

The French INRAE Biological Resource Center for pome fruits and roses: Plant and DNA collections of traditional and research genetic resources

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Abstract: The Biological Resource Center (BRC) 'Pome fruits and roses' is hosted by INRAE near Angers, France. It includes collections of apple, pear, quince and rose. The apple, pear and quince collections are preserved in orchards on site and as DNA samples. Research accessions of the *Rosa* genus are preserved both in the field and as DNA samples, whereas traditional accessions are primarily maintained as DNA samples. Traditional roses accessions are preserved in the field by different private and public rose gardens in France.

The main BRC's mission is to preserve these biological resources while improving and optimizing its collections. It also aims to gather and enrich data associated with the conserved genetic accessions, in particular by recording and centralizing phenotypic and genetic characterization data. This ensures the provision of suitable biological material and data for research and selection purposes. Additionally, these data support genetic resources management, especially in the framework of the apple and pear French networks coordinated by BRC. Thanks to these data, pedigrees could be unravelled and association studies implemented.

Keywords: genetic resources, Maloideae, Rosa, diversity, genebank, DNA

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Introduction

The French National Research Institute for Agriculture, Food and the Environment (INRAE) has historically hosted collections of traditional pome fruit genetic resources in Angers, France. Cultivars of apple (*Malus* Mill. spp.), pear (*Pyrus* L. spp.) and quince (*Cydonia* Tourn. ex Mill. spp.) were mainly introduced in the collections in the 1950s and 1960s from French nurseries, horticultural societies and botanical gardens. Botanical species were also introduced at this time from various European botanical gardens. Most of the accessions of cider apple, perry pear, apple and pear rootstocks came from field surveys carried out in the same years. In addition, the collections have been continuously enriched for breeding and for distinctness,

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uniformity and stability (DUS) testing activities, as well as for the conservation of heritage genetic resources. In particular, a duplication of old French varieties – identified as at risk of disappearing following a national genetic resources survey – was carried out in the 2000s.

The pome fruit collection of research genetic resources began to be built up in the 1980s with the creation of haploids, dihaploids and aneuploids. This collection was then considerably enriched since the 2000s thanks to the genetic mapping progenies that have served as references in a series of European projects.

The rose (Rosa L. spp.) collection was launched in 2003 when the Rosa genus was chosen as a model ornamental plant due to its economic importance and biological characteristics among ornamental woody plants. Since then, research has focused on understanding the key processes involved in quality development in ornamental plants such as plant architecture, flowering and disease resistance. This required the introduction and creation of original research genetic material, mainly progenies for genetic mapping. Due to their high importance in research, these mapping progenies have been preserved for further studies. These genetic resources are now being used to support national and international scientific collaborations. In addition, a DNA bank of wild individuals of Rosa gallica L. and traditional varieties conserved in rose gardens was established to study the evolution of the genetic variability in the Rosa genus.

The INRAE 'Pome fruits and roses' Biological Resources Centre (*RosePom* BRC) that gathers these collections is now hosted by the Research Institute on Horticulture and Seeds and the Horticultural Experimental Unit.

Collection description

For clarity and simplicity, accessions conserved in Rose-Pom are classified into two categories: traditional genetic resources and breeding/research genetic resources. These terms are defined in accordance with the classification proposed by the Multi-Crop Passport Descriptors (MCPD V.2.1) (Alercia et al, 2015) for the biological status of accessions. Traditional genetic resources include: (1) wild relative species (code 100), i.e. presumed wild specimens collected in a wild environment; (2) traditional cultivars (code 300), comprising heritage cultivars (French or foreign old cultivars of heritage interest), other old cultivars and botanical accessions of species (i.e. presumed wild specimens grown in botanical gardens, sometimes originating from seeds collected in other botanical gardens where some natural hybridization may have occurred between different conserved accessions, including old varieties); and (3) advanced or improved cultivars (code 500), which are cultivars obtained after 1945. Note that botanical accessions of species may or may not be declared of heritage interest, depending on the criteria used to define 'heritage interest'. These criteria are currently under discussion in France. Breeding/research genetic resources (code 400) include, among others, unnamed breeders' material (codes 410 to 420), cytogenetic stocks (code 422), and mapping populations (code 423). Note that we prefer to use the term 'mapping progenies' rather than 'mapping populations', since a progeny is the result of a cross between two parents, whereas a population may consist of several unrelated individuals.

In summary, *RosePom*'s collections include traditional resources of agricultural, industrial, economic, scientific, social and cultural interest as well as research resources, much of which consist of material for genetic and genomic studies.

More specifically, *RosePom* conserves approximately 8,800 reproductive clonal accessions (accessions conserved as plants in the field with the capacity to participate in the reproduction process), mainly from three genera, *Malus, Pyrus* and *Rosa* (Figure 1), each represented by multiple species. This includes around 3,500 traditional accessions (cultivars, botanical accessions and wild relatives) and 5,300 breeding/research accessions (breeding unnamed progenitors, research accessions composed of cytogenetic stocks and mapping progenies). *RosePom* conserves also several thousand additional non-reproductive accessions, in the form of leaves or DNA only, particularly for the *Rosa* genus.

Pome fruits

The pome fruits collection contains 4,300 apple, 2,300 pear and 60 quince accessions. These reproductive accessions have been introduced from different geographical origins and according to their use in fruit production, as rootstocks, for ornamental use or for research purposes. They therefore represent a large genetic diversity.

Traditional conserved genetic resources include: (1) wild accessions of relative species of Malus, Pyrus, Cydonia from all over the world including 47 taxa of western and eastern Pyrus species, (2) botanical accessions of Malus, Pyrus, Cydonia, (3) old or new cultivars of rootstocks of Malus, Pyrus, Cydonia, (4) old or new cultivars of dessert or cider apple (Malus domestica Borkh.), dessert European pear (Pyrus communis L.), perry pear (Pyrus nivalis Jacq.), nashi (Pyrus pyrifolia (Burm.f.) Nakai) and quince (Cydonia oblonga Mill.), and (5) old or new cultivars of ornamental apple and pear (various species and many interspecific cultivars). Among these, nearly 1,500 accessions are old cultivars from France (840 apple accessions, 640 pear accessions), old cultivars from other countries in Europe and some well-known old cultivars from America, Asia and Africa. In addition, a UPOV international reference collection of nearly 1,000 accessions of recent apple and pear cultivars complements the RosePom resources.

Resources originating from breeding and prebreeding programmes include over 1,000 accessions of material collecting traits of agronomic interest, in particular, (1) for apple, resistance to scab (*Venturia inaequalis* (Cooke) Winter), fire blight (*Erwinia amylovora* (Bur-

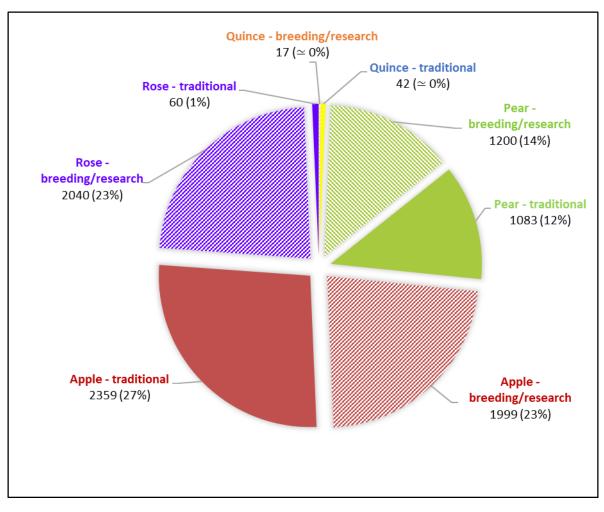


Figure 1. Reproductive collections: species groups and types. Repartition of the number of accessions of rose, apple, pear and quince according to the type of resources (traditional or breeding/research).

rill) Winslow *et al.*) and powdery mildew (*Podosphaera leucotricha* (Ellis & Everhart) Salmon), fruit texture, (2) for pear, resistance to scab, fire blight and pear psylla (*Cacopsylla pyricola* (Förster), and (3) for rootstocks, dwarfing, resistance to fire blight and abiotic stresses. It also includes 16 intergeneric hybrids between *Pyrus*, *Malus* and *Cydonia*.

Resources originating from research programmes include original material, in particular 46 accessions of haploids and double haploids and 1,400 accessions of mapping progenies segregating for disease and pest resistance. For apple, the two most important mapping progenies conserved by RosePom were created by crossing genotypes exhibiting different quantitative trait loci architecture (identified thanks to previous not conserved mapping progenies) for apple scab resistance: (1) 'TN10-8' hybrid crossed by the cultivar 'Fiesta' (260 accessions), and (2) 'Discovery' crossed by 'TN10-8' hybrid (149 accessions). For pear, RosePom conserves in particular a mapping progeny segregating for resistance to pear psylla and obtained by crossing the interspecific Pyrus bretschneideri Rehd. × Pyrus communis L. hybrid PEAR3, resistant to pear psylla, with the susceptible European pear cultivar 'Moonglow' (234 accessions).

From the point of view of a classification based on the type of use, among the accessions of cultivars and unnamed breeding material, there are 320 rootstock accessions (of which nearly 200 of *Malus*, 80 of *Pyrus* and 45 of *Cydonia*), 4,800 accessions of dessert or cider apple, dessert European pear, perry pear, nashi and dessert quince, and 120 accessions of ornamental apple and pear.

Roses

The rose collection conserves traditional biological resources (mostly in a non-reproductive form) and research genetic resources (in reproductive and nonreproductive forms).

Traditional resources include wild roses, botanical roses and cultivated varieties. Three thousand seven hundred (3,700) wild specimens are mainly of the species *R. gallica*, collected from more than 80 locations spread over 54 municipalities in France, with in general, 8 individuals per plot, depending on the size of the plot. Three sites, near Toulouse, France, were sampled more densely. Around 1,500 *Rosa multiflora* Thunb. accessions were collected in semi-natural/sown (MCPD code 130) sites in France. Botanical roses and cultivars

were sampled from 2004 to 2018 in French rose gardens and the Sangerhausen Rosarium (Germany). Sampled cultivars were mostly bred during the 19th and 20th centuries. The high genetic diversity of these accessions enables research teams to assess the impact of evolutionary history, natural selection and human activity on the *Rosa* genus.

Research resources are made up of mapping progenies or accessions selected for their particular characteristics. More specifically, these genetic resources include three diploid pseudo-F1 progenies linked by the use of the same male parent, an accession, abbreviated as Rw, which is an interspecific hybrid of Rosa wichurana Crép., conserved in the Jardin de Bagatelle in Paris, France. The three female parents are: Rosa chinensis Jacq. 'Old Blush', introduced into the United Kingdom by James Colvill around 1795 as 'Parsons' Pink China', the 'Fairy'. Polvantha variety bred in the United Kingdom in 1932 by Ann and John Bentall, and 'H190', a dihaploid obtained by haploidization of tetraploid Rosa 'MEIrilocra', commercially known as 'Zambra' bred in 1980 by Marie-Louise Meilland (Meynet et al, 1994). The size of the three progenies is roughly 1,050, 100 and 590 offspring. These segregating progenies, whose parents have a contrasting phenotype for different morphological traits (recurrent blooming ability, flower duplication, shrub habit) or disease resistance, can be used to answer questions about the genetic determinism of traits of interest.

Conservation

Conservation types

The main infrastructures (Figure 2) used by *RosePom* for the conservation of accessions are fields (15.5ha, including 1.5ha protected by Alt'Carpo nets, nets designed to prevent the entry of codling moth), insect-proof tunnels (480m²), freezers at -20°C and three cryopreservation tanks (total volume of 1,400L). *RosePom* also has access to glasshouses, a container yard, *in vitro* culture laboratories, cold chambers and -80°C freezers.

Reproductive resources are conserved as plants in the field or in pots in insect-proof tunnels, as shoots in *in vitro* culture and as budwood in liquid nitrogen (cryopreservation). Non-reproductive material such as leaves or petals are generally freeze-dried and stored at room temperature or in a cold chamber; DNA extracts are stored in freezers at -20°C.

Depending on various criteria, including in particular the value of interest, the rarity of the biological material and the type of biological material to be conserved, the conservation method or combination of conservation methods is defined according to four categories: (1) high level of conservation (at least two specimens) using a combination of conservation systems with special care for the specimen, (2) high level of conservation (two specimens) with one type of conservation system and special care for the specimen, (3) low level of conservation (one specimen) with special care for the specimen (i.e. propagation to be planned if the specimen is in danger of being lost), (4) low level of conservation (one specimen) without propagation even if the specimen is in danger of being lost.

Pome fruits

For pome fruits, the highest level of conservation is currently used for old French varieties, which are part of the French national heritage, with: (1) a specimen in an orchard protected by Alt'Carpo nets, used to protect trees from the insects that transmit fire blight (one of the main causes of apple and pear trees loss), (2) another specimen in an insect-proof tunnel, which provides protection from damage by pests and diseases transmitted by insects, such as pear decline (Candidatus Phytoplasma pyri Seemüller & Schneider) transmitted by pear psylla, and (3) ideally a specimen in cryopreservation. Cryopreservation is in progress for apples, though it remains a lengthy process requiring special care during the dehydration and freezing steps, which depend on the variety. For pears, the success rate is very genotype-dependant and is therefore not currently used. High-level conservation is also applied to specific apple and pear research resources, such as haploids and doubled haploids. These accessions, which tend to grow poorly in orchards, are maintained in in vitro culture chambers as well as in the field. Conversely, the lowest level of conservation is currently used for some progeny collections where the loss of some accessions is less detrimental to the overall collection.

In the orchard, trees are planted in the field with a distance of 4m between rows. Space between trees within rows ranges from 1.2m for those used only for conservation, to 2.5m between plants in the row for trees used both for conservation and other purposes (observation of the fruit and architecture of the trees, use as female parent in cross-breeding for research or pre-breeding, production of budwood).

Depending on the intended use beyond conservation, trees are managed with minimal pruning and without fruit thinning or according to industrial fruit production methods or pruned specifically to provide budwood.

Orchards are irrigated, except when planted in naturally wet soils, and trellised, except for trees pruned for budwood production. Trees are fertilized with organic fertilizers, except when the aim is precise fruit characterization – in this case, mineral fertilizers are applied to the soil. In all cases, mineral foliar fertilizers are applied. Trees are subject to preventive or curative phytosanitary treatment for diseases such as scab, powdery mildew and pests, in particular rosy aphid (*Dysaphis plantaginea* (Passerini)) and pear psylla, in accordance with sustainable agriculture standards.

Potted plants are grown in 3L pots for apples and 7.5L pots for pears and maintained in screened tunnels. Plants are spaced 25cm apart and heavily pruned to keep them small (about 1m high). Automatic watering in the tunnels is scheduled twice a day at fixed times, with frequency, amount and method varying according



Figure 2. Infrastructures used for the conservation of the accessions: a, field; b, orchards under Alt'Carpo nets; c, insect-proof tunnels; d, cryotanks; e, *in vitro* chamber for the conservation of living plant material; f, freezers at -20°C for the conservation of non-reproductive material.

to the season and weather conditions. Phytosanitary treatments are applied when pests or diseases threaten the plant's survival.

In addition to conserving accessions in our facilities, the preservation of old French cultivars, is managed at the national level through a national network for pome fruits genetic resources. The aim is twofold: first, to ensure that each heritage cultivar is conserved in at least two locations by different institutions; and, second, to ensure that some heritage cultivars are not conserved in too many copies, in order to optimize human and material resources.

Roses

For roses, shrubs are planted on agricultural tarpaulins in the field with 3.5m between rows and 1 or 1.5m

between plants in the row. The large space between rows was chosen to accommodate farm equipment used for pome fruits. Annual pruning is carried out when winter temperatures become stable, i.e. between late November and early January, followed by a copper treatment to protect the plant from fungal diseases.

Soil analysis is carried out to adjust the availability of nutrients to the needs of the plants. Fertilizers are applied to support the flowering period. A powdery mildew treatment in early spring and one or two aphicides per season are applied to these resources. Maintaining the edges of the agricultural tarpaulins and the base of the roses represents many hours of work. These plots are not irrigated. Traditional resources are conserved at *RosePom* only in a non-reproductive form, such as leaves or DNA. The wild accessions are conserved as reproductive forms in wild habitats, which in France are under the aegis of national botanical conservatories. Traditional varieties are being preserved in rose gardens, which are owned by the public sector or by private enthusiasts.

Health monitoring

For pome fruits, plant health monitoring is carried out throughout the year, but more intensively between April and October. It mainly involves visual inspection, but may also include analyses to confirm a diagnosis. The pathogens observed are mainly regulated organisms, including fire blight, European canker (*Neonectria ditissima* (Tulasne & C. Tulasne) Samuels & Rossman) and pear decline. For roses, field plants are regularly inspected for the absence of visible symptoms.

Identity validation after propagation and authentication

For pome fruits, after each cycle of propagation of the accessions, each plant planted in the field or in pots for conservation is tested with a set of five microsatellite (SSR) markers to check that the molecular identity of the plant obtained after propagation corresponds to the original plant. In the case of mutants, a visual comparison of the tree and fruit of the original plant and the new plant is necessary. This process generally takes one year (if the SSR control is sufficient) to three or four years (if it is necessary to check the fruit). The original trees are kept until all these checks are made.

Collaborative projects at European and international levels have enabled the comparison of molecular profile varieties from different collections in Europe and the United States, leading to the assignment of a unique code to each variety. This work helped identify duplicates of a variety represented by different accessions under different names and to determine the most probable varietal name of an accession with the same profile. This does not replace the historical authentication of varieties (i.e. checking the accuracy of the given variety name) but improves the knowledge of the identity of the accessions (Durel *et al*, 2023).

For roses, new plants are tested after propagation, where necessary with SSR markers, to validate their conformity to the mother plant.

Authentication of old cultivars is based on historical data and the expertise of rose garden managers, but it is rarely fully certain.

Accession description

Molecular and phenotypic characterization covers both traditional and breeding/research resources and is essential to ensure their trueness-to-type. To date, molecular characterization has mainly been carried out using SSR markers revealed by capillary electrophoresis or sequencing. Additionally, single nucleotide polymorphism (SNP) markers are now being used by research projects and revealed by high-throughput technologies. So far, 68% of pome fruit accessions and 41% of rose accessions have been genotyped.

RosePom carries out a part of the characterizations and also centralizes data generated by research teams using the *RosePom*'s genetic resources or supplying *RosePom* with new resources and associated data.

For pome fruits, *RosePom* uses a minimum list of descriptors for the management of pome fruit collections, including phenotypic characteristics (such as flowering time and harvest time) and simple morphological characteristics (such as fruit colour, shape and size, and tree habit). Characterization is based on the European Cooperative Programme for Plant Genetic Resources (ECPGR) reference documents (Lateur *et al*, 2022a,b) and the UPOV Guidelines for the distinctness, uniformity and stability of apple (UPOV, 2023) and pear (UPOV, 2000). Phenotypic characterization is carried out for certain characteristics (disease resistance, flowering, architecture, fruit quality, etc.) in the field, in the greenhouse or the laboratory.

For roses, the first characteristics used to help verify the identity of an accession are the colour of the flower, the number of petals and the plant's habit. Many other traits of morphological, disease susceptibility or biochemical nature, for example, can be phenotyped through research projects. The data obtained is then centralized by the *RosePom* information system.

Distribution

This material is regularly used in research and breeding programmes and is also distributed to thirdparty organizations and the international scientific community. Around 1,000 to 1,500 accessions are distributed per year mainly through collaborative projects. Depending on the availability of material, RosePom will distribute, in accordance with national and international regulations in force: (1) plant material in the form of plants or samples (grafts, cutting, pollen, leaves, petals, fruits, etc.), (2) extracted plant material such as DNA, and (3) data associated with this plant material, such as phenotypic or molecular data. The distribution service is available to public or private research bodies, institutes or breeders mainly in the frame of cooperative projects. It is also available to public or private actors in biodiversity conservation (conservatories managed by amateur associations or local authorities, nurseries specialized in the sale of old cultivars).

RosePom offers the opportunity to obtain resources on request by emailing crb-rosepom-contact@inrae.fr. Requests must be made in advance, considering legal and administrative constraints and the nature of the material requested. Distributions are made after the signature of a contract between INRAE and the recipient, with different requirements for the use of the resource, depending on the nature of the resource and the use planned by the recipient. *RosePom* does not guarantee the availability or quantity of requested material.

Quality management systems

RosePom's quality management system has been ISO 9001:2015 certified since February 2023. The certification covers the organization of activities related to the acquisition, conservation, characterization and distribution of *RosePom*'s genetic resources and associated data. The aim is to effectively meet the needs of its users. It ensures the traceability of living plant material, non-reproductive plant material and associated data.

The orchard is managed in accordance with the ISO 14001 environmental management system and the French 'Vergers Ecoresponsables' label.

Use of the resources

In breeding

RosePom collections have long been used as a source of germplasm for pre-breeding and breeding pome fruit programmes. These programmes have resulted in the release of 36 new plant breeders' rights (PBR) varieties. Pre-breeding programmes are currently being carried out in partnership with CEP-INNOVATION and NOVADI breeding companies.

RosePom's wild species and old apple and pear cultivars have long been tested for resistance to diseases and pests, particularly scab, fire blight, powdery mildew and pear psylla, and the more interesting accessions have been used to introduce resistance genes and QTLs coming from different genetic backgrounds by crossing with modern cultivars. The improved genetic stocks obtained have been introduced into RosePom's breeding material collections for use in the development of new varieties of dessert apple, cider apple and pear. Collections from research programmes, particularly mapping progenies established to study pest and disease resistance and fruit quality, have also been used to select improved material for dessert apple and pear, with the knowledge gained from these mapping progenies allowing the use of marker-assisted selection to pyramiding resistances to diseases and pests

Western and eastern Pyrus species from RosePom have been used in rootstock breeding to produce rootstocks more tolerant to global warming (six taxa including: P. cordata Desv., P. amygdaliformis Vill., P. amygdaliformis var. persica (Pers.) Bornm., P. elaeagrifolia Pall., P. syriaca Boiss.), biotic stress (P. calleryana Decne. and P. betulifolia Bunge) or to induce dwarfing of scions (P. nivalis Jacq.). Perry pear (P. nivalis Jacq.) cultivars conserved by RosePom have been used in the breeding of dwarfing rootstocks, as cytochemical analyses have shown that this compartment is divided into two sections: one of triploid genotypes, with a high vigour segregation in their progenies, and one of diploid genotypes, which are very homogeneous in terms of vigour. This triploid compartment has been used to create dwarfing rootstocks.

The cultivar collections of apple and pear varieties (dessert apple, cider apple, pear, rootstocks and ornamental apple and pear) have been used as reference material for DUS testing for official variety registration and PBR at the national and European levels. Thanks to these large collections, INRAE is an entrusted examination office to carry out the DUS technical examination on behalf of the Community Plant Variety Office (CPVO).

In research

Identity, diversity, relatedness and traits of interest are elucidated by characterizing the resources of *RosePom*.

Pome fruits

Characterizing genetic diversity. More than 20,000 apple cultivars are documented worldwide. An indepth analysis of the genetic diversity, structure and relatedness of old and recent apple cultivars conserved in RosePom and in institutional and associated germplasm collections at the French and European levels has been carried out by comparing more than 3,000 accessions from more than 20 European countries, USA and Canada, using SSR genotypic profiles (Leforestier et al, 2015; Suprun et al, 2015; Lassois et al, 2016; Urrestarazu et al, 2016; Durel et al, 2023). The highlighted main characteristics are a weak geographic structure and an important gene flow on a European scale, resulting from the numerous exchanges of graftwood over the centuries. A similar approach is also currently developed for European pear (Denancé et al, 2019; Bassil et al, 2023; Durel et al, 2023).

An apple core collection (287 accessions) has been developed from RosePom (Lassois et al, 2016) and further phenotyped for various traits (Lopez et al, 2015) including scab and fire blight resistance. Further, large multi-generation pedigrees were reconstructed from very old founders to elite cultivars thanks to a large SNP dataset, enlightening the history of apple empirical selection and the unexpected major role of a very limited number of founders such as the French cultivar 'Reinette Franche' and 'Margil' from the Renaissance period (Muranty et al, 2020; Howard et al, 2021). The amazing empirical selection of a high frequency of triploid cultivars (~20% of old apple cultivars are triploids) was also deciphered thanks to SNP-based pedigree analyses (Howard et al, 2023). Thanks to this work, INRAE's elite breeding population is now connected back to old founders with an accurate description of the transmission of genomic fragments across generations, giving a complete picture of haplotype sharing among all individuals.

Genetic mapping of disease/pest resistance factors.

Identifying new resistance genes/QTLs in pome fruit is an important goal to help breeding, especially for those pathosystems not yet sufficiently explored. Thanks to the conserved mapping progenies, numerous QTLs for pear resistance against scab, fire blight and psylla were identified (Montanari *et al*, 2015, 2016b; Perchepied *et al*, 2015, 2016). In apple, a major resistance gene against rosy apple aphids was fine-mapped thanks to plant accessions conserved in RosePom (Dall'Agata et al, 2018) with further development of tightly linked markers useful for breeding. Significant QTL (epistatic) interactions have been observed in both apple and pear progenies, which may correspond to the combined effect of favourable alleles for two or three genes along a metabolic pathway to promote strong resistance (van de Weg et al (2018) for apple/fire blight, Perchepied et al (2016) for pear/psylla). In traditional accessions, attempted genome-wide association studies (GWAS) for both apple scab and fire blight have so far been rather unsuccessful, although scab tests have been conducted with various strains in the greenhouse to account for V. inaequalis genetic diversity. For the V. inaequalisapple interaction, numerous low-frequency gene-forgene relationships in the core collection studied may have hampered QTL detection and may require a redesign of this collection. In contrast, GWAS performed for flowering and harvest dates or for eco-physiological traits successfully identified genomic regions controlling these traits (Urrestarazu et al, 2017; Coupel-Ledru et al, 2022).

Three scab resistance QTLs identified in the 'TN10-8' x 'Fiesta' progeny were subjected to in-depth analysis with the ultimate goal of cloning them and analyzing the metabolic pathway they control, in particular by looking for accurate co-localizations of OTLs controlling either disease resistance or metabolic compounds (Lapous et al, 2023). One (qT1) exhibits a specific interaction with V. inaequalis strains and has been shown to finely co-localize with the major scab resistance gene Rvi6/Vf. For the other two (qF11 and qF17), haplotype-sharing analysis allowed us to trace them in various genetic backgrounds along the reconstructed pedigree. In particular, qF17, initially mapped at almost the same position in two unrelated backgrounds, actually corresponded to the same SNPbased haploblock inherited from an as-yet-unknown common (and certainly ancient) ancestor (Durel, 2019).

The conserved progenies also allowed a very original work to be carried out, analyzing the combination of genetic (intrinsic) and plant resistance inducer (PRI)induced resistances to diversify/complement apple disease control methods. Putative synergistic or antagonistic effects between the two types of resistance were investigated using a genetic mapping approach. The F1 population 'TN10-8' x 'Fiesta' was genotyped and phenotyped for scab and fire blight resistance without and with PRI pretreatment (with acibenzolar-S-methyl – ASM -, a functional analogue of salicylic acid). QTLs (including qT1, qF11, and qF17) were detected in both situations, but with a rather limited impact of ASM on QTLs effect, indicating a mainly additive effect of both resistance mechanisms (Bénéjam *et al*, 2021, 2024).

In addition, other traits of interest were phenotyped on apple and pear mapping progenies, namely fruit texture/colour and sublethal genes (Ben-Sadok *et al*, 2015; Montanari *et al*, 2016a; Moriya *et al*, 2017). **Apple genome sequencing.** One of the double haploid accessions conserved by *RosePom*, the double haploid 'Golden Delicious' line (GDDH13), also coded X9273, obtained at INRA in 1963, has been used, thanks to the homozygosity of this line, to produce a high-quality de novo assembly of the apple genome (Daccord *et al*, 2017).

Roses

Characterizing genetic diversity. In the cultivated compartment, with more than 30,000 varieties, rose breeding activity has been very intensive, especially since the 19th century when old varieties of various origins and wild accessions were hybridized. The biological resources of 1,228 garden roses (botanical roses and old varieties) stored in RosePom (leaves and DNA) were genetically characterized using 32 microsatellite primer pairs (SSR). The genetic structure was revealed. The study of its evolution during the 19th century showed that the genetic background of European rose hybrids displayed a shift from an old European genetic background to an Asian one (Liorzou et al, 2016). This result is consistent with the introgression of old Chinese garden roses into European hybrids, especially for their continuous flowering. Indeed, the genotyping of the copia allele of the RoKSN gene, a homologue of TFL1 responsible for continuous flowering, on 270 accessions showed that this allele was selected in Europe during the 19th century (Soufflet-Freslon et al, 2021). All this work was carried out using an interdisciplinary approach, collaborating with historians to answer the same questions through both genetic resources and archival research, while considering the historical construction of rose diversity.

The 20th century was marked by the intensification of specific uses, such as cut and pot roses and the globalization of rose production and markets. These specificities were studied in a larger interdisciplinary approach with geographers, sociologists, economists and historians. Accessions were collected from rose gardens and private companies to constitute a large sample representative of time periods, usages and kinds of breeders. The first results on 1,796 accessions genotyped with 23 microsatellite primer pairs showed a decrease in genetic diversity during the 20th century, in line with the dominance of Tea hybrids. Cut roses appear to be a subset of garden roses.

In the wild compartment, 219 *Rosa gallica* populations represented by 901 plants collected in France by *RosePom* or by associated research teams and partners throughout Europe were genotyped by SSR sequencing of amplified fragments from 29 SSR primer pairs together with 717 cultivated accessions in order to investigate the diversity structure and origin of French populations. Diversity in France is much more structured than elsewhere in Europe, which can reveal multiple origins (Pawula, 2023). Furthermore, the identification of clones and sports (vegetative mutants), thanks to genotyping and phenotyping characterizations, is in progress.

Genetic mapping of traits of interest. With research genetic resources, genetic maps have been developed using SSR or SNP markers, allowing to anchor the genome sequence of Old Blush (Hibrand-Saint-Oyant et al, 2018) and to identify regions with important genes controlling traits of interest, such as floral characteristics, fragrance, disease resistance (Lopez-Arias et al, 2020) and prickle development (Zhou et al, 2020). For example, a study on the fragrance components (more than 30 components) was carried out on two pseudo-F1 populations conserved in RosePom's fields. Three genes were identified for the production of: geraniol, RhNUDX1-1 located on linkage group 2 (Magnard et al, 2015); 2-phenylethanol, RhPAAS located on linkage group 6 (Roccia et al, 2019); and farnesol, RhNUDX1-2 located on linkage group 7 (Sun et al. 2020).

All of these research projects have greatly enriched *RosePom*'s collections, either in terms of biological material or associated data. These resources and associated data are valuable for expertise, e.g. in DUS testing for pome fruits, or for supporting urban management decisions through knowledge of wild *R. gallica* populations.

Outreach

From an outreach point of view, *RosePom* is regularly presented to various audiences, including the general public, schoolchildren, students, professionals and scientists from other disciplines, such as historians, who see *RosePom* as a living archive. This is achieved through visits, stands at trade fairs and conferences.

Participation in networks and working groups

RosePom is one of the INRAE Biological Resource Centers that have joined forces with other French public institutions (CIRAD - French Agricultural Research Centre for International Development, IRD - French National Research Institute for Sustainable Development, and Institut Agro - French Institute for Higher Education & Research in Food, Agriculture & the Environment) in the BRC4Plants pillar (Bergheaud et al, 2025) of the National Agronomic Resources Research Infrastructure (AgroBRC-RARe). RosePom, as a member of the BRC4Plants pillar, is linked to the national structure coordinating plant genetic resources (Duval et al, 2023). Since 2023, the pome fruit collection has been one of the collections for which INRAE is recognized as an official manager of Plant Genetic Resources for Food and Agriculture by the French Ministry of Agriculture. This collection is also labelled as a 'National Collection' by the Conservatoire des Collections Végétales Spécialisées (Conservatory of Specialized Plant Collections).

At the national level, *RosePom* leads a national cooperative network on pome fruit genetic resources involving public and private partners, in accordance with the strategy drawn up as part of the National Charter for the Conservation of Genetic Resources. It is also involved as an expert in the national cooperation network on roses, whose members are French rose gardens.

At the international level, *RosePom* is involved in the European Cooperative Programme For Plant Genetic Resources (ECPGR) *Malus/Pyrus* Working Group, which helps to define common standards and protocols for these species. It is also involved in the ECPGR Cryopreservation Working Group.

Conclusion

The RosePom BRC plays an important role in the conservation of genetic resources of major fruit and ornamental plants, especially pome fruits. It has acquired considerable expertise in understanding the diversity of these genetic resources, both wild and cultivated. The conservation and knowledge of these genetic resources have proved very useful for three main activities: breeding, research and DUS testing. Interest in these resources is growing as crops are subject to many changes, in particular due to new regulations on the use of phytosanitary products, the emergence of pathogens and pests, and climate change. However, the conservation of these resources is costly in terms of human and material resources and faces multiple constraints. In order to maintain the collections in good condition despite these challenges, the management of all stages of the process must be carefully organized. The quality management system helps to achieve this objective. As highlighted by Engels et al (2024), collaborative networks are of primary importance for an efficient genetic resource conservation system. The organization in a network with different parties at the national and European levels makes it possible to share experiences, reflections and work to reduce the technical and financial constraints and optimize the process of conservation and valorization of these resources. Nevertheless, in order to enhance this activity of common interest for society, we emphasize the need to continuously raise awareness among the general public, researchers and policymakers of the importance of these genetic resources in view of their potential use in the future.

Author contributions

Writing – original: draft AP and LF, with contributions from all co-authors. Rose collections were described especially by AP, FF, TT, AC. Pome fruits collections were described especially by LF, CED, MHS, KG, ALH. Photos were provided by KG and TT. Writing editing: all authors, especially AP, LF, HM, FL. Review editing:AP and LF.

Conflict of interest statement

The authors have no conflicts of interest to report.

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References

- Alercia, A., Diulgheroff, S., and Mackay, M. (2015). FAO/Bioversity Multi-Crop Passport Descriptors V.2.1 (MCPD V.2.1) (Rome, Italy: Food and Agriculture Organization of the United Nations (FAO); Bioversity International). url: https://hdl.handle.net/ 10568/69166.
- Bassil, N., King, R., Nyberg, A., Zurn, J., Clare, S., Reinhold, L., Postman, J., Gilmore, B., Flores, G., Volk, G. M., Jenderek, M., Montanari, S., Chagné, D., Bus, V., Brewer, L., Dardick, C., Gottschalk, C., Durel, C.-E., and Denancé, C. (2023). Progress on the molecular characterization of the USDA National Pear Collection. *Acta Hortic* 1384, 273–280. doi: https://doi.org/10. 17660/ActaHortic.2023.1384.36
- Ben-Sadok, I., Tiecher, A., Galvez-Lopez, D., Lahaye, M., Lasserre-Zuber, P., Bruneau, M., Hanteville, S., Robic, R., Cournol, R., and Laurens, F. (2015). Apple fruit texture QTLs: year and cold storage effects on sensory and instrumental traits. *Tree Genet. Genomes* 11(119). doi: https://doi.org/10.1007/s11295-015-0947-x
- Bénéjam, J., Ferreira-De-Carvalho, J., Ravon, E., Heintz, C., Gaucher, M., Durel, C.-E., Brisset, M.-N., and Perchepied, L. (2024). Phenotyping data coupled with RNA sequencing of apple genotypes exhibiting contrasted quantitative trait loci architecture for apple scab (*Venturia inaequalis*) resistance. *Data Brief* 56, 110778. doi: https://doi.org/10.1016/j.dib.2024. 110778
- Bénéjam, J., Ravon, E., Gaucher, M., Brisset, M. N., Durel, C.-E., and Perchepied, L. (2021). Acibenzolar-S-methyl and resistance quantitative trait loci complement each other to control apple scab and fire blight. *Plant dis* 105, 1702–1710. doi: https://doi.org/10. 1094/pdis-07-20-1439-re
- Bergheaud, V., Audergon, J.-M., Bellec, A., Delaunay,
 A., Duminil, J., Dussert, S., Esnault, F., Geoffriau,
 E., Gouesnard, B., Jenny, C., Label, A., Lashermes,
 P., Maghnaoui, N., Marchal, C., Nuissier, F., Paulo-De-La-Réberdiere, N., Priet, A., Riecau, V., Térès,
 P., and Adam-Blondon, A. F. (2025). Organization of plant Biological Resource Centers for research in France: History, evolution and current status.

Genetic Resources (S2), 78–90. doi: https://doi.org/ 10.46265/genresj.ASZO2413

- Coupel-Ledru, A., Pallas, B., Delalande, M., Segura, V., Guitton, B., Muranty, H., Durel, C.-E., Regnard, J.-L., and Costes, E. (2022). Tree architecture, light interception and water-use related traits are controlled by different genomic regions in an apple tree core collection. *New Phytol* 234, 209–226. doi: https://doi.org/10.1111/nph.17960
- Daccord, N., Celton, J. M., Linsmith, G., Becker, C., Choisne, N., Schijlen, E., Van De Geest, H., Bianco, L., Micheletti, D., Velasco, R., di Pierro, E. A., Gouzy, J., Rees, D. J. G., Guerif, P., Muranty, H., Durel, C.-E., Laurens, F., Lespinasse, Y., Gaillard, S., Aubourg, S., Quesneville, H., Weigel, D., van de Weg, E., Troggio, M., and Bucher, E. (2017). High-quality de novo assembly of the apple genome and methylome dynamics of early fruit development. *Nature Genet* 49, 1099–1106. doi: https://doi.org/10.1038/ng.3886
- Dall'Agata, M., Pagliarani, G., Padmarasu, S., Troggio, M., Bianco, L., Dapena, E., Miñarro, M., Aubourg, S., Lespinasse, Y., Durel, C.-E., and Tartarini, S. (2018). Identification of candidate genes at the *Dp-fl* locus conferring resistance against the rosy apple aphid *Dysaphis plantaginea*. *Tree Genet. Genomes* 14(12). doi: https://doi.org/10.1007/s11295-018-1227-3
- Denancé, C., Ordidge, M., Lateur, M., and Durel, C.-E. (2019). Molecular characterization of an extensive set of European pear accessions with SSR markers. In XV EUCARPIA Fruit Breeding and Genetics Symposium, Prague.
- Durel, C.-E. (2019). Characterizing apple scab resistance: "the long and winding road". In XV EUCARPIA Fruit Breeding and Genetics Symposium, Prague.
- Durel, C.-E., Denancé, C., Muranty, H., Lateur, M., and Ordidge, M. (2023). MUNQ and PUNQ - a European and international apple and pear germplasm coding system. *Acta Hortic* 1384, 471–476. doi: https://doi. org/10.17660/ActaHortic.2023.1384.59
- Duval, C.-H., Didier, A., Delêtre, M., Omrani, M., Van Issum-Groyer, B., Bertoux, V., and Masson, F. (2023). French national coordination for conservation of plant genetic resources and their wild relatives: focus on horticultural species. *Acta Hortic* 1384, 199–205. doi: https://doi.org/10.17660/ActaHortic.2023.1384.26
- Engels, J. M. M., Ebert, A. W., and Van Hintum, T. (2024). Collaboration between private and public genebanks in conserving and using plant genetic resources. *Plants* 13, 247. doi: https://doi.org/10. 3390/plants13020247
- Hibrand-Saint-Oyant, L., Ruttink, T., Hamama, L., Kirov,
 I., Lakhwani, D., Zhou, N. N., Bourke, P. M.,
 Daccord, N., Leus, L., Schulz, D., Van De Geest, H.,
 Hesselink, T., Van Laere, K., Debray, K., Balzergue,
 S., Thouroude, T., Chastellier, A., Jeauffre, J., Voisine,
 L., Gaillard, S., Borm, T. J. A., Arens, P., Voorrips,
 R. E., Maliepaard, C., Neu, E., Linde, M., Paslier, M.C. L., Bérard, A., Bounon, R., Clotault, J., Choisne,

N., Quesneville, H., Kawamura, K., Aubourg, S., Sakr, S., Smulders, M. J. M., Schijlen, E., Bucher, E., Debener, T., De Riek, J., and Foucher, F. (2018). A high-quality genome sequence of *Rosa chinensis* to elucidate ornamental traits. *Nature Plants* 4, 473–484. doi: https://doi.org/10.1038/s41477-018-0166-1

- Howard, N. P., Micheletti, D., Luby, J. J., Durel, C.-E., Denancé, C., Muranty, H., Ordidge, M., and Albach, D. C. (2023). Pedigree reconstruction for triploid apple cultivars using single nucleotide polymorphism array data. *Plant. People. Planet* 5, 98–111. doi: https: //doi.org/10.1002/ppp3.10313
- Howard, N. P., Peace, C., Silverstein, K. A. T., Poets, A., Luby, J. J., Vanderzande, S., Durel, C.-E., Muranty, H., Denancé, C., and van de Weg, E. (2021). The use of shared haplotype length information for pedigree reconstruction in asexually propagated outbreeding crops, demonstrated for apple and sweet cherry. *Hortic. Res.* 8(202). doi: https://doi.org/10.1038/ s41438-021-00637-5
- Lapous, R., Magot, F., Muranty, H., Durel, C.-E., and Ferreira-De-Carvalho, J. (2023). Investigation of molecular mechanisms implicated in apple scab quantitative resistance using untargeted metabolic QTL mapping. In XVI EUCARPIA Symposium on Fruit Breeding and Genetics, Dresden-Pillnitz.
- Lassois, L., Denancé, C., Ravon, E., Guyader, A., Guisnel, R., Hibrand-Saint-Oyant, L., Poncet, C., Lasserre-Zuber, P., Feugey, L., and Durel, C.-E. (2016). Genetic diversity, population structure, parentage analysis, and construction of core collections in the French apple germplasm based on SSR markers. *Plant Mol. Biol. Rep* 34, 827–844. doi: https://doi.org/10.1007/ s11105-015-0966-7
- Lateur, M., Dapena, E., Szalatnay, D., Gantar, M. E., Guyader, A., Hjalmarsson, I., Höfer, M., Ikase, L., Kellerhals, M., Lacis, G., Militaru, M., Jiménez, C. M., Osterc, G., Rondia, A., Volens, K., Zeljković, M. K., and Ordidge, M. (2022a). ECPGR characterization and evaluation descriptors for apple genetic resources (Rome, Italy: European Cooperative Programme for Plant Genetic Resources), 57p. url: https: //www.ecpgr.org/fileadmin/bioversity/publications/ pdfs/2022_ECPGR_Malus_descriptors_final.pdf.
- Lateur, M., Szalatnay, D., Höfer, M., Bergamaschi, M., Guyader, A., Hjalmarsson, I., Militaru, M., Jiménez, C. M., Osterc, G., Rondia, A. T. S., Zeljković, M. K., and Ordidge, M. (2022b). ECPGR characterization and evaluation descriptors for pear genetic resources. European Cooperative Programme for Plant Genetic Resources (Rome, Italy: European Cooperative Programme for Plant Genetic Resources), 48p. url: https: //www.ecpgr.org/fileadmin/bioversity/publications/ pdfs/ECPGR_Pyrus_descriptors_Final_27-06-22.pdf.
- Leforestier, D., Ravon, E., Muranty, H., Cornille, A., Lemaire, C., Giraud, T., Durel, C.-E., and Branca, A. (2015). Genomic basis of the differences between cider and dessert apple varieties. *Evol. Appl* 8, 650– 661. doi: https://doi.org/10.1111/eva.12270

- Liorzou, M., Pernet, A., Li, S., Chastellier, A., Thouroude, T., Michel, G., Malécot, V., Gaillard, S., Briée, C., Foucher, F., Oghina-Pavie, C., Clotault, J., and Grapin, A. (2016). Nineteenth century French rose (*Rosa* sp.) germplasm shows a shift over time from a European to an Asian genetic background. *J. Exp. Bot* 67, 4711– 4725. doi: https://doi.org/10.1093/jxb/erw269
- Lopez, G., Pallas, B., Martinez, S., Lauri, P.-E., Regnard, J.-L., Durel, C.-E., and Costes, E. (2015). Genetic variation of morphological traits and transpiration in an apple core collection under well-watered conditions: towards the identification of morphotypes with high water use efficiency. *PLoS One* 10. doi: https://doi.org/10.1371/journal.pone.0145540
- Lopez-Arias, D. C., Chastellier, A., Thouroude, T., Bradeen, J., Van Eck, L., De Oliveira, Y., Paillard, S., Foucher, F., Hibrand-Saint-Oyant, L., and Soufflet-Freslon, V. (2020). Characterization of black spot resistance in diploid roses with QTL detection, metaanalysis and candidate-gene identification. *Theor. Appl. Genet* 133, 3299–3321. doi: https://doi.org/10. 1007/s00122-020-03670-5
- Magnard, J.-L., Roccia, A., Caissard, J.-C., Vergne, P., Sun, P., Hecquet, R., Dubois, A., Hibrand-Saint-Oyant, L., Jullien, F., Nicolè, F., Raymond, O., Huguet, S., Baltenweck, R., Meyer, S., Claudel, P., Jeauffre, J., Rohmer, M., Foucher, F., Hugueney, P., Bendahmane, M., and Baudino, S. (2015). Biosynthesis of monoterpene scent compounds in roses. *Science* 349, 81–83. doi: https://doi.org/10.1126/science. aab0696
- Meynet, J., Barrade, R., Duclos, A., and Siadous, R. (1994). Dihaploid plants of roses (*Rosa* x hybrida, cv 'Sonia') obtained by parthenogenesis induced using irradiated pollen and *in vitro* culture of immature seeds. *Agronomie* 14, 169–175. doi: https://doi.org/ 10.1051/agro:19940303
- Montanari, S., Brewer, L., Lamberts, R., Velasco, R., Malnoy, M., Perchepied, L., Guérif, P., Durel, C.-E., Bus, V. G. M., Gardiner, S. E., and Chagné, D. (2016a). Genome mapping of postzygotic hybrid necrosis in an interspecific pear population. *Hortic. Res.* 3, 15064. doi: https://doi.org/10.1038/hortres.2015.64
- Montanari, S., Guérif, P., Ravon, E., Denancé, C., Muranty, H., Velasco, R., Chagné, D., Bus, V. G. M., Robert, P., Perchepied, L., and Durel, C.-E. (2015). Genetic mapping of *Cacopsylla pyri* resistance in an interspecific pear (*Pyrus* spp.) population. *Tree Genet. Genomes* 11(74). doi: https://doi.org/10. 1007/s11295-015-0901-y
- Montanari, S., Perchepied, L., Renault, D., Frijters, L., Velasco, R., Horner, M., Gardiner, S. E., Chagné, D., Bus, V. G. M., Durel, C.-E., and Malnoy, M. (2016b). A QTL detected in an interspecific pear population confers stable fire blight resistance across different environments and genetic backgrounds. *Mol. Breed* 36(47). doi: https://doi.org/10.1007/s11032-016-0473-z

- Moriya, S., Kunihisa, M., Okada, K., Shimizu, T., Honda, C., Yamamoto, T., Muranty, H., Denancé, C., Katayose, Y., Iwata, H., and Abe, K. (2017). Allelic composition of MdMYB1 drives red skin color intensity in apple (*Malus x domestica* Borkh.) and its application to breeding. *Euphytica* 213, 78. doi: https://doi.org/10. 1007/s10681-017-1864-x
- Muranty, H., Denancé, C., Feugey, L., Crépin, J.-L., Barbier, Y., Tartarini, S., Ordidge, M., Troggio, M., Lateur, M., Nybom, H., Paprstein, F., Laurens, F., and Durel, C.-E. (2020). Using whole-genome SNP data to reconstruct a large multi-generation pedigree in apple germplasm. *BMC Plant Biol* 20(2). doi: https: //doi.org/10.1186/s12870-019-2171-6
- Pawula, C. (2023). *Rosa gallica* L. and other Gallic roses. Ph.D. thesis, Université d'Angers, Angers.
- Perchepied, L., Guérif, P., Ravon, E., Denancé, C., Laurens, F., Robert, P., Bouvier, L., Lespinasse, Y., and Durel, C.-E. (2016). Polygenic inheritance of resistance to *Cacopsylla pyri* in a *Pyrus communis* x *P. ussuriensis* progeny is explained by three QTLs involving an epistatic interaction. *Tree Genet. Genomes* 12(108). doi: https://doi.org/10.1007/s11295-016-1072-1
- Perchepied, L., Leforestier, D., Ravon, E., Guérif, P., Denancé, C., Tellier, M., Terakami, S., Yamamoto, T., Chevalier, M., Lespinasse, Y., and Durel, C.-E. (2015). Genetic mapping and pyramiding of two new pear scab resistance QTLs. *Mol. Breed* 35(197). doi: https: //doi.org/10.1007/s11032-015-0391-5
- Roccia, A., Hibrand-Saint-Oyant, L., Cavel, E., Caissard, J. C., Machenaud, J., Thouroude, T., Jeauffre, J., Bony, A., Dubois, A., Vergne, P., Szecsi, J., Foucher, F., Bendahmane, M., and Baudino, S. (2019). Biosynthesis of 2-phenylethanol in rose petals is linked to the expression of one allele of *RhPAAS*. *Plant Physiol* 179, 1064–1079. doi: https://doi.org/10.1104/pp.18.01468
- Soufflet-Freslon, V., Araou, E., Jeauffre, J., Thouroude, T., Chastellier, A., Michel, G., Mikanagi, Y., Kawamura, K., Banfield, M., Oghina-Pavie, C., Clotault, J., Pernet, A., and Foucher, F. (2021). Diversity and selection of the continuous-flowering gene, *RoKSN*, in rose. *Hortic. Res* 8, 76. doi: https://doi.org/10.1038/ s41438-021-00512-3
- Sun, P. L., Dégut, C., Réty, S., Caissard, J. C., Hibrand-Saint-Oyant, L., Bony, A., Paramita, S. N., Conart, C., Magnard, J.-L., Jeauffre, J., Abd-El-Haliem, A. M., Marie-Magdelaine, J., Thouroude, T., Baltenweck, R., Tisné, C., Foucher, F., Haring, M., Hugueney, P., Schuurink, R. C., and Baudino, S. (2020). Functional diversification in the *Nudix hydrolase* gene family drives sesquiterpene biosynthesis in *Rosa* x *wichurana. Plant J* 104, 185–199. doi: https://doi.org/10.1111/tpj.14916
- Suprun, I. I., Ushakova, Y. V., Tokmakov, S. V., Durel, C.-E., Denancé, C., and Ul'yanovskaya, E. V. (2015). Genetic diversity study of modern Russian apple (*Malus x domestica* Borkh.) cultivars by the SSR loci

analysis. *Agricultural Biology* 50, 37–45. doi: https://doi.org/10.15389/agrobiology.2015.1.37eng

- UPOV (2000). Pear Guidelines for the conduct of tests for distinctness, uniformity and stability (Geneva, Swiss: International union for the protection of new varieties of plants). url: https://www.upov.int/edocs/ tgdocs/en/tg015.pdf.
- UPOV (2023). Apple (fruit varieties) Guidelines for the conduct of tests for distinctness, uniformity and stability (Geneva, Swiss: International union for the protection of new varieties of plants). url: https:// www.upov.int/edocs/tgdocs/en/tg014.pdf.
- Urrestarazu, J., Denancé, C., Ravon, E., Guyader, A., Guisnel, R., Feugey, L., Poncet, C., Lateur, M., Houben, P., Ordidge, M., Fernandez-Fernandez, F., Evans, K. M., Paprstein, F., Sedlak, J., Nybom, H., Garkava-Gustavsson, L., Miranda, C., Gassmann, J., Kellerhals, M., Suprun, I., Pikunova, A. V., Krasova, N. G., Torutaeva, E., Dondini, L., Tartarini, S., Laurens, F., and Durel, C.-E. (2016). Analysis of the genetic diversity and structure across a wide range of germplasm reveals prominent gene flow in apple at the European level. *BMC Plant Biol* 16(130). doi: https://doi.org/10.1186/s12870-016-0818-0
- Urrestarazu, J., Muranty, H., Denancé, C., Leforestier, D., Ravon, E., Guyader, A., Guisnel, R., Feugey, L., Aubourg, S., Celton, J. M., Daccord, N., Dondini, L., Gregori, R., Lateur, M., Houben, P., Ordidge, M., Paprstein, F., Sedlak, J., Nybom, H., Garkava-Gustavsson, L., Troggio, M., Bianco, L., Velasco, R., Poncet, C., Theron, A., Moriya, S., Bink, M., Laurens, F., Tartarini, S., and Durel, C.-E. (2017). Genome-wide association mapping of flowering and ripening periods in apple. *Front. Plant Sci* 8(1923). doi: https://doi.org/10.3389/fpls.2017.01923
- van de Weg, E., DiGuardo, M., Jänsch, M., Socquet-Juglard, D., Costa, F., Baumgartner, I., Broggini, G. A. L., Kellerhals, M., Troggio, M., Laurens, F., Durel, C.-E., and Patocchi, A. (2018). Epistatic fire blight resistance QTL alleles in the apple cultivar 'Enterprise' and selection X-6398 discovered and characterized through pedigree-informed analysis. *Mol. Breed* 38(5). doi: https://doi.org/10.1007/s11032-017-0755-0
- Zhou, N., Tang, K. X., Jeauffre, J., Thouroude, T., Lopez-Arias, D. C., Foucher, F., and Hibrand-Saint-Oyant, L. (2020). Genetic determinism of prickles in rose. *Theor. Appl. Genet* 133, 3017–3035. doi: https://doi. org/10.1007/s00122-020-03652-7