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The Effect of Post-veneralization Temperature on Seedstalk Elongation and Flowering in Carrots[1]

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Additional index words. vernalization, bolting, photoperiod, low temperature, stem elongation, *Daucus carota*

Abstract. **Seedstalk height of carrot (*Daucus carota* L.) was reduced as the post-vernalization temperature increased from 15/21° to 27/32°C (night/day) with no significant effect on flowering and seed formation. Seedstalks of 'Royal Chantenay' carrot were most affected by the high temperatures and 'Scarlet Nantes' were the least affected while 'Danvers 126' was intermediate. Few plants had macroscopic seedstalk development 6 weeks after vernalization although the temperature during this period had a permanent influence on ultimate seedstalk height. Carrots grown at 27/32° during the initial 6 weeks following vernalization and then transferred to the optimum 15/21° grew no taller than plants held at 27/32°. Vernalization temperatures of 0°, 5°, and 10° for 10 weeks did not affect the percentage of plants flowered, time of bolting, or rate of seedstalk elongation. Ultimate seedstalk height was reduced only in 'Royal Chantenay' vernalized at 10°. Flowering was decreased by post-vernalization temperatures of 27/32° and 21/27°C when carrots were stored only 5 weeks at 5° but not after storage for 10 weeks or more. Increasing the vernalization time to 10 weeks hastened the rate of bolting in all three cultivars and increased ultimate seedstalk height in only 'Royal Chantenay' and 'Danvers 126.' Temperature during the first year of root growth, foliage removal from mature roots prior to storage, and photoperiod following vernalization did not affect seedstalk elongation or flowering.**

Stem elongation and flowering appear to be simultaneous events when vegetative rosette plants change to the reproductive stage, suggesting identity of the factors which control both processes. Experimental observations from many studies involving environmental factors, gibberellins, and growth retardants have definitely shown that a relationship may exist in certain species, but not for others (7, 15, 16). However, the relationship between stem elongation and flowering has received only limited attention experimentally in cold-requiring plants and was not mentioned in a review on stem elongation (11) and only briefly in a recent review on flower formation (17).

Carrots, a vegetative rosette plant, require an exposure to temperatures below a critical level (vernalization) for floral induction. Under optimum conditions, the induced plant shows rapid stem elongation ("bolting") to form a highly-branched, main seedstalk 3 to 4 feet tall. Two reports have shown ultimate height of carrot seedstalks to be inversely proportional to growing temperatures following the vernalization period (3, 10). Eisa and Wallace (3) further reported that the 'Royal Chantenay' carrot, when grown under relatively high greenhouse temperatures, exhibited very little or no seedstalk development, but flowered and matured a normal main umbel; i.e., a sessile flower. The literature has presented the concept of devernalization as either a complete inhibition of flowering and seedstalks or the formation of seedstalks without flowers ("barren seedstalks") (1). Inhibition of seedstalk elongation with normal flowering has been reported with photo-induced species (8).

The primary objective of this study was to determine the effect of post-vernalization temperatures on seedstalk elongation and flowering. In addition, the effect of vernalization time and temperature, growing temperature and foliage removal before vernalization, and photoperiod following vernalization were investigated.

Materials and Methods

Plant materials and general methods. Mature carrot roots were grown during the summers of 1970-72 on the Vegetable Crops Research Farm, Freeville, N.Y. using standard cultural practices. 'Royal Chantenay', 'Danvers 126', and 'Scarlet Nantes' carrots were selected to represent different bolting responses (2). Carrots (stecklings) were hand-harvested in September, and medium-sized roots of each cultivar were selected to reduce variability (4). Tops were cut off 2.5 cm above the crown; then the roots were rinsed to remove adhering soil and dipped in dicloran fungicide. Roots to be vernalized were placed in perforated plastic bags with vermiculite to prevent desiccation and stored in controlled temperature storage rooms. In addition, roots were potted after harvest and placed immediately at the different greenhouse temperatures. The vernalization period in all experiments, except those where time and temperature were variables, was 10 weeks at 5°C, previously reported to be optimal for carrots (2).

Upon removal from cold storage, individual roots were rolled in a mixture of thiram/benomyl/streptomycin sulfate/white quartz sand and planted immediately in standard 15 cm pots containing a peat/vermiculite/sand growing media at temperature regimes of 10°/15°, 15°/21°, 21°/27°, and 27°/32°C (night/day). Fertilization and pest control were on a weekly basis. A treatment unit consisted of 10 plants. The main seedstalk was measured every 2 weeks from the time elongation was visible and tied to bamboo stakes as necessary. All experiments continued after flowering until mature seeds were obtained. The statistical procedure used was analysis of variance, and the factorial treatments were partitioned to single degrees of freedom. Details of the statistical analysis are not presented since only highly significant and obvious differences are discussed.

Vernalization temperature and time. In 1970 stecklings were stored at 0°, 5°, and 10°C for 10 weeks and then grown at 10°/15°, 15°/21°, and 21°/27° greenhouse temperatures. In 1971 and 1972 stecklings grown in both the field and the greenhouse were stored at 5° for 5, 10, 20, and 30 weeks and subsequently grown at 15°/21°, 21°/27°, and 27°/32° greenhouse temperatures.

Growing temperature and foliage removal before vernalization. Carrots were grown from seed in 15 cm pots at 10°/15°, 15°/21°, and 21°/27°C greenhouse temperatures prior to the 10 weeks at 5° vernalization treatment. The tops were removed from half of the plants and left intact on the other half prior

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to cold storage. The roots were left undisturbed in the pots during vernalization under 3.2 klx fluorescent + incandescent light. These were grown at each of 2 greenhouse temperatures (15°/21° and 21°/27°C) following vernalization. Six plants were used per treatment.

Photoperiod following vernalization. Following the completion of the vernalization period in December, 3 photoperiod regimes were established at 15°/21° and 21°/27°C; short day of 8 hr, long day of 14 hr, and short day with a night interruption (NI). All treatments were uncovered at 8 AM and covered at 4 PM with black shading cloth to allow an 8 hr exposure to natural daylight. The long day plants received an additional 6 hr illumination from incandescent lights giving about 2.2 klx at plant level. The night interruption was given from 11 PM to 1 AM using similar incandescent lights.

Temperature during the early and late stagees of seedstalk development. In 1971 and 1972 carrot stecklings vernalized at 5°C for 10 weeks were planted in the greenhouse at 15°/21°, 21°/27°, and 27°/32°. After 3 weeks and 6 weeks, 10-plant lots of carrots were moved from each temperature to the other 2 temperatures and remained there until seedstalk development was completed. Control treatments were groups of plants which remained at the same temperature throughout seedstalk development.

Results and Discussion

The most striking result of these studies on carrot reproductive development was the effect of post-vernalization growing temperature on the elongation and ultimate height of seedstalks. Absolute values for seedstalk measurements differed only slightly from year to year, and the same relative responses to the different greenhouse temperatures occurred in all experiments; therefore, only one set of data is presented in this paper.

The ultimate seedstalk height was drastically affected by the greenhouse growing temperature following vernalization. Carrots bolted with normal seedstalk development at 10°/15° and 15°/21°C post-vernalization temperatures when the previous cold storage period was 5° or lower for 10 weeks or more (Fig. 1.). Plants of all three cultivars grown at 10°/15° developed slower than those at 15°/21°, but final seedstalk height did not differ (Table 1). Plants bolted quicker, seedstalks elongated faster, and umbel formation was completed earlier at 21°/27° and 27°/32° than at 15°/21°, but the ultimate seedstalk height was significantly shorter at 21°/27° and 27°/32° than at 15°/21° (Table 1). Seedstalk growth and height was more markedly affected in 'Royal Chantenay' at the high temperatures, 'Danvers 126' was always intermediate, and 'Scarlet Nantes' was least affected. Many plants, but more frequently 'Royal Chantenay'' formed normal umbels with little or no seedstalk elongation at the high temperatures (Fig. 2.) Dickson and Peterson (2) reported that carrot reproductive development was hastened at 21°/27°C. However, they did not investigate the effect of this temperature immediately following vernalization nor comment on ultimate seedstalk height.

Generally, vernalizing carrot roots for 10 weeks at different temperatures had only slight effects on the ultimate seedstalk height although the seedstalk height of 'Royal Chantenay' vernalized at 10°C was significantly shorter than at 0° and 5°. Variability in seedstalk height was greatest after vernalizing at 10° as indicated by the large standard errors of the mean (Table 2).

Carrots vernalized for 5 weeks at 5°C did not flower when subsequently grown at 27°/32°, some flowered at 21°/27° and about three fourths of them flowered when grown at 15°/21°. 'Royal Chantenay' and 'Scarlet Nantes' did not differ significantly in the percentage of plants which flowered but the seedstalk height of the 2 cultivars was affected by length of vernalization. As the vernalization time increased, the seedstalk height of 'Royal Chantenay' increased within each growing temperature and also as the growing temperature decreased, but there was no consistent effect of vernalization time on the seedstalk height of 'Scarlet Nantes' (Table 3). A similar experiment using carrots grown in the greenhouse at different temperatures before vernalization produced similar results on the effect of length of vernalization time. Seedstalk height of 'Royal Chantenay' was increased by longer vernalization periods, especially when subsequently grown at higher greenhouse temperatures, while 'Scarlet Nantes' showed no response.

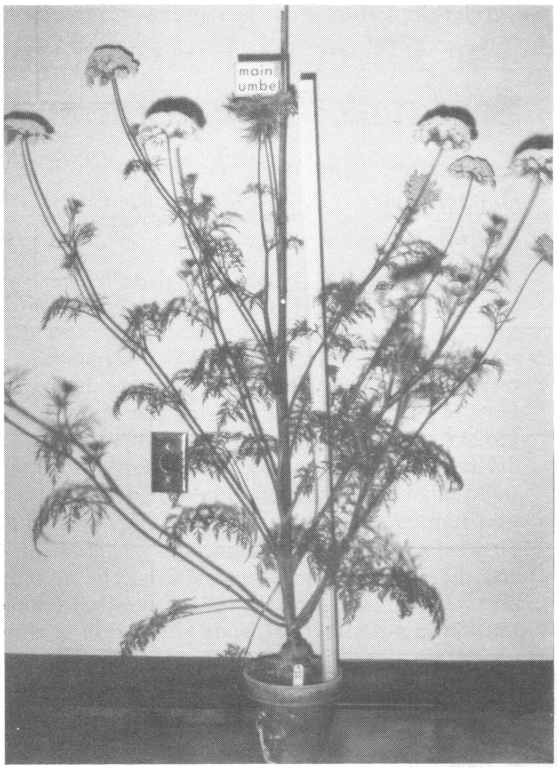

Fig. 1. Flowering carrot plant showing normal seedstalk elongation and branching. Grown at 15/21°C following vernalization at 5°C for 10 weeks.

Post-vernalization greenhouse growing temperatures during the initial 3 and 6 weeks following a 10-week vernalization period at 5°C had a significant effect on ultimate seedstalk height (Fig. 3). Although seedstalk elongation was evident macroscopically in only a few plants after 6 weeks, the temperature during this period had a lasting effect on seedstalk development. A period of 6 weeks at 27°/32°C reduced ultimate seedstalk height even when plants were moved to the more favorable growing temperature of 15°/21° (Fig. 3), and the ultimate seedstalk height was equal to that of plants grown continuously at 27°/32°, indicating that this temperature permanently inhibited seedstalk elongation. A period of 3 weeks at 27°/32° reduced seedstalk elongation when the plants were moved to 15°/21°, but those plants moved to 21°/27° were the same height as

Table 1. Seedstalk height of 3 carrot cultivars grown at different greenhouse temperatures following a vernalization period of 10 weeks at 5°C. Mean values of 10 plants.

Greenhouse temperature (°C)	Average seedstalk height (cm)		
	Royal Chantenay	Danvers	Scarlet Nantes
10/15	70.8 ± 4.5[z]	60.2 ± 4.6	71.9 ± 4.7
15/21	72.5 ± 3.1	58.8 ± 5.0	74.3 ± 4.1
21/27	16.7 ± 1.9	23.6 ± 2.0	46.5 ± 3.3
27/32	6.6 ± 0.6	25.8 ± 3.2	28.6 ± 6.8

[z]Mean ± standard error of the mean.

Table 2. The main effect of vernalization temperature on seedstalk height of carrots. Vernalization period was 10 weeks. Mean values of 10 plants.

Vernalization temperature (°C)	Average seedstalk height (cm)		
	Royal Chantenay	Danvers	Scarlet Nantes
0	58.7 ± 5.4[z]	47.9 ± 4.8	57.0 ± 4.3
5	56.0 ± 5.8	55.5 ± 4.4	70.9 ± 3.7
10	33.9 ± 8.3	46.6 ± 12.3	64.5 ± 7.3

[z]Mean ± standard error of the mean.

plants grown continuously at 21°/27° (Fig. 3). Seedstalk height of plants grown initially 6 weeks at 15°/21° and then moved to 27°/32° was greater than those plants grown continuously at 27°/32°, but was markedly shorter compared to plants grown continuously at 15°/21°, indicating that the higher temperature had inhibitory effects after the first 6 weeks. The temperature response followed the same pattern, but the high temperature effect was not as marked in 'Scarlet Nantes,' a faster bolting cultivar (Fig. 3). The "check" plants grown continuously at the same greenhouse temperature following vernalization responded similarly to those reported in Table 1.

The temperature during the vegetative development of the stecklings and the presence or absence of foliage during vernalization had no effect on rate of bolting or ultimate seedstalk elongation in the three cultivars when vernalized 10 weeks at 5°C.

The photoperiod following vernalization did not consistently affect the ultimate seedstalk height of these cultivars (Table 4). Stem elongation was not affected by photoperiod at 21°/27°C, but at 15°/21° the long day and night interruption treatments hastened seedstalk elongation compared to the short day treatment. Thermograph records revealed appreciable temperature increases under the incandescent lights so the increase in the rate of stem elongation was probably due to temperature and not photoperiod.

Vernalization temperatures of 0°, 5°, and 10°C resulted in nearly 100% flowering with normal umbel development and seed formation in all three cultivars in this study when the vernalization period was 10 weeks or longer, which agreed with earlier results of Dickson and Peterson (2). Development of lateral branches was greatly reduced on the short seedstalks of plants grown at the high greenhouse temperatures and this decreased the total number of umbels and potential seed yield (4). Umbel development was not affected by the higher greenhouse temperatures; however, seedset in the main umbels was not as good at 27°/32°C as at 15°/21°C. The seeds produced at the high temperature were viable and % germination was not affected.

Fig. 2. Carrot plant showing sessile flower. Grown at 21/27°C following vernalization at 5°C for 10 weeks.

While it has been known that the apical bud was the receptor of the flowering stimulus from vernalization, the effect of foliage during vernalization on rate of seedstalk elongation was not known. Kruzhilin and Shvedskaya (6) had reported that defoliation of carrots before vernalization resulted in no flowering, but they used only young seedlings in which no storage organ had developed prior to the vernalization treatments. The results obtained here indicate no effect of foliage during vernalization on seedstalk formation. The marked effect of temperature the first 3 and 6 weeks after vernalization reinforces the conclusion that foliage during vernalization had no influence on seedstalk elongation.

The percentage of plants that flowered was not affected by photoperiod as had been reported previously by Sakr and Thompson (12). The erroneous idea that "biennials" require long days to flower has appeared in the literature occasionally but has not been supported by experimental evidence (9, 14). Carrot breeders have been bringing carrots to flower in greenhouses during the short days of winter for many years, and commercial seed is produced during the long days of summer so photoperiod does not seem to be critical. In addition, most of the carrots used in this study and those studied by Dickson and Peterson (2) flowered under the short days of winter in the greenhouse. Imden (5) reported that long day treatments accelerated seedstalk elongation but were not essential for complete floral expression. The photoperiodic response he reported could have been effect of temperature, similar to the results of this study.

In these studies, carrots placed in the greenhouse immediately after harvest and grown continuously for nearly one year at 21°/27°C remained vegetative; however, approximately 50% of the carrots grown at 15°/21° flowered, and 100% flowered when grown at 10°/15°, indicating that the critical temperature for floral induction in carrots was higher than the commonly accepted 5° to 10°. Seedstalk height of carrots grown continuously at 10°/15° was comparable with that of carrots vernalized at 5° and then returned to 15°/21°; also, carrots grown continuously at 15°/21° and carrots returned to 21°/27° following vernalization had similar seedstalk height. Thus, as the vernalization temperature approached the critical temperature, both the percentage of plants that flowered and the height of the seedstalk decreased.

The results of this investigation indicated that the temperature optima for flowering of carrots was different than for

Table 3. Percentage of carrot plants that flowered and average seedstalk height as influenced by different vernalization periods at 5°C and greenhouse temperatures following vernalization. Mean values of 20 plants.

Weeks at 5°C	Greenhouse temp (°C)	Flowering plants (%)		Avg seedstalk height (cm)	
		Royal Chantenay	Scarlet Nantes	Royal Chantenay	Scarlet Nantes
5	15/21	71	83	19.4 ± 5.2[z]	63.4 ± 6.7
10		100	100	73.3 ± 4.7	91.4 ± 4.2
20		100	100	84.9 ± 4.5	90.9 ± 5.2
5	21/27	40	44	10.8 ± 2.9	53.3 ± 4.6
10		67	78	19.0 ± 5.5	56.6 ± 6.5
20		89	100	32.3 ± 3.1	64.1 ± 2.4
5	27/32	0	0	0.0	0.0
10		100	86	9.5 ± 1.3	32.7 ± 3.6
20		100	100	17.4 ± 1.7	33.5 ± 2.7

[z] Mean ± standard error of the mean.

Table 4. Percentage of carrot plants flowered and average seedstalk height as affected by 3 photoperiods at 2 greenhouse temperatures following 10 weeks vernalization at 5°C. Mean values of 10 plants.

Greenhouse temp (°C)	Photoperiod (hr)	Flowering plants (%)			Avg seedstalk height (cm)		
		Royal Chantenay	Danvers	Scarlet Nantes	Royal Chantenay	Danvers	Scarlet Nantes
15/21	8	70	100	86	72.7 ± 4.0[z]	52.1 ± 5.3	93.0 ± 2.7
	8 + NI[y]	80	100	100	70.5 ± 6.9	70.8 ± 6.4	91.6 ± 6.3
	14	70	100	100	78.6 ± 4.9	87.6 ± 5.4	92.4 ± 4.8
21/27	8	75	90	67	6.3 ± 0.9	27.6 ± 4.7	53.0 ± 4.8
	8 + NI[y]	63	88	78	9.2 ± 2.2	21.0 ± 4.7	41.1 ± 3.8
	14	63	100	78	8.4 ± 1.2	25.0 ± 4.6	44.6 ± 2.8

[z]Mean ± standard error of the mean.
[y]NI = night interruption from 11 PM to 1 AM.

seedstalk elongation, and that these processes were also affected differently by temperatures following vernalization. The results also suggested that an inherent difference existed among the cultivars in their vernalization requirements and their capacity to sustain the vernalized state under subsequent higher growing temperatures. The persistence of the vernalized state in other species has been documented by Lang (7).

Anatomical observation showed that carrots stored 6 weeks at 5°C were still in the vegetative or very early stage of apical meristem enlargement. After 9 weeks, apices were not advanced morphologically much more than at 6 weeks, but were apparently more advanced physiologically. The higher greenhouse temperatures following only 5 weeks storage at 5° inhibited further differentiation and other physiological processes necessary for floral induction; whereas, 10 weeks at 5° produced a physiologically fixed condition in the carrot apex and complete flowering resulted. If carrots were exposed to low temperature for a longer period (up to 30 weeks), later stages of umbel differentiation and even macroscopic seedstalk elongation occurred before planting in the greenhouse. Thus, low temperature had an "inductive" or a "direct" effect on carrots depending on the length of exposure (7).

A period of 10 weeks at 5°C was optimum to induce a "persistent vernalized state" (7) shown by the fact that temperatures as high as 27°/32° did not inhibit flower formation. The inhibition, or marked reduction, of seedstalk elongation by high temperature indicated a devernalizing effect contrary to most other species. High temperatures following vernalization have been reported to inhibit flowering but not stem elongation (1); however, no reports were found in the literature which indicated that flowering occurred without seedstalk formation in any species requiring low-temperature floral induction. Mur-

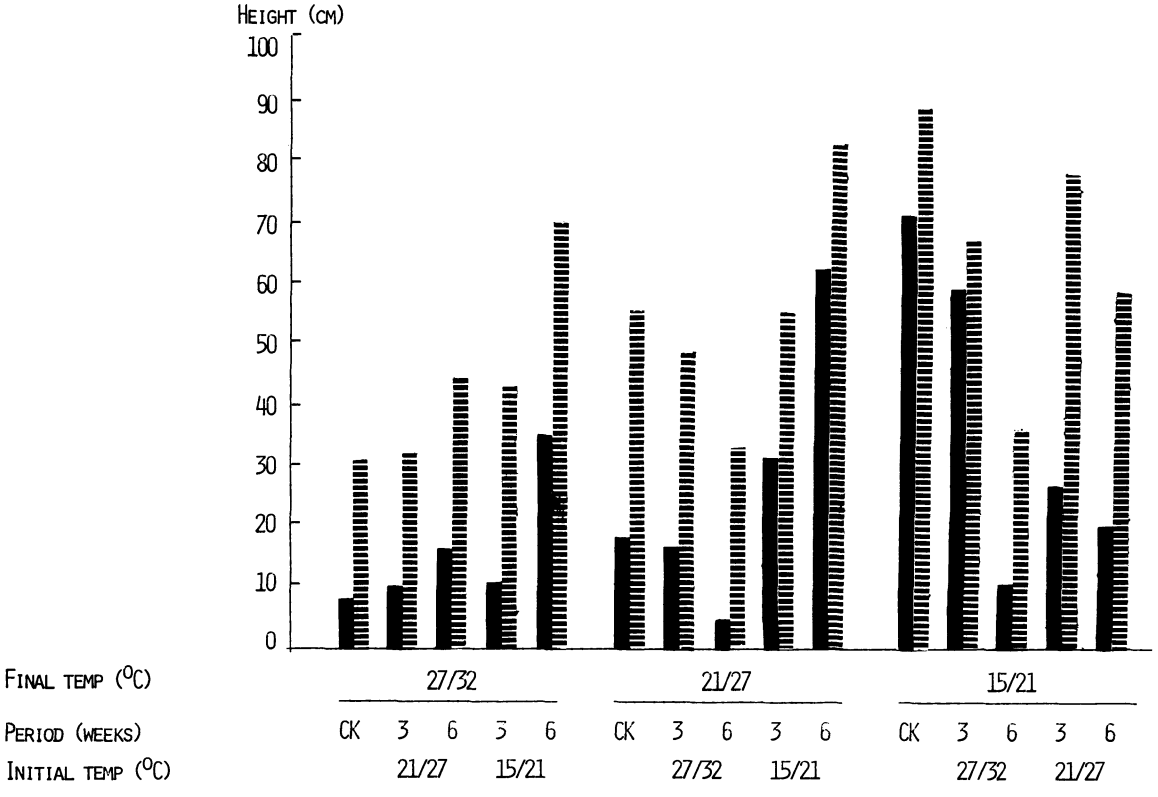

Fig. 3. The effect of greenhouse growing temperature during the initial 3 and 6 weeks following 10 weeks vernalization at 5°C on ultimate seedstalk height in Royal Chantenay (solid bar) and Scarlet Nantes (striped bar). (CK = at final temperature throughout the experiment)

neek (8) reported reduced seedstalk elongation and sessile flowers in *Rudbeckia* plants grown in a short photoperiod immediately following the inductive long day period.

Carrot cultivars have been shown to differ in the rate of bolting (2, 10). Microscopic observations in this study indicated that cultivars differed in rate of floral initiation both during and following vernalization, and that initial seedstalk elongation and umbel primordia differentiation occurred during the first 6 weeks following the 10 week vernalization period (article in preparation). Umbel primordia differentiation was always preceded by elongation of the subapical region and umbel primordia differentiation had begun by the time macroscopic seedstalks appeared. This observation agreed with that reported by Tsukamoto et al. (13). Exposure of carrots to high temperatures during this initial 6 week period inhibited further seedstalk elongation, but not floral differentiation, indicating that some aspect of cellular metabolism vital to stem elongation was affected irreversibly.

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The Effects of Fresh and Aged Bark Growing Media and Zinc Nutrition on the Growth, Zinc Uptake, and N Content of Tomato [1]

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Additional index words. Lycopersicon esculentum

Abstract. **Plant dry weight of tomato (*Lycopersicon esculentum* Mill.) grown in aged bark media was equal to or greater than that of those cultured in a control medium of perlite-sand. Plant growth in fresh bark was inhibited initially and then recovered. Zn concentration and total content per plant were high for plants cultured in bark media even when little or no Zn was applied. The intereaction between media and applied Zn was significant. Plant Zn increased with increasing amount of applied soluble Zn when cultured in perlite-sand, but did not normally change for plants cultured in bark. High Zn concentration of plants cultured in fresh bark was too low to account for the initial growth inhibition. N concentration and content per plant were normally lower for plants grown in fresh bark. N of plants in aged bark was similar to plants in the standard medium. Growth inhibition of plants in fresh bark did not appear to be due to N deficiency.**

Bark, an environmental hazard when treated as an unusuable waste product of the lumbering industry, can be used as a medium for growing plants. In most cases it has been used as a substitute for more expensive components such as peat in the culture of floral and foliage plants (8, 25, 29, 34, 35) and woody ornamentals grown in containers (12, 16, 17, 25, 26). Other experiments have shown lumbering wastes superior to soils for growing tomato (1, 9, 10, 32).

Organic matter (OM) has been shown to retain Zn (2, 5, 16), but the availability of the retained Zn is uncertain. Additions of OM have reduced Zn availability to plants in some cases (3, 22, 30) and increased it in others (13, 18, 19, 31). Zn retention by OM is most probably due to chelating compounds produced during degradation (2, 11, 14, 21, 23). Zn bound to humic acid is insoluble and unavailable, while that bound by organic acids or fulvic acid is available (33). Bark, particularly

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