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Hessian Fly (Diptera: Cecidomyiidae) Biology and Management in Wheat

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Abstract

The Hessian fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), is a major pest of wheat (*Triticum* spp. L.), reducing yields in many wheat producing countries around the world. The most commonly practiced and effective management techniques to control Hessian fly infestations are use of resistant wheat cultivars, adherence to optimum planting dates, destruction of volunteer wheat or 'green bridges', and insecticides. However, insecticide applications strictly for Hessian fly control is limited, owing to the temporality of seed treatments (~30 d), and associated cost and difficult timing of foliar applications. Adherence to optimum planting dates and destruction of volunteer wheat can also reduce the risk of infestation from other economically important wheat pests, e.g., aphids, fall armyworm (*Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae)), and wheat curl mite (*Aceria tosichella* Keifer (Acari: Eriophyidae)). This highlights that Hessian fly control tactics are more effective when used in an integrated pest management (IPM) program. A shortcoming of the current Hessian fly IPM program is the absence of reliable sampling methods for estimating the risk of Hessian fly damage and economic treatment thresholds. Instead management practices are used as either a preventative measure or in response to damage from the previous season. To ensure the use of the management practices is justified, pest detection surveillance strategies need to be advanced and/or developed in conjunction with economic thresholds, to help producers implement Hessian fly IPM programs.

Key words: *Mayetiola destructor*, wheat, integrated pest management, pheromone trap

The Hessian fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae), is present in most of the wheat (*Triticum* spp. L. (Poales: Poaceae)) producing regions of the world (CABI 2016). This fly is one of the oldest documented invasive species to North America, first reported in New York in 1779 (Pauly 2002). Multiple introductions of the Hessian fly to the United States have likely occurred (Morton and Schemerhorn 2013), resulting in the presence of Hessian fly in most wheat (a common host) growing regions of the United States (Ratcliffe and Hatchett 1997, Ratcliffe et al. 2000). The Hessian fly is a member of one of the largest family of flies, Cecidomyiidae (Gagne 1994), which contains many economically important species, including the sorghum midge, *Contarinia sorghicola* (Coquillett) (Diptera: Cecidomyiidae), and the sunflower midge, *C. schulizi* Gagne (Diptera: Cecidomyiidae) (Harris et al. 2003, Stuart et al. 2008). Gall formation is a feature associated with flies in this insect family (Harris et al. 2003), which provides a protective structure and induces a nutritive rich feeding site for larvae (Rohfritsch 1992). This has enabled the Hessian fly to become a major pest of wheat in the United States (Harris et al. 2003, Whitworth et al. 2009, Flanders et al. 2013). This article summarizes common management practices used to combat this pest, along with life history, host range, and dispersal behavior important to the understanding of Hessian fly management. The tactics reviewed can be used as part of a Hessian fly IPM program.

Geographic Distribution and Host Range

The Hessian fly originated in the Fertile Crescent region of the Middle East and is now present in Europe, North Africa, North America, and New Zealand (Stuart et al. 2012). Many grass species serve as hosts of this fly (Zeiss et al. 1993a), including at least 16 wild grass species found around the world (Harris et al. 2001), most belonging to the tribe Triticeae. Triticeae includes major cereal crops such as wheat, barley, and rye, but wheat is the optimum host for population increase (Harris et al. 2001, Chen et al. 2009a). In choice tests, Hessian fly prefers wheat, followed by rye, then barley (Harris et al. 2001, Chen et al. 2009a). Grasses in the tribe Bromeae are also hosts for Hessian fly in New Zealand (Prestidge 1992, Stewart 1992).

Life Stages

Adult

Hessian fly adults are brown or black, with females at times appearing reddish-brown owing to the presence of the orange eggs developing inside the abdomen (Fig. 1) (VanDuyn et al. 2003, Foster and Hein 2009). To distinguish Hessian fly from related species that appear similar, refer to appropriate taxonomic keys, e.g., Manual of Nearctic Diptera (McAlpine et al. 1981, Toolbox 2010).

Egg

Eggs (Fig. 2A) are found in the grooves on the upper side of the plant leaf, and take 3–12 d to hatch depending on the temperature, 50–85°F (10–29°C) (McColloch 1923, Packard 1928). Hessian fly eggs can be recognized by their orange color, elliptical shape, and small size (Flanders et al. 2013).

Larvae

Larvae are white, cylindrical, and develop a translucent green stripe down the middle of the back (Fig. 2B) (Gagne and Hatchett 1989, Flanders et al. 2013). There are three larval instars, and larval size varies between instar stages, doubling in length from the first (0.56–1.70 mm) to the second instar (1.70–4.00 mm) (Gagne and Hatchett 1989).

Pupa/Puparia

The third instar and pupae develop in the cuticle of the second-instar larva (Gagne and Hatchett 1989), termed the puparium. This stage is commonly referred to as the flax seed stage (Fig. 2C), due to the hardened, sclerotized, dark brown color, and shape of the cuticle, which resembles a seed of flax, *Linum usitatissimum* L. (Malpighiales: Linaceae).

Biology and Life History

Development and Establishment on Host

The Hessian fly can complete its life cycle in as few as 28 d, but development can be delayed during long periods of aestivation and diapause based on temperature. Upon hatching in seedling wheat, first-instar larvae move toward the base of the plant using parallel venation in the leaf as a guide and establish a feeding site on the stems within the plant crown (Stuart et al. 2012). In wheat plants that have elongated stems, the neonate larva establishes a feeding site on the stem beneath the leaf sheath at a node. Neonates require 12–24 h to move from the egg to the feeding site and larval mortality during this transit is high due to relative humidity, wind, cold, and rainfall (Packard 1928, Hamilton 1966). Only first- and second-instar larvae

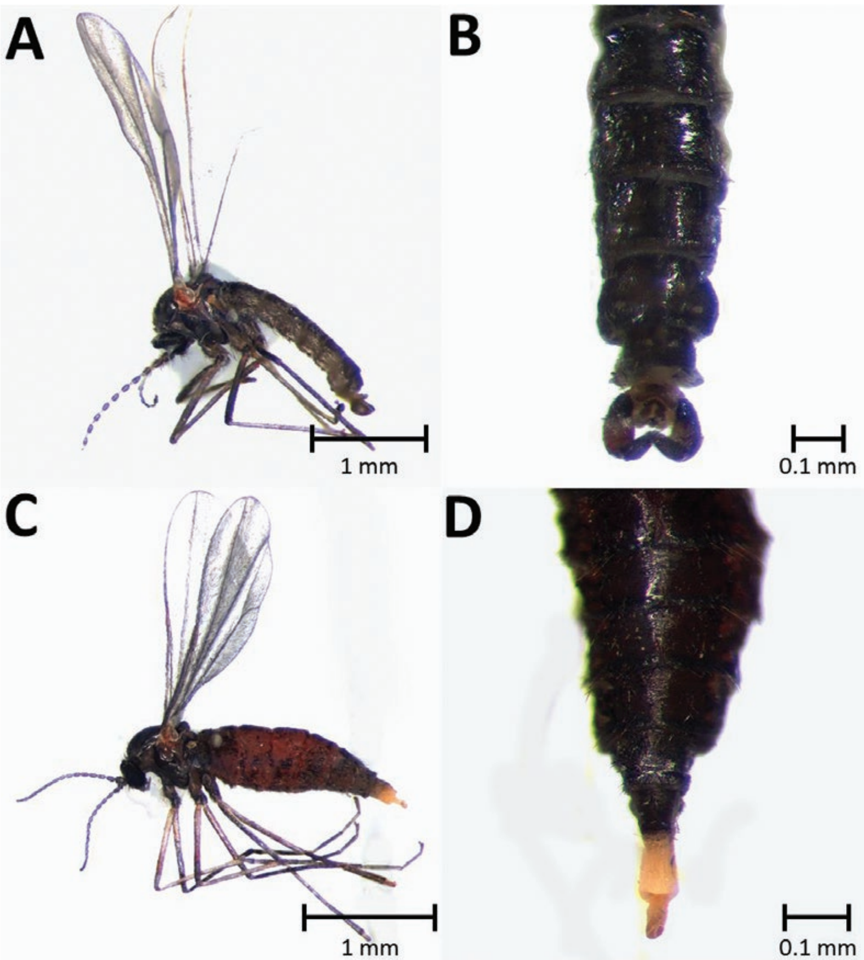

Fig. 1. Adult Hessian fly. (A) Male. (B) Male genitalia. (C) Female. (D) Female genitalia. (Photo credits (all): Alan Burke).

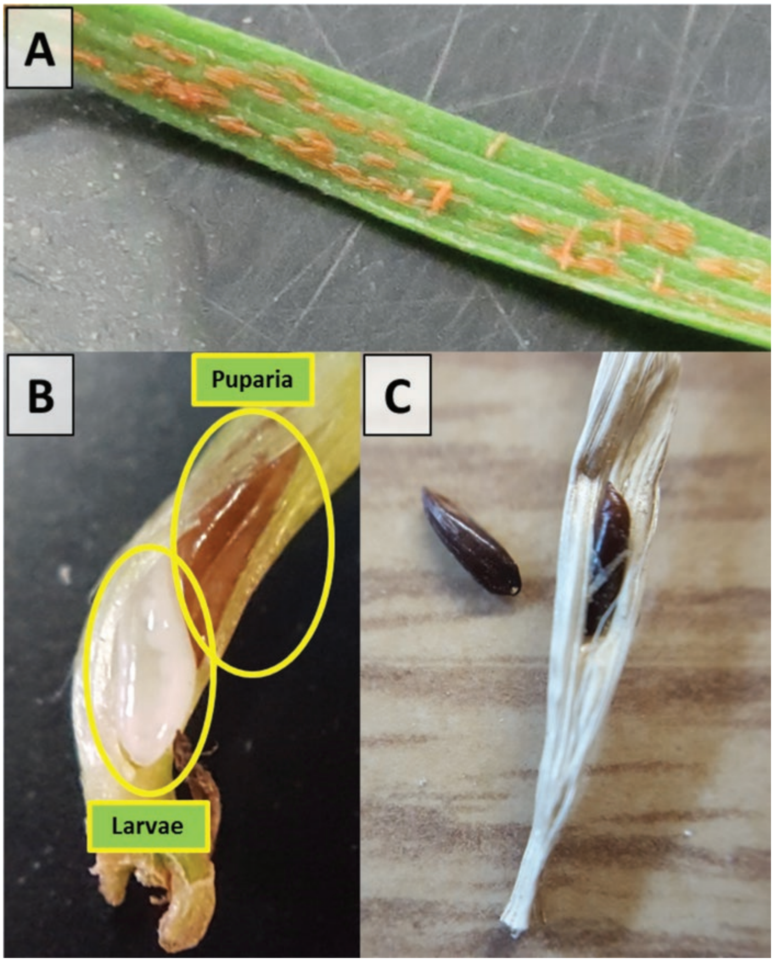

Fig. 2. Immature Hessian fly life stages. All photos are of wheat infested with Hessian fly. (A) Eggs. (B) Larvae and puparia. (C) Puparia (flaxseed).

feed, which last for 2–3 wk (Foster and Hein 2009). The length of the third instar/pupal stage typically ranges from 7 to 35 d depending on environmental conditions; unless the pupae enter a long dormant period known as aestivation (over-summer) or diapause (over-winter) when temperatures are too warm or cold to trigger eclosure of adults, respectively (Foster and Taylor 1975, Wellso 1991, Morgan et al. 2005, Chapin 2008). Adults typically eclose (emerge) after 10–14 d if temperatures remain ≥21°C (70°F), the optimum temperature for Hessian fly growth and development (Foster and Taylor 1975). High humidity and moisture in the surrounding environment must also be present for adult eclosure, although these conditions have not been quantified (Morgan et al. 2005, Stuart et al. 2012). Once a Hessian fly adult ecloses from the puparia, it will live for 1–4 d (Bergh et al. 1990, Harris and Rose 1991). During that time, females mate and oviposit on suitable host plants.

Since Hessian fly development, aestivation, and diapause are dependent on temperature and moisture, the number of generations varies across the regions of the United States. In the Northern states (Kansas, Missouri, Pennsylvania, and Nebraska), Hessian fly completes at least two generations every year, one spring and one fall (Boyd and Bailey 2000, Foster and Hein 2009, Whitworth et al. 2009, Tooker 2012). In the Southern United States (from Texas to the Carolinas), Hessian fly completes three to six generations each year, 1–3 in the fall and 1–3 in the spring (Lidell and Schuster 1990, Morgan et al. 2005, Flanders et al. 2013). Identifying generations is difficult as all individuals of a generation do not emerge as adults during the same time. Rather, individuals continue to emerge as adults for up to a year; therefore, a cohort of Hessian fly is termed a brood as it may be composed of progeny from several previous generations (McColloch 1923, Wellso 1991). The number of generations or broods, especially during the fall, has important implications for Hessian fly management strategies, specifically for delayed planting. Northern states typically can utilize delayed planting as an effective management strategy, while delayed planting is less effective in the Southern states. Delayed planting for Hessian fly management is discussed in greater detail in the *Management Options* section.

Dispersal and Flight

The Hessian fly has expanded its range to four continents and New Zealand (Stuart et al. 2012), making it highly successful at invading new regions of the world; however, their spread has been greatly aided by human movement and trade. On local landscape levels, wind and plant community composition are major factors affecting localized dispersal of Hessian fly. Early observations of Hessian fly infestations in Kansas fields concluded that adults, especially mated females, may be carried at least 3.2 km by the wind because no wheat or other hosts were within 3.2 km of the infested fields (McColloch 1917). More recently Withers et al. (1997) observed that ovipositing female Hessian flies disperse at a greater rate through areas of nonhost plants than areas with host plants. Wind speed also affects dispersal of female Hessian flies. As wind speed increases, females no longer exhibit upwind flights but instead exhibit more flights downwind, while remaining on plants for longer periods of time (Withers and Harris 1997). Additionally, Harris and Foster (1991) found that male Hessian flies exhibit upwind flight when exposed to components of the female Hessian fly sex pheromone. While the Hessian fly has been documented to move between a few meters to a few kilometers (McColloch 1917, Withers et al. 1997), wind likely plays a major role in local dispersal between wheat fields. However, what is not clear is the average or maximum dispersal range of adult Hessian flies, as observations of Hessian fly movement beyond a few meters are based on assumptions of the source plants (McColloch 1917). Knowledge of average and maximum distance travelled by adults will be important to understanding Hessian fly movement within the local landscape, field to field dispersal, or movement within a field.

Studies to date suggest that Hessian flies exhibit nonrandom movement, demonstrated by directed flights toward a pheromone, plant extract, a certain wavelength of color, or spatial configuration (Harris and Rose 1990, Withers et al. 1997, Anderson et al. 2012). Flight behavior is adjusted when changes in plant distribution are sensed through the use of chemoreceptors for host-specific chemicals, where females are much more likely to stay in an area when wheat is detected as opposed to a less attractive plant such as oats (Withers and Harris 1996). In other words, Hessian flies choose when and where to move based on cues from the environment.

Environmental Dispersal Cues

Females find their host plant using chemical, visual, and tactile cues (Harris and Rose 1990). Physical characteristics of hosts, such as the number and depth of vascular grooves, are also important for oviposition site selection (Kanno and Harris 2000a,b). The adaxial (upper) surface of the youngest leaf of the plant is the preferred oviposition site (Kanno and Harris 2000b, Ganehiarachchi et al. 2013). Larval survival is highest on the youngest leaf of the plant, and it is thought that the larvae need access to 'reactive' cells, which are plant cells easily manipulated to use as a food source (Ganehiarachchi et al. 2013).

Visual stimulants consisting of spectral and spatial information are important for attracting the fly from a distance. Females are attracted to the color green (530–560 nm) and brighter colors (Harris and Rose 1990, Harris et al. 1993). Besides spectral discrimination, females also approach and land more frequently on targets with vertical rather than horizontal contour lengths (i.e., horizontal lines) especially vertical lengths with higher density (Harris et al. 1993). The attraction of female Hessian flies to vertical contour lengths is not surprising, as a typical profile of wheat consists of many vertical contour lengths. While visual cues are important for Hessian fly oviposition, chemical cues are equally important.

Hessian flies are attracted to certain plant extracts over others during laboratory tests, specifically wheat extract (Harris and Rose 1990, Kanno and Harris 2000a). Their attraction to plant extracts can be enhanced when combined with other physical attractants. For example, combinations of wheat extract with color and/or tactile attractants result in a greater number of eggs laid by the Hessian fly than any of the three attractants alone (Harris and Rose 1990).

The female sex pheromone is another strong olfactory cue that attracts male Hessian flies (Morris et al. 2000, Andersson et al. 2009). A synthetic female sex pheromone was developed by Andersson et al. (2009). The pheromone lure has been tested in laboratory bioassays, small plot tests, and field tests and has been shown to be effective at attracting male Hessian flies (Anderson et al. 2012, Knutson et al. 2017). However, the effective range of the pheromone is not known, partly because the average daily dispersal range of the Hessian fly has not been quantified.

Associated Injury and Damage

Injury to wheat caused by feeding manifests itself in the form of a darker, almost blue-green, foliage color (Fig. 3D) and stunted

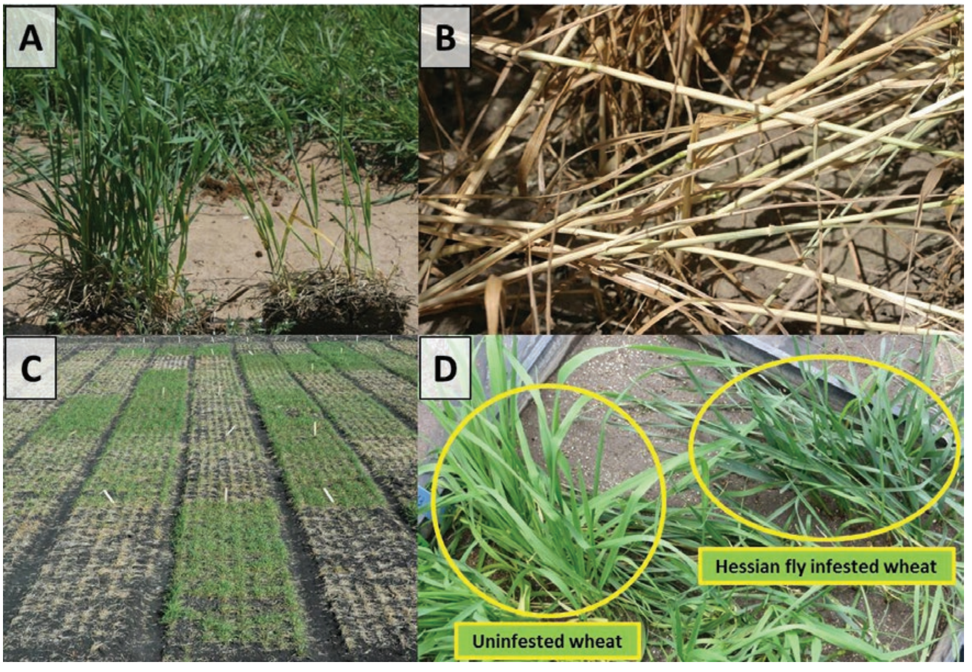

Fig. 3. Typical damage to wheat due to feeding by Hessian fly larvae. (A) Stunted growth of Hessian fly infested wheat compared to uninfested wheat (left) (photo credit: Tom A. Royer, Oklahoma State University). (B) Lodged wheat due to Hessian fly infestation (photo credit: Tom A. Royer, Oklahoma State University). (C) Wheat variety study containing Hessian fly resistant varieties (green plots) and susceptible varieties (brown plots). (D) Dark, blue-green, foliage of Hessian fly infested wheat compared to uninfested wheat (left).

growth (Whitworth et al. 2009). Seedlings sometimes compensate by increased tillering, but continued feeding on the plant will decrease growth of additional tillers (Anderson and Harris 2006, Anderson et al. 2011, Stuart et al. 2012). Yield loss caused by larval feeding on seedlings (Fig. 2B) results from stunted growth and death of tillers and seedlings (Fig. 3A, C). Larval feeding on wheat after stem elongation causes lodging from weakened stems, failure to produce a seed head, and a reduction in the number of seeds per spike and seed weight (Buntin 1999, Harris et al. 2003, Schwarting et al. 2016) (Fig. 3A–C).

In the United States, the Hessian fly is a potential economic pest in many of the wheat production regions (Smiley et al. 2004, Watson 2005, Alvey 2009). Damage caused by Hessian fly feeding can result in significant yield loss. From 1984 to 1989, the Hessian fly caused an estimated $4 million per year in damage in South Carolina, and an estimated $20 million in Georgia from 1988 to 1989 (Buntin et al. 1992, Chapin 2008). Buntin (1999) showed that the Hessian fly can cause an average annual yield loss of 5–10% in Georgia, with an estimated 21.1 kg/ha (0.31 bu/ac) yield loss occurring for each 1% infested tillers in autumn, and an 11.8 kg/ha (0.18 bu/ac) yield loss for each 1% increase in infested tillers in spring. In Oklahoma, regression analysis of winter wheat indicated that yield is reduced by approximately 386 kg/ha (5.74 bu/ac) over the growing season for every one Hessian fly immature per tiller (Alvey 2009).

Management Options

Since the discovery of the Hessian fly in the United States in the late 1700s, control practices have included burning and mowing stubble, application of lime, Paris green, Bordeaux mixture, and even kerosene emulsion (Headlee and Parker 1913, Webster 1915, Williamson 1917); however, such approaches were found to be either unsuccessful or unpractical for controlling Hessian flies in large commercial fields. Today common control measures include the use of resistant wheat cultivars, adherence to planting dates that escape early fall infestations (commonly referred to as the 'fly-free date'), destruction of volunteer wheat between plantings, and use of insecticidal seed treatments (Foster and Hein 2009, Whitworth et al. 2009, Royer et al. 2015).

Monitoring

Traps utilizing the Hessian fly female sex pheromone are an effective and efficient method for capturing adult male Hessian fly (Andersson et al. 2009, Schwarting et al. 2015, Knutson et al. 2017). Pheromone traps detect low densities of males in wheat fields; however, trap captures have not correlated to economically damaging larval infestations in the field and resulting crop damage (Schwarting et al. 2015, Knutson et al. 2017). Lack of correlations between trap catches and economically significant infestations could be due to high egg and neonate larval mortality prior to establishing a feeding site (Knutson et al. 2017). It is also important to note that the pheromone used in the Hessian fly traps only attracts male Hessian flies (Foster et al. 1991, Andersson et al. 2009), and this may also account for the lack of relationship between trap captures and field infestations.

There is currently no method developed to capture only female Hessian flies. Although the benefit of monitoring for female Hessian flies has not been studied, trapping females of other fly species such as Mediterranean fruit fly, *Ceratitis capitate* (Wiedemann) (Diptera: Tephritidae), and wheat bulb fly, *Delia coarctata* (Fallen) (Diptera: Anthomyiidae), has been valuable to pest management strategies (Bowden and Jones 1979, Hendrichs 1999, Katsoyannos et al. 1999, Broughton and Rahman 2017). It is important to consider monitoring for adult female Hessian flies in addition to males because female and male movement in the environment is dictated by different factors (Harris and Rose 1990, Harris and Foster 1991), which can result in their movement to different locations in the landscape. Male fly movement after emergence is primarily motivated to find mates. They respond to female sex pheromone to locate females, and mating typically occurs at the site of emergence (Bergh et al. 1990, Withers et al. 1997, Anderson et al. 2012). Female movement post-emergence is directed to oviposition site selection (Bergh et al. 1990, 1992), which is governed by multiple environmental factors, as mentioned in the *Environmental Dispersal Cues* and *Dispersal and Flight* sections (Harris et al. 1993, Withers and Harris 1997, Withers et al. 1997). Additionally, Withers et al. (1997) estimated that females are capable of moving long distances during oviposition, 660 m^2 in 2 h in host patches (wheat) and 1,500 m^2 in 2 h in nonhost patches (oat). The capability of females to move long distances during oviposition coupled with the differing factors that drive female and male Hessian fly movement may result in females being present in different locations than males post mating. Therefore, it is important to monitor for female Hessian flies in addition to males, as knowing where and when females are present in the landscape is important for understanding where infestations may occur because females are the primary agent of dispersal through selection of oviposition sites (Harris and Rose 1989). Thus, monitoring for female Hessian flies deserves further investigation.

Actively sampling and quantifying Hessian fly populations is not commonly adopted as part of the in-season, decision-making process because the nature of most Hessian fly management practices requires they be implemented before infestations have occurred (e.g., resistant cultivars, delayed planting dates, destruction of volunteer wheat). Hessian fly management should be implemented only when the threat of Hessian fly infestation exceeds an economic threshold. However, no economic treatment threshold has been developed for the Hessian fly (Shukle 2008), resulting in management practices being implemented either on a calendar schedule, i.e., fly-free date, or in response to historical crop failures for a given production field (with the exception of foliar insecticide application, which has limited application owing to the narrow window of effectiveness and associated cost). Additionally, the preventative nature of most Hessian fly control practices (resistant cultivars, delayed planting, destruction of volunteer wheat, and seed treatments) necessitates the need to assess the risk of Hessian fly damage weeks in advance of planting to ensure implementation of the practices is justified. The brief window of time (2–4 wk) between the beginning of fall brood emergence (September or October depending on location and weather) and optimum planting dates does not allow producers much time to purchase resistant cultivars, apply seed treatments, or destroy volunteer wheat if Hessian fly is detected in their field prior to planting. However, Hessian fly monitoring can inform producers when Hessian fly begins to emerge from summer aestivation and the level of adult activity in a localized area prior to and after planting (Anderson et al. 2012, Bradford 2014, Schwarting et al. 2015, Knutson et al. 2017). As weather conditions can cause brood emergence to vary from year to year and additional broods to occur (Drake and Decker 1932, Byers and Gallun 1972), early detection of brood emergence and brood levels prior to planting may aid producers when deciding on a planting date. Additionally, monitoring adult activity can warn producers of the need to check for Hessian fly infestations during the winter and spring months. If infestations of immature Hessian fly threaten crop yield, growers can limit crop inputs, e.g., fertilizer, fungicides, and irrigation, or switch fields from grain production to livestock forage (Knutson et al. 2017).

Plant Resistance

Planting resistant wheat cultivars has long been the most economical and effective control method (Berzonsky et al. 2003). To date, 34 Hessian fly resistant genes (R) have been identified (Li et al. 2013). Although effective, when widely planted over large areas in consecutive years, a resistant cultivar containing a single resistance gene can rapidly lose effectiveness due to selection for Hessian fly biotypes that overcome the R gene, typically within 6–8 yr after release (Gould 1986, Ratcliffe et al. 1994, Ratcliffe et al. 2000, Chen et al. 2009b). For example, research testing 21 and 22 R genes found that less than half provided effective protection of wheat against Hessian flies in the Southern United States (Cambron et al. 2010, Garces-Carrera et al. 2014). Hessian fly virulence is conditioned by inherited recessive genes (Hatchett and Gallun 1970, Formusoh et al. 1996, Zantoko and Shukle 1997). Hessian flies demonstrate genetic variation in virulence-related genes among individuals (Chen et al. 2010, Zhao et al. 2015), resulting in heterogeneity in fly populations in the field (Ratcliffe et al. 1994, Ratcliffe et al. 1996, Ratcliffe et al. 2000, Chen et al. 2009b, Cambron et al. 2010, Garces-Carrera et al. 2014). As a result of this heterogeneity, the planted resistant wheat cultivar selects for those virulent flies to resistant genes within that wheat cultivar. Thus, damaging outbreaks occur as resistance in the cultivar is lost. Rotating cultivars, each with a different source of resistance, to vary the R genes planted in subsequent years will help to mitigate loss of cultivar resistance (Gould 1986, Tooker and Frank 2012). Monitoring for virulent biotypes is also important for resistance management, since when these virulent biotypes begin to increase it may be possible to deploy new R genes in the field which are effective against the increasing proportion of virulent biotypes (Chen et al. 2009b, Garces-Carrera et al. 2014). As a result, area wide crop loss can be avoided. In the past, Hessian fly populations virulent to specific R genes were named but this is no longer practiced (Ratcliffe et al. 1994). Instead, Hessian fly populations are characterized by their virulence to specific R genes (Chen et al. 2009b, Garces-Carrera et al. 2014). Chen et al. (2009b) defined a gene as highly resistant to a Hessian fly population if ≥80% of the plants with that gene are resistant (no larval survival) in a virulence assay, moderately resistant to a population if 50–80% of the plants with that gene are resistant, and susceptible to a population if <50% of the plants are resistant.

Hessian fly virulence is expressed when saliva from actively feeding larvae causes R genes within the plant to trigger a combination of defensive mechanisms (Subramanyam et al. 2006, Giovanini et al. 2007, Harris et al. 2010, Liu et al. 2010). Some R genes deter additional Hessian fly larval feeding through protein production that specifically targets the larval midgut resulting in inhibition of metabolism and digestion through destruction of midgut microvilli, eventually resulting in larval death due to functional loss of digestion and absorption of nutrients (Giovanini et al. 2007, Liu et al. 2007, Subramanyam et al. 2008, Wu et al. 2008, Shukle et al. 2010). Another protein-encoding gene triggered by the Hessian fly in wheat is *HfrDrd*, which provides a disease resistance-like response against the Hessian fly (Subramanyam et al. 2013). Further advances in understanding the genetic basis for the mechanisms that Hessian fly larvae use to establish feeding sites could lead to the development of more durable resistance in wheat to Hessian fly (Zhao et al. 2015).

Temperature can also influence the effectiveness of R genes (Garces-Carrera et al. 2014). The resistant genes, *H3*, *H5*, *H10*, *H11*, *H12*, and *H18*, have been shown to lose resistance when the temperature rises above a certain threshold (Sosa and Foster 1976, Sosa 1979, Tyler and Hatchett 1983, Ratanatham and Gallun 1986, Buntin et al. 1990b, Cambron et al. 1996). For example, when wheat containing the resistant *H13* gene was exposed to heat stress of 40°C, it became susceptible to avirulent Hessian fly (Chen et al. 2014, Currie et al. 2014). The effect of temperature on some resistant genes can significantly affect the effectiveness of resistant cultivars commonly planted in the United States. Chen et al. (2014) documented that commonly used cultivars on the Great Plains, such as 'Bill Brown', 'Byrd', 'Endurance', 'Fuller', 'GA-031257-10LE34', and 'KS09H19-2-3', were susceptible at 20°C, but became resistant at lower temperatures. Plant resistance is also affected by the order of plant infestation by virulent and avirulent Hessian fly larvae. Infestation of virulent followed by avirulent larvae positively affects larval survival; established virulent larvae induce systemic susceptibility, thus providing refuge for later-infesting avirulent larvae and ultimately resulting in the survival of both (Baluch et al. 2012).

Although virulence assays can identify effective R genes, it is often not known what, if any, R genes are present in commercial wheat cultivars, as is often the case when breeding programs do not include Hessian fly resistance. Adoption of Hessian fly resistant cultivars is further complicated by the need to consider cultivar yield, disease resistance, and availability to producers in different regions of the United States. These hindrances to cultivar development coupled with the effects of temperature, virulent larvae infestations increasing avirulent larvae survival, and potential loss (6–8 yr after release) of R cultivar effectiveness due to regional buildup of resistant biotypes, reinforces the need for more comprehensive Hessian fly integrated pest management (IPM) programs.

Delaying Planting Date

Delayed planting until after a 'fly-free date' to escape Hessian fly infestation has been used in the Upper Midwest and Northern Great Plains states (ranging from North Dakota south to Kansas and extending east to Pennsylvania) since the early 1900s (Whitworth et al. 2009, Tooker 2012, Knodel et al. 2018). A fly-free date indicates when in the late fall adult Hessian fly activity has historically ceased due to cold weather, and thus avoiding infestation by ovipositing females. Fly-free dates are specifically tailored to the environmental conditions of different regions across the country. When the fly-free dates were first documented in the early 1900s, wheat producers held them in high regard. Reports surfaced of farmers secretly plowing under their neighbors' wheat fields that were planted before the fly-free (Satterthwait 1926). A potential drawback associated with the fly-free date is that later planting dates may increase the risk of winter kill due to cold weather (Campbell et al. 1991, Thiry et al. 2002). Consequently, finding a suitable planting date requires a farmer to weigh the risks of planting too early, which could result in Hessian fly and other key pest infestations, and planting too late, which could result in increased winter kill of tender wheat and reduced forage for fall grazing in Southern states like Texas, Oklahoma, and Kansas (Epplin et al. 1998, Carver et al. 2001). These factors were considered before the optimal fly-free planting dates were recommended (Drake et al. 1924, Walkden et al. 1944). However, new observations suggest that fly-free dates could be due for revision in some areas of the United States. For example, Davis et al. (2009) observed Hessian fly adult activity in Kansas later in the fall than previously recorded, and Schwarting (2014) recommended a revision of the fly-free dates in Kansas. It was noted early in the development of the fly-free dates that abiotic conditions, such as unseasonable wet or dry periods, can alter emergence or trigger secondary waves of emergence (Drake and Decker 1932). Even though these variables can affect the effectiveness of the fly-free dates, the technique still remains a good general guideline for a safe planting date to limit Hessian fly infestation in the North-central and Mid-western United States.

In many of the Southern wheat producing states, such as Georgia, Oklahoma, and Texas, fly-free dates are less effective due to intermittent periods of warm weather that occur throughout the fall and into early winter (Buntin and Chapin 1990, Morgan et al. 2005, Bradford 2014). The periodic warm weather allows adults to emerge and lay eggs, resulting in damaging larval infestations. Even though adult Hessian fly activity does not cease in the Southern states during the fall and winter months, delayed planting based on the number of fall broods and dates of brood emergence can still decrease damage caused by Hessian fly larval feeding (Buntin et al. 1990a, Morgan et al. 2005, Royer and Giles 2009, Knutson et al. 2017). For example, in North Central Texas 1–3 fall broods can occur during the fall, and delaying planting until November can help to avoid infestations by the early emerging fall broods (Lidell and Schuster 1990). Although less effective than the fly-free dates observed in the Northern states, delayed planting remains a viable option to reduce the risk of a fall Hessian fly infestation and other economically important pests like aphids, fall armyworm (*Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae)), armyworm (*Mythimna unipuncta* (Haworth) (Lepidoptera: Noctuidae)), wheat curl mite (*Aceria tosichella* Keifer (Acari: Eriophyidae)), and white grubs in Southern states (Kimura et al. 2017, McCornack et al. 2017). Monitoring Hessian fly activity with pheromone traps can identify periods of adult emergence in the fall and help refine planting dates.

Destruction of Volunteer Wheat

Volunteer wheat often emerges earlier in the fall than planted wheat, and can host early season development of Hessian fly populations that later lead to higher infestation rates in the subsequently planted wheat crop (Buntin et al. 1991). Much like fly-free dates, destruction of volunteer wheat has been recommended as an important control measure since the early 1900s (Headlee and Parker 1913). Despite the widespread practice of controlling volunteer wheat, surprisingly little research has been published on the subject. Parks (1917) determined that the presence of volunteer wheat before planting enhanced Hessian fly infestations and negated the benefit of planting after the fly-free date. Buntin et al. (1991) demonstrated that destruction of volunteer wheat prior to wheat planting reduced the risk of Hessian fly infestation. Timing of volunteer wheat destruction is important as it has been recommended to occur at least 2 wk before germination of the planted crop for the most effective results (Whitworth et al. 2009).

The value of tillage to destroy Hessian fly puparia in wheat residue varies. Studies of no-till systems compared to conventional tillage have mixed results (Chapin et al. 1992, Zeiss et al. 1993b, Castle del Conte et al. 2005). In these studies, successive tillage regiments and the depth that the residue was buried influenced fly survival and subsequent infestations in the wheat crop (Chapin et al. 1992, Zeiss et al. 1993b). Thus, tillage practices that sufficiently bury stubble (9–11 cm or 3.5–4.3 inches) and avoid repetitive tillage that can resurface buried flaxseed remains a valid method to destroy volunteer wheat to kill Hessian fly flaxseeds (Chapin et al. 1992, Zeiss et al. 1993b, Flanders et al. 2013). However, no-till systems designed to reduce soil erosion, improve soil structure, and increase organic matter content will likely continue to increase in popularity (Derpsch et al. 2010). Suppression of Hessian fly infested volunteer wheat through tillage will likely become a greater challenge for these producers, and thereby become a less utilized management tool in the future. Herbicides are an effective alternative to tillage for control of volunteer wheat to break the 'green bridge' and control pest insects like the Hessian fly (Bell et al. 2016). However, while herbicides will control volunteer wheat, they will not reduce the presence of wheat stubble from the previous crop that may harbor flaxseeds.

Insecticides

Systemic seed treatment products labeled for Hessian fly may control fall infestations of Hessian flies in winter wheat; however, they provide little to no protection from spring infestations (Wilde et al. 2001). In the Northern wheat producing states, seed treatments provide temporary control, ~30 d, which can be effective if there is only one fall generation of Hessian fly (Wilde et al. 2001, Whitworth et al. 2009). In Southern states such as Texas and Oklahoma, the 20–30 d of protection provided by seed treatments after germination again control the first brood of flies infesting wheat but are not effective against subsequent broods (Morgan et al. 2005, Royer et al. 2015). Seed treatments also control other early season insect pests (aphids) but the cost of investing in a preventative seed treatment for Hessian fly alone often cannot be justified. Seed treatments can be important when there is a history of high Hessian fly infestation and/or resistant cultivars are not available, and other management strategies, i.e., delayed planting and destruction of volunteer wheat, have been implemented if possible (VanDuyn et al. 2003, Morgan et al. 2005, Flanders et al. 2013).

Foliar-applied insecticides, typically pyrethroids, are targeted to control adults and neonate larvae before they reach the leaf sheath where they are protected from the treatment. Treatments are most effective when applied when seedling plants have 2–3 leaves. In the Southeastern United States, foliar applied insecticides can be considered when at least three of the following five conditions are met: 1) the current wheat crop was planted directly in or within 400 yards (365.8 m) of a wheat field of the previous year, 2) a resistant cultivar was not planted in the current field, 3) neonicotinoid seed treatment was not applied to the current field, 4) yield loss due to Hessian flies has occurred in nearby fields in previous years, 5) Hessian fly eggs are found on the wheat leaves of the current crop (VanDuyn et al. 2003, Flanders et al. 2013). However, foliar applications are only effective if applied when adults are laying eggs, eggs are present on leaves, and before larvae have established in the stems (VanDuyn et al. 2003, Buntin 2007) and because multiple broods occur throughout the growing season, multiple foliar insecticide applications would be necessary. The limited window of effectiveness, inconsistent infestation rate of Hessian fly, difficult timing of foliar applications, lack of efficient sampling methods and economic treatment threshold, and associated costs of multiple applications are the main reasons why foliar-applied insecticides remain one of the lesser-used management options (VanDuyn et al. 2003, Alvey 2009, Knutson et al. 2017).

Natural Enemies

Many species of Hymenopteran parasitoids (wasps) attack the Hessian fly. Gahan (1933) described 41 species of Hessian fly parasitoid wasps in North America and Europe. Most of these parasitoids belong to the superfamily Chalcidoidea, which attack the puparia of the spring generation of Hessian fly; however, five parasitoids in the family Platygasteridae attack the egg stage, which includes *Platygaster hiemalis* Forbes (Hymenoptera: Platygastridae) that parasitizes fall generations (Gahan 1933). Although the composition of parasitoid communities vary significantly among regions in the United States, three species (*P. hiemalis*, *Homoporus destructor* (Say) (Hymenoptera: Pteromalidae), and *Eupelmus allynii* French (Hymenoptera: Eupelmidae)) are widespread and are considered valuable parasitoids (Rockwood and Reeher 1933, Hill 1953, Schuster and Lidell 1990). Parasitoids cause significant mortality to Hessian fly populations, as high as 55, 87, and 98% parasitism observed in fields in Georgia, Texas, and Washington, respectively (Morrill 1982, Pike et al. 1983, Schuster and Lidell 1990). However, parasitism rates vary significantly between fields, generations, time of year, host density, and geographic location (Hill et al. 1939, Pike et al. 1983, Prestidge 1992, Wise 2007); owing to inconsistencies in their life history (egg vs puparia parasitoid, or attacking fall vs spring broods) and variation in population composition across regions. Inconsistent Hessian fly parasitism was highlighted by Schuster and Lidell (1990), who observed parasitism rates varied significantly from 0 to 87% in Texas wheat fields, with parasitism of fall Hessian fly generations rare compared to spring parasitism rates, and parasitoid species fluctuating widely between counties and years.

Pupal parasitoids result in Hessian fly mortality only after the larva has damaged wheat plants. When populations of Hessian flies in the Southern states break dormancy in the fall, populations can still rapidly increase during the two generations that can be completed before winter dormancy begins (Schuster and Lidell 1990, Knutson et al. 2002). Thus, in states where parasitoids are only active in late spring, parasitism does not protect the current crop, but spring parasitoids can reduce the number of Hessian fly entering summer aestivation (Schuster and Lidell 1990). This makes pupal parasitoids important for the protection of resistant cultivars, as parasitoids are capable of finding and parasitizing low densities of Hessian fly puparia (Knutson et al. 2002), which represent virulent biotypes that survive on resistant cultivars. The egg-larval parasitoid *P. hiemalis*, which attacks fall broods of Hessian fly, can significantly enhance the effectiveness of resistant cultivars, reducing Hessian fly larval survival to 2.5% (a 42% reduction compared to larval survival on solely the resistant cultivar) (Chen et al. 1991). The interaction between resistance and *P. hiemalis* was most effective when a cultivar of intermediate resistance was combined with the parasitoid (Chen et al. 1991). The ability of parasitoids to enhance resistant cultivars through increased Hessian fly mortality demonstrates the importance of conserving parasitism as a management technique. Practices that conserve Hessian fly parasitoids have not been investigated and more research is needed to understand how to increase Hessian fly parasitoid populations and improve the consistency of parasitism rates.

Integrated Management

Although the aforementioned control measures can impact Hessian fly populations if applied individually, they can be more effective at reducing Hessian fly losses when used in combination as part of an IPM program (Buntin et al. 1991, Chen et al. 1991, Buntin et al. 1992). Buntin et al. (1992) showed that a systemic insecticide combined with delayed planting is an economically effective Hessian fly management strategy when high-yielding resistant cultivars are not available. Also, parasitoids can enhance the control of Hessian fly in fields planted with wheat cultivars of intermediate resistance (Chen et al. 1991). Not only are Hessian fly management practices often compatible with each other, but they can be integrated with management plans for other insect pest of wheat. For instance, delayed planting not only reduces risk of Hessian fly infestation, but it also reduces the risk of other economically important pests like aphids, fall armyworm (*S. frugiperda*), armyworm (*M. unipuncta*), wheat curl mite (*A. tosichella*), and white grubs in Southern states (Kimura et al. 2017, McCornack et al. 2017). However, not all wheat management practices are compatible with all forms of Hessian fly management. Namely, no-till soil conservation does not comply with disk harrowing before planting to bury volunteer wheat/wheat stubble harboring flaxseed (Chapin et al. 1992). This highlights the need to improve upon the current Hessian fly monitoring technique (pheromone trap) to correlate trap capture with infestations, so that producers can select appropriate Hessian fly management practices that integrate with wheat field management (e.g., soil, insect, and weed management) or limit crop inputs (e.g., fertilizer, fungicides, and irrigation, or switch fields from grain production to livestock forage) (Knutson et al. 2017).

Conclusion

Since the introduction of the Hessian fly in the late 1700s (Pauly 2002), this pest is responsible for significant economic damage in many of the wheat production regions of the United States (Smiley et al. 2004, Watson 2005, Alvey 2009). As a result of the potential yield loss associated with Hessian fly larval feeding, multiple control tactics have been researched and developed into an IPM program that provides options for producers to integrate Hessian fly management with wheat production and control of other pest insects. Integrated Hessian fly management recommendations include:

- Incorporate resistant cultivars, adherence to optimum planting dates (i.e., 'fly-free dates' in Upper Midwest and Northern Great Plains states or delayed planting in Southern states to avoid the first fall brood), destruction of volunteer wheat 2 wk prior to planting, natural enemies, and insecticides to manage Hessian fly infestations.
- Foliar applied insecticides should only be considered when at least three of the following five conditions are met: 1) the current wheat crop was planted directly in or within 400 yards of a wheat field of the previous year, 2) a resistant cultivar was not planted in the current field, 3) neonicotinoid seed treatment was not applied to the current field, 4) yield loss due to Hessian flies has occurred in nearby fields in previous years, 5) Hessian fly eggs are found on the wheat leaves of the current crop (VanDuyn et al. 2003, Flanders et al. 2013). Insecticide application strictly for Hessian fly control is limited. Systemic seed treatments provide temporary control (~30 d) of fall infestations of Hessian flies in winter wheat; however, they provide little to no protection from spring infestations (Wilde et al. 2001).
- Resistant wheat cultivars have long been the most economical and effective control method (Berzonsky et al. 2003), and cultivars should be rotated, each with a different source of resistance, to vary the R genes planted in subsequent years to help mitigate loss of cultivar resistance (Gould 1986, Tooker and Frank 2012).
- If cultivars with only intermediate resistance are available, the fall parasitoid *P. hiemalis* can significantly enhance the effectiveness of those cultivars (Chen et al. 1991).
- Cultivar selection must balance the level of Hessian fly resistance with cultivar yield, disease resistance, and availability to producers in different regions of the United States.
- No single technique should be considered as a 'silver bullet' for management of Hessian fly in wheat. Instead, management practices should be used in conjugation when feasible and economically beneficial (e.g., a combination of volunteer wheat destruction with delayed planting, or integration of systemic insecticide with delayed plant) (Buntin et al. 1991, Buntin et al. 1992).
- Consider incorporating pheromone traps into the implementation of certain Hessian fly IPM tactics (i.e., delayed planting,

systemic seed treatment), as these traps can accurately and efficiently define periods of male Hessian fly activity.
- Hessian fly management tactics, i.e., delayed planting, destruction of volunteer wheat, and insecticides, should be integrated with wheat production practices (e.g., no-till) and additional pest management programs to reduce risk of other economically important wheat pests (e.g., aphids, fall armyworm, armyworm, wheat curl mite, and white grubs in Southern states) (Kimura et al. 2017, McCornack et al. 2017).

Future research on these management practices along with the development of sampling techniques, time to sample, and treatment thresholds can advance the effectiveness of Hessian fly IPM. Especially research focusing on the genetic mechanisms involved in the establishment a feeding site by Hessian fly larvae, which can lead to the development of new resistant cultivars. Additionally, a better understanding of egg and neonate mortality and weather conditions could improve the relationship between pheromone trap data and subsequent field infestations by Hessian fly larvae. Strategies examining attractants of female Hessian flies may improve correlations between trap catches and field infestations, and thus should also be the focus of future studies.

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