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PERSPECTIVES

Towards smart and sustainable development of modern berry cultivars in Europe

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SUMMARY

Fresh berries are a popular and important component of the human diet. The demand for high-quality berries and sustainable production methods is increasing globally, challenging breeders to develop modern berry cultivars that fulfill all desired characteristics. Since 1994, research projects have characterized genetic resources, developed modern tools for high-throughput screening, and published data in publicly available repositories. However, the key findings of different disciplines are rarely linked together, and only a limited range of traits and genotypes has been investigated. The Horizon2020 project BreedingValue will address these challenges by studying a broader panel of strawberry, raspberry and blueberry genotypes in detail, in order to recover the lost genetic diversity that has limited the aroma and flavor intensity of recent cultivars. We will combine metabolic analysis with sensory panel tests and surveys to identify the key components of taste, flavor and aroma in berries across Europe, leading to a high-resolution map of quality requirements for future berry cultivars. Traits linked to berry yields and the effect of environmental stress will be investigated using modern image analysis methods and modeling. We will also use genetic analysis to determine the genetic basis of complex traits for the development and optimization of modern breeding technologies, such as molecular marker arrays, genomic selection and genome-wide association studies. Finally, the results, raw data and metadata will be made publicly available on the open platform Germinate in order to meet FAIR data principles and provide the basis for sustainable research in the future.

Keywords: berry breeding, trait/genotype association, genomics, metabolomics, image analysis, consumer preference, plant genetic resources, BreedingValue project.

INTRODUCTION

Berries are highly appreciated for their flavor, appearance and nutrient content, including high levels of antioxidants that are beneficial for human health (Jimenez Garcia et al., 2013). Commercial production in 2020 exceeded 12.9 million tonnes globally and 3.4 million tonnes in Europe (FAO, 2021). The berries with the largest global production volumes were strawberries, raspberries, blueberries, currants, cranberries and gooseberries. In Europe, about 50% of the total production volume was strawberries, followed by raspberries and currants, each at approximately 20%, and blueberries at 5%. As well as being a berry producer, Europe is also a major importer of berries, and the import volume grew by nearly 40% between 2015 and 2020. The global production, import and export markets over the last 50 years are shown for strawberries as an example in Figure 1. The projected continuous increase in the market demand for berries is driving investments in global research and production, which will require increased breeding efforts. This has been recognized at the EU level by continuous support for EU-coordinated projects, the same as in the USA and China.

Breeding objectives include higher yields and yield stability, lower production costs, and better product quality (Capocasa et al., 2008; Cellon et al., 2018). In the past, breeders focused mainly on yield and production costs, but product quality is now a high priority (Mezzetti et al., 2016; Verma et al., 2017). This increases the complexity of breeding programs because additional traits must be combined in new cultivars (Akdemir et al., 2018). For berries in particular, traits related to consumer health and sensorial quality are becoming essential to compete on the global market (Mazzoni et al., 2016). The substances that confer aroma, flavor and taste need to be identified, along with the environmental stimuli and signaling mechanisms that lead to the accumulation of such bioactive compounds (Paredes-López et al., 2010). At the same time, new varieties must also incorporate traits that mitigate the impact of climate change, including resilience to abiotic stress factors such as water deficiency and high temperatures (Bisbis et al., 2019), as well as resistance to pests and diseases that are spreading to new areas (Bebber et al., 2013). Many climate change projections predict lower food availability, quality and nutritional value in the future (Challinor et al., 2014; Davies & Ribaut, 2017). Increasing the resilience of cultivars to biotic and abiotic stress not only ensures yield stability but may also allow crops to grow in different environments and cultivation systems. Strawberry cultivation has shifted in part from the open field to controlled/protected environments since the Montreal Protocol banned widely-used soil disinfectants. To meet the increasing market demand, all cultivation systems will be needed. Breeders must therefore provide a more diverse portfolio of cultivars, including those adapted to alternative cultivation systems, while meeting quality expectations.

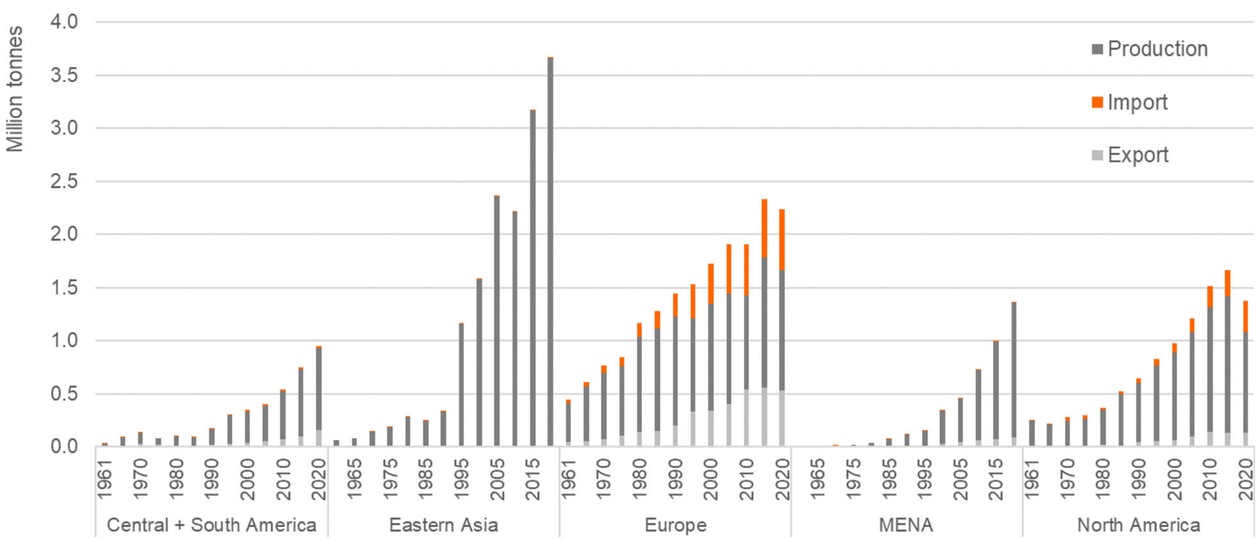

Figure 1. Strawberry production and trade volumes per market region from 1961 to 2020, showing stacked production and import volumes, and export volumes as part of the production volumes (FAO, 2021). MENA, Middle East and Northern Africa.

The steadily increasing production and import of berries in Europe may reflect consumer awareness of healthy diet and lifestyle choices (Santeramo et al., 2018). Breeders are therefore driven to consider the content of minerals, vitamins and favorable secondary metabolites in fresh fruits (Baselice et al., 2017). The high content of bioactive compounds in fresh berries, as opposed to processed fruits, can contribute to a healthy diet (Paredes-López et al., 2010; Skrovankova et al., 2015). The visual and sensory quality attributes of fresh fruits strongly influence the consumption rate (Barrett et al., 2010; Klee & Tieman, 2018). Furthermore, traders demand products with homogeneous or narrowly-defined qualities that are difficult to achieve for traits that are influenced by environmental conditions.

Fresh berries suffer from post-harvest losses at the retail level due to their short shelf life, which limits profitability and reduces the sustainability of production by increasing food waste. In 2020, the European Commission (EC) presented the Farm-to-Fork (F2F) Strategy as one of the basic concepts of the Green Deal for a more sustainable society. Accordingly, sustainable production is an important aspect of berry cultivation, and must ensure that quality and nutritional standards are maintained or improved. Smart production systems and advances in agricultural biotechnology are required to meet these challenges, including adaptation to new cultivation systems and high-precision mechanized farming. Such ambitious goals can be achieved by combining traditional and biotechnology-assisted production methods, including research that focuses on berry breeding (Sabbadini et al., 2021).

PREVIOUS BERRY RESEARCH AND BREEDING EFFORTS

Berry breeding is complex, not only due to the multi-dimensional targets discussed above, but also because many species are polyploid and/or interspecific hybrids. Genetic diversity is severely limited when only a few individuals are used for breeding without the development of further pre-breeding material (Diamanti et al., 2012). In many berry crops, related (sub)species are underutilized in breeding. Taking strawberry as an example, the genus *Fragaria* comprises 20 species and many subspecies ranging from diploid to decaploid (Liston et al., 2014). Today's cultivated strawberry mostly consists of the octoploid interspecific hybrid *Fragaria* × *ananassa* that was created in France in the late 1700s and bred in England in the early 1800s (Darrow, 1966). Raspberry and blackberry/bramble belong to the genus *Rubus*, which also provides several (sub)species for intercrossing. Similarly, blueberry, cranberry, bilberry and huckleberry belong to the genus *Vaccinium*, with bilberry considered a rich source of genetic diversity for the development of blueberry pre-breeding material (Podwyszynska et al., 2021).

To facilitate the development of pre-breeding material, previous research projects have characterized not only modern and ancient berry cultivars but also wild relatives to investigate their potential to increase the genetic diversity of cultivated berry species. Efforts to assess and maintain genetic resources for strawberry breeding in Europe started in 1994, revealing the loss of important material and narrowing genetic diversity. The EU-funded COST action 836 (1998–2004) characterized more than 1000 strawberry cultivars and ~400 wild accessions (Geibel et al., 2004). Follow-up projects were funded to maintain the identified core genetic resources, study additional genetic resources, include more traits, focus on the underlying genetics, and clarify technical issues in commercial production and laboratory protocols. In COST action 863 (2005–2010), 31 partners investigated environmental effects on the agronomic performance and metabolic profiles of fruit crops, and harmonized analytical standards for the metabolic profiles of small fruits (Mezzetti et al., 2009). The EU-funded projects GenBerry (2008–2012), RIBESCO (2007–2011) and EUBerry (2011–2014) characterized strawberry, raspberry, currant and blueberry genetic resources in order to assess genetic diversity and conserve the most valuable material. The genetic and phenotypic data generated in these projects were linked (including disease resistance), and techniques were harmonized between partners (Carrasco et al., 2007; Karhu et al., 2012; Lerceteau-Köhler et al., 2012; Mezzetti et al., 2016; Scalzo et al., 2005; Stafne et al., 2005; Zorrilla-Fontanesi et al., 2012). As an example, the GenBerry project highlighted the originality of old European cultivars, and focused on consumer preferences for fresh fruits with high nutritional value (Horvath et al., 2011). A platform was generated for data compilation, allowing the key characteristics of fruit quality to be screened in currants and blackberries (Krüger et al., 2012; Tavares et al., 2013), and a core collection of currant genetic resources was established (Antonius et al., 2012).

The GoodBerry project (2016–2020) brought together 17 European partners, and one each from Chile and China. They conducted multiple field experiments on strawberry, raspberry and blackcurrant, and collected genotypic, phenotypic and sensory data to provide the knowledge and procedures necessary for the development of elite cultivars that maintain high yields and quality in a range of environments (Allwood et al., 2019; Labadie et al., 2019; Pott et al., 2019, 2020a; Vallarino et al., 2018, 2019; Woznicki et al., 2016). Whereas earlier projects targeted key accessions and identified molecular markers to accelerate breeding as well as providing initial methods for sensory analysis and metabolomics, GoodBerry focused mainly on the secondary metabolites responsible for aroma, fruit quality and stress tolerance (Durán-Soria et al., 2021), while still covering environmental adaptation and genetic resources. Importantly, GoodBerry studied physiological and fruit quality traits in individuals from a biparental population planted in five European countries for a period of

3 years, highlighting the plasticity of strawberry (European Union, 2020). Furthermore, modern high-throughput screening tools were developed to combine omics datasets (Bolger et al., 2019; Labadie et al., 2019; Schwacke et al., 2019).

In the framework of the European Cooperative Programme for Plant Genetic Resources (ECPGR), a working group on berries was established in March 2019 (https://www.ecpgr.cgiar.org/working-groups/berries; Höfer, 2021). The main goal of the 51 members from 22 European countries is to coordinate activities between the national collections based on continuous long-term network cooperation in Europe to create synergies and establish contact points for berry research projects.

Outside the EU, one of the largest berry-related projects was funded from 2009 to 2019 by the USDA Specialty Crop Research Initiative (SCRI), and focused on the US market. RosBREED (Iezzoni et al., 2020) covered diverse species in the family *Rosaceae*, including strawberry and raspberry, and published genomic data and some phenotypic data in the Genome Database for Rosaceae (GDR; https://www.rosaceae.org), which is still regularly updated by researchers and breeders, and includes downloadable data and software for data visualization and analysis (Jung et al., 2019). The USDA-funded Vaccinium Coordinated Agricultural Project (VacCAP) was launched in 2020 to investigate the genetic basis of blueberry and cranberry fruit quality attributes, develop standard genotyping and phenotyping protocols, and develop or optimize tools and methods applied by the project partners. Wild accessions and related species were included in the project to develop new pre-breeding material. The project established the Genomic Database for Vaccinium (GDV; https://www.vaccinium.org), which is similar in function to GDR, but focuses on blueberry, cranberry and related berry species.

The knowledge from these projects allows the efficient use of genetic resources, and the creation of new breeding material that meets the current demands of growers and consumers. However, the genomic background of certain stress–response traits and the contribution of particular metabolites to the overall sensory qualities of berries remain unknown. Furthermore, a consumer survey across a wide geographic area has not yet been commissioned to inform future breeding objectives.

CLASSIFICATION OF BERRY GENETIC RESOURCES

Breeding alternates between increasing genetic variation and narrowing it by selection to create new cultivars. Selection is the beginning of a funnel effect that leads to domestication. The loss of diversity can result in negative as well as positive effects depending on the initial genetic diversity of the breeding material and the intensity and direction of breeding. For example, the negative effects of breeding include the loss of aroma and stress resistance (Aharoni et al., 2004; Ulrich et al., 1997). In strawberry, the comparison of old and modern cultivars revealed the loss of up to 35% of allelic diversity (Gil-Ariza et al., 2009; Horvath et al., 2011), in part reflecting the limited number of ancestral accessions used for initial hybridization in the 1700s (Hancock et al., 2010). High-performance cultivars are predominantly used in breeding programs worldwide to avoid linkage drag (inferior traits linked to target traits) from old cultivars or wild relatives. However, focusing on a small pool of accessions in breeding accelerates the loss of genetic diversity (Hardigan et al., 2018).

The diversity in current breeding programs can be assessed by studying the diversity of germplasm used to develop pre-breeding materials. By comparing the genetic diversity in old cultivars, modern cultivars, new releases and material currently undergoing breeding cycles, the genetic potential of future cultivars can be predicted. The most valuable genetic resources can then be defined and future selection gains can be estimated. The categories of strawberry germplasm recommended for inclusion in future studies are listed in Figure 2.

In the EU, plant breeders' rights are granted for new cultivars, giving the breeder exclusive control over propagation and the utilization and sale of harvested parts of the plant for a specified number of years. The breeder can choose to license the cultivar or become its exclusive marketer. The new cultivar must fulfill the criteria of registration and trialing. It must be new (not commercialized before), distinct from known cultivars, uniform and stable (characteristics must be genetically fixed, also with respect to reproduction). Plant materials that are not covered by plant breeders' rights can be subject to material transfer agreements that protect the intellectual property and material, and restrict its use. Such agreements can be applied to pre-breeding material, material that is not yet registered as a protected cultivar, or any other material that is not protected under other contracts or regulations.

NEW GENOMIC TOOLS FOR BERRY IMPROVEMENT

Berry breeding efforts have been accelerated by the development of high-throughput genotyping tools and efficient breeding strategies such as marker-assisted selection and genomic selection. Marker-assisted selection allows the rapid combination of traits in pre-breeding material, whereas genomic selection predicts genetic gains by applying knowledge about the effects of each marker. When genes or quantitative trait loci (QTLs) that follow Mendelian inheritance are identified, the use of molecular markers associated with the desirable traits can accelerate the introgression of the corresponding genomic regions because numerous markers can be analyzed simultaneously.

Panels of markers are available for strawberry (Whitaker, 2011), raspberry (McCallum et al., 2018) and

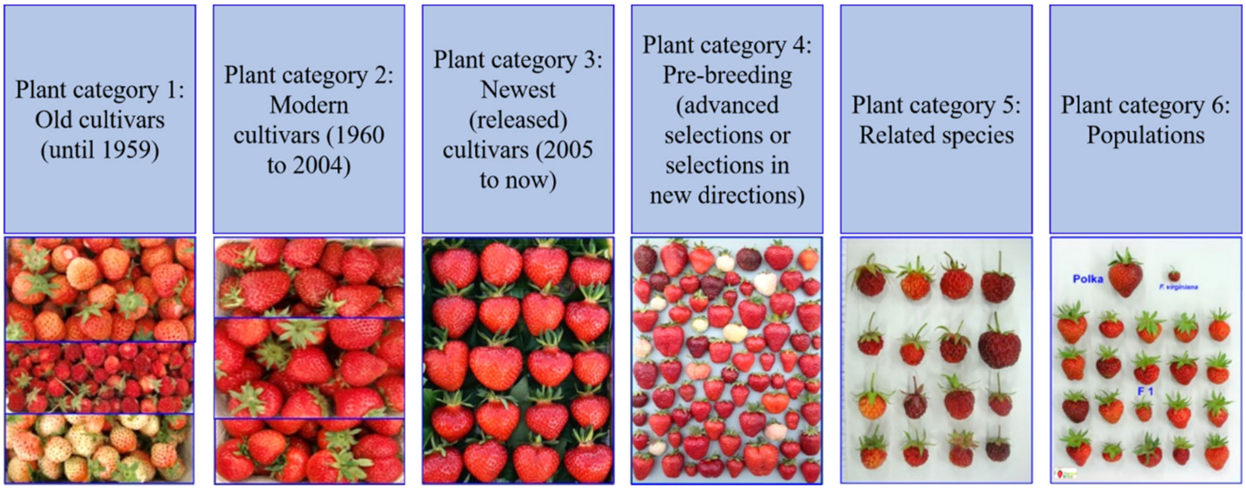

Figure 2. Proposed strawberry germplasm categories in chronological order for inclusion in future diversity studies.

blueberry (Rowland et al., 2011), and can be arranged on arrays. Genomic selection must be applied effectively to polygenic traits (Crossa et al., 2017), such as resistance to powdery mildew (*Podosphaera aphanis*), leaf scorch (*Diplocarpon earlianum*) and common leaf spot (*Mycosphaerella fragariae*) in strawberry, leaf rust (*Phragmidium rubi-idaei*) in raspberry, and sensory quality traits attributed to numerous metabolites.

Molecular markers are abundant, reliable and widely used for berry breeding. For example, Axiom 50K and 9K arrays have been developed to profile single-nucleotide polymorphisms (SNPs) in strawberry and raspberry, respectively (Hardigan et al., 2020; Jibran et al., 2018). Genome sequencing provides even more data to facilitate selection by the detection of functional genes and their roles in trait expression. The first strawberry genome sequence (diploid woodland strawberry) was therefore seen as a major breakthrough (Shulaev et al., 2011). Recent improvements have made it possible to obtain a phased genome of tetraploid blueberry (Colle et al., 2019). By contrast, improvements in long-read sequencing technology (Dumschott et al., 2020; van Rengs et al., 2022) coupled with open-source technologies (Chen et al., 2021; Cheng et al., 2021; Schrinner et al., 2020) have unraveled the black raspberry (VanBuren et al., 2018) and octoploid strawberry (Edger et al., 2019) genomes, and pangenomic analysis has shed light on the evolutionary history of strawberry (Feng et al., 2021; Hardigan et al., 2021; Liston et al., 2020; Qiao et al., 2021). For practical breeding purposes, high-quality genome resources should reflect the allelic diversity of cultivated strawberry, which was found to be generally high in cosmopolitan collections (Hardigan et al., 2021), but lower in a subset from California (Hardigan et al., 2018).

Studying diverse material representing all stages of the breeding program, including unexploited related species, pre-breeding accessions and advanced breeding material, facilitates population-based studies of breeding germplasm and the diversity within this genepool, allowing genome-wide association studies (GWAS), from which QTLs and genomic prediction models can be derived. GWAS and genomic selection often utilize the open-source software GAPIT (Tang et al., 2016) to detect genomic associations, and statistical tools such as ASReml-R (Butler et al., 2017) or BGLR (Pérez & Campos, 2014) to develop prediction models (Davik et al., 2020; Enciso-Rodriguez et al., 2018; Gezan et al., 2017). Such approaches have already been applied successfully to strawberry, for example in the context of stress resistance (Petrasch et al., 2022; Pincot et al., 2018).

COMPLETE PHENOTYPING – FROM METABOLOMICS TO IMAGE ANALYSIS

High-throughput phenotyping is needed in addition to genotyping for successful genomic selection. In berries, high-throughput phenotyping has mainly targeted fruit quality traits, including metabolomic profiles and fruit external morphology. Fruit sensory attributes are influenced by numerous traits and therefore have a complex genetic basis. In strawberry, the large-scale analysis of metabolite-based QTLs has identified loci that determine the content of sugars, organic acids, amino acids, polyphenols, volatiles and vitamin C (Davik et al., 2020; Lerceteau-Köhler et al., 2012; Pott et al., 2020a; Urrutia et al., 2016; Vallarino et al., 2019; Zorrilla-Fontanesi et al., 2012). Similar work is underway to identify QTLs that influence fruit quality traits in raspberry (Graham & Simpson, 2018; McCallum et al., 2018; Willman, 2019) and blueberry (Ferrão et al., 2020; Gilbert et al., 2015).

Metabolomics is the comprehensive biochemical analysis of metabolites by fractionation and chemical identification (Emwas, 2015), allowing fruit sensory traits to be associated with the abundance of particular compounds (Allwood et al., 2021). Following the fractionation of samples by gas chromatography (GC) or liquid chromatography (LC), the most prominent analytical techniques in plant metabolomics are nuclear magnetic resonance spectroscopy and mass spectrometry (MS; Roessner-Tunali et al., 2003; Sobolev et al., 2015). These methods are often combined as multi-platform metabolomics techniques such as GC/LC-MS or GC/LC-MS/MS (Ghatak et al., 2018). For example, the metabolic response of five strawberry cultivars to three different postharvest treatments over 10 days revealed the metabolic reconfiguration of the fruit, including the depletion of major sugars and acids, a modified volatile emission profile, and the accumulation of protective metabolites (Pott et al., 2020b). Metabolomics has also been used to evaluate the effect of breeding on fruit metabolomes (Durán-Soria et al., 2021; Vallarino et al., 2018; Zhao et al., 2019; Zhu et al., 2018). Metabolomics can profile metabolic diversity to identify: (i) accessions suitable as parents; (ii) metabolic markers for selection; and (iii) certification markers in different species to develop new strategies for crop improvement.

Berries are cultivated under a range of different environments and agronomic practices. The resulting plasticity (the ability of a genotype to produce distinct phenotypes in different environments) is known as the genotype × environment (G × E) interaction (Via & Lande, 1985), and can change the selection ranking of genotypes across environments (El-Soda et al., 2014). Understanding G × E interaction in berries is therefore necessary to predict growth and fruit quality, and to adapt breeding strategies for each targeted environment. The effects of G × E interactions, environment and agronomic practices on fruit quality have been investigated in strawberry (Di Vittori et al., 2018) and raspberry (Durán-Soria et al., 2021), and also in *Vaccinium* species (Karppinen et al., 2016).

Image analysis (2D and 3D) is a cost-effective high-throughput phenotyping tool (Feldmann et al., 2020; He et al., 2017; Li et al., 2020; Reynolds et al., 2019) used to analyze berry phenotypic traits in research and breeding or to sort fruits into quality classes during processing (Liming & Yanchao, 2010). The automated capture and analysis of images relating to plant architecture has accelerated the assessment of growth in model species, but this technology has not yet been widely applied to berry crops (Bernotas et al., 2019). However, an analytical pipeline based on the dissection of plants has been developed, combining multiscale 2D and 3D representations of plant architecture (Bolger et al., 2019; Cockerton et al., 2019; Labadie et al., 2019; Schwacke et al., 2019). Mechanistic models can integrate phenotyping information, and thus simulate crop responses to environmental variations and their integrated impacts on productivity (Benes et al., 2020; Hopf et al., 2022). In particular, 3D functional–structural plant models have been designed to integrate root and shoot data (Guan et al., 2022; Takahashi & Pradal, 2021), and simulate the effects of biotic and abiotic stress on 3D plant architecture (Braghiere et al., 2020).

QUALITY FROM A CONSUMER PERSPECTIVE

The basic concept of quality, including intrinsic product properties and user satisfaction, has evolved to pursue aims such as 'total customer satisfaction' or even 'customer delight' (Füller & Matzler, 2008; Yang, 2017). The quality of berries is based on key sensory parameters such as taste, flavor and texture, and these should be optimized to achieve market and consumer demands.

Various international standards exist to evaluate the sensory quality of fresh berries. A harmonized approach is needed for the evaluation and documentation of fresh fruit quality, including a standard lexicon consisting of agreed attributes and descriptive terms relevant to different berry species, and procedures for the analysis of different berries adapted for the use of trained panels. The documentation of small fruit genetic diversity for pre-breeding and commercial purposes will be improved by developing sensory profiles for selected sets of varieties and relating these to consumer preferences (Oliver et al., 2018a). Combinations of trained panel testing and laboratory analysis can be enhanced by collecting data from non-trained consumer surveys because these represent a greater number of participants covering a broader spectrum of geographic regions, social classes, ages and other demographic categories.

The motivation for food selection is generally based on nine factors: health, mood, convenience, sensory appeal, content of natural ingredients, price, weight control, familiarity, and ethical concerns (Steptoe et al., 1995). The relative importance of these factors varies according to the consumer's country of origin, but sensory appeal and health are often the highest ranking factors (Battino et al., 2019; Januszewska et al., 2011; Kalt et al., 2019; Pap et al., 2021). The recent review of consumer requirements and expectations for strawberry quality showed how modern consumer science methods can help to orient breeding strategies and commercial decision-making (Predieri et al., 2021). Consumer preferences for strawberry attributes have been solicited using methods such as check-all-that-apply (CATA) questionnaires to evaluate new cultivars compared with those already on the market (Lado et al., 2010). CATA questionnaires simultaneously capture information about 'overall liking' and the corresponding drivers, can segment consumers according to their preferences, and provide information useful for communication and marketing. They do not use a numeric scale. Instead, participants indicate whether a term is appropriate or not to describe a given product. This allows the investigation of sensory characteristics in the context of consumption, the willingness to purchase, and associated emotions. The effectiveness of this approach is evident from a strawberry questionnaire, which revealed no differences in 'overall liking', while responses to more specific questions about 'flavor liking' and 'willingness to pay' indicated significant differences in appreciation (Lado et al., 2010). The introduction of new technologies and methods to assess consumer acceptance can accelerate breeding and ensure new berry varieties meet market demands. The Napping test (Pagès, 2005) is another rapid sensory profiling technique, in which consumers follow their own criteria to differentiate between products, then use their own language to describe sensory differences using a consumer-friendly approach known as the ultra-flash profile (Perrin et al., 2008). The Napping test successfully segmented strawberry samples according to sensory traits by comparing the evaluations of untrained consumers with the judgments of a panel of trained experts (Oliver et al., 2018b). This revealed sensory and lexical similarities and differences between experts and consumers, helping to improve communication. The ultra-flash profile has been applied to 14 berry crops, including strawberry, bilberry and raspberry (Laaksonen et al., 2016).

As well as highlighting specific appealing traits, the fresh berry industry should point out innovative features related to sensory traits, environmental sustainability and health. In globalized food markets, innovation has become the key competitive force (Md Sohel Uz Zaman & Anjalin, 2011). Accordingly, data concerning the nutraceutical qualities of berries or their environmental impact during production are increasingly important for consumers, and are considered in addition to sensory traits when making purchase decisions.

BIG DATA MADE 'FAIR'

Information describing the attributes of germplasm collections should be readily available in data repositories so that users can access germplasm of interest alongside the associated data, otherwise the value and potential applications of that germplasm are hidden (Marx, 2013; Nandyala & Kim, 2016). Users from different application domains have different levels of expertise. It is therefore crucial that repositories offer entry points for casual, public and educational purposes, as well as the ability to support complex and powerful query and visualization tools required by expert users. The recording of experimental data from large, collaborative projects presents unique challenges that need to be addressed.

A common requirement of journals and funding agencies is that data are made publicly available in standard digital formats for utilization by others. This also ensures that germplasm variation identified or generated in research projects can be exploited by research and breeding communities. Guidelines have been established through initiatives such as FAIR, which stipulates that data should be findable, accessible, interoperable and reusable in order to facilitate (re)utilization (Wilkinson et al., 2016). Generalized repositories for genetic and genomic data are hosted by the National Center for Biotechnology Information (NCBI; https://www.ncbi.nlm.nih.gov), the European Molecular Biology Laboratory – European Bioinformatics Institute (EMBL-EBI; https://www.ebi.ac.uk) and the DNA Databank of Japan (DDBJ; https://www.ddbj.nig.ac.jp). Related initiatives such as the Proteomics Identifications Database (PRIDE) exist for proteins and peptides, and metabolite databases have been established for metabolomic data (Haug et al., 2020). However, it is challenging to set up a generalized repository for phenotypic data (Watt et al., 2020) or consumer perception and organoleptic qualities.

Furthermore, common standards serving all communities might not capture all metadata necessary to reproduce experiments with plants, where pot size or fertilizer input are examples of unique factors (Poorter et al., 2012). Therefore, all experimental and trial data should be collected along with informative and standardized metadata adhering to standards such as the Minimal Information About a Plant Phenotyping Experiment (MIAPPE; Ćwiek-Kupczyńska et al., 2016; Papoutsoglou et al., 2020). Solutions such as the Breeding Application Programing Interface (BrAPI) should also help to standardize data exchange (Selby et al., 2019).

To facilitate data reanalysis, it is important to specify in an unambiguous manner the focus of the study, the experimental design, experimental and environmental factors, and the tools, materials and methods used. Accordingly, standard operating procedures are especially important in research, along with a standardized vocabulary and ontologies to describe environments and/or plants and their parts. Relevant ontologies are usually developed in global communities to ensure they are widely accepted and understood, for example in the Planteome project (Cooper et al., 2018).

The efficient management and distribution of experimental data ensures the rapid incorporation of germplasm into research and breeding programs (Raubach et al., 2021). The dissemination of data within user communities is easier when standardized data formats and simple data structures exist, as exemplified by genomics data in the GDR (Jung et al., 2019). Phenotypic and organoleptic attributes require databases that allow users to query complex characterization and evaluation data, including effective visualization tools that provide a deeper understanding of the data, alongside tools for data export in formats suitable for downstream analysis. Open-source information systems such as Germinate (Raubach et al., 2021; Shaw et al., 2017) provide such functionality, and are used in the soft fruit, stone fruit and cereal communities. The interactive visual interfaces in Germinate provide access to information from plant genetic resources and pre-breeding experiments, and data can be exported as plain text if necessary. Germplasm and field trial sites can be represented using geographical maps. Complex phenotypic data can be displayed in a number of ways, including interactive matrix plots to show correlation, clustering and outliers in datasets comparing traits, or even the combined analysis of genetic and phenotypic data. These user-friendly options are particularly useful for queries spanning multiple genotypes.

THE BREEDINGVALUE PROJECT TO BOOST EUROPEAN SOFT FRUIT BREEDING

The challenges outlined above will be addressed by the new EU-funded project BreedingValue, in which we aim to connect European strawberry, raspberry and blueberry germplasm resources with breeding programs, and to transfer genetic resources, knowledge and tools to researchers, pre-breeders and other stakeholders. The holistic approach combines genomic and phenotypic data (including metabolomics and sensory quality attributes), and will meet future market and consumer requirements by applying consumer science (Figure 3). We will publish our results, raw data and metadata on the Germinate platform (Shaw et al., 2017).

A wealth of diverse berry germplasm is maintained among BreedingValue project partners. From these genetic resources, a core collection of plant material is planned to be maintained and utilized across the project, encompassing all six defined Plant Categories (Figure 2). For the first project period, more than 2200 genotypes and 33 breeding populations have been selected (Table 1). When choosing material for the core germplasm collection, accessions that are of interest for molecular investigation, for application of new phenotyping tools, and for consumer sensory tests will be prioritized.

The project will analyze strawberry genetic resources from all major European climate regions, integrating all historical and recent commercial knowledge from successful cultivars, and thus revealing the direction of different strawberry breeding programs in Europe. The strawberry germplasm collection includes more than 1700 genotypes from Plant Category 1 to 5, as defined in Figure 2. Furthermore, several hundreds of plants coming from 27 breeding populations complement the strawberry material characterization. Diverse raspberry and blueberry germplasm will also be investigated, albeit in less detail. The chosen raspberry germplasm collection will include over 400 genotypes of Categories 1–5, complemented by four breeding populations. The available blueberry germplasm collection consists largely of genotypes from a *Vaccinium corymbosum* genetic background, and includes 79 cultivars across

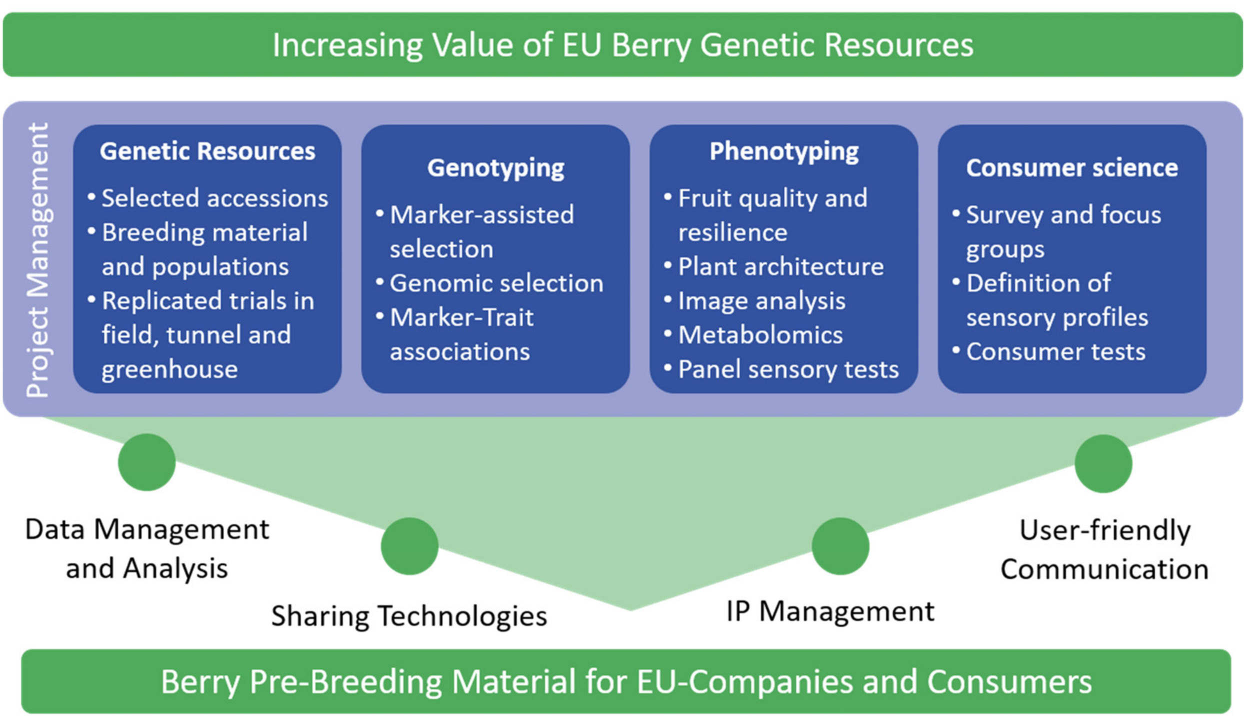

Figure 3. Organization and outputs of the BreedingValue project (©BreedingValue consortium, 2022).

Table 1 Germplasm planned to be included in the first project period per germplasm category and genus

Germplasm category	Number of genotypes included in BreedingValue		
	Fragaria sp.	*Rubus* sp.	*Vaccinium* sp.
1: Old cultivars (until 1959)	188	12	14
2: Modern cultivars (1960–2004)	312	20	35
3: Newest cultivars (2005–now)	144	15	8
4: Pre-breeding material	1019	354	20
5: Related species	72	8	2
Total (Cat. 1–Cat. 5)	1735	409	79
6: Number of populations[a]	27	4	2

[a]Each population represented by varying numbers of genotypes.

Plant Categories 1–5, as well as two populations (Table 1). The germplasm selection might undergo modifications in later project periods.

The majority of genotypes in the chosen collection will be assessed in field trials, and will serve as the foundation for genotyping, phenotyping and consumer science studies. Field trials will be performed by BreedingValue partners at the various cultivation sites across two growing seasons, with strawberry and raspberry germplasm assessed in replicated trials, and blueberry germplasm maintained in non-replicated plots. Traits related to plant performance will be assessed among project partners according to standard phenotypic descriptors defined in other EU projects (such as EUBerry, COST 836 and GoodBerry). Traits will include total yield across the season, fruit quality traits (such as size, color, shape, firmness and skin resistance) at the start and peak of the growing season, total sugar (°Brix) and titratable acids. These data, when compared with control cultivars, will allow the consortium to identify genotypes with higher yield and fruit quality across the different trial sites, and will increase the understanding of how the various genetic resources respond in different environments. Furthermore, a subset of genotypes will be assessed for resilience by evaluating water stress resistance (in strawberry and blueberry), and by assessing resistance to diseases (including powdery mildew and crown rot in strawberry, leaf rust in raspberry, and dieback and gall midge in blueberry) under artificial direct inoculation or natural high disease pressure. A Life Cycle Assessment (LCA) will also be undertaken on a subset of material in field trials to assess agronomic performance and sustainability. The LCA analysis will be performed using the standardized software Simapro v.9 with associated databases, and methodology based on ISO 14040 and ISO 14044.

The development of genomic tools for improved berry breeding efficiency will be facilitated through three approaches that will be extensively validated. Transfer of promising pre-breeding accessions, genomic tools and technologies to berry breeders outlines the strong focus of BreedingValue towards innovative technologies, and will have a strong impact on European berry breeding. Firstly, previously published markers for commercially important Mendelian traits in strawberry will be made publicly available for utilization by the breeding and pre-breeding communities. Markers linked to fruit quality traits (such as aroma, color, soluble acids and sugars, and anthocyanin content), flowering traits (everbearing) and disease resistances will be prioritized. A low-density SNP array for marker-assisted selection and cultivar identification will be developed by utilizing Fluidigm® SNP Type™ technology, which will allow for high-throughput, cost-effective and reproducible analysis of polyploid strawberry genotypes. Leaf samples of the BreedingValue strawberry germplasm collection extended by further accessions from commercial breeders (obtained through targeted calls) will be genotyped on the array, with data linked to phenotypes for those selections.

The second approach will employ GWAS and genomic prediction models to target commercially important polygenic traits with complex inheritance. The wide range of plant material from sources within and outside the project (obtained through targeted calls) will facilitate the model development. GWAS and genomic prediction models will mainly be applied to material defined in the BreedingValue germplasm collection, and those available from related studies. Genotyping of strawberry will be performed on the Axiom 50K SNP array (Hardigan et al., 2020), with powdery mildew resistance chosen as the candidate trait. A 9K axiom is available for raspberry (Jibran et al., 2018), but the results of a preliminary study will show if the marker density will be sufficient for our purposes. Alternatively, a genotyping-by-sequencing approach might be employed, with resistance to late leaf rust chosen as candidate trait. In addition, phenotypic data collected across the project for strawberry and raspberry will be utilized to identify genomic associations. For breeding programs involved with the project through targeted calls, both a marker-assisted approach and a genomic prediction approach will be utilized. For individual breeders, the best training set will be determined by selecting material that most closely correlates with the test sets (Akdemir & Isidro-Sánchez, 2019), as recently implemented using the R software environment (Ou & Liao, 2019). The predictive power of the models will be cross-validated rapidly, whereas full validation by the field-testing of selected accessions is a longer-term goal for a follow-up project. Simultaneously, material and technology transfer will take place to breeders and stakeholders by providing pre-breeding material and by training the participants of targeted calls in how to implement marker-assisted selection, GWAS or genomic selection in their breeding programs or companies, and how to use and improve the predictive models.

The third approach to develop genetic resources involves an allelic diversity study to assess genetic variation in strawberry material of the BreedingValue germplasm collection and further accessions provided by participants of targeted calls from Plant Categories 1, 2 and 3. Genotyping will be performed using the Axiom 50K SNP array. Genetic differentiation between the three categories can be assessed using the multiallelic extension of Wright's fixation index (F_{ST}), while phenotypic data can provide insight into the strength of selection on quantitative traits and the prevalence and effects of inbreeding. Extending the project dataset with historic or open-source data will additionally enable elucidating the achieved breeding progress in the different cultivar categories and the underlying factors (Tollenaar & Lee, 2002).

Accurate and efficient phenotyping is essential for cultivar improvement, and for developing marker-assisted selection and genomic prediction tools. The phenotyping work will focus on image analysis related to yield traits, and the analysis of sensory attributes and quality traits of ripe fruits using multi-platform metabolomics techniques. This will provide valuable information on the phenotypic properties of the BreedingValue germplasm collection, and investigate best methods for screening architectural, ripe fruit quality and post-harvest traits in large germplasm collections and pre-breeding material. Near-infrared spectroscopy will be used to image a subset of previously-phenotyped genotypes. These data will be used to establish protocols and predictive models for early screening of fruit ripening, fruit quality features, and biotic and abiotic stresses. Similarly, hyperspectral and 3D imaging of phenotyped strawberry, raspberry and blueberry germplasm will be analyzed to link imaging data to fruit quality traits and stress. Image analysis will be optimized to study plant architectural traits that correlate with yield, allowing the high-throughput selection of cultivars with better yields. A novel 3D plant model, calibrated on phenotypic data, will be developed to define ideotypes under various environmental conditions, in the open-source OpenAlea platform (Pradal et al., 2008).

Imaging and metabolite analysis will be performed on a subset of genotypes across two growing seasons. Data will be used to assess whether imaging techniques can be utilized as non-invasive and non-destructive alternatives to infer metabolite levels in fruit. Metabolic analysis will include quantification of folic acid and vitamin levels (particularly vitamin C). Primary metabolites of nutritive value (such as individual sugars, acids and phenolics) will be assessed using GC-TOF-MS (Osorio et al., 2011). Volatile compounds associated with aroma and flavor will be assessed by headspace GC-MS (Rambla et al., 2015), while secondary metabolites grouped into phenylpropanols, flavonoids, anthocyanins and proanthocyanins will be assessed by LC-MS/MS (Vallarino et al., 2018). In addition, mass spectral signatures will be used to identify unknown metabolites that contribute to fruit quality. The metabolomics approach will identify important genetic resources for conservation, thus enabling future selection gains and ensuring recovery from the loss of aroma in recent breeding programs. It will also enable the identification of key metabolites as selection markers and permit metabolomic data to be used for the certification of different berry species.

The fruit quality traits and sensory attributes of the diverse germplasm under investigation will also be characterized by trained panels, and the metabolomic data will be linked to these sensory profiles as the basis for automated sensory analytics. User-friendly and multilingual harmonized sensory analysis tools will be developed to describe the sensory properties that are important to consumers. Sensory profiles of a subset of diverse accessions will subsequently be obtained by panel testing. A broad consumer survey will be prepared to gain a high-resolution picture of consumer preferences relating to strawberries, raspberries and blueberries across the continent. A targeted call will allow breeders and pre-breeders across Europe to evaluate and feedback on the developed consumer sensory test tools and surveys. This will help to determine future breeding goals and requirements for the logistics and processing chain.

Finally, the development of new visualization components for Germinate, including consumer preference/organoleptic data types, will allow BreedingValue to benefit from the current features and functionality of this platform, while adding components specific to the soft fruit domain. This will also contribute to the Germinate open source codebase for the benefit of the worldwide plant breeding and research community.

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AUTHOR CONTRIBUTIONS

All authors contributed to the writing of this manuscript.

CONFLICT OF INTEREST

All authors of this manuscript declare no conflict of interest.

REFERENCES

Aharoni, A., Giri, A.P., Verstappen, F.W., Bertea, C.M., Sevenier, R., Sun, Z. *et al.* (2004) Gain and loss of fruit flavor compounds produced by wild and cultivated strawberry species. *Plant Cell*, **16**(11), 3110–3131.

Akdemir, D., Beavis, W., Fritsche-Neto, R., Singh, A.K. & Isidro-Sánchez, J. (2018) Multi-objective optimized genomic breeding strategies for sustainable food improvement. *Heredity*, **122**, 672–683.

Akdemir, D. & Isidro-Sánchez, J. (2019) Design of training populations for selective phenotyping in genomic prediction. *Scientific Reports*, **9**, 1446.

Allwood, J.W., Gibon, Y., Osorio, S., Araújo, W.L., Vallarino, J.G., Pétriacq, P. *et al.* (2021) Developmental metabolomics to decipher and improve fleshy fruit quality. In: Pétriacq, P. & Bouchereau, A. (Eds.) *Advances in botanical research*, Vol. **98**. London: Academic Press, pp. 3–34.

Allwood, J.W., Woznicki, T.L., Xu, Y., Foito, A., Aaby, K., Sungurtas, J. *et al.* (2019) Application of HPLC-PDA-MS metabolite profiling to investigate the effect of growth temperature and day length on blackcurrant fruit. *Metabolomics*, **15**, 12.

Antonius, K., Karhu, S., Kaldmäe, H., Lacis, G., Rugenius, R., Banilius, D. *et al.* (2012) Development of the Northern European Ribes core collection based on a microsatellite (SSR) marker diversity analysis. *Plant Genetic Resources*, **10**(1), 70–73.

Barrett, D.M., Beaulieu, J.C. & Shewfelt, R. (2010) Color, flavor, texture, and nutritional quality of fresh-cut fruits and vegetables: desirable levels, instrumental and sensory measurement, and the effects of processing. *Critical Reviews in Food Science and Nutrition*, **50**, 369–389.

Baselice, A., Colantuoni, F., Lass, D.A., Nardone, G. & Stasi, A. (2017) Trends in EU consumers' attitude towards fresh-cut fruit and vegetables. *Food Quality and Preference*, **59**, 87–96.

Battino, M., Forbes-Hernández, T.Y., Gasparrini, M., Afrin, S., Cianciosi, D., Zhang, J. *et al.* (2019) Relevance of functional foods in the Mediterranean diet: the role of olive oil, berries and honey in the prevention of cancer and cardiovascular diseases. *Critical Reviews in Food Science and Nutrition*, **59**, 893–920.

Bebber, D.P., Ramotowski, M.A.T. & Gurr, S.J. (2013) Crop pests and pathogens move polewards in a warming world. *Nature Climate Change*, **3**, 985–988.

Benes, B., Guan, K., Lang, M., Long, S.P., Lynch, J.P., Marshall-Colón, A. *et al.* (2020) Multiscale computational models can guide experimentation and targeted measurements for crop improvement. *The Plant Journal*, **103**(1), 21–31.

Bernotas, G., Scorza, L.C.T., Hansen, M.F., Hales, I.J., Halliday, K.J., Smith, L.N. *et al.* (2019) A photometric stereo-based 3D imaging system using computer vision and deep learning for tracking plant growth. *Gigascience*, **8**(5), 1–15. https://doi.org/10.1093/gigascience/giz056

Bisbis, M.B., Gruda, N.S. & Blanke, M.M. (2019) Securing horticulture in a changing climate—a mini review. *Horticulturae*, **5**, 56.

Bolger, A.M., Poorter, H., Dumschott, K., Bolger, M.E., Arend, D., Osorio, S. *et al.* (2019) Computational aspects underlying genome to phenome analysis in plants. *The Plant Journal*, **97**, 182–198.

Braghiere, R.K., Gérard, F., Evers, J.B., Pradal, C. & Pagès, L. (2020) Simulating the effects of water limitation on plant biomass using a 3D functional–structural plant model of shoot and root driven by soil hydraulics. *Annals of Botany*, **126**(4), 713–728.

Butler, D.G., Cullis, B.R., Gilmour, A.G., Gogel, B.G. & Thompson, R. (2017) *ASReml-R reference manual Version 4*. Hemel Hempstead, UK: *VSN International Ltd*.

Capocasa, F., Diamanti, J., Tulipani, S., Battino, M. & Mezzetti, B. (2008) Breeding strawberry (*Fragaria* X *ananassa* Duch) to increase fruit nutritional quality. *BioFactors*, **34**, 67–72.

Carrasco, B., Garcés, M., Rojas, P., Saud, G., Herrera, R., Retamales, J.B. *et al.* (2007) The Chilean strawberry [*Fragaria chiloensis* (L.) Duch.]: genetic diversity and structure. *Journal of the American Society for Horticultural Science*, **132**, 501–506.

Cellon, C., Amadeu, R.R., Olmstead, J.W., Mattia, M.R., Ferrao, L.F.V. & Munoz, P.R. (2018) Estimation of genetic parameters and prediction of breeding values in an autotetraploid blueberry breeding population with extensive pedigree data. *Euphytica*, **214**, 87.

Challinor, A.J., Watson, J., Lobell, D.B., Howden, S.M., Smith, D.R. & Chhetri, N. (2014) A meta-analysis of crop yield under climate change and adaptation. *Nature Climate Change*, **4**, 287–291.

Chen, Y., Nie, F., Xie, S.Q., Zheng, Y.F., Dai, Q., Bray, T. *et al.* (2021) Efficient assembly of nanopore reads via highly accurate and intact error correction. *Nature Communications*, **12**, 1–10.

Cheng, H., Concepcion, G.T., Feng, X., Zhang, H. & Li, H. (2021) Haplotype-resolved de novo assembly using phased assembly graphs with hifiasm. *Nature Methods*, **18**, 170–175.

Cockerton, H.M., Li, B., Vickerstaff, R.J., Eyre, C.A., Sargent, D.J., Armitage, A.D. *et al.* (2019) Identifying *Verticillium dahliae* resistance in strawberry through disease screening of multiple populations and image based phenotyping. *Frontiers in Plant Science*, no. 924.

Colle, M., Leisner, C.P., Wai, C.M., Ou, S., Bird, K.A., Wang, J. *et al.* (2019) Haplotype-phased genome and evolution of phytonutrient pathways of tetraploid blueberry. *Gigascience*, **8**(3), 1–15. https://doi.org/10.1093/gigascience/giz012

Cooper, L., Meier, A., Laporte, M.-A., Elser, J.L., Mungall, C., Sinn, B.T. *et al.* (2018) The Planteome database: an integrated resource for reference ontologies, plant genomics and phenomics. *Nucleic Acids Research*, **46**, D1168–D1180.

Crossa, J., Pérez-Rodríguez, P., Cuevas, J., Montesinos-López, O., Jarquín, D., de Los Campos, G. *et al.* (2017) Genomic selection in plant breeding: methods, models, and perspectives. *Trends in Plant Science*, **22**, 961–975.

Ćwiek-Kupczyńska, H., Altmann, T., Arend, D., Arnaud, E., Chen, D., Cornut, G. *et al.* (2016) Measures for interoperability of phenotypic data: minimum information requirements and formatting. *Plant Methods*, **12**, 44.

Darrow, G.M. (1966) *The strawberry; history, breeding, and physiology*. New York: Holt, Rinehart and Winston.

Davies, W.J. & Ribaut, J.-M. (2017) Stress resilience in crop plants: strategic thinking to address local food production problems. *Food and Energy Security*, **6**, 12–18.

Davik, J., Aaby, K., Buti, M., Alsheikh, M., Šurbanovski, N., Martens, S. *et al.* (2020) Major-effect candidate genes identified in cultivated strawberry (Fragaria × ananassa Duch.) for ellagic acid deoxyhexoside and pelargonidin-3-O-malonylglucoside biosynthesis, key polyphenolic compounds. *Horticulture Research*, **7**, 125.

Di Vittori, L., Mazzoni, L., Battino, M. & Mezzetti, B. (2018) Pre-harvest factors influencing the quality of berries. *Scientia Horticulturae*, **233**, 310–322.

Diamanti, J., Capocasa, F., Balducci, F., Battino, M., Hancock, J. & Mezzetti, B. (2012) Increasing strawberry fruit sensorial and nutritional quality using wild and cultivated germplasm. *PLoS One*, **7**, e46470.

Dumschott, K., Schmidt, M.H.-W., Chawla, H.S., Snowdon, R. & Usadel, B. (2020) Oxford nanopore sequencing: new opportunities for plant genomics? *Journal of Experimental Botany*, **71**(18), 5313–5322.

Durán-Soria, S., Pott, D.M., Will, F., Mesa-Marín, J., Lewandowski, M., Celejewska, K. *et al.* (2021) Exploring genotype-by-environment interactions of chemical composition of raspberry by using a metabolomics approach. *Metabolites*, **11**(8), 490.

Edger, P.P., Poorten, T.J., VanBuren, R., Hardigan, M.A., Colle, M., McKain, M. *et al.* (2019) Origin and evolution of the octoploid strawberry genome. *Nature Genetics*, **51**, 541–547.

El-Soda, M., Malosetti, M., Zwaan, B.J., Koornneef, M. & Aarts, M.G.M. (2014) Genotype×environment interaction QTL mapping in plants: lessons from Arabidopsis. *Trends in Plant Science*, **19**, 390–398.

Emwas, A.-H.M. (2015) The strengths and weaknesses of NMR spectroscopy and mass spectrometry with particular focus on metabolomics research. *Methods in Molecular Biology*, **1277**, 161–193.

Enciso-Rodriguez, F., Douches, D., Lopez-Cruz, M., Coombs, J. & de Los Campos, G. (2018) Genomic selection for late blight and common scab resistance in tetraploid potato (*Solanum tuberosum*). *G3*, **8**, 2471–2481.

European Union (2020) GoodBerry Project Reporting, periodic reporting for period 3 – GoodBerry (Improving the stability of high-quality traits of berry in different environments and cultivation systems for the benefit of European farmers and consumers), last update 14 October 2020. *European Union*, report no. 220214. https://cordis.europa.eu/project/id/679303/reporting (last accessed: 23 November 2021).

FAO (2021) FAOSTAT Food and agriculture database, Crops and livestock products, last update 21 December 2021. https://www.fao.org/faostat/en/#data/TCL (accessed and downloaded 02 February 2022).

Feldmann, M.J., Hardigan, M.A., Famula, R.A., López, C.M., Tabb, A., Cole, G.S. *et al.* (2020) Multi-dimensional machine learning approaches for fruit shape phenotyping in strawberry. *Gigascience*, **9**(5), 1–17. https://doi.org/10.1093/gigascience/giaa030

Feng, C., Wang, J., Harris, A.J., Folta, K.M., Zhao, M. & Kang, M. (2021) Tracing the diploid ancestry of the cultivated octoploid strawberry. *Molecular Biology and Evolution*, **38**, 478–485.

Ferrão, L.F.V., Johnson, T.S., Benevenuto, J., Edger, P.P., Colquhoun, T.A. & Munoz, P.R. (2020) Genome-wide association of volatiles reveals candidate loci for blueberry flavor. *New Phytologist*, **226**(6), 1725–1737.

Füller, J. & Matzler, K. (2008) Customer delight and market segmentation: an application of the three-factor theory of customer satisfaction on life style groups. *Tourism Management*, **29**, 116–126.

Geibel, M., Roudeillac, P., Masny, A., Trajkovski, K., Coman, M. & Simpson, D.W. (2004) The European strawberry database and building up a European core collection. *Acta Horticulturae*, **649**, 41–44.

Gezan, S.A., Osorio, L.F., Verma, S. & Whitaker, V.M. (2017) An experimental validation of genomic selection in octoploid strawberry. *Horticulture Research*, **4**, 16070.

Ghatak, A., Chaturvedi, P. & Weckwerth, W. (2018) Metabolomics in plant stress physiology. *Advances in Biochemical Engineering/Biotechnology*, **164**, 187–236.

Gil-Ariza, D.J., Amaya, I., López Aranda, J.M., Sánchez Sevilla, J.F., Botella, M.Á. & Valpuesta, V. (2009) Impact of plant breeding on the genetic diversity of cultivated strawberry as revealed by expressed sequence tag-derived simple sequence repeat markers. *Journal of the American Society for Horticultural Science*, **134**, 337–347.

Gilbert, J.L., Guthart, M.J., Gezan, S.A., Pisaroglo de Carvalho, M., Schwieterman, M.L., Colquhoun, T.A. *et al.* (2015) Identifying breeding priorities for blueberry flavor using biochemical, sensory, and genotype by environment analyses. *PLoS One*, **10**, e0138494.

Graham, J. & Simpson, C. (2018) Developmental transitions to fruiting in red raspberry. In: Hytönen, T., Graham, J. & Harrison, R. (Eds.) *The genomes of Rosaceous berries and their wild relatives*. Berlin/Heidelberg: Springer, pp. 199–212.

Guan, Z., Abd-Elrahman, A., Whitaker, V., Agehara, S., Wilkinson, B., Gastellu-Etchegorry, J.P. *et al.* (2022) Radiative transfer image simulation using L-system modeled strawberry canopies. *Remote Sensing*, **14** (3), 548.

Hancock, J.F., Finn, C.E., Luby, J.J., Dale, A., Callow, P.W. & Serçe, S. (2010) Reconstruction of the strawberry, Fragaria ×ananassa, using genotypes of *F. virginiana* and *F. chiloensis*. *Horticultural Science*, **45**, 1006–1013.

Hardigan, M.A., Feldmann, M.J., Lorant, A., Bird, K.A., Famula, R., Acharya, C. *et al.* (2020) Genome synteny has been conserved among the octoploid progenitors of cultivated strawberry over millions of years of evolution. *Frontiers in Plant Science*, **10**, 1789.

Hardigan, M.A., Lorant, A., Pincot, D.D.A., Feldmann, M.J., Famula, R.A., Acharya, C.B. *et al.* (2021) Unraveling the complex hybrid ancestry and domestication history of cultivated strawberry. *Molecular Biology and Evolution*, **38**, 2285–2305.

Hardigan, M.A., Poorten, T.J., Acharya, C.B., Cole, G.S., Hummer, K.E., Bassil, N. *et al.* (2018) Domestication of temperate and coastal hybrids with distinct ancestral gene selection in octoploid strawberry. *Plant Genome*, **11**(3), 180049.

Haug, K., Cochrane, K., Nainala, V.C., Williams, M., Chang, J., Jayaseelan, K.V. *et al.* (2020) MetaboLights: a resource evolving in response to the needs of its scientific community. *Nucleic Acids Research*, **48**, D440–D444.

He, J.Q., Harrison, R.J. & Li, B. (2017) A novel 3D imaging system for strawberry phenotyping. *Plant Methods*, **13**, 93.

Höfer, M. (2021) Coordination of genebank activities between different national collections of berry genetic resources in Europe in the frame of ECPGR. *Acta Horticulturae*, **1309**, 181–188.

Hopf, A., Boote, K.J., Oh, J., Guan, Z., Agehara, S., Shelia, V. *et al.* (2022) Development and improvement of the CROPGRO-Strawberry model. *Scientia Horticulturae*, **291**, 110538.

Horvath, A., Sánchez Sevilla, J.F., Punelli, F., Richard, L., Sesmero-Carrasco, R., Leone, A. *et al.* (2011) Structured diversity in octoploid strawberry cultivars: importance of the old European germplasm. *The Annals of Applied Biology*, **159**, 358–371.

Iezzoni, A.F., McFerson, J., Luby, J., Gasic, K., Whitaker, V., Bassil, N. *et al.* (2020) RosBREED: bridging the chasm between discovery and application to enable DNA-informed breeding in rosaceous crops. *Horticulture Research*, **7**, 1–23.

Januszewska, R., Pieniak, Z. & Verbeke, W. (2011) Food choice questionnaire revisited in four countries. Does it still measure the same? *Appetite*, **57**, 94–98.

Jibran, R., Dzierzon, H., Bassil, N., Bushakra, J.M., Edger, P.P., Sullivan, S. *et al.* (2018) Chromosome-scale scaffolding of the black raspberry (*Rubus occidentalis* L.) genome based on chromatin interaction data. *Horticulture Research*, **5**, 8.

Jimenez Garcia, S.N., Guevara Gonzalez, R.G., Miranda Lopez, R., Feregrino Perez, A.A., Torres Pacheco, I. & Vazquez Cruz, M.A. (2013) Functional properties and quality characteristics of bioactive compounds in berries: biochemistry, biotechnology, and genomics. *Food Research International*, **54**, 1195–1207.

Jung, S., Lee, T., Cheng, C.H., Buble, K., Zheng, P., Yu, J. *et al.* (2019) 15 years of GDR: new data and functionality in the Genome Database for Rosaceae. *Nucleic Acids Research*, **47**, D1137–D1145.

Kalt, W., Cassidy, A., Howard, L.R., Krikorian, R., Stull, A.J., Tremblay, F. *et al.* (2019) Recent research on the health benefits of blueberries and their anthocyanins. *Advances in Nutrition*, **11**, 224–236.

Karhu, S., Antonius, K., Rantala, S., Kaldmäe, H., Pluta, S., Rumpunen, K. *et al.* (2012) A multinational approach for conserving the European genetic resources of currants and gooseberry. *Acta Horticulturae*, **926**, 27–32.

Karppinen, K., Zoratti, L., Nguyenquynh, N., Häggman, H. and Jaakola, L. (2016) On the developmental and environmental regulation of secondary metabolism in Vaccinium spp. Berries. *Frontiers in Plant Science*, **7**, 655.

Klee, H.J. & Tieman, D.M. (2018) The genetics of fruit flavour preferences. *Nature Reviews. Genetics*, **19**, 347–356.

Krüger, E., Dietrich, H., Hey, M. & Patz, C.D. (2012) Effects of cultivar, yield, berry weight, temperature and ripening stage on bioactive compounds of black currants. *Journal of Applied Botany and Food Quality*, **84**(1), 40.

Laaksonen, O., Knaapila, A., Niva, T., Deegan, K.C. & Sandell, M. (2016) Sensory properties and consumer characteristics contributing to liking of berries. *Food Quality and Preference*, **53**, 117–126.

Labadie, M., Denoyes, B. & Guédon, Y. (2019) Identifying phenological phases in strawberry using multiple change-point models. *Journal of Experimental Botany*, **70**, 5687–5701.

Lado, J., Vicente, E., Manzzioni, A. & Ares, G. (2010) Application of a check-all-that-apply question for the evaluation of strawberry cultivars from a breeding program. *Journal of the Science of Food and Agriculture*, **90**, 2268–2275.

Lerceteau-Köhler, E., Moing, A., Guérin, G., Renaud, C., Petit, A., Rothan, C. *et al.* (2012) Genetic dissection of fruit quality traits in the octoploid cultivated strawberry highlights the role of homoeo-QTL in their control. *Theoretical and Applied Genetics*, **124**, 1059–1077.

Li, B., Cockerton, H.M., Johnson, A.W., Karlström, A., Stavridou, E., Deakin, G. *et al.* (2020) Defining strawberry shape uniformity using 3D imaging and genetic mapping. *Horticulture Research*, **7**, 115.

Liming, X. & Yanchao, Z. (2010) Automated strawberry grading system based on image processing. *Computers and Electronics in Agriculture*, **71**, S32–S39.

Liston, A., Cronn, R. & Ashman, T.L. (2014) Fragaria: a genus with deep historical roots and ripe for evolutionary and ecological insights. *American Journal of Botany*, **101**, 1686–1699.

Liston, A., Wei, N., Tennessen, J.A., Li, J., Dong, M. & Ashman, T.L. (2020) Revisiting the origin of octoploid strawberry. *Nature Genetics*, **52**, 2–4.

Marx, V. (2013) Biology: the big challenges of big data. *Nature*, **498**, 255–260.

Mazzoni, L., Perez Lopez, P., Giampieri, F., Alvarez Suarez, J.M., Gasparrini, M., Forbes Hernandez, T.Y. *et al.* (2016) The genetic aspects of berries: from field to health. *Journal of the Science of Food and Agriculture*, **96**, 365–371.

McCallum, S., Simpson, C. & Graham, J. (2018) QTL mapping and marker assisted breeding in *Rubus* spp. In: Graham, J. & Brennan, R. (Eds.) *Raspberry: breeding, challenges and advances*. Cham: Springer International Publishing, pp. 121–144.

Md Sohel Uz Zaman, A.S. & Anjalin, U. (2011) Evolution of service: Importance, competitiveness and sustainability in the new circumstances. *International Journal of Biodiversity Science, Ecosystems Services and Management*, **4**(3), 253–260.

Mezzetti, B., Balducci, F., Capocasa, F., Zhong, C.F., Cappelletti, R., Di Vittori, L. *et al.* (2016) Breeding strawberry for higher phytochemicals content and claim it: is it possible? *International Journal of Fruit Science*, **16**, 194–206.

Mezzetti, B., Nestby, R., Korbin, M., Denoyes Rothan, B., van Duijn, B. & Bodson, M. (2009) Cost action 863 euroberry research: from genomics to sustainable production, quality and health. *Acta Horticulturae*, **842**, 631–634.

Nandyala, C.S. & Kim, H.K. (2016) Big and meta data management for U-Agriculture mobile services. *International Journal of Software Engineering & Applications*, **10**(2), 257–270.

Oliver, P., Cicerale, S., Pang, E. & Keast, R. (2018a) Developing a strawberry lexicon to describe cultivars at two maturation stages. *Journal of Sensory Studies*, **33**, e12312.

Oliver, P., Cicerale, S., Pang, E. & Keast, R. (2018b) Comparison of quantitative descriptive analysis to the napping methodology with and without product training. *Journal of Sensory Studies*, **33**, e12331.

Osorio, S., Do, P.T. & Fernie, A.R. (2011) Profiling primary metabolites of tomato fruit with gas chromatography/mass spectometry. In: Hardy, N.W. & Hall, R.D. (Eds.) *Plant metabolomics, methods and protocols*. Totowa: Humana Press, Springer, pp. 101–110.

Ou, J.H. & Liao, C.T. (2019) Training set determination for genomic selection. *Theoretical and Applied Genetics*, **132**, 2781–2792.

Pagès, J. (2005) Collection and analysis of perceived product inter-distances using multiple factor analysis: application to the study of 10 white wines from the Loire Valley. *Food Quality and Preference*, **16**, 642–649.

Pap, N., Fidelis, M., Azevedo, L., do Carmo, M.A.V., Wang, D., Mocan, A. *et al.* (2021) Berry polyphenols and human health: evidence of antioxidant, anti-inflammatory, microbiota modulation, and cell-protecting effects. *Current Opinion in Food Science*, **42**, 167–186.

Papoutsoglou, E.A., Faria, D., Arend, D., Arnaud, E., Athanasiadis, I.N., Chaves, I. *et al.* (2020) Enabling reusability of plant phenomic datasets with MIAPPE 1.1. *The New Phytologist*, **227**, 260–273.

Paredes-López, O., Cervantes-Ceja, M.L., Vigna-Pérez, M. & Hernández-Pérez, T. (2010) Berries: improving human health and healthy aging, and promoting quality life--a review. *Plant Foods for Human Nutrition*, **65**, 299–308.

Pérez, P. & de los Campos, G. (2014) Genome-wide regression and prediction with the BGLR statistical package. *Genetics*, **198**, 483–495.

Perrin, L., Symoneaux, R., Maître, I., Asselin, C., Jourjon, F. & Pagès, J. (2008) Comparison of three sensory methods for use with the Napping® procedure: case of ten wines from Loire valley. *Food Quality and Preference*, **19**, 1–11.

Petrasch, S., Mesquida-Pesci, S.D., Pincot, D.D., Feldmann, M.J., López, C.M., Famula, R. *et al.* (2022) Genomic prediction of strawberry resistance to postharvest fruit decay caused by the fungal pathogen Botrytis cinerea. *G3*, **12**(1), jkab378.

Pincot, D.D., Poorten, T.J., Hardigan, M.A., Harshman, J.M., Acharya, C.B., Cole, G.S. *et al.* (2018) Genome-wide association mapping uncovers Fw1, a dominant gene conferring resistance to Fusarium wilt in strawberry. *G3*, **8**(5), 1817–1828.

Podwyszynska, M., Mynett, K., Markiewicz, M., Pluta, S. & Marasek-Ciolakowska, A. (2021) Chromosome doubling in genetically diverse bilberry (*Vaccinium myrtillus* L.) accessions and evaluation of tetraploids in terms of phenotype and ability to cross with highbush blueberry (*V. corymbosum* L.). *Agronomy*, **11**, 2584.

Poorter, H., Hler, J.B., van Dusschoten, D., Climent, J. & Postma, J.A. (2012) Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. *Functional Plant Biology*, **39**, 839–850.

Pott, D.M., Abreu E. Lima, F., de Soria, C., Willmitzer, L., Fernie, A.R., Nikoloski, Z. *et al.* (2020) Metabolic reconfiguration of strawberry physiology in response to postharvest practices. *Food Chemistry*, **321**, 126747.

Pott, D.M., Osorio, S. & Vallarino, J.G. (2019) From central to specialized metabolism: an overview of some secondary compounds derived from the primary metabolism for their role in conferring nutritional and organoleptic characteristics to fruit. *Frontiers in Plant Science*, **10**, 835.

Pott, D.M., Vallarino, J.G., Cruz-Rus, E., Willmitzer, L., Sánchez-Sevilla, J.F., Amaya, I. *et al.* (2020) Genetic analysis of phenylpropanoids and antioxidant capacity in strawberry fruit reveals mQTL hotspots and candidate genes. *Scientific Reports*, **10**(1), 1–15.

Pradal, C., Dufour-Kowalski, S., Boudon, F., Fournier, C. & Godin, C. (2008) OpenAlea: a visual programming and component-based software platform for plant modelling. *Functional Plant Biology*, **35**(10), 751–760.

Predieri, S., Lippi, N. & Daniele, G.M. (2021) What can we learn from consumers' perception of strawberry quality? *Acta Horticulturae*, **1309**, 987–994.

Qiao, Q., Edger, P.P., Xue, L., Qiong, L., Lu, J., Zhang, Y. *et al.* (2021) Evolutionary history and pan-genome dynamics of strawberry (*Fragaria* spp.). *Proceedings of the National Academy of Sciences of the United States of America*, **118**(45), e2105431118.

Rambla, J.L., López-Gresa, M.P., Bellés, J.M. & Granell, A. (2015) Metabolomic profiling of plant tissues. In: Alonso, J.M. & Stepanova, A.N. (Eds.) *Plant functional genomics, methods and protocols*. New York: Humana Press, Springer Protocols, pp. 221–237.

Raubach, S., Kilian, B., Dreher, K., Amri, A., Bassi, F.M., Boukar, O. *et al.* (2021) From bits to bites: advancement of the germinate platform to support prebreeding informatics for crop wild relatives. *Crop Science*, **61**, 1538–1566.

Reynolds, D., Baret, F., Welcker, C., Bostrom, A., Ball, J., Cellini, F. *et al.* (2019) What is cost-efficient phenotyping? Optimizing costs for different scenarios. *Plant Science*, **282**, 14–22.

Roessner-Tunali, U., Hegemann, B., Lytovchenko, A., Carrari, F., Bruedigam, C., Granot, D. *et al.* (2003) Metabolic profiling of transgenic tomato plants overexpressing hexokinase reveals that the influence of hexose phosphorylation diminishes during fruit development. *Plant Physiology*, **133**, 84–99.

Rowland, L.J., Hancock, J.F. & Bassil, N.V. (2011) Blueberry. In: Folta, K. & Kole, C. (Eds.) *Genetics, genomics and breeding of berries*. Enfield: Science, pp. 1–40.

Sabbadini, S., Capocasa, F., Battino, M., Mazzoni, L. & Mezzetti, B. (2021) Improved nutritional quality in fruit tree species through traditional and biotechnological approaches. *Trends in Food Science and Technology*, **117**, 125–138.

Santeramo, F.G., Carlucci, D., De Devitiis, B., Seccia, A., Stasi, A., Viscecchia, R. *et al.* (2018) Emerging trends in European food, diets and food industry. *Food Research International*, **104**, 39–47.

Scalzo, J., Politi, A., Pellegrini, N., Mezzetti, B. & Battino, M. (2005) Plant genotype affects total antioxidant capacity and phenolic contents in fruit. *Nutrition*, **21**, 207–213.

Schrinner, S.D., Mari, R.S., Ebler, J., Rautiainen, M., Seillier, L., Reimer, J.J. *et al.* (2020) Haplotype threading: accurate polyploid phasing from long reads. *Genome Biology*, **21**, 252.

Schwacke, R., Ponce-Soto, G.Y., Krause, K., Bolger, A.M., Arsova, B., Hallab, A. *et al.* (2019) MapMan4: a refined protein classification and annotation framework applicable to multi-omics data analysis. *Molecular Plant*, **12**, 879–892.

Selby, P., Abbeloos, R., Backlund, J.E., Basterrechea Salido, M., Bauchet, G., Benites-Alfaro, O.E. *et al.* (2019) BrAPI-an application programming interface for plant breeding applications. *Bioinformatics*, **35**, 4147–4155.

Shaw, P.D., Raubach, S., Hearne, S.J., Dreher, K., Bryan, G., McKenzie, G. *et al.* (2017) Germinate 3: Development of a common platform to support the distribution of experimental data on crop wild relatives. *Crop Science*, **57**, 1259–1273.

Shulaev, V., Sargent, D.J., Crowhurst, R.N., Mockler, T.C., Folkerts, O., Delcher, A.L. *et al.* (2011) The genome of woodland strawberry (*Fragaria vesca*). *Nature Genetics*, **43**(2), 109–116.

Skrovankova, S., Sumczynski, D., Mlcek, J., Jurikova, T. & Sochor, J. (2015) Bioactive compounds and antioxidant activity in different types of berries. *International Journal of Molecular Sciences*, **16**, 24673–24706.

Sobolev, A.P., Mannina, L., Proietti, N., Carradori, S., Daglia, M., Giusti, A.M. *et al.* (2015) Untargeted NMR-based methodology in the study of fruit metabolites. *Molecules*, **20**, 4088–4108.

Stafne, E.T., Clark, J.R., Weber, C.A., Graham, J. & Lewers, K.S. (2005) Simple sequence repeat (SSR) markers for genetic mapping of raspberry and blackberry. *Journal of the American Society for Horticultural Science*, **130**, 722–728.

Steptoe, A., Pollard, T.M. & Wardle, J. (1995) Development of a measure of the motives underlying the selection of food: the food choice questionnaire. *Appetite*, **25**, 267–284.

Takahashi, H. & Pradal, C. (2021) Root phenotyping: important and minimum information required for root modeling in crop plants. *Breeding Science*, **71**(1), 109–116.

Tang, Y., Liu, X., Wang, J., Li, M., Wang, Q., Tian, F. *et al.* (2016) GAPIT version 2: an enhanced integrated tool for genomic association and prediction. *Plant Genome*, **9**(2), 1–9.

Tavares, L., Figueira, I., McDougall, G.J., Vieira, H.L.A., Stewart, D., Alves, P.M. *et al.* (2013) Neuroprotective effects of digested polyphenols from wild blackberry species. *European Journal of Nutrition*, **52**, 225–236.

Tollenaar, M. & Lee, E.A. (2002) Yield potential, yield stability and stress tolerance in maize. *Field Crops Research*, **75**, 161–169.

Ulrich, D., Hoberg, E., Rapp, A. & Kecke, S. (1997) Analysis of strawberry flavour – discrimination of aroma types by quantification of volatile compounds. *Zeitschrift für Lebensmitteluntersuchung und -Forschung A*, **205**, 218–223.

Urrutia, M., Schwab, W., Hoffmann, T. & Monfort, A. (2016) Genetic dissection of the (poly)phenol profile of diploid strawberry (*Fragaria vesca*) fruits using a NIL collection. *Plant Science*, **242**, 151–168.

Vallarino, J.G., Abreu, E., Lima, F., de Soria, C., Tong, H., Pott, D.M. *et al.* (2018) Genetic diversity of strawberry germplasm using metabolomic biomarkers. *Scientific Reports*, **8**, 14386.

Vallarino, J.G., Pott, D.M., Cruz-Rus, E., Miranda, L., Medina-Minguez, J.J., Valpuesta, V. *et al.* (2019) Identification of quantitative trait loci and candidate genes for primary metabolite content in strawberry fruit. *Horticulture Research*, **6**, 4.

van Rengs, W.M., Schmidt, M.H., Effgen, S., Le, D.B., Wang, Y., Zaidan, M.W. *et al.* (2022) A chromosome scale tomato genome built from complementary PacBio and Nanopore sequences alone reveals extensive linkage drag during breeding. *The Plant Journal*, **110**, 572–588. https://doi.org/10.1111/tpj.15690

VanBuren, R., Wai, C.M., Colle, M., Wang, J., Sullivan, S., Bushakra, J.M. *et al.* (2018) A near complete, chromosome-scale assembly of the black raspberry (*Rubus occidentalis*) genome. *GigaScience*, **7**(8), giy094.

Verma, S., Zurn, J.D., Salinas, N., Mathey, M.M., Denoyes, B., Hancock, J.F. *et al.* (2017) Clarifying sub-genomic positions of QTLs for flowering habit and fruit quality in US strawberry (*Fragaria* × *ananassa*) breeding populations using pedigree-based QTL analysis. *Horticulture Research*, **4**, 1–9.

Via, S. & Lande, R. (1985) Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution*, **39**, 505–522.

Watt, M., Fiorani, F., Usadel, B., Rascher, U., Muller, O. & Schurr, U. (2020) Phenotyping: new windows into the plant for breeders. *Annual Review of Plant Biology*, **71**, 689–712.

Whitaker, V.M. (2011) Applications of molecular markers in strawberry. *Journal of Berry Research*, **1**, 115–127.

Wilkinson, M.D., Dumontier, M., Aalbersberg, I.J.J., Appleton, G., Axton, M., Baak, A. *et al.* (2016) The FAIR guiding principles for scientific data management and stewardship. *Science Data*, **3**, 160018.

Willman, M. (2019) *Genetic analysis of black raspberry breeding germplasm*, Masteral thesis. Columbus: The Ohio State University.

Woznicki, T.L., Heide, O.M., Remberg, S.F. & Sønsteby, A. (2016) Effects of controlled nutrient feeding and different temperatures during floral initiation on yield, berry size and drupelet numbers in red raspberry (*Rubus idaeus* L.). *Scientia Horticulturae*, **212**, 148–154.

Yang, C.-C. (2017) The evolution of quality concepts and the related quality management. In: Kounis, L.D. (Ed.) *Quality control and assurance*. Rijeka: IntechOpen.

Zhao, J., Sauvage, C., Zhao, J., Bitton, F., Bauchet, G., Liu, D. *et al.* (2019) Meta-analysis of genome-wide association studies provides insights into genetic control of tomato flavor. *Nature Communications*, **10**, 1534.

Zhu, G., Wang, S., Huang, Z., Zhang, S., Liao, Q., Zhang, C. *et al.* (2018) Rewiring of the fruit metabolome in tomato breeding. *Cell*, **172**, 249–261.e12.

Zorrilla-Fontanesi, Y., Rambla, J.-L., Cabeza, A., Medina, J.J., Sánchez-Sevilla, J.F., Valpuesta, V. *et al.* (2012) Genetic analysis of strawberry fruit aroma and identification of O-methyltransferase FaOMT as the locus controlling natural variation in mesifurane content. *Plant Physiology*, **159**, 851–870.