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Influence of Seedling Rootstock on Heterogeneity and Productivity in Fruit Trees: An Assessment and Discussion

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Abstract

Few studies have partitioned the variability in performance of a given cultivar between the effects of seedling rootstock heterogeneity i.e., the genetic influence of the rootstock, and edaphic factors. The relative contribution of genetic and environmental sources of variation to tree performance varies with orchard soil heterogeneity and the genetic heterogeneity among seedlings within species used as rootstocks. Identification and propagation of superior rootstocks, may greatly increase productivity in selected tree fruit species.

Fruit trees almost invariably represent compound genetic systems with the top or scion cultivar budded or grafted to rootstocks which are genetically uniform if propagated vegetatively or more heterogeneous if seedlings (i.e., sexual progeny) are used. Rootstocks have been shown to significantly influence the vigor of scion growth (5, 6, 9, 15, 19, 20, 22), and yield (5, 6, 10, 15, 20), including alternate bearing in deciduous tree fruit species (11). Rootstock trials have typically been employed to evaluate differences in scion performance attributable to different rootstock clones or clonal vs. seedling rootstocks. Although the variability among trees on seedling rootstocks has long been appreciated (12, 17, 18), there is a paucity of data to assess the variability in scion performance due to variability among seedlings used as rootstocks within the same scion/seedling rootstock combination.

We have selected an experiment performed by Serr and Forde (16) as the basis from which to explore this question. Tree growth and yield data were presented from a mixed planting of 30 individual trees of Persian walnut (*Juglans regia*) 'Eureka' grafted on Paradox hybrid (*J. hindsii* x *regia*) seedlings and 36 trees of 'Eureka' grafted on seedlings of the Northern California black walnut (*J. hindsii*). Serr and Forde (16) reported "wide differences in sizes of individual trees on both stocks" but did not consider the sources of variation. We have utilized their data i.e., tree size [estimated by trunk cross sectional area (TCSA)] and yield to calculate cropping efficiencies (CE), i.e., yield/TCSA. CE was calculated by the method of Westwood (21) to assess the relative partitioning of assimilates between fruit and vegetative growth within canopies of individual walnut trees. We have also analyzed these data statistically to partition the total inter-tree variation between genetic (potentially attributable to the heterogeneity among seedlings used as rootstocks) and nongenetic (soil, etc.) sources of variation in tree performance (3, 4).

There was a >5x variation in yields among 'Eureka'/Paradox seedling trees (Fig. 1, Table 1), and a positive relationship between tree size and yield/tree (Fig. 1). Of greater relevance to productivity, however, is the variation in CE among trees (Table 1). Yield varied >3x among 'Eureka' trees of the same size grafted on different Paradox seedling rootstocks (Fig. 1).

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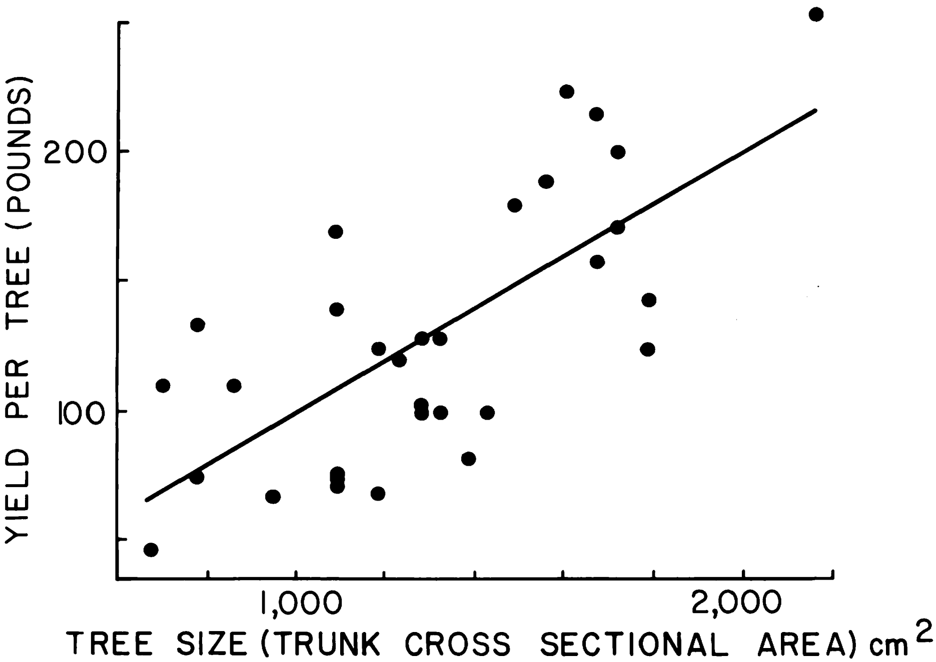

Figure 1. Relationship during one year between tree size (as estimated by TCSA) and yield tree^{-1} among 30, 40-year-old 'Eureka' walnut trees on seedling rootstocks of the Paradox hybrid. $r^2 = 0.5031$, $Y = 0.100x - 2.00659$.

Similar distributions were evident among 'Eureka'/*J. hindsii* trees (data not presented). The conspicuous variability among trees on both *J. hindsii,* and Paradox seedling rootstocks is expressed by the range of yield, TCSA, and CE (Table 1) which varied between 2.7 and 8.5 times. The C.V.'s for yield and C.E. in 'Eureka' trees were similar between Paradox and *J. hindsii* seedling rootstocks (Table 1). If only 50% of the difference between the average and highest C.E. of 'Eureka' trees on seedling rootstocks (Table 1) were attributable to the influence of seedling rootstock variation, we calculate that the productivity of the 'Eureka' orchard could be increased 30% and 50% in trees on Paradox and *J. hindsii* seedling rootstocks, respectively, by identifying and propagating the best rootstocks.

Regression analysis was used to partition environmental and genetic components for the yield data of Serr and Forde (16) and the derived CE's. Because of the limited amount of data and missing data points, (as well as some design limitations), these estimates should be regarded only as approximations. This analysis was somewhat unusual because the treatment effects (row and tree position in the plot) represent environmental components of variation. The 'error' term includes the genetic sources of variation and any sources of environmental variation not represented in the treatment effects. Error mean square equals the error variance. Mean square for treatments includes the variation due to the treatment effects as well as the error variance (7). The results of regression analyses for CE and yield of 'Eureka' on Paradox or *J. hindsii* rootstocks are presented in Table 2.

Examination of the results indicates that treatment effects (position in the

Table 1. Comparison of size (TCSA)† and yield of 30, 40-year-old 'Eureka' walnut trees on Paradox seedling rootstocks and 36, 40-year-old 'Eureka' on *J. hindsii* seedling rootstocks growing in a mixed planting. Calculations of cropping efficiency (CE) and statistics based on data of Serr and Forde (16).

Rootstock	Parameter	Mean	S.D.	C.V.	Range Low	Range High
Paradox	TCSA† (cm^2)	1307	367	28%	674 ——	2166
J. hindsii	TCSA† (cm^2)	1527	728	48%	436 ——	3070
Paradox	Yield (lbs)	127	51	40%	45 ——	254
J. hindsii	Yield (lbs)	113	47	41%	25 ——	213
Paradox	CE†† (lbs/cm^2)	0.098	0.032	32%	0.057 ——	0.154
J. hindsii	CE†† (lbs/cm^2)	0.078	0.026	33%	0.040 ——	0.159

†TCSA = Trunk cross sectional area.
††CE = Yield (lbs)/TCSA.

field) were significant for yield and accounted for a majority of the total variation in yield for both Paradox and *J. hindsii* rootstocks. However, when the environmental and genetic components of CE were assessed, treatment effects were not significant ($P > 0.05$), and 'genetic' variation represented a majority of the total variation. That is, tree size and yield varied over the plot to a considerably greater extent than CE. Apparently there were field effects (such as soil type) that had a significant effect on the overall vigor of the trees, (i.e. tree size and yield) but not on the relative partitioning of resources between vegetative and reproductive organs within the tree canopy. The variance (yield and CE) for Paradox and *J. hindsii* rootstocks were very similar, indicating that the genetic component of variation in this experiment was very similar between the two rootstock groups. Paradox rootstocks were apparently influenced by the local plot environment to a larger extent than the *J. hindsii* rootstocks.

We have selected a walnut orchard on a uniform soil and analyzed the variance of individual tree yields and CE's treated as a randomized block. Up to 70-80% of tree to tree variation in growth and productivity among 100 'Chico' walnut trees on *J. hindsii* seedling rootstocks may be associated with the heterogeneity of seedlings used as rootstocks (Weinbaum, et al. unpublished). This study is being continued to refine these estimates. We anticipate that total variation in growth and productivity among trees and the

Table 2. Mean square (MS), probability of >F, r^2, and % of total variation for cropping efficiency (CE) and yield of 'Eureka' walnut on Paradox of *J. hindsii* seedling rootstocks. Calculations of CE and statistics based on data of Serr and Forde (16).

Treatment	Parameter	Source	MS	P > F	r^2	% variation
Paradox	yield	treatments	15838	0.0008	0.41	89%
		error	1688	—	—	11%
	CE	treatments	2.58×10^{-3}	0.13	0.14	55%
		error	1.16×10^{-3}	—	—	45%
J. hindsii	yield	treatments	6160	0.05	0.16	68%
		error	1926	—	—	32%
	CE	treatments	2.37×10^{-4}	0.71	0.02	0.0%
		error	6.92×10^{-4}	—	—	100%

percentage of variation attributable to seedling rootstock heterogeneity should vary from orchard to orchard.

Tree age has also been shown to influence C.V. for yield (13). Coefficients of variation among 'Cox's Orange Pippin' apple trees on M.I. clonal rootstocks decreased from 40-50% as the trees came into bearing (0-7 years) to 20-30% in 11 year old trees. That is, the older the trees, the more uniform are yields among trees of the same scion/rootstock combination. Pearse's data also indicate higher initial C.V.'s for yield when seedling rootstocks were compared with clonal rootstocks (150% vs. 40-50%). However, the validity of this comparison was limited by the fact that the scions differed (seedlings were grafted to 'Worcester Pearmain').

The degree of heterogeneity within seedling rootstock populations presumably varies among tree fruit species, although definitive data appear to be lacking. Arulsekar and Parfitt (1, 2) have found significant differences in the amount of isozyme variability within cultivated peach (*P. persica*) and almond (*P. dulcis*). Breeding system (i.e., outcrossers vs. inbreeders), the ecological diversity of the species (provenance), and the origin of the parent trees may all influence the level of homogeneity within the seedling populations (19). For example, a significant amount of inbreeding has been reported in peach (14), and as a result much homogeneity due to homozygosity among seedling progeny may be anticipated. In contrast, all *Pistacia* spp. are dioecious and, therefore, obligate outcrossers. Walnut and pecan spp. are dichogamous and, therefore, seedlings used as rootstocks are also likely to arise as a result of outcrossing. The absence of published data reflecting the variability in tree growth and productivity within the same scion/seedling rootstock combination is somewhat surprising as the majority of the principal deciduous tree fruit industries in California (e.g., almond, apricot, cherry, peach, walnut, pecan, pistachio, kiwifruit, and persimmon) are cultured almost exclusively on seedling rootstocks.

The costs to tree fruit breeders of obtaining improved productivity via scion improvement are substantial because of large plant size, prolonged juvenile periods, and significant year-to-year variation in productivity which are superimposed over alternate-year bearing cycles (8). Thus, the potential for developing 'superior' rootstocks to increase the productivity of existing cultivars is appealing. The current interest in and development of the technology for clonal micro-propagation offers increased possibilities for clonally propagating rootstocks which support superior productivity in the grafted tree. In addition, rootstock breeding and selection is not limited by the need to maintain fruit quality as is the case when breeding scion cultivars.

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Book Review

RILANCIO DELLA COLTURA DEL PERO produced by the CENTRO OPERATIVO O RTOFRULTICOLO of Ferrara (Region's Romangna and Societa Orticola Italiana both of Bologna) is a collection of 21 papers reporting recent work on pear culture. The publication was coordinated by Dr. Silviero Sansavini and covers many aspects of pear culture including pruning, training, cultivars, disease problems and much more. It is written in Italian but contains brief summaries of most papers in English and is well illustrated with many colored pictures. This is an excellent reference providing an up to date treaties on many aspects of pear culture.

Book Review

MONOGRAFIA DI CULTIVAR DI PERO by A. Nicotra, D. Cobianchi, W. Faedi, and P. Munzo published by the Ministero dell 'Agricoltura e delle Foreste in 1979. This reference contains beautiful colored pictures of 66 pear cultivars as well as a written description of each. The publication contains 91 pages and is written in Italian.