The Crop Journal 10 (2022) 1528–1535

Contents lists available at ScienceDirect

The Crop Journal

journal homepage: www.keaipublishing.com/en/journals/the-crop-journal/

Wheat breeding for Hessian fly resistance at ICARDA

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ARTICLE INFO

Article history:
Received 11 April 2022
Revised 22 July 2022
Accepted 25 July 2022
Available online 13 September 2022

Keywords:
Breeding
Gene introgression
Hessian fly
Resistance

ABSTRACT

Hessian fly (HF), *Mayetiola destructor* (Say) is an important pest of wheat in North Africa, North America, Southern Europe, Northern Kazakhstan, Northwestern China, and New Zealand. It can cause up to 30% yield losses and sometimes can result in complete crop failure if infestation coincides with young stage of the wheat crop. Studies to-date have shown the availability of genetic diversity in the wheat genetic resources (landraces, wild relatives, cultivars, etc.) for resistance to Hessian fly. About 37 resistance genes have been reported from these wheat genetic resources for resistance to Hessian fly, of which, some have been deployed singly or in combination in the breeding programs to develop high yielding varieties with resistance to HF. Deployment of resistant varieties in different agro-ecologies with other integrated management measures plays key role for the control of HF. This paper summarizes the importance, life cycle, mechanisms of resistance, gene mining, and wheat breeding efforts for HF resistance.

Contents

1. Introduction

The name Hessian fly (*Mayetiola destructor*) is associated with the Hessen region of Germany, even though it is originated from the middle East. Currently, it is a destructive pest of wheat in North Africa, North America, Southern Europe, Northern Kazakhstan, Northwestern China, and New Zealand. Heavy populations are detected regularly in North America and western Mediterranean countries. In North Africa, especially in Morocco, grain yield losses have been estimated up to 36% [1].

A complete crop failure can occur if infestation coincides with young stage [2]. HF can be controlled using several integrated pest management (IPM) options that mainly consists of cultural, chem-

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https://doi.org/10.1016/j.cj.2022.07.021

ical, biological and genetic control methods [3]. Crop rotations, plowing of stubbles after harvest, removing and destroying volunteer wheat, nice seed bed preparation which helps early vigor establishment, application of chemicals, use of HF resistant wheat varieties, planting at the "HF free dates" are the most practical solutions. Chemical treatment is not an eco-friendly approach for the control of Hessian fly and hence it is not widely recommended. The use of resistant varieties in combination with early planting dates is the best method to control the menace of HF destruction, though planting date in the rainfed areas of Morocco is governed dominantly by the onset of rainfall in November/December.

2. Biology and life cycle of HF

Hessian fly belongs to the Cecidomyiidae family [4,5], one of the largest families within the Order of true flies (Diptera). Hessian fly adults do not feed and do not live long. HF female can lay 100–400 eggs on the adaxial surfaces of tender leaves in a short time (several hours up to 1 day). Eggs will hatch within 3–4 days at 20 °C. The newly hatched larvae will crawl down to the base of the leaf sheath and feeds on the stem above the crown for 2–3 weeks of its lifetime before it pupates. It is entirely the first- and second-instar larvae that causes damage by injuring the stem which leads into stunted growth, lodging, stem breakage and failure or few seed production [6,7]. The adult male and female flies, which in fact live only for few days (1–4 days), will mate and the cycle continues with the female laying eggs on the leaves [8,9]. The complete life cycle of HF takes 40–50 days (Fig. 1). However, after the second instar larvae reaches flaxseed stage, it could remain dormant for about 3–4 months whereby it overwinters and emerges in spring or over-summers in wheat stubble and emerges during the fall. Depending on environmental field conditions, Hessian fly can complete 2–3 generations/year [10,11].

Studies on the feeding mechanism of HF showed that through the mandibles, the larva injects salivary fluids containing enzymes and effector proteins into plants. Such molecules restrict plant growth and makes the cell wall permeable which in turn enables the larvae to suck the juice from the wheat leaf sheath and stem [12–14]. Infestation can happen during fall or spring. In case of severe HF infestation in the fall, the seedlings stunt heavily, become less winter hardy with few or no secondary tillers and eventually the whole plant dies immediately after the maturity of the larvae. If the infestation occurs in the spring, the larvae feeds on the area above the node between the leaf sheath and the stem. This inhibits stem elongation and nutrient transportation to the emerging spike and eventually results in poor seed production or stem breakage which even might resemble with hail damage [15]. In the early stage, the larvae can be examined by pulling out plants and peeling down the leaves at the base of the leaf sheath or at the point of attachment with the stem into the feeding site where the larva or flaxseed is located. Larvae can also be found in the internodes or lodged stems if infestation occurs in the older stage of the plant.

3. Categories of resistance to HF

Crop plants have different mechanisms to protect themselves from insect attacks. These mechanisms are classified in three categories.

3.1. Antixenosis

Antixenosis or non-preference is a modality that encompasses mechanisms of the plant which helps to protect itself from occupation or colonization by the insect [16]. Antixenosis can be considered as the first line of defense in plants against an insect damage. Plants that exhibit antixenotic resistance should have a reduced initial number of colonies early in the season. The mechanism could be antixenosis against oviposition or feeding [17]. Plants with pubescence such as hairiness of the foliage and or vascular bundles are able to deter insects with piercing and sucking

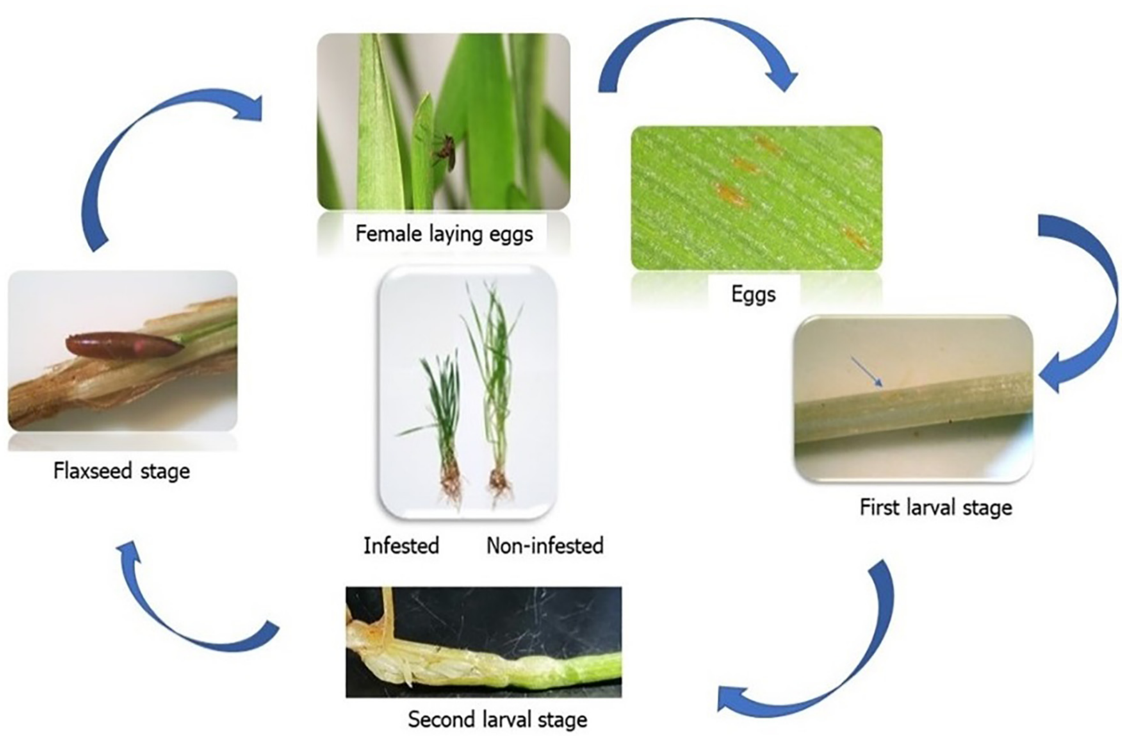

Fig. 1. Life cycle of Hessian Fly.

mouth parts. The simple trichomes deter oviposition and feeding by preventing the insect's ovipositor or proboscis from reaching the plant epidermis [18]. Pubescent wheat cultivar 'Vel' exhibits antixenosis to adults and larvae of the Hessian fly [19]. Hessian flies used their chemical, visual, and tactile senses to locate and identify host plants. Changes in information received by any of the three sensory modalities resulted in major reductions in the number of eggs laid on a treated substrate. In addition, significant interactions were observed when chemical, color, and tactile cues were combined [20].

3.2. Antibiosis

The primary resistance mechanism for HF is antibiosis [21]. Antibiosis genes in a wheat variety result in poor survival of larvae as they initiate feeding on the resistant plants. Generally, resistance is conferred by partially or completely dominant single genes and is manifested as larval antibiosis.

To date, 37 R genes against HF, have been identified in wheat and its wild relatives [22,23]. All 37 R genes are dominant except *h4*, which is recessive, and all are single effective genes except for *H7* and *H8*, which are two linked genes conferring resistance when they are together. No Hessian fly R gene in wheat has been cloned yet [24,25].

Hessian fly larvae become physically inactive in resistant wheat genotypes after 4–5 days and eventually die before developing into second instars [26,27]. Campos-Medina et al. [28] showed that larvae capable of generating compatible interactions successfully manipulated host plant chemical and morphological composition to susceptible plants and to create a more hospitable environment. Incompatible interactions (resistant plants to HF) resulted in lower host plant nutritional quality, thicker leaves, and higher phenolic levels using the spectral measurements techniques. Different types of defensive, toxic chemicals such as protease inhibitors, reactive oxygen species, toxic lectins, and secondary metabolites were induced specifically in resistant plants upon Hessian fly larval infestation [29,30].

Chen et al. [24] showed that genes involved in nutrient metabolism, RNA and protein synthesis exhibited lower transcript abundance in larvae from resistant plants, indicating that resistant plants inhibited nutrient metabolism and protein production in larvae. The same study identified several families of genes encoding secreted salivary gland proteins (SSGPs) that were expressed at the first instar larvae and with more genes with higher transcript abundance in larvae from resistant plants. Those SSGPs are candidate effectors with important roles in plant manipulation [24].

3.3. Tolerance

Tolerance is the plant's ability to maintain its fitness after insect damage through reproduction and growth [31]. Tolerance may also include compensation, or allowing regrowth, compared to a susceptible host with a similar population of pests [32]. Plant-insect interactions are highly dependent on the host plant, which will determine the tolerance level of the genotype. Tolerance relates to an insect's effect on a plant where a greater tolerance level results in less damage to the plant [33]. Tolerance also relates to the plant's response to insect injury through recovery and growth [34]. In wheat, an example of such mechanism is the ability of plants to tiller after seedlings being attacked by Hessian fly larvae. Of the three resistance categories, tolerance is perhaps the most difficult to identify since it requires more precise quantification of plant responses to the insect, preferably over a range of insect densities. On the other hand, tolerance theoretically places less selection pressure on the insect population relative to antixenosis and antibiosis [34].

Very little research has focused on HF tolerance in wheat. The hard-red spring wheat line 'Superb' can decrease yield loss from HF infestations by up to 65% compared to susceptible lines due to the partial tolerance and antibiosis present in the line [35]. This tolerance trait was explained as the ability of wheat stems to survive larval feeding without snapping [35]. The tolerant wheat line Pioneer brand variety 25R78 experienced significantly more leaf growth, biomass, and tillers versus the susceptible line infested with at least one Hessian fly larva. In Morocco, the bread wheat cultivar 'Massira' (unknown gene) which was released in 1994 has been reported to have some level of tolerance to Hessian fly. The successful regrowth and compensation of a tolerant variety depends on the availability of enough moisture/rainfall, which is one of the important limiting factors for wheat production in the rainfed environments such as Morocco [33].

4. Hessian fly biotypes

HF populations are constantly evolving in the field owing to genetic adaptation mechanisms formed in the long course of wheat-Hessian fly co-evolution [36] following a gene-for gene relationship between pest virulence and host plant resistance. The deployment and extensive use of resistant wheat varieties with the same resistance genes leads to the emergence of new virulent HF genotypes (biotypes) and hence the boom-and-bust cycle continues [37]. The presence of virulent Hessian fly biotypes has been reported for several wheat resistance genes. In the United States, 16 biotypes (GP and A to O) have been identified on the basis of their differential response to the resistance genes *H3*, *H5*, *H6*, and a gene combination *H7*/*H8* in wheat [38]. In Morocco, 10 resistance genes (*H5*, *H7*, *H8*, *H11*, *H13*, *H14*, *H15*, *H21*, *H22*, *H23*, *H25*, *H26*) were reported to be effective in addition to those from other uncharacterized sources [39,40]. Significant difference in the frequency of virulence among HF populations collected from the principal cereal-growing regions in Morocco was reported against *H5*, *H13* and *H22* genes indicating that a true virulence (biotype) is developing in Hessian fly populations in Morocco [41] which signifies the importance of continuous monitoring of the development of HF biotypes for designing effective gene pyramiding and cultivar deployment strategies.

5. Identification and introgression of HF resistance genes

The screening procedure that ICARDA follows is similar to the methodology described by Cartwright and LaHue [42]. Screening for Hessian fly can be carried out in hotspots in the field under natural infestation but also in the greenhouse. In the field, planting date needs to be adjusted so that 1–2 leaf stage of the crop coincides with the emergence of the flies. For example, in North Africa, a delayed planting date creates strong HF pressure on wheat plants. Fifteen seeds of each entry including the susceptible and resistant checks are usually sown in rows in standard plastic flats ($54 \times 36 \times 8$ cm) containing a mixture of soil and peat. After germination, the plants are covered with a mesh cloth, and about 50 mated females are released and allowed to lay eggs in each flat. Evaluation of resistant genotypes is usually made 3–4 weeks after infestation in the greenhouse or when the symptoms are clearly seen on the susceptible check. Susceptible plants show stunted growth and dark green color and contain live larvae, whereas the resistant plants exhibit normal growth and normal light green color and contain dead first-instar larvae. Following these procedures, wide arrays of wheat germplasm have been screened both in the field under natural infestation and in the greenhouse using

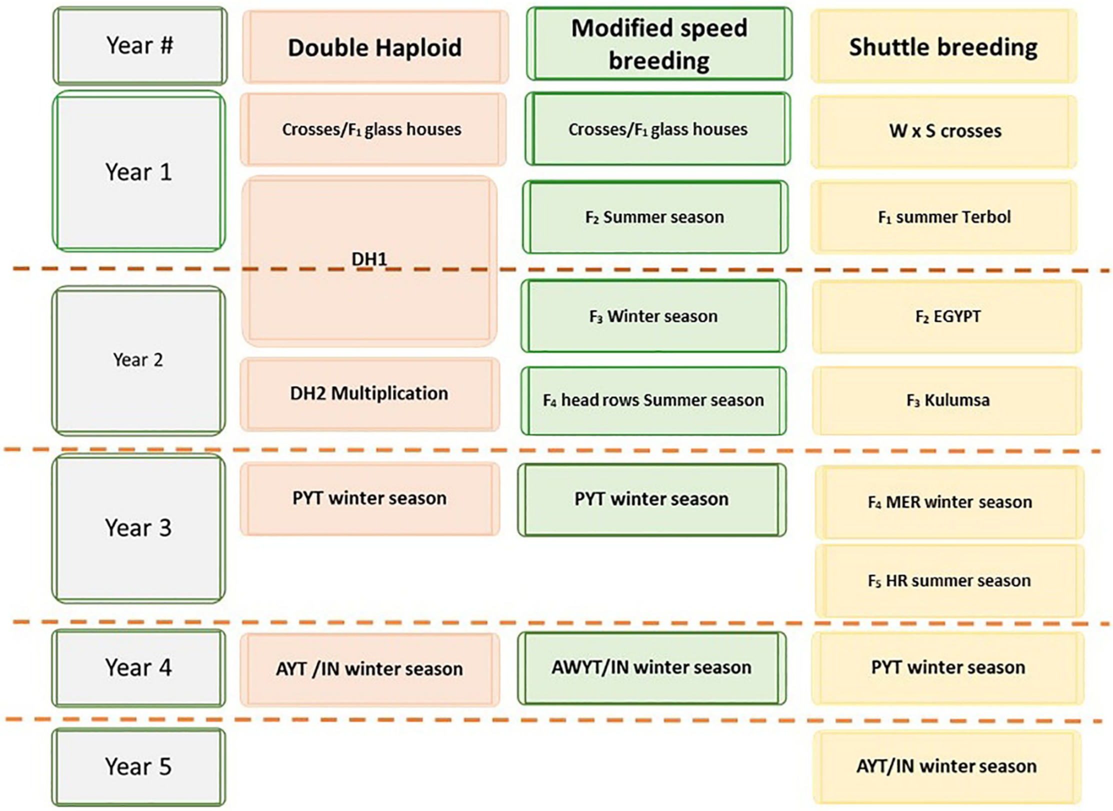

Fig. 2. Wheat breeding schemes at ICARDA. The doubled haploid scheme is used mostly for winter wheat breeding at Terbol, Lebanon station of ICARDA. For the modified speed breeding, elite × elite crosses and F_1s are managed in the greenhouse and segregating generations and head-rows are evaluated in the field at ICARDA- Merchouch research Station, in Morocco using summer × winter shuttle approach. Elite genotypes at F_6 stage evaluated across key locations for yellow and stem rusts resistance at Kulumsa (Ethiopia) and Izmir (Turkey), for heat tolerance at Wadmedani (Sudan) and for root diseases, drought tolerance, HF resistance at Merchouch and Sid Al Aydi stations in Morocco (Fig. 3).

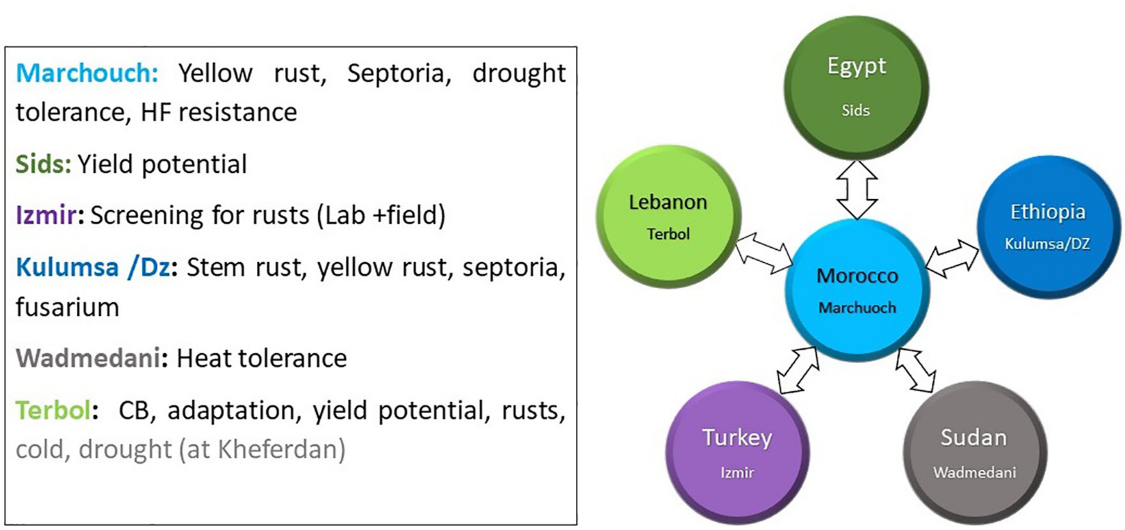

Fig. 3. Key locations for ICARDA's bread wheat breeding program.

artificial infestation. Many resistance genes against HF have been reported. To date, a total of 37 have been reported in wheat (Table S1) [42,43]. Most of the resistance genes for Hessian fly were identified from *Triticum aestivum* accessions such as Grant, Patterson, 86981RC1-10–3, 8268G1-19–49, KS89WGRC3 (C3), and KS89WGRC6 (C6). *Aegilops tauschii* accessions have been identified as excellent sources of Hessian fly resistance genes such as *H13*, *H22*, *H23*, and other insects including Greenbug *Schizaphis graminum* (Rondani) and Russian wheat aphid *D. noxia* [23,42,44]. Rye (*Secale cereale*) has been reported as the source of *H21*, *H25*, *Gb2* and *Gb6* for Greenbug while *Aegilops triuncialis* has been reported as the source of *H30* gene [45].

Table 1
Synthetic derived elite spring bread wheat genotypes from ICARDA combining yield potential, yellow rust (YR) resistance and 100% resistance to Hessian fly at Merchouch, Morocco, 2020.

No.	Name/Pedigree	Days to heading	Days to maturity	Plant height (cm)	Thousand-kernel weight (g)	Yield (t ha^{-1})
1	MUNAL #1/4/GIZA-168//SHUHA'S'/'O'UC'S'/'/'ESTONIA SR 24 + SR 26/7/WBLL1*2/4/YACO/PBW65/3/KAUZ*2/TRAP//KAUZ/5/KACHU #1/6/TRCH/SRTU//KACHU	108	159	113	36	8.397
2	MUNAL #1/4/GIZA-168//SHUHA'S'/'O'UC'S'/'/'ESTONIA SR 24 + SR 26/7/WBLL1*2/4/YACO/PBW65/3/KAUZ*2/TRAP//KAUZ/5/KACHU #1/6/TRCH/SRTU//KACHU	110	159	111	33	8.022
3	HUBARA-8/3/MON'S'/'L''S'/'B'W'S'/'/'R 22/CO 1213/5/05 W90045 U.S.A.-08CJ/PAVON SR 24 + SR 26 + SR 31/6/MON/IMU//ALD/PVN/3/BORL95/4/OASIS/2*BORL95/5/HUW234 + LR34/PRINIA//PBW343*2/KUKUNA/3/ROLF07/7/KRICHAUFF/2*PASTOR//SHUHA-8/DUCULA	110	160	116	33	7.790
4	ATTILA*2/RAYON//CATBIRD-1/3/AVYR 5 + 18/4/MILAN/MUNIA//SR 33 + SR 45 #23/5/PASTOR-6/6/QIMMA-12/REBWAH-13/3/NG8675/CBRD//MILAN/5/BABAX/LR42//BABAX*2/3/PAVON 7S3, +LR47/4/MELON//FILIN/MILAN/3/FILIN	101	160	100	37	7.527
5	PRL/2*PASTOR//SERI/4/MILAN/KAUZ//PRINIA/3/BABAX/5/AGT-YOUNG/6/KAMB2/PANDION	99	159	120	35	7.435
6	TERBOL/4/THELIN/WAXWING//ATTILA*2/PASTOR/3/INQALAB91*2/TUKURU 9Y-0B/5/BACANORA T 88/RUTH-2	95	154	107	35	7.315
7	DAJAJ-5/4/CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/3/KAUZ/8/WBLL1*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/5/KACHU/6/TRCH/SRTU//KACHU/7/DOY1/AE.SQUARROSA (447)/3/2*KA/NAC//TRCH	100	159	107	39	7.313
8	HEILO/3/OASIS/SKAUZ//4*BCN/7/ATTILA/4/WEAVER/TSC//WEAVER/3/WEAVER/5/ATTILA/HEILO/6/BABAX/LR42//BABAX/3/BABAX/LR42//BABAX	109	160	110	37	7.098
9	SERI.1B//KAUZ/HEVO/3/AMAD/4/HXL8246/KAUZ/6/REYNA-4//KAMB2/PANDION/5/PRL/2*PASTOR//SERI/4/MILAN/KAUZ//PRINIA/3/BABAX	107	160	116	35	7.082
10	HEILO/MIRIAM 41/6/02 W50807/5/PSN/BOW//SERI/3/MILAN/4/ATTILA	99	160	105	42	7.067
11	AMIRA-2//CHAM-6/SHUHA-14/3/SAMIRA-9/5/MILAN/KAUZ//PRINIA/3/BAV92/4/BAVIS	106	160	117	35	7.052
12	HEILO/3/SW89.5277/BORL95//SKAUZ/4/QUAIU*2/KINDE	108	160	104	41	7.050
13	02 W50807/RSMF8 704/5/BABAX/LR42//BABAX/3/BAVIACORA/4/HEILO	101	159	110	35	6.848
14	TUJAR/4/THELIN/WAXWING//ATTILA*2/PASTOR/3/INQALAB91*2/TUKURU 9Y-0B/5/DUCULA/2*PRINIA/4/SAFI-1//NS732/HER/3/SAADA	100	159	104	37	6.832
15	02W50807_1/4/PFAU/SERI.1B//AMAD/3/WAXWING/5/WBLL1*2/BRAMBLING//NIINI #1/3/VILLA JUAREZ F2009	100	160	100	38	6.800
16	ATTILA/3*BCN/3/CROC_1/AE.SQUARROSA (224)//OPATA/6/2*KAUZ//ALTAR 84/AOS/3/PASTOR/4/MILAN/CUPE//SW89.3064/5/KIRITATI/7/DOY1/AE.SQUARROSA (447)/3/2*KA/NAC//TRCH	110	160	110	36	6.725
17	TUJAR/4/THELIN/WAXWING//ATTILA*2/PASTOR/3/INQALAB91*2/TUKURU 9Y-0B/5/DUCULA/2*PRINIA/4/SAFI-1//NS732/HER/3/SAADA	106	160	105	33	6.718
18	02W50807_1/4/BL2064//SW89.5124*2/FASAN/3/TILHI/6/RAC 1192/5/2*ATTILA/4/WEAVER/TSC//WEAVER/3/WEAVER	108	160	102	33	6.682
19	Tesfa	109	169	100	35.3	8.02
20	Terbol	113	172	103	35.7	7.70
21	Atlas	110	169	105	39.6	7.10
22	Arrehane	101	156	101	31.25	4.31

Because of the co-evolution between wheat and insects, stacking of major R genes is very important for the development of durable resistance. This is mainly feasible for Hessian fly, since there are R genes clustered around the same chromosome intervals [43]. About 15 HF resistance genes were reported in close distances on the short arm of chromosome 1A (*H3*, *H5*, *H6*, *H9*, *H10*, *H11*, *H12*, *H14*, *H15*, *H16*, *H17*, *H19*, *H28*, *H29* and *Hdic)*; three genes on the long arm of chromosome 3D (*H24*, *H26*, *H32*) and three genes on the short arm of chromosome 6D (*H13*, *H23*, H_{WGRC4}). Some of these genes are tightly linked (*H9*/*H10* and *H26*/*H32*) and hence they can be easily introgressed simultaneously during the gene pyramiding process [16].

The resistance sources from wheat relatives and landraces do not have all the desired traits to be a variety by themselves. They can serve only as gene sources for the traits of interest such as insect resistance, drought and heat tolerance, disease resistance, etc. Introgression of such genes from wild relatives into common wheat is very difficult and requires efficient introgression techniques and approaches. Though there are successful natural gene introgressions as exemplified by wheat-rye translocations of 1BL.1RS and 1AL.1RS, which arose spontaneously from centromeric breakage and reunion, gene introgression/transfer in pre-breeding programs can be carried out using gene transfer through hybridization and chromosome mediated gene transfer approaches or through direct gene transfer using molecular approaches. The most successful and highly used gene introgression technique is the development of primary synthetic wheats ($2n = 6x = 42$, AABBDD) which is an amphiploidy developed by crossing the *T. turgidum* spp. *durum* ($2n = 4x = 28$, BBAA) with *Ae.* ($2n = 2x = 14$, DD) and chromosome doubling of the F_1 through colchicine treatment [83]. The primary synthetic wheats have served as a bridge to transfer important genes such as resistance to Hessian fly, aphids, Sunn pest and many other important genes for resistance to abiotic and biotic stresses [59,73,86–90].

Recently, Sabraoui et al. [91] showed that three synthetic hexaploidy wheat lines TRN/*Ae. tauschii* (700), GAN/*Ae. Tauschii* (248) and 68.111/RGBU//WARDRESEL/3/STIL/4/ *Ae. Tauschii* exhibited first combined resistance to both Moroccan Hessian fly and Syrian Sunn pest. In previous study, El Bouhssini et al. [92] reported that the level of resistance to Hessian fly in synthetic hexaploidy wheat ranged between 71% and 100%. To increase the efficiency of gene mining and gene introgression, identification and deployment of functional markers plays significant role. In this regard, KSAP markers are becoming more suitable in breeding programs since the cost per data point is low and it is convenient for medium to high throughput screening. KASP markers are available for *H32*, *h4*, *H7*, *H35*, and *H36* though they need to be validated before deploying them in marker assisted selection programs. Recently, two KASP markers, KASP-6B112698 and KASP-6B7901215, were recommended for marker assisted selection to deploy the HF QTL on 6BS (QHf.hwwg-6BS) [44].

6. Breeding for HF resistance

Breeding for insect resistance should be carried out in combination with other important traits targeting the regions where the insect pest is economically important. The wheat programs at ICARDA undertakes intensive characterization of parents for different traits such as yield potential, disease (root and foliar) resistance, heat and drought tolerance, insect resistance (Hessian fly, Sunn pest and Russian wheat aphid) and better nutritional quality. Once the progenitors are characterized, they are assembled in crossing blocks targeting the main challenges of the major wheat growing regions in developing economies. High yielding and adapted hall mark wheat cultivars representing the major agro-ecologies, synthetic derived hexaploidy wheats, and elite lines are included in the different crossing blocks. Simple, top and back-crosses are carried out commonly with the application of diagnostic markers for gene pyramiding in the F_2, F_1 top, and BC_1F_1 populations [93,94]. Selection of the segregating generation for different traits from F_2 to F_4 is carried out using the selected bulk or modified pedigree selection schemes as indicated (Fig. 2).

The bread wheat breeding program at ICARDA has utilized primary synthetic wheats intensively in the crossing program as sources of resistance for abiotic (heat and drought) stresses and biotic stresses (diseases and insects including HF) [87]. Out of the many released bread wheat varieties in Morocco, four varieties namely: Saada, Aguilal, Arrehane, and Snina are highly resistant to HF biotypes in Morocco [73,89].

Recently, as indicated in Table 1, elite genotypes with high yield potential, yellow rust resistance, drought and heat tolerance with 100% resistance to the Moroccan Hessian fly biotype have been identified and distributed to national programs in the CWANA region through ICARDA's international nursery distribution system for direct release and parentage purposes.

The HF genes in these wheat genotypes are not yet characterized though from the pedigree and the biotype information, it might be possible to expect that most of them may possess *H5* or *H22* genes.

Similarly, breeding programs in the USA have developed resistant varieties for the major insects such as Hessian fly, Russian wheat aphid, Greenbug, and Wheat stem sawfly. More than 60 Hessian fly resistant wheat varieties have been released in the USA between 1950 and 1983 and less than 1% yield loss have been reported in areas where resistant cultivars have been deployed [20,21].

7. Conclusions

Genetic diversity for resistance to biotic and abiotic stresses is the backbone for the success of any breeding programs. Studies to-date have shown the availability of sufficient genetic diversity in the wheat genetic resources (landraces, wild relatives, cultivars, etc.) for resistance to the most economically important insect pests such as Hessian fly. More than 37 resistance genes for HF have been identified from these genetic resources. Some of these genes have been deployed singly or in combination in the breeding programs to develop high yielding varieties with resistance to insects. Gene pyramiding using marker assisted selection is important to stack two or more resistance genes in an adapted cultivar in order to increase the durability of insect resistance. Breeding for tolerance traits would exert less selection pressure on insect pests to evolve the ability to overcome the deployed trait. It is also important to develop and deploy resistant varieties in a given agro-ecology instead of using a given variety across a large mega-environment along with integrated pest management options in order to slow down the development and spread of virulent biotypes of Hessian fly.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Wuletaw Tadesse: Visualization, Writing – original draft, Writing – review & editing. **Samira El-Hanafi:** Writing – review & editing. **Karim El-Fakhouri:** Writing – review & editing. **Imane Imseg:** Writing – review & editing. **Fatima Ezzahra Rachdad:** Writing – review & editing. **Zakaria El-Gataa:** Writing – review & editing. **Mustapha El Bouhssini:** Writing – review & editing.

Acknowledgments

This research was financially supported by the International Center for Agricultural Research in Dry Areas.

Appendix A. Supplementary data

Supplementary data for this article can be found online at https://doi.org/10.1016/j.cj.2022.07.021.

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