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Effects of Rootstock on Bud Development and Flower Formation of 'Starkspur Supreme Delicious' Apple*

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Abstract

Studies were conducted on mature 'Starkspur Supreme Delicious' trees growing on 17 rootstocks in Wooster, OH to examine differences in flowering and possible mechanisms for such differences. More dwarfing rootstocks had higher spur densities, but the relationship was weak. Spur density had no effect on flower density, but the proportion of spurs which formed flowers was closely related to flower density. Doming of the bud apical meristem, indicating a change to a floral state, only occurred after 20 appendages were present within the bud, and this critical number of appendages was constant across rootstocks and years. The timing of flower development was also unaffected by either rootstock or year. No differences in phosphorus concentration in spur leaves or in bud apical meristems were found among rootstocks, indicating no direct effect of P on flowering.

Rootstocks are used widely in commercial fruit production due to their beneficial effects on the growth and development of the scion. In apple, rootstocks have been shown to influence tree size, precocity, flowering, yield efficiency, dry matter partitioning and fruit quality (3, 20, 21, 27). The tendency for trees on dwarfing rootstocks to produce more fruit in relation to the size of the tree is well established (8, 20, 21). One of the limitations to achieving high yields in apple can be the production of flowers (7). The degree of bloom has been positively related with yield and yield efficiency (20). In a study with young, greenhouse-grown trees, cultivar influenced flowering to a greater extent than rootstock (10), but rootstock effects on flowering can also be dramatic (20). Despite its obvious importance, the mechanisms by which rootstocks influence flowering of the scion have not been studied.

Flowering of apple may be affected by many different influences, some of which may be modified or controlled by the rootstock. The basic unit of productivity in apple is the spur, and in particular the flowering spur. Among 'Delicious' strains, the density of spurs on a branch was negatively related to tree size, but positively correlated with yield efficiency (29). It is unclear however, to what extent differences observed in flowering among rootstocks can be explained by their effects on the production of spurs. The number of flowers borne on a branch is a function of the total number of spurs and the proportion of spurs which are reproductive. Rootstock effects on the development of individual buds have not been documented, and the possible mechanisms of such putative effects are many.

As apple buds develop, appendages (bud scales, transition leaves, true leaves and bracts) are added within the bud. In order for a flower to form within the bud, a critical number of appendages must be present. The critical number of appendages varied with cultivar (18), but rootstock effects have not been studied. If particular rootstocks lowered the complexity required in a bud prior to flower formation, in a sense it would be "easier" for flowers to form in such buds. The time during

*The data presented in this paper was taken from the PhD dissertation and related publications by P. M. Hirst.

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the season in which flowers are formed in buds may also be influenced by rootstock and may affect the proportion of buds in which flowers are formed.

Soil applications of phosphorus have been shown to increase flowering the year following application (22, 31). The response was mainly due to flower formation in a higher proportion of spurs, since effects on shoot growth were minimal. Rootstocks affect both the uptake of P from the soil (2, 6) and its transport across the graft union (14, 15) suggesting that rootstock effects on flowering may be mediated via influences on phosphorus nutrition.

This study was carried out to investigate several possible mechanisms of rootstock influence on flowering in apple. The study comprised three specific experiments. Firstly, we sought to determine the effects of rootstock on the number of spurs formed in scion branches and the proportion of those spurs which became reproductive. The relationships between shoot morphology and spur quality variables with flowering, precocity and productivity were described. In the second experiment, rootstock effects on bud development were described and their effects on the critical bud appendate number prior to flower formation, and time of flower formation determined. Thirdly, the concentration of P in spur leaves and the relative amounts of P in bud apical meristems of trees growing on 5 rootstocks was measured and related to the flowering and yield performance of these trees.

Materials and Methods

All studies were carried on 'Starkspur Supreme Delicious' apple trees growing on 17 rootstocks in Wooster, Ohio, as part of a rootstock evaluation program (20). The trees were planted in 1984 at a spacing of 5.5 x 3.5 m as randomized complete blocks with 10 single tree replicates. Trees were trained to a central leader tree form and standard commercial production practices were followed. Each year, trunk diameters were measured 20-30 cm above the soil from which trunk cross-sectional areas (TCSA) were calculated, and the total fruit yield per tree was weighted at harvest.

Experiment 1. In each year at bloom from 1988-1993, five shoots were selected around the periphery of each tree, and the 2-year-old section identified. The length of this section of branch was measured, and the number of flower clusters, spurs, and lateral shoots counted. The proportion of spurs and lateral shoots that flowered could thus be calculated as could the densities of flowers, spurs, and growing points (spurs + lateral shoots). Vegetative spurs were sampled in mid-September 1991 and various attributes of spur quality measured.

Experiment 2. From the experimental planting described above, 5 rootstocks were selected including: B.9, M.26EMLA M.7EMLA, P.18 and seedling. These rootstocks represented a wide range of tree size and productivity. In each year from 1991 to 1993, buds were sampled from the previous years' growth periodically during the growing season. On each sampling date, three (1991) or two (1992 and 1993) spurs were sampled from well illuminated positions of each tree, and their leaf number, leaf area, leaf dry weight and bud diameters measured. Buds were dissected under a dissecting microscope and their appendages counted and classified as either bud scales, transition leaves, true leaves or bracts. The bud meristem was classified as either vegetative (flattened) or floral (domed) and the critical appendage number prior to doming of the meristem was determined by linear discriminant analysis. Shoot growth was measured on 5 shoots per tree at various times throughout the growing season to determine the relationship between shoot growth and bud development.

Experiment 3. Leaves were pooled from the two (1992 and 1993) or three (1991) spurs sampled in experiment 2, and foliar mineral concentrations determined at the Research Extension Analytical Laboratory (REAL) using an ICP technique (30). Analysis of the relative levels of phosphorus, potassium, calcium, iron and sulphur in apical meristems prior to doming was measured using energy dispersive x-ray spectrophotometry (EDAX).

More detailed descriptions of the methodology employed in experiments 1-3 has been previously reported (9-13).

Results

Trees on seedling rootstock were among the most vigorous in terms of shoot length, while those on P.22 were the smallest, ranging from 27-50% the length of seedling (Fig. 1). Shoot lengths generally decreased from 1988 to 1990 as trees began to crop, but were reasonably constant from 1990 to 1993. Although the interaction between rootstock and year was statistically significant, it was of minor importance and accounted for less than 10% of the total treatment variation. Spur density generally followed an opposite trend to shoot length (Fig. 2, Table 1) and although more vigorous rootstocks tended to have lower spur densities, the relationship was not particularly strong ($r = 0.55$, $p < 0.05$). The variation in spur density among rootstocks was much lower than that for shoot length, with coefficients of variation (CV) below 13% of each year. Rootstocks had a large effect on the number of flower clusters per unit shoot length, with CVs as high as 61% in 1990 (Fig. 3). The differences in spur density among rootstocks, therefore, could not explain the differences observed in flower density. Overall, the flower densities were lower on more vigorous trees (Table 1), but trunk cross-sectional area (TCSA) or shoot length could only explain half the variation observed in flower density. Flower density was unrelated to spur density, but was closely related to the proportion of flowering spurs ($r^2 = 0.92$, $p < 0.001$). Therefore, rootstocks do not influence flowering via the production of higher numbers of spurs, but rather by affecting spur development and the proportion of spurs which undergo the transition from a vegetative to a floral state.

Table 1. Effect of rootstock on shoot length, spur density and flower density of 2-year-old branches of 'Starkspur Supreme Delicious' trees over a 6-year period.

Rootstock	Shoot length (cm)	Spur density ($no.m^{-1}$)	Flower density ($clust.m^{-1}$)
P.22	15.9	39.3	23.9
P.16	22.3	33.9	20.4
P.2	23.8	36.4	19.7
CG.10	24.5	37.2	19.6
B.9	26.2	31.1	20.9
MAC.39	28.5	36.2	20.3
M.26EMLA	30.4	36.2	17.5
C.6	28.8	35.4	20.4
P.1	32.2	34.1	22.1
M.7EMLA	34.3	31.7	21.0
M.4	37.6	33.8	21.0
MAC.1	33.7	35.6	20.3
CG.24	37.8	36.5	15.7
B.490	35.9	33.1	20.9
P.18	37.8	32.7	17.5
Ant.313	38.9	31.8	16.5
Seedling	38.1	34.0	17.5
LSD (p = 0.05)	2.0	1.7	3.0

Yield per tree was positively related to TCSA and shoot length in five or six years of the study, respectively (11). Yield efficiency, however, was negatively related to these characteristics in 6 or 3 years, respectively. Precocity (cumulative yield 1984-1988/TCSA 1988) and productivity (cumulative yield 1984-1993/TCSA 1993) were also negatively related to vigor as estimated by TCSA or shoot length. More precocious and productive rootstocks had more leaves per spur with higher specific leaf weights, but smaller spur leaf size than less productive rootstocks

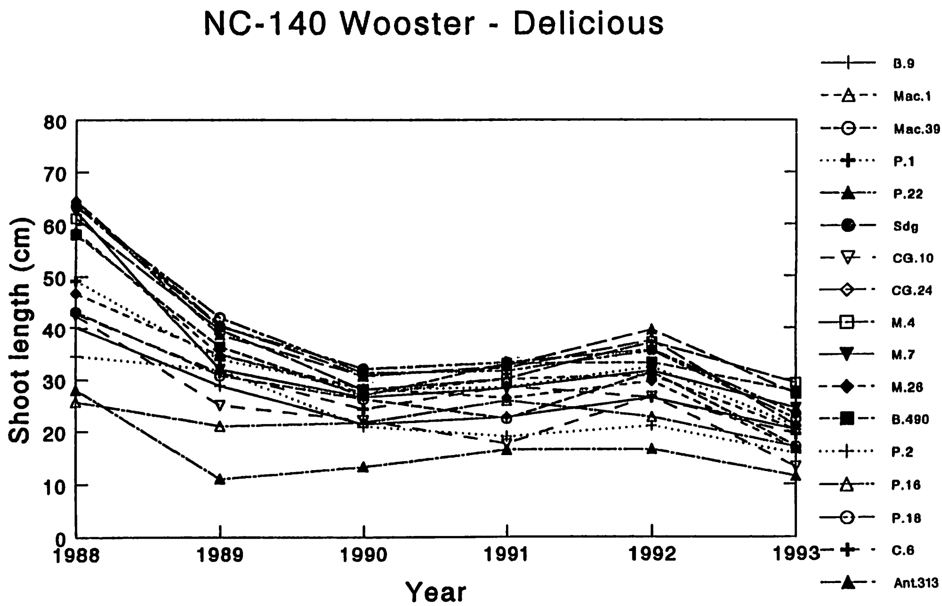

Figure 1. Length of the 2-year-old branch section of 'Starkspur Supreme Delicious' trees growing on 17 rootstocks in Wooster, OH, measured from 1988 to 1993. n = 50.

(11). During the period of study, extremes of temperature and rainfall were experienced, but despite this most of the yearly variation could be ascribed to cropping rather than environmental variables (11).

During each year from 1991 to 1993, the total number of bud appendages increased over the course of the growing season, but rootstock effects were only observed in 1991 (Fig. 4). The number of bud scales increased slightly during the early part of the season, but the numbers of transition leaves and true leaves remained reasonably constant (12). Most of the increase in appendage numbers was due to the production of additional bracts, but the time at which bracts were produced and the final bract number were unaffected by either rootstock or year (12). In 1991, rootstocks separ-

Table 2. Critical bud appendage number prior to doming of the bud apex as predicted by linear discriminant analysis of 'Starkspur Supreme Delicious,' and the proportion of buds correctly classified as either vegetative or floral by these predictive models.

	1991		1992		1993		All Years	
Rootstocks	app #	% correct	app #	% correct	app #	% correct	app #	% correct
B.9	19.6	94	19.3	84	20.8	96	19.6	92
M.26EMLA	19.8	95	19.8	91	---	--	19.9	96
M.7EMLA	19.7	92	20.2	85	19.6	98	19.9	94
P.18	19.1	93	20.2	89	18.4[z]	95	19.6	95
Seedling	20.2	97	20.2	84	18.2[z]	89	20.1	94
All rootstocks	19.7	95	19.9	91	19.7	97	19.8	94

[z]Based on < 5 floral buds.

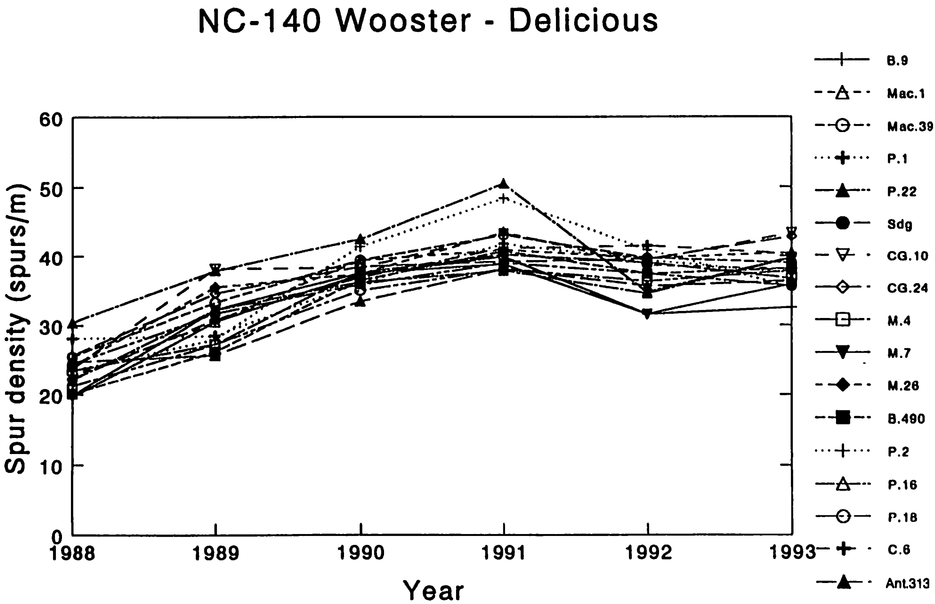

Figure 2. Spur density (spurs per meter of branch length) on the 2-year-old branch section of 'Starkspur Supreme Delicious' trees growing on 17 rootstocks in Wooster, OH, measured from 1988 to 1993. n = 50.

ated into 2 groups based on their final appendage number ($p \leq 0.05$) with trees growing on B.9 and M.7 EMLA having more appendages than those on M.26EMLA, P.18 or seedling rootstocks. The proportion of flowers evident in buds increased significantly from 91-109 days after full bloom (dafb) in 1991, after which a plateau was attained (Fig. 5). As with total appendage number, the rootstocks appeared to separate into the same 2 groups based on the proportion of buds in which flowers formed. During 1992 however, trees on all rootstocks exhibited a high degree of flower formation, which occurred from 89-107 dafb. Flower formation was sparse on trees of all rootstocks in 1993, but there was a slight trend for trees on B.9 and M.7EMLA to have a higher proportion of floral buds than trees on other rootstocks. Despite large differences in the degree of flower formation among years, doming of the apex occurred from approximately 90-110 days after full bloom in each year, which corresponded to the first weeks of August.

Linear discriminant analysis was used to determine the critical appendage number in the bud prior to flower formation. The critical appendage number calculated in this study was 20, and was constant among rootstocks and across years (Table 2). The models constructed allowed prediction of the floral status of buds based on their appendage number and in most cases more than 90% of buds were classified correctly using these models. More than 2100 buds were dissected over the 3 years of this study, and by pooling the data a model was constructed which allowed correct classification of 94% of all buds. It was, therefore, concluded that the critical appendage number is a property of the cultivar and was relatively stable across rootstocks and years. In this study, rootstock affected the proportion of buds which became floral in some years,

Table 3. Effect of rootstock, time of growing season (days after full bloom) and their interaction on the relative levels of P, K, Ca, Fe, and S in bud apical meristems of 'Starkspur Supreme Delicious' during 1991.

	Relative Mineral Nutrient Level (%)				
	P	K	Ca	Fe	S
Days after full bloom					
67	37.4	6.1	29.9	8.5	18.1
74	31.1	5.1	26.8	17.6	18.8
85	27.1	5.2	31.7	1.6.8	19.0
LSD (p = 0.05)	5.2	1.3	4.6	3.3	1.9
Rootstock					
B.9	32.2	4.8	30.3	13.7	18.2
M.26EMLA	31.4	6.9	30.1	13.8	17.4
M.7EMLA	27.6	5.3	33.3	14.6	19.0
P.18	34.8	4.8	28.1	12.1	20.1
Seedling	33.4	5.5	25.5	17.1	18.4
LSD (p = 0.05)	6.7	1.6	5.9	4.3	2.5
Source of Variation (%SS)					
Date	53.5***z	11.7	24.3	61.2***	5.9
Rootstock	18.5	33.7	40.4	10.2	28.2
Date X Rootstock	28.0	54.6	35.2	28.6	65.9

z,*,**,***Indicate significant at P ≤ 0.05, 0.01, or 0.001, respectively.

but the timing of flower bud differentiation, the critical appendage number and the type of bud appendage were all unaffected by rootstock.

Experiment 3.

Rootstock effects on the concentration of phosphorus in spur leaves were small and inconsistent among years (Fig. 6). Leaves from trees growing on M.26EMLA had the highest P concentration in 1991, but were among the lowest in 1992. In each year, foliar P levels declined over the course of the growing season, and these trends accounted for 70-97% of the total treatment variation. The decline in P levels with time was similar among all rootstocks with no interaction between rootstock and time of season evident in any year of the study. Spur leaf P concentrations were not associated with spur characteristics such as spur leaf number, spur leaf area, leaf dry weight or specific leaf weight (data not presented). The relative amounts of P in bud apical meristems during 1991 followed similar trends to those for foliar levels, with declines during the growing season and no rootstock influence (Table 3). Comparable results were evident in 1992 and 1993 (13).

In all 3 years, negative relationships between spur leaf P concentration and bud appendage number were evident, but the relationships were weak and accounted for less than 40% of the variation (13). The relative level of P in bud apices was related to bud and spur characteristics only in 1993, and the relationships were weak, accounting for less than 30% of the variation (13). The P concentration in spur leaves was unrelated to the level of P in bud apices.

Discussion

Many of the morphological attributes of shoots measured in these studies varied during most during 1988 and

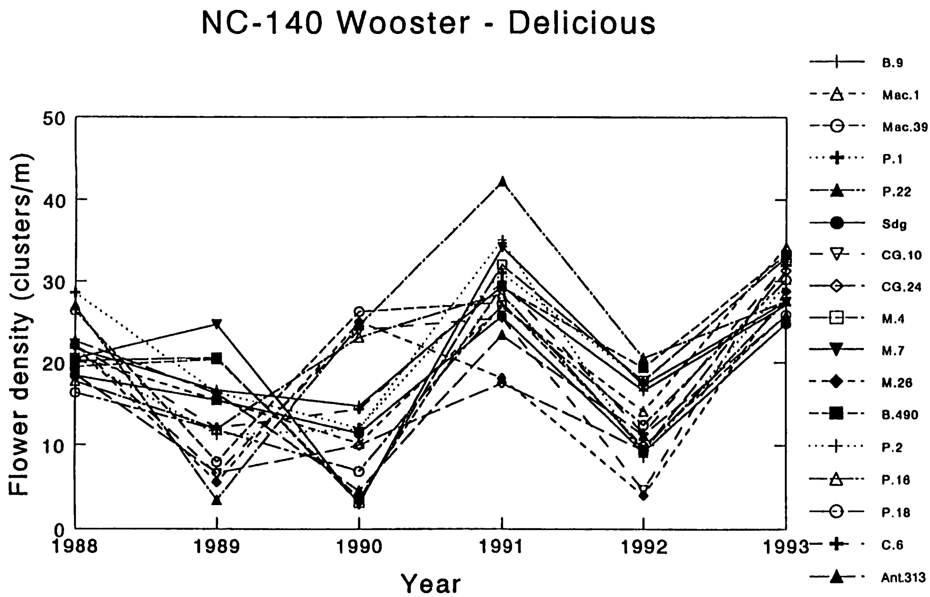

Figure 3 Flower density (flower clusters per meter of branch length) on the 2-year-old branch section of 'Starkspur Supreme Delicious' trees growing on 17 rootstocks in Wooster, OH, measured from 1988 to 1993. n = 50.

1989. These shoots grew 2 years earlier in 1986 and 1987, respectively, which corresponds to the time of first cropping. The cropping behavior of these trees may explain some of the variability in morphological attributes since cropping has been associated with reduced shoot growth (4), and many of the morphological variables studied were related to shoot growth.

Spur density was only minimally affected by rootstock, with P.22 generally having the highest spur density and Ant.313 the lowest. Similarly, Warrington et al. (29) reported that spur density differed more among 'Delicious' strains than within one strain growing on a range of rootstocks and also in a study with young trees, total growth was primarily controlled by rootstocks, whereas the distribution of growth was mainly a characteristic of the cultivar (10). In this study, spur density was not related to spur characteristics or yield variables indicating that rootstocks do not influence productivity by affecting the number of potential fruiting sites (spurs).

The number of flower clusters on a shoot was positively related to shoot length, but only half the variation in flower number could be explained by the number of spurs on the shoot. Flower density was unrelated to flower number and tended to be higher on trees with less vigor (as indicated by lower TCSA and shorter shoots), but the relationships were weak. The strong relationship of flower density with the proportion of flowering spurs and the weak relationship with shoot length indicated that rootstocks influence flower density not via shoot length effects, but by more direct control of bud development.

In all 3 years of this study, rootstock had no effect on the critical appendage number or the time of flower formation, indicating that the course of development of buds from vegetative to floral was controlled at a cultivar level. Rootstock did however, affect the pro-

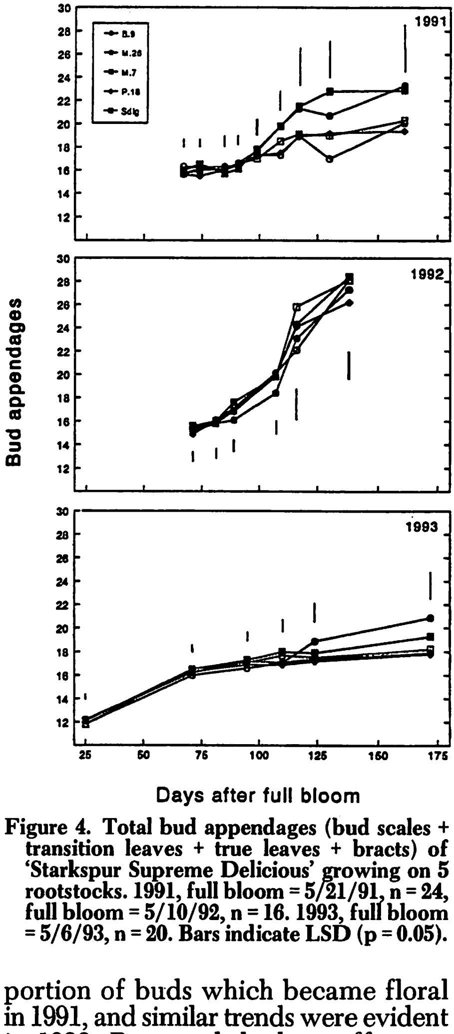

Figure 4. Total bud appendages (bud scales + transition leaves + true leaves + bracts) of 'Starkspur Supreme Delicious' growing on 5 rootstocks. 1991, full bloom = 5/21/91, n = 24, full bloom = 5/10/92, n = 16. 1993, full bloom = 5/6/93, n = 20. Bars indicate LSD (p = 0.05).

portion of buds which became floral in 1991, and similar trends were evident in 1993. Rootstock had no effect on the time of shoot growth cessation, which occurred at 40 days after full bloom in 1992 and at 70 days after full bloom in 1993. The earlier cessation of shoot growth in 1992 than in 1993 may have been due to soil moisture deficits since during the 40 days after bloom, rainfall was 84 mm and 43 mm lower than the long-term average in 1992 and 1993, respectively, and the trees were unirrigated. The cessation of shoot growth has been recognized as a prerequisite for flower initiation (1, 17, 28), and in this study earlier cessation of shoot growth (1992) was associated with a much higher degree of flower formation than when shoots terminated later in the season (1993). During the two years when shoots were measured, however, no rootstock effect on the time of shoot growth cessation or the degree of flower formation was apparent.

Although rootstocks differ in their ability to take up P from the soil (2, 6), no rootstock effects on spur leaf P concentration were found which is similar to previous reports for shoot

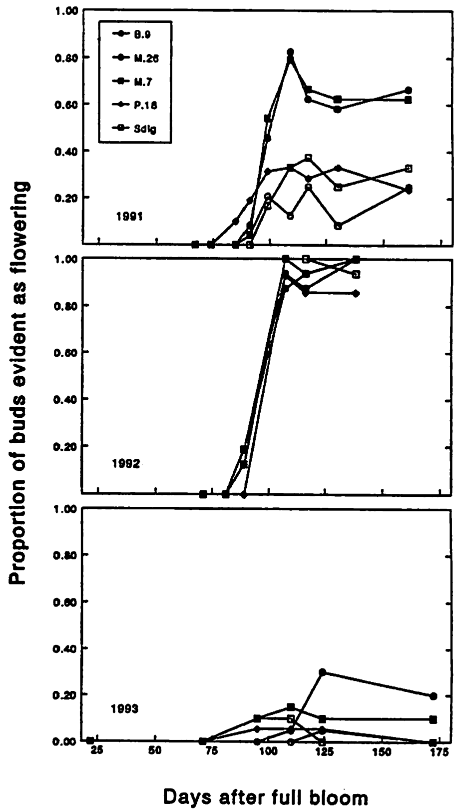

Figure 5. Proportion of sampled buds in which doming of the apex, indicating the first stages of floral development, was evident in trees of 'Starkspur Supreme Delicious' growing on 5 rootstocks. 1991, full bloom = 5/2/91, n = 24. 1992, full bloom = 5/10/92, n = 16. 1993, full bloom = 5/6/93, n = 20.

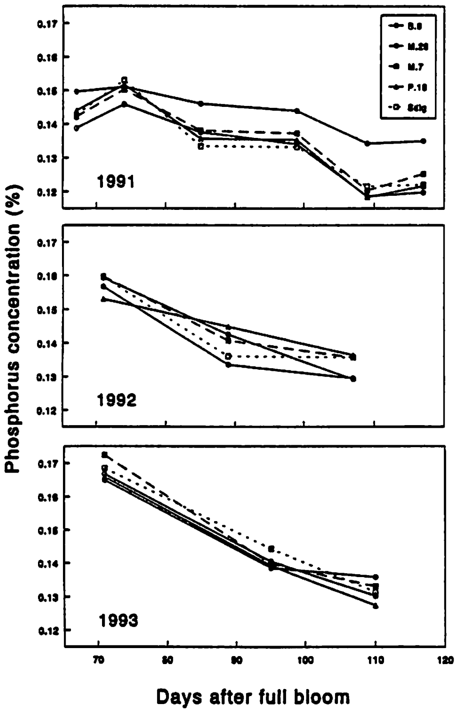

Figure 6. Spur leaf P levels of 'Starkspur Supreme Delicious' as influenced by 5 rootstocks over 3 years.

leaves where rootstock effects were small or absent (23, 25, 26). To our knowledge, this was the first study to use EDAX technology to examine mineral concentrations within a very localized area of the apical meristems of apple buds. Rootstocks did not affect the relative levels of P in bud apical meristems. Although the role for phosphorus in the mechanisms by which rootstocks influence flowering cannot be dismissed, a strong role is unlikely since P levels in spur leaves and bud meristems was unaffected by rootstocks. It would seem possible that the interaction between phosphorus levels and cytokinin biosynthesis shown for other crops (5, 19) may also be applicable in apple, and that the cytokinin so produced may promote flowering (16, 24) when transported to the scion.

In conclusion, although rootstocks had some effect on spur density, these differences did not explain the variations in flower density. Flower density was however, strongly related to the proportion of spurs which formed flowers. Although rootstocks affected bud development, they did not achieve this by altering the complexity at which flowers formed within buds, or the time at which flowers were formed.

Phosphorus levels have been shown to influence cytokinin biosynthesis in other crops (5, 19) and there are reports of apple rootstocks influencing P uptake (2, 6). Although there was no significant effect of rootstock on P levels in spur leaves or apical meristems in this study, the possibility cannot be dismissed that rootstock affected P levels in root tissue which may influence cytokinin production and ultimately flowering in the scion.

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