Proceedings of the Iowa Academy of Science

Volume 64 | Annual Issue Article 21

1957

The Effect of Mechanical Stimulation On the Collenchyma of Apium graveolens L.

Waldo S. Walker
State University of Iowa

The Effect of Mechanical Stimulation On the Collenchyma of *Apium graveolens* L.

By Waldo S. Walker

Introduction

Although the possibility that mechanical stimulation is a factor in the quantity of strengthening tissue in the stems of plants has been frequently suggested, few experiments have been designed to test this hypothesis. Although some work has been done on tensile strength of collenchyma (Ambronn 1881, Esau 1936, Curtis 1938), very little consideration has been directed to the study of the effect of mechanical stimulation on the structure and/or quantity of this tissue or any of the mechanical tissues of the plant. Venning (1949) reported that wind motion from an electric fan stimulated the development of collenchyma within the petioles of *Apium graveolens* L., but had no effect on the number of collenchyma bundles per petiole. He reported that stimulation by wind motion resulted in larger areas of collenchyma and in an increase in cell wall thickness of the collenchyma.

In Venning's experiment to determine the effects of the stimulation of wind motion on the collenchyma of celery a considerable increase in amount of collenchyma tissue resulted. These results raise another question. If one were able to provide mechanical stimulation with a minimum of wind motion and the resultant transpiration, would the collenchyma tissue respond in the same manner as that subjected to stimulation by the electric fan? In other words, was the response of the collenchyma due to the effect of the increased transpiration brought about by wind motion or was it due to the mechanical stress applied to the tissue through the force of the wind?

The primary purpose of the present investigation was to determine the effect of stimulation by mechanical means on the collenchyma of *Apium graveolens* L. (horticultural varieties Fordhook and Pascal). A secondary objective was to make a comparison of the effects, if present, of such stimulation attained by wind motion from an electric fan with that attained by a mechanical agitator which produced a minimum amount of wind motion. This would assist in the solution of the question raised by Venning's experiment.

Methods and Materials

Two horticultural varieties of celery (Pascal and Fordhook) were transplanted into greenhouse flats of twenty-one plants each. Each plant was 60 days old and approximately 6 inches tall at the beginning of the experiment.

One flat of each variety, which served as a control, was grown under normal greenhouse conditions.

One flat of each variety was subjected to wind motion from a sixteen inch electric fan. The fan was placed approximately three feet from the plants. The flats of celery were turned from day to day to insure an equal amount of wind motion from all sides. The plants were subjected to stimulation from the wind motion of the fan for nine hours per day (8:00 A.M. to 5:00 P.M.). The experiment was continued for 27 days.

One flat of each variety was placed on the platform of a mechanical agitator (Fig. 2). The agitator consisted of a platform mounted on wheels which were set on tracks so that the platform moved in two directions. The agitator was driven by an electric motor equipped with a reduction gear and a series of four large pulleys which made it possible to control the speed of agitation.

The experiment was begun on June 6 and terminated July 2. All three groups of plants were grown in the same room of the greenhouse to insure that the environmental factors for the three groups, with the exception of the introduced mechanical stimulation, were the same. The soil was kept moist throughout the experiment.

Celery was used in this experiment in an attempt to draw a correlation between the results of the writer and the results obtained by Venning. The celery petiole is crescent shaped in cross section. The collenchyma in celery is found in bundles immediately beneath the epidermal layer in the abaxial portion of the petiole. The two lateral edges of the crescent shaped petiole also have a considerable amount of collenchyma tissue (Fig. 3). There are no collenchyma bundles on the adaxial side of the petiole. There were seven to nine bundles of collenchyma in the mature petioles sampled at the termination of the experiment. Plants used in this experiment were grown under greenhouse conditions in rich sandy loam soil. Seeds germinated in approximately two weeks. At sixty days after germination the plants were large enough and of adequate uniformity to begin the experiment.

Samples were taken from all three groups on initiation of the experiment and subsequently on the 7th, 10th, 14th, 20th, and 27th days of the experiment. Forty samplings were made from each group during the experiment. When a plant was sampled it was removed from the respective flat and the two outermost leaves were removed. These leaves were the first leaves formed in the ontogeny of the plant body and did not offer a true representation of the mature celery petiole. Two samples were taken from each of the remaining petioles; one at the base of the petiole just above the petiolar wings

and one at approximately one centimeter below the point at which the first leaflets branch off the petiole.

Several methods were used in an attempt to make permanent mounts of the petiolar sections, but all proved inadequate due to the excessive shrinkage of the cell walls of the collenchyma as a result of dehydration. By the use of fresh mounts a true representation of the appearance of the cell wall was attained.

Free hand sections were used for making the mounts. The sections were cut, then stained in an aqueous solution of ruthenium red, and mounted in water on the slides.

The cross section of the entire petiole along with the collenchyma bundles of each section were outlined at a constant magnification (17 X) on paper by the use of the camera lucida.

Additional drawings of the collenchyma bundles were made at a high magnification (700 X). These drawings displayed the walls of the collenchyma cells in detail. One drawing was made from the most representative collenchyma bundle of each petiole. Upon completion of the experiment, the entire group of drawings was measured with a compensating polar planimeter. The total area of the petiole was measured and recorded. The areas of the collenchyma bundles within the petiole were measured and totaled. The percentage of petiolar area occupied by collenchyma was then computed.

Measurements of the cell wall thickness of the collenchyma were taken from the drawings with the higher magnification. Approximately fifty measurements were taken of the cell walls represented in each drawing. The average cell wall thickness was then computed from these figures.

A separate experiment was performed in an effort to determine the relative amount of transpiration which occurred in the three groups of plants. Six potted celery plants were used for this portion of the experiment. The soil was moistened and then the plots and soil were sealed by wrapping polyethylene plastic around them. The petioles and leaves of the plants were allowed to protrude through the plastic. This insured that the only avenue of water loss from the system would be by the transpiration through the leaves or petioles. The weights of the plants were recorded and then two plants were placed on the agitator, two were placed in front of the fan and two plants were used as a control. After 5 hours the plants were weighed again. The difference in weight between the first weighing and the second weighing expressed in grams the amount of water lost by transpiration of each group. This procedure was repeated three times. A week was allowed to pass between each determination in order to

gain a mean average of the water loss with consideration of variable light conditions and the increase in size of the plants.

Results

Measurements taken from the cross sectional drawings of the celery petioles during the course of the experiment indicated that: 1. the increase in the petiolar area was relatively constant between the three groups tested; 2. the percentage of petiolar area which was occupied by collenchyma showed a significant increase after stimulation by motion induced by the mechanical agitator and the electric fan; 3. the thickness of the collenchyma cell walls also showed a significant increase after such stimulation; 4. the petioles of the two experimental groups showed no increase in the number of collenchyma bundles per petiole over those of the control.

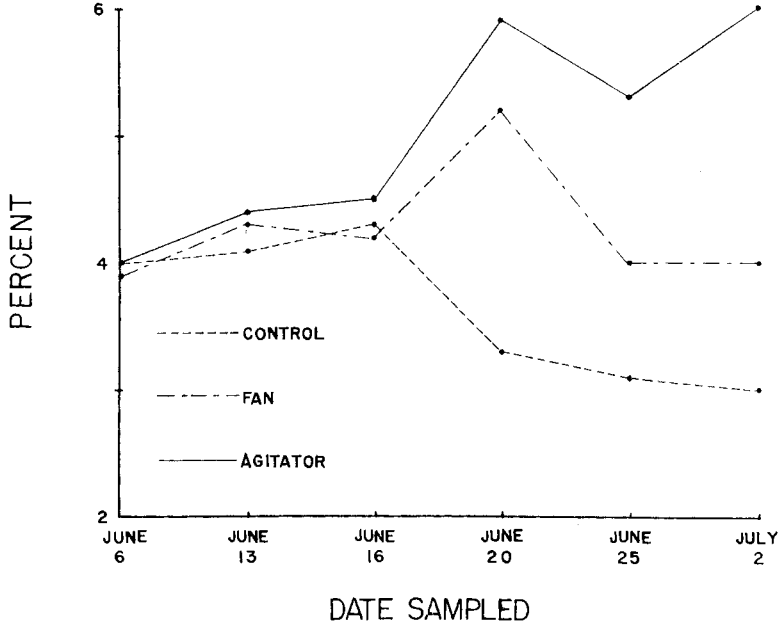

Figure 1. Average percentage of petiolar area occupied by collenchyma bundles determined at sampling dates.

The most striking result of the experiment was the increase in the proportion of the cross sectional area of the petiole which was occupied by collenchyma (Fig. 1). Whereas in the control plants the area of the petiole occupied by collenchyma decreased during the 27-day period of the treatment, the plants stimulated by the motion due to the fan contained essentially the same proportion of collenchyma at the end of the experiment as was present at the beginning

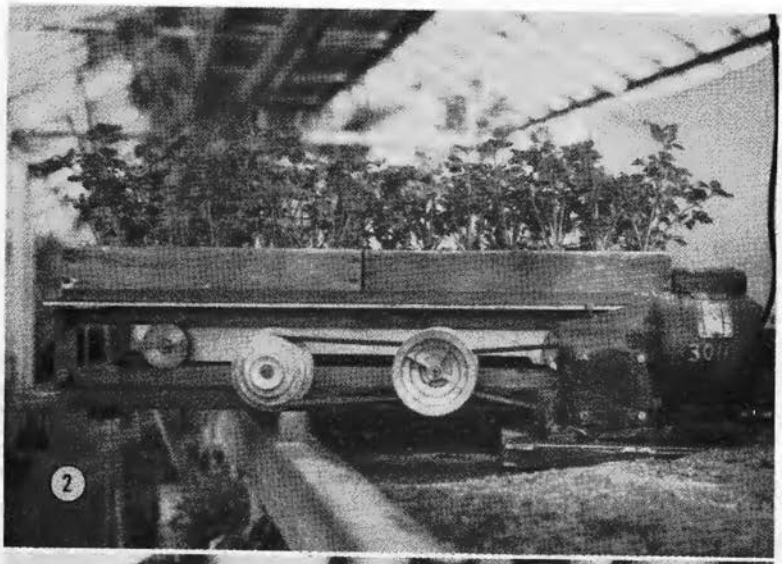

Figure 2. Side view of the mechanical agitator.

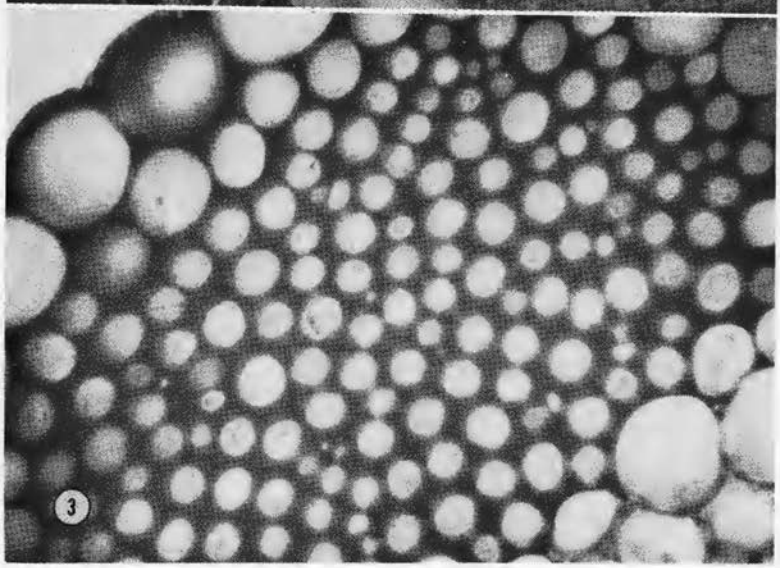

Figure 3. Transverse section of a portion of a celery petiole showing one of the collenchyma bundles. Taken from free-hand section (670 X).

and those stimulated by motion induced by the mechanical agitator showed an increase in the proportion of the petiole differentiated into collenchyma. The magnitude of these results is perhaps more evident when expressed in percentage of increase of the collenchyma in the experimental plants over that of the control. At the end of 27 days the plants which had received motion from the electric fan

had 33 percent more tissue differentiated into collenchyma than those of the control group while those agitated by the shaking table had 100 percent more collenchyma than the control. The greatest amount of increase in area of collenchyma in the two experimental groups occurred between the 10th and 15th days of the experiment (Fig. 1). The percentage of petiolar area occupied by collenchyma on the 10th day was 4.2 percent and 4.5 percent respectively for the fan group and the agitator group. On the 15th day percentage areas of collenchyma for the fan group and the agitator group were 5.2 and 5.9 respectively. Between the 15th and 19th days of the experiment the collenchyma area of the agitator group decreased to 5.3 percent. This decrease was followed by a sharp increase to 6 percent between the 19th and 27th days. The fan group displayed a definite drop in collenchyma area to 4 percent after the 15th day and gave no indication of a further increase after that time. The percentage of collenchyma area in the control plants maintained a steady average of about 4.1 percent for the first ten days of the experiment. After the 10th day the proportion of collenchyma to total petiolar area of this group declined steadily to the termination of the experiment. At the termination of the experiment the control group had only 3 percent of its petiolar area differentiated into collenchyma.

Although the measurements of collenchyma cell wall thickness indicate that an increase in thickness occurred in all three groups during the experiment, they indicate further that the increase which took place in the two experimental groups of plants was much greater than in the control plants (Table 1).

Table 1

Average Thickness of Cell Walls During Course of Experiment

Dates Sampled	Control Group	Fan Group	Agitator Group
June 6	2.2*	1.8	2.2
13	2.1	1.8	1.9
16	4.2	4.3	4.7
20	4.9	4.8	5.2
25	4.9	5.2	6.8
July 2	5.0	5.7	7.1

*Expressed in microns.

Results show that the three groups of plants maintained a parallel increase in cell wall thickness for the first 15 days of the experiment. During the last 12 days, however, a spread became apparent in the relative rates of increase of the wall thickness between the three groups. At the termination of the experiment the average thickness of the collenchyma cell walls in the control group was 5.0 microns while the average thickness of those of the plants which received

mechanical stimulation by the fan and the agitator measured 5.7 and 7.1 microns respectively. Thus the walls of the collenchyma cells in the fan group were 14 percent thicker than the walls of the control group. The collenchyma cell walls in the agitator group were 42 percent thicker than those of the control group.

Little difference was noted in the cell wall thickness between the sections taken at the base and those taken at the apex of the mature petioles. Results recorded for the two varieties of celery were relatively the same in all three groups throughout the experiment.

The result of the determination of the relative amount of water lost through transpiration by the three groups showed that the fan group transpired the greatest amount of the three groups (Table 2). The control group demonstrated the second highest amount of water loss by transpiration and the agitator group showed the least amount of water loss of the three groups.

Table 2

Grams of Water Lost per Celery Plant upon Subjection to Experimental Conditions for a Five-Hour Period

Experiment		Control Group	Fan Group	Agitator Group
1	Plant 1	20.0	36.0	17.0
	Plant 2	19.5	39.5	13.0
2	Plant 1	25.0	40.0	19.0
	Plant 2	25.0	54.5	20.0
3	Plant 1	33.5	56.5	27.5
	Plant 2	38.0	50.5	23.0

The amount of water lost by the transpiration of the plants placed in front of the fan was 130 percent greater than that lost by those placed on the agitator. The amount of water lost by the transpiration of the control plants was 35 percent greater than that lost by the plants on the agitator. Although the actual amount of water transpired by the three groups increased from week to week with the increase in size of the plants, the relative amount of increase among the three groups remained approximately the same.

Discussion

Collenchyma is the major support tissue found in the petioles of celery. Schlerenchymatous fibers are not present in the petiole. The only source of support present other than the collenchyma is that of the vascular tissue along with its accompanying bundle caps. Mature collenchyma cells retain a capacity for deposition of wall material for at least 87 days after germination.

Although it has been theorized (Haberlandt 1914) that a certain amount of direct accommodation to external conditions on the part

of the mechanical system may exist, little has been done quantitatively to support this hypothesis. The results obtained from this experiment show that an increase in mechanical motion of the celery petioles results in a significant increase in the amount of petiolar area which differentiates into collenchyma supplemented by an increase in the cell wall thickness of the collenchyma. Plants which had been subjected to mechanical agitation for 27 days showed that the amount of petiolar area occupied by collenchyma was as much as 100 percent greater than that of the control plants. In the same manner, the collenchyma cell wall thickness was as much as 42 percent greater due to such stimulation.

Structural stability of celery is related to the amount of collenchyma present within the petiole. Sayre (1929) demonstrated that collenchyma is the only tissue which has a definite relation to the stringiness of celery. The tensile strength of the collenchyma bundle has been measured by Ambronn (1881), Esau (1936), and Curtis (1938). Collenchyma has been found to have a breaking load of from two to four times that of the vascular tissue of the petiole plus its bundle cap (Esau 1936).

It follows that if structural stability of the petiole is due to the presence of collenchyma in the petiole and the amount of mechanical stimulation received by the petiole has a positive effect on the amount of collenchyma present, a cause and effect relationship exists between stability of the petiole and the amount of mechanical stimulation received by the plants during growth.

An examination of the results shown in Figure 1 shows that there was a decrease in the percentage area of collenchyma in the control group. The quantity of collenchyma in the fan group (in proportion to the total petiolar area) showed an initial increase which was followed by a gradual decrease which continued until the termination of the experiment. The agitator group displayed a relatively constant increase of collenchyma area throughout the experiment. Under normal conditions, such as were experienced in the control group, the amount of deposition of wall material of the collenchyma cells and the increase in the total area of collenchyma did not keep pace with the increase in petiolar area.

The wall thickness and the amount of petiolar area occupied by the collenchyma showed a greater increase in the group stimulated by the mechanical agitator than they did in the group which was stimulated by the wind motion derived from the electric fan. A possible reason for this difference lies in the fact that although the two types of stimulation appear to move the petioles approximately the same distance and supply the same amount of stress to the petioles, the agitator group receives the greatest amount of whipping motion. The stress applied by the fan is constant only in one direction while

that derived from the agitator is bi-directional. Although the agitator table moved only in one place, it moved back and forth. This caused the petioles to sway in one direction and then when the table moved in the opposite direction the petioles recovered and moved the same distance in the opposite direction. It would appear then, that twice the amount of stimulation was derived from the mechanical agitator as was achieved by the use of the electric fan. The greater area of collenchyma within the petioles of the agitator group and the greater thickness of the cell walls of this tissue was the result of this greater amount of agitation.

Venning (1949) stated that transpiration was probably one of the factors to which an increase in collenchyma could be attributed. It is clear that transpiration is not the major cause of increase in collenchyma area or cell wall thickness and may, in fact, have no relation to this increase whatsoever. Results of the experiment to determine the transpirational weight loss of the three groups show that little correlation may be drawn between an increase in transpiration and an increase in collenchyma area or collencyma cell wall thickness. Plants placed in front of the fan demonstrated a transpirational loss of water which was 130 percent greater than that of the plants placed on the agitator, however, the plants on the agitator exhibited 50 percent more collenchyma than the plants placed in front of the fan. Moisture loss due to transpiration in the control plants was slightly greater than that of the plants which had been subjected to agitation, but the latter group showed a 100 percent increase in collenchyma area over those of the control plants.

Summary

One group of celery seedlings was subjected to the wind motion of an electric fan for nine hours a day for 27 days. A second group of seedlings was placed on the platform of a mechanical agitator and subjected to mechanical agitation for the same period of time. A third group was grown under normal greenhouse conditions and was used as a control for the experiment.

1. Celery plants which have been stimulated by wind motion and mechanical agitation show a marked increase in collenchyma area and collenchyma cell wall thickness over those grown in an environment which lacks such stimulation.
2. Mechanical agitation of the celery plants resulted in a greater increase in collenchyma area and cell wall thickness than that derived from stimulation by wind motion.
3. A cause and effect relation exists between mechanical agitation and the quantity of collenchyma differentiated in celery petioles.

4. Weight tests showed transpiration in the fan group to be three times greater than that of the agitator group, however, the increase in collenchyma of the agitator group was more than twice that of the fan group. It was therefore concluded that transpiration was not a major factor in causing the increase in area and cell wall thickness of the collenchyma.

ACKNOWLEDGMENT

The author wishes to express appreciation to Dr. R. L. Hulbary for his advice on many facets of this problem and also to the Graduate College of the State University of Iowa for the equipment to make this work possible.

Bibliography

Ambronn, H. 1881. Ueber die Entwickelungsgeschichte und die mechanischen Eigenschaften des Collenchyms. Ein Beitrag zur Kentniss des mechanischen Gewebesystems. Jahrb. Wiss. Bot. 12:473-541.

Curtis, D. S. 1938. Determination of stringiness in celery. Cornell Univ. Agri. Exp. Sta. Mem. 212.

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

Haberlandt, G. 1914. Physiological plant anatomy. Macmillan and Co.

Sayre, C. B. 1929. Quality in celery as related to structure. Ill. Univ. Agr. Exp. Sta. Bul. 336:559-588.

Venning, F. D. 1949. Stimulation by wind motion of collenchyma formation in celery petioles. Bot. Gaz. 110:511-514.

DEPARTMENT OF BOTANY
STATE UNIVERSITY OF IOWA
IOWA CITY, IOWA