

# Global warming and increasing maize cultivation demand comprehensive efforts in disease and insect resistance breeding in north-western Europe

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## Abstract

Maize productivity is threatened by global climate change. Climate change scenarios suggest that north-western (NW) Europe will get warmer and drier during the main crop-growing period. In general, more northerly regions will benefit, whereas more southerly regions will suffer suboptimal rain-fed farming conditions. In these latter regions in particular, the resulting probable lower realized on-farm maize grain and biomass yields must be safeguarded. Breeding for resistance against already existing and emerging diseases and insect pests is one component to achieve yield stability across years. Durable multiple-disease resistance will become especially crucial. Herein, we focus on disease resistance breeding approaches in maize, especially related to north-western corn leaf blight and Fusarium ear rots, although virus and bacterial diseases will become more important as well. Continuous adjustments of disease resistance breeding strategies will be required. Insect pest resistance breeding must be improved considerably, as in a warmer world insects will thrive, probably causing detrimental direct (feeding, sucking, etc.) and indirect (vectors of pathogens, feeding wounds creating gateways for many pathogens, passive transport of inoculum across maize plants) effects. Four case studies on insects that are already prevalent in NW Europe or may be expected in the near future are covered in this review. Maize cultivars need to combine both durable multiple-disease and multiple-insect resistance, although the implementation of many different effective resistance resources in breeding programmes will be challenging, particularly if trade-offs among breeding goals appear.

## KEYWORDS

climate change, corn diseases, fungal pathogens, insect pests, resistance breeding, selection

## 1 | INTRODUCTION

Maize (*Zea mays*) contributes greatly to global food security. However, maize productivity is threatened by global climate change (Porter et al., 2019). For example, Lobell et al. (2011) reported that recent climate change between 1980 and 2008 has already reduced

the potential global maize production by about 3.8%, thereby countervailing some of the yield gains from breeding and other technological advances. In addition, maize is increasingly challenged by plant pathogens (Mueller et al., 2020), insect pests (De Groote et al., 2020), and other biotic and abiotic stress factors such as heat and drought (Cairns et al., 2012).

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In the European Union, maize is the second-most cultivated crop after wheat (*Triticum aestivum* subsp. *aestivum*, *T. turgidum* subsp. *durum*). In 2019, maize was cultivated on 8.9 million ha for grain maize and 6.4 million ha for silage (green) maize (EUROSTAT, 2020a, 2020b). Usually, maize is used as grain maize in the warmer regions and as silage maize in the cooler regions. In north-western (NW) Europe, about 85% of the maize production is designated to silage and biogas maize, while only 15% is grain maize (Galiano-Carneiro et al., 2021). With the promotion of green energy production via biogas in Germany, silage maize cultivation increased from 1.5 million ha (2000) to 2.7 million ha (2020), illustrating that maize cultivation can profit from both political decisions and from the future due to global warming (see below).

In general, in most parts of Europe, including NW Europe, it will get drier and warmer during the main crop-growing period including spring, summer, and autumn (Jacob et al., 2014), most probably increasing abiotic stress conditions for crops (Ceglar et al., 2019) including maize. Projected increased heat and water stress is especially detrimental during important growth stages of maize such as silking and kernel filling (Cairns et al., 2012). Drought and heat tolerance therefore deserve high priority in future crop breeding programmes (Ceccarelli et al., 2010; Chapman et al., 2012; Hammer et al., 2020) including those for maize (Cairns et al., 2012). On the other hand, global warming provides new opportunities for maize cultivation, particularly in the northern parts of NW Europe and at higher elevations. In addition, many plant pathogens, insect pests, and other harmful and beneficial organisms will also find new opportunities in NW Europe (Hakala et al., 2011; Miedaner & Juroszek, 2021).

One possibility to manage the increasing biotic risks in maize cultivation is breeding for resistance against already existing and potentially emerging plant diseases and insect pests (Cairns et al., 2012), which can be increasingly influenced by climatic and atmospheric changes (Deutsch et al., 2018; Garrett et al., 2006; Grünig et al., 2020; Gullino et al., 2018; Juroszek & von Tiedemann, 2011, 2013a, 2013b, 2013c, 2015; Lehmann et al., 2020). Herein, we focus on plant-pathogenic fungi and already important and emerging insect pests in maize in NW Europe, as insects feeding on maize can provide gateways for fungi such as *Fusarium* spp., eventually causing ear rots. We do not include insect vectors such as aphids and cicadas, which can transmit plant-pathogenic bacteria and viruses, although these

will become increasingly important as well (Jones & Barbeti, 2012; Trebicki, 2020). The long-term changes of diseases will be dependent on, for example, general crop health status, pathogen virulence including interactions with insects, and the location involved, but will inevitably lead to adjustments of future disease resistance breeding strategies (Li et al., 2020; Miedaner & Juroszek, 2021; Zhang et al., 2020). In addition, there will be effects on plant phenology such as alterations in the timing of flowering (Menzel et al., 2020; Racca et al., 2015) influencing diseases such as ear rots of maize that are caused by pathogens that infect plants at flowering (Gaikpa & Miedaner, 2019).

We will discuss three types of shifts caused by climate change, illustrated here by case studies: (a) shift in the importance of already established fungal pathogens (fungal leaf diseases); (b) adaptation of pathogen species/subspecies to warmer and/or drier conditions resulting in a higher fitness of the better-adapted species/subspecies within a disease complex (*Fusarium* disease complex in maize); and (c) shift of the ecological boundaries of thermophilic fungal pathogens (*Aspergillus* species) and insect pests (four case studies of herbivores) colonizing new areas that were formerly not warm enough. Herein, we focus on NW Europe including Norway, Sweden, Finland, Denmark, Germany, Belgium, the Netherlands, Luxembourg, northern France, Ireland, and the UK. However, most of our statements are also valid for other parts of Europe (e.g., Poland, Austria, Hungary, Romania, Spain, and Italy) and elsewhere, especially in the temperate and presumably also subtropical climate zones of Europe, because there are overlaps in pathogen and pest occurrence (Grünig et al., 2020).

## 2 | CHANGE IN THE RELATIVE IMPORTANCE OF FUNGAL LEAF DISEASES

When large-scale maize cultivation started in NW Europe after World War II, only two fungal diseases were frequently found in this area, *Fusarium* stalk rot caused by a complex of *Fusarium* spp. and common smut caused by *Ustilago maydis*. Both diseases were mainly controlled by the breeding of more resistant cultivars, and are of minor importance in NW Europe. However, recent European-wide monitoring activities (Ramos Romero, 2016) have detected several leaf diseases in European (Austria, Czech Republic, France, Germany, Poland, and the Netherlands were considered) maize fields (Table 1).

**TABLE 1** Already prevalent and emerging fungal leaf diseases of maize in north-west Europe according to Ramos Romero (2016) and Miedaner (2018)

Maize fungal leaf disease	Pathogen (causal agent)
Anthrachnose	<i>Colletotrichum graminicola</i>
Common rust	<i>Puccinia sorghi</i>
Grey leaf spot	<i>Cercospora zeae-maydis</i>
Kabatiella eyespot	<i>Aureobasidium zeae</i> , syn. <i>Kabatiella zeae</i>
Northern corn leaf blight	<i>Setosphaeria turcica</i> , teleomorph <i>Exserohilum turcicum</i>
Northern corn leaf spot	<i>Bipolaris zeicola</i> and two other <i>Bipolaris</i> species
Phoma leaf spot	<i>Phoma</i> species

Currently, mainly northern corn leaf blight (NCLB) caused by *Setosphaeria turcica* and common rust are prevalent in the more southern parts (southern Germany, Alsace), whereas Kabatiella eyespot and northern corn leaf spot are mainly prevalent in the more northern parts (northern Germany to Denmark) of NW Europe (Hanekamp, 2016). This increase in maize leaf diseases is most probably attributed to (a) the increasing cultivation of maize, (b) increased use of reduced/minimum tillage, and (c) simple crop rotations including monoculture (Miedaner, 2018). A comparison of isolates of *S. turcica* from South America and Europe suggested that aggressiveness of NCLB on maize in cooler climate zones will increase with rising temperatures (Navarro et al., 2021). In addition, recent climate change, namely warmer weather conditions throughout the year (e.g., mild and moist winters supporting inoculum survival and reproduction on maize residues) may also have favoured leaf diseases in maize (Miedaner, 2018). This is especially important, because all of the above-mentioned leaf diseases overwinter on maize residues, and consequently they could be effectively controlled by deep soil cultivation and diversified crop rotation, if farmers would frequently apply these preventive disease management methods.

There are a few review articles available among many others (compiled by Juroszek et al., 2020, see summary tables 1–3 therein) that focus considerably (Boland et al., 2004) or solely (Hooda et al., 2016; Juroszek & von Tiedemann, 2013c; Wu et al., 2011) on possible climate change effects on maize diseases. For example, Boland et al. (2004) speculate, based on their own expert knowledge, that the impact of most fungal leaf diseases of maize will be reduced by the end of the 21st century in Ontario (Canada) due to increasingly dry conditions during the maize growing period. Indeed, in NW Europe in the last 3 years (2018–2020), disease incidence of leaf diseases has been, in general, very low due to unusually warm conditions and lack of rainfall during the growing season. Boland et al. (2004) further expect that bacterial and viral diseases of maize will be more prevalent in Ontario due to global warming and consequently increased abundance of insect vectors. This might also be valid for other parts of the world (Hooda et al., 2016) including temperate regions such as recently reported for the USA (Ortiz-Castro et al., 2020). Juroszek and von Tiedemann (2013c) report, based on speculations and results of other researchers, that ear rot diseases in particular will continue to be a major problem in maize cultivation worldwide. Speculations based on expert knowledge (see above) and computer simulation studies of future disease risk (see below) are the two main methods of research to predict future impacts of diseases in crops (Juroszek & von Tiedemann, 2013b, 2015).

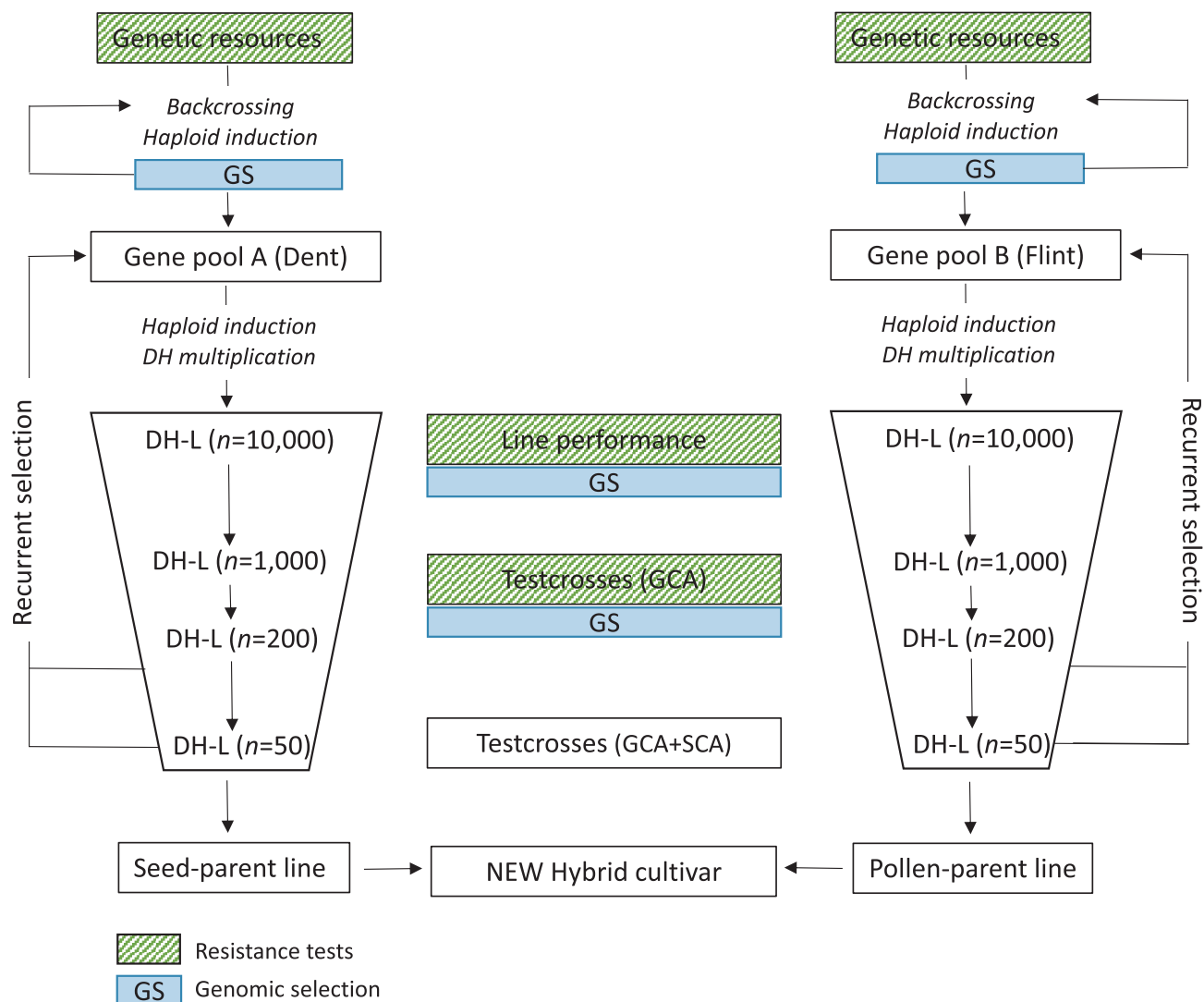
However, worldwide there are currently only four computer simulation studies available that project an altered risk of diseases in maize based on a modelling approach that is linked to a climate change scenario; two of these address Brazil (Ferreira & Miranda, 2020; Moraes et al., 2011), one addresses the Philippines (Salvacion et al., 2015), and one the entire globe (Ramirez-Cabral et al., 2017). Fortunately, the latter simulation study also considers Europe. According to this simulation study, the risk of common rust in Europe

caused by *Puccinia sorghi* and southern rust caused by *Puccinia polysora* in maize will increase in the future, both until the year 2050 and the year 2100 (Ramirez-Cabral et al., 2017). Therefore, breeders who are addressing European maize production systems will probably focus more attention on these two diseases in the future, particularly on common rust. Indeed, other maize diseases originally prevalent in tropical agroecosystems only are increasingly occurring in temperate agroecosystems (Mottaleb et al., 2019), another hint that global warming already increases the risk of maize diseases in Europe, until their supra-optimal temperature and suboptimal humidity conditions are met.

### 3 | BREEDING FOR RESISTANCE IN HYBRID MAIZE

Disease and insect resistance selection is a challenge in all breeding programmes because the different resistance traits are inherited independently and each disease or pest resistance adds to already existing breeding goals, especially agronomic traits like grain or dry matter yield, earliness, lodging resistance, and feed quality. Consequently, trade-offs among all these breeding goals are possible. The standard maize breeding pipeline in NW Europe (Figure 1) is divided in two gene pools, namely dent and flint. From each gene pool and breeding programme about 10,000 double-haploid lines (DH-L) are derived (Schmidt, 2004) from crosses by maternal haploid induction (Geiger & Gordillo, 2009). The resulting DH-L are multiplied and tested for their performance at a few locations for highly heritable traits like vigour, earliness, lodging resistance, and potentially also disease and insect resistance traits if the testing procedure is easy and robust enough. The positively selected DH-L are crossed with a tester from the opposite gene pool and the testcrosses are selected for their general combining ability (GCA) on multilocation tests that could also include disease and insect resistance traits. Whether resistance testing on this stage is performed or not, depends on the trait of interest. If the correlations between both generations are high enough, the breeder will prefer line testing. In some breeding programmes, a second testing on testcross basis is performed with at least two testers to select for GCA and specific combining ability (SCA). The selected DH-L can then be again multiplied and used for creating new hybrid cultivars. The best DH-L of the testcross steps are also used to generate the next breeding cycle in a recurrent selection (RS) scheme. If an off-season nursery is available, the standard breeding pipeline can be completed in 4 years. Afterwards, commercial hybrids are developed (Geiger & Gordillo, 2009).

Nowadays, the standard scheme explained above is supplemented by genomic selection (GS) on the basis of marker data achieved from medium- to high-density DNA arrays (Andorf et al., 2019). The prerequisite is the testing of a large training set where all traits of interest are investigated phenotypically across locations and years and associations with the respective marker data are calculated/estimated. If the training set is large enough and regularly



**FIGURE 1** Standard maize breeding scheme (Schmidt, 2004) supplemented by the introgression of genetic resources as resistance donor, recurrent selection, and genomic selection (GS, Geiger & Gordillo, 2009). DH-L, double-haploid line; GCA, general combining ability; SCA, specific combining ability; n, population size [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

updated, and consequently representative for the breeding material, it can be used to predict the genomic-estimated breeding values (GEBVs) of so far untested genotypes. In contrast to marker-assisted selection (MAS) that uses only a few significant marker-trait associations, GS exploits all known minor and major marker effects across the whole genome. However, GS must be performed separately for each heterotic group (Han et al., 2018). GS of DH-L can be based on associations from previous breeding cycles. This is especially valuable when the same resistance donors are used across cycles because genetic relationship is a key for a high prediction ability in GS. It has been proposed that GS could already take place directly after a successful haploid induction (Andorf et al., 2019). Mean phenotypic and GEBVs are combined to discard DH-L inferior in their overall breeding value before entering the costly testcross process. This could be repeated on the first testcross stage and a second testcross could then be discarded. A positive point is that GS is already used by commercial maize breeding for selection of grain yield. Therefore,

disease and insect resistance traits can be easily integrated (only the training populations have to be updated).

For integrating genetic resources as disease and insect resistance donors, a representative set of DH-L could be induced from the source populations and tested phenotypically for the respective resistance and adaptive traits (e.g., days to silking, plant height, lodging resistance, seed set; Gaikpa et al., 2021). Afterwards, a backcross procedure is necessary to further adapt the preselected material to the target environment. Here, GS can also be used for accelerating the introgression process. The phenotypically selected DH-L are backcrossed, and haploids are induced and genotyped. Only those with the highest GEBVs are further backcrossed (Geiger & Gordillo, 2009). For monogenic traits, the cheaper MAS could be performed instead of GS.

The above paragraphs explain how a disease and insect resistance breeding scheme is applied in general in hybrid maize breeding. More concrete resistance breeding approaches for specific



diseases and insect pests are highlighted in the following sections. In short, appropriate and specific resistance breeding approaches are foremost dependent on the type of resistance, namely if the available disease or insect resistance resource is qualitative (one or few *R* genes with major effects) or quantitative (usually many quantitative trait loci [QTLs] with minor additive effects). In this respect it is important to know, for example, if virulent races of a pathogen already exist in a location of interest, which can reduce the efficacy of a specific *R* gene. Then, it is better to use quantitative resistance, because usually they are effective against all races of a pathogen species, thus being more durable. Because of the minor phenotypic effects of most QTLs working additively together, several resistance alleles from diverse origins must be accumulated in one cultivar to reach a high level of resistance. For some diseases, like ear rots, only quantitative resistances are available, whereas for others like NCLB, both qualitative and/or quantitative resources can be used (see below).

#### 4 | LEAF DISEASE RESISTANCE BREEDING APPROACHES

Maize is a perfect model plant to study quantitative resistances, because this was historically the major pathway to implement disease resistance in maize and has been very successful, including NCLB resistance breeding in North America (Balint-Kurti & Johal, 2009). In general, major *R* genes (qualitative resistance, see above) play a much lower role in maize compared to wheat (Balint-Kurti & Johal, 2009) and are especially related to leaf diseases.

Plant breeders who address European maize production systems will need to pay attention to emerging leaf diseases in maize (see above). Presumably, bacterial and viral diseases will also gain more importance in NW Europe in the future. Therefore, plant breeders and plant pathologists are already highlighting that multiple-disease resistance is needed in maize (e.g., Jindal et al., 2019) and will be even more important in the future. Fortunately, there are increasingly more researchers focusing on this topic in maize (e.g., Balint-Kurti et al., 2010; Jindal et al., 2019; Martins et al., 2019; Wisser et al., 2006). For example, Wisser et al. (2018) found that a glutathione S-transferase (GST) gene was associated with modest levels of resistance to three different diseases in maize, suggesting a pleiotropic genetic basis.

In addition, certain breeding schemes may be more suitable for specific diseases than others, for example, depending on *R* gene or QTL distribution patterns within the chromosomes of maize, specifically if they are clustered (Wisser et al., 2006). A recent meta-analysis of 110 published studies reported 1,080 QTLs associated with disease resistance to fungi and viruses (Rossi et al., 2019). These are distributed over all 10 chromosomes, illustrating the complex nature of disease resistance breeding in terms of genetics and genomics. However, many more genes behind the QTLs must be characterized (Martins et al., 2019) and additional breeding schemes must be developed and/or existing ones adapted (Wisser et al., 2006) in order

to find a suitable way through the "jungle" of uncharacterized QTLs. One strategy is the development of an introgression library combined with high density marker coverage to resolve QTLs (Kolkman et al., 2020).

Where multiple-disease resistance cannot be implemented in breeding programmes easily, single-disease resistance breeding strategies should focus on the economically most important disease of a target region. For example, NCLB caused by *S. turcica* is at present the most troublesome leaf disease in European maize cultivation (Navarro et al., 2021), provided there is sufficient humidity for infection (Galiano-Carneiro & Miedaner, 2017) during the growing season. There are qualitative and quantitative resistance sources; however, some of the qualitative, race-specific *Ht* genes are already ineffective due to virulent pathogen populations. For example, within a European survey, conducted from 2011 to 2012, a total of 244 isolates of *S. turcica* were collected. Of these, 23.1% were identified as race 1 and 11% as race 3. In addition, the races 3N, 123, 23, 2, 13, 23N, and 12 occurred either solely or in various combinations with a combined frequency of 15.7% (Hanekamp, 2016b). These results, although somewhat different in the various regions, show that for all *Ht* resistance genes, including most of their combinations, presently used by breeders in maize cultivars, virulent isolates of *S. turcica* already exist in the fields of farmers in Europe. Therefore, breeders started to concentrate mainly on introducing quantitative resistance resources in maize cultivars to manage NCLB. In contrast, in Brazil and Argentina, race 0, which can be controlled by any *Ht* gene, still prevails (B. L. Navarro, University of Göttingen, Germany, personal communication). Thus, resistance strategies have also to be regionally adjusted. Similar to other pathosystems, a great array of resistance QTLs exists. In a recent study, 197 QTLs from 27 references were localized on all 10 chromosomes of maize (Miedaner et al., 2020). Again, the QTLs were not randomly distributed, but occurred in hotspots. The great number of QTLs does not suggest that it is "very easy" to achieve durable and stable NCLB resistance in maize, because the optimal number and effects of the major-effect QTLs to be combined needs to be assessed and validated in diverse germplasm. Also, possible penalties of the "most promising QTL combination" on yield- and quality-related traits must be evaluated.

Fortunately, a recently published study suggests that the introduction of Brazilian resistance donors can efficiently increase the resistance level of European maize germplasm (Galiano-Carneiro et al., 2021). This is of great interest to maize breeders in NW Europe and elsewhere, because in the subtropics and tropics, maize has already been challenged for a long time by NCLB. Consequently, it is likely that even more and better NCLB resistance resources can be identified in the future, for example, in Brazilian and Mexican maize germplasm for transfer to European maize germplasm. Therefore, international cooperation across continents (and climatic zones) and exchange of germplasm such as already promoted by CIMMYT (e.g., Cairns et al., 2012) is of overriding importance to adapt to changing environmental conditions, particularly in Europe, where quarantine (biosecurity) instructions must be strictly followed (Giovani et al., 2020).

While the genetic basis of resistance to fungal pathogens has been studied in maize relatively often, less is known about the genetic basis of bacterial and virus disease resistance (Qiu et al., 2020). However, ideally, in the future multiple-disease resistant (bacteria, fungi, and viruses) maize cultivars, even combined with multiple-insect resistances (see below) will hopefully be available, because they will be needed.

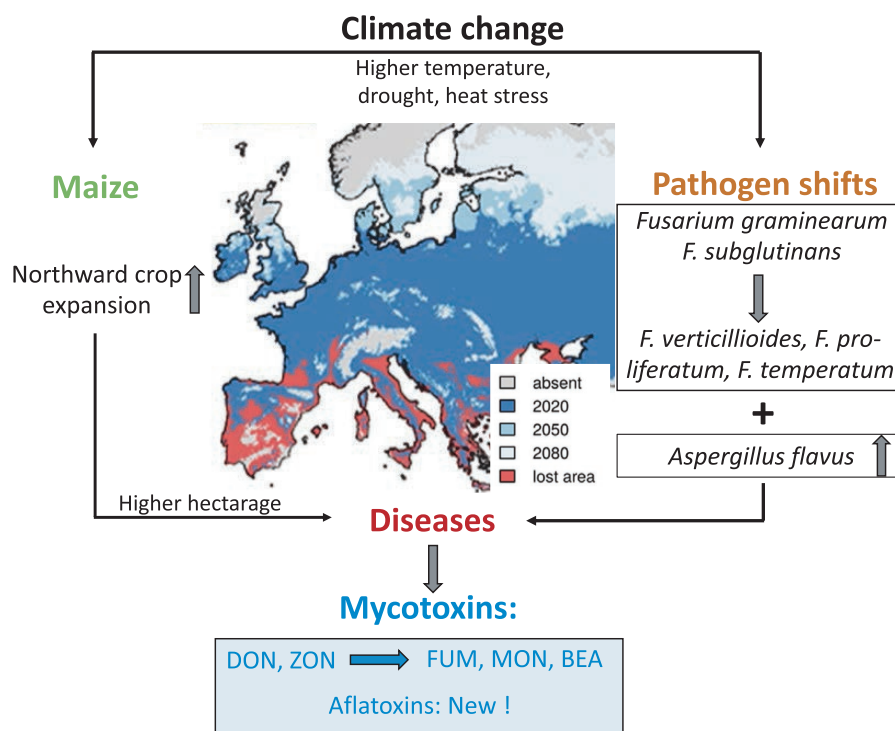
## 5 | MAIZE EAR ROTS AND RELATED MYCOTOXIN PRODUCTION

### 5.1 | *Fusarium* species

Internationally, two ear rot types are described caused by *Fusarium* species: Gibberella ear rot (GER) mainly caused by *F. graminearum* sensu stricto, and Fusarium ear rot (FER) mainly caused by the *Gibberella fujikuroi* species complex – *F. verticillioides*, *F. proliferatum*, and *F. temperatum*.

Maize production will expand in the future to Scotland and the southern parts of Norway, Sweden, Finland, and north-east Russia (Grünig et al., 2020, Figure 2). This northward maize expansion will also promote the geographic range expansion of *F. graminearum* ear rot and the contamination risk of the associated mycotoxins deoxynivalenol (DON), nivalenol (NIV), and zearalenone (ZON) (Parikka et al., 2012). In the more southern parts of NW Europe

the increasing temperature will influence the *Fusarium* species assemblage as well (Figure 2). It can be expected that GER might be outcompeted by FER due to warmer conditions. Indeed, 11 *Fusarium* species were identified in Germany that can cause ear rot of maize (Goertz et al., 2010). High temperatures at anthesis and during kernel development of maize favoured the occurrence of *F. verticillioides* and *F. proliferatum* in one year, including the associated fumonisin (FUM), moniliformin (MON), and beauvericin (BEA) contamination of maize kernels. In contrast, moderate temperature and higher moisture in another year promoted the prevalence of *F. graminearum* and *F. subglutinans*, resulting in higher concentrations of DON, NIV, and ZON. Under these circumstances, *F. avenaceum* and *F. subglutinans* also produced MON and BEA (Goertz et al., 2010). A recently published survey (Pfordt, Ramos Romero et al., 2020) approved these earlier findings in Germany: lower temperature and relative high precipitation caused a domination of *F. graminearum*, while a dry period with high temperatures during grain filling favoured *F. verticillioides* and *F. temperatum*, the latter being a descendant of *F. subglutinans*. Moreover, both a shortened grain-filling period and reduced relative humidity during maize flowering most likely contributed to a decreased DON content at harvest (Van der Fels-Klerx et al., 2013). Taken together, climate change effects will influence *Fusarium* species prevalence and associated mycotoxin profiles, consequently increasing the mycotoxin risk from FUM, MON, and BEA. Unfortunately, there are no EU legislative values available for the latter two mycotoxins. Moreover, their



**FIGURE 2** Potential impacts of climate change on maize cultivation, mycotoxigenic fungi, and plant-pathogen interactions resulting in altered mycotoxin production in north-west Europe until the end of the 21st century; arrows mark possible changes. DON, deoxynivalenol; ZON, zearalenone; FUM, fumonisin; BEA, beauvericin. Map from Grünig et al. (2020), open access [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



detection in grain is currently not possible using easy-to-handle immunotests.

In Poland, *F. verticillioides* is the most important *Fusarium* species causing ear rot in maize (Czembor et al., 2014). The second most important is *F. temperatum* (Czembor et al., 2014), which can produce MON, BEA, enniatins, and FUM B<sub>1</sub> (Scaufaire et al., 2012). *F. temperatum* appears to be very versatile, because it produced more MON, BEA, and fusaproliferin (FUS) at 30°C compared to 15°C (Scaufaire et al., 2012), which is unexpected (Fumero et al., 2016). Also, in Germany, *F. temperatum* was in third place after *F. graminearum* and *F. verticillioides* when isolated from naturally infected maize ears, with an even higher aggressiveness than the other two species (Pfordt, Schiwek, et al., 2020). Again, this example shows that we always have to be aware of *Fusarium* species shifts and that different *Fusarium* species colonize maize kernels at the same time (Reyes Gaige et al., 2020), including respective associated changes of mycotoxin profiles in maize kernels.

An increased insect damage of maize with rising temperatures (see last section) will also increase disease incidence of *Fusarium* species and mycotoxin contamination of maize, because the insects produce wounds due to feeding on kernels and these wounds are perfect gateways for mycotoxigenic fungi (Dowd, 2003), including *Fusarium* and *Aspergillus* species. Adult insects and their larvae can also passively transport inoculum across maize plants (Dowd, 2003). For example, the European corn borer (ECB) was found in the USA to enhance *F. verticillioides* incidence (Sobek & Munkvold, 1999). Accordingly, transgenic Bt maize can indirectly reduce *Fusarium* ear rot (Munkvold et al., 1997). Also, in Europe ECB feeding activity significantly increased the concentrations of seven monitored mycotoxins produced by *Fusarium* spp. of the Liseola section (Blandino et al., 2015), although this was not found for six other mycotoxins produced by *Fusarium* species of the Roseum and Discolor sections. Nevertheless, effective insect pest management is regarded as a very important method to reduce the risk of mycotoxin contamination (FUM, aflatoxin, DON, and ZON) in maize (Logrieco et al., 2021). To conclude, it can be expected that climate change, particularly global warming, will probably contribute to continuously increasing ear rot problems in maize caused by the many different *Fusarium* species, which can complement each other due to their individual ability to adapt successfully to various environmental conditions (JuroszeK & von Tiedemann, 2013c), also promoted by insect pest infestations such as ECB.

## 5.2 | *Aspergillus* species

A major concern for NW Europe is the potential occurrence of aflatoxins in maize kernels, especially AFB<sub>1</sub> which is usually most prevalent in cereals, produced by *Aspergillus flavus* and *A. parasiticus* due to warmer and drier weather conditions (Moretti et al., 2019). Aflatoxins are the most toxic mycotoxins and the strongest natural carcinogens known. Environmental stress, mainly drought or insect damage, can up-regulate aflatoxin production by the

fungi. Presently, aflatoxin contamination of plant products is mainly prevalent in tropical areas. Nevertheless, in southern Europe, aflatoxin contamination of plant products including maize kernels has increased since the 2000s, most likely caused by increasingly drier and warmer summers. Presumably, these conditions caused a shift from *F. verticillioides* to *A. flavus*, leading to high aflatoxin contents in maize kernels. In Hungary, aflatoxins could not be detected in a survey conducted from 2009 to 2011. However, in 2012, aflatoxin was found in 68.5% of samples taken, probably caused by hot and dry weather with prolonged drought during spring and summer (Kos et al., 2013). Subsequently, from 2013–2016, aflatoxin was frequently detected in Hungary, ranging from 5% to 72% of samples taken, with the exception of 2014, most likely due to cool and rainy weather conditions during this summer. In Serbia, aflatoxin was also detected several times (Janić Hajnal et al., 2017; Kos et al., 2018; Paterson & Lima, 2011). In northern Italy, in 2003, the first *A. flavus* outbreak occurred, probably due to very hot (>35 °C) and dry weather conditions (Medina et al., 2017). Consequently, the simulation study of Battilani et al. (2016) predicts that aflatoxin contamination of plant products will also become a problem in NW Europe including maize, both in 2050 and 2100.

A natural, biological control method to reduce the risk of aflatoxin production is the use of nontoxigenic *A. flavus* strains, certain strains that cannot produce aflatoxin. For example, a molecular study showed that the nontoxigenic strains can contain several single nucleotide polymorphisms (SNPs), deletions, or insertions in the aflatoxin biosynthesis gene cluster, thus preventing them from producing aflatoxins, although there are also other reasons for lack of aflatoxin production (Adhikari et al., 2016). These nontoxic strains (biological agents) can outcompete the naturally occurring toxigenic strains, provided they can share the same ecological niche (Dorner, 2004), herein maize plants. This procedure has been developed in the USA, where two products are permitted to control aflatoxin contamination in cotton, *Gossypium hirsutum* (AF36) and groundnut/peanut, *Arachis hypogaea* (Afla-guard), respectively, (Dorner, 2004). Recently, this technology has been adopted in sub-Saharan Africa for maize and peanut, where a product named Aflasafe contains four native nontoxigenic isolates of *A. flavus* isolated from local soils and specifically adapted to the country where it should be used (Senghor et al., 2020).

Across all these mycotoxin groups, the most promising measures related to preharvest management include genetic host plant resistance, effective insect pest management, and selecting locally adapted genotypes (e.g., concerning chilling tolerance, maturity, drought tolerance) (Table 2). Water management is specifically important for control of fumonisins and aflatoxins because the underlying diseases are both promoted by drought. Although available, no fungicide has been released in the EU for ear rot control. Therefore, farmers should change their management practices if required, especially soil management (e.g., more frequently ploughing instead of solely minimum or even zero tillage), rotation (e.g., no monoculture, less wheat–maize sequences), and also their choice of cultivars (e.g., resistant instead of high yielding only) to mitigate the effects of climate change on mycotoxin

**TABLE 2** Ranking of the five most important measures for minimizing preharvest mycotoxin contamination in maize according to votes of experts

Effective measure	Deoxynivalenol, zearalenone	Fumonisin	Aflatoxins
Host plant resistance	1	1	2
Insect control	4	2	4
Biocontrol	NM	NM	1
Locally adapted cultivars/hybrids	5	3	5
Good agricultural practices	NM	4	NM
Water management	NM	5	3
Crop rotation	2	NM	NM
Fungicide application	3	NM	NM
Total no. of measures	15	18	11

Note: 1 = most important, following Logrieco et al. (2021). NM, not mentioned specifically among the five most important measures, although important in an overall integrated pest management strategy.

contamination of food and feed. When adopting these integrated pest management (IPM) principles, farmers would also safeguard the durability of ear rot resistance of maize cultivars. However, mainly due to economic constraints, maize cultivation in NW Europe has become very intensive, whereby high nitrogen fertilizer levels, zero tillage, and minimum rotation are frequently used. Therefore, resistance breeding will become increasingly important in order to reduce the continuously increasing disease risks including maize ear rots and the associated mycotoxin contamination of maize kernels.

## 6 | EAR ROT DISEASE RESISTANCE BREEDING APPROACHES

Strategies of resistance breeding have been suggested recently for *Gibberella*, *Fusarium*, and *Aspergillus* ear rot diseases in maize, including genomics-based approaches (Gaikpa & Miedaner, 2019). In short, the underlying genetic architecture for resistances to all mycotoxigenic fungi in maize (see above) were found to be highly complex and under polygenic control. Resistance is predominantly governed by many small-to-medium effect QTLs that are scattered across the whole genome. In maize, a positive moderate correlation ( $r = 0.5$ – $0.6$ ) exists between *F. graminearum* and *F. verticillioides* resistances among 140 European inbred lines (Löffler et al., 2010). Accordingly, Löffler et al. (2010) found a high correlation between FUM and DON concentration ( $r = 0.70$ ) and also a high correlation between GER and FER resistances. In addition, the corresponding total mycotoxin concentration was also highly correlated ( $r = 0.83$ – $0.96$ ). The rather narrow associations in artificially infected plants under field conditions in screening trials could be exploited by just visually selecting for lines with low symptoms. Some genotypes were also reported to be resistant to two of the three ear rot diseases, namely GER, FER, and *Aspergillus* types (Gaikpa & Miedaner, 2019). Thus, it seems possible to select lines that are multi-resistant to several toxigenic pathogens.

Due to the high number of QTLs responsible for multiple ear rot resistance, GS rather than MAS is presumably better suited for

germplasm selection. Also, in wheat, GS was proposed to be successful for improving *Fusarium* head blight resistance and reducing DON contamination (Arruda et al., 2015; Herter et al., 2019; Rutkoski et al., 2012). Nevertheless, in a "near-final" selection stage, a mycotoxin test might be useful in order to confirm if the promising lines really do have a low mycotoxin content as proposed by GS. To broaden the genetic diversity for ear rot resistance, the exploitation of European landraces (Gaikpa et al., 2021) and of (sub)tropical germplasm is useful (Galiano-Carneiro et al., 2021).

## 7 | FOUR CASE STUDIES OF LEPIDOPTERAN AND COLEOPTERAN INSECTS

Insects are poikilothermic organisms, because their body temperature varies according to the surrounding temperature. Thus, their population dynamics are strongly affected by temperature. Consequently, global warming has the potential to significantly modify the actual distribution and population development of agricultural insect pests (Deutsch et al., 2018; Lehmann et al., 2020). Generally, insect damage will increase as a result of an increase in insect metabolic rates and their reproductive rates (Deutsch et al., 2018). However, there are complex interactions, also dependent on species and populations. Consequently, not all insect species will react the same way (Lehmann et al., 2020). Nevertheless, in NW Europe, there will be more insect species, often with greater populations during ambient environmental conditions, because most insect species are currently facing below optimum physiological temperature conditions, at least during most parts of the year. Therefore, it is likely that more direct (e.g., feeding, sucking) and indirect (e.g., creating wounds facilitating pathogen entry, pathogen transmission) damage caused by insects in maize in NW Europe can be expected, unless natural enemies of insect pests will perform better too (Litkas et al., 2019; Taylor et al., 2018). In conclusion: (a) many insect pests including ECB will migrate northward, for example, to Scandinavia;



(b) already occurring invasive species like the western corn root worm (WCR, *Diabrotica virgifera* var. *virgifera*) that first arrived in France in 2002, will continuously spread; and (c) new invasive species such as the Mediterranean corn borer (MCB, *Sesamia nonagrioides*) and the fall armyworm (FAW, *Spodoptera frugiperda*) are likely to invade NW Europe. Both are already causing severe crop damage in the Mediterranean region and the Near East, respectively (CABI, 2020).

### 7.1 | European corn borer (*Ostrinia nubilalis*, Lepidoptera)

The European corn borer (ECB) is an excellent example of a northward migrating insect pest. ECB is prevalent in many parts of the world (Gagnon et al., 2019), including Europe. In south-western Germany, ECB was detected in maize in the 1930s. However, due to the very small maize cultivation area at that time, it was not a serious pest. However, in 1990, ECB first invaded the Federal State of Northrhine-Westphalia in the western part of Germany. In 1995, it invaded eastern Germany, and in 2001, ECB was first detected near the Baltic coast in Mecklenburg-Western Pomerania (Heidel, 2015). By 2013, the insect affected maize almost everywhere in Germany (>90% of all districts), although the damage level varied greatly across German regions (Freier et al., 2015), with most damage in the south-west of Germany (see below). In Scandinavia, ECB was first detected in Denmark, in 2010. One year later, three sites in southern Sweden were infested (Lehmhus et al., 2012). Future risk simulations (year 2055) predict that ECB will likely establish in Norway, Sweden, Finland, Denmark, the United Kingdom, and Ireland, developing at least one generation per year (Svobodová et al., 2014). Today, ECB is not destructive in these countries, but it will become more important because it is (a) indirectly favoured by increasing maize acreage in northern parts of NW Europe (see Figure 2); and (b) directly favoured by global warming, because warming will promote feeding activity and fecundity among other ECB life cycle parameters. The CLIMEX model predicts that the area of arable land affected by ECB in Europe will increase by 61% (Kocmánková et al., 2011).

In the southern parts of NW Europe, more ECB generations per year will be produced. Since 2006, a bivoltine population of ECB, developing two generations per year, has already infested several thousands of hectares of maize in south-western Germany, between Freiburg and Basel. In 2017, a second area with the bivoltine population was detected near Mannheim, which is about 150 km further north of Freiburg. The south-west of Germany from Mannheim to the Swiss border is one of the warmest regions of NW Europe, thus a bivoltine population could establish there, presumably also already favoured by recent climate warming in Germany. The bivoltine ECB population attacks not only stalks (the first generation in particular) but also unripe maize ears (the second generation in particular) due to an overall longer infestation period compared to a univoltine ECB population. Consequently, a bivoltine ECB population produces much longer and greater feeding damage (stalks and ears) compared to a univoltine

ECB population. In addition, the wounds distributed throughout the ears of maize plants provide perfect gateways for secondary invasion of mycotoxinogenic *Fusarium* species (so far *Aspergillus* species are not detected in NW Europe). However, future global warming may favour northward migration of the bivoltine ECB population. In south-western Germany, even a third generation of ECB may develop successfully in the future, provided global warming continues as currently projected. For comparison, in the warm south-eastern USA, ECB currently regularly produces up to four generations per year.

### 7.2 | Western corn root worm (*Diabrotica virgifera* var. *virgifera*, Coleoptera)

The western corn root worm (WCR) is the most destructive maize insect pest in the USA. From there, this coleopteran insect pest was imported several times to Europe, presumably the first time in 1992 to Serbia (Miller et al., 2005). France and the Benelux countries were invaded in 2002 and 2003, respectively. WCR invaded Germany in 2007, presumably originating from the south of Europe (EPPO [European and Mediterranean Plant Protection Organization], 2012; Glas et al., 2009). It can be expected that WCR will pursue a similar invasion pattern like ECB in northern countries of NW Europe (see above), supported by milder winter and higher spring/summer/autumn temperatures. Given the great genetic variability of WCR, a gradual selection within the different WCR populations to cooler temperatures must also be considered.

### 7.3 | Mediterranean corn borer (*Sesamia nonagrioides*, Lepidoptera)

The Mediterranean corn borer (MCB) is already a serious maize pest in Mediterranean countries (Camargo et al., 2018). Due to global warming, MCB might invade large parts of NW Europe soon, because it has already occasionally been detected in southern Germany. MCB produces a similar damage pattern to ECB by feeding from either the stalk or the ear of maize. According to computer simulations by Maiorano et al. (2014), the potential geographical range of MCB could greatly increase until 2030 in NW Europe, possibly invading vast areas of central and eastern France, Belgium, the Netherlands, and western and northern Germany. In addition, MCB could potentially develop two generations per growing period in France and southern Germany (Maiorano et al., 2014).

### 7.4 | Fall armyworm (*Spodoptera frugiperda*, Lepidoptera)

The fall armyworm (FAW) is native to the tropical and subtropical Americas. It has not reached Europe yet. However, it recently conquered sub-Saharan Africa within about 3 years (2016–2018). It has spread to at least 28 African countries with a great potential for

economic damage of maize and other crops (CABI, 2020). The insect cannot overwinter in areas with temperatures below zero, except in sheltered and thus protected locations (e.g., heated greenhouses). In the USA, FAW survives the winter in the most southern regions (Texas, Florida), where it is frost-free during winter. However, during the maize growing period FAW spreads northward across the United States, even occasionally reaching southern Canada (Meagher & Nagoshi, 2004). In most of Europe, below zero winter temperatures limit the area for FAW establishment. However, Andalucia in Spain, Sicily in Italy, and some parts of Portugal and Greece are already suitable for year-round survival and establishment of FAW (Jeger et al., 2018). Provided FAW invades northern Africa, FAW can probably reach southern Europe such as Sicily (Jeger et al., 2018). Given the broad host range of FAW, many crops including maize are threatened. Due to global warming and increasingly milder winter temperatures, FAW has the potential to spread throughout NW Europe in the future, at least in summer when seasonal migrations from southern Europe might be supported by adequate weather conditions such as already occurring in North America (see above).

## 8 | INSECT PEST RESISTANCE BREEDING APPROACHES

Insect resistance in maize is a very broad topic, including pre- and postharvest insect pest resistance (Lopez-Castillo et al., 2018). Postharvest insect pest resistance is especially important in countries where postharvest conditions are critical. In NW Europe, preharvest insect resistance is particularly important, and still under investigation. In general, there are GMO (Genetically Modified Organisms) and non-GMO approaches in insect resistance breeding available, whereby in the NW European countries GMO approaches are not welcome due to public concerns. For insect pests, traditional non-GMO resistance breeding activities are lagging, particularly compared to breeding activities related to fungal pathogens. Important reasons include (a) lack of test sites with regular and homogeneous natural infestation; (b) mass-propagation of insect larvae is expensive; (c) plant-trait assessment conferring insect resistance is tedious; and (d) even with artificial infestation using laboratory-raised insect larvae in screening trials, heritability estimates are mostly low to moderate. This indicates that the genetic contribution is rather small and highly affected by non-genetic effects. For example, relatively small to moderate heritabilities ranging from 0.3 to 0.6 were reported by Schön et al. (1993), Bohn et al. (2000), and Badji et al. (2020, 2021), thus restricting gain from selection.

Host-plant resistance against insects is governed in principle by three mechanisms: (a) non-preference (antixenosis), (b) antibiosis, and (c) tolerance (Bohn et al., 2000; Franeta et al., 2019). A recently published review article related to strategies for enhanced crop resistance to insect pests is available by Douglas (2018). This review also considers recently advocated approaches such as exploiting microbiomes of insect pests either as target or vehicle for delivery of insecticidal agents.

In short, antixenosis operates by a lack of attractiveness of the host plant for the insect, for example, by stalk and leaf morphological characteristics (e.g., leaf toughness, trichomes, mesophyll content), and cell-wall fortification features (e.g., stover content of fibre, cellulose, lignin, and silica). However, it must be considered that compounds that lower insect attractiveness may also decrease digestibility of the maize stover, which is especially important for silage maize used for feeding. Additionally, a trade-off between MCB resistance and yield potential has been reported (Jiménez-Galindo et al., 2019). Insect-damaged maize plants constitute an additional indirect component of plant resistance, because damaged plants can emit volatile organic compounds that attract natural enemies of insect pests such as parasitoid wasps (Franeta et al., 2019).

Antibiosis increases the mortality of the larvae and decreases their feeding activity and consequently growth by specific plant secondary compounds. Clearly, this constitutes a multifaceted phenomenon depending on special secondary compounds like phenolic and/or dehydrodiferulic acid. Also, a hydroxamid acid, namely DIMBOA (2,4-dihydroxy-7-methoxy 2H-1,4-benzoxazin-3[4H]-one), was found to be a natural defence compound against ECB and other insect species (Klun et al., 1970). The concentration of DIMBOA inside the maize plant is mainly governed by the *bx1* gene and rapidly induced by insect damage (Butrón et al., 2010), whereby DIMBOA affects the enzyme endoprotease in the digestive system of ECB larvae, which finally died due to starvation.

Tolerance is the ability of the host plant to withstand the insect attack without significant loss of yield or quality. For example, vigorous growth is one element of tolerance in order to compensate for below-ground and/or above-ground maize biomass losses due to insect feeding.

Resistance against ECB is clearly a quantitative trait. For example, several QTLs in maize germplasm were detected affecting the length of tunnels produced by larval stalk mining and stalk damage ratings with mainly additive gene action (Bohn et al., 2000; Melchinger et al., 1998; Papst et al., 2004; Schön et al., 1993). Each QTL contributed 3%–15% to the phenotypic variation, with a maximum total explained genotypic variance of 50%. The authors concluded that conventional phenotypic selection (mainly visually in screening trials) for improving this kind of insect resistance type might be sufficient. A QTL analysis for MCB detected QTLs for stalk tunnelling that were in the same or adjacent bins to QTLs for ECB tunnelling, indicating gene clusters or common mechanisms of resistance to both corn borer species (Ordas et al., 2010). The authors suggested five candidate genes involved in cell wall biosynthesis or fortification that could explain the QTLs for stalk tunnelling in the bin 3.05 region. However, the three clustered QTLs detected in the bin 3.05' region had only low to moderate effects, all three together explaining only 33% of the total genotypic variance, illustrating that more genes and QTLs are presumably involved in stalk-tunnelling resistance. Also, with newer mapping technologies, only small-effect QTLs were found for MCB resistance (Jiménez-Galindo et al., 2019). The detected QTLs displayed large confidence intervals and their effects were usually not consistent across maize populations, thus

the stability of the resistance is lacking. Nevertheless, presumably in the future, GS will provide more success in increasing insect resistance in plants including maize (Badji et al., 2020, 2021), suggesting that entomologists and breeders should not be discouraged by less promising results at this early stage of research.

In the USA, traditional non-GMO genetic breeding work more or less stopped when the first GM maize cultivars were released in the second half of the 1990s, which expressed the Cry proteins in planta derived from *Bacillus thuringiensis* (Bt). These GM maize hybrids were able to control ECB and WCR effectively at their release. Nowadays, about 95% of the maize acreage in the USA is planted using GM hybrids (Alemu, 2020).

No significant direct side-effects on non-target organisms were found until now, when Bt and non-Bt maize cultivars were compared side by side, confirming a high specificity of the Bt-GMO method (Hellmich & Hellmich, 2012; Yin et al., 2020). However, it is possible that non-target insect pests are indirectly influenced. This was shown recently for pea aphid (*Acyrtosiphon pisum*), which was at least partly promoted by release from potato leafhopper (*Empoasca fabae*) competition due to insecticide application (Straub et al., 2020), and this indirect effect is also applicable to Bt-crops (Zeilinger et al., 2016). The latter authors have reported a competitive release and outbreak of non-target pests in transgenic Bt-cotton. Thus, Bt-crops including Bt-maize are not a "silver bullet" to solve all insect pest problems, although they can contribute to environmental and economic benefits through reduced insecticide use against target insect pests, provided that non-target insect pests do not need increased additional insecticide applications to be controlled.

However, the various specific Bt proteins expressed in GM maize plants had different effective periods until first resistances of insect pest populations were detected against them, thus reducing the efficacy of the GMO technology. For example, despite implementation of a high-dose refuge strategy with non-Bt host plants, the first resistances of WCR and FAW against the respective Cry3Bb and Cry1F proteins occurred 3 and 7 years following the first release in the USA, respectively (Tabashnik et al., 2013). On the other hand, Cry1Ab effectively controlled ECB in North America more than 15 years following its first release. The first case of field-evolved resistance of ECB to Cry1Ab Bt-maize was found in Nova Scotia, Canada, following 20 years of usage (Smith et al., 2019). In Spain, the first MCB individuals resistant to Cry1Ab protein were detected already in 2004–2005, 1–2 years after the first GM maize cultivation in 2003 (Andreadis et al., 2007). However, the estimated expected frequency of resistance of 0.0015 in this MCB population was extremely low, suggesting that the high-dose refuge strategy should be effective. A second survey in 2016 resulted in a frequency of resistance alleles of 0.0036 in the respective insect pest population. Although higher compared to the previous assessment, the difference was not statistically significant (Camargo et al., 2018). Thus, even 13 years after the first Bt-maize hybrid was grown in Spain, resistance in the target insect pest MCB did not significantly increase, and consequently efficacy of the GM maize remained high.

In addition to the high-dose refuge strategy, the commercialization of new Cry proteins and pyramiding of different Cry proteins are two strategies of the industry to improve durability of resistance (Douglas, 2018). Presumably, the introduction of natural non-GMO resistances in a GM maize genotype might help to enhance the durability of genetically modified Bt proteins in maize.

Of course, approaches other than host plant insect resistance are also important, such as alternative methods in Europe for controlling ECB by insecticides or by using endoparasitoids such as *Trichogramma brassicae*, and implementation of good agricultural practices such as a wider crop rotation and careful maize stubble management. For MCB, a biocontrol mechanism was described by the African parasitoid *Cotesia typhae* (Kaiser et al., 2017). In general, insect resistance breeding approaches should be combined with other direct and indirect methods to manage insect pests in maize in order to have an effective and durable strategy available according to IPM principles.

## 9 | CONCLUSIONS

Due to the projected milder winter and higher spring, summer, and autumn temperatures, many pathogen species will have the opportunity to migrate further north. The likely result is that countries in NW Europe will suffer from fungal diseases such as NCLB that are presently less problematic there. However, with a warmer and drier climate, insects might become especially important in NW Europe, among them vectors of plant pathogens such as bacteria and viruses. However, even non-vector insect species such as ECB can greatly promote plant disease incidence and severity. Insects feeding on maize plants results in wounds that can serve as gateways for fungal species, among them several *Fusarium* species that can produce mycotoxins (*Aspergillus* species are not yet detected in NW Europe). All these processes will be accelerated when maize cultivation is adopted throughout most parts of NW Europe, serving as an indirect driver of pathogen and insect pest spread. Thus, breeding maize cultivars (hybrids) with durable multi-disease resistance against diseases caused by bacteria, fungi, and viruses is of overriding importance. Equally important is the breeding of multi-insect resistant maize cultivars. Ideally, multiple-disease and multiple-insect resistance maize cultivars should be bred, although this is a challenging task (Kim et al., 2021), particularly when relying on traditional breeding methods only. These are supplemented today with off-season nurseries, doubled-haploid techniques, MAS, and GS procedures to reduce cycle length and enhance breeding population sizes (Miedaner et al., 2020; Sánchez-Martín & Keller, 2019).

Gene transfer and genome editing would greatly help against those pathogens and insect pests where no native resistances are available in elite breeding materials (Sánchez-Martín & Keller, 2019), such as for most insect resistances. This is especially true when new methods are applied that allow a faster cloning of genes than ever before (Hatta et al., 2019). Genome editing would be beneficial for a faster reaction of the plant breeders to a changing world. In

the short term, genomics-assisted resistance breeding will help to screen larger populations for the same costs and thus greatly accelerate breeding progress (Miedaner et al., 2020).

In any case, host-plant resistance breeding in maize will be more important in the future, including pathogens (bacteria, fungi, and viruses) and insect pests (both vectors and non-vectors). In Europe, traditional non-GMO plant breeding approaches must be preferred, because the public is still concerned about GM crops. There are researchers (e.g., Herve, 2018) who are optimistic that traditional non-GMO approaches such as exploiting natural quantitative variation in insect resistance, which is a promising and durable strategy, will be successful. However, these are currently not sufficiently investigated, presumably due to major obstacles such as relatively low heritability of traits and limited gain in selection. However, opportunities might be available when looking more carefully at potential beneficial traits such as screening for penetration resistance of maize stalks (e.g., Suby et al., 2020) in order to reduce infestation levels of boring larvae of insect pests. There may be many more potential traits conferring resistance to plant pathogens/diseases and insect pests that can be implemented in maize breeding strategies using traditional non-GMO approaches, in order to respect the vote of the European public.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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