CULTIVAR AND ENVIRONMENTAL IMPACT ON ONTOGENETIC CHANGES IN THE FRUIT CALCIUM STATUS OF PICKLING CUCUMBERS

By

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ABSTRACT

CULTIVAR AND ENVIRONMENTAL IMPACT ON ONTOGENETIC CHANGES IN THE FRUIT CALCIUM STATUS OF PICKLING CUCUMBERS

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A field experiment was conducted to determine the ontogenetic changes in calcium concentration and content in pickling cucumber fruit (Cucumis sativus L.) as related to seasonal changes in the environment. Factors studied, which may influence calcium accumulation, were planting date, genotypic variability (cvs. Castlepik 2012, PSX20580, Regal, Tamor), harvest date (0.5-5.5 cm fruit diameter) and tissue type, pericarp and endocarp. Changes in fruit growth were measured by fresh and dry weight, volume, and length:diameter ratio.

Mean fruit calcium concentration in a pickling cucumber fruit declined during ontogeny, while total fruit calcium content increased. Calcium concentrations in pericarp (1.1-0.7% dry wt.) and endocarp (0.8-0.2% dry wt.) tissues declined as fruits enlarged. Genotypic differences in fruit calcium concentration are attributable to differences in rates of fruit calcium accumulation and growth. Environmental factors, primarily soil moisture, had a significant and similar impact on rates of fruit calcium accumulation and growth.

To my parents, Marge and Stan Engelkes,
who taught me to walk. Your endless love,
support, and understanding have given me the
courage to take each new step.
This is <u>our</u> thesis.

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INTRODUCTION

Although an extensive body of knowledge exists concerning calcium nutrition of plants, Wallace and Soufi (1975) were compelled to comment that "in general the question of the calcium needs of plants is extremely confused, and calcium may be the least understood essential element."[1] Our lack of understanding of the function, uptake and transport of calcium in plants has slowed our progress in controlling the thirty-five known calcium-related disorders of fruits and vegetables and perhaps in recognizing other calcium disorders (109).

Fruit calcium concentration is highly correlated with fruit growth and quality in many crops. Calcium is involved in cell division and elongation, cell wall formation, maintenance of membrane integrity and function, and in enzyme activation. Certainly these physiological processes are vital to the normal growth and development of fruits.

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[1]A. Wallace and S. M. Soufi, "Low and Variable Critical Concentrations of Calcium in Plant Tissues," Commun. Soil Sci. Plant Anal., 6 (1975), p. 332.

The general calcium uptake characteristics or the calcium status of an entire plant are not indicative frequently of the calcium status of specific organs on the plant. Calcium deficiency symptoms may appear in plants grown on soils where the available calcium content is adequate as well as where the content is low. Deficiency symptoms are seldom expressed in the foliage of field-grown plants. Rather, they appear in fruits, storage roots, tubers and heart leaves of leafy vegetables.

Although a calcium-related disorder has never been identified positively in pickling cucumber fruits, Cucumis sativus L., the plant is a good model for investigating fruit calcium nutrition. The plant material is relatively accessible, as fruits may be harvested in less than fifty days after planting. Cucumber fruits may increase in fresh weight up to forty percent within a twenty-four hour period (89), accentuating calcium dilution through ontogeny. This was confirmed in a study of the mineral nutrition of pickling cucumbers by Widders and Price (1984), in which the mean fruit calcium concentration declined as fruits enlarged (137).

Other research results suggest that calcium may be a limiting factor in pickling cucumber fruit quality, as well as in fruit development. Adhikari (1980) reported a correlation between an increased incidence of misshapen cucumber fruits and a reduced fruit calcium content when chlorflurenol, an auxin tranport inhibitor, was applied

to induce parthenocarpic fruit set (2). Staub (1985) produced the "pillowing disorder", a putative symptom of calcium deficiency in cucumber fruits, by growing cucumbers in a calcium-deficient nutrient solution (119).

Most of the limited research on the calcium nutrition of pickling cucumbers has been conducted in controlled environments. In order to understand the importance of calcium in pickling cucumber fruit development and quality, further research is necessary in the field. The objectives of this research were: 1)to quantify the mean calcium concentration and total content in pickling cucumber fruits during fruit ontogeny; 2)to evaluate the ontogenetic changes in calcium accumulation rates relative to the growth rates of pickling cucumber fruits; and 3)to correlate various environmental parameters with fruit calcium accumulation and growth in several pickling cucumber cultivars.

LITERATURE REVIEW

Calcium has been recognized as an essential mineral nutrient in higher plants for over a hundred years (61,78,84,128). Although classified in the group of ten macronutrient elements, plant calcium requirements are often in the micronutrient range (18,59,60). A rediscovery of the importance of calcium nutrition on plant growth, development, and physiology has taken place in the last decade.

Calcium Functions

Calcium, an essential element for plant growth, is involved in cell division and specifically in increasing cell elongation (17,18). Root growth ceases within a few hours when calcium is absent in the nutrient medium (61). High calcium ion concentrations inhibit cell elongation (25,27,61). Cleland and Rayle (1977) propose that cytosolic calcium inhibits the biochemical processes of cell wall-loosening, either by competing for hydrogen ion binding sites or by altering wall proteins and/or polysaccharides, which are involved in hydrogen ion-enhanced enzyme reactions (25).

The highest calcium concentrations in plant cells are always found in the cell walls (27). By cross-linking pectic polymers, mainly in the middle lamella, calcium brings both structural and physiological stability to cell walls (18,20,23,24,27,34,128). During cell growth calcium is lost from the cell wall, changing the calcium-bridge structure (17,24,25,34,59).

Calcium plays a crucial role in maintaining plant membrane integrity. Membrane deterioration, identified by light and electron microscopy, is the first detectable sign of a plant calcium deficiency (4,59,61,62,77,98). Plant tissue senescence can be retarded by the addition of calcium. Corn leaf senescence was delayed by floating leaf disks in a calcium chloride ($CaCl_2$) solution (98). $CaCl_2$ sprays and dips are used commercially to reduce the incidence of bitter pit, a calcium disorder of apples associated with senescence (14,15,36,68,79,118). Membrane permeability and selective ion absorption are influenced by tissue calcium levels (17,18,20,31,59,61,65,77,84,98, 116,117,128,134). Calcium-deficient plant tissues are more subject to a heavy metal imbalance than tissues with high calcium concentrations (134).

Calcium plays a key role in plant cell metabolism through its involvement in enzyme systems: ATPase (4,28), alpha-amylase (59,131), NADH dehydrogenase (87), quinate-NAD^+ oxidoreductase (28), NAD and membrane-bound protein kinases (4,28,87), etc. Many of these enzymes are

calmodulin-dependent (28). Changes in cytoplasmic calcium concentrations activate calmodulin, a calcium-binding protein (28,98,120). Calcium is thought to alter enzyme activity, specifically membrane-bound enzymes, by maintaining membrane structure and thus enzyme configurations (4,27,59,61). The calcium-mediated activity of polygalacturonase (62) and phospholipase A2 (67) is linked with the onset of cell senescence and the loss of membrane integrity (34).

Recent reviews have cited increasing evidence that free calcium ions function as a secondary plant messenger (28,87,98,131). When plant cells perceive stimuli, like light or gravity, calcium ions are released into the cytosol (131). It is proposed that these changes in the cytoplasmic calcium concentration result in an activation of calmodulin. Calmodulin in turn activates certain enzyme systems, leading to various plant responses such as phototropism and gravitropism (28,98,131).

Calcium Uptake

Calcium is the major exchangeable cation in all but the very sandy and strongly acidic soils (43,58). Calcium moves to plant roots by mass flow in the soil solution (60, 83,104). The plant root surface area is highly correlated with calcium uptake (115,122). During exponential plant growth phases, calcium uptake is highly affected by the root growth pattern (70,104,140). Calcium uptake by apple

trees continues from flowering to harvest, but the rate tends to decline in the last two months of fruit development, when root growth decreases (56). If plant calcium uptake is neither selective nor active, continuous root growth and a high calcium concentration at the root surface are important for facilitating continuous calcium uptake by the plant.

The root calcium "absorbing zone" is believed to be restricted to tissues near the root tip (4,46,47,60,61). The movement of calcium ions into roots is virtually eliminated by suberization of the endodermis or by secondary root thickenings, suggesting that calcium follows the apoplast pathway (4,9,10,23,33,46,47,60,74). Calcium ions are adsorbed onto fixed, negatively charged cell wall surfaces (4,29,60,61,74,78,88). Proponents of passive calcium transport believe that calcium ions simply follow the influx of water into plant roots, moving by exchange reactions through the root cortex and into the xylem without ever being actively absorbed.

Calcium uptake is both concentration dependent, limited by the rate of diffusion at higher concentrations, and metabolically controlled, especially at low calcium concentrations (63,72). The metabolism-linked phase of uptake is probably the transport of calcium ions through the endodermis into the stele via the symplast pathway (9,10,46,60). Decreased calcium transmembrane transport, when root tissues are exposed to low temperatures

and metabolic inhibitors, provides evidence for an active calcium transport system (9,29,63,72,140). The symplast is not a major pathway for calcium transport, however, as the root cortical cytoplasm contains only micromolar concentrations of calcium and ion mobility is very limited (23,47,74).

Calcium Transport

The possible pathways of long distance calcium transport in higher plants are the xylem and/or phloem. Calcium is transported almost exclusively in the acropetal direction via the xylem (8,12,23,46,56,61,110,111,138,139). The ions move by exchange reactions along the fixed, negative binding sites of the xylem walls. Other divalent cations compete with calcium for these exchange sites, promoting calcium mobility (8). The xylem pathway has several advantages for distributing root-absorbed calcium ions (12,23,46,66,100,130). The volume and velocity of flow in the transpirational stream enhances the rate of calcium movement from the root to the shoot. The xylem can transport calcium throughout the plant in adequate quantities to support cell growth, since the extracellular xylem sap has virtually no calcium concentration restrictions, unlike the symplastic pathway.

Plant organs with a limited xylem water influx generally have low calcium contents (1,5,78,138). The importance of transpiration-driven calcium transport is

demonstrated by young, developing lettuce and cabbage leaves (7,94,125). Rapidly transpiring outer leaves accumulate significant quantities of ^{45}Ca in short-period (2-4 hour) uptake studies (94,125). The low transpiring enclosed leaves at the growing point accumulate little ^{45}Ca in the center one-half of the leaves and none at the leaf margins.

Although calcium translocation is often highly correlated with water transport (47,61,66,78,94,139), the relationship is not necessarily directly proportional (9,12,29,80,94,111). Since calcium undergoes continuous loss, exchange or gain with plant tissues as the ions ascend the xylem column, the rate of calcium transport relative to the volume flow rate of water may vary (12). Palzkill and Tibbitts (1977) report a decreasing ratio of ^{45}Ca transported to total plant water use with increasing transpiration rates (94). A reduction in transpiration, due to shoot excision, may not reduce calcium uptake on a short term basis (9). Likewise, a reduction in calcium translocation due to a metabolic inhibitor may not alter water transport.

Developing leaves, flowers and very young fruits are major and competing sinks for calcium and water via the xylem (23,37,139). The movement of calcium to these sinks may also be affected by endogenous plant hormones. Basipetal auxin transport seems to influence calcium transport, especially to shoot apices and into developing

fruits (3,37,61,118). Auxin synthesis and export from these tissues increases during flowering and fruiting (11). The auxin transport inhibitor, TIBA (2,3,5-triiodobenzoic acid), reduces the calcium concentration of apple fruits (118). It is proposed that during growth, endogenous auxins enhance calcium transport through formation of new cation exchange sites (61).

Plant ontogeny alters calcium translocation patterns within an intact plant (46,54,101,127). The distribution of ^{45}Ca in apple fruits at selected stages of development was monitored by thin section autoradiography, following root-feeding of small apple trees (37,85). Calcium accumulation rates in apple fruitlets are very high in the first 4 to 5 weeks after fruit set. As the fruitlets enlarge, the rate of accumulation gradually declines. After the apples reach the midway stage of fruit development at 11 to 14 weeks after full bloom, the isotope accumulates in the bark and leaves of fruit spurs but not in the flesh of apple fruits.

Wiersum (1966) postulates that the decline in the rate of calcium import into rapidly expanding storage organs is due to a change in the mode of water supply (139). Using Light Green dye as a visual tracer for water transport through the xylem, the patterns of distribution of root-absorbed ^{45}Ca and Light Green are highly correlated. During periods of high growth rates, no or only minimal amounts of Light Green or ^{45}Ca were translocated

into tomato and apple fruits, potato tubers, and seeds of broad beans via the xylem. Jones et al. (1983), calculating the probable limits to the influx of water into apple fruits via the xylem and phloem, also report two phases of calcium uptake into apple fruits (56). Although the two pathways may transport similar quantities of water early in the season, the phloem is the predominant mode of water supply into fruits later in the summer.

Young fruits have high transpiration rates and are photosynthetically active (37,42,46,57,61,101,127,139,140). The high water demand and the low requirement for additional assimilates can be supplied via the xylem, in which calcium moves freely. Although the import of water into fruits in the phloem is not restricted during the first few weeks of apple fruit development, it is probably rather unimportant compared with xylem transport (127). The rate of fruit transpiration decreases, due to a decline in the surface area to volume ratio, and the assimilate demand increases as fruits mature. Assimilates, nutrients, and water are transported from the leaves to the developing fruits via the phloem. The low calcium contents of mature apple and tomato fruits are similar to the known phloem sap calcium levels (46).

The phloem tissues cannot facilitate calcium transport like the xylem (23,33,73,100,102,127,138). Calcium is relatively immobile in the phloem symplasm

(4,33,46,47,56,57,60,78,127). The sieve tubes selectively exclude calcium (46,61), and the high pH and phosphate concentration of phloem sap would precipitate calcium as calcium phosphate (78). The obligatorily low calcium concentration of phloem sap is insufficient to support cell growth effectively (23,127). It is essential, therefore, that adequate supplies of calcium reach developing fruits via the xylem during the earliest stages of growth (37,46,78,85,101).

Calcium Distribution

Calcium is considered the most immobile plant nutrient among the essential elements (35,46). Since calcium moves with difficulty from cell to cell by symplasmic translocation, this element is unevenly distributed within plant organs (4,5,13,33,35,37,51,68,85,86,101,111, 137). Intact maize plants, fed ^{45}Ca for 24 hours, partition more of the isotope to apical than to mid or basal leaf segments (33). A declining calcium concentration gradient exists from the stem to the calyx end of tomato and apple fruits. An electron microprobe study for calcium in apple fruit tissues reveals a higher concentration in flesh versus peel tissues, vascular bundles versus the surrounding parenchyma tissue, and in lenticular versus non-lenticular peel tissues (86). Thin section autoradiography also identifies changing patterns in calcium distribution as apple fruits mature (37,85). Root-absorbed ^{45}Ca applied at 4 to 5

weeks after full bloom enters the vascular bundles throughout the whole fruit. The calcium concentration is highest in the core towards the stem end, intermediate in the peel, and least in the flesh tissue. Less ^{45}Ca accumulates in the outer cortex when applied at later stages of fruit maturity.

Once deposited in plant organs, calcium redistributes to other parts of the plant slowly or not at all (1,11,33, 35,46,61,63,69,78,102). Calcium will move out of fruits to shoot meristems via the xylem, particularly during periods of drought (56,127). If the amount of water imported into fruits through the phloem exceeds the cellular and transpirational tissue needs, further calcium may be exported out of fruits in the xylem (139). Older leaf tissues may have very high calcium concentrations (1,5,11,46,69,78, 111). This lack of calcium remobilization is primarily due to limited phloem mobility. Mature leaves contain large quantities of lignin, which has a high affinity for calcium (33,102,110). The suberin deposits in the vascular tissues of older leaves restrict calcium translocation out of the leaves. The deposition of insoluble calcium oxalate crystals in plant tissues is also a factor limiting calcium remobilization (21,37,39,46,49,53,78,82,100,133).

Any existing calcium regulatory mechanism in plants appears to operate in the direction of restricting rather than promoting calcium transport and distribution (4,9,55, 78). The calcium contents of plant organs are based on

metabolic removal from the vascular system (4,63), rather than on physiological demand (8). Loneragan and Snowball (1969) report deficient and luxury concentrations of calcium occurring simultaneously in different tissues of an individual plant (69). The calcium concentrations of leaf tissues are often several fold higher than those of fruit tissues (1,5,11,36,78,111,137). More calcium is distributed to fruits in the lower part of an apple tree than to fruits from the upper branches (16,57).

Calcium-related Disorders

Many researchers report a close correlation between the calcium concentration and quality of fruits, storage roots, tubers, and heart leaves of leafy vegetables. Calcium, due to its functions in plants, may affect quality by: reducing respiration (4,34), increasing fruit firmness (4,14,105), delaying fruit ripening and leaf senescence (4,34,76,105), increasing vitamin C content (4), reducing storage rot (4), reducing fruit splitting (19), and enhancing yield (84,135).

Although limestone and marl have been used in agriculture for hundreds of years, calcium has never received the attention growers give to their nitrogen, phosphorus, and potassium fertilizer regimes (58,84). Reports of plant calcium deficiencies are numerous, despite normal soil calcium levels being high enough to meet plant requirements (4,43,58,60,84). Applications of lime have

consistently failed to alleviate calcium-related disorders because the deficiencies are localized in the plant (4,58, 60,84,91,111,121). A calcium supply sufficient for leaves may not be sufficient to prevent calcium deficiency symptoms in fruits (111).

Shear (1975) lists thirty-five calcium-related disorders in different plant species (109). The characteristic feature of these disorders is a localized calcium deficiency (7,14,16,37,42,60,70). Although root and vegetative tissues may display calcium deficiency symptoms in the field, the most serious economic losses occur from deficiencies in reproductive tissues (84).

Localized calcium deficiencies occur in rapidly growing organs (1,4,16,40,44,56,57,91,95,109,111,125,126,133,139). A rapid growth rate results in a steady dilution of the plant organ calcium concentrations, especially if the rates of calcium import and accumulation are low. Normal fruit calcium concentrations, ranging between 200 and 3000 ppm dry weight, are only slightly higher than the fruits' functional requirements (69,134).

Rapid growth causes an increase in the calcium requirement, which the plant often cannot meet (4,40,125). Fruit enlargement, due primarily to cell expansion rather than cell division (113,114), decreases the formation of new calcium binding sites (61). Rapidly enlarging fruits are primarily supplied with water and nutrients, along with the necessary assimilates, in the phloem rather than

in the xylem, the major calcium transport pathway (37,57, 61,139). The influx of calcium into developing fruits via the xylem transpiration stream is further restricted as the surface to volume ratios of these fruits decline (4,61). Calcium is preferentially distributed to the more rapidly transpiring leaf tissues (4,56,57,61,78,111). It is for this reason that calcium deficiencies are positively correlated to the rate of vegetative growth (109).

Ferguson (1984) separates plant calcium-related deficiencies into two groups: disorders resulting from uneven calcium transport or distribution and senescent disorders (34). Some of the disorders caused by uneven calcium partitioning are blossom-end rot of tomatoes (40,60,61,75,81,90), blackheart of celery (44,60,61), leaf necrosis of seedling carrots (125,126), and tipburn of lettuce (7,60,61), cabbage (94,125), and cauliflower leaves (50). The occurrence of these localized calcium deficiencies indicates that higher plants are not able to adequately regulate their calcium distribution (4,61,78).

Bitter pit (34,37,51,60,61,109), senescent breakdown and decay of apples (14) are among the calcium disorders associated with senescence. Calcium retards senescence (4, 14,34,76,105), perhaps by maintaining membrane and cell wall structure (34,123) and by suppressing polygalacturonase activity (34,62,98).

Although high calcium concentrations are an advantage in delaying senescence and ripening, normal cell operation

requires low cytosolic calcium concentrations (34,74,105). To maintain enzyme activity and membrane functioning, eukaryotes must limit their free, cytoplasmic calcium concentrations to between 0.1 and 10 micromoles (100). The physiologically active calcium concentrations of fruits must decline in order for ripening to occur (14,34,61). Rin, the non-ripening tomato mutant, maintains high levels of calcium throughout ontogeny (98).

A calcium deficiency changes the ultrastructure of plant cells. The plasma and vacuolar membranes disintegrate (48,59,62,77), followed by a loss of cohesion in the cell wall (34,48,123). With increased membrane permeability, cell fluids invade the intercellular air spaces of calcium deficient leaf lamina and fruit tissues (40,48,75,81,112, 126). These tissues will appear translucent, which is the initial symptom of most calcium related disorders. This temporary phase is followed by tissue desiccation (1,4,40, 59,75,81,112,125,126). Necrosis is a diagnostic symptom of a plant calcium deficiency. Other observable symptoms which may appear are chlorosis (1,117), leaf cupping and curling (40,59,117), fruit cracking (19,26,112), and decreased root (59), leaf (35), fruit and/or seed (59) development or growth.

Factors Affecting the Plant Calcium Status

Loneragan and Snowball (1969) define a plant's functional nutrient requirement as "the minimal

concentration of nutrient within the plant organism which can sustain its metabolic functions at rates which do not limit growth."[2] Any factor, which affects calcium uptake, transport and distribution, plays a determinant role in meeting the plant's functional calcium requirements (40,109,111). Endogenous plant factors and almost every environmental parameter and cultural practice have been cited by researchers as either aggravating or ameliorating plant calcium deficiencies (46,75,109).

Plant Factors

The calcium content of a particular plant family, genus and species is to a large extent genetically controlled (61,75). Calcifuge plants attain maximum growth on acid soils (4,18). These plants have low soluble calcium contents and high concentrations of insoluble calcium oxalate (39). Calcicole plants thrive on soils with a high calcium content (4). A cucumber plant, classified as an obligate calcicole, may absorb forty times more calcium than wheat, a calcifuge plant (10,53).

Dicotyledons absorb more calcium from a given supply than do monocotyledons (70,75,103). The amount of calcium uptake is highly correlated with root parameters (104). Dicotyledonous roots have a higher cation exchange capacity,

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[2]J. F. Loneragan and K. Snowball, "Calcium Requirements of Plants," Aust. J. Agric. Res. 20 (1969), p. 471.

enhancing calcium adsorption (61). The differences in absorption may also be due to a greater total root surface area (70,103), more unsuberized root surfaces (45), and/or calcium specific binding sites (10) in dicotyledons.

The most effective control of calcium-related disorders is to develop resistant plant varieties. Genetic differences in calcium uptake and translocation have been discovered in apple seedlings (110). Festuca ovina populations have been classified as acidic or calcareous, depending on their ability to absorb calcium from low solution concentrations (116). Plant cultivars have already been identified with varying degrees of resistance to calcium-related disorders: tomato blossom-end rot (30, 43,81,90), cabbage tipburn (91,125), cauliflower leaf tipburn (50), lettuce tipburn (26), and seedling carrot leaf necrosis (126).

A number of heritable traits from the diverse plant germplasm pool have been selected for, which enhance resistance to calcium-related disorders. Genetic resistance may be due to more efficient or selective calcium absorption (30,43,50,116). Young developing tissues may differ in their calcium requirements (43,126) or in their calcium utilization (50). Plant cultivars may differ in their transpiration rates (126). Cabbage cultivars with reduced nightly stomatal opening are more resistant to tipburn injury (125). Barker and Maynard (1972) report a

difference in calcium accumulation in pea and cucumber shoots based on the form in which nitrogen is translocated from roots to shoots (6).

Since plants may grow differently in controlled environments than in the field, selections should be made under both conditions. Although artificial enclosure of young lettuce leaves encourages tipburn in the laboratory, natural leaf enclosure, such as occurs during heading, often does not initiate injury in the field (7). In controlled environments tipburn symptoms develop rapidly even on lettuce cultivars which are highly resistant to tipburn in the field (26).

Environmental Parameters

Climatic factors affect plant growth rates, which in turn significantly affect the rates of plant calcium uptake and accumulation (46,54,60,140). Water, essential for growth and development, is responsible for conducting minerals from the soil to plant organs. Bangerth (1979) cites water as one of the most "decisive" factors affecting plant calcium distribution (4). Soil moisture and the water potentials of plant organs may also determine the impact which secondary environmental factors, such as light and temperature, have on calcium distribution in the plant.

Optimum soil moisture affects the calcium concentration of the soil solution, provides a high soil-water potential, and maximizes plant water and nutrient uptake (125,140).

Excess soil moisture inhibits root growth due to reduced aeration (40,42,45,109,125). Since calcium is believed to be absorbed only by young, unsuberized root tissues, any reduction in root growth will retard calcium uptake (4,46,47,60,61). High soil moisture may also cause rapid fruit expansion, diluting the initial fruit calcium concentrations. In contrast, the calcium concentrations of leaf and fruit tissues of mildly drought-stressed plants are generally higher due to lower growth rates (16,90).

Low soil moisture may have either a positive or negative effect on calcium availability to the plant. Less calcium leaches out of the rhizosphere during a soil water deficit, but the mass diffusion of calcium ions to root surfaces will be decreased (90,109). A soil water deficit may also reduce calcium uptake by inhibiting root growth and reducing availability of energy rich metabolites to the root system (40,42,45,109,140). Xylem calcium transport is also depressed by a soil water deficit, due to low volume flow rates through the vessels (45,139). Even an intermittent soil moisture deficiency increases blossom-end rot of tomatoes (90). Calcium may be exported from fruits to leaves, due to competition for water and calcium (101,140).

Transpiration plays a major role in calcium accumulation, as previously mentioned. High relative humidity throughout the day increases the rates of plant growth and decreases calcium transport via the transpiration

stream (5,7,26,41,44,48,127,138). Tomato leaves may become calcium deficient after a prolonged period of cloudy, humid weather (1). Low relative humidity increases plant transpiration rates, but the transpirational stream may bypass low transpiring fruits and storage organs in favor of leaf tissues. This general trend did not occur in a 1983 study by Jones and Samuelson (57). They report that apple fruits with long bourse (swollen stem at base of inflorescence) shoots had higher fruit calcium concentrations than fruits associated with shoots of a lower leaf area. They propose that adequate evaporation from primary leaves plays an important role in achieving, rather than inhibiting, high fruit calcium concentrations.

Diurnal fluctuations in a plant's water potential facilitates calcium distribution to low transpiring plant organs (1,4,5,13,41,94,125,126). Root pressure develops when a plant stops transpiring or when the rate of water uptake exceeds the transpiration rate. A positive pressure develops in the xylem as the root pressure increases, moving calcium to the low transpiring plant organs. This is especially significant during the night when the growth rate of many storage organs is most rapid (4,13,26).

Changes in relative humidity and stomatal opening and closing create the diurnal fluctuations in plant-water potentials. High relative humidities only at night, adequate water, and low soil salinity favor root pressure development (1,4,5,13). Calcium-related injuries in the

field are more prevalent when periods of cool, moist weather are interrupted by warm, dry days (90,125).

Bradfield and Guttridge (1984) report that night-time humidities have a more significant effect on blossom-end rot incidence than the solute concentration in the soil solution during early tomato fruit development (13). Adams and Ho (1985) attribute a greater importance to high salinity in reducing tomato fruit calcium content than to low relative humidities (1). Transpiration rates and the soil solution concentration often interact, however, affecting calcium uptake. Plant uptake is selective for calcium over magnesium at low transpiration rates and soil solution concentrations (66).

In addition, calcium uptake is also affected by the soil pH and the presence of other anions and cations (72). The total amount of available calcium in the soil does not affect uptake as much as the concentration ratio of calcium to the other ions in solution (18,58,60,108). The uptake of monovalent ions by plant roots is largely dependent on the soil solution concentration of the specific ion, while the uptake of divalent cations is proportional to the total salt concentration (66). A low calcium to total salt concentration ratio increases the incidence of calcium-related disorders (40,41,90,109).

High salinity may influence calcium uptake by limiting plant water uptake (41,66,125). It also has an unfavorable effect on root pressure development, reducing calcium

distribution to low transpiring plant organs (13,41). High salinity also may alter a tomato plant's anatomical structure, increasing the internal resistance to xylem influx from the pedicel into the fruit (1).

Low soil pH depresses calcium uptake by many plants (22,64,72). Acid soils contain less available calcium (42). Hydrogen ions compete with calcium ions for uptake in acid soils between pH 3 and 5 (72). High levels of aluminum and manganese in the soil solution, which can be toxic to plants, interfere with calcium metabolism and uptake in acid soils (42,60,64,99).

The effect of other ions on calcium uptake may differ whether under field or controlled environment conditions. Soils provide a strong buffering capacity which hydroponic cultures cannot provide. Loneragan and Snowball (1969) also demonstrate convincingly that critical plant tissue calcium concentrations, below which a deficiency develops, are highly affected by the calcium concentrations under which a plant is grown (69). This diminishes the reliability of a critical tissue calcium concentration value apart from the particular experimental conditions under which it was determined.

Rapidly absorbed anions, NO_3^- > Cl^- = Br^- > SO_4^{2-}, enhance calcium absorption (60,72). Both a deficiency and an excess concentration of any of the essential plant cations also affect calcium uptake. The addition of any deficient plant nutrient can stimulate

calcium uptake (55,109). If aluminum is present in the soil solution, ammonium ions can stimulate calcium uptake (64). Of the monovalent ions, H^+ (72), K^+ (40,42,60, 64,72,121), and NH_4^+ (6,40,43,60,108) compete with calcium for absorption, while Li^+ and Na^+ have only slight effects (72). Excess nitrogen (40,60,90,91,109, 133), especially the NH_4^+-N source (38,109), potassium (18,40,42,90,109), magnesium (40,42,51,60,64, 66,109) and possibly phosphorus (109) depress plant calcium uptake and are correlated with calcium deficiencies.

Stimulation of excessive vegetative growth with nitrogen can be deleterious to the calcium supply of low transpiring plant organs (42,60,95,108,140). Excess nitrogen, phosphorus, and/or potassium can also stimulate fruit enlargement, diluting fruit calcium concentrations (95). Excess nitrogen fertilizers may increase calcium oxalate production due to enhanced nitrate assimilation (133). Ammonium fertilizers acidify soils, increasing calcium leaching. High NH_4^+-N levels are also associated with shorter plant roots and even injury to root tips, the active zone for calcium absorption (53,60,108).

An excess concentration of any ion changes the proportion of calcium to total ions in the soil solution and perhaps within the plant. Bitter pit of apples may be due more to a localized magnesium toxicity than to a calcium deficiency (51,109). High levels of fertilizers, such as ammonium fertilizers, may reduce plant water uptake

(60,108). Excess phosphorus may precipitate calcium from the root medium in an inactive form (43,55,109).

Other ions have a marked influence on calcium transport and distribution within plants (43,46). Boron may stimulate calcium movement into the petioles and midribs of apple leaves and increase the calcium concentration in apple fruits (42, 108, 109, 110, 111). NO_3^--N increases calcium transport and accumulation in mature leaves, while NH_4^+-N stimulates calcium partitioning into new leaves (110,111). Apple fruits, sprayed with a zinc salt solution, have a higher concentration of soluble calcium and less oxalate bound calcium (108). The oxalate may preferentially bind with zinc rather than with the calcium ions.

Warm soils encourage mineral and water uptake and may encourage root pressure flow (26,53,125,140). Lower soil temperatures, however, may favor calcium uptake over that of potassium if calcium uptake is passive (140). Potassium uptake is more sensitive to fluctuations in metabolic activity than calcium uptake. Warm soils also stimulate plant growth which may be detrimental to the calcium status of plant organs.

Cultural Practices

Both early planting and late harvesting lower the calcium concentrations and increase the incidence of tipburn of cabbages (91). Seeds sown into cold soils develop roots more slowly, limiting calcium uptake via the transpiration

stream. The cold soils also are not conducive to root pressure development. Late harvesting encourages further growth, diluting the calcium concentrations of plant organs.

In apple, close spacing may be favorable for the calcium status of plant organs if it decreases plant vigor, achieving slightly smaller and slower growing fruits (140). Close spacing is not beneficial to calcium accumulation if excess pruning is required (42). Excess pruning and thinning can excessively invigorate vegetative growth, resulting in large fruits with lower calcium concentrations (42,57,95). Moderate defoliation may reduce calcium-related disorders by slightly increasing the calcium concentration of fruits, without altering fruit size (95,109). During mild droughts, reducing older and extra foliage can be beneficial to the fruit calcium concentration (1).

Low fruit calcium concentrations may occur as a result of biennial bloom patterns. Inadequate thinning encourages heavy fruiting one year followed by a year with sparse, over-sized fruits. Over-sized fruits may also occur due to excessive tree vigor, poor fruit bud formation, an insufficient number of bees and desirable pollen, and frost damage (42). All of these factors will result in a growth-induced dilution of the fruit calcium concentration.

Judicious irrigation scheduling may be very beneficial for plant calcium uptake and accumulation in plants (95). Plant calcium nutrition is favored by steady growth rates.

Adequate soil moisture maintains uninterrupted, passive calcium uptake and upward translocation in the transpiration stream (140). Overhead misting of mildly water-stressed plants may also minimize the development of necrotic tissues, which is associated with a localized calcium deficiency (44).

Selective shading may encourage higher fruit calcium concentrations (95,106,109,127,139). More calcium accumulates in vegetative tissues which are growing under high light intensities. These tissues are major calcium sinks, due to their high growth rates and increased transpiration rates (109,127). Competition for available calcium between leaf and fruit tissues is accentuated. Higher light intensities also enhance photosynthesis, providing the necessary assimilates for increased fruit enlargement. This will further dilute the calcium that is able to move into the fruits (109).

It is desirable to reduce high vegetative transpiration rates which favor calcium distribution primarily to leaf rather than fruit tissues. In addition to shading, other means of reducing high transpiration rates are shelterbelts to reduce wind speeds, antitranspirant oil sprays, and overhead sprinkling (140).

Dilute or concentrated calcium sprays and dips are used to increase the calcium concentration of fruit flesh tissues (15,79,95,118). The calcium will move into the fruit tissues only if the spray is applied directly onto the

fruit surface (36,109). Although only very limited quantities of calcium can be supplied in this way, sprays reduce leaf necrosis in seedling carrots (125,126), sweet cherry splitting (19), and are commercially used to reduce bitter pit (36,68,118) and senescent breakdown (15) in apples. Lewis and Martin (1973) find calcium sprays to be much more effective in increasing the calcium concentrations of apple fruits than soil applications (68). Despite the benefit to fruits, calcium chloride sprays may cause leaf injury, especially following a wet, cool spring (15,42).

Proper timing of the spray applications is crucial to maximize the benefit. Rapidly growing leaf tissue may require daily sprays to prevent tipburn (125). Sprays applied closer to harvest are more effective in increasing apple fruit calcium concentration than sprays applied earlier in the season (15,19,42,118).

Although applications of TIBA, an auxin transport inhibitor, reduce the calcium concentration of apple fruits (4,118), exogenous auxin applications do not substantially increase the calcium content of pollinated fruits (3). If the seeds synthesize sufficient quantities of auxin, it is understandable that sprays would be ineffective. Foliar boron sprays reduce the calcium-related corking disorder of apples (42,109). Boron increases calcium accumulation, especially in plant tissues containing marginal calcium concentrations (108, 111). Shear and

Faust (1971) postulate that the boron effect may be due to an increased metabolic activity, especially if the tissue had been boron deficient (111).

MATERIALS AND METHODS

Field Experimentation

A field experiment was conducted at the Horticulture Research Center in East Lansing, Michigan in 1984. The field was a sandy loam soil with a sloping terrain running north to south. Due to soil fertility and moisture gradients, the four replications were arranged in an east to west direction (Table 1).

Table 1. Soil fertility values in experimental blocks.

Block	Soil pH	Lime index	P	K	Ca	Mg	Calc. CEC
			(lb./A)				
1	6.3	72	200	280	1347	240	5
2	5.7	70	233	320	1095	209	4
3	5.4	67	182	280	1263	228	8
4	5.6	64	292	296	1347	240	12

The experimental design was a split plot, with four planting dates and four pickling cucumber (Cucumis sativus L.) cultivars (Table 2). The main plots (planting date) were randomized within each block and the sub-plots (cultivar) were randomized within each main plot. Two

week intervals between successive plantings, June 7 to July 19, provided diverse environmental growing conditions. Potential genetic variability was assessed by planting four cultivars: Castlepik 2012, PSX20580, Regal and Tamor.

Table 2. Pickling cucumber split plot experimental design, 1984.

Main plot		Sub-plot	
4 planting dates		4 cultivars	
Planting	Date	Cultivar	Seed company
1	June 7, 1984	Castlepik 2012	Castle
2	June 20, 1984	PSX20580	Peto
3	July 5, 1984	Regal	Harris
4	July 19, 1984	Tamor	Asgrow

The main plots were disked prior to planting. Seeds were directly sown 5 cm apart within rows, using a Heath vacuum precision planter, on 3-row flat beds which were 2.13 m wide and 9 m long. Guard rows were planted between main plots and at the ends of each experimental block. The four replications were separated by 5.2 m alleys. At emergence plants were thinned to about 90 plants per row, resulting in a spacing of approximately 10 cm within and 71 cm between rows.

Approximately 2.5 cm of water was applied by sprinkle irrigation after sowing the seeds in the June 20 planting. No further irrigation was used in the experiment. The

July 5 planting (main plot) in replication 3 was lost due to a heavy rain after planting. The soil became crusted, thus preventing seedling emergence. Many seeds decayed in the water-logged soil.

Ethalfluralin (Sonalan), a pre-emergence herbicide, was applied after each planting. The main plots were cultivated twice. Weeds within rows were removed by hand. The striped cucumber beetle (Acalymma vittatum), which vectors bacterial wilt (Erwinia tracheiphila), was controlled with the insecticides, endosulfan (Thiodan) and malathion (Carbofos). Plants infected with bacterial wilt were removed from the field.

Fruit and Leaf Harvest

When the majority of plants in a main plot were flowering, post-anthesis flowers and the fruits were removed to insure that physiologically similar fruits were evaluated. The following day, beginning at anthesis, fruit samples were randomly harvested from the center row of each sub-plot. Fruits from the lowest fruiting node were selected approximately every other day for a total of six harvests per planting date (Table 3). In the third planting fruits were harvested 7 times. The sample size per sub-plot was 15 fruits in the first harvest and 8 fruits in the other harvests.

Twenty leaf samples were collected near anthesis from each sub-plot (Table 3). The most recent fully expanded

leaf, which was generally the fourth leaf from the apex,was selected. The leaves were rinsed in distilled water, separated into leaf lamina and petiole tissues, then placed into the drying ovens at 60° C.

Table 3. Pickling cucumber fruit and leaf harvest times for each main plot, 1984.

Fruit harvest number	Harvest dates							
	Planting 1		Planting 2		Planting 3		Planting 4	
	Date	DAA[z]	Date	DAA[z]	Date	DAA[z]	Date	DAA[z]
1	7-18	1	7-29	1	8-12	1	8-23	1
2	7-20	3	7-31	3	8-14	3	8-25	3
3	7-23	6	8- 2	5	8-16	5	8-27	5
4	7-25	8	8- 4	7	8-18	7	8-29	7
5	7-27	10	8- 6	9	8-20	9	8-31	9
6	7-30	13	8- 8	11	8-22	11	9- 2	11
7					8-27	16		
Leaf harvest								
	7-18	1	7-31	3	8-13	2	8-23	1

[z]Days after anthesis.

Growth Analysis

Fruit fresh weight. The peduncle and flower were excised from each fruit with a razor blade. Fruit samples from harvests 1 and 2 were massed, while fruits from the later harvests were individually weighed (g).

Volume. The volume of the massed fruit samples was determined using a graduated cylinder, 100 ml to 2000 ml size. The fruits were submerged in distilled water within a partially filled graduated cylinder. The new volume (ml) minus the initial volume (ml) of the distilled water in the graduated cylinder was recorded.

Length and Diameter. The length and diameter (cm) of each fruit from harvests 2 through 7 were measured.

Tissue Fresh Weight. Fruits from harvests 3 to 7 were cut longitudinally with a knife and sectioned into pericarp (fruit wall) and endocarp (seed cavity) tissues with a cork borer. The fresh weight (g) of each tissue was determined. Fruit tissue subsamples of approximately 20 g were selected for nutrient analysis, placed into pre-weighed pie tins, and then re-weighed.

Dry Weight. Whole fruit tissues from harvests 1 and 2 and pericarp and endocarp tissue subsamples from the later harvests were dried in an oven at 60^{o} C for 72 hours. Dry weights (g) of both fruit and leaf tissues were measured and percentage dry matter in the tissues was calculated.

Nutrient Analysis

Leaf and fruit samples were re-dried in an oven at 60° C overnight. Leaf tissues were ground in a Wiley mill to pass through a 20-mesh screen. Fruit tissues were ground with a mortar and pestle. Tissue samples of 0.1 g were weighed and placed into 50 ml volumetric flasks for wet-ashing. The tissue was digested overnight at room temperature (22° C) with 10 ml of analytical grade nitric acid. The mouth of each flask was covered with a washed marble. The nitric acid was evaporated off using an electric hot plate under a hood. When the acid digest was approaching dryness, several drops of hydrogen peroxide were added to each flask to complete the oxidation. The volumetric flasks were removed from the hot plate when the contents were almost colorless and allowed to cool. The flasks were made to volume with deionized water (10 mega v min. resistance). A 20 ml aliquot from each flask was transferred to a plastic vial for storage.

Calcium concentrations in leaf and fruit tissues were determined using an IL Video 12, atomic absorption/ emission spectrophotometer. Standard solutions were prepared, containing 1000 ppm lanthanum (La) from stock $LaCl_3$ solutions and varying concentrations of calcium (0.0, 0.5, 1.0, 2.0, 3.0 ppm). These standard solutions were used to produce a standard curve and tested until the instrument gave reproducible results. The unknown tissue samples were diluted with a $LaCl_3$ solution to

achieve a final La concentration of 1000 ppm and calcium concentrations in the range of 1 to 3 ppm. The calcium concentrations in the unknown samples were determined by atomic absorption spectrophotometry. The tissue calcium concentrations, expressed on a dry weight basis, were calculated by correcting for dilution.

Soil Moisture Content

Soil moisture content was determined gravimetrically. Soil samples, four per main plot, were gathered weekly from August 2 to September 2 from the main plot being harvested. Approximately 5 cm of top soil were removed with a shovel before inserting a Veihmeyer soil corer. The soil samples were from a 7 to 20 cm depth. Glass containers were weighed, the soil sample placed in the jar and then re-weighed. The dry soil weight was determined after oven-drying at 105^{o} C for 72 hours.

Statistical Interpretation of Data

Data gathered from the later harvest times are dependent on the earlier development of the fruit, preventing statistical analysis as a split-split plot, with harvest time as the sub-subplot factor. Analysis of variance using a split plot design was conducted on each harvest time and estimated mean fruit fresh weight. Significant differences between means were tested by the Least Significant Difference (LSD).

A Tektronix cubic spline computer program was used to estimate mean fruit fresh weight, pericarp and endocarp calcium concentrations, fruit calcium content, fruit growth rate and calcium accumulation rate at specific times after anthesis. A regression curve was generated by inputting the number of days after anthesis when fruits were harvested as the X variable and the mean fruit fresh weight data as the Y variable for each subplot. From this curve the number of days after anthesis to reach specific fruit fresh weights of 5, 25, 50, 75, 100, 125, 150 g could be estimated. Fruit growth rates for these estimated harvest times were determined by taking the first derivative of the regression curve function.

Regression curves were also generated for the time course changes in calcium concentration and content in developing pickling cucumber fruits. The X variable was again fruit harvest time (days after anthesis). The calcium concentrations of pericarp and endocarp fruit tissues and fruit calcium content were the Y variables. By inputting the previously estimated times when fruits reached 5, 25, 50, 75, 100, 125, 150 g fresh weight size, the fruit calcium status of these fruits was estimated from the curve. Calcium accumulation rates were estimated by calculating the first derivative of the regression curve function.

RESULTS AND DISCUSSION - SECTION 1

Calcium Status of Pickling Cucumber Fruits

Definition of Terms

Results of plant mineral analyses are expressed in terms of concentration and/or content. "Concentration is defined as the (net) amount of a particular element or substance which is present in a unit amount of a solution or compound (solid material); whereas content is defined as the amount of a particular element or substance present in a specific amount of a solution or compound, (such as a whole fruit)."[3]

The two terms cannot be used interchangeably. The calcium concentration and the content of developing pickling cucumber fruits are quite different (Figure 1). The calcium concentration, expressed on either a fresh or dry weight basis, declines as fruits mature. The calcium content of pickling cucumber fruits continues to increase as the fruits develop to marketable size.

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[3]M. B. Farhoomand and L. A. Peterson, "Concentration and Content," Agronomy Journal, 60 (1968), p. 708.

Figure 1 (A-B). The effect of planting date and cultivar on (A) the calcium concentration and (B) content of pickling cucumber fruits, harvested 1 to 11 days after anthesis, 1984. Each point is the overall treatment average of 4 replications x 4 planting dates x 4 cultivars.

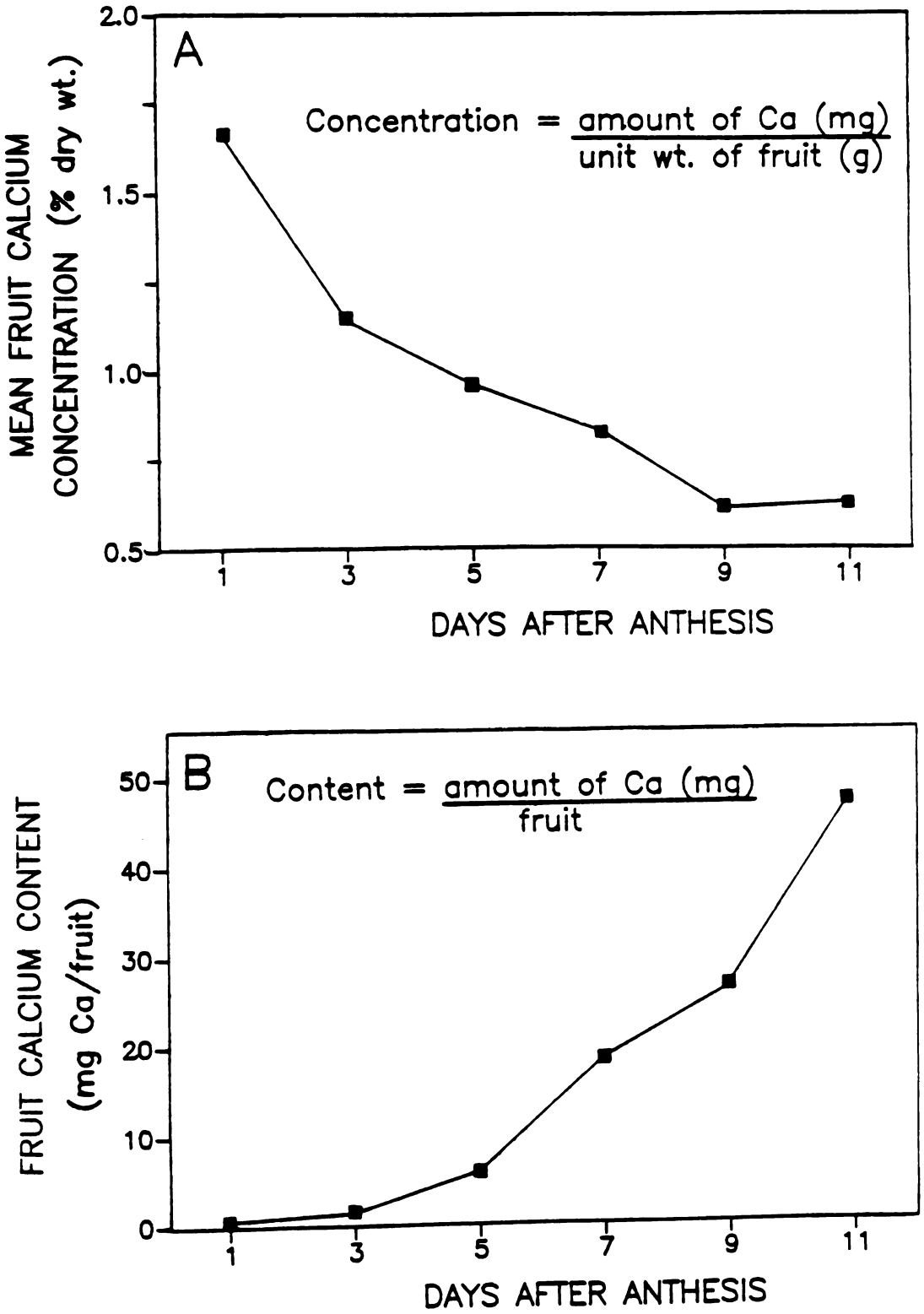

A
Concentration = amount of Ca (mg) / unit wt. of fruit (g)
MEAN FRUIT CALCIUM CONCENTRATION (% dry wt.)
2.0
1.5
1.0
0.5
1
3
5
7
9
11
DAYS AFTER ANTHESIS
B
Content = amount of Ca (mg) / fruit
FRUIT CALCIUM CONTENT (mg Ca/fruit)
50
40
30
20
10
0
1
3
5
7
9
11
DAYS AFTER ANTHESIS

Figure 1.

Although concentration is independent of the sample size, it is defined and influenced by both the amount of calcium present and the amount of plant biomass, which is determined by the growth rate of the fruit (32). An average pickling cucumber fruit at 3 days after anthesis has a calcium concentration of 1.13 percent on a dry weight basis (Figure 1A). By 11 days after anthesis the fruit calcium concentration averaged 0.62 percent dry weight. This decline could have been achieved either by a reduced rate of calcium import into the developing fruits or by a rapid fruit growth rate, which would have a dilutionary effect on the pickling cucumber fruit calcium concentration.

Content is dependent on the sample size (32). As the pickling cucumber fruits enlarged, the calcium content increased due to a continuous calcium uptake from 1 to 11 days after anthesis (Figure 1B). Although the fruit calcium concentration was approximately the same at 9 and 11 days after anthesis, the calcium content increased from an overall average of 26.19 mg per 85.65 g fruit to 47.74 mg per 148.23 g fruit during this period.

Fruit Calcium Concentration

The mean fruit calcium concentration declined from approximately 1.75 percent to less than 0.70 percent (dry weight basis) during fruit ontogeny (Table 4). This decrease in the calcium concentration was consistent with

the 1983 pickling cucumber calcium concentration data of Widders and Price (137). Since similar sized fruits were evaluated, rather than bulking all fruits on the vine, the differences in concentration between harvests were even more accentuated in this study.

The most rapid decline in the mean calcium concentration occurred during the first 5 days after anthesis (Table 4). During these early ontogenetic stages, the pickling cucumber fruit calcium concentrations were significantly affected by an interaction between planting date and cultivar. Fruits from the June 7 planting tended to have the lowest concentrations, while fruits from the July 19 planting had the highest calcium concentrations at 1 and 3 days after anthesis. Within the planting dates, there were no consistent differences between the declining fruit calcium concentrations of the four cultivars evaluated. It may be postulated that the very high relative growth rates of these developing fruits, combined with low rates of calcium import, resulted in the dramatic decline in the calcium concentrations.

By 7 days after anthesis the fruit calcium concentrations began to plateau (Table 4), coinciding with a leveling off of the relative growth rates of the pickling cucumber fruits (see Results and Discussion - Section 2). Both planting date and cultivar had an impact on the calcium concentrations of fruits from the later harvests. The calcium concentration of fruits from the July plantings were

Table 4. The effect of planting date and cultivar on the calcium concentration of pickling cucumber fruits, harvested 1 to 11 days after anthesis, 1984.

	Fruit calcium concentration (% dry wt.)					
	Days after anthesis					
Parameter	1	3	5	7	9	11
Planting date (PD)[z]						
June 7, 1984	1.37	1.05	0.90	0.69	0.50	0.52
June 20, 1984	1.71	1.05	0.85	0.93	0.78	0.79
July 5, 1984	1.62	1.16	1.04	0.87	0.62	0.60
July 19, 1984	1.94	1.26	1.04	0.83	0.52	0.59
LSD 5%[y]	0.19	0.14	0.12	0.09	0.05	0.04
1%	0.28	NS	NS	0.14	0.08	0.06
Cultivar (CV)[x]						
Castlepik 2012	1.67	1.15	0.96	0.89	0.59	0.65
PSX20580	1.76	1.14	0.95	0.80	0.68	0.65
Regal	1.61	1.10	0.97	0.91	0.61	0.66
Tamor	1.60	1.13	0.93	0.71	0.54	0.54
LSD 5%[y]	0.11	NS	NS	0.06	0.04	0.04
1%	NS	NS	NS	0.09	0.06	0.06
Interaction						
PD x CV	**	*	NS	NS	NS	NS

[z]Each entry is an average of 4 replications x 4 CV.

[y]LSD is significant at the 5% (*) or 1% (**) level or nonsignificant(NS).

[x]Each entry is an average of 4 replications x 4 PD.

similar and higher than the concentrations of fruits from the June plantings, harvested 5 days after anthesis. As the fruits matured, fruits from the June 20 planting tended to have higher calcium concentrations than fruits from the other plantings, while the lowest calcium concentrations were found in fruits from the June 7 planting. The higher calcium concentrations of fruits from the June 20 planting indicate that the fruit calcium accumulation rates relative to the rates of fruit growth were higher than those of fruits from the other plantings.

Cultivar differences in the pickling cucumber friut calcium concentration occurred from 7 to 11 days after anthesis (Table 4). Regal and Castlepik 2012 fruits had similar calcium concentrations. Tamor fruits were consistently low in calcium concentration throughout the experimental harvest period. By 11 days after anthesis, the mean calcium concentration of Tamor fruits was 0.54 percent dry weight, which was significantly lower than the calcium concentrations of Castlepik 2012, PSX20580 and Regal fruits. Tamor plants may be less efficient in calcium uptake, partition less calcium to the fruits and/or have a lower requirement for calcium within the fruit for normal development than the other cultivars.

It is interesting that the impact of environment and genotype on the calcium concentrations of pickling cucumber fruits varied throughout fruit ontogeny (Table 4). The main treatment effects on fruit calcium concentration were

consistent over a wide range of conditions for the more mature fruits. The differential effect of cultivar on the fruit calcium concentration under different environmental conditions indicates that pickling cucumber fruits are most sensitive to changes early in development. The plant has just completed the transition from a vegetative to a reproductive mode of growth, with major physiological changes in hormone and enzyme activity and in assimilate demand and partitioning. Any alteration in these physiological changes is likely to affect the rates of fruit calcium accumulation and growth, which determine the mean fruit calcium concentration.

Mean fruit calcium concentration does not indicate differences in specific fruit tissue calcium concentrations. Tracer studies with apple fruits, using radioactive calcium (^{45}Ca), have shown an uneven distribution of calcium throughout the fruits (68,85,86, 101). Calcium concentrations were highest in the core towards the stem end, intermediate in the peel, and lowest in the flesh tissue.

Differences in the calcium partitioning between pericarp and endocarp fruit tissues occurred with pickling cucumbers (Table 5). The pericarp calcium concentrations were always higher than those of the endocarp tissues. While the pericarp concentrations declined gradually with increasing fruit size, the endocarp calcium concentrations declined dramatically to a low of 0.20

percent dry weight or less at 11 days after anthesis. Such low calcium concentrations are considered a deficient level for growth in many plants (17,40,81,111,117,134).

The observed calcium concentration differences between the two pickling cucumber fruit tissues may be due to a higher growth rate and/or lower calcium accumulation rate of endocarp versus pericarp tissues (Table 5). The expansive cell growth rates of endocarp fruit tissues exceed the pericarp growth rates (see Results and Discussion - Section 2). A higher endocarp tissue growth rate relative to the calcium accumulation rate would cause a lower calcium concentration due to a greater dilutionary effect. The endocarp may also contain fewer vascular tissues than the pericarp. The necessary water for growth may diffuse into the endocarp tissues via the symplastic pathway, through which the calcium ions move with difficulty. This would decrease the rate of calcium import relative to the endocarp tissue growth rate.

The pericarp calcium concentrations of the pickling cucumber fruits were affected by both the time of planting and by cultivar (Table 6). At 5 days after anthesis the calcium concentration was higher in the pericarp of fruits from the July plantings in comparison with fruits from the June 20 planting. As the maturation period increased, fruits harvested from the June 20 planting maintained a higher calcium level in the pericarp tissues, whereas pericarp calcium concentrations of fruits from the June 7

Table 5. The mean calcium concentrations of pericarp and endocarp tissues of pickling cucumber fruits, harvested 5 to 11 days after anthesis, 1984.

	Calcium concentration (% dry wt.)[z]	
Days after anthesis	Pericarp tissue	Endocarp tissue
5	1.04	0.79
7	0.92	0.60
9	0.73	0.29
11	0.80	0.23

[z]Each entry is an average of 4 replications x 4 planting dates x 4 cultivars.

and July 19 plantings declined.

Tamor fruit tended to be the lowest in pericarp calcium concentrations (Table 6). The calcium concentrations of the pericarp tissues of Castlepik 2012 and Regal fruits were similar throughout the four harvests. These cultivars consistently maintained higher pericarp calcium concentrations than Tamor, except at 9 days after anthesis, when the concentrations were not significantly different. The calcium concentrations of PSX20580 pericarp tissues fluctuated at an intermediate level. Only at 9 days after anthesis did the mean concentration of PSX20580 pericarp tissue exceed the concentrations of the other three cultivars.

It should be noted that the trends in the pickling cucumber fruit pericarp concentrations changed at 11 days after anthesis (Table 6). The pericarp calcium concentrations, which declined from 5 to 9 days after anthesis, increased at day 11. Although this concentration increase was unexpected, it consistently occurred in all four planting dates and for all of the cultivars except PSX20580. It may be postulated that the observed calcium concentration increase was due to a decrease in the pericarp growth rate relative to the rate of calcium import into the tissue. Schapendonk and Brouwer (1984) report that pickling cucumber fruits in the lower nodes begin to lose their dominance by approximately 12 days after anthesis (106). If less water is transported into these fruits, the calcium

Table 6. The effect of planting date and cultivar on the calcium concentration of pericarp tissue of pickling cucumber fruits, harvested 5 to 11 days after anthesis, 1984.

	Pericarp tissue Ca concn (% dry wt.)			
	Days after anthesis			
Parameter	5	7	9	11
Planting date (PD)[z]				
June 7, 1984	1.00	0.75	0.61	0.68
June 20, 1984	0.92	1.03	0.92	0.99
July 5, 1984	1.14	0.98	0.77	0.79
July 19, 1984	1.09	0.90	0.61	0.75
LSD 5%[y]	0.14	0.11	0.08	0.06
1%	NS	0.16	0.11	0.08
Cultivar (CV)[x]				
Castlepik 2012	1.08	1.02	0.70	0.83
PSX20580	1.03	0.86	0.83	0.83
Regal	1.06	1.02	0.71	0.84
Tamor	0.98	0.77	0.67	0.70
LSD 5%[y]	0.07	0.08	0.06	0.06
1%	NS	0.11	0.08	0.08
Interaction				
PD x CV	NS	NS	NS	NS

[z]Each entry is an average of 4 replications x 4 CV.

[y]LSD is significant at the 5% or 1% level or nonsignificant (NS).

[x]Each entry is an average of 4 replications x 4 PD.

concentration would be higher, due to a lower dilutionary effect.

Planting date and cultivar also had an impact on the calcium concentrations of the endocarp tissues (Table 7). Fruits from the July 19 planting had the highest endocarp calcium concentrations at 5 and 7 days after anthesis. It is interesting that the concentrations of calcium in the pericarp (Table 6) and endocarp tissues were similar for fruits from this planting at 5 days after anthesis. By 9 days after anthesis, fruits from the June 20 planting had the highest mean endocarp calcium concentration.

Among the four cultivars examined, Tamor fruits had the highest mean endocarp calcium concentration at 5 days after anthesis and the lowest concentrations at 9 and 11 days after anthesis (Table 7). The calcium concentrations of the endocarp tissues were similar for Castlepik 2012 and Regal, as had been observed with the pericarp calcium concentrations (Table 6). PSX20580 fruits had intermediate concentrations of calcium in the endocarp tissues.

At 11 days after anthesis there was a significant interaction between the effects of planting date and cultivar on the endocarp calcium concentrations (Table 8). As with the main treatment effects, the June 20 planting consistently had the highest mean endocarp calcium concentration within the cultivars, although not always significant. Tamor fruits generally had the lowest endocarp calcium concentrations within the planting dates. Only in

Table 7. The effect of planting date and cultivar on the calcium concentration of endocarp tissue of pickling cucumber fruits, harvested 5 to 11 days after anthesis, 1984.

	Endocarp tissue Ca concn (% dry wt.)			
	Days after anthesis			
Parameter	5	7	9	11
Planting date (PD)[z]				
June 7, 1984	0.68	0.54	0.23	0.16
June 20, 1984	0.67	0.62	0.39	0.31
July 5, 1984	0.80	0.58	0.28	0.20
July 19, 1984	1.02	0.66	0.28	0.23
LSD 5%[y]	0.10	0.05	0.04	0.04
1%	0.15	0.07	0.05	0.06
Cultivar (CV)[x]				
Castlepik 2012	0.68	0.56	0.34	0.26
PSX20580	0.80	0.64	0.28	0.20
Regal	0.77	0.60	0.36	0.26
Tamor	0.91	0.60	0.20	0.18
LSD 5%[y]	0.08	0.04	0.03	0.03
1%	0.10	0.06	0.04	0.04
Interaction				
PD x CV	NS	NS	NS	*

[z]Each entry is an average of 4 replications x 4 CV.

[y]LSD is significant at the 5% (*) or 1% level or non-significant (NS).

[x]Each entry is an average of 4 replications x 4 PD.

the June 20 planting did PSX20580 have the lowest calcium concentration.

This interaction at 11 days after anthesis was as surprising as the rise in the pericarp calcium concentrations (Table 6,8). A treatment interaction had not affected either the total fruit or pericarp calcium concentrations of the more mature pickling cucumber fruits (Tables 4,6). It may be hypothesized that hormonal changes may have occurred as these fruits lost their dominance. Perhaps the auxin synthesized by the seeds increased the sensitivity of the fruits to environmental changes and of the genotypic response of the four cultivars, affecting the rate of calcium accumulation.

The concentration results may be confounded when comparing the calcium concentrations of pickling cucumber fruits from the four plantings according to harvest time. Differences may occur in fruit size and, consequently, in the physiological stage of development of these sampled fruits. Since the calcium concentration of any tissue is affected by the growth rate of the tissue, the calcium concentration data were estimated and standardized for similar fruit fresh weights (Figures 2,3). (A pickling cucumber fruit fresh weight of 100 g corresponds to a fruit diameter of approximately 2.5 cm.)

Planting date and cultivar treatments interacted, significantly affecting the pericarp calcium concentrations of 25 g pickling cucumber fruits and the endocarp calcium

Table 8. The interaction of planting date and cultivar on the calcium concentration of endocarp tissue of pickling cucumber fruits, harvested 11 days after anthesis, 1984.

	Endocarp tissue Ca concn (% dry wt)[z]			
	Cultivar (CV)			
Planting date (PD)	Castlepik 2012	PSX20580	Regal	Tamor
June 7, 1984	0.17	0.16	0.22	0.10
June 20, 1984	0.34	0.24	0.36	0.30
July 5, 1984	0.24	0.21	0.21	0.16
July 19, 1984	0.28	0.22	0.26	0.16

Significant effects

LSD 5% within PD 0.06

within CV 0.06

[z]Each entry is an average of 4 replications.

concentrations of 25 to 100 g fruits (Figures 2,3). It was surprising that this interaction occurred in the smaller fruits, since it had not been observed when analyzing the tissue calcium concentrations by harvest times. Variability in the fruit fresh weights apparently masked this interaction. It is also interesting that the endocarp tissue calcium concentrations were more sensitive to environmental changes and different genotypes than the pericarp calcium concentrations.

Planting date significantly affected the pericarp calcium concentrations of pickling cucumber fruits weighing 50 to 150 g (Figure 2). By eliminating the variability due to fruit size, the calcium concentrations of fruit pericarp tissues from the June 7 planting were not the lowest (Table 6). Fruits from the July 19 planting had the lowest pericarp calcium concentrations, while the pericarp tissues from the June 20 planting had the highest mean concentrations, though not always significant. The pericarp calcium concentrations increased only in mature fruits from the June 20 planting. The pericarp calcium concentrations of fruits from the June 7 and July 5 plantings were similar and intermediate, compared with the concentrations of fruits from the other plantings.

Planting date also had an impact on the endocarp calcium concentrations as pickling cucumber fruits enlarged to 125 to 150 g (Figure 2). The calcium concentrations of the endocarp tissues were similar in fruits harvested

Figure 2. The effect of planting date on the calcium concentrations of pericarp and endocarp tissues of pickling cucumber fruits of specific fresh weights, 1984. Each point is an average of 4 replications x 4 cultivars for 25 to 125 g fruits and an average of 3 replications x 4 cultivars for 150 g fruits.

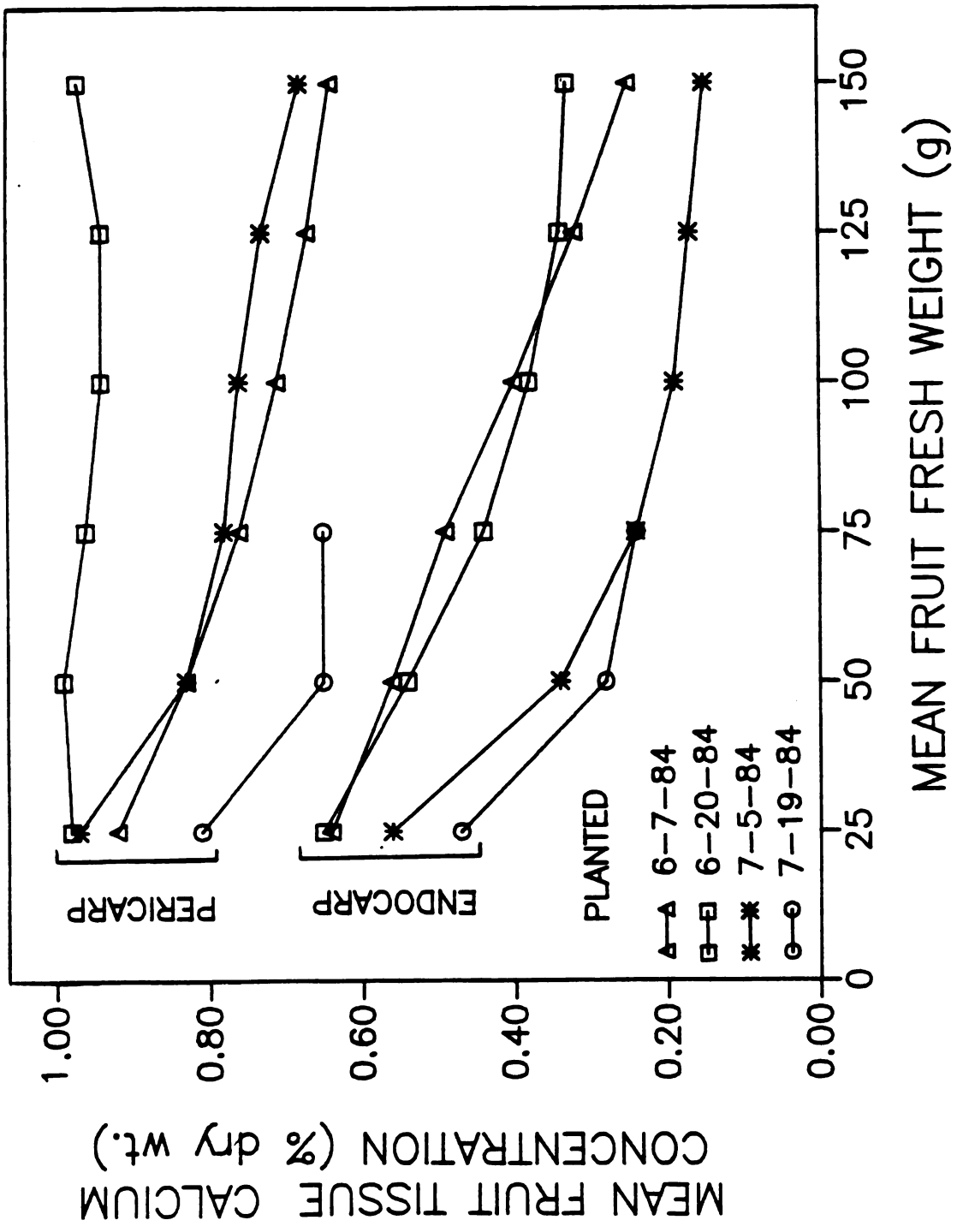

MEAN FRUIT TISSUE CALCIUM CONCENTRATION (% dry wt.)
1.00
0.80
0.60
0.40
0.20
0.00
0
25
50
75
100
125
150
MEAN FRUIT FRESH WEIGHT (g)
PERICARP
ENDOCARP
PLANTED
6-7-84
6-20-84
7-5-84
7-19-84

Figure 2.

Figure 3. The effect of cultivar on the calcium concentrations of the pericarp and endocarp tissues of pickling cucumber fruits of specific fresh weights, 1984. Each point is an average of 4 replications x 4 planting dates for 25 to 75 g fruits, an average of 4 replications x 3 planting for 100 to 125 g fruits, and an average of 3 replications x 3 planting dates for 150 g fruits.

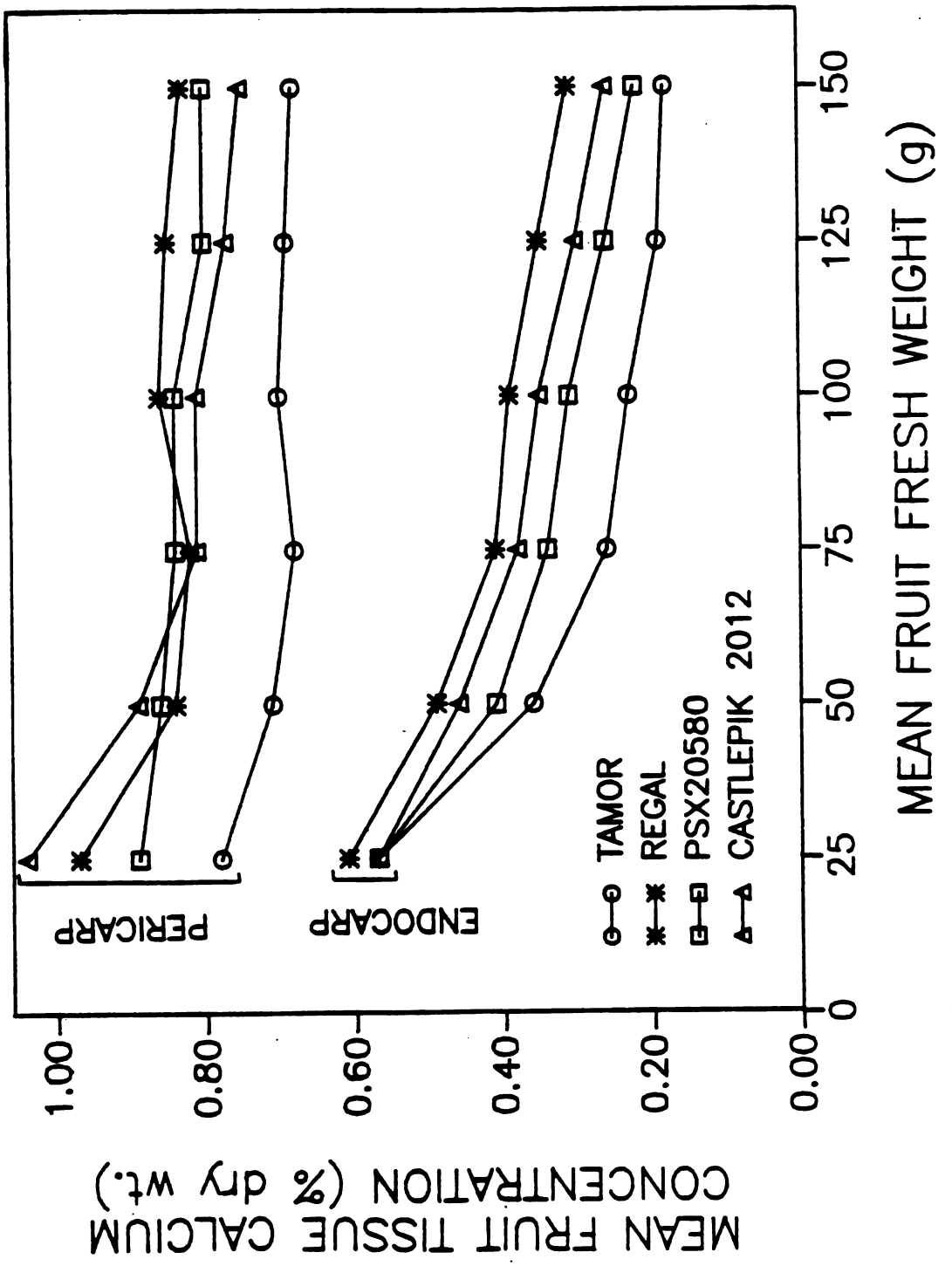

MEAN FRUIT TISSUE CALCIUM CONCENTRATION (% dry wt.)
1.00
0.80
0.60
0.40
0.20
0.00
0
25
50
75
100
125
150
MEAN FRUIT FRESH WEIGHT (g)
PERICARP
ENDOCARP
TAMOR
REGAL
PSX20580
CASTLEPIK 2012

Figure 3.

from the June plantings as compared with the similar and lower concentrations from the July plantings. It should be noted that while the endocarp tissue calcium concentrations declined as fruits from the June 20 planting matured, the calcium concentrations of the pericarp tissues remained relatively constant. This would suggest that the environment affects calcium import into and accumulation in pickling cucumber fruit tissues differently and perhaps also the growth rates of the pericarp and endocarp tissues. The drought during the early stages of development of fruits from the July 19 plantings and throughout development in the July 5 planting appeared to depress the calcium concentrations of endocarp tissues more than the pericarp concentrations.

Cultivar affected the pericarp calcium concentrations of 50 to 150 g fruits and the endocarp calcium concentrations of 125 to 150 g fruits (Figure 3). Regardless if the fruit tissue calcium concentrations were analyzed by harvest time (Tables 6,7) or by fruit fresh weight, Tamor consistently had the lowest calcium concentrations in both pericarp and endocarp tissues. Within the fruit fresh weight range of 25 to 150 g, Regal maintained the highest endocarp calcium concentrations.

Fruit Calcium Content

The mean calcium content of pickling cucumber fruits increased through ontogeny. The period of most rapid

calcium accumulation was generally between 9 and 11 days after anthesis, as the fruits approached harvestable size (Figure 4). This accumulation pattern is somewhat different from that of fruits of other species, which have a rapid increase in calcium content during the very early stages of fruit ontogeny but then level off as these fruits approach maturity and harvest (1,56,81,101,123,127). It must be recognized that pickling cucumber fruits are harvested at a relatively immature stage when the fruits are still rapidly growing, even though they may be relatively large at horticultural maturity.

At all harvest times, except 3 and 11 days after anthesis, planting date and cultivar interacted, having a significant effect on the calcium contents of pickling cucumber fruits (Figure 4). The calcium contents of the fruits harvested 3 days after anthesis differed significantly with respect to the time of planting only, while at 11 days after anthesis both planting date and cultivar had an impact on the fruit calcium contents. It is unknown why the treatment interactions were not significant at 3 and 11 days after anthesis. Since content is dependent on sample size, the differential effect of the four pickling cucumber cultivars on fruit calcium contents under different environmental conditions may have been largely due to the size of these fruits.

The calcium contents were similar and higher for fruits from the two June plantings, compared with the similar but

Figure 4 (A-B). The effect of (A) planting date and (B)cultivar on the calcium content of pickling cucumber fruits, harvested 1 to 13 days after anthesis, 1984. (A) Each point is an average of 4 replications x 4 cultivars. (B) Each point is an average of 4 replications x 4 planting dates.

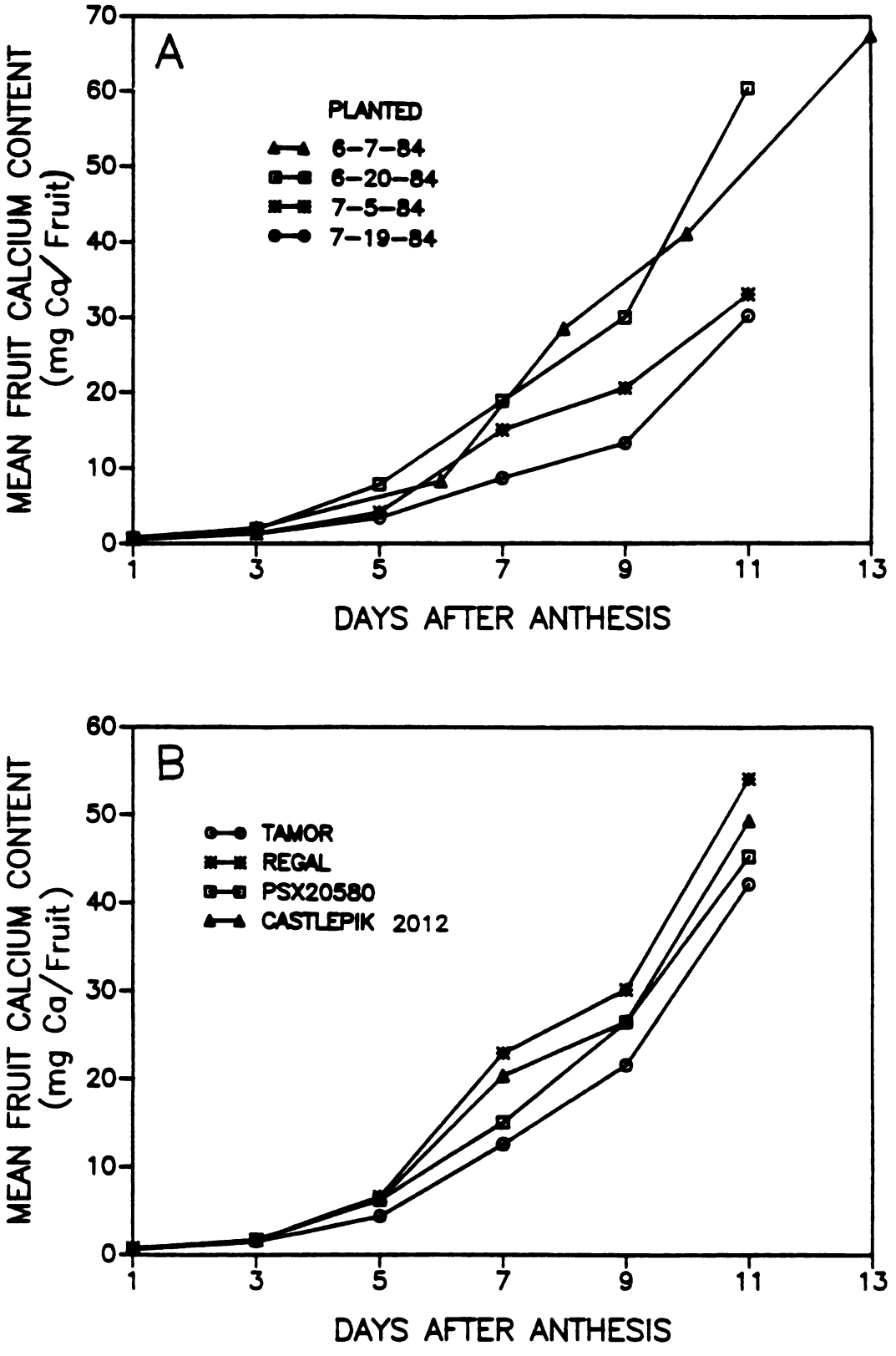

A
PLANTED
6-7-84
6-20-84
7-5-84
7-19-84
MEAN FRUIT CALCIUM CONTENT (mg Ca/ Fruit)
DAYS AFTER ANTHESIS
B
TAMOR
REGAL
PSX20580
CASTLEPIK 2012
MEAN FRUIT CALCIUM CONTENT (mg Ca/Fruit)
DAYS AFTER ANTHESIS

Figure 4.

lower fruit contents from the July plantings (Figure 4A). By the last harvest, the calcium content averaged 60 mg per fruit in the June plantings and was half that level in fruits from the July plantings. Fruits from the July plantings were smaller than those from the June plantings when compared at similar harvest times (see Results and Discussion - Section 2). The average fresh weight of fruits from the July 19 planting did not reach 100 g by 11 days after anthesis.

The greatest differences in calcium contents between the cultivars were encountered at the later stages of fruit maturity (Figure 4B). Tamor had the lowest content and Regal fruits generally accumulated the highest calcium levels of the four cultivars evaluated. Variability in the fruit sizes of the different cultivars at a specific harvest time, however, reduced the possibility of measuring significant cultivar differences, especially at the later harvests.

The fruit calcium content data were reevaluated and statistically analyzed again after standardization for fruit fresh weight (Figure 5). The calcium contents were similar for all fruits weighing 5 g. As the fruits enlarged to 25 and 50 g, the contents of the fruits differed due to an interaction between planting date and cultivar. By eliminating the variability in fruit size, this interaction became nonsignificant in affecting the calcium contents of fruits larger than 50 g. The contents of fruits within the

fresh weight range of 75 to 150 g were significantly affected by planting time and cultivar. Surprisingly, the calcium contents of 100 g fruits were affected only by cultivar.

Both 25 and 50 g Tamor fruits generally had the lowest calcium contents within the planting dates (Figure 5). Within the cultivars, 25 and 50 g fruits from the July 19 planting had the lowest calcium contents. The pickling cucumber fruit calcium concentrations were also the lowest in Tamor fruits and fruits from the July 19 planting, so the low fruit calcium contents were not surprising. It was also observed that a significant interaction affected the calcium concentrations of the pericarp and endocarp tissues of the smaller pickling cucumber fruits (Figures 2,3). This suggests that these fruits had low rates of calcium accumulation relative to the fruit growth rates.

The increase in calcium content relative to fruit weight was almost linear within the fruit fresh weight range of 5 to 150 g for planting date (Figure 5A). Once again, the June 20 planting tended to have fruits with higher calcium contents, while fruits from the July 19 planting tended to accumulate less calcium than fruits from the other plantings. Unlike the ontogenetic trends in calcium content evaluated by harvest time (Figure 4A), fruits from the June 7 and July 5 plantings had similar contents when the calcium content data were normalized for fruit fresh weight (Figure 5A). At 125 and 150 g, fruits from these

Figure 5 (A-B). The effect of (A) planting date and (B)cultivar on the calcium content of pickling cucumber fruits of specific fresh weights, 1984. (A) Each point is an average of 4 reps x 4 planting dates (PD) for 5 to 75 g fruits, an average of 4 reps x 3 PD for 100 to 125 g fruits, and an average of 3 reps x 3 PD for 150 g fruits. (B) Each point is an average of 4 reps x 4 cultivars (CV) for 5 to 125 g fruits and an average of 3 reps x 4 CV for 150 g fruits.

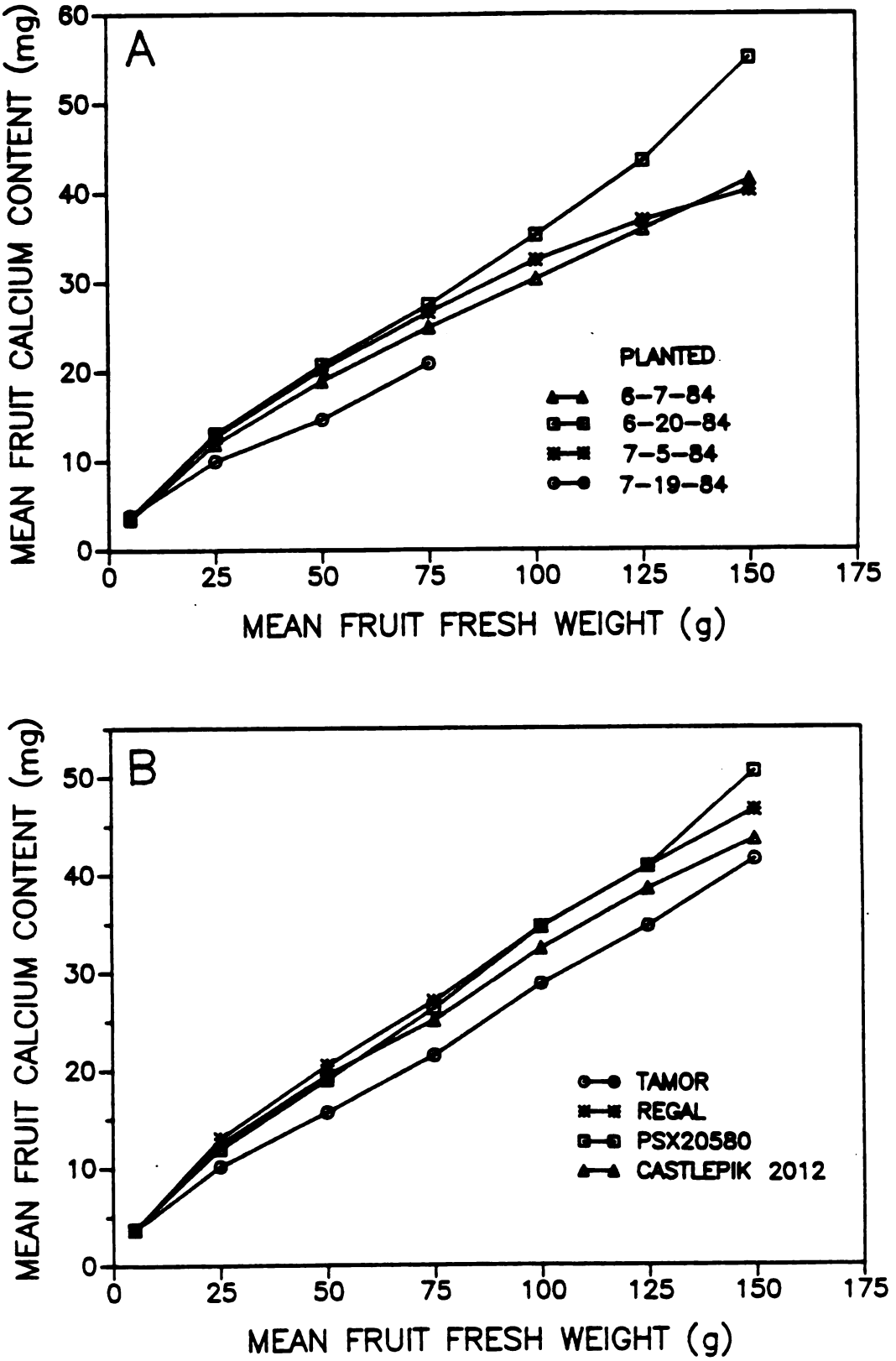

A
MEAN FRUIT CALCIUM CONTENT (mg)
MEAN FRUIT FRESH WEIGHT (g)
PLANTED
6-7-84
6-20-84
7-5-84
7-19-84
B
MEAN FRUIT CALCIUM CONTENT (mg)
MEAN FRUIT FRESH WEIGHT (g)
TAMOR
REGAL
PSX20580
CASTLEPIK 2012

Figure 5.

plantings remained similar in calcium contents and lower than those of fruits from the June 20 planting.

It was not unexpected that the trend differences between the fruit calcium contents analyzed by harvest time (Figure 4A) and by fruit fresh weight (Figure 5A) would be most notable in the larger pickling cucumber fruit sizes. The variability in fruit sizes between the planting dates was highest during the later harvests. The similarities between the lower calcium contents of fruits from the June 7 and July 5 plantings indicate that less calcium was being imported into these fruits than into fruits from the June 20 planting, when comparing fruits of equal fresh weight. It was very dry during the later stages of development for fruits from the June 7 and July 5 plantings, suggesting that water was a rate limiting factor in pickling cucumber fruit calcium accumulation and growth (see Results and Discussion - Section 4).

Even after normalizing fruit fresh weight, Tamor fruits usually had the lowest calcium contents (Figure 5B). This is consistent with the relatively low fruit tissue calcium concentrations previously discussed (Figure 3). The comparatively low calcium contents of Tamor fruits were established early in fruit development and maintained throughout ontogeny. The fruit calcium contents of the other cultivars fluctuated relative to one another as the fruits developed.

The calcium contents of the pericarp and endocarp fruit

tissues were analyzed by harvest periods (Figure 6). The calcium contents of pickling cucumber fruits are much higher in the pericarp tissues than in the endocarp tissues, consistent with the concentration data for these tissues (Tables 6,7). The pericarp calcium contents dramatically increased from 5 to 11 days after anthesis, while the endocarp tissues maintained low and nearly constant calcium contents. Variability in the size of the fruits and of the fresh weights of the two tissues being compared confound the content results, since content is dependent on sample size. The data do suggest, however, that there is a higher and continuous accumulation of calcium in the pericarp tissue than in the endocarp as a pickling cucumber fruit matures. It may be postulated that this is a result of more vascular tissues in the pericarp, facilitating calcium import into this tissue.

Fruit Calcium Accumulation Rate

The calcium accumulation rate of pickling cucumber fruits is the estimated amount of calcium (mg) which is imported into a fruit per unit time (day). The impact of planting date and cultivar on the fruit calcium accumulation rates is confusing (Figures 7,8). Genetic variability affected the calcium accumulation rates in small, immature pickling cucumber fruits, weighing 5 g (fresh weight). Planting date and cultivar interacted, affecting the import rates of calcium into 25, 50 and 150 g fruits. Only the

Figure 6. The effect of planting date and cultivar on the calcium content of pickling cucumber fruit tissues, harvested 5 to 11 days after anthesis, 1984. Each point is the overall average of 4 replications x 4 planting dates x 4 cultivars.

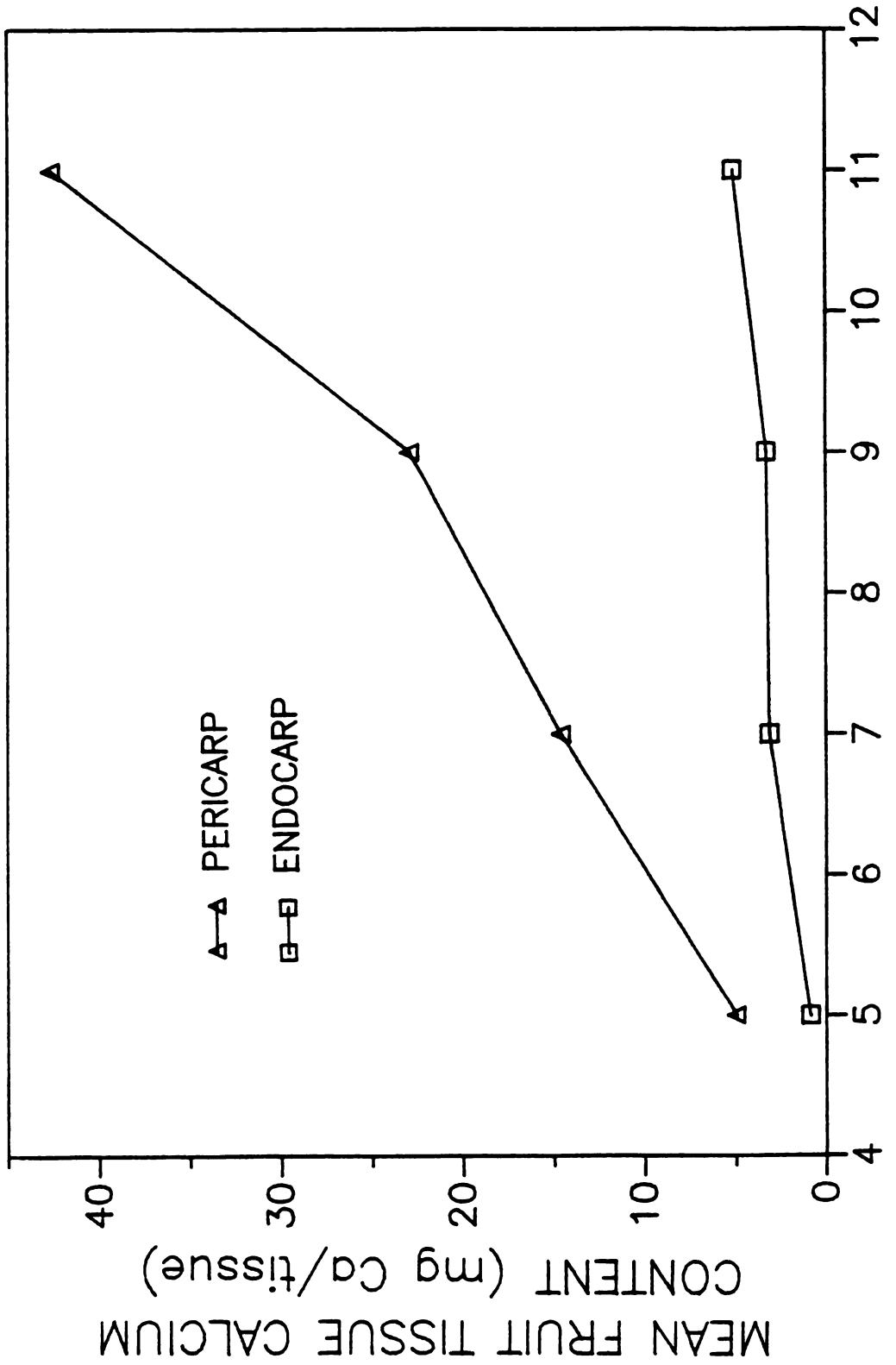

MEAN FRUIT TISSUE CALCIUM
CONTENT (mg Ca/tissue)
0
10
20
30
40
4
5
6
7
8
9
10
11
12
DAYS AFTER ANTHESIS
PERICARP
ENDOCARP

Figure 6.

planting date main treatment had a significant effect on the calcium accumulation rates of 75 to 125 g fruits.

Environmental conditions (see Results and Discussion - Section 4) appeared to have a significant effect on the ontogenetic trends in calcium accumulation rates (Figure 7). Similar rate trends were observed for fruits from the June 7 and July 5 plantings. Fruits from the June 7 planting reached their maximum import rate at 50 g and then plateaued at approximately 9 mg of calcium per day. The calcium accumulation rates for fruits from the July 5 planting were consistently low throughout ontogeny, suggesting that some factor was limiting calcium import into the pickling cucumber fruits. Upon reaching 75 g, fruits from the July 5 planting peaked in their calcium accumulation rates, which then declined to lower rates for 150 g fruits than for 5 g fruits. Fruits from the June 20 and July 19 plantings never reached their maximum calcium import rates, increasing continually in an almost linear manner. The fruits from the June 20 planting had a twenty-fold higher calcium import rate than that of 150 g fruits from the July 5 planting. Although fruits from the July 19 planting had an initially low calcium accumulation rate, 75 g fruits had similar rates as fruits from the June plantings.

It is interesting to note that the calcium import rates of Castlepik 2012, PSX20580 and Tamor fruits increased through ontogeny (Figure 8). Regal fruits had a rapid

Figure 7. The effect of planting date on the calcium accumulation rate of pickling cucumber fruits of specific fresh weights, 1984. Each point is an average of 4 replications x 4 cultivars for 5 to 125 g fruits and an average of 3 replications x 4 cultivars for 150 g fruits.

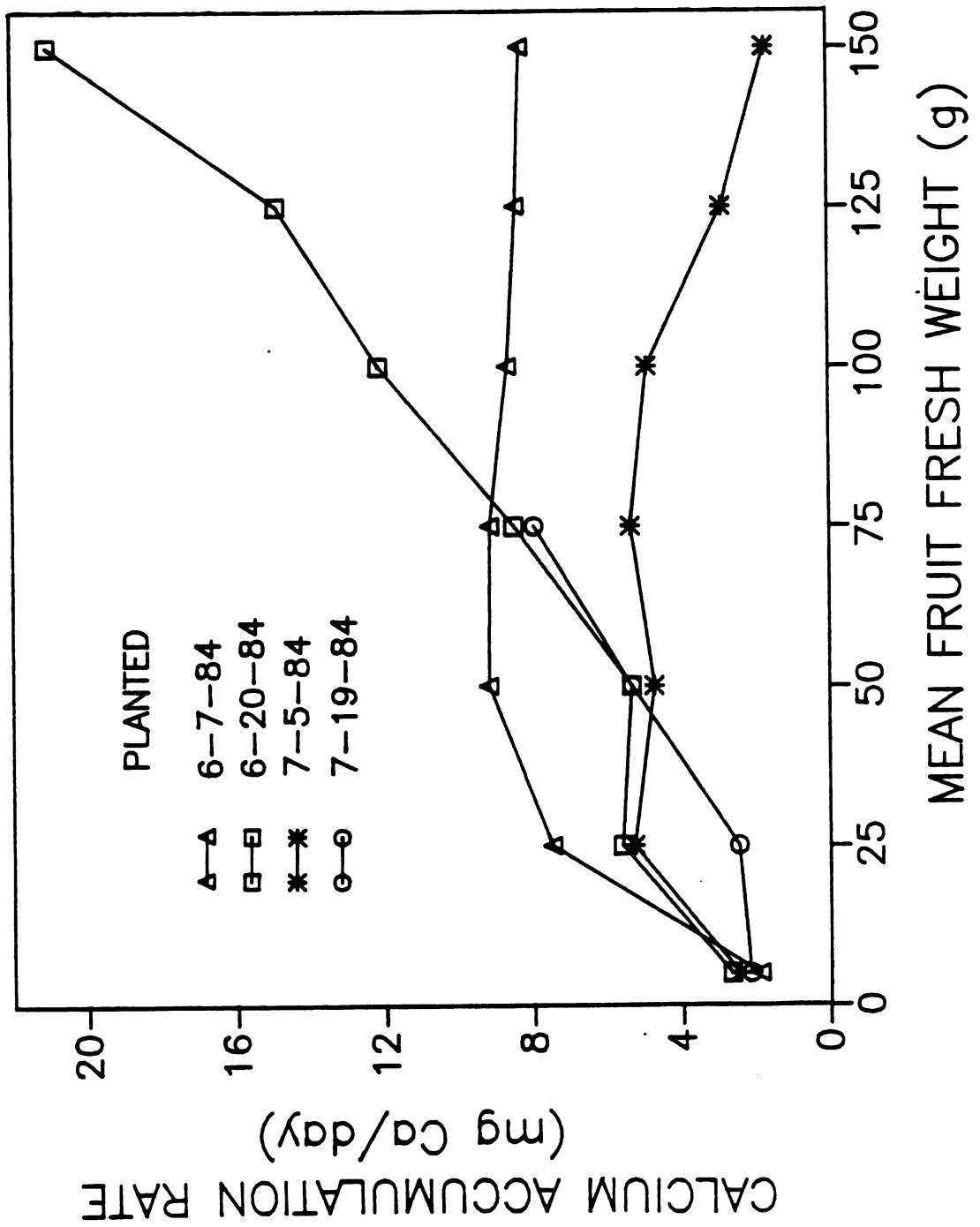

CALCIUM ACCUMULATION RATE
(mg Ca/day)
20
16
12
8
4
0
0
25
50
75
100
125
150
MEAN FRUIT FRESH WEIGHT (g)
PLANTED
6-7-84
6-20-84
7-5-84
7-19-84

Figure 7.

increase in import rates early in development but then began to level off in 75 g fruits. Tamor fruits, with low calcium concentrations and contents, had the lowest calcium accumulation rates during the earliest stages of development.

These results suggest that if calcium is proven to be critical for pickling cucumber fruit growth and/or quality, genetic variability could be exploited in a breeding program. Tamor fruits may have lower tissue calcium requirements, due to more efficient ion utilization. English and Barker (1983) report that tomato strains vary in calcium efficiency (30). Calcium-efficient strains grow well in a medium with a low calcium supply and accumulate less calcium compared with the calcium-inefficient strains. Pickling cucumber cultivars may have different fruit calcium accumulation rates because of varying efficiency in calcium uptake. Some cultivars may have more selective calcium absorption and/or differing efficiency of loading calcium ions into the xylem vessels. Pickling cucumber fruit growth is highly competitive with root growth (96,106). Perhaps this competitive sink strength differs among cultivars. Variable fruit growth rates may also affect the calcium accumulation rates of pickling cucumber fruits, due to dilutionary effects and altered fruit to shoot ratios.

Figure 8. The effect of cultivar on the calcium accumulation rate of pickling cucumber fruits of specific fresh weights, 1984. Each point is an average of 4 replications x 4 planting dates for 5 to 75 g fruits, an average of 4 replications x 3 planting dates for 100 to 125 g fruits and an average of 3 replications x 3 planting dates for 150 g fruits.

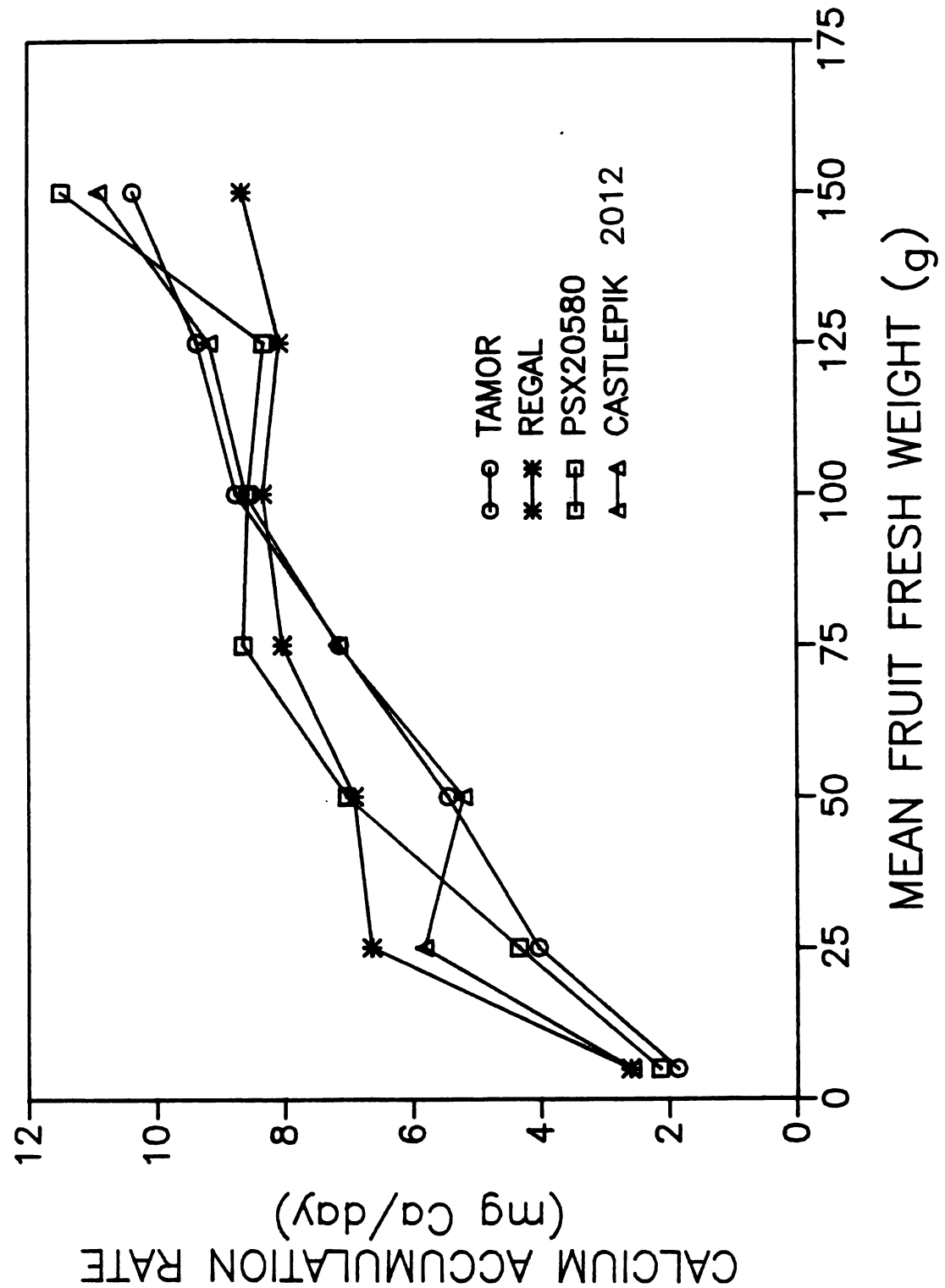

CALCIUM ACCUMULATION RATE
(mg Ca/day)
MEAN FRUIT FRESH WEIGHT (g)
TAMOR
REGAL
PSX20580
CASTLEPIK 2012
0
2
4
6
8
10
12
0
25
50
75
100
125
150
175

Figure 8.

RESULTS AND DISCUSSION - SECTION 2

Pickling Cucumber Fruit Growth

Fruit Fresh Weight and Volume

The growth of pickling cucumber fruits was measured by fresh weight, volume, dry weight, length and diameter. The mean fruit fresh weight (g) and volume (ml) of pickling cucumber fruits were highly correlated (Figure 9). For every 1 ml increase in volume there was a 0.96 g increase in the fruit fresh weight. The largest increase in fruit fresh weight and volume coincided, occurring between 9 and 11 days after anthesis (between 8 and 10 days after anthesis for fruits from the June 7 planting).

Planting date and cultivar had a similar effect on pickling cucumber fruit fresh weight and volume (Figure 9). The fruit density was not altered by the treatments. Both parameters were significantly affected by the planting date (Table 9). Cultivar also had an impact on the fruit fresh weights and volumes at all harvest dates except at 3 days after anthesis. Planting date and cultivar interacted at 7 days after anthesis, affecting pickling cucumber fruit size.

The largest fruits were from the June 7 planting, ranging in weight from 0.701 g to 216.83 g at 1 and 11 days

Figure 9. The effect of planting date and cultivar on the correlation between mean volume and fresh weight of pickling cucumber fruits, harvested 1 to 11 days after anthesis, 1984.

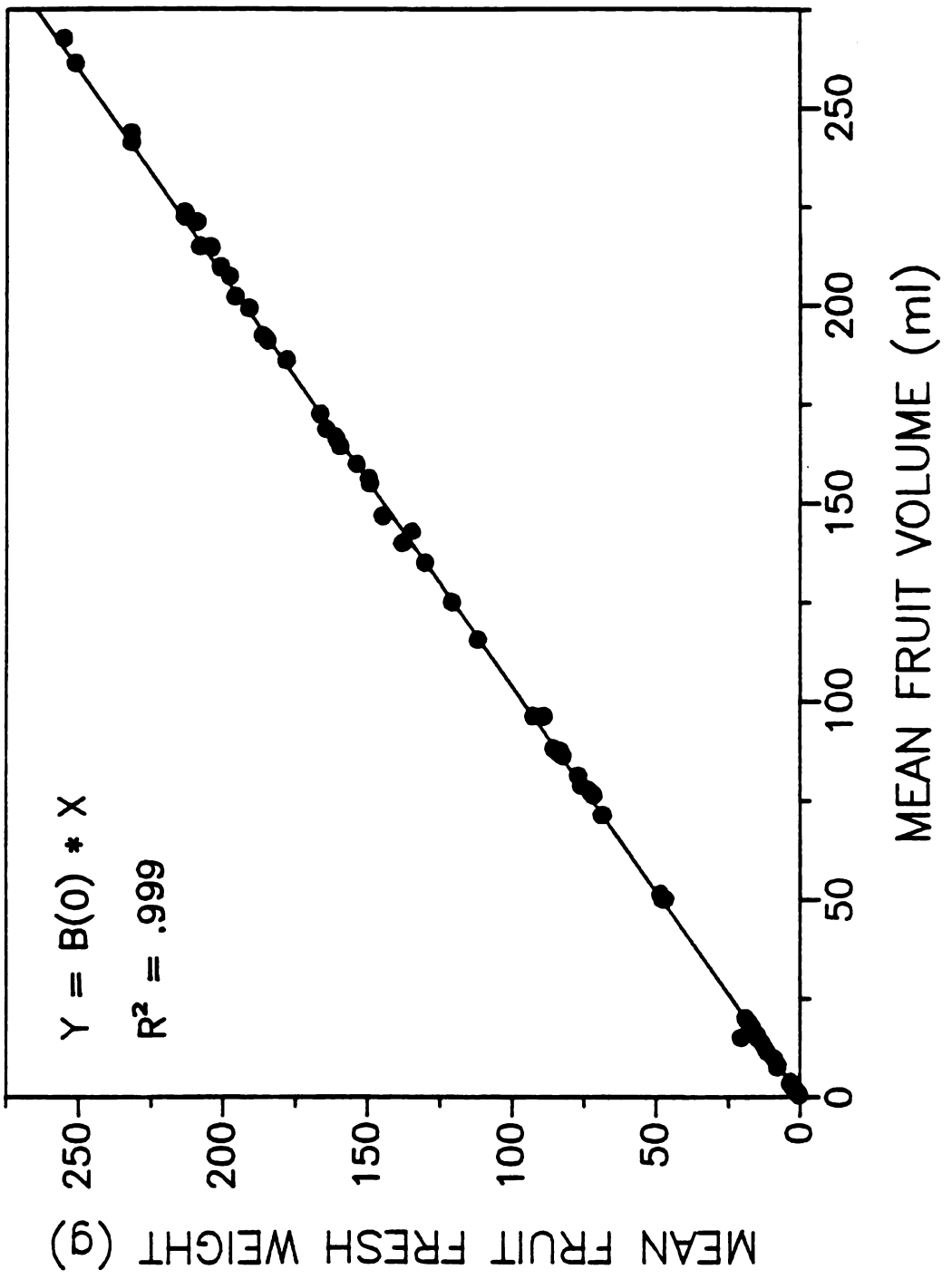

MEAN FRUIT FRESH WEIGHT (g)
MEAN FRUIT VOLUME (ml)
Y = B(0) * X
R² = .999
0
50
100
150
200
250

Figure 9.

after anthesis, respectively (Table 9). These higher fruit fresh weights were due to a one day delay in harvesting (Table 3) and to high fruit growth rates. Compared with the other plantings, fruits from the June 20 planting were intermediate in size. At 5 days after anthesis, fruits from the two June plantings had similar fresh weights, although the fruits from the first planting were more mature. Fruits from the two July plantings had low and similar fresh weights and volumes throughout the harvest period, averaging only a little more than 100 g (approximately a 2.5 cm diameter fruit) by 11 days after anthesis. Low soil moisture was a limiting factor to growth in both plantings (see Results and Discussion - Section 4).

Genetic variability generally resulted in higher individual fresh weights at the specific harvest times for Castlepik 2012 and Regal fruits than for PSX20580 and Tamor fruits (Table 9). Although the weights of Castlepik 2012 and Regal fruits were not significantly different, Regal produced the heaviest fruits throughout the harvest period. Both PSX20580 and Tamor fruits had lower growth rates, resulting in smaller fruits. It was observed that PSX20580 plants often wilted more quickly than the other pickling cucumber cultivars during periods of drought.

It is interesting that at 7 days after anthesis pickling cucumber fruit fresh weight and volume were affected by a significant treatment interaction (Table 9).

Table 9. The effect of planting date and cultivar on the mean fresh weight of pickling cucumber fruits, harvested 1 to 11 days after anthesis, 1984.

	Mean fruit fresh weight (g)					
	Days after anthesis					
Parameter	1	3	5	7	9	11
Planting date (PD)[z]						
June 7, 1984	0.701	2.913	14.168	75.46	157.80	216.83
June 20, 1984	0.411	1.905	12.747	41.63	83.05	169.81
July 5, 1984	0.386	1.672	6.426	30.246	58.31	101.18
July 19, 1984	0.425	1.281	4.358	17.091	43.44	105.10
LSD 5%[y]	0.104	0.291	3.357	15.15	17.10	28.01
1%	0.151	0.423	4.884	22.04	24.87	40.76
Cultivar (CV)[x]						
Castlepik 2012	0.503	2.033	10.355	44.88	90.55	152.31
PSX20580	0.383	1.951	9.875	37.294	76.51	135.30
Regal	0.558	2.061	10.440	49.10	98.03	161.16
Tamor	0.477	1.726	7.028	33.154	77.51	144.16
LSD 5%[y]	0.042	NS	1.552	4.21	9.89	15.95
1%	0.057	NS	2.089	5.67	13.32	NS
Interaction						
PD x CV	NS	NS	NS	**	NS	NS

[z]Each entry is an average of 4 replications x 4 CV.

[y]LSD is significant at the 5% or 1% (**) level or nonsignificant (NS).

[x]Each entry is an average of 4 replications x 4 PD.

Schapendonk and Brouwer (1984) report that maximum cucumber fruit abortion occurs at 8 days after anthesis, coinciding with a steadily decreasing amount of available assimilates (106). An assimilate shortage also inhibits the rate of pickling cucumber fruit growth. It may be hypothesized that the fruits are very sensitive to environmental and genetic variability during this critical fruit development period.

At the last four harvests, the fresh weights of the pericarp and endocarp fruit tissues were also analyzed. The pericarp tissues always weighed more than the endocarp tissues (Tables 10,11). Planting date and cultivar interacted, affecting the weights of the pericarp tissues at 5 and 7 days after anthesis and of the endocarp tissues at 7 days after anthesis. The main treatment effects of planting date and cultivar on the weights of both fruit tissues were highly significant at the later stages of fruit development.

Consistent with the total fruit fresh weight data (Table 9), fruits from the June 7 planting had the highest fresh weights for both the pericarp and endocarp fruit tissues (Tables 10,11). The tissue weights were usually intermediate for fruits from the June 20 planting and the lowest for the similar weight fruits from the July plantings. It is also not surprising that cultivar affected the specific tissue fresh weights and the total fruit fresh weights similarly over time. Castlepik 2012 and Regal fruits again tended to have similar and higher pericarp and

Table 10. The effect of planting date and cultivar on the mean fresh weight of pericarp tissue of pickling cucumber fruits, harvested 5 to 11 days after anthesis, 1984.

	Mean pericarp fresh weight (g)			
	Days after anthesis			
Parameter	5	7	9	11
Planting date (PD)[z]				
June 7, 1984	11.051	54.35	113.43	149.90
June 20, 1984	9.782	32.151	61.46	119.77
July 5, 1984	4.823	22.416	41.51	69.38
July 19, 1984	3.373	12.925	31.78	74.04
LSD 5%[y]	2.396	10.326	12.82	19.86
1%	3.487	15.024	18.66	28.89
Cultivar (CV)[x]				
Castlepik 2012	7.784	32.316	64.18	104.84
PSX20580	7.643	28.190	56.49	95.53
Regal	8.204	36.614	71.51	112.88
Tamor	5.398	24.718	56.00	99.83
LSD 5%[y]	1.152	2.996	6.87	11.33
1%	1.551	4.035	9.25	NS
Interaction				
PD x CV	*	**	NS	NS

[z]Each entry is an average of 4 replications x 4 CV.

[y]LSD is significant at the 5% (*) or 1% (**) level or nonsignificant (NS).

[x]Each entry is an average of 4 replications x 4 PD.

Table 11. The effect of planting date and cultivar on the mean fresh weight of endocarp tissue of pickling cucumber fruits, harvested 5 to 11 days after anthesis, 1984.

	Mean endocarp fresh weight (g)			
	Days after anthesis			
Parameter	5	7	9	11
Planting date (PD)[z]				
June 7, 1984	2.511	20.269	42.70	65.68
June 20, 1984	2.698	8.914	20.872	48.21
July 5, 1984	1.464	7.380	15.998	30.678
July 19, 1984	0.857	3.835	10.850	29.915
LSD 5%[y]	0.897	4.865	4.312	8.658
1%	1.305	7.078	6.274	12.596
Cultivar (CV)[x]				
Castlepik 2012	2.285	11.997	25.359	46.08
PSX20580	1.928	8.591	19.107	38.477
Regal	1.950	11.903	25.496	46.94
Tamor	1.368	7.927	20.458	42.99
LSD 5%[y]	0.378	1.259	3.045	4.914
1%	0.509	1.695	4.101	6.617
Interaction				
PD x CV	NS	**	NS	NS

[z]Each entry is an average of 4 replications x 4 CV.

[y]LSD is significant at the 5% or 1% (**) level or non-significant (NS).

[x]Each entry is an average of 4 replications x 4 PD.

endocarp tissue weights than PSX20580 and Tamor fruit tissues.

The ratios between the pericarp to endocarp fresh weights declined as the pickling cucumber fruits matured (Figures 11,12). The endocarp tissue weights increased more than the pericarp weights. Sinnott (1939) reports that cell division ceases first in the endocarp region and successively later in the outer tissues of Cucurbita pepo fruits (113). If this is also true in cucumber fruits, it would mean that greater cell expansion must occur in endocarp tissues than in pericarp tissues, in order to achieve the more rapid growth rates. This may also account for the dramatic calcium concentration decline which was observed in the endocarp fruit tissues (Table 5). There was generally an inverse correlation between the fruit tissue fresh weight and the tissue calcium concentration.

Planting date significantly affected the pericarp to endocarp fresh weight ratios of pickling cucumber fruits at 7 to 11 days after anthesis (Figure 10). The cultivar effect was highly significant throughout the sampling period (Figure 11). The treatments interacted only at 9 days after anthesis.

The highest fresh weight tissue ratio, although not significant, occurred at 5 days after anthesis for pickling cucumber fruits from the June 7 planting (Figure 10). It is very surprising that the ratio of these fruits then dramatically declined to the lowest value at 7 days after

Figure 10. The effect of planting date on the pericarp to endocarp fresh weight ratios of pickling cucumber fruits, harvested 5 to 11 days after anthesis, 1984. Each point is an average of 4 replications x 4 cultivars.

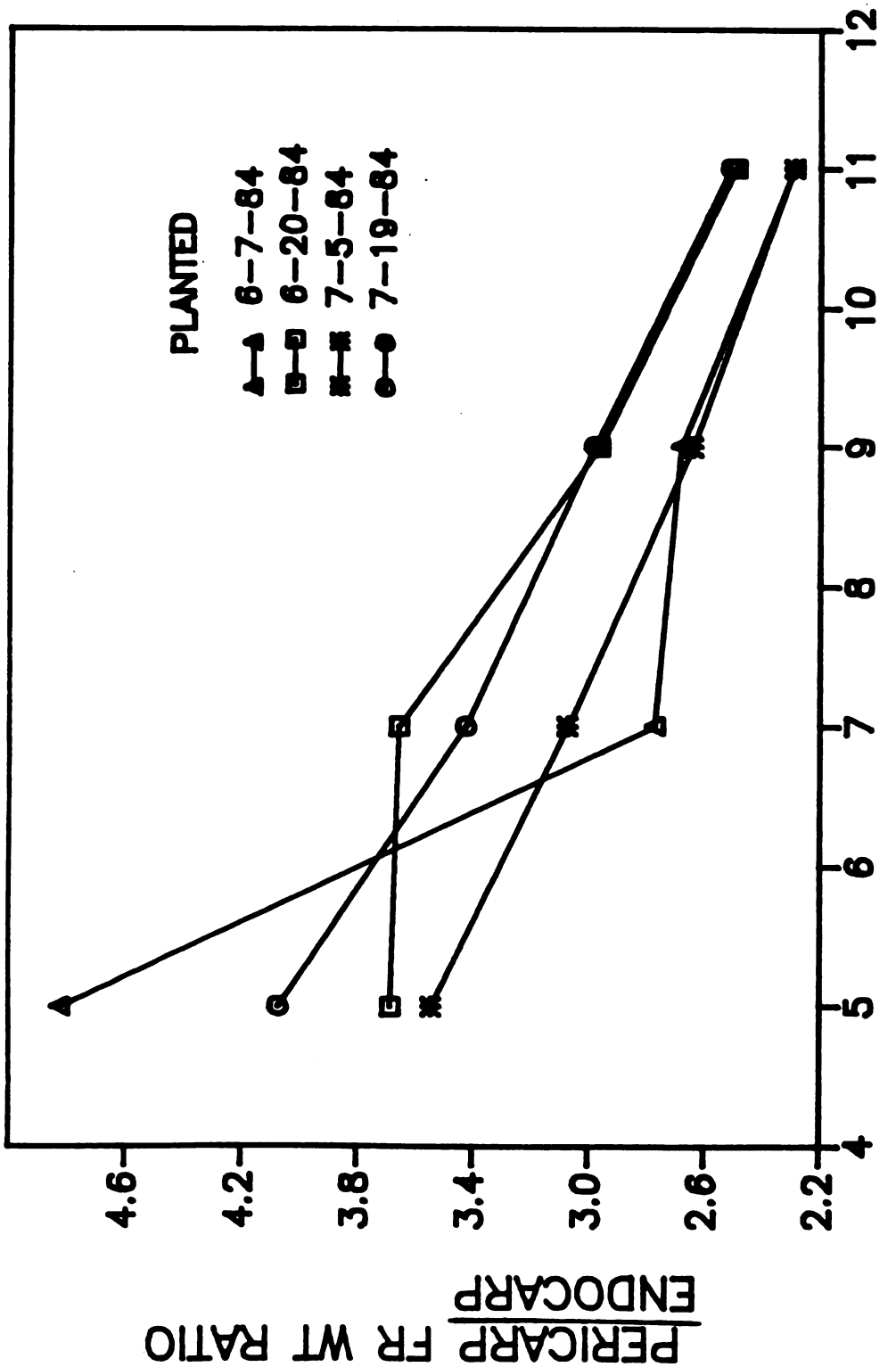

PERICARP FR WT RATIO
ENDOCARP
4.6
4.2
3.8
3.4
3.0
2.6
2.2
4
5
6
7
8
9
10
11
12
DAYS AFTER ANTHESIS
PLANTED
6-7-84
6-20-84
7-5-84
7-19-84

Figure 10.

Figure 11. The effect of cultivar on the pericarp to endocarp fresh weight ratios of pickling cucumber fruits, harvested 5 to 11 days after anthesis, 1984. Each point is an average of 4 replications x 4 planting dates.

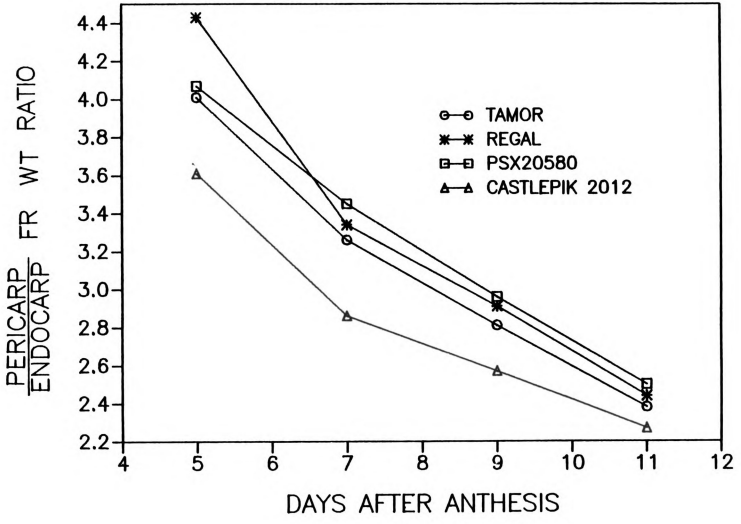

PERICARP / ENDOCARP FR WT RATIO
4.4
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
4
5
6
7
8
9
10
11
12
DAYS AFTER ANTHESIS
TAMOR
REGAL
PSX20580
CASTLEPIK 2012

Figure 11.

anthesis. Unlike the specific fruit tissue weight trends, the tissue weight ratio trends were similar for fruits from the June 7 and July 5 plantings and similar but higher for fruits from the June 20 and July 19 plantings. The ratios for fruits from the July 5 planting were consistently low throughout the sampling period. It was very dry during the early stages of fruit development in this planting. It should also be noted that the declining ratios leveled off between 5 and 7 days after anthesis in fruits from the June 20 planting and between 7 and 9 days after anthesis in the June 7 planting. It rained during both of these fruit growth periods.

Castlepik 2012 fruits, which had high fruit tissue weights, had low pericarp to endocarp weight ratios (Figure 11). While both Regal and PSX20580 fruits had significantly higher tissue weight ratios than Castlepik 2012 at 5 and 11 days after anthesis, all of the cultivars had higher ratios than Castlepik 2012 fruits at 7 days after anthesis. The greatest reduction in the pericarp to endocarp fresh weight ratios occurred between 5 and 7 days after anthesis.

It is somewhat surprising that cultivar had a greater impact than planting date on the pericarp to endocarp fresh weight ratios of pickling cucumber fruits (Figures 10,11). It may be postulated that genetic variability affects the partitioning of available water and metabolites into fruit tissues. The planting date effect was significant in later stages of fruit development. This may be due to

environmental factors, such as soil moisture availability, which limit fruit growth rates.

Fruit Growth Rate

Pickling cucumber fruits have high growth rates, with rates of fresh weight gain up to 3.3 g per hour (89,96). Cucumber fruits grow continuously, but the growth rate during the day is lower than during the night (96,129). Pharr et al. (1985) report that the dry weight loss from pickling cucumber leaves is higher at night in fruiting plants, indicating that starch is rapidly being mobilized from the leaves to the developing fruits (96).

The number of days after anthesis to reach a specific fruit fresh weight and the fruit growth rates were estimated from mean daily fruit fresh weight measurements, ignoring diurnal fluctuations in growth. In the later plantings flowering occurred earlier in time (Table 12), but the fruits enlarged more slowly (Table 13). Pistillate flower formation is enhanced by lower temperatures, short days, and decreased light intensity (107,132). In contrast, increased irradiance enhances fruit growth rates.

Planting date had a highly significant effect on the number of days after anthesis required to reach mean fruit fresh weights of 5 and 75 to 150 g (Table 13). Van de Vooren et al. (1978) also report that planting date affects earliness of pickling cucumber fruit production (132). As expected, the cultivar also affected the time required to

Table 12. The effect of planting date on the number of days from planting to anthesis for pickling cucumber fruits, 1984.

Planting date	Number of days from planting to anthesis
June 7, 1984	41
June 20, 1984	39
July 5, 1984	38
July 19, 1984	35

reach 5, 75, 100 and 125 g fruits (fresh weight basis). For 25 and 50 g fruits, there was a significant interaction between planting date and cultivar in affecting the number of days after anthesis required to reach these fresh weights. It is unknown why this interaction affected only the growth of smaller pickling cucumber fruits.

Pickling cucumber fruits from the July 19 planting grew more slowly than fruits from the June plantings, even during the earliest stages of fruit development (Table 13). Fruits from the June 20 planting required about 4 days from anthesis to enlarge to 5 g fresh weight, which was significantly less time than that required for fruits from the July 19 planting. Fruits from the July 19 planting did not average 100 g (approximately a 2.5 cm diameter fruit) by 11 days after anthesis, when the experiment was concluded. Since fruits from the July 5 planting required significantly more time to reach 100 to 150 g than fruits from the June plantings, fruits were harvested up through 16 days after anthesis. Fruits from the June plantings required only approximately 10 days to reach 150 g, compared to almost 14 days needed for fruits from the July 5 planting.

Tamor fruits, at an average weight of 5 g, grew more slowly than the other three cultivars examined (Table 13). Similarities occurred in the number of days required from anthesis to reach specific fresh weights for the more slowly growing PSX20580 and Tamor fruits as compared to Castlepik 2012 and Regal fruits. It should be noted, however, that

Table 13. The effect of planting date and cultivar on the number of days after anthesis for pickling cucumber fruits to reach specific fresh weights, 1984.

	Number of days after anthesis						
	Mean fruit fresh weight (g)						
Parameter	5	25	50	75	100	125	150
Planting date (PD)[z]							
June 7, 1984	4.39	6.54	7.40	8.07	8.70	9.38	10.28
June 20, 1984	3.97	6.08	7.56	8.62	9.40	10.03	10.40
July 5, 1984	4.72	6.87	8.69	9.99	11.15	12.43	13.88
July 19, 1984	5.20	7.78	9.17	10.18	---	---	---
LSD 5%[y]	0.57	0.32	0.40	0.51	0.62	0.53	0.58
1%	0.82	0.46	0.59	0.74	0.97	0.83	0.96
Cultivar (CV)[x]							
Castlepik 2012	4.44	6.49	7.93	8.96	9.55	10.44	11.57
PSX20580	4.50	7.07	8.51	9.51	10.09	11.05	11.92
Regal	4.49	6.56	7.86	8.86	9.28	10.10	10.97
Tamor	4.85	7.15	8.51	9.53	10.08	10.87	11.63
LSD 5%[y]	0.29	0.20	0.26	0.30	0.35	0.43	NS
1%	NS	0.27	0.35	0.40	0.48	0.58	NS
Interaction							
PD x CV	NS	**	*	NS	NS	NS	NS

[z]Avg. 4 reps x 4 CV for 5-75 g fruits, avg. 3 reps x 4 CV for 100-150 g fruits.

[y]LSD at the 5% (*) or 1% (**) level or nonsignif. (NS).

[x]Avg. 4 reps x 4 PD for 5-75 g fruits, avg. 4 reps x 3 PD for 100-125 g fruits, avg. 3 reps x 3 PD for 150 g fruits.

this statistically significant difference was usually only half a day in length, which is not meaningful by the regression method used to measure pickling cucumber fruit growth rates.

The fruit growth rates, g of fresh weight gained per day, were largely affected by planting date for fruits weighing 5 to 125 g (Figure 12). Similar trends occurred in the growth rates of fruits from the June 7 and July 5 plantings and from the June 20 and July 19 plantings. These growth rate trends are positively correlated with pickling cucumber fruit calcium accumulation rate trends (Figure 8), which will be further discussed in Section 4 of Results and Discussion. The maximum growth rates for fruits from the June 7 and July 5 plantings were attained in 100 g fruits. It is interesting to note that the maximum average growth rates for fruits from the July 5 planting were about half the maximum rates of fruits from the June 7 planting. Fruits from the June 20 and July 19 plantings never reached their maximum growth rates by 11 days after anthesis. The highest average growth rate, 50.28 g per day, was estimated for 150 g fruits from the June 20 planting.

Cultivar had a significant effect on the growth rate of 25 g fruits only (Figure 13). Castlepik 2012 and Regal fruits grew at a faster rate than 25 g fruits of PSX20580. Planting date and cultivar interacted, having a significant effect on the growth rate of 150 g fruits (Table 14). This would suggest that an environmental parameter rather than a

Figure 12. The effect of planting date on the growth rate of pickling cucumber fruits of specific fresh weights, 1984. Each point is an average of 4 replications x 4 cultivars for 5 to 125 g fruits and an average of 3 replications x 4 cultivars for 150 g fruits.

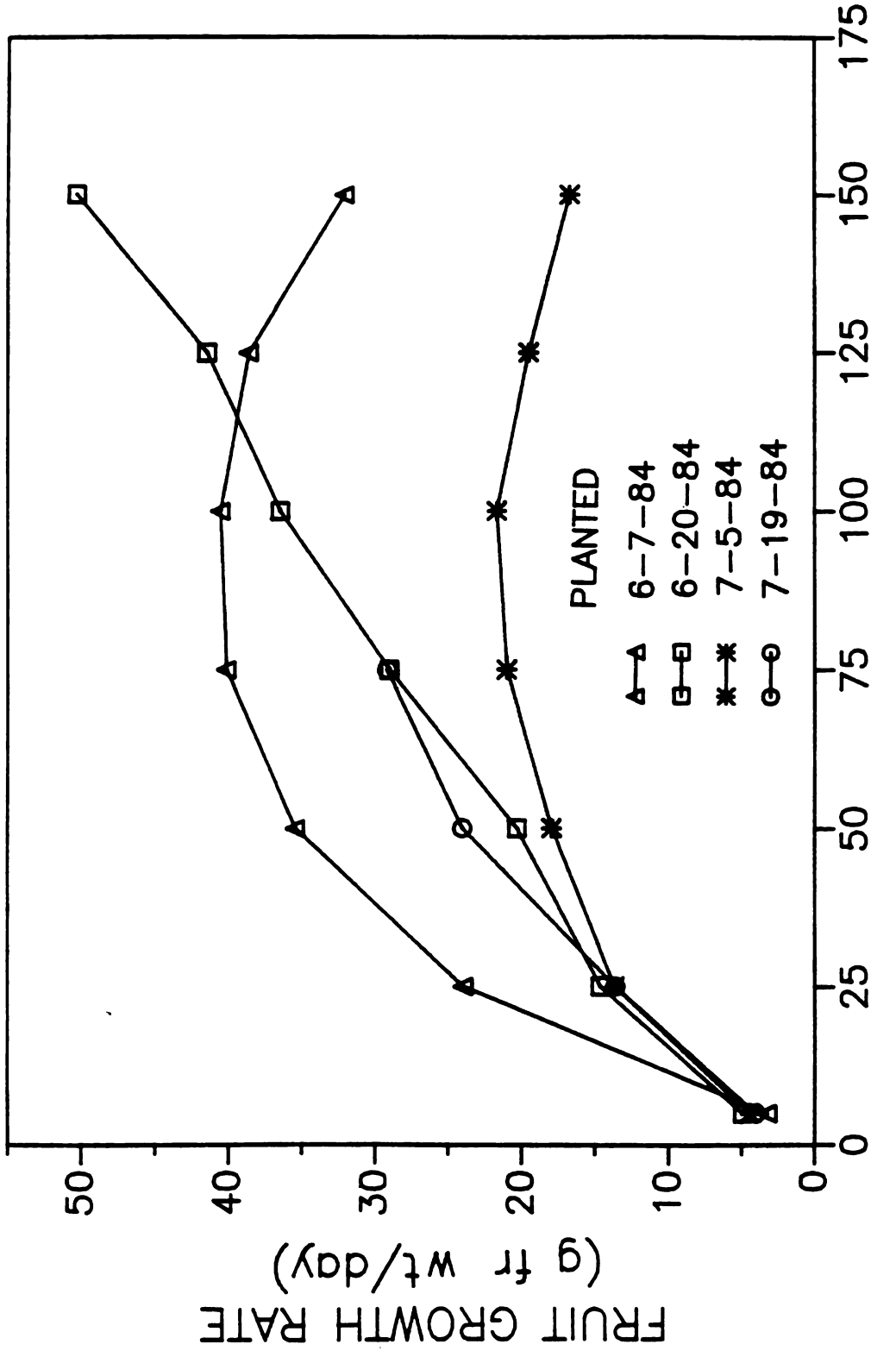

FRUIT GROWTH RATE
(g fr wt/day)
MEAN FRUIT FRESH WEIGHT (g)
PLANTED
6-7-84
6-20-84
7-5-84
7-19-84
0
10
20
30
40
50
0
25
50
75
100
125
150
175

Figure 12.

genetic trait was the major limiting growth factor throughout pickling cucumber fruit development.

The single environmental parameter that varied the most between planting dates was the amount and timing of the rainfall (see Results and Discussion - Section 4). Hughes (1978) notes that few crops suffer more than cucumbers during a drought (52). The growth rates of water-stressed plants are much lower than those of non-stressed cucumber plants (92). Larger fruits, which appear to be more efficient at fruit osmotic adjustment, are less affected by drought than the smaller pickling cucumber fruits. The larger fruits continue to enlarge by withdrawing the needed moisture from the smaller fruits on the vine. The observed significant interaction affecting the growth rate of 150 g fruits (Figure 13) may have resulted from varying cultivar efficiencies in osmotic adjustment, in response to the different moisture conditions in the four plantings (Table 14).

It is useful to look at pickling cucumber development per unit fresh weight of fruit (Figure 14). It is not surprising that the relative growth rates declined as the fruits enlarged. Cell division in the fruits of Cucurbit species may be completed by anthesis (113). After cell division ceases, all further fruit growth is due to cell expansion. Sinnott (1939) reports that the final fruit size of three Cucurbita pepo races is almost directly proportional to differences in cell size rather than to cell

Figure 13. The effect of cultivar on the growth rate of pickling cucumber fruits of specific fresh weights, 1984. Each point is an average of 4 replications x 4 planting dates for 5 to 75 g fruits, an average of 4 replications x 3 planting dates for 100 to 125 g fruits and an average of 3 replications x 3 planting dates for 150 g fruits.

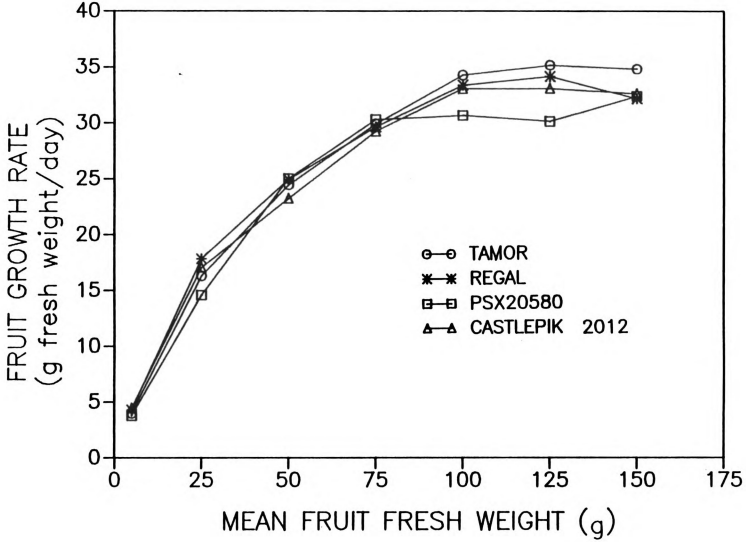

FRUIT GROWTH RATE
(g fresh weight/day)
MEAN FRUIT FRESH WEIGHT (g)
TAMOR
REGAL
PSX20580
CASTLEPIK 2012
0
5
10
15
20
25
30
35
40
0
25
50
75
100
125
150
175

Figure 13.

Table 14. The interaction of planting date and cultivar on the growth rate of 150 g pickling cucumber fruits, 1984.

	Fruit growth rate (g fr wt/day)[z]			
	Cultivar (CV)			
Planting date (PD)	Castlepik 2012	PSX20580	Regal	Tamor
June 7, 1984	25.94	28.26	35.78	38.20
June 20, 1984	59.26	53.30	43.52	45.05
July 5, 1984	12.64	15.63	17.21	21.23

Significant effects

Within PD	LSD 5%	9.70
	1%	13.46
Within CV	LSD 5%	12.14
	1%	18.38

[z]Each entry is an average of 4 replications.

number (113).

The statistical significance of the planting date and cultivar treatments on relative fruit growth rates (Figure 14) was the same as that on the pickling cucumber fruit growth rates (Figure 12). Fruits from the June 7 planting generally had the highest relative growth rates, as was observed with the growth rates during the early stages of fruit development. The relative growth rates of fruits from the July 5 planting were consistently low. This was probably due to limited moisture availability, which resulted in low cell expansion rates. Unlike the fruits from the other plantings, the relative growth rates of fruits from the June 20 planting remained almost constant for 50 to 150 g fruits. This constant relative growth rate during fruit ontogeny indicates that large numbers of fruit cells continued to expand over a long period of time.

Fruit Dry Weight

The dry weights of the pickling cucumber fruits were also measured. Pharr et al. (1985) state that the dry weight percentage of a cucumber (cv. Calypso) fruit is about 5 to 6 percent of its fresh weight throughout ontogeny (96). The fruit dry weight percentages of the pickling cucumber cultivars evaluated in this study were higher than 5 to 6 percent during early fruit development (Table 15). Both planting date and cultivar had a significant effect on the dry weight percentages of the fruits. Only at 5 days

Figure 14. The effect of planting date on the relative growth rate of pickling cucumber fruits of specific fresh weights, 1984. Each point is an average of 4 replications x 4 cultivars for 5 to 125 g fruits and an average of 3 replications x 4 cultivars for 150 g fruits.

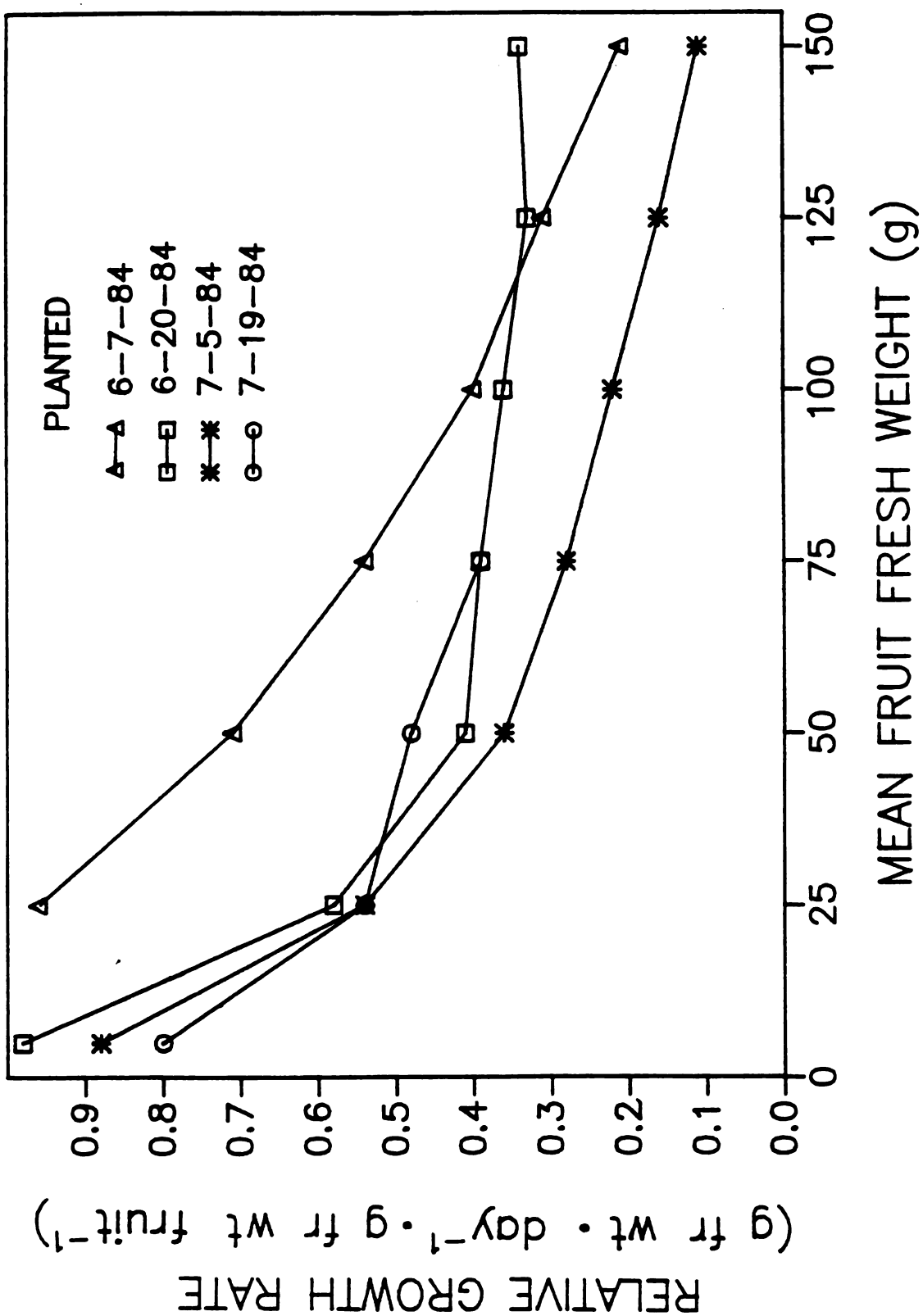

PLANTED
6-7-84
6-20-84
7-5-84
7-19-84
RELATIVE GROWTH RATE
(g fr wt • day⁻¹ • g fr wt fruit⁻¹)
MEAN FRUIT FRESH WEIGHT (g)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0
25
50
75
100
125
150

Figure 14.

after anthesis was the cultivar effect nonsignificant.

The ontogenetic trends in the dry weight percentages of fruits from the June 7 and July 5 plantings were similar (Table 15). During the early stages of fruit development, fruit percent dry weight was high, approximately 8.6 to 8.9 percent but declined to approximately 5.5 to 6.0 percent as the fruit grew and matured. The observed changes in the dry weight percentages for fruits from the June 20 and July 19 plantings were significantly greater, declining during fruit development from greater than 9 percent to less than 5 percent. It should be noted that these differences between the planting dates can be attributed in part to differences in fruit size at each of the specific harvest times.

Pickling cucumber fruit growth rates were similar for the June 7 and July 5 plantings as compared to the June 20 and July 19 plantings (Figure 12). Pickling cucumber fruit growth rates are inversely correlated with fruit dry weight percentages. Fruits from the June 7 and July 5 plantings had higher dry weight percentages (Table 15) when the fruit growth rates plateaued in the later stages of development. The linear increases in growth rates of fruits from the June 20 and July 19 plantings coincided with lower fruit dry weight percentages.

Differences in the dry weight percentages due to genetic variability were more consistent throughout fruit ontogeny than those due to planting date effect (Table 15). Although not always significant, Castlepik 2012 fruits had

Table 15. The effect of planting date and cultivar on the dry weight percentages of pickling cucumber fruits, harvested 1 to 11 days after anthesis, 1984.

	Dry weight percentage of fruit					
	Days after anthesis					
Parameter	1	3	5	7	9	11
Planting date (PD)[z]						
June 7, 1984	8.92	6.94	6.50	5.49	5.17	6.02
June 20, 1984	10.18	9.64	7.22	4.90	4.65	4.54
July 5, 1984	8.62	6.59	6.23	5.76	5.83	5.46
July 19, 1984	9.35	8.19	7.60	6.04	5.95	4.93
LSD 5%[y]	0.76	0.59	0.44	0.41	0.60	0.47
1%	1.11	0.86	0.63	0.59	0.87	0.68
Cultivar (CV)[x]						
Castlepik 2012	8.88	7.50	6.63	5.44	5.28	5.10
PSX20580	9.55	7.80	6.93	5.52	5.51	5.30
Regal	9.35	7.94	6.96	5.47	5.31	5.14
Tamor	9.28	8.12	7.03	5.77	5.50	5.41
LSD 5%[y]	0.35	0.37	NS	0.12	0.18	0.16
1%	0.47	NS	NS	0.16	NS	0.22
Interaction						
PD x CV	NS	NS	NS	NS	NS	NS

[z]Each entry is an average of 4 replications x 4 CV.

[y]LSD is significant at the 5% or 1% level or nonsignificant (NS).

[x]Each entry is an average of 4 replications x 4 PD.

the lowest dry weight percentages, ranging between 5.10 and 8.88 percent. The percentages of PSX20580 and Tamor fruits were similar at all harvests, except at 7 days after anthesis when Tamor fruits had the highest dry weight percentage, 5.77, of the cultivars. Regal fruits had dry weight percentages of 9.35 and 7.94, similar to those of PSX20580 and Tamor fruits, at 1 and 3 days after anthesis, respectively. Due to high fruit growth rates (Figure 12), however, the dry weight percentages of Regal fruits declined to similar percentages as those of Castlepik 2012 fruits from the last three harvests.

Fruit Length and Diameter

The length and diameter of each fruit were measured in the morning following harvest. Tukey (1964), using a linear displacement voltage transducer, discovered that pickling cucumber (cv. Ohio MR 200) fruits enlarge in diameter during both daylight and night hours if the soil moisture is adequate (129). Cultivar and planting date significantly affected both fruit length and diameter (Tables 16,17), as expected. The genotypic characteristics of fruit length and diameter were very stable for the pickling cucumber cultivars evaluated. Regal fruits were the longest and Castlepik 2012 fruits generally had the largest diameters.

Fruits from the June 7 planting tended to be the longest and thickest, while fruits from the last planting, July 19, were generally the smallest (Tables 16,17). Both

the length and the diameter of the pickling cucumber fruits were less from plantings later in the season. As mentioned previously, decreasing irradiance later in the season decreases the rate of pickling cucumber fruit growth. Fruit growth rates of water-stressed pickling cucumber plants are much less than those of non-stressed plants (92). This is consistent with the observed lower lengths and diameters of fruits from the July plantings, during which the percent soil moistures were generally low (see Results and Discussion - Section 4).

The fruit length to diameter (L/D) ratios of the pickling cucumber fruits generally declined as the fruits matured (Figures 15,16). Both cultivar and planting date had a highly significant effect on the L/D ratios. Only at 7 days after anthesis did the two main treatments interact, affecting the fruit L/D ratios. As previously mentioned, approximately 8 days after anthesis seems to be a critical period in pickling cucumber fruit development, which may explain this interaction.

Consistent with the statistical results of fruit lengths and diameters, Castlepik 2012 fruits had the lowest L/D ratios, although not always significant (Figure 15). Regal fruits had the highest L/D ratios. The L/D ratios of PSX20580 and Tamor fruits were similar throughout the harvest period.

Fruits from the June 7 planting had the highest average L/D ratio of 3.68 at 3 days after anthesis

Table 16. The effect of planting date and cultivar on the mean length of pickling cucumber fruits, harvested 3 to 11 days after anthesis, 1984.

	Mean fruit length (cm)				
	Days after anthesis				
Parameter	3	5	7	9	11
Planting date (PD)[z]					
June 7, 1984	3.5	5.9	9.9	12.1	13.0
June 20, 1984	3.0	5.5	8.5	10.5	12.8
July 5, 1984	2.9	4.6	7.6	9.3	10.9
July 19, 1984	2.5	3.8	6.0	8.0	10.6
LSD 5%[y]	0.2	0.5	0.8	0.7	0.5
1%	0.3	0.8	1.1	1.0	0.7
Cultivar (CV)[x]					
Castlepik 2012	3.0	4.9	8.0	9.8	11.4
PSX20580	2.9	4.9	7.6	9.4	11.2
Regal	3.2	5.5	9.1	11.1	13.0
Tamor	2.8	4.5	7.4	9.6	11.6
LSD 5%[y]	0.2	0.3	0.3	0.4	0.4
1%	0.2	0.4	0.4	0.5	0.5
Interaction					
PD x CV	NS	NS	NS	NS	NS

[z]Each entry is an average of 4 replications x 4 CV.

[y]LSD is significant at the 5% or 1% level or nonsignificant (NS).

[x]Each entry is an average of 4 replications x 4 PD.

Table 17. The effect of planting date and cultivar on the mean diameter of pickling cucumber fruits, harvested 3 to 11 days after anthesis, 1984.

	Mean fruit diameter (cm)				
	Days after anthesis				
Parameter	3	5	7	9	11
Planting date (PD)[z]					
June 7, 1984	1.0	1.7	3.4	4.5	5.1
June 20, 1984	0.9	1.7	2.6	3.4	4.5
July 5, 1984	0.9	1.4	2.4	3.0	3.7
July 19, 1984	0.8	1.2	1.9	2.6	3.8
LSD 5%[y]	0.1	0.2	0.3	0.2	0.3
1%	0.1	0.3	0.4	0.3	0.5
Cultivar (CV)[x]					
Castlepik 2012	1.0	1.6	2.7	3.5	4.4
PSX20580	0.9	1.5	2.5	3.3	4.2
Regal	0.9	1.5	2.6	3.5	4.2
Tamor	0.9	1.3	2.4	3.2	4.2
LSD 5%[y]	0.0	0.1	0.1	0.2	0.2
1%	0.1	0.1	0.2	0.2	NS
Interaction					
PD x CV	NS	NS	NS	NS	NS

[z]Each entry is an average of 4 replications x 4 CV.

[y]LSD is significant at the 5% or 1% level or nonsignificant (NS).

[x]Each entry is an average of 4 replications x 4 PD.

(Figure 16). By 11 days after anthesis these fruits had lower L/D ratios than those of fruits from the other plantings. It is surprising that the L/D ratio trends of pickling cucumber fruits from the first planting are so different from the ratio trends of the other plantings. Fruits from the later plantings had similar L/D ratios throughout ontogeny. Since the growth rates of fruits from the June 20 and July 19 plantings were similar (Figure 12), it was expected that the L/D ratios of fruits from these plantings would be similar. It was not expected that fruits from the July 5 planting, which had much lower growth rates, would have similar L/D ratios. It should be noted that the data were not normalized according to fruit size, which may have affected the L/D ratio results.

Results generated by other researchers support the hypothesis that conditions which are conducive to rapid fruit growth increase pickling cucumber fruit L/D ratios. O'Sullivan (1980) reports that both irrigation and nitrogen fertilizer increase L/D ratios (93). In contrast, lower temperatures during fruit development increase pickling cucumber L/D ratios, due to slower fruit growth rates (115). Drought (93) and soil compaction (115) reduce pickling cucumber fruit L/D ratios. L/D ratios are decreased when the plant population is higher or lower than optimum (93). At high plant populations, neighboring plants compete for limited environmental resources, while at low plant populations the greater number of fruits

Figure 15. The effect of cultivar on the length to diameter ratios of pickling cucumber fruits, harvested 3 to 11 days after anthesis, 1984. Each point is an average of 4 replications x 4 planting dates.

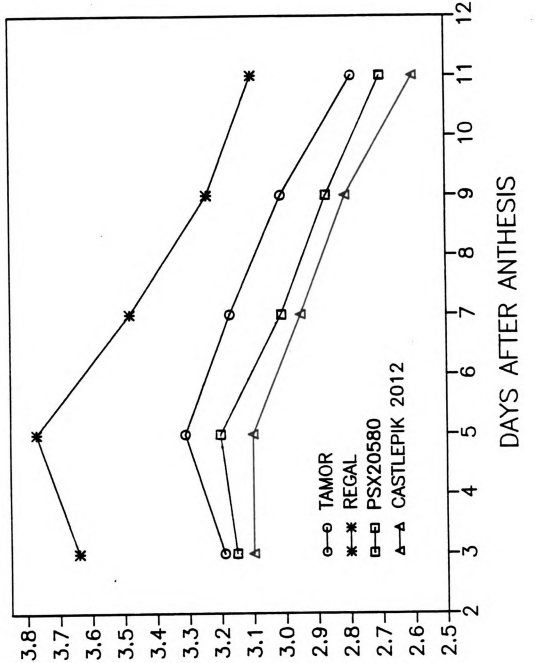

MEAN FRUIT LENGTH / DIAMETER RATIO
3.8
3.7
3.6
3.5
3.4
3.3
3.2
3.1
3.0
2.9
2.8
2.7
2.6
2.5
2
3
4
5
6
7
8
9
10
11
12
DAYS AFTER ANTHESIS
TAMOR
REGAL
PSX20580
CASTLEPIK 2012

Figure 15.

Figure 16. The effect of planting date on the length to diameter ratios of pickling cucumber fruits, harvested 3 to 13 days after anthesis, 1984. Each point is an average of 4 replications x 4 cultivars.

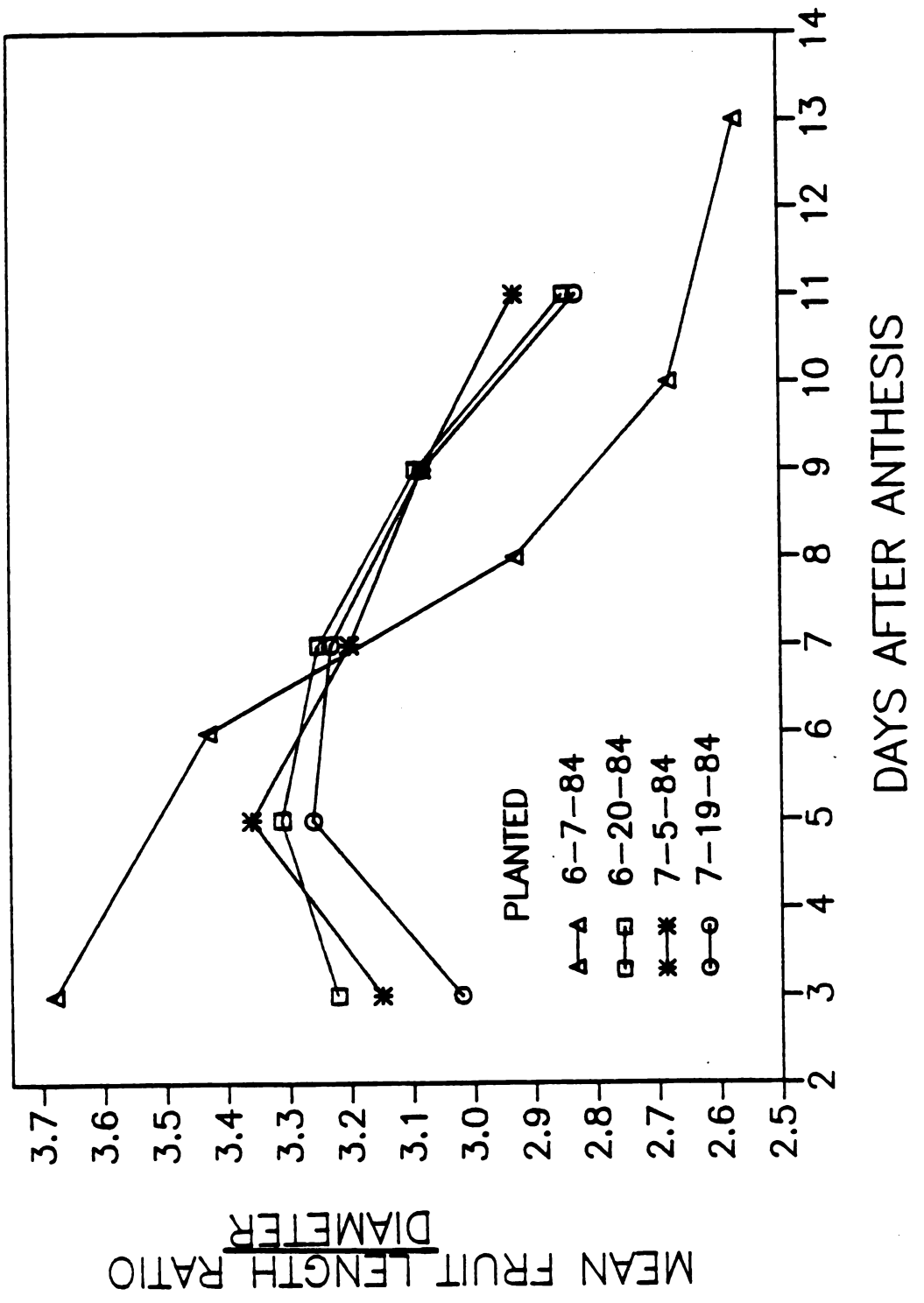

MEAN FRUIT LENGTH RATIO
DIAMETER
3.7
3.6
3.5
3.4
3.3
3.2
3.1
3.0
2.9
2.8
2.7
2.6
2.5
2
3
4
5
6
7
8
9
10
11
12
13
14
DAYS AFTER ANTHESIS
PLANTED
6-7-84
6-20-84
7-5-84
7-19-84

Figure 16.

per plant may result in within plant competition for available nutrients and water.

RESULTS AND DISCUSSION - SECTION 3

Calcium and Growth Analyses of Leaf Tissues

Leaf Calcium Concentration

A pickling cucumber plant is classified as an obligate calcicole because it must grow on calcareous soils (53). The vegetative tissues continue to accumulate calcium ions throughout pickling cucumber plant growth (11,54). This deposition of calcium in leaf tissues may be an adaptive mechanism, which allows pickling cucumbers to grow on highly calcareous soils. The calcium regulatory mechanism appears to restrict calcium remobilization. The older leaves often have a high calcium content, which is not required physiologically (53,54,78). Since calcium is relatively immobile in the phloem, little if any calcium will be exported from the leaf tissues once deposited. Calcium remobilization out of mature leaves is also limited by the increasing lignification of the vascular tissues. Lignin has a high affinity for calcium, providing an expanding reservoir for the accumulation of calcium ions (111).

In this experiment the calcium status of the most recently expanded pickling cucumber leaves was determined (Table 18). These leaves were expanding during the same

time period as the fruits were enlarging. Uneven calcium partitioning between fruit and leaf tissues occurred in the pickling cucumber plant. The calcium concentration of the leaf lamina tissue rose to higher than 3 percent and the fruit endocarp tissue concentration (Table 7) declined to lower than 0.20 percent (dry weight basis).

It may be hypothesized that more calcium is partitioned into leaf tissues than into maturing fruit tissues due to higher leaf transpiration rates and more efficient short distance calcium transport in leaf lamina. Picken (1984) postulates that veins develop in cucumber leaves to optimize short distance transfer of water and metabolites (97). The average maximum number of cells between leaf mesophyll cells and vascular tissues is maintained at approximately 7 throughout plant ontogeny.

The calcium concentrations of the laminar tissue were significantly affected by the date of planting only, while the petiole calcium concentrations were not altered by the planting date or by cultivar (Table 18). The highest average laminar calcium concentration of 3.10 percent (dry weight) was measured in leaves from the June 7 planting. Significantly lower calcium levels were observed in leaves from the June 20 and July 19 plantings. The lowest lamina calcium concentrations occurred in leaves from the July 5 planting.

The calcium concentration of the leaf lamina tissue was always higher than that of the petiole tissue (Table 18).

Table 18. The effect of planting date and cultivar on the calcium concentration and content of pickling cucumber leaf tissues[z], 1984.

	Ca concentration (% dry weight)		Ca content (mg Ca/tissue)	
Parameter	Lamina	Petiole	Lamina	Petiole
Planting date (PD)[y]				
June 7, 1984	3.10	1.84	14.25	1.09
June 20, 1984	2.36	1.45	7.96	0.54
July 5, 1984	1.85	1.54	4.41	0.33
July 19, 1984	2.42	1.76	9.05	0.62
LSD 5%[x]	0.31	NS	2.30	0.19
1%	0.45	NS	3.35	0.28
Cultivar (CV)[w]				
Castlepik 2012	2.56	1.75	9.11	0.60
PSX20580	2.42	1.66	8.87	0.68
Regal	2.30	1.60	8.39	0.64
Tamor	2.46	1.58	9.30	0.65
LSD 5%[x]	NS	NS	NS	NS
Interaction				
PD x CV	NS	NS	NS	NS

[z]The most recent fully expanded leaf.

[y]Each entry is an average of 4 replications x 4 CV.

[x]LSD is significant at the 5% or 1% level or nonsignificant (NS).

[w]Each entry is an average of 4 replications x 4 PD.

High metabolic activity during the period of leaf expansion promotes calcium movement into and accumulation in the leaf laminar tissues (111). This may explain the small differences between the leaf lamina and petiole calcium concentrations observed in the third planting when the overall calcium concentrations in the plant were low, 1.85 and 1.54 percent calcium on a dry weight basis, respectively.

Iwahashi et al. (1982) propose that the mechanism of calcium accumulation in cucumber leaf tissues is very different from that in stem and petiole tissues (54). Petioles and stems accumulated calcium steadily from 5 to 30 days after germination, while the rate of leaf calcium accumulation declined once the leaf tissues reached their maximum fresh weights. It is ironic that most leaf tissue elemental analyses, which are conducted to determine the adequacy of the calcium levels in the plant, only sample the petiole tissue rather than also evaluating the lamina tissue. The current results suggest that the calcium concentration of the pickling cucumber petiole tissue is not as sensitive to changes in the environment as the leaf lamina tissue. It may, therefore, be more accurate to sample leaf lamina rather than petiole tissue for non-mobile nutrients like calcium.

It should be noted that leaf tissue is not a good indicator of mature fruit tissue calcium concentrations (111). At 1 day after anthesis the fruit calcium

concentrations and the petiole concentrations were similar (Table 18). As the fruits enlarged, the calcium concentrations of the fruits (Table 4) were affected differently by the environment than were the leaf calcium concentrations. Although the leaves from the June 7 planting had the highest calcium concentrations, the fruits generally had the lowest concentrations among the four plantings. This would suggest that factors other than calcium uptake by the plant are contributing to variations in calcium levels within a plant.

Leaf Calcium Content

Planting date had a similar effect on the calcium concentrations and contents of the leaf lamina tissues (Table 18). The calcium contents of the leaf lamina from the June 7 planting were the highest, intermediate from the June 20 and July 19 plantings, and lowest from the July 5 planting. Although the petiole calcium concentration differences were nonsignificant for the four plantings, planting date significantly affected the petiole calcium contents. Leaves from the June 7 planting also had the highest petiole calcium contents. Petioles from the July 19 planting accumulated more calcium than leaf petioles from the July 5 planting. The calcium contents of the leaf lamina and petiole tissues from the July 5 planting were three times lower than the leaf tissue contents from the first planting. These content differences were attributed

largely to differences in tissue weights.

Leaf Dry Weight

Cultivar affected the dry weights of the petiole tissues (Table 19). It is not surprising that Castlepik 2012, a determinate pickling cucumber cultivar with shortened internodes, had the lowest petiole dry weights. The dry weights of both the leaf lamina and petiole tissues were affected by the time of planting. The trends in pickling cucumber leaf weight due to planting date reflected those seen for the leaf calcium status. Leaf lamina dry weights were highest from the June 7 planting and lowest from the July 5 planting. Similarly, petiole dry weights from the July 5 planting were significantly lower than those from the other plantings. Due to these weight differences, it was not unexpected that the calcium contents would be higher for the larger leaves from the June 7 planting than those from the July 5 planting.

The June 7 planting had the longest vegetative period (Table 12), probably due to the long day photoperiod. This planting also received a substantial amount of rain 10 days before anthesis, when the examined leaf tissues would have been expanding. The low leaf tissue dry weights from the July 5 planting were unexpected (Table 19). Among the four plantings, the July 5 planting had the greatest amount of rainfall 10 days before anthesis, which should have stimulated vegetative growth. Due to the high air

Table 19. The effect of planting date and cultivar on the dry weights of pickling cucumber leaf tissues, 1984.

	Dry weight of 20 leaves (g)[z]	
Parameter	Lamina	Petiole
Planting date (PD)[y]		
June 7, 1984	9.192	1.194
June 20, 1984	6.733	0.727
July 5, 1984	4.669	0.412
July 19, 1984	7.401	0.699
LSD 5%[x]	1.118	0.080
1%	1.626	0.117
Cultivar (CV)[w]		
Castlepik 2012	6.757	0.660
PSX20580	6.980	0.796
Regal	6.960	0.767
Tamor	7.299	0.810
LSD 5%[x]	NS	0.060
1%	NS	0.080
Interaction		
PD x CV	NS	NS

[z]The 20 most recent fully expanded leaves.

[y]Each entry is an average of 4 replications x 4 CV.

[x]LSD is significant at the 5% or 1% level or nonsignificant (NS).

[w]Each entry is an average of 4 replications x 4 PD.

temperatures during leaf expansion, however, much of the available water was probably depleted by evaporation from the soil surface.

It is also surprising that the June 20 and July 19 plantings had similar leaf tissue dry weights (Table 19). The soil moisture level was lower in the July 19 planting during vegetative growth than in the June 20 planting. It was observed that the pickling cucumber plants from the July 19 planting produced fewer leaves than in the earlier plantings. This decreased vegetative growth was probably a response to both the lower soil moisture and to the short day photoperiod. A more complete understanding of the environmental effect on pickling cucumber leaf growth would have been gained by weighing the entire plant. It could have then been determined if leaf number and/or weight were/was affected by planting date.

RESULTS AND DISCUSSION - SECTION 4

Environmental Impact on Rates of Fruit Calcium Accumulation and Growth

Calcium Accumulation Rate Relative to Fruit Growth Rate

The effect of the transition from a vegetative to a reproductive mode of growth in annual species appears to have a significant impact on calcium uptake capabilities of the plants (22). For cucumbers the pattern of water and calcium uptake follows very closely the pattern of root growth (104,122). Pickling cucumber fruit growth is highly competitive with root growth (96). Since root growth often stops after the onset of fruiting (106), calcium uptake may be severely reduced.

High growth rates usually result in lower mineral concentrations of the whole plant and can cause a significant decline in the calcium concentration of the fruits (4,56,95,125). Steady fruit growth rates are preferable to high fruit growth rates in maintaining adequate calcium levels in fruits (139). This is especially true during the early fruit ontogenetic stages. Tromp (1979) noted a negative correlation between the calcium concentrations of apple fruits of 2 g dry weight

and the rate of fruit growth, while the calcium concentrations of more mature apple fruits of 20 g dry weight were positively correlated to the rate of fruit growth (127).

Comparing the graphs of calcium accumulation rates (Figure 7) with those of fruit growth rates (Figure 12), similarities can be seen in these trends for pickling cucumber fruits. Rates of calcium accumulation and growth did not differ as significantly between the cultivars as might have been anticipated. Environmental factors had a significant and similar impact on the rates of calcium import and growth. The trends in calcium accumulation rates and in fruit growth rates were similar for fruits from the June 7 and July 5 plantings and from the June 20 and July 19 plantings. The average maximum calcium accumulation rate peaked in 50 g fruits from the first planting, while in the July 5 planting the maximum rate occurred in 75 g fruits. Growth rates declined after fruits averaged 100 g fresh weight in the June 7 and July 5 plantings. The fruits from the June 20 and July 19 plantings exhibited a continual rise in rates of calcium accumulation and growth throughout the harvest period.

These trend similarities suggest that a correlation exists between the rates of pickling cucumber fruit growth and calcium accumulation (Figures 7,12). This is depicted in the scatter plots of fruit growth rates versus calcium accumulation rates for 75 and 150 g fruits from the four

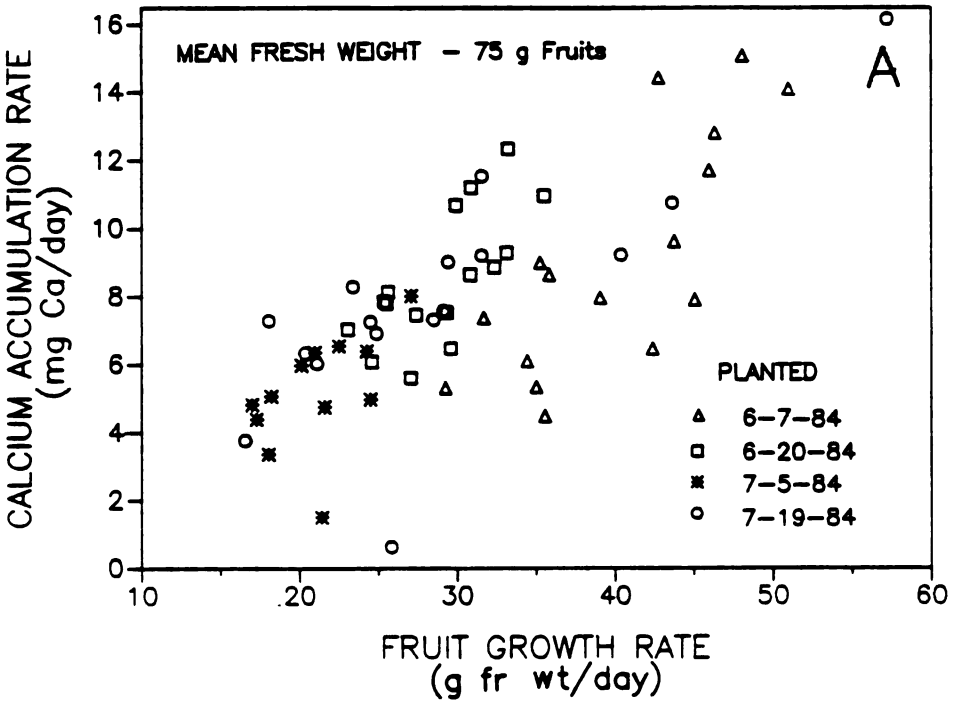
plantings (Figure 17). Even though the environment during fruit development was different for these plantings and affected both growth and calcium import (Figures 7,12), the rates of fruit growth relative to the rates of calcium accumulation were similar. The points form a nearly linear band at a 45° angle. At both 75 and 150 g, fruits from the July 5 planting maintained low calcium import rates relative to growth rates, compared with the rates of fruits from the other plantings.

It is important to note that under certain environmental conditions a significantly higher rate of calcium accumulation was achieved for a given fruit growth rate. This relationship can be seen by comparing the relatively high calcium accumulation rates of the June 20 planting with the lower rates of the June 7 planting (Figure 17). Although environmental conditions could not be controlled in the field, it is interesting to speculate which environmental parameters differentially affected the calcium accumulation rates relative to the fruit growth rates of pickling cucumbers.

Environmental Conditions During the Growth Periods

Rainfall, pan evaporation, air and soil temperatures were measured daily at the Horticulture Research Center by the Michigan State Weather Service (136). The greatest amount of rain fell during the growth periods of pickling cucumbers planted June 20 and July 5 (Table 20). Pickling

Figure 17 (A-B). The effect of planting date on the fruit growth rates versus calcium accumulation rates for (A)75 g and (B)150 g pickling cucumber fruits, 1984. The rates for each planting date were estimated from regression curves of the fruit calcium concentration and fresh weight of 4 cultivars, each replicated 4 times. The July 5 planting had 3 replications.


MEAN FRESH WEIGHT – 75 g Fruits
A
CALCIUM ACCUMULATION RATE
(mg Ca/day)
FRUIT GROWTH RATE
(g fr wt/day)
PLANTED
6-7-84
6-20-84
7-5-84
7-19-84
0
2
4
6
8
10
12
14
16
10
20
30
40
50
60

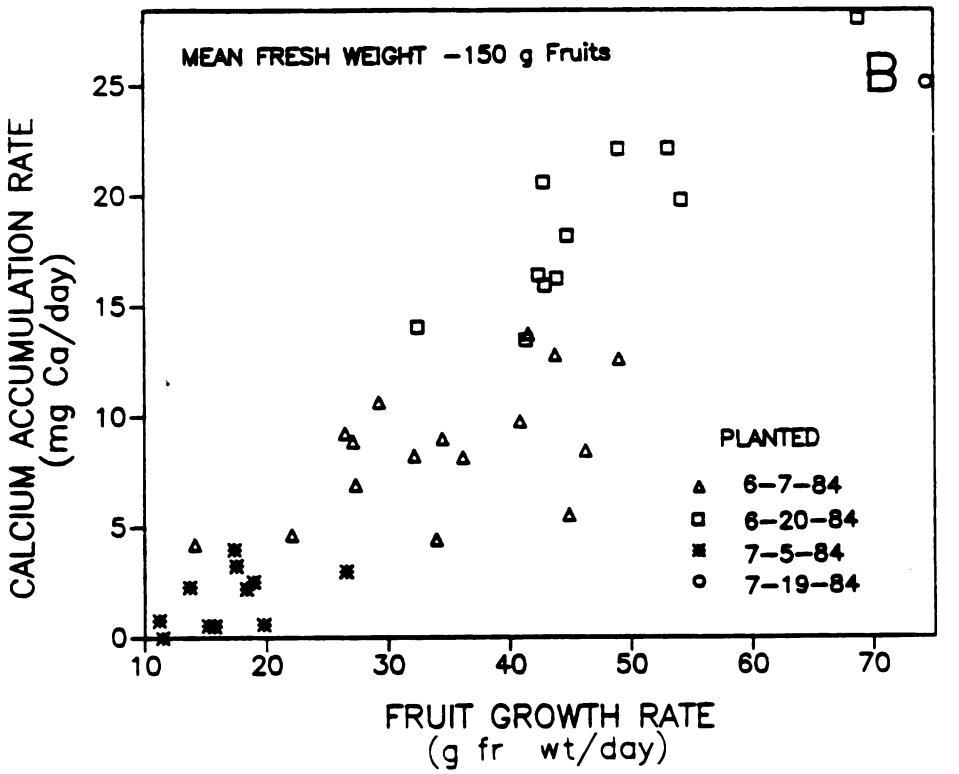

MEAN FRESH WEIGHT –150 g Fruits
B
CALCIUM ACCUMULATION RATE
(mg Ca/day)
FRUIT GROWTH RATE
(g fr wt/day)
PLANTED
6-7-84
6-20-84
7-5-84
7-19-84
0
5
10
15
20
25
10
20
30
40
50
60
70

Figure 17.

Table 20. Cumulative rainfall and pan evaporation during pickling cucumber vegetative and fruit development periods, 1984.

	Cumulative water (cm)[z]			
	Planting date			
	June 7	June 20	July 5	July 20
Rainfall plus irrigation				
Vegetative period	7.46	8.02	11.16	6.68
10 days before anthesis	3.73	0.71	5.97	0.00
Fruiting period	0.71	5.10	0.00	0.91
Growth period total	8.17	13.12	11.16	7.59
Pan evaporation				
Vegetative period				
Total	29.18	26.60	23.75	20.70
Daily mean	0.71	0.68	0.62	0.59
10 days before anthesis				
Total	6.88	5.66	5.61	5.89
Daily mean	0.68	0.56	0.56	0.58
Fruiting period				
Total	7.77	6.60	9.63	6.14
Daily mean	0.60	0.60	0.60	0.56
Growth period				
Total	37.81	33.20	33.38	26.84
Daily mean	0.70	0.66	0.62	0.58

[z]Data measured by the Michigan State University Weather Service at the Horticulture Research Center.

cucumbers planted June 7 and July 19 received similar but lower amounts of rainfall. For the June 7 and July 5 plantings, the majority of the rain fell during the vegetative growth period, with small quantities or no rainfall during fruiting, respectively. For the June 20 planting the amount of rain was more equally divided, with 8 cm of rain during the 39-day vegetative period and 5 cm during the 11-day fruiting period. The least amount of rain, less than 1 cm, fell during the fruiting period of the July 19 planting.

Pan evaporation averages were the highest for the growth period of the June 7 planting and declined successively at later planting times (Table 20). The average daily pan evaporation amount during fruiting was 0.60 cm for all plantings except the July 19 planting, which had only a slightly lower average of 0.56 cm. These averages do not reflect the daily fluctuations in the amount of evaporation, due to variations in temperature and relative humidity.

The water gain due to rainfall and the loss due to transpiration from the plant and evaporation from the soil surface resulted in varying soil moisture levels within the main plots (Table 21). Differences in soil moisture percentages between replications were very notable. Replication 1 consistently had the lowest percent soil moisture, while replication 4 had the highest percentages. The percent soil moisture was very high on August 11 due to

Table 21. Gravimetric soil water percentage within the pickling cucumber main plots, 1984.

		% Soil moisture (g/g)[z]			
		Replication			
Planting date	Sampling date	1	2	3	4
June 20	August 2	7.88	8.86	9.40	10.34
July 5	August 11	12.31	13.44	19.77	20.87
	August 19	6.99	8.71	14.07	15.95
July 19	August 26	7.49	9.42	9.10	18.82
	September 2	5.32	7.33	6.94	18.12

[z]Average of 4 soil samples at a 7-20 cm depth.

heavy rainfall on the preceeding days. There was a large decline in the soil moisture percentages from the August 11 to the August 19 sampling in the July 5 main plot. The lowest soil moisture percentages were measured in replications 1, 2 and 3 of the July 19 main plot.

The average air and bare soil temperatures differed by only 4^{o} C during both vegetative and fruit growth periods for all planting dates (136). The average bare soil temperatures at a 10 cm depth were higher than the average air temperatures. There were large fluctuations in the daily minimum and maximum air temperatures during the growth periods of all plantings (Figure 18). The differences between the minimum and maximum daily air temperatures were greater than for soil temperatures (Figure 19).

It is interesting to note how the air temperatures varied within the four fruiting periods (Figure 18). For the June 7 planting the minimum temperatures were approximately 8^{o} C at the beginning and end of fruiting and rose to 32^{o} C in the middle of the harvest period. For the June 20 planting the minimum and maximum daily air temperatures continued to rise throughout the harvest period. During the fruiting period of the July 5 planting there were large differences between the minimum and maximum daily air temperatures. The change in the maximum temperatures was not as great as the declining minimum air

Figure 18. Maximum and minimum daily air temperatures during the pickling cucumber growth period of the 4 planting dates, 1984. (Data measured by the Michigan State University Weather Service at the Horticulture Research Center.)

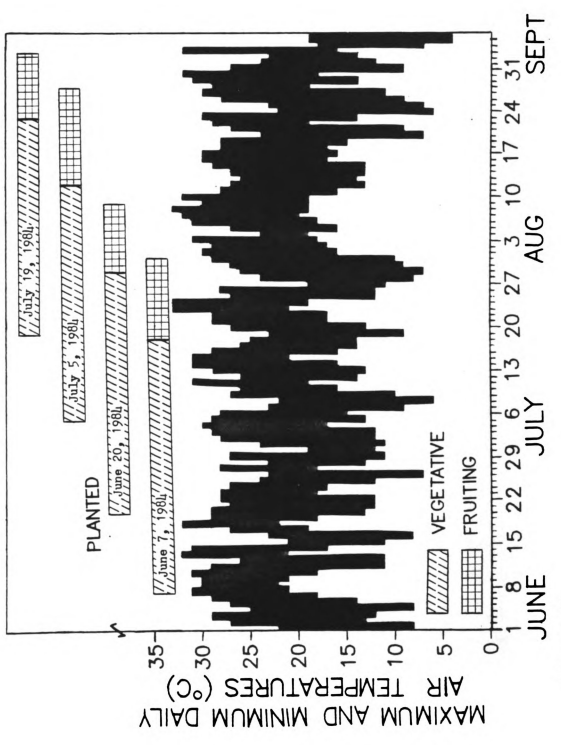

MAXIMUM AND MINIMUM DAILY AIR TEMPERATURES (°C)
0
5
10
15
20
25
30
35
PLANTED
June 7, 1980
June 20, 1980
July 5, 1980
July 19, 1980
VEGETATIVE
FRUITING
1 8 15 22 29 6 13 20 27 3 10 17 24 31
JUNE
JULY
AUG
SEPT

Figure 18.

Figure 19. Maximum and minimum daily soil temperatures during the pickling cucumber growth period of the 4 planting dates, 1984. (Data measured by the Michigan State University Weather Service at the Horticulture Research Center.)

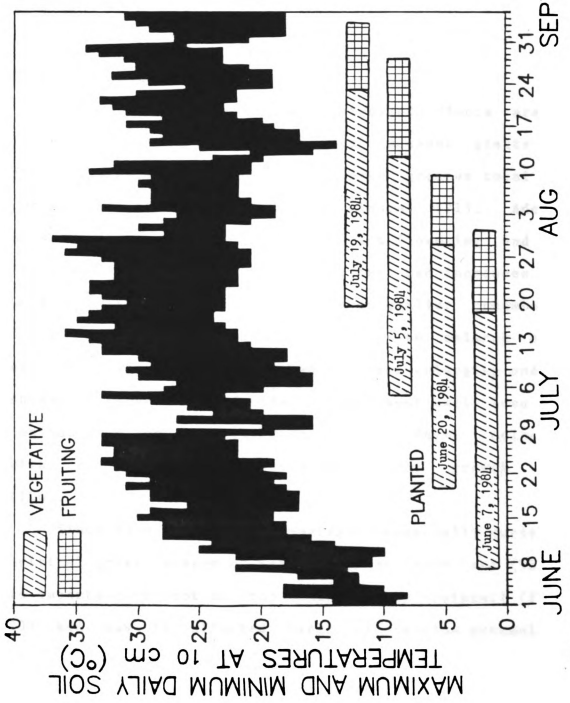

MAXIMUM AND MINIMUM DAILY SOIL TEMPERATURES AT 10 cm (°C)
40
35
30
25
20
15
10
5
0
VEGETATIVE
FRUITING
PLANTED
June 7, 1984
June 20, 1984
July 5, 1984
July 19, 1984
1 8 15 22 29 6 13 20 27 3 10 17 24 31
JUNE
JULY
AUG
SEPT

Figure 19.

temperatures. The air temperatures generally increased from 1 to 8 days after anthesis for the July 19 planting and then declined.

Effect of Rainfall

The growth rates of water-stressed plants are much lower than those of non-stressed cucumber plants (92). Fruiting plants tend to have an even greater total water consumption than nonfruiting plants (71). Adequate moisture is especially critical during flowering and early fruit set (93), when the rate of water use increases (71). Larger fruits are less affected than smaller cucumbers by drought (92). Large fruits continue to enlarge at the expense of the small fruits, which cease enlarging and then shrivel. These larger fruits in the lowest axils lose their dominance after approximately 12 days, coinciding with a period of decreasing fruit growth rates (106).

Since moisture is very important, especially during the critical growth stages of early cucumber fruit set (93), it is important to look at the timing of the rainfall (Figure 20) and how it affected rates of calcium accumulation (Figure 7) and fruit growth (Figure 12). It may be hypothesized that pickling cucumber fruits that receive adequate moisture should have the highest rates of calcium accumulation and growth. More calcium should be available in the soil solution. Optimum soil moisture

Figure 20. Daily rainfall during the growth period of pickling cucumbers from 4 planting dates, 1984. (Data measured by the Michigan State University Weather Service at the Horticulture Research Center.)

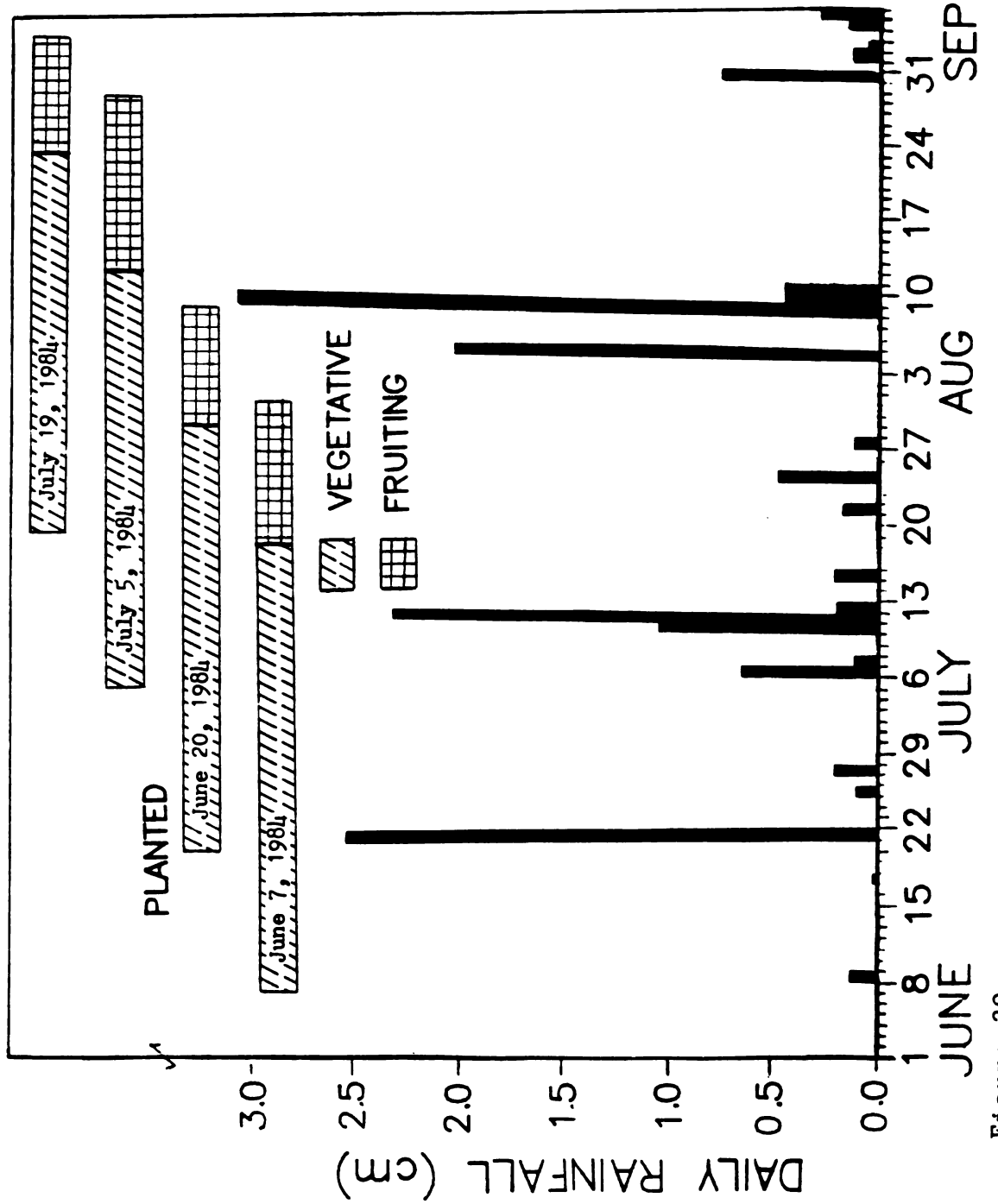

DAILY RAINFALL (cm)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
JUNE
1
8
15
22
29
JULY
6
13
20
27
AUG
3
10
17
24
31
SEPT
PLANTED
June 7, 1984
June 20, 1984
July 5, 1984
July 19, 1984
VEGETATIVE
FRUITING

Figure 20.

levels during the vegetative growth period supports cucumber root growth, providing new sites for calcium uptake. During expansive fruit growth, net water movement into fruits via the xylem occurs in response to a water potential gradient. Calcium import into the developing pickling cucumber fruits via the xylem should be enhanced to some extent by the greater volume of water, also.

It is interesting to note that fruits from both the June 7 and July 5 plantings exhibited maximum rates of calcium accumulation (Figure 7) and growth (Figure 12) at or before the average fruit fresh weight reached 100 g. While the June 7 planting received approximately 8 cm of rain during the vegetative growth period, the July 5 planting received the largest amount of rain, 11 cm (Figure 20). Substantial amounts of the rain during the vegetative growth periods fell 10 days prior to anthesis for the June 7 and July 5 plantings, 3.73 and 5.97 cm, respectively. The June 7 planting also received 0.71 cm of rain during the fruiting period.

Fruits from the June 7 planting peaked in their calcium accumulation rates at 7 days and growth rates at approximately 9 days after anthesis (Figures 7,12). Among the four plantings, fruits from this first planting had the highest rates of calcium accumulation and growth until the average fruit fresh weights exceeded 75 g and 100 g, respectively. There was a sharp rise in the rates after the 0.15 cm rain at 4 days after anthesis (Figure 20). No

increase in calcium accumulation rates and only a small increase in fruit growth rates occurred following the 0.46 cm rain at 7 days after anthesis. The fruit calcium accumulation rates remained almost constant as fruits enlarged from 75 to 150 g. The fruit growth rates declined, especially as fruits enlarged from 125 to 150 g.

Since the July 5 planting received the largest amount of rain 10 days prior to anthesis, water should not have been a limiting factor to early pickling cucumber fruit growth (Table 20). Small fruits, weighing 50 g or less, from this planting did have similar calcium accumulation and growth rates as those of fruits from the other plantings (Figures 7,12). When the fruits from the third planting reached 75 g and larger, the rates declined to the lowest levels among the plantings. This was the only planting that received no rain during the fruiting period (Table 20).

Several hypotheses may be proposed to explain the calcium accumulation rate and growth rate trends for the June 7 and July 5 plantings (Figures 7,12). As the initial pickling cucumber fruit enlarges and new fruits begin to develop on the vine, the assimilate demand increases. Due to the low amounts of rainfall during fruiting, there may have been a shortage of both water and assimilates in the later stages of pickling cucumber fruit development. As previously mentioned, maximum cucumber fruit abortion occurs at 8 days after anthesis, coinciding with a steadily

decreasing amount of available assimilates (106). The maximum calcium accumulation and growth rates peaked around 8 days after anthesis in the June 7 planting. The brief rain shower at 7 days after anthesis probably was not sufficient to maintain the high rates of fruit calcium accumulation and growth. At 6 and 7 days after anthesis, the minimum night air temperatures of 21° and 19° C, respectively, were the highest in the fruiting period (Figure 18). These high temperatures further accentuated the water stress.

The large fluctuations in moisture between the vegetative and the fruit growth periods may be deleterious (Figure 20). The plants cannot grow at a steady rate. Plant metabolism may be traumatized by water stress. Plants from the July 5 planting often wilted in the afternoons. During the night the plants would regain turgidity. This would slow fruit growth as more energy was expended for maintaining the water-stressed cells, decreasing the energy available for further growth.

Fruit hormonal changes also may have affected the calcium accumulation and growth rates. The larger, dominant pickling cucumber fruits may have grown by drawing moisture and assimilates from any smaller fruits on the vine. The July 5 fruits reached their maximum rates (Figures 7,12) at approximately the time that the fruits in the lower nodes would begin to lose their dominance (106).

The fruits from the June 20 and July 19 plantings had

an almost linear increase in the rates of calcium accumulation and growth (Figures 7,12). Since these fruits never reached their maximum rates, this would suggest that there was not an assimilate or water shortage. Both plantings received about 7 cm of rainfall during their vegetative growth periods, of which 0.71 cm and none fell 10 days before anthesis for the June 20 and July 19 plantings, respectively (Figure 20). It rained 5.10 cm during fruiting in the June 20 planting, the highest amount amongst the four plantings. The July 19 planting received 0.91 cm of rain during the fruiting period.

It took a greater number of days after anthesis to reach a specific fruit fresh weight for the July 19 planting (Table 13). Fruits from the last planting averaged only 75 g at 10 days after anthesis. The pickling cucumber plants started fruiting earlier in plant development than in the other plantings. This would suggest that there was less photosynthetic leaf area, decreasing the production of assimilates. The percent soil moisture was low at the beginning of the fruiting period, which also affected fruit development and calcium accumulation rates (Figures 7,12). The 25 g fruits from this planting had significantly lower calcium accumulation rates than fruits from the other plantings. It is possible that these fruits were drawing water from the smaller fruits on the vine, thus decreasing calcium import more than growth.

The pickling cucumber plants from both the June 20 and

July 19 plantings received rain between 6 and 8 days after anthesis (Figure 20). This is the critical period of time during which assimilates often become limiting for pickling cucumber fruit growth (106). Both calcium accumulation and fruit growth rates increased for 25 and 50 g fruits from the July 19 and June 20 plantings, respectively, following these rains (Figures 7,12).

In contrast to the declining rates for the June 7 and July 5 plantings, fruits from the June 20 planting continued to increase in calcium accumulation and growth rates as they enlarged to greater than 100 g (Figures 7, 12). It had been cloudy during the last two harvests, which may have increased water and calcium movement to the fruits by enhanced root pressure flow. Since the final pickling cucumber harvest was at 11 days after anthesis, it is unknown if fruits from the July 19 planting would have continued to increase in their rates of calcium accumulation and growth like fruits from the June 20 planting or would have reached maximum rates like the fruits from the June 7 and July 5 plantings.

Relationship of Pan Evaporation

Diurnal fluctuations in plant transpiration rates, created by dry days, humid nights and good soil moisture levels, increase the import of calcium into weakly transpiring tomato fruits (1). Root pressure flow only develops at night when the transpiration rate is low. This

would suggest that the development of a positive root pressure at night may be extremely important for facilitating calcium transport into developing pickling cucumber fruits.

Scatter plots were prepared of the total daily pan evaporation amounts versus the rates of calcium accumulation and growth on the day pickling cucumber fruits weighed 25, 75 and 150 g (fresh weight). The location of points in the different quadrants are nearly identical for both the calcium accumulation rate and the growth rate plots (Figure 21). The location of these points from the different planting dates differed for the three fruit weights. Since there was greater separation of points from the different plantings for 150 g fruits, only these plots are presented.

The points for each planting date (Figure 21) are almost stacked in ascending order of the amounts of rainfall received during fruiting (Table 20). The July 5 planting had the lowest rainfall and rates of fruit calcium accumulation and growth, the June 7 planting had intermediate values, and the June 20 planting had the highest rainfall and rates. The points for the June 7 planting overlapped more with the July 5 points for fruit growth rates than for calcium accumulation rates. This may be due to greater growth rate differences among cultivars for 150 g fruits.

Pan evaporation did not have a major effect on either calcium accumulation rates or fruit growth rates in this

Figure 21 (A-B). The relationship between daily pan evaporation on the (A) calcium accumulatin rates and (B)fruit growth rates of 150 g pickling cucumbers from 3 planting dates, 1984. The rates for each planting date were estimated for regression curves of the (A) fruit calcium concentration and (B)fruit fresh weight of 4 cultivars, each replicated 4 times. The July 5 planting had 3 replications. (Evaporation measured by the Michigan State University Weather Service at the Horticulture Research Center.)

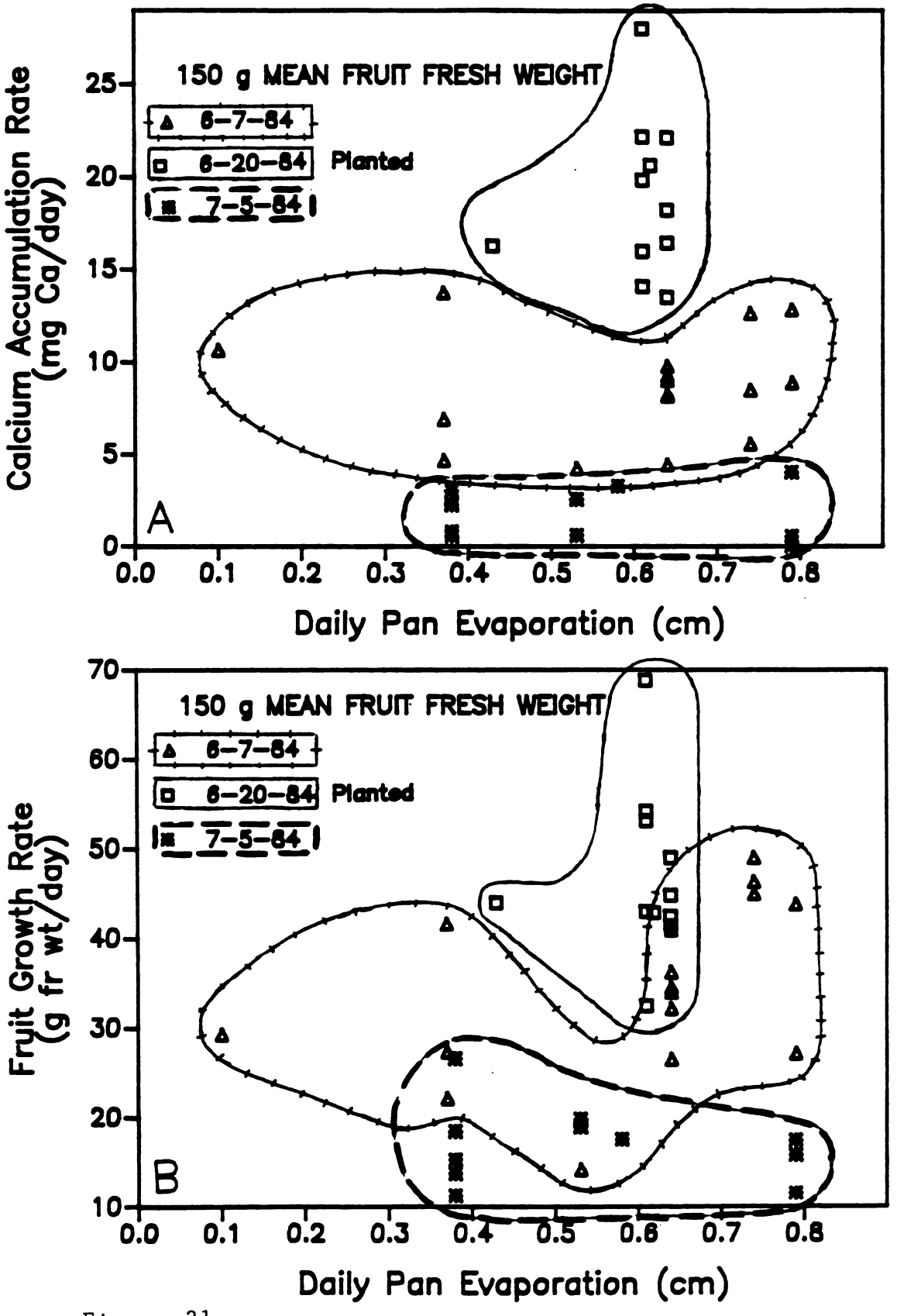

150 g MEAN FRUIT FRESH WEIGHT
6-7-84
6-20-84 Planted
7-5-84
Calcium Accumulation Rate (mg Ca/day)
A
Daily Pan Evaporation (cm)
150 g MEAN FRUIT FRESH WEIGHT
6-7-84
6-20-84 Planted
7-5-84
Fruit Growth Rate (g fr wt/day)
B
Daily Pan Evaporation (cm)

Figure 21.

experiment (Figure 21). At any one pan evaporation amount the rates of pickling cucumber fruit calcium accumulation and growth were very different. The lack of response may be due to the fact that the pan evaporation data were daily totals, which do not reflect diurnal fluctuations. A positive root pressure, which develops during the night, may be very important in affecting water and calcium movement into the pickling cucumber fruits. Also, the other environmental parameters could not be controlled in the field as the amount of daily pan evaporation changed.

Pan evaporation is not the same as transpiration from a plant. Water is evaporating from an open pan rather than from a leaf with stomatal opening and closing or from the small lenticels of fruits. Cucumis is one of the most sensitive crop species to ultraviolet beta (UV-beta) radiation, which decreases the leaf diffusive resistance to water vapor (124). In mild water-stressed Cucumis species, UV-beta radiation reduces stomatal closure. Transpiration rates also increase in fruiting versus nonfruiting cucumber plants.

Effect of Soil Moisture

No clear trends occur between percent soil moisture and the rates of pickling cucumber fruit calcium accumulation and growth (Table 22). Due to the differences in fruit maturity and environmental conditions, comparisons can only be made between replications at each sampling time but not between samplings. At 1 and 4 days after anthesis the

percent soil moisture was around 20 percent in replication 4 of the July 5 and 19 plantings. The calcium accumulation rates and fruit growth rates were reduced at these high soil moisture levels. Replication 4 was flooded from the heavy rain on August 4 and 8 (Figure 20). This most likely created anaerobic conditions in the rhizosphere, which are not conducive to water and nutrient uptake by the pickling cucumber roots.

At 8 days after anthesis soil moisture was positively correlated with the rates of fruit calcium accumulation and growth, since percent soil moisture was not in excess (Table 22). As noted previously, water plays a crucial role in pickling cucumber fruit growth and calcium accumulation. More frequent soil sampling would have provided a broader base from which to draw conclusions about the effect of soil moisture on these rates. Although the highest calcium accumulation rates are usually associated with the highest fruit growth rate at any given soil moisture percentage, there were some exceptions at 1,5 and 8 days after anthesis (Table 22). Further work is needed to assess why these differences occur. It would also be interesting to compare the rates of numerous fruits of similar sizes to determine if soil moisture affects calcium accumulation rates and fruit growth rates differently at various ontogenetic stages of fruit development.

Table 22. The effect of blocking on the percent soil moisture and on the rates of fruit calcium accumulation and growth of pickling cucumbers, 1984.

Planting date	Sampling time DAA[z]	Rep	% Soil moisture (g/g)[y]	Ca accum. rate (mg Ca/day)[x]	Growth rate (g fr. wt./ day)[x]
June 20	5	1	7.88	4.52	9.72
		2	8.86	5.84	11.49
		3	9.40	3.82	7.90
		4	10.34	4.64	9.36
July 5	1	1	12.31	0.32	0.32
		2	13.44	0.10	0.38
		4	20.87	0.14	0.26
	8	1	6.99	3.18	10.12
		2	8.71	1.00	14.69
		4	15.95	5.25	18.51
July 19	4	1	7.49	0.87	0.92
		2	9.42	1.56	2.32
		3	9.10	0.98	1.34
		4	18.82	0.61	0.78
	11	1	5.32	11.98	41.16
		2	7.33	7.32	22.88
		3	6.94	7.16	22.27
		4	18.12	11.70	41.90

[z]Days after anthesis.

[y]Average of 4 soil samples at a 7-20 cm depth.

[x]Average of 4 cultivars.

Effect of Temperature

Warm soils encourage mineral and water uptake and positive root pressure development, which should stimulate fruit growth and/or calcium transport rates. The rate of pickling cucumuber fruit production was reported to have increased as the night temperatures rose (132). Schapendonk et al. (1984) attributed earliness of fruit production to increased irradiance rather than to higher temperatures (107).

Scatter plots were prepared of the maximum (Figure 22) and minimum (Figure 23) daily soil temperatures for the days when pickling cucumber fruits weighed 25, 75 and 150 g versus the rates of calcium accumulation of fruits at these specific fresh weights. Similar scatter plots were also generated for maximum and minimum daily soil temperatures versus fruit growth rates and maximum and minimum daily air temperatures versus the rates of fruit calcium accumulation and growth, which will not be presented. The points for both the calcium accumulation and growth rates were in similar locations for all of the temperature plots. The plots were also similar for the air and soil temperatures. The soil temperatures showed a corresponding increase as the maximum daily air temperatures increased, but the daily soil minimum and maximum temperatures fluctuated less than the air temperatures.

Ingestad (1973) noted an increase in ion uptake in cucumbers (cv. Bestseller OE 0219) with an increase in root

temperatures. In the present experiment, similar soil temperatures were associated with very different calcium accumulation rates at the different fruit weights examined (Figures 22,23). The calcium accumulation rates did increase with increasing minimum soil temperatures for 150 g fruits (Figure 23C). For 150 g fruits from the different plantings, the points were in separate quadrants of the plots, arranged in the order of the amount of moisture received during fruiting (Table 20). If a positive root pressure affects both ion and water uptake in pickling cucumbers, the primary effect of water may have altered the secondary effect of temperature on calcium uptake (4). Since only the main effects of soil moisture and temperature on the rate of fruit calcium accumulation were studied, this possible interaction was not identified.

The points for the different planting dates overlapped in the plots of 25 and 75 g fruits (Figures 22A-B,23A-B). The 25 g fruits from the June 7 planting had higher calcium accumulation rates at the higher maximum daily soil temperatures. Points for the June 20 and July 5 plantings overlapped for both minimum and maximum soil temperatures. There was adequate moisture for fruit growth in both main plots at this fruit size. The lowest calcium accumulation rates generally occurred in 25 g fruits from the July 19 planting and in 75 g fruits from July 5 planting (Figure 7). At these low calcium accumulation rates, it was extremely dry. The high minimum and maximum daily soil

Figure 22 (A-C). The effect of maximum daily soil temperatures on the calcium accumulation rates of (A)25 g, (B)75 g, and (C)150 g pickling cucumber fruits from the different planting dates, 1984. The rates for each planting date were estimated from regression curves of the fruit calcium concentration of 4 cultivars, each replicated 4 times. The July 5 planting had 3 replications. (Temperatures measured by the Michigan State University Weather Service at the Horticulture Research Center.)

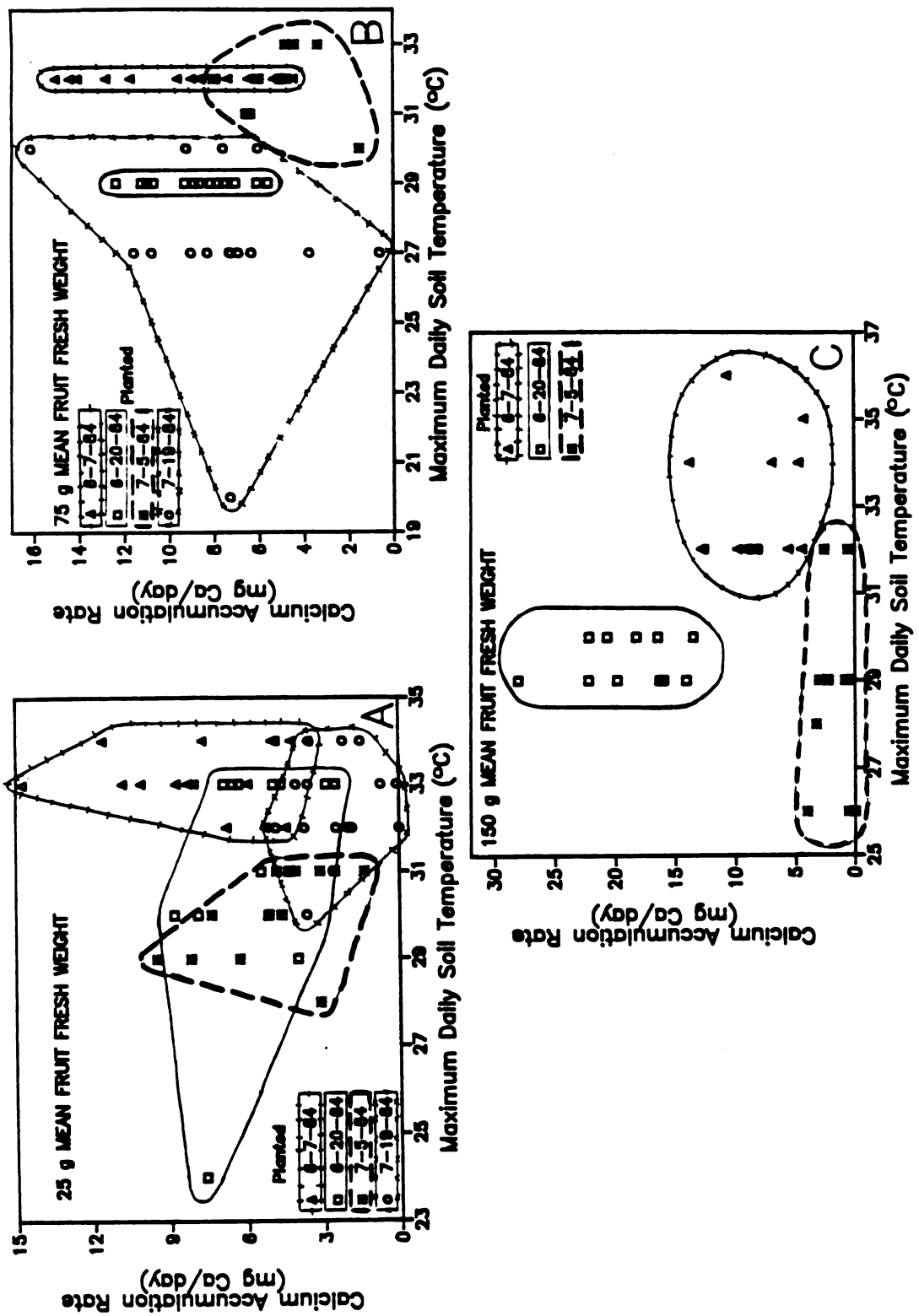

25 g MEAN FRUIT FRESH WEIGHT
75 g MEAN FRUIT FRESH WEIGHT
150 g MEAN FRUIT FRESH WEIGHT
Planted
6-7-84
6-20-84
7-5-84
7-19-84
A
B
C
Calcium Accumulation Rate (mg Ca/day)
Maximum Daily Soil Temperature (°C)

Figure 22.

Figure 23 (A-C). The effect of minimum daily soil temperatures on the calcium accumulation rates of (A)25 g, (B)75 g, and (C)150 g pickling cucumber fruits from the different planting dates, 1984. The rates for each planting date were estimated from regression curves of the fruit calcium concentration of 4 cultivars, each replicated 4 times. The July 5 planting had 3 replications. (Temperatures measured by the Michigan State University Weather Service at the Horticulture Research Center.)

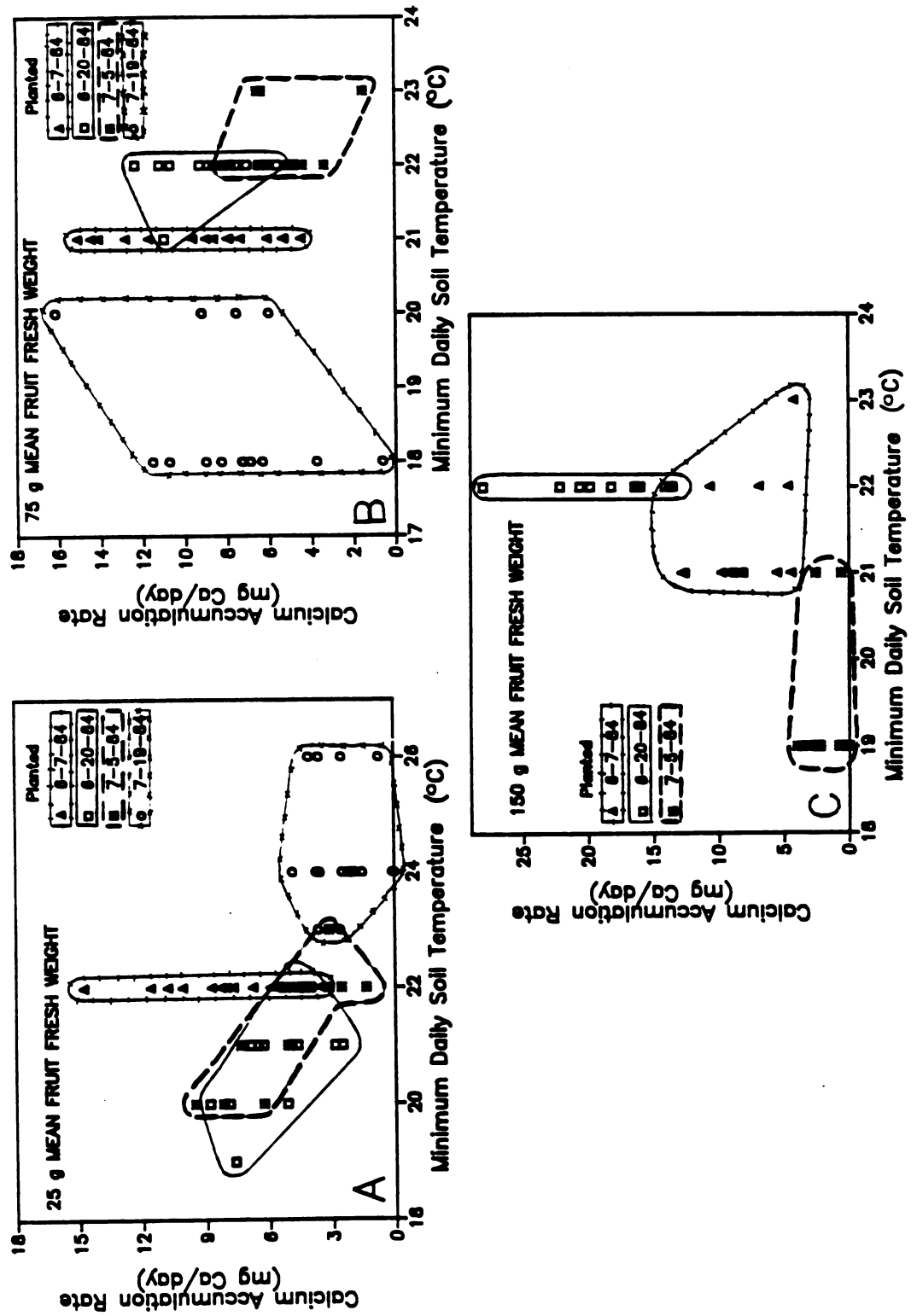

25 g MEAN FRUIT FRESH WEIGHT
75 g MEAN FRUIT FRESH WEIGHT
150 g MEAN FRUIT FRESH WEIGHT
Planted
6-7-84
6-20-84
7-5-84
7-19-84
A
B
C
Calcium Accumulation Rate (mg Ca/day)
Minimum Daily Soil Temperature (°C)

Figure 23.

temperatures would have further depleted the limited available moisture by evaporation and transpiration. The plants would not have been able to regain turgidity as rapidly during the night, due to the high temperatures and lack of moisture.

SUMMARY

Mean Calcium Concentration and Content in Pickling Cucumber Fruits During Ontogeny

The mean pickling cucumber fruit calcium concentration declined from approximately 1.75 percent to less than 0.70 percent (dry wt.) during fruit ontogeny. The most rapid decline in calcium concentration occurred during the first 5 days after anthesis. The differential effect of cultivar on the fruit calcium concentration under different environmental conditions indicates that pickling cucumber fruits are most sensitive to changes early in development. Planting date and cultivar had an impact on the calicum concentration of fruits from the later harvests. Fruits from the June 20 planting had the highest calcium concentrations (0.78-0.93% dry wt.) from 7 to 11 days after anthesis. Tamor had the lowest fruit calcium concentrations (0.54-1.60% dry wt.) throughout ontogeny.

Differences in calcium partitioning between pericarp and endocarp tissues occurred in pickling cucumber fruits. While the pericarp calcium concentration (1.1-0.7% dry wt.) declined gradually with increasing fruit size, the endocarp calcium concentration (0.8-0.2% dry wt.) declined

dramatically to a low of 0.20 percent, a deficient concentration for many crops. Expansive cell growth rates of the endocarp fruit tissues exceeded pericarp growth rates in the more mature pickling cucumber fruits, having a dilutionary effect on the tissue calcium concentration. The endocarp may also contain fewer vascular tissues than pericarp tissues, decreasing the rate of calcium import into the tissue. Endocarp tissue calcium concentrations are more sensitive to environmental changes and different genotypes than the pericarp calcium concentrations.

A higher concentration of calcium accumulated in leaf tissues (3.1% dry wt.) than in pickling cucumber fruits (1.94% dry wt.). The calcium concentrations of leaf lamina tissue (1.8-3.1% dry wt.) were always higher than petiole tissue (1.4-1.8% dry wt.) calcium concentrations of pickling cucumbers. The petiole tissue calcium concentration is not as sensitive to changes in the environment as the leaf lamina tissue. It may, therefore, be more accurate to sample leaf lamina rather than petiole tissue for non-mobile nutrients like calcium. Leaf tissue is not a good indicator of mature fruit tissue calcium concentrations, suggesting that factors other than calcium uptake by a plant are contributing to variations in calcium levels within the plant.

As pickling cucumber fruits enlarged, the calcium content (0.54-67.74 mg Ca/fruit) increased due to a continuous calcium uptake during ontogeny. The period of

most rapid calcium accumulation was generally 9 to 11 days after anthesis, as the fruits approached harvestable size. The increase in calcium content relative to fruit fresh weight was almost linear within the fruit fresh weight range of 5 to 150 g for planting date. The June 20 planting tended to produce fruits with the highest calcium contents (3.71-55.03 mg Ca/fruit), while fruits from the July 19 planting generally had the lowest calcium contents (3.92-20.89 mg Ca/fruit). The greatest differences in fruit calcium contents between cultivars occurred in the more mature fruits. The comparatively low calcium contents of Tamor fruits (3.62-41.54 mg Ca/fruit) were established early in fruit development and maintained throughout ontogeny.

If calcium is proven to be critical for pickling cucumber fruit development and quality, it would be advantageous to increase the fruit calcium concentration. Calcium sprays or dips, which are used to increase the concentration in apple fruit flesh, could not increase the low calcium concentrations of endocarp tissues. The applied calcium only moves superficially into fruit tissues. Calcium fertilizers may increase fruit calcium concentration if applied during the early stages of fruit development. Genetic variability could be exploited in a pickling cucumber breeding program. A pickling cucumber cultivar, such as Tamor, may have a lower tissue calcium requirement due to more efficient ion utilization, more selective calcium absorption and/or differing efficiency of loading

calcium ions into xylem vessels.

The calcium contents of plant organs are based on metabolic removal from the vascular system rather than on physiological demand. The effect of calcium competition between fruits on a vine needs to be studied. More calcium may be distributed to fruits lower on the vine than from the upper nodes. It is also unknown if ontogenetic changes in pollinated pickling cucumber fruit calcium concentration and content are the same as in a parthenocarpic fruit. It has been proposed that endogenous auxin formed by seeds may enhance calcium transport. In this study the mean fruit calcium concentration was quantified. A calcium fractionation study would elucidate if the calcium is in a soluble and/or insoluble form and if the solubility changes through ontogeny. Further research is also needed to determine the physiological consequences of the changing calcium status of pickling cucumber fruits.

Ontogenetic Changes in Calcium Accumulation Rates Relative to the Growth Rates of Pickling Cucumber Fruits

The calcium accumulation rate of a pickling cucumber fruit is the amount of calcium (mg) imported into the fruit per unit time (day). The fruit growth rate is the fresh weight (g) gained per unit time (day). Environmental factors had a significant and similar impact on the rates of pickling cucumber fruit calcium import and growth.

Trends in calcium accumulation rates and growth rates

were similar for fruits from the June 7 and July 5 plantings and from the June 20 and July 19 plantings. The average maximum calcium accumulation rate peaked in 50 g fruits from the June 7 planting (9 mg Ca/day) and in 75 g fruits from the July 5 planting (5 mg Ca/day). Growth rates declined after fruits averaged 100 g in the June 7 and July 5 plantings at 40.5 and 21.6 g/day, respectively. Fruits from the June 20 and July 19 plantings exhibited a continual rise in rates of calcium accumulation and growth throughout the harvest period. The highest average calcium accumulation rate (21 mg Ca/day) and growth rate (50.3 g/day) were estimated for 150 g fruits from the June 20 planting. Pickling cucumber fruits from the July 19 planting grew more slowly than fruits from the June plantings, averaging less than 100 g by 11 days after anthesis.

It is important to look at the calcium accumulation rate relative to the growth rate, as a high growth rate and/or low calcium import rate will cause a decline in the pickling cucumber fruit calcium concentration. Even though the environment during fruit development was different for these plantings and affected both growth and calcium import, the rates of growth relative to rates of calcium accumulation were similar. The largest increase in pickling cucumber fruit fresh weight and volume occurred between 9 and 11 days after anthesis, which was also the period of most rapid calcium accumulation. These trend similarities suggest that a correlation exists between the rates of

pickling cucumber fruit calcium accumulation and growth.

Approximately 7 days after anthesis appears to be a critical period in pickling cucumber fruit development. Planting date and cultivar interacted, affecting fruit fresh weight, volume, and length to diameter ratios. Fruits from the June 7 planting reached their maximum rates of calcium accumulation and growth during this time period. Schapendonk and Brouwer (1984) report that maximum cucumber fruit abortion occurs at 8 days after anthesis (106). Available assimilates often become limiting during this period of high fruit growth rates. In this study, pickling cucumber fruit growth rates were inversely proportional to the fruit dry weight percentages.

Steady fruit growth rates are preferable to high fruit growth rates in maintaining adequate calcium levels in pickling cucumber fruits. Closer plant spacing may favor the calcium status of pickling cucumber fruits if plant vigor is reduced slightly, resulting in smaller, slower growing fruits. Further research is needed to identify the physiological plant processes which control calcium accumulation. If these processes are the same as those controlling growth, it would suggest further methods of increasing the fruit calcium status.

Effect of Various Environmental Parameters on Pickling Cucumber Fruit Calcium Accumulation and Growth

Under certain environmental conditions a significantly higher rate of calcium accumulation was achieved for a given fruit growth rate, suggesting that differences exist in calcium transport or accumulation efficiency in pickling cucumber fruits. Soil moisture significantly increased the rates of pickling cucumber fruit calcium accumulation and growth, if the soil moisture did not exceed 20 percent. Optimum soil moisture affects the calcium concentration of the soil solution, provides a high soil-water potential, and maximizes plant water and nutrient uptake.

Pickling cucumber plants from the June 7 and July 5 plantings received the majority of rain during their vegetative growth phases. Fruits from both plantings reached their maximum fruit growth rates and calcium accumulation rates before the fruits averaged 100 g. The lowest rates of fruit calcium import and growth occurred in the July 5 planting, the only planting which received no rain during fruiting. Fruits from the June 20 and July 19 plantings, which never attained maximum rates of calcium accumulation and growth, received 5.10 cm and less than 1 cm of rain during fruiting, respectively. This rain fell between 6 and 8 days after anthesis, the critical time period during which assimilates often become limiting to pickling cucumber fruit growth. Both the rates of fruit

calcium accumulation and growth increased following these rains.

Pickling cucumber fruits, especially in the early stages of development, are very sensitive to water stress. It would be interesting to compare rates of fruit calcium accumulation and growth of pickling cucumbers of similar size to determine if soil moisture affects these rates differently at various ontogenetic stages. Judicious irrigation scheduling, especially around 8 days after anthesis, would appear to be very beneficial for pickling cucumber fruit calcium accumulation and growth.

Neither pan evaporation nor temperature had a direct effect on pickling cucumber fruit calcium accumulation or growth. If a positive root pressure affects both ion and water uptake in pickling cucumbers, the primary effect of water may have altered the secondary effects of pan evaporation and temperature on calcium uptake. Since only the main effects of pan evaporation and temperature on rates of fruit calcium accumulation and growth were studied, these possible interactions were not identified.

Diurnal fluctuations in a plant's water potential facilitates calcium distribution to low transpiring plant organs in many crops. Adequate water, low relative humidity at night, and low soil salinity favor root pressure development. High vegetative transpiration rates, which enhance calcium distribution primarily to leaf rather than to fruit tissues, may be reduced by selective plant

shading, overhead sprinkling, and shelterbelts to reduce wind speeds.

BIBLIOGRAPHY

BIBLIOGRAPHY

1. Adams, P. and L. Ho. 1985. Two disorders but one cause. Grower 103(12):17-27.

2. Adhikari, R. R. 1980. Effect of nitrogen, plant population, and chlorflurenol on gynoecious parthenocarpic pickling cucumber (Cucumis sativus L.). M.S. Thesis, Michigan State University.

3. Bangerth, F. 1976. A role for auxin and auxin transport inhibitors on the Ca content of artificially induced parthenocarpic fruits. Physiol. Plant. 37:191-194.

4. Bangerth, F. 1979. Calcium-related physiological disorders of plants. Ann. Rev. Phytopath. 17:97-122.

5. Banuelos, G. S., G. P. Offermann, and E. C. Seim. 1985. High relative humidity promotes blossom-end rot on growing tomato fruit. HortScience 20(5):894-895.

6. Barker, A. V. and D. N. Maynard. 1972. Cation and nitrate accumulation in pea and cucumber plants as influenced by nitrogen nutrition. J. Amer. Soc. Hort. Sci. 97(1):27-30.

7. Barta, D. J. and T. W. Tibbitts. 1986. Effects of artificial enclosure of young lettuce leaves on tipburn incidence and leaf calcium concentration. J. Amer. Soc. Hort. Sci. 111(3):413-416.

8. Bell, C. W. and O. Biddulph. 1963. Translocation of calcium. Exchange versus mass flow. Plant Physiol. 38:610-614.

9. Bengtsson, B. 1982. Uptake and translocation of calcium in cucumber. Physiol. Plant. 54:107-111.

10. Bengtsson, B. and P. Jensen. 1982. Uptake of calcium in wheat and cucumber roots. Physiol. Plant. 55:273-278.

11. Bengtsson, B. and P. Jensen. 1983. Uptake and distribution of calcium, magnesium and potassium in cucumber of different age. Physiol. Plant. 57(4): 428-434.

12. Biddulph, O., F. S. Nakayama, and R. Cory. 1961. Transpiration stream and ascension of calcium. Plant Physiol. 36:429-436.

13. Bradfield, E. G. and C. G. Guttridge. 1984. Effects of night-time humidity and nutrient solution concentration on the calcium content of tomato fruit. Sci. Hort. 22:207-217.

14. Bramlage, W. J., M. Drake, and J. H. Baker. 1979. Changes in calcium level in apple cortex tissue shortly before harvest and during postharvest storage. Commun. Soil Sci. Plant Anal. 10(1&2):417-426.

15. Bramlage, W. J., M. Drake, and S. A. Weis. 1985. Comparisons of calcium chloride, calcium phosphate, and a calcium chelate as foliar sprays for 'McIntosh' apple trees. J. Amer. Soc. Hort. Sci. 110(6):786-789.

16. Brun, C. A., J. T. Raese, and E. A. Stahly. 1985. Seasonal response of 'Anjou' pear trees to different irrigation regimes. II. Mineral compostion of fruit and leaves, fruit disorders, and fruit set. J. Amer. Soc. Hort. Sci. 110(6):835-840.

17. Burstrom, H. 1954. Studies on growth and metabolism of roots. X. Investigations of the calcium effect. Physiol. Plant. 7:332-342.

18. Burstrom, H. G. 1968. Calcium and plant growth. Biol. Rev. 43:287-316.

19. Callan, N. W. 1986. Calcium hydroxide reduces splitting of 'Lambert' sweet cherry. J. Amer. Soc. Hort. Sci. 111(2):173-175.

20. Carolus, R. 1975. Calcium relationships in vegetable nutrition and quality. Commun. Soil Sci. Plant Anal. 6(3):285-298.

21. Christiansen, M. N. and C. D. Foy. 1979. Fate and function of calcium in tissue. Commun. Soil Sci. Plant Anal. 10(1&2):427-442.

22. Clarkson, D. T. 1965. Calcium uptake by calcicole and calcifuge species in the genus Agrostis L. J. Ecol. 53:427-435.

23. Clarkson, D. T. 1984. Calcium transport between tissues and its distribution in the plant. Plant, Cell and Environ. 7:449-456.

24. Cleland, R. 1960. Effect of auxin upon loss of calcium from cell walls. Plant Physiol. 35:581-584.

25. Cleland, R. E. and D. L. Rayle. 1977. Reevaluation of the effect of calcium ions on auxin-induced elongation. Plant Physiol. 60: 709-712.

26. Collier, G. F. and T. W. Tibbitts. 1984. Effects of relative humidity and root temperature on calcium concentration and tipburn development in lettuce. J. Amer. Soc. Hort. Sci. 109(2):128-131.

27. Demarty, M., C. Morvan, and M. Thellier. 1984. Calcium and the cell wall. Plant, Cell and Environ. 7:441-448.

28. Dieter, P. 1984. Calmodulin and calmodulin-mediated processes in plants. Plant, Cell and Environ. 7:371-380.

29. Drew, M. C. and O. Biddulph. 1971. Effect of metabolic inhibitors and temperature on uptake and translocation of ^{45}Ca and ^{42}K by intact bean plants. Plant Physiol. 48:426-432.

30. English, J. E. and A. V. Barker. 1983. Calcium efficiency among tomato strains depends on nitrogen regimes. J. Plant Nutr. 6(8):725-734.

31. Epstein, E. 1961. The essential role of calcium in selective cation transport by plant cells. Plant Physiol. 36:437-444.

32. Farhoomand, M. B. and L. A. Peterson. 1968. Concentration and content. Agron. J. 60:708-709.

33. Ferguson, I. B. 1979. The movement of calcium in non-vascular tissue of plants. Commun. Soil Sci. Plant Anal. 10(1&2):217-224.

34. Ferguson, I. B. 1984. Calcium in plant senescence and fruit ripening. Plant, Cell and Environ. 7:477-489.

35. Ferguson, I. B. and E. G. Bollard. 1976. The movement of calcium in germinating pea seeds. Ann. Bot. 40:1047-1055.

36. Ford, E. M. 1979. Effect of post-blossom environmental conditions on fruit composition and quality of apple. Commun. Soil Sci. Plant Anal. 10(1&2):337-348.

37. Ford, E. M. and J. D. Quinlan. 1979. The distribution of ^{45}Ca in apple fruits when supplied to the roots at three times during the season. J. Hort. Sci. 54(3):181-188.

38. Fukumoto, M. and K. Nagai. 1983. Possible roles of calcium and ammonium in the development of bitter pit in apple. Physiol. Plant. 59:171-176.

39. Gallaher, R. N. 1975. The occurrence of calcium in plant tissue as crystals of calcium oxalate. Commun. Soil Sci. Plant Anal. 6(3):315-330.

40. Geraldson, C. M. 1957. Control of blossom-end rot of tomatoes. Proc. Amer. Soc. Hort. Sci. 69:309-317.

41. Geraldson, C. M. 1979. Minimal calcium stress using the gradient mulch production system. Commun. Soil Sci. Plant Anal. 10(1&2):163-169.

42. Greene, G. M. 1984. Penn State research project cites factors that influence calcium. Goodfruit Grower 35(17):16-18.

43. Greenleaf, W. H. and F. Adams. 1969. Genetic control of blossom-end rot disease in tomatoes through calcium metabolism. J. Amer. Soc. Hort. Sci. 94:248-250.

44. Gubbels, G. H. and R. L. Carolus. 1971. Influence of atmospheric moisture, ion balance, and ion concentration on growth, transpiration and blackheart of celery (Apium graveolens L.). J. Amer. Soc. Hort. Sci. 96(2):201-204.

45. Haber, M. F., E. Young, and M. Faust. 1983. Effects of PEG-induced water stress on calcium uptake in peach seedlings. J. Amer. Soc. Hort. Sci. 108(5): 737-740.

46. Hanger, B. C. 1979. The movement of calcium in plants. Commun. Soil Sci. Plant Anal. 10(1&2):171-193.

47. Harrison-Murray, R. S. and D. T. Clarkson. 1973. Relationships between structural development and the absorption of ions by the root system of Cucurbita pepo. Planta 114:1-16.

48. Hecht-Buchholz, Ch. 1979. Calcium deficiency and plant ultrastructure. Commun. Soil Sci. Plant Anal. 10(1&2):67-81.

49. Himelrick, D. G. and C. E. Walker. 1982. Seasonal trends of calcium, magnesium, and potassium fractions in apple leaf and fruit tissues. J. Amer. Soc. Hort. Sci. 107(6):1078-1080.

50. Hochmuth, G. J. 1984. Variation in calcium efficiency among strains of cauliflower. J. Amer. Soc. Hort. Sci. 109(5):667-672.

51. Hopfinger, J. A. and B. W. Poovaiah. 1979. Calcium and magnesium gradients in apples with bitter pit. Commun. Soil Sci. Plant Anal. 10(1&2):57-65.

52. Hughes, G. R. 1978. These steps help produce good fall cucumber crop. Southeast Farm Press, p. 38.

53. Ingestad, T. 1973. Mineral nutrient requirements of cucumber seedlings. Plant Physiol. 52:332-338.

54. Iwahashi, M., Y. Tachibana, and Y. Ohta. 1982. Accumulation of calcium, magnesium, potassium and sodium with growth of individual leaves, petioles and stems of cucumber plants. Soil Sci. Plant Nutr. 28(4):441-449.

55. Jakobsen, S. T. 1979. Interaction between phosphate and calcium in nutrient uptake by plant roots. Commun. Soil Sci. Plant Anal. 10(1&2):141-152.

56. Jones, H. G., K. H. Higgs, and T. J. Samuelson. 1983. Calcium uptake by developing apple fruits. I. Seasonal changes in calcium content of fruits. J. Hort. Sci. 58(2):173-182.

57. Jones, H. G. and T. J. Samuelson. 1983. Calcium uptake by developing apple fruits. II. The role of spur leaves. J. Hort. Sci. 58(2):183-190.

58. Jones, J. B., Jr. 1975. Calcium - its soil and plant chemistry. Commun. Soil Sci. Plant Anal. 6(3): 205-206.

59. Jones, R. G. W. and O. R. Lunt. 1967. The function of calcium in plants. Bot. Rev. 33:407-426.

60. Kirkby, E. A. 1979. Maximizing calcium uptake by plants. Commun. Soil Sci. Plant Anal. 10(1&2):89-113.

61. Kirkby, E. A. and D. J. Pilbeam. 1984. Calcium as a plant nutrient. Plant, Cell and Environ. 7:397-405.

62. Konno, H., T. Yamaya, Y. Yamasaki, and H. Matsumoto. 1984. Pectic polysaccharide breakdown of cell walls in cucumber roots grown with calcium starvation. Plant Physiol. 76:633-637.

63. Koontz, H. V. and R. E. Foote. 1966. Transpiration and calcium deposition by unifoliate leaves of Phaseolus vulgaris differing in maturity. Physiol. Plant. 19:313-321.

64. Kotze, W. A. G. 1979. Ionic interactions in the uptake and transport of calcium by apple seedlings. Commun. Soil Sci. Plant Anal. 10(1&2):115-127.

65. LaHaye, P. A. and E. Epstein. 1971. Calcium and salt toleration by bean plants. Physiol. Plant. 25: 213-218.

66. Lazaroff, N. and M. G. Pitman. 1966. Calcium and magnesium uptake by barley seedlings. Aust. J. Biol. Sci. 19:991-1005.

67. Leshem, Y. Y., S. Sridhara, and J. E. Thompson. 1984. Involvement of calcium and calmodulin in membrane deterioration during senescence of pea foliage. Plant Physiol. 75:329-335.

68. Lewis, T. L. and D. Martin. 1973. Longitudinal distribution of applied calcium, and of naturally occurring calcium, magnesium, and potassium, in Merton apple fruits. Aust. J. Agric. Res. 24:363-371.

69. Loneragan, J. F. and K. Snowball. 1969. Calcium requirements of plants. Aust. J. Agric. Res. 20:465-478.

70. Loneragan, J. F. and K. Snowball. 1969. Rate of calcium absorption by plant roots and its relation to growth. Aust. J. Agric. Res. 20:479-490.

71. Loomis, E. L. and P. C. Crandall. 1977. Water consumption of cucumbers during vegetative and reproductive stages of growth. J. Amer. Soc. Hort. Sci. 102 (2):124-127.

72. Maas, E. V. 1969. Calcium uptake by excised maize roots and interactions with alkali cations. Plant Physiol. 44:985-989.

73. Macklon, A. E. S. 1975. Cortical cell fluxes and transport to the stele in excised root segments of Allium cepa L. II. Calcium. Planta 122:131-141.

74. Macklon, A. E. S. and A. Sim. 1981. Cortical cell fluxes and transport to the stele in excised segments of Allium cepa L. IV. Calcium as affected by its external concentration. Planta 152:381-387.

75. Malavolta, E., P. R. Camargo e Castro, V. F. da Cruz, and T. Yamada. 1975. Calcium and its relationship to blossom-end rot in tomato. Commun. Soil Sci. Plant Anal. 6(3):273-284.

76. Mallick, M. F. R., M. Masui, A. Ishida, and A. Nukaya. 1984. Respiration and ethylene production in muskmelons in relation to nitrogen and calcium nutrition. J. Japan. Soc. Hort. Sci. 52(4):429-433.

77. Marinos, N. G. 1962. Studies on submicroscopic aspects of mineral deficiencies. I. Calcium deficiency in the shoot apex of barley. Amer. J. Bot. 49:834-841.

78. Marschner, H. 1974. Calcium nutrition of higher plants. Neth. J. Agric. Sci. 22:275-282.

79. Mason, J. L. 1979. Increasing calcium content of calcium-sensitive tissues. Commun. Soil Sci. Plant Anal. 10(1&2):349-371.

80. Masuda, M. and K. Gomi. 1984. Mineral absorption and oxygen consumption in grafted and non-grafted cucumbers. J. Japan. Soc. Hort. Sci. 52(4):414-419.

81. Maynard, D. N., W. S. Barham, and C. L. McCombs. 1957. The effect of calcium nutrition of tomatoes as related to the incidence and severity of blossom-end rot. Proc. Amer. Soc. Hort. Sci. 69:318-322.

82. Maynard, D. N. and A. C. Gentile. 1963. The distribution of calcium in cells of the roots of carrot (Daucus carota L.). Physiol. Plant. 16:40-43.

83. McLean, E. O. 1975. Calcium levels and availabilities in soils. Commun. Soil Sci. Plant Anal. 6(3): 219-232.

84. Millaway, R. M. and L. Wiersholm. 1979. Calcium and metabolic disorders. Commun. Soil Sci. Plant Anal. 10(1&2):1-28.

85. Millikan, C. R. 1971. Mid-season movement of ^{45}Ca in apple trees. Aust. J. Agric. Res. 22:923-930.

86. Mohr, W. P. and G. M. Jamieson. 1984. The use of an electron microprobe to monitor the uptake of calcium and chloride in apples. Can. J. Plant Sci. 64:349-354.

87. Moore, A. L. and K. E. O. Akerman. 1984. Calcium and plant organelles. Plant, Cell and Environ. 7: 423-429.

88. Moore, D. P., L. Jacobson, and R. Overstreet. 1961. Uptake of calcium by excised barley roots. Plant Physiol. 36:53-57.

89. Motes, J. E. 1977. Pickling cucumbers. Production and harvesting. Extension Bulletin E-837, Cooperative Extension Service, Michigan State University.

90. Mullins, C. A. and J. D. Wolt. 1983. Effects of calcium and magnesium lime sources on yield, fruit quality, and elemental uptake of tomato. J. Amer. Soc. Hort. Sci. 108(5):850-854.

91. Nieuwhof, M., F. Garretsen, and D. Wiering. 1960. Internal tipburn in white cabbage. II. The effect of some environmental factors. Euphytica 9:275-280.

92. Ortega, D. G. and D. W. Kretchman. 1982. Water stress effects on pickling cucumber. J. Amer. Soc. Hort. Sci. 107(3):409-412.

93. O'Sullivan, J. 1980. Irrigation, spacing and nitrogen effects on yield and quality of pickling cucumbers grown for mechanical harvesting. Can. J. Plant Sci. 60:923-928.

94. Palzkill, D. A. and T. W. Tibbitts. 1977. Evidence that root pressure flow is required for calcium transport to head leaves of cabbage. Plant Physiol. 60:854-856.

95. Perring, M. A. 1979. The effects of environment and cultural practices on calcium concentration in the apple fruit. Commun. Soil Sci. Plant Anal. 10(1&2): 279-293.

96. Pharr, D. M., S. C. Huber, and H. N. Sox. 1985. Leaf carbohydrate status and enzymes of translocate synthesis in fruiting and vegetative plants of Cucumis sativus L. Plant Physiol. 77:104-108.

97. Picken, A. J. F. 1984. Quantitative morphology of the developing cucumber leaf. Ann. Bot. 53:527-539.

98. Poovaiah, B. W. 1979. Role of calcium in ripening and senescence. Commun. Soil Sci. Plant Anal. 10(1& 2):83-88.

99. Poovaiah, B. W. 1985. Role of calcium and calmodulin in plant growth and development. HortScience 20 (3):347-352.

100. Raven, J. A. 1977. H^+ and Ca^{2+} in phloem and symplast:Relation of relative immobility of the ions to the cytoplasmic nature of the transport paths. New Phytol. 79:465-480.

101. Redmond, W. J. 1975. Transport of calcium in apple trees and its penetration into the fruit. Commun. Soil Sci. Plant Anal. 6(3):261-272.

102. Ringoet, A., G. Sauer, and A. J. Gielink. 1968. Phloem transport of calcium in oat leaves. Planta 80:15-20.

103. Rorison, I. H. and D. Robinson. 1984. Calcium as an environmental variable. Plant, Cell and Environ. 7: 381-390.

104. Sachan, R. S. and R. B. Sharma. 1981. Calcium absorption as an index of root parameters of cucumber (Cucumis sativus L.). Plant Soil 59:129-133.

105. Sams, C. E. and W. S. Conway. 1984. Effect of calcium infiltration on ethylene production, respiration rate, soluble polyuronide content, and quality of 'Golden Delicious' apple fruit. J. Amer. Soc. Hort. Sci. 109(1):53-57.

106. Schapendonk, A. H. C. M. and P. Brouwer. 1984. Fruit growth of cucumber in relation to assimilate supply and sink activity. Sci. Hort. 23:21-33.

107. Schapendonk, A. H. C. M., H. Challa, P. W. Broekharst, and A. J. Udink Ten Cate. 1984. Dynamic climate control; an optimization study for earliness of cucumber production. Sci. Hort. 23: 137-150.

108. Shear, C. B. 1975. Calcium nutrition and quality in fruit crops. Commun. Soil Sci. Plant Anal. 6(3):233-244.

109. Shear, C. B. 1975. Calcium-related disorders of fruits and vegetables. HortScience 10(4):361-365.

110. Shear, C. B. and M. Faust. 1970. Calcium transport in apple trees. Plant Physiol. 45:670-674.

111. Shear, C. B. and M. Faust. 1971. Value of various tissue analyses in determining the calcium status of the apple tree and fruit, p. 75-98. In: R. M. Samish (ed.). Recent advances in plant nutrition. Gordon and Breach, New York.

112. Simon, E. W. 1978. The symptoms of calcium deficiency in plants. new Phytol. 80:1-15.

113. Sinnott, E. W. 1939. A developmental analysis of the relation between cell size and fruit size in cucurbit fruits. Amer. J. Bot. 26(4):179-189.

114. Sinnott, E. W. 1945. The relation of growth to size in cucurbit fruits. Amer. J. Bot. 32(7):439-446.

115. Smittle, D. A. and R. E. Williamson. 1977. Effect of soil compaction on nitrogen and water use efficiency, root growth, yield, and fruit shape of pickling cucumbers. J. Amer. Soc. Hort. Sci. 102(6):822-825.

116. Snaydon, R. W. and A. D. Bradshaw. 1961. Differential response to calcium within the species Festuca ovina L. New Phytol. 60:219-234.

117. Spiers, J. M. 1983. Elemental leaf content and deficiency symptoms in rabbiteye blueberries. 2. Calcium and magnesium. J. Plant Nutr. 6(12):1073-1086.

118. Stahly, E. A. 1986. Time of application of calcium sprays to increase fruit calcium and reduce fruit pitting of apples sprayed with TIBA. HortScience 21 (1):95-96.

119. Staub, J. 1985. Personal communications with Irvin Widders.

120. Stosic, V., C. Penel, D. Marme, and H. Greppin. 1983. Distribution of calmodulin-stimulated Ca^{2+} transport into membrane vesicles from green spinach leaves. Plant Physiol. 72:1136-1138.

121. Sundstrom, F. J. and S. J. Carter. 1983. Influence of K and Ca on quality and yield of watermelon. J. Amer. Soc. Hort. Sci. 108(5):879-881.

122. Tachibana, Y. and Y. Ohta. 1983. Root surface area, as a parameter in relation to water and nutrient uptake by cucumber plant. Soil Sci. Plant Nutr. 29(3): 387-392.

123. Tandon, D. K. and S. K. Kalra. 1984. Pectin changes during the development of mango fruit cv Dashehari. J. Hort. Sci. 59(2):283-286.

124. Teramura, A. H., M. Tevini, and W. Iwanzik. 1983. Effects of ultraviolet-B irradiation on plants during mild water stress. I. Effects on diurnal stomatal resistance. Physiol. Plant. 57:175-180.

125. Tibbitts, T. W. and D. A. Palzkill. 1979. Requirement for root-pressure flow to provide adequate calcium to low-transpiring tissue. Commun. Soil Sci. Plant Anal. 10(1&2):251-257.

126. Tibbitts, T. W., R. Setiamihardja, D. P. Palzkill, and D. M. Olszyk. 1983. Calcium-related leaf necrosis of seedling carrots. J. Amer. Soc. Hort. Sci. 108(6):1017-1019.

127. Tromp, J. 1979. The intake curve for calcium into apple fruits under various environmental conditions. Commun. Soil Sci. Plant Anal. 10(1&2):325-335.

128. True, R. H. 1922. The significance of calcium for higher green plants. Science 55:1-6.

129. Tukey, L. D. 1964. A linear electronic device for continuous measurement and recording of fruit enlargement and contraction. Proc. Amer. Soc. Hort. Sci. 84:653-660.

130. Van de Geijn, S. C. and C. M. Petit. 1979. Transport of divalent cations. Cation exchange capacity of intact xylem vessels. Plant Physiol. 64:954-958.

131. Vanderhoef, L. N. and T. Kosuge. 1984. The molecular biology of plant hormone action: research directions for the future. Amer. Soc. of Plant Physiologists, p. 31-33.

132. van de Vooren, J., P. J. A. L. de Lint, and H. Challa. 1978. Influence of varying night temperatures on a cucumber crop. Acta Hort. 87:249-255.

133. van Egmond, F. 1979. Fate of calcium in the sugarbeet plant. Commun. Soil Sci. Plant Anal. 10(1&2): 311-323.

134. Wallace, A. and S. M. Soufi. 1975. Low and variable critical concentrations of calcium in plant tissues. Commun. Soil Sci. Plant Anal. 6(3):331-337.

135. Waters, W. E. and V. F. Nettles. 1961. The influence of hydrated lime and nitrogen on the yield, quality, and chemical composition of the Charleston Gray watermelon. Proc. Amer. Soc. Hort. Sci. 77: 503-507.

136. Weather Service Bureau, 1984, Michigan State University, Horticulture Research Center, East Lansing, Michigan.

137. Widders, I. and H. Price. 1984. The effects of plant density on the mineral nutrition of two pickling cucumber cultivars, Tamor and Castlepik. Michigan State University Research Report, 18 p.

138. Wieneke, J. 1979. Calcium transport and its microautoradiographic localization in the tissue. Commun. Soil Sci. Plant Anal. 10(1&2):237-250.

139. Wiersum, L. K. 1966. Calcium content of fruits and storage tissues in relation to the mode of water supply. Acta Bot. Neerl. 15:406-419.

140. Wiersum, L. K. 1979. Effects of environment and cultural practices on calcium nutrition. Commun. Soil Sci. Plant Anal. 10(1&2):259-278.