

# Differential Growth Responses of Apple Species to Chilling and Root Pruning

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*Additional index words.* chilling requirement, dormancy, root regeneration potential, root regeneration capacity, budbreak, *Malus domestica*, *Malus anis*, *Malus prunifolia*, *Malus x robusta*, *Malus antonovka*, *Malus borwinka*, *Malus ranetka*

**Abstract.** *Malus domestica* Borkh., *M. anis*, *M. prunifolia* Borkh., *M. x robusta* Rehd., *M. antonovka*, *M. borwinka*, and *M. ranetka* bare-root seedlings were chilled at 5C for 0, 400, 800, 1200, or 1600 hours. After chilling treatments, one-half of the seedlings were root-pruned and all seedlings were placed in a greenhouse for 15 days. Quantitative differences between species in the timing and magnitude of new root and shoot growth responses to chilling were observed. Root pruning decreased and delayed the production of roots <0.6 mm in diameter in response to chilling, while the production of larger roots was less affected. Regeneration of both root types differed among species. For new large ( $\geq 0.6$  mm in diameter) root growth criteria, interactions between chilling hours and species were apparent. Chilling requirements and growing degree hour requirements for vegetative budbreak of each species were estimated.

## Materials and Methods

Recent studies indicated an enhancement of root regeneration potential in *M. domestica* following exposure to chilling temperatures (Young and Werner, 1984b, 1985b, 1986). Similar enhancements of root growth following artificial chilling or exposure to winter conditions have been reported for other species (DeWald et al., 1985; Farmer, 1975; Lathrop and Mecklenburg, 1971; Stone and Norberg, 1979; Webb, 1976, 1977). For *M. domestica* (Young and Werner, 1985b) and *Taxus cuspidata* Sieb. and Zucc. (Lathrop and Mecklenburg, 1971), this enhancement is thought to be perceived by the root system. However, quantitative data on chilling enhancement of *M. domestica* root growth are lacking.

Differences among species in root regeneration capacity following exposure to various levels of chilling have been reported (Webb, 1977). Differences in root regeneration capacity in response to exposure to chilling temperatures have also been reported between commercial apple rootstock (Young and Werner, 1984b, 1985b) and between half-sib families of *Pinus taeda* L. (DeWald et al., 1985). Such differences in root and shoot growth responses to chilling might be useful in apple cultivar and rootstock breeding. While root pruning has often been shown to reduce subsequent new shoot growth (Arnold and Struve, 1989a, 1989b; Geisler and Ferree, 1984) and sometimes root regeneration capacity (Arnold and Struve, 1989b), we found no information on the interaction of root pruning and chilling on root growth or on the effect of root size on the chilling response.

The objectives of this experiment were to: 1) quantify the effect of chilling on root and shoot growth, 2) determine if differences in root regeneration potential exist between species of *Malus*, 3) determine if root pruning alters root and shoot growth responses to chilling, and 4) estimate the chilling requirements and growing degree hour requirements for vegetative budbreak of the species included in this study.

One-year-old seedlings of *M. domestica*, *M. anis*, *M. antonovka*, *M. prunifolia*, *M. x robusta*, *M. borwinka*, and *M. ranetka* were lifted bare-root in early November from the nursery (Lawyer's Nursery, Plains, Mt.) after receiving <200 chilling hours. After lifting, seedlings were wrapped in polyethylene with roots surrounded by moist sphagnum peat, enclosed in waxed cardboard boxes, and shipped to Raleigh, N.C. There, they were placed in a cooler maintained at 13C until 15 Jan. 1988, then placed in a 5C cooler. After 0, 400, 800, 1200, and 1600 hr of chilling, 10 uniform seedlings of each species were removed from the cooler. Average seedling fresh weight (g), shoot length (cm), and number of vegetative buds were 16, 40, 34 for *M. domestica*; 18, 45, 32 for *M. anis*; 24, 45, 26 for *M. prunifolia*; 25, 106, 46 for *M. x robusta*; 22, 40, 25 for *M. antonovka*; 17, 45, 33 for *M. borwinka*; and 22, 97, 45 for *M. ranetka*. All seedlings were single stem whips (i.e., not more than one terminal bud per seedling) and only vegetative buds were present. On five seedlings of each species, all lateral roots were removed and the taproot pruned to 20 cm (root-pruned seedlings). Fresh weights of the removed root tissues were recorded. The remaining five seedlings of each species were left intact (unpruned seedlings). Total fresh weights were measured directly. Root fresh weights were determined nondestructively by the method of Young and Werner (1984a). Shoot fresh weights were determined by subtraction. Seedlings were planted in waxed cardboard milk cartons (2.3 liters) containing Turface (Applied Industrial Materials Co., Deerfield, Ill.) medium and placed in the greenhouse in a completely randomized design. Weekly, 125 mg N/liter from 20N-8.7P-16.6K water-soluble fertilizer (Peters Fertilizer Products, Fogelsville, Pa.) was applied. Temperatures were set at 24/18C (day/night) for 9 and 15 hr, respectively. Natural photoperiods were used.

At 3-day intervals, the number of buds broken (green showing between bud scales) and number of new shoots elongating 3 mm or more were recorded. Seedlings were destructively harvested at day 15. Characteristics measured included new and old shoot lengths, new and old shoot fresh weights, new shoot dry weight, total number of buds, old root fresh weight, new root fresh and dry weights, number and length of roots  $\geq 0.6$  mm in diameter (large roots), and number of roots <0.6 mm in diameter (small roots). Diameters of a random sample of large roots per plant were measured under a dissecting microscope. New root : new shoot ratios, percent budbreak (number of buds

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Table 1. Least squares means significance levels for hours of chilling at SC (C), species (S), root pruning (P), and interactions for various growth characteristics of apple seedlings.

Treatment	Root surface area	New root fresh wt	New root dry wt	Large root length	No. small roots	No. large roots	Root to shoot dry wt	Percent budbreak	Percent shoots >3 mm	New shoot length	New shoot fresh wt	New shoot dry wt
c	NS	NS	*	NS	***	NS	NS	***	***	***	***	S**
s	**	***	**	**	***	***	**	**	**	**	**	S**
P	NS	NS	NS	NS	***	NS	NS	NS	NS	***	***	***
C x S	**	**	NS	*	NS	NS	NS	NS	NS	NS	NS	NS
C x P	NS	NS	NS	NS	***	NS	NS	NS	NS	***	***	***
S x P	*	**	**	*	***	**	NS	NS	NS	NS	***	***
CXSXP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

\*\* \* \*\* \*NS Significant at  $P \leq 1\%$ ,  $0.1\%$ ,  $0.01\%$ , or not significant, respectively.

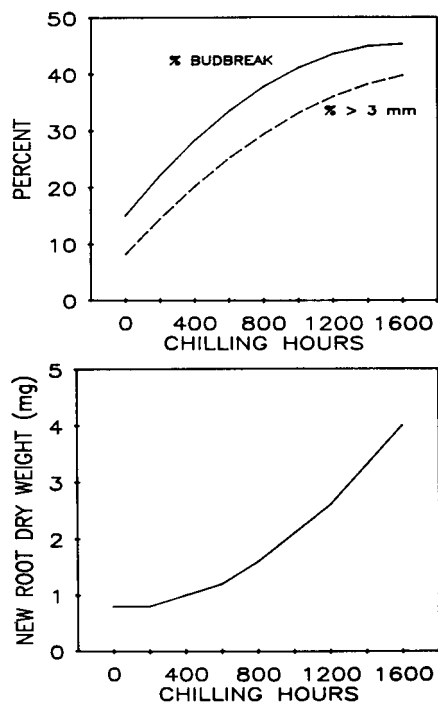


Fig. 1. Main effects of chilling hours at 5C (across species and root-pruning treatments) on budbreak, percent buds elongating  $\geq 3$  mm, and new root dry weight of seedlings after 15 days in a greenhouse. Regression equations are presented in Table 2.

broken/total number of buds), large root surface area ( $3.14 \times \text{radius} \times \sqrt{\text{radius}^2 + \text{new root length}^2}$ ), and growing degree hours (GDH) ( $\{[(\text{day temperature} - 4.5 \text{ C}) \times \text{hours at day temperature}] + (\text{night temperature} - 4.5 \text{ C}) \times \text{hours at night temperature}\} \times \text{days}$ ) required to reach 90% of maximum observed budbreak were calculated. After factorial analysis (7 species  $\times$  5 chilling levels  $\times$  2 root pruning levels) appropriate interactions and main effects were analyzed using least-squares means procedure and polynomial regression (SAS Institute, 1985).

### Results and Discussion

**Shoot growth responses.** No 3-way interactions were significant at the 1% level (Table 1), allowing the interpretation of main effects and 2-way interactions not involved in significant higher level interactions. Across species and root-pruning treatments, final percent budbreak (after 15 days in the greenhouse)

began to decrease in rate after  $\approx 1200$  chilling hours (CH) (Fig. 1, Table 2). The number of buds elongating  $\geq 3$  mm after 15 days in the greenhouse followed a similar pattern, but did not plateau until near 1600 CH (Fig. 1). Across chilling and root-pruning treatments, species differences in final percent budbreak were evident. A larger percentage of buds broke in *M. prunifolia*, *M.  $\times$  robusta*, *M. ranetka*, and *M. antonovka* than in *M. domestica*, *M. anis*, and *M. borwinka* (Table 3).

Regardless of chilling treatment, root pruning tended to reduce new shoot growth as measured by length, fresh weight, and dry weight (Table 4). The effect was significant in *M. prunifolia*, *M.  $\times$  robusta*, *M. antonovka*, and *M. ranetka* (Table 4). Across species, the tendency for root pruning to reduce shoot growth was evident regardless of chilling treatment (Fig. 2, Table 2). As CH increased, the effect became more pronounced (Fig. 2). The rate of increase in new shoot fresh and dry weights with increasing CH was less for root-pruned plants than unpruned plants through 1600 CH. Also, the rate of new shoot growth of root-pruned plants began to decrease between 1200 and 1600 CH, whereas the rate of new shoot growth in unpruned plants was not affected (Fig. 2). Reductions in shoot growth due to root pruning have been reported (Arnold and Struve, 1989a, 1989b; Geisler and Ferree, 1984). Although the basis for this effect in this experiment is unknown, various factors may be involved. The removal of root tissue at planting may reduce nutrient and carbohydrate reserves as well as the root surface area available for water and nutrient uptake. Additionally, sources of hormones may have been decreased. Root tips are sources of cytokinins (Richards and Rowe, 1977; Skene, 1975), and all intact root tips were removed from root-pruned plants. Substances with gibberellin-like activity also occur in apple rootstock (Ibrahim and Dana, 1971). Changes in root and shoot growth following root pruning may be the result of alterations in source/sink relationships (Geisler and Ferree, 1984; Young and Werner, 1982).

Chilling up to 1600 hr hastened the rate of budbreak in all species, although the magnitude of the response differed between species. Following 1600 CH, only 3 to 6 days were required for *M.  $\times$  robusta* and *M. ranetka* to reach maximum percent budbreak (Fig. 3), whereas *M. prunifolia* required  $\approx 9$  days followed by *M. domestica*, and *M. anis*, *M. antonovka*, and *M. borwinka*, which required between 9 and 12 days (Fig. 3). Some budbreak occurred in all species even in the absence of chilling (Fig. 3). Following 400 CH, there were substantial increases in the rates of budbreak and the final percent budbreak. An additional 400 hr (to 800 CH) substantially increased the rates of budbreak and the final percent budbreak in *M. do-*

Table 2. Formulas for polynomial regression equations used in Figs. 1-4. In equations: CH = chilling hours at 5C, D = days in greenhouse, BB = budbreak, NRFW = new root fresh weight (g), TLR = total large root length (mm), and LRSA = large root surface area (mm<sup>2</sup>).

Equation	R <sup>2</sup>	P value
<i>Figure 1</i>		
Final % BB = 0.150 + 0.00038*CH - 0.000000119*CH <sup>2</sup>	0.26	0.0001
% buds elongating ≥ 3 mm = 0.0823 + 0.000334*CH - 0.0000000856*CH <sup>2</sup>	0.41	0.0001
New root dry weight (g) = 0.000783 + 0.0000000127*CH <sup>2</sup>	0.04	0.0002
<i>Figure 2</i>		
New shoot fresh weight of pruned plants (g) = 0.0653 + 0.000358*CH	0.43	0.0001
New shoot fresh weight of unpruned plants (g) = 0.270 + 0.000000575*CH <sup>2</sup>	0.38	0.0001
New shoot dry weight of pruned plants (g) = 0.0263 + 0.0000468*CH + 0.0000000352*CH <sup>2</sup>	0.50	0.0001
New shoot dry weight of unpruned plants (g) = 0.0712 - 0.0000156*CH + 0.000000147*CH <sup>2</sup>	0.40	0.0001
Total shoot length of pruned plant (mm) = 28.8 + 0.000176*CH <sup>2</sup> - 0.0000000617*CH <sup>3</sup>	0.50	0.0001
Total shoot length of unpruned plants (mm) = 64.4 + 0.000143*CH <sup>2</sup>	0.45	0.0001
Number of small roots on pruned plants = 0.895 - 0.00379*CH + 0.00000346*CH <sup>2</sup>	0.11	0.0001
Number of small roots on unpruned plants = 29.8 + 0.0000445*CH <sup>2</sup>	0.14	0.0001
<i>Figure 3</i>		
% BB for <i>M. domestica</i> at:		
0 CH = -0.009 + 0.000622*D <sup>2</sup>	0.27	0.0001
400 CH = -0.0261 + 0.00126*D <sup>2</sup>	0.60	0.0001
800 CH = -0.0153 + 0.00154*D <sup>2</sup>	0.71	0.0001
1200 CH = -0.0194 + 0.0233*D	0.57	0.0001
1600 CH = -0.00657 + 0.0480*D - 0.00159*D <sup>2</sup>	0.56	0.0001
% BB for <i>M. anis</i> at:		
0 CH = -0.0103 + 0.000476*D <sup>2</sup>	0.44	0.0001
400 CH = -0.0177 + 0.000813*D <sup>2</sup>	0.34	0.0001
800 CH = 0.0104 - 0.0115*D + 0.00148*D <sup>2</sup>	0.58	0.0001
1200 CH = -0.0159 + 0.00409*D <sup>2</sup> - 0.000151*D <sup>3</sup>	0.63	0.0001
1600 CH = -0.0125 + 0.00792*D <sup>2</sup> - 0.000395*D <sup>3</sup>	0.70	0.0001
% BB for <i>M. prunifolia</i> at:		
0 CH = -0.0252 + 0.0188*D	0.57	0.0001
400 CH = -0.0104 + 0.00185*D <sup>2</sup>	0.70	0.0001
800 CH = -0.0233 + 0.00586*D <sup>2</sup> - 0.000260*D <sup>3</sup>	0.72	0.0001
1200 CH = -0.0556 + 0.0141*D <sup>2</sup> - 0.000744*D <sup>3</sup>	0.21	0.0001
1600 CH = 0.0263 + 0.0708*D - 0.00279*D <sup>2</sup>	0.76	0.0001
% BB for <i>M. ×robusta</i> :		
0 CH = -0.00395 + 0.000216*D <sup>2</sup>	0.35	0.0001
400 CH = -0.00668 + 0.0215*D	0.33	0.0001
800 CH = -0.0537 + 0.0341*D	0.54	0.0001
1200 CH = -0.0239 + 0.0876*D - 0.00325*D <sup>2</sup>	0.67	0.0001
1600 CH = 0.0127 + 0.167*D - 0.0183*D <sup>2</sup> + 0.000638*D <sup>3</sup>	0.53	0.0001
% BB for <i>M. antonovka</i> :		
0 CH = -0.0177 + 0.0162*D	0.39	0.0001
400 CH = -0.0218 + 0.00175*D <sup>2</sup>	0.77	0.0001
800 CH = -0.0279 + 0.00377*D <sup>2</sup> - 0.000139*D <sup>3</sup>	0.85	0.0001
1200 CH = 0.0148 + 0.00705*D <sup>2</sup> - 0.000347*D <sup>3</sup>	0.64	0.0001
1600 CH = 0.0218 + 0.00846*D <sup>2</sup> - 0.000430*D <sup>3</sup>	0.72	0.0001
% BB for <i>M. borwinka</i> :		
0 CH = -0.00876 + 0.000538*D <sup>2</sup>	0.42	0.0001
400 CH = -0.0105 + 0.00128*D <sup>2</sup>	0.58	0.0001
800 CH = -0.0125 + 0.00128*D <sup>2</sup>	0.70	0.0001
1200 CH = 0.00994 + 0.00162*D <sup>2</sup>	0.55	0.0001
1600 CH = -0.0114 + 0.00639*D <sup>2</sup> - 0.000312*D <sup>3</sup>	0.69	0.0001
% BB for <i>M. ranetka</i> :		
0 CH = -0.000763 + 0.00879*D	0.16	0.0018
400 CH = -0.0302 + 0.0238*D	0.35	0.0001
800 CH = -0.0121 + 0.0239*D	0.38	0.0001
1200 CH = 0.0428 + 0.00668*D <sup>2</sup> - 0.000327*D <sup>3</sup>	0.38	0.0001
1600 CH = 0.00591 + 0.142*D - 0.0155*D <sup>2</sup> + 0.000537*D <sup>3</sup>	0.50	0.0001

continued

Table 2. (Continued)

Equation	$R^2$	$P$ value
<i>Figure 4</i>		
For <i>M. domestica</i>		
NRFW = $-0.0218 + 0.000000479 \cdot \text{CH}^2 - 0.00000000280 \cdot \text{CH}^3$	0.12	0.0532
TLRL = $-6.93 + 0.00118 \cdot \text{CH}^2 - 0.000000688 \cdot \text{CH}^3$	0.09	0.1039
LRSA = $-473 + 0.0145 \cdot \text{CH}^2 - 0.00000851 \cdot \text{CH}^3$	0.10	0.0745
For <i>M. anis</i>		
NRFW = $0.000152 + 0.0000000140 \cdot \text{CH}^2$	0.09	0.0345
TLRL = $31.4 - 0.000137 \cdot \text{CH}^2 + 0.000000134 \cdot \text{CH}^3$	0.11	0.0903
LRSA = $-16.9 + 0.000646 \cdot \text{CH}^2$	0.09	0.0312
For <i>M. prunifolia</i>		
NRFW = $-0.00178 + 0.0000000142 \cdot \text{CH}^2$	0.20	0.0011
TLRL = $20.2 + 0.0000295 \cdot \text{CH}^2$	0.10	0.0291
LRSA = $123 + 0.441 \cdot \text{CH}$	0.08	0.0521
For <i>M. × robusta</i>		
NRFW = $0.00483 - 0.0000204 \cdot \text{CH} + 0.0000000201 \cdot \text{CH}^2$	0.22	0.0032
TLRL = $22.3 - 0.0757 \cdot \text{CH} + 0.0000745 \cdot \text{CH}^2$	0.19	0.0076
LRSA = $195 - 0.711 \cdot \text{CH} + 0.000695 \cdot \text{CH}^2$	0.20	0.0048
For <i>M. ranetka</i>		
NRFW = $0.0166 - 0.0000536 \cdot \text{CH} + 0.0000000362 \cdot \text{CH}^2$	0.13	0.0338
TLRL = $26.8 - 0.728 \cdot \text{CH} + 0.0000571 \cdot \text{CH}^2$	0.12	0.0514
LRSA = $355 - 1.15 \cdot \text{CH} + 0.000877 \cdot \text{CH}^2$	0.13	0.0428

Table 3. Main effects of species on root and shoot growth of apple seedlings of seven species of *Malus*.<sup>1</sup>

Criterion	<i>Malus domestica</i>	<i>Malus anis</i>	<i>Malus prunifolia</i>	<i>Malus × robusta</i>	<i>Malus antonovka</i>	<i>Malus borwinka</i>	<i>Malus ranetka</i>
Budbreak (%)	28 a	26 a	41 b	39 b	37 b	28 a	39 b
Shoots ≥ 3 mm (%)	23 ab	21 a	33 c	30 c	31 c	22 ab	28 bc
New root to shoot dry wt (g.g <sup>-1</sup> )	0.005 a	0.002 a	0.002 b	0.001 b	0.001 b	0.002 b	0.001 b

<sup>1</sup>Within criteria means followed by the same letter are not significantly different at  $P \geq .01$ . Values are means of 25 observations.

*mestica* and *M. × robusta*, whereas, for *M. prunifolia* and *M. antonovka*, the rates of budbreak increased, but the final percent budbreak did not. For *M. anis*, *M. borwinka*, and *M. ranetka*, little change in the rates of budbreak or the final percent budbreak were evident when chilling was increased from 400 to 800 hr. An increase from 800 to 1200 and 1200 to 1600 CH resulted in a substantial increase in the rate of budbreak for all species. For some species, this increase represented shoot growth enhancement due to over-chilling (beyond the CH required for maximum final percent budbreak). Changes in rate or extent of budbreak following 800 and 1200 CH and/or between 1200 and 1600 CH depended on whether the species' chilling requirement had been satisfied. Enhancement of budbreak by prolonged chilling has been reported for *M. domestica*, *Prunus avium* L., *Prunus persica* (L.) Batsch, and *Pyrus communis × Pyrus pyrifolia* (Burm) Nakai (Couvillon and Erez, 1985).

Chilling hour requirement data (estimated by the lowest 5C CH curve for budbreak that plateaued) indicated that *M. prunifolia* had the lowest CH requirement (between 800 and 1200 CH, but closer to 800 CH), as evidenced by a reduced rate of budbreak beginning at 800 CH (Fig. 3, Table 2). We cannot account for the greater budbreak for *M. prunifolia* at 1200 CH than at 1600 CH. *Malus antonovka*, *M. × robusta*, and *M. ranetka* also had CH requirements between 800 and 1200 CH, but higher than that of *M. prunifolia* (Fig. 3). *Malus domestica*,

*M. anis*, and *M. borwinka* had the highest CH requirements, between 1200 and 1600 CH (Fig. 3). Based on the lowest CH curve to plateau for each species (Fig. 3), the growing degree hour (GDH) requirements for 90% of maximum observed budbreak of all species, except for *M. × robusta*, were calculated to be between 3402 and 4536 GDH. *Malus × robusta* had a lower GDH requirement, between 2268 and 3402 GDH, than the other six species. CH requirements agreed with those reported for some clonal *M. domestica* rootstock, but GDH requirements were somewhat lower than those reported for *M. domestica* and *M. antonovka* clones (Young and Werner, 1985a).

*Root growth responses.* Since nearly all small roots regenerated from lateral roots that existed at planting, root pruning greatly reduced the number of small roots regenerated in all species (Table 4) and at all chilling treatments (Fig. 2). In this respect, species tended to fall into three groups: *M. prunifolia* and *M. × robusta* producing many small roots; *M. antonovka* and *M. ranetka* moderate numbers; and *M. domestica*, *M. anis*, and *M. borwinka* the fewest (Table 4). Across species, the number of small roots regenerated by unpruned plants remained low for the first few hundred chilling hours and then began to increase, whereas the number on root-pruned plants remained near zero through 1600 CH (Fig. 2). Root pruning affected both the timing and magnitude of small root regeneration. Root pruning drastically reduced the number of small roots regenerated, par-

Table 4. Interactions between root pruning and species on root and shoot growth of seven species of *Malus* averaged across chilling treatments.<sup>z</sup>

Species	Root pruned	New large root							
		No. new roots		Surface area (mm <sup>2</sup> )	Length (mm)	Fresh wt (g)	New shoot		
		<0.6 mm	≥ 0.6 mm				Length (mm)	Fresh wt (g)	Dry wt (g)
<i>Malus domestica</i>	Yes	2 a	20 a	4331 a	409 a	0.14 a	148 a	0.44 a	0.11 a
	No	25 a	5 b	811 b	83 b	0.02 b	165 a	0.56 a	0.14 a
<i>M. anis</i>	Yes	1 a	5 a	802 a	98 a	0.02 a	100 a	0.32 a	0.08 a
	No	20 a	2 a	404 a	46 a	0.01 a	121 a	0.44 a	0.11 a
<i>M. prunifolia</i>	Yes	1 a	1 a	128 a	10 a	0.01 a	125 a	0.41 a	0.12 a
	No	195 b	5 a	824 a	87 a	0.02 a	247 b	1.47 b	0.35 b
<i>M. × robusta</i>	Yes	1 a	1 a	116 a	10 a	0.00 a	143 a	0.31 a	0.10 a
	No	104 b	3 a	471 a	56 a	0.01 a	279 b	0.97 b	0.21 b
<i>M. antonovka</i>	Yes	0 a	1 a	89 a	10 a	0.00 a	100 a	0.34 a	0.10 a
	No	76 b	3 a	338 a	39 a	0.01 a	226 b	1.07 b	0.26 b
<i>M. borwinka</i>	Yes	3 a	5 a	1342 a	117 a	0.03 a	96 a	0.32 a	0.08 a
	No	16 a	2 a	305 a	32 a	0.01 a	157 a	0.53 a	0.13 a
<i>M. ranetka</i>	Yes	0 a	1 a	359 a	23 a	0.01 a	121 a	0.32 a	0.09 a
	No	73 b	2 a	187 a	24 a	0.00 a	217 b	0.72 b	0.20 b

<sup>z</sup>Within species and criteria means followed by the same letter are not significantly different at  $P \leq 0.01$ . Values are means of 35 observations. <sup>y</sup>< 0.6 mm = small and  $\geq 0.6$  mm = large roots.

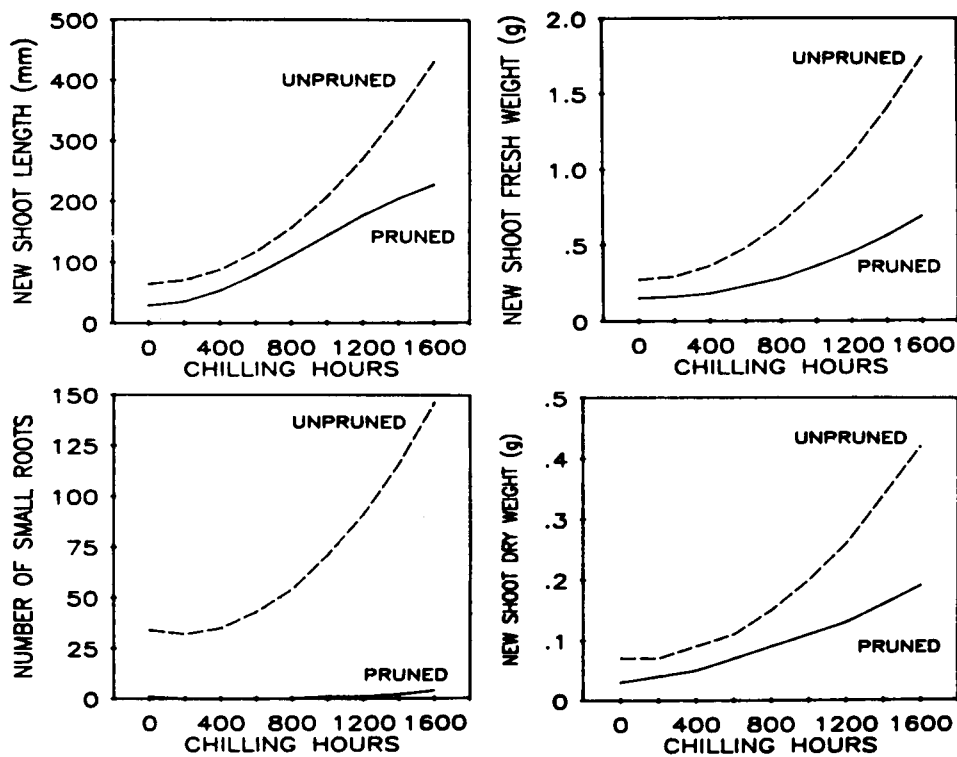


Fig. 2. Interactions between root pruning and chilling hours at 5C on new shoot fresh weight, new shoot dry weight, total new shoot length, and the number of small roots of seedlings (across seven species) after 15 days in a greenhouse. Regression equations are presented in Table 2.

ticularly at higher chilling levels (Fig. 2). Increases in the number of small roots regenerated (Fig. 2) occurred earlier in unpruned plants (400 to 800 CH) than in root-pruned plants (800 to 1200 CH). This result agrees with those of DeWald and Feret (1987) on *Pinus taeda* L.—when shoots were dormant or quiescent, new root growth consisted primarily of elongation of existing roots, rather than initiation of new roots.

Species differences in responses of large roots to chilling and root pruning were also apparent. Across chilling treatments, the number of large roots regenerated was unaffected by root prun-

ing for all species, except *M. domestica*, in which root pruning stimulated root production (Table 4). This same pattern was reflected in the root length, root surface area, and new root fresh weights (Table 4). Species differences in the number of roots regenerated were also reported by Gilman and Yeager (1988) in studies on autumn root regeneration of some deciduous hardwood species, although they did not distinguish between root sizes.

Across species, new root dry weights began to increase after  $\approx 400$  CH and continued to increase through 1600 CH (Fig. 1).

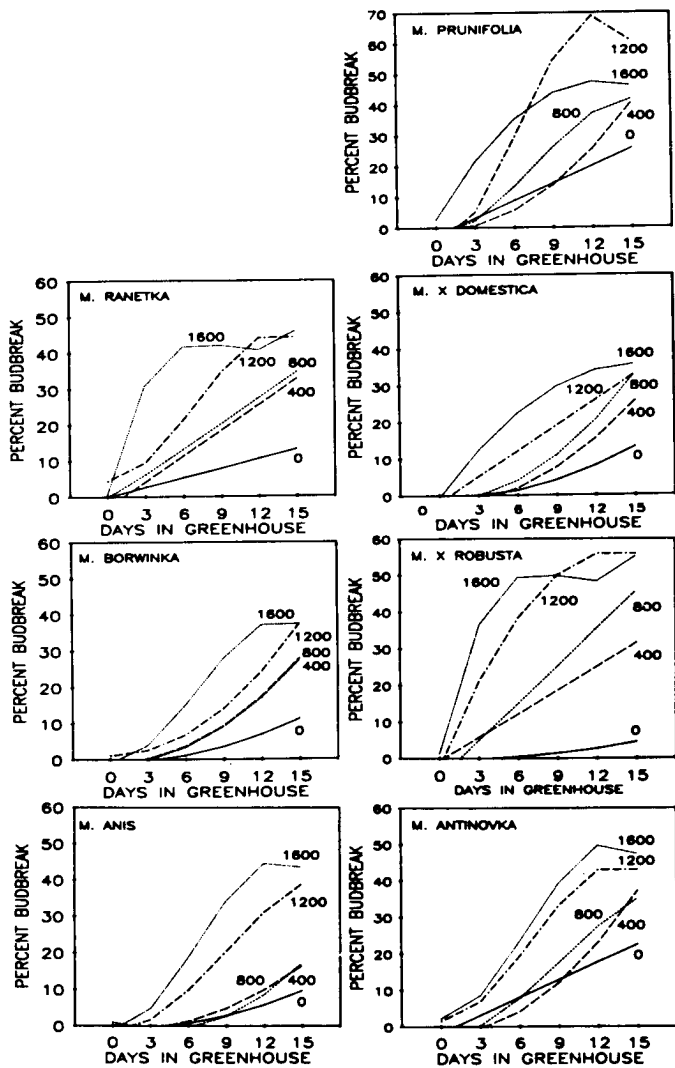


Fig. 3. Effects of chilling hours (CH) at 5C on budbreak of seven species of *Malus*. Regression equations are presented in Table 2.

Also, the ratio of dry weights of regenerated large roots to that of new shoots was greater for *M. domestica* than for other species (Table 3). While these effects on the large root dry weight were significant (Table 1), the weights fell near the precision error of the balance used ( $\pm 5$  mg), and thus may not be as reliable as other measures of large root regeneration (large root fresh weight, total length, and surface area).

Across root pruning treatments, two patterns of responses of large roots to chilling were apparent, and all three measures of root growth followed the same pattern (Fig. 4, Table 2). For *M. domestica*, regeneration of large roots began to increase before 400 CH, rose through 1200 CH, then decreased to 1600 CH. In *M. anis*, *M. prunifolia*, *M. × robusta*, and *M. ranetka*, regeneration remained at a low level or decreased slightly through 800 CH and then increased through 1600 CH. Regression coefficients (for the three characteristics vs. CH) were not significant in *M. antonovka* and *M. borwinka*.

Increases in-root regeneration potential during winter (outdoors) or during artificial chilling have been reported in *M. domestica* (Young and Werner, 1984b, 1985b, 1986), *Quercus rubra* L. (Farmer, 1975), *Fraxinus americana* L. (Webb, 1976), *A. saccharum* (Webb, 1977), *Pinus ponderosa* (Stone and Nor-

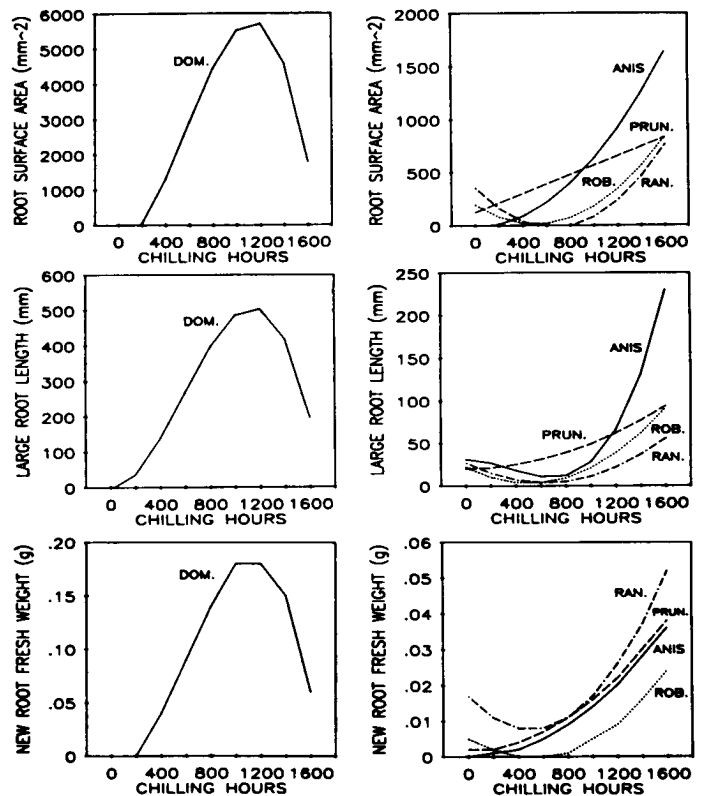


Fig. 4. Interactions between species and chilling hours at 5C on new root fresh weight, total large root length, and large root surface area of seven species of *Malus*. Abbreviations on graphs are: DOM. = *Malus domestica*, ANIS = *Malus anis*, PRUN. = *Malus prunifolia*, ROB. = *Malus × robusta*, RAN. = *Malus ranetka*. Regression equations are presented in Table 2.

berg, 1979), *P. taeda* (DeWald et al., 1985), and *Taxus cuspidata* (Lathrop and Mecklenburg, 1971). Differences in root regeneration in response to chilling between *M. domestica* rootstock (Young and Werner, 1984) and half-sib families of *P. taeda* (DeWald et al., 1985) have also been shown. The present study demonstrates quantitative differences between species of *Malus* in root growth responses to chilling. Because differences in root regeneration potential between half-sib families of *P. taeda* (DeWald et al., 1985) and *Pinus radiata* Don (Nambiar et al., 1982) are highly heritable, such differences may be exploitable traits for apple rootstock breeding.

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