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ORIGINAL ARTICLE

Paving the way towards future-proofing our crops

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Abstract

To meet the increasing global demand for food, feed, fibre and other plant-derived products, a steep increase in crop productivity is a scientifically and technically challenging imperative. The CropBooster-P project, a response to the H2020 call 'Future proofing our plants', is developing a roadmap for plant research to improve crops critical for the future of European agriculture by increasing crop yield, nutritional quality, value for non-food applications and sustainability. However, if we want to efficiently improve crop production in Europe and prioritize methods for crop trait improvement in the coming years, we need to take into account future socio-economic, technological and global developments, including numerous policy and socio-economic challenges and constraints. Based on a wide range of possible global trends and key uncertainties, we developed four extreme future learning scenarios that depict complementary future developments. Here, we elaborate on how the scenarios could inform and direct future plant research, and we aim to highlight the crop improvement approaches that could be the most promising or appropriate within each of these four future world scenarios. Moreover, we discuss some key plant technology options that would need to be developed further to meet the needs of multiple future learning scenarios, such as improving methods for breeding and genetic engineering. In addition, other diverse platforms of food production may offer unrealized potential, such as underutilized terrestrial and aquatic species as alternative sources of nutrition and biomass production. We demonstrate that although several methods or traits could facilitate a more efficient crop production system in some of the scenarios, others may offer great potential in all four of the future learning scenarios. Altogether, this indicates that depending on which future we are heading toward, distinct plant research fields should be given priority if we are to meet our food, feed and non-food biomass production needs in the coming decades.

KEYWORDS

crop productivity, crop yield, future-proofed crops, future world scenarios, plant research

1 | INTRODUCTION

The increasing global population, projected to reach 9 billion by 2050, increasing consumer expectations, health-related recommendations for a more diverse diet and ambitions to transition to a more sustainable bio-industrial base will result in an ever-increasing demand for food, feed, fibre and other plant-derived products (Aschemann-Witzel et al., 2019; de Boer et al., 2014). Projections from the current rates of annual crop yield gains suggest that the global production will fall 40–70% short of this future demand if new land is not made available (Ray et al., 2013). The planet, however, has reached the maximum sustainable capacity for agricultural land, while a doubling of the current global agricultural productivity per hectare will be needed to meet this projected

goal. An increase on this scale would provide food and nutrition security, as well as sufficient feedstocks to enable a thriving bio-economy.

While recognizing the importance of the food production system as a whole, the H2020 CropBooster-P project is drafting a roadmap for the development of new and improved crops critical for the future of European agriculture, taking into account a changing geopolitical landscape, climate change and agricultural priorities (Baekelandt et al., 2022; Harbinson et al., 2021). The CropBooster-P expert panel identified those key broad traits that will need to be optimized to improve crop productivity (Baekelandt et al., 2022), focusing on increased yield potential (Burgess, Masclaux-Daubresse, et al., 2022), yield stability (Gojon et al., 2022) and nutritional quality (Scharff et al., 2021). Thus, CropBooster-P includes all recognizable traits

related to increased yield potential (Burgess, Masclaux-Daubresse, et al., 2022) and yield stability under unpredictable environments (Gojon et al., 2022), with increased resource use efficiency (Gojon et al., 2022) and nutritional quality (Scharff et al., 2021). We fully recognize that although these are individually important target traits, they cannot be pursued individually and that an integrated approach is imperative. CropBooster-P has been focussing on the genetic basis for crop improvement delivered by conventional breeding and/or integrated with more advanced biotechnological methods (Table 1) and thus, on traits that can be transferred between plant species using both empirical and directed methods.

Considering a multitude of global trends and key uncertainties, a scenario exercise was carried out and four future scenarios were developed (Cornelissen et al., 2021). These learning scenarios depict complementary future socio-economic developments, taking into account numerous policy and socio-economic challenges and constraints. Whilst none of these, at least in isolation, are likely to accurately and precisely portray the future, together they form a starting point for setting the boundaries around the future space in which the crop improvement options will need to be positioned and assessed. By examining these scenarios, we will reach a better understanding of the diversity of possible future outcomes and how these could inform and direct plant research, focussing on the three overarching traits of crop yield (potential), yield stability (sustainability) and nutritional quality. With this, we aim to indicate which crop improvement approaches are most appropriate for our four future world scenarios. We will further explore some key options for future research that are, in fact, common for yield, nutritional quality and sustainability, such as the development of

modelling and phenotyping approaches and improved methods for breeding and genome editing. Besides relying on conventional agricultural practices, we provide a preliminary look into the potential of diverse platforms of food production, for example, the use of underutilized terrestrial and aquatic species as alternative sources of nutrition and agricultural production. Tapping into these species as a source for food, feed and non-food biomass might be crucial in the coming decades.

2 | FUTURE WORLD SCENARIOS AND HOW TO PRIORITIZE FUTURE PLANT RESEARCH

The four future learning scenarios were developed to encapsulate complementary future socio-economic developments that take into account numerous policy and socio-economic challenges and constraints (Cornelissen et al., 2021). It should be noted, however, that two major global developments have occurred since we formulated these scenarios; the Covid-19 pandemic in 2020 and the outbreak of war in Europe in 2022. Although these events illustrate the versatility and the fragility of the world food production and trade system, and will potentially have major effects on the direction the future will take, we still believe that the future will lie somewhere in the option space defined by our scenarios, which allow a multitude of outcomes depending on the global environmental, agricultural, social, political, technological and economic trajectory.

The four possible future learning scenarios (Figure 1) were named 'Bio-Innovation', 'My Choice', 'Food Emergency' and 'REJECTech' (Baekelandt et al., 2022;

TABLE 1 Impact assessment of the four learning scenarios (focus on technologies)

	Bio-Innovation	My Choice	Food Emergency	REJECTech
Conventional breeding				
Breeding based on phenotype-based selection	No limitations	No limitations	No limitations	No limitations
Biotechnology				
Molecular breeding, for example marker-assisted selection and genomic selection	No limitations	No limitations	No limitations	No limitations
Genome editing, for example CRISPR/Cas technologies	No limitations	With limitations	No limitations	Not desired Not accepted
Classical genetic modification, for example gene transfer	No limitations	With limitations	No limitations	Not accepted

The impact of the four learning scenarios on the methods and technologies that could be used to improve crop productivity is shown. Methods and technologies are subdivided in conventional breeding and biotechnology, and their acceptance and/or limitations are shown for each of the four learning scenarios 'Bio-Innovation', 'My Choice', 'Food Emergency' and 'REJECTech'. In the 'Bio-Innovation' scenario, the acceptance of the technologies is driven by innovations in a flourishing bio-economy, while in the 'Food Emergency' scenario, they are accepted because they are required to safeguard food security.



FIGURE 1 Impact assessment of the four learning scenarios (focus on traits). Four future world scenarios were developed within the CropBooster-P program, depicting complementary future socio-economic developments that take into account numerous policy and socio-economic challenges and constraints: ‘Bio-Innovation’, ‘My Choice’, ‘Food Emergency’ and ‘REJECTech’. For each of the scenarios, several key determinants, characteristics and impacts are presented, for example, the impact on what plant traits should be prioritized, including yield potential (depicted by a plant), yield stability (depicted by a droplet) and nutritional quality (depicted by a light bulb), whether genome engineering methods and technologies (depicted by a DNA helix) would be accepted and what the envisaged impact would be on the environmental sustainability (depicted by a landscape).

Cornelissen et al., 2021). By design, each of these four is an extreme but plausible scenario and hence, the reality in the year 2050 is likely impacted by elements coming from each of the four learning scenarios, emphasizing the importance to define and start tracking short-term and mid-term indicators for the scenarios, and utilize these to seek the most robust way forward.

2.1 | Future learning scenario ‘Bio-innovation’

In the ‘Bio-Innovation’ scenario, financial means, growth and technological options are assumed to be unlimited (Table 1). There would be no restrictions on research and the development of technology, and the full range of conventional and biotechnological options can be exploited to meet the future needs. Key options can be implemented relatively quickly (3–5 years) and technologies will allow targeted gene modification and/or transfer between all species in a very short time frame. Also, the targeted manipulation of more complex traits will be possible by 2030 (Parisi & Rodríguez-Cerezo, 2021). The shorter technological turnover time will enable researchers to use the most recent discoveries immediately to explore new research fields and determine the best options for improvement, allowing them to relatively quickly detect any shortcoming and subsequently optimize performance features on

a whole-plant and field level. The widespread use of artificial intelligence and integrated modelling strategies would further allow increased accuracy in predicting how to improve our future crops most efficiently, allowing a very precise approach to crop improvement.

In this scenario, it will be possible to improve or add multiple complex traits in an integrated way within the same crop using a variety of technologies (Table 1), allowing fast crop improvement and decreased adverse environmental impacts (Figure 1). A range of processes, such as resource use and photosynthesis, could be improved, resulting in larger and more stable yields, more sustainable production, and better nutritional quality. This could be achieved by exploiting both natural variation and biotechnological approaches (genome editing, introducing new genes and pathways, etc.). This scenario would enable, in the longer term, the development of ‘breakthrough’ designer crops, such as N-fixing cereals and perennial crops, and the conversion of C3 crops to C4.

In the ‘Bio-Innovation’ scenario, significant effort could be put in breeding new crops or crops cultivated with traditional or alternative farming approaches, for example, specific breeding programmes for underused or new crops in alternative cropping systems that can provide a reliable yield in a more uncertain climate (Burgess, Cano, & Parkes, 2022). The potential of, amongst others, the fast growing C4 tropical leafy vegetable amaranth, seaweeds or extremophile species could be relatively easily and

efficiently exploited in Europe following timely improvement based on major breeding efforts utilizing the biological variability in these species. In addition, they may be used as model crops for harnessing other crops. Although important in all future scenarios, in the 'Bio-Innovation' future, priority might also be given to the generation of crops that contribute to mitigate global climate change via carbon sequestration deep in the soil (Jansson et al., 2021) or reduce temperature rises by planting trees and bushes optimized for urban planting or for green walls (Fineschi & Loreto, 2020). This scenario also offers great opportunities to efficiently and rapidly breed non-food species that can be used as cover crops, relay crops or intercrops such as N-fixing plants or species specifically dedicated to eco-system services, including N uptake, C sequestration, soil covering, pollination and pest control.

Within the 'Bio-Innovation' model, an equal thrust across yield potential, yield stability (sustainability), and nutritional quality can be envisaged to improve crop productivity (Figure 1), resulting in broader consumer choices, tailored diet options, a larger product variety, longer shelf lives and sustainable agriculture. It is worth noting that a large part of the major modifications needed to fulfil the 'Bio-Innovation' future world depend on the use of new genomic techniques (NGTs, Table 1).

2.2 | Future learning scenario 'My Choice'

The 'My Choice' scenario focusses on the consumer's preference, that is, consumers drive the market, similar to personalized medicine. Accordingly, there would be a need for a greater variety of crops and a diversity of nutrients to meet the specific requirements from different subgroups of consumers, likely resulting in less domination of the current major crops. In this scenario, the restrictions on the application of plant breeding and biotechnology technologies are limited (Table 1). The high degree of personalization could, however, significantly slowdown the speed of delivery. In addition, the starting costs to develop such technologies could be higher than in the 'Bio-Innovation' scenario, given the high degree of personalization and the shift to small-scale production.

Although improving crop yield remains necessary, it can be envisaged that in a 'My Choice' scenario, emphasis is put on nutrient quality and alternative nutrition sources that are produced in an environmentally sustainable manner (Figure 1). When compared to 'Bio-Innovation', however, the distinct focus on diversity could result in increased crop diversification, a decrease in industrial farming and a value shift from commodity crops to food and specialty crops. In this scenario, we can also speculate that

consumer demand would lead to the introduction of new traits for taste and other sensory properties, specific compounds, food supplements or drugs to produce nutraceutical or medical food, alongside with an increased demand for alternative nutrient sources and nutrient dense foods, alternative crops, superfoods and crops with improved micronutrient content and specialized metabolites with nutritive roles. Examples include crops with increased concentrations of antioxidants, polyphenols or the use of alternative crops such as *Camelina* as a plant-based source of essential fatty acids (Scharff et al., 2021). It is expected that biofortification with micronutrients might become a key priority in this scenario. We can also foresee an industrially driven demand for engineered crops that produce high-value compounds, such as additives for fuel industry (Ortiz et al., 2020) or molecules for pharmaceutical industry (Burnett & Burnett, 2020).

Whilst conventional breeding can be used to obtain the desired traits in the 'My Choice' scenario, biotechnological solutions will be more efficient, leading to a slightly increased period (5–10 years) of safety regulation and rigorous testing before innovations would be made commercially available (Table 1). For example, NGTs have been used to increase the amount of healthy omega-3 long chain poly-unsaturated fatty acids in oilseeds, and these could potentially be used to improve human nutrition either directly or indirectly via animal or fish feed (Napier et al., 2019). The fatty acid example is also accompanied by significant environmental benefits, because it decreases the demands on oceanic capture fisheries, which are already at their limits of productivity in many places. In this scenario, it is also expected that some aspects of social acceptance and consumer choice will shift towards, for instance, crops generated via NGTs. Despite the major benefits that nutritional enhancement may provide, crops of this kind have not been adopted by agriculture nor demanded by consumers, as can be seen by consumer rejection of Golden rice, enriched in Vitamin A (Kettenburg et al., 2018). Concerning yield, a major application of this scenario might be to increase transportability, shelf life and longevity demands, including delayed senescence. Technologies used in this scenario would include a combination of NGTs and conventional breeding (Table 1), screening heritage crops for the genetic diversity present in ancestral genomes.

2.3 | Future learning scenario 'Food Emergency'

In the 'Food Emergency' scenario, the focus is on maximizing yield potential and yield stability (sustainability) in the face of extreme weather events caused by global

climate change or other unforeseen natural or man-made disasters that put a pressure on the food production system. This will probably require the production of a limited number of the most robust and high-yielding varieties of a few specific species, or could be based on a diversification of varieties, for example, early and late maturing varieties, at a farm level to ensure a more global production stability. Global climate change is not the only factor that could serve to trigger this kind of scenario. Indeed, recent events have demonstrated that the occurrence of a global pandemic and the outbreak of war on the European continent have major effects on food prices and security and thus can potentially lead to this scenario, even though it initially appeared unlikely in Europe. The worldwide Covid-19 outbreak has exposed the vulnerability of the global food system, showing that free market mechanisms cannot be relied upon as a tool for food security and that the import of food into the European Union must no longer be taken for granted. In addition, the outbreak of war in Ukraine is threatening approximately 30% of the globally traded wheat and sunflower, and causing increases in fossil energy prices, resulting in increased farm fuel costs and costs of nitrogenous fertilizer. In addition, Ukraine, Russia and Belarus are major suppliers of synthetic fertilizers. Amongst the many problems arising from the Ukrainian conflict, are difficulties in the supply chain, strong increases of nitrogenous fertilizer prices and an unprecedented demand for biomass to produce biogas (Moussu, 2022).

In the 'Food Emergency' scenario, food security is under threat and accordingly, any solution that delivers food security will be exploited, even at the expense of environmental sustainability (degradation and damage, Figure 1). In this scenario, we therefore envisage that any technologies that are available to increase food security will be exploited, and these will be focussed on yield-delivering innovations for a selected number of key crops. In response to the food security crisis, it would be expected that new varieties with high and stable yield, whether produced by conventional breeding or NGTs, would be prioritized and adapted as rapidly as possible with the minimum of regulatory obstacles. These yield increases would be achieved by, for instance, increasing photosynthesis, organ growth and development, and (re)mobilization and partitioning of nutrients to the harvestable biomass. Alternatively, it may also focus on shortening the crop cultivation periods to enable multiple harvests per season. Modelling approaches could further contribute to identify crops, best varieties and crop traits with the highest potential to improve productivity in a specific soil and climate environment. Due to the food pressure, little to no emphasis is likely to be put on increasing nutritional quality. In addition, environmental sustainability is likely not

to be given priority, putatively resulting in, for example, overexploitation of natural resources such as fresh water, extended fertilizer use or soil pollution.

In the 'Food Emergency' scenario, most emphasis will likely be put on increasing food and feed biomass production, with yield potential and stability under stressful conditions being the main drivers for innovation in the agri-food system (Figure 1). Interestingly, pathways underlying yield stability have been shown to be coupled with those improving yield potential (Welcker et al., 2022), whereas physiological processes involved in stress adaptation have not been selected so far, leaving margins of progress in that direction. In this scenario, very little effort will be put towards non-food biomass production. The priority is likely to be set on calorie production, probably also resulting in decreases of tailored diet options. Although the lack of environmental sustainability means that this approach will not work in the long-term, there is a need to develop safeguards in the event of a climate crisis to ensure global food security while preserving options for the production of sustainable, nutritious and diverse crops.

2.4 | Future learning scenario 'REJECTech'

In contrast to the other three scenarios, a large number of biotechnological breeding methods, including NGTs, are not desired or even accepted by society in a 'REJECTech' scenario (Table 1). This could result from a general mistrust in science, policymakers and the conventional agri-food systems. Even some classical methods of gene modification like mutagenesis may be prohibited. Accordingly, conventional breeding programmes would be prevailing, along with more traditional agricultural practices.

In this case, improvement of crop productivity would need to rely on the exploration of the genetic diversity in wild, related species and the introgression of traits through traditional breeding techniques, such as marker-assisted selection. Reliance on classical selection will slow down the process with several years and limit the exploitation and combination of the traits of interest within the selected species and thus many potential improvements will not be possible. In addition, introgression, which is based on the transfer of sometimes large chromosomal fragments by crossover, is less precise and less effective than gene transfer or modern precision editing techniques. This is likely to lead to more variation from wild relative traits but perhaps less predictability, as well as the concomitant transfer of undesirable traits. Another alternative would be to invest in the development of currently underutilized species, such as *Camelina*, to improve crop

nutritional quality and lupins to improve phosphorous use efficiency. However, yield increase and stabilization, nutritional quality optimization or improving pest resistance for these underutilized species will likely need major time and efforts.

As food security is likely to decline in this scenario, the focus will be on improving crop yield and yield stability, rather than nutritional quality (Figure 1). Wild species germplasm and underutilized crop species could be exploited to adapt to 'REJECTech' conditions, but domestication and breeding for high productivity or reductions of putative antinutrients often present in ancestral crops will take very long based on conventional breeding programmes (30–50 years). In addition, technological innovations will be limited, and the bio-economic potential low. In a 'REJECTech' future world, the possible crop improvement technologies that can be used to improve crop yield will depend on the technologies that will be rejected and/or accepted by society, for example, classical genetic modification versus genome editing (Table 1). Similar as in the 'Food Emergency' scenario, any solution that delivers food security will be exploited in the 'REJECTech' scenario, even at the expense of environmental sustainability (degradation and damage, Figure 1). The limited use of technologies that can be used in the 'REJECTech' scenario could, however, also promote a more sustainable production through crop management adaptation to mitigate climate change, by including intercropping cereals with legumes for example.

Growing concerns over food security in the 'REJECTech' scenario could, in the medium term, develop into the 'Food Emergency' scenario.

3 | OPTIMIZING BREEDING AND GENETIC ENGINEERING METHODS TO INCREASE CROP PRODUCTIVITY

Next to classical forward and reverse genetics, mapping of quantitative trait loci and genome-wide association studies are currently the preferred means to identify natural genetic variants positively influencing certain plant traits. Whilst being extremely valuable, conventional breeding approaches based exclusively on phenotypic diversity can be slow and it can take several years or decades to introduce the desired traits by crossing. In addition, this methodology then needs to be followed by several backcrosses to get rid of potential undesired traits (Ramstein et al., 2019). In contrast, molecular methods taking into account diversity at the DNA level may allow a more rapid and cleaner introduction of desired alleles. This is especially valuable for complex traits that require multiple changes. This

involves, however, the identification of the genetic element underpinning variation in a trait and if there is no information available on what that element might be, then conventional breeding might be quicker. Genetic engineering methods depend on a detailed knowledge about the underlying pathways, which is usually missing, even for well understood processes.

Biotechnology also offers the opportunity to transfer genes between species, which may allow rapid and significant progress. The molecular methods encompass modern plant breeding approaches like marker-assisted selection/breeding or genomic selection, gene transfer technologies and NGTs, including novel DNA mutagenesis technologies, such as CRISPR/Cas, and synthetic biology approaches, allowing the transfer of complete metabolic and/or genetic pathways. Contrary to plants obtained by the other molecular methods, which benefit from similar regulations in most jurisdictions worldwide, plants obtained by NGTs are presently considered as genetically modified organisms (GMOs) in Europe, whereas numerous countries in North and South America, Africa, Asia and Oceania treat them as non-GMO (Menz et al., 2020). Based on the same scientific knowledge regarding the safety of these technologies and the products made using these technologies, it is unfortunate that divergent decisions have been taken, allowing only a part of the countries to freely exploit the benefits of NGTs in terms of production and sustainability.

To improve crops using what is known about loci, genes and gene regulatory networks that control plant traits, breeding technologies are required that can either introgress natural, modified or edited alleles into elite germplasm, or specifically modify the genome of the elite germplasm directly using site-directed mutagenesis. To meet our future crop productivity demands in time, **several breeding technologies require further development**, including genomic selection, speed and fast breeding, double haploid (DH) breeding, accelerated domestication and precision breeding.

Genomic selection. Traits are often under the control of multiple loci, which need to be selected for to improve crop productivity (Boyle et al., 2017). Genomic selection consists of devising a model that allows the prediction of agronomic performance of a genotype based on its entire genome, as such accounting for multiple, often minor, loci in a single breeding step. It has been widely adopted by seed companies in recent years. The model is based on a large data set previously acquired by genotyping and phenotyping a training set of (related) genotypes (Millet et al., 2019). This training set is used to develop a multivariate model that correlates the genome with the phenotype and with this

model, the phenotype of any related genome could be predicted. Genomic selection reduces costs (fewer field experiments) and time (fewer generations) and allows more readily the simultaneous exploitation of minor quantitative trait loci. The improvements needed for a more general use of the technology include the handling of epistasis between loci and the use of knowledge about gene function for more accurate predictions or the application to genetically distant material (Hickey et al., 2019; Voss-Fels et al., 2019).

Speed and fast breeding. A game changer in (marker-assisted) plant breeding is 'speed breeding'. Using highly controlled environments in growth chambers with tailored light regimes allows rapid cycling of generations and shortens the classical breeding process (Ghosh et al., 2018; Hickey et al., 2019). In a complementary approach, the generation time of crops can be reduced by introducing transgenes such as *FLOWERING TIME* (van Nocker & Gardiner, 2014) or by using precision breeding to knock out floral repressors such as *TERMINAL FLOWER1* (Charrier et al., 2019), which is particularly beneficial in perennial species. Future research needs to address the fine-tuning of the genetic approaches and the transfer to other crop species.

Doubled haploid breeding. The DH technology induces the loss of one set of chromosomes to form a haploid, which is followed by doubling of the remaining set of chromosomes, to restore in one step a fully homozygous diploid. In maize, *in planta* DH breeding has considerably shortened breeding times, and the identification of *MATRILINAL (MAT)/NOT LIKE DAD (NLD)* as the gene responsible for haploid induction (Gilles et al., 2017; Kelliher et al., 2017) allowed the transfer of the DH technology to other species such as rice and wheat (Liu et al., 2019; Yao et al., 2018). However, improvement of DH induction rates and transfer to a wider range of crops are needed (Chaikam et al., 2019).

Accelerated domestication or neodomestication. The domestication of wild to crop plants by early Neolithic farmers took centuries or even millennia (Gepts, 2002). Precision breeding could allow accelerated domestication or neodomestication of wild species with desirable traits (Gutaker et al., 2022) in a single generation through the simultaneous editing of previously identified domestication genes (e.g. fruit size). Proof-of-concept has been provided by the simultaneous editing of four key genes to domesticate *Solanum pimpinellifolium*, a wild relative of tomato (Li et al., 2018) and sufficient knowledge exists in at least two other crop species (Zsögön et al., 2018), to suggest that they would also be amenable for domestication.

Also in horticulture, this might harbour great potential, because there are many yet unexploited ornamentals and mutants of colour and shape of flowers and fruits.

Precision breeding. Among the recently developed tools, only the CRISPR/Cas technology is a technology that is revolutionizing our ability to create genetic variation leading to novel traits and to speed up the introduction of existing favourable traits in crops (Gao, 2021). CRISPR/Cas-mediated genome editing provides a seductive alternative to transgenesis. It has the important advantage of site-specific, precise modifications of target genes without the addition of (foreign) genetic material through mutagenesis by non-homologous end joining or base editing (Yin et al., 2017). In addition, CRISPR/Cas also allows the introduction of foreign DNA at a specific/chosen site in the genome through homologous recombination, although still largely inefficient in plants (Čermák et al., 2015). The potential of CRISPR/Cas is tremendous and since its discovery in 2012, almost 300 proof of concepts for improved traits under greenhouse conditions have been obtained, of which several further confirmed by field experiments (Modrzejewski et al., 2018, '<https://www.eu-sage.eu/genome-search>'). However, to efficiently apply this form of precision breeding to all major crop species and to elite genotypes within the species, several technological hurdles still need to be overcome. First, despite the precision of genome editing, there remains the risk of pleiotropic effects that may have undesirable effects on farming and post-harvest quality. Second, *cis*-regulatory elements rather than coding sequences may need to be targeted to modify specific aspects of gene expression profiles, such as the developmental timing and/or tissue specificity (Swinnen et al., 2016). Third, to more widely obtain edited plants no longer carrying the editing tool, and as such not being classed as GMO, transient DNA (Veillet et al., 2019) or DNA-free genome editing technologies need to be further developed, especially for the many clonally propagated crops in which the transgene cannot be crossed out (Anders., 2022; Dong et al., 2021; Liang et al., 2018; Svitashv et al., 2016; Zhang et al., 2016). Fourth, genome editing requires tissue culture, to which not all species or cultivars are amenable, so successful genome editing on specific species or genotype may require the optimization of nutrients and plant hormones used in tissue culture. The application of genetic tools such as expression of morphogenic transcription factors (Kong et al., 2020; Lowe et al., 2016) can also contribute significantly to improve transformation efficiency. Finally, to make the genome accessible to any type of editing, advanced CRISPR-based technologies such as

base editing and prime editing (Anzalone et al., 2019) need to be harnessed for plants and engineered and so-called PAM-less versions of the classical Cas9 enzyme could be interesting to develop (Rosello et al., 2022).

Gene transfer technologies. Since genome editing only allows the modification of existing genes, the transfer of complete metabolic and/or genetic pathways may in certain cases not be achievable via genome editing and will require the use of classical gene transfer techniques, previously successfully used to improve biotic (e.g. in BT maize (Brookes, 2019)) or abiotic stress tolerance (e.g. in rice (Oladosu et al., 2019) and maize (Adee et al., 2016)) or increase nutritional quality (e.g. omega3-canola (Lin et al., 2022)). An example is the transfer of symbiotic nitrogen fixation pathways from legumes to other botanical families. Recently, bacterial, cyanobacterial (Lin et al., 2014; López-Calcano et al., 2020; Nayak et al., 2022; South et al., 2019) or unicellular green algae genes were successfully used to improve growth and productivity of higher plants (Lin et al., 2014; López-Calcano et al., 2020; Nayak et al., 2022; South et al., 2019). If the homologous recombination rate could be improved, the CRISPR/Cas technology could be used to target the insertion site of the transgene in plant genomes, making the process even less prone to variability.

4 | THE POTENTIAL OF NOVEL AND UNDERUTILIZED TERRESTRIAL AND MARINE PLANT SPECIES

Currently, 70% of the calories consumed by humans come from just 15 major crops, of which more than half comes from maize, rice and wheat grain (Khoury et al., 2014; Massawe et al., 2016; Ross-Ibarra et al., 2007) and a large proportion of the calories produced serve to feed animals (Poore & Nemecek, 2018). Numerous other crops have important nutritional, taste and other properties, or can grow well in environments where other crops fail (FAO, 2010). However, these crops are often neglected and largely ignored by local and national governments, given inadequate support to enable their trading, improvement and consumption in Europe. In addition to a diversification of existing crops, there is in all the future scenarios a strong need to further investigate the potential value of germplasm of a wild, non-domesticated relative of a crop plant and the use of wild species, and to promote the further development of terrestrial and marine species that are currently still underutilized in Europe. Besides terrestrial plants, seaweeds represent a great opportunity for feed, food and biomass production without competition

for arable land and water but, to date, they are largely underutilized in Europe (Directorate-General for Maritime Affairs and Fisheries, 2021; Torres-Tiji et al., 2020).

4.1 | De novo domestication of wild crop species

A vast amount of genetic diversity in important traits that is present in ancestral crops and wild germplasms has been lost due to the genetic bottlenecks that occurred during the domestication process and during the selection of modern cultivars. Many staple crops fail to meet the micronutrient demands, resulting in deficiencies (Jiang et al., 2021) and crop yields are challenged by climate change. Wild relatives and landraces that have been collected could be used as breeding resources. To date, they have been largely underexploited owing to a limited genetic information but development of genomics and bioinformatics techniques may help to explore and identify the available genetic structure and variation that could be introgressed in elite lines. For example, rice landraces collected from various agro-ecological regions in Northern India showed a large variation for mineral content ranging for iron from 0.25 to 34.8 µg/g and for zinc from 0.85 to 195.3 µg/g (Roy & Sharma, 2014), illustrating the wide range of possible gain. More recently, genomics and bioinformatics techniques allowed to identify the pan-genomic R genes related to rust resistance from wild diploid wheat (Arora et al., 2019). These examples illustrate how new technologies, together with de novo domestication/redomestication of wild relatives or ancestors of crop species may open the way to increase crop yield and, more importantly, provide yield stability when plants face suboptimal conditions (Zhang & Batley, 2020).

4.2 | Underutilized terrestrial species

The Neglected and Underutilized Species (NUS) include more than 7000 species worldwide whereas the mainstream agricultural systems currently still rely on <100 crop species and only three species (rice, wheat and corn) provide 60% of the food energy intake (Khoshbakht & Hammer, 2008; Prescott-Allen & Prescott-Allen, 1990). To satisfy the protein demand, Europe depends for about 25% on the import of protein crops, primarily soybean meal for feed use (Eurostat, e.g. EU protein balance sheet 2011–17. xls (de Visser et al., 2014)). To secure future access, the EU is, amongst other measures, promoting the development of fodder crops and protein crops such as lupin, pea or lentil, but the grain legume cultivation in Europe is currently still insufficient to meet the demand (European

Commission, 2018; Kezeya Sepngang et al., 2020; Watson et al., 2017; Zander et al., 2016). In view of the comprehensive shift in human nutrition from meat to plant proteins, the quality of protein crops must be adjusted in their composition to ensure a versatile and healthy human diet (van Vliet et al., 2020). To enable (re-)scaling and economic return, the protein crops need to show improved yield potential and stability, need to be optimized for consumption, and need to fit into the post-harvest processing chain. For instance, the broader use of lupin is limited due to allergens and the presence of anti-nutritional compounds, which adversely affect livestock health. Furthermore, these underutilized species can have poor biotic or abiotic stress tolerance and yield stability. Hence, breeding efforts are particularly needed to target yield stability and seed quality (Abraham et al., 2019). This can be accelerated exploiting the increased genome sequence information and using molecular markers and/or advanced breeding techniques (Hane et al., 2017; Książkiewicz et al., 2017). Another example of a nutritious crop that is currently still underutilized in Europe is amaranth, a C4 dicot which is harvested and used as a fast growing leafy vegetable or cereal (Onyango et al., 2008; Rastogi & Shukla, 2013) with a nutritional value superior to several commodity crops (Rastogi & Shukla, 2013). In addition, if sufficient water is supplied in the early season, amaranth species are drought tolerant. Despite some breeding efforts, this species is not widely grown (Williams & Haq, 2002) but its diverse genetic base offers interesting perspectives for further breeding in relation to nutrition and adapting agricultural systems to climate change (Rastogi & Shukla, 2013).

Currently, agriculture relies heavily on annual grain crops, which produce about 80% of the world's food (Ross-Ibarra et al., 2007). Perennial grain crops, however, offer several potential advantages, including reduced soil erosion, improved soil health and enhanced resource and water use efficiency. Moreover, perennial species are generally more stress tolerant and resilient because their extensive and long-lived root system provides a better buffer to unfavourable conditions. An example of a perennial that could replace wheat is *Thinopyrum intermedium*. *T. intermedium* has a similar nutritional value quality as annual wheat and provides promising but a yet unexploited yield potential for animal feed and human food production (DeHaan et al., 2014). Currently, however, development is slower and yields are lower compared to modern yields for wheat, demonstrating that further research and breeding on this intermediate wheat will be required if we want to unlock the full potential of this crop.

Given that climate change predictions suggest that future agriculture will be challenged more due to more extreme weather conditions and in particular salinity, the potential of halophytic crops should also be explored. An

example of a crop that tolerates well saline conditions and has a high nutritional quality is *Chenopodium quinoa* (quinoa). Quinoa contains a high crude protein content ranging from 13.8% to 21.9% depending on the variety and is considered the only plant that provides all the essential amino acids, carbohydrates and lipids in proportions ideal for human and animal nutrition (<https://www.fao.org/documents/card/es/c/3638200-e-1fbb-4d7e-a359-d8f582b1d082/>). In the future, the broad genetic variability for this species, with several varieties displaying even superior nutrient composition, offers the potential to meet our future crop productivity demands globally. Moreover, it is particularly suitable in those areas faced with increased groundwater salinity due to sea level rise or the needs to irrigate with brackish water, problems that reduce the yield of most crops. In addition, quinoa can be used for salt sequestration, giving the crop a dual functionality that allows for a more sustainable use of the soil (Böhm et al., 2018).

4.3 | The potential of marine species

Around 10,000 species of macroalgae are known, of which five genera represent more than 95% of the current seaweed production and value: the brown algae *Saccharina* (*kombu*) and *Undaria* (*wakame*), and the red algae *Pyropia*/*Porphyra* (*nori*), *Kappaphycus*/*Euचेuma* and *Gracilaria*. Green seaweeds are less used, but genera like *Ulva* and *Caulerpa* are also being cultivated (Chopin & Sawhney, 2009). Seaweeds, or macroalgae, are used for direct human consumption as a vegetable, a source of flavouring and as a thickener in the Asian cuisine. Nutritionally, seaweeds are often rich in minerals and vitamins (Radulovich et al., 2015). Generally, the content of lipids and digestible carbohydrates are low but some species have a relatively high protein content ranging from 10% to 30%, with red and green seaweeds typically having higher contents than brown algae (Fleurence, 1999). Accordingly, protein-rich seaweeds, such as *Palmaria palmata* and *Porphyra* spp., are potential substitutes for animal proteins or plant-based proteins, such as those derived from soybean. Further studies also have the potential to find new strains and species with higher protein and caloric content. Seaweeds are also used in industry as a source of colloids used as thickeners in food and feed, and minor uses include fertilizers, bioenergy, agrichemicals, cosmetics, nutraceuticals and pharmaceuticals (Cai et al., 2021).

Intertidal seaweeds are typically more tolerant to physical and abiotic stressors than subtidal species. This is often correlated with more efficient antioxidative systems, such as increased activity of reactive oxygen-degrading enzymes and antioxidants, including vitamins, found higher up in the intertidal, where abiotic stress is more prevalent (Collén & Davison, 1999; Dring, 2005).

Conversely, subtidal species are more tolerant to negative biotic interactions than intertidal ones. Such differences may be exploited as a way of improving productivity and quality of seaweeds produced in aquaculture, for example, through breeding aimed at increasing the antioxidant capacity and resistance to oxidative stress. In fact, increased stress due to daily exposure to air in cultures of the red alga *nori* (*Porphyra* and *Pyropia* species) is used to control grazers, diseases and epiphytes (Blouin et al., 2011).

Despite the major potential that seaweeds offer, they remain largely understudied and currently still relatively few molecular tools are available to study and possibly engineer them (Badis et al., 2021; Blomme et al., 2021; Ichihara et al., 2022). Investment in the characterization of their biology, reproduction, growth and development and the development of more efficient classical breeding techniques accompanied with modern analyses and molecular biological tools would be advantageous to further leverage the potential of this crop type and to allow aquatic species to become a competitive resource. With increasing knowledge of seaweed physiology and genetics, combined with molecular biological tools, new strains could potentially be generated to meet the future demands. One complication in seaweed aquaculture is that it is done in open plots in the sea (Cai et al., 2021) with the potential of spreading of cultivated genotypes in ocean currents. In addition, cultivated species are often growing next to their wild counterparts, thus improved knowledge of the ecological and genetic effects of seaweed aquaculture is very important.

Seaweeds are the most rapidly expanding aquaculture sector. However, the diversity of seaweeds that can currently be cultivated has yet to reach full potential. Currently, most seaweed production (95%) is through aquaculture, rather than harvested from the wild, and is located in Asia, with China as main producer (Buschmann et al., 2017; Ferdouse et al., 2018). Research is ongoing to explore further production in Europe and to optimize culture systems (Azevedo et al., 2019; Marinho et al., 2019; Steinhagen et al., 2021). The absence of competition for arable land makes algal aquaculture at sea an interesting candidate for increased food and non-food production. There is, however, some competition for available plots from other aquaculture activities such as fish and shellfish cultures, as well as tourism and transport across waterways. However, there is increased interest for integrated multi-tropic aquaculture to increase nutrient availability for the algae and reduce the environmental footprint of fish aquaculture. If offshore farming of seaweeds can be achieved, which is currently being tested in several pilot studies (<https://www.h2020united.eu/>; Interreg, 2022), the potential area for cultivation is also virtually unlimited, for example, in windmill parks. In the future, also additional studies will need to be performed to further

investigate whether aquaculture of coastal species is possible and profitable in these environments (<https://www.northseafarmers.org/news/220627wwharvest/>). These examples of de novo domestication and the use of underutilized terrestrial and marine species are relevant to all four scenarios, but might be of particular importance in the 'REJECTech' scenario, in which society will need to rely mostly on the available crops, species and germplasm. However, relying on classical genetics to get rid of the undesirable traits may take decades. In the 'Bio-Innovation' and 'My Choice' scenarios, the (re)domestication of wild crops or introduction of interesting traits could be achieved in a rapid and targeted manner using NGTs. They constitute an effective tool to accelerate breeding for improved yield, while retaining or reintroducing the traits related to nutritional quality or yield stability from ancestral species. There are currently several barriers limiting the integration of NUS into the agri-food system that can be grouped into three main classes: (1) the lack of recognition value from the national and international research systems and a local negative perception, (2) disabling policies that often promote major cereal staple crops and are reluctant to allow more traditional products to enter wider marketplaces and the required infrastructures and markets for NUS, and (3) limited and fragmented data available both at molecular, nutritional and processing level and a lack of relevant information accessible to policymakers and practitioners (Franzo et al., 2013; IPES-Food, 2017). However, a holistic approach, including an increase in knowledge, appreciation, awareness, breeding, processing, social acceptance and advertisement initiated in Brazil, Kenya, Sri Lanka and Turkey, has successfully targeted some NUS to improve diet and human nutrition (review by Hunter et al., 2019; Siddique et al., 2021). Similar multi-stakeholder approaches could be undertaken at wider scale to meet the challenges of malnutrition, yield stability, environmental sustainability and biodiversity preservation.

5 | CONCLUDING REMARKS AND FUTURE OUTLOOK

Within the CropBooster-P project, four learning scenarios were developed, depicting contrasting future socio-economic developments and taking into account numerous policy, socio-economic challenges and constraints that could potentially develop (Baekelandt et al., 2022; Cornelissen et al., 2021). Based on this analysis, it appears that each future world scenario might have a different impact regarding to which plant research fields should be prioritized. Whereas increasing yield potential and stability will for instance be of utmost priority in a 'REJECTech' or 'Food Emergency' scenario, the 'Bio-Innovation' and

'My Choice' scenarios allow for more diverse methods to improve crop productivity and equal efforts can be made to also improve the nutritional quality of crops. Whilst many traits that contribute to yield potential (Burgess, Masclaux-Daubresse, et al., 2022), yield stability (Gojon et al., 2022) and nutritional quality (Scharff et al., 2021) have been described and might provide promising targets for exploitation, also more knowledge on breeding and biotechnological approaches is needed. In addition, in all four scenarios, a better exploitation of novel and underutilized marine and terrestrial species might harbour great potential to meet the future crop productivity demands. Generating crops that can meet the future needs and help to deliver food security in an environmentally sustainable way could ideally be done by combining conventional breeding approaches, including molecular variants such as marker-assisted breeding or genomic selection, and biotechnological crop breeding techniques, such as genetic engineering and/or the fast-evolving genome editing technologies (Zhang et al., 2019). The latter might however not be possible in a 'REJECTech' scenario (Table 1).

Another important point that has to be considered is that quality can relate to nutritional quality for humans and animals (e.g. proteins, fatty acids and vitamins), but also to digestibility for humans and cattle (e.g. digestibility and antinutrients) and industrial quality (e.g. fibres, conversion of biomass, digestibility and composition in specific high-value compounds). For non-food purposes, quality concerns plant characteristics that determine the specific application for which the crop is used. For instance, fibre digestibility for cattle or fibre quality for industry represent different requirements. To meet future demands, plants should be bred that have both a higher yield of harvestable parts used for food and feed production, as well as a non-food or feed residue with properties maximally suited to match requirements to produce non-food commodities, such as liquid fuel or biomaterials. In this way, multipurpose crops can be grown that have a minimal environmental footprint per tonne produced by optimizing land use and diversifying economic use. It is conceivable that such crops can deliver quality food and feed, as well as raw materials for bioprocessing systems of environmentally friendly processes and ecosystem services. An example is increasing the efficiency of extracting and degrading lignin, which is a major limitation in the conversion of biomass to fermentable sugars (Chen & Dixon, 2007; Van Acker et al., 2013). Although the biosynthetic pathways underlying the production of cell wall components are well characterized, the mechanisms regulating their deposition are far from understood and differ between species (Camargo et al., 2019). In addition, reducing the amount of lignin in plants is often accompanied by yield reduction (Bonawitz & Chapple, 2013;

De Meester et al., 2022). Although several hypotheses explaining the molecular basis of these responses have been proposed (Muro-Villanueva et al., 2019), the mechanisms that lead to dwarfism remain not fully understood. However, recent advances in genomics and bioinformatics highlighted several strategies that can be exploited to engineer the host species without the yield reduction (De Meester et al., 2018, 2020; Ralph et al., 2019). Alternatively, completely different lignin polymers with different composition and properties can be engineered using genes from other biosynthetic pathways or other taxa in a synthetic biology approach (Hoengenaert et al., 2022; Oyarce et al., 2019; Wilkerson et al., 2014). This opens promising perspectives (De Meester et al., 2022), particularly in the context of the 'Bio-Innovation' and 'My Choice' scenarios.

Despite the differences in priorities to improve yield potential, yield stability and/or nutritional quality in the different scenarios, we have to acknowledge that in practice this may run into scientific and technical challenges. For instance, the major crop traits for yield potential, yield stability and nutritional quality have mostly a complex multigenic nature and are highly interlinked. The genes and pathways underlying individual traits may therefore have the potential to affect many other important traits, in a positive or in a negative manner. Increasing the above-ground yield might, for instance, influence the allocation of carbon to roots or have an impact on the nutritional value of a crop. Consequently, it is essential for each scenario that future research is holistic and considers these interactions and how they can be optimized best, rather than individually considering a single trait. The development of (very) high-throughput functional phenotyping facilities will be necessary to assess the complexity of the plant system and to capture the extensive local and systemic physical, metabolic and signalling exchanges between plant tissues and organs. To decrease undesirable trade-offs among traits and/or breed for new traits, for instance, it will be crucial to integrate the phenotyping of different traits and to study the impact of manipulations on the performance of the whole canopy. Therefore, detailed phenotyping will require further development in the context of controlled conditions, as well as in relevant growth conditions, and also to increase the power of phenotyping in relevant growth conditions, such as in field conditions. With this respect, roots are among the plant organs in which responses to many external stimuli take place that contribute to the plant acclimation and adaptation to various environmental conditions (Calleja-Cabrera et al., 2020; Lombardi et al., 2021; Lynch et al., 2022; Meister et al., 2014; Muller et al., 2019; Tardieu et al., 2017; Vives-Peris et al., 2020). Capturing root architecture, development and activity is complex and time consuming. Several root phenotyping facilities are available but there

is a major need to develop phenotyping techniques and infrastructures to deepen our knowledge and move faster towards a functional root characterization.

A next critical success factor is to install a dynamic flow with feedback loops from findings in the lab on how complex traits work to measuring performance of optimized crops in the field. Detailed measurements on field-grown crop plants will also be fundamental to refine and validate crop modelling outcomes and integrate the impact of physical and biological soil properties on plant development. Subsequent development and distribution of more sophisticated crop models incorporating a wider range of biological pathways and processes could be of great help to identify the traits to explore and design ideotypes and enable better predictions about the most powerful approaches to increase crop performance (Chenu et al., 2017; Hammer et al., 2019; Muller & Martre, 2019; Peng et al., 2020). In the future, dynamic models should not only include an update on real-time trends associated with climate change, but also year-to-year variations, extreme events such as heat waves and late frost, and the effect that rapid fluctuations in environmental factors have on specific crop traits, such as irradiance on photosynthesis, or water availability on development and therefore on crop yield and quality. Further development of models to better account for multiple stresses such as nutrient availability, genetic variability, physiological processes and adaptive responses, and their interconnected dependencies, will in the future be essential to predict plant behaviour in response to a changing environment and nutrient availability. Development in artificial intelligence, combined with availability of massive phenotyping and genotyping data sets, will probably be helpful to address such complexity. Combined with the societal needs and expectations, this may allow to identify the most relevant alleles, genes, traits and techniques that can and need to be used to future-proof our crops. To make this work, a virtual network between academia, breeders, producers and consumers will make the difference. Information flow in both directions of the value chain will help to focus on the right topics and questions, and will enable time and resource effectiveness.

The complexity and interactions between the traits amenable to breeding requires a holistic approach mobilizing also other disciplines (agronomy, ecophysiology, soil science and social sciences) to consider the role of each crop within the food and farming system, as well as its potential to mitigate climate change and environmental damage.

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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 analyzed in this study.

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