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Recent Advances in Cherry Breeding

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ABSTRACT

Sweet and sour cherries belong to the *Prunus* spp. and are extensively grown both in the old and new world with an estimated annual production of over 3 million tons. Both cherries are believed to be native to the region between Eastern Europe and cold parts of Russia from where it spread to other parts of the world. Several breeding programs aim to continuously improve cherries with different objectives such as season extension, self fruitfulness, resistance to biotic and abiotic factors and yield. Molecular advances that have augmented crop improvement in several other species have also been utilised for acceleration of cherry breeding. In this short review we have discussed the recent advances that have impacted on cherry improvement and culture.

Keywords: *Prunus* species, allotetraploid, self fruitfulness, rootstocks, land races, biotic and abiotic stress, fruit cracking
Abbreviations: AFP, anti-freeze protein; **AFLP**, amplified fragment length polymorphism; **IQF**, individually quick-frozen; **PCR**, polymerase chain reaction; **RAPD**, randomly amplified polymorphic DNA; **RFLP**, restriction fragment length polymorphism; **S-RNA**, stylar ribo nucleic acid; **SSR**, single satellite repeat; **TSS**, total soluble solids

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ORIGIN AND HISTORY

Cherries are one of the oldest fruit crops known to mankind. It is believed that Theophrastus has mentioned cherries roughly 300 years BC (Hedrick 1915). Another earlier writing suggests that Lucullus brought cherries back to Italy when he returned from the Pontus region in present day Turkey. Thus cherries have a rich history behind them. The origin of sweet and sour cherries is one of the subjects of debate that is ongoing. A number of reviews have been written on this topic. Sweet cherry is believed to have originated in the south side of the Caucasian mountains with a likely secondary dissemination into Europe (De Candolle [1886] in Faust and Surányi 1997). However, Webster (1996) has reported that sweet cherries are indigenous to the region between northern Iran, the Ukraine and other countries to the south of the Caucasus Mountains, thus giving it a much wider area of possible origin. Similar situation exists for sour cherries as well with diverse opinion floated out regarding its origin. While Webster (1996) suggests that sour cherry may have originated from the same area as sweet cherries, earlier reports include a much wider area from Switzerland to the Adriatic Sea and from the Caspian Sea to the north of Europe (Hedrick 1915). Another study suggests that sour cherry is possibly a spontaneous inter-specific hybrid between ground cherry (*P. fruticosa*) and sweet cherry (Olden and Nybom 1968). Molecular analysis such as isozyme analysis, genomic *in situ* hybridization and karyotyping strongly suggest that *P. cerasus* is an inter-specific hybrid (Hancock and Iezzoni 1987; Santi and Lemoine 1990; Schuster and Schreiber 2000). Further, it has also been established that majority of the chloroplast genome of sour cherry is likely inherited maternally from ground cherry, thus validating an inter-specific origin for sour cherry (Brettin *et al.* 2000). Thus it appears that sweet, sour and ground cherries are native to a vast area in the near East but probably concentrated in the region south of the Caucasian mountains (Brown *et al.* 1996; Srinivasan *et al.* 2004). As with several other crops having such a long history, both sweet and sour cherry were eventually spread to

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the other parts of the world from the center of origin through natural means including animals, birds and humans.

Most of the early sweet cherry cultivars, including the highly popular 'Bing', were developed by astute growers and nurseries in the various sweet cherry growing regions of the world (Bargioni 1996). However, controlled hybridization using established parents is the favored method of improvement now, which has resulted in a number of regionally important cultivars. The situation is quite similar with sour cherry as well with most of the early selections made from local genotypes and probably propagated through root suckers (Iezzoni 1984). Such selections probably resulted in several land races in Eastern Europe thus strengthening the genetic diversity in this region (Faust and Surányi 1997). Although a number of public breeding programs started in 1900s, only a handful is still functional along with a few private breeding programs.

GENETIC RESOURCES

It has been recently reported that a rich genetic resource for sweet cherries exists in the mountainous region of China (Cai *et al.* 2007). However, very little is known to the outside world on this particular resource. Outside of this, most of the sweet cherries that are cultivated now can be traced to their European origin. Recent molecular tools have provided interesting information on the genetic nature of the existing varieties. Analyses such as RAPD, SSR, AFLP and isozymes analyses have been done by several labs to ascertain the relationship within the existing cultivars. Almost all of these analyses suggested only a low level of polymorphism (Bošković and Tobutt 1998; Gerlach and Stösser 1998; Wünsch and Hormaza 2002; Zhou *et al.* 2002). Further, Wünsch and Hormaza (2002) suggested based on their SSR analyses of ancient European cultivars that they all fall into two groups, either from southern Europe or northern Europe. This is probably due to the adaptation of northern European cultivars to cold. The situation is even more alarming in North America where there are only four breeding programs. Almost all the varieties that were developed by these programs can be traced back to only five founding cultivars (Choi and Kappel 2004). Earlier studies indicated that there could be two potential landraces in sour cherries as well – one tracing its origin to mild winter regions of Western Europe and the other to a colder Russian region in the east. However, subsequent studies dispute this theory, as there seem to be a continuum in the cold hardiness levels (Hillig and Iezzoni 1988). Unlike sweet cherries, sour cherry growing is limited to a very small number of cultivars, mostly regional. In Central Europe the main sour cherry cultivar is 'Schattenmorelle', a self-compatible and highly productive cultivar with dark red fruits and juice. In North America, 'Montmorency' – a self-compatible variety with bright red fruits and clear juice- is the cultivar of choice. It is likely that both these cultivars originated in France. Among the other notable varieties, 'Pandy' (and its derivatives) are popular in Hungary and Romania, although it is self-sterile. It is likely that the cultivars in cold regions such as Canada and Russia have *P. fruticosa* in their lineage as this species incorporates the much needed cold tolerance (Bors 2005). In spite of its much narrower genetic base, it is suggested that sour cherry is more polymorphic than sweet cherry (Beaver *et al.* 1995), probably due to its allotetraploid nature.

Cherries all around the world are predominantly propagated on two rootstocks –Mazzard (*P. cerasus*) or Mahaleb (*P. mahaleb*). Original Mazzard selections were from progenies of native forest trees (Webster and Schmidt 1996). A number of dwarfing rootstocks belong to *P. cerasus* or derivatives from its hybrids. Mahaleb is still the rootstock of choice in several European countries (Central and Southern) and parts of Asia. Among the other species, *P. canescens and P. fruticosa* have been preferred as parents for rootstock breeding projects (Wolfram 1996; Rozpara and Grzyb 2005).

Several *Prunus* species have potential in breeding programs due to their cross compatibility. However, interspecific hybridization is extremely limited in cherries for scion varieties. Few interspecifc hybrid rootstocks have been developed and are in sporadic use (Iezzoni *et al.* 1990; Webster and Schmidt 1996). The following interspecific hybrids are identified to have potential in cherry rootstock breeding (Iezzoni *et al.* 1990; Webster and Schmidt 1996): *P. avium* x *P. pseudocerasus*; *P. incisa* x *P. serrula*; *P. cerasus* x *P. maackii*; *P. cerasus* x *P. avium*; *P. cerasus* x *P. canescens*; *P. cerasus* x *P. fruticosa*; *P. fruticosa* x *P. avium*; *P. subhirtella* x *P. yedoensis*; *P. mahaleb* x *P. avium*; *P. avium* x *P. kurilensis*; *P. avium* x *P. incisa*; *P. canescens* x *P. incisa*; *P. canescens* x *P. tomentosa*; and *P. cerasus* x *P. pensylvanica*.

ECONOMIC IMPORTANCE

Total cherry production is steadily increasing in both traditional as well as new regions as sweet cherries are still a seasonal fruit that creates a unique buzz in the market, world-wide. The conspicuous spurt in the world production is due to the release of improved cultivars including improvements such as self fertile varieties. Recent awareness of consumers to added health benefits from fruits including cherries, due to their high antioxidant content has given a new lease on life for cherries.

The estimated world annual production of cherries is little over 3 million tons over the past five years with a steady increase since 1990. Turkey is the leading producer of cherries followed by the US and Russia. Germany, which used to be one of the top cherry producing countries, is currently in the seventh place. Total value of the cherry trade worldwide is approximately US$500 million in 2005, though it may have risen in the past few years. While Turkey is the leading producer, US still is the largest exporter of cherries, Japan and Germany account for the top two importers based on the value of the product.

Sweet cherries are primarily consumed as fresh fruit while sour cherries are mostly processed (Kaack *et al.* 1996). Cherries can be frozen in bulk or individually quick-frozen (IQF) for further processing. Canned sour cherries are used for pie-fillings. Both cherries, after dehydration, are included in the dry fruit mix and breakfast cereals. Other forms of processing such as jams and jellies are also made from both cherries. Sweet cherries are also bleached and re-coloured for use in drinks and desserts. Cherry liqueur and wine are the other notable products. Both cherries are excellent functional foods due to their high antioxidant capacity and several new antioxidants have been identified in dried sour cherries (Wang *et al.* 1999) which can be further exploited for their role in health promotion.

BREEDING OBJECTIVES

Improved fruit quality in sweet cherries

Irrespective of the situation, fruit quality is the foremost character that cherry breeders always look to improve upon. Fruit size, sugar content and firmness are the general areas of improvement for getting quality fruits. Large fruit size is favored these days in most markets and thus there is a conscious trend in breeding for this attribute (Christensen 1995). Kappel *et al.* (1996) have suggested that a fruit weight of approximately 12 g is the ideal size with a total soluble solid (TSS) of 17-19% from a consumer perception and hence this should be the standard to look for in new cultivars. In addition most sensory panelists also favored a nice sugar acid balance in that study. However, certain markets as in Japan prefer more sugars in the fruits and so is the case with processing. Among the chemical constituents, anthocyanins are the key components to improve upon while in sour cherries a good anthocyanin and ascorbic acid content (Šimunic *et al.* 2005) will enhance the nutraceutical value of the fruits.

Resistance to fruit cracking in sweet cherries

Fruit cracking, normally associated with sudden rainfall following extensive dry periods, is a major problem in many cherry growing regions of the world. Even in drier growing areas, such as the west coast of North America, it can pose a threat occasionally. It appears largely a physiological phenomenon, determined by environmental fluctuations than genetic, thus hampering the breeding process. While there are suggestions that cultivars with firmer fruits tend to be more susceptible to cracking (Brown *et al*. 1996), it has also been challenged in some other regions (Kappel *et al*. 2000). It is a challenge to breeders to make any significant forward strides in developing crack tolerant varieties as there are no useful tools either at the phenotypic or molecular levels. This attribute has been and will be a challenge and a primary goal in sweet cherry breeding programs throughout.

Extension of the ripening season

Since sweet cherries are a highly seasonal fruit, cultivars producing at either end of the season always command premium price in the market. Thus developing varieties 'outside the existing window' remains a high priority in breeding. While this may be attractive in mild winter cherry growing regions, growers are still reluctant to embrace cultivars that are either too early or too late in colder regions such as Eastern Canada. Such an extension in season remains still attractive as the dividends are high in the Northern Hemisphere cherry growing countries (O'Rourke 2006). It is likely that the cherry growers in southern hemisphere will also be benefited at such season extensions.

Biotic stress tolerance

A lot of pests and diseases attack cherries as with any other fruit crops, thus necessitating a number of sprays during cropping. Brown rot (*Monilinia* spp.), bacterial canker (*Pseudomonas* spp.) are the most destructive diseases while cherry fruit fly (*Rhagoletis* spp.) and black cherry aphid (*Myzus cerasi* Fab.) are the major insect pests attacking sweet as well sour cherries. In the western North American growing regions powdery mildew is a serious problem in both cherries. While there is a fair degree of tolerance exists among the available cultivars for most of these pest and diseases (e.g. 'Hedelfingen' is quite resistant to powdery mildew), true resistance is still elusive. It is not known if there is any resistance to *Monilinia* spp. among the wild species. Cultivars released from John Innes Institute such as 'Mermat' and 'Inge' exhibit good resistance to bacterial canker (Mathews and Dow 1983).

Abiotic stress tolerance

As cherry growing extends to new areas, which are often in the periphery of traditional areas, the risk of winter injury, spring frost or heat stress also increase. It is well established that low temperatures during late autumn and early winter hamper the production of sweet cherries (Caprio and Quamme 2006). Heat stress tends to encourage fruit doubles; however, cultivars such as 'Rainier' and 'Jubilee' seem to have very low doubling potential thus pointing to the availability of resistance in the existing gene pool.

Precocity

In perennial species such as cherries a quicker return on investment is a priority and the only way to achieve this is through developing precocious cultivars as well as rootstocks. Some cultivars such as 'Sweetheart' are very precocious even when grafted on standard rootstocks such as 'Mazzard', while some of the newer rootstocks (e.g. 'Gisela' series) can also incorporate precocity. Since sour cherries are grown predominantly for processing, productivity is as important as precocity. In general sour cherries are self-compatible, although self-incompatible and partially self-compatible cultivars do exist. Sour cherry fertility is not fully understood as that of sweet cherry. Just as the sweet cherries, sour cherries also exhibit gametophytic self-incompatibility (Tobutt *et al*. 2004; Hauck *et al*. 2006).

Self-fertility

Of late, self-fertility has become an important trait in cherry breeding programs. Currently self-fertile cherry cultivars have been developed in almost all the breeding programs. In Canada, sweet cherry cultivars such as 'Stella', 'Skeena' and 'Staccato' from Summerland, and 'Vandalay' and 'Theranivee' from Vineland are increasingly popular both as a cultivar and as a breeding parent. It appears that in future only self-fertile cultivars will be preferred by growers as constancy of production is favored over negative attributes of self fertile cultivars such as over cropping and fruit size reduction (due to clusters). This is further fueled by the fact the marketing is now going global demanding the industry to put consistency in production over quality attributes.

Mechanical harvesting

Of late, mechanical harvesting is becoming an important objective due to non availability and escalating labor costs. While such mechanical harvest might be acceptable for processing cherries but for cherries intended for the fresh market mechanical harvesting might compromise the quality and until a market for stem less sweet cherries is developed, this will be an enormous challenge for growers and breeders alike. To facilitate a successful cultivar for mechanical harvesting, factors such as tree architecture, stem retention and tolerance to bruising are important. There are varieties and selections with low stem retention force that can be used to augment cultivar development to meet this goal, although it will be a time consuming effort.

MOLECULAR APPROACHES IN BREEDING PROGRAMS

Cherries have a longer pre-bearing age. A minimum of 4-5 years is required from seeds to first fruits in seedlings. Unlike annual horticultural crops or grain crops, there is no homozygous parent used in breeding programs to predict the genotype of the offspring. Thus a lot of hybridizations have to depend on speculations than accurate predictions. This is a hard and time consuming job where the results will not be known for a long time. In such situations, the use of molecular markers to aid selection on the basis of genotype rather than phenotype will be extremely useful as it not only can help to potentially reduce the time (although this is not a very practical one), but also the huge amount of space required to grow the hybrid seedlings to fruition. For instance, if reliable molecular markers have been developed, one can screen the seedlings in a greenhouse itself and plant only the desired seedlings based on the genotype analysis. However, it must be admitted that this field is rather in its infancy in cherries, since the traits of importance vary based on the region of cultivation or universal traits such as fruit quality are often complex quantitative traits involving a number of genes, thus requiring several generations of analyses. Genotyping of 75 sweet cherry cultivars using peach SSR markers has lead into the demarcation of two well defined groups based on their geographical origin, thus demonstrating the useful of markers from a closely related species (Wünch and Hormaza 2002). Since fruits are the parts of economic importance in both cherries, most of the molecular studies are directed towards ripening-related and disease resistance genes. Recently, there is added interest in studying the antioxidant genes and genes that encode human allergens such as thaumatin-like proteins – Pru a1 and Pru a2 (Fils-Lycaon *et al.* 1996; Inschlag *et al.* 1998). With the peach genome sequencing nearing its completion many useful markers may be found from those results to improve sweet and sour cherries.

Barring certain cultivars of sweet and sour cherries, it is safe to say they are self-incompatible. Sweet cherry is an obligate out crossing species, due to gametophytic incomepatibility, requiring compatible pollen sources for commercial cultivation. Thus this trait invoked a lot of interest among the molecular breeders. A lot of earlier work depended on stylar protein S-RNAse isozymes to study this problem. However, of late PCR S-allele detection is largely carried out using PCR based approaches, which is far more accurate and effective (Sonneveld *et al*. 2005). Further PCR based genotyping of most commercial cultivars have also been done in almost all regions (see Kappel *et al.* 2009 for details). Since the release of self-compatible varieties, there is an increasing interest in utilising the mutant *S*-allele (originally developed by irradiation) that is responsible for the self compatibility. Molecular markers for self compatibility have been identified recently (Ikeda *et al.* 2004; Zhu *et al.* 2004). Further characterization of the S-allele has revealed that there are some deletions or frame shifts resulting in pollen mutation (Sonneveld *et al*. 2005). Although these studies have resulted in very useful and practicable markers, it is unlikely that they will make a significant shift in the conventional breeding involving large populations. Perhaps they will be a very effective tool in the 'pre-selected' (conventional selections made based on phenotype evaluation) population to confirm the self-compatibility.

Being a tetraploid, sour cherries exhibit a typical disomic inheritance pattern which adds to the complexity of linkage map development. Tetraploid sour cherry cultivars have been primarily identified by single-dose restriction fragment (SDRF) low density RFLP linkage (Wang *et al.* 1998). They have also further identified that four of the sour cherry linkage groups may be identical with peach and almond.

Genetic linkage maps are not yet ready for cherries, although attempts have been made in both sweet (Stockinger *et al*. 1996) and sour cherries (Canli 2004). However, with the genome of peach almost ready to be published and availability of linkage maps in other *Prunus* species such as almonds should be quite readily transferable to cherries. The high levels of synteny and marker co-linearity (Arus *et al*. 2006) should facilitate such transfer quite effectively. Rapid strides are being in the development of bioinformatics for *Rosaceae* (Genomic Database of Rosaceae; Jung *et al*. 2008) which should greatly augment improvement in this species. With plant regeneration and genetic transformation still in its infancy in most *Prunus* members including cherries, it is safe to assume that genetically modified cherries are quite far away, although these techniques can accelerate crop improvement.

TISSUE CULTURE AND GENETIC TRANSFORMATION

Plant regeneration through *in vitro* culture techniques is not as advanced as in other species in the *Prunus* genome. In general most *Prunus* spp. show a high degree of recalcitrance for *in vitro* regeneration. Cherries however, are relatively better and plant regeneration is achieved fairly well. The earliest attempts on *in vitro* culture of sweet cherries date back to 1933 when embryos from controlled hybridization involving early cultivars were cultured on artificial media to get plants (Tukey 1933).

Young leaves of several sweet cherry cultivars have responded well in tissue culture and plants have been regenerated successfully by several groups. Several important cultivars including, 'Hedelfingen', 'Napolean' and 'Schneiders' (Tang *et al*. 2002), 'Kristiina' (Vasar 2000), 'Bing', 'Sweetheart' and 'Lapins' (Feeney *et al*. 2007) have been successfully regenerated. In sour cherries regeneration from *in vitro* derived leaf explants of 'Montmorency' has been reported (Song and Sink 2005). As with any other crop several nutrient media have been studied and reported useful in successful regeneration. From all these reports it appears that the woody plant medium (Lloyd and McCown 1981) seems to be the best. Since microbial contamination is an inherent problem in the explants when obtained from the field aseptic shoot cultures are often preferred. Such use of aseptic cultures also facilitates the availability of young leaves throughout the year. The use of antioxidants, such as dithiothreitol is reported to have a significant effect in root formation but very little on acclimatization (Vasar 2000). Micropropagation is of great use in multiplying and mobilising clean rootstocks, especially with several viral diseases threatening the cultivation of these crops. In crops with numerous cultivars, a major problem is genotype dependency on regeneration and cherries are no exception either (Bhagwat and Lane 2004; Song and Sink 2005).

In spite of the number of reports on developing regeneration systems for both sweet cherries (Bhagwat and Lane 2004) and sour cherries (Tang *et al*. 2000, 2002), very little success in obtaining stable transformation of cherries has been achieved. This is partly due to the fact that the above mentioned systems are largely organogenic based and hence stable transformation occurs at a very low frequency. Both *Agrobacterium*-mediated as well particle bombardment systems have been attempted for cherry transformation (Druart *et al*. 1998). More recently stable transformation of 'Montmorency' and 'Gisela-6' rootstock has been achieved, although only reporter genes such as *β-glucuronidase* gene have been used (Song and Sink 2006). Genetic transformation with useful genes such as phytochrome related genes can help to control the tree size (Piagnani and Scotti 2006). Transgenic sour cherry with anti-freeze protein (AFP) has been reportedly regenerated, although the functionality of the AFP could not be proven on the regenerated plants (Dolgov 1999). Transgenic rootstock cultivar 'Colt' expressing the rice *phytochrome* A (*phy* A) gene shows reduced apical dominance and increased branching in field testing (Muleo and Iacona 1998). Genes encoding polyphenol oxidase (PPO) is currently of interest and transgenic cherries are being developed in private laboratories.

FUTURE PERSPECTIVES

Crop improvement through conventional breeding in cherries is a long term as well as an expensive process. However, it is the most successful one so far as evidenced from the number of new cultivars that have been released from various breeding programs. This is truer with sweet cherries than sour cherries where the numbers of bred cultivars are far less than the sweet cherries. Recent advances in molecular marker and other biotechnological approaches offer the potential to accelerate the cultivar development process. Perhaps these advances can help in developing more self fruitful cultivars with precise characteristics as per industry and consumer demands and expand cherry growing to more non-traditional regions as well. Plant regeneration and transformation has been achieved in both cherries which can immensely help to improve existing cultivars for specific traits. Varietal preference or brand loyalty among consumers is very much in existence in cherries, which can be retained by transformation techniques. A more plausible approach is to transform rootstocks and thus avoid the presence of transgene in the final product, the fruit. The completion of peach genome sequencing is a very significant step for all *Prunus* species and will augment crop improvement in these species in the immediate future.

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