

Influence of Rootstock, Scion, and Water Deficits on Growth of 'Colt' and 'Meteor' Cherry Trees

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Abstract. Growth and physiological characteristics were evaluated in autografted and reciprocally grafted plants of *Prunus avium* L. × *pseudocerasus* Lindl. 'Colt' and *Prunus cerasus* L. 'Meteor'. Containerized plants were grown for 150 days in a greenhouse under either well-watered or water-stressed conditions. Both the scion and rootstock influenced growth (relative growth rate, \bar{R}), morphological [leaf area : root surface area (LARSA) and specific leaf area (SLA)], and physiological (mean net assimilation rate, \bar{E}) characteristics of grafted plants. Regardless of the watering regime, plants with 'Meteor' scions and 'Colt' rootstocks maintained higher \bar{R} than plants with 'Colt' scions and 'Meteor' rootstocks. This enhanced growth occurred as a result of higher \bar{E} . Measurements on water-stressed plants also showed that the graft combination of 'Meteor' on 'Colt' had the lowest LARSA, while the reciprocal combination of 'Colt' on 'Meteor' had the highest. Differences in LARSA among water-stressed plants primarily reflected changes in SLA, as influenced by both rootstock and scion, and not in partitioning of dry weight between these organs.

A wide range of morphological and physiological characteristics has been found to be affected by rootstocks, scions, and their resulting interactions (Lockard and Schneider, 1981; Syvertsen, 1985; Tubbs, 1973). Many of these characteristics have the potential for improving plant water relations and growth during water stress. For example, rootstocks have been found to influence transpiration rate and crop water-use efficiency in peach (*Prunus* spp.) (Natali et al., 1983), leaf conductance in apple (*Malus* spp.) (Giulivo et al., 1985), leaf osmotic potential at full turgor and calculated hydraulic conductivity in apple (Olien and Lakso, 1986), root distribution in citrus (*Citrus* spp.) (Castle and Krezdorn, 1975, 1977), and midday leaf water potentials in citrus (Castle and Krezdorn, 1977), peach (Natali et al., 1983), and apple (Giulivo et al., 1985; Olien and Lakso, 1986). Few of these experiments, however, have examined how the influence of different rootstocks and scions can contribute to whole-plant growth and maintenance of growth under water stress.

Classical plant growth analysis provides a comprehensive method for evaluating whole-plant growth that integrates growth over time and permits the partitioning of growth into

morphological and physiological components (Hunt, 1982). Plant growth analysis has been used extensively as a method for evaluating and comparing growth of various species and progenies (Cain and Ormrod, 1984; Grime and Hunt, 1975; Ledig and Perry, 1969; Pollard and Wareing, 1968; Sweet and Wareing, 1968), the effects of water stress on growth processes (Ashenden et al., 1975; Jarvis and Jarvis, 1963), and the influence of rootstocks on plant growth and structure (Dudney, 1974; Vyvyan, 1955).

In this study, we combined the reciprocal grafting protocol of Vyvyan (1955) and plant growth analysis to examine the relationships between scion, rootstock, and water stress in two cherry cultivars with varying growth habits: *Prunus cerasus* 'Meteor', a strongly determinate grower, and *P. avium* × *pseudocerasus* 'Colt', a strongly indeterminate grower. The objective of this study was to evaluate the relative influence of rootstock and scion on plant growth and partitioning patterns in graft combinations of 'Meteor' and 'Colt' cherry trees under well-watered and water-stressed conditions.

All plant material was clonal and ranged in stem caliper from 1 to 2 cm. Stems were pruned to a uniform length of 20 cm from the stem-root junction. Root systems were pruned to a uniform overall dimension of 21 cm in diameter and 30 cm in length to conform to container dimensions. Cleft grafts, consisting of two scions with three buds each, were made between 2 and 23 Feb. 1985. Plants were then placed in the dark at 5°C with roots packed in moist peat before being planted.

Plants were potted on 14 Mar. 1985 in 11.4-liter black plastic containers with 8 liters of medium consisting of 2 sand : 1

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Table 1. Mean relative growth rate (\bar{R}), mean net assimilation rate (\bar{E}), and leaf area ratio (LAR) for graft combinations of 'Meteor' and 'Colt' cherry after 150 days of well-watered or water-stressed conditions.

Treatments	\bar{R} (mg·g ⁻¹ ·wk ⁻¹)	\bar{E} (mg·cm ⁻² ·wk ⁻¹)	LAR (cm ² ·g ⁻¹)
Well-watered			
Meteor/Colt	86.4	4.1	19.5
Meteor/Meteor	79.2	3.5	21.8
Colt/Colt	71.8	2.1	34.9
Colt/Meteor	64.0	1.8	38.3
Water-stressed			
Meteor/Colt	31.2	3.0	15.4
Meteor/Meteor	22.4	2.0	14.8
Colt/Colt	21.9	2.1	16.4
Colt/Meteor	14.4	1.4	16.4
Single degree-of-freedom contrasts			
Irrigation (Irr.)	**	**	**
Scion	**	**	**
Stock	*	**	NS
Scion × stock	NS	NS	NS
Irr. × scion	NS	**	**
Irr. × stock	NS	NS	NS
Irr. × scion × stock	NS	NS	NS
LSD _{0.05}	16.1	0.6	5.2

NS,*,**Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively, $n = 5$.

sphagnum peat : 1 soil (by volume) that had been pasteurized and screened through 1.3-cm² mesh hardware cloth. Pea-sized gravel (1.1 liters) was placed in the bottom of each container to prevent loss of medium. Plants were grown in a glasshouse in Ithaca, N.Y., under natural light with the air maintained between 16 to 24°C. Once plants broke dormancy and success of the graft union was assured, plants were pruned to one scion containing two growing buds. Water-soluble fertilizer (10N-10P₂O₅-10K₂O) was applied at 10-day intervals at 200 mg N/liter. All plants were well-watered before the initiation of treatments.

The experiment was arranged as a three-way factorial (2 scions × 2 rootstocks × 2 watering regimes) in a completely randomized design. The graft combinations consisted of 'Meteor' and 'Colt' grafted onto

rootstocks of the same cultivar ('Meteor'/'Meteor' and 'Colt'/'Colt') and plants reciprocally grafted onto the rootstock of the alternate cultivar ('Meteor'/'Colt' and 'Colt'/'Meteor').

The two watering regimes consisted of a well-watered and water-stressed treatment initiated on 18 Apr. 1985. Water-stressed plants were watered to container flow-through at 10-day intervals to provide repeated periods of water stress over the duration of the experiment. Well-watered plants were irrigated daily.

Five plants from each treatment combination were harvested 150 days after planting. Leaf areas (L_A) were measured with a leaf area meter (Model 3100; LI-COR, Lincoln, Neb.). Roots were washed free of soil, and root lengths were determined on roots <5 mm in diameter using a video image

analysis system as described by Barnett et al. (1987). Root volumes were determined for the same root samples by volume displacement (Johnson, 1983). Root surface area was then calculated based on length and volume, assuming roots were round in cross section with uniform diameter. Because of the extensive time and labor required for measuring root length and surface area, these measurements were taken on the water-stressed plants only. Dry weights were determined for leaves, roots, and stems after 96 h at 70°C. A sample of 10 plants (five of each species) was harvested at planting to estimate initial plant dry weights for use in growth analysis. These dry weights were estimated for each plant based on individual fresh weights and a dry : fresh weight regression equation ($R^2 = 0.988$). Regression analysis showed no species × fresh weight interaction ($P = 0.22$). Thus, data were pooled and one regression equation was used to predict dry weight regardless of rootstock or scion.

Mean relative growth rate (\bar{R}), the mean change in dry weight per unit time per unit dry weight, was calculated according to (Radford, 1967):

$$\bar{R} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1},$$

where W_1 and W_2 = total dry weight at times (t) 1 (planting) and 2 (harvest), respectively.

Mean net assimilation rate (\bar{E}), also known as mean unit leaf rate, is defined as the mean rate of increase in total dry weight per unit of leaf area per unit of time (Ledig, 1974) and was calculated according to Radford (1967) as:

$$\bar{E} = \frac{2(W_2 - W_1)}{(L_{A,2} + L_{A,1})(t_2 - t_1)},$$

where $L_{A,1}$ and $L_{A,2}$ = leaf area at times 1

Table 2. Influence of scion, rootstock, and irrigation treatment on leaf area (L_A), leaf weight : root weight, specific leaf area (SLA), specific root area (SRA), leaf area : root length (LARL), and leaf area : root surface area (LARSA) for 'Meteor' and 'Colt' cherry after 150 days of irrigation treatments.

Treatments	L_A (cm ² , 1000s)	Leaf wt : root wt (g·g ⁻¹)	SLA (cm ² ·g ⁻¹)	SRA (cm ² ·g ⁻¹)	LARL (cm ² ·cm ⁻¹)	LARSA (cm ² ·cm ⁻²)
Well-watered						
Meteor/Colt	5.28	0.40	102	---	---	---
Meteor/Meteor	5.32	0.33	124	---	---	---
Colt/Colt	10.3	0.74	124	---	---	---
Colt/Meteor	10.6	0.69	136	---	---	---
Water-stressed						
Meteor/Colt	1.32	0.23	97	44	0.12	0.51
Meteor/Meteor	1.47	0.18	115	36	0.23	0.89
Colt/Colt	1.55	0.18	129	30	0.23	0.84
Colt/Meteor	1.77	0.17	137	23	0.29	1.14
Single degree-of-freedom contrasts						
Irrigation (Irr.)	**	**	NS	---	---	---
Scion	**	**	**	NS	**	*
Stock	NS	NS	**	NS	**	**
Scion × stock	NS	NS	*	NS	NS	NS
Irr. × scion	**	**	**	---	---	---
Irr. × stock	NS	NS	NS	---	---	---
Irr. × scion × stock	NS	NS	NS	---	---	---
LSD _{0.05}	0.76	0.12	7.2	21	0.05	0.29

NS,*,**Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively. Values are means; $n = 5$ for L_A , leaf weight : root weight, and SLA; $n = 3$ for SRA, LARL, and LARSA.

and 2, respectively. Both \bar{R} and \bar{E} were calculated as mean rates averaged over the period from planting to harvest. Leaf area ratio (LAR) was calculated as the ratio of L_A per plant dry weight. To avoid assumptions regarding the integration of LAR over time (Radford, 1967), LAR is presented as an instantaneous value as measured at the terminal harvest.

Predawn (0400–0500 HR) leaf water potentials were measured using a pressure chamber (Plant Moisture Status Console, Soil Moisture Corp., Santa Barbara, Calif.) on replicate plants included in the experiment for that purpose. Measurements of predawn water potential were taken starting 70 days after planting and again at 20-day intervals thereafter. These dates coincided with the last day of a given dry-down cycle. One measurement was taken per plant on the third or fourth fully expanded leaf.

Because of differences in evaporative demand over the treatment period, the level of stress for each 10-day dry-down period varied. Mean predawn water potentials for water-stressed plants were -2.6 , -2.0 , -0.8 , -3.6 , and -1.3 MPa at the end of individual dry-down intervals measured on days 70, 90, 110, 130, and 150, respectively.

Growth analysis. \bar{R} decreased for all graft combinations in response to water stress (Table 1). However, plants with 'Meteor' scions maintained higher \bar{R} than plants with 'Colt' scions, irrespective of the irrigation treatment. The rootstock influenced \bar{R} such that plants with 'Colt' rootstocks had higher \bar{R} than plants with 'Meteor' rootstocks, irrespective of the irrigation treatment.

As was found for \bar{R} , \bar{E} typically decreased in response to water stress and was significantly affected by both the rootstock and scion. Plants with 'Meteor' scions maintained higher \bar{E} than plants with 'Colt' scions; however, this pattern was accentuated under well-watered conditions. Plants with 'Colt' rootstocks maintained higher \bar{E} than plants with 'Meteor' rootstocks, regardless of the irrigation treatment. Under well-watered conditions, plants with 'Meteor' scions had lower LAR than did plants with 'Colt' scions. However, values of LAR were similar under water-stressed conditions. There was no effect of the rootstock on LAR.

Plants with 'Colt' scions had a larger L_A than plants with 'Meteor' scions, but only under well-watered conditions (Table 2). The larger L_A of well-watered plants with 'Colt' scions most likely resulted due to the indeterminate nature of 'Colt'. There was no effect of the rootstock on L_A .

Partitioning of dry weight. The leaf weight : root weight ratio decreased in response to water stress for all plants; however, plants with 'Colt' scions showed a greater decrease than did plants with 'Meteor' scions (Table 2). There were also significant changes in the partitioning of dry weight within the leaf and roots. The scion, rootstock, and irrigation regime influenced specific leaf area (SLA) (leaf area : leaf dry weight) such that plants with 'Meteor' scions had lower SLA than did those with 'Colt' scions; however, this effect

was greatest under water-stressed conditions and for plants with 'Colt' rootstocks. There were no treatment effects on root surface area : rootstock dry weight. Although there were no significant differences in leaf : root weights among water-stressed plants, differences in SLA resulted in significant differences in the ratio of leaf surface : root surface area (LARSA) as influenced by both rootstock and scion. The L_A : plant length ratio showed similar trends.

\bar{R} is a function of two components: 1) the ratio of assimilatory surface area : plant dry weight (LAR) and 2) the net assimilation rate of the leaf surface area (\bar{E}) (Hunt, 1982). In this study, 'Meteor'/'Colt' plants maintained higher \bar{R} than did 'Colt'/'Meteor' plants while having similar or lower LAR, depending on the watering regime. The higher \bar{R} of 'Meteor'/'Colt' plants therefore was achieved as a result of a higher \bar{E} . This trend held under both well-watered and water-stressed conditions.

Under water-stressed conditions, a higher \bar{E} may contribute to improved drought resistance. Ashenden et al. (1975) found that under drought, populations of orchard grass (*Dactylis glomerata* L.) from dry sites had higher \bar{E} than populations from moisture sites, suggesting that maintenance of high \bar{E} under drought conditions may provide for improved growth, adaptability, and tolerance to water stress.

\bar{E} is a measure of photosynthetic efficiency per unit leaf minus losses of CO_2 due to respiration (Ledig, 1974). The effect of the scion on \bar{E} was anticipated because species often vary in photosynthetic rate and canopy architecture. Because well-watered 'Colt' scions typically had larger L_A than 'Meteor' scions, the higher \bar{E} of well-watered plants with 'Meteor' scions may have resulted from lower L_A with higher light interception per unit L_A .

The significant effect of the rootstock on \bar{E} was less expected and may be the result of several rootstock influences. Lack of a significant rootstock effect on L_A indicates the influence of the rootstock on \bar{E} was not one of variation in total light interception. One potential influence of the rootstock on \bar{E} could result from the indirect effect of the rootstock on leaf morphology. In our study, plants with 'Colt' rootstocks had lower SLA and higher \bar{E} than did plants on 'Meteor' rootstocks. SLA has been found to be negatively correlated with rates of photosynthesis within a wide variety of woody plants (Jurik, 1986; Nelson and Michael, 1982; Oren et al., 1986). Association of high rates of photosynthesis with low SLA may be due to increased mesophyll cell surface area per unit L_A (Nobel et al., 1975). \bar{E} in this study was negatively correlated ($P < 0.05$) with SLA in both well-watered ($r = -0.82$) and water-stressed plants ($r = -0.66$) and may represent a significant mechanism by which rootstocks can influence \bar{E} .

LARSA is a measure of transpirational surface area to root absorptive area and may be an important factor in the ability of a plant to function and grow under water stress. Dif-

ferences in LARSA among plants under water stress primarily reflected changes in partitioning patterns within leaves (SLA). A lower LARSA may improve water uptake per unit of leaf area and the ability to maintain turgor and stomatal conductance, resulting in an improved \bar{E} .

The low LARSA and SLA and high \bar{R} and \bar{E} associated with the 'Meteor' scion is consistent with drought-adapted ideotypes (Brown, 1980). Observations made in the field also indicate that plants with 'Meteor' scions typically show less evidence of stress under drought conditions than do other cherry cultivars (J. Cummins, personal communication). Conversely, the low LARSA and SLA and high \bar{R} and \bar{E} associated with the 'Colt' rootstock suggest that scions on 'Colt' rootstocks would be better adapted to drought than scions on 'Meteor' rootstocks.

Success of any plant under drought conditions depends on its ability to acquire and use water such that photosynthesis and growth can be maintained under increasingly dry conditions. Selection of more drought-resistant rootstocks with extensive and deep root systems has been pursued with citrus (Castle and Krezdorn, 1977). However, little attention has been given to the influence of both the rootstock and scion on physiological and morphological traits and their potential influence on growth under water stress. The results of this study indicate that both rootstock and scion can affect a variety of characteristics that influence growth under both well-watered and water-stressed conditions.

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