Thresholds and prediction models to support the sustainable management of herbivorous insects in wheat. A review

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Abstract

Wheat is one of the most important arable crops grown worldwide, providing a significant proportion of the daily calorific intake for countries across the globe. Wheat crops are attacked by a diverse range of herbivorous invertebrates (pests) that cause significant yield loss. It is anticipated that yield loss caused by pests will increase in response to a changing climate. Currently, these pests are primarily controlled using pesticides, however there is an increased need for more sustainable pest management solutions. Economic thresholds represent one avenue that can support the sustainable management of pests. Briefly, thresholds are the number of pests above which there is sufficient risk of yield loss.

Here we review the economic thresholds and prediction methods available for sustainable pest management in wheat. We focus on five economically damaging pests affecting wheat crops in the UK and Europe. For each we highlight the key period of crop risk to pest attack, identify economic thresholds, and provide an overview of current decision support models that can help estimate crop risk and advise sustainable pest management; we end by proposing areas for future improvement for each pest. Furthermore, we take a novel approach by discussing economic thresholds and their applications to sustainable pest management within the context of crop physiology and the capacity for crops to tolerate pest damage, a consideration that is often overlooked when developing pest management strategies. We use the stem-boring pest, the gout fly, as a case-study and use the economic injury level equation to conduct a theoretical assessment of the appropriateness of the current gout fly threshold. This theoretical assessment indicates that wheat crops can tolerate greater gout fly damage than currently considered, and shows that by incorporating crop physiology into sustainable pest tolerance schemes we can work towards developing more appropriate physiological-based pest thresholds.

Keywords

Aphids, Blossom midge, Crop Tolerance, Economic Threshold, Economic Injury Level, Gout Fly, Insect Pests, Integrated Pest Management, Prediction Models, Wheat bulb fly

Contents

1. Introduction

Wheat (*Triticum aestivum*) is one of the most important crops grown across the world (Curtis and Halford 2014). Wheat provides 25% of the daily calorific intake for the UK, and the reliance on wheat as a source of calories is higher (up to 61%) in countries with greater food insecurity (Mottaleb et al. 2022). Wheat crops are attacked by a myriad of herbivorous invertebrates (hereafter referred to as pests) across the growing season, with both winter and spring wheat exposed to a range of co-occurring pests (Fig. 1). Pests can cause significant levels of damage, potentially reducing yields by up to 80% (Rogers et al. 2015; Nancarrow et al. 2021; Perry et al. 2000), and various factors influence the extent to which they damage crops, including the feeding mechanism, the plant tissue fed on, and the development stage of the crop during the period of herbivory. The main pests affecting wheat in the UK, and their periods of activity, are detailed in Fig. 1. This review will focus on the most economically important insect pests in the UK and northern Europe, denoted by an asterix in Fig. 1.

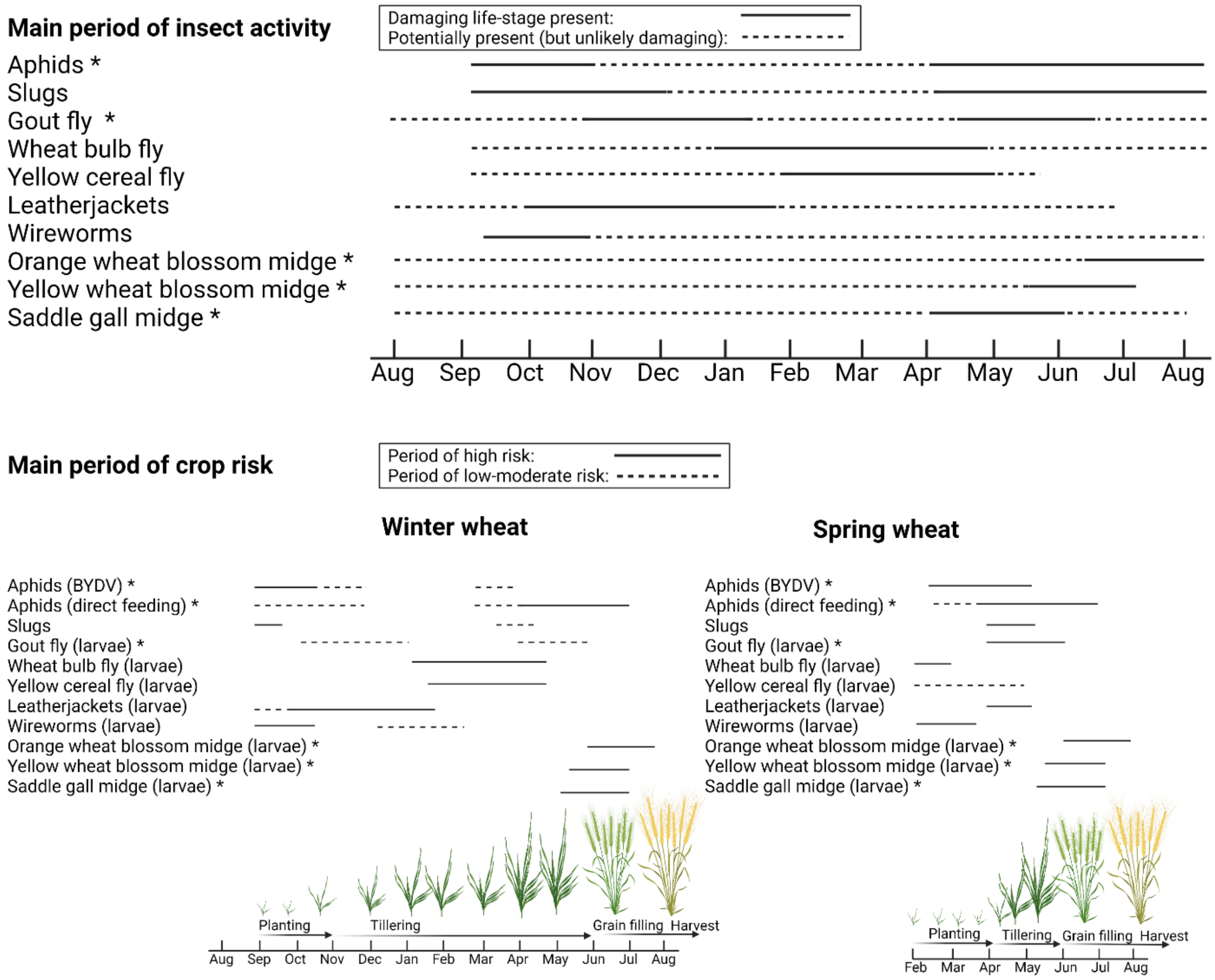


Fig. 1: Periods of activity for the damaging stage(s) of the main pests affecting wheat crops in the UK and the main period of crop risk of herbivory for each pest. * indicates herbivorous invertebrates that will be a focus for this review.

Currently, pest populations are primarily controlled using insecticides. However, due to more stringent regulations (EU 2009) and environmental concerns around insecticide use (Goulson 2013), alongside the emergence of pest populations that have reduced sensitivity, or resistance to, insecticides (Bass et al. 2015;

Walsh et al. 2020a; Walsh et al. 2020b; Leybourne et al. 2023b), there is a growing need for more sustainable pest management options (Mc Namara et al. 2020). Economic thresholds (hereafter referred to as thresholds) represent one avenue that can support the sustainable management of pests. Briefly, thresholds are the number of pests per plant, or unit area, above which there is sufficient risk that the level of crop damage caused will result in economic yield loss (Higley and Pedigo 1993; Pedigo et al. 1986). In the UK, thresholds have been devised for the main pests of wheat (Table 1), although not all of these thresholds have been experimentally validated.

Table 1: The main herbivorous insects affecting wheat crops in the UK.

Pest	Growth stage during which crop is at highest risk	Level of economic damage	Current accepted threshold(s)	Additional comments	References
Aphids (*Sitobion avenae, Rhopalosiphum padi*): Virus vectors	Up to GS 31.	20- 80% yield loss if BYDV prevalence is high	One apterous adult	Plants can still be infected after GS31, but there is little impact on yield.	(Perry et al. 2000; Nancarrow et al. 2021).
Aphids (*S. avenae, Metapolophium dihordum*): Feeding damage	Emergence to two weeks before the end of grain filling.	10-13% yield loss if infestation high	Two thirds of tillers infested between GS 31 and two weeks before grain filling finishes. 50% of tillers infested before GS 61.	Drought can increase impacts due to lower reserves of soluble stem carbohydrates.	(George and Gair 1979; Tatchell 1989; Oakley and Walters 1994).
Orange wheat blossom midge (*Sitodiplosis mosellana*)	GS 54-59	Up to 79% yield loss if infestation is high.	Over 120 males per trap per day; One midge per three ears (feed crop); One midge per six ears (milling and seed crops)	Once the majority of the crop is in flower the risk has passed.	(Olfert et al. 1985; Kurppa and Husberg 1989; Larsson 1992; Pivnick and Labbé 1993; Oakley 1994; Ellis et al. 2009; Senevirathna et al. 2023).
Yellow wheat blossom midge (*Contarinia tritici*)	GS 43-49	Extent of potential yield loss unknown.	No current thresholds, most growers follow orange wheat blossom midge thresholds	Once the majority of the crop is in flower the risk has passed.	(Ellis et al., 2014).
Saddle gall midge (*Haplodiplosis marginate*)	GS 31-39	13-70% yield loss	600-1,200 larvae m^{-2}	This threshold has only been proposed, it has not been tested and validated	(Golightly and Woodville 1974; Ellis et al. 2014).
Wheat bulb fly (*Delia coarctata*)	GS 21-31	Up to 4.8 t ha^{-1} yield loss	250 eggs m^{-2} for crops sown before November; 100 eggs m^{-2} for crops sown after November	Well-tillered crops can tolerate damage.	(Gough et al. 1961; Rogers et al. 2015).
Gout fly (*Chlorops pumilionis*)	GS 21-31	30-50% yield loss	Winter wheat: 50% of tillers infested with eggs; Spring wheat: 10% of tillers infested with eggs at GS31-32		(Derron and Goy 1990; Bryson et al. 2005; Ramsden et al. 2017).

Despite their widespread use (Ramsden et al. 2017), the scientific foundations for most thresholds are based on decades-old biological and phenological observations (Frew 1924; Gough et al. 1961), and the majority of thresholds do not account for crop traits that can influence the extent to which a specific crop at a specific growth stage can tolerate a specific pest. For example, damage from a pest that destroys wheat shoots can be better tolerated if the plant is able to produce additional shoots through tillering, and ignoring such crop traits can lead to an underestimation of the pest pressure that can be tolerated (Leybourne et al. 2022). By placing greater emphasis on crop physiology and physiological tolerance to herbivorous insects, thresholds should be revisited and, if necessary, revised and updated so that they better account for the natural physiological tolerance of the crop. A threshold-based tolerance approach has been developed in other crop-pest systems, with tolerance in oilseed rape against the pollen beetle *Meligethes spp.* a key example (Hansen 2004; Skellern and Cook 2018; Ellis and Berry 2011). Developing similar tolerance-based thresholds for other important pests will help with the development of more sustainable management practices. This approach was previously when re-examining the thresholds of the damaging wheat pest, the wheat bulb fly (*Delia coarctata*); here the authors found that the current thresholds likely underestimate the level of pest pressure that can be tolerated and, through predictive modelling, found that wheat crops could potentially tolerate *D. coarctata* damage through an increase in shoot number production (Leybourne et al. 2022).

Thresholds can be used as a baseline to advise when pest management interventions should be considered, and Fig. 2 provides a graphical overview of the decision-making processes involved. A key step in the process is effective determination of pest populations, however monitoring pests within the field is challenging; pests can be difficult to find when numbers are low (for some pests even small populations are damaging) and difficult to identify, pest distribution may be patchy across field(s), and areas to be monitored can be large (Ramsden et al. 2017). Predictive models can be used to support sustainable management practices by helping farmers and growers estimate insect abundance, predict insect activity or gauge crop tolerance (Leybourne et al. 2023a). This allows for monitoring effort to be concentrated on times and locations at which damaging pest populations are likely to occur. Several models have been developed to support the management of pests in wheat (Leybourne et al. 2023a). Together, thresholds and models that predict the abundance or activity of pests represent a foundation from which future integrated pest management schemes can be developed, as recently described for *D. coarctata* (Leybourne et al. 2022).

Here, we briefly describe how crop physiology, particularly the physiological basis of yield determination in wheat, can be used to produce more robust physiological-based thresholds. Following this, we review the thresholds and available predictive models for the main pests of wheat (Fig. 1; Table 1). We revise current thresholds by placing greater emphasis on crop physiology in order to incorporate natural crop tolerance into thresholds, as achieved previously for *D. coarctata* (Leybourne et al. 2022), and we use the gout fly (*Chlorops pumilionis*) as a case study for this. We conclude by highlighting how threshold-based tolerance schemes can be used to develop future sustainable pest management schemes.

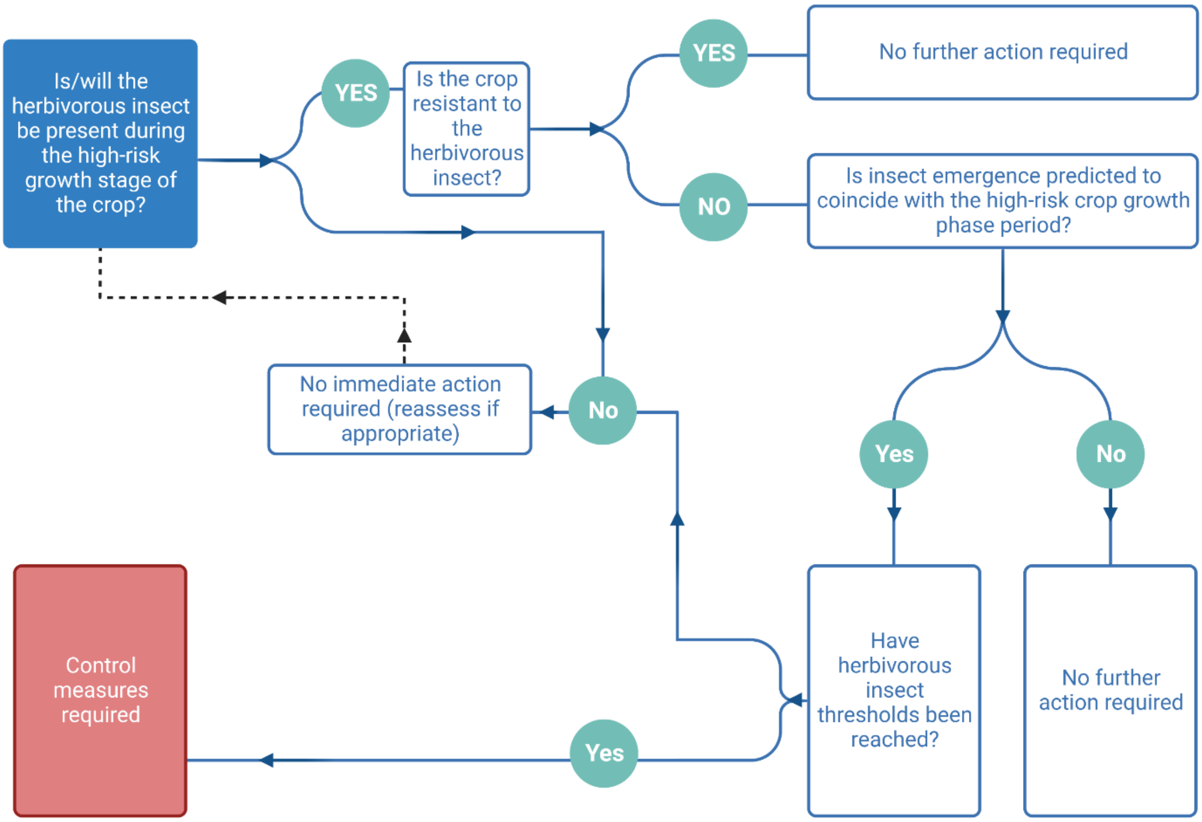


Fig. 2: General overview of the threshold-based management process This image was created with BioRender.com

2. The physiological basis of yield determination in wheat crops and its incorporation into herbivorous insect thresholds

2.1. The physiological basis of yield: Sink or source

We have a firm understanding of the physiological factors that determine yield formation in wheat (Murchie et al. 2023; Slafer et al. 2023). These factors can help estimate the degree of tolerance a wheat crop will have against a specific pest at a given growth stage. The key factor determining yield is whether yield formation is sink or source limited (Fischer 2007; Parry et al. 2011; Bingham et al. 2007). For example, yield determination in barley and oilseed rape is dictated by the number of seeds m^{-2}; therefore, factors that influence seed number during the early phases of the crop growth stage are key limiting factors in yield formation for these crops (Bingham et al. 2007). This is known as sink limitation (Slafer et al. 2023). Conversely, for wheat the number of available grain sites is usually high enough that the limitation for yield is the rate at which these grain sites can be filled. Consequently, wheat yield is determined by grain assimilation (i.e., the availability of photosynthetic assimilates to fill grains), and this is known as source limitation (Murchie et al. 2023). If a wheat crop has insufficient access to resources required to fill seeds, or suffers from resource loss (i.e., herbivory) during this key grain-filling period then the achievable yield of the crop will suffer (Foulkes et al. 2011). Therefore, herbivorous insects that are active during the critical grain-filling growth phase represent the herbivorous insects of critical importance in determining yield for wheat.

Whether or not a crop is source or sink limited will determine how tolerant it will be to pest injury at different crop growth stages. A crop which is sink limited will be particularly vulnerable to damage during the period when the number of grains m^{-2} is determined. For example, barley would be expected to have a low tolerance to pests which reduce tiller numbers because this would reduce seeds m^{-2} and sink size (Bingham et al. 2007). A crop which is source limited will have a low tolerance to pests which reduce the supply of resources to the growing grains. For example, wheat would have a low tolerance to pests which reduce green area during seed filling as this will reduce photosynthesis and the supply of photo-assimilate for filling the grains. For most wheat pests, impact on early growth stages between plant establishment and the start of stem extension typically occurs in October through to April (Fig. 1), although they can be present in the wheat crop during a wider period. These pests include slugs, gout fly, wheat bulb fly, yellow cereal fly, leatherjackets, wireworms, and saddle gall midge. Wheat is tolerant to yield-loss inducing damage during early phases of growth and will therefore have greater tolerance to these pests. Pests which impact on later phases of growth, and are therefore of greater concern to wheat growers, include: orange and lemon wheat blossom midges which attack during flowering and damage the grain, aphids that directly reduce resource use by wheat during the grain-filling stage by removing sugars and carbohydrates during feeding, and viruses transmitted by aphids which affect growth and resource accumulation during all growth stages.

2.2. Incorporating crop physiology into thresholds: Developing physiological-based thresholds

Wheat has a substantial ability to compensate for damage caused by insect herbivory. This is readily achieved by: 1) Producing a greater number of shoots and ears, as well as a greater number of grains per ear, to compensate for plant loss; 2) Producing more grains per ear and larger grains to compensate for shoot loss; 3) Producing larger grains to compensate for grain loss; and 4) Increasing the remobilisation of stored soluble carbohydrates to compensate for a reduction in the supply of photo-assimilate during grain filling. From these, the first can be actively manipulated by farmers and growers to produce crops that are more capable of tolerating insect damage: increasing shoot and plant number to ensure sufficient fertile shoots remain after herbivory. This can be achieved through increasing seed rate and/or sowing earlier; however, this requires an estimate of the predicted level of pest damage. Here, predictive models can be beneficial in determining the pest risk ahead of sowing, enabling growers to adapt the seed rate and sowing date as required.

3. The current thresholds and predictive models for key wheat pests

Thresholds have been developed for most wheat pests (Table 1; Ramsden et al., 2017). However, the majority of these thresholds were developed over 25 years ago, and since then agronomic practices have changed and our understanding of the biology of these insects has improved. It is therefore important that these thresholds are reviewed and, if appropriate, updated and developed into more reliable thresholds. Accounting for crop physiology, and by association the natural tolerance of wheat to a specific pest, is a potential way to update thresholds. Incorporating this information into thresholds will help develop more sustainable pest management practices where natural crop tolerance can be manipulated to develop a crop robust enough to tolerate a predicted level of pest pressure, as recently proposed for *D. coarctata* (Leybourne et al. 2022).

In order to follow thresholds growers must monitor, or be able to accurately estimate, insect populations and use this to determine the level of crop risk. As mentioned above, this is often difficult to do under field conditions (Ramsden et al. 2017) and predictive models can assist in this regard. Such models have been developed to estimate the abundance of pest populations, predict the occurrence of phenological events (e.g. migration), and to determine the overall level of crop risk to a specific pest (Leybourne et al. 2023a). These models are useful standalone tools that can help with the monitoring and management of pest populations, and they can also be combined with thresholds to better support sustainable management practices. A population prediction model that can be used as the foundation for a threshold-based pest management system was recently described (Leybourne et al. 2022). This system combines models estimating seasonal insect abundance and crop development to generate dynamic thresholds based on crop tolerance, and so provides a prescriptive pest management tool.

Below we review the current thresholds, economic injury levels, and prediction models for each pest identified in Table 1. For the stem-boring insect *C. pumilionis* we also provide a theoretical revision of the economic injury level and describe a potential physiological crop tolerance level, similar to thresholds revisions previously conducted for *D. coarctata* (Leybourne et al. 2022).

3.1. Aphids: Virus transmission and direct-feeding damage

Cereal aphids are the primary sap-feeding insect pests of wheat. Cereal aphids damage winter crops through two mechanisms: direct feeding damage and the transmission of phytoviruses such as barley yellow dwarf virus (BYDV) (Dedryver et al. 2010; Nancarrow et al. 2021; Perry et al. 2000). The main cereal aphids affecting wheat crops in Europe are the bird cherry-oat aphid *(Rhopalosiphum padi)*, the English grain aphid *(Sitobion avenae)*, and the rose-grain aphid *(Metapolophium dirhodum)*. *R. padi* and *S. avenae* are the main autumn vectors of BYDV in winter wheat (Aradottir and Crespo-Herrera 2021), with *M. dirhodum* and *S. avenae* more abundant in summer when direct feeding damage occurs (Honek et al. 2018). *S. avenae* and *M. dirhodum* are also important vectors of BYDV in spring-sown wheat (Aradottir and Crespo-Herrera 2021). A key driver of aphid risk in Europe is the emergence of aphids with reduced sensitivity to insecticides (Foster et al. 2014; Walsh et al. 2020a; Walsh et al. 2020b; Leybourne et al. 2023b).

3.1.1.Period of crop risk

The main period of crop risk from BYDV is plant emergence to GS31, after which a crop should suffer minimal yield loss from new infections (Doodson and Saunders 1970). The risk period for direct feeding damage is up to two weeks before grain filling (Oakley and Walters 1994). Virus transmission occurs in autumn (Aradottir and Crespo-Herrera 2021) during the sink determination phase of crop growth, with the detrimental effects of virus infection (stunted crop growth and reduced green leaf area) restricting sink development and resource assimilation. The period of crop risk to direct feeding damage coincides with the source determination phase of crop growth and restricts photosynthetic assimilation. For some cereal aphid species, infestation can also initiate the redistribution of soluble carbohydrates away from the sink and towards the aphid feeding site.

3.1.2. Overview of current thresholds

The current threshold for virus-vectoring aphids is exceptionally low (Nancarrow et al. 2021; Ramsden et al. 2017; Ellis et al. 2014). Currently, the UK threshold for virus-vectoring aphids is one apterous (wingless) aphid within the crop (Ellis et al. 2014). These thresholds are based on several factors: The high risk of substantial yield loss following BYDV transmission, that only a single aphid is needed to infect a plant, that monitoring these pests is difficult, and that pyrethroid insecticides are relatively cheap. However, these thresholds make two broad assumptions: 1) That every aphid present in a cereal field in autumn carries BYDV; and 2) Every aphid transmits BYDV with 100% efficiency. These assumptions are flawed as surveys have shown that the proportion of aphids harbouring BYDV is often less than 10% in the UK (Plumb 1976), though more recent surveys are needed. It is also important to note that the efficiency of virus transmission differs between cereal aphid species and clones (Kern et al. 2022; Halbert and Pike 1985; Lucio-Zavaleta et al. 2001). Currently, the level of virus incidence within the aphid population and the transmission potential of the local aphid population are not incorporated into BYDV thresholds.

In the UK, the threshold for direct feeding damage is 50% of tillers infested with cereal aphids from GS31 to GS61, and 66% of tillers infested from GS62 to two weeks before grain filling (Oakley and Walters 1994). As with the BYDV threshold there is scope for improvement as the degree of infestation is not considered, only the proportion of tillers affected. Under the current threshold, a crop infested with one aphid per two tillers would be placed in the same risk category as one infested with 20 aphids on one out of two tillers. Clearly, under the second scenario the crop is suffering from a greater level of pest pressure. Other European countries have attempted to place the cereal aphid direct feeding damage thresholds into more defined categories: In Germany and Denmark the threshold is approximately five aphids per ear at the flowering stage (Merbach et al. 1980; Hansen 2006) and in Sweden the threshold is seven aphids per tiller (Larsson 2005). Similar to the BYDV thresholds, there is no distinction made between the different aphid species.

3.1.3. Overview of current predictive models that can help estimate crop risk

There are several prediction models available that can help growers assess BYDV and aphid risk. In the UK, the main model is a T-sum degree-day model that predicts when the second wingless generation of aphids will emerge. This generation is thought to be responsible for initiation of secondary crop infection (i.e. the aphids responsible for spreading the virus to plants neighbouring those initially infested and so increasing the proportion of the crop infected). The model helps growers to target their in-field crop monitoring efforts to the appearance of the most damaging pest stages, however the origins of this model are unknown. Other models have been developed for the UK (Kendall et al. 1992; Morgan 2000) but their use has not been adopted, primarily due to lack of suitable technology at the time of development. Models for BYDV have been developed for other countries; for example predicting virus incidence and yield loss in Australia (Thackray et al. 2009), autumn aphid abundance in New Zealand (Lankin-Vega et al. 2008), and infection and secondary spread in France (Gillet et al. 1990; Leclercq-Le Quillec et al. 2000).

Prediction models have also been developed for the direct feeding damage summer populations, in the UK this includes models that predict the occurrence of summer migration (Harrington et al. 1991; Howling et al. 1993) and the potential level of in-field infestation (Mann et al. 1986). However, the majority of the BYDV and direct feeding damage models are outdated and no longer fit for purpose.

3.1.4.Proposed areas for improvement and future development

For both BYDV and direct damage thresholds, the key areas for improvement centre on better linking the level of insect infestation (e.g., the proportion of aphids carrying BYDV or actual aphid abundance) with potential yield loss, incorporating treatment costs into spray guidance into the decision-making process, and to better understand how a wheat crop could naturally tolerate virus and aphid infestation through compensatory growth. Developing a greater understanding of this would enable scientists to develop, test, and validate more realistic thresholds for aphid and virus tolerance. One key avenue for future development should be to revise the thresholds by incorporating the level of virus incidence present in the local aphid population; virus incidence can be readily detected from trap-caught aphids (Bates et al. 2020) and could be used as the foundation to develop a more accurate threshold scheme.

3.2. Orange wheat blossom midge (Sitodiplosis mosellana) and yellow wheat blossom midge (Contarinia tritici)

The wheat blossom midges, *S. mosellana* and *C. tritici*, are two sporadically-occurring pests. The potential host range for *S. mosellana* covers the majority of the UK and Central Europe (Olfert et al. 2016) and the insect is also widespread across China (Duan et al. 2013). The larvae of *S. mosellana* feed on the grain and *C. tritici* larvae feed on the flower, which can cause significant crop damage if infestation is high. *S. mosellana* damage can also promote secondary infection with wheat pathogens, including fusarium head blight (Miao et al. 2023). Whilst *S. mosellana* damage is sporadic, in years of significant infestation losses can be high, for example a 2004 outbreak in the UK was estimated to cause crop losses of £60 million (Oakley et al. 2005). The risk of *S. mosellana* has decreased due to breeding for crop resistance (McKenzie et al. 2002; Thomas et al. 2005; Blake et al. 2011). Further information on the biology and management strategies for *S. mosellana* are described in a recent comprehensive review (Dufton et al. 2022).

3.2.1.Period of crop risk

The period of insect activity and crop risk differs slightly between the two insects: Crops are at risk of *C. tritici* damage during the booting stage (GS43-49), where the larvae feed on the stigma and the anthers (Oakley 1994; Dufton et al. 2022) which limits grain development and prevents successful pollination. Crops are at risk of *S. mosellana* damage between GS54-59, where the larvae feed on the developing grain, reducing grain size, premature sprouting, reductions in quality and increased risk from diseases. For both insects, the damage occurs during the source determination stage of crop growth.

For both insects, the level of annual crop risk is variable and dependent on the co-occurrence of the at-risk crop growth stage with the period of pest activity. The timing of the booting stage is a key factor that determines whether a crop is at risk of *C. tritici* infestation, as adults oviposit between the lemma and palea, and larvae are unable to survive once a crop has been pollinated. For *S. mosellana*, the timing of ear emergence in relation to midge oviposition activity is the key factor that influences the extent of damage that can be caused (Pivnick and Labbé 1993; Helenius and Kurppa 1989). Once wheat is flowering the period of risk for *S. mosellana* has passed. The extent of *S. mosellana* risk is also influenced by various environmental factors that dictate whether *S. mosellana* larvae break their overwintering diapause in the soil and subsequently pupate or return to diapause (Miao et al. 2019; Hinks and Doane 1988). The main environmental factors influencing this are soil temperature (extended low temperatures to break diapause followed by above 13ºC to form a pupa) and soil moisture (Miao et al. 2019; Oakley et al. 1998). Adult migration is a key risk factor that can determine crop risk to *S. mosellana* (Miao et al. 2013). Modelling studies have predicted that female *S. mosellana* can migrate long distances, 28-197 km, through wind-borne dispersal (Miao et al. 2013). Air temperature can also influence the flight ability of *S. mosellana* adults (Hao et al. 2013).

3.2.2. Overview of current thresholds

The perceived risk for *S. mosellana* has decreased in recent years as *S. mosellana* resistant wheat varieties have become commercially available (Blake et al. 2011). However, *S. mosellana* thresholds and alternative management strategies are still important as not every commercial variety contains *S. mosellana* resistance, and other varietal traits (e.g., BYDV or pathogen resistance) might be more important to a specific grower. Therefore, thresholds and crop tolerance still represent a key management strategy for *S. mosellana*. The current thresholds for *S. mosellana* depend on the type of wheat crop being grown. For feed crops, the current threshold is one adult per three ears, with this decreasing for milling and seed crops to one adult per six ears (Oakley 1994). In-field counts of adults are challenging for farmers as the process involves parting the crop and counting the number of adults that take flight; due to these challenges a trap-based threshold of >120 male *S. mosellana* per day has been suggested as an alternative threshold. Trials with pheromone traps have found a strong relationship with trap abundance and in-field abundance (Bruce et al. 2007), and a similar relationship was found between adult *S. mosellana* caught on yellow sticky traps and infestation (Hao et al. 2014). As with cereal aphids, the current thresholds do not account for the level of damage a given crop could compensate for and tolerate.

Currently, no threshold has been developed for *C. tritici*. Most growers follow the *S. mosellana* thresholds, although this approach has not been experimentally tested and validated.

3.2.3. Overview of current predictive models that can help estimate crop risk

There are two predictive models that can estimate the development and emergence of *S. mosellana* in wheat crops (Jacquemin et al. 2014; Oakley et al. 1998). The most efficient of these models is the stage-structured Jacquemin et al. (2014) model. This model uses various environmental factors to estimate the occurrence of three key phenological events: 1) larval emergence (occurring after 250-degree days above 3 ºC from 1st

January); 2) larval movement and pre-pupation (occurring after larval emergence when soil temperature exceeds 13 ºC); 3) adult emergence (starting with the first rainfall event following the end of event 2 and concludes after 160 degree days above 7 ºC). Research on temperature-dependent flight ability of *S. mosellana* (Hao et al. 2013) could also be incorporated into flight risk models, particularly for models designed to estimate *S. mosellana* risk under future climate scenarios.

3.2.4.Proposed areas for improvement and future development

There are several avenues that could be explored to improve *S. mosellana* and *C. tritici* management. For *S. mosellana*, we propose that a key area for improvement is to combine the Jacquemin et al. (2014) model with a crop development model. This approach could be used to estimate crop risk during the growing season by predicting *S. mosellana* adult emergence and estimating the likelihood of this co-occurring with the at-risk growth stage. Several cereal development models have already been described and can act as the foundation from which an integrative system could be developed (Basso et al. 2016; Soltani et al. 2013; Manschadi et al. 2022). Recent genome sequencing of *S. mosellana* (Gong et al. 2022) should also stimulate more fundamental research into pest biology and pest-plant interactions.

A key focus of future research for *C. tritici* should be the development, testing, and validation of a specific threshold. The lack of a threshold for *C. tritici* is likely a result of the insect only being a minor pest of wheat.

3.3. *Saddle gall midge* (Haplodiplosis marginata)

Saddle gall midge, *H. marginata,* is a pest affecting wheat across many northern European countries (Rowley et al. 2016) that causes crop damage through larval feeding. During feeding, the larvae form galls that disrupt the flow of nutrients within the plant stem (Golightly and Woodville 1974). This disruption of nutrient flow can result in reductions in ear length, thousand grain weight, and stem length while also causing grains to under develop (Woodville 1970, 1973; Golightly and Woodville 1974; Popov et al. 1998). Additional indirect yield loss can be caused if the weakened stem lodges (Woodville 1973; Golightly and Woodville 1974). It has been suggested that more than six *H. marginata* galls per tiller is sufficient to cause a significant yield reduction (Woodville 1973; Schütte 1983; Golightly and Woodville 1974) and that if 70% of wheat stems are infested, crop losses could reach 2.2 t ha^{-1}. Comprehensive reviews of *H. marginata* biology and management are provided in Censier et al. (2015) and Rowley et al. (2016).

3.3.1.Period of crop risk

Adult *H. marginata* can emerge as early as mid-April, but the typical period of adult activity is between May and early July (Censier et al. 2015; Rowley et al. 2016). Adult males emerge first, search for emerging females, and reproduce. Adults only live for around 1-7 days, with females laying around 60-120 eggs in raft-like patterns along the veins of young leaves (Censier et al. 2015). Larvae emerge 1-2 weeks following oviposition and begin to burrow into the leaf (Golightly and Woodville 1974). Larvae feed for 4-6 weeks, during which time they produce galls along the wheat stem (Censier et al. 2015). Upon reaching maturity, larvae fall to the ground, tunnel into the soil, and activate their diapause (Censier et al. 2015). The pupation process starts from March of the following year and adults start to emerge 2-4 weeks later (Censier et al. 2015). Crops are most susceptible if *H. marginata* eggs are laid during the stem extension stage, GS31-39. The crop is considered to be no longer at risk after the booting stage, GS45, as only negligible impacts on yield are observed from this growth stage onwards (Golightly and Woodville 1974). Larval feeding impacts sink determination. Various environmental and agronomic factors determine the extent of damage caused by *H. marginata* in a given year (Censier et al. 2016a; Golightly and Woodville 1974).

3.3.2. Overview of current thresholds

There is no established threshold for *H. marginata* (Censier et al. 2015; Ramsden et al. 2017). However, Golightly and Woodville (1974) previously proposed two thresholds. One based on the abundance of larvae in the soil: 600-1200 larvae m^{-2}; and a second based on the number of eggs per stem: five eggs per stem (Golightly and Woodville 1974). Although neither of these thresholds have been tested and validated. A subsequent threshold, based on the number of larvae per plant, suggested a tolerance threshold of 30 larvae per plant (Popov et al. 1998). However, the relationship between larval abundance in the soil and the extent of larval infestation is unclear, so it is difficult to equate plant-based larval tolerance with soil-born larval density (a metric that would be easier to assess, measure, or estimate). Additional thresholds based on the number of galls per stem have been proposed in several countries (Schütte 1983; Skuhravý et al. 1993; Woodville 1973) but they are impractical as, by this point, control treatments are unlikely to be effective (Rowley et al. 2016). The lack of tested and validated thresholds is a key knowledge gap for sustainable *H. marginata* management.

3.3.3. Overview of current predictive models that can help estimate crop risk

Models for *H. marginata* control have primarily been developed to predict adult emergence (Rowley et al. 2017; Rowley et al. 2016), as this is the life-stage most effectively controlled with insecticides. Incorporation of rainfall into the model significantly increased predictive accuracy (Rowley et al. 2016), and the most robust model uses the date of first rainfall (falling on or after 1st March) as the start date and estimates that adult emergence will occur after 512-degree days above 0 ºC (Rowley et al. 2017). Testing of this model at ten sites across three seasons predicted adult emergence within four days (Rowley et al. 2017).

3.3.4. Proposed areas for improvement and future development

As with *S. mosellana*, we suggest that a focal area for future *H. marginata* research should be to combine a crop development model with the *H. marginata* simulation models (Rowley et al. 2017; Rowley et al. 2016) to develop an integrated system that can predict *H. marginata* emergence and estimate the likelihood of this co-occurring with the at-risk wheat growth stage, thereby minimising monitoring effort. Monitoring effort could be minimised further by continued development, testing, and validation of *H. marginata* pheromone traps (Rowley et al. 2018; Censier et al. 2016b). These traps can potentially help growers target insecticide application during high-risk periods (Censier et al. 2016b; Censier et al. 2016a), but future work should also aim to better associate *H. marginata* abundance with potential crop risk.

Future research should also focus on further developing and validating a *H. marginata* threshold. Currently, the relationship between the number of larvae in the soil and level of crop damage caused is tenuous (Popov et al. 1998) and the proposed threshold of 600-1,200 larvae m^{-2} has not been experimentally tested or validated

(Golightly and Woodville 1974). Strengthening the confidence in this relationship will enable the risk assessment process for *H. marginata* to be refined into a more sustainable method; indeed, a significant knowledge gap is whether *H. marginata* could be sustainably managed through compensatory growth (an avenue being explored for stem-boring larvae). If a link between larvae abundance and crop damage was developed, then a future *H. marginata* management scenario could combine this information with the combined models proposed above into the following process:

1. Running of *H. marginata* emergence models to predict the adult emergence period;
2. Running of a crop development model to estimate whether adult emergence will co-occur with the at-risk growth stage;
3. If emergence and crop-risk periods co-occur: Monitoring of soil samples to determine in-field *H. marginata* abundance and estimate the level of potential yield risk;
4. Implementation of a management intervention if yield risk is high.

It may be possible to include a crop tolerance factor into future *H. marginata* thresholds, however the first step in achieving this would be to develop a model that can predict annual *H. marginata* risk (i.e., larvae abundance) not just adult emergence. If this can be achieved, then we believe that it could be possible to incorporate a crop tolerance element into a future *H. marginata* scheme by producing a crop that is able to tolerate a higher number of galls per plant. It has been suggested that around 6-10 galls per tiller can cause a yield reduction (Woodville 1973; Schütte 1983; Skuhravý et al. 1993; Golightly and Woodville 1974); therefore if a crop has 1,000 shoots m^{-2} then 5000 galls m^{-2} can be tolerated, a crop with 500 shoots m^{-2} will be able to tolerate 2500 galls m^{-2}, etc. However, key knowledge gaps in basic *H. marginata* biology mean that possibilities for developing a robust crop tolerance factor beyond this basic incorporation of gall number are currently limited. Knowledge gaps that need to be filled include: The proportion of *H. marginata* eggs that survive and develop into larvae, the number of galls produced per larva, and a means of improving crop tolerance to the damage. If this information is gathered, a crop tolerance component can be incorporated into future *H. marginata* management schemes.

3.4. Gout fly (Chlorops pumilionis)

Chlorops pumilionis is a stem-boring pest that infests both winter-sown and spring-sown wheat, but spring wheat is usually at higher risk to damage than winter wheat (Derron and Goy 1990). Infestation results in smaller grains and a loss of tillers, with significant potential yield losses (up to 30-50% in spring wheat if unmanaged).

3.4.1.Period of crop risk

C. pumilionis can go through two to three generations per year, with adult emergence occurring after 295-degree days above 4.5 ºC (Derron and Goy, 1990). After emergence, the adults mate and females lay individual eggs on the leaves of young wheat plants (GS10-37); it has been estimated that a single female can lay 50-100 eggs (Frew 1924; Empson and Gair 1982). Larval emergence occurs 8-10 days after egg laying, although a minimum temperature of 15 ºC is required for larval emergence (Derron and Goy 1990). Larvae cause crop damage by boring into individual shoots where their feeding restricts plant development, affecting the source determination stage of yield determination (Fig. 1). A single *C. pumilionis* larva is thought to only infest one shoot (Frew 1924). Larval development takes approximately one month and the pupation stage around five weeks (Gratwick 2012). The level of attack and corresponding yield loss differs between seasons and crop; spring-sown wheat suffers more damage than autumn-sown wheat (Derron and Goy 1990; Bryson et al. 2005). Generally, damage is greatest when adult emergence coincides with the at-risk crop growth stage, GS31-37 for spring-sown crops (Derron and Goy 1990) and GS12 for winter-sown crops (Ellis et al. 2014). It is thought that winter wheat crops that are sown from mid-October can escape *C. pumilionis* attack, since the second-generation adults will have finished laying eggs by the time the crop emerges (Derron and Goy 1990; Lilly 1947); however, this assumption is based on outdated observations and requires revalidation as agronomic practices and climate have changed significantly since this was suggested.

Currently, there are no chemical control methods approved for *C. pumilionis* management in the UK. Therefore, predicting risk and developing cultural control methods (such as growing a sufficiently robust crop capable of tolerating damage) represent the main management options available to growers.

3.4.2. Overview of current thresholds

There have been two thresholds proposed for *C. pumilionis*. For winter wheat the proposed threshold in the UK is the presence of *C. pumilionis* eggs on 50% of plants at GS12, however there is no scientific basis for this (Ramsden et al. 2017). In Switzerland, a threshold of 15% of tillers infested with eggs has been proposed for spring wheat (Derron and Goy 1990).

3.4.3. Overview of current predictive models that can help estimate crop risk

The prediction of adult gout fly emergence would be a useful tool for agronomists and farmers. An adult emergence model has been developed in Switzerland (Derron and Goy 1990). This model predicts emergence of the spring generation using accumulated degree days from January 1, with a baseline degree days temperature of 4.5°C. If validated further, this model could assist in timing monitoring efforts at the period of adult emergence, which could then be used to estimate the potential size of the pest population. Due to phenological differences between *C. pumilionis* generations, it is unlikely that this model would accurately predict emergence of the second generation of adults in late summer. For example, adult emergence and egg laying for the first generation are highly correlated and occur in quick succession compared to the second generation (Derron and Goy 1990; Lilly 1947).

3.4.4. Assessing the appropriateness of the current threshold

The current thresholds for *C. pumilionis* are 15% of tillers infested (spring wheat) and 50% of tillers infested (winter wheat; Table 1). It is possible to theoretically test the appropriateness of these thresholds through a series modelling scenarios, as achieved previously for the wheat bulb fly (Leybourne et al. 2022). Below, we detail two theoretical scenarios where we tested spring wheat and winter wheat under three levels of larval infestation: 50%, 75%, and 100% infestation.

For the winter wheat threshold, we used a wheat shoot number prediction model (Leybourne et al. 2022) to predict the number of shoots m^{-2} for a typical wheat crop drilled in October at three different plant population levels: low (150 plants m^{-2}), medium (250 plants m^{-2}), and high (350 plants m^{-2}). The number of shoots lost to *C. pumilionis* was assumed to be one per plant. Any plant with eggs on at GS12 is assumed to lose one tiller to *C. pumilionis*. Which tiller is lost depends on what growth stage the plant is infested at: If infested early at GS12 then the main shoot is the most likely shoot to be lost, later infestations mean that later formed tillers will be vulnerable to loss. This is because there is only one shoot at GS12, and while only 65% of gout fly eggs are likely to become shoot damaging larvae and eggs are laid individually, there can be several eggs on each plant (Bryson et al., 2005). Therefore, the risk of at least one egg becoming a shoot damaging larva was assumed to be 100%.

The wheat shoot number model was used to estimate the impact of losing either the main shoot, or any of the primary tillers produced up to GS25. While *C. pumilionis* infested shoots don't necessarily die (Gratwick 2012), we take a cautious approach and assume that an infestation results in the loss of one tiller, including all subsequent tillers developing from the infested shoot. This cautious approach ensures that we are testing the thresholds under a worst-case scenario, thereby ensuring there is a relatively conservative level of insurance built into the estimations. Where the shoot number falls below 400 shoots m^{-2} at GS31 it is assumed that the crop will not be able to achieve its potential yield. If the shoots m^{-2} fall to between 400 and 500 shoots m^{-2} then the crop might be able to achieve a moderate potential yield of about 8 t ha^{-1} (Spink et al. 2000b; Spink et al. 2000a).

For all nine larval infestation and plant population scenarios, our modelling indicated that losing one of the second or subsequent primary tillers would be unlikely to affect yield as the number of shoots m^{-2} produced by GS31 would be > 500 shoots m^{-2} in all cases (Table 2). Where the main shoot was lost, the same was observed for medium and high plant populations with infestation levels of 50%, however our modelling scenario indicated that low plant populations might struggle to reach the potential yield in this scenario. If 75% of plants were to be infested at GS12 and the main shoot lost, a low plant population is unlikely to reach its potential yield, and average plant populations may also struggle to reach their potential yields. In a theoretical worst-case scenario where 100% of plants are infected with gout fly and the main shoot lost, none of the plant population levels tested are likely to reach their potential yield if the main shoot is infested (Table 2), and the low plant population may also struggle to reach its potential yield if the first primary tiller is infested (i.e. around GS21). These scenarios have been calculated assuming there is no additional secondary tillering to compensate for the lost shoots, but we acknowledge that this might happen due to the damage coming so early in the crop development (~GS12), which may reduce the risk of yield loss to gout fly (Bryson et al. 2005).

Table 2: The number of remaining shoots (shoots m^{-2}) produced by GS31 for three different plant populations (low, medium and high), and three different levels of larval infestation (a. 50%, b. 75% and c. 100% plants infested) scenarios for winter wheat. Red cells indicate shoot numbers below 400 shoots m^{-2} (high risk of yield loss). Orange text indicates shoot numbers between 400-500 shoots m^{-2} (moderate risk of yield loss). Values that are not highlighted are expected to produce the potential yield.

Plants m^{-2}	**Shoots with no damage**	**Main Shoot lost**	**1st Primary Tiller lost**	**2nd Primary Tiller lost**	**3rd Primary Tiller lost**	**4th Primary Tiller lost**	**5th Primary Tiller lost**
50% larval infestation (number of shoots remaining, shoots m^{-2})							
150	701	477	567	621	657	675	675
250	878	597	710	777	822	845	845
350	961	656	777	851	900	925	925
75% larval infestation (number of shoots remaining, shoots m^{-2})							
150	701	364	499	580	634	661	661
250	878	457	625	727	794	828	828
350	961	503	684	795	869	906	906
100% larval infestation (number of shoots remaining, shoots m^{-2})							
150	701	252	432	540	612	648	648
250	878	316	541	676	766	811	811
350	961	350	592	740	838	888	888

In spring wheat crops, the risk period for *C. pumilionis* damage is GS31-37 (Derron and Goy 1990). By this growth stage, the maximum number of shoots will have been produced by the crop, and therefore the impact on total shoot number is likely to be lower because destroying a shoot does not result in the death of tillers that later form from this shoot. The possible impact on shoot number is summarised in the scenarios outlined in Table 3. In the spring crop scenario, it is assumed that eggs are laid on separate shoots (because gout fly eggs are laid individually (Frew 1924; Gratwick 2012)), and approximately 65% of gout fly eggs are likely to become shoot damaging larvae.

Table 3: The number of shoots m^{-2} remaining after gout fly damage in spring sown wheat crops for a range of shoot numbers and gout fly egg numbers

Shoots m^{-2} at GS31	50 eggs m^{-2}	100 eggs m^{-2}	150 eggs m^{-2}	200 eggs m^{-2}
500	468	435	403	370
600	568	535	503	470
700	668	635	603	570

The threshold for *C. pumilionis* in winter wheat is currently 50% of plants infested at GS12 (Ramsden et al. 2017). This matches the prediction for low plant populations in our tested scenario, assuming the main shoot is infested. However, our hypothetical scenario suggests that for average and high plant populations, it may be possible to increase the threshold to a higher infestation level. This is supported by Bryson et al. (2005) who found infestation levels of up to 50% of plants caused no significant reduction in yield. It is also expected that crops sown earlier will have greater tolerance to *C. pumilionis* damage because more of their tillers have been produced at the time of infestation. Further research is needed to accurately identify a threshold level for average and high plant populations.

3.4.5.Incorporating crop physiology to develop a tolerance scheme for C. pumilionis

Our theoretical test of the current threshold above indicates that the current thresholds could be increased for winter wheat crops. As *C. pumilionis* are stem-boring pests that occur during the early stages of winter wheat growth, it is also possible to incorporate crop tolerance into pest management schemes by calculating the economic injury level and developing a crop sufficiently capable of tolerating anticipated infestation levels (Stern et al. 1959). To achieve this, we employed an approach previously used for a similar stem-boring pest, the wheat bulb fly (Leybourne et al. 2022).

The following factors determine how much damage a cereal crop can sustain from a stem-boring pest before the damage becomes economically damaging. These factors can be used to provide a more comprehensive estimation of economic thresholds for the target pest, as was previously reported for the wheat bulb fly (Leybourne et al. 2022):

1. The number of shoots a larva can destroy
2. The minimum number of fertile shoots a crop requires to achieve a yield potential
3. The maximum number of shoots a crop is expected to produce in winter
4. Viability of the herbivorous insect eggs

These factors can be used to revise the economic thresholds using Equation 1.

$$EIL = \frac{(SN - SN_{MIN})/SN_{KILL}}{Egg\ Viability}$$

Equation 1: Economic Injury Level (EIL) equation used to estimate wheat tolerance against stem-boring insects. SN = the number of shoots per m^{-2} in winter, SN_{MIN} = the minimum number of fertile shoots m^{-2} required to achieve a yield potential, SN_{KILL} = the number of shoots killed by an individual larva, and Egg Viability the proportion of eggs that develop into larva.

In order to update the gout fly threshold (i.e., predict the number of wheat shoots needed to tolerate a *C. pumilionis* infestation) we estimated the above factors in addition to the average number of eggs laid per m^{-2} by a *C. pumilionis* adult. For the number of shoots a single *C. pumilionis* larva can destroy, it is well reported that *C. pumilionis* larvae only infest and pupate within one tiller (Gratwick 2012). So this value remains at one and is not adjusted during our EIL calculations.

For the minimum number of fertile shoots a crop requires to achieve a potential yield, Spink et al. (2000b) found that 400 shoots m^{-2} are required to achieve a potential yield of 8 t ha^{-1}, however to provide insurance against achieving too few shoots 500 shoots m^{-2} was used when reviewing the *D. coarctata* thresholds (Leybourne et al. 2022).

We estimated the egg viability of *C. pumilionis* at 0.65 (range: 0.3-1). This was based on previous research (Frew 1924) where the egg viability was estimated to be 59% (range: 26% - 94%), we estimated a higher egg viability as *C. pumilionis* eggs hatch relatively quickly when compared with other stem-boring insects with a similar estimated viability (e.g., *D. coarctata*).

Using the estimated values described above, Fig. 3 demonstrates the EIL for *C. pumilionis*, created by adjusting each parameter from its likely minimum value to its maximum value. It should be recognised that this approach is likely to overestimate the EIL (number of eggs needed to cause economic injury) because it assumes that each larva only kills one shoot in total, but doesn't account for the death of any additional shoots that would have formed from the injured shoot. The approach used could be applied more realistically to the impact of C. *pumilionis* on spring wheat because this crop is usually infested after tillering is complete, so the death of one shoot will not impact on the subsequent formation of later shoots. Of the three parameters tested (minimum ears m^{-2}, maximum shoots m^{-2} and egg viability) the number of shoots m^{-2} has the greatest influence on the EIL threshold which could be as low as 154 eggs m^{-2} for a shoot number of 600 shoots m^{-2} or as high as 1692 eggs m^{-2} for a shoot number of 1600 of shoots m^{-2}. In contrast, the EIL threshold ranges from 1,667 eggs m^{-2} for an egg viability of 0.3, to 500 eggs m^{-2} for an egg viability of 1. Therefore, even if all eggs survive, shoot number still has the greatest influence on the EIL.

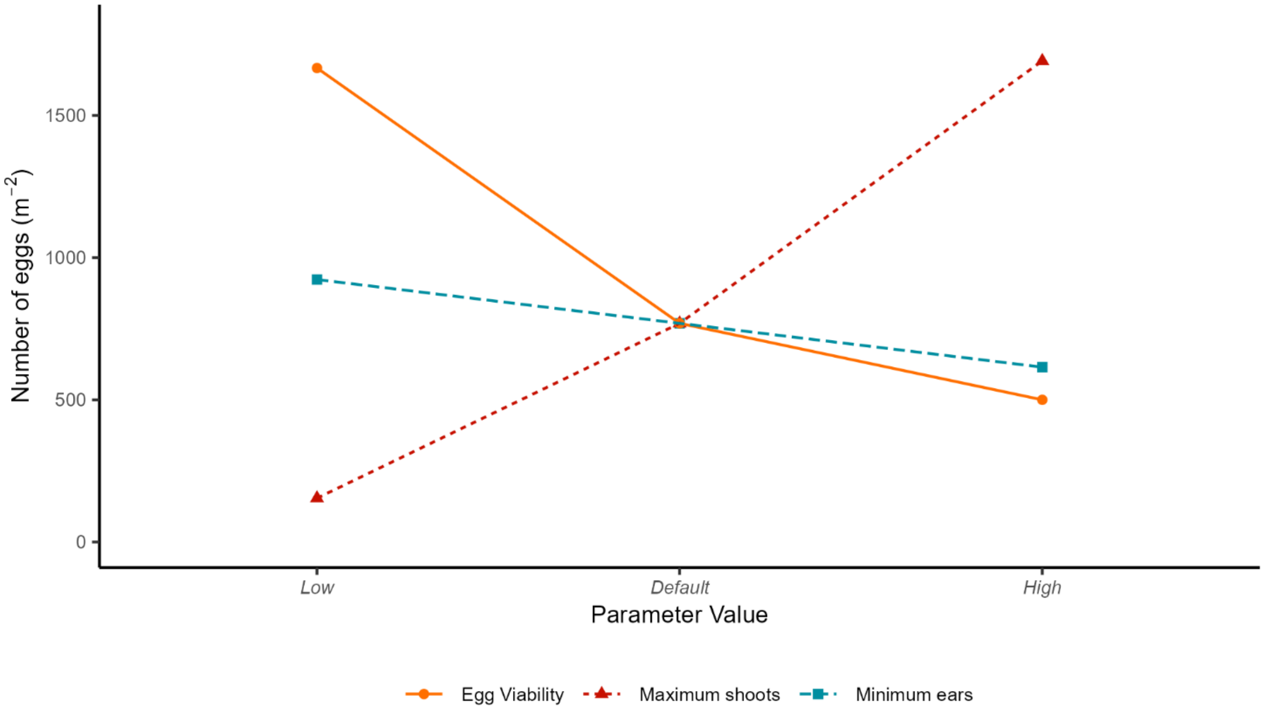
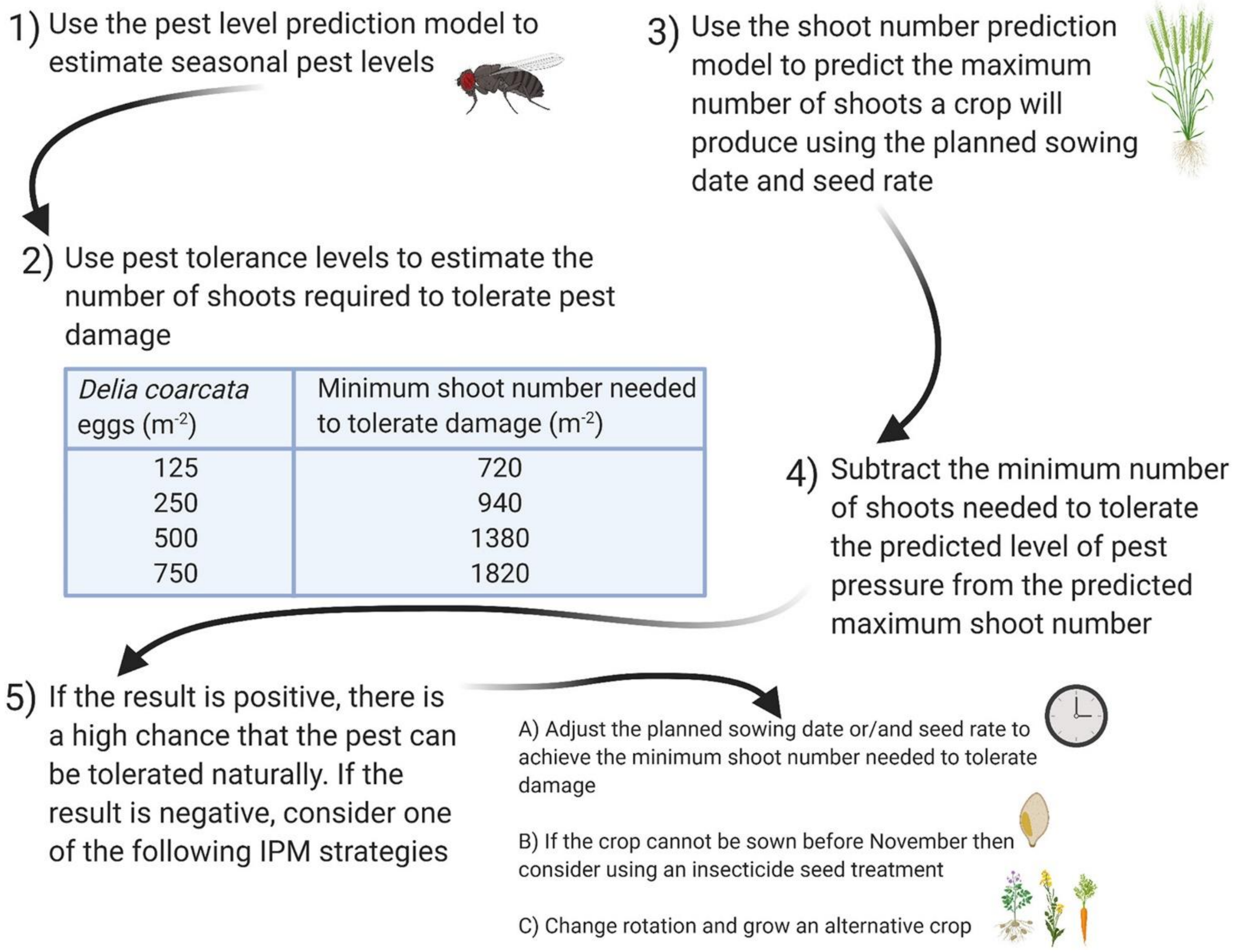


Fig. 3: Economic injury level sensitivity analysis for gout fly, *C. pumilionis*

3.4.6.Proposed areas for improvement and future development

Future research should focus on testing and validating the proposed *C. pumilionis* tolerance scheme for autumn and spring sown wheat, developing a prediction model that can estimate seasonal risk of *C. pumilionis*, and integrating these into a threshold-based pest tolerance scheme, as done recently for *D. coarctata* (Fig. 4).



1) Use the pest level prediction model to estimate seasonal pest levels

2) Use pest tolerance levels to estimate the number of shoots required to tolerate pest damage

Delia coarcata eggs (m^{-2})	Minimum shoot number needed to tolerate damage (m^{-2})
125	720
250	940
500	1380
750	1820

3) Use the shoot number prediction model to predict the maximum number of shoots a crop will produce using the planned sowing date and seed rate

4) Subtract the minimum number of shoots needed to tolerate the predicted level of pest pressure from the predicted maximum shoot number

5) If the result is positive, there is a high chance that the pest can be tolerated naturally. If the result is negative, consider one of the following IPM strategies

A) Adjust the planned sowing date or/and seed rate to achieve the minimum shoot number needed to tolerate damage

B) If the crop cannot be sown before November then consider using an insecticide seed treatment

C) Change rotation and grow an alternative crop

Fig. 4: A graphical overview of the *D. coarctata* threshold-based pest tolerance scheme proposed in Leybourne et al. (2022). Image reproduced with permission. Original image created with BioRender.com

4. Conclusion: Towards physiological-based thresholds

Here we have reviewed important information relevant to the determination of thresholds for a range of important insect pests affecting wheat crops. For each insect, we review the period of crop risk, the current thresholds, available prediction models, and highlighted focal areas for future research. This illustrates the large potential for improving economic thresholds for the invertebrate pests of wheat. Crop tolerance is a key component that could be used to improve thresholds, and we propose that this should be explored for three of these pest insects: *H. marginata*, *C. pumilionis* and aphids causing direct feeding damage. For *C. pumilionis* we conduct a theoretical test of the current thresholds, with our results suggesting that the current threshold for winter crops is likely too conservative, and carry out a preliminary assessment of the viability of developing a tolerance-based insect management scheme for *C. pumilionis*, similar to a previous scheme developed for the wheat bulb fly (Leybourne et al. 2022). It is important to emphasise that at the moment these are purely theoretical updates and future research projects should focus on testing and validating these.

We also note a knowledge gap in fundamental factors that can influence both the risk of a given herbivorous insect as well as agronomic and crop physiological factors that will likely influence the level of damage that can be tolerated. These include considerations of varietal tolerance and incorporation of more robust economical consideration (such as treatment costs) into the management processes. We highlight these as additional areas worthy of future research, especially as crop production moves towards more holistic practices. The introduction of varietal considerations into the development of future thresholds is increasingly important as growers are provided with a greater varietal choice, including varieties with resistance or tolerance to specific herbivorous insects: for example orange wheat blossom midge resistant varieties (McKenzie et al. 2002; Thomas et al. 2005; Blake et al. 2011) and BYDV tolerant varieties (Jarošová et al. 2016; Will et al. 2021).

5. Declarations

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5.2. Conflicts of Interest

The authors have no conflict of interests to declare. Funders had no role in the design or conduct of the study.

5.3. Ethics approval

Not applicable.

5.4. Consent to participate

Not applicable.

5.5. Consent for publication

Not applicable.

5.6. Availability of data and material

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

5.7. Code availability

Not applicable: No datasets were generated or analysed during the current study.

5.8. Authors’ contributions

Conceptualisation: DJL, KES, PMB, SW; Funding Acquisition: DJL, PY, SW; Literature Search and Investigation: AM, NM, ST, LA, SW, SE, PMB, KES, DJL; Synthesis: DJL, KES; Writing – Original Draft: DJL; Writing – Critical Revisions and Edits: KES, PMB, SW, PY; Visualisation: DJL. All authors read and approved the final manuscript.

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