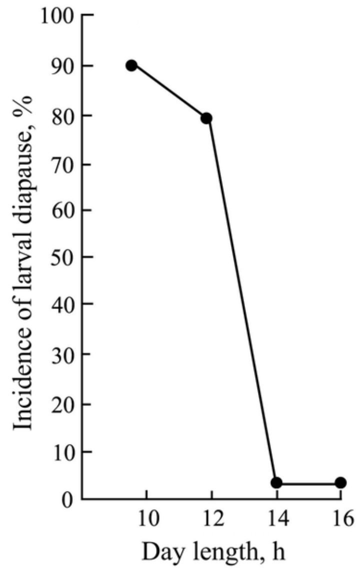

Fig. 3. Photoperiodic control of larval diapause induction in *Diachrysia chryson* (Esper) at 20°C (population from Honshu Island, Japan; 36.1° N, 138.1° E; after Yamamura et al., 2008a).

Polychrysia moneta (Fabricius, 1787) is a hygrophilous montane species preferring humid and cool biotopes. It has a Euro-Siberian subboreal range and is distributed in the Western Palaearctic from the north of Spain to the south of Norway, Sweden, and Finland (Matov and Kononenko, 2012), and can also be found in the South Urals (Sukhareva, 1999; Goater et al., 2003). The species is polyphagous, its larvae feeding on plants from five families (Klyuchko, 2006; Matov and Kononenko, 2012). The seasonal cycle is multivoltine: only one generation a year is completed in the greatest part of the range but the second generation is sometimes recorded in part of the population. Adults of the overwintered generation fly in June–July. In the south of the range, if the second generation is completed its adults fly in August–September (Sukhareva, 1999; Goater et al., 2003; Klyuchko, 2006). Middle-instar larvae overwinter to complete their development and pupate in May of the following year. Young larval instars differ in coloration from the older ones, which is also typical of other species of Plusiinae. Larvae of the second generation are known to grow very quickly (Goater et al., 2003; Berdys, 2016), suggesting the existence of exogenous (photoperiodic) growth rate regulation, which is characteristic of many insect species from different orders (Musolin and Saulich, 1997; Saulich and Musolin, 2007).

Plusia festucae (Linnaeus, 1758) has a trans-Palaearctic temperate range (Matov and Kononenko, 2012). The species occurs in the entire Palaearctic, from Morocco to Siberia to the Korean Peninsula, China, and Japan (Goater et al., 2003). The species is polyphagous, its larvae occurring on 11 families of monocots (Merzheevskaya, 1971; Klyuchko, 2006; Matov and Kononenko, 2012).

In European Russia (Sukhareva, 1999), Germany (Koch, 1958), Western Ukraine (Klyuchko, 2006), and Belarus (Merzheevskaya, 1971) *P. festucae* produces two generations a year. Adults of the overwintered generation fly in May–July in Germany (Koch, 1958) and in May–June in European Russia; adults of the summer generation fly in August–September.

The population of *P. festucae* from the temperate zone of Russia (Belgorod Province, Belogorye Nature Reserve, 50° N, 36° E) was studied experimentally (Saulich and Musolin, 2016). Larvae were kept under two alternative photoperiodic regimes: long day (18 h of light a day) and short day (12 h). Since the 11th day after hatching, the body mass of the larvae was noticeably (nearly by 3 times) lower in the short than in the long day; the difference increased as the larvae grew (Fig. 4).

By the 30th day, the larvae from the long-day regime reached the weight of about 100 mg and pupated; adults emerged from the pupae approximately two weeks later. By the same day, the mean body mass of larvae in the short-day regime was only slightly greater than 12 mg. These larvae slowly gained weight and practically stopped growing by the 100th day. The growth arrest was not related to pupation but indicated

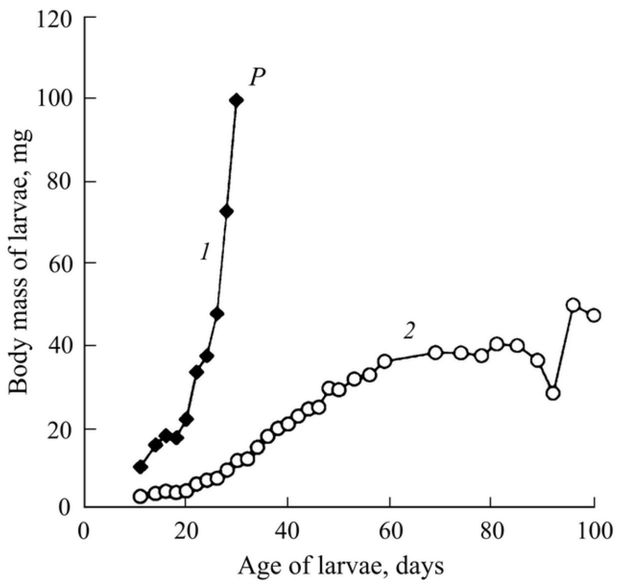

Fig. 4. Body mass dynamics of the larvae of *Plusia festucae* (L.) depending on the photoperiodic regime and their physiological state at 20°C (population from Belgorod Province, Belogorye Nature Reserve, 50° N, 36° E; our data): (*1*) physiologically active larvae in a long-day regime (18 h of light a day); (*2*) diapausing larvae in a short-day regime (12 h of light a day); *P*, the moment of pupation of the active larvae.

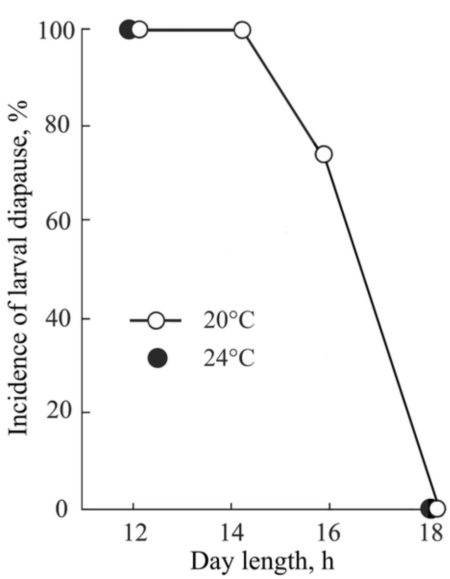

Fig. 5. Photoperiodic control of larval diapause induction in *Plusia festucae* (L.) at 20 and 24°C (population from Belgorod Province, Belogorye Nature Reserve, 50° N, 36° E; our data).

the onset of larval diapause. The larvae remained in this state for several months and showed no signs of spontaneous reactivation.

The onset of diapause in IV instar larvae of *P. festucae* was controlled by the long-day PhPR (Fig. 5). At the lower of the studied temperatures (20°C) under short-day conditions (12 and 14 h of light a day), all the larvae entered diapause. The fraction of diapausing individuals was reduced at 16-h photoperiod, while in the long-day regime (18 h) all the larvae developed actively.

These experimental results shed light on the seasonal strategy of the species in the temperate zone of Russia. According to our phenological observations and experimental data, adults of the overwintered generation fly in the second decade of June. Larval development takes about one month at the mean temperature of 20°C; therefore, it should be completed by the end of July when the day length is about 17 h. The long-term mean temperature of the warmest month (July) in the region is 21°C (*Agroclimatic Resources*..., 1972). In a year with the mean temperature of July exceeding the long-term average or nearly equal to it, no less than 80% of the larvae will remain physiologically active (Fig. 5). They will complete feeding, pupate, and the adults emerging from the pupae will give rise to the second generation; this scenario is consistent with the literature data for Ukraine (Klyuchko, 2006) and Belarus (Merzheevskaya, 1971). Larvae of the second generation will develop in August or early September, and the great majority of them will diapause because the day length shortens to 14 h and continues to decrease during that period.

By contrast, if temperatures in the middle of summer during a particular season remain below the long-term average, the larvae of the summer generation will encounter the short-day conditions and form diapause already in the first generation. Even in this case, however, the second generation may develop in part of the population, because the larvae will reach the IV instar at day lengths still close to the critical value; correspondingly, some of the "earlier" larvae will continue development and pupate before the autumn temperatures drop below the lower threshold.

Thus, depending on the conditions of a given season, *P. festucae* in the temperate zone of Russia has the univoltine type of development in cold years and the bivoltine type in warm years. The bivoltine cycle is realized more frequently than the univoltine one in this region. In both cases, the seasonal development of the species is controlled by the day length, according to the parameters of photoperiodic diapause induction typical of the local population. This type of seasonal cycle allows the species to use the vegetation season quite efficiently, and also ensures the preservation of a considerable part of the population should the second generation perish.

Syngrapha ottolenguii (Dyar, 1903) is a typical alpine species with a Holarctic North-Pacific boreal range; it was recorded within the Russian territory in Magadan Province, Kamchatka, Sakhalin and Kuril Islands, and also in China, the Korean Peninsula, and Japan (Matov et al., 2008; Yamamura et al., 2008b; Matov and Kononenko, 2012). This is an oligophagous species whose larvae are known to feed only on plants of the family Ericaceae (Klyuchko, 2006; Yamamura et al., 2008b; Matov and Kononenko, 2012).

The population of *S. ottolenguii* from Japan (38° N, 140° E; Zao Mt., 1800 m above sea level) was experimentally studied. This typically alpine moth has two expressed seasonal strategies: a short-day arrest of development of the II and III instar larvae in autumn and winter, and long-day inhibition of reproduction in summer. As a result, oviposition is delayed till autumn, and the late cold-resistant larvae overwinter under the snow cover.

Experiments with rearing this species on artificial nutrient medium in the laboratory showed that inhibition of larval development was controlled by PhPR. The larvae pupated in less than 40 days in long-day photoperiodic regimes (16 and 15.5 h of light a day), whereas under short-day conditions (12 h) pupation occurred only approximately on the 100th day (Fig. 6). Particularly high variation of the duration of larval development was observed at photoperiods of 12 and 14.5 h, at which the first pupae appeared on the 30th day, and the last ones, only on the 140th day (Fig. 6). This inhibition of larval development was interpreted as labile diapause because the larvae continued feeding, though at very low rates judging by the amount of excrements produced (Yamamura et al., 2008b).

To determine the effect of the photoperiod on ovariole development, the females were kept for 40 ± 1 days after hatching at three different photoperiods: 12, 16, and 24 h of light a day; the latter regime simulated the middle of the Arctic summer. No oviposition was recorded in any of the regimes, even in the presence of males and food. The females kept at 12 h of light contained on average about 500 eggs in their ovarioles; those kept at 16 h produced no more than 200 mature eggs, and under the conditions of constant light the mean number of mature eggs was no greater than 100. As shown in Fig. 7, the maturation of females was clearly affected by the photoperiodic conditions: the long day inhibited the gonad development while the short day promoted it.

Thus, *S. ottolenguii* revealed a combination of two photoperiodically controlled processes: inhibition of maturation of adults (at least females) under long-day conditions in summer and arrest (delay) of larval development under short-day conditions in autumn and winter. The cited authors interpreted these inhibition periods as two separate seasonal adaptations maintaining the univoltine seasonal cycle under the boreomontane conditions. In terms of developmental physiology, they may be considered as two typical labile diapauses that are timed to different seasons of the year and appear at different stages of development, namely the summer adult diapause and the autumn-winter larval diapause showing the typical features of these states.

Syngrapha ain (Hochenwarth, 1785) has a Eurasian boreomontane range and is distributed from the west of the Alps to the Russian Far East, Japan, and the Korean Peninsula (Yamamura and Sasaki, 2008; Matov and Kononenko, 2012). The adults fly in July–August. The species prefers mountain coniferous forests, and in central and eastern Asia, light birch-larch forests. It is an oligophage, presently known to feed only on plants of the family Pinaceae (Matov and Kononenko, 2012). The larvae have a positive phototaxis and concentrate in the upper part of the tree crown. They overwinter and complete their feeding in May–June of the following year. *Syngrapha ain* is a univoltine species with an obligate larval diapause (Yamamura and Sasaki, 2008).

Syngrapha interrogationis (Linnaeus, 1758) has a Holarctic boreomontane range; it is distributed in Alaska, Canada, and from Iceland to the continental Europe and Siberia to Japan (Matov and Kononenko, 2012). In Europe, the species is common in the northern and central parts while in the south it prefers alpine areas, being recorded up to 2400 m above sea level in the Alps. This moth is almost ubiquitous in Eastern Europe (Goater et al., 2003; Matov et al., 2008). The species is polyphagous, its larvae feeding on plants of five families (Klyuchko, 2006; Matov and Kononenko, 2012). The seasonal cycle is probably univoltine. The larvae overwinter and complete their feeding in May–June of the following year. The adults fly from June to mid-August.

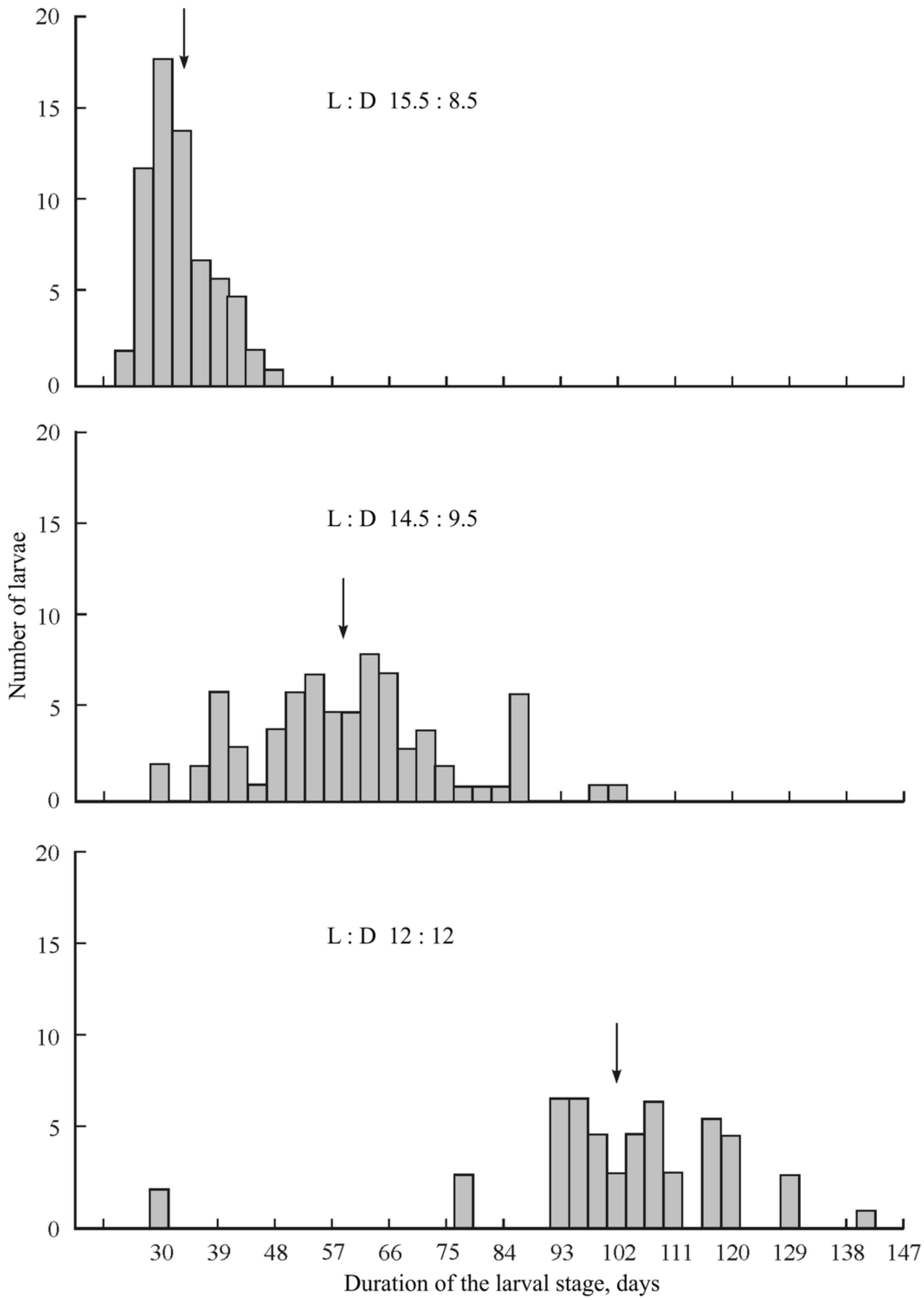

Fig. 6. Influence of the day length (L : D) on the duration of larval development of *Syngrapha ottolenguii* (Dyar) at 20°C (population from Japan, 38° N, 140° E). Arrows mark the mean duration of larval development in each regime (after Yamamura et al., 2008b).

Syngrapha devergens (Hübner, [1813]) is a typical element of the alpine fauna. It is distributed in the Alps and in the mountains of Tien Shan and Altai, extending up to the snow line. The species is oligophagous, its larvae being known to feed on plants of three families (Goater et al., 2003; Yamamura et al., 2008b). This is one of the few species of the subfamily Plusiinae having a semivoltine life cycle. Its larvae regularly overwinter twice and mature (complete their feeding) in June–July. The adults can be recorded in July–August (Goater et al., 2003; Yamamura et al., 2008b).

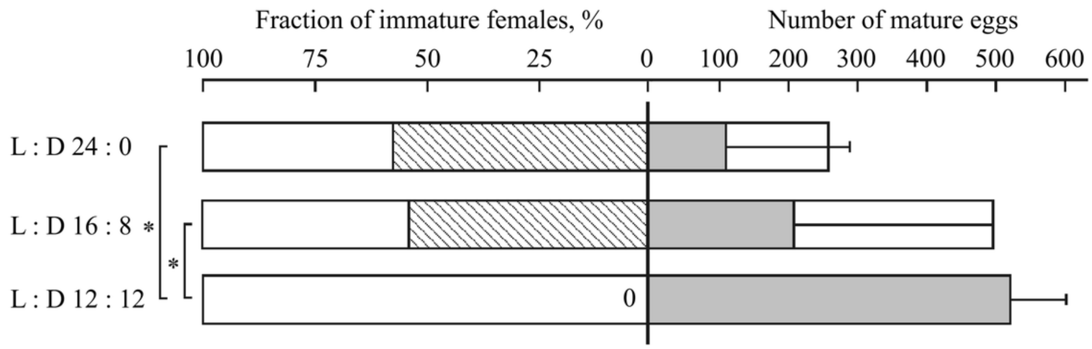

Fig. 7. Influence of photoperiodic conditions (L : D) on maturation of females of *Syngrapha ottolenguii* (Dyar) at 20°C (population from Japan, 38° N, 140° E). Left: fraction of females with mature eggs (unshaded) and without mature eggs (shaded) 40 ± 1 days after hatching; right: mean number of mature eggs in all the females (shaded) and in females with mature eggs (unshaded) 40 ± 1 days after hatching; * differences are significant at 5% confidence level (after Yamamura et al., 2008b).

3. TRIBE ABROSTOLINI

This tribe includes only two genera: the small North American genus *Mouralia* Walker, 1852 with a single species *M. tinctoides* Guen, 1852 and one of the large genera of the subfamily Plusiinae, *Abrostola* Ochsenheimer, 1816. The Palaearctic fauna comprises 22 species of the genus *Abrostola*, most of which occur in temperate regions.

The dark spectacle ***Abrostola triplasia*** (Linnaeus, 1758) has a trans-Palaearctic subboreal range (Matov and Kononenko, 2012). This is an oligophagous species whose larvae occur on plants of three families (Matov and Kononenko, 2012).

The population of *A. triplasia* from Belgorod Province of Russia (Belogorye Nature Reserve, 50° N, 36° E) was studied experimentally (Saulich et al., 2015). The onset of facultative pupal diapause in the dark spectacle was controlled by qualitative PhPR of the long-day type with the critical photoperiod of over 17 h at 20°C. As the day length increased to 18 h (which was close to the maximum day length in the study region), the fraction of diapausing individuals decreased abruptly to 0% (Saulich et al., 2015). In the nature, these non-diapausing individuals can give rise to the next generation. The seasonal cycle of the studied population should be characterized as potentially bivoltine, which was confirmed by the data of phenological surveys using a light trap (Fig. 8).

Adults of the overwintered generation emerge very late, in mid-June, so that larvae of the first generation of the new season develop when the day length is close to the critical level; this determines the presence of both diapausing and physiologically active pupae in this generation. The diapausing pupae overwinter, while the adults emerging from the active pupae form the second generation, whose pupae also overwinter. Therefore, the overwintering pool of the dark spectacle is formed by individuals of both the first and the second generation. The fractions of the two generations in the total number of overwintering pupae depend on the weather conditions in the given year: pupae of the first generation prevail in cold years, and those of the second generation prevail in average and warm years. Thus, *A. triplasia* in the study region has a very flexible seasonal cycle which allows it to utilize the whole vegetation season by forming two generations and at the same time to form the reserve of overwintering pupae already in the first generation, which would be helpful if the weather conditions do not allow the second generation to complete.

Abrostola tripartita (Hufnagel, 1766) has a Eurasian subboreal range (Matov and Kononenko, 2012). It is distributed over the whole western part of Eurasia except for the northernmost regions of Fennoscandia; in the east of Eurasia it occurs in the southern regions of Siberia as far eastward as Japan. This is a polyphagous moth whose larvae feed on plants of five families (Matov and Kononenko, 2012). The species overwinters as pupae and has a multivoltine (bivoltine) seasonal cycle, forming two generations a year both in Germany and Ukraine (Koch, 1958; Klyuchko, 2006).

Abrostola asclepiadis ([Denis et Schiffermüller], 1775) has a Eurasian subboreal range covering Southern and Central Europe, as far northwards as Sweden and Finland (Matov and Kononenko, 2012). Within Eastern Europe, the species has been recorded in the South Urals. It is also distributed in the Caucasus and Asia Minor (Förare, 1995; Goater et al., 2003; Matov et al., 2008). This is an oligophagous species; at pre-

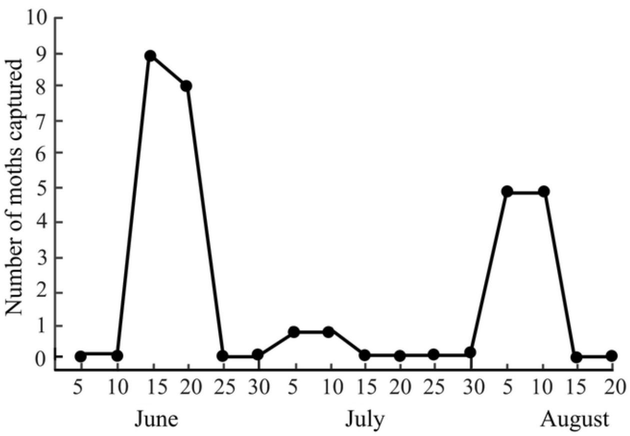

Fig. 8. Light trap captures of *Abrostola triplasia* (L.) in Belogorye Nature Reserve (Belgorod Province, 50° N, 36° E; after Saulich et al., 2015).

sent, its larvae are known to feed only on plants of the family Asclepiadaceae (Matov and Kononenko, 2012). At least some species of this plant family contain alkaloids and the glycoside vincetoxin and are rarely consumed by other insects (Förare, 1995).

The species overwinters as pupae and has a multivoltine seasonal cycle. One generation a year was recorded in Ukraine (Klyuchko, 2006) and Germany (Koch, 1958), whereas in Sweden two generations may develop in some years (Förare, 1995).

4. TRIBE OMORPHINI

This poorly studied tribe includes one species, *Omorphina aurantica* Alpheraky, 1892 from Tibet (Kitching, 1987); there are no data on the control of its seasonal cycle.

CONCLUSIONS

Analysis of the data on seasonal adaptations in Plusiinae has shown that the responses controlling the seasonal development of these moths are still poorly understood. However, even the scanty material available demonstrates a considerable diversity of seasonal schemes realized by different species of Plusiinae in different regions. Representatives of this small subfamily reveal practically all the pattern of seasonal cycles known in Insecta, from homodynamic to various modifications of the heterodynamic cycle.

The homodynamic cycle (continuous physiological activity, with a sequence of generations developing without diapause all the year round) was studied in detail in species from different tribes: *Trichoplusia ni*, *Ctenoplusia agnata* (Argyrogrammatini), and *Autographa gamma* (Plusiini). The seasonal development of these southern moths is complicated by regular interzonal migrations. They can extend far to the north, complete a different number of generations per season depending on the local climatic conditions, and form temporary seasonal populations whose existence is limited by the vegetation period. Adults of some species may be able to migrate back to the south before the onset of unfavorable conditions, but in a more probable scenario, the temporary seasonal populations perish due to their inability to survive a prolonged winter. Their dependence on the environmental conditions is very strong, which was demonstrated by the example of *Macdunnoughia confusa* (Merivee, 1971), also capable of long-distance migrations.

The heterodynamic seasonal cycle, including a special overwintering state, practically ensures the existence of insects under the conditions of expressed climatic seasonality. Species with this type of seasonal development usually have vast ranges covering territories with a broad and diverse spectrum of environmental conditions. The heterodynamic type includes univoltine, multivoltine, and semivoltine development.

Univoltinism based on an obligate diapause is typical of many species, including *Autographa buraetica*, *A. excelsa*, and *Syngrapha ain* which inhabit high latitudes (including the Subarctic) and mountain landscapes up to the subalpine belt. Strong and genetically determined diapause ensures their resistance to low temperatures and a prolonged absence of food. However, in *Syngrapha ottolenguii* (a species morphologically close to *S. ain*) the same effect is achieved by the presence of two diapauses controlled by the day length: the autumn-winter larval diapause and the summer adult one (Yamamura et al., 2008).

According to the published data, the semivoltine seasonal cycle is known only in one species of the subfamily Plusiinae, namely in *Syngrapha devergens*, whose larvae regularly overwinter twice during their development (Yamamura et al., 2008).

Multivoltinism is very common in the tribe Plusiini. Depending on the latitude, different species of this taxon produce from 1 to 4 generations a year while their middle-instar larvae overwinter in a facultative diapause. However, the properties of the diapause vary strongly between the species: diapause can be deep and strong (as in *Diachrysia chrysitis*) or labile and thus insufficient for successful overwintering and maintaining stable population abundance (as in *Macdunnoughia confusa*; Merivee, 1971).

Some ecological adaptations of Plusiinae used in the formation of the specific seasonal cycle of a species or its population are very close to the adaptations typical of representatives of other insect orders. These are migrations, winter and summer diapauses, photoperiodic regulation of the larval growth rate, and seasonal polyphenism in the larval coloration (Saulich and Musolin, 2017). On the whole, the system of seasonal adaptations of Plusiinae, as in other insects, is totally determined by the local environmental conditions and only weakly related to the taxonomic position of particular species of tribes.

Species of the tribe Abrostolini stand apart in the phylogenetic scheme of the subfamily (Kitching, 1987; Nomura, 1987). They differ from the rest of Plusiinae not only in morphological characters but also in specific traits of seasonal development: they overwinter exclusively as pupae and thus have a different structure of the entire seasonal cycle.

ACKNOWLEDGMENTS

The authors are very grateful to A.Yu. Matov (Zoological Institute of the Russian Academy of Sciences, St. Petersburg) and Prof. S. Yamamura (Tamagawa University, Tokyo, Japan) for valuable advice and help with obtaining some literature. This work was partly supported by the Russian Foundation for Basic Research (grant 17-04-01486A).

REFERENCES

1. *Agroclimatic Resources of Belgorod Province* (Gidrometeoizdat, Leningrad, 1972) [in Russian].
2. Belozerov, V.N., "Dormant Stages and Their Participation in Adjustment and Regulation of Life Cycles of Harvestmen (Arachnida, Opiliones)," Entomologicheskoe Obozrenie **91** (1), 180–216 (2012) [Entomological Review **92** (6), 688–714 (2012)].
3. Belozerov, V.N., "Seasonal Aspects of the Life Cycles of Pseudoscorpions (Arachnida, Pseudoscorpiones)," Entomologicheskoe Obozrenie **92** (1), 142–166 (2013) [Entomological Review **93** (5), 634–652 (2013)].
4. Berdys, H., Golden Plusia *Polychrysia moneta* (2016). http://www.gardensafari.net/en_picpages/polychrysia_moneta.htm (accessed 01.06.2016).
5. Chapman, J.W., Bell, J.R., Burgin, L.E., Reynolds, D.R., Pettersson, L.B., et al., "Seasonal Migration to High Latitudes Results in Major Reproductive Benefits in an Insect," Proceedings of the National Academy of Sciences **109**, 14924–14929 (2012).
6. Chapman, J.W., Drake, V.A., and Reynolds, D.R., "Recent Insights from Radar Studies of Insect Flight," Annual Review of Entomology **56**, 337–356 (2011).
7. Danilevsky, A.S., *Photoperiodism and Seasonal Development of Insects* (Leningrad State University, Leningrad, 1961) [in Russian].
8. Danks, H.V., *Insect Dormancy: An Ecological Perspective* (Biological Survey of Canada, Ottawa, 1987).
9. Danks, H.V., "The Elements of Seasonal Adaptations in Insects," Canadian Entomologist **139**, 1–44 (2007).
10. Denlinger, D.L., "Dormancy in Tropical Insects," Annual Review of Entomology **31**, 239–264 (1986).
11. Denlinger, D.L., Yocum, G.D., and Rinehart, J.P., "Hormonal Control of Diapause," in *Insect Endocrinology*, Ed. by L.I. Gilbert (Academic Press, London, 2012), pp. 430–463.
12. Dingle, H., *Migration: the Biology of Life on the Move* (Oxford University Press, N.Y., 1996).
13. Förare, J., "The Biology of the Noctuid Moth *Abrostola asclepiadis* Schiff. (Lepidoptera, Noctuidae) in Sweden," Entomologisk Tidskrift **116** (4), 179–186 (1995).
14. Goater, B., Ronkay, L., and Fibiger, M., *Noctuidae Europaeae*, Vol. 10: *Catocalinae, Plusiinae* (Entomological Press, Sorø, 2003).
15. Goryshin, N.I. and Saulich, A.Kh., "Studies of Seasonal Adaptations in Homodynamic Lepidoptera. II. Cold Tolerance and Survival at Low Above-Zero Temperatures," Zoologicheskii Zhurnal **61** (1), 36–46 (1982).
16. Goryshin, N.I. and Saulich, A.Kh., "Studies of Seasonal Adaptations in Homodynamic Lepidoptera. III. Development under the Temperate Climate Conditions," Zoologicheskii Zhurnal **62** (2), 222–232 (1983).
17. Goto, S.G. and Numata, H., "Insect Photoperiodism," in *Insect Molecular Biology and Ecology*, Ed. by K.H. Hoffmann (CRC Press, Boca Raton, 2015), pp. 217–244.
18. Hill, J.K. and Gatehouse, A.G., "Effects of Temperature and Photoperiod on Development and Pre-Reproductive Period of the Silver Y Moth *Autographa gamma* (Lepidoptera: Noctuidae)," Bulletin of Entomological Research **82**, 335–341 (1992a).
19. Hill, J.K. and Gatehouse, A.G., "Genetic Control of the Pre-Reproductive Period in *Autographa gamma* (L.) (Silver Y Moth) (Lepidoptera: Noctuidae)," Heredity **69**, 458–464 (1992b).
20. Hill, J.K. and Gatehouse, A.G., "Phenotypic Plasticity and Geographical Variation in the Pre-Reproductive Period of *Autographa gamma* (Lepidoptera: Noctuidae) and Its Implications for Migration in This Species," Ecological Entomology **18**, 39–46 (1993).
21. Honěk, A., "Food Induced Variation in Thermal Constants of Development and Growth of *Autographa gamma* (Lepidoptera: Noctuidae)," European Journal of Entomology **99**, 241–252 (2002).
22. Johnson, C.G., *Migration and Dispersal of Insects by Flight* (Methuen, London, 1969).
23. Kaisila, J., "Immigration und Expansion der Lepidopteren in Finland in den Jahren 1869–1960," Acta Entomologica Fennica **18**, 1–452 (1962).

24. Kaneko, J., "Existence Ratio of the Silver Y Moth, *Autographa gamma* (L.) after Overwintering in a Cabbage Field at Sapporo, Japan," Annual Report of the Society of Plant Protection of North Japan **44**, 124–126 (1993).
25. Kaneko, J., "Differences in Cold-Hardiness between Silver Y-Moth, *Autographa gamma* (L.) and Asiatic Common Looper, *A. nigrisigna* (Walker)," Japanese Journal of Applied Entomology and Zoology **40**, 303–308 (1996) [in Japanese].
26. Kipyatkov, V.E. and Lopatina, E.B., "Seasonal Cycles and Strategies in Ants: Structure, Diversity, and Adaptive Traits," in *Strategies of Adaptations of Terrestrial Arthropods to Adverse Environmental Conditions* (*Proceedings of the Biological Research Institute, Vol. 53*), Ed. by A.A. Stekolnikov (St. Petersburg State University, St. Petersburg, 2007), pp. 107–192 [in Russian].
27. Kitching, I.J., "Spectacles and Silver Y's: a Synthesis of the Systematics, Cladistics and Biology of the Plusiinae (Lepidoptera: Noctuidae)," Bulletin of the British Museum (Natural History). Entomology **54**, 75–261 (1987).
28. Klyuchko, Z.F., *Noctuoid Moths of Ukraine* (Izdatelstvo Raevskogo, Kiev, 2006) [in Ukrainian].
29. Koch, M., *Wir bestimmen Schmetterlinge* (Radebeul, Berlin, 1958).
30. Koch, M., "Warum wandern einige Schmetterlingsarten?" Entomologischen Abhandlungen **32**, 203–211 (1965).
31. Koštál, V., "Eco-Physiological Phases of Insect Diapause," Journal of Insect Physiology **52**, 113–127 (2006).
32. Lafontaine, J.D. and Poole, R.W., "25.1. Noctuoidea, Noctuidae (Part): Plusiinae," in *The Moths of America North of Mexico*, Ed. by R. Dominick (Wedge Entomological Research Foundation, Washington, 1991).
33. Lafontaine, J.D. and Schmidt, B.C., "Annotated Check List of the Noctuoidea (Insecta, Lepidoptera) of North America North of Mexico," ZooKeys **40**, 1–239 (2010).
34. Li, C., Fu, X., Feng, H., Ali, A., Li, C., and Wu, K., "Seasonal Migration of *Ctenoplusia agnata* (Lepidoptera: Noctuidae) over the Bohai Sea in Northern China," Journal of Economic Entomology **107** (3), 1003–1008 (2014).
35. Matov, A.Yu. and Kononenko, V.S., *Trophic Associations of the Larvae of Noctuoid Moths in the Fauna of Russia (Lepidoptera, Noctuoidea: Nolidae, Erebidae, Euteliidae, Noctuidae)* (Dalnauka, Vladivostok, 2012) [in Russian].
36. Matov, A.Yu., Kononenko, V.S., and Sviridov, A.V., "Noctuidae," in *Catalogue of the Lepidoptera of Russia*, Ed. by S.Yu. Sinev (KMK Scientific Press, Moscow, 2008), pp. 239–296 [in Russian].
37. Merivee, E.E., "Criteria of Lability of Photoperiodic Response and Their Relation to Cold Tolerance in Noctuid Moths *Plusia chrysitis* L. and *Macdunnoughia confusa* Stph.," in *Cold Tolerance in Insects and Acarines: Proceedings of a Symposium, April 19–21, 1971*, Ed. by V.Yu. Maavara (Tartu, 1971), pp. 79–83.
38. Merivee, E.E., *Cold Tolerance in Insects* (Estonian SSR Academy of Sciences, Tartu, 1978) [in Russian].
39. Merzheevskaya, O.I., *Larvae of Noctuidae: Their Biology and Morphology* (Nauka i Tekhnika, Minsk, 1967) [in Russian].
40. Musolin, D.L. and Saulich, A.Kh., "Photoperiodic Control of Nymphal Growth in True Bugs (Heteroptera)," Zoologicheskii Zhurnal **76** (5), 530–540 (1997) [Entomological Review **77** (6), 768–780 (1997)].
41. Musolin, D.L. and Saulich, A.Kh., "Diapause in Pentatomoidea," in *Invasive Stink Bugs and Related Species (Pentatomoidea): Biology, Higher Systematics, Semiochemistry, and Management*, Ed. by J.E. McPherson (CRC Press, Boca Raton, 2017), pp. 475–542.
42. Navas, C.A., and Carvalho, J.E. (Eds.), *Aestivation: Molecular and Physiological Aspects (Progress in Molecular and Subcellular Biology 49)* (Springer-Verlag, Berlin-Heidelberg, 2010).
43. Nomura, M., "Allozyme Variation and Phylogenetic Analyses of Genera and Species of Japanese Plusiinae (Lepidoptera: Noctuidae)," Applied Entomology and Zoology **33** (4), 513–523 (1998).
44. Novák, I., "Hibernation of the Silver Y-Moth *Autographa gamma* L. (Lepidoptera: Noctuidae) under the Climatic Conditions of Central Europe," in *Proceedings of the XIII International Entomological Congress, August 2–9, 1968. Vol. 1* (Moscow, 1968), p. 533.
45. Novák, I., "Prezimovani mury gama (*Autographa gamma* L., Lepidoptera: Noctuidae) ve Stredni Evrope," Ochrana Rostlin **8**, 305–312 (1972).
46. Saito, O., "Notes on Larval Hibernation of the Alfalfa Looper, *Autographa gamma* (L.) on Cabbage Plant in Sapporo, Hokkaido," Annual Report of the Society of Plant Protection of North Japan **39**, 217 (1988).
47. Saito, O., "Diapause-Like Prolongation of Larval Duration under Short-Day Photoperiod and Low Temperature Conditions in the Silver Y Moth, *Autographa gamma* L. (Lepidoptera: Noctuidae)," Applied Entomology and Zoology **42** (3), 391–395 (2007).
48. Saulich, A.Kh., *Seasonal Development and Dispersal Potential of Insects* (St. Petersburg State Univ., St. Petersburg, 1999) [in Russian].
49. Saulich, A.Kh. and Musolin, D.L., "Times of the Year: the Diversity of Seasonal Adaptations and Ecological Mechanisms Controlling Seasonal Development of True Bugs (Heteroptera) in the Temperate Climate," in *Strategies of Adaptations of Terrestrial Arthropods to Adverse Environmental Conditions* (*Proceedings of the Biological Research Institute, Vol. 53*), Ed. by A.A. Stekolnikov (St. Petersburg State University, St. Petersburg, 2007), pp. 25–106 [in Russian].
50. Saulich, A.Kh. and Musolin, D.L., "Seasonal Cycles in Stink Bugs (Heteroptera, Pentatomidae) from the Temperate Zone: Diversity and Control," Entomolo-

gicheskoe Obozrenie **93** (2), 263–302 (2014) [Entomological Review **94** (6), 785–814 (2014)].

51. Saulich, A.Kh. and Musolin, D.L., "Seasonal Development of *Plusia festucae* and Its Environmental Control," in *The Kataev Memorial Readings – IX. Dendrobiotic Invertebrates and Fungi and their Role in Forest Ecosystems. Proceedings of the International Conference*, Ed. by D.L. Musolin and A.V. Selikhovkin (St. Petersburg State Forest Technical University, St. Petersburg, 2016), pp. 106–107.
52. Saulich, A.Kh. and Musolin, D.L., "Seasonal Cycles of Pentatomoidea," in *Invasive Stink Bugs and Related Species (Pentatomoidea): Biology, Higher Systematics, Semiochemistry, and Management*, Ed. by J.E. McPherson (CRC Press, Boca Raton, 2017), pp. 543–585.
53. Saulich, A.Kh. and Sokolova, I.V., "Seasonal Adaptations in Noctuid Moths (Lepidoptera, Noctuidae)," Entomologicheskoe Obozrenie **81** (3), 529–546 (2002) [Entomological Review **82** (9), 1127–1141 (2002)].
54. Saulich, A.Kh. and Volkovitsh, T.A., *Ecology of Photoperiodism in Insects* (St. Petersburg State Univ., St. Petersburg, 2004) [in Russian].
55. Saulich, A.Kh., Sokolova, I.V., and Musolin, D.L., "Seasonal Development of the Dark Spectacle *Abrostola triplasia* (L.) (Lepidoptera, Noctuidae) and Its Environmental Control," Entomologicheskoe Obozrenie **94** (3), 481–488 (2015) [Entomological Review **95** (6), 687–692 (2015)].
56. Saunders, D.S. (with Steel, C.G.H., Vafopoulou, X., and Lewis, R.D.), *Insect Clocks*, 3rd ed. (Elsevier Science, Amsterdam, 2002).
57. Speidel, W., Faner, W., and Naumann, C.M., "Phylogeny of the Noctuidae (Lepidoptera)," Systematic Entomology **21** (3), 219–251 (1996).
58. Storey, K.B. and Storey, J.M., "Aestivation: Signaling and Hypometabolism," Journal of Experimental Biology **215** (9), 1425–1433 (2012).
59. Sukhareva, I.L., "Family Noctuidae," in *Insects and Acarines as Agricultural Pests*, Vol. 3: *Lepidoptera, Part 2*, Ed. by V.I. Kuznetsov (Nauka, St. Petersburg, 1999), pp. 332–376 [in Russian].
60. Tauber, M.J., Tauber, C.A., and Masaki, S., *Seasonal Adaptations of Insects* (Oxford University Press, New York, 1986).
61. Vojnits, A., "Az 'igazi' vándorlepkék," Folia Entomologica Hungarica **8**, 167–175 (1966).
62. Volkovitsh, T.A., "Diapause in the Life Cycles of Lacewings (Neuroptera, Chrysopidae)," in *Strategies of Adaptations of Terrestrial Arthropods to Adverse Environmental Conditions* (*Proceedings of the Biological Research Institute, Vol. 53*), Ed. by A.A. Stekolnikov (St. Petersburg State University, St. Petersburg, 2007), pp. 234–304 [in Russian].
63. Yamamura, S. and Sasaki, M., "Some Notes on Larval Development and Diagnosis in *Autographa buraetica* (Staudinger) (Lepidoptera: Plusiinae) in Japan," Japan Heterocerists' Journal **240**, 269–272 (2006) [in Japanese with English summary].
64. Yamamura, S. and Sasaki, M., "Larval-Pupal Bionomics of *Syngrapha ain* (Hochenwarth) (Noctuidae, Plusiinae) in the Japanese Population Based on Artificial Rearing and Field Observation," Japan Heterocerists' Journal **248**, 412–417 (2008) [in Japanese with English summary].
65. Yamamura, S., Ikarashi, M., and Sasaki, M., "A Critical Photoperiod which Induces Larval Diapause, and Observation of Its Development in *Diachrysia chryson* (Esper) (Noctuidae: Plusiinae)," Japan Heterocerists' Journal **249**, 434–437 (2008a) [in Japanese with English summary].
66. Yamamura, S., Ikarashi, M., and Sasaki, M., "Dual Photoperiodic Regulation to Enable Univoltine Life Cycle in Alpine Silver-Y Moth, *Syngrapha ottolenguii* (Noctuidae: Plusiinae) without Obligatory Diapause," Applied Entomology and Zoology **43** (1), 105–112 (2008b).
67. Yathom, S., and Rivnay, E., "Phenology and Distribution of Phytometrinae in Israel," Zeitschrift für Angewandte Entomologie **61** (1), 1–16 (1968).