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Quantitative and Qualitative Characterization of Carrot Root Periderm during Development

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Abstract. **Periderm from the roots of carrot (*Daucus carota* L.) was isolated enzymatically and analyzed anatomically and chemically during development. The outer transverse walls of the phellem layer formed a continuous, external membrane containing chloroform/methanol-soluble lipids. Separated by thin layer chromatography, these lipids contained at least 6 major chemical groups, the most abundant of which cochromatographed with fatty acids. Scanning electron microscopy revealed the absence of surface fine structure. The periderm membrane decreased in weight with development of the root, attributable to reductions in both chloroform/methanol-soluble and insoluble material per unit area.**

The roots of crops such as carrot, beet, and turnip are covered by periderm tissue at maturity (5). A lipid polymer, suberin, is a characteristic component of the periderm cell wall (13) and has been partially characterized in 6 crops (14). In addition, wax-like materials have been collected and identified from these plants (7). Suberin-containing portions of the periderm can be separated from adjacent tissue with enzymatic methods commonly employed to isolate cuticular membranes from aerial plant parts (14). The root periderm outer surface and the cuticular membrane of aboveground plant parts are similar in structure and function. The cuticle is a noncellular, nonuniform membrane consisting of a cutin matrix which is impregnated with wax often present as elaborate fine structure on the outer surface (epicuticular wax). Cellulose and pectin lie between a layer of cutin and the cell wall and thus the cuticle can be released by digestion with cellulase and pectinase. The chemistry of cutin and suberin are similar in that both are composed in part of long chain fatty acids, hydroxy fatty acids, and related aliphatic compounds (13). Phenolic constituents are present in both polymers (23) but to a greater extent in suberin (12). Many of the soluble lipids associated with suberin are those typical of cuticular waxes, i.e., alkanes, esters, alcohols, and fatty acids (7, 26).

The structure, location, and chemistry of the cuticle limits water loss and provides a barrier to the uptake of foliar-applied chemicals (15, 18). In addition, the cuticle serves as a protective barrier to insect and disease infestation (17). The suberized cell walls of the carrot periderm also may function as the primary barrier to substances moving into and out of the root. Although the suberin and its associated soluble lipids exist as a lamellar structure within the cell wall, and are not extracellular as in cutin, the periderm probably plays a similar role in preventing water loss from internal tissue (4, 25). As in the cuticle (3, 10, 24), it is the waxes of the suberin complex which appear to constitute the greatest impedence to water vapor diffusion (25).

An anatomical description of carrot root development was published by Esau (6). The activity of the cambium and secondary tissues displaces the cortex early in the life cycle of the plant and the periderm forms the outer protective layer. Although the chemical composition of carrot suberin (14) and its associated waxes (25) has been partially analyzed for mature roots, there is no developmental study of the periderm with respect to its chemistry. The following investigations were initiated to form a basis for physiological studies on the carrot periderm, particularly the portion forming the outermost surface of the root. Also reported are findings on changes in qualitative composition of these suberin-enriched cell walls during growth in a greenhouse situation.

Materials and Methods

Plant material and culture. Carrots for the characterization work were grown at the Michigan State University Muck Soils Research Farm in Laingsburg. 'Tito', 'A Bak', MSU 1414 B, MSU 1410 B, and MSU 1389 B were obtained from the department of horticulture's carrot-breeding program. Seeds of 'Gold Pak', 'Danvers', and 'Spartan Fancy' were purchased from Joseph Harris Co., Rochester, N.Y. All were grown with standard cultural procedures.

For the development study, seeds of 'Scarlet Nantes' (Harris Seed Co.) were sown in 10-liter plastic pots filled with vermiculite and placed on a greenhouse bench. This medium greatly facilitated the harvest and subsequent analyses as the particles were easily rinsed from the root with minimum damage to the periderm. Fertilizer was provided by weekly applications of half-strength modified Hoagland's and soluble 20N–8.8P–16.6K (rate = 200 ppm N). No other chemicals were applied. A randomized complete-block design with 4 blocks was utilized; 20 to 30 roots formed an experimental unit. Six equally distributed sampling dates began 78 days after sowing and ended on day 147. At each harvest, average root fresh weight and total periderm membrane weight per unit area were determined. The periderm membrane was further divided into its chloroform-soluble and insoluble components which also were quantitated on a unit area basis. The soluble lipids were examined by thin layer chromatography (TLC).

Isolation of periderm membrane. Peels from mature carrot roots were boiled for 15 min in distilled water, drained, and treated with a 1% (w/v) solution of fungal pectinase (United States Biochemical Corporation, Cleveland, Ohio) in citrate-phosphate buffer (pH 3.8). Complete removal of cellular debris (as determined by microscopic examination) usually occurred after 4 days with mechanical agitation and required at least one

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change of solution during this period. For accurate determination of membrane weight per unit area, 100 discs of 6 mm diameter were punched with a cork-borer and excised from the root surface with a razor blade in preparation for enzyme treatment. Following digestion of the excess internal tissue, the resultant cell-free membranes were thoroughly rinsed, drained, and air-dried.

Extraction of soluble lipids. About 150 mg of isolated, air-dried membranes were refluxed for 2 hr in 50 ml chloroform/methanol ($CHCl_3$/MeOH, 2 : 1, v/v) and filtered (Whatman no. 1 paper). All solvents were glass-distilled. This procedure was repeated with clean solvent and the extracts were combined. Extracts were concentrated by evaporation under a stream of N_2 to about 3 ml, transferred to screw-capped test tubes for complete drying, and sealed under N_2 until used in qualitative analyses. The membranes were weighed before and after extraction for calculation of soluble lipid weight.

TLC. Soluble lipid extracts from 3 lines and 2 cultivars lines in the characterization study were dissolved in chloroform (10 mg/ml) and extracts from the development work ('Scarlet Nanks') were adjusted to reflect 250 cm^2 area extracted/ml based on their calculated weight/cm^2. The lipids were applied as spots (10.0 µl) or 0.5-mm bands (200 µl) to 0.25-mm silica gel G plates (Uni-plate, Analtech, Inc., Newark, Del.) which were prewashed in redistilled benzene, prepared as described by Flore and Bukovac (8). Cabbage leaf wax of known composition (2, 8) was applied as a standard to compare with the lipids of the 5 different lines. Spotted plates were developed in benzene and wax constituents were localized by charring (160°C) after spraying with 50% H_2SO_4. For quantitative analysis of major wax fractions by weight, larger (10 mg) quantities of soluble lipid from MSU 1410 B were applied as a 16-cm band to 0.5-mm silica gel G plates. Plates were again developed in benzene and then exposed to iodine vapor for detection of the separated fractions. Prominent bands were outlined to facilitate location after the stain evaporated. Each band was scraped from the plate and extracted with 10 ml $CHCl_3$/MeOH (2 : 1, v/v) at 60° for 2 hr. The slurry was washed through Whatman no. 1 paper into clean tubes. Chromatography of each fraction was repeated and the bands collected as before but into tared tubes. Solvent was evaporated under N_2 and the tubes were weighed. Amount of wax in each fraction was calculated as a percentage of total by weight.

Light microscopy. Isolated membrane discs and fresh carrot root pieces (2 or 3 mm) containing periderm were surrounded with Tissue-Tek II O.C.T. (Lab Tek Products, Naperville, Ill.) and quick-frozen on metal stubs in an International Harris Model CTD cryostat. Following the method of Norris and Bukovac (19), tissue was sectioned 6–12 µm thick, mounted on glass slides, and stained with a saturated solution of ethanolic Sudan III and IV for 30 sec. After rinsing and air-drying, cover slips were affixed with 1% (w/v) phenol in 1 : 1 (v/v) water and glycerol.

Scanning electron microscopy. Small (2 to 3 mm^2) pieces of tissue were cut from the surface of 'Tito' roots, frozen on dry ice, and lyophilized. Some sections received a pretreatment which consisted of wiping the surface with $CHCl_3$/MeOH-soaked cotton prior to freezing to remove any superficial wax deposits. For microscopy, sections were coated with approximately 20 nm gold. Photographs were taken with a JEOL Model JSM 35C instrument operated at 15 kV.

Transmission electron microscopy. Samples 2 to 3 mm^2 were fixed for 2 hr in cold (0°C) 4% glutaraldehyde in 0.1 M phosphate buffer; postfixed with 1% osmium tetroxide in 0.1 M phosphate buffer, dehydrated in ethanol, and embedded in a 1:1 mixture of Mollenhouer's and Spurr's resins (11). Sections (80 nm) were examined on a Phillips 300 instrument operating at 60 KV.

Results and Discussion

Light microscopy. A section through the root surface taken midway between the crown and the tip of a mature carrot root ('A Bak') indicated that rectangular-shaped phellem cells comprised the outermost layer of periderm (Fig. 1A). The darkened walls of these cells were stained with Sudan III and IV, a stain that has been used in histological studies to detect cutin and suberin (19, 22). In some areas, the suberized cells occurred in 2 layers but the densest staining occurred on the outermost surface.

Periderm cells containing suberin are expected to resist digestion by pectinase and this indeed was the case with carrot root. Enzyme treatment for 96 hr left only the outer periclinal wall with fragments of anticlinal and inner periclinal wall adhering (Fig. 1B). These results indicated that a continuous membrane was formed mainly by the outer transverse wall of the phellum, and that this layer could be isolated intact from the underlying tissue.

This observation leads to the first parallel (with some restrictions) that can be drawn between the carrot periderm and a characteristic leaf cuticle. Both the carrot root and the typical leaf are covered by an outer, continuous membrane structure; however, in the case of the leaf, the cuticle is formed on top of the epidermal cell walls and is noncellular. The cutin-containing matrix of the leaf cuticle is cleanly separated from epidermal walls upon pectinase treatment (10, 19, 20). Adjacent phellem cells of the carrot periderm released their outer walls intact upon digestion of the tissue. The suberin contained within these walls probably forms continuous bands across the areas of the radial cell walls (4, 25) and thus lends continuity to the surface of the root.

Transmission electron microscopy. The high magnification obtained with the transmission electron microscope showed the dark-staining material in the outer periderm cell wall to be continuous across the area of the radial wall (Fig. 1C). The continuity in the surface of the root allowed the outer wall material to be isolated in large sections. The lamellar structure common to the potato tuber periderm walls (25) was not observed in these sections.

Scanning electron microscopy. Scanning electron microscopy was employed to determine if soluble lipid fine structure typical of leaf and fruit waxes (2, 16) existed on the outside of the root. Micrographs (Fig. 2) revealed no regular pattern of wax crystals. The surface debris and ridge-like matter were not greatly reduced by $CHCl_3$/MeOH extraction. Typical leaf and fruit wax compounds would have been removed by this treatment (1, 19, 21). The superficial structure seen (Fig. 2) evidently was not a lipid or at least not a free (soluble) lipid form. These observations illustrate a major difference between roots and cuticularized organs.

Isolation of membrane and extraction of soluble lipid. The weight per unit area of the isolated membrane was found to vary with cultivar and ranged from 470 to 790 µg/cm^2 (Table 1). Although some of the observed differences could be due to environmental and location effects, significant variation was shown among the 5 subjects grown in the same experimental plot. The proportion of the total membrane which was extracted with $CHCl_3$/MeOH ranged from 7.0% to 11.0% of the total membrane, or 33 to 70.4 µg/cm^2. The hot solvent extraction removed all lipids and other lipophilic organic compounds other than those cova-

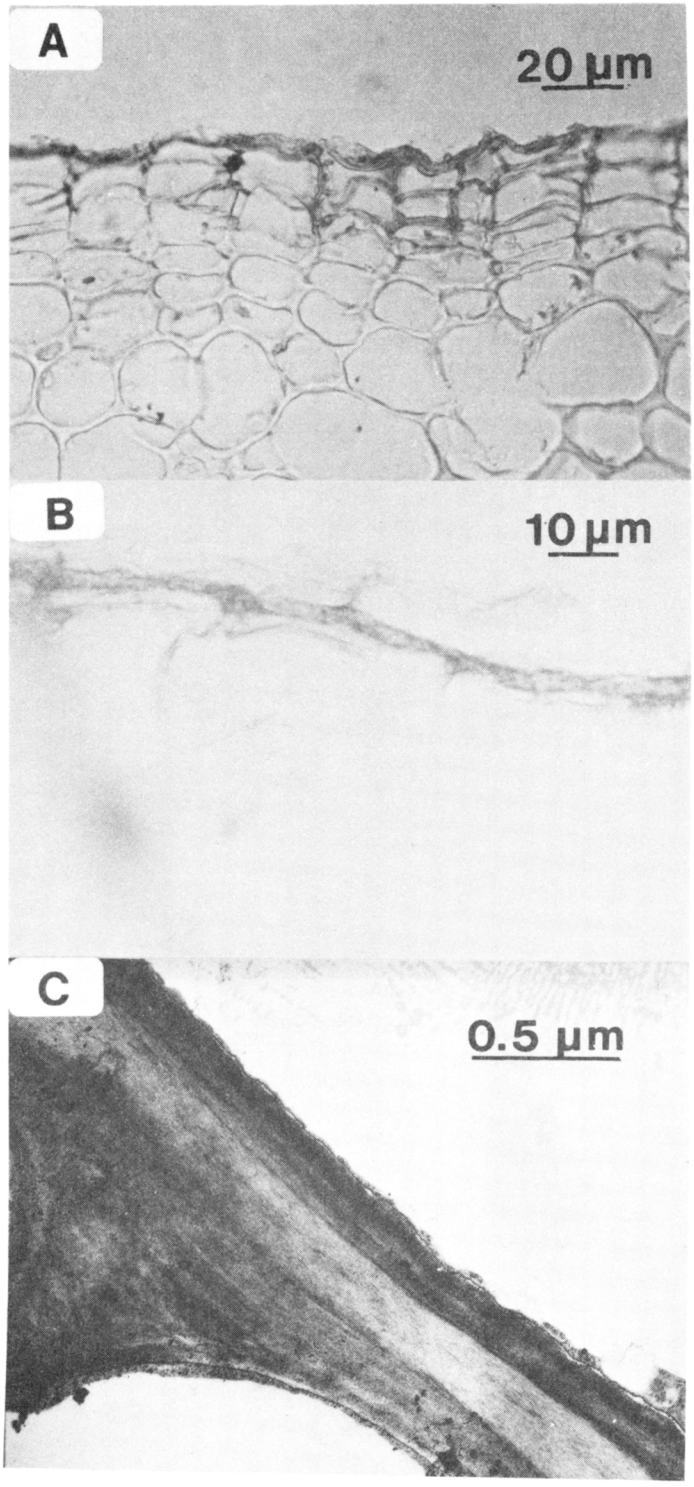

Fig. 1. Cryostat sections of 'A Bak' carrot root stained with Sudan III and IV. A. A 7-µm section from the midsection of mature carrot root surface. B. Periderm section (10 µm) following 96 hr of treatment with pectinase. C. Transmission electron micrograph of a 'Scarlet Nantes' periderm cell section (80 nm). Stained as described in text.

lently bound as part of the suberin polymer (14). The lipid proportion in the periderm was less than that generally found in the cuticle; however, the amount of lipid soluble material per unit area was similar to that reported for many cuticular membranes (17).

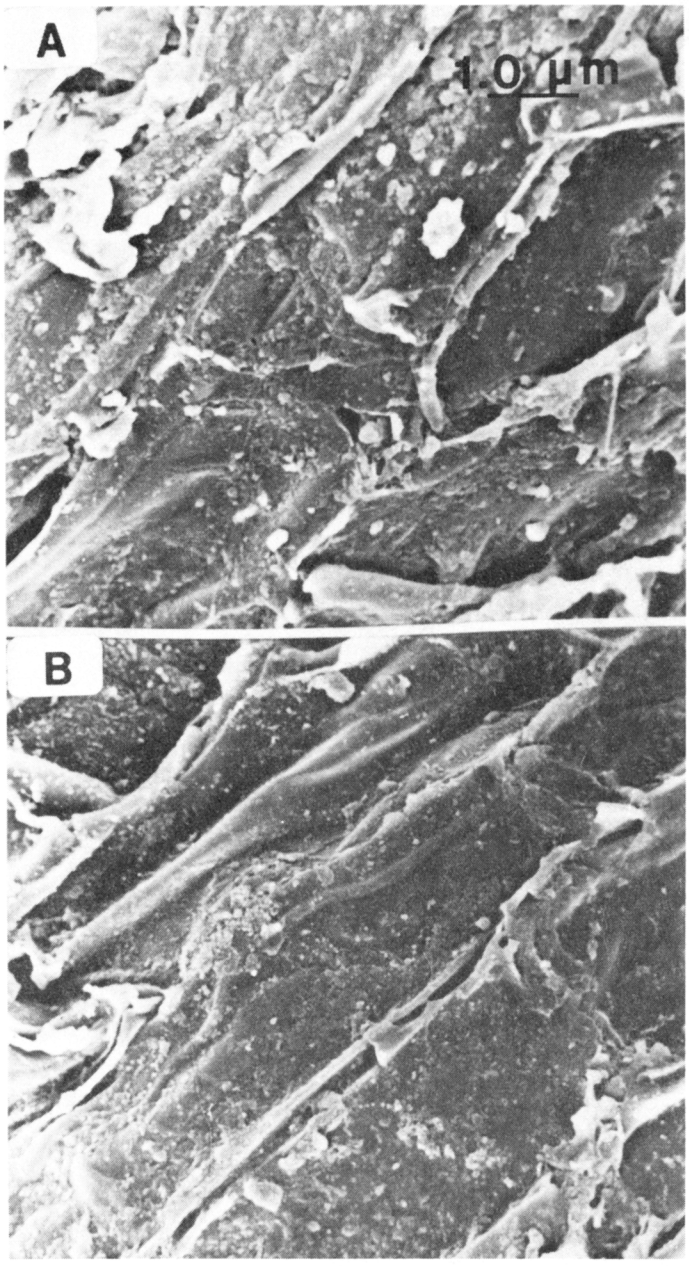

Fig. 2. Scanning electron micrograph of 'Tito' root surface. A. Normal surface. B. Surface after wiping with $CHCl_3$/MeOH-soaked cotton.

TLC. Major wax groups from the soluble lipids isolated from membrane material of 3 carrot lines and 2 cultivars were separated by TLC. A nonpolar solvent, benzene, was selected to separate out hydrophobic classes from the crude extract (2, 8), and cabbage wax previously characterized was used for comparison with the carrot extracts (Fig. 3). Nonpolar compounds, migrating above the origin, were shown to constitute a portion of the soluble lipids in the periderm membrane. The 6 most prominent spots were collected from preparative layer plates for gravimetric analysis. The most polar fraction, 6, was also the predominant one (Table 2), confirming the findings of Espelie et al. (7). Relatively small amounts of very nonpolar classes (i.e., fractions one and 2) were recovered. The opposite was found to be true of cabbage wax in one study (8), where alkanes made up 26% of the total and fatty acids only 3.5%. Collectively then, the carrot periderm lipids are relatively more polar than

Table 1. Total membrane weight and $CHCl_3$/MeOH soluble content of periderm membranes isolated with pectinase from different lines and cultivars of carrot.

Cultivar[z,y]	Total membrane wt ($\mu g/cm^2$)	$CHCl_3$/MeOH soluble (%)
Spartan Fancy	470 ± 50	7.0 ± 2
Danvers	640 ± 60	10.0 ± 3
Gold Pak	790 ± 70	8.0 ± 1
MSU 1389 B	710 a[x]	8.3 a
A Bak	710 a	9.6 a
MSU 1410 B	640 b	11.0 a
Tito	630 b	10.6 a
MSU 1414 B	600 b	10.7 a

[z]The first 3 cultivars were grown in different locations.
[y]The 5 accessions were grown in the same experimental plot; values represent the average of 3 replications.
[x]Mean separation within columns by Duncan's multiple range test, 5% level.

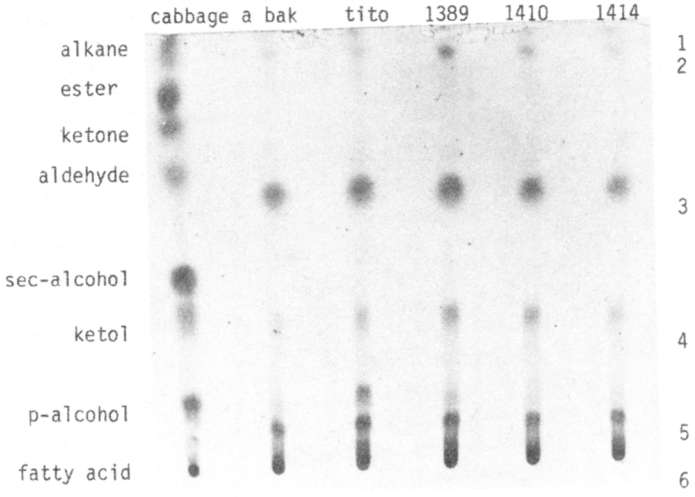

Fig. 3. Thin layer chromatogram of soluble lipids from periderm membrane of 3 carrot lines, 2 cultivars, and leaf wax from cabbage. Development in benzene.

Table 2. Quantitative fractionation of soluble lipid from MSU 1410 B by thin layer chromatography in benzene.

Fraction[z] number	R_f	% of total
1	1.0	1.52
2	0.95	4.57
3	0.61	2.03
4	0.33	4.06
5	0.10	14.21
6	0.00	65.49

[z]From Fig. 3.

the cabbage wax and would be expected to lend different permeability characteristics to the suberized cell walls. The contribution of various chemical classes to the effectiveness of leaf wax as a barrier to penetration has been documented (3, 9) but similar studies have not to our knowledge been performed for suberin-associated waxes.

Developmental studies. Data taken during carrot growth enabled us to correlate periderm components with root development. Total periderm membrane weight/cm^2 and root fresh weight were plotted against time (Fig. 4). The weight of the isolated membrane decreased with time as the size of the root increased. The weight/unit area of the soluble lipids and insoluble components decreased during the course of the study, by 50% and 37%, respectively (Fig. 5). Since the root is rapidly expanding over the period in which these observations were made, it is likely that the synthesis of periderm wall components did not keep pace with the increase in the surface area of the root. The data in this study support this explanation since all membrane components decreased in quantity and at about the same rate.

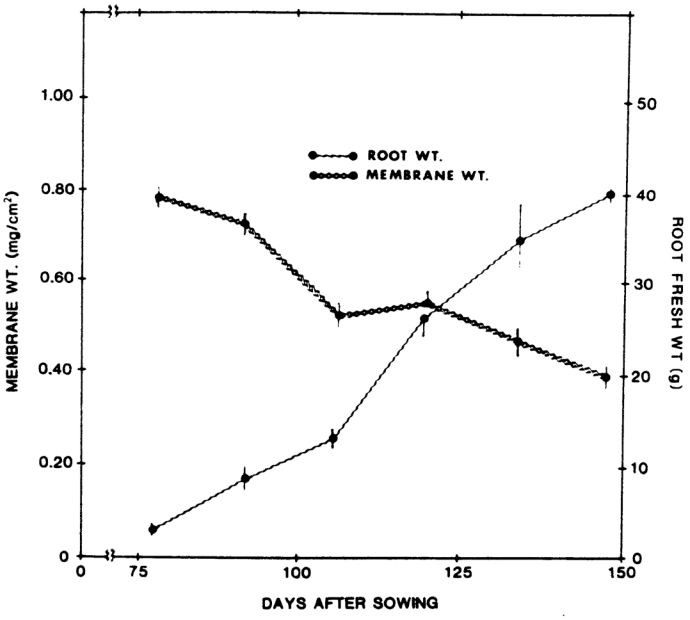

Fig. 4. Changes in periderm membrane weight and root fresh weight with time in greenhouse-grown 'Scarlet Nantes'. Each point is the average of 4 replicates of 10–15 roots. Vertical bars indicate SE.

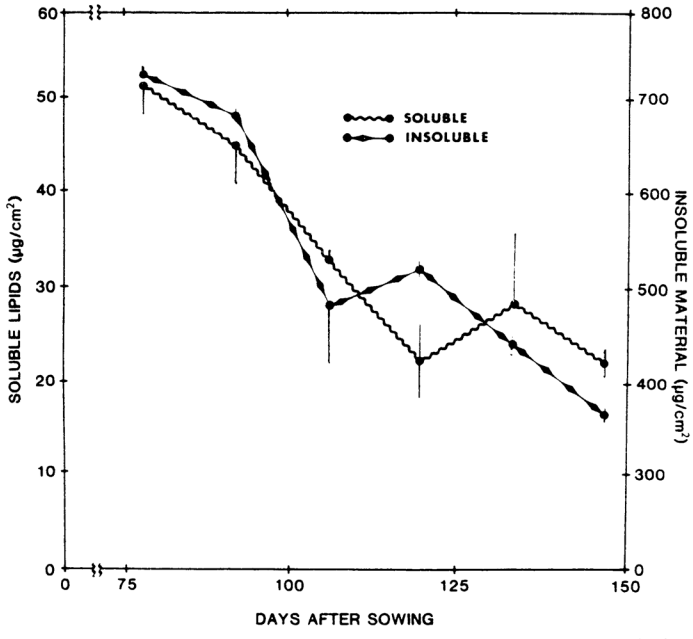

Fig. 5. Changes in the composition of the periderm membrane during the growth of 'Scarlet Nantes.' Each point is the average of 4 replicates of 10–15 roots. Vertical bars indicate SE.

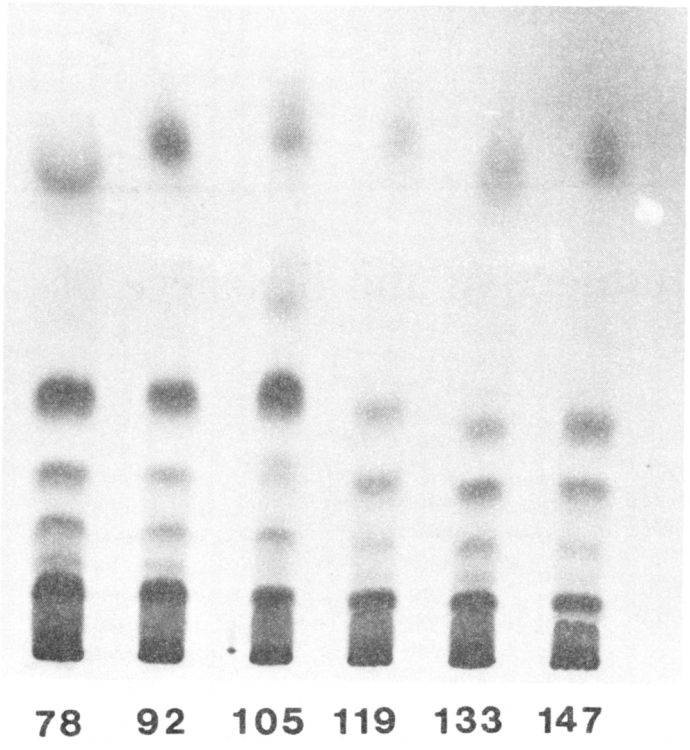

Fig. 6. Thin layer chromatogram of soluble lipids from isolated 'Scarlet Nantes' periderm at various harvest dates. Number of days after sowing is indicated below each sample. Developing solvent = benzene. Each band contains the soluble lipids from 250 cm^2 of root surface.

Cuticular lipids have been shown to undergo changes in composition during maturation (4, 16); however, qualitative differences in wax between sampling dates were not observed with TLC (Fig. 6).

Conclusions

The outer cell walls of the carrot root periderm form a continuous membrane over the root surface. Soluble lipids comprise about 10% of the membrane and the bulk of them are relatively polar in comparison to those found in cabbage leaf cuticle. These components appear to be entirely embedded rather than superficial. However, synthesis of the suberized portions of the periderm and the associated soluble lipids does not proceed at the same rate as root expansion as seen by a progressive decrease in the weight per unit area of the membrane.

Although the stability of periderm characteristics was not investigated, differences in membrane weight between cultivars suggest the possibility of genetic manipulation. As with cuticular waxes, chemical and environmental manipulations of the waxes may be possible.

The physical and chemical properties discussed here suggest a protective role for this portion of the root periderm. When compared to a leaf cuticle, however, the periderm membrane lacks some features which are very important to the function of the leaf cuticle, i.e., surface wax fine structure and a high concentration of very hydrophobic lipid classes. Additional reports on periderm permeability to water vapor diffusion are forthcoming. The contribution of individual components to permeability characteristics of the carrot periderm and require additional study before further analogies can be drawn between the protective role of the cuticle and the suberized tissues.

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Effects of Processing upon Objective and Sensory Variables of Carrots

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Abstract. **Four hybrids of carrot (*Daucus carota* L.) were analyzed raw, fresh-cooked, canned-cooked, or frozen-cooked for sensory and objective parameters. Processing reduced the carotenoid and volatile terpenoid concentrations of all hybrids. Relative to raw carrots, sugar content was reduced in canned-cooked and frozen-cooked carrots, but was increased in fresh-cooked samples. Depending on the hybrid, 6% to 32% of the free sugar was reducing sugar in raw samples; however, sugars in processed samples were 15% to 33% reducing sugar. Fresh-cooked and frozen-cooked carrots exhibited a 10-fold reduction in shear pressure texture relative to raw texture, while canned carrots had a 30-fold reduction. Harsh flavor was reduced greatly by canning and freezing, but was not reduced as much in fresh-cooked samples. These differences in harsh flavor could be accounted for by variation in volatile terpenoid levels. Differences in sweetness found between raw sampling hybrids also were observed for corresponding samples after processing. Reducing sugars and volatile terpenoids contributed to variation in sweetness and preference.**

Processing usually alters the flavor, vitamin content, and texture of vegetables. Upon canning, tomatoes lose volatile acids and low-boiling volatiles, whereas carbonyl compounds, high-boiling volatile oil, and methyl sulfide concentrations increase (6, 9, 14). Carrots have been reported to lose approximately half of their high-boiling volatile terpenoids upon canning (3) and 15% to 20% of their carotenoids (1, 7, 16). In addition, cultivar differences have been noted for canned snap bean flavor volatiles (15) and processed carrot firmness (4, 8).

In a recent review, Lund (5) has stressed the need for basic data describing quantitative changes in food quality as a function of processing parameters. Sizable genetic differences in raw carrot volatile terpenoids, sugars, carotenoids, and flavor have been reported (10, 11, 12, 13). This paper considers the effect of some current processing practices upon these objective and sensory variables for several carrot hybrids.

Materials and Methods

Plant materials and sample preparation. Four USDA carrot hybrids—(B6373 x B6345) x B6274 (A), B8080 x B6274 (B), (B3640 x B3080) x F524 (C), and (B3640[2] x B3316) x F524 (D)—were grown at Zellwood, Fla., shipped via air to Wisconsin, washed, and stored at 5°C. Raw carrots were either evaluated within 6 days of harvest or were processed and evaluated within 20 days.

Raw carrots were prepared and evaluated as described previously (10, 11). Three methods of processing were used. Fresh-cooked carrots were sliced (1 cm thick), placed into 2 parts boiling salted water (0.5% NaCl) for about 3 min, simmered about 8 min, drained, and evaluated. Canned-cooked carrots were prepared by slicing raw carrots, packing into glass pint jars with brine (0.5% NaCl), and still-retorted at 115°C for 30 min; prior to evaluation, canned-cooked samples were simmered 5–10 min in canning liquid and drained. For frozen-cooked carrots, whole roots were blanched 4 min in boiling water, drained, cooled, sliced, immersed into Freon 115 until colder than −25°, sealed in polyethylene bags, and stored at −12°; prior to evaluation, frozen-cooked carrots were immersed in boiling salted water (0.5% NaCl) for about 2 min and drained.

Laboratory and sensory measurements. Methods of laboratory and sensory measurements were as described previously (10, 11). Included were carotenoids, sugars, volatile terpenoids, and flavor attributes. Descriptive profiling was performed by 25 to 30 panelists. The texture measurements were made using a Kramer shear press (16) and a sensory panel which scaled textures on a semistructured scale (coded on a 7-point basis) from soft to crisp.

Data were analyzed on a Univac 1110 computer at the Univ. of Wisconsin-Madison, using the BMD P2R stepwise regression program (2).

Results and Discussion

Objective variables. Carotenoid and volatile terpenoid concentrations in carrots were reduced by all processing procedures used (Table 1). Depending on cultivar, carotenoid levels diminished 11% to 20% for fresh-cooked, 8% to 12% for canned-cooked, and 7% to 20% for frozen-cooked. A loss of 70% to 85% of total volatile terpenoids was realized for fresh-cooked, whereas either canning or freezing resulted in a 65% to 80% reduction. In general, individual volatile terpenoid quantities diminished by the same percentage upon processing, although frozen samples retained relatively less myrcene and α-phellandrene than did fresh-cooked or canned-cooked carrots. Fresh-

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