A Review of Ecological Factors Associated with Wild Host Plants as Refuges for Suppressing Pesticide Resistance in Agricultural Arthropod Pests

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Abstract

Arthropod pests continue to occur throughout the year by inter-plant movement and dispersal between cultivated host plants that are applied with pesticides and wild host plants that serve as refuges in the area of cultivation. This paper reviews the relationship between the host range and status of pesticide resistance in agricultural arthropod pests in Japan. The decisive factors for determining the development of pesticide resistance were concluded with attention paid to wild host plants as refuges. The arthropod pests that developed pesticide resistance were as follows: (1) monophagous species infesting cultivated crops treated with pesticides, (2) polyphagous species with a host range restricted to cultivated plants lacking wild host plants, and (3) certain populations of polyphagous species develop resistance in habitats such as tea fields and greenhouses with year-round cultivation because they are relatively isolated from the surrounding populations that do not develop resistance due to the abundance of refuges. In all cases, pest populations inhabit environments where they are restricted to mate with the susceptible populations from refuges of wild host plants.

Key words: pesticide resistance, wild host plants, refuge, tea field, year-round cultivation

Introduction

The world grain production doubled during the 40 years between 1970 to 2010, reaching 2.2 billion tons (Alexandratos and Bruinsma, 2012). However, productivity improvement remains essential considering that the current world population of 7.6 billion is expected to reach 9.8 billion in 2050 (UN, 2017), but there is a limit to the possible expansion of the crop cultivation area. Agricultural chemicals have played a principal role in crop production alongside the development of high-yielding varieties and cultivation techniques. In the practice of integrated pest management (IPM), biological control using agents against arthropod pests is not possible without applying pesticides to lower the initial pest density in Japan because pest density increases rapidly during warm weather (Masui et al., 2014; Yamanaka, 2009).

However, pesticides are inevitably subjected to the development of resistance. There has been a rapid increase in the number of cases of resistance development due to the wide use of these products, reaching up to 586 species in 2014 (Sparks and Nauen, 2015). Recent topics on pesticide resistance are on the brown rice planthopper, *Nilaparvata lugens* Stål (Hemiptera: Delphacidae); melon aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae); and green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) which developed resistance to neonicotinoids (Bass et al., 2015; Matsuura and Nakamura, 2014). Additionally, studies have focused on the diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae); smaller tea tortrix, *Adoxophyes honmai* Yasuda (Lepidoptera: Tortricidae); and the beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) which developed resistance to diamides (Fukuda and Hayashikawa, 2014; Nauen and Steinbach, 2016; Okamoto, 2018; Troczka et al., 2012; Uchiyama and Ozawa, 2014).

Theoretical studies on pesticide resistance began in the 1970s by Georgiou and Taylor (1977a, b), who introduced the “refuge” concept alongside other factors that can...
influence the rate of the evolution of pesticide resistance. A refuge is an area where pesticides are not applied, and thus allow the production of susceptible populations. Studies have demonstrated that the recruitment of susceptible individuals from a refuge into a pest population delays resistance development (Comins, 1977; Georgiou and Taylor, 1977b, 1986). Since transgenic plants expressing insecticidal proteins from the bacterium *Bacillus thuringiensis* Berliner (Bt), Bt crops were grown commercially in 1996, cultivation of Bt crops such as corn and cotton has expanded, reaching 101 million hectares (ha) in 26 countries in 2017 (ISAAA, 2017). Farmers were required to plant non Bt-protein expressing cultivars as a refuge to suppress the resistance to Bt toxins, based on “high dose-refuge strategy” (Gould, 1998; USEPA, 2017). Although seven insect pests developed resistance to Bt crops, the other insects have remained susceptible to major crops for more than 20 years (Tabashnik and Carrière, 2017).

Sparks and Nauen (2015) and Whalon et al. (2008) demonstrated that most of the top 20 resistant species share similar biological characteristics, such as a short generation time, high mobility, and high fecundity by summarizing the current status of arthropod resistance to pesticides. FAO (2012) comprehensively demonstrated many factors accelerating resistance development, but the dominant factor was not clear. Although studies on resistance management in Bt crops have revealed that non-Bt cultivars play an important role as a refuge in delaying the development of resistance (Huang et al., 2011; Tabashnik and Carrière, 2017), there has been a lack of discussion regarding on the role of refuge in pesticide resistance management (Carrière et al., 2012). Wild host plants, non-Bt varieties and other cultivated host crops that do not produce the targeted insecticidal Bt toxins act as refuges in Bt crop cultivation. Only wild host plants, however, provide refuge in the regular cultivation of crops because effective pesticides are usually registered on most major crops (Morishita, 2019). Although little is known regarding the size of the population outside the area or the magnitude of migration between areas (Roush and Daly, 1990), the immigration of susceptible populations has been considered a major factor suppressing the development of pesticide resistance (Tabashnik, 1990).

This paper describes how arthropod pests continue to occur throughout the year on both the cultivated hosts that are applied with pesticides and wild hosts that serve as refuges. It determines the effect of these occurrences and dispersal in the area of cultivation on the status of pesticide-resistance in major arthropod pests in Japan. Additionally, it extracts the factors that accelerate the development of pesticide resistance, focusing on wild host plants as a refuge.

**Monophagous pests infesting cultivated crops**

Strictly speaking, monophagous means feeding on only one species of plant, but the term is usually extended to include species feeding on plants within a single genus, whereas polyphagous refers to insects feeding on a relatively large range of plants from different families (Bernays and Chapman, 1994).

Monophagous arthropod pests infesting only cultivated crops could develop resistance to pesticides because they are always under pesticide application on cultivated crops. However, the pests that feed on both cultivated crops and crop wild relatives growing around crop fields do not develop pesticide-resistance because the latter acts as a refuge.

The rice stem borer, *Chilo suppressalis* (Walker) (Lepidoptera: Crambidae), and rice leaf beetle, *Oulema oryzae* Kuwayama (Coleoptera: Chrysomelidae), are monophagous insect pests infesting rice plants. The rice stem borer has two major host plants; rice, *Oryza sativa* L., and the water-oats, *Zizania latifolia* L. Since there is reproductive isolation between the populations feeding on rice (rice population) and water-oats (water-oats population), each population is considered to be monophagous (Matsukura et al., 2006). The other example, *O. oryzae*, mainly feeds on rice, sometimes feeding on the wild host, such as *Phragmites australis* (Cav.) Trin. ex Steud., and *Leersia sayanuka* Ohwi (Sato and Suzuki, 1988). *C. suppressalis* developed resistance to organophosphates (Koyama et al., 1987; Tanaka et al., 1982). Resistance to BHC in *O. oryzae* was first reported in the late 1960s and the 1970s, followed by organophosphates and carbamates (Kidokoro, 1997), and then fipronil after the 2000s in northern Japan (Ishimoto et al., 2004; Ueno and Saito, 2005). Their resistance was attributed to feeding only or mainly on rice plants, which were usually treated with granule pesticides.

The persimmon fruit moth, *Stathmopoda masinissa* Meyrick (Lepidoptera: Stathmopodidae), and *Ponticulothrips diospyrois* Haga et Okajima (Thysanoptera: Phlaeothripidae)
are monophagous insect pests that infest persimmon, *Diospyros kaki* Thunb. *S. masinissa* has bivoltine life cycles; larvae appear in June and August, and old larvae overwinter in a cocoon under the bark of persimmon trees (Oda, 1983). *P. diospyros* hibernates as adults under bark in and around persimmon orchards and disperses to form marginal roll galls on the young leaves of persimmon trees (Sota, 1988). *S. masinissa* and *P. diospyros* have been well controlled for more than 30 years with pesticides (Hennni and Hashimoto, 1984; Tsueda and Taera, 2014); no reports on their development of pesticide-resistance have been detected in Japan. Since the wild persimmon, *D. kaki* var. sylvestris Makino, grows around persimmon orchards in Japan, it could act as refuges for these two pests.

**Polyphagous pests utilizing few wild host plants**

Whether polyphagous pests could develop resistance to pesticides depends on the abundance of wild host plants they feed on. Pests using a small number of wild host plants develop resistance to pesticides.

First, I describe the relationship between resistance development and the utilization of wild hosts in the two polyphagous *Tetranychus* spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae) and the Kanzawa spider mite, *Tetranychus kanzawai* Kishida (Acari: Tetranychidae), infesting horticultural and ornamental crops in Japan. *T. urticae* is highly polyphagous and is reported to occur on more than 900 different host plants in more than a hundred countries (Bolland et al., 1998; Migeon et al., 2009). In contrast, the distribution of *T. kanzawai* is mainly limited to the western Pacific area, including Japan, Taiwan, China, Korea, and Thailand (Ehara, 1999), although *T. kanzawai* has been recorded at various locations around the world (Bolland et al., 1998). *T. urticae* revealed high resistance to almost all acaricides (Kuwahara et al., 1983; Morishita, 1993a; Van Leeuwen et al., 2010) and was in first place among the top twenty resistant arthropod pests (Whalon et al., 2008). This spider mite has been collected from most of the cultivated plants in Japan (Hinomoto et al., 2001; Takafuji et al., 1989), and the devastating resistance problem of *T. urticae* has been occurring in strawberry, chrysanthemum and rose plants which are vegetatively propagated (Haruyama and Matsumoto, 2013a; Kiriake and Yanagita, 2015; Kunimoto, 2010). Conversely, *T. kanzawai*, which occurs on vegetable and fruit crops, remains susceptible to acaricides in Japan (Kuwahara et al., 1983; Morishita, 1993a).

To clarify the factor responsible for the difference between these two spider mite species in their susceptibility to acaricides, Morishita (2001b) and Morishita and Takafuji (1999) studied the occurrence and inter-plant movement of the two spider mites in the fields of the pea-watermelon cropping system. *T. kanzawai* maintained a low-density population on the wild hosts, *Clerodendrum trichotomum* Thunb. and *Akebia quinata* (Houtt.) Decne., in the border vegetation, and then dispersed into the pea fields when the peas were sown. The *T. kanzawai* population increased in density in the pea fields, reaching a peak in November or December. Conversely, *T. urticae* were not observed on border vegetation but lived on chrysanthemum throughout the year, including the cultivation and nursery period, moving into pea fields in September (Fig. 1). *T. urticae* continuously reproduced only on cultivated plants (chrysanthemum, pea, and watermelon), which were treated with acaricides year-round, whereas *T. kanzawai* occurred on both cultivated and non-cultivated plants, resulting in population mixing with the susceptible population on border vegetation. These differences in their life cycles could explain the differences in susceptibility between the two mite species; *T. urticae* developed high resistance to acaricides while *T. kanzawai* remained susceptible.

Another comparison was made in the common cabbageworm, *Pieris rapae crucivora* Boisduval (Lepidoptera: Pieridae) and the closely related species, *Pieris melete* Ménetriés (Lepidoptera: Pieridae). Both of them demonstrate similar preferences for oviposition: cruciferous crops and wild plants. However, while the former prefers sunny places in plains and feeds on cruciferous crops, mainly cabbage, the latter prefers shaded habitats and feeds on Japanese radish, *Raphanus sativus* L., and two cruciferous wild plants, bitter cress, *Cardamine appendiculata* Franch. & Sav. and Indian yellow cress, *Rorippa indica* (L.) Hiern (Ohsaki, 1979). As for the pesticide-resistance in *P. r. crucivora*, there have been several reports on the development of resistance to organophosphorus pesticides such as dichlorvos and phenthoate (Asakawa, 1975; Morishita, 1993c). Resistance to DDT and trichlorphon has also been found in the United States and China (McEwen and Chapman, 1952; Mu et al., 1984). Conversely, *P. melete* has not developed resistance to pesticides. The habitat preference of *P. rapae* for sunny places may lead to increased dependence on cultivated
The diamondback moth has become the most destructive insect of cruciferous crops throughout the world because of the development of resistance to pesticides such as pyrethroids, Bt toxins and diamides (Fukuda and Hayashikawa, 2014; Makino and Horikiri, 1985; Morishita, 1998; Tanaka and Kimura, 1991). The Indian marshcress, *Rorippa indica* (L.) Hiern.; Verginia pepperweed, *Lepidium virginicum* L.; Shepherd’s Purse, *Capsella bursa-pastoris* (L.) Medik.; and bitter cress, *Cardamine flexuosa* With., were reported as wild hosts in Japan (Begum et al., 1996; Yamada, 1983). Morishita et al. (1992) determined the susceptibility to three pesticides, one pyrethroid, one nereistoxin, and one Bt, in the diamondback moth collected from cabbage fields and a colony of a wild host, *Raphanus sativus* L., which grows adjacent to the cabbage fields. No differences in the LC$_{50}$ values of the three pesticides were observed between the two populations, suggesting that the small colony size of cruciferous wild plants could not produce enough susceptible individuals to suppress pesticide resistance by mating with the resistant individuals immigrating from cruciferous vegetables.

*S. exigua*, originated in Southeast Asia, became a cosmopolitan species (Che et al., 2013). It is a polyphagous pest that infests many kinds of vegetative and ornamental crops (Horikiri, 1986; Zheng et al., 2011) and has also developed resistance to permethrin, EPN, etofenprox, and diamides (Iguchi et al., 2003; Okamoto, 2018; Takai, 1991). The pesticide-resistant larvae were collected from the area where the Welsh onion was cultivated successively throughout the year (Suenaga and Tanaka, 2000) and the greenhouse cultivation area of the pea-watermelon cropping system where it occurred on watermelon from spring to summer and on peas from autumn to spring (Okamoto, 2018). Curly dock, *Rumex japonicus* Houtt. and common knotgrass, *Polygonum aviculare* L. were recorded as wild host plants from Japan (Horikiri, 1986), and two pigweeds, *Amaranthus retroflexus* L., *A. hybridus* L., and a sunflower, *Helianthus annuus* L. were recorded from the United States (Greenberg...
et al., 2001; Showler, 2001). Since the growth of these wild hosts is seasonally restricted, year-round cultivation of vegetable host plants surrounded by wild host plants growing in restricted seasons appears to force S. exigua to develop resistance to pesticides.

On the other hand, the following three polyphagous species have not developed resistance to pesticides presumably because they reproduce mainly on wild hosts. The brown-winged green stink bug, *Plautia stali* Scott (Heteroptera: Pentatomidae), is a seed feeder that mainly reproduces on the cones of *Cryptomeria japonica* (Thunb. ex L. f.) D. Don and *Chamaecyparis obtusa* (Sieb. et Zucc.) Endl. (wild host plants) and immigrates to fruit orchards to feed on fruit crops (Oda et al., 1980; Yamada and Miyahara, 1980). Although fruit orchards have been treated with pesticides, the status of resistance has not been reported (Yamanaka, 1998). *Thrips hawaiiensis* (Morgan) (Thysanoptera: Thripidae) is a polyphagous thrips species that inhabits many kinds of wild and cultivated flowers and infests fruits such as mandarin oranges, fig fruits and pea pods (Kakimoto, 2018; Miyazaki and Kudo, 1988; Teramoto et al., 2001). Pesticide resistance of this thrips has not been detected in Japan (Haruyama and Matsumoto, 2013b; Kakimoto, 2018). The rice skipper, *Parnara guttata guttata* (Bremer et Grey) (Lepidoptera: Hesperiidae), which is polyphagous, feeding on both rice plants and wild host plants such as *Echinochloa crus-galli* (L.) Beauv. and *Phragmites karka* (Retz.) Trinius (Nakasui, 1981), has not developed pesticide resistance.

**Inability to overwinter in open fields**

The inability of arthropods to overwinter in open fields means that there is a season when they cannot utilize wild host plants as a refuge. Populations overwintering on cultivated crops under pesticide applications in greenhouses establish open field populations in summer. This life cycle results in the development of resistance to pesticides.

A comparison was made between the two invasive thrips species, the melon thrips, *Thrips palmi* Karny (Thysanoptera: Thripidae), and the western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), in relation to pesticide-resistance and whether they overwinter in the open fields. *T. palmi* is considered to originate from Southeast Asia since it was first collected in Indonesia in 1921 (Kajita et al., 1996). *F. occidentalis* was originally distributed in the western area of the United States, and had spread to other countries in the 1970s and the 1980s (Tommasini and Maini, 1995). The former and the latter were introduced to Japan in 1978 and 1990, respectively (Hayase and Fukuda, 1991; Tommasini and Maini, 1995).

*F. occidentalis* developed resistance to pesticides in both greenhouse and open field populations in Japan (Hamasaki et al., 2014; Imura et al., 2013; Morishita, 1993b). *T. palmi* feeds on a wide range of wild host plants such as Asteraceae, Amaranthaceae and Cucurbitaceae families (Miyazaki and Kudo, 1988). However, since thrips cannot overwinter in open fields because of a low cold tolerance (Tsumuki et al., 1987), the individuals intensively selected by the application of pesticides in the greenhouse in winter dispersed to establish populations on open-field crops (Matsuzaki et al., 1985; Morishita and Azuma, 1989). This life cycle is responsible for the development of pesticide resistance.

When *F. occidentalis* populations, which had already developed pyrethroid resistance, were introduced to Japan, the thrips populations were susceptible to the new pesticides available on the market thereafter in Japan (Katayama, 1997; Morishita, 2001a). Since *F. occidentalis* occurs in both cultivated and wild host plants such as henbit, *Lamium amplexicaule* L., and chickweed, *Stellaria neglecta* (Weihe), around ornamental fields and orchards throughout the year (Table 1) (Katayama, 2006; Morishita, 2005), these wild host plants are considered to provide refuge for *F. occidentalis*. Therefore, the difference in pesticide susceptibility between the two thrips species in Japan has been attributed to whether they can overwinter on weeds in open fields.

**Habitat characteristics isolating resistant population**

1. **Year-round cultivation in greenhouses**

As mentioned above, *F. occidentalis* populations have not developed resistance to new pesticides in Japan. However, certain populations of *F. occidentalis* occurring in the greenhouse of year-round sweet pepper cultivation developed resistance to spinosad and chlorfenapyr which became available on the market after the invasion (Okazaki et al., 2007, 2014). Similar to these cases, in the United States in the 1990s, *F. occidentalis* developed high pesticide resistance in greenhouses, while the pesticide-susceptible populations of *F. occidentalis* were collected from open fields (Brødsgaard, 1994; Immaraju et al., 1992). Resistance to spinosad has also been reported in Spain and the United States (Bielza et al., 2007; Loughner et al., 2005). Most of these resistant
populations were observed in the greenhouses of the Transvaal daisy, Gerbera jamesonii Bolus ex Hook. f. where the harvest started from the third month of planting and continued for up to two years. An enclosed greenhouse environment places populations under intense selection for resistance because of constant exposure to pesticides and limiting immigration of susceptible individuals (Denholm et al., 1999; Immaraju et al., 1992). Therefore, the pest population in a greenhouse for year-round cultivation is isolated from the pest populations surrounding the greenhouse.

2. Tea fields

In open crop fields, pest populations could mate with the populations outside of the crop fields. However, large-scale cultivation prevents pest populations in the crop field to mate with the population outside the crop fields. Taylor and Georghiou (1979) theoretically demonstrated that the larger the population size in the sprayed area, the lower the effect of retarding the development of resistance by diluting the resistance gene pool. There are large tea fields in several areas: a typical plantation can be seen in Makinohara, Shizuoka Prefecture where tea trees are planted in 5,000 ha out of 6,100 ha of the district area (Yamamoto et al., 2005). In addition, evergreen tea trees provide a stable habitat including overwintering sites and steady food throughout the year. As a result, pests tend to develop resistance to pesticides in large-scale tea cultivation.

Three polyphagous arthropod pests, T. kanzawai, Scirtothrips dorsalis Hood (Thysanoptera: Thripidae) and A. honmai infest both tea plant and deciduous fruit crops (T. kanzawai also infests vegetable crops). The populations of these three species in tea fields developed resistance to pesticides, while the populations occurring on deciduous fruit crops remained susceptible. I elucidate factors specific to tea fields that contribute the difference in susceptibility to pesticides between these two populations.

The tea-inhabiting populations of T. kanzawai developed high resistance to acaricides such as fenbutatin oxide and CMP (Hamamura, 1984; Osakabe, 1968). This spider mite passes ten generations from spring to autumn and overwinters on tea plants (Ehara and Hamamura, 1993). Thus, spider mites in tea fields continue to occur in spite of spraying acaricides with little chance of mating with individuals from the surrounding vegetation, resulting in the development of acaricide resistance. In contrast, the spider mite establishes a population on deciduous fruit trees by dispersal from the ground cover and adjacent areas, and the population collapses when leaves fall off. This dispersal is critical for the T. kanzawai populations on pear plants to remain susceptible to acaricides (Yamazaki and Itoyama, 2014).

S. dorsalis was distributed in Japan, Korea, South-east Asia, and Australia in the 1980s, and thereafter, it has been widespread in South Africa, Israel, and the United States (Kumar et al., 2014; Nishino and Kodomari, 1988). Although the pesticide susceptibility of thrips collected from vineyards was high (Shibao, 1997), its tea-inhabiting populations showed low mortality against caltap, methomyl, and pyrethroids (Ichida and Kudo, 2001; Kodomari, 1978). Since the adults were not observed in vineyards in winter (Shibao et al.,

### Table 1. Seasonal occurrence of Frankliniella occidentalis on weeds in a persimmon and the adjacent mandarin orange orchard (modified Morishita 2005)

| Orchard           | Weed                  | Adult number per head or shoot* |
|------------------|-----------------------|---------------------------------|
|                  | Jan | Mar | May | June | July | Aug | Sep | Oct | Nov |
| Persimmon        |     |     |     |      |      |     |     |     |     |
| Veronica persica | —   | 0   |     |      |      | 0.40| —   | —   | 0   |
| Solanum americanum | —   | —   |     |      |      | 6.00| —   | —   | —   |
| Acalypha australis | —   | —   |     |      |      | 0.17| 5.45| —   | —   |
| Stellaria neglecta | 0.01| —   | —   |      |      | 0.33| —   | 0.06| 0.07|
| Digitaria ciliaris | —   | —   |     |      |      | 1.75| —   | —   | —   |
| Setaria viridis  |     | —   | —   |      |      | 41.5| —   | —   | —   |
| Mandarin orange  |     |     |     |      |      |     |     |     |     |
| Geranium carolinianum | —   | —   |     |      |      | 8.46| —   | —   | —   |
| Vicia angustifolia | —   | —   |     |      |      | 0.37| —   | —   | —   |
| Stellaria neglecta | 0.02| 0   | 0.27| 0.38 | 0.24| —   | —   | —   | 0   |
| Lamium amplexicaule | 0.04| 0   | 0.12| —   | —   | —   | —   | —   | —   |
| Amaranthus viridis | —   | —   | —   |      |      | 1.88| —   | 0.70| —   |

*: Head in D. ciliaris and S. viridis and shoot (5–10 cm from the top) in the other hosts.
—: There is no data because of no existing host.
1990, 1991), adults that overwintered in evergreen trees such as big-leaf podocarp trees, *Podocarpus macrophyllus* (Thunb.), were supposed to immigrate to the vineyards and reproduced on vine leaves from June to September. In tea fields, in contrast, these thrips inhabited tea leaves throughout the year, overwintering as pupae in the soil under tea plant litter (Okada and Kudo, 1982). Consequently, tea-inhabiting populations have relatively little chance of mixing with the populations outside of the tea fields.

*A. honmai* is distributed in Japan and Korea (Lee et al., 2005; Yasuda, 1998) and passes four to five generations a year. While resistance to pesticides has not been reported in populations collected from deciduous fruit crops such as persimmon, the populations collected from tea fields have developed resistance to organophosphates, pyrethroids, insect growth regulators and diamides (Kosugi, 1999; Uchiyama and Ozawa, 2014; Uchiyama et al., 2013). In tea fields, this species occurred throughout the year; the larvae were observed to feed on tea leaves even in winter (Minamikawa and Osakabe, 1979). Since the larvae of *A. honmai* could not overwinter in deciduous fruit orchards because of defoliation (Henmi, 1986), the population in deciduous fruit orchards was established by the adults of overwintering generations immigrating from evergreen wild hosts such as *Quercus phillyreoides* A. Gray, where larvae could grow in winter, followed by the emergence of larvae in June. Discontinuous occurrence during the winter and establishment by immigrants in early summer contribute to the moth population of deciduous fruit crops to remain susceptible to pesticides.

**Conclusion**

In this review, I have discussed ecological factors that may accelerate the rate of resistance development. Fig. 2 classifies the arthropod pests according to the development of resistance to pesticides, based on host range, abundance of wild host plants and population isolation by environment. First, monophagous arthropod pests such as *C. suppressalis* and *O. oryzae* feeding on cultivated host plants that were treated with pesticides developed resistance to pesticides. Second, while polyphagous insect pests such as *P. stali*, and *T. hawaiensis* which fed on abundant wild host plants did not develop pesticide resistance, polyphagous insect pests such as *T. urticae*, *T. palmi*, *P. xylostella*, and *S. exigua* which does not have enough wild host plants have developed resistance to pesticides. Finally, pest populations isolated from the surrounding populations could develop pesticide-resistance. Year-round cultivation in enclosed greenhouses causes *F. occidentalis* populations to be isolated from outside populations. Large-scale tea fields force the populations of three pest species (*T. kanzawai*, *S. dorsalis* and *A. honmai*) to continue to occur on evergreen trees throughout the...
year and to hinder mating with susceptible individuals from other hosts of the tea fields.

**Perspective**

This review referred to a limited number of pests that developed resistance to pesticides. The cotton aphid, *A. gossypii*, is a devastating pest in vegetable and ornamental crops and has developed resistance to organophosphates, pyrethroids and neonicotinoids (Hosoda et al., 1993; Matsuura and Nakamura, 2014; Saito, 1990). However, it was left out of this review since its life cycle illustrates five types in Japan and its host preferences, host alternations, and biotypes are complicated (Komazaki and Toda, 2008); moreover, it is difficult to draw a scheme demonstrating the relationship between the status of pesticide resistance and characteristics. Further investigations covering the number of arthropod pests, including cotton aphids, are needed to determine the factors that accelerate the development of pesticide resistance.

Agricultural arthropod pests are divided into two groups: pesticide-resistant pests and non-resistant pests (Fig. 2). We can naturally take different strategies for these two groups. As the best approach to retard resistance development is to reduce pesticide use, particularly the number of treatments and the proportion of the population that is treated (Tabashnik, 1990), biological control is especially important for farmers tackling highly pesticide-resistant pests. For example, the two predatory mites *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) for controlling *T. urticae* and *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae) for *T. palmi* have been widely applied with pesticides, which hardly affect these biocontrol agents (Yamanaka, 2009; Yanagita, 2019). Several studies have demonstrated that the rotation of various pesticides is effective in suppressing resistance (Immaraju et al., 1990; Prabhaker et al., 1998), and farmers are recommended to apply pesticides in rotation to avoid continuous spraying of pesticides with the same mode of action (MoA). To control the non-resistant group, however, farmers should spray economical and efficient pesticides without paying attention to the rotation. In practice, pyrethroids and neonicotinoids have been used for over 20 years in persimmon orchards to control *P. stali* which is a non-resistant insect pest in Japan.

As mentioned above, resistance to pesticides in *T. hawaiiensis* has not been detected in Japan (Fig.2). This thrips, however, developed resistance to pesticides in banana plantations in south China (Fu et al., 2018, 2019). Pesticides have been applied against thrips by most growers in several areas, with more than 20 applications per banana-growing cycle (Fu et al., 2018). Large-scale banana plantations up to 1000 ha in China may force the thrips populations to prevent the immigration of susceptible populations into banana plantations. This is similar to the case in which the three pests developed resistance to pesticides only in the tea fields of Japan. Therefore, we must focus on the large-scale cultivation of evergreen crops in terms of the development of pesticide-resistance in non-resistant arthropod pests.

The level of resistance in *F. occidentalis* against pesticides in greenhouses varied widely (Immaraju et al., 1992; Okazaki et al., 2014), suggesting that the level could be affected by different cultivation practices in each greenhouse such as crop type and cultivation period. In addition, new cultivation practices such as large-scale farming in greenhouses where tomato and strawberry plants are mainly cultivated on a scale of 1–2 ha have increased since the 1990s in Japan (Yamada, 2008). In large-scale farming, the larger the greenhouse, the fewer the adults that could mate with individuals outside of the greenhouse. These changes in cultivation practices need to be taken into consideration in the development of pesticide-resistance.

Arthropod pests continue to occur throughout the year via dispersal between cultivated host crops and wild host plants in the area of cultivation. As expected, most studies on pest ecology have been carried out mainly in crop fields because crops are economically damaged by pests. Consequently, researchers have paid less attention to the abundance of wild hosts as a pest refuge, occurrence of pest on wild hosts, and dispersal of pest between crops and wild host plants. However, as mentioned above, immigration of susceptible individuals is essential to retard the development of pesticide resistance. Further research should be conducted on wild hosts as a refuge of susceptible individuals to better understand the dynamics in the development of pesticide resistance.

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Masahiko Morishita: Ecological factors suppressing pesticide resistance

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