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Reviewed paper

Conclusions from 38 years apple breeding at Agroscope in Waedenswil

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Abstract

Apple breeding at Waedenswil has a long tradition dating back almost to the foundation of the research station in 1890. 38 years ago, in 1984, breeding was newly oriented towards including disease resistance as well as performing crosses annually. Accessions with desired traits were acquired by international cooperation and exchange, as well as through the analysis of indigenous genetic resources and the development of the institute's own collection of advanced selections. In the last decades, new objectives and methods as well as advanced data management were implemented to render the breeding process more precise and efficient. Breeding is also oriented towards the requirements of organic apple growing.

Keywords: apple breeding, disease resistance, molecular selection, fruit quality

Introduction

The Breeding objectives have evolved over the 38 years, but the main goals have remained:

- High fruit quality
- Broad resistance to biotic and abiotic stress factors
- Good and regular production

A key initial spark for the breeding program's focus on disease resistance was the collaboration with the apple breeding program at East Malling (UK) and the phytopathology group of ETH in Zürich. East Malling had established parental material with a broad range of genetic resistance, also based on material from the Coop Breeding Program in the USA. The IOBC meeting of the Working Group "Intergrated Plant Protection in Orchards", Subgroup "Integrated control of pome fruit disease" held in Brissago, Switzerland, in 1988, was a key event in initiating joint efforts to breed new apple and pear varieties with sustainable disease resistance (Kellerhals, 1989; Alston, 1989; Lespinasse, 1989). Gessler (1989) presented the genetics of the interaction *Venturia inaequalis*-*Malus*: the conflict between theory and reality during that meeting and Valsangiacomo *et al*. (1989) discussed aspects of host resistance and pathogenesis in the interaction *Venturia inaequalis*-apple leaves. By the end of the 1980's, developments in molecular genetic analysis had advanced to the point where the first applications in practical breeding became possible. In 1992, it became obvious and confirmed, that the *Vf* (*Rvi6*) scab resistance can indeed be broken down by emerging strains of the pathogen (Parisi *et al*., 1993). Earlier reports (Fischer *et al*., 1983) were not considered fully credible by the scientific community. The need to breed for more durable resistance became obvious. Kellerhals & Furrer (1994) presented "Approaches for breeding apples with durable disease resistance", a topic still in discussion today. The European Apple Genome Mapping Project (EAGMAP) was a joint effort to develop and apply these methods in apple breeding. The starting point were DNA-RAPD and DNA-RFLP markers, e.g. for the *Vf* (*Rvi6*) scab resistance. At the 1993 meeting of the Eucarpia Fruit Breeding Section in Waedenswil/Einsiedeln, Switzerland, molecular markers were a topic for the first time in those meetings and scientists from Europe (King, 1994), the USA (Weeden, 1994) and New Zealand (Gardiner, 1994) presented their research.

The number of molecular markers related to relevant agronomic traits as well as the number of marker types increased in the following years (Patocchi *et al*., 2009). The work of Jänsch

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et al. (2015) enabled the gradual transition from SSR to SNP marker analysis. A series of EU-funded projects allowed developments in DNA-informed breeding: EAGMAP (King *et al*., 1991) DARE (Durable Apple Resistance in Europe), HiDRAS (High Quality Disease Resistant Apple Varieties), Fruitbreedomics (bridge the gap between scientific genetics research and application in breeding) and INVITE (Innovation in Variety Testing). Agroscope Apple Breeding was involved in all these projects. The newly achieved developments at the molecular level and in phenotyping were successfully integrated into the selection of the breeding program. Molecular markers allowed the application of the concept of pyramiding multiple resistance genes against the same pathogen or pest in one genotype (Baumgartner *et al.,* 2015) in order to prevent resistance breakdown.
The perspectives of polygenic resistance in breeding for durable disease resistance have been outlined among others by Lindhout (2002), Laurens (2004) and Kellerhals *et al*. (2012). The exploitation of new sources and genetic backgrounds of disease resistance is a useful approach to develop more resilient varieties. At Agroscope, we were able to define the distinctive accessions of Swiss apple genetic resources, in total around 1400, and screen them for valuable traits related to disease resistance and fruit quality (Kellerhals *et al*., 2018). Specific accessions were used as parents in the breeding programs of Agroscope and Poma Culta (Kellerhals *et al.,* 2018). The progenies are currently under evaluation. The use of genetic resources in apple breeding and for sustainable fruit production was already discussed by Kellerhals *et al*. (2004) and so-called “old” or “heirloom” accessions have been considered in crosses. The same paper also discussed the concept of variety mixtures as an additional approach to reduce disease and pest pressure in orchards. Fruit quality requirements must always be given high priority when developing disease and pest resistant cultivars. Sensory work with consumers, experts and trained panels is important and is taken into account in Agroscope’s apple breeding program (Inderbitzin *et al*., 2019).

Material and Methods

Scab resistance screening
A method for artificial apple scab resistance screening was established in 1986 based on knowledge acquired at East Malling (UK) and at INRA Angers (F). The basis were diseased leaves from apple trees not sprayed with fungicides. Subsequently, diseased leaves from seedlings in the greenhouse screening were used and from time to time new material from orchards was added. The method of the phenotypic scab screening in the greenhouse has been improved considerably over the 38 years and is very reliable nowadays (Kellerhals *et al.*, 2014). When major scab resistance genes are included, screening is carried out according to the scale of Chevalier *et al.* (1991). When polygenic resistance is included, a scale derived from Lefrancq *et al* (2004) is applied. However, currently the question arises whether to adjust the inoculum to the field situation, where scab strains breaking *Rvi6* resistance become more abundant. Therefore, it might be useful to add specific resistance breaking strains to the inoculum.
Molecular selection
The initial RAPD markers linked to the scab resistance gene *Vf* (*Rvi6*) were transformed into more reliable and reproducible markers that can be used directly in apple breeding (Gianfranceschi *et al*., 1996). CAPS and SCAR-markers were developed which allow determining the allelic status of the *Vf* (*Rvi6*) locus (Kellerhals *et al.*, 1998). Gradually the development moved towards the use of SSR markers instead of CAPS and SCAR markers. SSR markers are codominant, highly distributed throughout the genome, and highly reproducible with low quantity and quality of DNA. In order to make marker analyses of progeny plants more affordable, Dilworth & Frey (2000) developed a rapid method for high-throughput DNA extraction from plant material for PCR amplification. Frey *et al*. (2004)

developed a new multiplex PCR-based method for reliable and low-cost high-throughput molecular screening. Using this method, they screened 3366 apple seedlings with an average hands-on time from DNA extraction to analysable data of less than 4 h/96 plants and at a cost below US$ 0.5 per marker per plant. The method was most efficient when the data were analysed only for presence/absence of the desired alleles, which can be done in less than 1h/96 plants. Even then, the method was very robust and informative.
In 2005, markers were available for a number of apple disease resistance genes such as *Vf, Vr, Vbj, Pl1, Pl2, Pld* and *Plw*. However, the *Vr* resistance, originating from Russian apple R12740-7A, seemed to comprise different gene loci (*Rvi2*, *Rvi4*). In 2009, Bus *et al*. presented a new proposal for the nomenclature of *Venturia inaequalis* races. The new name *Rvi6* for *Vf* as example is based on its association with race 6. The strategy of pyramiding (combining) resistance genes against the same pathogen in one genotype was successfully applied, bearing in mind that molecular data had to be seriously examined for plausibility (Baumgartner *et al.*, 2016). A performant pedigree information system is therefore crucial.
The range of diseases and pest against which selection has been carried out has increased during the 38 years. Resistance to fire blight (*Erwinia amylovora*), *Diplocarpon mali* (*Marssonina coronaria*), *Neofabraea* spp., rosy apple aphid (*Dysaphis plantaginea*), were considered. The relevant selection tools have been developed or adapted, evaluated, incorporated and options for molecular selection developed in cooperation with other research teams. Molecular analysis of parents and progeny plants is carried out in external private labs using defined markers developed by Agroscope or ETH Zürich and the international scientific community.

Fruit quality, storage and consumer acceptance

Based on phenotypic and molecular data, selection of parental material for resistances and fruit quality traits was established. Storage potential of advanced selections and released varieties was systematically evaluated in preliminary and exact storage trials, respectively (Dällenbach *et al*., 2020). Consumer acceptance of disease tolerant apple cultivars was evaluated by means of instrumental and sensory evaluation (Inderbitzin *et al*., 2019). Agroscope apple breeding established a hedonic sensory evaluation of advanced selections by experts or consumer groups, complemented with analytical data (mainly Pimprenelle robotic machine (Setop, Cavaillon, France)) and sensory information from a trained panel.

Results

Scab resistance screening

The results from the artificial apple scab resistance screening in the greenhouse in 2021, according to Chevalier *et al.* (1991), correspond to the expectations based on molecular analyses of the parents (Table 1 and Figure 1). The segregation follows a 1:1 ratio for cross combinations (CrCo) 2019 and 2021, and a 3:1 ratio for CrCo 2020, 2022 and 2023. The offspring of CrCo 2019 and 2021 carry either *Vf* (*Rvi6*) at a heterozygous stage or no monogenic resistance, leading to the prediction of 50% resistant seedlings. The offspring of CrCo 2020, 2022 and 2023 carries either *Vf* (*Rvi6*) heterozygous or homozygous or no monogenic resistance, leading to the prediction of 75% resistant seedlings.

Table 1: Molecular analysis of cross combinations (CrCo). *Rvi6*: scab resistance; *Pl2*: mildew resistance; fire blight resistance QTL: FB_F7

CrCo	Mother (Loci)	Father (Loci)	No of plants
2019	ACW 21276 (*Rvi6*)	XX5912 (-)	**1453**
2020	ACW 21931 (*Rvi6*)	XX3678 (*Rvi6*)	**764**
2021	ACW 20235 (*Rvi6-FB_F7*)	XX7469 (-)	**819**
2022	ACW 24010 (*Rvi6-Pl2*)	ACW 22772 (*Rvi6-FB_F7*)	**234**

2023	ACW 14886 (*Rvi6*)	Rusticana (*Rvi6*)	**726**
Control	Gala (-)	Braeburn (-)	**109**

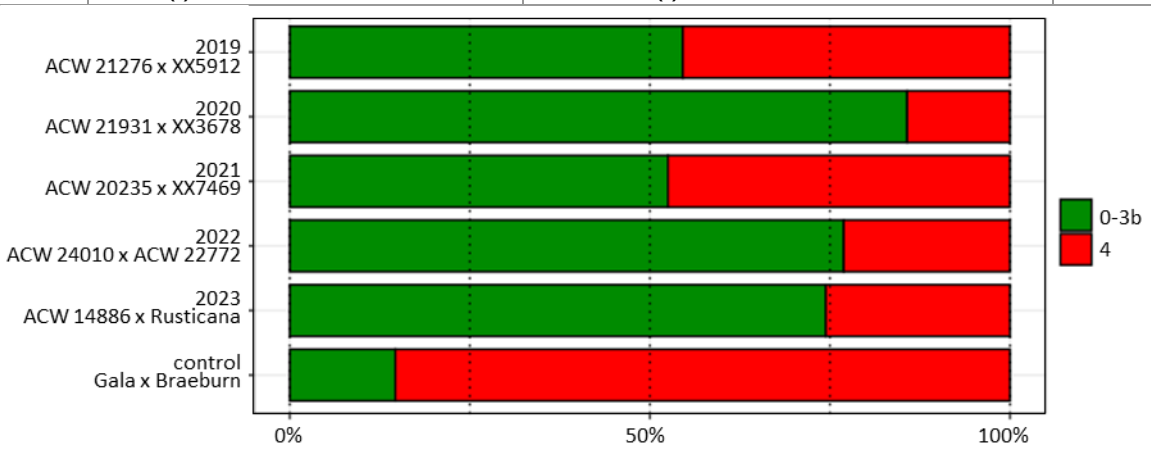

Figure 1: Segregation of the seedlings per cross combination (CrCo) according to Chevalier et al. (1991) into "resistant" (classes 0 to 3b) or "susceptible" (class 4) plants.

Molecular selection

Table 2 shows current molecular analysis of selected cross combinations designed for pyramiding disease resistances combined with high fruit quality from the year 2020. It illustrates the pyramiding of resistances genes. In addition, these results allow for a valuable and stringent pre-selection of progenies. However, phenotypic scoring of the performance of the selected plants is still required.

Table 2: Molecular analysis of cross combinations (CrCo) designed for pyramiding scab resistance (A) and their segregation in % (B). *Rvi2, Rvi4, Rvi6*: scab resistance; *Pl1, Pl2*: mildew resistance; fire blight resistance QTL: FB_F7

A)

CrCo	Mother (Loci)	Father (Loci)	No of plants
1905	ACW 22107 (*Rvi2-Rvi6*)	ACW 24850 (*Rvi2-Rvi4-Rvi6Rvi6-Pl2*)	**282**
1906	ACW 21336 (*Rvi2-Rvi6*)	ACW 24929 (*Rvi2-Rvi4-Rvi6-Pl1-Pl2*-FB_F7)	**296**
1907	ACW 24917 (*Rvi2-Rvi4-Rvi6-Pl1-Pl2*-FB_F7)	ACW 27741 (*Rvi2-Rvi4-Rvi6-Pl1*)	**66**

B)

CrCo	Rvi2	Rvi2Rvi2	Rvi4	Rvi4Rvi4	Rvi6	Rvi6Rvi6	Pl1	Pl2	FB_F7
1905	48	26	44	0	54	46	NA	42	0
1906	49	30	53	0	50	22	NA	30	53
1907	52	17	32	41	47	20	NA	47	52

The example of selection ACW 11567 illustrates that careful interpretation of molecular marker results obtained in the laboratory is required. Molecular analysis of this selection usually indicated the presence of a signal for *Rvi2* and *Rvi4*. While analyzing the reasons, it became obvious that the parent Milwa also displayed a signal for *Rvi4*. This must be a false positive signal, as there is no source for *Rvi4* in the pedigree of Milwa (Figure 2) and the variety is not scab resistant. However, for *Rvi2* the source is obviously R12740-7A. A good pedigree information database is therefore extremely helpful for correct interpretation of molecular data.

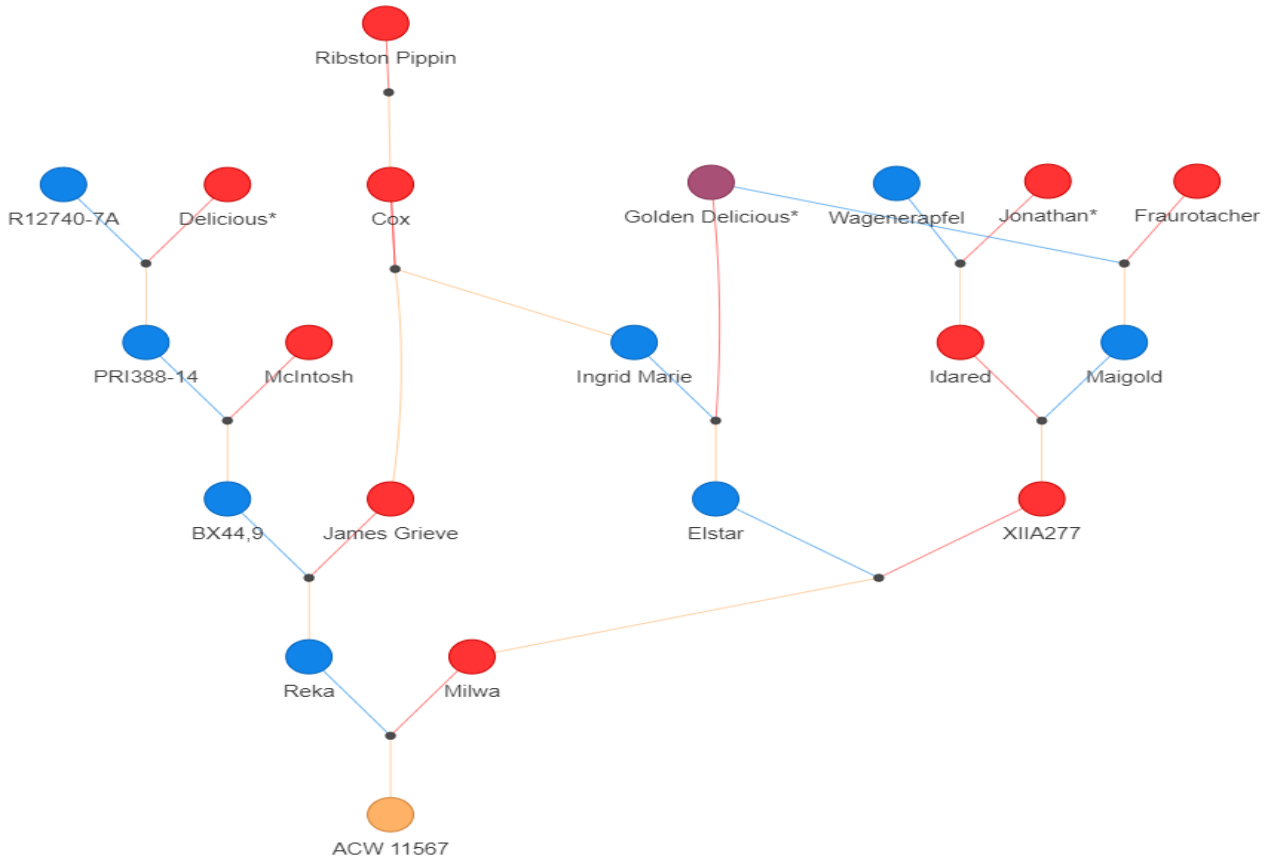

Figure 2: Pedigree of ACW 11567 (female parents in red, male parents in blue)

Fruit quality

A consumer test with high school students (N=40) in June 2021 with five advanced Agroscope selections and three standard cultivars stored under CA conditions revealed that samples with good firmness and a balanced sugar/acid-ratio are preferred (Table 3). High acidity in ACW 21274 was not perceived negatively at this late time of storage season. However, low sugar, low acidity and low firmness in Gala Schnitzer was not well rated.

Table 3: Consumer rating (high school students, N = 40) for eating quality (good, medium, low), analytical (Pimprenelle) measurement (°Brix, Malic acid, Firmness) and sensory evaluation by a trained panel (sweet, acid, firm, scale 1 to 100 with increasing intensity) of advanced Agroscope selections compared to standard varieties (Mariella, Nicogreen and Gala Schnitzer)

	% good	% medium	% low	°Brix	Malic acid (g/kg)	Firmness (kg/cm²)	sweet	acid	firm
ACW 14886	75	18	7	13.1	6.4	7.5	54.1	46.6	61.3
ACW 21274	68	25	7	14.4	8.5	8.1	50.8	60.3	65.3
ACW 17220	62	33	5	14.4	6.4	7.4	52.7	52.5	51.4
Mariella	60	25	15	12.2	2.9	9.5	44.1	28.4	74.0
Nicogreen	57	25	18	9.5	4.8	7.4	30.2	39.6	53.9
Gala Schnitzer	40	25	35	10.2	2.7	5.9	53.7	17.6	30.3
ACW 19896	38	40	22	13.1	5.1	6.6	45.8	27.3	30.9
ACW 22800	35	38	27	14.1	4.6	6.8	40.3	21.5	41.2

All of the disease-resistant varieties released from the Agroscope apple breeding program up to now carry only scab resistance *Vf* (*Rvi6*) (Table 4). However, advanced selections with pyramided resistances and high fruit quality are in the pipeline. In parallel, advanced selections with polygenic resistance are in evaluation.

Table 4: Agroscope apple varieties released and their disease resistance setup

	Scab resistance	Mildew resistance	Fire blight tolerance
Ariwa	*Rvi6*	*Pl1*	-
CH 101-Galiwa®	*Rvi6*	-	-
Ladina	*Rvi6*	-	FB_F7
Rusticana	*Rvi6*	-	-

Discussion and Conclusions

Apple breeding at Agroscope is based on long-term oriented breeding aims. A modern selection scheme was established that includes reliable phenotypic disease screenings, tree and fruit evaluation and fruit quality analysis on sensory and instrumental levels. At the beginning, phenotypic evaluation and breeder's knowledge were crucial. More and more molecular and data management tools were integrated, leading to more efficient selection in a broader context. The challenges for the future are to further streamline the breeding process with advanced molecular methods combined with innovative phenotyping tools and adequate data processing (bioinformatics). Peace (2017) established the term DNA-informed breeding. Genomic prediction of breeding values and genomic selection are expected to be the next steps (Roth *et al.,* 2020; Jung *et al*., 2020).

Climate change is an increasing challenge, also for breeding. Plants are permanently exposed to environmental changes and the mechanisms by which they adapt need to be further elucidated. According to Perrin *et al.* (2019), perennial and clonally reproducing plants may have developed particular mechanisms allowing them to adapt to these changes and transmit this information to their offspring. It has been proposed that the mechanisms allowing this plasticity of response could come in the form of epigenetic marks that would evolve throughout a plant's lifetime and modulate gene expression. Anyway, new challenges related to climate change arise for apple cultivation and therefore also for breeding.

Critical pedigree analyses and considerations about the narrow genetic basis (Bannier *et al.*, 2011) underlined the necessity to broaden the genetic basis. The long-standing tradition of apple breeders worldwide to exchange breeding material and to collaborate as a community in international research projects is important and continues up to now, even though many breeding programs are more economically and privately oriented. However, the worldwide breeding efforts for more resilient cultivars are not sufficiently recognized by fruit growing and marketing. Only a few disease resistant apple varieties gained some economic impact. Even in organic apple production, retailers often prefer non-resistant cultivars. Therefore, the benefit of breeding efforts for the organic sector is underexploited. Apple production is still dominated by classical varieties requiring a high number of plant protection interventions. On the market side and for the consumer the varietal choice is limited and rather uniform and the desired extrinsic factors such as outstanding flavor and texture and the desired diversity are not yet available, leading to lower consumption. This is somehow questioning the orientation and efforts of breeding programs and the underpinning research.

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