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Variations in leaflet orientation among soybean cultivars

Thomas J. Wofford

To the Graduate Council:

I am submitting herewith a thesis written by Thomas J. Wofford entitled "Variations in leaflet orientation among soybean cultivars." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Plant, Soil and Environmental Sciences.

Fred L. Allen, Major Professor

We have read this thesis and recommend its acceptance:

R. R. Shrode, V. H. Reich

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

I am submitting herewith a thesis written by Thomas J. Wofford entitled "Variation in Leaflet Orientation among Soybean Cultivars." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Plant and Soil Science.

Fred L. Allen

Fred L. Allen, Major Professor

We have read this thesis and recommend its acceptance:

Robert R. Shrode

Vernon H. Reich

Accepted for the Council:

L. Evans Roth

Vice Chancellor
Graduate Studies and Research

VARIATION IN LEAFLET ORIENTATION AMONG SOYBEAN CULTIVARS

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Thomas J. Wofford

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Special thanks to my wife Nancy, and to our family for their love, prayers and encouragement. Most of all, thanks be to God whose grace and power enable me to live.

ABSTRACT

Significant variation was observed among five cultivars of soybeans (Glycine max L., Merr.) in the degree of leaflet orientation at two stages of growth. The degree of leaflet orientation of Ogden, Forrest, Essex, York and Dare was measured hourly beginning at 7:00 a.m. and continuing until 7:00 p.m. (EST) and 8:00 p.m. (EDT) during V10 and R3, respectively. The cultivars tended to change the vertical inclination of the center leaflets of a trifoliolate while keeping the horizontal inclination relatively constant, whereas, the reverse was true of the side leaflets. Maximum variation in leaf movement was noted from 10:00 a.m. until 5:00 p.m. During the V10 stage of growth Ogden and Essex exhibited the greatest amount of orientation while Forrest and Dare were intermediate and York exhibited the least response. During R3 Ogden attained and maintained the highest angle of orientation of the center leaflet followed by Essex and Forrest. Dare and York changed very little. Forrest, Dare and York exhibited the most horizontal movement of the side leaflets (R3) followed by Ogden and Essex which exhibited less movement. More variation was observed during the reproductive stage of growth than was observed during the vegetative stage. Analyses indicate that sufficient statistical information about the variation can be attained from two-days' measurements.

Potassium levels were significantly higher ($P > .01$) in the pulvini of plants collected in the "tense" state than those from plants collected when pulvini were in the "relaxed" stage. The shifts in potassium

concentration in the pulvinus apparently has some role in the bending and straightening of the pulvinus which in turn moves the leaflet. Some differences were observed among cultivars in the fine structure of the pulvinus but these differences could not be adequately defined in this study. The effects of light intensity, sun angle and ambient temperature on leaflet orientation of the soybean cultivars were negligible based on correlation and regression values.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

The arrangement and orientation of leaves in plant communities has been investigated by researchers working with many plant species. This interest is due primarily to the substantial role which leaves play in the growth of plants by providing a medium for the interaction of the plant with its environment. Previous investigations of leaf canopy arrangements and the orientation of leaves have dealt primarily with agronomic species which demonstrate a particular foliar arrangement that does not change over time. However, the spatial orientation of the leaves of some plant species is not static, but, in fact, they demonstrate the ability to change their leaf arrangement in a matter of a few minutes in some cases. The literature refers to both of these phenomena as simply leaf orientation without distinguishing between the two types. To clarify this, leaf orientation of species whose leaves do not change spatially over time will be referred to as "static" leaf orientation, while the orientation observed in species whose arrangement and orientation can be freely altered by the plant will be referred to as "dynamic."

Many advances have been made in understanding the role of different static leaf arrangements on the penetration and distribution of light within plant communities. These phenomena need to be examined for the complex situation of dynamic leaf orientation characteristic of soybeans (*Glycine max* spp.).

Donald (2), in 1968, proposed the concept of plant ideotypes for crop species. He stated that the efficient production of dry matter by a monotypic community depends on the ability of the individual plant to make maximum use of the resources of the limited environment in which it grows, and to encroach to a minimum degree on the environment of its like neighbors. In his paper Donald introduced a theoretical model for breeding crop ideotypes. One character of this model was that of erect foliage. He suggested that erect foliage in a dense community permits adequate illumination of a greater area of leaf surface than occurs in a canopy of long, horizontal or drooping leaves, because in the later case, the upper leaves would be overlit and the lower leaves harmfully shaded. Donald surmised that crop species with the most erect foliage operate with the least amount of demand on the light resources. He based this conclusion on the observation that the modern rice varieties (*Oryza sativa*) grown in Japan and Taiwan yielded more than the rice varieties of the tropics. All of the higher yielding varieties had erect foliage.

Duncan (5), in 1971, conducted computer simulations to see if there was a way to estimate the quantitative significance of leaf angle modification. He found that the highest yielding combination of leaf arrangements always had vertical leaves in the upper layers of the canopy and horizontal layers below. He stated also that for any position of the sun there is an optimal arrangement of the leaves.

In terms of static leaf orientation, the advantage of more vertical leaf orientation, as proposed by Donald, has been demonstrated through research with corn, barley and sugar beets.

Many authors have reported on the advantages of vertically oriented leaves in corn. Russell (21), in 1972, stated that most varieties of maize (Zea spp.) grown in the corn belt demonstrate horizontal or flat-leaf patterns, and that variation of leaf angles among varieties was evident. He further suggested that if leaves were more erect, greater penetration of sunlight into the canopy should result, thus increasing total leaf area receiving the greater light intensity. The end result of this should be increased dry matter production per unit area of field space.

Pendleton, Egli and Peters (19) reported that under field conditions all the leaves on corn plants are not light saturated, even at low plant populations. From this they concluded that light appears to be the primary ecological factor limiting the grain yield of corn grown under highly productive conditions. It appears from their research that, in the static leaf orientation of corn, an increase in the number of upright leaves would be advantageous to high yield.

In a later experiment, Pendleton, Smith, Winter and Johnston (20) measured apparent photosynthesis on individual corn leaves. They discovered that the relative efficiency of CO_2 fixation per unit of incoming sunlight increased steadily as the leaf angle decreased. This suggests further advantages to breeding corn varieties with more vertical orientation of their leaves.

Early et al. (6), in 1967, reported similar information that supports leaf arrangements which increase the amount of sunlight available to corn plants. They considered the effects of reducing the amount of sunlight available to the crop, on the morphology, grain yield, and chemical composition of two corn hybrids, at the vegetative, reproductive and maturity phases of growth. They found that shading the plants caused significant reductions in all components measured except those established prior to treatment.

Other authors have reported that corn yields can be increased when corn plants have leaves which are more vertically oriented, as compared to normal corn leaf habits (10, 35). Lambert and Johnson (16) concluded that upright leaf orientation is an important characteristic to select for in breeding corn varieties.

Investigations with other crops showing static leaf orientation have been conducted. Gardner (9) in 1966, reported higher yields for barley (Hordeum spp.) cultivars with narrow, upright leaves which showed deep penetration of light into the leaf canopy. He found lower yields for those cultivars which had long, wide, drooping leaves and which showed strong interception of the sunlight by the upper leaves of the canopy. Also, Pearce et al. (18) conducted leaf orientation research with barley plants. In their experiment, the barley plants were positioned in flats which caused the plants to grow at different angles to the source of light and from this they demonstrated that differing leaf orientations cause different rates of photosynthesis. They reported that more vertical leaves resulted in a higher rate of net photosynthesis, allowing greater penetration of light into the canopy at higher Leaf Area Indices (LAI's) than horizontal leaves.

Watsun and Witts (32), in 1969, studied the effects of static leaf orientation on light distribution in sugar beets. They found that, although the net assimilation rates of wild and cultivated sugar beets were similar, the cultivated beets produced more dry matter at high LAI's than the wild beets. They attributed this difference to the inherent disparity in leaf orientation.

Just as the static orientation of leaves has a definite effect on the productivity of the plant, plants which are capable of dynamic leaf movement attain various benefits from this ability. The majority of plants having the characteristic of dynamic leaf movement are in the family Leguminosae, which includes Albizzia julibrissin, Glycine spp., Mimosa pudica and members of the Phaseous genera. These species change the degree of alignment of their leaves in accord with the different stimuli impinging on the plant (4, 34).

Dubetz (4) reported on the movement of the leaves of bush bean (Phaseolus vulgaris). He noted that under conditions of extreme drought and intense sunlight the leaves of bush bean oriented themselves parallel to the incident light. He observed also that they followed the course of the sun in this position, and by morning, they assumed their normal position. Similarly, Wien and Wallace (34) reported that four cultivars of Phaseolus demonstrated differing degrees of leaflet orientation under a given light intensity. They further explained that light from the side caused the leaflets to orient themselves in a plane parallel to the source point of the incoming radiation. In this way the leaves were in a position which enabled them to intercept more light energy. On the other hand, light directed from above caused the leaflets to orient themselves in such a way that they intercepted less energy.

Kawashima (13), in 1969, reported on the "leaf orientation-adjusting movement" in soybeans. He measured the azimuth of leaves and the angle of leaf inclination on all the leaves on one hill of a soybean plant community of the variety Azeminori. From the data he collected, he showed how the angle of the leaves in this hill of soybeans varied under different weather conditions and light intensities.

In a similar study, Kawashima (14) used a soybean plant of the Madison variety. He observed that the pattern of leaf orientation acted to equalize the light intensity on the leaf surface of all the leaves of the plant community. He found that soybean leaves orient themselves in relation to the source-direction of the strongest light.

The morphological structure which facilitates this movement is the pulvinus. The pulvinus is a specialized organ, sensitive to environmental stimuli, and capable of controlling leaf and leaflet movement in many plants (7).

The physiological mechanism which causes the pulvini of plants to alter the orientation of their leaves is not fully understood. Satter and Galston (23) reported, in 1971, that fluxes in potassium ion concentrations is a "common feature of Albizzia leaflet movement." Whether or not potassium flux is responsible for leaf movement in soybeans is not known at this time.

As with static leaf orientation, it seems that dynamic leaf orientation would offer many advantages to those plant species which possess it. Such advantages are: (1) allowing the plant to obtain an optimum arrangement of its leaves at any given time in order to increase the light available to each leaf which should increase leaf photosynthesis, (2) increasing the production of assimilates close to the site of photosynthate demand, (3) decreasing the amount of abscission of pods (soybeans) and (4) helping to regulate leaf temperature and transpiration by minimizing the amount of area exposed to direct sunlight.

Most researchers agree that there is room for improvement in the photosynthetic efficiency of soybeans. Dornhoff and Shibbles (3) have implicated leaf photosynthesis as the primary process which ultimately delimits soybean yield. To understand leaf photosynthesis and the factors which limit or enable it to increase, the biological principles which are involved in its operation need to be examined and understood.

One such principle is the fact that all dry matter produced by a plant is a function of the solar radiation intercepted by the plant (26). This is true because essentially all dry matter present in higher plants originates from photosynthetic carbon dioxide reduction (8). Hence, the amount of dry matter produced is influenced by the concentration and orientation of the leaves within the crop canopy because this affects the distribution of solar radiation throughout the canopy. Since the amount of dry matter produced depends on the amount of sunlight available to all the leaves of the canopy, production should increase if the available light is distributed uniformly so that the fraction of leaves exposed to light intensities beyond saturation and below compensation is minimal (8).

Weil and Ohlrogge (33), in 1976, stated that the poor yield of the bottom nodes of soybeans might be attributed to inadequate light for maximum photosynthesis at the lower levels of the canopy due to shading by the upper leaves during the pod-filling period. Earlier studies of Verhagen et al. (31) showed that production can be increased if lower leaves receive more light.

In soybeans this deficiency in light at the lower levels of the canopy is due to the fact that as light penetrates into the community, its intensity decreases exponentially as a result of leaves shading each other (12). Sakamoto and Shaw (22) conducted a study in 1967 to determine the pattern of light interception and distribution in a field soybean community. They stated that because of a large amount of self-shading and predominant interception at the periphery of the canopy, many of the lower leaves were not receiving adequate radiation. They proposed further that an increase in yield possibly could be achieved through selecting varieties whose natural leaf inclination leads to deeper penetration of useful energy to a greater number of leaves. Shaw and Weber (28), in 1967, reported very similar findings with soybeans. They reported that the largest part of light interception occurs in the outer 15 to 30 cm of the plant canopy. They found that greater light penetration, resulting in a greater amount of the plant canopy receiving a light intensity above 150 foot candles, generally resulted in higher yields.

Johnson et al. (11) also found that because of inter- and intra-plant competition for light, middle and bottom soybean leaves do not reach their photosynthetic potential under field conditions. To test this they added light and found that this increased the yields of the bottom, middle and top canopy positions of the plants 30, 20, and 2 percent, respectively. Light-rich plants had more seeds, nodes, pods, branches, pods per node, seeds per pod and a higher oil content than normal plants. Schou et al. (24) similarly increased the light available to a soybean community. They reported that the yield increase was much greater than they expected from the amount of light that was added.

Another beneficial purpose of dynamic leaf orientation in some plant species is the fact that it increases the production of assimilates close to the site of photosynthate demand. This is particularly useful in soybeans due to the primarily localized movement of assimilates within the plant. Thaine et al. (29), in 1959, obtained information which showed that the distribution of assimilates in soybeans is localized. In other words, the assimilates from the upper leaves moves primarily to the apex, and assimilates in younger and lower leaves move to the roots, while assimilates from the middle leaves move both up and down, to some extent. Thrower's (30) work of 1962, with soybeans, essentially agreed with Thaine's. He stated that the export of assimilates from an expanded leaf to the apex and root is inversely proportional to its distance from these sinks.

In 1966, Belikov and Pirskii (1) established, with help of the tracer atom method, that in soybeans the beans of each node receive nutrition through assimilates from primarily the same node in the axil on which they are located. This can be seen to be true by the manner in which the beans on the lower nodes are often shed or become less valuable.

An important question to be raised at this point is how efficient and productive are the lower leaves of soybeans. Shibles and Weber (25) demonstrated that the lower leaves of soybeans are not "parasitic" upon the rest of the canopy. They showed that the production of dry matter in soybeans did not decline at a LAI greater than that required for the interception of full solar radiation. Therefore, they do not detract from the net production of photosynthate by the soybean community.

Other important benefits are realized in crops demonstrating dynamic leaf orientation in terms of decreasing leaf temperatures and transpiration losses. Dubetz (4), from his work with bush beans, stated that leaf orientation and movement presumably are adaptations which minimize transpiration rates and perhaps prevent thermal death. Stevenson and Shaw (27), in 1971, experimented with tying the leaves of soybeans upright. They discovered that leaf resistance values for upright leaves were less than those of naturally exposed leaves on eight of nine sunny days. Similarly, leaf temperatures were less for upright leaves.

The last important benefit from dynamic leaf movement to be considered is its indirect influence on reducing the amount of pod loss. Mann and Jaworski (17), working with soybeans, reported that shading to 63 percent of ambient light caused abscission in half of the pods of one variety. The greater penetration and distribution of light along with the reduced shading brought about by dynamic leaf orientation should reduce pod loss indirectly through its direct influence on leaf photosynthesis and higher photosynthate production from leaves deeper in the canopy.

Dynamic leaf orientation is an important characteristic which gives plant species flexibility in controlling and modifying various physiological processes. Furthermore, it seems logical to assume that if variation exists within species for this type of leaf orientation, then it should be possible for plant breeders to develop improved cultivars that can more efficiently utilize the environment in which they grow, particularly in terms of utilization and conservation of sunlight and moisture.

The objectives of this study were to determine:

1. if variation exists among five soybean cultivars for the orientation response of their leaflets during the course of a day,

2. how much daily leaf movement takes place in any one cultivar,

3. the variation present during a vegetative stage of the plant's growth versus that present during a reproductive stage,

4. what role potassium flux plays in the leaf orientation response of soybeans, and

5. if there are differences in the fine structure of the pulvini of different soybean cultivars.

CHAPTER II

MATERIALS AND METHODS

The experimental procedure was divided into three sections. The first portion of the experiment was designed to obtain a measurement of the amount of dynamic leaflet movement which occurs in five soybean cultivars throughout the course of a day. A second dealt with the microscopic examination of the pulvini and the final segment was an analysis of the concentration of potassium in the pulvini at the two extremes of leaflet orientation.

Five cultivars of soybeans (*Glycine max* L.) were planted in the greenhouse at the University of Tennessee in February of 1978. The five cultivars were: Ogden, Forrest, Essex, York and Dare. The experiment was set up as a randomized complete block design with three replications. Each cultivar was planted separately in plastic pots 28 centimeters in diameter, containing 4500 grams of a 2:1:1 mix of soil, peat and perlite, respectively. Lime and fertilizer were added to properly adjust the pH and fertility for optimum plant growth.

When the plants reached the V10 stage of growth (plants in vegetative stage of growth with 10 nodes), the trifoliolate at the eighth node of each plant was positioned in such a way that the center leaflet was facing due east. Later in the experiment, when the plants were at the R3 growth stage (plants in reproductive stage of growth with pods approximately 5 cm in length), the trifoliolate at the seventeenth node was positioned to face due east. At both stages of growth, angle measurements were taken on the vertical and the horizontal inclination of the left, center, and right leaflets of the above designated trifoliolate. The angle of vertical inclination (upward and downward) of each leaflet measured was designated as the main angle of that leaflet. The angle of horizontal inclination (side-to-side) of each leaflet was designated as the sub-angle. Measurements were taken with a clinometer positioned along the mid-rib and perpendicular to the mid-rib of each leaflet for main and sub-angle, respectively.

A complete set of measurements was taken on each variety on four different days at both growth stages. During the V10 stage of growth, measurements were taken on April 7, 10, 12, and 14, 1978. During R3, measurements were taken on four consecutive days, June 20-23, 1978.

Each of the daily measurements began at 7:00 a.m. (Eastern Standard Time during V10 and Eastern Daylight Time during R3) and continued every hour throughout the day until the light intensity declined to five or less British Thermal Units (BTU's). Also, three independent variables were recorded hourly: temperature, light intensity and the angle at which the sun was positioned relative to the experiment.

The specimens for the other two portions of the experiment were obtained from the plants in the greenhouse after all the measurements had been obtained for the first portion. Approximately 50 pulvini were excised from plants of each cultivar in mid-afternoon (approximately 2:00 p.m.) and again in late evening (approximately 10:00 p.m.) in order to obtain samples which would exemplify the extremes of dynamic leaf orientation. By mid-afternoon most cultivars were nearing maximum leaflet orientation, and the pulvini were in an "elbow" shape. In late evening the leaflets had returned to a more "normal" position and the pulvini were more or less straight. The former will be referred to hereafter as the "tense" position of pulvini and the latter as the "relaxed" position.

Ten pulvini of each cultivar for each position were immediately fixed in a 3:1 solution of ethanol and acetic acid, respectively. They were then dehydrated and embedded in paraffin, sectioned (cross and longitudinally) and stained with fast-green and counter stained with safarin. The sections were viewed under the microscope at 31.25X magnification, and the number of layers of cortical cells between the vascular system in the center of the pulvini and the epidermis were counted.

Approximately 40 pulvini in the tense position for each cultivar were placed in paper bags and dried in an oven at 68° Celsius for 30 to 34 hours. The dried tissue was digested with various acids (HNO_3, $HCLO_4$ and HCL), in an aluminum digestion block. The digested samples were then analyzed for potassium concentration on a Perkin-Elmer Atomic Absorption Analyzer. The same procedure was followed for pulvini in the relaxed position for each cultivar.

CHAPTER III

RESULTS AND DISCUSSION

The first step in determining the amount of variation present among the five cultivars is to answer some basic questions relating to the overall variation observed. These questions are:

1. Are different patterns of response present in either the horizontal or the vertical movement of the leaves? If there are differences, which movement best defines the plant's leaf orientation response?
2. Do the left, center and right leaflets of a trifoliolate all respond similarly, or do they operate independently?
3. Should leaflet orientation of soybean cultivars be measured during the vegetative or reproductive phases of growth, or does it matter?
4. During which time of the day are cultivar differences maximum?
5. Are the responses of the plants and the degree of variation similar on different days? On how many days should measurements be taken to allow one to obtain a reasonable measure of the leaflet orientation of a cultivar?

The first question deals with the relative importance of the vertical versus the horizontal movement of soybean leaves. Figure 1 illustrates the changes in the main (vertical) angle and Figure 2 the changes in the sub- (horizontal) angle of the left, center and right leaflets during the V10 and R3 stages of growth. The points represent means averaged across

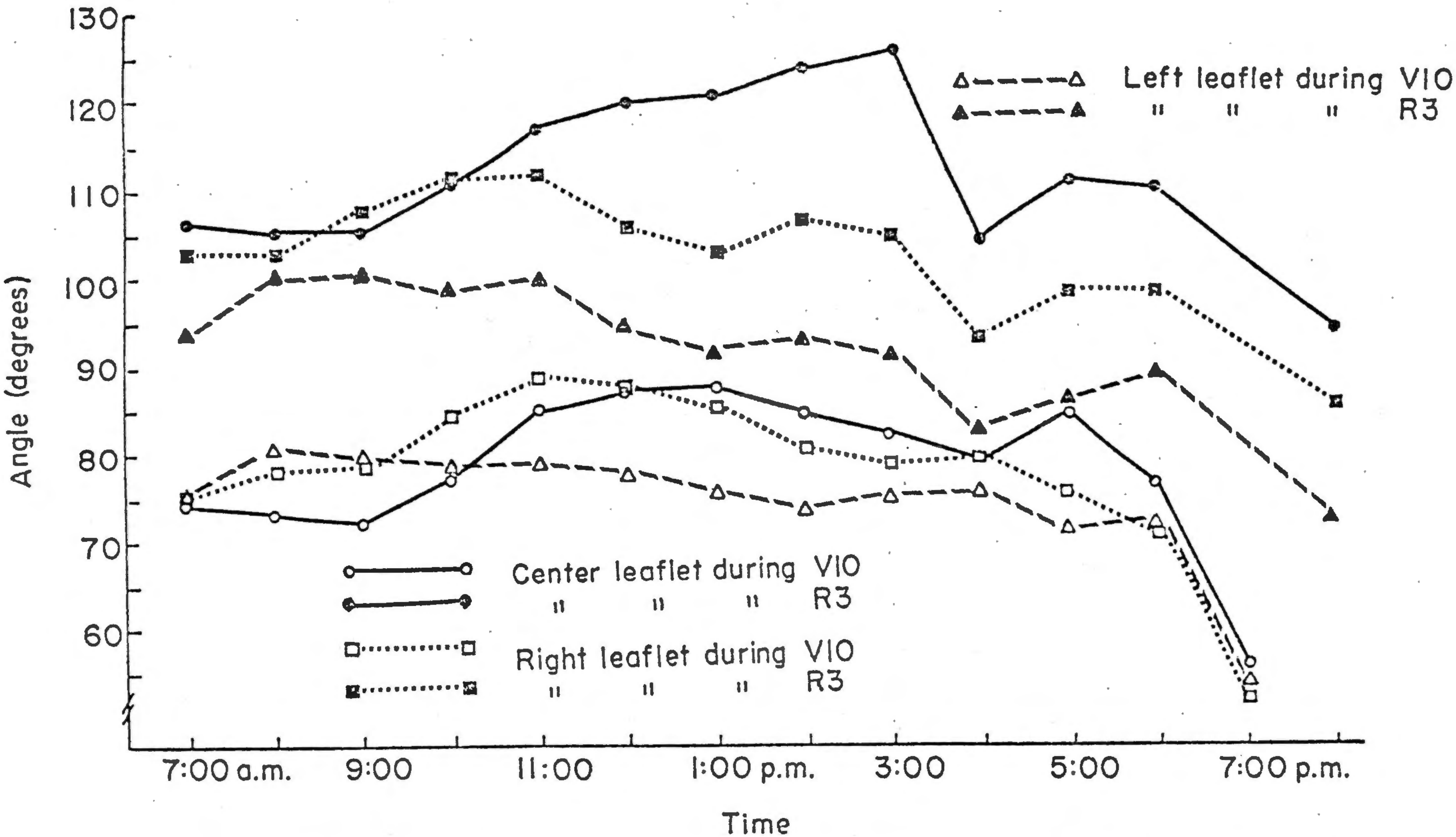

Figure 1. The average vertical orientation (main angle) of the left, center and right leaflets of all five soybean cultivars.

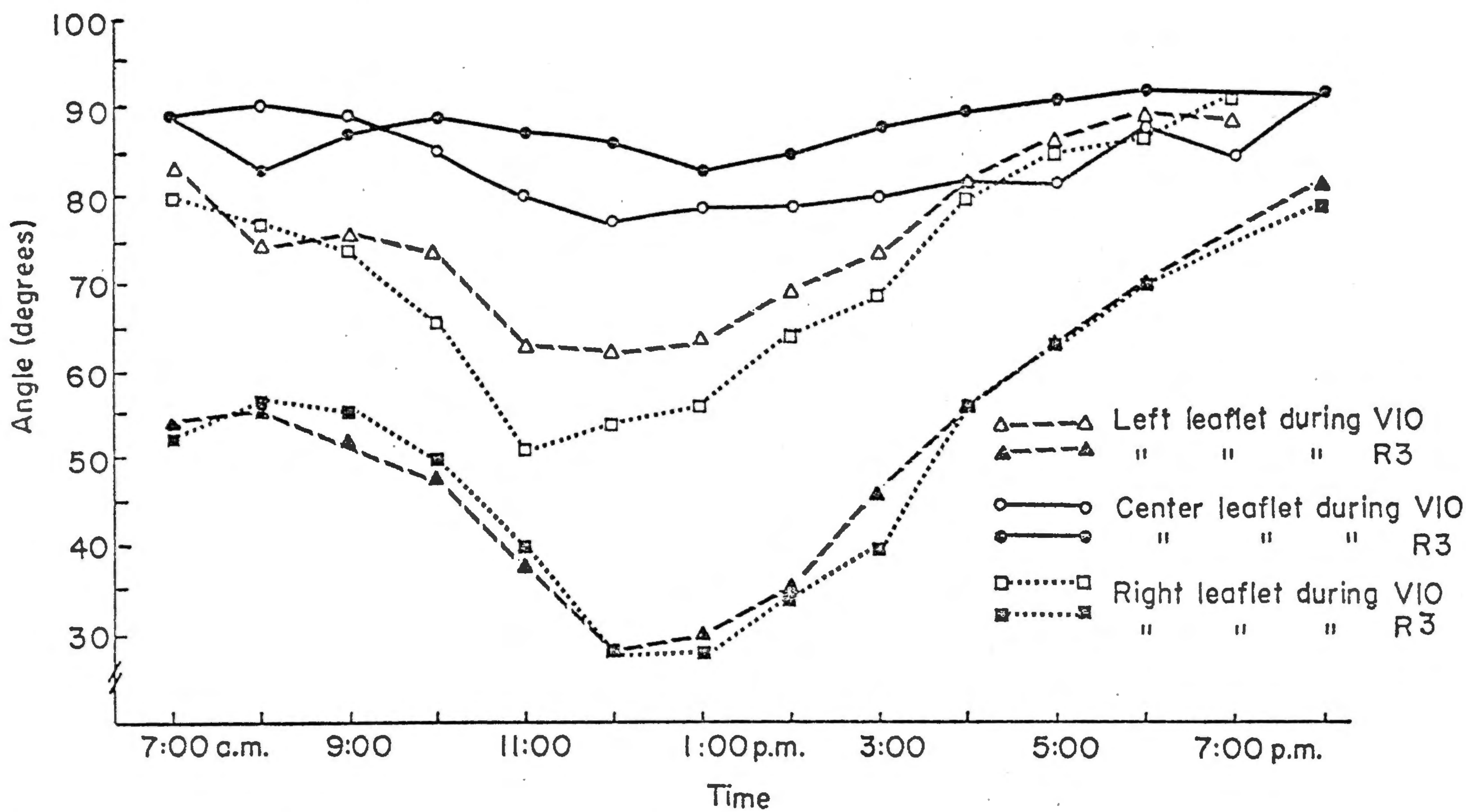

Figure 2. The average horizontal orientation (sub-angle) of the left, center and right leaflets of all five soybean cultivars.

cultivars, replications and dates of measurements within each growth stage. The data indicate that both directions of movement are important depending on the leaflet considered. The center leaflet gives one response, and the side leaflets (right and left) give a different response. The center leaflets of the trifoliolates had more change in the main than in the sub-angle throughout the course of the day during both growth stages, whereas, the right and left leaflets of the trifoliolates had more change in the sub- than in the main angle. Hence, there is a distinct pattern of response which is present in the center leaflet and a different pattern present in the side leaflets. This can be illustrated clearly by considering the response of individual cultivars. Figures 3 through 17 illustrate the main and sub-angle changes for the right, center and left leaflets of each individual variety during the V10 and R3 stages of growth. During R3, all varieties show similar trends in that the main angle of the right and left leaflets show the least response over the duration of the day, whereas, the greatest response is present in the sub-angle measurements. On the other hand, the center leaflet shows the main angle to have the greatest response over time and substantially less change is seen in the sub-angle. During V10, Ogden (Figures 3-5), Essex (Figures 9-11) and York (Figures 12-14) follow the same trends as above, but Forrest (Figures 6-8) and Dare (Figures 15-17) deviate slightly. For the latter two variaties during V10, neither the main nor sub-angles of the right, center and left leaflets changed appreciably throughout the day. Thus, the main response of the center leaflet is in the form of vertical

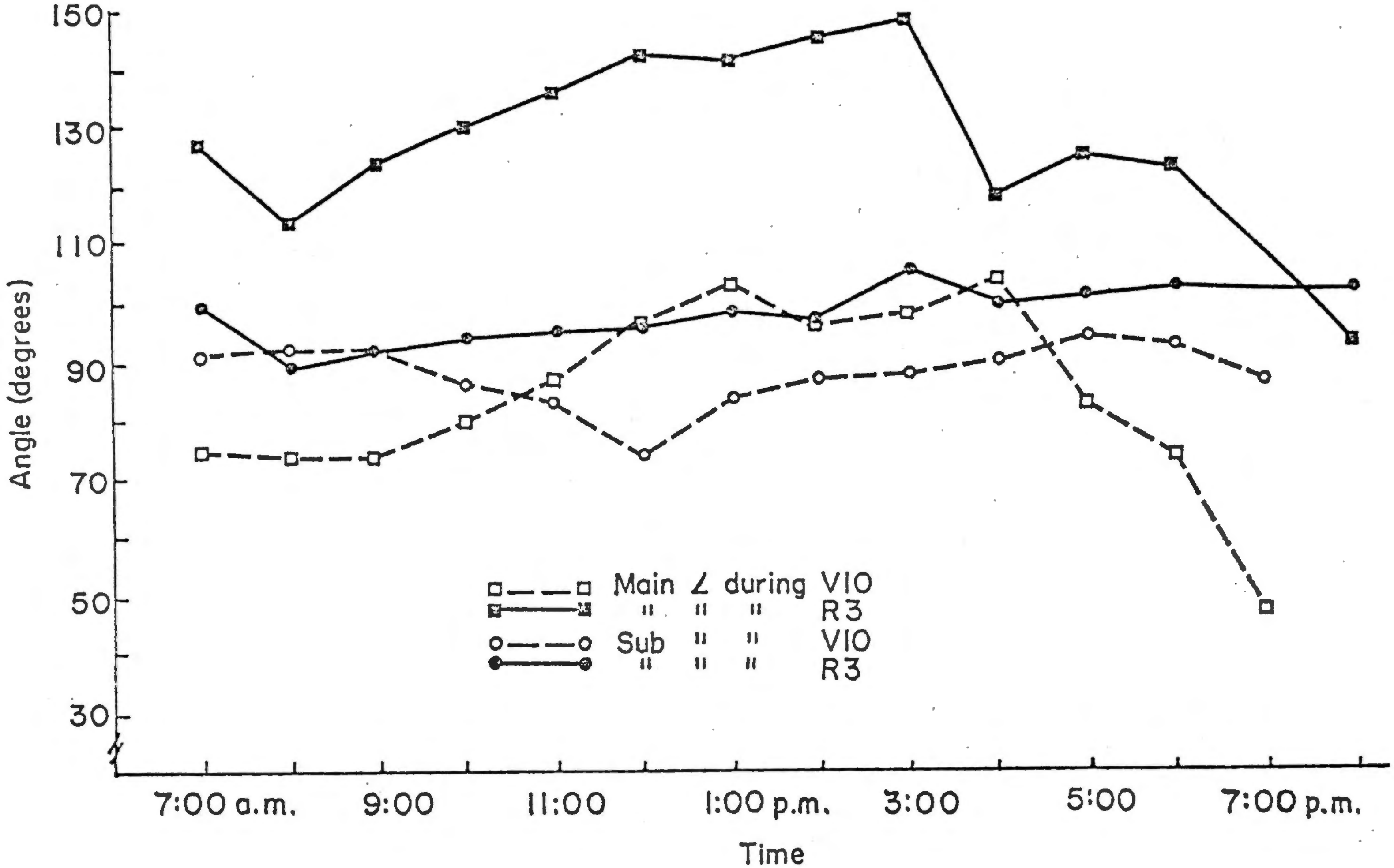

Figure 3. The mean horizontal and vertical orientation of the center leaflet of Ogden during two growth stages.

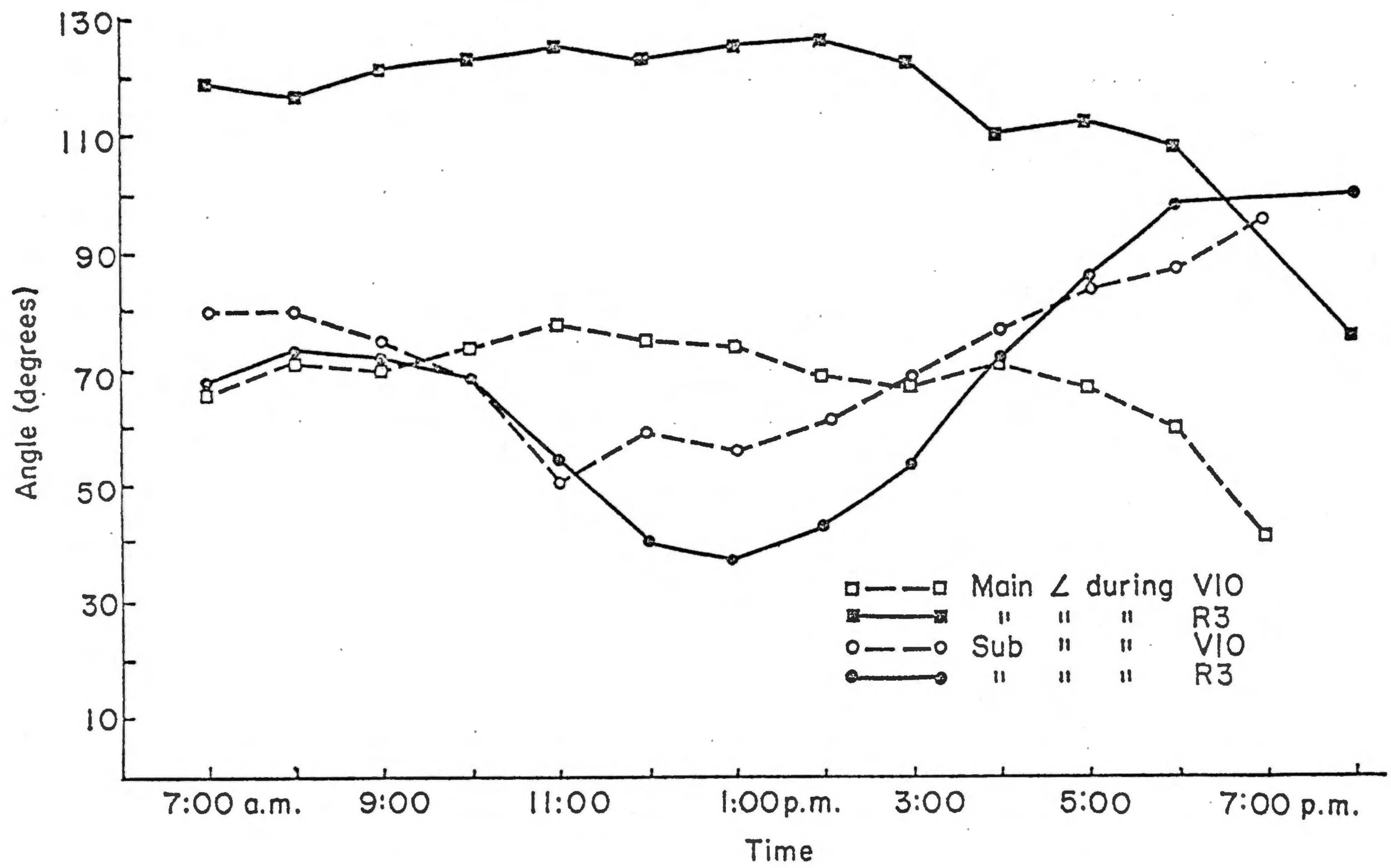

Figure 4. The mean horizontal and vertical orientation of the right leaflet of Ogden during two growth stages.

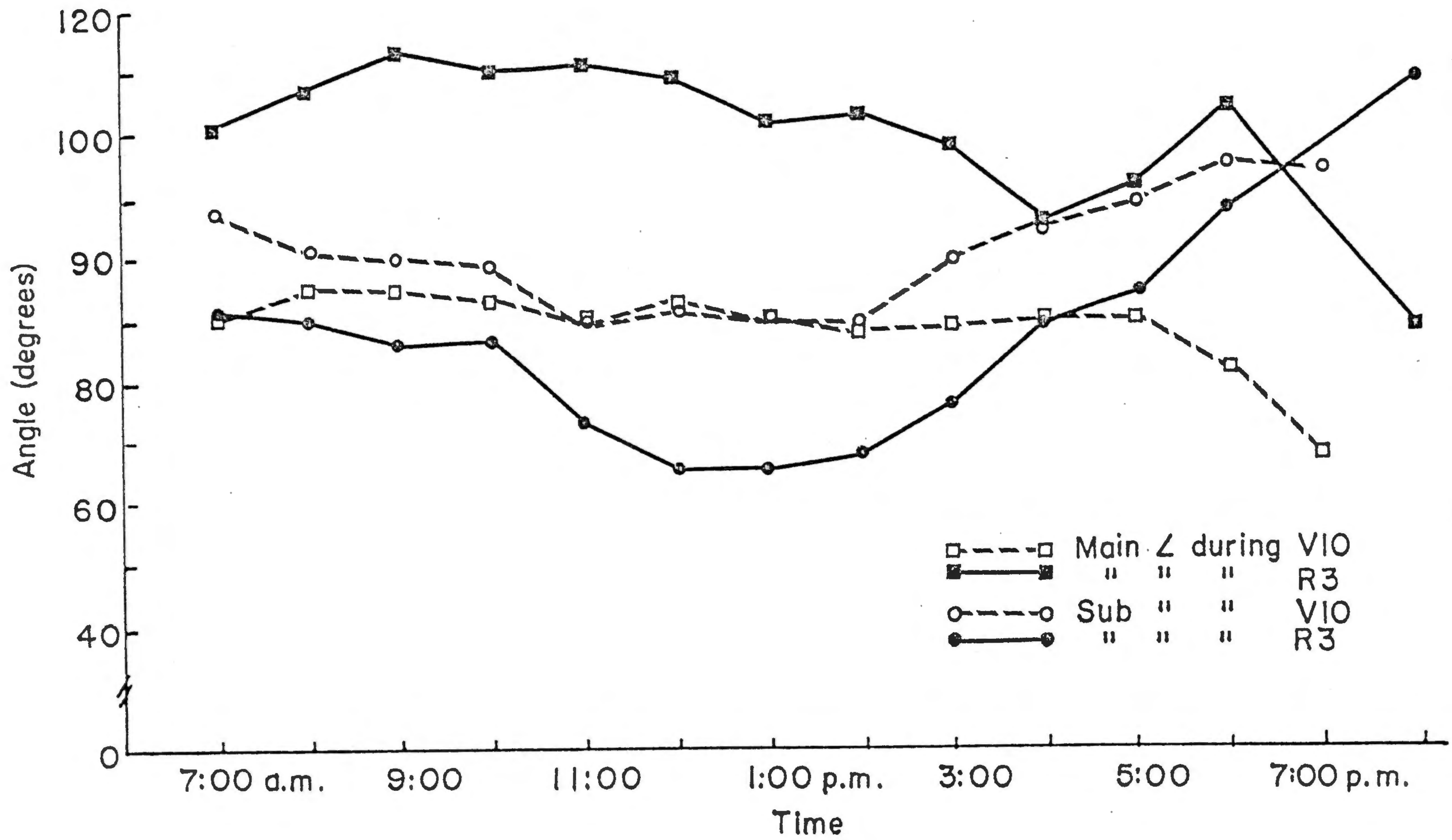

Figure 5. The mean horizontal and vertical orientation of the left leaflet of Ogden during two growth stages.

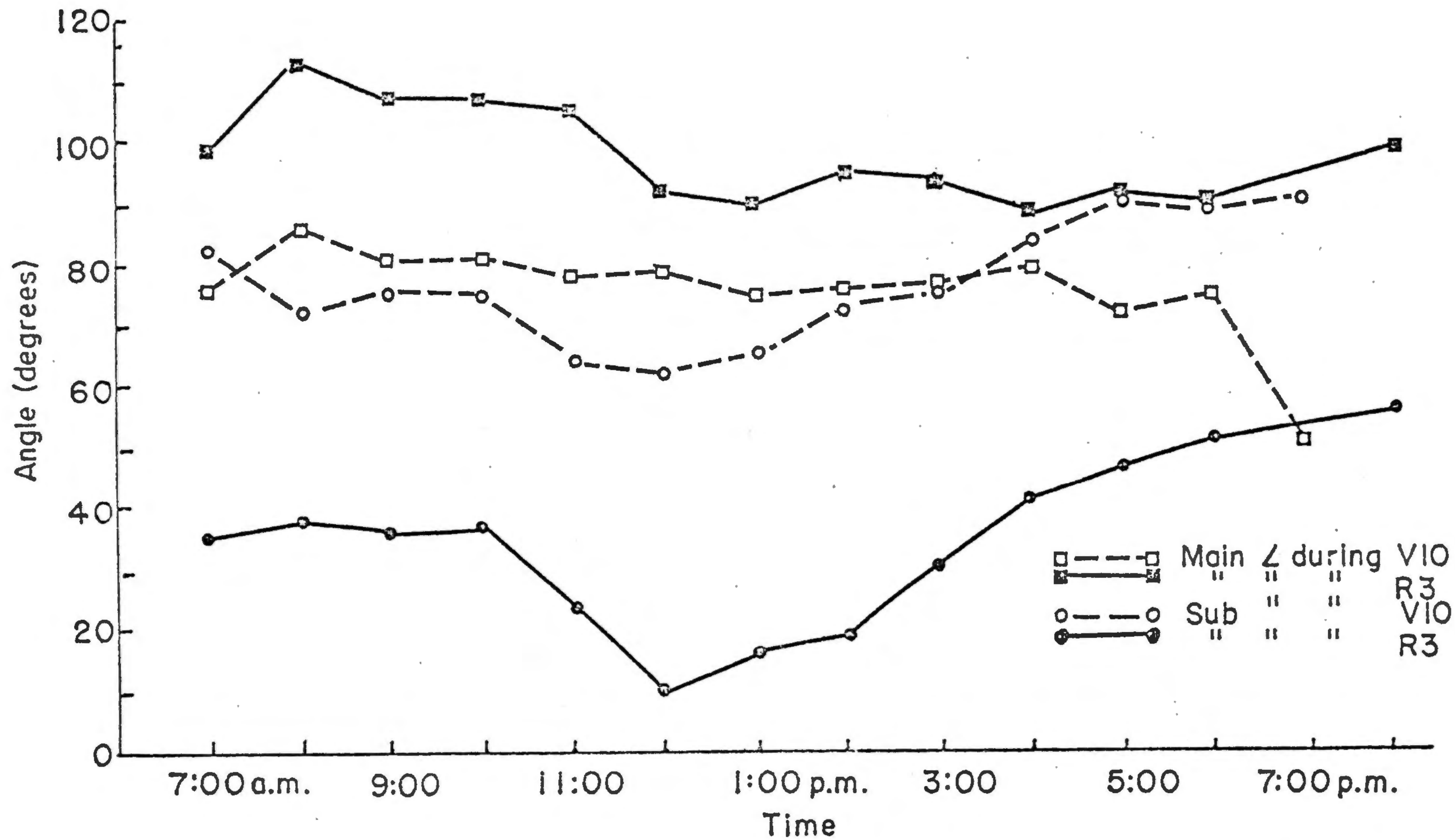

Figure 6. The mean horizontal and vertical orientation of the left leaflet of Forrest during two growth stages.

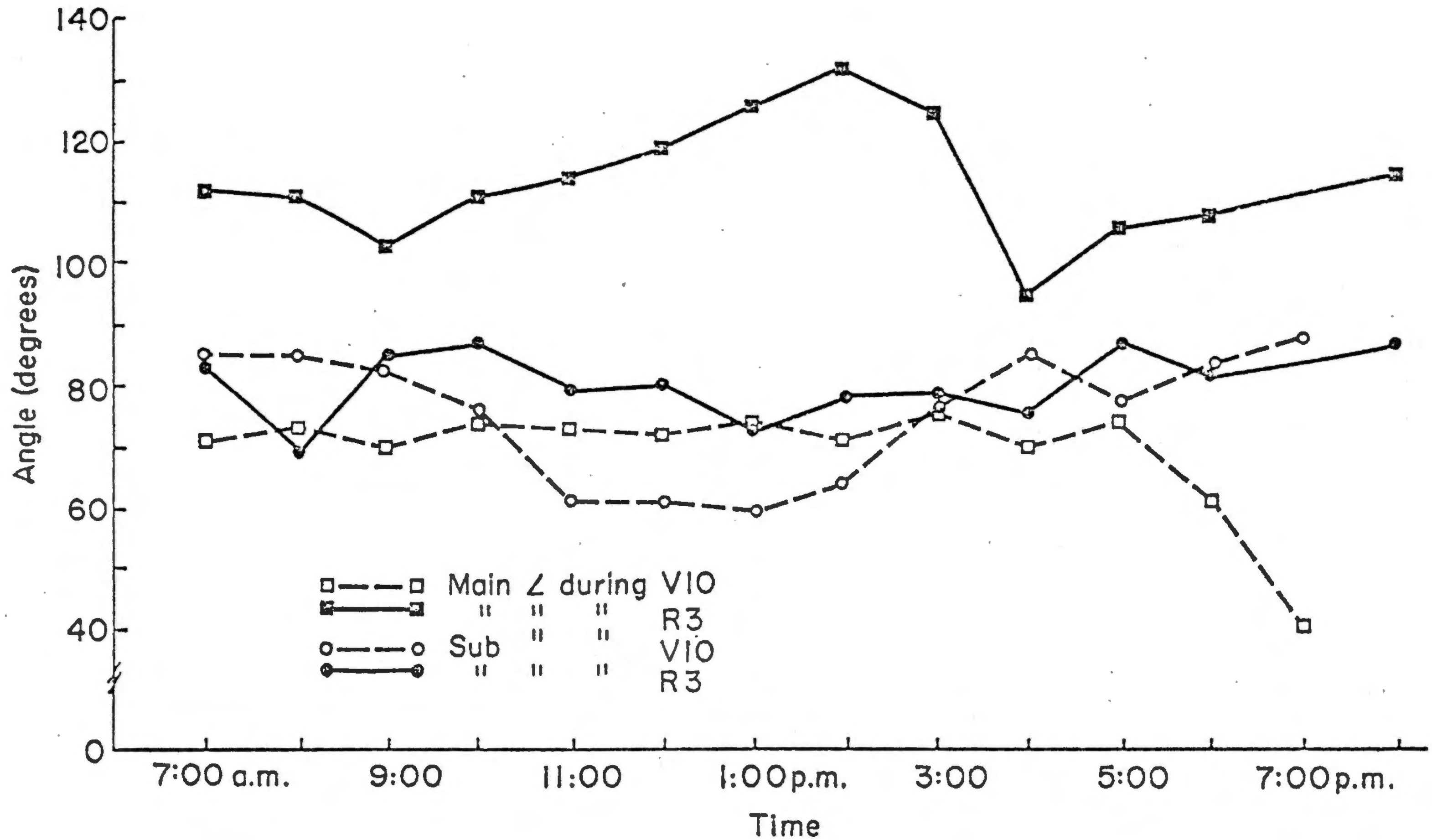

Figure 7. The mean horizontal and vertical orientation of the center leaflet of Forrest during two growth stages.

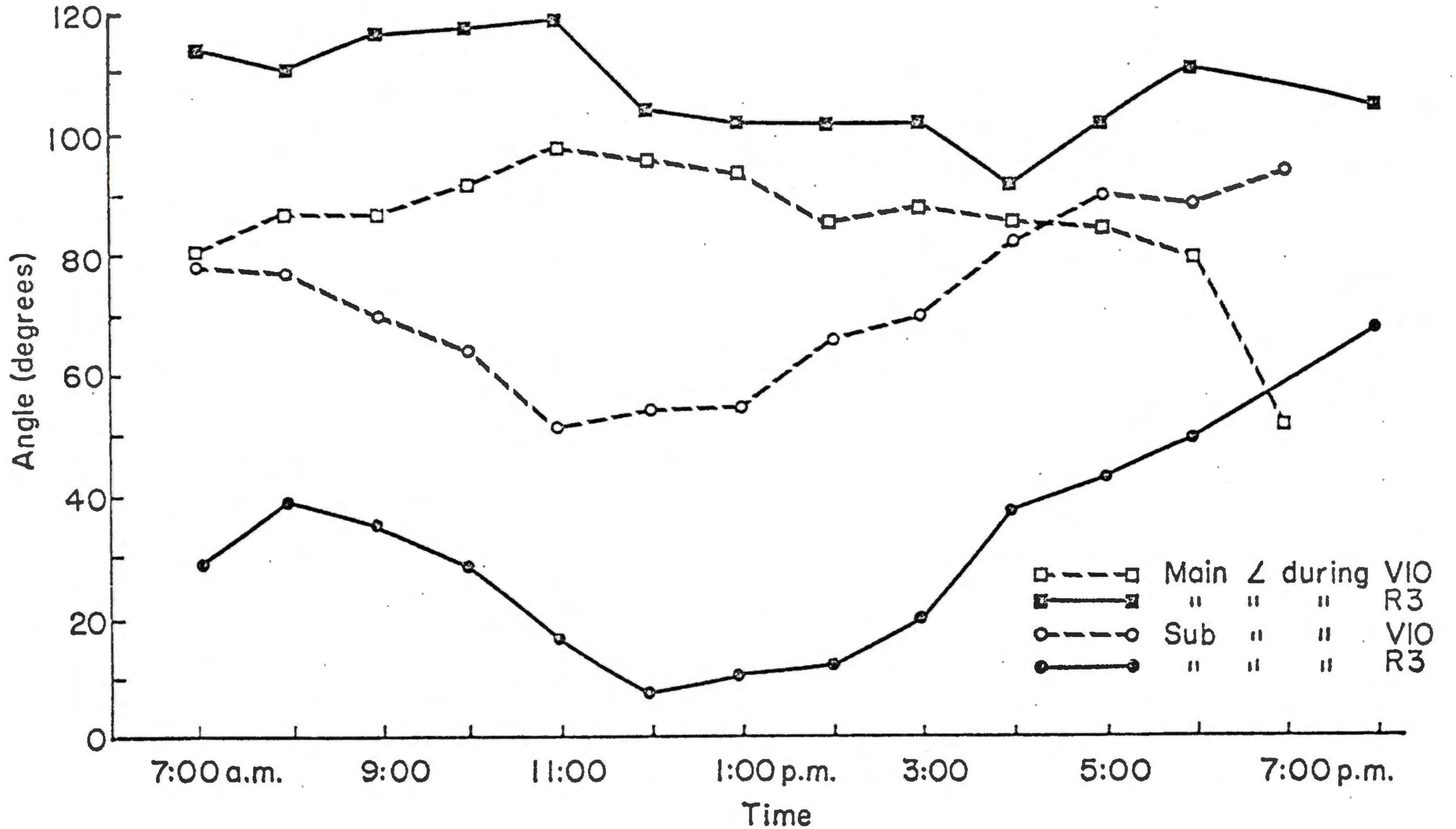

Figure 8. The mean horizontal and vertical orientation of the right leaflet of Forrest during two growth stages.

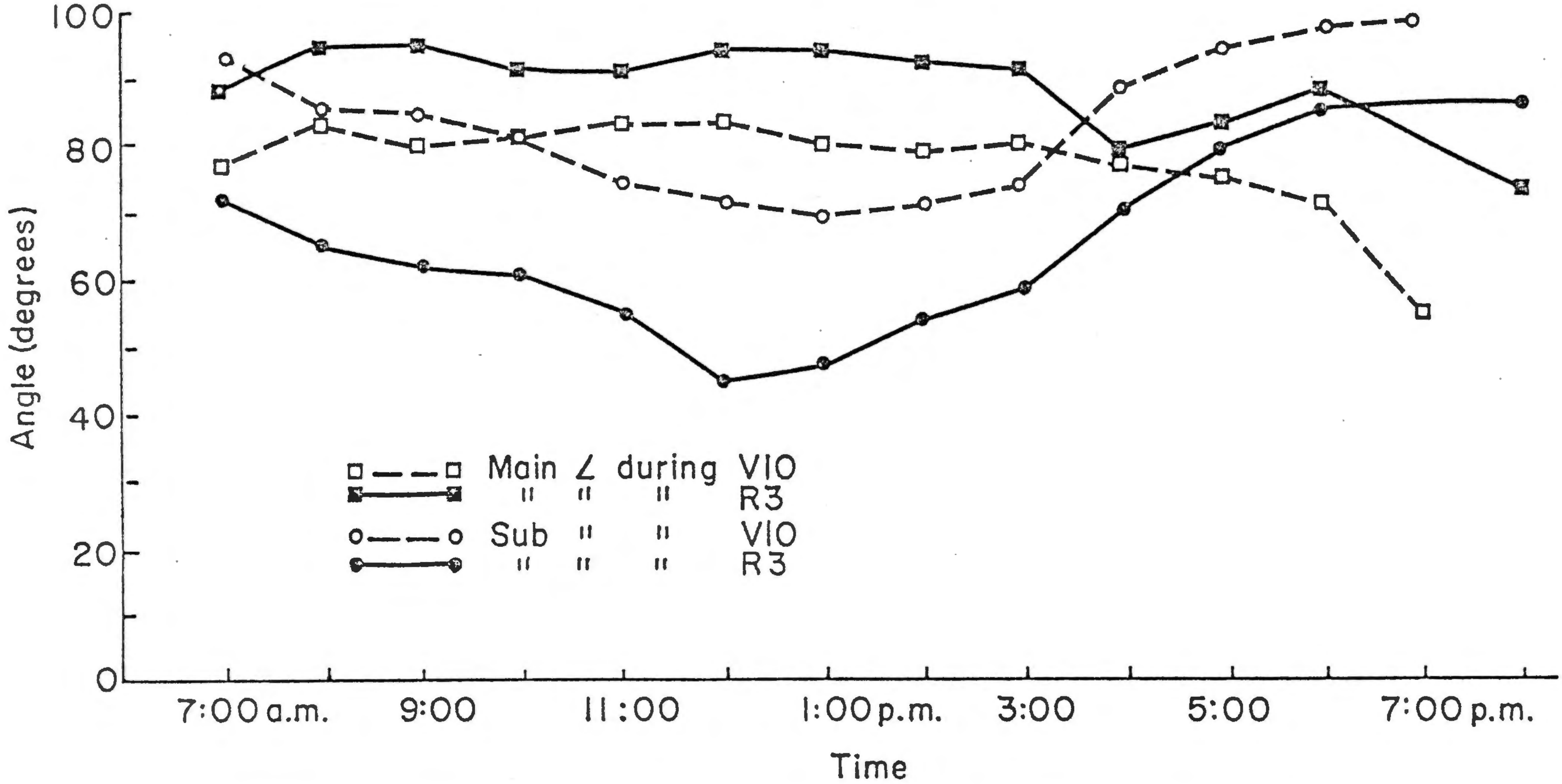

Figure 9. The mean horizontal and vertical orientation of the left leaflet of Essex during two growth stages.

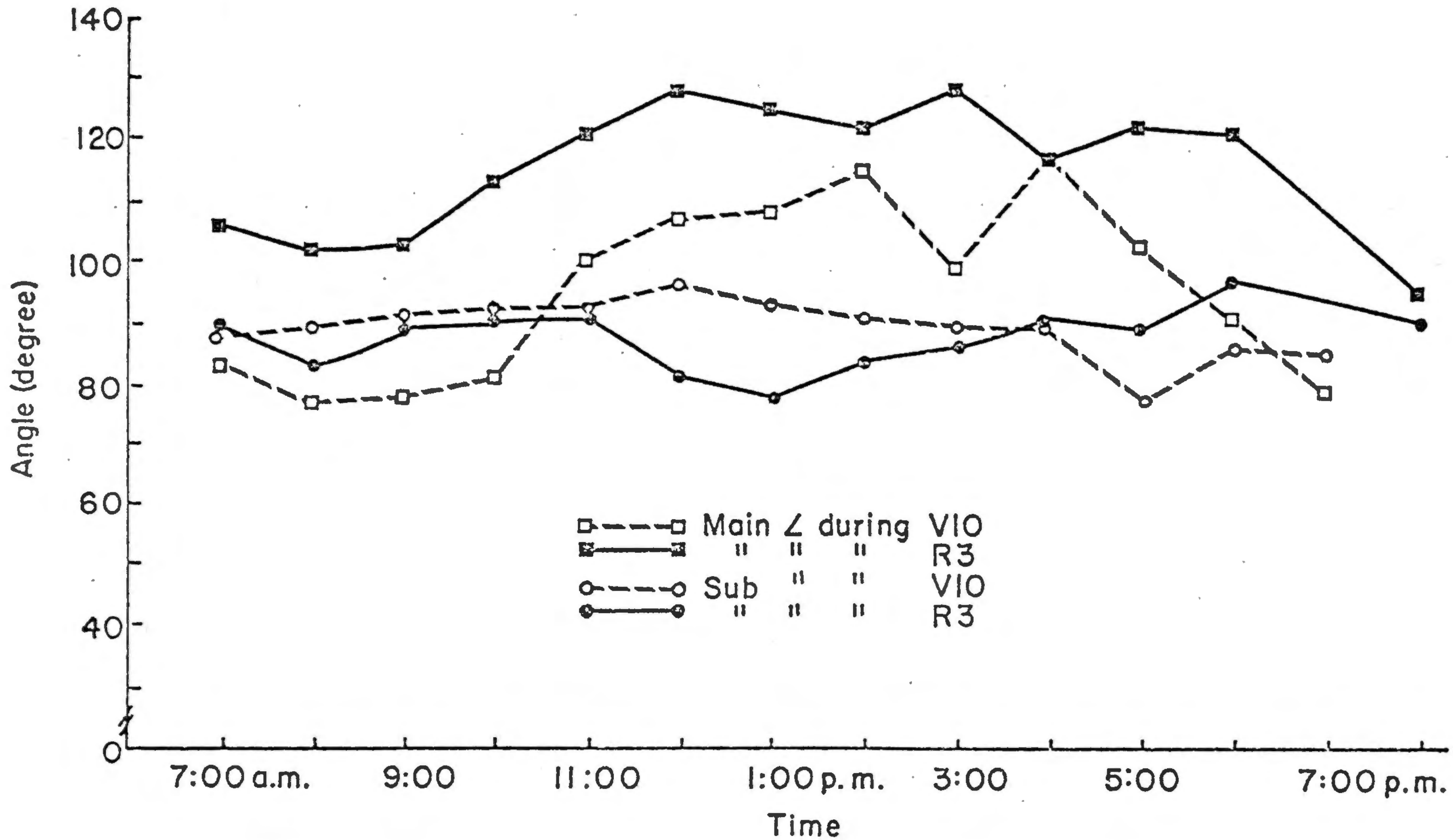

Figure 10. The mean horizontal and vertical orientation of the center leaflet of Essex during two growth stages.

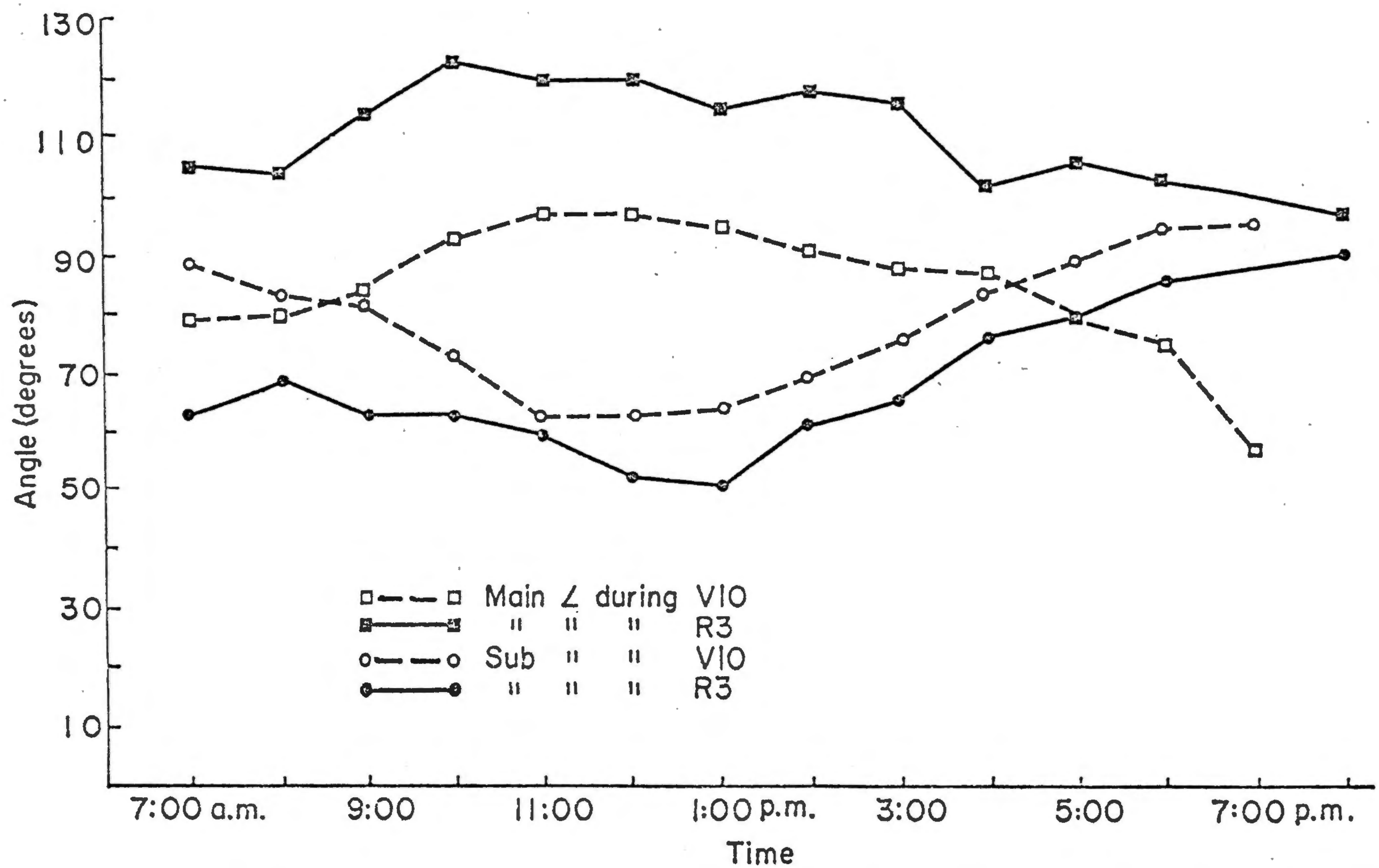

Figure 11. The mean horizontal and vertical orientation of the right leaflet of Essex during two growth stages.

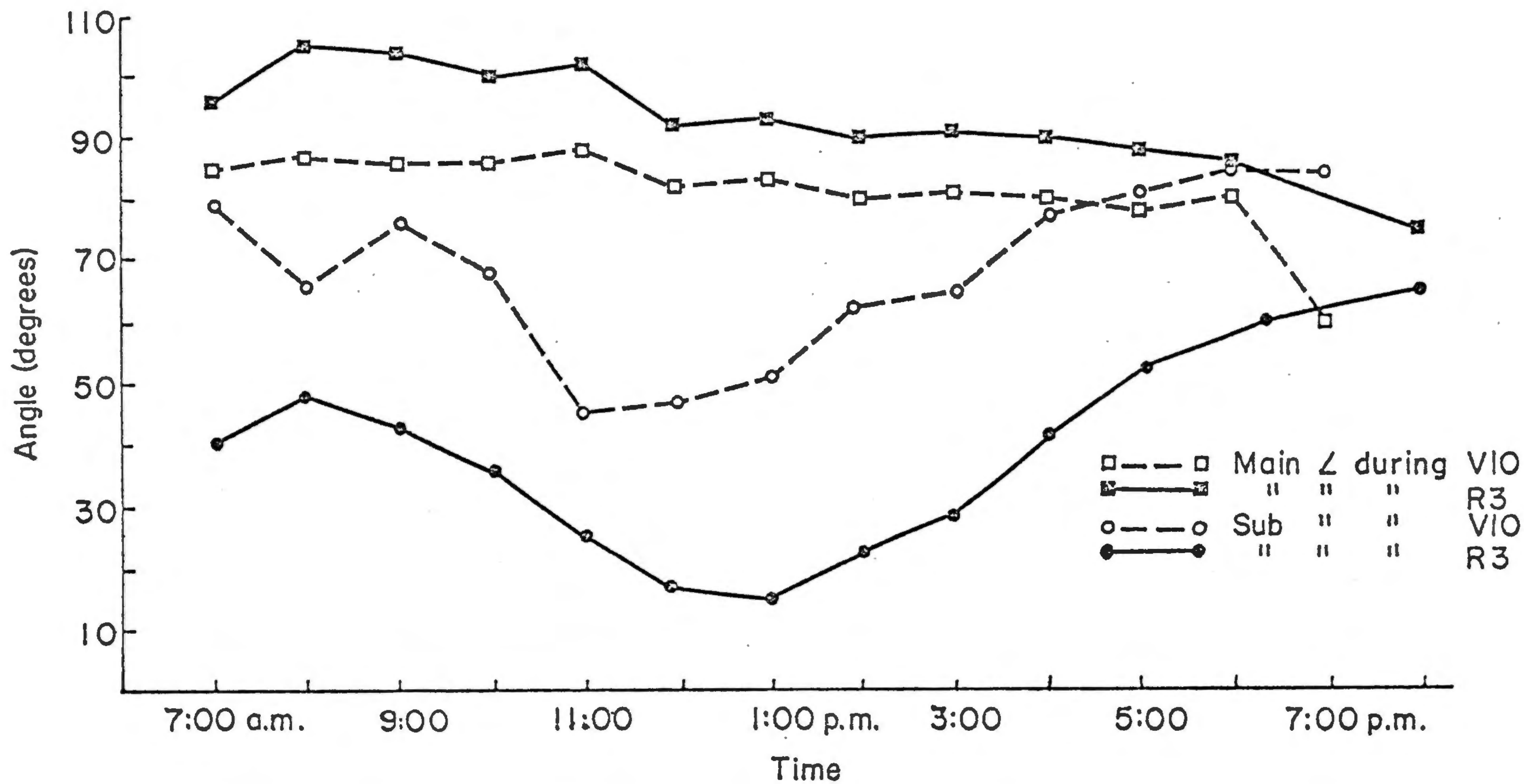

Figure 12. The mean horizontal and vertical orientation of the left leaflet of York during two growth stages.

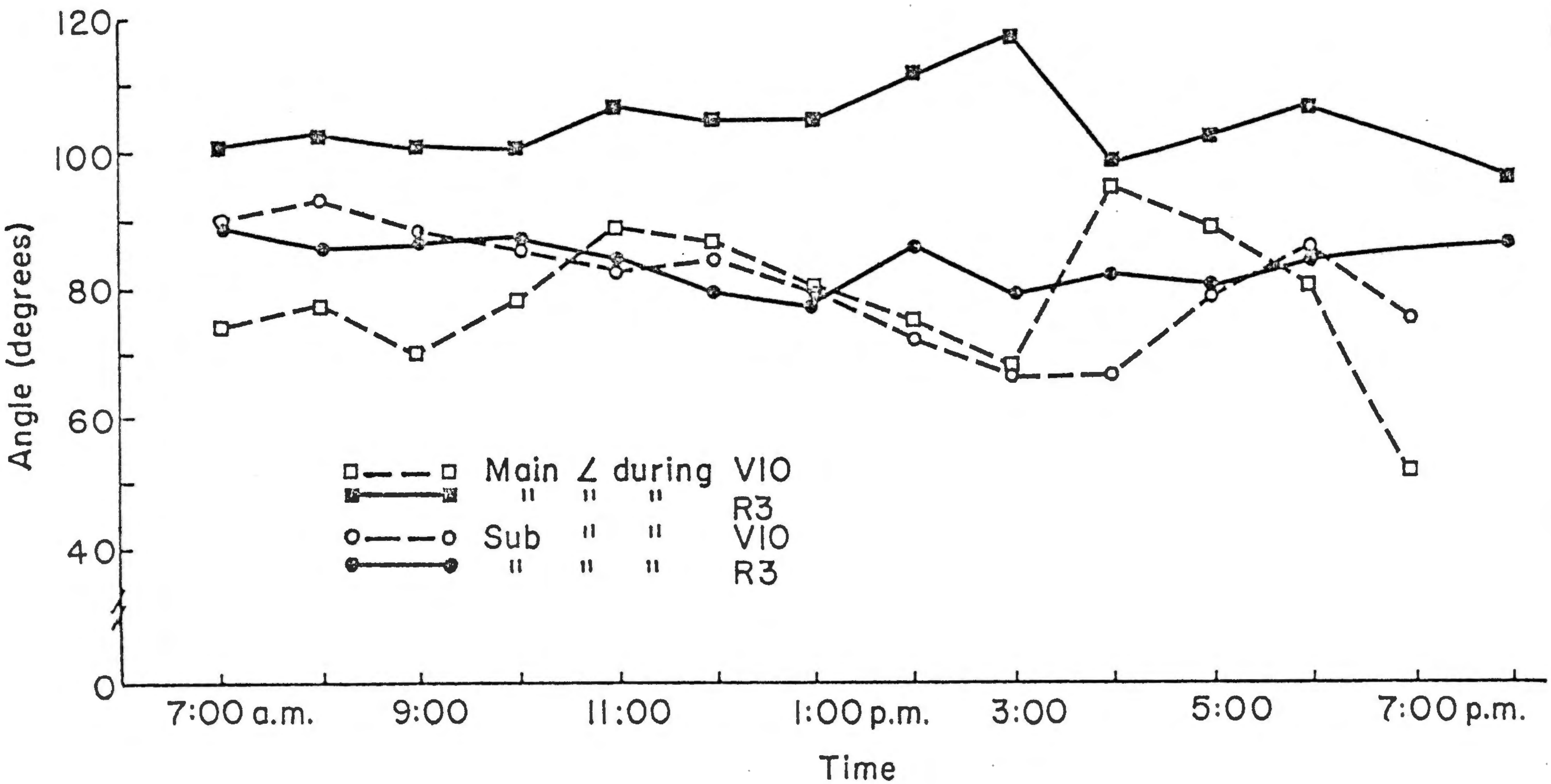

Figure 13. The mean horizontal and vertical orientation of the center leaflet of York during two growth stages.

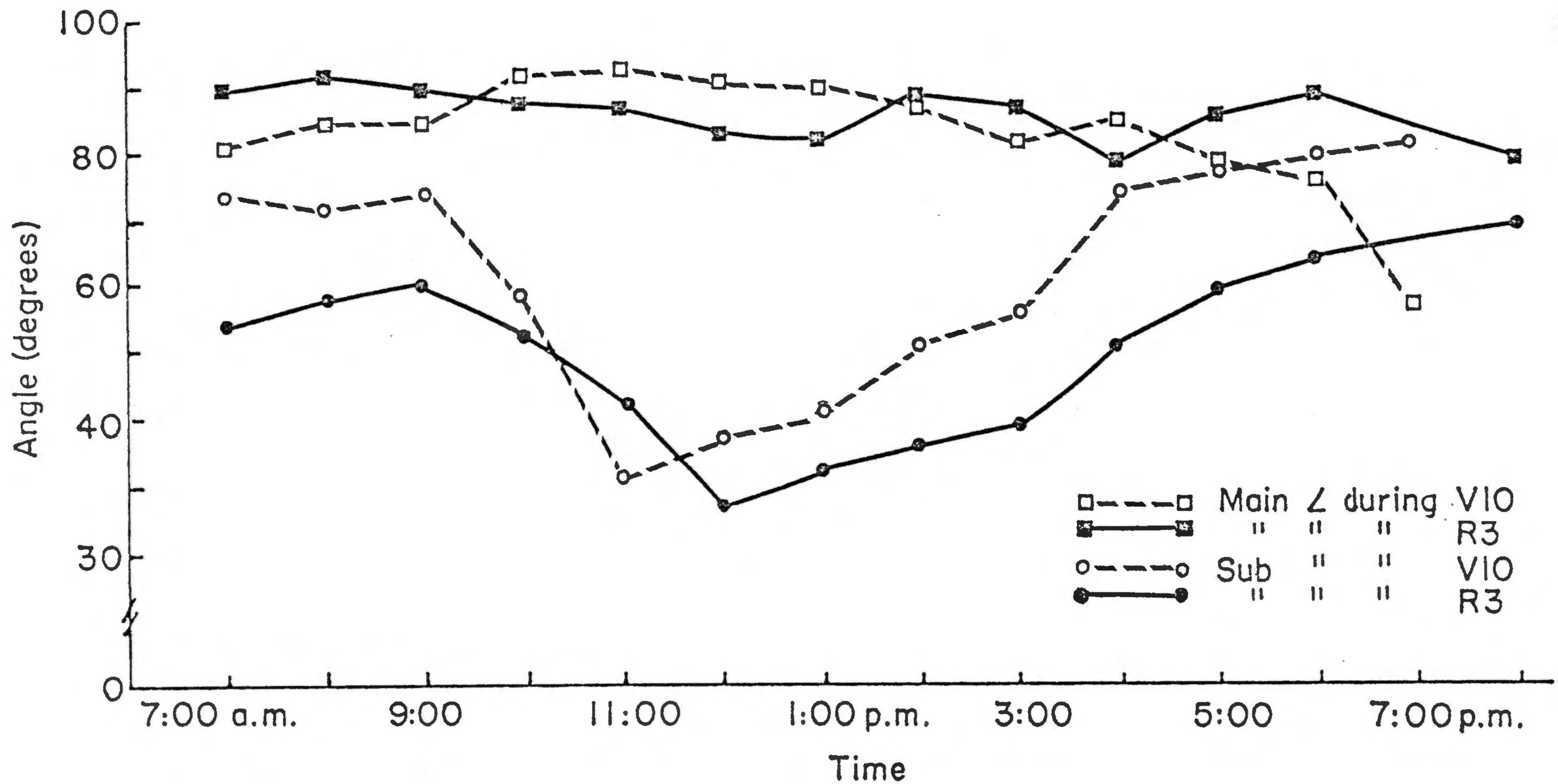

Figure 14. The mean horizontal and vertical orientation of the right leaflet of York during two growth stages.

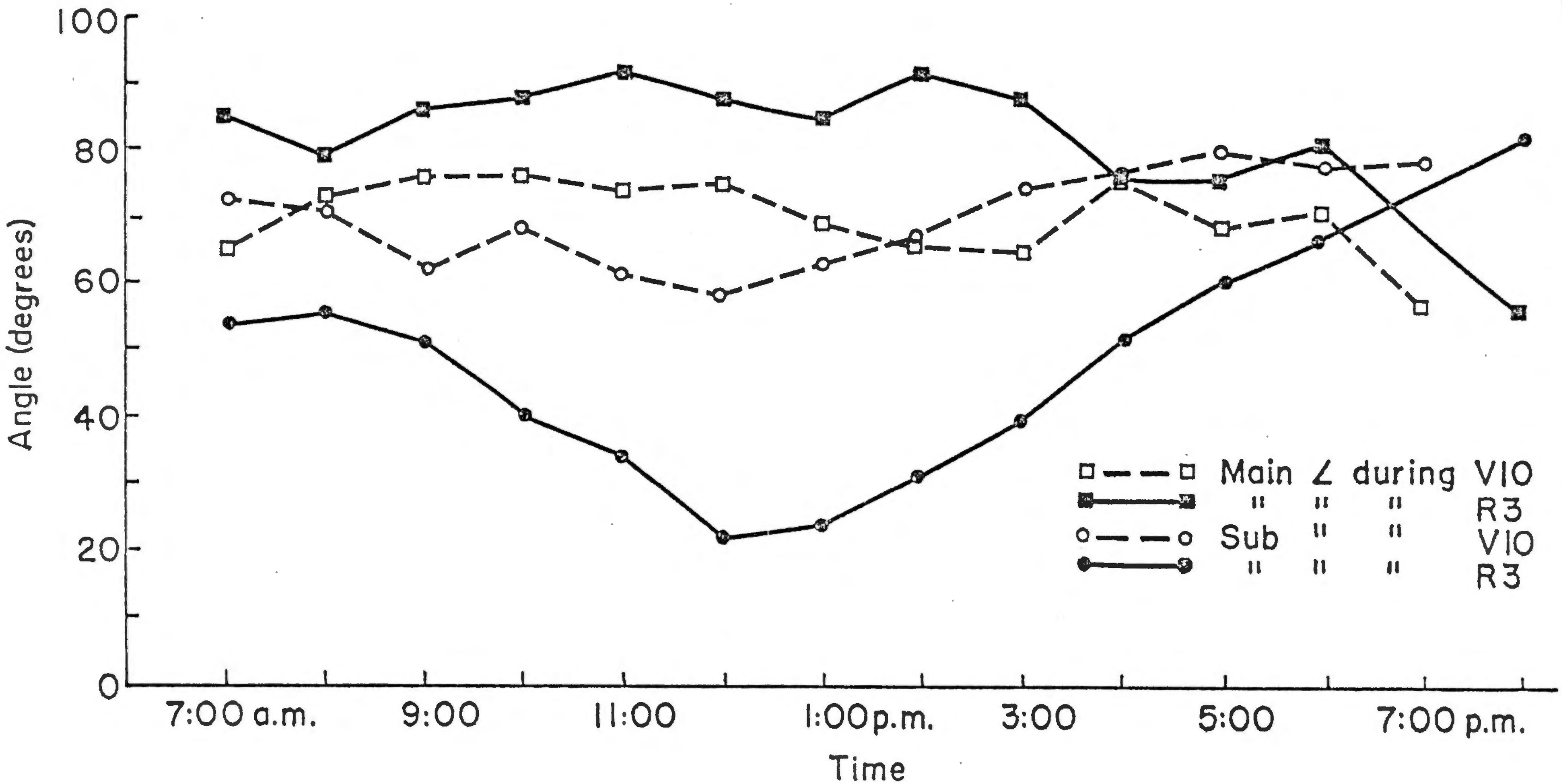

Figure 15. The mean horizontal and vertical orientation of the left leaflet of Dare during two growth stages.

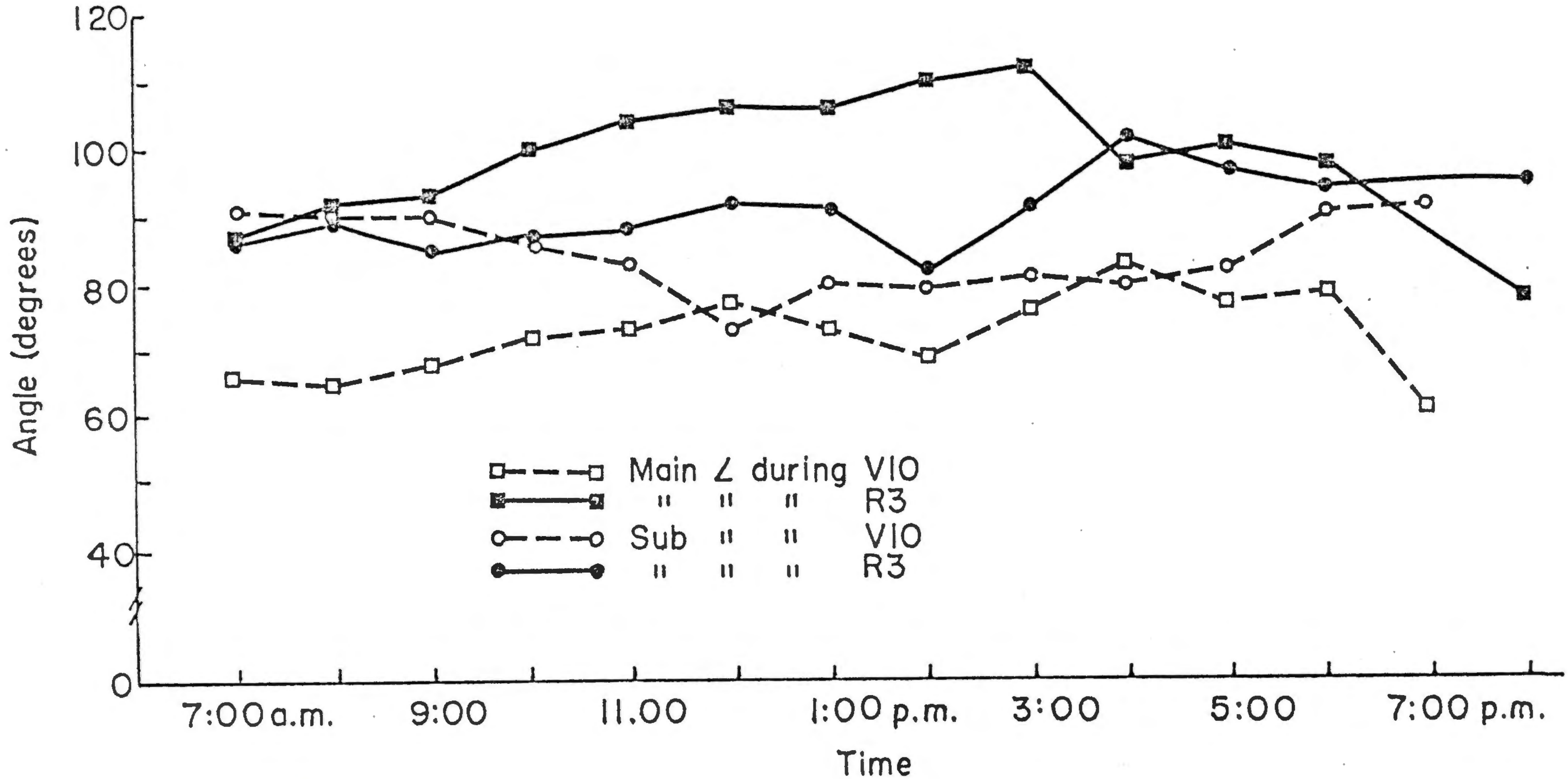

Figure 16. The mean horizontal and vertical orientation of the center leaflet of Dare during two growth stages.

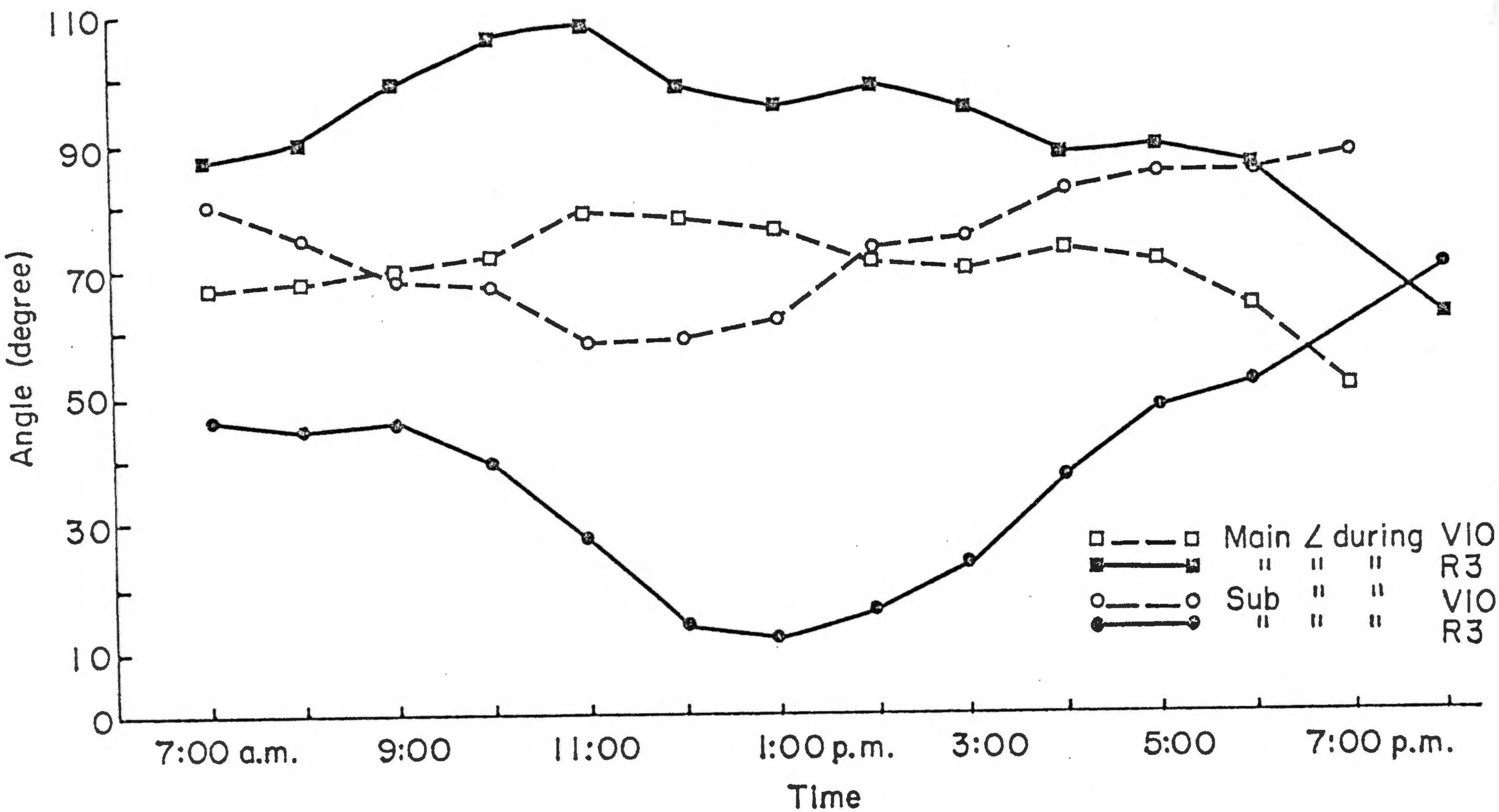

Figure 17. The mean horizontal and vertical orientation of the right leaflet of Dare during two growth stages.

movement, while the main response of the side leaflets is in horizontal movement.

The second question has been partially answered, i.e., there is variation in the response of the different leaflets. The next problem is to determine from which of the leaflets the data should be collected to yield sufficient, accurate information about the varietal variation. In order to answer this, one needs to examine the differences among the leaflets. The data indicate very similar patterns of response of the left and right leaflets. This is particularly true of the sub-angle measurements in which there were no significant differences in the leaflets (during V10) except at four times of the day: 10:00, 11:00, 12:00 and 1:00 (Table 1). The corresponding information for the main angle of the right and left leaflets shows a greater amount of variation than exhibited in the sub-angle. During V10, the main angle of the right leaflet was primarily equal to, but sometimes greater than, that of the left leaflet (Table 1). The pattern of response was very similar during R3, showing the left and right leaflets to behave in much the same manner, the main difference being that the main angle of the right leaflet was significantly greater than that of the left at 12 out of the 13 times (Table 1).

The results indicate that measurements of the center leaflet of a trifoliolate and either one of the side leaflets would give an accurate representation of the movement that is taking place. However, the question arises as to why the main angle of the right leaflet was often greater than that of the left leaflet. One possible explanation is that

Table 1. Comparison of mean main angles of orientation of left, center and right leaflets of soybean trifoliolates at different times of the day during the V10 and R3 stages of growth.*

Time	Growth Stage	Leaflet Left	Leaflet Center	Leaflet Right
0700	V10	$75^{ghijklm}$**	74^{ijklm}	$75^{ghijklm}$
	R3	94^{op}	106^{efghi}	103^{ghijkl}
0800	V10	81^{cdefg}	73^{jklm}	78^{fghijk}
	R3	100^{jklmno}	105^{ghijkl}	103^{ghijkl}
0900	V10	80^{defghi}	72^{lm}	$79^{defghij}$
	R3	101^{hijklm}	105^{ghijkl}	108^{efg}
1000	V10	$79^{defghij}$	$77^{ghijklm}$	85^{bcde}
	R3	99^{klmno}	111^{def}	112^{def}
1100	V10	$79^{efghijk}$	85^{bcde}	89^{ab}
	R3	100^{ijklmn}	117^{cd}	112^{de}
1200	V10	$78^{fghijkl}$	87^{b}	88^{b}
	R3	95^{mnop}	120^{bc}	106^{efghij}
1300	V10	$76^{ghijklm}$	88^{b}	86^{bc}
	R3	92^{pq}	121^{bc}	104^{ghijkl}
1400	V10	74^{ijklm}	85^{bcd}	81^{cdefg}
	R3	94^{nop}	124^{ab}	107^{efgh}
1500	V10	75^{hijklm}	83^{bcdef}	$79^{defghij}$
	R3	92^{pq}	126^{a}	105^{ghijkl}
1600	V10	$76^{ghijklm}$	94^{a}	80^{cdefgh}
	R3	83^{r}	105^{fghijk}	94^{nop}
1700	V10	73^{klm}	85^{bcd}	$76^{ghijklm}$
	R3	87^{qr}	112^{de}	99^{lmno}
1800	V10	72^{m}	$77^{fghijklm}$	71^{m}
	R3	90^{pq}	111^{def}	99^{mno}
1900	V10	54^{n}	56^{n}	51^{n}
2000	R3	74^{s}	95^{mnop}	84^{r}

*Each mean represents the average of four days' measurements on all five cultivars.

**Numbers followed by the same letter(s) are not significantly different (P < .05) according to Duncan's New Multiple Range Test. The comparisons are only valid within a particular growth stage, i.e., comparison cannot be made of a measurement during V10 with a measurement during R3.

this was caused by the sun not being directly over the center of the trifoliate throughout the day, and, in fact, it was positioned more over the left leaflet than the right, resulting in a greater vertical inclination in the right leaflet. Assuming this to be the cause of the observed differences, measurements of one or the other of the side leaflets, plus measurements of the center leaflet should yield adequate information for one to evaluate the leaflet orientation of a soybean cultivar. Data from the center leaflet would provide evidence as to the vertical leaf movement exhibited, and data from either of the side leaflets would provide evidence as to the horizontal leaf movement of the cultivar. The general trend of change in the main angle of the center leaflet was to increase continuously until 3:00 or 4:00 p.m., while the angle of the side leaflets generally decreased during this same period.

The third question deals with whether plants respond in the same manner during V10 and R3. The results obtained tend to support the conclusion that the orientation of the leaves follows the same general pattern of movement in both growth stages (Figures 1 and 2, pages 16 and 17). However, there does seem to be a difference in the degree and range of the responses. More specifically, the measurements obtained when the plants were at the R3 stage of growth tended to be larger for the main angle and smaller for the sub-angle, illustrating greater movement of the leaves in both cases (Figures 1 and 2). Also, the range of measurements tended to be larger at the R3 stage of growth. Because of the observations that: (1) the same general pattern of movement holds throughout both growth stages, (2) the R3 stage of growth brings out the extreme measurements of the main and sub-angles and (3) that the range of variation is larger in the reproductive growth stage, combined with the idea that more demands are placed on the plant during this reproductive stage, it is concluded that measurements taken when the plants are in the reproductive stages of growth should provide better information on the orientation response of cultivars than those taken during vegetative stages.

Another question to be asked is: During what period of the day was the most variation among cultivars exhibited? The data showed that the time period during which there was the greatest amount of variation in vertical orientation of the center leaflets was from 10:00 a.m. until 4:00 or 5:00 p.m. (Figures 18 and 19). During the period from 7:00 to 10:00 a.m., the measurements of all five cultivars at V10 were clustered in an array separated by a maximum of 10 to 20 degrees. However, beginning at 10:00 a.m. and going through approximately 5:00 p.m., the graph illustrates a dispersion of responses or an increase in the variability among cultivars. From 4:00 p.m. until the end of the day there was some variation in the response of each cultivar, but the differences were not as large as those from 10:00 a.m. until 4:00 p.m. At the R3 stage of growth the cultivars differed only about 30 to 35 degrees from each other during most of the day, and the ranking of the cultivars was practically unchanged. Sub-angle measurements of the side leaflets from 10:00 a.m. until 5:00 p.m. should give adequate information about the response of each plant. Throughout the day the array of the

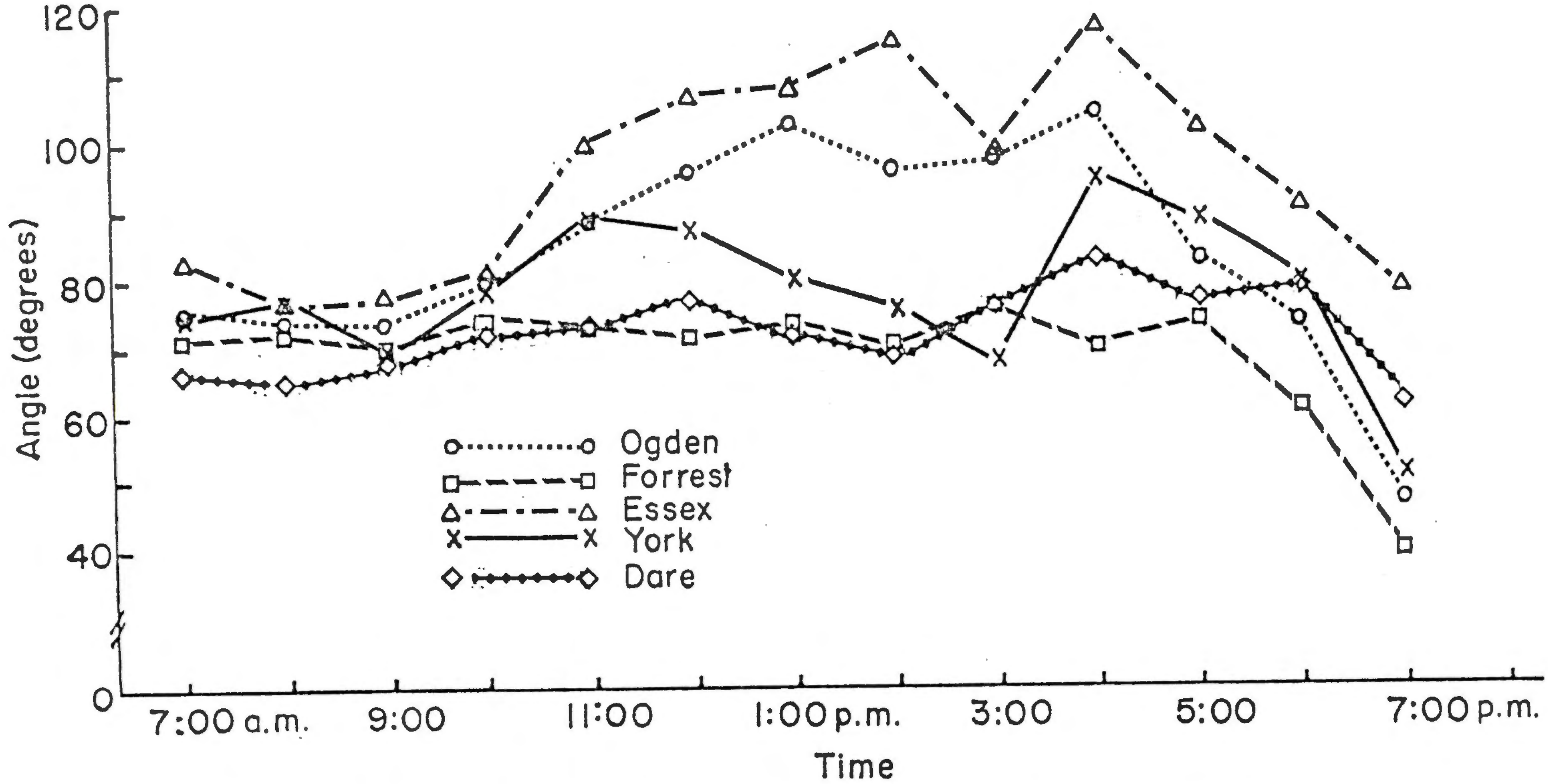

Figure 18. The average main angle of the center leaflet of five soybean cultivars during the V10 stage of growth.

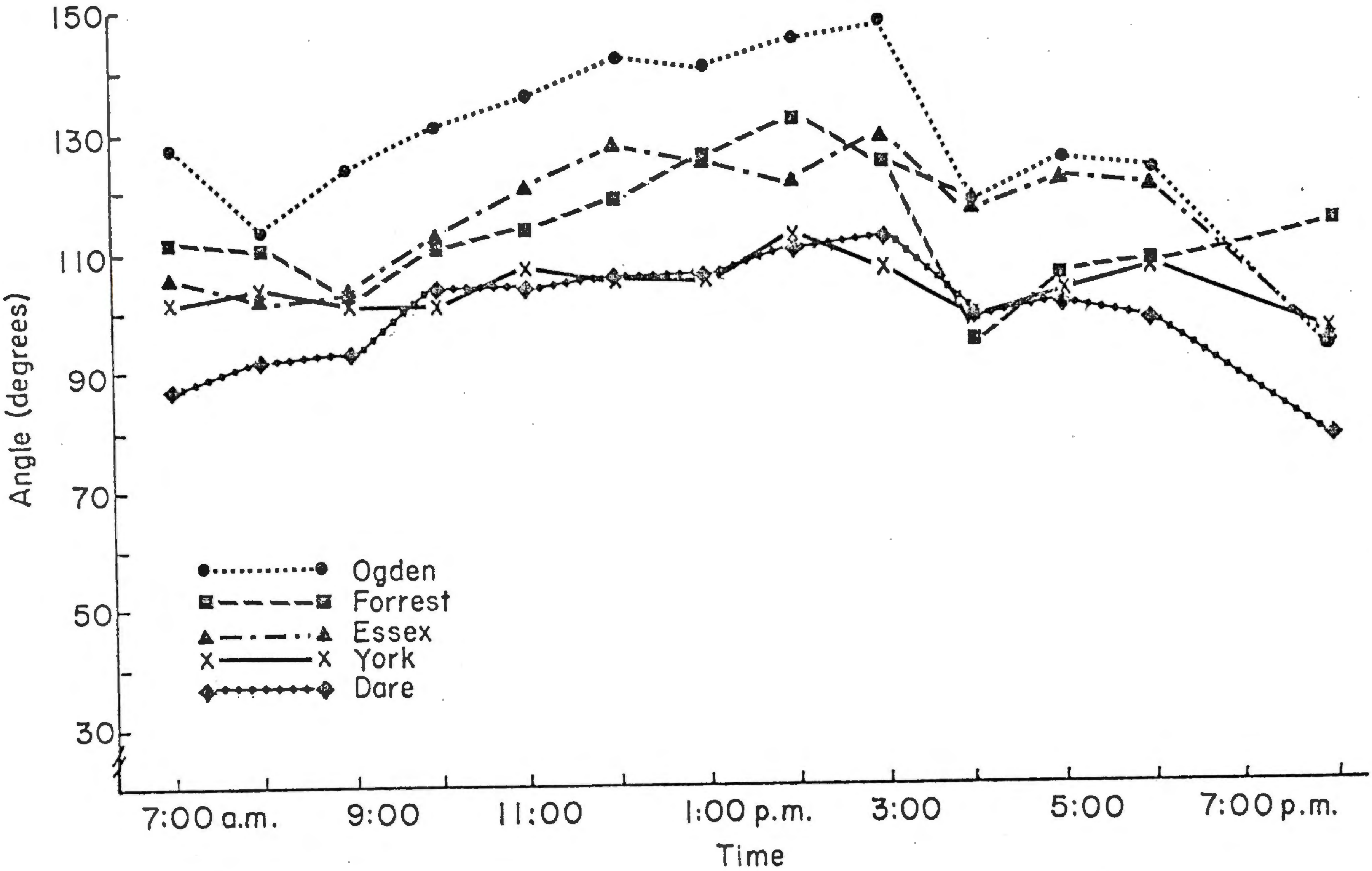

Figure 19. The average main angle of the center leaflet of five soybean cultivars during the R3 stage of growth.

responses of the side leaflets changed very little (Figures 20 and 21). In the morning and afternoon hours when less variation was observed, there was probably less demand on the plants.

A consistent drop in the alignment of all the cultivars' center leaflets was observed between 3:00 and 4:00 p.m. followed immediately by an increase during the following hour in leaflet angle during both growth stages (Figures 18 and 19). The clearest manifestation of this phenomenon occurred at R3 when the angle of every cultivar reached a peak at 2:00 or 3:00 p.m. and then declined an average of 20°, followed by an increase in the angle of orientation of about 5° (Figure 19). At V10 the pattern is more sporadic and not as clearly defined, but there is an equivalent drop in the angle of the leaflets of each cultivar of about 7° which is followed by an increase and then the expected decline until dark (Figure 18). This phenomenon could be due to a regulatory mechanism within the plant which is not activated within closely specified limits due to its dynamic nature. For example, if the orientation is the result of turgor pressure within the pulvinus, the physiological structure of the pulvinus may be such that the plant overreacts in the movement and an equilibrium must subsequently be established. This explanation would be satisfactory if a fluctuation in potassium concentration in the pulvinus is at least partially responsible for turgor changes.

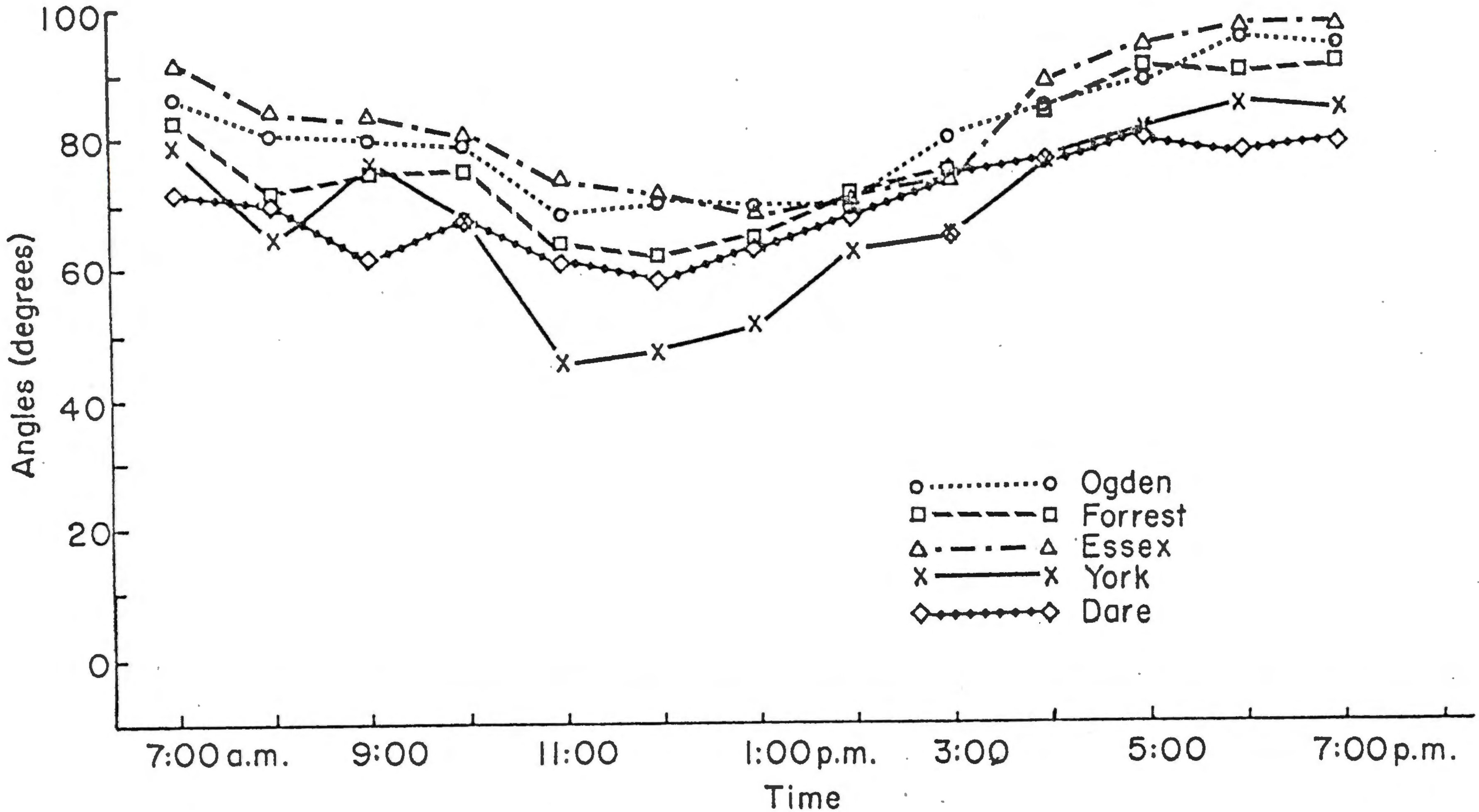

Figure 20. The average sub-angle of the left leaflet of five soybean cultivars during the V10 stage of growth.

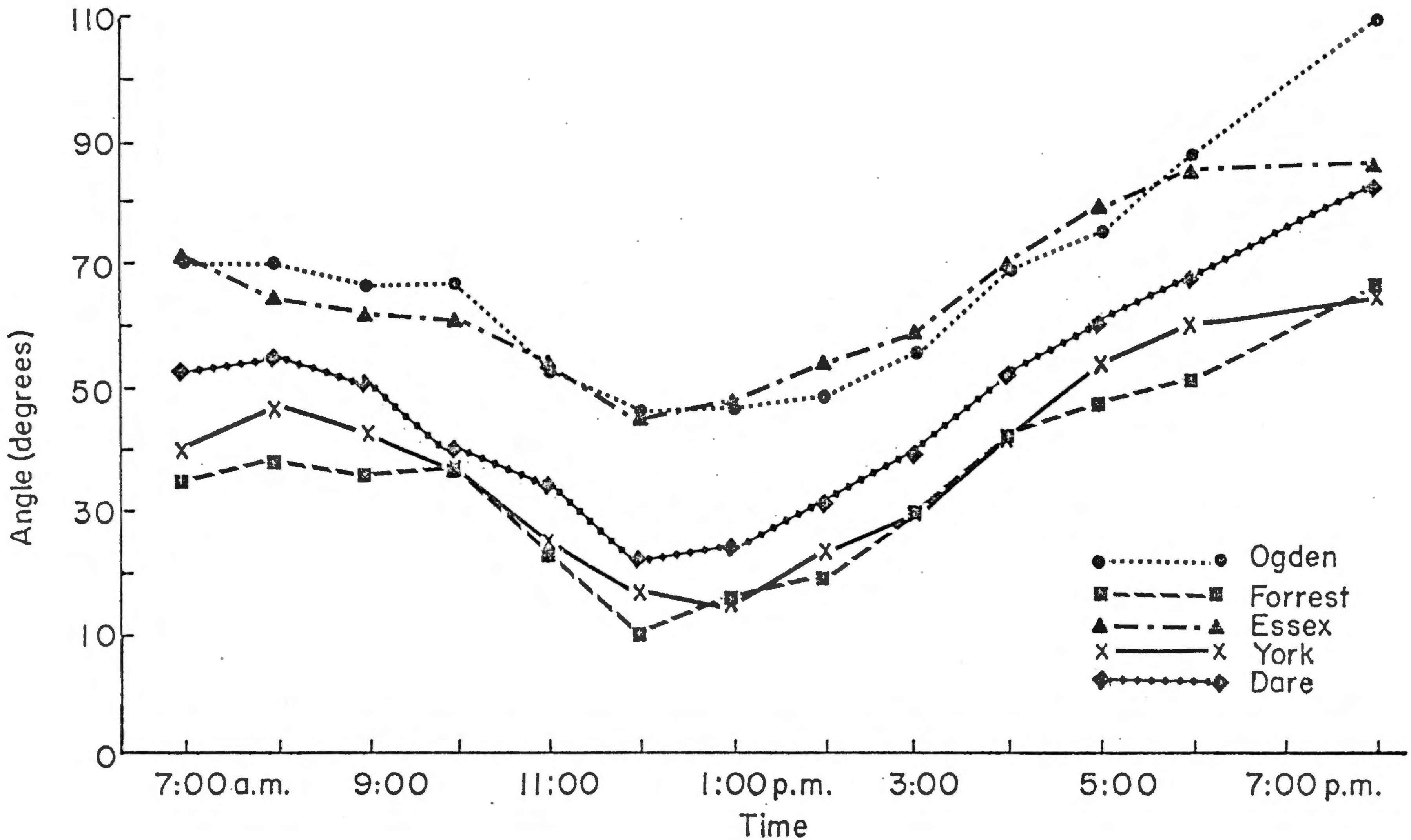

Figure 21. The average sub-angle of the left leaflet of five soybean cultivars during the R3 stage of growth.

Potassium Concentration in the Pulvinus During the Extremes of Leaflet Orientation

Satter and Galston (23) postulated that potassium had a role in the movement response observed in Albizzia pulvini. One objective of the present study was to determine if potassium could be implicated as having a role in the movement of the pulvinus which in turn orients the leaves of the soybean plant. Presented in Table 2 are the potassium concentrations during the extremes of pulvinus position for 4 different cultivars of soybeans. Each cultivar showed a consistently higher concentration of potassium in the pulvinus during the "tense" position than during the "relaxed" position. The average potassium concentration in the pulvinus of cultivars during the tense position was 19,401 ppm compared to 15,456 ppm during the relaxed position. The average difference in potassium concentration between the two extreme positions was 3,944 ppm which is significant ($P < .01$) according to a paired-observation t test. Another important point is that there were differences among the cultivars in potassium concentration during both the tense and relaxed positions of the pulvini. During the tense position, the Ogden cultivar had the highest concentration of potassium in the pulvinus, 22,166 ppm, followed by Dare (20,037 ppm), Forrest (19,314 ppm) and York, being the lowest, with 16,087 ppm. During the relaxed position of the pulvinus, Forrest had the highest concentration of potassium with 18,108 ppm followed by Ogden (16,430 ppm), York (14,650 ppm) and Dare with the lowest, 12,638 ppm. Also, cultivars differed considerably in the amount of change in potassium concentration

Table 2. Potassium concentration in soybean pulvini at the "tense" and "relaxed" positions during leaflet orientation.

	Potassium Ion Concentration (ppm)		
Cultivar	Tense	Relaxed	Difference
Ogden	22,166	16,430	5,736
Forrest	19,314	18,108	1,206
York	16,087	14,650	1,437
Dare	20,037	12,638	7,399
Average	19,401	15,456	3,944**

**Indicates significance ($P < .01$) according to a paired observation "t" test.

in the pulvinus between the relaxed and the tense positions. Dare exhibited the largest change of 7,399 ppm followed by Ogden with 5,736 ppm. York and Forrest had considerably less change in K, 1,437 and 1,206 ppm, respectively. Thus, the results indicate that there are definite changes in the potassium concentration in the pulvinus of soybean cultivars during the process of leaflet orientation. It appears that potassium does have some role in the process responsible for "bending" and "straightening" of the pulvinus which in turn moves the leaflet in a specific direction. Whether or not there is an association between the capacity of a cultivar to drastically change the concentration of K in the pulvinus and the extent of leaflet orientation of the cultivar is not clear, nor is it possible to determine this from the present study.

Another basic question which needs to be answered asks how many days measurements should be taken to define adequately the variation present. Statistical analysis of the data revealed that measurements of leaflet orientation taken over a two-day period should yield sufficient statistical information about the variation. This conclusion was reached after performing the analysis of variance of one day's measurements, two days' measurements, three days' measurements, and four days' measurements (Table 3). The analysis of variance of one day's data did not reveal sufficient differences in the responses of the cultivars. In the other analyses, where the date component was present, there were no significant differences in the Date × Cultivar interaction, and the cultivars were always significantly ($P < .01$) different. Therefore, while variation in the amount of orientation was observed in each

Table 3. Mean squares for the main angle during the V10 growth stage for one, two, three, and four days of measurements.

Component of ANOVA	Mean Squares			
	One Day	Two Days	Three Days	Four Days
Cultivar	8,833.17	7,386.97**	9,560.75**	15,712.72**
Date		68,627.70	59,768.27*	54,997.58**
Time	883.59	7,006.05	6,479.09	7,660.35
Trifoliolate	3,345.00**	2,462.87	3,042.05	5,824.88
Cultivar × Time	333.01**	294.66	313.51*	384.46**
Cultivar × Date		4,574.56	3,337.08	2,856.91
Time × Trifoliolate	412.17**	934.78**	928.73**	1,223.10**

*P < .05.

**P < .01.

cultivar, the relative ranking of the cultivars did not change significantly from one day to the next. Even though measurements taken on two days should illustrate the orientation response differences in the cultivars, some accuracy is lost in analyzing the variation when the data are collected over fewer days due to decreasing the sample size. Hence. if there is interest in second- or third-order interactions, measurements should be taken over four days to give more definitive results.

Orientation of Individual Cultivars

Ogden

After providing some answers to the basic questions concerning leaf orientation, the response of individual cultivars can be examined. The main angle of the center leaflet of Ogden during the V10 stage of growth was approximately 75° from 7:00 to 9:00 a.m. and then steadily increased to approximately 100° at 1:00 p.m. (Figure 3, page 19). It remained at nearly 100° from 1:00 to 4:00 p.m. and then steadily decreased to 47° at 7:00 p.m. During this time the sub-angle (center leaflet) remained relatively constant throughout the day. The angle was near 90° from 7:00 to 9:00 a.m. and began to decrease until it reached 74° at 12:00 noon. The leaflet then began to move back toward a near flat, horizontal position, reaching 89° at approximately 5:00 p.m.

During the R3 stage of growth, the pattern of response was similar to that during the day at V10, but the angle of inclination, both vertical and horizontal, was generally highest during R3. The vertical angle of inclination of the center leaflet was consistently higher in

R3 than in V10 for Ogden (Figure 3, page 19). The average daily main angle during V10 was 85° but it was 128° during R3 (Ogden, Table 4). There was not as much difference between the sub-angles of the center leaflet at the two growth stages. The average daily sub-angle of the center leaflet for Ogden during V10 was 88° compared to 98° during R3 (Table 4).

It appears from this information that the center leaflet of Ogden at the V10 stage of growth is positioned in such a manner that it receives maximum exposure to the incoming radiation from the morning hours of 7:00 to 9:00 a.m. and throughout the day until 4:00 p.m. The measurements of leaflet orientation obtained during this time period indicate an increase in the angle of measurement consistent with the increase in the angle of the incoming radiation. This trend towards maximization of the solar energy appears to diminish from 4:00 p.m. to 7:00 p.m., during which time the earth is in such a position that the radiation from the sun is striking the trifoliolate from the west. During this time period the leaflet is positioned in such a way that it is having minimum exposure to the sunlight.

During the R3 growth stage, it appears that the center leaflet is positioned in such a manner that it captures very little of the incoming light, and, in fact, appears to minimize its exposure to sunlight by virtue of its orientation. If the movement of the leaflets is actually minimizing the plant's exposure to sunlight during the reproductive phase, this movement could be a mechanism which keeps the transpiration rate of the plant in check and thus aids in optimal utilization and conservation of the assimilates available to the plant.

Table 4. Means of the main and sub-angle of each leaflet of a trifoliolate for five cultivars of soybeans at the V10 and R3 stages of growth.

	Center Leaflet		Left Leaflet		Right Leaflet	
Cultivar	V10	R3	V10	R3	V10	R3
			Main Angle (°)			
Ogden	85	128	69	99	68	116
Forrest	70	114	76	99	86	108
Essex	96	116	78	89	85	111
York	79	104	82	93	84	86
Dare	73	99	71	82	70	93
			Sub-Angle (°)			
Ogden	88	98	80	66	72	66
Forrest	75	80	76	35	72	30
Essex	89	88	82	65	78	68
York	67	83	80	38	61	49
Dare	70	91	84	47	73	36

The side leaflets of Ogden appear to have a response nearly opposite to that observed in the center leaflet. In the side leaflets the main angle does not exhibit much change over the course of the day, while the sub-angle of the side leaflets shows a definite pattern of tracking the position of the sun.

The main angle of the side leaflets of Ogden during the V10 stage of growth was approximately 70° from 7:00 a.m. until 4:00 or 5:00 p.m. at which time it began decreasing to about 40°-45° at 7:00 p.m. (Figures 4 and 5, pages 20 and 21). During this same time period the sub-angle of these leaflets exhibited more change. At the beginning of the day the average angle was recorded to be around 80°-90°, and it gradually decreased to 50°-70° at 11:00 a.m. at which time it stabilized and began a steady increase through the rest of the day to about 95° at 7:00 p.m.

During the R3 stage of growth, the pattern of response was similar to that observed during V10, but the angle of inclination was both highest and lowest during R3. The vertical angle of inclination was consistently higher in R3 than in V10 (Figures 4 and 5). The average daily main angles were 69° and 68° during V10 for the left and right leaflets, but they were 99° and 116° during R3 (Ogden, Table 4). On the other hand, the horizontal angle was usually lowest in the R3. The average daily sub-angles for the left and right leaflets of Ogden were 80° and 72° during V10 and 66° during R3 (Table 4).

From this information it appears that at times the leaflets are positioned in such a way that they receive maximum exposure to sunlight while at other times of the day they are positioned in such a manner that they receive minimum exposure. All three leaflets appear to be accomplishing the same thing; but the side leaflets obtain maximum and minimum exposure primarily through horizontal orientation, whereas, the same exposures are achieved primarily through vertical movement in the center leaflets.

Basically it seems that nearly maximum light interception occurs throughout the day during V10 through horizontal orientation of the side leaflets of Ogden. The leaflets turn toward the east in the morning, and, as the sun reaches its zenith, the average angle of the leaflets begins to increase and they achieve a more parallel position. After this point they proceed to tilt toward the west as the radiation continues to impinge more from a westerly direction.

During R3, the right leaflet of a trifoliolate of Ogden, was inclined at about 70°, from 7:00 a.m. until approximately 10:00 a.m., and it, therefore, intercepted much of the available light. From 11:00 a.m. through 1:00 or 2:00 p.m. the angle reached a low of about 35°-45° while the sun was directly overhead; thus, the interception of light energy tended to be minimized. From approximately 3:00 p.m. until 8:00 p.m. the angle increased, and some light was intercepted, but much less than if the leaflet was perpendicular to the source of light.

Forrest

The main angle of the center leaflet of Forrest during the V10 stage of growth remained relatively constant, approximately 70°, throughout the day from 7:00 a.m. through 5:00 p.m. (Figure 7, page 23). It decreased from 5:00 p.m. to a low of 40° at 7:00 p.m. In the same manner, the sub-angle of the center leaflet showed only a small amount of change during this time period. It remained nearly level, approximately 85°, until 10:00 a.m. when it decreased to a low of 60°. It remained at 60° from 11:00 a.m. through 1:00 p.m. and then increased through the afternoon and evening up to 88° at 7:00 p.m.

During the R3 stage of growth, a somewhat different pattern was observed. At this growth stage the main angle of the center leaflet stayed close to 110° from 7:00 a.m. through 10:00 a.m. and then it increased continuously to an angle of 132° at 2:00 p.m. From this high point reached at 2:00 p.m., the leaflet declined rather sharply to 90° at 4:00 p.m., and then the angle slowly increased to 115° at 8:00 p.m. (Figure 7, page 23). During this growth stage the sub-angle oscillated around 80°, showing relatively little variation. Again, the vertical angle was consistently higher in R3 than it was in V10 with the average main angle of the center leaflet being 114° during R3 and 70° during V10 (Table 4, page 49). In terms of the sub-angle, there was only a 5° average difference in the two growth stages, with 75° being the average during V10 and 80° being the average during R3.

In the V10 stage of growth it seems that the relatively constant orientation of the center leaflet of Forrest (slightly below horizontal at 70° for the main angle and approximately 70° for the sub-angle), allows the plant to capture an appreciable amount of the incoming radiation throughout most of the day without much movement taking place. This appears to be a very conservative approach which allows primarily a maximum exposure to sunlight. During R3 the center leaflet appears to have an opposite response. At this reproductive stage of growth the movement observed appears to be a positioning of the center leaflet such that it receives minimum exposure to sunlight throughout the day. This conclusion is reached because of the vertical inclination (110°) of the leaflet that was viewed in the morning when the sunlight was impinging from a low angle in the east accompanied by a greater vertical inclination being attained as the angle of the sunlight reached its highest point of the day. As the sunlight began to impinge from a more westerly direction, the angle dropped drastically (from 132° to 95°) and increased only a very small amount until the end of the day (114°).

The side leaflets of Forrest exhibited an opposite response (compared to that of the center leaflet) in that the majority of the movement recorded was in horizontal orientation of the leaflets. At V10 the main angle of the side leaflets had very little change throughout the day. The change in the left leaflet was not significant from 7:00 a.m. through 6:00 p.m., ranging from 72° to 86°, however at 7:00 p.m. there was a significant decrease to 51° (Figure 6, page 22). Similarly, the right leaflet showed significant differences only at 7:00 a.m., 6:00 p.m. and 7:00 p.m., and the angle ranged from 80° to 98° (Figure 8, page 24). The only exception was at 7:00 p.m. when it was 52°. The horizontal (sub-angle) movement of the side leaflets was substantially more during V10. The right leaflet began at 78° and decreased to 50° at 11:00 a.m., then increasing until 7:00 p.m. when it reached an angle of 94°. The left leaflet maintained an angle of approximately 75° from 7:00 a.m. to 10:00 a.m. decreasing to 62° at noon. Afterward, it gradually increased to 92° at 7:00 p.m.

The side leaflets of Forrest showed a pattern of response in the R3 stage of growth similar to that in the V10, with the angles observed in R3 being much more extreme. The sub-angle of the right leaflet decreased most of the morning from a beginning high of 39° at 8:00 a.m. to an average low of 7° at noon and then increased through the rest of the day to 68° at 8:00 p.m. The left leaflet began at 35° and decreased to an average low of 10° at noon and then increased to 56° at 8:00 p.m. During this time the vertical inclination of each leaflet was rather stable, showing a slight decrease throughout the day (113°-105°). The differences between the V10 and the R3 stages of growth can be seen in the average daily angles obtained (Table 4, page 49). For example, the average main angle of the left leaflet was 99° in R3 and 76° in V10, while the average sub-angle was 35° in R3 and 76° in V10.

It appears from these data that the same mechanisms are at work in the side leaflets as in the center leaflets. In V10 an overall trend of movement to facilitate maximum reception of light energy is apparent. During R3 the movement seems to be resulting in a minimization of the light being received.

Essex

Essex showed a sizeable amount of response in the main angle of its center leaflet during V10 (Figure 10, page 26). From 7:00 a.m. until 10:00 a.m. the angle of orientation remained at approximately 80°, then increasing to 115° at 2:00 p.m. From 2:00 p.m. until 7:00 p.m. the angle decreased to 79°. The change in sub-angle orientation of the leaflet was negligible, remaining at approximately 90°. The orientation observed for the main angle during R3 was similar in pattern to that observed in V10, but the average angles observed in R3 were consistently greater than or equal to those recorded during V10. During R3 the leaflet remained at about 103° from 7:00 a.m. through 9:00 a.m. and then increased to a high of 128° at noon. It held this same high angle until 3:00 p.m. and then decreased to 95° at 8:00 p.m.

With Essex it appears that the orientation response observed in V10 serves to minimize the amount of solar radiation which is received. In the morning, for example, when the main angle was about 80°, very little light was being intercepted, and, as the angle of the sun increased, the angle observed in the vertical inclination increased also. As the sunlight began to come more from a westerly direction, the angle of the center leaflet decreased. The same thing occurred at R3, but it was more pronounced, such that less light was intercepted throughout the day.

The side leaflets of Essex showed some response in both the main and the sub-angles with most of the change occurring in the sub-angle. At V10 the main angle of the right leaflet began at 80° and increased to an average of 97° at 11:00 and 12:00 and then decreased to 57° at 7:00 p.m. (Figure 11, page 27). The left leaflet, however, remained around 80° all day until the last hour, at which time it had decreased to 55° (Figure 9, page 25). The sub-angle of the right leaflet at V10 decreased from 88° at 7:00 a.m. to about 63° from 11:00 to 1:00 p.m. and then increased to 96° at 7:00 p.m. The left leaflet displayed a similar pattern. At R3 the pattern of the change was similar to that during V10 but was of a higher magnitude. The main angles of the side leaflets were

89° for the left leaflet during R3 and 78° during V10 and 111° for the right leaflet during R3 and 85° during V10 (Table 4, page 49). The sub-angle was smaller in the side leaflets during R3 than V10, with the left leaflet averaging 65° (R3) and 82° (V10) and the right leaflet averaging 68° (R3) and 78° (V10).

York

The main angle of the center leaflet of York was approximately 75° from 7:00 to 10:00 a.m. at the V10 stage of growth (Figure 13, page 29). The leaflet then rose to an angle of 89° at 11:00 a.m. and then gradually decreased to an angle of 68° at 3:00 p.m. From 3:00 to 4:00 p.m., the leaflet changed from a relatively relaxed alignment of 68° to the greater-than-level orientation of 95°. From this point the angle of the leaflet receded to 52° at 7:00 p.m. During this same period of time, the horizontal inclination of the center leaflet underwent a small degree of change. At 7:00 a.m. the average sub-angle was 90°, from this level position the pattern of leaflet orientation was that of an overall decrease in the angle to 66° at 3:00 p.m., from which time the angle increased to just below level at 86° at 6:00 p.m., and then dropped to 75° at the close of the day (7:00 p.m.).

The pattern of leaflet orientation for the center leaflet of York at the R3 stage of growth was somewhat different from that just discussed in the V10 stage for the main angle. Even though some differences were present, the primary difference between the V10 and R3 stages was the larger magnitude of the angles at R3. At R3 the average daily main angle recorded was 104°, while, at V10 it was only 79° (Table 4, page 49). The horizontal inclination of the center leaflet in terms of the pattern of orientation was very similar at both stages of growth with the greatest differences between the two showing up at 2:00, 3:00, and 4:00 p.m. This two-hour time period showed the greatest divergence. The main angle of the center leaflet of York at R3 remained stable at approximately 101° from 7:00 to 10:00 a.m., then it increased to about 105° and remained at about this inclination from 11:00 a.m. to 1:00 p.m. It then increased to a peak of 117° at 3:00 p.m. and finally decreased in inclination to 96° at 8:00 p.m.

The side leaflets of York appear to have a somewhat opposite orientation response compared to that of the center leaflet. The main angle of both side leaflets remained relatively constant in the V10 stage of growth with an average daily angle of 82° for the left leaflet and 84° for the right leaflet (Table 4, page 49). Neither of the leaflets showed variation in the sub-angle (70°) from 7:00 to 9:00 a.m. during the V10 stage of growth. From 9:00 to 11:00 a.m. the average angles of each leaflet decreased, to 31° for the right leaflet and 45° for the left leaflet (Figures 12 and 14, pages 28 and 30). They both increased through the remainder of the day to an average of 84° and 82° for the left and right leaflets, respectively, at 8:00 p.m.

During R3 the behavior of the side leaflets was very similar to that observed in V10, but during R3 more extreme orientation responses were noted. As an example, the average daily angle of vertical inclination of the left leaflet was 93° in R3 and 82° in V10, and the average daily sub-angle was 38° in R3 and 67° in V10 (Table 4).

Dare

There was not much change in the vertical inclination of the center leaflet of Dare over time, however, some change did take place (Figure 16, page 32). The average main angle increasing from 66° at 7:00 a.m. to 77° at noon. It then decreased to an average inclination of 69° at 2:00 p.m., increased to 83° at 4:00 p.m. and then decreased to 61° at 7:00 p.m. The average hourly angles were not significantly ($P > .05$) different from each other from 7:00 a.m. through 3:00 p.m.

In terms of horizontal inclination, the sub-angle of Dare did show a small amount of change throughout the day during V10. It began at 91° at 7:00 a.m. and remained almost constant through the morning until 11:00 a.m., then decreasing to 73° at 12:00 noon and then increasing to 80° at 1:00 p.m. From 1:00 p.m. to 5:00 p.m. it changed very little, remaining around 80°; then, between 5:00 and 6:00 p.m., the average angle of horizontal inclination rose to 91° and was at 92° at 7:00 p.m.

At the R3 stage of growth the average main angle of the center leaflet increased from 7:00 a.m. until 3:00 p.m., beginning at 87° and increasing to 112° at 3:00 p.m. From 3:00 p.m. until 8:00 p.m. it gradually declined until it was at 78°. During R3 the sub-angle was virtually level at approximately 88° from 7:00 a.m. to 1:00 p.m., then decreasing to 82° at 2:00 p.m., rising to 102° at 4:00 p.m., leveling off toward the close of the day, with the last angle of the day averaging 95°. The overall differences of the two growth stages are seen in the fact that the average daily main angle was 99° at R3 and 73° at V10 and the average daily sub-angle was 91° at R3 and 84° at V10 (Table 4, page 49).

The main angle of the side leaflets of Dare shows little movement during V10, and remained around 70° (Figures 15 and 17, pages 31 and 33). However, the sub-angles of the side leaflets at this growth stage do show more variation. In this case, the average 7:00 a.m. measurement (sub-angle) is 80° for the right leaflet and 72° for the left leaflet, then the angle of inclination decreased to 58° at 11:00 a.m. and at noon for the right and left leaflets, respectively. From this low point of orientation (58°), the average angles increased to 88° and 79° at the close of the day (7:00 p.m.), for the right and left leaflets, respectively.

The response of the side leaflets during R3 was similar to that during V10, but during R3 more extreme angles were observed (Figures 15 and 17). At the R3 stage of growth the average main angle of the right leaflet of Dare was 87° at 7:00 a.m., then, from 7:00 to 11:00 a.m., the angle increased to an average angle of 108°. From 11:00 a.m. until the last measurement of the day (8:00 p.m.), the angle of the leaflet declined to 62°. From 7:00 a.m. to 9:00 a.m., the sub-angle remained about 45°, then it decreased to an extreme of 12° (average) at 1:00 p.m. From 1:00 p.m. to 8:00 p.m. the average sub-angle increased to 70°. The amount of difference between the growth stages can be seen in Table 4 (page 49) which shows the average respective daily main angles of the left and right leaflets to be 82° and 93° at R3 and 71° and 70° at V10. On the other hand, the average respective daily sub-angles were 47° and 36° for the left and right leaflets at R3 and 70° and 73° at V10 (Table 4).

Similarities and Differences Among Cultivars

At least three postulates can be posed as to the function of dynamic leaflet orientation in soybeans. The first is that, in response to certain stimuli, the leaflets are positioned such that they receive maximum exposure to sunlight and therefore the rate of photosynthesis is enhanced. The second is that, in response to stimuli, the leaflets are positioned to receive minimum exposure to sunlight, thus reducing the amount of transpiration. The third is that, since both of the above can operate in the plant during the course of a day, the response which takes place depends on the particular stresses placed upon the plant and the current demand for photosynthates. Speculation can be made as to the particular postulate which is in effect at a particular time for a given cultivar. Certain similarities and differences among cultivars can be observed in terms of which postulate appears to be dominant.

Center Leaflet, V10 Growth Stage

It appears from the information on the response of individual cultivars that at the V10 stage of growth the leaflet orientation responses of the center leaflet of Ogden and Essex are very similar (Figure 18, page 38). The center leaflet of each appears to be positioned in such a manner that it receives maximum exposure to the incoming radiation from the morning hours of 7:00-9:00 a.m., and throughout the day until 4:00 p.m. The measurements of leaflet orientation obtained during this time period show an increase in the angle consistent with the increase in the angle of incoming radiation. This trend toward maximization of the solar energy received appears to diminish from 4:00 p.m. until 7:00 p.m., during which time the earth is in such a position that radiation from the sun is striking the trifoliolate from the west. During this latter time period the center leaflets are positioned in such a way that they are having minimum exposure to the sunlight. Thus, it seems that the first postulate is in effect for the major portion of the day, but, in the late afternoon, the second postulate of minimization of exposure to sunlight seems to be in effect also. Because both a minimization and a maximization of exposure to sunlight is seen in the response of these cultivars, the third postulate also is in effect, and the particular response of the leaflet at each time of the day is presumed to be dependend upon the particular stresses placed on the plant at that time.

Forrest and Dare demonstrate similar vertical inclination of the center leaflets during the V10 stage of growth (Figure 18, page 38). However, the similar responses of Forrest and Dare are different from that of Ogden and Essex. The orientation of the center leaflet of Forrest and Dare was relatively constant at about 70° over most of the day. This particular orientation of the leaflet is such that it tends to capture a large amount of the impinging sunlight during most of the day. This response of primarily maximizing photosynthesis over most of the day conforms to the first postulate. However, the orientation response of Forrest and Dare has the appearance of being much more conservative than that of Ogden and Essex. In fact, at times the response is so conservative that it is questionable as to whether or not the center leaflets of Forrest and Dare are positioned to optimize the available energy.

In viewing the overall response of the vertical inclination of the center leaflets of the five cultivars, one can see that York's response is a little different from that of the other four cultivars (Figure 18, page 38). From 7:00 to 11:00 a.m. it seems to behave very much like Ogden and Essex, in that the angle of the center leaflet becomes larger and appears to be receiving a large portion of the available sunlight. However, from 11:00 to 3:00 p.m. the angle of the leaflet declines and results in minimizing the radiation striking the leaf surface. This tendency seems to hold true until the close of the day. Therefore, postulate one seems to be in effect in the morning and late evening hours while the second postulate predominates during mid-day. Therefore, it is again suggested that the inherent environmental stresses placed on the plant determine its particular response.

Center Leaflet, R3 Growth Stage

The conclusions suggested about the maximization or minimization of the photosynthetic rate or the transpiration rate at the R3 stage of growth are somewhat different from those applicable to the center leaflets of the five cultivars at V10. At R3 the response of the average main angle of the center leaflet of all five cultivars appears to be one which conforms to the second postulate and allows for minimum exposure of the leaflets to sunlight and, hence, minimization of the rate of transpiration (Figure 19, page 39).

Even though all five varieties appear to be operating in accord with the second postulate, some varieties are more closely related to each other in their response than are others. At this growth stage (R3) the center leaflet of Ogden displays the largest angle of vertical inclination over the bulk of the day, and appears to be positioned such that a plane extending down the mid-rib of the leaflet would lie nearly parallel to the plane of the incoming radiation. Therefore, Ogden has every appearance of receiving the least amount of sunlight possible during this time when considerable photosynthate demands are placed on the plant.

The center leaflets of Forrest and Essex are very similar to each other in vertical response at the R3 stage of growth (Figure 19, page 39). Again, the second postulate seems to be preeminent, and the amount of light intercepted is small relative to the amount of energy available. However, the response of the center leaflets of Forrest and Essex is not as extreme in orientation as that of Ogden.

The other two cultivars, York and Dare, are likewise very similar to each other in their pattern of vertical orientation (Figure 19). Because of the initial upright orientation of the leaflets and the rise in the angle of orientation of the leaflets accompanying the increase in angle of the sun, the center leaflets of York and Dare are aligned during the day in a manner that causes them to receive only a relatively small amount of the incoming sunlight. The curve representing the average incline of the leaflet is seen not to be as steep for York and Dare as it is for the other three cultivars. This seems to indicate that the main angle of York and Dare at R3 does not minimize the transpiration rates to the same extent as it does in Ogden, Forrest and Essex.

Side Leaflets, V10 Growth Stage

The side leaflets of the five cultivars also appear to follow one or more of the postulates which were posed about the function of dynamic leaflet orientation in soybeans. In the case of the side leaflets, the primary mode of expression is through horizontal orientation, which is in contrast to the center leaflets where the most significant movement is that of vertical orientation. As with the center leaflets, various similarities and differences among the five cultivars at both growth stages can be observed.

At the V10 stage of growth, the horizontal movement of leaflet orientation of the side leaflets is very similar in all five cultivars (Figure 20, page 41). To aid in illustrating this movement, the orientation of the left leaflet of each cultivar will be discussed. At this growth stage (V10) Essex and Ogden show the smallest amount of change over time. They begin the day positioned at about 90° and consistently turn their leaflets more toward the direction from which the sunlight is coming until around 11:00 a.m. at which time the angle of the leaflets stabilizes and remained at about 70° until 1:00 p.m. During this time period (11:00-1:00 p.m.), the sun was reaching its apex and passing overhead. Throughout the remainder of the day, as the bearing of the sun became more westerly, the left leaflet of Essex and Ogden was observed, correspondingly, to have an increase in angle of orientation. This results in the apical surface of the leaflets receiving more of the available energy from the sun. To summarize the response of Essex and Ogden in terms of the previously stated postulates, it appears that throughout the day, during V10, the side leaflets are positioned such that they receive maximum exposure to sunlight, and, therefore, the rate of photosynthesis is enhanced.

The left leaflets of Forrest and Dare behaved very similarly to each other at the V10 stage of growth (Figure 20, page 41). Their orientation response was only slightly more than that of Essex and Ogden. In terms of the stated postulates, Forrest and Dare also appeared to attain maximum exposure throughout the day. The primary difference between the response of Forrest and Dare and that of Essex and Ogden is that the average angle attained for Forrest and Dare tends to be less than that of Essex and Ogden during most of the day. Because of the relationship of the sub-angle of a side leaflet to the angle of the sun, a smaller angle seems to result in less sunlight being captured. So it is theorized that the side leaflets of Forrest and Dare receive slightly less of the impinging radiation than do Essex and Ogden. However, they are probably receiving a majority of the sunlight.

The side leaflets of York responded to a greater extent than did those of the other four cultivars (during V10, Figure 20). This is evidenced by the fact that the average sub-angle of York's left leaflet reached a low of 45°, while the lowest average angle of the other four cultivars was 64°. The overall pattern of York's movement was very similar to the other cultivars' movement except that the leaflets attained orientations which gave measurements that were smaller in degrees and thus indicating more extreme movement. However, York did receive an appreciable amount of the available energy.

Side Leaflets, R3 Growth Stage

During the R3 stage of growth the cultivars fall into two very similar groups exhibiting similar patterns of movement, being different only in the rate of change (Figure 21, page 42). The angle of the leaflets of one group remains about 20° higher than that of those of the other group. The group whose angle of orientation is the highest is composed of Ogden and Essex. The side leaflets of Ogden and Essex were, on the average, positioned at an angle of 71° at 7:00 a.m. From this time until noon, the leaflets tilted toward the east, and reached an average angle of 45°. During these morning hours, it cannot be determined whether the movement of the leaflets facilitates maximization of the photosynthetic rate or minimization of transpiration. A large portion of the light is probably being captured since the ventral surface of the leaflet is turned toward the east from which direction the sunlight is coming, and, therefore, photosynthesis is probably being carried out at a moderate rate. From noon until 8:00 p.m. the angle of the side leaflets of Ogden and Essex increases to around 95°. This probably causes a portion of the direct sunlight to be intercepted by the leaflet surface, but less than the maximum amount being intercepted. Thus, the first postulate was probably in effect due to the horizontal orientation of the side leaflets of Ogden and Essex at the R3 stage of growth. This is opposite to the conclusions drawn at V10 where the second postulate appeared to be in effect.

The sub-angles of the side leaflets of Dare, York and Forrest exhibited very similar patterns of orientation at the R3 stage of growth

(Figure 21, page 42). At 7:00 p.m. their leaflets were positioned at an orientation of 43°, on the average. From this orientation the average sub-angle of each decreased to an average low of 17° at noon. Because the leaflets were slanted at such small angles, it seems that this results mainly in minimizing the amount of light striking the leaflets. From noon until 8:00 p.m., the edge of the leaflet which is the most easterly begins to move upward, and the average angle reached at the end of the day was 71°. During this time, since the sun had passed overhead, very little light could strike the surface of the leaflets. Thus, the second postulate again appears to be predominant, and Dare, York and Forrest are probably losing less of their available moisture to transpiration than if the leaflets had been positioned at angles of orientation resulting in greater illumination of the ventral surface of the leaflets.

In summary, these results illustrate that during V10 both the side and center leaflets of all five cultivars act primarily to maximize the exposure of the leaflets to the sunlight. Ogden and Essex exhibit the greatest response followed by Forrest and Dare, which exhibit a more conservative response. York, on the other hand, is characterized by following a somewhat different pattern of response, but it still tends to have maximum exposure to the sunlight. During the R3 stage of growth a different pattern was observed for all the cultivars, with the response resulting primarily in a minimum exposure of the leaves to the sun. During this period of time Ogden and Essex demonstrate the least amount of change which was a more moderate response than the other cultivars.

In the morning hours the side leaflets were positioned such that they received a medium amount of the available energy while in the afternoon a minimum exposure was obtained. Dare, Forrest, and York demonstrated the greatest amount of change with the leaflets positioned at very steep angles resulting in the least amount of light being intercepted. The differences between the growth stages probably resulted from minimum stresses being on the plants during V10 (where all the varieties received maximum exposure), and with more stresses on the plants during R3 resulting in an orientation of the leaflets to attain minimum exposure to the light. The consistent and inherent differences in the response of the cultivars reflects the genotypic variation among cultivars.

Regression and Correlation of Independent Variables

Hourly measurements were taken of three independent variables to determine what effect changes in these variables have on the orientation of soybean leaflets. The variables were sun angle, ambient temperature and light intensity (BTU). In Table 5 are listed the hourly measurements of these variables averaged over four days of observations. The values were used in a multiple regression and correlation model to determine the best possible one-variable, two-variable and three-variable models, as well as the coefficients of partial regression and of determination of each (Table 6). The largest R-square value attained was 0.1540 for the three-variable model which means that a maximum of 15.40 percent of the variation of the leaflet orientation can be explained by multiple regression on the three independent variables. The remaining variation is unexplained.

Table 5. The average hourly ambient temperature, light intensity and angle of the sun for four days' measurements of leaflet orientation of soybean cultivars during the V10 and R3 stages of growth.

Time	Temperature		Light Intensity		Sun Angle	
	V10*	R3**	V10	R3	V10	R3
	(Celsius)		(BTU)		(Degrees)	
7:00 a.m.	17	23	15	14	15	8
8:00	16	24	65	35	20	20
9:00	20	26	98	74	38	35
10:00	26	28	158	119	50	36
11:00	25	31	193	218	74	55
12:00	28	36	179	276	91	73
1:00	31	38	171	255	109	85
2:00	28	37	153	226	120	94
3:00	29	36	113	235	131	111
4:00	29	33	93	138	143	133
5:00	27	31	49	85	154	142
6:00	24	31	13	66	165	150
7:00	23		6		120	
8:00		27		11		165
Average	25	31	100	135	95	85

*Eastern Standard Time.

**Daylight Saving Time.

Table 6. The regression and correlation coefficients obtained for sun angle, ambient temperature and light intensity with the main angle (vertical) of orientation of the center leaflet and the sub-angle (horizontal) of the right leaflet of soybean cultivars as dependent variables.

Independent Variables	b Value		R-Square (%)	
	V10	R3	V10	R3
	Main Angle/Center Leaflet			
Sun Angle	0.02	-0.06	0.1	1.2
Temperature	-0.11	0.07	0.1	1.5
BTU	0.06	0.04	1.9	3.8
Temp/BTU			1.9	4.1
BTU/Sun A			1.9	4.8
Temp/Sun A			0.4	4.1
Temp/BTU/Sun A			2.0	4.8
	Sub-Angle/Right Leaflet			
Sun Angle	0.08	0.17	4.1	2.7
Temperature	-0.32	-0.80	2.6	4.0
BTU	-0.09	-0.02	13.9	6.7
Temp/BTU			14.0	6.7
BTU/Sun A			14.5	9.0
Temp/Sun A			10.8	10.2
Temp/BTU/Sun A			15.4	10.3

The single-variable model which produced the largest R-square during V10, for both the center and right (side) leaflets, was with light intensity as the independent variable. It accounted for only 1.9 percent of the main angle variation of the center leaflet, and 13.9 percent of the sub-angle variation of the right leaflet. This same model (light intensity) also explained the most variation (for a single-variable model) during R3, accounting for 3.8 percent of the variation of the center leaflet (main angle) and 6.7 percent of the variation of the right leaflet (sub-angle). The best two-variable model during V10 contained light intensity and either temperature or sun angle and explained 1.9 percent of the variation present in vertical movement of the center leaflet. Variation in the horizontal movement of the right leaflet (V10) was 14.50 percent accounted for by the two-variable models containing light intensity and angle of the sun. During R3 the best two-variable model was the one with light intensity and sun angle as independent variables and the main angle of the center leaflet as the dependent variable, but it accounted for only 4.8 percent of the variation. The best two-variable model for the sub-angle, right leaflet, as the dependent variable contained temperature and sun angle as independent variables and accounted for 10.2 percent of the variation. Thus, it appears that the factor of primary importance is the inherent capacity of an individual cultivar to orient its leaves in response to these different stimuli.

Fine Structure of the Pulvini

Another objective of this research was to examine the fine structure of the pulvini of the five soybean cultivars and to determine if differences exist. To accomplish this objective, it was necessary to define some standard cytological techniques which would facilitate measurement of variable characteristics, and which could be defined in such a manner as to yield themselves to quantitative analyses. It was originally thought that this could be accomplished by comparing cultivars with respect to cell volume measurements obtained from cells in the immediate vicinity of the vascular system and cells adjacent to the epidermis. After examination of several microscopic sections, it was concluded that statistical analyses of these cell measurements would not yield a valid estimate of the actual variation present. This conclusion was drawn on the basis of the fact that an extremely large sample would be required to account adequately for the variation encountered as a result of not being able to obtain consistently the microscopic sections from the same location in each pulvinus. This analysis did not lead to any consistent patterns of variation between the different cultivars during the tense and relaxed states, suggesting that the variation present was due to the sampling techniques and the sample size. However, observation of the general cell anatomy led to the conclusion that some differences among cultivars might exist. One example of an apparent difference was in the cross-sectional view of the shape of the vascular tissue of the various cultivars. Observation of the vascular systems lead to the hypotheses that Ogden has a characteristic indentation in its vascular system which is not characteristic of the other cultivars. This could possibly allow more flexibility in the movement of the pulvini in Ogden than in the other cultivars. Cytological differences of this nature could partially explain the different rates of orientation observed in the different cultivars. For example, Ogden did exhibit much orientation of its leaflets.

CHAPTER IV

SUMMARY AND CONCLUSIONS

The angle of orientation of left, center and right leaflets of Ogden, Forrest, Essex, York and Dare cultivars of soybeans was measured during the V10 and R3 stages of growth. The horizontal and vertical inclinations of each leaflet, designated as main and sub-angles, respectively, were measured hourly beginning at 7:00 a.m. and continuing until 7:00 p.m. during the V10 growth stage and until 8:00 p.m. during the R3 stage. Measures were recorded on four separate days during both growth stages.

The results indicate that the orientation of the center leaflets of a trifoliolate differs from that of the side leaflets. Cultivars tend to change the vertical inclination of the center leaflet while keeping the horizontal inclination relatively constant, whereas, the reverse is true of the side leaflets. That is, the cultivar tends to change the horizontal inclination of the side leaflets while keeping the vertical inclination relatively constant. This was generally true of all five cultivars. Because of this trend significant differences were observed between the main (vertical) and sub- (horizontal) angles. However, the center and side leaflets appear to be accomplishing the same purpose. Due to the physical locations of the leaflets in relation to the sun, the center leaflet was able to minimize or maximize its exposure to the radiation through vertical movement, and the side leaflets did the same thing by rotating from side to side.

Cultivars differed in the degree of orientation of their center and side leaflets at different times of the day during V10 and R3. The period of the day in which differences were maximum was from approximately 10:00 a.m. until 5:00 p.m. This time span appears to be best for measuring the leaflet orientation and detecting differences among soybean cultivars.

Of the cultivars measured in this study, Ogden and Essex exhibited the greatest amount of orientation during the V10 stage of growth. Forrest and Dare were somewhat intermediate, and York exhibited the least orientation during V10. During the R3 growth stage, Ogden attained and maintained the highest angle of orientation of the center leaflet, beginning at 128° at 7:00 a.m. and reaching a maximum of 148° at 3:00 p.m. Essex and Forest were intermediate beginning near 110° at 7:00 p.m. and increasing to approximately 130° at 3:00 p.m. Dare and York changed very little over the course of the day, beginning at approximately 94° at 7:00 a.m. and increasing to only 110° at 4:00 p.m. Ogden and Essex exhibited similar horizontal movement of the side leaflets, and Forrest, Dare, and York differed from Ogden and Essex but were similar to each other. However, the movement of the side leaflets of Ogden and Essex was less than that of the latter three cultivars. Thus, the data indicate that Ogden and Essex attain more of their leaflet orientation through vertical movement of the center leaflet, whereas, Dare and York attain more of their leaflet orientation through horizontal movement of the side leaflets and less through vertical movement of the center leaflet. During R3, Forrest exhibited vertical and horizontal movement of the center as well as the side leaflets.

All cultivars had a higher angle of orientation of leaflets during R3 than during V10. Also, there was more variation among cultivars during the reproductive than during the vegetative stage. On the basis of this evidence, it appears that measurements of leaflet orientation during the reproductive stages of growth would allow one to obtain better estimates of the potential orientation of a cultivar and to detect differences among cultivars.

An unusual phenomenon was observed in that all five cultivars exhibited a consistent decline in the angle of their center leaflets between 1:00 and 4:00 p.m. followed by an immediate increase in the angle during the following hour. This pattern was clearly defined during R3 during which the orientation of every cultivar reached a peak at 2:00 or 3:00 p.m., then declined about 20°, then immediately increased about 5° and then decreased until the close of the day. During V10 the same phenomenon occurred, but it was more sporadic and less distinct, occurring between 1:00 and 4:00 p.m., with a decline of about 7° after the peak, followed by an increase of a few degrees and then a decline until dark. This phenomenon could be due to changes in turgor pressure within the pulvinus occurring in such a manner that the plant overreacts in movement and an equilibrium must subsequently be reached.

Statistical analysis of the data from measurements from one day measurements, two days, three days and four days revealed that measurements of leaflet orientation taken over a two-day period of time should yield sufficient statistical information about the variation. However, in order to obtain reliable information about second- or third-order interactions, measurements should be taken over more than two days.

It appears that potassium can be implicated as having a role in the orientation of soybean leaflets. The data revealed that there was a consistently higher concentration of potassium in the pulvini of four cultivars (Ogden, Dare, Forrest, and York) observed during the "tense" position compared to those during the "relaxed" position. Also, cultivars differed in their capacity to attain high and low levels of potassium in the pulvini during both the tense and relaxed states. In addition, the cultivars differed considerably in the amount of change in the concentration between the two extremes of orientation.

Microscopic examination of the anatomy of the pulvinus did not lead to an acceptable description of variation among the cultivars. The variation observed in the anatomy of pulvini appeared to be no more than random. Variation among observations on the same cultivar tended to be as great as that among observations on different cultivars. However, some qualitative differences were observed such as was seen in the arrangement of the vascular tissue in the pulvinus of Ogden when compared to that of the other cultivars.

The effects of light intensity, sun angle and ambient temperature on leaflet orientation of the soybean cultivars were negligible. It appears that the cultivar effect was the overriding factor in determining the amount of leaflet orientation. The coefficients of determination of variation in leaflet orientation by the three independent variables were small, with the largest R-square obtained being 15.40 percent when all

3 variables were included in the model. Likewise, the regression coefficients were small, ranging from 0.17 for leaflet orientation on sun angle during R3 to a negative 0.80 for leaflet orientation on temperature during R3. This reveals that only a small portion of the change in the leaflet orientation can be explained by its regression on these independent variables.

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