SPECIAL ISSUE ARTICLE

Physiologia Plantarum

New approaches to improve crop tolerance to biotic and abiotic stresses

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Funding information
Ramon y Cajal contract from Spanish Ministerio de Economía y Competitividad, Grant/Award Number: RYC-2016-19325; CNR project Green & Circular Economy, Grant/Award Number: FOE-2019 DBA.AD003.139; Generalitat Valenciana/Fondo Europeo de Desarrollo Regional, Grant/Award Number: IDIFEDER/2018/010; Universitat Jaume I, Grant/Award Number: UJI-B2019-24

Edited by: J. Kapuganti

Abstract

During the last years, a great effort has been dedicated at the development and employment of diverse approaches for achieving more stress-tolerant and climate-flexible crops and sustainable yield increases to meet the food and energy demands of the future. The ongoing climate change is in fact leading to more frequent extreme events with a negative impact on food production, such as increased temperatures, drought, and soil salinization as well as invasive arthropod pests and diseases. In this review, diverse "green strategies" (e.g., chemical priming, root-associated microorganisms), and advanced technologies (e.g., genome editing, high-throughput phenotyping) are described on the basis of the most recent research evidence. Particularly, attention has been focused on the potential use in a context of sustainable and climate-smart agriculture (the so called "next agriculture generation") to improve plant tolerance and resilience to abiotic and biotic stresses. In addition, the gap between the results obtained in controlled experiments and those from application of these technologies in real field conditions (lab to field step) is also discussed.

1 | INTRODUCTION

Crop plants are continuously exposed to multiple abiotic and/or biotic stressors, leading to hindered growth and development and, subsequently, loss of productivity and crop quality. Examples of such stress factors include both abiotic factors such as drought, salinity, and heat, as well biotic stressors such as attack by fungal pathogens and insects, among others. The severity of the effect of such stressors can be clearly attested by multi-billion dollar losses in yield (FAO 2017 report, http://www.fao.org/3/I8656EN/i8656en.pdf).

Recent climate model projections show that the Mediterranean basin is one of the regions that will be influenced mostly by climate change (IPCC, 2019). For this reason, improvement of the tolerance, of relevant crops, to water deficit and heat crucial to adapt to climate changes. In this context, reducing crop yield losses and increasing agricultural water use efficiency (WUE) in the Mediterranean region,

which is one of the highest crop-producing areas in Europe, are a priority. Hence, improving plant response to adverse environmental conditions is in fact particularly important for sustainable food security. Upon water deficit and salinity conditions, as well as under extreme temperatures, plants adapt through physiological and metabolic responses, mostly regulated at the transcriptional level (Gupta et al., 2020; Hirayama & Shinozaki, 2010). Recent evidence show that plants respond to combinations of stress by activating a complex transcriptional module, which differs from their single-stress responses and is related to the actual environmental conditions encountered (Rejeb et al., 2014). Consequently, considerable attention should be directed toward enhancing plant tolerance to combinations of multiple abiotic and biotic stresses, hence approaching real-life agricultural conditions. Understanding the mechanisms involved in plant responses to multiple simultaneous stresses is therefore crucial for the development of broad-spectrum strategies applicable for the improvement of stress-tolerance in crops. Despite the fact that several advancements in the development and application of sustainable technologies to improve plant resilience have been made in the last decade, a gap in the knowledge between controlled conditions and open field studies is still present. This is probably due to the complexity of the natural environment that can "mask" the effects, but also to the difficulties of studying complex plant traits, i.e. root traits, in the field. To fill in this gap is a relevant challange for present, as well as for future researchers. In this review, diverse strategies used to improve plant tolerance and resilience to abiotic and biotic stresses are described and discussed based on recent research.

2 | EXPLOITING THE DIFFERENCES IN GENOTYPES: ANCIENT/LOCAL VERSUS MODERN

2.1 | Overview of crop domestication and achievements up to modern era crop breeding

The study of the human trophic level during the Pleistocene has revealed an increasing carnivorous trend beginning from *Homo habilis* at the lowest level to the highest peak in *Homo erectus*. This trend was reversed during the Upper Paleolithic (hunter-gatherer) and more in the Neolithic, culminating with the advent of agriculture in which humans learnt to cultivate and domesticated edible wild plant species (Figure 1; Ben-Dor et al., 2021). Plant domestication is defined as the process of identifying natural variants of edible plants with valuable agronomic traits, collecting them, and adapting to artificial growth conditions in which watering and fertilization are provided on demand by growers (Chen et al., 2021). Traditionally, this task has been carried out by growers themselves by selecting naturally-occurring variants with enhanced productivity and quality albeit reduced toxicity. This activity has progressively moved to breeders who plan, design and execute plant breeding programs leading to varieties improved in specific plant traits, not only yield-related ones, but also those correlated to resistance to pathogens and/or pests, plant architecture changes
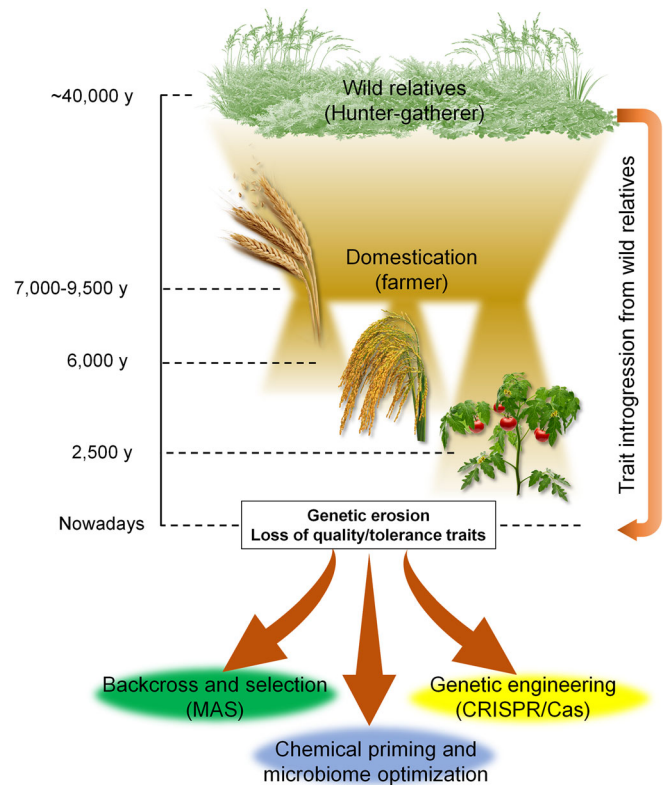

FIGURE 1 Overview of the domestication process of wheat, rice, and tomato from Upper Paleolithic to present day

and morphological traits associated to edible organs (e.g., fruits or different vegetative parts such as roots, stems, or leaves). Throughout history, the domestication process has been associated to dramatic phenotypic changes mirroring variations in the genetic constitution, emphasizing the fact that domesticated crops are indeed genetically-modified versions of their natural parental species. To this respect, domestication has not been a one-way only process but the result of several and often unintended admixtures of different genetic backgrounds that have contributed to shape all currently existing genotypes. Early agriculture domestication served essential feeding purposes but nowadays, market requirements and, lately, climatic constraints are defining new plant breeding targets (Alseekh et al., 2021). When evaluating the world agricultural production, one should focus on staple crops such as wheat or rice and also horticultural crops that constitute an important percentage of edible agricultural products, namely tomato (Abberton et al., 2015; Lobell & Gourdji, 2012). However, woody crops constitute an important portion of the agricultural production in the Mediterranean area, primarily iconic species such as grapevine, olive, and citrus, which are important targets for breeding. Owing to their perennial nature, the effects of climate change can affect different plant processes, ultimately influencing productivity and quality in the middle and long terms. Therefore, in clear contrast to annual staple crops, the productivity of woody crops might be limited by environmentally-driven developmental cues rather than abiotic stress factors, as already discussed in De Ollas et al. I(2019).

Each plant species has its own genetics and reproductive issues, which makes it necessary to treat domestication of each group separately. Modern bread wheat (*Triticum aestivum*) is a hexaploid resulting from two polyploidization events arising from diploid *Triticum urartu* (AA genome) and an *Aegilops speltoides*-related species (BB genome), followed by a more recent addition of the *Aegilops tauschii* genome (DD genome) (Wang et al., 2018). The genus *Triticum* consists of several species among which the diploid *T. urartu* (AA genome donor) is only found in the wild whereas *Triticum monococcum*, almost extant, is cultivated. The tetraploid wheats *Triticum turgidum* and *Triticum dicoccoides*, *Triticum dicoccum*, and *Triticum timopheevii* (Zhuk.) Zhuk. are found either as wild or cultivated forms and the hexaploids *Triticum zhukovskyi* Menabde & Ericz. and *T. aestivum* exist only as cultivated forms. All these species are native to the Near East including Eastern Mediterranean, Southeast Turkey, Northern Iraq, and Western Iran. As a general consensus, allopolyploidization via, hybridization with *A. tauschii* is considered the major force driving diversification during the evolution of the *Triticum* species (Matsuoka, 2011). Domestication of wheat introgressed several morphological and physiological traits such as larger fruits, increased apical dominance, loss of seed dormancy, and synchronized growth and flowering. These are known as "domestication traits" and are important for cultivated wheat to adapt to its agroecological environment, distinguishing crops from their wild progenitors. In cereal crops, including wheat and rice, a common domestication trait is the loss of natural seed dispersal resulting in the seed being retained in the spike facilitating its harvest (Matsuoka, 2011). The complex genetic structure makes breeding of wheat a daunting task. Although hybridization to introgress interesting traits is, to some extent, possible, the effects of the introgressed genes might not be expressed due to the outstanding genome plasticity which, paradoxically, contributes to retaining interesting variations in cultivated wheat. Despite the fact that *T. aestivum* has acquired an outstanding adaptive capacity to a wide range of environmental conditions, there are important traits related to abiotic stress tolerance that need to be introgressed in cultivated wheat to improve resilience to climate change (Choudhary et al., 2019). It is worth noting that the adaptation during domestication can also affect root exudate composition. This is particularly interesting considering that root exudates influence the interactions in the rhizosphere (Williams & de Vries, 2020). An original study on the impact of domestication and crop evolution on root exudate composition has been performed by Iannucci et al. (2017) through metabolite profiling for a panel of 10 genotypes corresponding to the key steps in domestication of tetraploid wheat (wild emmer, *T. dicoccoides*; emmer, *T. dicoccum* and durum wheat, *T. turgidum* subsp. *durum*). These authors showed that, in addition to soil type, the composition of the rhizosphere metabolites is associated with differences among the genotypes of the wheat domestication groups.

Rice is another important staple crop, which constitutes an essential component of diets and livelihoods of nearly 3500 million people worldwide, especially in Asia (Wing et al., 2018). Population genetics modeling and phylogenomics based on high-quality whole genome sequences of different varietal groups and wild *Oryza* species suggest a complicated picture of rice evolution, in which extant rice populations originated from different ancestral populations of *Oryza rufipogon* and/or *O. nivara*, diverging ~300,000–400,000 years ago. According to the most accepted model, de novo domestication seems to have occurred only once in japonica landraces and the subsequent introgression of japonica alleles into wild rice or proto-indica led to the origin of other Asian rice populations, which nowadays contribute to the different rice varietal groups. The genes introgressed from japonica landraces are important for rice domestication such as the Non-shattering allele which, as in wheat, hampers dispersal of seeds and facilitates harvesting; color gene RC that leads to the typical white grain color and the PROG1 gene is responsible of the erect growth that prevents yield loss due to lodging (Matsuoka, 2011; Wing et al., 2018). Separate individual events led to the rise of *O. sativa* in Asia from *O. rufipogon* and *O. glaberrima* in West Africa from *O. barthii*. Interestingly, both species were selected for the same traits involving the same or similar genes, suggesting that rice quality traits are common to different cultures. Conversely to wheat, the domestication of rice included the introgression of traits related to abiotic stress tolerance, such as the HAK5 gene encoding a high-affinity potassium transporter, which confers salinity tolerance along with 10 other loci found in African rice cultivars (Wing et al., 2018). Studies performed in the two major indica rice varieties (generated by independent breeding programs in China and Southeast Asia) identified 200 genomic regions including gene functions associated with important agronomic traits: plant height (SD1), nitrogen assimilation (AMT1.1), XA3, and XA4 involved in disease resistance (Wing et al., 2018), and SUB1A that encodes an Ethylene response factor that confers tolerance to submergence (Bailey-Serres et al., 2010). Among horticultural crops, tomato (*Solanum lycopersicum* L. Mill) is the most important cultivated member of the Solanaceae family. It is thought to have arisen from a bunch of wild ancestors native to the Andean South America and the Galapagos Islands. Accessions of *Solanum pimpinellifolium* L. is thought to be the closest wild ancestors to the cultivated tomato and are native to Coastal Perú and Ecuador. These accessions can be divided into three main genetic groups or ecotypes linked to environmental differences found in the coastal regions of Northern Ecuador, in the montane region of Southern Ecuador and Northern Peru, and the coastal region of Perú (Blanca et al., 2015). In turn, *S. lycopersicum* is divided into two varieties or cultivars, var. cerasiforme with small round-shaped berries (cherry tomatoes) and var. *lycopersicum* with pear-shaped fruits. Whereas *Solanum lycopersicum var. cerasiforme* requires more humid environments to thrive, *S. pimpinellifolium* can occupy both drier to more humid environments, being an important contributor to the development of modern cultivated tomato varieties. There is no biological barrier for *S. pimpinellifolium* and *S. lycopersicum* to cross, therefore, where no geographical barriers such as Andes mountains are present (e.g., Mesoamerica, Ecuador, or central Perú) the possibility for spontaneous hybridization is high, contributing to the development of *Solanum lycopersicum var. lycopersicum*. Nevertheless, this is possibly the most controversial part as it would imply the migration of *S. pimpinellofolium* to Mesoamerica as a wild species where it would

have been domesticated into *S. lycopersicum var. lycopersicum*, however, this possibility, in the absence of any agricultural interest, is quite unlikely. On the contrary, it is more likely that, in a first step, early farmers selected natural accessions of *S. pimpinellifollium* or *S. lycopersicum var. cerasiforme* that were exported to Mesoamerica, where these predomesticated *S. lycopersicum var. cerasiforme* could be further domesticated in a second step. Indeed, the European accessions originated from these Mesoamerican *S. lycopersicum var. lycopersicum* accessions, and is thus a bottleneck for subsequent breeding of tomato in Europe (Blanca et al., 2015), making it necessary to collect wild germplasm accessions for the search for interesting traits. In the last century, breeding efforts in tomato have focused on disease resistance and adaptation to diverse production areas, productivity, and yield uniformity. The introgression of traits coming from *S. pimpinellifolium* or other more distant *Solanum* species have contributed to broaden the genetic diversity of cultivated tomato. The traits selected over the domestication process have been primarily related to fruit size, weight, shape (*FAS*, *SUN*, *OVATE*, and *LC* genes), and ripening (*RIN*, *NOR*, *TDR4*, and *CNR* genes), leading to the identification of several genes responsible of these traits (Lozano et al., 2009; Paran & Van Der Knaap, 2007). In recent years, the introgression of traits related to disease and pest resistance as well as abiotic stress tolerance in cultivated tomato have become a prioritized breeding target. To this respect, an interesting source of tolerance and resistance genes is the tomato wild relative *Solanum pennellii* L. This genotype has shown an outstanding ability to tolerate dehydration (Egea et al., 2018) as well as resistance to the attacks of the red spider mite (Maciel et al., 2018; Maluf et al., 2010; Resende et al., 2002) and the tomato pinworm (Maluf et al., 2010; Rakha et al., 2017). These arthropod pests cause severe damage and important losses in production of tomato and, therefore, generation of resistant lines is a prioritized breeding target. However, it must be taken into consideration that this is a long-term objective.

2.2 | Modification of traits related to abiotic and biotic stress tolerance

Plant water stress tolerance is a complex trait that produces profound modifications of the plants morphological, physiological, and metabolic characteristics. Among all described plant mechanisms associated to increased drought tolerance, control of leaf stomatal closure and root system growth promotion are important to reduce water loss and increase WUE. Although an efficient root system better adapted to changing soil and environmental conditions has been proposed to be essential to maintain productivity in stressed environments (Calleja-Cabrera et al., 2020), regulation of root functional traits and how these traits are related to whole plant strategies to respond to diverse (and often concurring) stress conditions, and also how they influence the interactions with soil microorganisms, is still to be fully investigated. Starting from the classical crop breeding programs, researchers have mapped hundreds of quantitative trait-loci (QTLs) modulating plant morphological and physiological traits to water

stress such as leaf rolling and drying, stomatal aperture and density, leaf cuticular wax thickness and composition, abscisic acid (ABA) content, leaf relative water content, root water potential, root/shoot ratio, and root system architecture (RSA; root volume, root length, and root thickness). Moreover, the application of new sequencing technologies has boosted the identification of molecular markers which could be used for the controlled QTLs introgression, by marker-assisted selection (MAS), into elite varieties (Harris et al., 2007; Landi et al., 2007; Neeraja et al., 2007; Steele et al., 2006). For instance, more than 40 QTLs modulating leaf morphology or increasing the plant WUE have been identified in rice (Ishimaru et al., 2001; Laza et al., 2010) and soybean (Mian et al., 1998). In addition, researchers have focused on roots, which are crucial to detect and initiate the plant responses to the water stress (Dinneny, 2019), and identified a high number of QTLs modulating the dynamics of roots. The development of new tomography techniques and three-dimensional root imaging analysis have increased the number of QTLs identified by medium/high throughput root phenotyping under different growth conditions in different crops, including wheat and tomato (Hargreaves et al., 2009; Helliwell et al., 2017; Hu and Xiong, 2014; Teramoto et al., 2020; Tracy et al., 2010). However, the relative low contribution of most of the QTLs identified to water stress tolerance together with the normal stress combination occurring in crop field trials and undesired phenotypic side-effects have reduced the success-rate of the improvement of crops in the field (Cobb et al., 2019). Global approaches or -omics such as transcriptomics, proteomics, and metabolomics, as well as classical genetic screenings have identified hundreds of key genes/activities involved in morphological, physiological, and metabolic processes with the potential to improve the water stress tolerance in crops. Hence, a more controlled and defined tolerance is obtained when these genes putatively involved in the crop response to water stress are introduced into plants by *Agrobacterium tumefaciens* gene transformation, generating genetically modified (GM) plants. Functional genomics studies have been carried out by overexpressing or suppressing the expression of these genes in crops, focusing on putative regulatory genes such as transcription factors or protein kinases that could potentially activate multiple water stress mechanisms leading to crop tolerance (Hu & Xiong, 2014). For instance, overexpression of drought-induced transcription factors *OsDREB1A* in rice or *SlAREB1* in tomato produce more tolerant plants (Ito et al., 2006; Orellana et al., 2010). In addition to regulatory genes, an increase in the level of expression of genes involved in phytohormone metabolism or in plant osmotic adjustment, such as the rice *OsDSM2* gene that codes a β-carotene hydroxylase 1 or *OsTSP1* that codes a trehalose-6-phosphate synthase activity, have produced more tolerant rice plants (Du et al., 2010; Li et al., 2011). More recently, genome editing technologies such as CRISPR/Cas (Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR-associated protein), TALEN (Transcription Activator-Like Effector Nucleases) and ZFN (Zinc-Finger Nucleases) with hundreds of editing events generated in staple crops up to date (Biswas et al., 2021; Chen et al., 2019) have facilitated the transfer of knowledge from model plants like *Arabidopsis thaliana* to cultivated species, and thus crucial for the

breakthrough in producing water stress tolerant crops. In addition, the use of new technologies, some of them based on CRISPR/Cas systems, to control the expression of plant stress regulatory genes, thus inducing or repressing plant responses according to the environmental conditions, is very promising and opens new fields of interest for crop improvement (Selma et al., 2019). From the editing technologies, CRISPR/Cas9-based genome editing has been used in about 20 crop species during the last years (including rice, tomato, maize, wheat, potato, citrus, and grape) and the results have been summarized in several recent reviews (Biswas et al., 2021; Chen et al., 2019; Jaganathan et al., 2018; Kim et al., 2021). In general, genome-editing application has mainly focused on various traits including yield improvement, nutritional value, biotic and abiotic stress management, improving disease resistance as well as tolerance to abiotic stresses such as drought and salinity. From these, we have highlighted the genome editing events conferring tolerance to biotic and abiotic stresses in tomato, wheat, and rice in Table 1. However, all these genome-editing technologies may produce deleterious effects in crops by genome-wide off-target mutations, making the generation of new water stress tolerant crops by genome editing a little bit more complex than expected. More problematic is the public concern raised against these technologies. This has provoked the establishment of strict regulatory rules concerning the use of genetically-modified or genome edited organisms (collectively labeled as GM) in several countries including the European Union, slowing down the production of water stress tolerant crops. Indeed, only Monsanto has a maize event, which is tolerant to drought stress approved for public use according to the GM approval database (https://www.isaaa.org/gmapprovaldatabase/default.asp). To answer the concern of the society, considerable effort has been made to obtain crops with genome modifications but, without sequence integration of foreign DNA. For example, genome of immature embryos or protoplasts has been edited using CRISPR–Cas9 ribonucleoprotein complexes, obtaining very promising results for a high number of species, including wheat, maize, and potato (Andersson et al., 2018; Liang et al., 2017; Svitashev et al., 2016). In the case of biotic stresses, introgression of QTLs by MAS has been widely used in cereals, including rice and wheat, to obtain varieties less susceptible to late fungal blight (*Phytophthora infestans* L.), bacterial blight (*Xanthomonas campestris* L.), or powdery mildew (*Podosphaera xanthii* L.) (Collard & Mackill, 2008).

TABLE 1 List of reported gene editing strategies to enhance biotic and abiotic stress tolerance in wheat, rice and tomato (adapted and expanded from Biswas et al., 2021)

Crop	Phenotype	Gene(s)	Molecular event	References
Rice	Bacterial blight resistance	*OsSWEET11, 13 and 14*	Base insertion/deletion	Xu et al. (2019)
	Drought tolerance	*OsSRL1, OsSRL2*	Base deletion	Liao et al. (2019)
	Salinity tolerance	*OsRR22*	Base insertion	Zhang, Liu, et al. (2019)
	Drought and salinity tolerance	*OsDST*	Base deletion	Kumar et al. (2020)
	Phosphate deficiency	*OsACS*	Base insertion/deletion	Lee et al. (2019)
	Bacterial blight resistance	*OsXa13/Os8N3*	Base deletion	Kim et al. (2019) Yu et al. (2021)
	Drought tolerance	*OsERA1*	Base insertion/deletion	Ogata et al. (2020)
	Salinity tolerance	*OsHDA710*	Base deletion	Ullah et al. (2020)
	Salinity tolerance	*OsNAC041*	Base insertion/deletion	Bo et al. (2019)
	Multiple abiotic stress tolerance	*OsNAC006*	Base insertion/deletion	Wang et al. (2020)
	Bacterial blight resistance	*OsAvrXa7*	OsSWEET14 promoter base deletion	Zafar et al. (2020)
Wheat	Resistance to *Fusarium graminearum*	*TaNFXL1*	Base insertion/deletion	Brauer et al. (2020)
	Drought Tolerance	*TaDREB2, TaERF3*	Base insertion/Deletion	Kim et al. (2018)
Tomato	Bacterial speck Resistance	*SlJAZ2*	Base deletion	Ortigosa et al. (2019)
	Enhanced resistance to *Pepper mottle virus*	*SleIF4E1*	Base deletion	Yoon et al. (2020)
	Drought Tolerance	*SlNPR1*	Base insertion/Deletion	Li et al. (2019)
	Powdery mildew. Tolerance	*SlPMR4*	Base insertion/deletion/ inversion	Martínez et al. (2020)
	Enhanced resistance to *Pseudomonas syringae* pv. tomato, *Phytophthora capsici* and Xanthomonas spp	*SlDMR6-1* and *SlDMR6-2*	Base deletion	Thomazella et al. (2021)
	Salinity tolerance	*SlHKT1;2*	Base substitution	Vu et al. (2020)
	Salinity tolerance	*SlHyPRP1*	Base deletion	Tran et al. (2021)

These QTLs have been introgressed and accumulated into elite cultivars using a gene pyramid strategy with consecutive rounds of introgression and selection of the resistant traits, finally obtaining several QTLs that define different resistance genes into a single genetic background such as resistance to leaf and stem rust in wheat (Zhang, Chi, et al., 2019), blast resistance in rice (Singh et al., 2001), or strip rust resistance in barley (Castro et al., 2003). However, the use of genetic engineering to generate GM crops has boosted the obtention of varieties resistant to some of the most devastating pest and diseases (Douglas, 2018). Particularly, the production and accumulation in several crops of Bt toxins naturally produced by the soil bacterium *Bacillus thuringiensis* have been successful against a great diversity of phytophagous insects, particularly lepidopterans. Nowadays, more than 250 GM events in crops are approved for public use according to the GM approval database. Other important target traits are those related to metabolite constitution that provide fruits and other edible parts of plants with attractive colors, aromas, and nutritional properties (Fernie & Schauer, 2009; Nadi et al., 2019) as well as production of metabolites involved in plant defense against pathogens and pests (Arbona & Gómez-Cadenas, 2015). In the process of domestication, the first set of metabolites has been fixed and favored, whereas the second array of compounds that crops have evolved to survive and thrive in a threatening environment has been progressively reduced. This has led to virtually defenseless plants with poor competitive abilities compared to their wild relatives (Szymański et al., 2020). To this respect, certain volatile organic compounds or VOCs are considered damage-associated molecular patterns (DAMPs) acting in plant–plant communications to induce plant defenses in nearby same plant populations (Meents & Mithöfer, 2020). herbivore-induced plant volatiles (HIPVs) have drawn attention as interesting targets for breeding owing to their ability to modify trophic interactions between plants, pests, and their natural enemies (Turlings & Erb, 2018). Furthermore, some of them also show an effect on surrounding plants activating their defense responses before the pest or disease strikes (Pérez-Hedo et al., 2021). Catola et al. (2018) demonstrated that VOCs emitted by stressed tomato plants induced VOC emission in unstressed receivers, also increasing the attraction of parasitic wasps, potentially improving protection against aphid attacks under conditions of reduced water availability. Moreover, VOC profile is influenced by the type of plant-pathogen interaction, being different after infection with virulent or avirulent bacterial strains in tomato. In virulent interactions, VOC blend is enriched in esters of (Z)-3-hexenol with acetic, propionic, isobutyric, or butyric acids, and several hydroxylated monoterpenes (e.g., linalool, α-terpineol, and 4-terpineol), whereas plants mainly emit monoterpenes and SA derivatives in avirulent interactions (López-Gresa et al., 2017). Resistance to phytophagous spider mites is also reflected in differences in the VOC profile in tomato, involving metabolites that induce defensive responses in surrounding plants (Weinblum et al., 2021). Indeed, treatments with (Z)-3-hexenyl propionate and (Z)-3-hexenyl butyrate, known as green leaf volatiles, resulted in stomatal closure, pathogenesis-related gene induction and enhanced resistance to bacterial infection. These results point toward the potential application of green leaf volatiles as

inducers of protection against biotic and abiotic threats (López-Gresa et al., 2018). It has recently been shown that exposure of tomato to different HIPVs induces changes in endogenous metabolite biosynthesis preparing plants to endure the attack of the two-spotted spider mite *Tetranychus urticae* and the tomato pinworm *Tuta absoluta* by reducing pest survival, worsening pest reproductive traits and, subsequently, reducing the damage induced (Pérez-Hedo et al., 2021). Indeed, some species of lepidopterans have been evolved to secrete an enzyme, glucose oxidase, that causes stomatal closure in tomato and soybean inhibiting the emission of several HIPVs (e.g., (Z)-3-hexenol, (Z)-jasmone, and (Z)-3-hexenyl acetate), as important airborne signals inducing defense responses in surrounding plants (Lin et al., 2021). Moreover, VOCs produced by different soil microorganisms have also been shown to induce defense responses in plants and attract natural enemies in different plant species (D'Alessandro et al., 2014; Singh, Singh, et al., 2021), hence, playing an important role in multitrophic interactions (Piechulla & Degenhardt, 2014). Physiological and biochemical responses induced by plant or microorganism volatiles could also be advantageous under abiotic stress conditions, both exerting overlapping roles (ul Hassan et al., 2015; Vickers et al., 2009).

Defense responses also involve endogenous changes in metabolites and enzyme activities that participate in the protection of plant cells from attack of microorganisms and arthropod pests. The array of endogenous metabolites induced in response to pathogen or pest attacks varies depending on the plant species, the pre-existing defenses, and the intensity of the attack (Ahuja et al., 2012; He et al., 2018; Piasecka et al., 2015). Indole glucosinolates and camalexin are the most important defense metabolites in the model plant *A. thaliana* (Buxdorf et al., 2013; Schuhegger et al., 2006); glycoalkaloids (Friedman, 2000) and acyl-sugars from epidermal glandular trichomes (Paspati et al., 2021; Schilmiller et al., 2010) in tomato, while benzoxazinoid metabolites (4,7-dimethoxy-1,4-benzoxazin-3-one or DIMBOA and its hydroxylated and glycosylated derivative HDMBOA-glc) are relevant in corn (Ahmad et al., 2011). Their abundance and distribution in plant tissues have an impact on the ability of plants to defend themselves from pathogens and pests. Therefore, constituting important metabolite traits for selection of cultivars and accessions (Chu et al., 2011; Jogawat et al., 2021).

With the advent of high throughput metabolite profiling techniques, it has been possible to screen large amounts of plant accessions for defense-related compounds that could constitute an advantage under field conditions contributing to reduce pesticide input (Arbona & Gómez-Cadenas, 2015).

Several bioinformatics tools to process and analyze metabolomics data are already available and constitute well-established methods. These are available either as integrated packages that perform extraction of features, alignment, and their annotation or as separate tools that can be used sequentially. More importantly, the increasing number of comprehensive metabolite databases has boosted the nontargeted metabolome screening and the identification of metabolite features important in defining plant phenotypes (Table 2).

2.3 | Boosting abiotic and biotic resistance traits discovery: the importance of high throughput plant phenotyping technologies

Plant stress response traits are part of the plant phenotype, that is the observable and measurable plant characteristics that are the product of the interaction of the genome (G), the environment (E) and, in agriculture context, the agronomical management (G × E × M; Hawkesford & Riche, 2020). Plant phenotyping is a cornerstone in plant breeding: the selection of plants with favorable traits requires considerable efforts, investment and it is quite time consuming. Among other approaches, the exploitation of natural biodiversity (Araus et al., 2018; Huang & Han, 2014) and the exponential growth of genome editing technologies (Miladinovic et al., 2021; Zhan et al., 2021) offer great opportunities for crop improvement. To obtain solid results, it is usual to phenotypically screen hundreds of genetic lines and plants under diverse climatic conditions, either in controlled environments or open field experiments. Plant phenotyping for crop

TABLE 2 List of databases for annotation of metabolites in nontargeted analyses

Database name and website	Analytical information available	Query type	Publicly availability	Interconnection with metabolomics pipelines
Metlin https://metlin.scripps.edu/	Experimentally confirmed mass spectra of metabolites in different ionization modes and CID energies.	Precursor mass, specific precursor-to-product mass transitions, neutral loss as single or batch queries.	Public, users need to sign up	Can be queried from xcms Connects with KEGG and PubChem
Human Metabolome Database https://hmdb.ca/	Experimental or theoretical mass spectra of metabolites in different analytical platforms, ionization modes and CID energies, contains chemical, clinical, and biochemical information of metabolites, including specific tissue or cellular location accumulation.	Compound name, Precursor mass, Precursor-to-product fragmentation pattern, GC/MS peak lists, 1D or 2D NMR.	Publicly available, no sign up required. Several databases can be freely downloaded.	Metfrag in-silico fragmentation tool https://ipb-halle.github.io/MetFrag/
Biological Magnetic Resonance Data Bank https://bmrb.io/metabolomics/	Fully downloadable experimental Nuclear Magnetic Resonance Data.	Compound name, mass, structure, 1D or 2D NMR peak lists.	Publicly available, no sign up required.	—
Mass Bank http://www.massbank.jp/ https://massbank.eu/MassBank/	Experimental mass spectra of metabolites in different analytical platforms, ionization modes and CID energies.	Basic search includes compound name, mass, or molecular formula. Advanced search allows peak lists, peaks derived from molecular formulas or peak differences.	Publicly available, no sign up required.	—
Golm metabolome database http://gmd.mpimp-golm.mpg.de/	GC/MS spectra of derivatized compounds, provides peak relative abundance and retention indices of compounds relative to the column used (VAR5 or MDN35)	Curated spectrum of the compound of interest. Allows batch processing of several GC/MS runs through TargetSearch[a] or TagFinder[b] software. Databases are free to download in text mode.	Publicly available, no sign up required.	TargetSearch and TagFinder for batch processing of several GC/MS runs.
Metabolights https://www.ebi.ac.uk/metabolights/index	Fully downloadable series of metabolomics experiments (MS or NMR-based), contains information on metabolites (retention time, mz or NMR chemical shift)	Organism, technology, or organism part.	Publicly available, no sign up required.	—

[a]Cuadros-Inostroza et al. (2009).
[b]Luedemann et al. (2008).

genetic improvement often requires multiannual and multilocation trials with invasive and disruptive sampling (Sellami et al., 2019; Zhang et al., 2021), implying intense manual operations, that in turn weaken the significance and the precision of the results. While, we over the last decades have seen a rapid progresses in the development of genomic tools, such as next generation sequencing technologies that has allowed for an unprecedented, efficient, and low-cost sequencing of plant genomes, plant phenotyping has become the bottleneck in plant breeding programs aimed at establishing or selecting genotypes that maintain or increase crop performance. In the last years, new technological approaches has emerged and rapidly grown under the so-called plant phenomics, with the objective of developing high throughput plant phenotyping (HTPP) methods and tools for fast and noninvasive studies of the phenotypes (Fiorani & Schurr, 2013; Furbank & Tester, 2011; Pasala & Pandey, 2020; Tardieu et al., 2017). Plant phenomics promotes transdisciplinary and cross-border technology applications, taking advantage of the incredible developments in the fields of electronics, sensors, computer science, robotics, Information and Communication Technologies (ICT), data science and artificial intelligence. Plant phenomics has been defined as the development and application of a suite of tools and methods to accomplish three major goals: (1) capture information on structure, function, and performance of large numbers of plants, together with their environment; (2) analyze, organize, and store the resulting datasets; and (3) developed models able to disentangle and simulate plant behavior in a range of scenarios (Pasala & Pandey, 2020). In a typical phenotyping platform configuration, information is captured by optical sensors able to detect plant tissue reflectance at various wavelengths (RGB, IR, NIR, SWIR, fluorescence, 3D CT/PET/NMR, hyperspectral, and multispectral) or signals coming from physical or chemical sensors detecting changes on plants or environmental parameters. Sensors are normally mounted on mobile carriers, typically gantry systems in greenhouses or in open field and UAVs or phenomobile in open field, that move over the plants and canopies to detect the reflectance signals (Madec et al., 2017). In an alternative configuration under a protected environment, plants can be transported by conveyors to fixed sensors mounted in imaging chambers. Data are then stored in specific repositories and analyzed via, algorithms and pipelines to extract the main plant features and traits, which are then examined by statistical and data science approaches. Images are analyzed by imaging procedures implementing computer vision approaches or, more recently, artificial intelligence pipelines (deep learning, machine learning) (Li, Zhang, & Huang, 2014; Singh, Jones, et al., 2021).

It is worth noting that HTPP can be carried out at different scales and levels of biological organization, spanning from laboratory, to controlled conditions infrastructures, to open field (Figure 2; Daoliang et al., 2021). In a typical laboratory set-up, benchtop robotic platforms and instruments allow the study of traits at plant and cellular level, particularly on model plants such as *Arabidopsis*, characterized by fast and very compact growth. Growth chambers and greenhouses offer protected environments in which experimental plants can be grown under controlled or semi-controlled environmental conditions. These infrastructures are equipped with sophisticated automated platforms that manage potted plants and shoot images with various sensors present either in imaging chambers (plant-to-sensor configuration) or on gantry system (sensor-to-plant configuration). Greenhouse or growth chamber HTPP is generally performed to carefully study plant responses under specific growth conditions, trying to detect morphological and physiological traits associated with the response. Open field HTPP platforms relay on experimental design and sites carried out on field plots, a typical approach largely used in plant breeding and agronomy. Open field HTPP platforms operate in real conditions trying to capture the complexity of the G × E interaction under uncontrollable environmental factors and stresses. According to their usage scenarios and imaging distance, field HTPP platforms can be categorized into ground-based and aerial platforms.

The three types of HTPP platform described above, should not be considered mutually exclusive, but rather as complementary tools to better assess plant traits and gather more insights into gene function. The choice of HTPP platforms and approaches to be used must be evaluated case by case and should be driven by specific scientific questions. Indeed, the different levels of HTPP approaches are characterized by different levels of investment intensity and costs that must be carefully considered (Reynolds et al., 2019). As suggested by Costa et al. (2019), the application of field-phenotyping technologies to monitor plant/crop responses should be expanded to assess a larger number of varieties and replicates upon natural growth conditions at a lower cost. This could be particularly important in the several areas bordering the Mediterranean sea that are especially prone to be subjected to the effects of climate change. Outputs from whole plant/ecosystem phenotyping should be integrated with molecular phenotyping (transcriptomics, proteomics, metabolomics, etc.) for improving practical application (Costa et al., 2019).

Many national and international initiatives and networks are active worldwide to establish high-level research infrastructures for HTPP, to create research infrastructure able to comprehensively address multiscale plant phenotyping under different agroclimatic scenarios. Several of them have been developed in Europe, allowing to measure the diversity of traits contributing to plant performance and enabling prediction-making (Pieruschka & Schurr, 2019). Particularly, the project EMPHASIS (https://emphasis.plant-phenotyping.eu), supported by the ESFRI program under the 2016 roadmap, structured a multi-node European infrastructure of plant phenotyping platforms that allow access to researchers, breeders and agri-food industry, paving the way to boost crop genetic improvement (Mir et al., 2019; Yang et al., 2020).

HTPP has already been proven to be very relevant in speeding up discoveries in many areas of plant science, including plant physiology (Janni et al., 2019; Muller & Martre, 2019), genetics (Singh, Jones, et al., 2021), breeding (Yang et al., 2020), and phytopathology (Mahlein et al., 2018). HTPP was clearly shown to be efficient in detecting plant stress response both in greenhouse conditions and in open field.

The success of genomic assisted breeding for plant stress response is related to the precision in marker-trait association and estimation of genomic breeding values, mostly depending on coverage
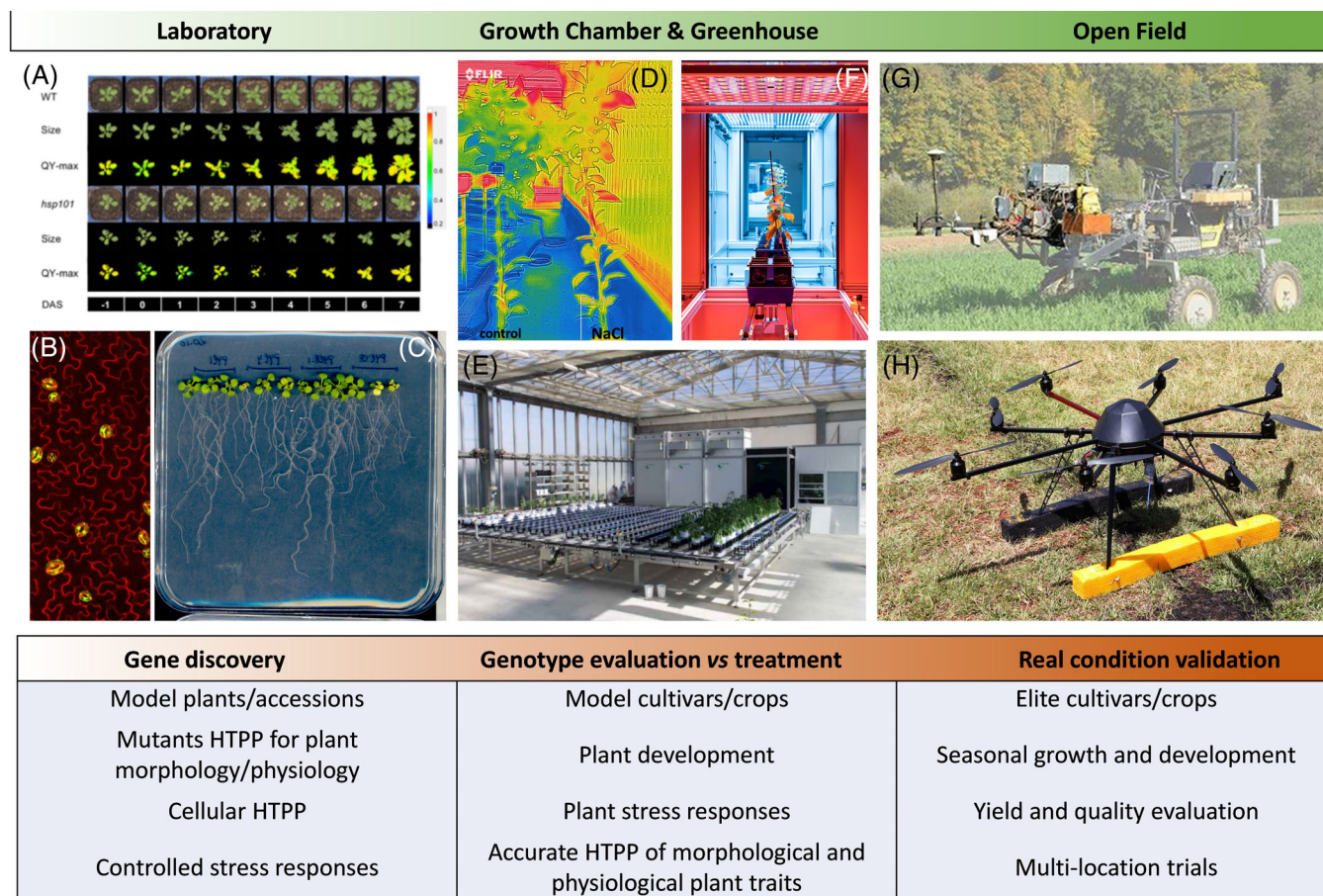
FIGURE 2 Overview of high throughput plant phenotyping (HTPP) multiscale strategies. HTPP embraces technologies that can be applied at different scales and sizes, from lab, to controlled (growth chambers) or semi-controlled (greenhouses) conditions, to open field. Images illustrate some relevant examples and applications of these approaches. The table in the bottom summarizes the main targets and features of the studies carried out at the specific HTPP scale. Comparison of rosette size of Col-0 plants grown under four control conditions and 3, 6, and 9 h of heat stress (45°C) treatment, from Gao et al. (2020) (bioRxiv https://doi.org/10.1101/838102, CC-BY-NC-ND) (A) guard cell-targeted GFP overexpression, by A. Baker, CC BY-SA-NC (B) *Arabidopsis thaliana* seedlings growing in vertical agar plates, credit: Miguel González-Guzmán (C) thermographic image of *Citrus sinensis* subjected to salt stress (left) and control conditions (right) from Gonzalez-Guzman et al. (2021) (D) poplar trees on the phenotyping system in ORNL's Advanced Plant Phenotyping Laboratory. Credit: Carlos Jones/ORNL, U.S. Dept. of Energy CC-BY (E), Phenotyping facility at ALSIA Basilicata (Italy), credit: Francesco Cellini (F), phenotyping platform PhenoTrac 4 of the Chair of Plant Nutrition from the Technical University of Munich, from Barmeier and Schmidhalter (2017) *Frontiers in Plant Science*, 8, 1920. doi: 10.3389/fpls.2017.01920 CC BY (G) and an unmanned aerial vehicle (UAV) to be used for data collection International Potato Center (https://wle.cgiar.org/news/attack-drones) CC-BY (H)

and precision of genotyping and phenotyping. For several important agronomic traits, there is a wide gap between the discovery and practical use of QTL for crop improvement. This limitation has been associated to the low accuracy in QTL detection resulting from low marker density and the manual collection of phenotypes of complex agronomic traits. Using high-throughput genotyping (HTG) in combination with high-throughput digital phenotyping it is possible to increase marker density and improve the precision and resolution of QTL detection (Bhat et al., 2020). The quantitative measurement of drought resistance phenotyping markers (i.e., transpiration or leaf moisture content) in addition to automated HTPP platforms provides an opportunity to correlate traditional and novel DR traits and also perform DR-related genes mining. Using LemnaTec's Scanalyzer3D, 44, and 21 DR QTLs were identified in a set of wild barley

introgression lines (Honsdorf et al., 2014) and a wheat RIL population under water stress (Parent et al., 2015), respectively. Using a similar approach, 51 DR traits (including digital and traditional traits) were identified in an association panel and a recombinant inbred line (RIL) population. As a result, 93% of the loci found by genome-wide association studies or GWAS co-localized with previously reported DR-related QTLs and different loci containing known DR-related genes were identified. This study rendered 69 trait–locus associations identified by both GWAS and linkage analysis. Moreover, the role of a DR gene, *OsPP15*, was confirmed by genetic transformation experiments, demonstrating that the combination of HTPP and genetic mapping is a promising approach for the discovery of novel DR genes (Guo et al., 2018) as well as other interesting traits.

Recently, HTPP was applied on a germplasm panel formed by a set of 36 genotypes of durum wheat, selected from a core set of 452, called the single seed descent (SSD) collection, produced by SSD from a worldwide durum wheat germplasm collection (Danzi et al., 2019), with the aim to identify genotypes that are resilient to water stress for breeding purposes. The results indicate that HTPP can discriminate genotypes that use soil water more efficiently. Plant imaging is quite powerful in detecting early stress response in fruit crops as well. Leaf angle and leaf area index in grape are two traits correlated with drought stress response. Particularly, in the drought stress experiments carried out in grapevine mentioned above, leaf angle was collected during drought imposition using automatic HTPP platforms employing a 3D imaging reconstruction method based on multi-view stereo and structure from motion and 2D RGB images. The digital traits were well correlated with the same traits measure by standard methods, and at the same time represented early proxies of drought response (Briglia et al., 2020).

In addition to genetic analysis and ecophysiological measurements, it is very useful to determine variations in crop yield of selected panels to changes in resource availability in field experiments. Progress in sensors, aeronautics, and high-performance computing as well as in user-friendly data management have increased the use of field HTPP (Araus & Cairns, 2014). Another example on how HTPP approaches can be very useful under open field conditions to monitor stress responses related to nitrogen use efficiency and WUE was provided by experiences on the PhénoField® platform (Beauchêne et al., 2019). PhénoField® manages a moving rainout shelter and irrigation systems that allow the application of different drought conditions in field, all equipped with environmental sensors for the control of drought stress intensity. PhénoField® uses a high-throughput phenotyping technologies set (imaging sensors RGB, NIR/VIS, LiDAR) mounted on an automated gantry, allowing frequent and noninvasive high-resolution measurements of the canopy. An experiment was carried out on a panel of 22 winter bread wheat varieties tested with two different water regimes and two nitrogen levels. The study demonstrated the capacity of the HTPP system to characterize drought and nitrogen stress impact on wheat growth, with the accuracy needed to differentiate wheat varieties.

HTPP approaches are also powerful to put the hidden plant organ, the roots, under the spotlight. Roots are involved in water and nutrient uptake from the soil, and therefore act as the sensor of soil abiotic stresses, such as drought and salt. Furthermore, roots interact with rhizosphere microbiota, influencing the RSA, and in a way modulating the adaptation of plants to the soil environment. RSA and root plasticity are very important traits for plant abiotic stress tolerance, but breeders too often do no target these traits because of the inherent difficulties in following them throughout the experiments. Since roots are buried in the soil, they have to be shoveled out to be examined with the risk of destroying the architecture. In the past, scientists developed simple soil-free systems to follow root development using seedlings on agar, hydroponic or paper pouches. These systems allow the strict control of the experimental conditions but are far from the soil environment. Soil is a very heterogeneous nonsterile environment

and has a strong influence on the root growth and makes monitoring the intact root system for analysis difficult. The advent of plant phenomics stimulated many research groups to develop HTPP imaging technologies for plant roots grown in soil (Gandullo et al., 2021; Joshi et al., 2017; Nagel et al., 2012; Rellán-Álvarez et al., 2015).

The importance of HTPP for root phenotyping has been thoroughly discussed (Atkinson et al., 2019) prospecting great advanced in this area for plant science and crop breeding. A summary of the different HTPP approaches, applications and goals is provided in Figure 2.

3 | PRIMING TO THE RESCUE

Different methodologies have been employed for enhancing climate change-related stress tolerance in plants and therefore increase crop WUE; some are particularly time-consuming (e.g., conventional breeding) and others such as plant genetic modification are currently unacceptable in many countries around the world, and Europe in particular (Hu & Xiong, 2014). As an attractive alternative, priming is a rapidly emerging field in plant stress physiology and crop stress management (Mauch-Mani et al., 2017; Sako et al., 2020; Savvides et al., 2016). Stimuli from pathogens and pests, beneficial microorganisms, natural and synthetic compounds, nanomaterials as well as the presence of abiotic stresses at mild levels induce the activation in plants of a specific physiological state called "priming," which is marked by an enhanced activation of induced defense mechanisms (Alagna et al., 2020; Mauch-Mani et al., 2017). After stimulus perception, changes may occur in the plant at the physiological, transcriptional, post-translational, metabolic, and epigenetic levels. Under subsequent stimuli, the plant effectively mounts a faster and/or stronger defense response that results in increased resistance and/or stress tolerance (Mauch-Mani et al., 2017; Pieterse et al., 2014). Stress impacts on plant growth and yield in primed plants are remarkably reduced in comparison with nonprimed plants (Hu & Xiong, 2014). However, information on the mechanisms underlying the improved tolerance is still patchy, or in several cases unknown, hindering the development of novel products and practices; thus, further research is needed to better understand how plants adapt to multiple environmental constraints after priming and design stress management practices based on chemical and/or biological priming. Focus has so far been placed primarily on the evaluation and development of chemical treatments (Sako et al., 2020), which lead to an efficient induction of defense pathways without resorting to genetic modifications. Furthermore, root-associated microorganisms, such as arbuscular mycorrhizal (AM) fungi and plant growth promoting bacteria (PGPB), are also important actors in this context (often being classified as biostimulants) and the optimization of their real utilization has a great potential in an innovative and sustainable agriculture context, providing benefits to plant growth and health through an increase in plant nutrition, conferring plant tolerance to abiotic stresses and improving resistance to biotic threats (Balestrini et al., 2018; Busby et al., 2017). On one hand, PGPB can act as "priming stimulus" through diverse mechanisms such as modifications in phytohormonal levels,

antioxidant compounds, osmolytes (proline), and polyamines, regulation of stress responsive genes, changes in root morphology, and emission of VOCs (Alagna et al., 2020 and references therein). They can also produce complex blends of VOCs, as observed in *Pseudomonas chlororaphis*, as signal for developing priming and systemic responses in themselves and neighboring plants (Brilli et al., 2019). On the other hand, an important role of AM fungi is that of bio-fertilizing microorganisms, thanks to their ability to establish mutualistic symbioses with the roots of most crop species. These symbiotic fungi are essential elements for plant nutrition as their root-colonizing hyphae can extend for many meters in the ground helping plants to acquire mineral nutrients and water present in the soil, while in turn receiving carbon compounds (Balestrini et al., 2020). However, additional information on the best plant-microorganism combinations, important for an optimization of the practical use of beneficial soil microorganisms in agriculture particularly under unfavorable conditions, must be still obtained. The application of these beneficial fungi as priming agents in the field still requires new knowledge on the molecular mechanisms involved in nutrient transfer, metabolic pathways affected by single, multiple and combined stresses, and physiological mechanisms leading to improved tolerance (Alagna et al., 2020). Notably, the interplay between chemical and biological priming is gaining interest among researchers in plant priming and biostimulation owing to its potential to maximize the primed status (e.g., Irankhah et al., 2020). In addition, actions aimed at crop diversification include the adoption of drought-tolerant crops particularly indigenous plant species well adapted to local climatic conditions, as well as crop varieties that are resistant to pests and diseases, reducing the need for pesticides and, as a consequence, reducing carbon emissions by decreasing pesticide demand and the number of in-field applications. In the last years, several efforts have been made to develop sustainable plant protection strategies with a low impact for the environment. Among them, nonpathogenic plant viruses may have important beneficial roles in plants, mainly under harsh environments where they can confer tolerance to drought and extreme soil temperatures (Roossinck, 2015), serving as endogenous priming agents, at least in experiments carried out under controlled conditions (Alagna et al., 2020 and references therein). Additionally, spray-induced gene silencing through the foliar application of double-strand RNA (dsRNA) might have high potential in defense priming, acting on a target pathogen and inducing enhanced plant resistance (Nerva et al., 2020).

Priming can be applied at different developmental stages, i.e. from seed (Li, Peng, et al., 2014; Paparella et al., 2015) to adult generative plants (Saleethong et al., 2016), and using different application methodologies (Filippou et al., 2013). Although existing literature has mainly focused on the application of chemical agents after seed germination and at later developmental stages, interest has recently started shifting to the application of priming agents to the seed stage, i.e. seed chemical priming, as it shows outstanding advantages. Treatment of seeds prior sowing would be easier in practice, economically more efficient and cleaner than treatments at later developmental stages, as priming treatments are applied specifically to seeds in low amounts avoiding release of chemicals and/or microorganisms to the environment and, hence, implying a low risk of toxic exposure for operators while at the same time having a positive impact that improves seed germination and seedling establishment (Johnson & Puthur, 2021) even under adverse environmental conditions (Dragicevic et al., 2013). Furthermore, recent studies indicated that seed priming may be a method of improving tolerance through memory imprint (i.e., changes in the epigenome, Jiménez-Arias et al., 2015), suggesting a prolonged protection against abiotic stress at later stages of development (Hu & Xiong, 2014). In addition, seed priming can be further improved through the employment of advanced nanomaterials as coating agents, which act as nanocarrier systems offering controlled release of the priming agent (Ioannou et al., 2020), while seed nano-priming with nanoparticles showed antimicrobial properties in addition to having a stimulatory effect in plant growth (do Espirito Santo Pereira et al., 2021). Interestingly, seed priming demonstrates great potential as a green strategy for the improvement of traits of underutilized (orphan) crops or deprecated cultivars of widespread crops, which despite showing outstanding organoleptic traits are often inferior in productivity, show low seed germinability, and are challenged more intensely by adverse environmental conditions (Tadele, 2019).

4 | PERSPECTIVE IN THE EXPLOITATION OF THE ROOT-ASSOCIATED MICROBIOTA TO COPE WITH CLIMATE CHANGE

It is already known that diverse plant species or genotypes can be selected for different soil microbial communities. Selective pressure is mainly strong in the rhizosphere, the area around the roots that is directly influenced by root processes and is inhabited by the rhizosphere microbiome. It is already known that plants have a key role in shaping their microbiomes, and this can drive the selection of plant traits that sustain beneficial microbiomes (Bakker et al., 2020). Particularly, root exudates might play a primary role in selecting rhizosphere microbiota. It has been proposed that influencing the rhizosphere microbiome by the alteration of the root exudation patterns might open up new opportunities to increase plant performance, with positive effects on crop production (de Vries et al., 2020). Although an important body of knowledge has been generated on different biological, physiological, and ecological aspects of the interactions between plants and beneficial microorganisms (Bakker et al., 2020; Toju et al., 2018), most information often comes from noncrop plants in controlled experiments whereas the functional potential of the plant associated microbiota (i.e., the plant microbiome) remains largely unknown (Toju et al., 2018). The widespread use of -omics technologies has recently enabled the dissection of the microbial actors as well as the molecular mechanisms involved in the complex interactions in plant associated microbiomes (Toju et al., 2018). Several aspects of these interactions, including the mechanisms at the basis of the regulation of plant defenses in the presence of beneficial microorganisms, have not been fully elucidated. Additionally, optimization of plant-microbial associations is acknowledged as a challenging task mainly

due to the complexity of plant-microorganism and microorganism–microorganism interactions, and the reliance of those interactions on environmental conditions (Singh et al., 2020).

Improving plant resilience requires highlighting how these interactions are affected over time under stressed conditions, mainly focusing on growth of crop species under diverse pedoclimatic conditions following different plant, soil, and water management approaches. The outcome of these overlapping interactions is environment-dependent, and interactions may be beneficial or harmful depending on the actual conditions, often rendering interactions not sufficiently stable for practical application. The exploitation of these microorganisms for real field application requires improvement in the knowledge of how they interact with plants and the environment, providing information on the complex feedbacks between plants and microbes during, and mainly after, a stress event (de Vries et al., 2020). Large-scale adoption of these practices still remains to be explored mainly for the inconsistency in the efficacy upon diverse environmental conditions. It is also important to remark that the underlying abiotic stress events in different climate-sensitive soils can affect microbial soil and rhizosphere communities (Jansson & Hofmockel, 2020), both in terms of diversity and structure, leading to subsequent changes depending on the stress level and recovery. These changes in soil microbial communities can lead to a modification of the interactions with roots under severe or mild persistent drought with the creation of diverse plant-microbial interactions during the recovery, potentially affecting future plant and soil responses to drought (de Vries et al., 2020). An additional step, to understand the potential of the soil microbiome and to predict the impacts of environmental stresses on its key function, is to move from metagenomes studies to the so-called soil "metaphenome." This approach has been described in Jansson and Hofmockel (2018) as the product of expressed functions encoded in microbial genomes (metagenome) and the environment (resources available; spatial, biotic, and abiotic constraints). A point that should be stressed by ongoing research projects is the exploration of the soil microbial biodiversity that is still unknown. As reported by Wurtzel et al. (2019), over 99% of bacteria and archaea are uncultured or undiscovered, suggesting that several prokaryotic enzymes and metabolic pathways (with a prospective to be re-used in plants) remain to be identified.

AM fungi are among the beneficial soil microbes with a role in improving crop tolerance to abiotic stresses. Exploitation of AM fungi has been extensively discussed in the context of agriculture, considering that the AM symbiosis is the dominant mycorrhizal symbiosis formed by most crops (an exception being e.g., species in the Brassicaceae) and its potentially positive, multifunctional role in plant nutrition, pathogen protection, stress tolerance, and soil structure provision (Chen et al., 2018). In applied research focused on these symbioses, attention should be paid to the improvement in the production and application of the mycorrhizal fungal inoculum, directly addressing the decline in mycorrhizal abundance in agricultural fields. "Mycorrhizal technology"—described as the set of measures to optimize local mycorrhizal abundance and diversity in terms of functioning for attaining sustainability of agroecosystems (Rillig et al., 2016)—needs to be supported by research such as (1) a better understanding of the relative contribution of AM symbiosis to any aspect of sustainability; (2) defining which parameters influence symbiosis effectiveness, helping to prevent other agricultural management approaches from interfering with the mycorrhizal-mediated benefit; (3) expanding the response variables for documenting mycorrhizal effects. Further efforts should be done to translate the information derived from fundamental research to innovation in crop, soil, and water management, with the development of beneficial microbial-based strategies and practices designed for environmentally sustainable crop production and tailored to a specific environment. Such a holistic approach requires a tight linkage of highly controlled phenotyping experiments, a network of field trial sites in contrasting climate conditions, field phenotyping approaches, long-term experiments under field conditions and the development of accessible data repositories. The development and the application of bioinformatics tools useful to study the complex interactions among diverse functional groups of microorganisms is also a point that should be taken in consideration in future research projects. Recent studies have shown that the physiological changes in host plants can vary depending on the community structure of associated microbiomes. Different bioinformatic approaches have been developed to study the microbial diversity as well as the interaction networks discovered by high-throughput DNA sequencing, although they often are applied separately for bacteria and fungi (Toju et al., 2018). Microbiome-based innovations may also contribute to the policies for the development of sustainable practices, in line with the Sustainable Development Goals (SDGs, https://sdgs.un.org/goals), and international cooperation in microbiome research projects has been suggested to be an essential point for a sustainable future (D'Hondt et al., 2021). Additionally, researchers should focus on understanding how inoculants influence the native microbial communities, and vice versa, as well as how microbial inoculants interact with the plants in the field, which are crucial points for a wider application of microbial consortia (Compant et al., 2019). Interestingly, diversity and efficiency of microorganisms, as well as the microbial networks, are correlated to crop plant species/varieties and soil/environmental conditions (Toju et al., 2018).

5 | CONCLUSIONS

In the last years, the need to safeguard food security (and safety) and prepare to face the current climate change has become increasingly important, and efforts are made to transform agriculture and adopt practices that are "climate-smart," contributing to the achievement of SDGs adopted by all United Nations Member States as core part of the 2030 Agenda for Sustainable Development (https://sdgs.un.org/goals). Although several countries are developing policies and strategies designed to support climate change mitigation and adaptation and sustainable development, there is a lack of adequate research findings on sustainable practices for the various agroecosystems, soil types, farming system, temperature, and so on. It is worth noting that domestication has focused on yield related traits and not on stress tolerance or disease resistance traits, which consequently need to be

recovered from wild relatives by introgression that takes long periods, and fails when concurring stress conditions appear, or genetic engineering that currently constitutes an unfeasible strategy in Europe. Priming strategies, including rhizosphere and root-associated microbiota, are also crucial actors in this context, having a huge potential in development of a next generation agriculture. These approaches in fact aim at boosting the existing endogenous plant potential to endure abiotic and biotic constrictors, having potentially long-lasting effects and, in principle, does not negatively modify other interesting crop traits such as quality of edible organs and yield. Moreover, advancement in technology, such as the use of high-throughput platforms to quantify crop performance and tolerance traits of different crop genotypes upon different treatments (e.g., inoculation with beneficial microbes, plant response to diverse environmental stresses, etc.) provides an opportunity to characterize the plant responses of a subset of varieties under tightly controlled growth conditions or in the field, where real-life agricultural conditions are found.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Writing-original draft preparation: Miguel González Guzmán, Francesco Cellini, Vasileios Fotopoulos, Raffaella Balestrini, Vicent Arbona. *Writing-review and editing*: Miguel González Guzmán, Francesco Cellini, Vasileios Fotopoulos, Raffaella Balestrini, Vicent Arbona; All authors have read and agreed to the published version of the manuscript.

DATA AVAILABILITY STATEMENT

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

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