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Enhancement of Calcium Transport to Inner Leaves of Cabbage for Prevention of Tipburn[1]

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Abstract. **Heading cabbage plants, *Brassica oleracea* L. (Capitata group) grown under humidity conditions which allowed root pressure flow to occur during the dark period, as indicated by the occurrence of guttation from the leaf margins, remained free of tipburn. Plants grown under conditions which prevented root pressure flow from occurring developed tipburn on both wrapper and inner head leaves. The effect of root pressure flow on ^{45}Ca transport was studied in cabbage plants in the rosette stage of growth. Heads were simulated by covering the inner leaves of the plants. ^{45}Ca was readily transported to inner "head" leaves under high humidity which allowed root pressure flow to occur, while very little ^{45}Ca was moved to these leaves under low humidity which prevented root pressure flow. The data indicate that root pressure flow is required to move adequate amounts of Ca to prevent tipburn in head leaves of cabbage.**

Several studies have indicated that tipburn of cabbage is due to deficient Ca levels in the inner head leaves (23, 25, 32). Although large amounts of Ca are absorbed by the roots, as indicated by high Ca concn in the outer leaves, only small amounts of Ca reach the inner leaves. It has been suggested that tipburn results when certain environmental factors restrict Ca transport to marginal tissue of internal head leaves (31).

Ca transport from the roots to the shoots of plants is thought to occur via the transpiration stream (1, 2, 3, 5, 20, 30), undergoing a series of exchange reactions at negatively charged sites in the xylem as it moves through the plant (1, 3). Some evidence indicates that Ca can also be transported with water moved by root pressure flow (4, 6); however, there is no evidence that this process is necessary to move Ca to any plant tissues. Since transpiration from inner head leaves of cabbage is greatly restricted by surrounding leaves, we have hypothesized that root pressure flow is necessary for transport of adequate Ca to inner head leaves of cabbage.

The experiments reported here were conducted to study tipburn development and Ca transport under conditions that encourage root pressure in comparison to conditions that encourage rapid transpiration.

Methods

Tipburn studies with heading plants. Seeds of 'Sanibel' cabbage, were planted in trays of vermiculite, and watered with nutrient solution containing Na, K, Mg, Ca, NO_3, SO_4, H_2PO_4, and Cl at 0.5, 3.0, 2.0, 5.0, 7.5, 2.0, 0.5 and 0.5 meq/liter, respectively; and Fe, B, Mn, Zn, Cu, and Mo at 2.3, 0.25, 0.25, 0.0025, 0.01, and 0.005 ppm, respectively. Fe was added as FeEDTA. The trays were placed in an Environmental Growth Chamber Model M-3 reach-in growth chamber with a plexiglass barrier, with temp 20 ± 1°C, relative humidity (RH) 62 ± 3% and illumination 21.5 ± 1.1 klx (2000 ft-c, 310 μE $m^{-2}sec^{-1}$). Illumination was continuous with input wattage for cool-white fluorescent and incandescent lamps of 90 and 10%, respectively. Air temp was measured with an exposed iron-constantan thermocouple, relative humidity with a psychormeter, and illumination with a Weston illumination meter and Lambda quantum meter. Air movement down through the plant bed was 20–30 m min^{-1} as measured with a hot-wire anemometer.

The trays were covered with paper for 2 days to prevent drying of the germinating seeds. Following emergence, distilled water or nutrient solution was added to the trays on alternate days. Two weeks after seeding, when the first true leaves were about 1.5 cm long, seedlings were transplanted into 10.8 liter containers filled with peat soil from a newly opened marsh in Wisconsin. Each container of soil was fertilized with solutions containing 1.32 g of KH_2PO_4, 4.95 g of KNO_3, 4.76 g of $MgSO_4$, 11.54 g of $Ca(NO_3)_2 \cdot 4H_2O$, 11.54 g of $Ca(H_2PO_4)_2 \cdot H_2O$, 6.23 mg of FeEDTA, 3.32 mg of KCl, 1.38 mg of H_3BO_3, 0.75 mg of $MnSO_4 \cdot H_2O$, 0.51 mg of $ZnSO_4 \cdot 7H_2O$, 0.11 mg of $CuSO_4 \cdot 5H_2O$, and 0.016 mg of $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$. Previous studies with lettuce had demonstrated that these were desirable nutrient levels for this soil. The plants were placed in a Sherer Gillett Model Cel 512-37 growth chamber maintained at 21.5 ± 4.3 klx (2000 ft-c, 307 μE $m^{-2}sec^{-1}$), 20 ± 2°C, and 45 ± 10% relative humidity, with a 16 hr light:8 hr dark cycle. Plants were watered twice daily, once to the point where water dripped from the drain holes in the containers. Two weeks after transplanting, the plants, which had about 12 true leaves, were paired and separated into 2 groups of 6 plants each. The plants of 1 group were individually enclosed during each dark period until harvest with polyethylene film overlain with brown paper to decrease transpiration and to encourage water movement by root pressure flow. The plants of the second group were maintained within the chamber without covering to encourage water movement by transpirational flow.

Plants were harvested 59 days after transplanting when the largest plants were approx 75 cm in diam, with heads approx 10 cm in diam. Data were collected on tipburn occurrence, no. of leaves longer than 1 cm, fresh wt, and dry wt.

^{45}Ca transport studies. Cabbage plants were grown for 2 weeks in vermiculite as in the previous study, then transplanted into polyethylene lined containers containing 400 ml of the same nutrient solution used for starting the seedlings in the tipburn study. The solutions were aerated continuously and brought to vol with distilled water daily and replaced every 4 days. One day prior to treating the plants with ^{45}Ca, the solutions were again replaced. Plants were used for ^{45}Ca transport studies when they were in a rosette stage of growth and had 6-7 leaves longer than 1 cm. Heading of some of the plants was simulated by covering the inner 3-4 leaves with a polyethylene film overlain with aluminum foil. Five different treatments with 4 single plant replicates were included and the experiment was repeated.

Plants for the different treatments were maintained in either an illuminated chamber at 21.5 klx, 20°C and 50% RH, or in a darkened chamber at the same temp and relative humidity. Four plants were maintained without any covering, as controls, in the illuminated chamber to encourage transpiration from all leaves (Treatment A). Four "heading" plants were placed in both the illuminated and darkened chambers (Treatments B and C). The

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partial covering restricted transpiration from the inner leaves, but did not restrict transpiration from the outer leaves. Four additional "heading" plants were maintained in the darkened chamber and completely enclosed in a polyethylene bag to reduce transpiration from all leaves and encourage the development of root pressure flow (Treatment D). Finally, 4 "heading" plants were placed in the illuminated chamber for a 4 hr period, followed by a period in the darkened chamber with the plants completely enclosed in a polyethylene bag (Treatment E).

After 2-3 hr of equilibration under the various light conditions indicated above (illuminated conditions for Treatment E), the nutrient solution of each plant was replaced with 400 ml of nutrient solution containing 10 μC of ^{45}Ca as $CaCl_2$. The plants were maintained under the indicated conditions for 4 hr for absorption and translocation of ^{45}Ca and then harvested, except for the plants of treatment E. Plants of treatment E were maintained in the illuminated chamber for 4 hr, and then maintained in the darkened chamber with all leaves covered until guttation was observed from each plant (10-15 min) before harvest.

Plants were harvested by severing the stem at the base of the cotyledonary node. The plant tissue was dried at 70°C for 2 days, and dry wt of various plant parts were determined. Outer and inner leaves were digested separately as follows: Dried tissue was placed in a 100 ml test tube and covered with nitric acid for at least 30 min. The tissue-acid mixture was heated over a flame until the tissue was disintegrated. Approximately 2 ml of perchloric acid was then added and the solution was heated until it was clear and colorless. Often, additional nitric acid, ~1 ml, was added during the second heating to achieve complete oxidation. To the ~1 ml of solution remaining, distilled water was added to bring the vol to 30 ml, from which a 1 ml aliquot was taken for ^{45}Ca determination. The 1 ml aliquot was added to 10 ml of scintillation solution, and the cpm of ^{45}Ca present was determined on a scintillation counter. The scintillation solution consisted of 9.6 g of 2,5-diphenyloxazole (PPO), 0.2 gm of p-bis-[2-(5-phenyloxazolyl)]-benzene (POPOP), and 1 liter of Triton X-100 mixed with 2 liters of toluene.

Results

Tipburn studies with heading plants. Covering heading plants during the dark period to saturate the atmosphere around their outer leaves completely prevented tipburn whereas exposure to a 45% RH atmosphere during the dark period encouraged tipburn in 5 of the 6 plants. Root pressure flow, as indicated by guttation, occurred in the covered plants. Tipburn was first observed on the uncovered plants 46 days after transplanting as heads were just beginning to form. As the plants continued to grow, tipburn occurred on successive developing leaves within the head. The uncovered plant which did not develop tipburn was the smallest plant in the treatment, and because of its slower growth rate, it may have been less susceptible to tipburn. Growth of plants in the 2 treatments was similar as indicated by the data for fresh and dry wt and no. of leaves (Table 1).

^{45}Ca transport studies. Accumulation of ^{45}Ca in the inner leaves was greatly altered by the different treatments (Table 2). When inner leaves were exposed to an atmosphere at 50% RH, they accumulated large amounts of ^{45}Ca (Treatment A). When inner leaves were covered to reduce transpiration from them, and outer leaves remained exposed (Treatments B and C), inner leaves accumulated much less ^{45}Ca than the inner leaves of plants of treatment A. When transpiration was reduced from all leaves (Treatment D), root pressure flow occurred, as indicated by guttation, and inner leaves accumulated significant amounts of ^{45}Ca. Accumulation in covered inner leaves of plants in treatment D was several times greater than accumulation in covered inner leaves of plants in which outer leaves were left uncovered and free to transpire (Treatments B and C).

Covering of plants for a 10-15 min period to just initiate guttation (Treatment E) did not significantly increase ^{45}Ca accumulation in the inner leaves.

Accumulation of ^{45}Ca in the outer leaves of plants in the different treatments, both in the light and dark, was similar except for the smaller accumulation in the treatment in which all leaves were covered and root pressure flow occurred.

Discussion

These studies demonstrate that Ca transport to protected inner leaves of cabbage plants is enhanced when transpiration is inhibited from the outer leaves and that tipburn is prevented by the same conditions. Inhibiting transpiration from outer leaves allowed root pressure flow to occur, as indicated by guttation from the plants. These findings support the hypothesis that root pressure flow is required to supply adequate amounts of Ca to enclosed leaves of heading cabbage plants, and thus prevent tipburn.

While it is likely that root pressure flow is unimportant to the water economy of the plant, as discussed by Kramer (17), its importance to other processes within the plant are not as well known. Some workers have suggested that root pressure flow could serve a necessary role in ion transport (8, 14, 16), especially in non-transpiring or slowly transpiring plants (14, 16); however, direct evidence for the necessity of root pressure flow to transport ions in plants has not been presented previously.

Experiments similar to the one reported here on heading plants have been performed by other workers on heading cabbage plants (33) and on cauliflower plants (18). These workers found that high night/low day relative humidity prevented Ca-related disorders of these plants, and suggested that the relative humidity pattern caused a diurnal fluctuation in the direction of flow within the xylem supplying the low transpiring organs of these plants: during the day, water is drawn out of the head leaves or the curd to supply the transpiring leaves, during the night, water from the roots, containing Ca, reenters the organs until they become fully turgid. Krug et al. (18) and Wiebe (34) presented data indicating that there was such a diurnal fluctuation in water within the low-transpiring organs, and that the Ca concn of the cauliflower curd was increased under these condi-

Table 1. Tipburn and growth of heading cabbage plants in which root pressure flow was controlled.

Treatment	No. of plants tipburned	No. of leaves[z]	Fresh wt[z] (g)	Dry wt[z] (g)
Covered at night, root pressure flow encouraged	0 of 6	40.8 ± 2.1[y]	636.0 ±32.0[y]	54.2 ± 4.2[y]
Not covered at night, root pressure flow discouraged	5 of 6	39.7 ± 2.1	597.8 ± 41.4	57.8 ± 6.4

[z]Average of 6 values ±SD.

[y]The values for no. of leaves, fresh wt and dry wt are not significantly different at the 5% level.

Table 2. Accumulation of ^{45}Ca in the inner and outer leaves of cabbage following a 4 hr absorption period under different humidity and light conditions.

Treatment	Leaf covering: Outer leaves	Leaf covering: Inner leaves	Light conditions	Treatment intended to represent:	^{45}Calcium accumulation[z] cpm/mg dry wt: Inner leaves	^{45}Calcium accumulation[z] cpm/mg dry wt: Outer leaves
A	uncovered	uncovered	light	Plant before heading, in light period, transpiration occurring	1066a[y] ± 295	927a ± 212
B	uncovered	covered	light	Plant after heading, in light period, transpiration occurring	68b ± 30	1093a ± 222
C	uncovered	covered	dark	Plant after heading, in dark period, transpiration occurring	146b ± 88	904a ± 195
D	covered[x]	covered	dark	Plant after heading, in dark period, transpiration not occurring	586c ± 241	528b ± 67
E	uncovered[w]	covered	light[w]	Plant after heading during evening period when transpiration decreases and plant water potential rises	197b ± 52	1118a ± 411

[z]Avg of 8 plants from 2 experiments ± SD. [y]Mean separation within columns by Duncan's multiple range test, 5% level.
[x]Transpiration decreased sufficiently to allow root pressure flow to occur as indicated by the occurrence of guttation.
[w]The 4 hr treatment period was extended with the entire plants covered and placed in a darkened chamber until guttation occurred (10-15 min).

tions. Our data for treatment E indicate that as plant water potential increases from that existing in the plants under the illuminated conditions of this study to that existing in the plants at the initiation of guttation, very little ^{45}Ca was moved to "head" leaves of cabbage. However, a substantial amount of ^{45}Ca was moved to these leaves when the reduced transpiration conditions were maintained for 4 hr following the initiation of guttation, allowing root pressure flow to occur during this period.

Regulation of root pressure flow. Root pressure flow occurs in plants growing under conditions which discourage transpiration and which favor ion and water uptake by the roots (17). Root pressure flow is encouraged at night in many plants by stomatal closure which reduces transpirational water loss. However, root pressure flow in cabbage is not favored in this manner, for cabbage stomata are open most of the night as reported by Loftfield (21), and confirmed by measurements made during these studies. Thus, cabbage requires a near-saturated atmosphere to decrease transpiration rates so that root pressure can develop. A near-saturated atmosphere occurs during periods of precipitation and at night when radiational cooling reduces the air temp to, or close to, the dew-point temp. During nights when air temp are considerably above the dew-point temp, transpirational water loss from cabbage will be favored instead of root pressure flow.

In addition to being dependent upon the transpiration rate, root pressure flow is dependent upon uptake of water and ions by the roots. Low soil water potentials will restrict root pressure flow by limiting water uptake. Low potentials can result from reductions in soil water content or from increases in salt concn of the soil. Root pressure flow is stopped in several plants at soil water potentials of −0.5 to −3.0 bars (17), while transpirational flow still occurs at these and lower soil water potentials. Thus, Ca cannot move to protected, (non-transpiring) leaves of cabbage when the soil is dry or has a high salt concn, but can move to exposed, transpiring leaves under these conditions.

Decreasing temp of the soil reduces root pressure flow. At low soil temp, the rate of ion uptake into the xylem is decreased and resistance to water movement in the root is increased (17). If soil remains cold over a period when above ground conditions are warm and favor rapid growth, root pressure may not develop sufficiently to move adequate Ca to the inner leaves of the plant.

Oxygen is required for the development of root pressure (17). Low O_2 levels, as in very wet soils, would reduce ion uptake and prevent the development of root pressure. Low O_2 conditions can also lead to root decomposition, destroying the roots ability to develop root pressure.

Several of the factors which limit root pressure flow, such as dry soils (15), soils with a high salt concn (15, 28), and flooded soils (32), have been reported to encourage tipburn of cabbage in the field.

Ca-related disorders of other plants. There are several other Ca-related disorders which occur in low-transpiring organs, including internal browning of Brussels sprouts (8, 22, 24), tipburn of lettuce (19, 29), blackheart of celery (12), bitter-pit of apple (7, 10), and blossom-end rot of tomato (13, 26, 27). With small amounts of transpirational water movement, root pressure flow may be necessary to translocate adequate Ca to these organs during rapid growth. Lower incidence of tomato blossom-end rot has been noted when transpiration is reduced (13) and when guttation occurs (27).

Proposed controls for Ca-related disorders. Knowledge that root pressure flow can translocate Ca to inner head leaves of cabbage suggests several different procedures for prevention of cabbage tipburn and other Ca-related disorders. A procedure that would saturate the atmosphere at night, or that would maintain a moisture layer on the leaf surfaces, such as the use of night misting might be beneficial. Application of chemicals that reduce stomatal opening or planting wind breaks to reduce air movements over the plants may also be effective. Maintenance of adequate soil water, prevention of excessive water accumulation in the soil, and maintenance of optimum fertility should all favor root pressure build-up and Ca movement to low-transpiring organs.

In growth chambers, where Ca-related disorders are a common problem, it is suggested that the disorders may be prevented by regulation of the dark period conditions to maintain a high relative humidity and air temp less than soil temp to encourage the build-up of root pressure.

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Effect of Ethephon and SADH on Quality of Clipped and Nonclipped Tomato Transplants[1]

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Abstract. **(2-Chloroethyl)phosphonic acid (ethephon) and succinic acid-2,2-dimethylhydrazide (SADH, daminozide) improved quality and uniformity of clipped and nonclipped transplants of tomato (*Lycopersicon esculentum* Mill.). The materials were effective when applied singly or in combination and with or without a fungicide (maneb). Ethephon applied at 150 to 300 ppm reduced the percentage of transplants bearing flowers and fruits, reduced stem elongation and stimulated root development. SADH at 5,000 ppm reduced stem elongation and yellowing of foliage. Foliage, root, and stem quality were enhanced by using the materials in combination. Neither yields nor fruit quality were adversely influenced by the treatments.**

Southern Georgia has been a major source of transplants for tomato fields in Eastern and Midwestern states for more than 40 years (2). Plants of early maturing cultivars, such as 'Campbell 28', often flower and occasionally set fruits before they are harvested for shipment to northern tomato growers. Plants bearing fruits are slow to recover and resume growth after transplanting and do not produce a normal crop. Clipping has been used to produce plants of uniform size and to maintain them within a usable size range for 7–10 days. Clipping is a hazardous practice because of the possibility of spreading plant pathogens. A more effective method for holding plants within an acceptable size range is needed to facilitate mechanical harvesting and packing for shipment without further sorting. Most plant regulator studies have been with very young seedlings or plants approaching maturity (1, 3, 6, 7, 8, 9, 10, 12). These experiments were designed to determine whether flowering, fruiting and plant height of transplant could be effectively controlled with plant growth regulators.

Materials and Methods

All experiments were conducted on the Joseph Campbell farms near Climax, GA, during the spring seasons of 1973 to 1975. Seedlings of 'Campbell 28' were grown on beds 2 m wide.

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