Journal of American Pomological Society 54(1):18-22 2000

# Rootstock Influences the Construction Costs of 'Starkspur Supreme Delicious' Apple Trees

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## Abstract

The construction costs ($CC_{comp}$) of vegetative and reproductive components, and total tree (total CC) and net ($CC_{net}$) construction costs were calculated using the gross heat of combustion, percentage ash content, and total nitrogen for 'Starkspur Supreme Delicious' apple trees (*Malus domestica* Borkh) grafted onto MAC.24, M.7 EMLA, M.26 EMLA, M.9 EMLA, MAC.9, and M.27 EMLA. The $CC_{comp}$ in Oct./Nov. of 1-yr wood, 2-yr wood, and roots was lower in trees grafted onto more dwarfing rootstocks than in those on more vigorous rootstocks. Leaves had the highest $CC_{comp}$. Frame, 2-yr, 1-yr, shoot, and root had similar $CC_{comp}$. Fruit and spurs had the lowest $CC_{comp}$. As tree size decreased, total CC and $CC_{net}$ decreased.

While partitioning studies measure the dry weights of different growth components and demonstrate the patterns of distribution of dry matter as influenced by rootstock, the construction cost (CC) of tissues varies according to the molecular composition of the tissue (3, 17). These studies have reported the energy costs of specific tissues, but there is no information on the effects of rootstock on the net energy costs of an apple tree. Partitioning differences influenced by rootstocks may result in different total and net CC and, therefore, represent different energy demands for growth. If rootstocks influence growth demands, it may be possible to optimize production through revised management practices designed for the variable growth requirements of tree components that are induced by the different rootstocks.

The objective of this study was to calculate total tree (total CC) and net construction costs ($CC_{net}$) from the gross heat of combustion ($dH_c$), percentage ash content (A), and total nitrogen (N) and determine the effects of six rootstocks on these construction costs in 'Starkspur Supreme Delicious' apple. Rootstocks were selected to represent a range of vigor classes.

## Materials and Methods

Energy budget analysis was performed on components of 'Starkspur Supreme Delicious' trees grafted on MAC.24 (vigorous), M.7 EMLA (semi-dwarf), M.26 EMLA, M.9 EMLA (dwarf), MAC.9 (dwarf), and M.27 EMLA (sub-dwarf) planted in 1980/81 as part of the NC-140 apple rootstock trial (4, 12, 13). Components were sampled destructively twice, once in Mar. 1990 and again with different trees in Oct./Nov. 1990. The components sampled in Mar. were: frame; 2-yr, 1-yr, and spur wood; and root. In Oct./Nov. 1990, in addition to the aforementioned components, current season's growth, spur and shoot leaf, and fruit were also collected. Composite subsamples, amounting to approximately 5% of the total dry weight of each of the components, were made from each tree. Wood, 2-yr, 1-yr, current season's growth, spur, and root components were first put through a chipper. All components were then finely ground and small subsamples appropriate for each analytical technique were removed. All components from two-tree replicates were analyzed for gross heat of combustion (dHc), percentage ash content (A), and total nitrogen (N). The dHc was measured on 1.0 g pelletized samples using a Parr 1241 Adiabatic Bomb Calorimeter (14) and standard operating procedures (14). An ashing oven was used for A determination of a 1.0g sample, while analysis of total N (0.25 g oven-dried sample) was via the

Oregon Agricultural Experiment Station Technical Paper No. 11600.
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micro-Kjudahl method. Construction cost ($CC_{comp}$) of each component was calculated using the equation:

$$CC_{comp} = [(0.06968*dH_c-0.065)(1-A)+N/14.0067*180.15/24)*1/E_g$$

where $E_g$ is the growth efficiency (19). A value of 0.87 was used in this study as an estimate of growth efficiency (15). Total tree construction cost (total CC) (kg glucose) was calculated by multiplying the $CC_{comp}$ (g glucose.$g^{-1}$DW) of each component by the dry weight (DW) for that component, then summing all components for that tree. New growth CC was the summation of fruit, shoot and spur leaf, and current season's growth DW multiplied by their respective $CC_{comp}$'s. The net construction cost ($CC_{net}$) (glucose, g.$g^{-1}$DW) was then calculated for trees on each rootstock by dividing the total CC by the total-tree or new-growth DW.

Data were analyzed using a general linear model procedure of the Statistical Analysis System software (16). Means separations were by the Waller-Duncan k-ratio t-test, k-ratio = 100.

## Results and Discussion

The six rootstocks used in this study did not, in general, influence $CC_{comp}$ (Table 1). There were differences observed for 1-yr wood in Mar., and 2-yr and 1-yr wood and root in Oct./Nov. The differences in $CC_{comp}$ observed between the same wood components on different rootstocks are not easily explained. It is possible that the rootstock influences the types of compounds (i.e., lignins, lipids, etc.), but more likely that the percentage of each class of compounds varies within components. Wood components on smaller trees were proportionately smaller. This woodst may have a higher percentage of bark and vascular tissue and less structural tissue. Therefore, it is probable that the wood from smaller trees had higher carbohydrate levels and contained lower amounts of the much more energy-costly lignins.

More apparent are the differences between components. In Mar., frame, 2-yr and 1-yr wood, and root had the highest $CC_{comp}$, followed by spur wood (Tables 1 and 2). Shoot leaf $CC_{comp}$ was highest, followed by spur leaf $CC_{comp}$ in the Oct./Nov. sample (Table 2). Wood components had similar $CC_{comp}$'s ranging from 1.31 g.$g^{-1}$DW for 2-yr wood to 1.27 g.$g^{-1}$DW for current season's wood, while fruit and spur wood were lowest at 1.19 g.$g^{-1}$DW and 1.20 g.$g^{-1}$DW, respectively. Construction costs of different classes of molecular compounds which make up plant material can help to explain the observed differences. While these classes include a wide range of compounds, the variation in construction cost between classes is much greater than the variation of compounds within a class. The lipid fraction has the highest CC (2.85 g.$g^{-1}$DW), followed by lignins (2.07 g.$g^{-1}$DW), nitrogenous compounds (1.61 g.$g^{-1}$DW), carbohydrates (1.17 g.$g^{-1}$DW), and organic acids (0.91 g.$g^{-1}$DW) (15). In contrast to other plant components, leaves are higher in nitrogenous compounds (25 to 30%) and lipids (4 to 5%), and lower in carbohydrates (60 to

**Table 1. Construction cost of components ($CC_{comp}$) of 'Starkspur Supreme Delicious' on six rootstocks, Mar. 1990.[z]**

| | | $CC_{comp}$ (glucose, g.$g^{-1}$DW) | | | |
|---|---|---|---|---|---|
| Rootstock | Frame | 2-yr wood | 1-yr wood | Spur | Root |
| MAC.24 | 1.32 | 1.31 | 1.27bc | 1.18 | 1.34 |
| M.7 EMLA | 1.30 | 1.33 | 1.30ab | 1.18 | 1.29 |
| M.26 EMLA | 1.32 | 1.32 | 1.32a | 1.22 | 1.27 |
| M.9 EMLA | 1.30 | 1.28 | 1.25c | 1.19 | 1.24 |
| MAC.9 | 1.30 | 1.27 | 1.25c | 1.16 | 1.30 |
| M.27 EMLA | 1.28 | 1.27 | 1.28b | 1.21 | 1.22 |
| Mean | 1.30a | 1.30a | 1.28a | 1.19b | 1.28a |

[z]Mean separation in columns and across component means was by Waller-Duncan k-ratio t-test, k-ratio = 100. Means were of two replications.

**Table 2. Construction cost of components ($CC_{comp}$) of 'Starkspur Supreme Delicious' on six rootstocks, Oct./Nov. 1990.[z]**

| | $CC_{comp}$ (glucose, $g.g^{-1}$DW) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Rootstock | Frame | 2-yr | 1-yr | Shoot | Spur | Root | Shoot leaf | Spur leaf | Fruit |
| MAC.24 | 1.30 | 1.32abc | 1.33a | 1.27 | 1.17 | 1.39a | 1.42 | 1.30 | 1.20 |
| M.7 EMLA | 1.30 | 1.33ab | 1.34a | 1.26 | 1.21 | 1.30b | 1.44 | 1.40 | 1.20 |
| M.26 EMLA | 1.31 | 1.33a | 1.31a | 1.30 | 1.20 | 1.30b | 1.46 | 1.36 | 1.18 |
| M.9 EMLA | 1.29 | 1.29cd | 1.25b | 1.28 | 1.22 | 1.19c | 1.47 | 1.40 | 1.18 |
| MAC.9 | 1.27 | 1.27d | 1.25b | 1.26 | 1.18 | 1.26b | 1.47 | 1.35 | 1.20 |
| M.27 EMLA | 1.31 | 1.30bcd | 1.24b | 1.27 | 1.21 | 1.27b | 1.48 | 1.40 | 1.20 |
| Mean | 1.30a | 1.31c | 1.29c | 1.27c | 1.20d | 1.28c | 1.46a | 1.37b | 1.19d |

[z]Mean separation in columns and across component means was by Waller-Duncan k-ratio t-test, k-ratio = 100. Means were of two replications.

65%), resulting in the highest construction cost of all components studied, as was found by Souci et al. (17). The difference between shoot and spur leaves might be related to a difference in physiological age. Spur leaves were approaching senescence and probably had begun recycling nitrogenous compounds and carbohydrates into storage organs of the trees. Wood components contain high percentages of cellulose (75 to 80%) and lignin (20 to 25%), resulting in the next highest $CC_{comp}$'s as shown by Farmer (3). Fruit and spur wood had the lowest $CC_{comp}$. Since fruit is high in carbohydrates (93%) and low in nitrogenous compounds (2 to 2.5%) and lipids (2 to 2.5%), it is not surprising that the $CC_{comp}$ is close to that for carbohydrates (3).

Rootstocks influence total tree DW (18), therefore, we anticipated differences in total CC for trees grafted onto different rootstocks. On both sample dates, trees on MAC.24 had the highest total CC, followed by M.7 EMLA, M.26 EMLA, M.9 EMLA, MAC.9, and M.27 EMLA. The total CC reflected differences in total DW (Table 3).

Trees on all rootstocks had lower $CC_{net}$ in Oct./Nov. than in Mar. because the presence of fruit, which had a low $CC_{net}$, out weighed the presence of leaves, which had a high $CC_{net}$ (Table 3). In general, as tree size decreased, the total CC also decreased. Since the percentage of total dry weight partitioned to fruit increases as tree size decreases (2, 5, 6, 18) and $CC_{net}$ of fruit is lower than other components, then it is not surprising that whole-tree $CC_{net}$ would decline as the tree size declines. The same trend in $CC_{net}$ relative to vigor was also observed in Mar., when the presence of fruit was not a factor. In general, trees on more dwarfing rootstocks, when contrasted to more vigorous rootstocks, partition a higher percentage of the total

**Table 3. Whole-tree and new-growth total (total CC) and net construction cost ($CC_{net}$) of 'Starkspur Supreme Delicious' on six rootstocks, Oct./Nov. 1990.[z]**

| | Total CC (glucose, kg) | | | $CC_{net}$ (glucose, $g.g^{-1}$DW) | | | |
|---|---|---|---|---|---|---|---|
| | Whole tree | | | Whole tree | | | |
| Rootstock | Mar. | Oct./Nov. | New growth[x] | Mar. | Oct./Nov. | New growth | Construction efficiency[y] (glucose/leaf DW, $kg{\cdot}kg^{-1}$) |
| MAC.24 | 75a | 118a | 43a | 1.32a | 1.28a | 1.22a | 11.44 |
| M.7 EMLA | 53b | 105a | 41a | 1.30c | 1.27b | 1.22a | 10.73 |
| M.26 EMLA | 33c | 67b | 27b | 1.31b | 1.26c | 1.20c | 11.65 |
| M.9 EMLA | 14d | 32a | 16c | 1.28e | 1.23e | 1.20c | 14.51 |
| MAC.9 | 12de | 22cd | 11c | 1.29d | 1.24e | 1.21b | 14.57 |
| M.27 EMLA | 3e | 5d | 3d | 1.25f | 1.25d | 1.22a | 14.47 |

[z]Mean separation in columns was by Waller-Duncan k-ratio t-test, k-ratio = 100. Means were of four replications.
[y]Construction efficiency = new growth total CC (glucose, kg) ÷ leaf DW (kg).
[x]New growth CC's were calculated from fruit, current season's growth, and shoot and spur leaves dry weights and construction costs.

tree DW to spurs and roots (18). The $CC_{comp}$ of spurs is lower than frame costs. Also, there was a tendency for $CC_{comp}$ to decrease within a component as rootstocks became less vigorous and trees decreased in size (Table 1). These two factors may have contributed to the decrease in $CC_{net}$, calculated for the Mar. sampling, as tree vigor declined.

A measure of how efficiently a rootstock "constructs" new biomass, or construction efficiency, was calculated by using the total CC of new growth and dividing it by total spur and shoot leaf DW (Table 3). Although only significant at $p = .17$, there was a tendency for trees which partition more biomass to fruit and were less vigorous to have a higher construction efficiency (Table 3). Hansen (8) determined that heavy fruiting reduces total leaf area, but the increase in total tree DW is higher in fruiting than in non-fruiting trees. The increase in fruit weight more than balances the loss of vegetative growth (1). The explanation most commonly given for this is increased photosynthesis, photosynthetic efficiency, and transport in the presence of a strong sink such as fruit (7, 8, 11). This has been supported by studies which show that as the leaf area decreased with cropping, the net assimilation rate per $cm^2$ leaf area of $^{14}CO_2$ increased (9). Another possible contributing factor is the changing source-sink relationship during the growing season. As new shoots begin to grow, they act as sinks, importing reserves from the rest of the tree. The longer the shoot grows, the longer it acts as a sink (10) and requires more energy to produce the leaves and shoots. Later, as extension growth slows and eventually stops, the new leaves on the these shoots begin exporting carbohydrates. Since new growth is less on smaller trees, it creates less demands on tree reserves and current photosynthates and new shoots begin exporting earlier in the season, thereby increasing the available photosynthate for partitioning to fruit.

It is probable that all of these explanations contribute to the increase in dry weight per leaf area observed as fruiting increases and vegetative vigor decreases. (2, 5, 6, 18) The known benefit of increased productivity of apple trees grafted onto dwarfing rootstocks may partially be explained by the availability of more photosynthate to produce more fruit because of the lower net energy demand to produce fruit and the reduction in the production of the "expensive" leaf and woody tissues.

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**Journal of American Pomological Society 54(1): 22-27 2000**

# Relationship Between Trunk Cross-sectional Area, Harvest Index, Total Tree Dry Weight and Yield Components of 'Starkspur Supreme Delicious' Apple Trees

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## Abstract

The relationship between trunk cross-sectional area (TCSA) and total tree dry weight (DW), and between harvest index (HI) and yield efficiency (YE) of 'Starkspur Supreme Delicious' (*Malus domestica* Borkh.) apple trees on nine different rootstocks was examined. In general, as tree size increased, the reliability of TCSA as a predictor of total tree DW decreased. A log transformation increased the accuracy of the estimate. The relationship between YE and HI was improved when a log transformation of TCSA is used to compute the YE. A comparison of tree evaluations based on TCSA and total tree DW revealed that trees on M.27 EMLA had a greater partitioning of dry matter to flowers and fruit when actual DW was used in calculations. The larger trees on MAC.24 and M.7 EMLA rootstocks, ranked higher in YE and flower density when TCSA was used instead of DW as a basis for accounting for tree size. The rootstocks with the highest HI's, ranging from 0.46 to 0.48, were M.9, M.27 EMLA, M.9 EMLA, MAC.9, and O.3. OAR1, M.26 EMLA, M.7 EMLA, and MAC.24 were contained in a second grouping with HI's ranging from 0.33 to 0.39. M.27 EMLA had one of the lowest YE's but had a high HI. M.7 EMLA had a relatively high YE but a low HI. OAR1 had the lowest YE but not the lowest HI.

Clonal rootstocks are widely used to provide size control, induce precocity, and increase productivity in tree fruit species. Evaluations of rootstocks commonly include yield efficiency (YE), a measure of productivity defined as the fresh weight (FW) yield divided by the trunk cross-sectional area (TCSA) (6). TCSA has been positively correlated with the total above-ground tree FW (7). Therefore, YE provides an estimate of the FW yield (kg) per kg of above-ground tree FW.

A widely used measure of productivity of annual crops is the harvest index (HI), defined as the fraction of the total plant DW that is partitioned to the harvested sink, or the ratio of the yield DW to the total plant DW. The similarity in theory of YE and HI is apparent, since both are a measure of yield relative to the total plant weight. However, the relationship between these terms has not been studied. Destructive sampling of trees in the 1980-81 NC-140 apple rootstock trial provided an op-

Oregon Agricultural Experiment Station Technical Paper No. 11602.
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