## Studies on the effect on

root growth of continued rotation
about a horizontal axis.

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## Studies on the effect on root growth of

 continued rotation about a horizontal axis.
## Abstract

An attempt has been made to discover whether or not the growth rate of roots rotated about a horizontal axis is affected by the speed at which the rotation occurs.

The method entailed a double selection of the roots to ensure that all the roots used in each experiment were straight and of equal initial length. Pea roots were used and the seedlings were intact throughout the experiment. The roots were held horizontally in jars which were supported in horizontal cradles. These cradles were attached to rotary spindles driven electrically and connected by driving chain to a geared klinostat so that their rotary speeds could be varied. The whole apparatus was enclosed in a box from which the light was excluded. The roots were photographed every half hour through a vertical slit in the wall of the box, a light being switched on momentarily inside while the exposure was made. The negatives were developed and the roots at successive half hourly intervals were measured from these negatives with a travelling microscope. The increases in length and hence the growth rates were calculable. This was repeated at various speeds. Graphs of growth rate against time have been
plotted. Correlation coefficients have been calculated for growth rate on time and regression lines have been drawn. Some statistical analyses have also been done. There appears to be no well defined effect of speed of rotation on growth rate although rotated roots seemed to have a lower growth rate than vertical non-rotated roots and, in general, the slower the speed of rotation the lower the growth rate. Time does seem to affect the growth rate trend and appears to have most effect when the growth rate is generally high and also when the speed of rotation is high.
N.B. Figures $1-8$ will be found in the text and Figures 9-25 will be found in the Appendix.

# Studies on the effect on root growth of continued rotation about a horizontal axis. 

## Statement of the problem

The problem was to discover whether rotation and speed of rotation of pea roots revolving about a horizontal axis had any effect on the growth rate of those roots. Origin of the Problem

Mrs M.E. Brownbridge ("Studies on Geotropism in the roots of Pisum sativum with particular reference to the effects of exposure to auxins and antiauxins" - Ph.D. Thesis The intlevence of July 1954) who used a klinostat to eliminate/gravity during an investigation on the effect of hormones on the curvature of roots, observed that there appeared to be a decrease in the growth rate of the roots at high klinostat speeds and an increase at low speeds. This effect could not be investigated immediately but when Mrs Brownbridge had completed her work I took up the problem and attempted to discover whether or not speed was a factor influencing growth rate.

## History of the Problem

Several workers studied this problem towards the end of the 19th century. Schwartz 1881, Elving 1883, Sachs 1887 and Luxburg 1905, as a result of their investigations, concluded that, if rotation did influence growth rate it was only to a very slight extent.

Zollikofer 1921, observed fluctuating growth rate when he rotated Avena Coleoptiles about a horizontal axis.

Konigsberger l922, could not find any effect of rotation about the horizontal axis on the growth rate of Avena Coleoptiles, although this rotation did seem to have an effect on the growth rate when the Coleoptiles were returned to the vertical position.

Brain 1935 and 1942, rotated both roots and shoots parallel to the horizontal axis for several days at one revolution per hour. He noticed a considerable decrease in the growth rate of the roots, but the shoots in general grew faster than normal under such conditions.

Cholodny 1932, found no effect on the growth rate of roots when rotated.

Cholodny and Navez 1932, discovered that a drop of water at the tip of a root may decrease the growth rate. Such a drop tends to accumulate when the root is in the vertical position but not to such a great extent in the horizontal position.

Larsen 1952, rotated whole seedlings of Artemisia parallel to the horizontal axis of the klinostat at speeds ranging from 0.25 minutes per revolution to 128 minutes per revolution. At all speeds the average growth rate of roots was lower than that of roots rotated in the normal position parallel to the vertical axis of the klinostat.

Method used in the experiments about to be described
Outline of the method
Peas were grown until the roots were from 1 to $2 \frac{1}{2}$ centimetres long. They were then put into holders in the horizontal position and rotated in the dark about ap horizontal axis. The speed of rotation was varied for each set of experiments and ranged from l revolution every 8 seconds to 1 revolution every 73 minutes 30 seconds, there being 10 speeds altogether. Roots were also grown in the vertical position but not rotated. The rotated roots were photographed every half hour and the rotation was continued for five and a half hours.

The negatives were developed and the increases in length of the roots were measured from the negatives using a travelling microscope, but in the case of the vertical roots these were measured directly every half-hour, the microscope being turned vertically through $90^{\circ}$ for this purpose. A comparison of the growth rates of the rotated roots with those of the vertical roots was made, and the effects of speed of rotation on the growth rate was investigated.

Detail of the method
The peas used were uniform genetically pure seed of the variety 'Meteor' supplied by Sutton and Sons of Reading.


Half to three-quarters of a pint of peas were soaked for each experiment. A special soaker was used to allow the peas to be aerated as well as immersed. The soaker consisted of a 750 cc . inverted conical flask which contained the peas. This was fitted with a rubber bung A, which carried a wide glass tube $B$. Rubber bungs $C_{1}$ and $C_{2}$ sealed the ends of the tube B. A narrow straight glass tube passed through the bungs $C_{1}$ and $C_{2}$, and was arranged so that the end in the flask was approximately $\frac{1}{4}$ inch from the top of the inverted flask. Water from the flask passed through this tube into the sink after passing over the peas in an upward direction. A right angled glass tube passing through the bung $C_{2}$ led air and water to the cavity of the wide glass tube $B$. The bung $C_{1}$ was chanelled along its outer surface so that water and air from the tube $B$ could enter the flask through the passage thus formed. When the apparatus had been assembled the whole was inverted as the diagram Figure 1 shows. The connections to the tap and to the air supply were made. The upward flow of air and water into the flask agitated the peas so that the air was able to circulate well amongst them.

The peas were put into the soaker at 3 p.m. and were ready for planting at 3 p.m. the next day Two to three shallow plant pots (depth 2 inches and diameter $7-8$ inches) were filled with washed sand and the whole sterilised in
the autoclave at 15 pounds per square inch gauge steam pressure (temperature $250^{\circ}$ Fahrenheit) for fifteen minutes. The sand was damped uniformly with distilled water and the pots were covered with glass plates previously washed in alcohol. Sterilisation killed any fungi or bacteria which may have attacked the peas. The glass. plates prevented spores which may have been in the atmosphere from falling onto the sterile sand. When the pots were cool the peas were planted in the sand, the point of emergence of the radicle being directed downwards so that the roots would grow straight. The pots were covered with the glass plates and placed in the dark at a temperature of $25^{\circ}$ Centigrade for eighteen hours. At 10 a.m. the following day, seventy seedlings having straight roots of the same length were selected, each root then being about $\frac{3}{4}$ of a centimetre long. The seedlings were intact throughout the experiment.

The selected seedlings were washed by dipping them into distilled water and then they were placed in a perforated perspex holder over water. Each root was placed vertically through a perforation in the holder. The roots were put into a closed box at a temperature of $25^{\circ}$ Centigrade for twenty four hours. The water below the perspex holder did not touch the roots but maintained a moist atmosphere inside the box. Throughout the procedure care was taken so as not to damage the roots.

At 10.0 a.m. the next day (second after planting) sixteen seedlings with equal length of straight root,were selected from the seventy previously put into the perspex holder. The roots at this stage were $1 \frac{1}{2}$ to $2 \frac{1}{2}$ centimetres in length. These sixteen seedlings were the ones used in the experiment. They had presumably equal metabolic rates since the growth rates of their respective roots had been very similar during the selection period. The purpose of double selection was to ensure that sixteen roots with equal growth rates were available.

During rotation the seedlings were enclosed in two glass jars each containing eight seedlings. The jars were of length 4 inches, breadth 1.9 inches and depth 6 inches, the internal dimensions being slightly less.

At approximately $\frac{3}{4}$ inch from the top of the jar was fixed a perspex platform pierced with holes through which the roots of the seedlings passed. Since the length of the platform was slightly larger than the internal dimension of the vessel, the platform was kept in place by the lateral pressure exerted on it by the walls of the vessel.

A series of lines was drawn, with a diamond, parallel to the upper edge of each jar, i.e. parallel to the perspex platform and about $\frac{1}{5}$ inch apart. These. lines extended from $\frac{1}{2}$ to $1 \frac{1}{2}$ inches below the upper edge of the jar and on that
side adjacent to the camera during photography. These were reference base lines used during measurement of the negatives. See Figure 2.


FIG.2 - GLASS JAR TO HOLD SEEDLINGS DURING ROTATION -


About 80 c.c. of distilled water were put into each of the two jars. Fight of the seedlings were arranged on the perspex platform of each jar so that their roots were hanging vertically through the perforations in the platform. The
arrangement of the seedlings is shown in the diagram. Fig 3.

## FIG.3-Y LEW OF JAR LOADED READY FOR ROTATION.



## VIEW OF LOADED JAR FROM ABOVE

PEA SEED LING


Cotton wool was packed loosely between the peas to prevent them from moving during rotation. Any slight

## FI9.4-POSITION OF JAAS IN HOLDEAS AT THE MOMENT OF PHOTOGRAPHING.



THE PART PHOTOGRAPHED IS THAT BETWEEN PLANES ab AND cd.
movement would have vitiated the results as it would inevitably have been a movement of withdrawal. Another method of packing the peas had been investigated - that of using glass wool packing. This was unsatisfactory as the glass wool lacked flexibility and was too stiff. Cotton wool, being resilient, served the purpose much better. No solution which could attack the cotton wool was used during the experiments. The method of cotton wool packing was therefore adopted. The rim of each glass jar was coated with vaseline. A glass plate with a central hole, diameter $\frac{1}{4}$ inch, was pressed tightly down on the rim of each jar, which was then tilted slowly until it rested in the horizontal position. This was the position occupied by the jars throughout rotation. All handling was carefully done in order to minimise shock. The object of this initial tilting to the horizontal position was to enable the level of the water in the jar to be adjusted so as to lie between two adjacent pea roots, more distilled water being added through the hole in the glass plate lid if necessary. This adjustment ensured that none of the roots was obscured by the water surface during photography. (Figure 4)

The jars were then returned to their normal standing position with the roots vertical. They were left in the dark for one hour so that if the metabolism of the seedlings had been affected by transfer to the platforms, it could return to normal before the start of the experiment.

At the end of an hour the two jars were placed horizontally in the two cradles of the klinostat, the roots being on the side adjacent to the camera. As the cradles rotated the roots were alternately wetted and aerated, each root being wetted once every revolution. A separate apparatus was constructed which would alternately wet and aerate vertical non-rotated roots at approximately the same rate. A control experiment, in which eight roots were grown vertically in the dark at the same temperature as the rotating roots and at the same rate of wetting, was set up. The wetting device for the control experiment consisted of a glass jar $B$ of capacity 300 cc. sealed with a rubber bung through which three glass tubes $E, A$ and $C$ passed. Tube E, having a bore of half a centimetre and two right angled bends, led with a long vertical leg to a 250 cc. separating funnel $F$ situated at a lower level than the bottom of the jar B. (Figure 5)


The stem of the funnel $F$ passed into a glass jar $G$ fitted with a perspex perforated platform $Q$.

The seedlings, having been doubly selected, were arranged on the platform as previously described and were packed in with cotton wool. A plate covered the top of the jar as in the case of the rotating jars. A thermometer and the funnel stem passed through holes in the plate. The capacity of the jar between " $\ell$ " and $Q$ was somewhat less than the capacity of the funnel F. Tube $A$, of bore $\frac{1}{2}$ inch, led water from the supply main into the jar B. Tube C, also of bore $\frac{1}{2}$ inch, led water from jar $B$ to the sink. All the joints were made airtight. The apparatus was set up with distilled water filling the jar $G$ up to the platform $Q$ and with the tap $P$ of the funnel open. The water supply tap was turned on and water from tube A filled jar $B$ and the tube $C$ and part of tube $E$. When jar $B$ was full, the pressure of water from the supply, via A, forced water from B up through $C$ and over to $D$, hence the siphon CD started to act. The water was also pushed up into tube E but the horizontal part of this tube was too high to allow water to pass over into funnel $F$ before the siphon started to remove water from B. $\dot{X}$ As water siphoned out of B, air was pulled, in through the tube $E$ to take its place, and consequently the water from jar $G$ was pulled up into the funnel F. When the water level - $\dot{X}$. The free discharge rate of flow through $C$ to waste, was designedly, greater than the incoming supply rate of flow th rough $A$. The latter was uneler control and could be regulated.
in $G$ was lower than the level " $\ell$ " air broke through into $F$ and hence into $E$ and $B$. This air passed from $B$ into $C$ and thus broke the siphon stream. Water from $A$ then started to refill B. When B was again full the pressure of water from $A$ forced water over into $C$ to set the siphon working again. As B filled, air was forced out through E and into $F$ so that the water drained out from $F$ into $G$ and re-immersed the roots. The time between one immersion and the next was found to be approximately the same as the wetting interval in the rotation experiment when the klinostat was geared at 9 F. (see page 21). The jar containing the vertical roots was covered with a black cloth which was removed only during measurements. The temperature was carefully noted and maintained as near as possible to that of the rotation chamber $\left(21-22^{\circ} \mathrm{C}\right)$.

The first measurement was made one hour after the seedlings had been arranged on the perspex platform. This interval allowed the metabolism to settle down. The measurements were made with a travelling microscope arranged in the vertical position, the roots being immersed during measurement. The reason why they were measured immersed, was that they always carried a drop of water at the tip when not immersed, and this obscured the root tip. When fully
immersed the root tip was more clearly visible, and care was taken to measure squarely to the root to eliminate the effect of refraction. Measurements of all the vertical roots were made every half hour at the same time as the photograph of the rotating roots was taken. All measurements were recorded. Two of these control experiments were carried out in May. A comparison of these with the winter control experiments was made to see if there were any seasonal cycle in the natural growth rate. Graphs of growth rate against time were plotted for both experiments and the graphs were compared with those of the vertical experiments carried out during the winter. See Graphs, Figures $9 a, 9 b$, and 20.

The accompanying diagrams show the rotational apparatus and camera set-up. (Fig. 6(a), (b) and (c)) The klinostat with its rotational cradles was enclosed in a large box so that rotation could be carried out in the dark. One side of the box was hinged to form a door giving access to the klinostat. Another tiny door at the back of the box enabled the gears of the apparatus to be changed without opening the large door. The roots were photographed through a glass panel in one side of the box. (Fig. 6(a) and (b)) The camera was supported on another wooden box placed on its side so that it cauld be used as a cupboard for slides. The camera was screwed tightly down on to a movable platform, this in its turn being screwed at one end onto the box. Between


Flab(c)
the camera lens and the glass panel on the klinostat box was a black cardboard funnel $20 \frac{1}{2}$ inches long and $15 \frac{1}{2}$ inches diameter at its widest section where it made contact with the klinostat box. The mouth of the funnel at the point of contact was closed by a black cardboard partition having a vertical slit $12^{\prime \prime}$ long and $0 \cdot 6$ i.e. $\frac{6}{10}$ inch wide, thus light ( $L^{\prime}$ and $L^{\prime \prime}$ ) from the klinostat chamber could pass through the slit, through the camera lens and be focussed on the plate at the back of the camera (Figure 6(c)). The shape of the movable platform carrying the camera is shown in, the diagram (Fig. 6(c)).

[^0]When the jars containing the seedlings were in their cradles ready to be photographed and the crades vertically placed for that purpose, a 40 watt lamp was switched on inside the rotation chamber and a black matt board was arranged behind the jars so that there was no glare. The roots, now arranged as shown in the diagram, Figure 4, were viewed through the plate at the back of the camera.

The focussing was adjusted by means of the usual focussing screw at the side of the camera. If the roots were not visible through the slit, the funnel was moved laterally until all the root tips were in view. Light was prevented from entering the rotational chamber at the large end of the funnel by means of a black cloth. Two photographic plates were used for each experiment. When the changeover of plates was made, an inspection of the roots was carried out through the frosted plate on the camera, to make sure they had not grown out of the range afforded by the slit in the cardboard partition of the funnel. The lines "ab" and "cd" on the diagram (Fig. 4) represent the edges of the slit through which the photographs were taken. The catch on the camera was then moved to give $\frac{1}{10}$ of a second exposure. ... The shutter was set and a photographic plate (Kodak P.1500) in its holder was inserted in place of the frosted plate at the back of the camera. The pointer of the platform bearing
the camera was moved to interval 7 and an exposure was made. The light in the klinostat chamber was switched off and the cradles were set in motion by the switch on the camera support (Figure 6(a)). The shutter was set in readiness for the next exposure and the pointer was moved to interval 8. Thus successive photographs of the roots were arranged side by side along the negative (Figure 7). This procedure was carried out as quickly as possible so that the light in the box would not raise the temperature of the roots.


## FIG:7

For all speeds except the faster ones photographs were taken while the cradles were rotating.

At the faster speeds the cradles had to be stopped in the vertical position or else a blurred negative would have resulted. The cradles were set in motion again immediately the exposure had been made, and indeed in some cases the cradles merely slowed down, never actually coming to a stop. This interruption of rotation lasted for only a fraction of a second and its effect on the responses of the rotated Dots was probably negligible.

It may have caused a slight imperceptible bending since the force of gravity would be acting unilaterally at the moment when the rotation was stopped. I do not think that the growth rate would be affected sufficiently to be measurable as the time of stoppage was very short.

It was thought that the camera distorted the image especially at the sides of the negative. This was overcome to some extent by using the central portion of the negative, and using two negatives for each experiment, ie. 7 exposures on one negative and 5 on the other. The amount of distortion was determined by measurements, however.
i. A piece of mm . graph paper was put into the rotation chamber and photographed, with the pointer of the platform at each successive position on the arc of the circle centre A. The negative was developed and the length of a large ( 10 mm. ) square was measured from the successive exposures.

Any change in the apparent length of this square as the position of the pointer moved from one extreme end of the arc to the other, was noted. The figures ( 2 sets) are recorded below/ Page The lengths of several ten millimetre squares was then measured directly from the graph paper. Measurements in all cases were made with a travelling microscope.

It was found, on examination of the two sets of figures, that there was no marked directional fluctuation in the length of the square. Thus the central part of the negative only was used and any distortion was regarded as negligible.

The average length of square measured from the negative and the average length of square measured direct from the graph paper were used to determine the scale factor by which the direct readings (from the vertical roots) must be divided to make them correspond with the rotational readings which had been reduced in scale by photography. Thus all recorded rotational readings were not absolute or true lengths but were $4 \cdot 722$ times too small, i.e. the scale was $\frac{1}{4 \cdot 72}$ of full size. This does not affect the overall picture since it is a comparison which is being made. All average vertical readings have been divided by 4.722 before using them in the results.

Passing from $X$ to $Y$ on the arc (Figure 6(c)), length measurements of the 10 mm . square from the negative were
as follows:-
Two sets of readings were taken, using square $A$ for the first set and square $B$ for the second set.

| Length of square $A$ at $X$ | $2 \cdot 15 \mathrm{~mm}$. |
| :---: | :---: |
| Length of square A at lst mark | 2.05 mm . |
| Length of square $A$ at 2nd mark | $2 \cdot 13$ |
| Length of square $A$ at 3 rd mark | $2 \cdot 15$ |
| Length of square A at 4 th mark | 2.06 mm |
| Length of square A at 5th mark | 2.06 |
| Length of square A at $Y$ | 2.09 |
|  | $\underline{14.69}$ |
| Length of square $B$ at $X$ | 2.16 mm |
| Length of square $B$ at lst mark | 2.11 mm |
| Length of square $B$ at 2nd mark | $2 \cdot 16 \mathrm{~mm}$ |
| Length of square B at 3rd mark | 2.13 mm |
| Length of square $B$ at 4 th mark | $2 \cdot 14$ |
| Length of square $B$ at 5 th mark | $2 \cdot 12$ |
| Length of square B at Y | $2 \cdot 17$ |
|  | $\underline{14.99}$ |
| Total | 29.68 |
| Average Len | 2-12 |

Length measurements of several 10 mm . squares direct from the graph paper are as follows:-
$10 \cdot 04 \mathrm{~mm}$.
$10 \cdot 00 \mathrm{~mm}$.
10.00 mm . $9 \cdot 99$.mm. 10.03 mm . 10.01 mm . 10.07 mm . 10.02 mm . 10.07 mm . 10.07 mm . 10.01 mm . 9.97 mm . 9.99 mm . 9.92 mm . $\overline{140 \cdot 19 \mathrm{~mm} \text {. }}$

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Average Length = 10.014 mm.
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Thus a length of 10.014 mm . appears on a negative as $2 \cdot 12 \mathrm{~mm}$.

The conversion factor is therefore $\frac{10 \cdot 014}{2 \cdot 12}=4 \cdot 722$.
The klinostat itself is best explained by reference to the diagrams (Figure 8).

It consisted of a metal box containing the electric motor which rotates a spindle $S$. The motor is geared so that the spindle can be rotated at different speeds. A movable dial $D$ on one side of the metal box alters the gearing. There are twelve different gear positions and for each a fast and a slow speed, thus giving 24 speeds. A lever L moving along in a groove adjusts to Fast or Slow.

The rotary spindle is fitted with a cog-wheel or sprocket and this is connected by a chain to two similar sprockets vertically above it, each driving one of the cradles carrying the jars. Thus both the jars are rotated by the motor in the same direction as the motor spindle. The temperature inside the dark rotation chamber was controlled by a thermostat (21-2 $2^{\circ}$ C). The electricity supply to the klinostat was controlled by two switches, one on the klinostat itselfand the other on the camera support. The former switch was always left on while the electricity supply was reguiated by the latter switch.

The speed of rotation of the jars was altered for different experiments by altering the gearing. This was
done by rotating the numbered dial $D$ until the gear number required was opposite an arrow on the motor casing. Then the fast and slow lever was adjusted. The speed of rotation of the jar cradles was timed for a wide range of gearing.
GEARING OF KIINOSTAT MOTOR

GEAR NUMBER

SPEED

TIME FOR ONE REVOLUTION minutes

Fast
Slow
Fast
Slow 17
Fast Slow . 42
Fast 49
Slow 1 : 42

Fast
Slow
Fast
slow
Fast
Slow
Fast
Slow
Fast
2
4 • 12
5 . 0
10
12
24
31
73
81

3
7
8
20

42
0
12
0
21 34
6
15
30
24


The speeds used for the experiments were within the range limited by the arrows in the left hand column.

The roots were photographed every half hour but where the slow speeds made this difficult, photographs were taken when the jars were vertical and the roots adjacent to the camera. In this case the time between each photograph was carefully recorded and a calculation was made to convert the measured growth, to growth per half hourly interval so making the readings correspond with all the others.

When the roots had been photographed the plates were developed and fixed. Kodak developer D6la and fixer F54a were used. One part of the developer was used with one part of water and the plates were immersed for five to eight minutes. They were then rinsed in cold water and put into the fixing bath for ten minutes. After this the plates were washed in cold, running water for one to two hours, dried slowly and examined. The developing and fixing was carried out in total darkness. The diamond lines on the jar had photographed as well as the roots and these lines acted as base lines for measurement of the roots (Figure 7).

Each root was measured at consecutive exposures i.e. at consecutive half hours of the growth period. From these growth measurements, increases in growth for each half hourly period, i.e. the growth rates, were calculated. Although eight roots were photographed from each jar it was not always possible to get a complete record of the growth rate of each root because some of them curved slightly during rotation and so could not be measured. Only those roots which remained straight during the experiment were used in the analysis. ins, This curving of some of the roots may be a Geotonus effect $\because$ but it was not investigated further at this point.

## Faults of Method and Apparatus

One of the main defects in this method lies in the klinostat itself which occasionally did not rotate as smoothly

as it ought to have done. This was due to some fault in the motor which may possibly be rectified if the motor were overhauled. A mechanical klinostat would, in some ways, have been preferable to the ele ctrically driven one. The current may alter and this would affect the speed of rotation irrespective of the gearing. A mechanical klinostat would have given constant power although it may not have produced a smooth rotation.

Another possible source of error, not easy to eliminate, lay in the variation of the intrinsic vitality of the peas. Peas vary in the rate of respiration, the metabolic rate and hence in the growth rate of their roots. If there is an intrinsic variation in the growth rate of the roots then it becomes very difficult to assess variation due to speed of rotation.

However it is assumed that there will be the same intrinsic variation among the peas of one experiment as between those of another. Any other variation due to experimentation would be apparent over and above this. The effect of this intrinsic variation on the results was, however, reduced by the method of double selection described previously. By this method only those peas having approximately the same root growth rates were chosen. The size of root selected was approximately the same throughout all experiments and all such roots had grown for the same length of time. Thus throughout the range of experiments performed all roots used
had approximately equal growth rates.
The rotating roots were not revolving around the spindle axis at equal radii. Those roots at the end of the perspex platform were revolving in a larger circle about the axis than were those roots situated at the middle of the platform. The centrifugal forces experienced by the roots would, therefore, be unequal, and this would affect the response of the roots although probably to an extent too small to be measurable.

During soaking, the peas may not have been agitated equally since the air stream did not pass evenly through them. This may have upset the respiration and the subsequent growth rates.

Again there may have been a personal error in judging the degree of dampness of the sand in which the peas were grow. This would affect their initial growth but, as mentioned earlier, the double selection method would lessen this effect.

During rotation of the roots in the glass jars they would be immersed once every revolution. They would therefore be subjected to the impact of the water on them. This too may have affected the respiration rate and consequently the growth. The controls were not subjected to sudden impact of the water which, in their case, rose and immersed them gradually. This discrepancy could only have been overcome
by a wetting device which ejected the water onto the controls from a jet. This would have entailed boring the container to carry the jet and also boring it underneath to run off the water. An automatic device for controlling the amount of water ejected each time would also have been needed. Since this research was not concerned so much with differences between a control and a rotational experiment but rather with the effect of rotational speed, an elaborate wetting device was not constructed. If more extensive work were to be done on control roots, and rotated roots, then an ejector device for wetting the controls should be designed and used to make the two experimental set-ups more comparable. Larsen sugeests that a drop of water at the root tip decreases the growth. If this is the case, as is very probable since the root would thus find some of its sustenance without searching for it, all the roots in every experiment herein considered probably had a reduced growth rate since the method of wetting inevitably leaves arop of water on each root after immersion.

It is probable that there is some slight error due to personal equation in the measurement of the roots and negatives by means of the travelling microscope. However, since the same person has done the measuring throughout, the error should be the same in all cases and hence, although it may have affected the absolute $\operatorname{Values,~it~will~not~have~affected~the~}$
trends of the response of the roots. In addition I think it should be pointed out that in the measurement of such small lengths as $\cdot 05$ to $\cdot 1 \mathrm{~mm}$. i.e. less than $\frac{1}{2540}$ inch, a more sensitive instrument than the travelling microscope is needed for very accurate results.

It was in some cases difficult to decide where the actual end of the root was, on the negative.

This was due to:-
(1) Focussing: depending on whether the cradles carrying the roots were absolutely vertical when the exposure was taken.
(2) The root tips having a 'halo' due to reflected light since they were creamy in colour and shiny.
(3) The root tips having a 'furry' edge - probably due to cells flaking off.
(4) Water film present on roots.

These sources of error are very difficult to eliminate.

## Recording of Results

The half hourly measurements from the controls and from the negatives of each experiment were recorded directly in a table. The increases in growth of each root for each experiment were calculated from these direct readings and inserted in a second table. The average growth increases of all the roots of each experiment were then calculated for
each half hourly period of time. These recordings were made for all experiments at every speed. A set of tables (Tables II to XII) was then drawn up showing the following average growth rates for each of the ten speeds and for the vertical roots:-
N.B. All the growth rates are based on growth per half hour.
(1) The average increases in the growth of all the roots of each experiment for each half hourly period of time.
(2) The average growth rate of all the roots of each experiment for the whole time period of that experiment.
(3) The grand average growth rate for each half hourly period. This is calculated for each half hourly period fromall the roots of all the experiments performed at any one speed.
(4) The grand mean growth rate, i.e. the grand mean growth per half hour. This is calculated from all the roots of all the experiments at any one speed for the whole time period of these experiments.

## Analysis of Results

It was thought that the speed of rotation may not affeet the overall growth rate but that it may affect the influence of time on the growth rate. For the purpose of illustration let us consider that the growth rate of a root rotated at

Speed A remains constant for the first two hours of growth. Then it increases gradually for the next three hours, reaching a maximum at the fifth hour and then gradually falling again. This state of affairs would be represented graphically thus:-


Now let us consider another root having the same intrinsic vitality as the first root but rotated at a different speed B. Suppose the graph of growth rate with time of this second root follows the dotted line. From the two graphs it is apparent that the time course of the growth rate of the second root is altered because of the alteration in speed of rotation. The growth rate remains constant for an hour longer than in case A and the maximum growth rate is maintainedepor twice as long. Otherwise there is little overali alteration of the growth rate. In this way the rotational speed may affect the influence of the time-factor on the growth without affecting the average growth


In order to find out whetheror not this was the case with the experimental roots, graphsf pf growth rate against
time were plotted for each experiment at each speed and also for the controls. (Please see graphs Figures 9-2ld

These graphs were originally plotted on squared paper with a small vertical scale. On the finished graphs the vertical scale has been increased to aid plotting and also to show the divergencies more clearly. The fluctuations in growth rate appear from some of these graphs to be large but they rarely exceed $\frac{1}{10} \mathrm{~mm}$. If the vertical scale were reduced the graphs would be smoother and the fluctuations apparently less but the graphs would not have been as useful for study. This plotting scale effect should be noted when reading the graphs.

Since no marked effect of time was apparent, correlation coefficients were calculated for each experiment to see whether there was a real correlation between time and growth rate.

If the correlation coefficient is equal to 1 (unity) then there is a very strong positive correlation between growth rate and time and growth rate increases with increasing time interval from the start of the experiment.

If the coefficient equals -1 (minus one) then the correlation is markedly negative and the growth rate decreases with the progression of time. The correlation coefficient, which is usually denoted by ' $r$ ', can neither be greater than +1 nor less than -1 .

If 'r' is zero then there is absolutely no correlation between time and growth rate. For the calculation of values of ry and for a table of coefficients please see the
appendix/Table $\frac{\overline{I X} \text { and }}{\text { appendix } I}$
Some of the correlation coefficients were sufficiently significant to warrant further investigation. The significance level of these coefficients (found from Statistical Tables by Fischer and Yates) is placed at the side in a second column. A significance level of 0.05 has been adopted and only those coefficients with a greater significance than this have been considered. A significance of $0 \cdot 01$ means that a coefficient with this significance level would occur by chance in only one out of every hundred cases. The fact that it has occurred during a particular experiment is therefore significant at the adopted level and indicates some factor other than chance affecting it.

In order to appreciate the full significance of these correlation coefficients, it was necessary to calculate the regression coefficients and plot regression lines. The calculation of the regression coefficient, which is the slope of the regression line, is shown immediately after the calculation of correlation coefficient in the Appendix, pages no. $\bar{X}$ and $\overline{\underline{X I}}$.

The regression lines were plotted on a graph having growth rate as the " $X$ " axis and time from the beginning of the experiment as the "x" axis. There is one regression line for each experiment. Each line passes through the mean time and also through the mean growth rate for each experiment The slope of each line i.e. the regression coefficient, was calculated from the correlation coefficient of each experiment
using the formula:-
Regression Coefficient $\neq r \frac{\sqrt{V_{G}}}{\sqrt{V_{T}}}$

$$
\text { where } \begin{aligned}
r & =\text { Correlation Coefficient } \\
V_{G} & =\text { Variance of growth rate } \\
V_{T} & =\text { Variance of time }
\end{aligned}
$$

A graph of regression coefficients against speed of rotation was then plotted (Figure 33). The regression coefficients were plotted along the " $y$ " axis and the Rotational speed along the "x" axis. The regression coefficients of each speed were represented by a vertical line, the maximum regression coefficient marking the upper limit, and the minimum coefficient marking the lower limit of the line, other coefficients for each speed being plotted along the line.

The graph therefore shows the range of regression coefficient for each speed and also the trend of the coefficient ovef the experimental speed range. In order to make this trend more apparent, another graph of mean regression coefficient against speed was drawn (Figure 34). The mean regression coefficient was plotted along the "y" axis and the rotational speed along the "x" axis. This graph is really the same as the one previously described but in this case all the coefficients for any one speed have been averaged and the mean value plotted.

An analysis of variance was next carried out to determine whether or not the trend of regression coefficient with speed was really significant. The analysis is set out in the
appendix, page no. $\overline{\text { XII }}$.
To find out whether there was any effect of speed on the overall growth rate of the roots, a graph of grand mean growth rate against speed was plotted (Appendix Figure 35). The grand mean for each speed was found by averaging all the half-hourly growth rates for each experiment and then combining these averages from all the experiments at any one speed. At any one speed the maximum mean growth rate is indicated by a dot above each plotted point of the graph and the minimum mean growth rate is shown by a dot below the plotted point of the graph. For the calculation of mean growth rates please see the appendix - Tables of Averages, Tables II to XII. Again an analysis of variance of mean growth rate and speed was carried out to determine the significance of the graphical trend, page no. Appendix $\overline{X V}$

## Consideration of Results

A comparison of the growth rate - time graphs of the control Winter experiments and the control Summer experiments shows no. outstanding differences either in overall growth rate or in the trend of growth rate with time.

Consider the graph of average growth rate against time in which all the different speeds are represented together. The plotting of several graphs on the same co-ordinate field has ....e. enabled a $\nabla$ isual comparison to be made (Figures 2la and b) . il No well defined effect of speed on growth rate is apparent from the graphs. : There appears to be little effect of speed on the overall growth rate since any upward fluctuation is balanced by a nother in the opposite direction.

At higher speeds of rotation ( 8 secs. per revolution to 300 seconds ( 5 minutes) per revolution), the fluctuation in growth rates was more pronounced than at lower speeds ( 10 minutes 21 seconds per revolution to 73 minutes 30 seconds per revolution). This is to be expected since the metabolism of the root is more likely to be upset at high rotational speeds than at low speeds.

At the higher speeds of rotation the growth rate gradually decreased from a comparatively high figure until rotation had continued for about two hours, after which it increased again. After the seventh half hour the growth rate appears to have dropped markedly, after which it fluctuated.

At the lower speeds of rotation the growth rate decreased slightly during the first two hours of rotation after which on the whole it remained steady.

When a root is growing vertically the force of gravity is acting on it parallel to its direction of growth. When a root is placed horizontally it curves downwards so that the tip is again parallel to the line of the gravitational force. Since the force of gravity so markedly acts on a horizontal root, causing it to curve at the tip, there is every reason to suppose that this same force acts to the same extent on a vertical root but its effects are less apparent. If a horizontal root is rotated about a horizontal axis so that the effect of the force of gravity is virtually eradicated, then perhaps any difference in growth rate between this root and a vertical one may in some part be due to the effect of gravity. This
suggestion may partially explain the decrease in growth rate at the start of rotation and the slight reduction in growth rate of slowly rotated roots when compared with vertical roots. The overall growth rate of the vertical roots appears to have been somewhat higher than that of roots rotated slowly. This effect becomes obliterated when all the speeds are considered together because at the higher speeds the fluctuations of the growth rate become more marked.

It would be expected that the growth rate of the vertical roots would be greater than that of rotated roots owing to the mechanical shock suffered by the latter. The surface cells of the rotated roots are subjected alternately to tension and compression as they are rotated, the upper side of the root being under tension and the lower side under compression. Vertical roots growing in solution are subjected to an even tension, since they are virtually growing in space and not in a resistant medium, and so experience much less mechanical shock than rotated roots. It is well known that bushes which are repeatedly brushed or touched by passers -by, grow much less vigorously than if they are growing undisturbed by repeated contact.

In some of the experiments performed on vertical roots the growth rate initially decreased with time. This may have been due to slight disturbance of metabolism due to handing and such a disturbance may also have contributed to the initial decrease in the growth rate ref the rotated roots.

Those rotational experiments performed at Speed 9F were
particularly compared with the vertical experiments to find out whether rotation had any marked effect on growth rate without the complications arising from varying the rotational speed. Speed 9F was used because the wetting interval was equal to that of the vertical experiments. The averages of all vertical experiments and all $9 F$ experiments were used and were recorded in a graph of growth rate against time.

A calculation of the Least Significant Difference showed that the variations between the growth rates of the rotated and the vertical roots were not significant. Statistical analyses of vertical and rotational values for each half hourly time period also were not significant at the 5\% level of variance.

From observations made on the graphs of growth rate against time (Figures 9 - 21) it appears that during vertical growth the growth rate was somewhat higher than with rotated roots. Although there was a considerable fluctuation in the growth rate of the vertical roots, the general trend tended to be steady. Considering all the rotational experiments together the general trend shows a gradual decrease of growth rate as time progressed in the early portion of the experimental period, followed by an increase in rate towards the middle of the experiment, and ending in a fluctuating or a decreasing rate.

The initial decrease was very probably due to handing shock. . The increase in the midale of the experiment may have represented a rallying of the roots to their former behaviour
or an acclimatization of the roots to the rotation effects. The final decrease was most likely the result of the long term disturbance of the roots by rotation.

In order to find out whether there was a real correlation between growth rate and time it was necessary to calculate the correlation coefficients for each experiment. The calculation used is explained in the appendix, page no. $\bar{X}$. An explanation of the correlation coefficients may be found previously under "Analysis of Results", page 29

Only those coefficients significant at the -05 level have been considered. The degree of significance is indicated in the third column of the table of Correlation and Regression Coefficients (Table I). Appendix I.

Considering all the experiments, those for which the correlation coefficient is at all significant, at the adopted level of $\cdot 05$, represent only $\frac{15}{44}$ of the total number of experiments. There is a greater proportion of significant coefficients for those experiments performed at a rotational speed of less than 1 revolution per 5 minutes ( $6 F$ ). Thus it would appear that at slower rotational speeds the correlation between time and growth rate is greater than at higher speeds of rotation. The time factor therefore seems to influence the growth rate more when the speed is slow than when it is fast.

Having studied the correlation coefficient it is necessary to discover exactly what is the effect of time on growth rate.

This was done by calculating the regression coefficient and plotting regression lines as explained previously under "Analysis of Results" (Figures 22-32).

For the vertical growth experiments, there was agreement between four regression lines in one direction and a similarity between the remaining three regression lines in the opposite direction (see Figure 22). In experiments 2, 5, 6 and 7 the growth rate declined slowly with time. In experiments 1,3 and 4 the growth rate increased with time but it is only in experiments 1 and 4 that the correlation coefficient is significant. In over $50 \%$ of the vertical experiments the growth rate decreased slightly with time but the two experiments with significant correlation coefficient show that the growth rate increased considerably with the progression of time.

At speed ${ }^{\text {Fo }}{ }^{23} \mathrm{~F}_{\mathrm{A}}$ the only experiment with a correlation coefficient significant at the $5 \%$ level indicates that growth rate decreased considerably with time. : The other two in experiments also indicate a decrease of rate with time but ws they do not agree very well as to slope.

Fig 24
At speed $9 \mathrm{~F}_{\mathrm{N}}$ five experiments have regression lines $\quad$. which are more or less horizontal, that is, their regression coefficients are very small. These lines suggest that at this speed there was very little regression of growth rate on time. In other words the time factor affected the growth rate only slightly. In experiments la, 5a and 13 the growth rate tended to increase with time whereas in experiments Ba.
and 7a the rate decreased with time (Figure 24). The remaining experiments, except $2 a$, indicate a definite decrease of growth rate as time progressed. Experiment 6a is the only one for this speed which has been found to be significant by statistical analysis.

Two of the four experiments performed at speed 9S (Figure 25) have very similar regression lines pointing to a growth rate declining very slightly as time went on. The other two experiments at this speed conflict with one onother. Experiment 14 shows an increasing growth rate with the progression of time while 16 shows a decreasing rate.

Negligible regression of growth rate on time is shown by those experiments performed at speed 7F (Figure 26).

At speed 6F (Figure 27) two of the experiments show a slight positive regression of growth rate on time while the third indicates a very significant negative regression of growth rate on time.

At speed 6S (Figure 28) and 5F (Figure 29) there appears to have been a marked negative regression of growth rate on time in all the experiments. At speed $5 S$ (Figure 30) the regression was again negative.

At speed 4F (Figure 31) the growth rate decreased with the progression of time but the degree of this regression varied fron experiment to experiment. The two experiments at speed 4 S (Figure 32) provide conflicting data, one indicating a positive regreasion and the other a negative regression.

Considering all the experiments together, $75 \%$ of them have negative regression lines and in $39 \%$ of these the correlation between growth rate and time was significant at the $5 \%$ level. It may be noted also that for rotational speeds of 1 revolution
per 120 seconds, 42 seconds, 20 seconds, 8 seconds, the experiments with positive correlation represent $31.5 \%$ of the total number of experiments performed at these speeds. For speeds of 1 revolution per 5 minutes, 10 minutes 21 seconds, 12 minutes 34 seconds, 24 minutes 6 seconds, 31 minutes 15 seconds and 73 minutes 30 seconds, the experiments with positive correlation represented $16 \cdot 6 \%$ of the total number of experiments performed at these speeds. Thus it would seem that at the fast rotational speeds the tendency for the growth rate to increase with time is twice as great as at slower rotational speeds. This statement depends of course on the arbitrary division of high and low speeds. This division however seems most naturally to fall between speeds $6 F$ and 7F, the former being in the category of slow speeds and the latter belonging to the higher speed group.

However, the main trend throughout the whole series of experiments seems to have been a negative regression of growth rate on time. This is to be expected since the stresses and consequent strains imposed upon the root by rotation undoubtediy profoundly affect its growth over a long period of time. At the higher speeds the rotation probably so distorted the true growth of the root that little consistency in the growth rate trend can be traced. This is evident in the high proportion of positive regressions.

The graph of mean regression coefficient against speed of rotation (Figure 34) shows that none of the rotational
speeds had a positive mean regression coefficient. The vertical mean regression coefficient however was positive. This graph (Figure 34) seems to show a definite trend of regression coefficient with speed of rotation. As speed of rotation decreases from a high value at lof to a low value at $4 S$ the trend of regression coefficient with speed shows a marked increase in regression coefficient followed by a sharp decrease which in its turn is followed by a steady increase as the speed becomes slower.

This graph (Figure 34) shows that at speed 6S the negative regression of growth rate on time was most marked. At speeds $7 F$ and $4 S$ the negative regression of growth rate on time was least. In the vertical experiments the regression was positive.

In order to find out whether this apparent trend of mean regression coefficient with speed was real or not, a statistical analysis of variance between regression coefficients and speed was carried out and may be found in the appendix, page no. XII. The value of $F$ obtained by this analysis lies at approximately the $15 \%$ level of significance. This significance is low since such a value of $F$ could easily occur by chance. The analysis therefore indicates that there is very little effect of speed on the regression coefficient. A $15 \%$ level of significance is not good enough to constitute proof but is sufficient indication that more work on this subject is worth doing and is evidently needed before the question can be answered satisfactorily.

The graph $\begin{aligned} & \text { Fig } 35, \\ & ,\end{aligned}$ of grand mean growth rate against speed of rotation also shows an interesting trend. The mean growth rate was a maximum at speed loF. The rate then decreased until speed 7F was reached, after which it increased and then finally decreased steadily. The growth rate was generally lower at slower speeds.

It is interesting to compare this graph with that of mean regression coefficient against speed of rotationl: Fig 34 . It will be observed that where there is a maximum at lof on the former graph there is a minimum on the regression graph. When there is a minimum on the growth rate curve at 7 F there is a maximum on the regression graph. At speeds slower than 7F the two graphs are also directly opposed to one another. The growth rate curve increases and then decreases whereas the regression curve decreases and then increases. Thus where the growth rate is high there is a correspondingly significant regression coefficient. As the mean growth rate fluctuates so does the regression coefficient. When the growth rate is high there is a marked regression of growth rate on time. When the growth rate is low the regression of rate on time is very slight. Thus the time factor seems to have played a much more important part in influencing growth rate when that growth rate tended to be high than when it tended to be low. The graph of grand mean growth rate against speed shows that there was a very slight tendency for the growth rate to be higher at higher speeds and so there is an indication that the time factor may have
influenced the growth rate more at higher speeds than at lower ones.

An analysis of variance between growth rate and speed has been set out in the appendix, page no. $\overline{X V}$, but from this, speed does not appear to have influenced growth rate in the least since $F$ is smaller than the $20 \%$ level of significance.

## Summary of the Conclusions

(1) No well defined effect of speed of rotation on growth rate was apparent although the growth rate was generally lower at slower rotational speeds.
(2) At higher speeds of rotation the fluctuation in growth rate as time progresses was more pronounced than at lower speeds.
(3) The growth rate of vertical roots was somewhat higher than that of rotated roots.
(4) Observations made from the graphs of growth rate against time show that there was a gradual decrease of growth rate with time in the early periods of the experiment, followed by an increase in rate towards the middle of the experiment and ending in a fluctuating or decreasing rate..
(6) At fast rotational speeds there were twice as many experiments in which growth rate increased with time as there were experiments iat slower rotational speeds in which growth rate increased with time.
(7) From regression lines the main trend throughout seems to have been a negative regression of growth rate on time.
(8) Graphical representation of the results shows a definite trend of regression coefficient with speed of rotation Analysis of variance does not strengthen this indication. It shows that there is no effect of speed of rotation on the trend of the regression coefficient.
(9) Graphical representation shows a definite trend of mean growth rate with speed of rotation but again this is not supported by the analysis of variance, which shows that there is absolutely no effect of speed of rotation on the mean growth rate.
(10) The passage of time seems to have played a much more important part in influencing growth rate when that growth rate was high than when it was low.
(ll) There is an indication that the passage of time may have' influenced the growth rate more at intermediate speeds than at higher or lower speeds.

Appendix I
CORREIATION AND REGRESSION COEFFICIENT
TABLE I

Speed
Vertical

| Vertical | $\begin{array}{r} \cdot 5056 \\ -\cdot 1543 \end{array}$ |  | $\begin{array}{r} .00415757 \\ -.00116969 \end{array}$ |
| :---: | :---: | :---: | :---: |
|  | -2490 |  | . 0018546 |
|  | -8379 | .001 | -0062454 |
|  | --4160 |  | -. 0014633 |
|  | --1139 |  | -.0010543 |
|  | - -1842 |  | -.0009819 |
| 10 F | - -7247 | . 01 | -.0091824 |
|  | - -1203 |  | -.001027 |
|  | - - 4850 |  | -.00467272 |
| 9 F | -0362 |  | -00089696 |
|  | -2974 |  | -00321818 |
|  | - -1852 |  | -.0001454 |
|  | - - 4207 |  | -.0021454 |
|  | - - 4726 |  | -.0045158 |
|  | -1215 |  | . 00050908 |
|  | - -5286 |  | -.0083998 |
|  | - -1316 |  | -.00076342 |
|  | - - 4950 |  | -.00369096 |
|  | -02287 |  | -0001184 |
| 9S | -4608 |  | -0045819 |
|  | - -2289 |  | --0014723 |
|  | - 6071 | . 05 | -.00509053 |
|  | - -2385 |  | --00143634 |
| $7 F$ | 0 |  | $0 \cdot 10$ |
|  | -. 0628 |  | - 00034542 |
| 6 F | -. 7878 | . 01 | -.00746353 |
|  | . 08478 |  | -0008092 |
|  | . 04007 |  | -00019996 |
| 65 | -. 7686 | . 01 | -.0061187 |
|  | -. 5278 |  | -.00438181 |
| 5 F | -. 5835 | . 02 | -•00306364 |
|  | -. 6037 | .02 | --0050546 |
|  | -. 7630 | . 01 | --00378155 |
|  | -.8287 | .001 | -•00353635 |
| 5 S | -. 8194 | . 01 | --00426364 |
|  | -.3806 |  | --0010724 |
| 4 F | --8806 | -001 | --0048455 |
|  | --2201 |  | - 000179088 |
|  | -.6591 | .05 | --003365 |
|  | -. 3193 |  | - 00013726 |
|  | --8498 | -001 | --0053454 |
| 4 S | . 6181 | -05 | -00172 |
|  | - 8841 | -001 | - -00224 |

Regression Coefficient -00415757
-. 00116969 . 0018546
-0062454
-. 0014633
-.0010543
-.0009819
-.0091824
-.00467272
-00089696
-00321818
-.0001454
-.0021454
.0045158
00050908
-.00076342
-•00369096
-0001184
0015819
-. 00509053
-. 00143634
-00 ${ }^{0} 34542$
-•00746353
-00019996
-.0061187
-•00438181
-.00306364
-. 00378155
-•00353635
-•00426364
--0010724
-.0048455
--003365
-•0013726
-•0053454
-00172

- 00224

Appendix II

## TABLES OF AVERAGES (for all experiments)

(1) Average Increases of all roots of each experiment for each successive half-hour.
(2) Grand sverages of all roots of all experiments for each successive half-hour at each speed.
(3) Mean of the Grand Averages (Grand Mean) for each speed. For example: Consider the Vertical Roots: (I) For the first half-hour of Experiment 1 the growth rate average for all the roots of that experiment was 083 ; (2) Considering all the experiments (Vertical) together the growth rate average for the first half-hour was -0779; (3) The Grand Mean is the Absolute Average.

TABLE II VERTICAL Experiments 1, 2, 3, 4, 5, 6, 7.

| Time in |  |  |  |  |  |  |  |  | $\frac{\text { Grand }}{\text { Average }}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| hours |  | Average Growth Rate |  |  |  |  |  | Total |  |
| $\begin{aligned} & \text { from start } \\ & \text { of Expt. } \end{aligned}$ | 1 | 2 | 3 | 4 | 5 | 6 | 7 |  |  |
| $\frac{1}{2}$ | . 083 | -161 | . 075 | .038 | . 075 | . 053 | . 060 | - 545 | . 0779 |
| 1 | -057 | -121 | -064 | -093 | - 073 | -036 | -009 | -453 | -0647 |
| $1 \frac{1}{2}$ | -038 | -100 | -104 | -064 | -047 | -006 | -002 | -361 | -0516 |
| 2 | -053 | -114 | -072 | -075 | -047 | -072 | -045 | -478 | -0683 |
| $2 \frac{1}{2}$ | -062 | -093 | -045 | -070 | -072 | -075 | -019 | -436 | -0623 |
| 3 | -110 | -083 | -053 | -083 | -053 | -012 | -009 | -403 | -0576 |
| $3 \frac{1}{2}$ | -093 | -121 | -072 | -100 | -048 | -012 | -004 | -450 | -0643 |
| 4 | -114 | -106 | -083 | -106 | -057 | -070 | -019 | -555 | -0793 |
| $4 \frac{1}{2}$ | -087 | -112 | -053 | -121 | -053 | -083 | -028 | -537 | -0767 |
| 5 | $\cdot 075$ | -142 | $\cdot 131$ | -104 | -043 | -006 | -028 | -529 | -0756 |
| Aver ${ }^{\frac{1}{2}}$ |  |  | -083 | -114 | -064 | -021 | -021 | -303 | -0606 |
| for each |  |  |  |  |  |  |  |  | -7389 |
| Expt. | -0772 | -1153 | -0759 | - 088 | -05745 | -0405 | -02218 | Grand | $.067173$ |

## Appendix III

TABLE III SPEED 10F (1 rev. every 8 seconds)
Experiments 8, 9, 10
Time in
hours from

| Experiment | 8 | 9 | 10 |
| :---: | :---: | :---: | :---: |
| $\frac{1}{2}$ | -23 | -112 | -15 |
| 1 | -14 | . 06 | . 053 |
| 11 | -12 | -057 | -07 |
| 2 | -13 | -05 | -06 |
| $2 \frac{1}{2}$ | -12 | -053 | -033 |
| 3 | -12 | -053 | -038 |
| $3 \frac{1}{2}$ | -10 | -113 | -08 |
| 4 | -075 | -023 | -063 |
| $4 \frac{1}{2}$ | -12 | -040 | -045 |
| 5 | -07 | -068 | -045 |
| $5 \frac{1}{2}$ | $\cdot 11$ | -092 | -058 |
| Averages |  |  |  |
| for each | -12136 | -06555 | . 06318 |
| Expt. |  |  |  |


| Total | $\frac{\text { Grand }}{\text { Average }}$ |
| :---: | :---: |
| -492 | -164 |
| -253 | -084 |
| -247 | -082 |
| -240 | -080 |
| -206 | -069 |
| -211 | -070 |
| -293 | -098 |
| -161 | -054 |
| -205 | -068 |
| -183 | -061 |
| -260 | -087 |
|  | .917 |
| $\left.\begin{array}{l}\text { Grand } \\ \text { Mean }\end{array}\right\}$ - 08336 |  |



TABIE V SPEED 9S (1 rev. every 42 seconds)
Experiments 14, 15, 16, 17

| $\frac{\text { Time in }}{\text { hours from }}$ | Average Growth Rate |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| start of | 14 | 15 | 16 | 17 | Total | $\frac{\text { Grand }}{\text { Average }}$ |
| $\frac{1}{2}$ | -065 | - 0 | -126 | .10 | -381 | -095 |
| 1 | -046 | - 07 | -065 | .06 | -241 | -060 |
| $1 \frac{1}{2}$ | -060 | -05 | -031 | . 036 | -177 | -044 |
| 2 | -040 | -047 | -041 | . 05 | -178 | -045 |
| $2 \frac{1}{2}$ | -08 | -047 | -038 | . 06 | -225 | -056 |
| 3 | -08 | -024 | -034 | -05 | -188 | -047 |
| 31 | -164 | -076 | -035 | . 076 | -351 | -088 |
| 4 | -066 | -060 | -040 | . 034 | -200 | -050 |
| $4 \frac{1}{2}$ | -091 | -040 | -046 | . 073 | -250 | -063 |
| 5 | -091 | -032 | -035 | -038 | -196 | -049 |
| $5 \frac{1}{2}$ | ${ }^{\circ} 084$ | -083 | -030 | -067 | -264 | -066 |
| Averages |  |  |  |  |  | -663 |
| for each Expt. | -07882 | $\cdot 05627$ | -04736 | -05855 | Miean | -0603 |

TABLE VI SPEED 7F (1 rev. every 2 minutes) Experiments 18,19
Time in

| $\frac{\text { hours from }}{\text { start of }}$ | Average Growth Rate |  | Total | $\begin{aligned} & \text { Grand } \\ & \text { Average } \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: |
| Experiment | 18 | 19 |  |  |
| $\frac{1}{2}$ | -11 | -05 | -16 | -08 |
| 1 | -047 | -063 | -11 | -055 |
| $1 \frac{1}{2}$ | -065 | -046 | -111 | ${ }^{-056}$ |
| 2 | -048 | $\bigcirc 40$ | -088 | -044 |
| $2 \frac{1}{2}$ | -052 | -024 | -076 | -038 |
| 3 | -06 | -08 | -140 | -070 |
| $3 \frac{1}{2}$ | -082 | -044 | -126 | -063 |
| 4 | -05 | -044 | -094 | -047 |
| $4 \frac{1}{2}$ | -075 | -03 | -105 | $\cdot 053$ |
| 5 | -066 | -04 | -106 | -053 |
| $5 \frac{1}{2}$ | -082 | -08 | $\cdot 162$ | $.081$ |
| Averages |  |  |  |  |
| for each | -067 | -04918 | Grand Mean | -0582 |


| Experiments 20, 21; 22 |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Time in |  |  |  |  |  |
| hours from Average Growth |  |  |  |  |  |
| start of Grand |  |  |  |  |  |
| Experiment | 20 | 21 | 22 | Total | Average |
| $\frac{7}{2}$ | -122 | . 095 | . 08 | -297 | .099 |
| 1 | -08 | -133 | . 067 | -280 | .093 |
| $1 \frac{1}{2}$ | -083 | -068 | -09 | -241 | -080 |
| 2 | -065 | -067 | -08 | -212 | -071 |
| $2 \frac{1}{2}$ | -097 | -073 | -082 | -252 | -084 |
| 3 | -077 | -078 | -11 | -265 | -088 |
| $3 \frac{1}{2}$ | -09 | -123 | -118 | -331 | -110 |
| 4 | -02 | -075 | -066 | -161 | -054 |
| 4- $\frac{1}{2}$ | -06 | -099 | -09 | -249 | -083 |
| 5 | -04 | -058 | .083 | -181 | -060 |
| $5 \frac{1}{2}$ | $\cdot 023$ | -117 | . 07 | -210 | $\cdot 070$ |
|  |  |  |  |  | -892 |
| Averages |  |  |  |  |  |
| for each | -06882 | -08782 | - 08509 | Mean | -0811 |
| Experiment |  |  |  |  |  |

TABLE VIII SPEED 6S (1 rev. every 10 minutes 21 seconds)
Experiments 23, 24

| Time in |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
| hours from Average Growth Rate |  |  |  |  |
| start of |  |  |  | Grand |
| Experiment | 23 | 24 | Total | Average |
| $\frac{1}{2}$ | -126 | -12 | -246 | -123 |
| 1 | -099 | -102 | -201 | -101 |
| $1 \frac{1}{2}$ | -053 | -055 | -108 | -054 |
| 2 | -087 | -028 | -115 | -058 |
| $2 \frac{1}{2}$ | -071 | -067 | -138 | -069 |
| 3 | -047 | -048 | -095 | -048 |
| 31 2 | -072 | -07 | -142 | -071 |
| 4 | -063 | -041 | -104 | -052 |
| 4 $\frac{1}{2}$ | -05 | -061 | -111 | -056 |
| 5 | -036 | -036 | -072 | -036 |
| $5 \frac{1}{2}$ | -053 | $\cdot 067$ | -120 | -060 |
| Averages |  |  |  |  |
| for each | . 06882 | . 06318 | Grand Mean | . 0.0662 |

TABIE IX SPEED 5F (I rev. every 12 minutes 34 seconds) Experiments 25, 26, 27, 28

Time in

| hours from | Average Growth Rate |  |  |  |  | $\frac{\text { Grand }}{\text { Average }}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\frac{\text { Start of }}{\text { Experiment }}$ | 25 | 26 | 27 | 28 | Total |  |
| $\frac{1}{2}$ | .079 | -117 | . 084 | -071 | $\cdot 351$ | . 088 |
| 1 | .036 | -070 | . 067 | -055 | -228 | - 057 |
| $1 \frac{1}{2}$ | -072 | -071 | -055 | -049 | -247 | -062 |
| 2 | .04 | . 066 | . 048 | -046 | -200 | 050 |
| $2 \frac{1}{2}$ | -076 | -099 | . 067 | -037 | -279 | - 069 |
| 3 | -053 | . 042 | . 049 | -049 | -193 | -048 |
| $3 \frac{1}{2}$ | . 037 | . 073 | . 041 | -024 | -175 | 044 |
| 4 | . 040 | . 041 | . 065 | -029 | -175 | -044 |
| $4 \frac{1}{2}$ | -046 | . 018 | .052 | -028 | -144 | -036 |
| 5 | . 041 | .046 | . 032 | -035 | -154 | -039 |
| $5 \frac{1}{2}$ | .031 | -072 | -029 | -031 | -163 | $\cdot 041$ |
| Averages |  |  |  |  |  | . 578 |
| for each | -05009 | -065 | -05355 | -04127 | Grand | -05255 |

TABLEX SPEED 5S (1 rev. every 24 minutes 6 seconds)
Experiments 29, 30
Time in

| hours from | Average Growth Rate |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
| start of |  |  |  | Grand |
| Experiment | 29 | 30 | Total | Average |
| $\frac{1}{2}$ | -081 | -062 | -143 | . 072 |
| 1 | -066 | -055 | -121 | -061 |
| $1 \frac{1}{2}$ | -042 | -066 | -1083 | -054 |
| 2 | -046 | -062 | -108 | -054 |
| $2 \frac{1}{2}$ | . 056 | -047 | -103 | -052 |
| 3 | -050 | . 059 | -109 | -055 |
| $3 \frac{1}{2}$ | -025 | . 050 | -075 | -038 |
| 4 | .031 | -040 | -072 | . 036 |
| $4 \frac{1}{2}$ | -037 | -070 | -107 | -054 |
| 5 | . 029 | .054 | -083 | -042 |
| $5 \frac{1}{2}$ | -032 | . 045 | -077 | -039 |
| Averages |  |  |  | - 557 |
| for each |  |  | Grand |  |
| Expt. | -045 | -05545 | Mean | -05064 |

TABLE XI SPEED 4F (1rev. every 31 minutes 15 seconds)
Experiments 31, 32, 33, 34, 35
Time in
hours from

| $\begin{aligned} & \text { Start of } \\ & \text { Experiment } \end{aligned}$ | 31 | 32 | 33 | 34 | 35 | Total | $\frac{\text { Grand }}{\text { Average }}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\frac{1}{2}$ | .077 | -108 | . 085 | . 051 | -098 | . 236 | . 059 |
| 1 | -061 | -087 | -082 | -048 | . 066 | -264 | -066 |
| $1 \frac{1}{2}$ | -054 | -063 | -061 | -022 | -070 | -210 | -053 |
| 2 | -036 | -022 | -041 | -033 | -041 | -133 | -033 |
| $2 \frac{1}{2}$ | -028 | -021 | -055 | -029 | .058 | - 137 | -034 |
| 3 | -035 | -041 | -053 | -022 | -054 | -153 | -038 |
| $3 \frac{1}{2}$ | -039 | -050 | -060 | -017 | -058 | -165 | -041 |
| 4 | -033 | -074 | -043 | -035 | -046 | -189 | -047 |
| $4 \frac{1}{2}$ | -031 | -039 | .036 | .029 | .033 | -133 | . 033 |
| 5 | -015 | -07 | - | .037 | -023 | -146 | -037 |
| $5 \frac{1}{2}$ | -020 | -07 | - | -027 | .035 | -153 | -038 |
| Averages |  |  |  |  |  |  | -479 |

Averages
for each
Expt. .039 .05864 .05733 .03182 .05291 Mean .04355
N.B. The plate from Experiment 33 was fogged on the last two exposures. [foe the note the puge bexing the full roguto Triferibl

TABLE XII SPEED 4S (1 rev. every 73 minutes 30 seconds)
Experiments 36, 37
Time in
hours from Average Growth Rate

| start of |
| :---: |
| Experiment |
| $\frac{1}{2}$ |
| $\frac{1}{2} \frac{1}{2}$ |
| 2 |
| $2 \frac{1}{2}$ |
| $3 \frac{1}{2}$ |
| $4 \frac{1}{2}$ |
| $4 \frac{1}{2}$ |
| 5 |

Averages
for each
Expt.

| 36 | 37 | Total | $\frac{\text { Average }}{\text { Aver }}$ |
| :--- | :--- | :--- | :--- |
| .044 | .061 | .105 | .053 |
| .044 | .061 | .105 | .053 |
| .036 | .052 | .088 | .044 |
| .036 | .052 | .088 | .044 |
| .037 | .048 | .085 | .043 |
| .037 | .048 | .085 | .043 |
| .057 | .042 | .099 | .049 |
| .057 | .042 | .099 | .049 |
| .055 | .038 | .093 | .047 |
| .055 | .038 | .093 | .047 |
|  |  |  | .047 |
| .0458 | .0482 | Grand | .472 |
|  |  | Mean | .0472 |

## Appendix IX

Explanation of the Statistical Analysis Carried Out to Find the Correlation Coefficient between Growth Rate and Time, for each Experiment

In these calculations
$G=$ Growth Rate
$T=$ Time
$\Sigma G=$ The Sum of the Growth Rates
$\Sigma T=$ The Sum of the Times
$G T=$ The Growth Rate $x$ the Time, for each time period
$\Sigma G T=$ The Sum of all the GT quantities
$\Sigma G^{2}=$ The Sum of (G2 for each time period)
$\Sigma T^{2}=$ The Sum of (Tín for each time period)
$\bar{G}=$ The mean growth rate - found by dividing the $K G$ by the number of time periods used
$\bar{T}=$ The mean time - found by dividing the $\Sigma T$ by the number of time periods used.

The Correlation Coefficient between $G$ and $T$ is given by:-

$$
r=\frac{\frac{1}{N} \sum G T-\bar{G} \bar{T}}{\sqrt{V_{G} \bar{V}_{T}}}
$$

where $N$ is the number of time periods or number of $G$ and $T$ pairs used,
$\nabla_{G}=$ variance of $G$ which is equal to $\frac{1}{N} \sum G^{2}-(\bar{G})^{2}$ $\nabla_{T}=$ variance of $T$ which is equal to $\frac{1}{N} \sum T^{2}-(T)^{2}-\operatorname{lot}$ It will be noted that the time periods have not been calculated in hours but in numerical order starting from the beginning of the experiment. For instance in Experiment 1

## Appendix X

the first half hour of the experiment has been numbered 1 , the second half hour of the experiment has been numbered 2 , and so on. At the end of three and a half hours of rotation we should be at the end of time period seven. By this method each half hour has a definite place in the time scale from the beginning of the experiment to the end and also bears a definite relationship to the other time periods in the scale.

For each experiment the growth rate averages for all the roots for each time period have been used. These are the same averages which are set down in the Tables of Averages. (Please see previously). Tables I ToXll.

For each experiment the average growth rate and timeperiod number for each time period have been set down in two corresponding tables. From these a table of GT quantities has been compiled. The totals from each of these tables gives the quantities $\Sigma G, \leqslant T$ and $\sum G T$ respectively.

From here the quantities $\bar{G}\left(\frac{\sum G}{N}\right), \bar{T}\left(\frac{\sum T}{N}\right), \bar{G} \bar{T}$, $\bar{G}^{2}$ and $\bar{T}^{2}$ are easily calculated.

The quantity $\frac{1}{N} \sum G T$ is found and $V_{G}$ and $V_{T}$ are calculated remembering that $V_{G}=\frac{1}{N}\left\langle G^{2}-(\bar{G})^{2}\right.$ and similarly for $V_{T}$.
$\sqrt{\bar{V}_{G}}$ and $\sqrt{\bar{V}_{T}}$ are next evaluated so that finally $r$ the Correlation Coefficient can be found.

To find the regression coefficient from these calculations the following equation is used

Regression coefficient $=r \frac{\sqrt{V_{G}}}{\sqrt{\bar{V}_{T}}}$

## Appendix XI

This regression coefficient represents the slope of the regression line when it is plotted with the growth rate as the $y$ axis and the time as the $x$ axis. The position of the regression line is defined by three requirements:1. It must pass through the mean growth rate $\bar{G}$.
2. It must pass through the mean time $\overline{\mathrm{T}}$.
3. It must have a slope given by the regression coefficient. The line represents the regression, if any, of growth rate on time. (For further explanation of these lines please see text Page 30).
ANALYSIS OF VARIANCE - Regression Coefficient and Speed

$N=$ Number of Items in each respective column.
Total Number of Items $=44=N_{T}$
$\begin{aligned} \text { Correction Factor }=\frac{T^{2}}{N_{T}}=\frac{79.6616^{2}}{44}=\frac{6345 \cdot 97}{44}=\underline{144 \cdot 2266}\end{aligned}$
$\begin{aligned} \text { Between Squeelafs Sum of Squares } & =298 \cdot 4415-144 \cdot 2266 \\ & =\frac{154 \cdot 2149}{\text { Degrees of Freedom }=11-1}=10\end{aligned}$
$N=$ Number of Items in each respective column.
Total Number of Items $=44=N_{T}$
$\begin{aligned} \text { Correction Factor }=\frac{T^{2}}{N_{T}}=\frac{79.6616^{2}}{44}=\frac{6345 \cdot 97}{44}=\underline{144 \cdot 2266}\end{aligned}$
$\begin{aligned} \text { Between Squeelafs Sum of Squares } & =298 \cdot 4415-144 \cdot 2266 \\ & =\frac{154 \cdot 2149}{\text { Degrees of Freedom }=11-1}=10\end{aligned}$

$N=$ Number of Items in each respective column.
Total Number of Items $=44=N_{T}$
$\begin{aligned} \text { Correction Factor }=\frac{T^{2}}{N_{T}}=\frac{79.6616^{2}}{44}=\frac{6345 \cdot 97}{44}=\underline{144 \cdot 2266}\end{aligned}$
$\begin{aligned} \text { Between Squeelafs Sum of Squares } & =298 \cdot 4415-144 \cdot 2266 \\ & =\frac{154 \cdot 2149}{\text { Degrees of Freedom }=11-1}=10\end{aligned}$


[^1]TABIE OF ANALYSIS OF VARTANCE

| Source of | Sum of | Degree of | Variance |
| :--- | :---: | :---: | :---: |
| Variation | Squares | Freedom | Estimate |
| Between Speeds | 154.2149 | 10 | 15.42149 |
| Within Speeds | 322.849 | 33 | 9.7832 |
| Total | 477.0639 | 43 |  |

$$
\begin{aligned}
F & =\frac{15 \cdot 42149}{9 \cdot 7832} \text { with d.f. } 10 / 33 \\
& =1.576324
\end{aligned}
$$

$$
\text { F from Tables: } \begin{aligned}
-5 \% & =2 \cdot 18 \\
10 \% & =1.8 \\
20 \% & =1.48
\end{aligned}
$$

ANALYSIS OF VARIANCP - Mean Growth Rate and speed

$N=$ Number of Items in each respective column.
Totàl 1 Number of Items $=44=N_{T}$
Correction Factor $=\frac{T^{2}}{\mathrm{~N}_{\mathfrak{W}}}=\frac{280 \cdot 071^{2}}{44}=\frac{78439 \cdot 765041}{44}=1782 \cdot 7219$
Between Squeplay Sum of Squares $=1835 \cdot 937-1782 \cdot 7219=53 \cdot 2151$

|  | 10 F | 9 F | 9S | 7 F | 6 F | 6 S | 5 F | 5 S | 4F | 4S | V |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 147．282 | $104 \cdot 857$ | 62.126 | 44.89 | 47．362 | 47.362 | 25.09 | 2025 | $15 \cdot 21$ | 20.976 | 59．5984 |
|  | $42 \cdot 968$ | 106.709 | 31.663 | 24.187 | $77 \cdot 124$ | 39．917 | $42 \cdot 25$ | $30 \cdot 747$ | 34．387 | 23．232 | 132.941 |
| 魷 | 39.917 | 37．704 | $22 \cdot 429$ |  | 72.403 |  | $28 \cdot 676$ |  | 32．867 |  | $57 \cdot 623$ |
|  |  | $114 \cdot 276$ | 34－281 |  |  |  | 17.032 |  | $10 \cdot 125$ |  | 77.44 |
|  |  | 29．746 |  |  |  |  |  |  | 27． 995 |  | 33.005 |
| \％ |  | $21 \cdot 837$ |  |  |  |  |  |  |  |  | 16.443 |
|  |  | 33－224 |  |  |  |  |  |  |  |  | 4.9195 |
| 成 |  | 7.097 |  |  |  |  |  |  |  |  |  |
| 思 |  | 46.731 |  |  |  |  |  |  |  |  |  |

$$
\begin{aligned}
& \text { Grand Total }=2001 \cdot 1279 \quad \text { Degrees of Freedom }=43 \\
& \text { Total Sum of Squares }=2001 \cdot 1279-1782 \cdot 7219=\underline{218 \cdot 4060} \\
& \begin{aligned}
\text { Within Sqregale Sum of Squares } & =\text { Total S. of } \mathrm{S} \cdot-\text { Between Spaeds } \mathrm{S} \cdot \text { of } \mathrm{S} . \\
& =218 \cdot 4060-53 \cdot 2151 \\
& =\underline{165 \cdot 1909} \text { Degrees of Treedom }=43-10 \\
& =33
\end{aligned}
\end{aligned}
$$

TABIE OT ANALYSIS OF VARIANCE

| Source of | Sum of <br> Variation | Degree of <br> Squares | Variance |
| :--- | :---: | :---: | :---: |
| Fetween Speeds | 53.2151 | 10 | 5.3215 |
| Wistimate |  |  |  |
| Within Speeds | 165.1909 | 33 | 5.0058 |
| Total | 218.4060 | 43 |  |

$$
\begin{aligned}
F & =\frac{5 \cdot 3215}{5 \cdot 0058} \text { with d.f. } 10 / 33 \\
& =1.0631
\end{aligned}
$$

F from Tables:- $20 \%=1 \cdot 48$

NOTE ON GRAPHS
It should be noted that the "growth rate" in these graphs does not represent the absolute rate of extension of the roots but the rate of change in length of the photographic images. To convert these values to absolute growth rate of roots in mm. per half hour they should be multiplied by the factor 4.72 (see pages 18-20).





























[^0]:    A is the point of attachment of the platform to the box. The pointer of the platform moves along the arc of a circle centre $A$ and radius "a". This arc was drawn on the box and was marked off at $\frac{3}{4}$ inch intervals. The intervals. were numbered from $X$ to $Y$. The light rays from the klinostat chamber entered the camera as shown and were focussed on the frosted plate at the back of the camera. As the pointer of the platform was moved from $X$ to $Y$ the image of the slit on the plate moved from "x" to "y". When photographs were being taken the pointer was moved only along the middle part of the arc (between intervals 7 and 13) so that images appeared on the central portion of the plate, i.e. between "p" and "q". This was to avoid any slight distortion.

[^1]:    Grand Total $=621 \cdot 2905$ Degrees of Freedom $=43$
    Total Sum of Squares $=621 \cdot 2905-144 \cdot 2266=477 \cdot 0639$
    Within Spreads Sum of Squares $=$ Total $S$ of $S$ - Between Speeddes $S$ of $S$ $=43-10$
    $=33$

