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Lateral Shoot Development in Six Diverse Seedling Populations of Apple

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Abstract

Growth and branching habit of seedling populations originating from open-pollinated trees of *Malus prunifolia* Borkh., *M. ranetka* Borkh., and four cultivars of *M. domestica* Borkh. ('Antonovka,' 'Bittenfelder,' 'Borowinka,' 'Golden Delicious') were characterized. The decreased rate at which new lateral shoots developed was directly related to decreases in terminal growth rate, since all lateral budbreak throughout the growing season occurred within 20 cm of the shoot tip. 'Borowinka' sdlg., 'Golden Delicious' sdlg., and *M. ranetka* populations were most vigorous and, generally, had the greatest number of lateral budbreaks and branches. However, lateral budbreak and branching were not strongly related to terminal growth rate, evidenced by poor correlations with terminal shoot length. cross-sectional area, and internode length.

Introduction

Variation among commercial apple cultivars in vigor and tendency to branch is well documented (4, 5, 7). Many cultivars exhibit limited branching and are induced to branch, manually or chemically, in the nursery or immediately after planting. The early yields and high production potential of a high-density orchard can only be realized when a significant number of well-distributed branches develop. Knowledge of which traits are highly correlated with branch development would be beneficial in developing new cultivars which branch more freely than those currently available. The objectives of this study were: (1) to demonstrate the wide variation in growth and branching habit among a collection of genetically diverse seedling populations and (2) to examine the relationship between terminal shoot growth and lateral shoot development.

Materials and Methods

Study 1. In Nov. 1991, 20 one-year-old upright shoots were randomly selected from each of six sets of 9-year-old seedling trees. Each set of trees (seedling populations) originated from open-pollinated trees of either *Malus prunifolia* Borkh., *M. ranetka* Borkh., or one of four cultivars of *M. domestica* Borkh. ('Antonovka,' 'Bittenfelder,' 'Borowinka,' 'Golden Delicious'). The parent trees were grown together in a single block. The seedling populations were located in Raleigh, NC in a compact hedgerow consisting of a permanent network of horizontal

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Table 1. Growth characteristics of upright shoots of six seedling populations after one (1991) and two (1992) years of growth.

Population	Cross-sectional area (CSA) (cm^2)		Total terminal shoot length (m)		Internode length (cm)		Total lateral budbreaks		Branches (>=5cm) Primary		Branches (>=5cm) Primary + secondary	Total branch length (m) Primary		Total branch length (m) Primary + secondary
	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992	1992	1991	1992	1992
Antonovka sdlg.	0.92 b[z]	2.95 b	1.13 b	1.83 bc	1.79 b	1.90b	12.3 c	43.6 bc	7.2 b	18.0 b	23.6 cd	0.77 c	3.99 c	4.79 c
Bittenfelder sdlg.	0.52 c	1.16c	1.07 b	1.38 d	1.47 c	1.43 d	21.2 c	33.6 c	12.8 b	18.0 b	20.1 d	1.49 bc	3.90 c	4.22 c
Borowinka sdlg.	1.35 a	3.41 b	1.62 a	2.27 a	1.85 b	1.87 b	34.9 b	76.2 a	27.3 a	34.6 a	41.9 ab	3.75 a	8.72 b	9.50 b
G. Delicious sdlg.	0.90 b	2.68 b	1.39 a	2.03 ab	1.40 c	1.43 d	52.9 a	82.2 a	31.5 a	37.8 a	38.6 bc	2.47 ab	5.78 bc	5.87 bc
M. prunifolia	1.05 b	2.97 b	1.06 b	1.63 cd	1.69 b	1.71 c	12.6 c	45.4 bc	9.7 b	19.6 b	20.4 d	1.40 bc	4.45 c	4.56 c
M. ranetka	1.48 a	6.47 a	1.39 a	2.31 a	2.37 a	2.36 a	19.5 c	55.4 b	16.5 b	39.3 a	58.7 a	2.82 ab	14.93 a	19.28 a

[z]Mean separation within columns by LSD at 0.05 level.

Table 3. Correlations between pairs of growth parameters for all six seedling populations (n = 120), after one (1991) and two (1992) years of growth.

	Correlation coefficient (r): Shoot cross-sectional area		Terminal shoot length		Internode length		No. lateral budbreaks		No. branches	
	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992
Terminal shoot length	0.83	0.75	---	---						
	p = 0.0001	p = 0.0001	---	---						
Internode length	0.49	0.54	0.39	0.49	---	---				
	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.0001	---	---				
No. lateral budbreaks	0.46	0.43	0.72	0.72	-0.06	0.03	---	---		
	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.5703	p = 0.7592	---	---		
No. branches (> = 5cm)	0.58	0.56	0.75	0.70	0.08	0.22	0.93	0.80	---	---
	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.4002	p = 0.0260	p = 0.0001	p = 0.0001	---	---
Total branch length	0.76	0.83	0.77	0.72	0.23	0.45	0.72	0.56	0.86	0.81
	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.0187	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.0001	p = 0.0001

branches approximately 75 cm above the soil line and numerous upright shoots removed each dormant season. All upright growth was removed in Feb. 1992 except the selected shoots (120 total), which were allowed to grow through the 1992 season. Terminal shoot length, shoot diameter (at 12 cm from shoot base), number of lateral budbreaks, and number and length of both primary and secondary branches ($\geq$ 5cm) were measured in Nov. 1991 and again in Nov. 1992. In addition, in Nov. 1991, the length of each terminal shoot was marked off into four equal parts. The number of nodes, lateral budbreaks, and branches ($\geq$ 5cm), as well as total branch length in each quarter were ascertained in Nov. 1991 and Nov. 1992.

Study 2. Following the removal of all upright growth in Feb. 1993, 60 current-season upright shoots were randomly selected in April/May from each of the six seedling populations. All other upright growth was removed. When the selected shoots of a population were 20-30 cm in length (week 0) and again after 1, 3, 5, 7, 11, 15, and 19 weeks, terminal shoot length was measured and the number of lateral budbreaks counted. To monitor the position of newly-occurring budbreaks along each terminal shoot during the growing season, the lengths of terminal growth occurring between measurement dates were considered separate zones. The number of budbreaks in each zone was counted at each of the previously indicated times [budbreak in the first zone (spring budbreak to week 0) was counted eight times during the growing season, budbreak in the second zone (week 0-1) was counted seven times, etc.]. Data were subjected to analysis of variance procedures and regression analysis. Treatment means were separated using the least significant difference test ($p \leq 0.05$).

Results

Study 1. 'Borowinka' sdlg. and *M. ranetka* populations were the most vigorous at the end of one year (Nov. 1991) and two years (Nov. 1992) of growth, generally having greater shoot cross-sectional area (CSA), terminal shoot length, and branch length than other populations (Table 1). 'Borowinka' and 'Golden Delicious' sdlg. populations generally had the greatest number of lateral budbreaks and branches ($\geq$ 5cm) after one year and, along with *M. ranetka*, the greatest total branch length. 'Borowinka' sdlg., 'Golden Delicious' sdlg., and *M. ranetka* had the greatest percent lateral budbreak (Table 2). In all six populations, almost all of the budbreak, branching, and branch length occurred in the lower half of the current-season terminal shoot in 1991, suggesting that

Table 2. Percent lateral budbreak in each quarter of 1991 portion or upright shoots of six seedling populations, after one (1991) and two (1992) years of growth.

	Lateral budbreak (%)									
	Quarter 1[z]		Quarter 2		Quarter 3		Quarter 4		Quarters 1-4	
Population	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992
Antonovka sdlg.	24.7 b[y]	39.0 b	40.3 b	59.9 b	13.1 c	80.8 a	0.7 b	87.4 ab	18.3 b	68.8 c
Bittenfelder sdlg.	37.5 b	52.7 b	41.4 b	50.3 b	22.6 bc	42.4 b	1.2 b	23.9 d	24.4 b	40.9 d
Borowinka sdlg.	69.7 a	83.7 a	63.9 ab	84.9 a	22.5 bc	88.6 a	0.2 b	91.9 a	37.5 a	87.4 a
G. Delicious sdlg.	77.5 a	91.0 a	73.8 a	88.5 a	46.1 a	83.9 a	6.4 a	66.3 c	49.4 a	82.4 ab
M. prunifolia	34.8 b	51.3 b	36.5 c	87.5 a	10.1 c	83.0 a	0.0 b	74.2 bc	17.8 b	72.5 bc
M. ranetka	66.2 a	84.9 a	76.6 a	96.9 a	33.8 ab	92.4 a	2.0 b	93.8 a	37.6 a	92.0 a

[z]Quarter 1 = basal; quarter 4 = apical.
[y]Mean separation within columns by LSD at 0.05 level.

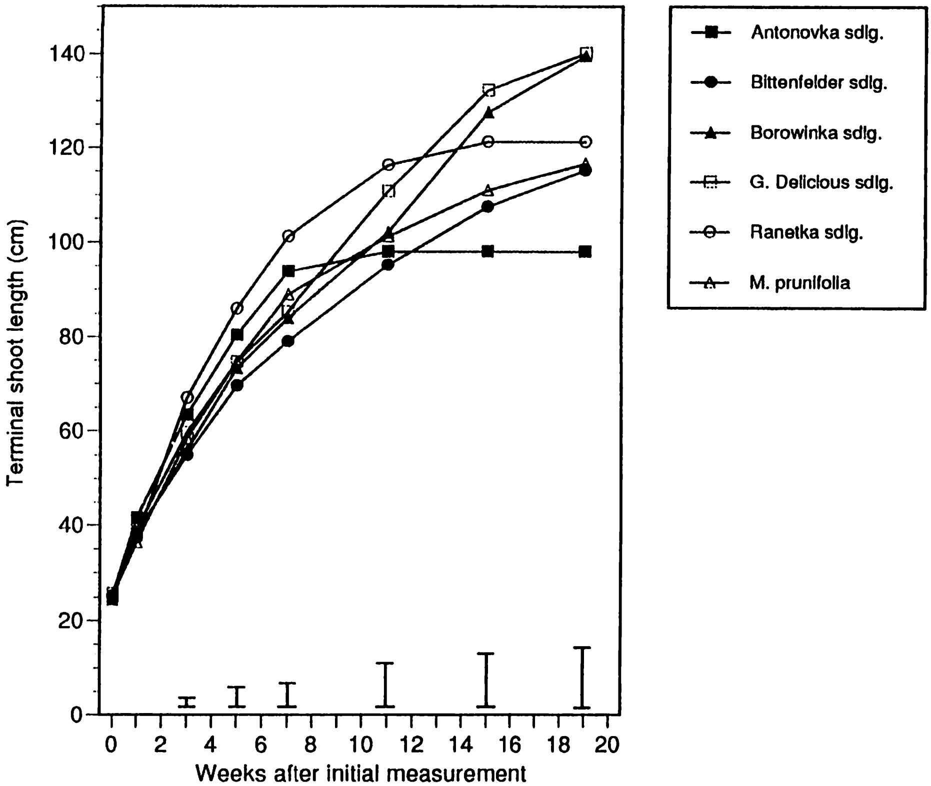

Figure 1. Terminal shoot length of upright shoots of seedling trees of five open-pollinated cultivars and one species of apple throughout the 1993 growing season. Vertical bars indicate LSD at 0.05 level. Error bars smaller than symbol size not shown.
'Antonovka' seedling ($y = 30.4 + 11.2x - 0.42x^2$, $r^2 = 0.84$);
'Bittenfelder' seedling ($y = 28.7 + 8.74x - 0.22x^2$, $r^2 = 0.81$);
'Borowinka' seedling ($y = 27.9 + 9.19x - 0.18x^2$, $r^2 = 0.90$);
'Golden Delicious' seedling ($y = 28.2 + 10.1x - 0.22x^2$, $r^2 = 0.86$);
***M. prunifolia* ($y = 27.3 + 10.5x - 0.31x^2$, $r^2 = 0.76$);**
***M. ranetka* ($y = 27.1 + 13.4x - 0.45x^2$, $r^2 = 0.76$).**

the majority of lateral budbreak occurred early in the growing season, when terminal shoot growth was most rapid. Only 'Golden Delicious' sdlg. had a considerable number of budbreaks in the uppermost quarter of current-season growth. Lateral budbreak was absent from the non-vigorous terminal growth which occurred the second year (1992) with all populations.

Overall, terminal shoot CSA correlated poorly with lateral budbreak and branching (Table 3). These correlations were considered low, despite being significant ($p \leq 0.05$) due to the large number of replications ($n = 120$). After one year, 'Bittenfelder' sdlg. and *M. ranetka* populations had a similar number of lateral budbreaks and branches even though terminal shoot CSA of *M. ranetka* was three times greater than that of 'Bittenfelder' sdlg. (Table 1). However, CSA of 'Golden Delicious' sdlg. was strongly correlated with both lateral budbreak ($r = 0.89$, $n = 20$, $p = 0.0001$) and branching ($r = 0.90$, $n = 20$, $p = 0.0001$). Internode

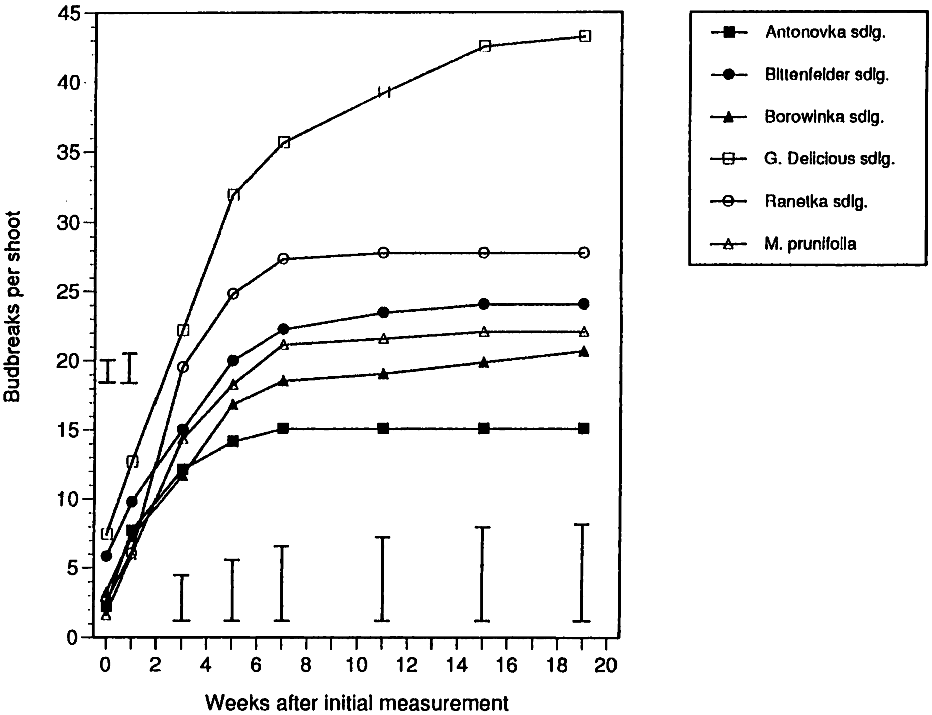

Figure 2. Lateral budbreak of upright shoots of seedling trees of five open-pollinated cultivars and one species of apple throughout the 1993 growing season. Vertical bars indicate LSD at 0.05 level. Regression equations correspond to weeks 0-11 only.
'Antonovka' seedling ($y = 3.51 + 3.14x - 0.19x^2$, $r^2 = 0.29$);
'Bittenfelder' seedling ($y = 5.96 + 3.69x - 0.19x^2$, $r^2 = 0.27$);
'Borowinka' seedling ($y = 3.40 + 3.54x - 0.19x^2$, $r^2 = 0.28$);
'Golden Delicious' seedling ($y = 7.00 + 6.27x - 0.30x^2$, $r^2 = 0.70$);
***M. prunifolia* ($y = 1.75 + 4.66x - 0.26x^2$, $r^2 = 0.52$);**
***M. ranetka* ($y = 1.90 + 6.37x - 0.37x^2$, $r^2 = 0.80$).**

length was not strongly correlated with lateral budbreak or branching. Lateral budbreak was correlated with internode length only with 'Golden Delicious' sdlg. ($r = 0.47$, $n = 20$, $p = 0.0401$ (1991)) and *M. prunifolia* ($r = 0.68$, $n = 20$, $p = 0.0015$ (1991)). Similarly, branching was correlated with internode length only with 'Golden Delicious' sdlg. ($r = 0.69$, $n = 20$, $p = 0.0012$ (1991)) and *M. prunifolia* ($r = 0.62$, $p = 0.0044$ (1991); $r = 0.64$, $n = 20$, $p = 0.0029$ (1992)).

***Study* 2.** Time of spring budbreak ranged from mid-March with *M. ranetka* to mid-April with 'Golden Delicious' sdlg. (Table 4), resulting in a three-week range in the time of initial measurement. *M. ranetka* and 'Antonovka' sdlg. had the greatest terminal growth rate over the first seven weeks, but decreased rapidly thereafter (Fig. 1). 'Golden Delicious' sdlg. and 'Borowinka' sdlg., which grew at a similar rate, continued to grow for a much longer period than other populations. The decreased rate at which new lateral shoots developed was directly related to decreases in terminal growth rate, because lateral budbreak did not occur more than 20 cm from the shoot tip.

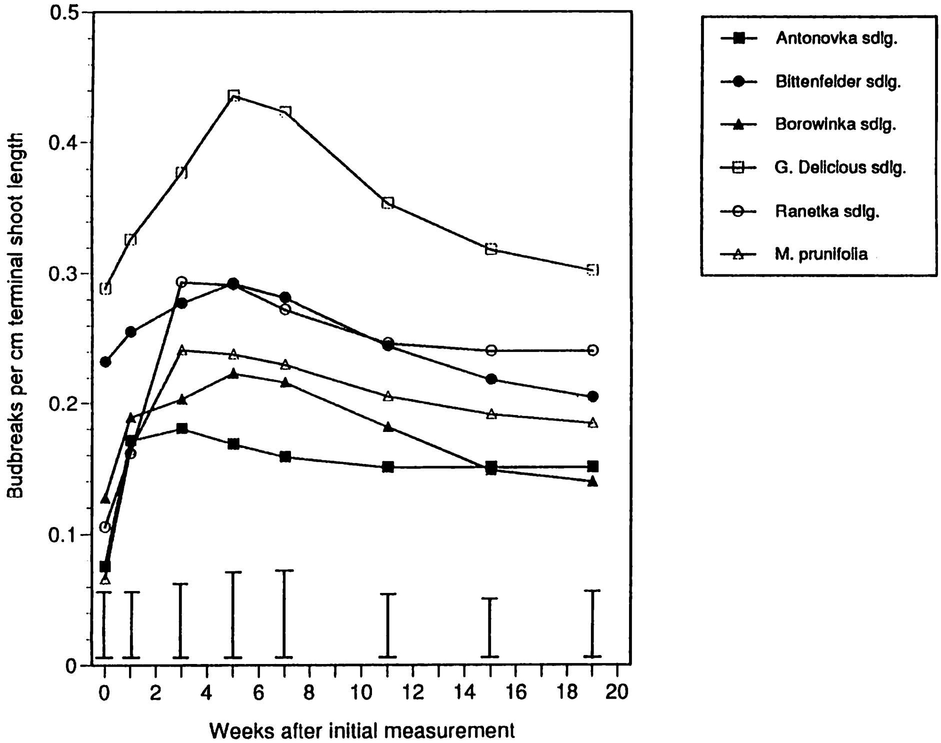

Figure 3. Lateral budbreak of upright shoots of seedling trees of five open-pollinated cultivars and one species of apple throughout the 1993 growing season in relation to terminal shoot height. Vertical bars indicate LSD at 0.05 level. Regression equations correspond to weeks 0-11 only.
'Antonovka' seedling ($y = 0.11 + 0.002x - 0.0017x^2$, $r^2 = 0.06$);
'Bittenfelder' seedling ($y = 0.23 + 0.019x - 0.0016x^2$, $r^2 = 0.02$);
'Borowinka' seedling ($y = 0.14 + 0.026x - 0.0021x^2$, $r^2 = 0.05$);
'Golden Delicious' seedling ($y = 0.29 + 0.045x - 0.0035x^2$, $r^2 = 0.19$);
***M. prunifolia* ($y = 0.10 + 0.048x - 0.0035x^2$, $r^2 = 0.30$);**
***M. ranetka* ($y = 0.12 + 00.56x - 0.0041x^2$, $r^2 = 0.42$).**

With all seedling populations, most of the lateral budbreaks occurred by week 5 (Fig. 2). 'Golden Delicious' sdlg. had two to three times the number of lateral budbreaks as other populations by week 19. Budbreak occurred at every node of most 'Golden Delicious' sdlg. shoots through week 7. However, one-half of the lateral shoots were less than 5 cm long, and therefore not considered branches. Throughout the growing season, 'Golden Delicious' sdlg. had the greatest number of lateral budbreaks in relation to terminal shoot length (Fig. 3), due to the large number of budbreaks early in the growing season and to the substantial budbreak which occurred after week 7.

Discussion

Even though terminal shoot growth and branching habit were quite variable within each seedling population, differences between populations were distinct and were greater than those which exist between most commercial cultivars. Environmental factors may have been partially responsible for the differences in growth rates seen by mid-summer. All populations, except 'Golden Delicious' sdlg., were derived from very cold-hardy parents (1) and,

Table 4. Dates of spring budbreak (1993) for six seedling populations.

Population	Budbreak date[z] (Julian days)
Antonovka sdlg.	89 b[y]
Bittenfelder sdlg.	98 c
Borowinka sdlg.	97 c
G. Delicious sdlg.	103 c
M. prunifolia	85 b
M. ranetka	77 a

[z]Each date represents mean of four trees.
[y]Mean separation within column by LSD at 0.05 level.

therefore, may have been adversely affected by extended high summer temperatures. The sharp decrease in the terminal growth rate of 'Antonovka' sdlg. shoots coincided with the onset of high temperatures (> 30C). Many shoots of *M. prunifolia* exhibited a dramatic shortening of internodes and small, malformed leaves at the shoot tip by late summer. Grochowska et al. (3) associated this "June effect" with a substantial reduction of root-produced gibberellins in the xylem and elevated phloem levels during high summer temperatures. Since shoot growth was not compared at specific dates, but at certain intervals following spring budbreak, a single period of high temperatures (or other environmental condition) may have affected each seedling population differently.

With all of the seedling populations, most of the branching on current-season growth occurred early in the growing season, when terminal growth was most rapid. Branching did not occur on the non-vigorous current-season growth of the second year. Short internodes have been associated with low vigor and limited branching in apple (2). However, Zagaja and Faust (6) found that shoot cross-sectional area and branching were not necessarily linked with internode length and suggested that different genetic mechanisms operate to control these traits. In our study, even though the terminal shoots with the greatest length and cross-sectional area within each population generally had the most branches and longest internodes, there were many equally vigorous shoots with a small number of branches and/or short internodes. Terminal shoot vigor obviously plays a role in lateral shoot development, but several genetic factors seem to be involved.

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Nitrogen Source and Timing for Blueberry

Nitrogen fertilizer increased yields and leaf nitrogen compared to unfertilized controls. Split application of urea (half at budbreak and half at petal fall) resulted in 10% higher yields than the same amount in a single application. Urea and two controlled release materials with different dissolution rates (3 to 4 months, 8 to 9 months) resulted in similar yields and leaf N levels when compared at the same rate of N. From Hanson and Retamales. *HortScience* 27(12):1265-1267, 1992.