ROSE BREEDING: PAST, PRESENT, PROSPECTS.

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In this review the PAST, PRESENT and PROSPECT will be considered as three separate periods in the history of the breeding and development of rose cultivars. The recurring theme is the genetic variation. This theme was chosen because there is justified doubt as to sufficient genetic variation available among current progenitors to ascertain the vitality and productivity of future cultivars in cross-breeding. This seems particularly true for glasshouse cultivars.

The above three periods are defined as follows. PAST: the era from pre-history until about the year 1875, the PRESENT era from about 1875 until 1967, and the PROSPECT (future) from 1967 onwards.

With probably over 5000 years, the PAST covers the longest time lapse. It ended around the year 1875, with the discovery of aimed cross-breeding. Not accidentally, Mendel published his famous laws about inheritance about simultaneously. It is remarkable that many rose breeders still like to think in terms of Mendelian or qualitative inheritance. Quantitative inheritance or additive gene action, seems either little known or not used.

The PRESENT period started with the knowledge about aimed cross-breeding, and ended with the introduction of biotechnology in rose breeding in 1967. This period has covered about 90 years only.

The PROSPECT, which in fact is the FUTURE era, has already begun in 1967, and is about 28 years on the way.

To start with, the breeding and genetic variation occurring in the PAST period will be considered. It is assumed that early horticulturists sampled desirable rose species from the wild and planted them in collections. According to Wiley (1955) and Krussmann (1987), several species and most likely cultivars of them too, were grown in gardens in China, Persia, Mesopotamia, Egypt, Greece and in Italy, long before the beginning of the Christian era. It is uncertain, however, whether all the roses of ancient horticulture were seedlings, or that certain strains were already vegetatively propagated. A fact is, that during this whole period, new cultivars exclusively arose by sowing the seeds that resulted from open-pollination.

Particularly in the beginning, domestication of species and their probable inter-specific hybrids supposedly was a slow process. However, as unsuitable primitive forms were discarded and propagation methods improved, progress towards tame forms was more rapid. Introduction of new genotypes and exchange of species and cultivars by travellers, considerably broadened the genetic variation available to horticulturists. It should be noted, by the way, that domestication of a species, any species in fact, necessarily involves a narrowing of the genetic variation available. In a few cases only, early breeders kept record of the female parent and the year of introduction of a new cultivar. These records, however, have enabled to ascertain part of the descent of later cultivars Although it was instinctively felt that neighbouring plants in collections had a relation to the new forms obtained, breeders did not yet realize that characters of the male parent could be turned over by pollination.

Afterwards, it was established that from initially mainly diploid, gradually new cultivars were and later tetraploids. Particularly nowadays, important cultivars are almost exclusively tetraploid. Modern research demonstrated that in crossing diploid and

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tetraploid species, triploids arise with relative ease. Although most triploids appear to be female sterile, a number of them has fertile, diploid pollen that may successfully fertilize tetraploid forms. It is notable that particularly among recurrent flowering cultivars, vigour of the plants increased with the ploidy level. If this knowledge would have been applied by breeders, it would have opened interesting possibilities to introduce new characters from diploid species to tetraploid cultivars. Such introductions would have taken two generations of cross-breeding only.

By correlating the rose flowers pictured in old manuscripts or heads on coins with later established endemic species, taxonomists are more or less certain that the following species have played a role in earliest horticulture.

R. alba L	2n = 6x	= 42
R centifolia L.	2n = 3x/4x	= 21/28
R damascena Mill.	2n = 4x/5x	= 28/35
R gallica L.	2n = 4x	= 28
R moschata Herrmann	2n = 2x	= 14
R pimpinellifolia L.	2n = 4x	= 28
R sempervirens L.	2n = 2x/3x/4x	= 14/21/28
R wichuraiana Crépin	2n = 2x	= 14

The relative importance of most of the species that have contributed to the cultivars raised in the PAST and PRESENT periods, is presented in Table 1 (Krussmann, 1986).

Two imports into Western Europe have put their stamp more on new forms than any others. These are the four diploid ‘Stud China‘s’ (*R. chinensis* Jacquin), which introduced both the hitherto unknown phenomena of resurrent flowering and the bush type of plant. Further, the likewise diploid *R. multiflora* Thunberg, that brought shoots with an umbel of many flowers.

At the end of the PAST period, an overview can be given of the most important groups of cultivars and the species on which these groups were based. A simplified diagram is presented in Table 2 (Stewart, 1969).

Depending on the taxonomist, between 240 and 300 rose species are being distinguished nowadays. It has been estimated, however, that genotypes of only 10 - 20 of these species have contributed to modern cultivars. Because most rose species are cross-compatible, one would have expected the involvement of many other species. Because these species must have been known to Man, the choice of these 10 - 20 species might not have been accidental, but based on easy availability, attractive characters or favourable seed set.

The above course of events indicates that:
- there 15 an enormous potential of characteristics that is still unused and waiting to be exploited in breeding
- the genetic base of cultivars at the end of the past period covers only small part of the total variation available within the genus *Rosa*.

Looking back, the highlights of rose breeding in the PAST period can be summarised as follows:
- numerous species were sampled and grown in collections
- few species only have contributed to cultivars of the PRESENT period
- Inter-specific hybridization is a natural process
- new cultivars resulted from open-pollination only
- breeding was concentrated in Western Europe and USA
- a natural tendency from diploidy to tetraploidy
- initially large genetic variation
- domestication of species decreased variation
- descents of cultivars before about 1875 are speculative

The PRESENT era has ended exactly 28 years ago, when Hill (1967) in England successfully induced somatic embryos in callus of the climbing Hybrid Tea The Doctor' With that highlight, the introduction of biotechnology in rose breeding became a fact.

Looking back at the PRESENT era, it is clear that on the one hand, it is characterized as one of very large and important developments in plant biological research. On the other hand, the world-wide important crop rose appears to be somewhat destitute of scientific research. Lack of research is most strongly illustrated when one leaves through older editions of Plant Breeding- or Horticultural Abstracts. Among the thousands of annual entries, those of the rose are conspicuous by their absence.

Within the rose, scientific research has mainly concentrated on taxonomy, cytology, physiology, morphology, growing conditions, as well as variety and rootstock testing. Breeding research aiming at: inheritance of characters, facilitating the process of cross-breeding, improving direct and indirect selection, adaptation to low-energy conditions and resistance to pests and diseases has been rare and lagged seriously behind that in fruit, for example. If breeding research was carried out at all, it was confined to universities and horticultural institutions. Unfortunately there has been little recognition of its merits.

With regard to the genetic variation available within the classes of roses in vogue, the PRESENT era started with two important new introductions.

The first novelty was the yellow coloured, resurrent blooming, large flowered 'Soleil d'Or', bred by Pernet in the year 1900. This cultivar was, in fact, the first success of an aimed species-cross. It is notable, however, that all yellow pigmentation, which is controlled by additive gene action, originates from 'Soleil d'Or'. All present-day yellow cultivars descent from that one cultivar only (Paris and Maney, 1944).

The second introduction was about 1920, when the ancient dwarf cultivar of *R. chinensis minima*(Sims)Voss, 'Pompon de Paris', was re-discovered in Switzerland by Colonel Roulet. The new species, now named *R.roulettii* Correvon, was the beginning of a range of miniature cultivars. Owing to the fact that dwarfness is controlled by one dominant gene (Dubois and De Vries, 1987), breeders like Jan de Vink, Pedro Dot and Ralph Moore, achieved a large number of miniatures in a relative short period. Thanks to the fact that the breeders of the thirties were not afraid to publish the progenitors of their new cultivars, it was not difficult to demonstrate that, like the Hybrid Teas, miniatures evolved from diploid, via triploid to the present tetraploid level.

Without any doubt, the largest genotypic variation created by Man, was available at the beginning of the PRESENT era. The distance between cultivars and their wild ancestors was not yet far, while mixing of classes was not yet common.

Overlooking this enormous genepool, breeders of the PRESENT era seized their opportunity. Progenitors were chosen or discarded, methods of crossing were developed, while the whole breeding process was increasingly carried out indoor.

With some perseverance, many different progenitors appeared to be cross-compatible. As a consequence, the original clear borders between classes of cultivars gradually faded. At first this yielded a multitude of unexpected desirable new forms. The significance of hybridization among all roses available is, however, that the specific genetic variation that first was conserved within classes containing several cultivars, now became divided over numerous, in fact non-classed cultivars. In it self, this was not a wrong action. But as cross-incompatible cultivars were gradually discarded, the first reduction of a broad genetic variation had started.

Another important development towards reduction of genetic variation occurred in the thirties, when cultivars were divided into the categories garden and glasshouse roses.

Encouraged by demands from each category, breeders began to develop genotypes that seemed suitable to each specific environment. Today, breeders mainly specialize in one category only. The fact that royalties for glasshouse cultivars are 3 to 5 times that for a garden rose, made the glasshouse category particularly attractive. Owing to still sufficient large genetic variation among cultivars, breeding efforts in both categories were remarkably successful. Gradually, particularly for the glasshouse, a new classification, mainly used at flower auctions, was introduced: small-flowered, medium large-flowered and large-flowered cultivars.

Generally speaking, there is no basic difference between the breeding of garden and cut roses. As to the selection process, breeders of both categories apply positive, but mainly negative selection to their seedlings. Roughly 99% of the plants in each seedling population are discarded during some stage of selection. Maintenance of this strict selection in millions of new seedlings each year, over a range of almost 100 years, must have led to severe genetic erosion. To make things worse, almost every selectionist looks for the same desirable phenotype, thus applying the same selection criteria.

In studying collections of modern cut roses, it is not difficult to conclude that these plants not only have become adapted to the glasshouse environment, but that their habitus is more or less similar as well. Hence, cultivars show more uniform bud shape, flower shape, flower size, number of petals, stem length and thorniness within each flower colour.

However much the external quality of cultivars, which is the appearance of the plants or parts of them, may have improved, this is not the case with their internal quality. If internal quality contains for example, vigour, adaptation to low energy environments, vase life of flowers or resistance to pests and diseases, manners stand badly for roses. Unfortunately, breeding programmes for internal quality have been unpopular and are rarely pursued by private breeders.

As to external quality, it is seen that most breeders experience increased uniformity of seedling populations as a positive result of their efforts. It Is questionable, however, whether this is really favourable or not. Particularly for cut roses, there is only a restricted number of progenitors available to obtain desirable seedlings with specific characters. When a broader range of progenitors is claimed, they appear to be descendants of cultivars already involved. If this is true, which is to be feared, the conclusion is that, with few exceptions only, most new cultivars have several common progenitors. In turn, this indicates that new cultivars more and more result of some form of inbreeding. Whereas in self-pollinating crops inbreeding may lead to favourable varieties, this is not the case in outbreeding crops like the rose. In outbreeding crops, heterozygosity is the basis of maintaining vigour and productivity.

Experiments at CPRO-DLO with selfing or sibbing rose cultivars have shown that these rigorous forms of inbreeding are absolutely deleterious to both the vigour and the plant habitus of seedlings. It is not difficult to show that also milder forms of inbreeding have already led to decrease of vigour (De Vries and Dubois, 1987).

The above inbreeding situation has been recognized by prominent breeders. Their much voiced complaints are: "seedling populations must be larger each year" and "it is increasingly difficult to find something better". There Is not one simple answer to the question how this state of affairs in the rose has originated. Afterwards a number of factors appear to have played a role:

- rose breeding is relatively easy
- rose breeding is often a side-line for horticulturists
- rose breeders are more old-fashioned than in other crops
- rose breeders are interested in cultivars, not in experimentation
- breeding woody ornamentals is laborious, time-consuming and advances slowly
- scientists like fast crops
- little contact between breeders and scientists

Coming to the end of the PRESENT era, some conclusions are justified:
- Initial tremendous gain of new forms
- more uniform cultivars owing to selection
- high external quality

- low internal quality
- serious reduction of genetic variation
- onset of inbreeding depression
- little co-operation science: breeders

As a consequence of the actions in the PRESENT era, the pass-word of the PROSPECTS or FUTURE era is: introduction of new genes that contribute to the internal quality of a partly inbred crop. Obviously, the most proper and cheapest action would be to introduce new genetic information from rose species by cross-breeding. Information from both specials yet unused and from new genotypes of those already incorporated. The second possibility is offered by biotechnology.

The option of biotechnology appears not to be a free choice for breeders. In the early stages, biotechnology was in the hands of a few Universities and State Institutes only. Gradually, however, big chemical and old companies invested in the genetic modification of financially attractive crops. The rose was not excepted. Today, genetic modification of roses is also in the hands of biotech companies like Mogen, Calgene Pacific, Keygene and several other commercial laboratories. The most important conclusion is not that these companies may promise more than they can realize, but that the rose, that formerly was in the safe hands of horticulturists only, now suddenly is out of reach of that group.

Completely apart from the technical developments in rose breeding, the consequences of too many human beings living per square kilometer must be taken into account. This is particularly conspicuous in the Western hemisphere. Not unjustly, therefore, environmentalists are increasingly involved in the safer culture of crops. Many of their initial demands have presently become laws in Western countries. Hence, environmental laws contain: reduction of the use of fungicides, pesticides, nematicides and of the use of vase water conditioners. That is true for both commercial and private users. In some countries, chemicals for agricultural use can be obtained on prescription only. This means that characteristics of cultivars that formerly were desirable only, now have become demands. Survival of the beautiful crop rose may depend on adequately meeting these demands. While breeders of many other important crops have recognized and anticipated these demands by creating resistant genotypes, to our best knowledge the traditional rose breeder hardly has an answer.

This state of affairs means another tremendous stimulance to biotechnology. Together with the established centers of research, commercial biotech labs develop, isolate and construct new genes, and invent methods to introduce these genes Into plants. Introduction of foreign genes seemingly meet the requirements in a way that can hardly compete with cross-breeding. Some of the PROSPECTS offered by biotechnology, that might be realized before the year 2000 are:

- resistance to vase water bacteria
- resistance to beetles and caterpillars
- resistance to mildew and/or blackspot
- introduction of new flower pigments

In order to further protect environment and meet future wishes of growers and nurserymen, several other items may be predicted which, given the proper funding may ultimately be met by biotechnology:

- resistance to white fly, red spider and thrips
- resistance root knot bacteria
- resistance to root nematodes
- rootstocks with increased vigour
- cultivars that root more easily
- cultivars with improved fragrance
- cultivars that can be harvested at one go
- cultivars that are daylength sensitive

The Introduction of patented genes into cultivars that are already protected by breeders rights, has put a time bomb under the position of the traditional rose breeder. Under the present Plant Varieties and Seeds Act, sports of protected cultivars can be protected as independent cultivars. In the new bill for Plant Varieties and Seeds Act, which is not yet accepted as a law, owners of cultivars are better protected than in the present one. For example, in the new bill, the term derived variety has been proposed to distinguish sports. Owners of the mother variety will have a say in the introduction of derived varieties. It seems rather simple, too simple in fact, to consider a cultivar into which one or more patented genes have been introduced, as just a derived variety. Although within the European Union cultivars cannot not be patented, a precedence has already been created by a recent plant patent for soy bean. It Is this new adjudication that rightly should alarm owners of protected cultivars.

In the above pictured situation, there seem few options left to the breeder of the second millennium. Trading on as before may wear out new possibilities in a few decades. If breeders decide to remain their own master, a renewed co-operation with scientific institutions must be established. Another option is a Joint-venture with specialized biotech companies, thus sharing the royalties of protected cultivars and patented genes.

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Table 1. Distribution of classes of roses in the last 400 years. After R.E.SHEPHARD (1954) and G.KRüSSMANN (1986), completed until 2000.

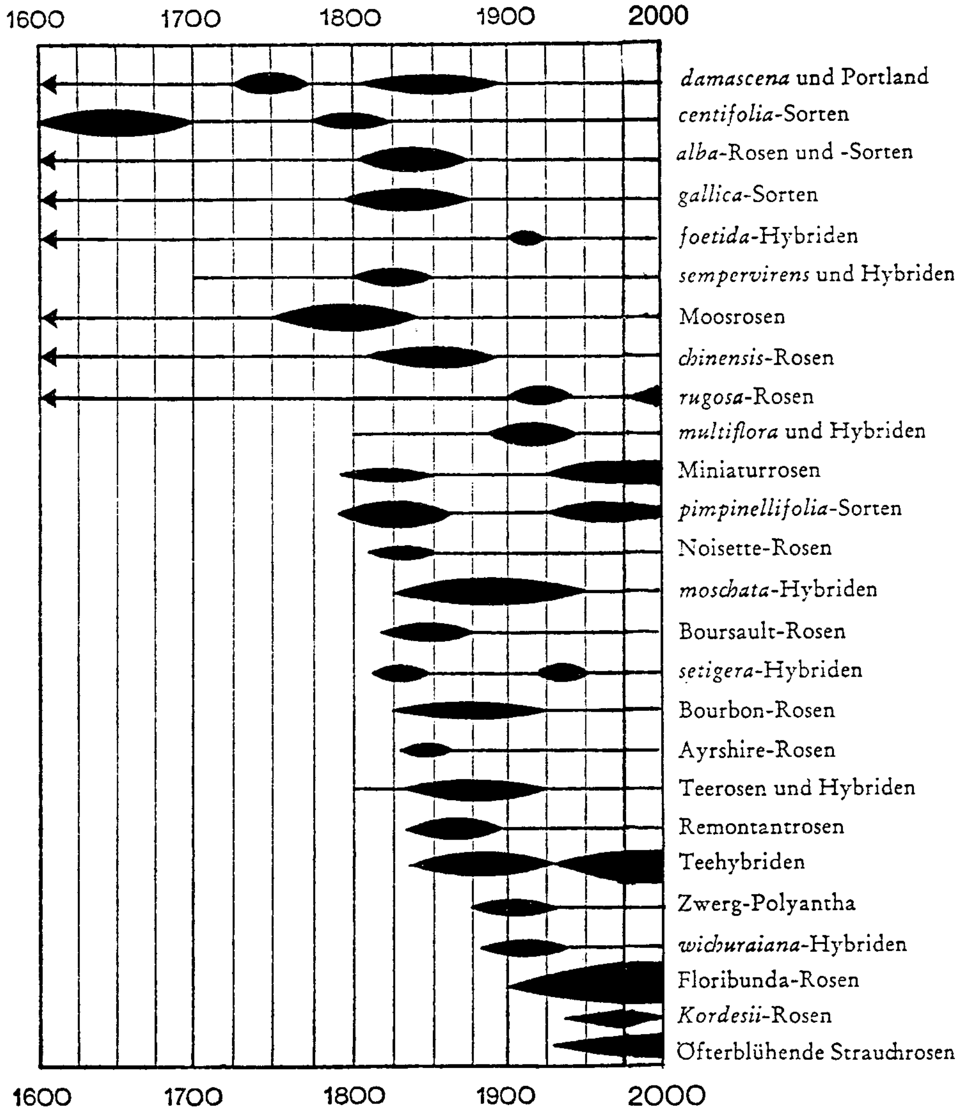

Table 2. The origin of the modern cultivated rose. After STEWART (1969)