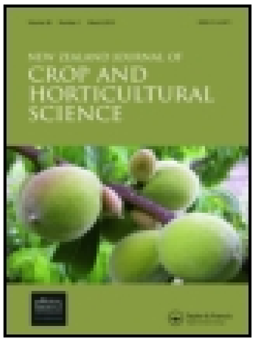

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Review

Breeding rootstocks for tree fruit crops

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Abstract Identification of problems and prioritising breeding objectives based on those problems are essential first steps in a rootstock improvement program. For all tree fruits, incorporating resistances to critical diseases and pests will facilitate fruit production in a social environment demanding reduction in pesticide usage. Diseases caused by various *Phytophthora* species are important and can be catastrophic for all major tree fruit crops; breeding for resistance to *Phytophthora* has generally been successful. Very large initial seedling populations are required to permit suitably rigorous early screening; the breeding team should anticipate odds of $1{:}10^4$ to $1{:}10^6$ that any given seedling will be commercially successful. In preliminary orchard tests, positive selection for dwarfing and precocity induction can be made by the fifth year. More rigorous second tests should be made with a number of commercial varieties in several locations. Although almost all rootstock improvement programs now rely on conventional breeding methods, through application of genetic engineering, the Malling 26 apple (*Malus domestica*) rootstock has been successfully transformed from being highly susceptible to fire blight to being moderately resistant.

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INTRODUCTION

Johnny Appleseed is the quintessential picture of our transition from the hunter-gatherer stage of fruit production to our increasingly refined orchard technologies of today. Our first stages in the long climb from hunter-gatherer involved the simple planting of seeds from the fruit we had just eaten—the peach (*Prunus persica* L.) pit and the apple (*Malus domestica* Borkh.) core, carefully tamped into the soil. In many parts of the world, this primitive pomology persists even today; the 'criollo' peaches of Mexico and the village apricots (*Prunus armeniaca* L.) of Afghanistan are good examples of such seedling orchards.

That certain individual trees may be far superior to the run-of-the-mill has been recognised for thousands of years. Our viticulturists capitalised on the easy-rooting of their commodity long, long ago by utilising cuttings to propagate superior grapevines (*Vitis vinifera* L.). By the time Jesus of Nazareth was walking the hills of Galilee, the grafting of olive (*Olea europaea* L.) trees was a commonplace practice, and the writings of Pliny make it evident that grafting superior varieties onto rootstocks was well known in numerous fruit species.

It is impossible to estimate when the horticulturist began to recognise that just as selection and propagation of superior fruiting varieties could be carried out on a routine basis, so might also be superior rootstocks on which to graft those varieties.

In its earliest beginnings, commercial fruit production was based on the seedling-rooted tree. When I (JNC) was a boy growing up in the hills of Southern Illinois, our orchards of apples, pears (*Pyrus communis* L.), and peaches were all growing on seedling rootstocks, and so were the trees in every orchard across North America. Those big trees were tolerant of their physical environments, tolerant of the diseases and pests that attacked them, and tolerant of the often rather casual treatment of the farmer. Even today, most stonefruit trees being planted are on seedling rootstocks, and likely almost half the hectarage of apple and pear trees being planted are on seedling. Citrus crops of course fall into a unique class— the peculiarities of citrus seed production permit the propagator to produce clonal rootstocks with apomictic seeds.

First serious commercial deployment of clonal rootstocks probably began in the apple orchard a hundred years ago. Initially clonal rootstocks were tried primarily to limit tree size; 'Yellow Metz'—now Malling 9 and its many substrains—is the only commercial survivor of those early selections. Here in the southern hemisphere, you began using 'Northern Spy' and its derivatives to escape the ravages of woolly apple aphid (WAA) (*Eriosoma lanigerum* Hausmn.). We're all familiar with the story of the WAA-resistance breeding program initiated at the John Innes Institute in 1922 and the cooperation with East Malling that eventually led to the introduction of the Merton Immune series and the Malling-Merton's. The New Zealand, Australian, and South African apple industries are based on these rootstocks today.

BREEDING PRINCIPLES

Developing new varieties was once the province of the pomologist-breeder working alone, but that approach is no longer viable. The team approach initiated at John Innes Institute more than 70 years ago continues to evolve. On the modern breeding team, we expect to see not only the pomologist-breeder and the pathologist, but also often the biochemist, the biotechnologist, and the stress physiologist.

Although the basic principles and methods relating to breeding fruiting varieties are applicable to breeding better fruit tree rootstocks, the rootstock breeder does face certain unique factors: (1) the physical environment of the root system is very different from that of the fruiting portion of the tree. Temperature regimes, gas exchange systems, and moisture environment are obviously different. Further, within the rhizosphere of a particular plant there are substantial variations in environmental conditions, and the variations in rhizosphere from tree to tree are far greater than those of the same trees aboveground. (2) The biotic environment in which the rootstock lives is much different from that of the scion variety. The stock is subject to the hazards of water moulds, sucking insects, nematodes, chewing mammals, and soil-borne viruses. In many instances a symbiotic relationship with mycorrhiza is important, perhaps essential. We need to remember that it is much more difficult for the orchard operator to deal with these challenges below ground than with the challenges encountered aboveground. (3) The influences of root system on scion and of scion on root system are profound. Many of the most important horticultural attributes of the tree as a biotic unit may be substantially influenced by the stock—vigour, blossom initiation, fruit set, and phenology are but examples. (4) Under modern production and merchandising regimes, no genetic diversity is acceptable in the scion variety. In the rootstock, though, a certain amount of genetic diversity is acceptable and may well be highly desirable.

BREEDING STRATEGY

In the beginnings of our apple rootstock breeding work at Geneva, United States, we were struck with the historical failure to identify critical problems, to derive from these problems appropriate breeding objectives, and to attack these objectives systematically. We came to believe that a rootstock breeding program should be designed on a problem:objective basis, and that a program in progress should be frequently reviewed and revised on this basis. Our basic sequential approach is probably broadly applicable, regardless of commodity:

(1) Define problems, both existing and potential.
(2) Define objectives, based on real problems.
  (a) Establish standards, both minimal and optimal.
  (b) Establish priorities among the objectives.
  (c) Weight objectives differentially for specific producing situations.
(3) Develop screening methods and sequences.
  (a) Plan to produce very large populations and then to eliminate early and ruthlessly.
  (b) When working toward resistance objectives, determine and include physiological races of each pest.
  (c) After screening, confirm that the survivors are indeed stress-resistant under field conditions.
(4) Plan the hybridising program.
  (a) Identify potential parents. Search (but do not trust!!) the literature. Parent identification

will involve extensive evaluation of germplasm.
   (b) Obtain the chosen parents or secure sources of pollen.
   (c) Estimate numbers of seedlings required to produce appropriate numbers of individuals to be orchard-tested. Orchard testing phase is limiting factor on seedling numbers.

(5) Make crosses; harvest, stratify, and germinate seed. (Easiest part of program!)

(6) Conduct early screening, preferably in a greenhouse, beginning with seedlings as young as possible.

(7) Plant survivors as candidates in nursery trials. Eliminate preselections that do not meet essential objectives such as form, brittleness, or root type.

(8) Propagate the apparent best candidates from phase I nursery. Three trees on each candidate rootstock should suffice. Bud to test variety that will best display characteristics of interest, e.g., tree vigour.

(9) Proceed to second test level as early as possible. Use several fruiting varieties that will have continuing commercial impact. Second tests should be planted in different locations. Plots of 4–10 trees should be used, under commercial orchard conditions.

(10) By the end of fifth or sixth year at second test level, the very best candidates in each vigour class may be bulked up for extensive semi-commercial scale third test.

IDENTIFYING PROBLEMS

What problems are limiting for the particular crop? Are some more amenable to attack by cultural methods than by breeding? Will loss of a particular chemical make genetic control critically important? Is there evidence that a "better" rootstock would solve the problem over the long haul?

Environmental hazards

Environmental hazards that in the north-eastern United States limit survivability of our apple trees include: fire blight (*Erwinia amylovora* (Burr.) Winslow et al.), crown rot (*Phytophthora* spp.), the "Southern root rots" (*Clitocybe, Armillaria, Corticum, Xylaria,* and *Dematophthora*), tomato ringspot virus (only on MM.106, Mark, and M.26 at present), low winter soil temperatures (but rarely in New York), drought, and waterlogging. Important, but usually not limiting, are nematodes, specific replant problem, WAA, and high summer soil temperatures. Here in the southern hemisphere, of course WAA take on a much more sinister value.

Horticultural problems

Horticultural problems of the rootstock include poor anchorage, brittleness and breakage, excessive suckering, lack of precocity, and limited production efficiency.

The nurseryman has only modest demands on the rootstock: (1) it must be economically propagable; (2) it should be relatively free of spines both in stoolbed and in the liner nursery; (3) it must survive well on being transplanted, both into the nursery and into the orchard; (4) the liner must take the bud well and there must be no incompatibility with common cultivars; and (5) there must be no problem with "blow-outs" of the budling shoots.

In addition, the nurseryman would like to be able to avoid spraying against black spot and powdery mildew; it would be convenient to have red or otherwise distinctive foliage; it would be very helpful to have a stock that would cause the finished tree to mature early in the fall and so permit early digging.

The fruit grower, once he/she plants a tree, is permanently committed to the rootstock decision. The genetic makeup of that rootstock cannot be altered, and there is relatively little that can be done after planting to permanently modify its environment. The fruitgrower is concerned first of all that a tree survives whatever environmental hazards it encounters; that it comes into commercial production early, and that it produces heavy crops of well-sized, high quality fruit every year. Crown rot and fire blight are the most important factors influencing survivability of apple trees in New York, but in Quebec winter hardiness is most critical. Tomato ringspot virus and *Phytophthora* are the tree killers in the Shenandoah Valley.

We group problems that may be suitable for the rootstock breeder to address into four classes:

(1) Hazards of the physical environment

Soil problems—poor internal drainage, droughty, pH too high or too low (= lime chlorosis or Al-toxicity and Mn-toxicity), and deficient in essential nutrients; low temperatures; and high temperatures.

(2) Hazards of the biotic environment

Fungi, bacteria, nematodes, arthropods, viruses and viroids, mycoplasmas and spiroplasmas, and rodents.

(3) Horticultural problems—orchard

Tree size control, poor anchorage, excessive suckering, burrknots, lack of precocity, low production efficiency, smaller fruit size, diminished fruit quality, and delayed incompatibility.

(4) Horticultural problems—nursery

Difficult propagability, spines in stoolbed and liner row, budbreak too early, fall maturity too late, limited period for budding, and poor compatibility.

RESISTANCE BREEDING

It is technically possible to breed rootstocks resistant to a very broad spectrum of diseases and other pests. In apple, for example, we could very well be including resistance to black spot, powdery mildew, apple blotch, *Xylaria mali*, *Clitocybe*, *Armillaria*, and *Corticum*, along with fire blight and *Phytophthora*, in our list of objectives. To accomplish such multiple resistances, though, would take many generations; the odds to achieve a single seedling with these resistances would be c. 250 000 to 1.

Every one of our fruit crops has only limited tolerance to *Phytophthora*. We find extreme sensitivity in almost all peaches and apricots; Mazzard cherries (*Prunus avium*) have some tolerance, but not Mahaleb (*P. mahaleb*). Some *P. domestica* are reasonably tolerant and many Myrobolans and Mariannas can survive quite severe infection pressure. There is wide variation in sensitivity in apples and pears, from the very sensitive MM.104 apple to tolerant 'Winter Nelis' pear seedlings.

Because *Phytophthora* attack so often results in a dead tree, tolerance for all the endemic *Phytophthora* species is usually an appropriate essential objective in breeding rootstocks for all our crops. Species, races, isolates, and biotypes certainly complicate the matter; we know, for example, that at least four of the *Phytophthora* species that attack apple are economically serious.

Some diseases may affect rootstocks only in the nursery, e.g., the mildews. Such diseases have only minute economic impact, given the long life of a fruit tree; they are relatively simply controlled with chemicals; and they seldom result in death of a tree. We feel they should not be included as significant objectives.

Cotton root rot, *Phymatotrichum omnivorum*, is endemic to two great subtemperate belts around the globe. Where this pathogen is present, it is virtually impossible to grow any fruit crop. So far as we have been able to discover, only a few *Vitis* species are tolerant. Here is a disease that merits close attention by breeders working on a regional focus. Similarly, *Rosellinia necatrix* severely limits fruit growing in many subtropical and subtemperate regions. If we were trying to develop rootstocks for apples to survive in central Texas or the Nile Delta, these two diseases would be at the top of our list—and *Phytophthora* and fire blight would be in the minor leagues.

Our most important job in resistance breeding is to identify and prioritise the problems.

ESTABLISHING OBJECTIVES

General breeding goals

Certain general problems are common to almost all commodities in almost all locations. The most obvious include:

Tree longevity

The tree must survive under prevailing conditions with minimum of chemical and cultural manipulation (except irrigation, if normally practiced).

Propagability

Whether by seed or by vegetative means, the candidate rootstock must meet the propagation requirements of the commercial nurseryman. However, it may be that some relatively simple modifications of propagation methods could make an otherwise unacceptable rootstock suitable. Passage of Ottawa 3 apple rootstock through micropropagation greatly enhanced the stoolbed propagability.

Graft compatibility

Graft compatibility with at least most commercial cultivars is essential. Especially when working with *Prunus* rootstocks, broad testing must be carried out and compatibilities determined.

Productivity

Productivity evaluation must include flower production, fruit set, fruit size, and year-to-year consistency of production.

Prioritised objectives in apple rootstock breeding

Objectives in the Geneva apple rootstock breeding program are based on needs for horticultural performance and for adaptation to the environment. Since not every desirable goal can be achieved, we prioritised our objectives as "essential", "important", or "helpful", and set standards for each (Table 1).

Cherry rootstock breeding objectives

An array of objectives for a cherry rootstock breeding program in a mid-temperate region such as Central Otago, New Zealand or New York and Michigan, United States would have many similarities (Table 2).

Setting objectives for other tree fruits

Sets of objectives that are similar in principle can be designed for any commodity and for any region. An apple rootstock breeding program in New Zealand would certainly be moving WAA-resistance to the highest priority and would likely lower the priority on winter hardiness and early leaf fall; in southern Brazil resistance to *Rosellinia* would be on the essential list. A grapevine rootstock breeding project in California would no doubt establish a high priority for chloride-exclusion and fan-leaf hypersensitivity. Citrus rootstock breeders will want resistances to the resident *Phytophthora* and to a considerable spectrum of nematodes, tolerance to tristeza, plus good compatibility and easy propagation.

PRESCREENING

Negative selection should be accomplished as early in the total evaluation sequence as can possibly be programmed. This "prescreening" is normally applied to very young seedlings in the greenhouse; in our apple and pear rootstock programs, we begin when seedlings are c. 20 mm tall. The breeding team should plan to take to the nursery a set of preselections from which have been eliminated a large percentage of plants that ultimately would have been judged as unsuitable. Early elimination for susceptibility/sensitivity to pathogens and pests is the type of prescreening that has been most successfully used.

Table 1 Prioritised objectives for apple (*Malus* × *domestica*) rootstock breeding.

Objectives	Standard
Essential objectives	
Dwarfing: range of vigour	M.27 to MM.111
Production: early, heavy as	MM.106
Crown rot: resistant as	M.9
Fire blight: resistant as	M.7
Burrknots: relatively free, as	M.2
Winter hardy: tolerant as	MM.111
Fall hardening: relatively early as	M.7
Propagability: relatively easy as	M.9
Liners: clean-shanked; thrifty as	MM.111
Important objectives (but not essential)	
Anchorage: related to vigour-modest for dwarfing, rigorous for full-sized trees	
Spring budbreak: relatively late, as	M.27
Suckers: relatively few, as	MM.106
Woolly aphids: resistant as	MM.106
Tomato ring spot virus: resistant as	M.7
Latent viruses: tolerant as	M.9
Voles: resistant as	Novole
Helpful objectives	
Identifiability: red or otherwise distinctive foliage	Bud.9; Ottawa 3
Powdery mildew: resistant as	M.9
Fruit maturation: early as	M.9
Drought: tolerant as	M.7
Alkali soils: tolerant as	MM.106
Acid soils: tolerant as	Maruba-kaido
Apple scab: resistant as	Novole

Caution must be exercised, however, that prescreening be based on the determined objectives of the program; a particular screen should not be used merely because it is technically attractive. It would be possible to use a *Phytophthora cactorum* screen to eliminate 75% of seedlings in a pear **variety** breeding program—but this would not be in keeping with a likely set of objectives for such a program. Similarly, an early screen for *Venturia inaequalis* would be easy to apply in an apple rootstock breeding program—but it would not be appropriate for an objective of tertiary priority.

To meet the above set of objectives of our apple rootstock breeding program, we find it reasonable to run very early sequential screens for survival after inoculation with *Phytophthora* and *Erwinia amylovora*. For a stonefruit rootstock project, probably only a *Phytophthora* screen would be useful. In breeding citrus rootstocks, prescreening for resistance to *Phytophthora* and perhaps to some nematodes would seem to be appropriate.

For many of the pathogens with which a rootstock breeding team should be interested, no useful prescreening protocols have yet been developed. In the cotton belt, for example, it would be highly useful to be able to prescreen for *Phymatotrichum omnivorum* tolerance in any of the fruit crops. In California and southern Brazil, we would like to be able to screen young apple seedlings for resistance to *Rosellinia necatrix*. We urgently need *Verticillium*-resistant *Prunus* rootstocks, but we have no technique now on hand.

Often the first step that must be taken in prescreening is to develop an effective technique. It is essential that the breeding team demonstrate that application of a presecreening technique will ultimately result in a selected population that is significantly superior for the attribute tested. For all our crops, for example, we must assure ourselves that if we screen young seedlings for *Phytophthora* tolerance, then years later the population of trees being tested in the orchard have enhanced tolerance to these pathogens.

Usually inoculum concentration and incubation conditions can be adjusted to yield 25–35% survival in most prescreening protocols. In screening apple and pear rootstock seedling populations with *Phytophthora*, for example, we have been able to adjust flooding conditions and soil temperatures to dependably kill 70–80% of the seedlings. Controlling ambient temperature in the 20–25°C range has given dependable results with fire blight screening. Eliminating predators with appropriate pesticides and following appropriate temperature regimes have been very helpful in maximising infestation with WAA.

Table 2 Prioritised objectives for cherry (*Prunus* spp.) rootstock breeding.

Objectives	Standard
Essential objectives	
Phytophthora tolerance: at least as tolerant as	F12/1
Anchorage: as good as	F12/1
Early bearing: inducing fruiting as early as	Gisela 148/1
Productivity: inducing efficiency as good as	Gisela 148/1
Crown gall: tolerant as	Hartz Mountain Mazzard
Buddable: liner diameter as great as	Gisela 148/1
Graft-compatible: with all sweet cherries	
Soil pH: tolerant in 5.5–7.0 range	
Important objectives	
Low temperature: tolerant as	F12/1
Suckering: no heavier than	F12/1
Propagable: no more difficult than	F12/1
Micropropagation: no significant epigenetic effects	
Tomato ring spot virus: hypersensitive	
Prune dwarf virus, prunus necrotic ring spot virus, and X-Disease: tolerant	
Spines: free	
Helpful objectives	
Resistant to cherry leafspot in nursery	
Resistant to powdery mildew in nursery	

NURSERY EVALUATIONS

Centrepiece for the nurseryman is propagability. Most apple rootstocks are propagated by some form of layering, and this seems a reasonable method to use in evaluation. Most clonal rootstocks of pear, peach, and plum are propagated by hardwood cuttings, and application of good cuttage techniques would seem appropriate. Making judgement based on micropropagation capability or with plant material derived from micropropagation is not generally advisable.

Thorns or spines are often conspicuous in nursery liners of apples and pears, as well as some *Prunus* and *Citrus*. Spines may be associated with juvenility, but the juvenility effects are usually minimised by the third year. Depending on the priority assigned to the "spine-free" objective, thorny individuals can be eliminated after the third year in the nursery. In contrast, individuals that are spine-free in the first nursery year are almost invariably spine-free permanently.

On apples and a very few *Prunus*, burrknot initials are discernible by the second or third year. In some families, e.g., Alnarp 2 × MM.111, 100% of the seedlings will show significant burrknot infestation by the third year. In our view, these individuals should be eliminated because in the orchard tree, burrknots may lead to girdling of the tree and are attractive to a number of borer species.

In general, we would like to have our rootstock to become dormant relatively early in the autumn and to remain dormant relatively late in the spring. Early autumn maturation permits earlier harvest in the stoolbed and nursery and may later reduce low temperature sensitivity of the fruiting tree in the orchard.

Up to this point, our central focus has been on eliminating the unfit on the basis of the likelihood of having problems later in the life of the tree. Now we also include some positive selection, for example with apple rootstocks, selecting for straight, clean shanks, easy rooting and freedom from burrknot initials.

ORCHARD EVALUATION

This is the most expensive phase of a rootstock breeding program, so it is critical that the populations of candidates to be tested in the orchard have been rigorously screened beforehand. We are now following a protocol similar in principle to that of the classical tree fruit breeder: first, test with just a few individuals; second, test in replicated trials; and third, test in semi-commercial scale-up. At first test level, we will be consciously combining negative screening with positive selection. In the orchard, we will be evaluating our rootstock candidates for: (1) tree size control; (2) induction of early fruiting; (3) induction of efficient production; (4) fruit quality and fruit size; (5) anchorage; (6) suckering; (7) tolerance of physical environments, including high and low temperatures, and high and low moisture; (8) delayed incompatibility; and (9) responses to orchard infections of viruses.

We are now using only three trees grafted onto each rootstock in our first tests, set as replicated single tree plots with M.9, M.26, M.7, and MM.106 as controls. This gives us good opportunity for estimating within 5 years the dwarfing potential, tendency to produce suckers and develop burrknots, and potential for inducing early fruiting. For first testing, we use a variety that is vigorous and late to come into production. We have used 'Northern Spy' and 'Mutsu' very successfully. Now, because of reduced cost for spraying, we are using 'Liberty'. We select c. 20% of the candidates in the first test orchard.

Liners of selected candidates are budded to a number of varieties for second testing. These are distributed to cooperating scientists across North America, usually set in single-tree plots with 8 replicates per location. Second test gives us hard data on all the attributes listed above and much information on regional and edaphic adaptability of the candidate rootstocks. Third test orchards should focus on just a few elite candidates, grown in replicated plots of 5–10 trees each in a formal system suitable for each size class. The data from these trials greatly facilitates introduction decisions.

UNCONVENTIONAL METHODS FOR ROOTSTOCK IMPROVEMENT

At Geneva, the Aldwinckle-Norelli biotechnology group has now succeeded in transforming M.26 with genes from the cecroptin moth (H. S. Aldwinckle & J. Norelli pers. comm.). Normal M.26 plants are highly susceptible to fire blight; the transgenic M.26 plants are moderately resistant. Further work now in progress is aimed at producing blight-resistant M.9 and 'Royal Gala'.

Almost every rootstock now available to the nurseryman could be improved greatly with the change of a single characteristic. Longer fusiform initials in M.9 and Budagovski 9 would reduce brittleness. Resistance to *Phytophthora* would radically improve the utility of MM.106, Mahaleb and Manchurian apricot stocks. Absence of burrknots would make M.26 and P.1 much more usable. Such changes may well be possible in future through DNA manipulation similar in principle to the M.26 protease insertions already accomplished.

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