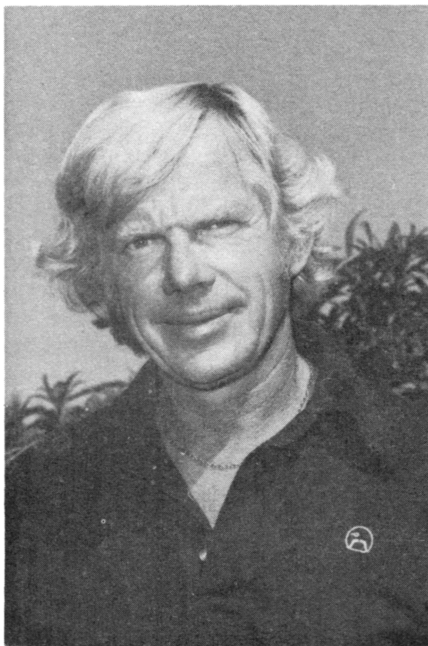


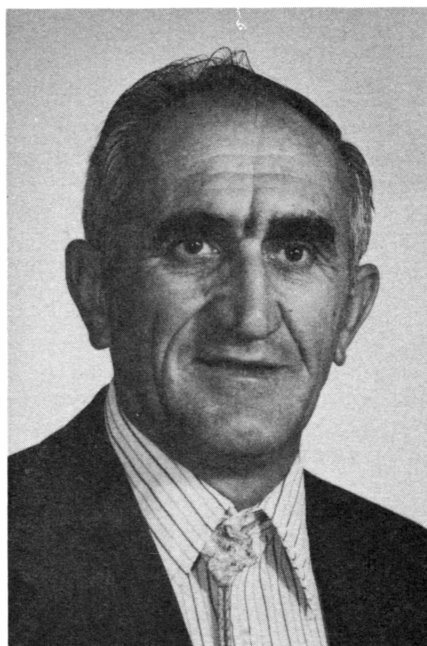
Genetic Remodeling of Fruit and Nut Trees to Facilitate Cultivar Improvement¹

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Numerous studies show there is great genetic variability in tree fruit and nut species (24). Where quantitative genetic analyses have been made they generally reveal that most of this genetic variability is additive (18, 19, 20, 21, 22). Consequently, the simplest, least expensive breeding method (mass selection) should be as effective as any for improving tree fruit and nut cultivars. Furthermore, most tree fruit and nut species are perennial¹ and can be readily cloned (most commonly by bud grafting). These properties provide geneticists powerful engineering tools that are unavailable in most agronomic and

vegetable species. Taken together, these facts suggest that the genetic techniques so successful in improving agronomic and vegetable cultivars should be even more effective when applied to tree fruit and nut crops. However, this is not the case because large plant size and long periods of juvenility severely impede the process of cultivar improvement in tree fruit and nut species.

How large plant size impedes cultivar improvement

It is well known that the high cost of rearing trees renders it impracticable for geneticists to screen seedling populations (for genotypes with favorable combinations of fruit or nut traits) comparable in size to those in agronomic or vegetable breeding stocks screened for analogous traits. For example, table beets are normally planted at a density of about 250,000/ha at a current cost of about

\$2,500/ha (V. Rubatsky, personal communication). The same number of peach seedlings, even when planted at 10 times their normal density, would occupy about 100 ha and cost about \$250,000/year to maintain. Thus one could expect the cost of maintaining peach breeding stocks to be at least 100 times that of maintaining table beet breeding stocks of the same size. Due to such huge cost differentials, agronomic and vegetable breeding stocks typically contain 100 to 1,000 times as many seedlings as are found in tree fruit and nut breeding stocks. All other things being equal, this difference in number of seedlings screened means that the likelihood of any given genetic recombinant arising in tree fruit or nut breeding stocks is 100 to 1,000 times less than the likelihood of an analogous recombinant arising in agronomic or vegetable breeding stocks. In other words, the capability of breeders of

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tree fruit and nut crops to aggregate favorable alleles, affecting fruit or nut quality, into common genotypes (via genetic recombination) is *at best 100 times less* than that of breeders of agronomic or vegetable crops with analogous objectives. This would not be a problem if the particular combinations of recombinational events we sought arose reasonably frequently. Unfortunately they arise *very rarely*.

For example, in an apple breeding stock studied by Williams (48), the frequency of progeny that could be expected to have acceptable mildew resistance was 40%, the frequency of progeny with acceptable fruit size was 20%, season of maturity 20%, flavor 10% and color of skin 10%. Assuming that these characters are inherited independently, the probability of one seedling arising in a population of 1,000 seedlings, that possessed a combination of the five traits at an acceptable level of expression, is only 0.15. The number of apple seedlings one must rear and screen to raise this expectation to 0.50 is 4,300. Of course, were we after a combination of the five traits with *superior* rather than merely *acceptable* performance our likelihood of success would drop much lower.

What makes matters worse is the fact that our objectives are generally far more, rather than less, ambitious than that cited in this example. After all, we neglected the first requirement of an apple cultivar: acceptable yield. We also neglected other important traits, e.g., cold hardiness, fruit shape, firmness, juiciness, storage ability. We leave to your own imagination the sample size required to provide a 50% expectation of having a seedling arise in which all of these characteristics are combined at acceptable levels.

The importance of screening large numbers of seedlings has been understood by various fruit breeders. For example, ultra-high density plantings have been used in the peach breeding program at the University of Florida in an effort to mitigate some of the adverse effects of large plant size (40).

Another adverse consequence of large plant size on cultivar improvement is that it effectively precludes increasing their productive potential (i.e., number of fruits of desired size produced/unit area). Because of the large size of these plants, rearing the number of replicate propagules required to obtain reasonably precise estimates of yield potential is simply too expensive. But without reasonably precise estimates of yield potential, genetic differences among seedlings cannot be distinguished. Where genetic differences among seedlings cannot be distinguished, selection is bound to be ineffective—regardless of the nature of the trait's inheritance. Consequently, the genetic potential for

productivity in these crops has been largely untapped, and remains largely untapped.

The effects of juvenility on cultivar improvement

One of the two relevant effects of juvenility on the process of developing better cultivars is to extend the minimum length of selection cycles. The consequence is a very low rate of cultivar improvement. This stems from the fact that rate of response to selection is inversely proportional to the length of selection cycles; i.e., the longer the juvenile period the lower the rate of response to selection. The minimum length of selection cycles in tree fruit and nut breeding stocks, due to juvenility, ranges between 2 to 10 times that achievable in agronomic or vegetable breeding stocks. All other things being equal (and ignoring the effects of large plant size), this means that juvenility, by itself, reduces the theoretical rate of cultivar improvement in these species to between 1/2 and 1/10th that which can be expected in agronomic or vegetable breeding stocks.

The other adverse consequence of juvenility is that it increases the cost per unit genetic improvement in almost direct proportion to the length of the juvenile period. This is because the cost of rearing and evaluating tree seedlings, for fruit or nut quality or productivity, is almost directly proportional to the length of time required to rear them to sexual maturity. Juvenile periods of 6 to 8 years in these large plants are imposing exorbitant costs on genetic improvement.

The combined effects of large plant size and juvenility on cultivar improvement

The joint effects of large plant size and juvenility on cost and rate of cultivar improvement can be illustrated by examining the table beet-peach example through 1 selection cycle. Since beets are biennial the minimum length of selection cycles is ordinarily 2 years. However, selection on beet root traits can be practiced at the end of the 1st year thereby reducing the number of plants to be intercrossed in the 2nd year, to perhaps 0.1% of the original number, or to 250 plants in our example. Thus, the cost of rearing a table beet breeding stock, initially comprising 250,000 seedlings, might be about \$2,500 for the 1st year but could drop to \$500 or less the 2nd year. This would amount to about \$3,000 per selection cycle. The cost per unit response to selection would be \$3,000/R, where R is the amount of response per selection cycle.

As pointed out above, under the same

set of assumptions employed for the table beets, the cost of rearing 250,000 peach seedlings probably would be about \$250,000/year. The minimum length of selection cycles in peach breeding stocks is ordinarily 4 years, due to the 1 to 2 year juvenile period in this species. Selection on fruit characteristics analogous to beet root characteristics ordinarily could be practiced in the 3rd year, reducing the number of selected plants to be intercrossed the 4th year to 0.1% of the original number, or to 250 plants in this example. Thus the cost of maintaining such a breeding stock for 1 selection cycle would be roughly \$250,000 per year for the first 3 years; and it might be as low as \$2,000 the 4th year. (The 4th year cost could well be 10 times greater, or more, due to the fact that the 250 selected seedlings would be randomly distributed over 100 ha and could not be consolidated onto a single hectare without extending the length of the selection cycle by 2 years. Such a ploy would reduce the rate of response to selection from 1/2 to 1/3 that achievable in the table beet breeding stock.) This amounts to about \$752,000 per selection cycle. The cost per unit response to selection would thus be \$752,000/R.

Comparing the costs of the 2 programs, we find that plant size and juvenility, together, impose a cost burden on the peach program that is about *250 times greater* than that pertaining in the table beet program. Comparing the rates of response in the 2 programs, we find that juvenility, by extending the minimum length of selection cycles in peach to 4 years, limits rate of response to selection in peach breeding stocks to *only half* that possible in table beet breeding stocks.

Were the resources available in the peach program no larger than those available in the table beet program (which is close to reality), i.e., \$3,000 per selection cycle in our example, the number of seedlings screened for superior recombinant genotypes would have to be reduced from 250,000 to about 800. All other things being equal, this would mean that were the probability of a given (superior) recombinant genotype arising in the table beet breeding stock equal to 0.50, the probability of an analogous recombinant arising in the peach breeding stock would be about 0.002 or *250 times lower*. Clearly, under such constraints, cultivar improvement objectives readily achievable in agronomic and vegetable species are far out of reach of those attempting to improve tree fruit and nut cultivars.

Indeed these comparisons are based on crude approximations of costs and thus may considerably underestimate actual costs. However, even if one assumes the cost differentials in this

example are 10 fold greater than actually pertain (which we believe is unlikely), still, the basic conclusion drawn would be the same: *Plant size and juvenility profoundly influence both the rate at which geneticists can exploit the genetic potential that exists in these species and the cost of the process. The rate of cultivar improvement that they dictate is very low and the cost is very high.*

Prospects for reducing tree stature and eliminating the juvenile phase

Genetic dwarfs. Gregor Mendel (32) in 1866 first reported single gene control of plant dwarfism (the garden pea, *Pisum sativum*). By 1964, genetic dwarfs had been reported in at least 17 families of angiosperms (35). In those taxa that have been subject to significant genetic study, dwarfism is among the more frequent mutations observed, e.g. at least 11 different dwarf mutants besides the one reported by Mendel, *le*, are now known in the garden pea. Other examples of genetically dwarfed plants employed in food production are wheat (10), rice (10), barley (1), sorghum (38), tomato (42), cucumber (36), squash (13), and watermelon (33). Today one could probably document the existence of such genes in all crop plants.

Dwarfed wheat and rice provide models of the genetically-dwarfed plants that have recently become important in agriculture. (In the agronomic literature they are termed "semi-dwarf" to distinguish them from short-statured genotypes with dwarf reproductive as well as vegetative organs. The reproductive organs of "semi-dwarfs" are not reduced in size.) In the commercially important "semi-dwarf" cultivars of wheat and rice (and in a number of other species of agricultural importance) dwarfism results from shortened shoot internodes, due primarily to fewer cells per internode. The physiological basis for this phenomenon in wheat and rice, among others such as peach (49), appears to be interference with functioning of gibberellin. Dalrymple (10) points out some of the relevant effects of these genetic dwarfs: their shoot stature does not adversely affect vitality. They are better suited than their standard counterparts to mechanized production. They incorporate a greater portion of available nutrients into reproductive organs (seeds or fruits) than do their standard counterparts and thus increase the "harvest index" (economic yield/biological yield). They are often significantly more productive (per unit area) than their standard counterparts under conditions of high nutrient input and high density.

Strong (43) reported in 1867 that the 'Van Buren Golden Dwarf' peach

(discovered by Mr. J. Van Buren of Clarksville, Georgia, in 1857) had

"... wood so short-jointed; and so thickly set with fruit-buds not being more than a quarter of an inch apart. I should judge that the tree would rarely exceed four feet in height; and it will bear full crops at half that height..."

This dwarf habit is no stunted growth: on the contrary, the growth and foliage are most luxuriant, the leaves being of the richest green... Considering its productiveness, and the small space required, we may say that, in habit of growth, it is the ne plus ultra for forcing.

Now as to the quality of the fruit, ... As one of the fruits of the late war, we have been deprived of this fruit use to this date. Mr. Van Buren had just prepared to send out his stock of trees when the war broke out..."

Mr. Josiah Hooper reported in the same 1867 issue of the *American Journal of Horticulture*, an 'Italian Dwarf' peach

"loaded... with snow white fruit... that is much dwarfer in habit (3 feet in stature at maturity) than the Van Buren dwarf..." (23)

There are numerous more recent reports that, in the aggregate, indicate that genes which induce dwarf shoot stature are widespread in tree fruit and nut species (see 2, 11, 27, 41). Furthermore, dwarfism appears to be one of the most common aberrant phenotypes induced by mutagenic agents applied to these species (4, 5, 6, 12, 29, 30) suggesting that mutant forms of any of a number of different genes induce dwarfism. Thus, direct screens for mutant genes that induce dwarfism should be quite successful. The objective, of course, would be to screen for those that dwarf shoot stature without adversely affecting the productivity of the plant, or the quality of its fruits or nuts.

Juvenility. T. Visser's inspired analyses have provided objective quantitative evidence that considerable genetic variation for the length of the juvenile period exists in the apple and pear breeding stocks he studied (45, 46, 47). Subjective observations by others suggest that such genetic variation is common in fruit and nut breeding stocks (3, 8, 14, 31, 39, 41, 50). Visser has also shown that, in the populations he studied, the genes influencing this trait are primarily additive (47). Thus simple mass selection should be effective in genetically reducing the length of juvenile periods. In fact, using Visser's data (47), (and the standard formula relating heritability, selection intensity, and response to selection,) we have calculated an expected reduction in the juvenile period of between 10 and 14 months in one selection cycle, were parents chosen

among the 10% of breeding stock that have the shortest juvenile period. Thus, in a single selection cycle we could expect an increase in the rate of response to selection (for all other traits) of nearly 20%, along with a similar reduction in costs. It seems likely that rate of response to selection would drop off after the first selection cycle, but quantitative genetic theory and the results of hundreds of selection experiments suggest further responses can be expected.

A feasibility study

From the above it is evident that both plant size and length of juvenility in these species can be manipulated genetically. However, we need to know if large plant size and long periods of juvenility are prerequisites for high productive efficiency and high fruit and nut quality in these species. If not, the sooner we engineer smaller plants, and reduce the length of their juvenile period, the sooner we shall be able to exploit their genetic potential at a reasonable rate and cost.

There is some evidence that large plant size is not a prerequisite for high productivity per unit area in these species. For example, high density plantings of fruit crops that have been significantly reduced in stature (*via* scion rootstock interactions or pruning), are widely known to produce higher per unit area yields than when planted at normal densities and allowed to reach their normal stature (15, 16, 25, 34, 37, 44). However, we know of no objective quantitative evidence bearing on yield potential or on fruit or nut quality of trees carrying mutant alleles that dramatically reduce shoot stature, such as, for example, the 'Van Buren Dwarf' or 'Italian dwarf' peach.

Along with C.O. Hesse (University of California, Davis), we initiated 2 experiments in 1975 to establish whether "genetic dwarfs" (trees carrying mutant alleles that dramatically reduce shoot stature) are capable of high productive efficiency (yield per unit area) and high fruit quality. We used the recessive *dw* gene, that induces brachytic dwarfism in peach, as a model system (28). The shoots of plants homozygous for the *dw* allele have drastically shortened internodes. Consequently, at maturity they reach only about 1.8 m in stature. This is about 60 cm taller than the brachytic dwarf discovered by Van Buren in 1857, and about 90 cm taller than the brachytic 'Italian Dwarf' reported by Hooper in 1867. The *dw* gene appears to be analogous with those mentioned above in "semi-dwarf" wheat and rice in that it is recessive, it interferes with gibberellin function (49), and it reduces internode length without affecting the size of reproductive organs.

One experiment was designed to establish whether or not plants of this dwarf genotype could produce unit area yields equivalent to plants of normal stature. The other experiment was designed to establish whether or not this dwarfing gene had serious adverse effects on fruit quality. (Presently available peach cultivars dwarfed by this gene produce inferior fruit; the 3 most important tangible defects of which are reduced skin color, soft flesh, and low soluble solids.) This experiment was designed to establish whether these defects in fruit quality are consequences of the *dw* allele or whether they are consequences of alleles of other genes carried by the plant in which the *dw* mutation arose. The specific objective of the second experiment was to establish whether or not fruit skin color (tone and amount), fruit firmness, and percent soluble solids (a trait highly correlated with fruit flavor) of *dw/dw* genotypes could be improved to meet commercial standards.

Yield. In April 1976, we established a yield trial at the Kearney Field Station (near Fresno) of the University of California, (Fig. 1). We used the dwarf peach strain 54P455 (kindly supplied by Mr. Fred Anderson of Merced, California) budded onto Nemaguard rootstocks about 45 cm above the ground. The 54P455 genotype is derived from the 'Flory Dwarf' and 'Swatow Dwarf' peaches that were independently introduced to the U.S. from China as seeds (7). These dwarf trees were planted in hexagonal configurations at

densities of 1,250, 2,500, 3,750, 5,000, and 7,500 per ha. A randomized complete block design was used. About 30 trees per density treatment were planted in each of 3 blocks. Guard rows were planted around all treatments.

The average diameter of fruit from this yield trial was between 7 and 7.5 cm, showing that the gene that dwarfs tree stature does not adversely affect fruit size. More than 90% of the fruit produced exceeded a diameter of 6 cm, presently the minimum for commercial acceptability.

Yield estimates from the 1,250, 2,500, and 3,750 tree/ha plots of these dwarf trees, obtained in 1977, 1978, and 1979, are depicted in Fig. 1 along with average yields of standard clingstone peach orchards of the same age. The optimum planting density for these dwarf trees has not yet been determined. However, these results clearly demonstrate that dwarf peach trees, of the *dw/dw* genotype, can produce high yields (yields that appear to surpass that of mature, 7-year-old, standard peach trees) at least 2 years sooner than standard genotypes, as they are normally grown in California. Standard genotypes potentially could produce high yields when less than 4 years old, but as most commonly grown they do not because of the considerable (and costly) pruning they require to establish the shape necessary for acceptable productivity at maturity. In contrast, peach trees dwarfed by the *dw* gene require little, if any, pruning during this time.

The maximum yields thus far ob-

served for these dwarf trees were 73 MT/ha for 4-year-old dwarf trees planted at 2,000/ha (Fig. 2). This is more than *triple* that of standard clingstone peaches of the same age that are planted at 3750/ha, and 68 MT/ha for 4-year-old trees planted at the usual 270 trees per ha. It is *double* the 34 MT/ha average of mature (7-year-old) standard clingstones grown in California (9). Clearly the dwarfing gene does not adversely affect maximum potential productivity, unless it induces a premature termination of the productive life of the plant, which appears highly unlikely. On the contrary, these results suggest that this dwarfing gene may well facilitate a doubling of productivity.

Production economics. In California between 5 and 7 years are normally required for standard peach orchards to pay off the costs of establishment. James Beutel (Cooperative Extension Specialist, University of California) estimated the economics of establishing genetically dwarfed peach orchards of 3,750 trees/ha over a 7-year period, in order to compare required investments and returns with those associated with standard peach cultivars (17). The comparison is based on the assumption that productivity of dwarf cultivars would not increase beyond that observed during the 4th year of this experiment; namely, that it would not exceed 68 MT/ha. Furthermore, it is based on the assumption that genetically dwarfed cultivars with fruit of commercially acceptable quality can be developed.

Estimates of the accumulated net income obtainable from standard trees (270 trees/ha) and from genetically-



Fig. 1. Plants and fruit of dwarf peaches, 4th year.

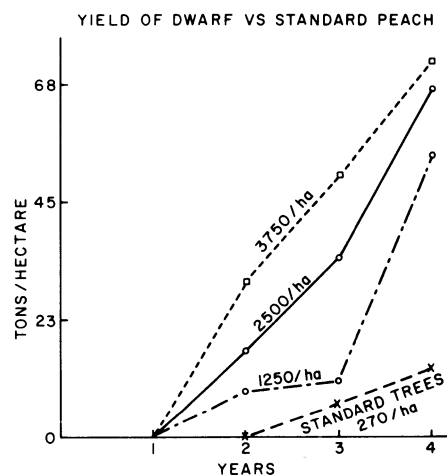


Fig. 2. Yield estimates of dwarf peach strain 54P455 (budded onto Nemaguard rootstocks) during the first 4 years of orchard establishment. The SE of these estimates are less than 6%. The yield estimates for standard trees planted at 270 trees/ha were obtained from the California Crop and Livestock Reporting Service (9) and are statewide averages of clingstone peach orchards under commercial production.

dwarfed trees (3,750 trees/ha) are plotted in Fig. 3 for the 7 years generally required to recapture accumulated costs of establishing standard peach orchards. From this analysis it appears that genetically-dwarfed peach trees have the potential of offering producers major economic advantages over standard peach trees, even if their productivity at maturity is no greater than that observed in the 4th year of this yield trial. Although the initial investment would be greater for establishing a dwarf peach orchard, the investment would appear to be recoverable 2 to 3 years sooner than that required to establish a standard peach orchard. Once the investment required to establish the orchard was recovered, and assuming the 68 MT/ha yield we observed during the 4th year of this trial would be maintained, the expected annual net income from a dwarf peach orchard would appear to be about triple that of an established standard peach orchard.

Fruit quality. Estimates of the effect of genes from *dw/dw* parents on the phenotypic variance of fruit size, color, firmness and percent soluble solids were obtained from a population of "F₁" seedlings derived by crossing 4 selected *dw/dw* genotypes with selected *Dw/Dw* genotypes from the standard peach breeding stock of the University of California, Davis. Two offspring, randomly sampled from each of 61 "F₁" families (i.e., 122 offspring), were included in this analysis.

Fruit size was estimated by the average diameter (in cm through the cheeks) of 10 randomly sampled fruits per tree. Fruit color tone and amount were subjectively estimated on a scale of 1 (low) to 5 (high) from the 10 fruits sampled to determine fruit size. Fruit firmness was subjectively estimated, on a 1 to 5 scale, by squeezing one randomly sampled fruit per genotype between the thumb and forefinger. Percent soluble solids was measured with a refractometer from one randomly sampled fruit per genotype.

Estimates of the effects of genes, introduced into the University of California breeding stock by the *dw/dw* parents, on the heritabilities of fruit size, color (tone and amount), firmness and percent soluble solids were obtained by regressing measurements of the randomly sampled "F₁" offspring on measurements of their mid-parents. Details of the analytical procedure are reported elsewhere (20).

The introduction of this dwarfing gene into the peach breeding stock fortuitously tripled the phenotypic variance, among seedlings, for amount of skin color tone, and doubled the phenotypic variance of fruit size, percent soluble solids, and fruit firmness (Table 1). This additional variation is apparently due to the segregation,

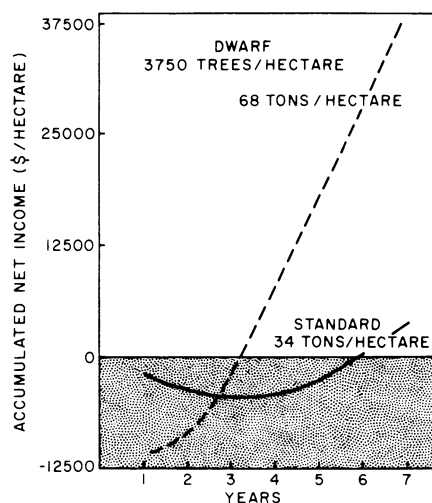


Fig. 3. Economics of establishing orchards of standard and dwarf peach trees. See (17) for details.

among "F₁" seedlings, of other genes carried by the dwarf parents.

The effects of the newly introduced genes on fruit firmness, fruit color tone, fruit size and percent soluble solids must be almost entirely additive, since heritability estimates of these traits increased in direct proportion to the increase in phenotypic variance among seedlings (Table 1).

The estimated heritabilities for fruit skin color (tone and amount), firmness, size and percent soluble solids are high enough to suggest that these traits can be improved to meet commercial standards within 1 or 2 selection cycles. For example, estimates taken from 23 families segregating for dwarfs indicate that fruit produced by dwarf trees is, on the average, 2% lower in soluble solids than that of their standard siblings. However, the estimated heritability of percent soluble solids in this breeding stock (0.19) is sufficiently high to indicate this deficiency can be corrected in 2 selection cycles by choosing parents among the 5% of the breeding stock with highest soluble solids. All the other measures of fruit quality have higher heritability estimates than percent soluble solids and consequently should re-

spond to selection more rapidly.

Summary and conclusions

Quantitative genetic studies of several fruit and nut breeding stocks have revealed that substantial genetic potential for improvement exists in these crops. But, nonetheless, expected (and actual) rates of improvement are very low in comparison with that of typical agronomic or vegetable crops, and costs per unit improvement are very high. In fact, the costs per unit improvement are becoming unsupportable (14).

Plant size and seedling juvenility are the major barriers to exploiting this genetic potential at a reasonable rate and cost.

Numerous reports in the literature demonstrate plant size and length of the juvenile period in these species can be readily altered by well-known, straightforward genetic techniques. *These barriers to cultivar improvement can be removed.* However, the effects of reducing plant size and juvenility on production efficiency or on fruit and nut quality have not been reported.

The results of our yield trial demonstrate that these plants can be genetically dwarfed without adversely affecting productivity on a unit area basis. On the contrary, they suggest dwarfing peach trees can directly facilitate major increases in productivity. The results of Beutel's economic analysis suggest peach trees dwarfed by the *dw* gene could offer producers significant economic advantages over trees of normal stature. These dwarf trees obviously also offer safety advantages, since they eliminate the necessity for any ladder operations. The results of our genetic study indicate large plant stature is not an *a priori* requirement for high fruit quality. They indicate there is more than sufficient genetic potential in this breeding stock to correct, within 1 or 2 selection cycles, the 3 most important tangible quality defects of fruit produced by presently available *dw/dw* genotypes: fruit firmness, skin color and percent soluble solids.

Table 1. Estimates of means, variances, and heritabilities (h^2) in the University of California's peach breeding stock before (standard) and after (F₁) introducing the *dw* allele. The estimates pertaining to color tone, firmness, size, and percent soluble solids were taken from Hansche et al. (20).

Character	Means		Phenotypic variances		h^2	
	Standard	F ₁	Standard	F ₁	Standard	Dwarf
Firmness	2.7	2.9	0.3	0.8	.13 ± .02	.26 ± .14
Color						
Tone	3.0	3.0	0.3	0.8	.03 ± .02	.57 ± .16
Amount ²	—	2.5	—	0.6	—	.41 ± .08
Size (cm) ³	6.8	5.9	0.3	0.6	.26 ± .02	.65 ± .15
Soluble solids (%)	11.1	11.3	2.7	4.7	.01 ± .02	.19 ± .15

²This trait was not measured in the "standard" population.

³Fruit number per plant in the "standard" population was controlled by thinning. No such control was applied to the F₁ population.

Dwarfing the large plants used to produce tree fruits and nuts, and shortening their juvenile period, requires a temporary—but major—shift in the primary focus of selection goals: from developing better cultivars to developing biological systems more amenable for genetic engineering. However, the potential rewards of remodeling these biological systems are great—and the cost of delaying this process is rapidly becoming exorbitant.

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