This is to certify that the

thesis entitled

HORMONAL, METABOLIC AND PHYSIOLOGICAL CHANGES IN CELERY PETIOLES DURING THE INDUCTION OF PITH

presented by

Michelle K. Mitchell

has been accepted towards fulfillment
of the requirements for

M.S. degree in Horticulture

Hugh C. Price
Major professor

Date 8/9/82

O-7639

HORMONAL, METABOLIC AND PHYSIOLOGICAL CHANGES IN CELERY PETIOLES DURING THE INDUCTION OF PITH

By

Michelle K. Mitchell

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Horticulture

1982

ABSTRACT

HORMONAL, METABOLIC AND PHYSIOLOGICAL CHANGES IN CELERY PETIOLES DURING THE INDUCTION OF PITH

By

Michelle K. Mitchell

Abscisic acid (ABA) applied at 10^{-6}, 10^{-5}, 10^{-4} M or benzyladenine (BA) at 5, 10 or 20 ppm, as either a soil drench at 50-ml per 20-cm pot or a foliar spray did not increase pith development, nor did removal of various amounts of the roots or leaves. Metabolic changes were followed during a four day stress of celery petioles. Electrolyte leakage (EL) and CO_2 production increased after one day of wilting, while water content (WC) decreased. Upon rehydration, EL and WC returned to normal, but CO_2 production remained high. A second period of wilting increased electrolyte leakage from stressed tissue, and resulted in significant correlations between pith severity and WC, EL and CO_2 production. Electrolyte leakage remained high following rehydration, indicating that the tissue was no longer capable of complete repair. Ethylene production increased in stressed petioles following one wilting; however, by the fourth day of the experiment no treatment differences were apparent. Ethylene production was never correlated with pith severity and ethephon application did not induce pith.

To those who quest for knowledge

ACKNOWLEDGMENTS

The guidance and encouragement of Dr. Hugh C. Price is gratefully acknowledged. I would like to thank my committee members, Drs. Frank G. Dennis, Jr. and Clifford J. Pollard for their input, assistance and editing.

A special thank you is extended to Mrs. Christine Reynolds whose attentiveness to the growth and maintenance of the plant material is appreciated. I am also grateful to all of my fellow graduate students who have helped and encouraged me, especially Mr. James Wolpert who was willing to help a novice.

Last but not least, I would like to thank my parents who have made it all possible.

TABLE OF CONTENTS

SECTION I

BENZYLADENINE, ROOT AND LEAF REMOVAL: LACK OF EVIDENCE FOR THEIR IMPORTANCE IN PITH FORMATION IN CELERY

SECTION II

WATER CONTENT, ELECTROLYTE LEAKAGE, AND CO_2 AND ETHYLENE PRODUCTION IN CELERY PETIOLES AS AFFECTED BY WATER STRESS

APPENDIX

LIST OF TABLES

Table Page

SECTION I

SECTION II

LIST OF FIGURES

Figure Page

SECTION I

SECTION II

APPENDIX

LITERATURE REVIEW

Celery (*Apium graveolens* L. var. dulce, Pers.) is a member of the Umbelliferae family; it exhibits a biennial flowering habit and is amorphic (the petiole morphology changes with each new leaf). In the first year a well developed root system, a short crown stem and a rosette of leaves are produced. In the second year, if vernalization has occurred, the seed stalks elongate and become greatly branched, producing a shrubby plant 2-3 feet tall (Hayward 1947).

Anatomy of the Celery Petiole

The edible portion of the celery plant is the petiole, anatomically a part of the leaf structure. The crescent-shaped petioles occur in a whorl around the stem, overlapping at the stem junction due to their broadened bases.

The abaxial surface of the petiole is prominently ribbed. The ribs are collenchyma strands which provide mechanical strength for the petioles. The strands are the major contributors to the characteristic stringiness associated with celery (Esau 1936). The adaxial surface, in contrast, is smooth and does not contain collenchyma strands; instead reinforcement is achieved by the heavily thickened cell walls of the 2-3 layers of subepidermal parenchyma cells (Hayward 1947). Stomata occur on both the abaxial and adaxial surfaces, with the greatest number on the abaxial surface. The stomata on the abaxial surface are arranged in rows in the furrows between the ridges of collenchyma strands. The outer epidermal cell walls are thickened to form a well-defined cuticle. These cells exhibit considerable irregularity in shape; in general they are quadrangular with the greatest dimension being parallel to the long axis of the petiole (Hayward 1947).

The mesophyll layer of the petiole consists of parenchymatous cells having large intercellular spaces. The principal vascular bundles lie in a semicircle immediately inside the collenchymatous strands, with the phloem caps directed toward the abaxial surface. Minor vascular bundles can be found between the major bundles, depending on the cultivar. Numerous oil ducts occur in the phloem with general distribution throughout the parenchymatous tissue adaxial to the main vascular semicircle (Hayward 1947).

General Growth Characteristics of Celery

During the first 80 days of growth (120 day crop), only 2% of the final fresh weight of the whole plant is added. Approximately 50% of the final fresh weight is gained during the 21 days prior to harvest. During this dramatic increase in fresh weight the percent dry weight actually decreases (Zink, 1963). Burdine, et al. (1961) suggest that following a rapid growth phase of 3-4 weeks (approximately 70-91 days after transplanting) celery plants enter a 2-3 week rest period. During this time there is no net increase in fresh weight; in fact the petiole size actually decreases. This rest stage coincides with the period of pith development. Because the rest period is accompanied by actual weight loss; the authors suggest that the metabolic processes within the plant are changing.

Total N, Mg and Na tend to decrease as the plants approach marketable maturity. Ca levels remain relatively constant, while P and K fluctuate throughout the entire growing season. Maximum nutrient uptake coincides with the period of maximum growth rates (Zink 1963).

Comparisons Between Harvested and Stored Celery

Tissue potassium levels do not differ between outer and inner petioles at harvest or during storage. Nitrate N and alcohol insoluble solids are higher in outer than in inner petioles at harvest (Hall 1957).

Metabolic functions continue during the storage of celery with more activity occurring at 13° C (70° F) than at 4° (40° F). Hall (1957) reported greater dry weight increases in outer petioles than in inner or heart petioles when stored for one week at 4°. However, at 13° dry weight increases were as great in the heart petioles, as in the outer petioles.

Storage of petioles at 4° or 13° increases total sugars, reducing sugars, and sucrose with the largest increases occurring at 13°, as compared to levels prior to storage. Sugars increase to the greatest extent in heart petioles with somewhat smaller increases in the inner and very little change in the outer petioles (Hall 1957). Some translocation of sugars occurs. Since there are no significant decreases in sugar content of the outer petioles it is unlikely that translocation from other petioles is occurring. The sugars are probably transported from the stem (a storage organ) to the heart petioles, the major sink, and to a lesser extent into the inner petioles. White-Stevens (1935) reported a decrease in reducing sugar, starch and total carbohydrates, measured as total hexose, in the crown during the first 35 days of storage.

Organic N is utilized during storage. At harvest the heart petioles contain the highest amount and the outer petioles the least. Organic N decreases in the outer and inner petioles during the first week of storage, while increasing in the heart petioles. On the other hand, crude fiber increases more in outer than in heart petioles.

Pithiness in Celery

General

Millions of dollars worth of celery are lost each year due to breakdown of the tissue. Generally, this occurs during the final weeks prior to harvest, and can be recognized in the field by lacunae and cell collapse at the base of the oldest petioles on the stalk. No other externally visible symptoms are evident. Internally, pith begins as white spots progressing to small lacunae and finally becoming so severe the stalk is completely hollow. Pith is thought to be a physiological rather than a pathological disorder (Aloni and Pressman 1979). Esau (1936) characterized pith as the breakdown of the large parenchyma cells. Hayward (1947) notes:

> "in plants that tend to be pithy, the parenchyma breaks down schizogenously at various points, leaving irregular internal cavities."

Generally, pith development is thought to occur from the base of the petiole upward and from the outer petioles inward.

Two different types of pith have been reported, the first occurring only on older maturing outer petioles, the second affecting all of the petioles when the plant is very young, resulting in total loss. The second type of pith is controlled by a single dominant gene (Emsweller 1932). The first type of pith is of greatest concern, as it is responsible for the economic losses. A new type of pithiness was reported (Prendville 1964), which develops in 12-week old plants and is confined to the oldest, outer petioles. Cultivars exhibiting this type of pith are Utah 15, Utah Golden Crisp, Latham Blanching, Golden Self Blanching, Stoutheart and Golden Marvel.

In the cultivars Utah, Emerson Pascal, Utah 15, Utah 10B, Utah 52-70, Summer Pascal and Utah Pascal, Coyne (1962) associated the development of pith during storage with a decline in fresh and dry weight of the petiole. The decline in fresh weight was largely attributed to moisture loss from transpiration, while increased respiratory activity of pith tissue was thought to be responsible for the decline in dry weight. Increases in the rate of respiration were associated with greater pith development. However, differences in respiratory rates among cultivars were not correlated with cultivar susceptibility, as rapid increases in the respiration rate occurred only after the development of moderate to severe pith. Those cultivars which had the smallest parenchyma cells possessed the greatest resistance to pith (Coyne 1962).

Saline conditions increase the development of pith. Water stress (by deprivation) increases pith within 5 days, while nutrient deficiency and water logging are effective only after 25 days. In general, the relative water content (RWC) tends to decrease with an increase in pith formation. Upon rehydration, after 3 days of water deprivation, the RWC does not increase to that of non-stressed plants (Aloni and Pressman 1979).

Nutritional Factors

Although pith is not considered to be induced by nutrient deficiency, very little data on the effects of nutrition have been published. Burdine and Guzman (1963) found that increasing the nitrogen rate from 0 to 28 kg/ha (0 to 150 lbs/acre) significantly decreased the frequency of pith. The frequency of nitrogen application did not affect pith development and maximum growth was achieved with 14 kg/ha (75 lbs/acre). The authors concluded, that a nutrient balance which keeps the plants vegetative delays pith formation, but did not suggest that low N levels alone were responsible for pith formation. Low calcium levels in celery often induce blackheart, a disorder in which the leaves of the heart petioles turn black and are subsequently infected with secondary rot organisms. Boron deficiency increases the thickness of the ground parenchyma cell walls (Spurr 1957). No data are known which provide evidence for a correlation between levels of any nutrient and pith formation.

Hormonal Regulation

Immersion in benzylaminopurine (BA) improves the appearance and rating values of harvested celery. Although BA slows the rate of deterioration and respiration of celery stored at temperatures ranging from 4-21° C (40-70°F), thus reducing weight losses attributable to respiration (Wittwer et al. 1962), there is no indication that it reduces pith formation.

Gibberellin (GA) applications to celery plants prior to harvest reduce respiration during storage but increase the incidence of pith (Bukovac et al. 1960). The parenchyma cells of GA-treated celery are longer and thinner, and thus may increase pith.

Although GA_3 treatment increases the incidence of pith, pith does not develop when GA_3 is applied in conjunction with aqueous sodium chloride solutions ranging from 0.2% to 1.0%; if the plants are fully rehydrated, after treatment with GA_3 and salt much more pith develops (Aloni and Pressman 1980). The authors concluded that plants treated with salt acquired intrinsic properties which reduced the effect of GA_3, and that plant size was not involved, as the fresh weights of control plants and those treated with the lower concentration of salt were approximately identical.

Aloni and Pressman (1979) suggest that ABA may be responsible for pith formation in celery, for they observed that the abscisic acid (ABA) content of leaves on intact plants increased with water stress. Rehydration lowered the ABA content but not to the original level. ABA application to detached celery petioles increased pithiness in a concentration-dependent fashion.

Ethylene concentrations of 1000 ppm cause splitting of celery petioles along the adaxial surface, increase pithiness, and stimulate respiration (Mack 1927). However, the author did not indicate whether the celery was stored, and if so how long or at what temperature. Although there is no indication that respiration increased during pith development, rot increased and therefore the increased respiration was probably a result of rotting.

Summary

Pithiness in celery occurs prior to harvest and during storage. Both inbalances in fertilization and environmental stresses increase pith. Drought, flooding, ethylene, GA and ABA all reportedly increase the incidence of pith, and rehydration of stressed petioles further accentuates pith. Increased respiration appears only to be an after-effect of severe pith and cell deterioration, but GA can both increase pith and decrease respiration. Despite considerable effort devoted to research on pith in celery, very little information is available on how or why it is formed.

This thesis was undertaken with the following objectives:

1. to determine where pith occurs and how it progresses.
2. to elucidate whether ethylene is responsible for increases in pith.
3. to assess the role of cytokinin in preventing pith.
4. to determine what metabolic changes occur during the induction of pith.

LITERATURE CITED

LITERATURE CITED

Aloni, B. and E. Pressman. 1980. Interaction with salinity of GA_3-induced leaf elongation, petiole pithiness and bolting in celery. Scientia Hort., 13, 135-142.

_______ 1979. Petiole pithiness in celery leaves: Induction by environmental stresses and the involvement of abscisic acid. Physiol. Plant., 47, 61-65.

Bukovac, M.J., S.H. Wittwer and J.A. Cook. 1960. The effect of preharvest foliar sprays of gibberellin on yield and storage breakdown of celery. Quart. Bull. Michigan Agr. Exp. Stat., 42,764-770.

Burdine, H.W., V. L. Guzman and C. B. Hall. 1961. Growth changes in three celery varieties on Everglades organic soils. Proc. Amer. Soc. Hort. Sci., 78, 353-360.

_______ and V.L. Guzman. 1963. Some factors associated with the development of pith in winter grown Everglades celery. Proc. Florida State Hort. Soc., 76, 233-238.

Coyne, D.P. 1962. Chemical and physiological changes in celery in relation to pithiness. Proc. Amer. Soc. Hort. Sci., 81, 341-346.

Emsweller, S.L. 1932. An hereditary pithiness in celery. Proc. Amer. Soc. Hort. Sci., 29, 480-485.

Esau, K. 1936. Ontogeny and structure of collenchyma and of vascular tissues in celery petioles. Hilgardia, 10, 432-465.

Hall, C.B. 1957. Composition and organoleptic evaluation of portions of celery stalks. Proc. Florida State Hort. Soc., 70, 204-208.

Hayward, H.E. 1947. The structure of economic plants. p. 451-484. MacMillan, New York.

Mack, W.B. 1927. The action of ethylene in accelerating the blanching of celery. Plant Physiol, 2, 103.

Prendville, M. 1964. Hollow stem in very young celery plants. Nature, 202, 1238-1239.

Spurr, A.R. 1957. The effect of boron on cell wall structure in celery. Amer. Jour. Bot., 44, 637-650.

White-Stevens, R.H. 1936. Observations on the changes of pectic substances and sugars in celery during cold storage. Sci. Agr., 17, 128-136.

Wittwer, S.H., R.R. Dedolph, V. Tuli and D. Gilbart. 1962. Respiration and storage deterioration in celery (*Apium graveolens* L.) as affected by post-harvest treatments with N^6 benzylaminopurine. Proc. Amer. Soc. Hort. Sci., 80, 408-416.

Zink, F.W. 1963. Rate of growth and nutrient absorption of celery. Proc. Amer. Soc. Hort. Sci., 82, 351-357.

SECTION I

BENZYLADENINE, ROOT AND LEAF REMOVAL: LACK OF EVIDENCE FOR THEIR IMPORTANCE IN PITH FORMATION IN CELERY

BENZYLADENINE, ROOT AND LEAF REMOVAL: LACK OF EVIDENCE FOR THEIR IMPORTANCE IN PITH FORMATION IN CELERY

M. K. Mitchell and H. C. Price[1]
Department of Horticulture
Michigan State University
E. Lansing, Michigan 48824

Additional index words: Apium graveolens, pithiness, stress, abscisic acid

Abstract: Abscisic acid (ABA) at 10^{-6}, 10^{-5} or 10^{-4} M, or benzyladenine (BA) at 5, 10 or 20 ppm, applied as either a soil drench at 50-ml per 20-cm pot or a foliar spray did not increase pith development, nor did removal of various amounts of the roots or leaves.

Celery (*Apium graveolens* L. var dulce) develops an economically devastating disorder, termed "pith". In its earliest stages pith appears as small white areas either between the vascular bundles or in the center of the petiole. As it progresses, cells continue to collapse and eventually the entire petiole becomes hollow. Pith is thought to be a physiological rather than a pathological disorder (1), which develops schizogenously throughout the petiole (9), and involves the breakdown of the large parenchyma cells (6). Generally pith occurs (at harvest) as the plants approach maturity, occurring first in the outer petioles and moving inward, from the base of the petiole upward (8). Balanced fertilizers which provide adequate nitrogen for growth delay the development of pith during the growing season, but once the plants reach maturity previous treatments are ineffective in preventing its formation (8). Burdine and Guzman (3) report a rest period of 2-3 weeks in the growth of celery in which petiole size decreases and pith

---

[1] Graduate research assistant and Professor, respectively

development begins. Flooding, nutrient deficiency, and particularly drought stress reportedly induce pith (1), leading to the hypothesis that pith is a senescence phenomenon. Abscisic acid (ABA) normally promotes senescence (21). Under stress conditions induced by water deprivation or osmotic solution endogenous levels of ABA increase (1,15). ABA decreases transpirational rates in tobacco plants (15), closes stomates in detached barley and wheat leaves (14), and increases pith in detached celery petioles (1). Mizrahi (15) suggested that stress, whether achieved through water deprivation or high osmotic stress, changes the cytokinin to ABA ratio in the leaf. Stressed sunflower plants exude less kinetin-like substances from severed stems than do non-stressed plants (12).

Chibnall (4) was the first to suggest that root hormones inhibit leaf senescence by regulating leaf protein metabolism. Cytokinins have since been implicated as being the active factor (20). In several cases, cytokinins are capable of replacing roots; for example, they promote the retention and development of inflorescences on unrooted grape cuttings, as well as branching of inflorescences in cultured explants of <u>Carex</u> <u>flacca</u> (20).

Evidence has accumulated indicating that leaves are capable of synthesizing and/or transforming cytokinins (10,11), and Mizrahi, et al. have hypothesized that leaf water content is the primary signal for modification of the plant hormone system (16). Endogenous cytokinin levels in leaf tissue decrease both with the approach of maturity and under conditions of water stress (2,13).

BA application restores the incorporation of leucine into protein in stressed tobacco leaf discs (2), and prevents the decline of RNA and protein synthesis in stressed sugar beet leaves. Aging of plant tissue is accompanied by reductions in the levels of protein and RNA (17), and senescence can be delayed in intact bean plants by treatment with BA (7).

Our purpose was to determine what effect ABA, root pruning, leaf removal and BA might have on pith formation in celery.

Materials and Methods

All of the experiments were conducted on celery plants (Florida 683) grown from seed in the greenhouse under supplemental lighting. The plants were fertilized weekly, and maintained in an actively growing state prior to treatment. All experiments were conducted on four-month-old plants growing in 20-cm clay pots and arranged in a completely randomized design with three replicates, except where otherwise noted. Pith evaluations were made on a scale from 1-5 as follows: 1-no pith; 2-white areas evident; 3-small holes present; 4-large holes scattered about the petiole; 5-hollow center seen. All petioles on the plant were evaluated at five locations: the base, 5-cm from the base, 10-cm from the base, below the first pulvinus and above the first pulvinus. The scores were combined for each plant and subjected to standard analysis of variance techniques.

Stress treatments consisted of alternatively wilting (by withholding water) and rewatering for 2-3 cycles per week, which previous studies indicated was sufficient time for pith to develop.

Experiment 1

ABA (10^{-4}, 10^{-5} or 10^{-6} M) was applied either as a 50-ml soil drench or as a foliar spray, water being applied to the control plants. The plants were watered normally and evaluated three and seven days after treatment. The data were analyzed separately for each evaluation date.

Experiment 2

Two separate root pruning experiments were conducted. In both experiments the following amounts of the root system were removed: half removed horizontally; half removed longitudinally; three-quarters removed horizontally. The control plants were not pruned. In the first experiment three-month-old plants were watered normally and no wilting occurred. The experiment was conducted for one week and replicated four times. In the second experiment four-month-old plants were stressed for one week prior to evaluation.

Experiment 3

Various amounts of leaf area were removed by severing all leaves distal to a given pulvinus. The amounts of leaf area removed were: none; all leaves distal to the outermost pulvinus (1); all leaves distal to the second pulvinus; all leaves distal to the third pulvinus. The plants were evaluated following a one week period of stress.

Experiment 4

In the final experiment BA (5, 10 or 20 ppm) was applied either as a 50-ml soil drench or as a foliar spray to run-off, with water serving as a control. The plants were evaluated after one week of stress.

Results and Discussion

ABA applied to whole plants either as a drench or foliar spray had no effect on pith formation (Table 1). Aloni and Pressman (1), using the same concentrations of ABA, reported a concentration-dependent increase in pith development following continuous incubation. In our study only one application was made, hence all of the ABA may have been metabolized and therefore was not available for transport.

Removal of large amounts of the root system did not increase pith when the plants were maintained on a daily watering schedule (Experiment 1 Table 2). However, pith readily developed following stress in all treatments including the control, suggesting that stress itself contributed more to pith development than did either the roots or factors produced in the roots (Experiment 2 Table 2). Removal of various amounts of the leaf area also had no significant effect on the development of pith (Table 3), although all treatments gave higher values than the control.

If a deficiency of cytokinins or a reduction in the cytokinin/ABA ratio induced by water stress caused pith formation, applications of BA should partially or wholly offset the effects of the stress. However, BA had no effect (Table 4). This inactivity could be due to insufficient uptake or to metabolism. However, BA dips at the same concentrations were effective in reducing respiration and improving appearance ratings of stored celery (22).

Three-quarters of the root system was removed with no detectable effect on pith formation. Such a treatment should greatly reduce the amount of cytokinin moving from the root system

Table 1. Effect of abscisic acid, applied as a soil drench or as a foliar spray, on pith development[z] in petioles of intact celery plants.

	Pith Severity			
	Time of evaluation (days after treatment)			
	Three		Seven	
ABA (M)	Spray	Drench	Spray	Drench
0	2.48	2.28	2.64	2.37
10^{-6}	2.51	1.75	2.76	2.84
10^{-5}	2.07	2.53	2.55	2.59
10^{-4}	2.28	2.24	2.48	3.31

[z] Rated from 1 (no pith) to 5 (hollow petiole). Treatment effects non-significant at the 5% level.

Table 2. Effect of root removal on pith development in petioles of intact celery plants.

	Pith Score[z]	
Treatment	Experiment 1 (plants not stressed)	Experiment 2 (plants stressed)
Control	1.44	4.14
3/4 Roots removed horizontally	1.12	4.19
1/2 Roots removed horizontally	1.14	4.21
1/2 Roots removed longitudinally	1.53	4.21

[z] Rated from 1 (no pith to 5 (hollow petiole). Treatment effects non-significant at the 5% level.

Table 3. Effect of leaf removal on pith development in petioles of intact celery plants.

Pulvinus location of leaf removal	Pith rating[z]
Control	2.77
First	3.40
Second	3.56
Third	2.92

[z]Rated from 1 (no pith) to 5 (hollow petiole). Treatment effects are non-significant at the 5% level.

Table 4. Effect of benzyladenine, applied as a soil drench or as a foliar spray, on pith development[z] in petioles of intact celery plants.

	Method of application	
Benzyladenine (ppm)	Foliar	Drench
0	2.69	2.52
5	2.57	2.48
10	2.36	2.58
20	2.78	3.09

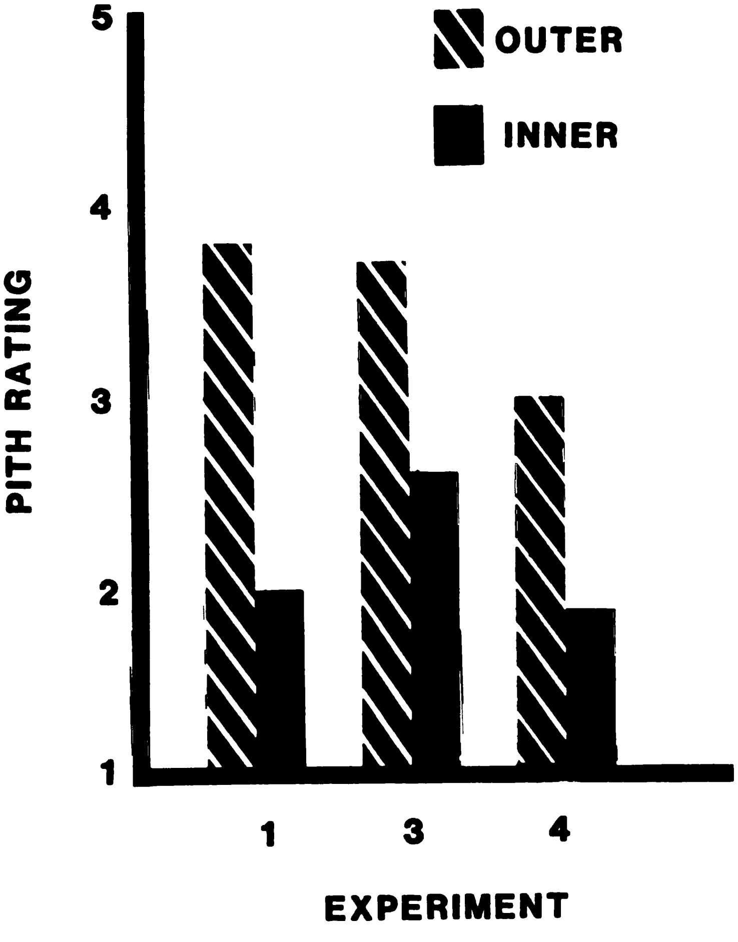
[z]Rated from 1 (no pith) to 5 (hollow petiole). Treatment effects are non-significant at the 5% level.

through the xylem. Yet pith developed only when the plants were subjected to drought stress, and pith formation was independent of the area of root present.

If the leaves are more important in cytokinin production than the roots, leaf removal should stimulate pith formation, but it did not. Thus, the results of these experiments do not indicate that pith is a result of lower cytokinin levels.

Throughout all of these experiments the outer petioles developed significantly more pith than did the inner petioles (Figure 1). The inner petioles wilted to the same degree as the outer petioles, yet little pith developed. Thus, either the inner petioles were not physiologically mature enough for cellular breakdown to occur, or the parenchyma cells were not large enough for pith to develop. Coyne (5) found that those cultivars with the smallest parenchyma cells were the most resistant to pith formation. Petiole enlargement is a function of cell enlargement due to water uptake; when the plants are small cell size is small and as the petioles enlarge the cells also enlarge. As the cells enlarge they may lose their elasticity and the shock of water loss coupled with rehydration may result in cellular breakdown. However, Prendville (18) reported pith development in outer petioles of 12-week old plants. Therefore, an age-size interaction may be involved in pith formation. Pith is obviously not a simple disorder and much more work is needed to elucidate its cause.

Figure 1. Pith formation in outer vs. inner petioles of celery in three different experiments. Evaluations were made seven days following treatment and values for the outer and inner petioles are pooled over all of the experiments.


5
4
3
2
1
PITH RATING
OUTER
INNER
1
3
4
EXPERIMENT

LITERATURE CITED

LITERATURE CITED

1. Aloni, B. and E. Pressman. 1979. Petiole pithiness in celery leaves: Induction by environmental stresses and the involvement of abscisic acid. Physiol. Plantarum, 47, 61-65.

2. Ben-Zioni, A., C. Itai, and Y. Vaadia. 1967. Water and salt stresses, kinetin and protein synthesis in tobacco leaves. Plant Physiol., 42, 361-365.

3. Burdine, H.W. and V.L. Guzman. 1963. Some factors associated with the development of pith in winter grown Everglades celery. Proc. Florida State Hort. Soc., 76, 233-238.

4. Chibnall, A.C. 1939. Protein metabolism in the plant. Yale Univ. Press, New Haven Connecticut.

5. Coyne, D.P. 1962. Chemical and physiological changes in celery in relation to pithiness. Proc. Amer. Soc. Hort. Sci., 81, 341-346.

6. Esau, K. 1936. Ontogeny and structure of collenchyma and of vascular tissues in celery petioles. Hilgardia, 10, 432-465.

7. Fletcher, R.A. 1969. Retardation of leaf senescence by benzyladenine in intact bean plants. Planta, 89, 1-8.

8. Guzman, V.L., H.W. Burdine, E.D. Harris, Jr., J.R. Orsenigo, R.K. Showalter, D.L. Thayer, J.A. Winchester, E.A. Wolf, R.D. Berger, W.G. Genung and T.Z. Zitter. 1973. Celery production on organic soils of south Florida. Florida Agr. Ext. Bull. 757.

9. Hayward, H.E. 1947. The structure of economic plants. p. 451-484 MacMillan, New York.

10. Hewett, E.W. and P.F. Wareing. 1973. Cytokinins in Populus x robusta: Changes during chilling and bud burst. Physiol. Plantarum, 28, 393-399.

11. ______1973. Cytokinins in Populus x robusta: Qualitative changes during development. Physiol. Plantarum, 29, 386-389.

12. Itai, C. and Y. Vaadia. 1965. Kinetin-like activity in root exudate of water-stressed sunflower plants. Physiol. Plantarum, 18, 941-944.

13. ______1971. Cytokinin activity in water-stressed shoots. Plant Physiol., 47, 87-90.

14. Mittelheuser, C.J. and R.F.M. VanSteveninck. 1969. Stomatal closure and inhibition of transpiration induced by (RS)-abscisic acid. Nature, 221, 281-282.

15. Mizrahi, Y., A. Blumenfeld and A.E. Richmond. 1970. Abscisic acid and transpiration in leaves in relation to osmotic root stress. Plant Physiol., 47, 169-171.

16. ______1971. Abscisic acid and cytokinin contents of leaves in relation to salinity and relative humidity. Plant Physiol., 48, 752-755.

17. Osborne, D.J. 1962. Effect of kinetin on protein and nucleic acid metabolism in Xanthium leaves during senescence. Plant Physiol., 37, 595-602.

18. Prendville, M. 1964. Hollow stem in very young celery plants. Nature, 202, 1238-1239.

19. Shah, C.B. and R.S. Loomis. 1965. Ribonucleic acid and protein metabolism in sugar beet during drought. Physiol. Plantarum, 18, 240-254.

20. Skene, K.G.M. 1975. Cytokinin production by roots as a factor in the control of plant growth. p. 365-396. In: J. G. Torrey and D. T. Clarkson (eds.) The development and function of roots. Academic Press, New York.

21. Wareing P.F. and I.D.J. Phillips. 1981. Growth and differentiation in plants. Pergamon Press, New York.

22. Wittwer, S., R.R. Dedolph, V. Tuli and D. Gilbart. 1962. Respiration and storage deterioration in celery as affected by post-harvest treatment with N^6 benzylaminopurine. Proc. Amer. Soc. Hort. Sci., 80, 408-416.

SECTION II

WATER CONTENT, ELECTROLYTE LEAKAGE, AND CO_2 AND ETHYLENE PRODUCTION IN CELERY PETIOLES AS AFFECTED BY WATER STRESS

WATER CONTENT, ELECTROLYTE LEAKAGE, AND CO_2 AND ETHYLENE PRODUCTION IN CELERY PETIOLES AS AFFECTED BY WATER STRESS

M. K. Mitchell and H. C. Price[1]
Department of Horticulture
Michigan State University
E. Lansing, Michigan 48824

Additional index words: *Apium graveolens*, pith

Abstract: Water content (WC), electrolyte leakage (EL), and CO_2 and ethylene production were followed during four days of stress to determine what changes occurred during the induction of pith. EL and CO_2 production increased in celery (*Apium graveolens* L.) petioles after one day of wilting, while WC decreased. Upon rehydration, EL and WC returned to normal, but CO_2 production remained high. A second period of wilting increased electrolyte leakage from stressed tissue, and resulted in significant correlations between pith severity and WC, EL and CO_2 production. Electrolyte leakage remained high following rehydration, indicating that the tissue was no longer capable of complete repair. Ethylene production increased in stressed petioles following one wilting; however, by the fourth day of the experiment no treatment differences were apparent. Ethylene production was never correlated with pith severity and ethephon application did not induce pith.

In celery, *Apium graveolens* L., the physiological disorder, pith, is economically devastating. It has been characterized as the breakdown of large parenchyma cells (10), occurring schizogenously throughout the petiole (12). Pith development occurs first in the outer petioles and moves inward (11,17). Development occurs rapidly following drought or salt stress, but more slowly following flooding or nutrient deprivation (2).

Respiration of stored celery increases with increasing pith, but high respiration rates do not appear to cause pith and cultivars which are resistant to pith tend to have lower respiration rates (8).

---

[1] Graduate research assistant and Professor, respectively

Post-harvest benzyladenine dips reduce respiration and improve the appearance of celery (21), whereas gibberellin applied prior to harvest increases both petiole length and pith while decreasing the respiration rate (7).

Ethylene is considered to be a senescence promoter (20). Stress, whether induced by chemical injury, water deprivation, chilling or flooding, increases ethylene production (4,5,6,14,16,18). Electrolyte leakage increases with both water stress and chilling injury (14,19), and is used to monitor membrane integrity. Ethylene is not believed to disrupt membrane permeability (1). Little information is available concerning specific changes in metabolic processes during the induction of pith by water deprivation. Experiments were therfore conducted to determine what changes occur in respiration, water content, electrolyte leakage, and ethylene production, and ethephon was applied to determine whether high concentrations of ethylene would increase pith formation.

Materials and Methods

Celery plants, cultivar Florida 683, were grown from seed in the greenhouse in clay pots and were maintained on a weekly fertilization schedule until four months of age.

Pith-free petioles were removed from the plants at the soil level. Four petioles were placed in each of 16, two-liter containers containing 200 ml of water. A plastic sheath was placed around the petioles to protect the leaves from excessive transpiration, but was open at the top to allow free gas exchange. The petioles in eight of the 16 containers were sprayed with 10 ppm ethephon daily and maintained in a growth chamber at 22° C for 4 days (the duration of the experiment). The remaining 8 containers were placed in a separate growth chamber at 22° C to prevent ethylene contamination. Petioles in 4 containers in each growth chamber were stressed, the remaining 4 were not. Water stress was induced by withholding free water and removing the plastic sheath to reduce the relative humidity, thereby resulting in flaccid petioles. One day (24 hrs) of stress was alternated with one day of rehydration (the petioles were turgid following rehydration), for a total of four days. The following parameters were measured daily for each petiole after cutting into 25 six mm crescents: water content, electrolyte leakage, and CO_2 and ethylene production.

Water content was obtained by subtracting the dry weight (the crescents were dried in a drying oven for at least 24 hrs) of 5 petiole crescents from the fresh weight, and expressing the difference as grams of water per gram of dry weight.

Electrolyte leakage was determined by incubating five celery crescents for 24 hours in 25 ml of distilled water in a test tube. After determining the conductivity of the bathing solution on a Beckman Solu-bridge, the crescents and the solution were heated to 80° C for one hour, then cooled before reading the conductivity again. Values are expressed as conductivity prior to heating as a percentage of that after heating.

Ethylene and CO_2 production rates were obtained by placing five crescents into a 30 ml airtight syringe sealed with a serum cap. Gas samples were taken after one hour, which preliminary experiments indicated was sufficient time to detect treatment differences. CO_2 was analyzed on a 8700 Carle gas chromatograph, and ethylene on a Varian Aerograph Series 1200.

Visual ratings of pith were determined using a severity scale of 1 to 9 as follows: 1-no pith; 3-white areas evident; 5-small holes appearing; 7-holes scattered throughout the petiole; 9-severe pith development affecting the entire petiole. Two, 4, 6 and 8 indicate intermediate stages of development.

All experiments were conducted twice. Analysis of variance was determined separately for each day, and mean separation was performed by orthogonal comparisons (planned F tests).

Results and Discussion

After one cycle of wilting and rehydration, there were no apparent differences among treatments in pith severity (Table 1). However, pith was induced in detached petioles after the second period of wilting (day 3). Rehydration (day 4) allowed the petioles to regain their turgor, but pith severity remained significantly greater than for non-stressed petioles. Ethephon did not affect pith formation in either stressed or non-stressed petioles.

As expected, the water content was significantly lower in the wilted tissue on days one and three (Table 1 and Figure 1A). After the first rehydration (day 2), the difference was not significant. Apparently the cells were capable of fully rehydrating, although some of the water may have accumulated in the intercellular air spaces. After the second rehydration (day 4), the difference was not significant at the 5% level but it was significant at the 10% level. The cells were beginning to lose their ability to completely hydrate, in agreement with the findings of Aloni and Pressman (2) who reported that whole plants are capable of returning

Table 1. Main effects of water stress and ethephon (10 ppm) on pith formation, water content, percent electrolyte leakage, CO_2 and ethylene production in celery petioles.

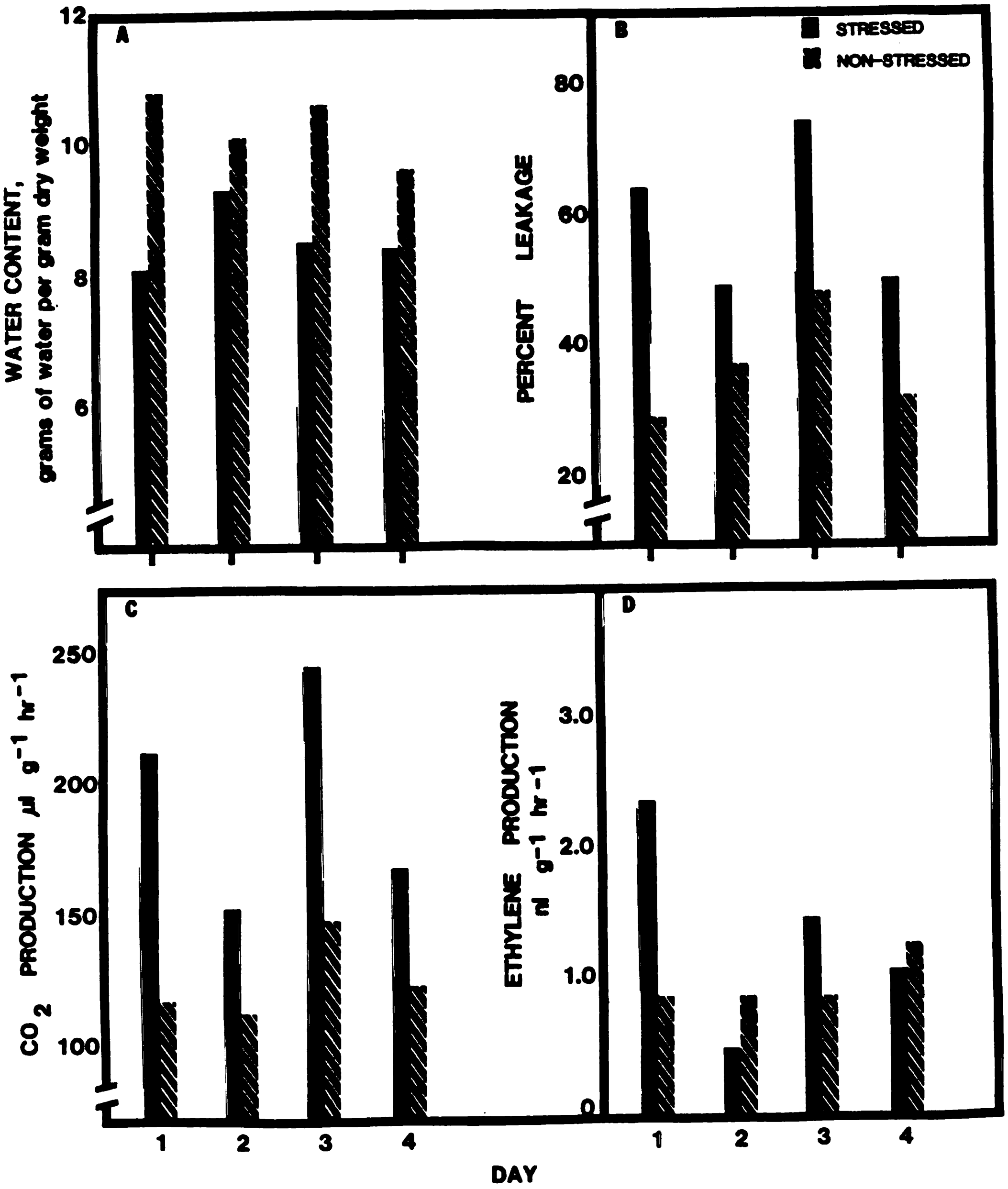
Water Stress	Ethephon (10 ppm)	Day of observation 1	2	3	4
		Pith severity[z]			
0		4	5.5	4.5	6
+		4	6	8***	9***
	0	3.5	5.5	5.7	7.5
	10	4.5	5.7	6.7	7.5
Interaction		NS	NS	NS	NS
		Water content (gram per gram dry weight)			
0		10.88	10.16	10.74	9.74
+		8.23***	9.38	8.62***	8.54*
	0	11.07	9.89	10.28	9.60
	10	8.04	9.64	9.08	8.69
Interaction		NS	NS	NS	NS
		Electrolyte leakage %			
0		28.75	37.00	46.75	31.50
+		64.25***	49.25	74.12***	49.50**
	0	43.75	40.12	58.00	41.50
	10	49.25	46.12	62.88	39.50
Interaction		NS	NS	NS	NS
		CO_2 production ul g^{-1} hr^{-1}			
0		116	112	150	152
+		216	156**	247***	177
	0	121	130	174	158
	10	211	139	223	172
Interaction		***	NS	NS	NS
		Ethylene production nl g^{-1} hr^{-1}			
0		0.934	0.888	0.840	1.271
+		2.404**	0.491***	1.506	1.144
	0	1.752	0.748	0.850	1.273
	10	1.586	0.631	1.496	1.142
Interaction		NS	NS	***	NS

---

[z] Rated from 1 (no pith) to 9 (severe).

*Significantly different from respective controls at 10(*), 5(**) or 1(***) % level by ANOVA.

Figure 1. Effect of water stress on water content (A), electrolyte leakage (B), CO_2 (C) and ethylene production (D) in celery petioles. Stressed petioles were wilted on days one and three and rehydrated on days 2 and 4.


A
B
C
D
■ STRESSED
▨ NON-STRESSED
WATER CONTENT, grams of water per gram dry weight
12
10
8
6
PERCENT LEAKAGE
80
60
40
20
CO$_2$ PRODUCTION µl g^{-1} hr^{-1}
250
200
150
100
ETHYLENE PRODUCTION nl g^{-1} hr-1
3.0
2.0
1.0
0
1
2
3
4
DAY

to the same relative water content as controls when deprived of water for short periods of time (3 days or less) but not when stressed for longer periods of time. Again, the ethephon treatment had no effect on water content, nor was the interaction significant.

The percentage of electrolytes lost after one wilting (day 1), was significantly greater in stressed than in non-stressed petioles (Table 1 and Figure 1B). Stressed petioles lost 64% of their total electrolytes, whereas non-stressed lost only 29%. Upon rehydration (day 2), the differences in electrolyte leakage were non-significant (Table 1), indicating membrane repair had occurred. After a second wilting (day 3), the stressed petioles lost 74% of their total electrolytes, which was significantly greater than 47% lost by the non-stressed petioles. The wilted tissue continued to lose electrolytes after a second rehydration period (day 4), 50% being lost vs. 32% for non-stressed tissue. The additional stress imposed by the second wilting period appeared to have damaged the membranes beyond complete repair. The WC was never significantly correlated with electrolyte leakage. However, in plum leaves water loss is significantly correlated with electrolyte leakage (14). Based on these data wilting induced metabolic changes which subsequently increased electrolyte leakage.

Greater rates of CO_2 production were evident after one wilting (day 1) but the difference was not significant (Table 1). Rehydration (day 2) did not appear to relieve the stress imposed on the petioles, since CO_2 production did not decrease but was significantly greater in stressed tissue (Figure 1C), and remained higher following a second wilt period (day 3). Differences were no longer apparent upon rehydration (day 4). Respiration rates may have fallen either because cellular death occurred, reducing the number of cells capable of respiring, or because the petioles were no longer capable of responding to additional stress. Pith severity was positively correlated with CO_2 production (r=.91) (Table 2) on day 4, therefore the former hypothesis is more probable. Pith also increased in the control petioles during this time, which may account for the lack of difference in respiration. Ethephon increased CO_2 production only in stressed tissue, the interaction between stress and ethephon being significant at 0.1% (Figure 2) level. However, the interaction was not significant on day 3.

Initially (day 1), stressed tissue produced significantly more ethylene than non-stressed (Table 1 and Figure 1D). However, upon rehydration (day 2) stressed tissue produced significantly less ethylene than non-stressed. Since electrolyte leakage was not significant on day 2 the reduction in ethylene production in stressed tissue was probably not due to the membranes inability to sustain ethylene synthesis (membranes are thought to be the site of ACC synthesis, the precurser of ethylene) (13,15). The added ethylene may have acted as a feedback inhibitor inhibiting ethylene biosynthesis. Following a second day of wilting (day 3) the interaction between ethephon and stress was significant, more ethylene being produced following ethephon appliction to stressed vs. non-stressed petioles (Figure 3). After rehydration (day 4) no significant differences between treatments were apparent (Table 1). Ethylene production may have leveled off because the stressed tissue was no longer responsive to additional stress, or the membranes were

Figure 2. Effect of stress and ethephon, applied to the petiole at 10 ppm until run-off, on CO_2 production, after one day of wilting. The interaction is significant at the 1% level.

Figure 3. Effect of stress and ethephon, applied to the petiole at 10 ppm until run-off, on ethylene production, following a second wilt cycle (day 3). The interaction is significant at the 1% level.

disorganized to the extent that they would not sustain ethylene synthesis. The electrolyte data indicate a high degree of cellular leakage on day 4, supporting the latter hypothesis; however, the tissue was capable of producing ethylene in the range of 0.50 - 2.50 nl g^{-1} hr^{-1}, which is a significant amount.

Although ethylene production was higher in stressed tissue, the difference was no more than four fold, which is considered inadequate to account for a physiologically significant hormonal response. The only significant differences in pith ratings were between stressed and non-stressed tissue; ethephon treated petioles did not develop more pith, and ethylene production was never correlated with pith severity. In experiments conducted on whole plants (unreported) ethylene as a gas or ethephon applied either as a foliar spray or a soil drench at physiologically active levels of 1, 5 or 10 ppm did not increase pith development. These data suggest that ethylene does not control pith formation.

During the first two days of the experiment, neither water content, EL or CO_2 production was correlated with pith severity (Table 2). However, following the second wilt period (day 3) all parameters were significantly correlated at the 1% level or higher with pith; WC r=.70 (negative), EL r=.73 and CO_2 r=.65. At this time WC was also significantly correlated with CO_2 production. Upon rehydration (day 4), pith was still significantly correlated with both EL (r=.81) and respiration (r=.91).

Respiration rates were higher in stressed tissues (differences were significant only on days 2 and 3) indicating changing metabolic conditions. Stressing celery leaves reportedly increases their

Table 2. Statistical significance of correlation coefficients (r values) for pith vs. water content, electrolyte leakage and CO_2 production.

	r Value			
Correlation	Day 1	Day 2	Day 3	Day 4
Pith vs. Water content	NS	NS	0.70**	NS
Pith vs. Electrolyte leakage	NS	NS	0.73**	0.81***
Pith vs. CO_2	NS	NS	0.65**	0.91***
Water content vs. CO_2	NS	NS	0.88***	NS

NS non-significant, ** significant at the 1% and *** .1% level.

sensitivity of malate dehydrogenase activity by KCl to a level similiar to mature leaves (3). In contrast to Coyne's (8) findings that respiration of stored celery increased only after pith developed, our data indicate that CO_2 production increases in stressed tissue prior to pith development. Although differences in respiration were not apparent on day 4, pith severity remained significantly correlated with respiration. CO_2 production was not significantly correlated with pith on days 1 and 2; therefore increased respiration rates may be an indication of changing metabolic processes within stressed petioles which in turn result in pith.

Similarily, electrolyte leakage does not appear to cause pith, since the correlations were not significant until after pith developed. The EL data do indicate that a great deal of membrane disruption occurs during wilting and that the membranes become more disorganized with additional stress.

The mechanism for pith development is thought to be the same regardless of how it is induced (2). Water deprivation followed by hydration rapidly brings about pith formation and other metabolic changes, whether these changes are similar to those which occur when pith forms under other conditions remains to be elucidated.

LITERATURE CITED

LITERATURE CITED

1. Abeles, F.B. 1973 Ethylene in plant biology. Academic Press, New York.

2. Aloni, B. and E. Pressman. 1979. Petiole pithiness in celery leaves: Induction by environmental stresses and the involvement of abscisic acid. Physiol. Plantarum 47:61-65.

3. ______E. Pressman and R. Shaked. 1981. Effects of salts on NADH-malate dehydrogenase activity in celery leaves during their maturation and senescence. Plant Sci. Letters 20:239-250.

4. Ben-Yehoshua, S. and B. Aloni. 1974. Effect of water stress on ethylene production by detached leaves of Valencia orange (Citrus sinensis Osbeck). Plant Physiol. 53: 862-865.

5. Bradford, K. 1977. Ethylene production, epinasty, and growth of tomato plants as influenced by root aeration. MS Thesis, Mich. State Univ., E. Lansing.

6. Bressan, R.A., L. LeCureaux, L.G. Wilson, and P. Filner. 1979. Emission of ethylene and ethane by leaf tissue exposed to injurious concentrations of sulfur dioxide or bisulfite ion. Plant Physiol. 63:924-930.

7. Bukovac, M.J., S.H. Wittwer and J.A. Cook. 1960. The effect of preharvest foliar sprays of gibberellin on yield and storage breakdown of celery. Quart. Bull. Michigan Agr. Expt. Stat. 42:764-770.

8. Coyne, D.P. 1962. Chemical and physiological changes in celery in relation to pithiness. Proc. Amer. Soc. Hort. Sci. 81:341-346.

9. Elster, E.F. and J.R. Konze. 1976. Effect of point freezing on ethylene and ethane production by sugar beet leaf discs. Nature 263:351-352.

10. Esau, K. 1936. Ontogeny and structure of collenchyma and of vascular tissues in celery petioles. Hilgardia 10:432-465.

11. Guzman V.L., H.W. Burdine, E.D. Harris,Jr., J.R. Orsenigo, R.K. Showalter, D.L. Thayer, J.A. Winchester, E.A. Wolf, R.D. Berger, W.G. Genung and T.Z. Zitter. 1973. Celery production on organic soils of south Florida. Florida Agr. Ext. Bull. 757.

12. Hayward, H.E. 1947. *The structure of economic plants*. MacMillan, New York.

13. Ismail, H. and D.P. Murr. 1980. Control of ethylene production in apple by calcium. HortScience 15:422. (Abstr.).

14. Kobayashi, K., L.H. Fuchigami, and K.E. Brainerd. 1981. Ethylene and ethane production and electrolyte leakage of water-stressed 'Pixy' plum leaves. HortScience 16:57-59.

15. Lieberman, M. and S.Y. Wang. 1980. Preservation of the ethylene forming system in deteriorating (senescent) postclimacteric apple tissue slices by calcium and magnesium. Plant Physiol. 65:41. (Abstr.).

16. McMichael, B.L., W.R. Jordan and R.D. Powell. 1972. An effect of water stress on ethylene production by intact cotton petioles. Plant Physiol. 49:658-660.

17. Mitchell, M.K. and H.C. Price. Benzyladenine, root and leaf removal: Lack of evidence for their importance in pith formation in celery. Unpublished.

18. Peiser, G.D. and S.F. Yand. 1979. Ethylene and ethane production from sulfur dioxide injured plants. Plant Physiol. 63:142-145.

19. Stergios, B.G. and G.S. Howell, Jr. 1973. Evaluation of viability tests for cold stressed plants. J. Amer. Soc. Hort. Sci 98:325-330.

20. Wareing, P.F. and I.D.J. Phillips. 1981. *Growth and differentiation in plants*. Pergamon Press, New York.

21. Wittwer, S.H., R.R. Dedolph, V. Tuli and D. Gilbart. 1962. Respiration and storage deterioration in celery (*Apium graveolens* L.) as affected by post-harvest treatment with N^6 benzylaminopurine. Proc. Amer. Soc. Hort. Sci. 82:351-357.

APPENDIX I

THE ONTOGENETIC DEVELOPMENT OF PITH IN CELERY PETIOLES

THE ONTOGENETIC DEVELOPMENT OF PITH IN CELERY PETIOLES

There is some discrepancy in the literature concerning the initial location and progression of pith. Generally, pith has been reported to progress from the base of the petiole upward, and from the outer petioles inward (2,3,4). However, Prendville (5) noted more pith 7.5 cm (3") above the base of the petiole, than at the base and Aloni and Pressman (1) found the greatest degree of pith development below the first pulvinus (node) following water stress. My purpose was to trace the development of pith to determine where it first occurs and how it progresses within the petiole.

Materials and Methods

Celery (Apium graveolens L. cv. Florida 683) plants were grown in clay pots (20-cm diameter) in the greenhouse under supplemental lighting. They were fertilized weekly and maintained in an actively growing state. Evaluations began when the plants were four months of age and continued at weekly intervals for a total of five weeks. Each petiole longer than 10-cm, from each of ten plants was removed at the soil level each week and examined at five locations: the base; 5-cm from the base; 10-cm from the base; below the first pulvinus; above the first pulvinus. Pith was evaluated on the following scale: 1-no pith; 2-white areas beginning; 3-small holes; 4-holes scattered throughout the petiole; 5-one large hole through the petiole. The data were pooled and mean values for the ten plants are presented.

Results and Discussion

The greatest amount of pith occurred in the outer petioles decreasing inward regardless of time of sampling (Figure 1 A-E), as previously reported (2,3,4,5). Severity changes were larger in petioles 1-4 than 5-7.

During the first week, pith ratings were higher below than above the pulvinus, which were higher than those 10-cm from the base, which in turn were higher than those at the base or 5 cm from the base. Pith severity was greater near the pulvinus (above and below), the second week, than at the base. However, at week 3 pith severity was greatest above the pulvinus and decreased successively toward the base. The most severe pith continued to be above the pulvinus in the fourth week, whereas the base exhibited intermediate to high pith ratings. At the final evaluation, week five, a good deal of pith had developed in all petiole positions. Severity was greatest above the pulvinus and least at the base and below the pulvinus.

Considerable interaction between location and petiole position make it difficult to draw conclusions, but does account for the discrepency in the literature. Generally, more pith occurs above the pulvinus than at the base. Pith has not been clearly established to form in any particular direction, indeed during the course of this study pith was found midway up the petiole with no formation either distal or proximal to it.

These data do not rule out the role of senescence in pith formation. It is clear that over the five week period the most severe pith occurred in the outer petioles, progressively decreasing

Figure 1.

A-E Effect of celery petiole position (from oldest (1) to youngest (7) on 4-month-old plants) and location on the petiole on pith ratings on a scale from 1 (no pith) to 5 (severe pith). A-week 1, B-week 2, C-week 3, D-week 4, E-week 5.

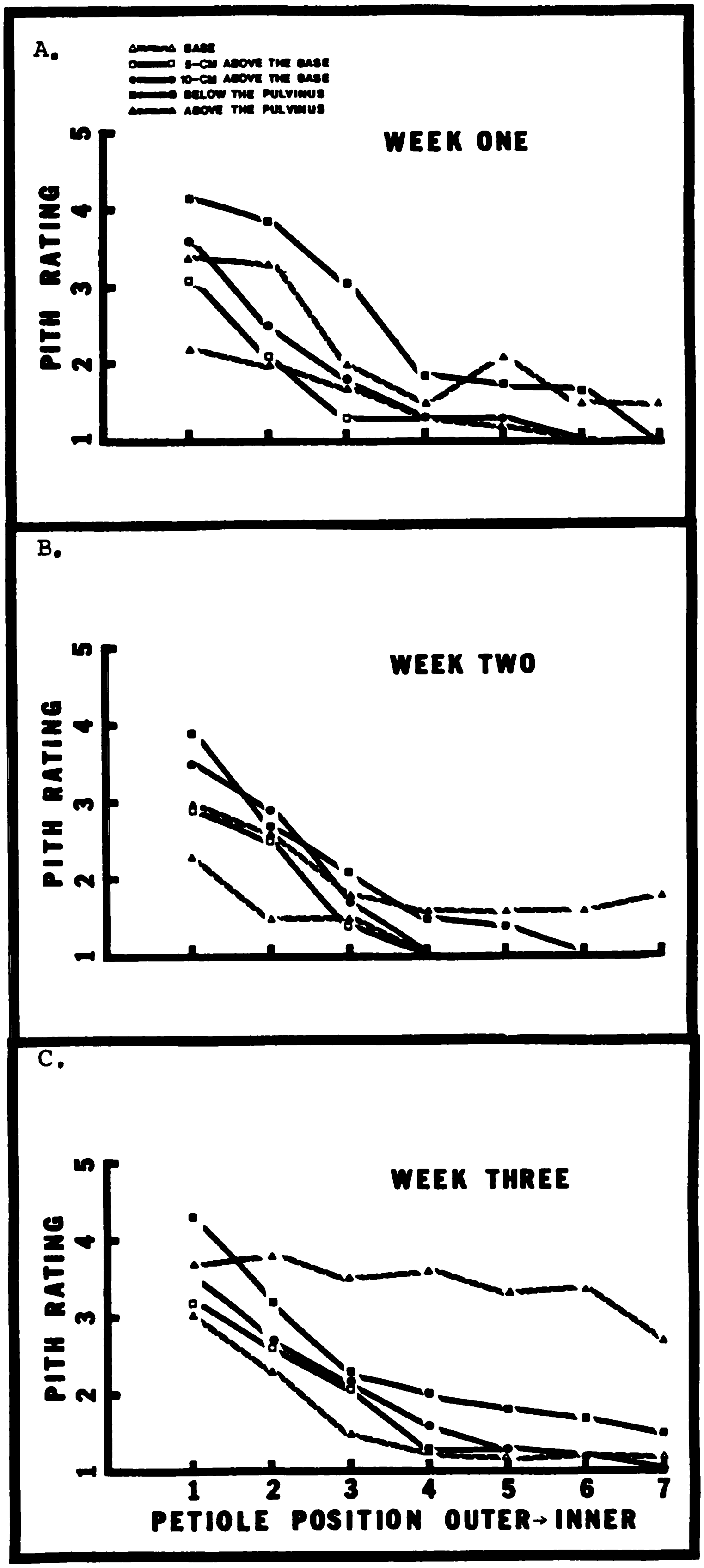
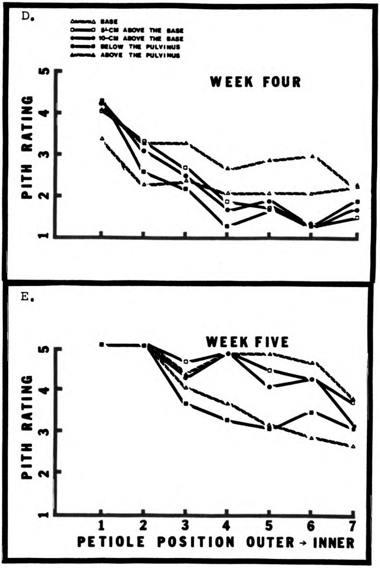

A.
BASE
5-CM ABOVE THE BASE
10-CM ABOVE THE BASE
BELOW THE PULVINUS
ABOVE THE PULVINUS
WEEK ONE
PITH RATING
1
2
3
4
5
B.
WEEK TWO
PITH RATING
1
2
3
4
5
C.
WEEK THREE
PITH RATING
1
2
3
4
5
1
2
3
4
5
6
7
PETIOLE POSITION OUTER→INNER

Figure 1 (cont'd.)



in the inner petioles as found by others (2,3,4,5). The outer petioles, were older and more mature than the inner and considerably more yellowed at the final evaluation, indicating their senescent condition. It is imperative to determine what role senescence plays in pith formation, as well as what stage leaf maturation occurs. Until we understand when pith occurs within the leaf's life cycle, we cannot properly evaluate metabolic or hormonal changes within the petioles or leaves.

LITERATURE CITED

LITERATURE CITED

1. Aloni, B. and E. Pressman. 1979. Petiole pithiness in celery leaves: Induction by environmental stresses and the involvement of abscisic acid. Physiol. Plantarum, 47,61-65.

2. Burdine, H. W. and V. L. Guzman. 1963. Some factors associated with the development of pith in winter grown Everglades celery. Proc. Florida State Hort. Soc., 76, 233-238.

3. Coyne, D.P. 1962. Chemical and physiological changes in celery in relation to pithiness. Proc. Amer. Soc. Hort. Sci., 81, 341-346.

4. Guzman V.L., H.W. Burdine, E.D. Harris, Jr., J.R. Orsenigo, R.K. Showalter, D.L. Thayer, J.A. Winchester, E.A. Wolf, R.D. Berger, W.G. Genung, and T.Z. Zitter. 1973. Celery production on organic soils of south Florida. Florida Agr. Ext. Bull. 757.

5. Prendville, M. 1964. Hollow stem in very young celery plants. Nature, 202, 1238-1239.