Chilling of Endodormant Peach Propagules: II. Initial Seedling Growth

James W. Frisby¹ and Schuyler D. Seeley²

Plants, Soils, and Biometeorology Department, Utah State University, Logan, UT 84322-4820

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Abstract. We observed initial peach [*Prunus persica* (L.) Batsch] seedling growth after endodormant (ED) seeds ('Johnson Elberta') had been stratified for five durations (20 to 60 days) at eight constant temperatures (0 to 18C). Seedling growth increased and became more normal when seeds were stratified for longer durations at chilling temperatures. Stratification (St) at 0 to 6C (especially 2C) produced seedlings with more abnormal growth than St at higher temperatures (8 to 10C) at intermediate St durations (30 to 50 days). Growth of the primary stem increased with additional St (0 to 14C). Abnormal (epinastic) leaf development decreased following longer St treatments at 4 to 14C. Lateral shoot growth increased initially, then decreased after longer treatments at low temperatures (0, 4, and 6C) and decreased after St at higher temperatures (8 to 10C).

Seedlings from peach seeds or excised embryos that have received a minimal St treatment usually grow abnormally (Chao and Walker, 1966; Flemion, 1934; Flemion, 1936; Flemion and De Silva, 1960; Pollock, 1962; Tukey and Carlson, 1945). This abnormal seedling growth, called physiological dwarfing (PD), is characterized by small size, especially of the primary stem, abnormal (epinastic) leaf development on the primary stem, and normal leaf development on lateral branches (Flemion, 1959; Pollock, 1962). Occasionally, severely dwarfed seedlings appear to begin normal growth, but this is due to growth of a lateral branch originating near the terminal end of the primary stem (Davidson, 1934; Tukey and Carlson, 1945; Wang and Beardow, 1968). Physiological dwarfing of peach seedlings does not prevent normal root growth and development (Flemion and Waterbury, 1945).

Abnormal leaf development has been used as an indicator of PD (Flemion, 1959; Pollock, 1959; Pollock, 1962). However, Wang and Beardow (1968) suggested that PD and abnormal leaf development are separate growth problems. They characterized PD by the small size and short internodes of seedlings, and determined that less St is required to overcome true dwarfing than is required to overcome abnormal leaf development. They suggested that apex abortion coupled with abnormal leaves causes a plant to appear dwarfed that would otherwise have grown normally.

How is PD related to ED? Some suggest that delayed foliation (Chandler et al., 1937) and PD are manifestations of the same problem (Pollock, 1962), which is consistent with the fact that seed St enhances both germination and normal seedling growth. To clarify the relationship between ED and PD we quantified seedling growth following optimal and marginal St treatments. The treatments were designed to produce normal and physiologically dwarfed seedlings. The data from this study will also be used to compare initial seedling growth with the chilling responses of seeds (germination and emergence), seedlings (second season),

and cuttings after similar chilling treatments (Frisby and Seeley, 1993b).

Materials and Methods

Seedlings for this experiment were identical to those from the emergence experiment reported by Frisby and Seeley (1993a). Five replications of 10 seeds were used for each treatment. Seeds were stratified at 0, 2, 4, 6, 8, 10, 14, and 18C for 20, 30, 40, 50, and 60 days in factorial treatment combinations. After St, the seeds were planted in a completely randomized design in standard plastic flats (6 × 25 × 52 cm) that contained soilless medium (1 peat : 1 vermiculite : 0.5 perlite, by volume). Seeds from each replication were planted 3 cm deep in two adjacent rows of five seeds each. Four or five replications were planted in each flat. The greenhouse was maintained at 27/21C (day/night). A 16-h photoperiod was provided by natural sunlight supplemented with artificial light provided by 1000W high-pressure sodium lamps. Treatments to control mites, thrips, aphids, and fungus gnats included tricyclohexylhydroxystannane (cyhexatin) (50% WP, Dow Chemical Co., Midland, Mich.), O,O-diethyl O-(2-isopropyl-6-methyl-4-pyrimidinyl) (Diazinon), (25% EC, Chevron Chemical Co., San Ramon, Calif.), and (3-Phenoxyphenyl) methyl (+)-*cis*, *trans*-3-(2,2-dichloroethenyl)-2,2-dimethylcyclopropanecarboxylate (permethrin) (25.6% EC, ICI Americas, Wilmington, Del.).

After 56 days, the seedlings were harvested and the medium was washed from the roots. Seedling replicates were each placed in a plastic bag and stored at 0 to 2C until measured (within three weeks). Stems were separated from the roots at the cotyledonary node. Lateral shoots 21.5 cm were cut off and measured separately. Leaves were removed from the stems and shoots. Leaf area and dry weight (70C) of abnormal (epinastic) and normal leaves on the primary stems and leaves on lateral shoot were recorded separately. Primary stem length and dry weight, total lateral shoot length, and dry weight and number were recorded. The only root measurement was dry weight. The average plant size, instead of the total for the replication, was used in all calculations. A matrix of correlation coefficients was created to indicate relationships between the various growth characteristics. A two-way factorial

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¹Graduate Research Assistant.

²Professor.

Abbreviations: ED, endodormant; PD, physiological dwarfing; St, stratification.

Table 1. ANOVA of peach seedling ('Johnson Elberta') growth following seed St. Growth was averaged to a per seedling size before ANOVA. The factorial treatment combinations included five St durations (20, 30, 40, 50, and 60 days) at seven temperatures (0, 2, 4, 6, 8, 10, and 14C) in a completely randomized design. Leaf measurements included area (square centimeters) and dry weight (milligrams) of normal and abnormal leaves on the primary stem and leaves on lateral shoots. Stem measurement included length (millimeters) and dry weight of the primary stem and length, dry weight, and number of lateral shoots. Root dry weight was also recorded. Linear and polynomial trend analysis is also provided for significant main effects and interactions.

Source of variation	df	Mean squares										
		Leaf measurements						Stem measurements				
		Normal leaves		Abnormal leaves		Leaves on LS		Primary stem		Lateral shoots		
		Dry wt	Area	Dry wt	Area	Dry wt	Area	Length	Dry wt	Length	Dry wt	Number
Duration (D)	4											
Linear (.)	1	1955560***	48608.15***	134138.7***	1881.05***	97430***	3373.54***	2102.55***	650136***	262.62***	896.3 ^{NS}	9.96***
Quadratic (.)	1	92304***	1260.69***	247.2 ^{NS}	65.76*	19329**	812.71***	101.71***	44705***	97.84***	4053.6***	1.27**
Cubic	1	4403 ^{NS}	40.57 ^{NS}	4202.3*	116.20**	514 ^{NS}	21.53 ^{NS}	1.02 ^{NS}	18 ^{NS}	4.36 ^{NS}	119.1 ^{NS}	0.03 ^{NS}
Quartic	1	45354***	597.67**	453.8 ^{NS}	16.86 ^{NS}	339 ^{NS}	20.35 ^{NS}	24.40*	11083**	0.02 ^{NS}	7825.5***	0.21 ^{NS}
Temperature (T)	6											
Linear	1	177506***	4170.55***	15423.8***	186.28***	202866***	5574.31***	186.01***	11262**	656.99***	30407.2***	11.25***
Quadratic	1	3932 ^{NS}	16.74 ^{NS}	3815.4*	32.98 ^{NS}	5980 ^{NS}	232.26 ^{NS}	2.95 ^{NS}	5321 ^{NS}	14.32 ^{NS}	494.2 ^{NS}	0.54 ^{NS}
Cubic	1	65142***	1626.06***	23109.6***	287.50***	14650**	259.87*	51.18**	5428 ^{NS}	34.75*	2956.9**	0.16 ^{NS}
Residual	3	25975***	710.19***	597.9 ^{NS}	10.38 ^{NS}	11791***	343.43**	35.81***	11311***	34.27**	1939.2***	0.52*
D x T	24											
D ₁ x T ₁	1	9748 ^{NS}	189.89 ^{NS}	183.2 ^{NS}	20.61 ^{NS}	184 ^{NS}	1.20 ^{NS}	1.72 ^{NS}	850 ^{NS}	1.29 ^{NS}	0.1 ^{NS}	0.02 ^{NS}
D ₁ x T _q	1	148093***	3580.22***	16145.4***	203.77***	20078**	748.77***	109.04***	38198***	76.13***	2548.9**	1.69***
D _q x T ₁	1	27675**	665.97**	1372.0 ^{NS}	14.48 ^{NS}	13933*	635.56**	8.90 ^{NS}	860 ^{NS}	69.41**	2127.2**	1.77***
D _q x T _q	1	20221**	372.78*	437.6 ^{NS}	17.02 ^{NS}	1398 ^{NS}	28.25 ^{NS}	5.05 ^{NS}	1734 ^{NS}	3.69 ^{NS}	201.8 ^{NS}	0.04 ^{NS}
Residual	20	10995***	293.62***	936.7 ^{NS}	14.71 ^{NS}	4135**	118.28*	14.82***	4663***	17.00***	846.9***	0.32**
Error	135	2707	82.75	709.2	10.62	1778	60.19	5.01	1620	6.31	276.9	0.15
												4427

^{NS,*,***} Nonsignificant or significant at P = 0.05, 0.01, or 0.001, respectively.

analysis of variance (ANOVA) was used to analyze seedling growth data.

Results and Discussion

Very few seedlings were obtained after seed St at 18C. Therefore, only St temperatures between 0 to 14C were used in the ANOVA. Few seedlings were obtained after treatment for 20 and 30 days at 14C. These values are suspect due to the few seedlings obtained and are presented for comparison only. Due to the many temperature treatments, all replications for each temperature were treated in one temperature-controlled chamber simultaneously. We understand that this caused the error terms to underestimate the true variability of the systems. However, the probabilities for the F tests were extremely low and indicate significance with much larger error terms (Table 1).

All seedling growth measurements were significant for the main effects of St duration and temperature (Table 1). All growth measurements were significant for the duration by temperature interaction except root dry weight. Although many values were significant, only representatives for each group are presented.

The main effect of St duration (averaged over all St temperatures) showed a divergence between normal and physiologically dwarfed seedling growth and development as St time increased (Fig. 1). When seeds were stratified for longer durations, primary stem, normal leaf, and root dry weights increased, while lateral shoot, lateral shoot leaf, and abnormal leaf dry weights decreased. The biggest changes in seedling growth and development took place after 40 days of seed St. Seedling growth has been reported by others to increase with longer St treatments (Sharma and Singh 1978; Toit et al., 1979; Zigas and Coombe, 1977a).

A similar divergence in dry weights was noticed for the main effect of St temperature [averaged over all St durations (Fig. 2)]. Seedlings obtained from St at 2C had less primary stem growth and

more normal leaf development than those obtained from St at other tested temperatures. These seedlings also had more lateral stem growth and leaves on lateral stems. Seedlings obtained from St at relatively high St temperatures (8 to 14C) had good primary stem growth with less lateral growth and abnormal leaf development.

Fleming and Waterbury (1945) reported that root growth of physiologically dwarfed seedlings is normal. We, however, saw significant changes in root dry weight according to the seed St treatment (Figs. 1 and 2). To help explain this discrepancy an ANOVA was calculated on the root : shoot ratio. Neither the main effects of duration and temperature nor the interaction were significant for root : shoot ratio (data not presented). Therefore, the

Fig. 1 Main effect of seed St duration on seedling ('Johnson Elberta') primary stem (PS), normal leaf (NL), root (R), abnormal leaf (AL), lateral shoot (LS), and lateral shoot leaf (LSL) dry weights (Bars = LSD 0.05). Values were averaged over seven St temperatures (0, 2, 4, 6, 8, 10, and 14C). Trend analysis is provided in Table 1.

Fig. 2. Main effect of St temperature on seedling ('Johnson Elberta') primary stem (PS), normal leaf (NL), root (R), abnormal leaf (AL), lateral shoot (LS), and lateral shoot leaf (LSL) dry weights (Bars = LSD 0.05). Values were averaged over five St durations (20, 30, 40, 50, and 60 days). Trend analysis is provided in Table 1.

differences in root growth were only due to the different sizes of the seedlings due to the seed St treatment. Thus, our data supports the observations of Flemion and Waterbury (1945).

The main effects of St duration and temperature give only generalized results, since the interactions were significant (except for root dry weight). Responses observed after chilling at 2C are

difficult to explain without investigating the results of interactions between St duration and temperature.

Primary stem and normal leaf growth varied in response to seed St temperature and duration (Fig. 3). All seedlings that emerged after only 20 days of seed St had short primary stems with some normal leaf area. Primary stem and normal leaf growth increased when the seeds were stratified for longer times at all temperatures. Enhanced primary stem and normal leaf growth was first observed after 30 days of St at the higher temperatures ($\geq 8^{\circ}\text{C}$). Seeds stratified at 2C did not show greatly improved primary stem or normal leaf growth after longer seed St treatments.

Lateral shoot length (total per seedling) changed more elaborately than primary stem growth in response to seed St duration and temperature (Fig. 3). Lateral shoot growth after seed St at 2C was high and stable despite the length of the St treatment. Lateral shoot length after seed St at 0, 4, or 6C increased between 20 to 30 days of St, but decreased as the St duration increased. Lateral shoot growth decreased with additional St at 8 and 10C. Seedlings obtained after St at 14C never developed significant lateral shoot growth after any chilling duration.

Abnormal leaf area was highest after seed St at 4 and 6C for 20 and 30 days (Fig. 3). It decreased to near zero after additional seed St at 4 to 14C. However, abnormal leaf area did not change significantly with longer St treatments at 0 or 2C.

Correlation coefficients for comparisons between dry weight and area were high for each corresponding leaf type (Table 2). High correlations between normal leaf dry weight and normal leaf

Fig. 3. Interactions between seed St duration (20, 30, 40, 50, and 60 days) and temperature (0, 2, 4, 6, 8, 10, and 14C) on seedling ('Johnson Elberta') primary and lateral shoot lengths, and normal and abnormal leaf areas. Values for seedlings stratified for 20 and 30 days at 14C were obtained from few seedlings. The bars equal the LSD 0.05 for differences among duration and temperature combinations. Trend analysis is provided in Table 1.

Table 2. Correlation coefficients for comparisons between primary stem and lateral shoot growth with normal and abnormal leaf dry weight and area and lateral shoot (LS) leaf dry weight of peach seedlings ('Johnson Elberta').

Measurements	Correlation coefficients (<i>r</i>) for linear regression				
	Normal leaves		Abnormal leaves		LS leaves
	Dry wt	Area (NLA)	Dry wt (ALDW)	Area (ALA)	Dry wt (LSLDW)
LS leaf area	-0.64***	-0.65***	0.33***	0.37***	<u>0.98***</u>
LSLDW	-0.64***	-0.61***	0.35***	0.36***	
ALA	-0.72***	-0.69***	<u>0.97***</u>		
ALDW	-0.71***	-0.71***			
NLA	<u>0.98***</u>				

Correlations for values underlined explained >70% of the variability.

***Significant at *P* = 0.001.

Table 3. Correlation coefficients for comparisons between primary stem length and dry weight, lateral shoot length, dry weight and number, root dry weight, lateral shoot leaf area (LSLA), and normal (NLA) and abnormal (ALA) leaf area on the primary stem of peach seedlings ('Johnson Elberta'). Multiple regression equations for primary stem growth are also included (see also Table 2).

Measurements	Correlation coefficients (<i>r</i>) for linear regression					
	Primary stem		Lateral shoots			Root
	Length	Dry wt (PSDW)	Length (LSL)	Dry wt (LSDW)	No. (LSN)	dry wt (RDW)
LSLA	-0.63***	-0.53***	<u>0.97***</u>	<u>0.94***</u>	<u>0.93***</u>	-0.22**
NLA	<u>0.94***</u>	<u>0.92***</u>	-0.57***	-0.61***	-0.65***	0.68***
ALA	-0.59***	-0.54***	0.36***	0.36***	0.34***	-0.34***
RDW	0.65***	0.76***	-0.17*	-0.12 ^{NS}	-0.32***	
LSN	-0.68***	-0.61***	<u>0.90***</u>	0.82***		
LSDW	-0.57***	-0.44***	<u>0.98***</u>			
LSL	-0.60***	-0.49***				
PSDW	<u>0.95***</u>					
Multiple regression equations for PS growth ²						<i>R</i> ²
PSDW	= 47. + 4.1 × NLA*** + 3.1 × ALA*** + 0.26 × LSDW*					<u>0.88***</u>
PSL	= 51. + 2.0 × NLA*** + 0.92 × ALA*** - 0.12 × LSL**					<u>0.89***</u>

²Values for the equations were dry weight in milligrams, length in millimeters, and leaf area in square centimeters.

Correlations for values underlined explained >70% of the variability.

^{NS,*,***} Nonsignificant or significant at *P* = 0.05, 0.01, or 0.001, respectively.

area, abnormal leaf dry weight and abnormal leaf area, and lateral shoot leaf dry weight and lateral shoot leaf area were expected.

Primary stem and lateral shoot dry weights correlated highly with primary stem and lateral shoot length, respectively (Table 3). Primary stem and lateral shoot length also correlated highly with normal leaf and lateral shoot leaf area, respectively (Fig. 4). Correlations between normal stem growth (length, dry weight) and abnormal leaf or lateral shoot growth (length, dry weight) were significant and could indicate competition; however, the correlation coefficients were very low. Also, multiple regression showed that normal leaf, abnormal leaf, and lateral shoot growth all correlated positively with primary stem dry weight (Table 3). Yet, lateral shoot growth correlated negatively with primary stem length, also using multiple regression. Root dry weight did not correlate highly with any measurement reported.

No simple index that would explain all the seedling growth responses to various St treatments was found, probably due to a confounding affect of the condition that produces abnormal leaves as suggested by Wang and Beardow (1968). Unstratified or insufficiently stratified seeds or seeds stratified at ineffective tempera-

tures (i.e., 14C for 20 days, Fig. 3) would produce seedlings that would exhibit true PD. These seedlings would exhibit limited growth. If the shoot apex died due to the abnormal leaf condition, extensive lateral shoot growth would not occur due to the limited growth of the true PD. Seeds stratified for a longer time or at more effective temperatures would not have the limited growth due to true PD. Death of the shoot apex due to the abnormal leaf condition of these seedlings would encourage lateral shoot growth. True PD was partly overcome with 20 days of St at 0 to 10C (see lateral shoot growth, Fig. 3). Not all seedlings with abnormal leaves had apex abortion (by observation). If the shoot apex did not die because of the abnormal leaf condition, then the primary stem would continue to grow, although not normally, and lateral shoot growth would be inhibited by apical dominance, which was probably what happened after St at 4 to 10C for 50 to 60 days. Likewise, PD might be continuous, with semidwarfed seedlings being possible without the anomalous leaf problem. Therefore, primary stem and lateral shoot growth were confounded by the abnormal leaf condition and by true PD.

Seeds stratified at 0 and 2C had a substantial amount of

Fig. 4. Correlations between primary stem length and normal leaf area and lateral shoot length and lateral shoot leaf area of peach seedlings ('Johnson Elberta'). Seedlings were obtained after St treatments of 20 to 60 days at temperatures from 0 to 14C.

abnormal leaves, even with long St durations (Fig. 3). The abnormal leaf condition that caused apex abortion was not overcome after longer St treatments at 2C. Thus, seeds stratified at 2C produced seedlings with inhibited primary stem growth and forced lateral shoot growth due to an inability to overcome the abnormal leaf condition.

This confounding may explain why lateral shoot and abnormal leaf growth had both negative and positive correlations (Table 3). Lateral shoot growth and abnormal leaf growth are symptoms of problems that can prevent primary stem growth. This situation is evident by the negative correlation coefficients for linear regressions. Yet, abnormal leaf growth, when present, could provide nutrients to the primary stem, although not as efficiently as normal leaves. Likewise, the abnormal leaf condition did not always cause apex abortion. However, lateral shoot growth occurred only after apex abortion, being a symptom of terminated primary stem growth. The lateral shoot may have provided some nutrients to the primary stem, causing it to be heavier, but the length was fixed before lateral stem growth was induced.

Experiments by Zigas and Coombe (1977a, 1977b) give some

clues about the hormonal control of the induction of the abnormal leaves. Their experiments show a requirement of both gibberellic acid (GA) and abscisic acid (ABA) before abnormal leaves are produced. They postulated that ABA is provided by the seed coat and GA is released or produced during St. It has been reported that ABA levels decrease (Bonamy and Dennis, 1977; Diaz and Martin, 1972) and that GA levels increase (Mathur et al., 1971) during peach seed St.

We speculate that 0 and 2C may have been excellent St temperatures for GA release or production in peach seeds, especially with short St durations. Evidence for this was the rapid seedling emergence promoted by St at these temperatures (Frisby and Seeley, 1993a). Likewise, 0 and 2C may not have been favorable for degradation of ABA, or ABA production was enhanced during forcing. We speculate that 8 and 10C were good temperatures for ABA degradation but not as good for GA production. This relationship suggests that alternating seed St temperatures may provide better seedling growth than isothermal temperatures as suggested by Erez and Couvillon (1987) for chilling of peach buds.

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