J. AMER. SOC. HORT. SCI. 115(5):722-727. 1990.

Response of Seed Carrot to Various Water Regimes. II. Reproductive Development, Seed Yield, and Seed Quality

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Additional index words. *Daucus carota* var. sativa, seed germination, seed vigor, water deficit, biological yield components

Abstract. **Seed yield and quality of carrot *(Daucus carota* var. sativa DC.) were influenced by a wide range of water application regimes and levels. Irrigation treatments were imposed beginning at the time of extension of the primary umbel and extending throughout the reproductive development period. The three application regimes used were: 1) a high-frequency, low water deficit treatment [100% of daily accumulated crop evapotranspiration (ET_c)]; 2) a series of five low-frequency (irrigated after 30 mm of accumulated ET,) application treatments with a range of water deficits from moderate to minimal (40% to 120% of ET_c applied); and 3) a series of three treatments that had rapidly developing water deficits applied by terminating irrigation at 7, 5, and 2 weeks before harvest after being grown under low-stress conditions. Pure live seed (PLS) yield was optimized by different treatments within each of the three application regimes. Maximum yields were achieved with short-term (2-week) rapidly developing water deficits near harvest, moderate deficit irrigation with 60% to 80% of ET_c applied after 30 mm of ET_c, or with a low water deficit, high-frequency application. Seed germination percentage decreased as the amount of applied water increased. This effect was more pronounced in the later-developing umbel orders. However, seed quality measured as seedling root length was improved with increasing water application.**

The seed carrot plant grows in an indeterminate fashion, producing seed in umbels that arise from multi-rank ordered branches. This general growth form results in seed of different maturity stages being present on the plant at the same time. Therefore, when the seed of the primary umbel is mature and ready for harvest, seed from secondary and tertiary umbels may not be mature, and tertiary and quarternary umbels may still be in flower. As a result, there is a great deal of variability in the maturity of the seed at harvest. Since genetic efforts to improve the carrot plant have been directed primarily toward improved root production and quality, carrot reproductive development has remained much the same as that of undomesticated relatives (Braak and Kho, 1958).

The effects of water management on carrot seed production and quality are not well-understood, with limited published information available (George, 1985). MacGillivray and Clemente (1949) indicated that as the amount of water applied was increased, total seed yield also increased, although no statistical difference was shown. In their study, the seed produced by the treatment receiving the least irrigation always ranked first for viability. Hawthorn (1952) reported that low and moderate water applications (significantly lower than full estimated ET_c requirements) resulted in the highest seed yields when compared to high water application treatments. The high water application treatments also resulted in lodged plants and lower seed quality. Hawthorn and Pollard (1954) showed that under dry conditions during bolting and umbel development, seed yields were increased and seed quality improved when compared to treatments receiving larger amounts of applied water. Salter and Goode (1967) concluded after reviewing the literature that there is no consistent evidence for moisture-sensitive stages during the growth of carrots for seed.

The purpose of this experiment was to determine if carrot seed yield and quality are affected by diverse water regimes. Particular attention was given to the effects of the water management treatments on the rate and variability of flowering and seed development of the several umbel orders as related to the biological yield components.

Received for publication 27 Nov. 1989. This research was supported, in part, by a grant from the California Agricultural Technology Institute, California State Univ., Fresno. Contribution no. 900903 of the California Agricultural Technology Institute. Use of trade names does not imply endorsement by the USDA-ARS or California State Univ., Fresno. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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Abbreviations: ACLW, accumulated change in total leaf weight; AUM, average umbel maturity; DOY, day of year; ET_c, crop evapotranspiration; PLS, pure live seed.

Materials and Methods

All methods for field plot establishment and maintenance are described earlier (Hutmacher et al., 1990). Three irrigation treatment regimes were used: 1) high frequency (low water deficit), 100% ET_c daily irrigation (100-D); 2) low frequency (gradually developing water deficit series), with water applied after ≈ 30 mm ET., with the treatments replacing 40%, 60%, 80%, 100%, and 120% of calculated ET_c (40-L, 60-L, 80-L, 100-L, and 120-L, respectively); and 3) low-frequency, terminated irrigation (rapidly developing water deficit series), with water applications the same as treatment 100-L, but water withheld at 7, 5, and 2 weeks before harvest (100-L-7W, 100-L-5W, and 100-L-2W, respectively). Plant phenology and reproductive development were determined every 14 days, starting 6 May and ending 2 July 1985, from five plants sampled from each plot of the low-water deficit and gradually developing water deficit series treatments. The rapidly developing water deficit plots were sampled only on 7 June and 3 July. The plants were divided into leaf, stem, and flower components. Only completely green, non-necrotic or nonyellowed leaves were sampled. The flower components were divided into those produced by primary, secondary, tertiary, and quarternary umbels. The umbels were characterized on a 1 to 10 scale for stage of maturity as: 1, bud (new), new bud visible, no apparent swelling, found between the stem and subtending leaf; 2, bud (tight), bud beginning to swell, bud is firm when pinched; 3, bud (loose), bud is swelled but remains closed, bracts have begun to be separated from one another due to swelling, distinctive white umbel structure visible between bracts; 4, umbel, definite umbel structure present, progresses from slightly opened to completely opened, general appearance is wet, as with wet, brushed hair; 5, pre-anthesis, florets are distinct but anthers are not present, umbel appears dry; 6, anthesis, anthers are visible, no apparent swelling of the pistil; 7, seed set, seed is filling, ranges from slightly swollen ovaries to moderately swollen; 8, seed mature (green), seed completely filled, seed is distinct, the twin seed produced from each floret can be clearly seen; 9, seed mature (brown), seed mature and. browning or brown, no shattering; 10, seed shatter, umbel has browned, seed is shattering or capable of shattering.

Six meters of row from each experimental unit of low and gradually developing water deficit series treatments were harvested on 16 July, and 5 m of row were harvested from the rapidly developing water deficit series treatments on 17 July. The umbels were divided into the four umbel orders, dried, and the seed threshed and cleaned. Seed samples were tested for germination percentage and the seedlings evaluated according to the methods of the Assoc. of Official Seed Analysts (1978). Dry weights of two replications of 100-seed samples were determined. Seedling root length was determined after 12 days in the germination chamber. Two replications of 20 seeds from each treatment and umbel order were used for all seedling evaluation tests. PLS production was determined by multiplying total seed yield with percentage germination data for each umbel order based on the 12-day germination test (Copeland and McDonald, 1985). Two reproductive efficiency calculations were made by dividing PLS yield by total inflorescence and above-ground biomass.

All variables were correlated with the amount of total applied water using the Pearson method (Snedecor and Cochran, 1980). Regression analysis was used to analyze the quantitative variable series for the gradually developing water deficit treatments. All differences are reported at $P = 0.05$ unless otherwise stated.

Results and Discussion

Whole plant response to water application. Total plant dry matter production increased with the amount of applied water ($r = 0.98$; $P = 0.01$), regardless of application regime. When compared to rapidly stressed plants, plants exposed to gradually accumulating soil water deficits (40-L, 60-L, and 80-L) were better able to sustain at least some photosynthate production through maintenance of partially open stomata with somewhat reduced leaf areas (Hutmacher et al., 1990). Plants subjected to rapidly developing water deficits responded with at least 3-fold reductions in leaf stomatal conductance, relative to plants in the 100-L treatment, within 7 days after termination of irrigation, followed by substantial losses in the viable leaf area and significant abscission of leaves within 10 to 15 days after termination of irrigation (Hutmacher et al., 1990). These changes in leaf area are reflected in the ACLW during the growing season (Fig. 1]. Values of ACLW <0.0 indicate a net loss in effective leaf matter. The 120-L treatment resulted in a stable ACLW through the season. Treatments 100-D and 100-L exhibited slight decreases in ACLW with time. A rapid differentiation of ACLW values occurred after DOY 154. Final ACLW values on DOY 182 were negatively correlated with total applied water (Fig. 1 insert). Once rapidly developing water deficits were imposed, the only compensation in nonreproductive growth was a reduction in leaf area to regulate water losses. Presumably, photosynthate availability was reduced during this period as indicated by substantial reductions in stomatal conductance (Hutmacher et al., 1990). Leaf weight at the end of plant sampling was negatively correlated with total applied water ($r = 0.972$; $P = 0.0001$).

Effects of water application on umbel growth and development. Primary and secondary umbel production were unaffected by water application, but tertiary and quarternary order umbel production increased with increasing applied water (Fig. 2A). Total dry weight and weight per umbel of secondary, tertiary, and quarternary umbel orders increased with increasing amounts of applied water (Fig. 2 B and C).

The average rate of development of the different umbel orders

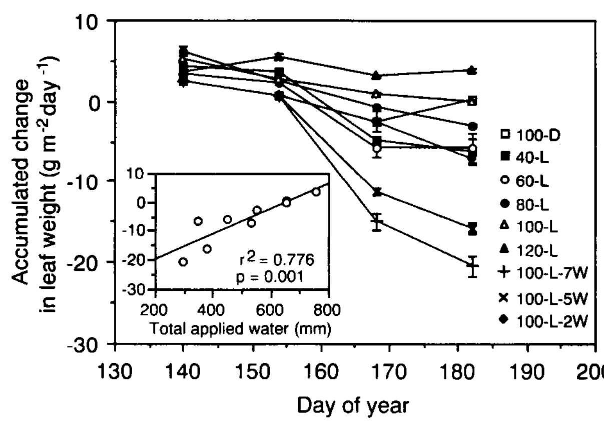

Fig. 1. Effect of nine irrigation treatments on ACLW of seed carrot grown at Fresno, Calif., in 1985. Inset graph shows the relationship between total applied water for the season and ACLW at the last sampling date. Irrigation treatments are: 100-D = daily application at a rate equivalent to 100% of ET_c; 40-L, 60-L, 80-L, 100-L, 120-L = 40%, 60%, 80%, 100%, and 120% ET_c application after 30 mm of accumulated ET=; and 100-L-7W, 100-L-5W, 100-L-2W = 100% application after 30 mm of accumulated ET_c until DOY 142, 156, and 178, respectively, when water applications were stopped. Bars indicate standard error of the mean.

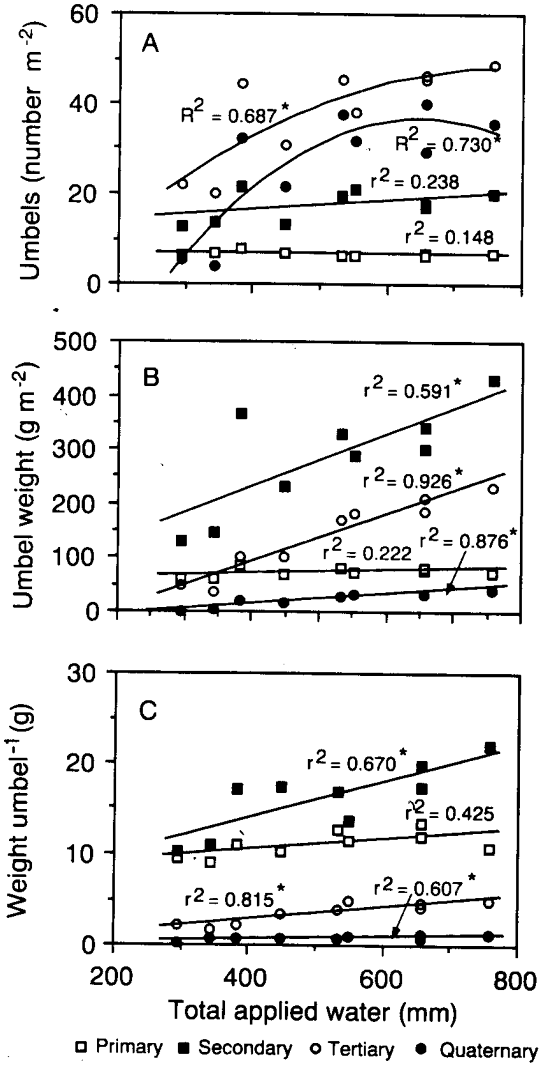

Fig. 2. Effect of total applied water from nine irrigation treatments on: **(A)** number of umbels produced; **(B)** umbel weight; and (C) weight per umbel of primary, secondary, tertiary, and quaternary umbel orders of seed carrot grown at Fresno, Calif., in 1985. Linear and quadratic coefficients of determination (r^2 and R^2, respectively) marked with * are significant at $P \leq 0.05$.

was unaffected by the three application regimes (data not shown). Primary and secondary umbels reached the AUM stage of development 8 (seed full-sized, green) between DOY 154 and 168 (Fig. 3A). A small percentage of the tertiary and quaternary umbels reached this stage of development at this same time (<30% and <5%, respectively). Since the plants in treatments 100-L-7W and 100-L-5W were in a rapid state of decline as a result of diminishing leaf weight by DOY 168 (Fig. 1), there was most likely a limitation of available photosynthate to support continued umbel formation and complete seed development, particularly in the tertiary and quaternary umbel orders.

The rapidity with which soil water deficits become severe enough to restrict plant growth and maintenance depends on soil type, plant size, and rooting depth, and on the evaporative demand (Kramer, 1969). These cumulative effects did not become severe enough to cause a significant association between amount of applied water and leaf weight until DOY 154 (Table 1). Tertiary and quaternary umbel numbers were correlated with leaf weight ($P = 0.10$) at DOY 168 and more strongly correlated at DOY 182 ($P = 0.05$) (Table 1). The number of sec-

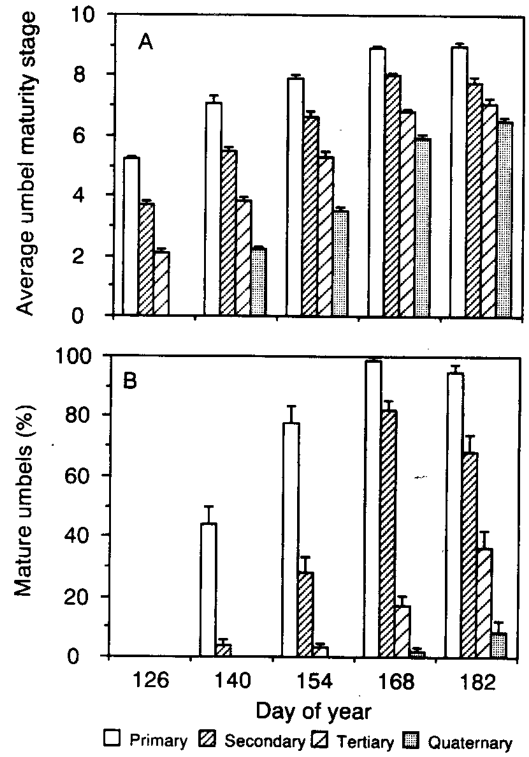

Fig. 3. Reproductive development of four umbel orders of seed carrot grown at Fresno, Calif., in 1985. **(A)** AUM stage index (8 = seed mature, green, and fully filled); and **(B)** percent of total umbels that were mature. Values shown are the average of nine irrigation treatments. In treatments 100-L-7W and 100-L-5W, irrigation was terminated on DOY 142 and 156, respectively. Vertical bars indicate standard error of the mean.

Table 1. Correlation coefficients *(r)* from five sampling dates for plant leaf weight with amount of applied water and number of umbels per plant of seed carrot grown at Fresno, Cal if., in 1985. Results are for the gradual accumulating stress treatments (n = 5).[z]

Sample date (DOY)	Amount of applied water	Umbel order		
		Secondary	Tertiary	Quaternary
126	– 0.42	–0.74	– 0.48	–0.17
140	–0.17	–0.57	–0.19	0.09
154	0.30	0.62	0.26	–0.06
168	0.94	0.72	0.86	0.84
182	0.99	0.86	0.90	0.91

[z]Correlation coefficients $\geq$ 0.808, 0.878, and 0.959 are significant at $P \leq 0.10$, 0.05, and 0.01, respectively.

ondary umbels was not correlated with leaf weight ($P = 0.10$) until DOY 182. The apparent reduction in leaf development and thus possible limitation to photosynthate availability at a time when <5% of the tertiary and quaternary umbels had reached maturity suggests why these two umbel orders contribute relatively little to the overall seed yield of the plants. Therefore, late in the season, it can be expected that substantial competition existed among umbel orders for diminishing, limited photosynthetic resources needed to complete umbel maturity.

Umbel order effect on seed yield and seed quality. For all irrigation regimes, the secondary order umbels contributed the greatest portion of the total seed produced (Fig. 4C). The primary order umbels produced more seed than the tertiary orders under lower water application regimes (treatments 40-L, 100-L-7W, and 100-L-5W), but with less water stress, relatively

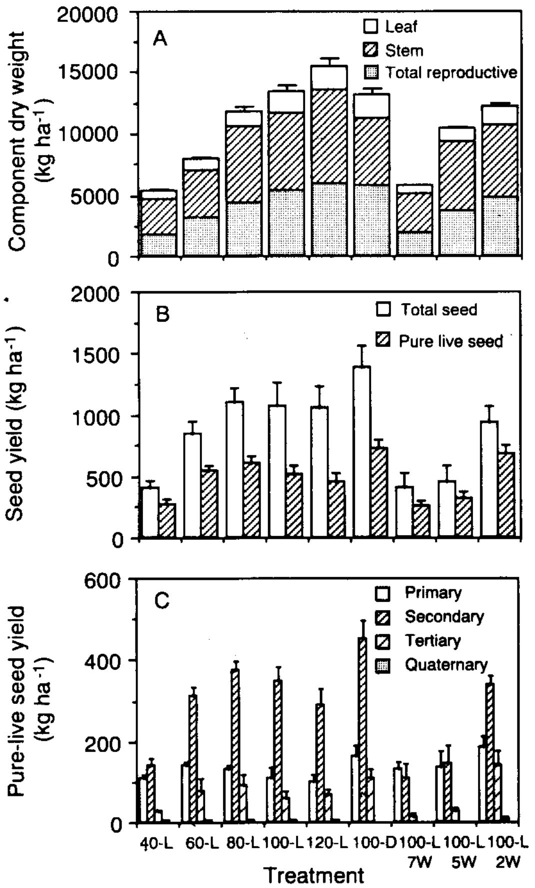

Fig. 4. Effect of nine irrigation treatments on **(A)** above-ground phytomass yield components on DOY 183; **(B)** total and PLS production; and **(C)** PLS production of four umbel orders of seed carrot grown at Fresno, Calif., in 1985. Vertical bars indicate standard error of the mean. Irrigation treatments are the same as Fig. 1.

equal amounts of seed were produced. The quaternary order umbels were of no consequence to final seed yields in any of the treatments. Hawthorn et al. (1962) reported that both the secondary and tertiary umbel orders were the largest contributors to final yield. It is not possible to determine whether differences in umbel order contribution to final yield in our results as compared with those described by Hawthorn et al. (1962) - were due to cultivar differences or differences in the manner in which the seed crops were produced. In this study, the crop was grown from stecklings, while Hawthorn and coworkers used a direct-seeded crop.

Similar to data reported by Borthwick (1932), earlier-developing umbels produced seed that was higher in viability (as determined by 6- and 12-day germination tests) than later-developing umbels. The average 12-day germination for all treatments from the primary, secondary, tertiary, and quaternary umbel orders was 69%, 58%, 48%, and 29%, respectively.

Effects of water application on seed yield. The 100% ET_c daily irrigation treatment (100-D) produced the highest total seed yield (Fig. 4B). Total seed yield was reduced in the more severe irrigation termination treatments 100-L-7W and 100-L-5W, compared to treatment 100-L-2W. The magnitude of the yield reduction was similar to that observed with treatment 40-L. The plants from treatment 100-L-2W had similar total seed production as those in the 60-L, 80-L, 100-L, and 120-L treatments.

PLS production was correlated with total seed production (r = 0.898; P = 0.001). Secondary and tertiary umbels were the yield components affected most by the water application treatments, with the secondary order being the most significant contributor to PLS yield except for the most water-stressed treatments (Fig. 4C). Secondary umbel PLS yield was similar to that of the primary umbels for the more stressed treatments 40-L, 100-L-7W, and 100-L-5W. Tertiary umbel PLS was greatly reduced in these treatments also. This indicates that available water was not adequate to sustain the plants and mature seeds in these umbel orders. Since AUM through DOY 140 was similar across all irrigation treatments, the timing of severe water deficits determined whether umbel orders reached maturity. At the time irrigations were terminated, treatments 100-L-7W and 100-L-5W had secondary and tertiary umbel orders with AUM values of <3.75 and <2.00, respectively, and few mature umbels for any of the umbel orders (Fig. 3 A and B). Treatment 40-L, which was the most severe deficit irrigation-treatment, had similar secondary and tertiary umbel production as the two earlier irrigation termination treatments.

The reproductive efficiency of the crop measured as the ratio of PLS to total reproductive weight (PLS :TRW) and PLS to total above-ground dry weight (PLS :TDW) is given in Fig. 5. Only the quantitative series for the deficit treatments 40-L, 60-L, 80-L, 100-L, and 120-L was examined by regression analysis. The ratios of PLS:TRW and PLS:TDW were optimized for treatment 60-L, with reductions in both measures of reproductive efficiency with lesser or greater deficit percentages. The 100-D treatment, which received one of the highest total amounts of water, had a PLS:TRW ratio similar to 60-L. The efficiency of 100-D was much greater than the 100-L and 120-L treatments because of increased PLS production but similar total dry matter production (Fig. 4 A and B). Therefore, there was an effect due to frequency of application.

In the most severe irrigation termination treatment (100-L-7W), reproductive efficiency measured as either PLS:TDW or PLS:TRW was higher than the 100-L-5W treatment because water deficits severely restricted umbels from developing past initial growth stages along with a reduction in total dry matter production. For treatment 100-L-5W, seed development was

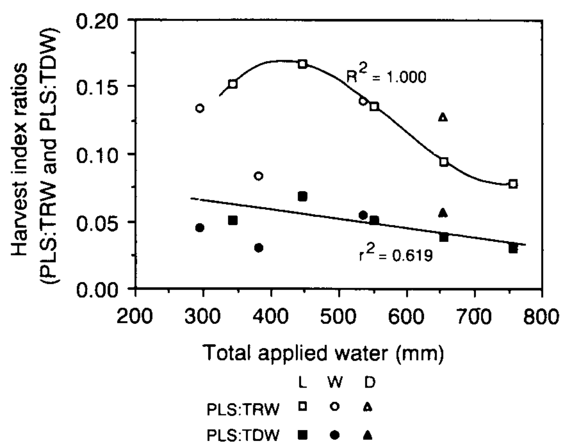

Fig. 5. Effect of total applied water from nine irrigation treatments on two harvest index ratios of seed carrot grown at Fresno, Calif., in 1985. PLS:TRW = pure live seed yield ÷ total reproductive weight and PLS:TDW = pure live seed yield ÷ total above-ground phytomass. L, W, and D = gradually accumulating stress, rapid developing stress, and low-stress treatment regimes, respectively. Regression analyses are fitted to the L regime treatments only. R^2 and r^2 are significant at $P \leq 0.05$ and 0.10, respectively.

also restricted, but total dry matter production was greater than treatment 100-L-7W. There was no relationship between PLS:TRW or PLS:TDW and total or PLS yield over all treatments or within the deficit irrigation series (regressions not shown).

Effects of water application on seed germination. Twelve-day germination percentage for seed from the primary umbel order was greatest in the three irrigation termination (100-L-7W, 100-L-5W, 100-L-2W) treatments (Fig. 6). In the secondary through quaternary orders, this advantage was for the two more severe cut-off treatments (100-L-7W and 100-L-5W). The two more severe rapidly developing water deficit treatments had adequate soil water (equivalent to 100-L) to mature seed produced in the primary and secondary umbels. However, when subjected to rapidly developing water deficits after initial high water availability, these two treatments could not support normal seed development in the two later-maturing umbel orders. This was probably due to the rapid loss of leaf area as a result of the rapidly developing water deficits after DOY 154 (Fig. 1).

Gradually accumulating water stress enhanced the germination percentage as the irrigation deficit percentage increased (*r* = – 0.93, – 0,94, – 0.96, and – 0.97 for 6-day germination, and –0.91, –0.94, –0.93, and –0.98 for 12-day germination; *P* = 0.05). This effect was more pronounced in the tertiary and quaternary umbel orders (Fig. 6). Significant differences existed between 6- and 12-day germination percentages as increasing amounts of water stress were applied, indicating possible reduced seed vigor. This effect was also more pronounced in the later-developing umbel orders.

A possible explanation for reduced seed germination with increased water application may be competition between umbels that are maturing seed and those being initiated. Since the number of tertiary and quaternary umbels produced by the end of the growing season increased with increasing amounts of applied water (Fig. 2A), less photosynthate may have been available within each umbel order per sink to complete seed maturation. A negative relationship was found between number of tertiary and quaternary umbels and final seed germination percentage within umbel orders (Table 2).

Likewise, inter-order competition existed for available resources to complete seed maturation. The number of primary umbels per plant was unaffected by moisture level, since it is fixed at one per plant. The total weight of primary umbels (as well as weight per umbel) was also unaffected by the different treatments, probably because >80% were mature by the time of rapid leaf weight reduction at DOY 154 (Fig. 1 and 3B). The number of secondary order umbels, which developed relatively early in the season in all treatments, was unaffected by water applications, but total umbel weight and weight per umbel increased with increasing water levels (Fig. 2 B and C). The number of umbels, total umbel weight, and weight per umbel of tertiary and quaternary umbel orders all increased with increasing applied water. Since these orders must also compete for available photosynthate to maintain and mature developing seeds, any increase in later-developing umbels reduced available photosynthate supply for maturing seed. This-would be particularly true in treatments that were rapidly losing leaf weight due to rapid or accumulating water deficits. Seed germination percentage for primary, secondary, and tertiary umbel orders was negatively correlated with the number of umbels produced by the next higher order (Table 2).

Braak and Kho (1958) suggested that increasing umbel number may be a possible factor that decreases carrot seed quality but did not investigate this factor any further. Their study showed that the reproductive biology of domestic carrot often differed from wild carrot in that wild forms produced little seed in the later-developing umbels due to the presence of mostly male flowers. Since these umbel orders primarily contributed male gametes, they would not require large amounts of plant resources late in the season to complete seed development. This trait appears to have been selected away from in the domestic carrot and may explain the inefficiency of prolific flowering under nonstressed conditions that are counterproductive to seed germination and PLS yield.

The more severe irrigation termination treatments (100-L-7W and 100-L-5W) produced lower 100-seed weights and shorter seedling root lengths than the other treatments (Fig. 7). This dif-

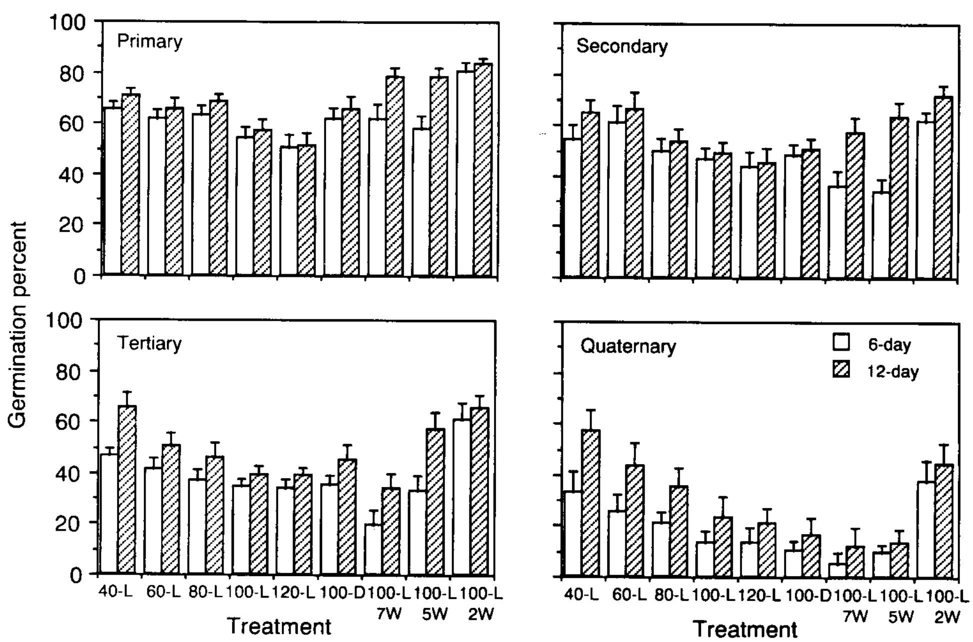

Fig. 6. Effect of nine irrigation treatments on 6- and 12-day seed germination percentage of four umbel orders of seed carrot grown at Fresno, Calif., in 1985. Vertical bars indicate standard error of the mean. Irrigation treatments are the same as Fig. 1.

Table 2. Correlation coefficients *(r)* for sampling DOY 168 of seed germination with number of umbels per plant produced within and among four umbel orders of seed carrot grown at Fresno, Calif., in 1985. Results are for the gradual accumulating stress treatments (n = 5).

	Source of competition	
Umbel order	Intra-order	Inter-order
	Umbel order	
	Primary	Secondary
Primary	0.00[z]	–0.90
	Secondary	Tertiary
Secondary	–0.78	–0.87
	Tertiary	Quaternary
Tertiary	– 0.91	– 0.95
	Quarternary	
Quaternary	–0.94	---[y]

[z]Correlation coefficients ≥ 0.878 and 0.959 are significant at $P \leq 0.05$ and 0.01, respectively.
[y]Inter-order correlation could not be determined since quintenary order umbels were not sampled.

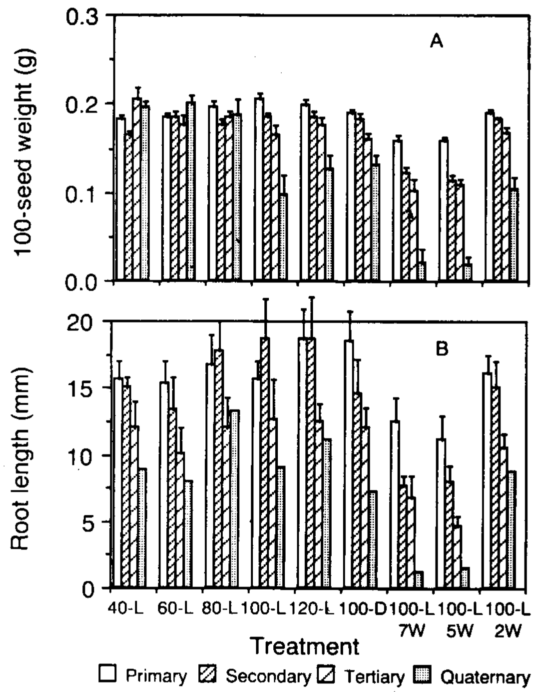

Fig. 7. Effect of nine irrigation treatments on **(A)** 100-seed weight; and **(B)** seedling root length after 12-day germination test of seed carrot grown at Fresno, Cal if., in 1985. Vertical bars indicate standard error of the mean. Irrigation treatments are the same as Fig. 1.

ference, in part, may explain the difference between early and late germination counts in these treatments. Similarly, in the more stressed deficit treatments, the later-developing umbel orders also had reduced 100-seed weights. The 40-L, 60-L, and 80-L treatments exhibited relatively uniform 100-seed weights for all umbel orders. Since it is possible to change germination percentage but not 100-seed weight, it is important to maximize germination percentage because low-germination carrot seed cannot be separated by conventional seed-conditioning processes such as seed specific weight (D. Bilsland, personal communication, 1990).

Seedling root length (Fig. 7B) was correlated with 100-seed weight (r = 0.83, 0.88, 0.85, and 0.79; P = 0.01 for primary, secondary, tertiary, and quaternary umbel orders, respectively). Seedling root length for the four umbel orders was positively correlated with total applied water (r = 0.80, 0.79, 0.68, and 0.63; P = 0.01, 0.01, 0.05, and 0.10, respectively). Only for the primary and secondary umbel orders was 100-seed weight correlated with total applied water (r- = 0.81 and 0.73; P = 0.01 and 0.05, respectively). These findings indicate that even when there is an improvement in seed germination percentage by reduced water (higher stress) applications, the actual seed vigor quality may be reduced. The relationship between seedling root length and final field stand establishment needs to be determined to decide whether this vigor criterion is a seed quality trade-off with germination percentage.

Carrot seed plants grown in a relatively coarse-textured soil, with low to moderate water-holding capacity, are not capable of regulating a rapidly developing water deficit and still producing substantial quantities of good quality seed. Total seed yield was positively correlated with amount of applied water. However, germination percentage was negatively correlated with amount of applied water. The late-season termination of irrigation and higher percent deficit treatments overcame reductions in total seed yield by improved germination percentage. Yield of PLS was optimized by the 2-week termination (100-L-2W), daily (100-D), and gradual deficit stress (40-, 60-, and 80-L) treatments.

One-hundred seed weight was most uniform among the various umbel orders in the higher-deficit irrigation percentage treatments. Lower-deficit irrigation and rapidly developing stress treatments adversely affected 100-seed weight in the tertiary and quaternary orders. Only primary and secondary umbel order 100-seed weights were positively correlated with amount of applied water. Increasing amounts of applied water increased seedling root length for all umbel orders. It is therefore possible to increase seed germination percentage with increased water deficits, but at the same time this may reduce seed vigor quality.

These findings are contrary to those of MacGillivray and Clemente (1949), who indicated that higher seed yields occurred with increasing amounts of applied water, with no effect of rate of applied water on seed quality; and Salter and Goode (1967), who found seed carrot to not be sensitive to different water levels. This study is in general agreement with Hawthorn (1952) and Hawthorn and Pollard (1954), who found carrot seed yield was enhanced by slight amounts of water stress.

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