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A Review of Geographic Distribution, Overwintering and Migration in *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae)

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ABSTRACT

The beet armyworm, *Spodoptera exigua* Hübner 1808 is an outbreak herbivore and results in serious economic losses in many areas of the world. One of causes of population outbreak could be attributed to miss the optimal control chance based on incomprehension of the population source. We reviewed the advances of overwintering and migration of *S. exigua* based on geographic distribution to understand the population sources. The distribution regions of *S. exigua* increased 34 countries since 1972. Population dynamics of *S. exigua* during winter were different, but the overwintering regions are still vague and migratory trajectories are incomplete. The migratory phenomena, demonstrating moths have strong flight capacity, had been recorded in the United States, United Kingdom, Fennoscandia and Japan in spring and early summer, and back track in the United Kingdom and China in fall. On the basis of monsoon, geographic distribution and population dynamics during winter, we speculated that the population of *S. exigua* migrate northward in spring and early summer in China, and southward in fall in the United States and Japan.

Key words: Spodoptera exigua, geographic distribution, population dynamic, overwintering, migration, population source.

INTRODUCTION

Low temperature during winter is a huge challenge for surviving of many insects. Insects have evolved various strategies to endure these environmental stresses. Hibernation and migration are the two major strategies for winter survival in seasonal adaption of insects (Tauber *et al.*, 1986). Understanding the overwintering regions and migratory trajectories could provide helpful information for predicting the population dynamics following winter and for establishing effective population monitoring and forecasting (Bale, 2002).

The beet armyworm, *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae) is an important and cosmopolitan agricultural crops pest (Brady and Ganyard, 1972), and results in serious economic losses in recent years across a wide distribution in the world, particularly in the America and Asia. In addition, the phenomenon of devastating outbreak was recorded in many regions, such as China (Luo *et al.*, 2000) and the

United States (Burris *et al.*, 1994). Theoretically, the population outbreak could put down to miss the optimal control chance (for example, population management of the first generation). However, *S. exigua* is a migratory species (Mitchell, 1979) and can overwinter in some regions, e. g., California (Trumble and Baker, 1984) and Kagoshima (Suenaga and Tanaka, 2000). So, the primary question that the population source of outbreak regions migrated from southern provinces, or arose from local or both needs to answer.

Indeed, it is beneficial for IPM (Integrated Pest Management) on the basis of understanding the population source of outbreak pests. But the first we have to clarify is the population dynamics of pests during winter. Here, we reviewed the advances of overwintering and migration of *S. exigua* based on geographic distribution, to understand the population dynamics during winter as the basis for analyzing the population source, monitoring and forecasting for this species.

GEOGRAPHIC DISTRIBUTION

Geographic distribution is one of the major characteristics of an insect, and was considered as a basis for analyzing the population source, especially for invasive and outbreak species. *S. exigua* is considered to be an outbreak pest with a worldwide distribution. Its migratory capacity significantly contributes to the population outbreak and facilitates the geographic expansion of population (French, 1969; Mikkola, 1970; Kimura, 1991; Feng *et al.*, 2003). Older synoptic describing regarding the distribution of *S. exigua* in the world was published by Commonwealth Agricultural Bureaux (CAB, 1972). They reported that *S. exigua* distributed in 67 countries in the world, about 70 % of which were recorded in Africa and Asia. However, an extensive survey of the literatures of this species indicated that its distribution regions increased to 101 countries in the world. A majority of expansion in geographic regions were mostly in the northern Europe (e. g., Norway, Finland, Sweden, etc.) and South America (e. g., Brazil, Bolivia, Chile, etc.) (Table 1). Furthermore, many researchers considered the geographical locations of *S. exigua* ranging on latitude from 57° N to 45° S. However, moths were monitored at Sotkamo (64.13° N) in Finland through light-traps for many years (Mikkola, 1970). Therefore, the geographical locations of *S. exigua* should be revised to range from 64° N to 45° S.

POPULATION DYNAMICS OF *S. EXIGUA* DURING WINTER

Historical data demonstrated that study on population dynamics of *S. exigua* during winter focused on temperate regions in the Northern Hemisphere (Fig. 1). There was no literature reported this information though it has been spread to the Southern Hemisphere and boreal regions in the Northern Hemisphere (Table 1, Fig. 1).

Beet armyworm is a temperate species, and their overwintering strategies (e. g., migration or hibernation) vary with latitude so that population dynamics during winter are different. However, the overwintering regions of *S. exigua* are vague. On the one hand, its northern boundary of overwintering is unclear. For example, 44° N was considered as the northern boundary of overwintering (Mikkola and Salmensuu, 1965). Literatures recorded that *S. exigua* also could not overwinter at some southern regions of the northern boundary of overwintering, including the United States: delta and hill regions of north Mississippi (Adamczyk *et al.*, 2003) and Tennessee; Japan: Akita Prefecture (Kimura, 1991); China: Beijing (Feng *et al.*, 2003), Daxian State of Sichuan Province (Zeng *et al.*, 2003) and Wenzhou City of Zhejiang Province (Chen *et al.*, 2005; Xu *et al.*, 2007); United Kingdom (Hurst, 1965; French, 1969) and Fennoscandia (Mikkola, 1970). Moreover, as shown in Figure 1, the northmost overwintering site of *S. exigua* was reported at Bayramaly (37.6° N) in Turkmenistan. It maybe considered that the northern boundary of overwintering is 37.6° N. However, whether *S. exigua* can overwinter ranging on latitude from 37.6° N to 44° N, which was also considered as northern boundary of overwintering by other researchers (Mikkola and Salmensuu, 1965), it needs further study. On the other hand, the population dynamics of *S. exigua* have excited a lively controversy in some regions (Fig. 1). In Shandong Province in China, population outbreak were considered by some researchers to have migrated from southern provinces (Feng *et al.*, 1995), while others insisted that the insects arose from local overwintering populations (Wang *et al.*, 2002). A similar debate was also raised concerning population source in Henan Province (Wu *et al.*, 2000; Guo *et al.*, 2005). Moreover, whether *S. exigua* appears to overwinter in Georgia in the United States, opinions on this issue are at opposite poles (Carlson, 2008; Sparks and Riley, 2008).

Table 1. Increased geographic distribution of *Spodoptera exigua* in the world since 1972.

Latitude	Distribution
60° N-75° N	Norway (Aarvik, 1981), Finland (Mikkola, 1970), Sweden (Brown, 1975)
45° N-60° N	EUROPE: Ireland (Thompson and Nelson, 2003), United Kingdom (Michael, 2009), Germany (Kranz *et al.*, 1977), Norway (Aarvik, 1981), Netherlands, Belgium, Denmark, Sweden, Poland, Latvia, Ukraine (Brown, 1975); NORTH AMERICA: Minnesota (Abrahamson and Luhman, 2001)
30° N-45° N	EUROPE: Malta (Baron, 2007), Montenegro and Serbia (Vajgand, 2009); ASIA: Georgia, Turkmenistan (Kurdov, 1986, 1987), Armenia, Uzbekistan (Khamraev and Davenport, 2004);
15° N-30° N	AFRICA: Mauritania; PACIFIC ISLANDS: Polynesia (Nishida, 2008); NORTH AMERICA: Dominica (Brown, 1975)
0°-15° N	AFRICA: Uganda (Brown, 1975); ASIA: Malaysia (Azidah and Sofian–Azirun, 2006); SOUTH AMERICA: Nicaragua (Todd and Poole, 1980), Honduras (Passoa, 1991)
0° -15° S	AFRICA: Zambia (Brown, 1975); SOUTH AMERICA: Peru, Bolivia (Hernández *et al.*, 2005)
15° S-30° S	AFRICA: Mauritius (Van Wyk *et al.*, 2008); SOUTH AMERICA: Brazil, Bolivia (Hernández *et al.*, 2005), Chile (Angulo and Jana, 1982)
30° S-45° S	AUSTRALASIA AND PACIFIC ISLANDS: New Zealand (Brown, 1975); SOUTH AMERICA: Chile (Angulo and Jana, 1982)

Although the overwintering regions of *S. exigua* are unclear, some overwintering sites of *S. exigua* have already been confirmed. For example, pupae appeared to overwinter in California: San Diego, Orange and Ventura County (Trumble and Baker, 1984); Jordan (Al-Abbadi, 2001); Turkmenistan: Bayramaly (Kurdov, 1986, 1987); China: Dali State (Li, 2005) and Hengyang City (Yin *et al.*, 1994). Larvae appeared to overwinter in Japan: Kagoshima Prefecture (Suenaga and Tanaka, 2000). Furthermore, larvae were investigated on *Spinacia oleracea* L. and *Brassica* *compestris* L. var. *purpurea* Bailey during winter (2008-2009) in Wuhan City (114.31° E, 30.52° N, Hubei Province), and on *Allium schoenoprasum* L. during winter (2009-2010) in Yibin City (104.6° E, 29.8° N, Sichuan Province). Meanwhile, moths also were monitored by sex pheromone during winter (2009-2010) in Yibin City (unpublished data). Furthermore, no phenomenon of overwintering had also been observed, and all stages of this insect were found throughout the year in China: Taiwan, Shenzhen, Hongkong and Xiamen (Chen *et al.*, 1988; Lv *et al.*, 1992; Fang *et al.*, 1998; Dai *et al.*, 1999); United States: Hastings, Belle Glade and Alachua of Florida (Tingle and Mitchell, 1977; Foster, 1989; Mitchell and Tumlinson, 1994), Texas (Mascarenhas *et al.*, 1998), Arizona (Fye and Carranza, 1973), Alabama and Mississippi (Hendricks *et al.*, 1995). Information of the overwintering and perennial damage sites of *S. exigua* is helpful for analyzing the population source in the severe regions in the northern high latitude.

MIGRATION OF *S. EXIGUA*

Migratory mechanism of *S. exigua*

Migratory behavior is a seasonal to-and-fro movement of populations between regions where conditions are alternately favorable or unfavorable (including one region in which breeding occurs) (Dingle and Drake, 2007) and a key process in the population dynamics of many insects (Williams, 1957). As known to all, meteorology should be integrated into research on migration, especially when trying to understand the timing of migration, migratory routes, orientation, etc. (Shamoun-Baranes *et al.*, 2010). From numerous studies over the years, it is clear that of all atmospheric conditions wind plays a most important role in insect migration (Chapman *et al.*, 2008), because the insects climb to heights where the wind speed exceeds their own flying speed through the airflow. Especially, the wind systems encountered by night-flying insects occur over a range of sizes up to thousands of kilometers (Burt and Pedgley, 1997). This view has been proved in *S. exigua* (French, 1969; Mikkola, 1970).

Migratory insects uses by day or / and night-flying. Day-flying insects primarily make use of the sun (Oliveira *et al.*, 1996), polarized light (Hyatt, 1993), Earth's magnetic (Pérez *et al.*, 1999), antennae (Christine *et al.*, 2009) for orientation. The orientation mechanisms of nocturnal moths (night-flying) that migrate have not been well studied. For *S. exigua*, we only know that it may migrate with airflow, but are unclear whether it has orientation mechanisms for this round trip.

Migratory trajectories in late spring and early summer

The northmost overwintering site of *S. exigua* was recorded at Bayramaly (37.6° N) in Turkmenistan (Fig. 1). So, a common question that most people wondering about is where the population sources come from beyond 37.6° N?

In fact, population originates from southern perennial damage and/or overwintering regions. Migratory trajectories are from southern to northern regions in late spring and early summer. Because of the prevalent monsoon in late spring and early summer is helpful for *S. exigua* migrating from south to north according to the migratory mechanism. For example, in the British Isles, sources of *S. exigua* came from the south according to recorded capture and a wind track from a southerly direction into the British Isles. In February, March and April, *S. exigua* migrated with the wind to the British Isles from Canary Islands or Madeira (perennial damage regions). After May, *S. exigua* arrived in the British Isles from Spain and Portugal (overwintering regions) or the offspring of moths carried from Africa to the Iberian Peninsula earlier in the year (French, 1969). The similar phenomenon was observed in Fennoscandia. The moths were captured in the night at Parikkala, Houtskär, Helsink and Sotkamo in Fennoscandia by light-traps in operation per night in southern areas in August. The moths source was supposed to come from the overwintering regions at north-east of the Caspian Sea (Figs. 1 and 2) (Mikkola, 1970). Subsequently, some moths were observed at Öland and Västerås from August to September in Sweden during 1995-1998 (Ryrholm, 1998). Moreover, the phenomenon migrating of *S. exigua* from south to north in late spring and early summer had also been recorded in Japan (Kimura, 1991) and the United States (Mitchell, 1979; Westbrook, 2008).

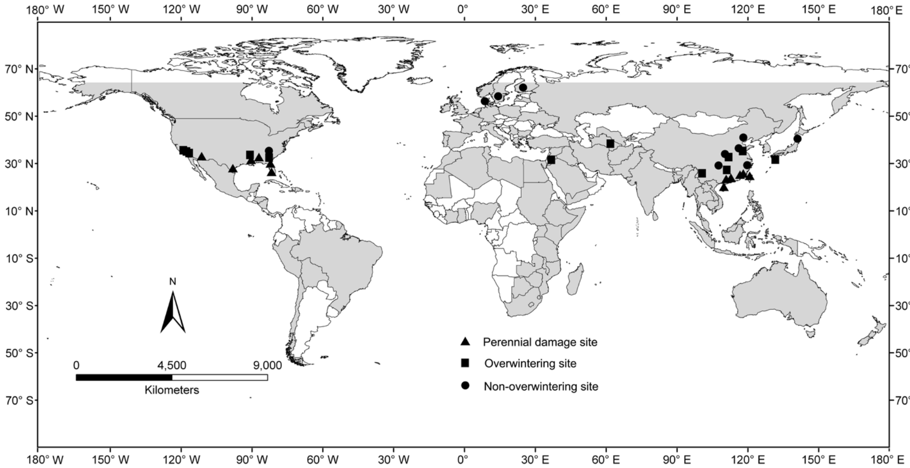

Fig. 1. Geographic distribution of *S. exigua* (gray background in the map) in the world and population dynamics during winter.

The worsening pest problem of *S. exigua* on various crops in the northern regions in China is at least partially attributed to its strong migratory capacity (Han *et al.*, 2004). However, it was only reported that *S. exigua* migrated from northern to southern areas in September in China. Therefore, the population sources and migratory trajectories are unclear. It is worth to mention that the southeast monsoon, prevalent in South Asia and Southeast Asia, usually move from eastern pacific to southern cities (in April) to middle and lower Yangtze (in late May to early July) to north and northeast cities (in late July to early August) in China. On the basis of monsoon, distribution and population dynamics during winter, the hypotheses of migratory trajectories of *S. exigua* in spring and early summer in China were provided: (1) migration from southern to northern areas in May to July; (2) migration from southern to middle areas in May, and later from middle to northern areas in July; (3) migration from middle to northern areas in July (Fig. 2).

Migratory trajectories in fall

Generally, many species have the seasonal to-and-fro movement, such as *Danaus plexippus* (Lepidoptera: Danaidae) (Froy *et al.*, 2003). In fact, *S. exigua* has the similar behavior (Fig. 2; Heppner, 1998; Feng *et al.*, 2003), because it is unable to survive at high latitude during winter (Mikkola and Salmensuu, 1965). It is worth to mention that equatorward airflows suitable for carrying migrants to south occur during fall. The migratory destinations are the southern overwintering or perennial damage regions. For example, back track of *S. exigua* was observed with radar and with a simultaneously-operated searchlight trap and ground light-trap in late September (from 22 September to 1 October) at a site in Langfang (39.5° N, Hebei Province) in China, and provided possible path of migration on those nights with north or northeast winds (Feng *et al.*, 2003). But we still do not know the migratory destination was either overwintering or perennial damage regions. Moreover, although many entomologists accepted the viewpoint that *S. exigua* could migrate southward in fall in the United States, no evidence was found to support this suggestion. According to the monsoon and distribution in the United States, the hypotheses of back track of *S. exigua* in fall were provided: (1) southward to overwintering regions (e. g., California); (2) southward to perennial damage regions (e. g., Arizona and Florida). In Japan, the prevalent of northeast monsoon in October was beneficial for back track of *S. exigua*. Therefore, we speculate that it is southward to overwintering regions (e. g., Kagoshima Prefecture) based on the monsoon and distribution (Fig. 2).

Overall, we supposed that migration of *S. exigua* has the common rule which moths migrate northwards in the spring and early summer, and southwards in the fall according to the habit of round trip in other migratory nocturnal species (Beerwinkle *et al.*, 1994).

SUMMARY

The distribution of *S. exigua* increased from 67 to 101 countries since 1972. Hibernation and migration are the two major strategies of *S. exigua* for winter survival. However, the overwintering regions are still unclear and migratory trajectories are incomplete. Therefore, it is difficult to accurately determine the status of *S. exigua* field population due to lacking of systemic understanding of the population dynamics during winter in the world.

The best way is to combine many methods to improve the precision of forecast in future study, such as winter climatic analysis, simulation of spring emergence of the overwintering generation, light trap monitoring, field population surveys, ovarian dissecting of the light trap catches and analyses of historical light trap data. These results are helpful for understanding the population dynamics and analyzing the population source of *S. exigua* in the outbreak regions of Northern Hemisphere.

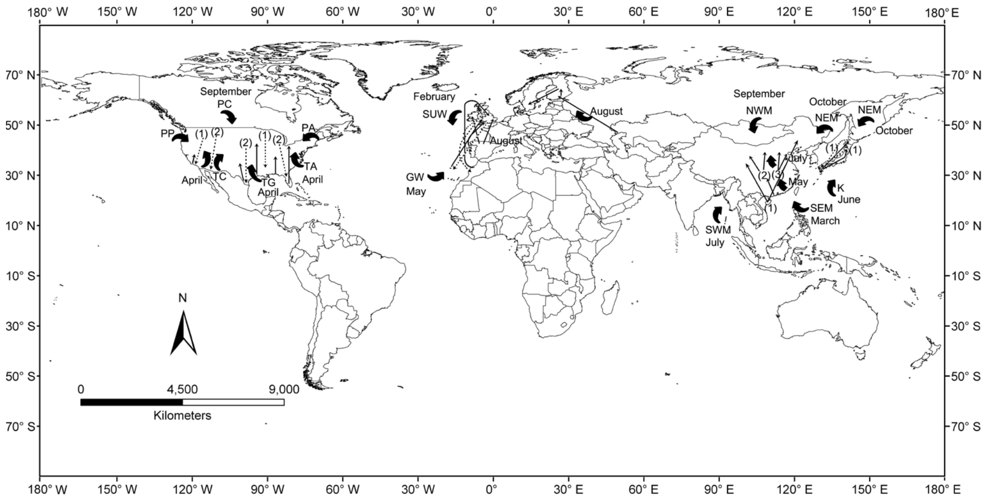

Fig. 2. Migratory trajectories of *S. exigua* in United States (Data from Trumble and Baker, 1984; Heppner, 1998; Westbrook, 2008), United Kingdom (Data from Hurst, 1965; French, 1969), Fennoscandia (Data from Mikkola, 1970), Japan (Data from Kimura, 1991) and China (Data from Feng *et al*., 2003). The continuous parts of the lines with thin arrows indicates the direction of the migration, the broken ones are back track. The big arrow indicates the direction of air-flows with month. Back track of *S. exigua* in the United States: (1) Supposed southward to overwintering regions; (2) Supposed southward to perennial damage regions. Back track of *S. exigua* in Japan: (1) Supposed southward to overwintering regions. Migratory trajectories of *S. exigua* in China: (1) Supposed migration from perennial damage to non-overwintering regions in July; (2) Supposed migration from perennial damage to overwintering regions in May, and later from overwintering to non-overwintering regions in July; (3) Supposed migration from overwintering to non-overwintering regions in July. TA: Tropical Atlantic; TC: Tropical continental; TG: Tropical Gulf; PA: Polar Atlantic; PC: Polar continental; PP: Polar Pacific; SEM: Southeast monsoon; SWM: Southwest monsoon; SUW: Surface and upper winds; NEM: Northeast monsoon; NWM: Northwest monsoon; GW: Geostrophic winds; K: Kuroshio.

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