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A STUDY OF THE WATER RELATIONS

OF

GALANTHUS NIVALIS AND GALANTHUS ELWESI

with Special Reference to the Relationship  
between Transpiration and the Degree of  
Development of the Conducting Tissues in  
the Growing Region of the Leaf.

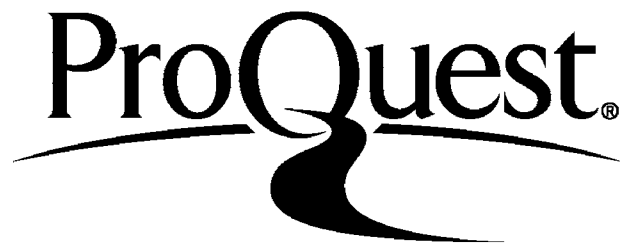
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C O N T E N T S.

	Page.
I. INTRODUCTION -----	1
II. WATER CONTENT IN GALANTHUS NIVALIS -----	7
(1) Methods -----	7
(2) The resting bulb -----	8
(3) The growing bulb -----	10
III. ABSORPTION -----	14
(1) Methods -----	14
(2) The absorption at intervals during the season -----	16
(3) The total absorption during the season -----	18
(4) The relation between the amount of water absorbed and the amount transpired -----	19
IV. TRANSPIRATION -----	22
(1) Methods -----	22
(2) Presentation of results -----	25
(3) The Transpiration of different individuals at different intervals during the season -----	27
(4) The Transpiration of the same individual plants at different intervals in the season -	30
(5) The transpiration of plants planted on 21st Dec. compared with those planted 21st Oct. --	32

C O N T E N T S (cont.)

(6) Comparison of transpiration from adaxial and abaxial leaf surface -----	34
(7) The transpiration of cut leaves -----	39
(8) The condition of the stomata -----	40
(9) Conclusions -----	41
V. TRANSPIRATION AND THE CONDUCTING SYSTEM OF THE LEAF	43
(1) Methods -----	43
(2) The conducting system of the leaf -----	45
(3) The area of the conducting tissue in growing region of the leaf -----	51
(4) The relationship between transpiration and the 'conducting area' -----	55
(a) in <u>Galanthus nivalis</u> -----	56
(b) in <u>Galanthus Elwesi</u> -----	59
(5) Conclusion -----	60
VI. COMPARISON WITH OTHER PLANTS -----	62
(1) Transpiration -----	62
(2) Vascular supply to the leaf -----	66
(3) Absorption -----	67
(4) Conclusion -----	68

C O N T E N T S (cont.)

VII.	OBSERVATIONS ON THE FOOD RESERVE †)-----	72
	(1) Changes within the storage cells -----	72
	(2) Changes in thickness of the storage leaves and foliage leaf bases -----	74
	(3) The dry weight of plants at different periods of growth -----	75
VIII.	GENERAL CONCLUSIONS -----	77
IX.	SUMMARY -----	92
X.	LITERATURE CITED -----	97
XI.	APPENDIX-----	I.

S E C T I O N I.INTRODUCTION.

In England a number of bulbous plants occur wild or are commonly cultivated among these are - Galanthus, Hyacinthus, Muscari, Narcissus, Scilla and Tulipa. Most of these plants flower in the spring; their leaves appear above ground early in the year at a time when the temperature is low and frosts are common, so that one would expect the absorption of water by the roots to be very small. Hales<sup>6</sup> speaking of snowdrops, crocuses etc., conjectures that these "forward hardy plants do probably partake much of the nature of evergreens in perspiring little", but so far as I know the water relations of these plants has never been investigated.

The season of growth of these plants, their characteristic form and method of growth, and the absorption of water by adventitious roots arising annually at the periphery of the stunted stem led one to think that the study of their water relations might yield interesting results.

It is well known that in certain monocotyledons particularly bulbous plants, the growth of the leaf is intercalary, the growing region being situated in the



basal part of the leaf; in this respect they differ from the majority of flowering plants. Little is known of the anatomy of this growing region but recently Wicks (20a) has investigated the leaf anatomy of some Amaryllidaceous plants e.g. Narcissus poeticus, N. Elvira, Zephranthes candida, Galanthus nivalis, Haemanthus and Brunsvigia. She finds that the vascular tissue is much less developed in the growing region than it is in the mature parts of the leaf; this difference is particularly striking in the young leaf and at this stage the conducting tissue is represented in the growing region by a few small protoxylem elements only.

It has often been suggested that there is a close connection between transpiration and the degree of development and type of element composing the conducting tissues through which the water passes on its way from the roots to the transpiring leaf surface but there appears to be some disagreement as to the nature of this relationship.

Kerner (10) considers that the construction of the conducting strands varies according to the needs of the transpiring surface and as an illustration of this cites the example of climbing plants in which the size of the conducting vessels varies according to the length of the stem and size of the transpiring leaves. Haberlandt (5) appears to hold the same view and in support of it quotes a number of examples, including the work of Jost, who found that the suppression of

the transpiring surface resulted in a reduction of its vascular supply and the work of Schenck and Kohl. The last two named workers compared the degree of development of the vascular tissue in damp and dry air and concluded that the greater the transpiration the better developed is the xylem.

Other workers hold the view that intensity of transpiration is directly affected by the conducting tissue. Among these are Krutizky and Farmer (4). Krutizky found that the transpiration of individual hawthorn leaves was increased if the number of leaves on the twig was reduced, this he attributes to the increased water supply to the remaining leaves. This work of Krutizky is not published but is mentioned by Maximov (12). Farmer studied quantitatively the relative efficiency of different types of wood. He found that the wood of deciduous trees was more efficient than the evergreen types, having a higher specific conductivity, and he considers that the low specific conductivity of the evergreen wood accounts for the xerophytic nature of their leaves and low rate of transpiration. Farmer attributes the higher specific conductivity of the deciduous woods to the greater length and diameter of the individual elements composing the wood. The anatomy of wood in relation to its efficiency has been more fully investigated by Holmes (7) and

Rivett (16). The former compared the wood of ash and hazel and considers that the higher specific conductivity of hazel wood over ash wood is due to the greater number of conducting elements per unit area. Rivett made a study of the wood of the evergreens Rhododendron ponticum and Ilex Aquifolium: she considers that the length of the vessel is the most important anatomical feature affecting specific conductivity.

A constant quantitative relationship between intensity of transpiration and the total area of the vascular tissue at the base of the leaf was observed by Yasuda (21) in the rice plant.

Rubel (17) and Huber (8) have shown that the vascular tissue is less developed in shade leaves than in sun leaves and also that the intensity of transpiration is less suggesting close connection between vascular tissue and transpiration. They calculated the rate at which the water flowed in the conducting channels and shewed that the rate of flow is more rapid in shade plants.

In bulbous Monocotyledons all the water passing to the transpiring leaf surface must pass through the meristematic region at the base of the leaf. It was thought therefore that a study of the water relations of these plants might, with other results, give interesting information regarding the relationship between conducting tissue and transpiration.

Work has been carried out on Galanthus nivalis and Galanthus Elwesi. The reasons for selecting these species

are given below;-

- 1) The small size of the plants. Plants could be grown in small pots and their transpiration measured by weighing potted plants on an ordinary balance.
- 2) The simple structure of the plants. Church (3) describes the structure of the bulb in Galanthus: only two foliage leaves, one with a sheathing base are present in Galanthus nivalis and Galanthus Elwesi, these are surrounded by a sheathing leaf. During their period of growth these three leaves accumulate food in their bases, and form the storage structures in the succeeding year. Thus three storage leaves are present in the bulb, the outer ones are continuous cylinders but the inner one is not, (see fig34 ) as the base of the inner foliage leaf, which it represents, is not sheathing. The bulb is protected by three membranous scales - the remains of the storage organs of the previous season. In three seasons the cycle of foliage leaf base, storage organ, membranous scale is passed through.
- 3) The snowdrop is the earliest of the bulbous plants to flower in Britain. In an average season the shoots of Galanthus nivalis appear above ground towards the end of December; the leaves break through the sheath some two weeks later and are gradually expanded. Early in

February the flower bud appears, opening about two weeks later. The leaves remain green for several weeks after the flower has withered, the length of time varying according to external conditions. For example on 24th May, 1934 leaves of plants growing in long grass were still green whereas those on plants growing in the more exposed conditions of a flower bed had withered completely. In Fig. 34a-f drawings of plants are given at different stages of growth. These plants were grown in water during the season 1933 - 4 and flowered later than those observed during the two following seasons. This was probably due to weather the fact that the spring of 1934 was colder than the two following.

S E C T I O N II.WATER CONTENT IN GALANTHUS NIVALIS.

An attempt was made to follow the changes in the water content of plants of Galanthus nivalis during their growing season, since the water content of a plant reflects its water balance i.e, the relationship between transpiration and absorption.

Method.

The bulbs were obtained commercially and were grown in an unheated green-house.

1933 - '34 bulbs were grown some in tap-water and some in a Knop's culture solution, the bulbs being supported by means of perforated zinc metal sheet in large glass vessels, so arranged that the base of the bulb touched the water while the metal remained above water level. The roots were protected from light by black paper and in the early stages light was excluded from the shoots also. At monthly intervals the water or culture solution was changed and water added more often so that it remained at about the same level in the vessels. As the surface of the water was large and freely exposed to the air it was thought that sufficient air for the roots would be present in the water.

In 1934 - '35 bulbs were grown in ordinary potting soil, ten bulbs in each pot.

In 1933 - '34 the bulbs were marked and weighed in batches of three before planting, and in 1934 - '35 in batches of ten.

At intervals during the season plants were taken from the glass vessels (two batches from water and two from culture solution) or dug up and washed free from soil (one batch); after careful drying with a linen cloth and blotting paper the plants were weighed and dried in an oven at a temperature of 97°C. In this way the fresh weight and the water content was obtained for resting bulbs and growing bulbs at different stages of their development.

#### The Resting Bulb.

The water content of bulbs was determined in the Autumn of 1933 and of 1934 just before planting took place. Bulbs were considered singly and in batches of ten.

The results obtained are given in table (1) and appendix 1.

Table I. % Water Content of Resting Bulbs.

8th November 1933.

20th October 1934.

A	B	C	D	E	F	G	H
10 Individual bulbs	10 Individual bulbs	Batch of 10 bulbs	Batch of 10 bulbs	8 Individual bulbs	8 Individual bulbs	Batch of 10 bulbs	Batch of 10 bulbs
67.8	64.5			64.3	63.5		
60.5	62.2			63.7	61.0		
59.8	60.8			62.4	60.6		
59.4	59.4			61.5	59.1		
59.4	58.5			60.7	58.5		
59.3	57.7			58.8	57.6		
56.9	56.7			58.7	56.1		
55.6	56.1			58.0	56.0		
53.1	55.6						
53.1	54.8						
Mean of 10 bulbs	58.4	58.2	56.4	Mean of 10 (or 8) bulbs 61.1	59.1	63.6	61.7
Mean of 40 bulbs	57.7		Mean of 36 bulbs		61.4		



These figures show that the percentage water content of single bulbs may vary considerably, a range of 11.4% occurring in the 1934 values and 12.5% in the 1935 values. If the average of ten bulbs is considered the variation is much less, being only 1.4% in the four batches considered in 1934 and 4.5% in 1935. The lower values obtained in 1933 may be due to:-

- 1) Loss of water during storage: the estimations were carried out nearly three weeks earlier in 1934 than 1933.
- 2) Difference in growth during the preceeding seasons: the bulbs obtained in autumn 1933 were rather larger than those in 1934 and this was probably a reflection of the different conditions under which the plants had been grown in the previous spring.

#### The Growing Bulb.

The water content of plants was determined from the resting stage through the seasons as the leaves and flowers developed until the plants died down in late spring, when the bulbs were air-dried to restore them to a condition comparable with that in which they were planted the previous autumn. The leaves withered rather early compared with plants growing naturally in a garden, probably because the latter were more protected from excessive transpiration than the plants in pots and glass vessels. The results obtained are given in Table II and Appendix 2.

Table II. The Percentage Water Content of Plants during Growth.

		Season 1933 - 4			Season 1934 - 5		
Date	Tap Water		Culture Solution			Soil	
	A Batch of 3 bulbs	B Batch of 3 bulbs	C Batch of 3 bulbs	D Batch of 3 bulbs	C & D Mean	Date	Batch of 10 bulbs
4th Dec.	59.3	59.1	59.2	60.1	57.8	21st Nov.	59.9
17 " "	60.3	60.5	60.4	60.5	59.5		
1st Jan.	65.8	65.2	65.5	60.2	61.9		
8th "	60.9	70.2	65.6	60.3	61.5		
15 " "	68.5	59.4	64.0	64.6	63.2	14th Jan.	63.9
12 " Feb.	70.7	74.4	72.6	74.5	72.3	4 " Feb.	77.7
19 " "	74.5	71.4	73.0	75.1	74.7	20 " "	82.4
26 " "	72.8	72.8	72.8	74.0	74.4	6 " Mar.	84.1
12 " Mar.	78.9	77.6	78.3	77.4	76.1	19 " "	83.9
27 " "	82.5	77.2	79.4	80.5	80.7	29 " "	87.3
20 " Apr.				76.4	76.5		
15 " May	43.1	50.2	46.7			3rd May	77.7

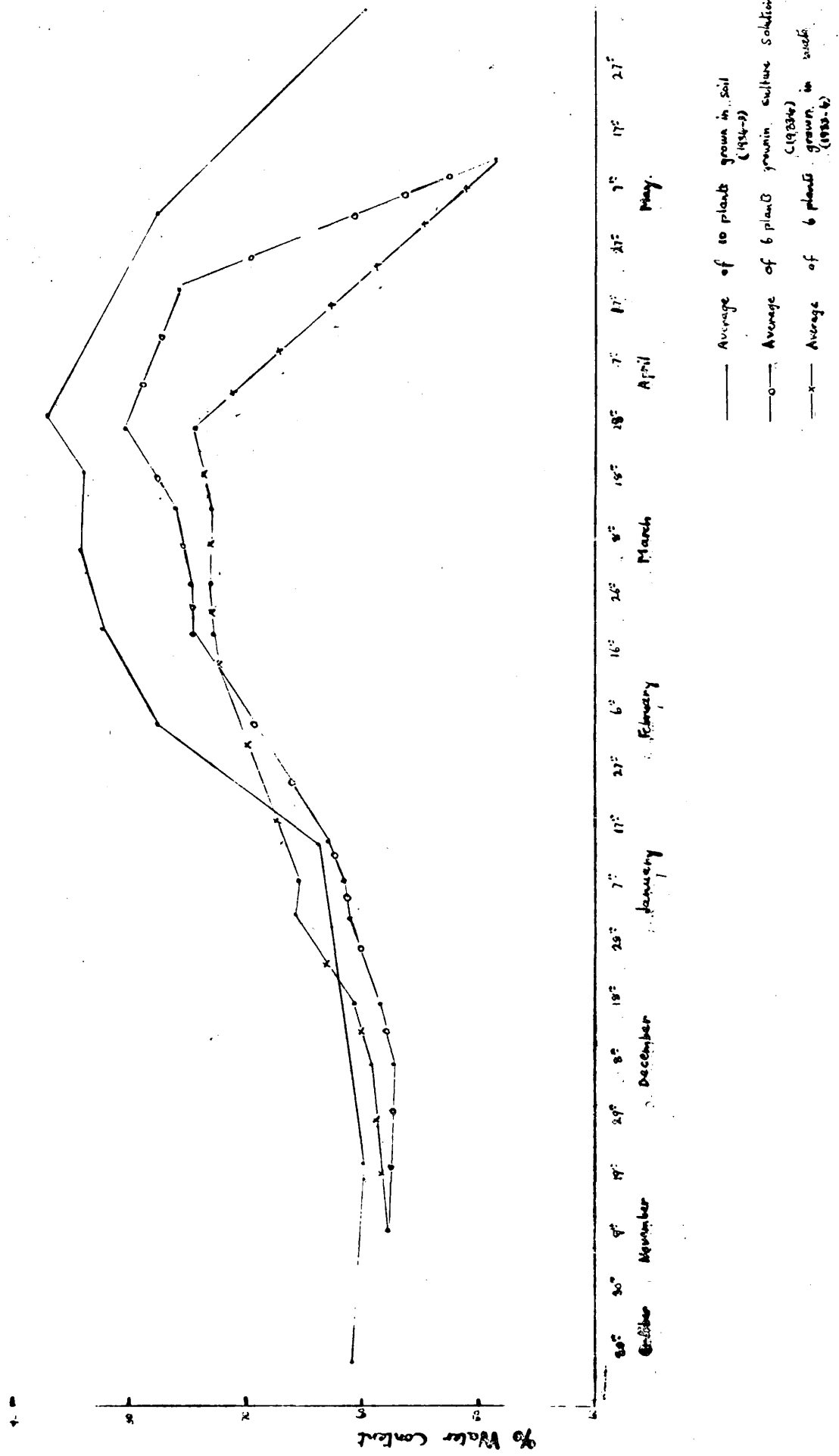
The average of these results obtained at different dates are shewn graphically in Fig. 1, which gives the changing water content during the season. The fresh weight of plants (average of 10) planted in autumn has been compared with that found at intervals during the season. The percentage change in fresh weight during the season is shewn graphically in Fig. 2, and the figures are given in Appendix 3.

From a consideration of the data given it may be deduced that:-

- 1) The percentage water content of the plants increases from the time of planting until they begin to die down at the end of the season's growth. This increase is slow at first but from about mid-January onwards, when the shoot has appeared above ground and the leaves and flowers are developing, it is much more rapid. Compared with the storage leaves the shoot and roots contain a relatively large quantity of water and a maximum water content occurs near the end of the season when the root and shoot systems are fully developed; as these wither the water content falls rapidly.
- 2) The percentage increase in fresh weight follows the same course as the water content, increasing slowly at first, then more rapidly and finally falling as the shoot and root shrivel.

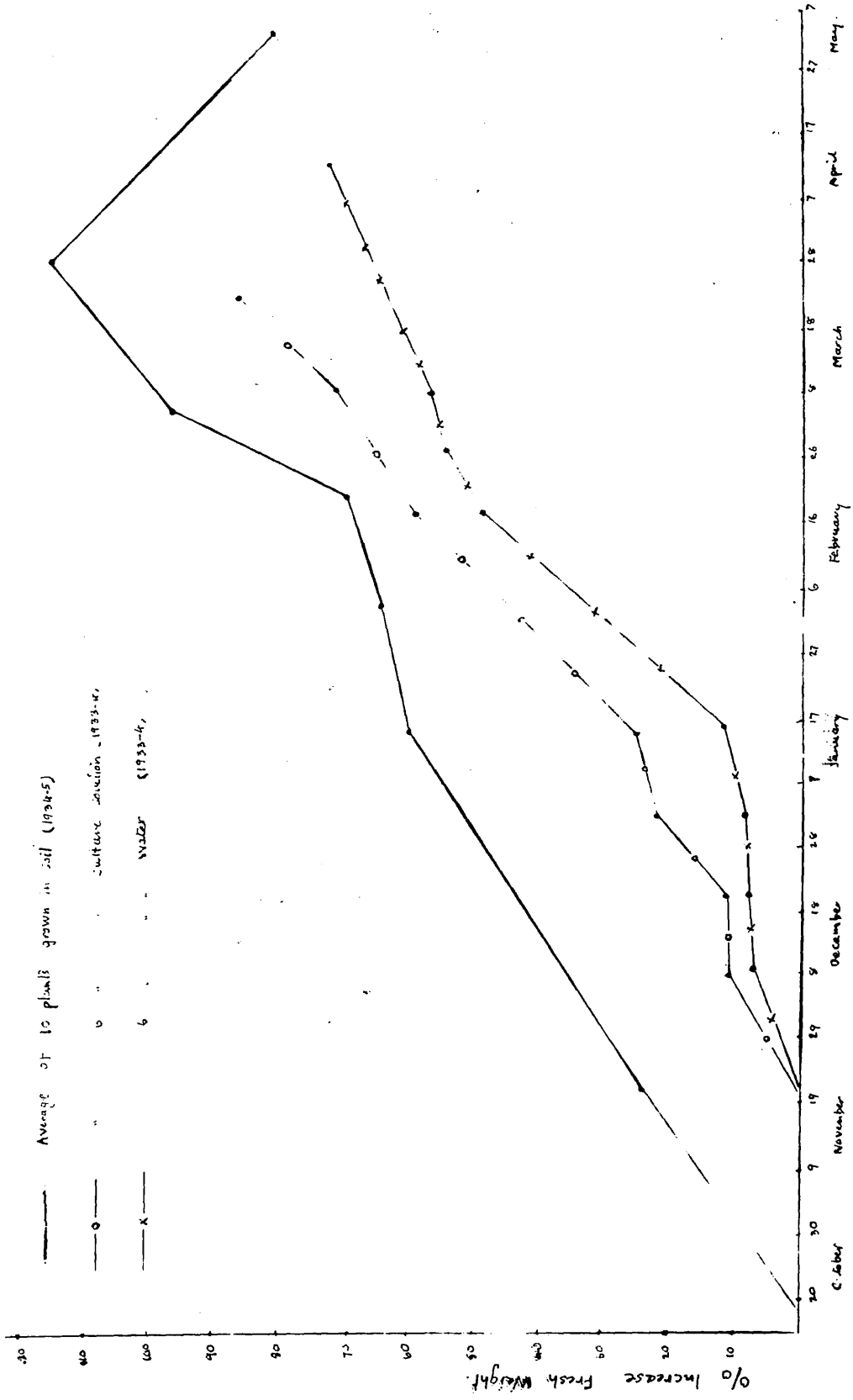
3) Little distinction can be drawn between plants grown in tap-water and culture solution as regards their changes in percentage water content or fresh weight.. The absence of mineral salts did not appear to impoverish the plants and their growth in tap-water was fully as luxuriant as in the culture solution. The plants grown in soil show a rather higher percentage water content and increase in fresh weight and this may be due to the fact that the root system of these plants was better developed than that of plants grown in water - the difference in root development doubtless being an outcome of differences in aeration in the two media.

Fig 1 *Gobionthus muriei* - Percentage water content of plants at different stages of growth.



— Average of 10 plants grown in soil (1934-5)  
 -o- Average of 6 plants grown in culture solution (1933-4)  
 -x- Average of 6 plants grown in water (1933-4)

Fig 2 Galanthus nivalis - Percentage increase in fresh weight of plants at different stages in growth compared with the fresh weight when planted the previous Autumn.



### S E C T I O N III.

#### ABSORPTION.

In Galanthus the shoot is expanded rapidly at a time of year when temperature is low, absorption taking place by means of adventitious roots it was thought therefore that information regarding absorption in these plants might be of interest. Experiments were therefore undertaken to determine:-

- (a) Absorption at different stages of development during the growing season.
- (b) Amount of water absorbed during growth.
- (c) The relation between absorption and transpiration.

#### Methods.

Plants were grown in U-tubes of the type shown in Fig. 3. A snowdrop bulb was supported in the wide arm by means of sheet bees-wax so that the base of the bulb was in water, the wax was melted to make an air-tight seal. The tubes were filled with water or with Knop's culture solution up to the level marks on the arms and the narrow arm was plugged with cotton wool preventing

evaporation. The U-tubes were fitted into boxes packed with cotton wool to protect the roots from light and sudden changes in temperature. At intervals, when required the U-tubes were filled up to the marks from a burette; a temporary small hole being made by a needle in the bees-wax so that the water was at atmospheric pressure in both arms of the U-tube. The water was aerated each week by blowing in air with a pipette. The plants were kept in an unheated greenhouse, but when transpiration was measured they were brought up into a laboratory where the temperature ranged from 16 - 19°C. A record of the maximum and minimum daily temperatures and midday wet and dry bulb thermometer readings in the greenhouse was kept for reference.

A control experiment set up with dead instead of living bulbs showed that little evaporation took place from the tubes, not more than 0.5c.c. in five months. The error on filling up the U-tubes from the burette was found to be  $\pm$  0.5 c.c.

Transpiration was measured by weighing the plants in the U-tubes.

To trace the course taken by the water absorbed some experiments were made with dyes. Plants grown in water were transferred to dilute solutions of dyes and after an interval hard-sections were cut and examined rapidly in water or liquid paraffin. A number of dyes were tried



including methylene green, methylene blue, fuchsin and eosine; last named was the only dye taken in to any appreciable extent, but it was unsatisfactory as it had an obviously toxic effect on the plants, the tissues shriveling wherever the dye accumulated.

The Absorption at Intervals during the Season.

Eight plants of Galanthus nivalis were used; their growth was rather poor compared with plants growing in soil but they flowered at about the same time as plants in a garden. The mean values obtained for these plants <sup>are</sup> is shown in Table III and figures for individual plants are given in Appendix 3.

Table III.

Average Absorption of water at intervals during the Season  
by Galanthus nivalis.  
(8 plants)

Dates (1934)	No. of Days	c.c. absorbed between dates (measured)	c.c. absorbed per day (calculated)
29 Nov. - 9 Feb.	72	3.56 - .05	0.050
9 Feb. - 1 Mar.	20	1.10	0.055
1 Mar. - 13 Mar.	12	2.04	0.17
13 Mar. - 27 Mar.	14	0.17	0.30

It appears that absorption is higher in the latter part of the season than it is at the beginning. This may be attributed to:-

- (a) a higher temperature towards the end of the season
- (b) a better developed root system
- (c) increase in transpiration due to the greater development of the leaf surface and to external conditions

Observations on the intake of dyes by plants of different ages confirmed the fact that absorption increases with the age of the plants. Young plants of Galanthus nivalis in which the foliage leaves were still enclosed in the sheath (early January) were examined after their roots had been in dilute eosine for 14 days. It was found that the dye had not penetrated beyond the base of the bulb and very little dye had accumulated in the plants. A month later when the leaves had broken through their sheath and were partly expanded the dye entered more rapidly and in four days dye was seen in the leaves 2 cm. above the base. At the flowering stage (early March) penetration was still more rapid and the dye accumulated considerably in the leaves, resulting in their withering three days after the plants were first placed in the dye. Similar results were obtained in Galanthus Elwesi.

Total Absorption during the Season.

The volume of water absorbed between 20th November 1933 and 20th April 1934 by twenty four plants of Galanthus nivalis was measured and the data is given in Appendix 4 and represented graphically in Fig. 3, covering a growing period from autumn to summer resting stages. The plants flowered at about the same time as those growing in a garden and produced healthy leaves but their root systems were poorly developed. The individual plants studied varied considerably in their water requirements and some of the values are surprisingly low. Since the plants were growing in water under unnatural conditions the data obtained are of limited application, but they are of interest as they show that a bulbous plant such as Galanthus nivalis can if necessary expand its leaves and flower with very little water, one plant absorbed only 4 c.c. in five months.

An attempt was made to determine the relative water requirements of plants of Galanthus nivalis, i.e. the amount of water given out per unit of dry matter formed, a conception introduced by Briggs and Shantz (2). Before planting bulbs were weighed and the dry weight of each calculated (see page 8). At the end of the season the dry weight of each plant was found, including dead leaves, flowers etc. which were collected as they were shed. It was found that the final dry weight of the plants was less than the original

Autumn dry weight so that in these circumstances the relative water requirement cannot be calculated. The data obtained are given in Appendix 4.

The plants were grown in the U-tubes in water and doubtless loss in weight during the growing season may be attributed to this unnatural condition. The expansion of the shoot possibly took place at the expense of the food reserve stored in the bulb and the plant was unable to replace this amount during the season.

It was thought that observations on the amount of food reserve and its distribution in the bulb at different stages might be of interest and some observations were made on this subject and are given in Section VII.

#### Absorption and Transpiration.

It has been shown that in Galanthus nivalis the water content increases with age, suggesting that absorption is greater than transpiration. Attempts were made to determine this experimentally but as the actual amounts of water involved were unexpectedly small the experimental error is relatively large and in some cases rises to 1.5%. Estimations of absorption and transpiration were made over periods of about three days and the following data obtained.

Table IV.Absorption and Transpiration in Galanthus nivalis.

Date		Absorption ±0.5 c.c.	Transpiration ± .001grm
Mar. 22 - 24	Plant A	3.5	2.5
	" B	1.5	2.0
	" C	0.9	1.4
	Mean of A,B,C.	2.0	2.0
May. 3 - 7	Plant D	7.5	6.9
	" E	6.8	7.1
	" F	5.0	5.1
	Mean of D,E,F.	6.5	6.4

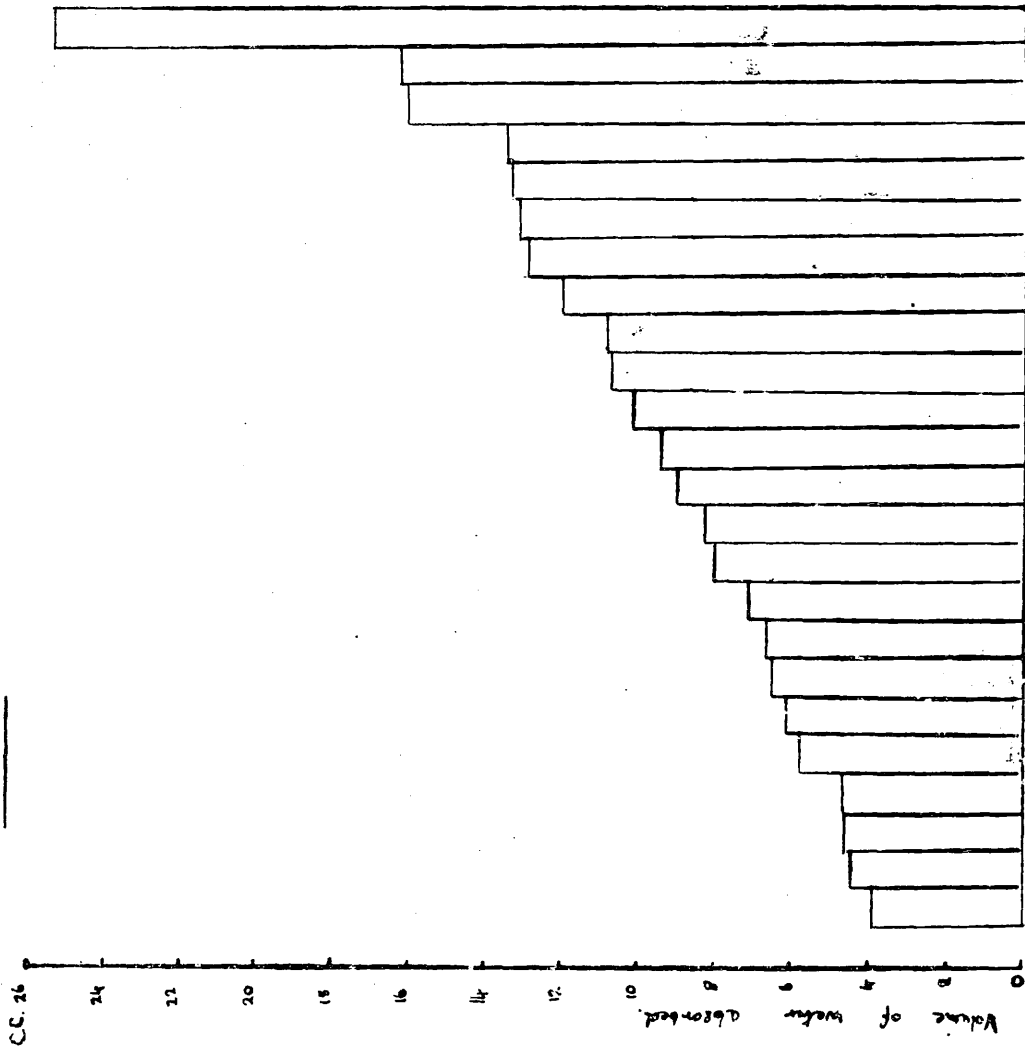
In Table V similar data is given for Galanthus Elwesi.

Table V.Absorption and Transpiration in Galanthus Elwesi.

Date		Absorption ± .05 c.c.	Transpiration ± .001grm
Feb. 25 - 26	Plant A	0.5	0.34
	" B	0.5	0.34
	Mean of A,B.	0.5	0.34
Mar. 8 - 12	Plant C	2.0	1.9

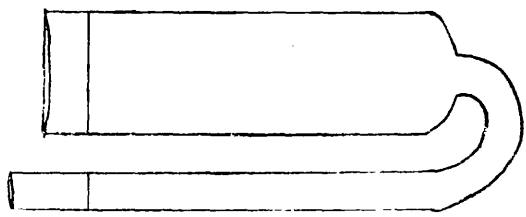
From the data given in Table IV and V it appears that absorption and transpiration are about equal in Galanthus nivalis and in Galanthus Elwesi is slightly greater, but in view of the large experimental error no great importance can be attached to these figures. Calculations show that even when the water content of the plants of Galanthus nivalis is increasing most rapidly ( c f Table II ) the increased water content of an individual plant could be brought about if absorption were only .015 c.c. greater than transpiration per day.

Fig 4 Gadus nas nivalis. Total volume of water absorbed during the growing season (2<sup>nd</sup> November - 20<sup>th</sup> April 1984) by plants grown in water.



Each rectangle represents the total volume of water absorbed by one plant between 2<sup>nd</sup> November and 20<sup>th</sup> April.

Fig 3 Type of U-tube used for measuring absorption.



SECTION IV.TRANSPIRATION.Methods.

Transpiration was measured by determining (a) the loss of weight of the plant or (b) by means of cobalt chloride paper.

(a) By Weighing.

A wax-seal method such as that described by Briggs and Shantz (2) was used. In October snow-drop bulbs were planted separately in garden soil in glass specimen tubes ( $1\frac{1}{2}$  by  $3\frac{1}{2}$  inches), a layer of charcoal at the bottom providing drainage. The tubes were kept in a cold greenhouse and watered when necessary. The plants grew healthily and flowered at about the same time as plants growing in a garden. The day before an experiment was to be made the flower was cut off at the base of its stalk and the cut end waxed, the sheath was also waxed; a layer of silver sand was put on the surface of the soil and over this was poured just molten paraffin wax (melting point  $36^{\circ}\text{C}$ ) and the tube gently rocked to give a good seal. This wax was found to be hard enough at the temperatures of these experiments and did not injure the young shoots. The total



weight of the plant in its pot was about 100 grammes. The plants were weighed on a balance correct to 2 milligrammes this represents an error of not more than .5% of the total loss due to transpiration in all but the two first experiments of 1935; in the experiment of 1-5th January 1935 where the total transpiration may be less than 20 milligrammes per day the error rises to 5%. In the next experiment the error is not more than 2%.

(b) By cobalt-chloride paper.

Stahl's method as elaborated by Livingston and Shreve (II) was used. A Livingstone clip was used to press the paper to the leaf surface. All readings were taken on growing plants in a garden between the hours of Noon and 2 p.m. They were taken always in the same part of the leaf, namely near the median line at approximately 5 centimetres below the leaf tip. At least two readings and generally more have been made in each case and both surfaces of the leaves considered. The results are given in tables in the form of - time required for the cobalt chloride paper to change from the initial to the final standard colours.

The area of the leaves was obtained as follows:-

The leaves were not detached from the plant, they were held between sheets of glass in front of a bright light and the area traced with a pencil on the graph paper (c f Appendix II). The drawing was cut out and weighed or else the area

estimated by means of counting the squares on the paper, both methods gave close agreement. Since the leaves of Galanthus have a simple linear shape it was possible to check the areas by measuring the length and average breadth of the leaf. Allowance was made for changing area due to growth during an experiment, in some cases this was as much as two square centimetres per day; the average width of the leaf at the base where elongation takes place and the increase in length of the shoot were measured each day and allowance made accordingly.

#### Evaporation.

A measure of the evaporating power of the air was obtained by recording the loss from a free water surface weighed at the same intervals as the plants. Four circular basins were used (two of diameter 55 millimetres and two 44 millimetres) these were distributed among the plants. The identical four basins were used in all the experiments so that the total water surface was the same throughout; they were filled to the same level each morning (i.e. approximately 5 millimetres from the brim) Thomas and Ferguson (18) have pointed out that evaporation from a circular free water surface is not necessarily proportional to the square of the radius and emphasise the importance of taking into account the depth of the water surface from the brim. In these experiments

the height of the water level was kept fairly constant, the changing level due to evaporation being not more than 2 millimetres per day. It was thought that by these methods a standard for comparing the evaporation power of the air on different days might be obtained; the losses have not been reduced to unit area. Details of the way in which the data has been treated to calculate the evaporating power of air ("Evaporation") are given in the appendix. ( $p \times v$ )

Records of temperature and humidity were kept for reference, by means of self recording apparatus.

The experiments were conducted as far as possible under similar conditions in an artificially heated laboratory (temperature 16 - 21°C), by an east window where there was no direct sunlight and the air was still.

Plants were watered just before an experiment and if necessary during an experiment.

#### Presentation of Results.

The experimental results are presented as (a) Transpiration per unit area of leaf surface, (b) the "relative transpiration ratio".

As a rule these are presented graphically and the figures from which they have been calculated are given in Tables of the Appendix. The method of calculation requires some further explanation.

(a) Transpiration per unit area.

This represents loss in weight in milligrams per square centimetre of leaf surface per day. It is usual to use the hour as the unit of time but in the present series of experiments the rate of transpiration is very small and it was thought that a day would be a more suitable time unit. All results have therefore been calculated taking 24 hours as the unit of time. When an experiment has been extended over more than one day the average daily rate of transpiration during the experiment has usually been calculated.

(b) The Relative Transpiration Ratio.

In 1906 Livingstone defined "Relative Transpiration" as the amount of water lost per hour from one square centimetre of plant surface divided by the amount lost per hour from one square centimetre of water surface under similar atmospheric conditions. He considered that the effect of the atmosphere is eliminated and "relative transpiration" may therefore be used to express the intrinsic transpiring power of the plant.

This concept has been criticised by Knight (10<sup>6</sup>) and others on the grounds that transpiration and evaporation are not equally affected by changes in external conditions and unreliable results are obtained particularly when there is considerably <sup>moist</sup> increment of the air but no more satisfactory way of comparing transpiration on different days has been devised.

It has been previously explained that a measure of the evaporating power of the air was obtained by measuring the water loss from a free water surface but this loss was not reduced to unit area and that the unit chosen in measuring transpiration was one day. The ratio of "transpiration per unit area" to "evaporation" has been calculated in the present work, this differs from Livingstone's ratio but is proportional to it. Skene (18) suggests that the value obtained by dividing transpiration from any constant area by evaporation from any constant area may be referred to as the "relative transpiration ratio" and this term has been adopted in the present work. No exact quantitative significance is attached to the individual values but it was thought that in a laboratory where the air was still and temperature and light were not subject to sudden changes, the values obtained would give information making it possible to compare the transpiration of plants at different periods of their growth.

(a) Transpiration of different individuals at intervals during the season.

Transpiration was measured by weighing.

Galanthus nivalis.

In 1934 the "daily march of transpiration" was determined for three periods, 21st - 23rd March, 3rd - 5th May, 24th - 25th May. In each experiment three plants

potted separately were used and the evaporation from the free water surface was estimated. The average results of each group of plants are recorded graphically in Figure 5 and these suggest that:-

- (1) The relative transpiration ratio increases during the season.
- (2) The relative transpiration ratio appears to be higher during the day than it is during the hours of darkness.

In 1935 another series of six experiments was carried out during the growing season. Five or more plants were used in each experiment and the plants were weighed twice daily. At the end of each experiment the plants were killed in order to estimate the area of their conducting system.

The results obtained are given in Appendix 5 and 7 and represented graphically in Figures 7 and 8.

In Figure 7 the "relative transpiration ratio" of one plant over a given period is represented as a plain rectangle. The mean value obtained for plants of the same age is also shown (shaded) in spite of the variation in individual plants. of the same age it may be deduced that the "relative transpiration ratio" increases through the season, that is with the age of the plants.

Since 1934 it was found that the "relative transpiration ratio" was higher during the day than at night (c f

figure 5) the observed increase in the ratio with age might be attributed to a longer daily period of daylight during the latter part of the season. The "relative transpiration ratio" was therefore calculated in each experiment for a period of daylight (10.45 a.m. - 4.45 p.m.) and also during the remainder of the twenty-four hours. The average results obtained are shown graphically in figure 8 and the figures given in Appendix 8. A tendency for increase in relative transpiration with the age of the plant is still observed.

It is interesting to note that Figure 8 shows that the "relative transpiration ratio" is not always lower at night than during the day. No adequate explanation of this fact can be offered.

#### Galanthus Elwesi.

The transpiration of plants to Galanthus Elwesi was measured under the same conditions and at the same time as plants of Galanthus nivalis. The results obtained are given in Appendix and Figure 6 and 9. It will be seen that in this series also, the relative transpiration ratio tends to increase slightly through the season. As these plants died down rather early it was not possible to continue the experiments after 9th March.

Comparison of Figures 7 and 9 shows that relative transpiration ratio is lower in Galanthus Elwesi than

Galanthus nivalis under the same external conditions.

(b) Transpiration of the same individual plants at different times in the season.

Galanthus nivalis.

The transpiration of four selected plants was determined at intervals throughout the season. The experiments were made at the same time as those described on previous pages. The results obtained are given in the Appendix. In figure 10 is shown graphically the change in the relative transpiration ratio for each plant at different ages, the average daily rate of transpiration over a period of three days being given; the average of the four plants is also given.

From a consideration of the data it may be deduced that:-

(1) The relative transpiration ratio increases more or less steadily as the plant ages but is exceptionally high 21st - 25th February; the reason for this is not known.

(2) The intensity of transpiration varies in the different plants and this difference may be as much as 100% for two plants under the same conditions.

(3) A plant which has the lowest (or highest) intensity at one period does not necessarily have the lowest (or highest) at another period.



In the last experiment (3rd - 5th April) the variation between the plants is very marked two of them showing a much higher intensity of transpiration than the other two; this difference may be due to the fact that the plants were beginning to show signs of withering, the tips of the leaves were yellow and the abscission layer along which the green part of the leaf separates from its smaller storage basal region was already recognisable; the two plants with the lower intensity of transpiration showed more definite signs of withering than the others. Sections of the abscission layer showed that at this period the vascular supply was not interfered with. Owing to the fact that these four plants had been exposed to higher temperatures during previous experiments than other plants used for transpiration experiments mentioned they were rather more mature; the latter plants showed no signs of withering by 5th April and the abscission layer was not clearly defined.

Galanthus Elwesi.

The transpiration of two plants was measured at different ages: the results obtained are presented in Appendix and Figure 11 and these show that in this series also,

- (1) Relative transpiration tends to increase with age

but in the last experiment it was found to be lower than previously, this may be due to the fact that the leaves were already showing signs of withering at this time.

(2) The relative transpiration of the two individual plants used was not equal under the same external conditions.

(c) The Transpiration of the Plants planted on December 21st compared with those planted on October 21st.

The planting of some bulbs was delayed by two months. These did not all grow well but some plants of Galanthus nivalis developed healthily though they were naturally backward compared with those planted earlier and flowered three to four weeks later. The transpiration of these plants was measured under the same conditions as that of the October plants by means of weighing and by cobalt chloride paper.

Galanthus Nivalis.

From March 7th to 9th two of these younger plants were weighed along with five of the older plants, and their transpiration estimated. The figures are given in Appendix 5e. The average values obtained for transpiration per unit area and the relative transpiration ratio are shown in Figure 12. It will be seen that there is considerable variation in plants of the same age but it may be deduced

that the intensity of transpiration is lower in the younger plants, confirming the fact that an increase in the relative transpiration ratio takes place as the plants grow older.

Similar results were obtained from these plants by the cobalt chloride method; these are given in table VI.

Table VI.

Transpiration of plants planted in October and December  
under the same conditions.

	planted October	planted December
19th March	3 mins. 5 secs.	3 mins. 10 secs.
Temperature 17°C	1 " 50 "	2 " 25 "
	0 " 53 "	1 " 40 "
20th March	0 " 46 "	1 " 37 "
Temperature 18°C	0 " 43 "	0 " 57 "
	0 " 42 "	0 " 54 "
21st March	0 " 35 "	0 " 45 "
Temperature 23°C	0 " 28 "	0 " 45 "
	0 " 22 "	0 " 37 "
Mean of both surfaces given.		

Galanthus Elwesi

No data is available for this species as the bulbs

planted late did not develop well.

The data obtained from these retarded plants is therefore of interest as it confirms the fact that an increase in transpiration takes place with age.

(d) A comparison of the Intensity of Transpiration on the adaxial and abaxial leaf surfaces in Galanthus nivalis, Galanthus Elwesi and Narcissus.

Measurements were made by means of cobalt chloride paper on the same leaf of these species to determine the rates of transpiration on the two surfaces.

Galanthus nivalis.

Results obtained are given in Table VII. The average of two or more readings for the two surfaces in a number of different leaves are given:-

Table VII.

Galanthus nivalis.

Comparison of Transpiration from adaxial and abaxial surface of the leaf.

Date of Expt.	Upper Surface	Lower Surface
18th March, 1935 (Temp. = $16\frac{1}{2}^{\circ}\text{C}$ ) Average	4mins 36secs 2 " 0 " 3 18	1min 5secs 1 " 45 " 1 25
19th March (Temp. = $17^{\circ}\text{C}$ ) Average	5 " 0 " 3 " 40 " 3 " 0 " 2 " 45 " 2 " 20 " 2 " 10 " 1 " 45 " 1 " 30 " 2 46	1 " 20 " 2 " 30 " 1 " 30 " 1 " 20 " 1 " 33 " 1 " 10 " 1 " 10 " 2 " 0 " 1 22
20th March (Temp. = $18^{\circ}\text{C}$ ) Average	2 " 52 " 1 " 6 " 1 " 0 " 0 " 56 " 0 " 52 " 0 " 50 " 1 16	0 " 20 " 0 " 25 " 0 " 35 " 0 " 38 " 0 " 40 " 0 " 20 " 0 30
21st March (Temp. = $23^{\circ}\text{C}$ ) Average	1 " 17 " 0 " 40 " 0 " 42 " 1 33	0 " 17 " 0 " 20 " 0 " 17 " 0 18
4th May (Temp. = $24^{\circ}\text{C}$ ) Average	0 " 50 " 0 " 25 " 0 " 20 " 0 " 19 " 0 28 $\frac{1}{2}$	0 " 22 " 0 " 12 " 0 " 15 " 0 " 16 " 0 16
5th May (Temp. = $24^{\circ}\text{C}$ ) Average	0 " 19 " 0 " 15 " 0 17	0 " 16 " 0 " 12 " 0 14
Readings opposite each other to the two surfaces of the same leaf. Readings below each other all refer to different leaves.		

These results indicate that the intensity of transpiration is definitely higher on the lower surface than it is on the upper surface. Wicks (20a) has shown that in the greater portion of the leaf limb the number of stomata per unit area on the lower surface is about twice as great as it is in the corresponding portion of the upper surface and the higher rate of transpiration is probably an outcome of this fact.

Galanthus Elwesi.

Results obtained are given in Table VIII.

TABLE VIII.

Galanthus Elwesi.

Comparison of Transpiration from Upper and Lower leaf Surfaces.

Date.	Upper Surface.	Lower Surface.
4th May	0 mins. 23 secs.	0 mins. 12 secs.
Temperature 24°C	0 " 17 "	0 " 20 "
	0 " 14 "	0 " 24 "
	0 " 10 "	0 " 15 "
	0 " 8 "	0 " 10 "
Average	14 Secs.	16 Secs.
5th May	0 " 25 "	0 " 20 "
Temperature 24°C	0 " 24 "	0 " 35 "
	0 " 17 "	0 " 22 "
Average	22 Secs.	46 Secs.
Readings opposite each other refer to the two surfaces of the same leaf.		
Readings below each other refer to the different leaves.		

This data suggests that intensity of transpiration is slightly greater on the upper surface in Galanthus Elwesi. The stomatal frequency has not been worked out in detail but examinations of a number of strips of the upper and lower epidermis showed that the number of stomata per unit area is slightly greater on the upper surface than on the lower surface in Galanthus Elwesi in contrast to Galanthus nivalis in which the lower surface has the greater number of stomata per unit area ( c. f. Table IX).

TABLE IX.

Species	Number of stomata per unit area of leaf surface	
	Adaxial Surface	Abaxial Surface
<u>Galanthus nivalis</u>	0.29	0.62
<u>Galanthus Elwesi</u>	0.47	0.42

Narcissus poeticus.

Data obtained is given in Table. X

TABLE X.

Narcissus poeticus.

Comparison of Transpiration in adaxial and abaxial  
surfaces of the leaf.

Date	Upper Surface	Lower Surface
March 19th	0 mins. 55 secs.	1 min. 10 secs.
Temperature -17°C	0 " 55 "	0 " 55 "
Average		
March 20th	0 " 24 "	0 " 25 "
Temperature -18°C	0 " 20 "	0 " 20 "
Average		
March 21st	0 " 33 "	0 " 36 "
Temperature -23°C	0 " 33 "	0 " 35 "
	0 " 25 "	0 " 25 "
	0 " 19 "	0 " 23 "
Average		
May 5th	0 " 15 "	0 " 20 "
Temperature -24°C	0 " 12 "	0 " 20 "
Average		
<p>Readings opposite each other refer to the two surfaces of the same leaf.</p> <p>Readings below each other refer to different leaves.</p>		



Intensity of transpiration on the two surfaces therefore appears to be influenced by the number of stomata per unit area. Wicks (20 a and b) has studied the stomatal distribution in these and other Amargylli-daceous plants and finds that the number of stomata per unit area increases, part from local irregularities, from the base of the leaf to near the apex. This increase is due to a decrease in the size of the epidermal cells. The increase in relative transpiration observed in leaves of Galanthus, with increasing age cannot, therefore, be attributed to an increase in the number of stomata per unit area of leaf surface.

In Narcissus the intensity of transpiration on the two surfaces appears to be about equal. Wicks (20a) has shown that the stomatal frequency is very nearly equal on the two surfaces of the leaf.

Leaves were cut from a plant under water and thrust through a slit in the cork of a specimen tube filled with water and the cork was sealed with wax. The tubes were weighed at intervals.

(e) The Transpiration of cut Leaves of Galanthus nivalis.

The transpiration of the cut leaves in water was compared with that of leaves still attached to a rooted plant, under the same conditions. The results obtained

are shown graphically in Figure 13. They show again considerable variation of the individuals and irregular transpiration but indicate that the transpiration per unit area of the cut leaves is on the whole rather lower than that of the attached leaves.

(f) Condition of Stomata.

Attempts were made to determine the degree of opening of the stomata in plants of Galanthus nivalis and Galanthus Elwesi during the course of an experiment. The methods employed were those recommended by Lloyd (\*11). Small pieces of epidermis were rapidly stripped from a leaf, fixed in Absolute Alcohol, cleaned and mounted. The width of the stomatal aperture was measured by means of a micrometer eye piece. A great range in size was found to occur in the apertures of any one strip; this might be due to a number of causes:-

- (1) Actual variation in the size of the stomatal apertures in the living leaf.
- (2) Poor stripping and fixation. Strips were fixed at a large number of different times, using fresh alcohol each time and one might have expected that at least one strip would be properly fixed and yield uniform results; this was not the case.
- (3) Unsuitability of the method. Recently Madel (13) and

Oppenheimer (14) have criticised the method and shown that it is unsuitable for use with certain plants, yielding unreliable results. They do not mention monocotyledonous plants such as Galanthus.

(g) Conclusions.

By investigating the transpiration of a number of different plants of Galanthus nivalis and Galanthus Elwesi of different ages it has been established that the "relative transpiration ratio" increases through the season, as the plants age. The transpiration of selected plants has been measured at different stages in their growth and it was again found that an increase in the "relative transpiration ratio" of the plants takes place with increasing age. The results of observations made on the rate of transpiration of retarded plants confirmed the fact that the "relative transpiration ratio" increases with the age of the plants.

Assuming that the "relative transpiration ratio" gives a measure of the intrinsic transpiring power of the plant, the effect of external conditions having been eliminated, one may suggest that the observed increase in this ratio as the plants grow older is due to internal factors affecting the rate of transpiration.

By comparing the rate of transpiration and the number of stomata per unit area on the two surfaces of the leaf in

Galanthus nivalis, Galanthus Elwesi and also Marcissus poetisus it was found that in these plants the intensity of transpiration appears to be affected by the number of stomata per unit area. The observed increase in the relative transpiration ratio might be explained if the number of stomata per unit area increases as the leaf ages. Wicks (20a) has however shown that the contrary is the case: in each successive new piece of leaf interpolated into the leaf limb by intercalary growth there is a decrease in the number of stomata per unit area. Some other factor than stomatal distribution on the leaf surface must therefore be sought to account for increasing intensity of transpiration with increasing age.

Data are given which suggest that the transpiration of cut leaves of Galanthus nivalis in water is slightly lower than that of leaves attached to a growing plant. It is suggested that this may be due to the fact that the large amount of mucilage present in the leaves tends to block the cut ends of the conducting channels, resulting in diminution of transpiration. This suggested explanation emphasises again the close connection between transpiration and the conducting channels supplying in transpiring leaf surface.

Fig. 5 *Galanthus nivalis* - Daily March of Transpiration at Three Different Periods in the Season.

— Average Relative Transpiration of 3 plants weighed separately. 21<sup>st</sup> - 23<sup>rd</sup> March 1924  
 - - - Average Relative Transpiration of 3 plants weighed separately. 8<sup>th</sup> - 9<sup>th</sup> May 1924  
 - - - Average Relative Transpiration of 3 plants weighed separately. 24<sup>th</sup> - 25<sup>th</sup> May 1924

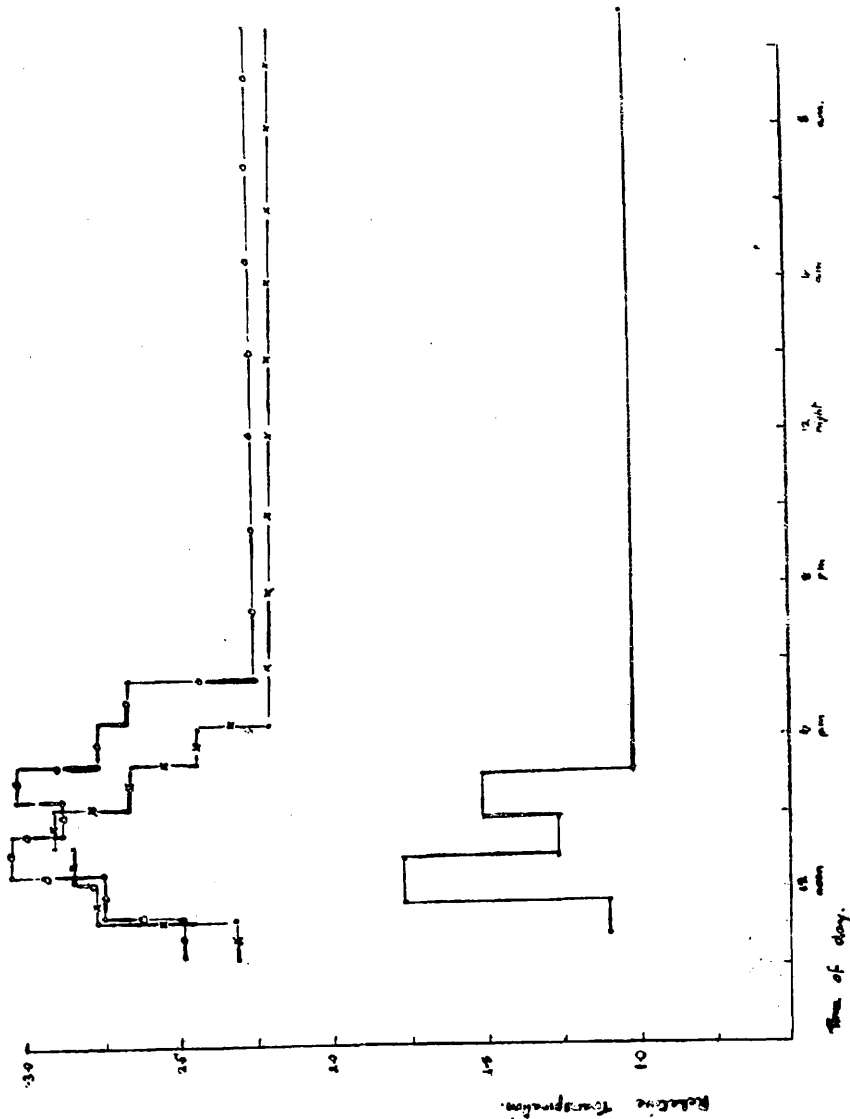


Fig. 6. Concentration Ethylol. Relative Transpiration of Individual Plants

at Different Periods in The Season

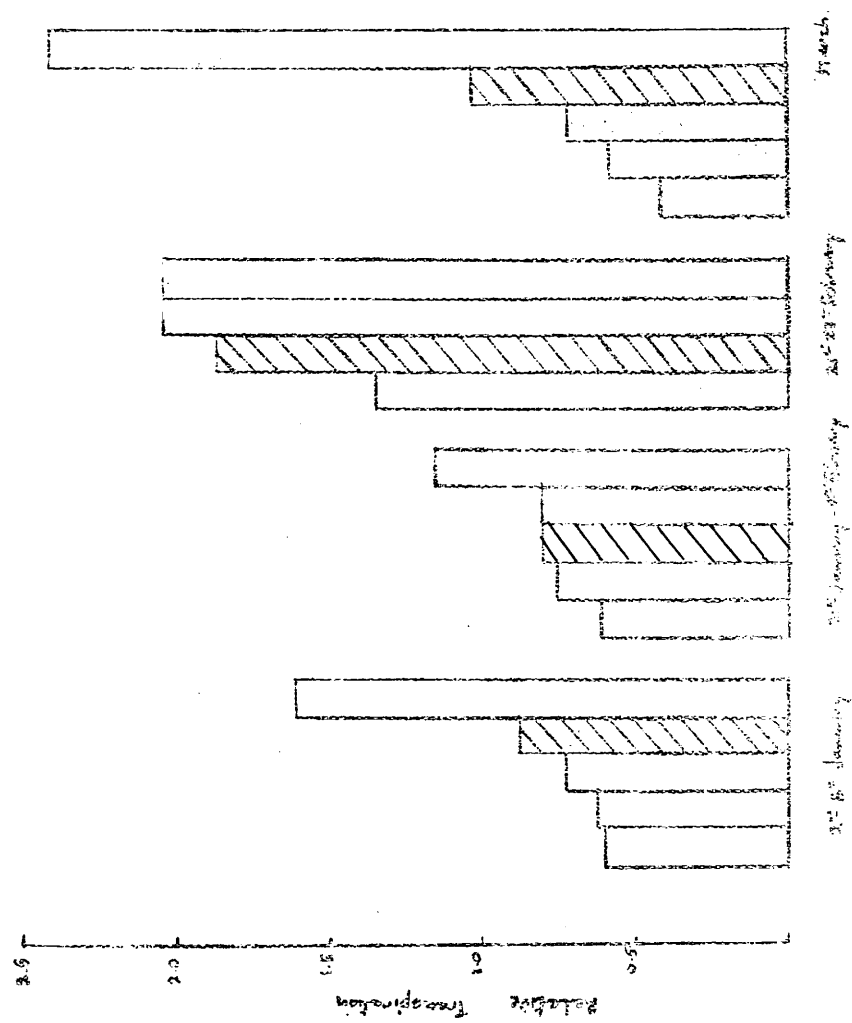
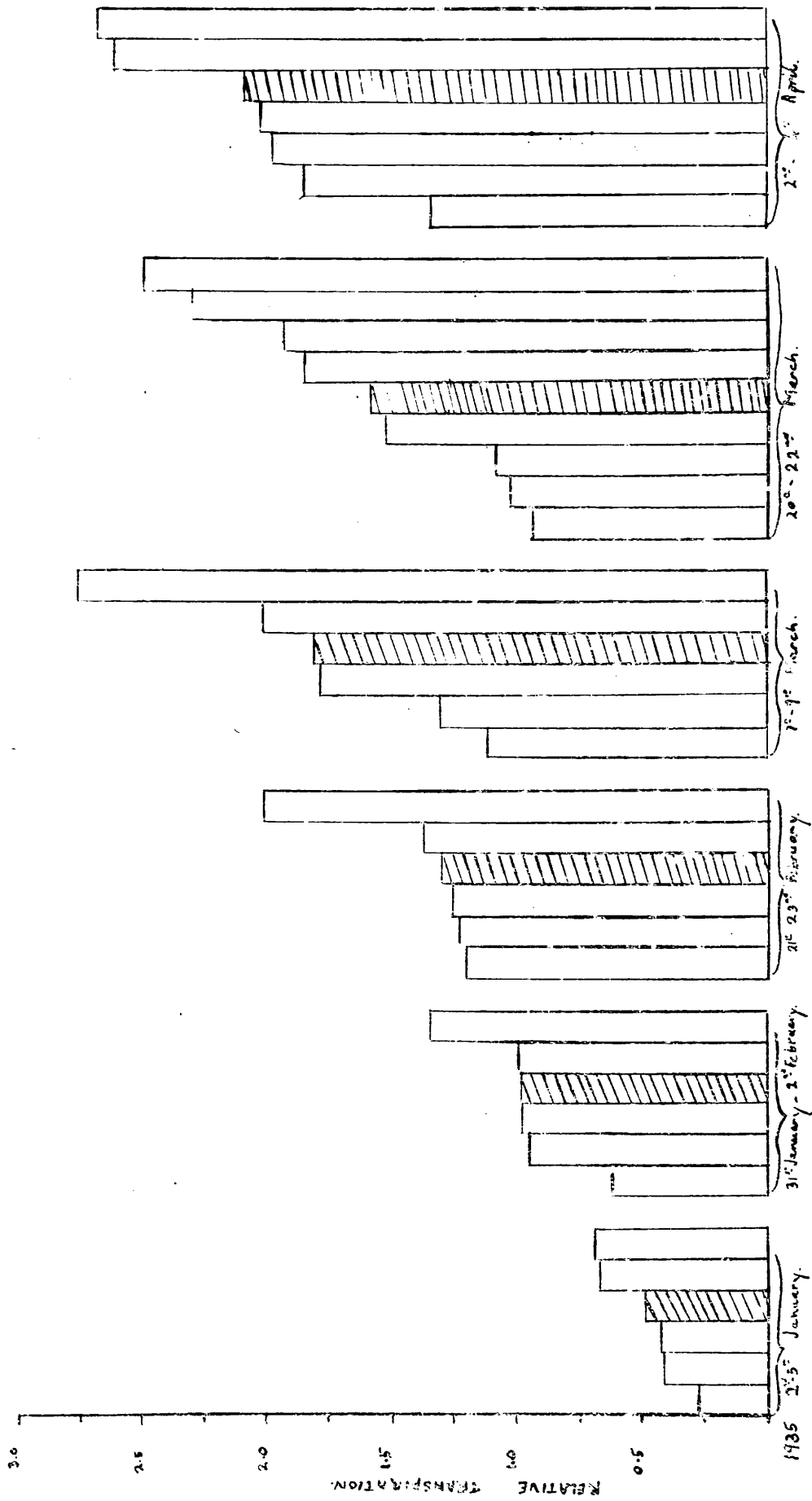


Fig 7. *Galarinus rivealis*. Relative Transpiration of Individual Plants at Different Periods in the Season.



Each rectangle represents the average relative transpiration of one plant at the date given. (Average shaded).

Fig 8. Galenthus niveus. "Relative Transpiration" of Plants of Different Ages, Measured During

Day and Night Periods.

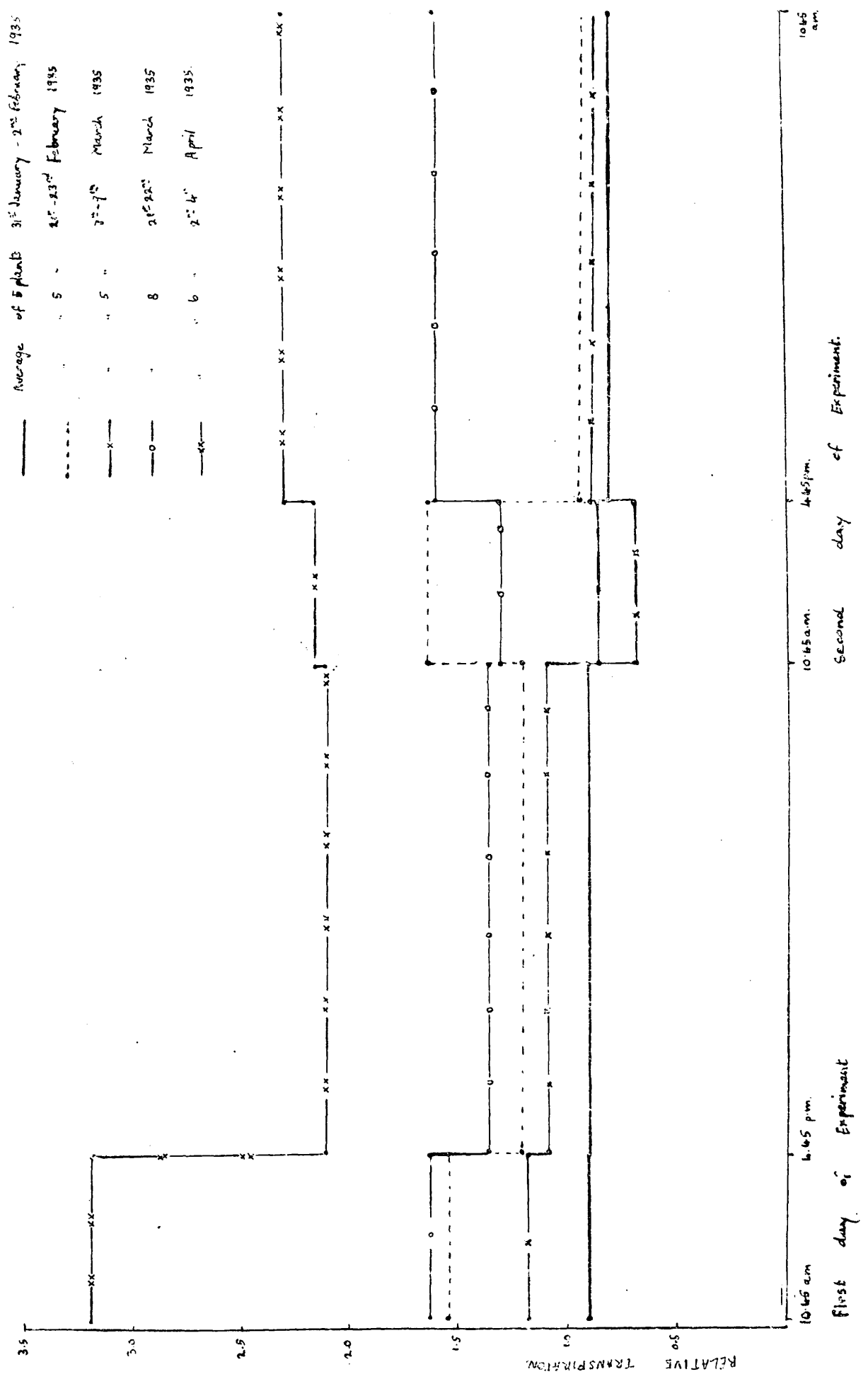




Fig 9. *Galanthus Elwesii*. Average "Relative Transpiration" of Plants of Different Ages Measured During Day and Night Periods.

— Average of Plants 31<sup>st</sup> January - 2<sup>nd</sup> February 1956  
 - - - - - " " 21<sup>st</sup> - 22<sup>nd</sup> February " "  
 ..... " " 7<sup>th</sup> - 9<sup>th</sup> March " "

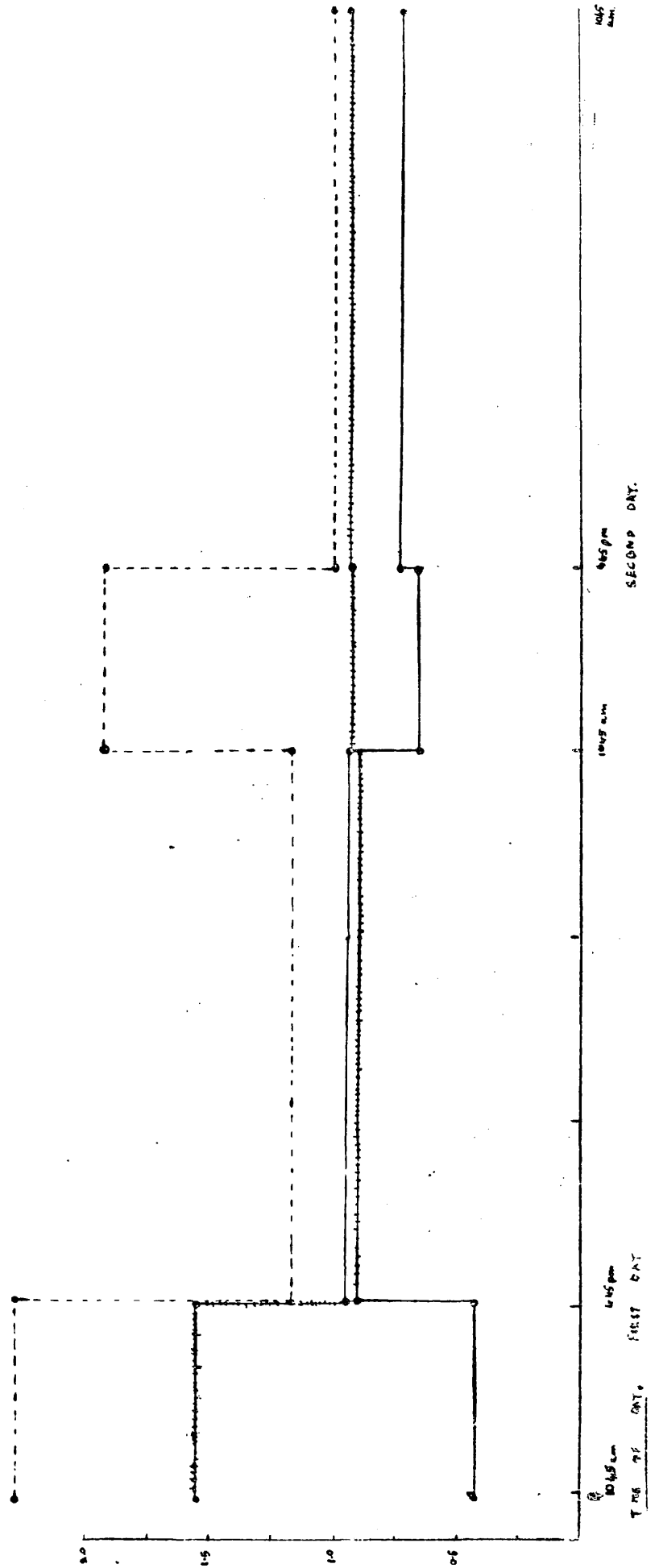


Fig 10

Gaeanthus nivalis

Average 'relative transpiration' of four plants at different periods in the season.

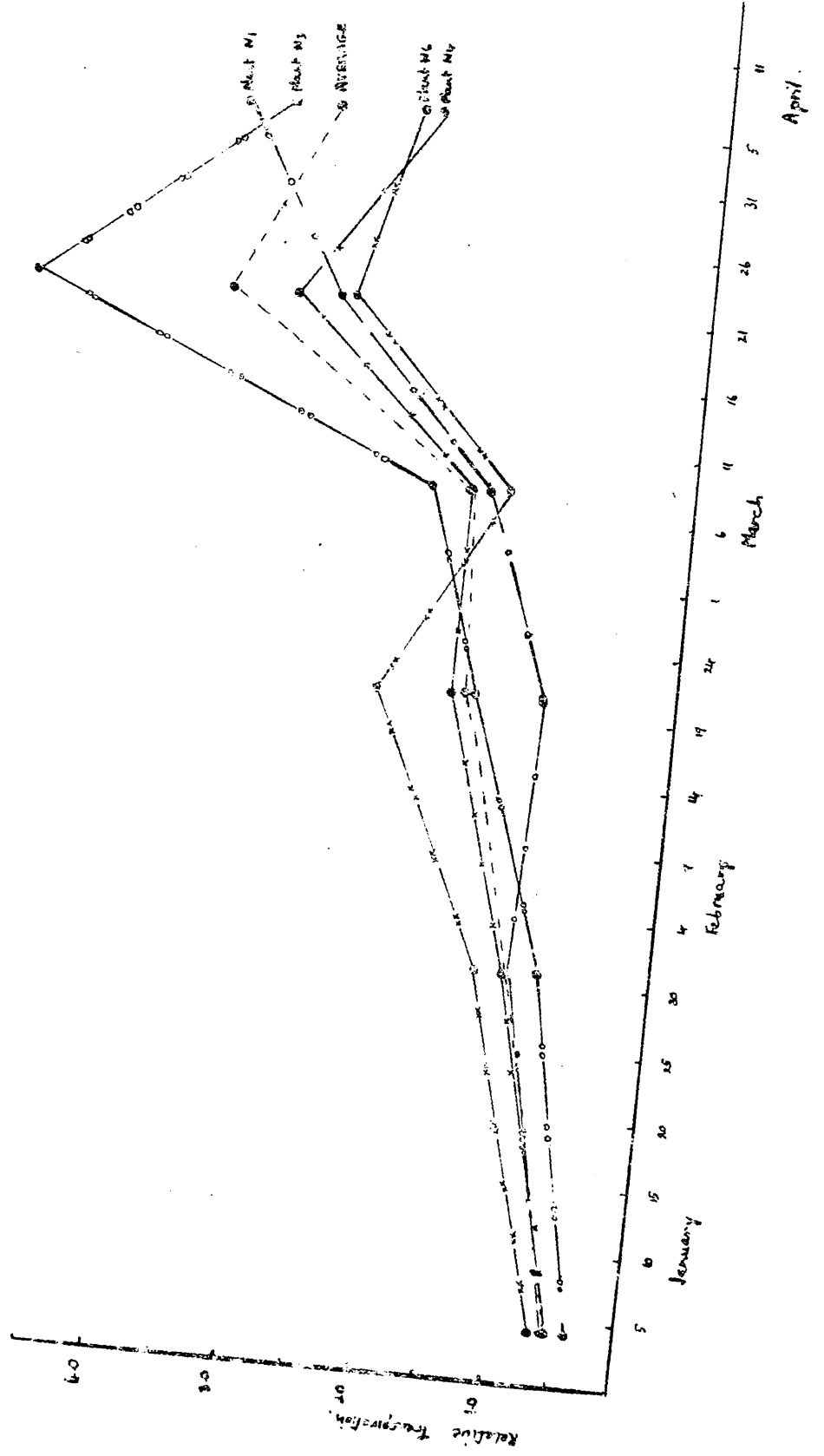
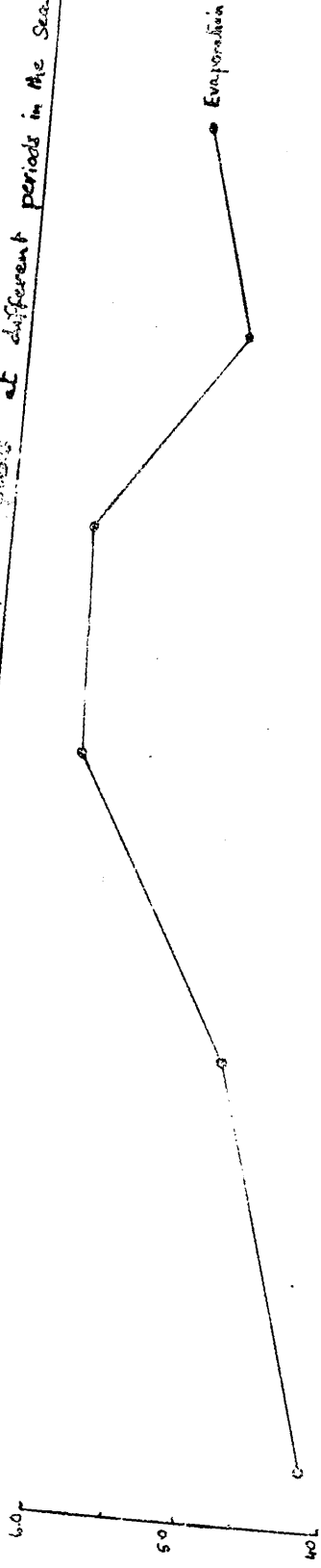


Fig. III. *Culcasia Elmeri*. Average "Relative Transpiration" of Two Plants at Different

Periods in The Season.

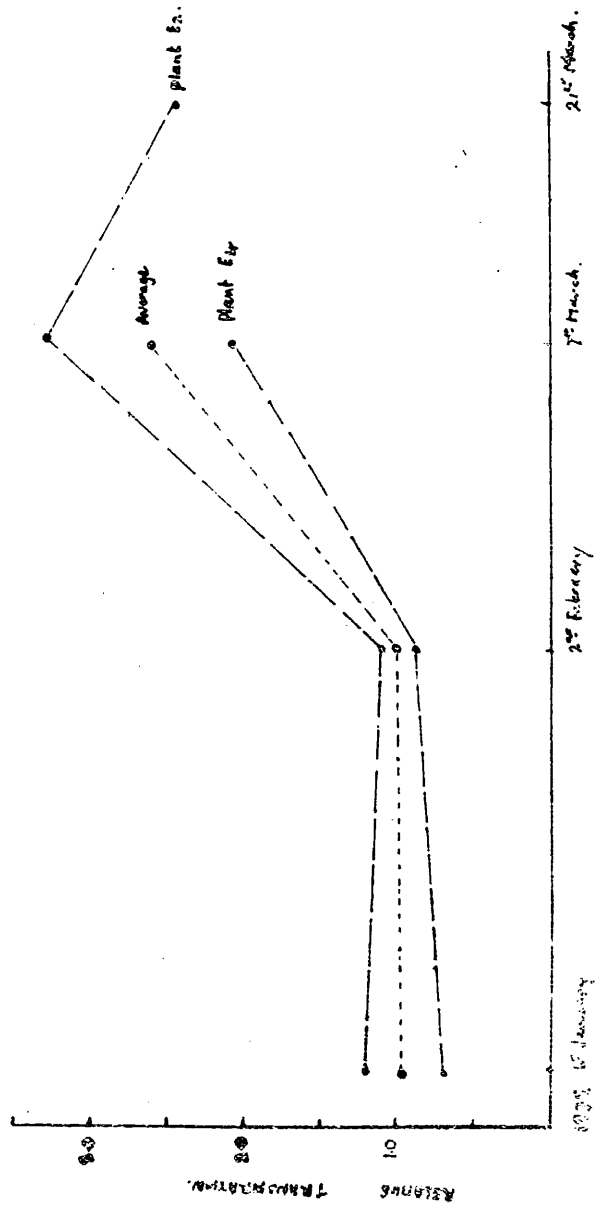
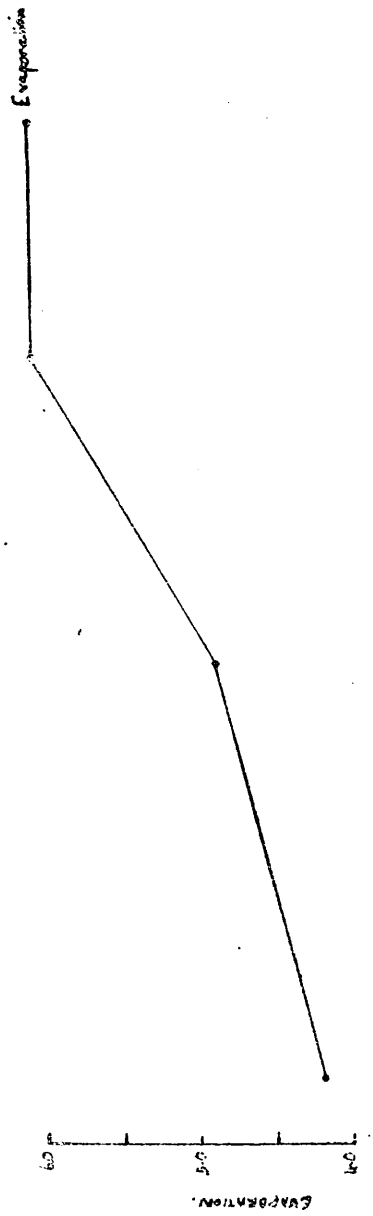


Fig 12. *Galambus nivalis* . Comparison of Intensity of Transpiration in Plants of Two  
Different Ages Under The Same Conditions.

Fig 12(a)

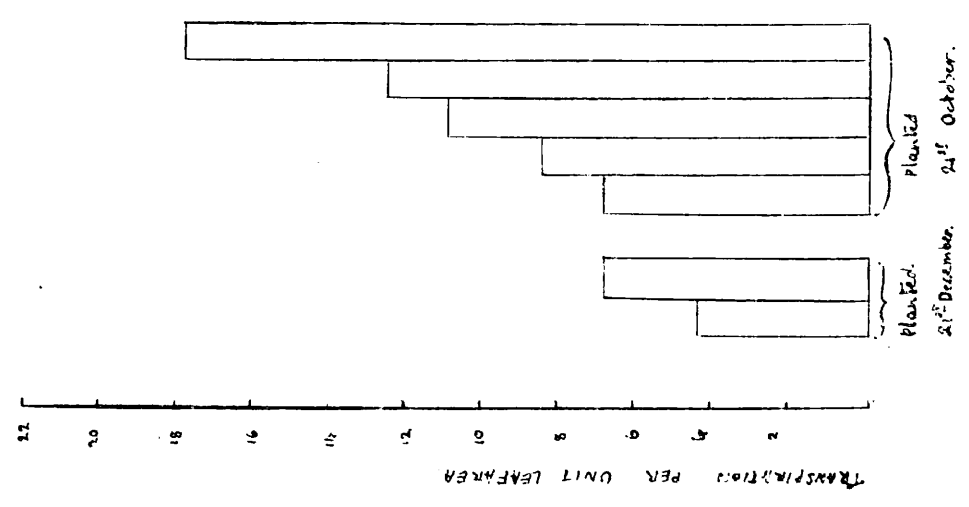


Fig 12(b)

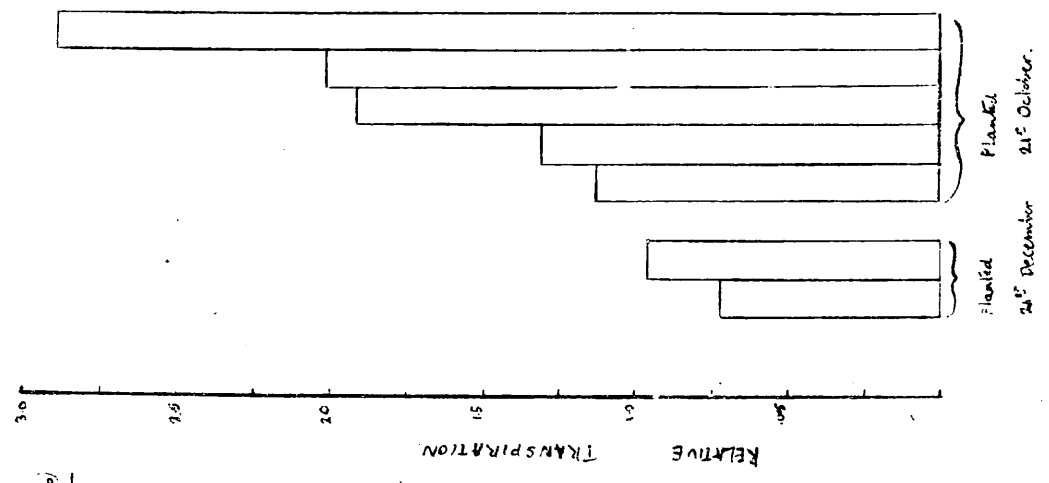
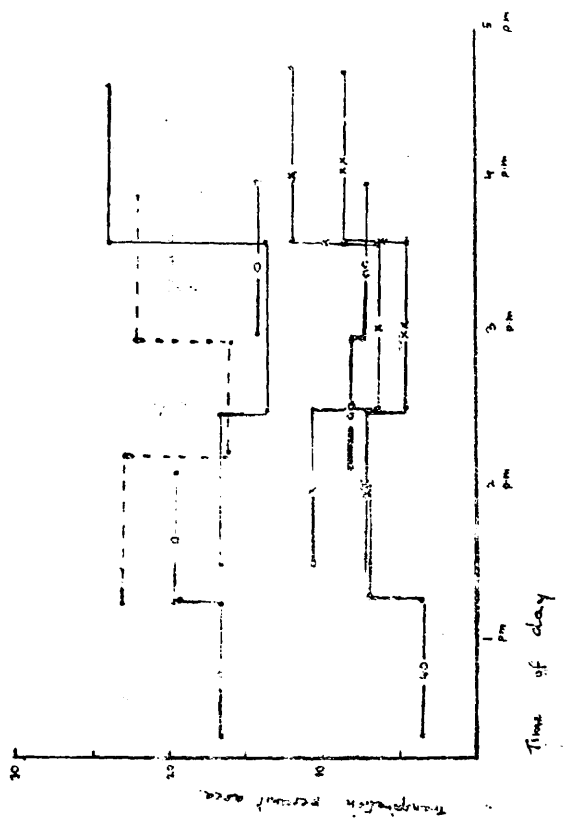
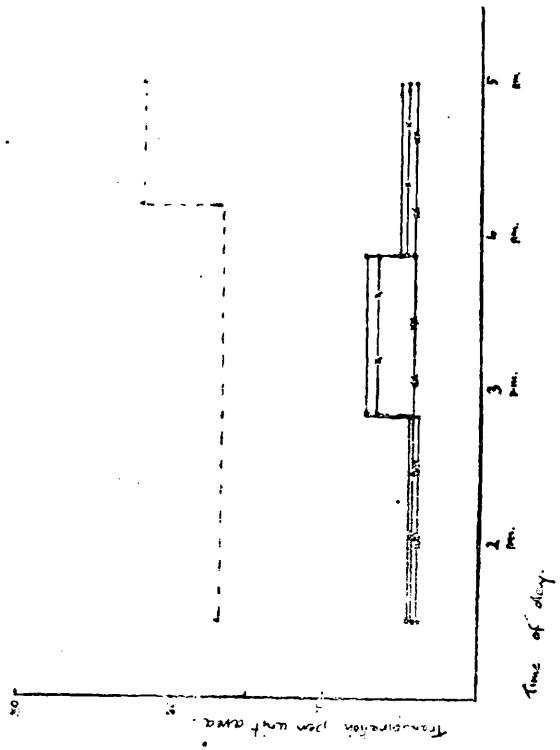


Fig 13. *Galanthus nivalis*. Transpiration per unit area of cut leaves and leaves attached to growing plants compared under the same external condition, at two different dates.

— Transpiration per unit area of 9 cut leaves  
 - - - Transpiration per unit area of attached plant



23 May 1934



24 May 1934

S E C T I O N V.TRANSPIRATION AND THE CONDUCTING SYSTEM IN THE LEAF  
OF GALANTHUS NIVALIS AND OF GALANTHUS ELWESI.

In this section the changes which take place in the conducting tissue in the growing region of the leaf with increasing age are described and the transpiration at different times in the season is considered. Quantitative measurements are given, (for one and the same plant), of the cross-sectional area of the xylem cavities in the growing region and of the intensity of transpiration, for a number of plants of different ages.

A. Methods.(1) Anatomy.

The anatomy of the growing region was studied mainly by means of hand-sections of fresh material and of material fixed in 70% alcohol. Microtome sections were also cut in some cases, particularly in the dormant stages and stained with gentian violet and bismark brown.

(2) The Region of Growth.

The region of growth of the leaf was determined by following the growth of marked leaves. Soil was scraped away from round the bulb of a potted plant, the storage

organs and sheath were slit down at one side so as to expose one of the foliage leaves to its base and this leaf was marked at intervals of 1 mm. with indian ink using a fine camel hair brush, so as not to damage the young leaf. When the ink was dry, silver sand was poured on up to the original soil level to protect the leaf.

(3) Leaf area.

This was measured by means of the methods described on page

(4) Cross-sectional area of the xylem in the growing region.

The cross-sectional area of the xylem in the growing region was estimated for the plants used in the series of transpiration experiments made in 1935.

After the transpiration of the plants had been measured they were dug up, fixed in 70% alcohol, and hand sections of the two foliage leaves were cut in the lower part of the leaf where the growing region was known to be situated (see below). The section showing the least amount of mature xylem elements (i.e., those fully lignified and with no contents) was selected and mounted in safranine glycerine jelly. Some contraction probably occurs during this treatment. A trial was made by measuring the area of the xylem cavities in a section of fresh material and again after treatment with 70% alcohol and with glycerine jelly, and it was found that the amount of contraction was small and appeared to be uniform. This error has therefore

been neglected throughout:

The cavities of the mature xylem elements were drawn with the aid of a camera lucida at a linear magnification of 800 diameters and the drawings cut out and weighed. Trails were carried out to find a suitable paper and a thick graph paper was chosen, which in addition to having a constant area / weight relationship (see appendix 11) enabled a check by counting squares to be made. This method of checking was found useful in the earlier experiments where the area involved was small.

Duplicate sets of drawings were made of the sections and the areas obtained are given in appendix 12. The results obtained indicate that the total error is not more than 1.8%.

B. The Conducting System of the Leaves of Galanthus nivalis and of Galanthus Elwesi.

Wicks (20a) has described in detail the anatomy of the foliage leaf in Narcissus poeticus and Narcissus Elvira. She finds that the leaf may be roughly divided into three regions:-

- (a) the leaf limb
- (b) the growing region
- (c) the sheathing base

The zones are not sharply defined and the growing region passes gradually into the limb above and the base below. In the resting bulb the tissues in the limb and base are already mature and these regions undergo little elongation when the



leaf expands in the following season: the great increase in the size of the leaf during the growing season is due to rapid expansion of the tissues in the growing region and in this part of the leaf the tissues are immature. In the leaf limb and sheathing base little groups of mature tracheids occur in the vascular bundles but as these pass through the growing zone less xylem is found, only one or two protoxylem elements being differentiated as annular or spiral tracheids; these are capable of undergoing considerable stretching as the leaf is elongated. The metaxylem is unlignified and at this stage the young tracheids contain considerable cell contents, later as the leaf ages the metaxylem gradually matures, the contents disappear and the walls thicken so that when the leaf is half grown the extent of lignified tissue in the growing region is much greater than it was in the dormant leaf. By the time the leaf is half grown all the metaxylem in the upper part of the growing region may be lignified and above this level small secondary tracheids appear in the bundles. Wicks notes that the tracheids are always arranged linearly in the growing region while they tend to occur in groups in the sheathing base and limb regions.

Further Wicks distinguishes the same three regions in the leaf of Zephranthes candida and Galanthus nivalis and found that the changes taking place in the vascular bundles as they pass through the growing region are similar to those observed

in Narcissus. The amount of lignified tissues in the growing region increases with age in both these plants. She gives no figures of Galanthus nivalis.

The observations of Wicks in Galanthus nivalis and Galanthus Elwesi, has been confirmed and extended.

Leaves of these plants were marked during January and early February, and it was found that the region of maximum elongation was situated within the bulb near the base of the leaf. This region extended over a length of about 1 centemetres in Galanthus nivalis and 1.5 centemetres to 2 centemetres in Galanthus Elwesi below this it passed into the sheathing base of the leaf, where little or no elongation was observed; above it faded gradually into a mature region where the tissues had ceased to expand. In figure 14 a typical example is shown. On 15th January a leaf of Galanthus nivalis 47 mm. long was marked at intervals of 1 mm. and the increase in length of each interval noted eight days later. No increase took place above 15 mm. from the base, but below this elongation is taking place rapidly, reaching a maximum at about 5 mm. from the base. Lower down the extent of elongation decreases and ceases just above the extreme base of the leaf.

The region of elongation was found to be the same in five other bulbs examined.

The vascular tissue in the three regions of the leaf has been studied in Galanthus nivalis and Galanthus Elwesi. In the median bundle of the dormant leaf small groups of tracheids

were found in the base and limb regions, in the growing region only a few protoxylem elements were differentiated as shown in Figure 28b for Galanthus Elwesi and Figure 30a for Galanthus nivalis; changes taking place in the median bundle of the leaf where it passes through the growing region with increasing age of the leaf are illustrated in Figure 29a - c for Galanthus Elwesi and Figure 30b - d for Galanthus nivalis. In the resting bulb the young metaxylem elements can be distinguished as large thin walled cells with dense contents and nuclei; and these gradually mature during the season so that by the time the plant is in flower all the metaxylem is fully lignified and without any contents. . After flowering small secondary elements are seen in the bundles in the growing region. These may be observed at a much earlier date higher up in the leaf limb; as Wicks noted in Narcissus they are small and hexagonal in cross-section and appear to be formed from a cambium such as Arber (14 p. 40) has described in several monocotyledonous leaves.

The elements formed at different times in the season vary in diameter, at the beginning of the season small protoxylem elements are formed followed by large metaxylem elements and later small secondary tracheids. A variation in length was also found, in table 8 are given data obtained by measuring with a micrometer eye-piece the diameter of elements in cross-sections and the length as seen in macerated material.

Table XI.

Galanthus nivalis and Galanthus Elwesi diameter and length of vascular elements in leaf.

	Galanthus nivalis			Galanthus Elwesi		
	Proto-xylem	Meta-xylem	Secondary Elements	Proto-xylem	Meta-xylem	Secondary Elements
Diam. ( $\mu$ )	7-10	20-40 Averg 30	5-8	10	30-50 Averg 40	10
Length (mm.)	0.7 - 1.14	1.8 - 3.0 Averg 2.8	1.25-1.75	0.8 - 1.1	4.0 - 4.7 Averg 4.4	1.0-1.6

The elements appear to be rather long, for Haberlandt (15 page 82) states that the average length of tracheids rarely exceeds 1mm.

The changes shown in Figs 29 - 32 take place in the median bundle of the leaf but numerous bundles occur in each leaf and in these similar changes take place but the nearer a bundle is to the median line of the leaf the greater is the extent of lignified tissue in it at any time. In the young leaf no lignified elements occur in the side bundles and by the time their protoxylem elements are lignified much of the metaxylem in the median bundles is mature. The individual elements in the side bundles are smaller as well as fewer in number than are the corresponding elements in the central bundles. The degree of development of region of the leaves

of successive ages are shown in Fig. 31 a-d Galanthus Elwesi and Fig. 32 a-d Galanthus nivalis.

Comparison of figures 31 and 32 shows that the xylem matures more rapidly in Galanthus Elwesi than in Galanthus nivalis; this to be expected for although the two species appear above ground at about the same date the former species flowers at least three weeks earlier than the latter. The elements of Galanthus Elwesi tend to be rather larger than those of Galanthus nivalis, (See Table XI)

The individual bundles are connected at intervals by side veins (See Figure 32f). By the time the shoot appears above ground the tracheids in these side veins are fully thickened in the leaf limb but in the growing region they remain unligified until the leaf is almost mature. The lateral veins connect the secondary elements of the bundles (Figure 32f) as they do in other monocotyledonous leaves described by Arber (1).

Wicks found that the immature xylem in Narcissus was unable to conduct watery solutions of eosine, this has been confirmed for Galanthus nivalis and Galanthus Elwesi using the methods described previously. Only fully lignified elements were found stained with eosine, the thin walled metaxylem elements with contents being entirely free from stain. The last formed elements were invariably most densely stained and the protoxylem most lightly stained. It was found that in the

growing region most of the stain travelled up the central bundles to the leaf limb where it travelled along the transverse veins towards the margin of the leaf. Some of the veins towards the side of the leaf were free from stain, although containing mature elements in the growing region, this suggests that even under the warm dry conditions of the experiment the vascular tissue in the growing region was more than sufficient to supply the needs of the transpiring leaf limb.

C. The Area of the Conducting Tissue in growing region of the leaf in *Galanthus nivalis* and in *Galanthus Elwesi*.

From the description given above of the changes taking place in the vascular tissues in the growing region of the leaf as it matures it is evident that the total amount of conducting tissue in this region increases throughout the season (See Figs. 31, 32). In the spring of 1935 the actual cross-sectional area of the lignified xylem elements in the growing region, (for briefness this will be called the "conducting area,") was measured in a number of plants of different ages in the two species of Galanthus. The unit of area selected was one square millimetre.

The plants investigated were those used to determine the transpiration at different stages of growth. The experiments were made at intervals from the time when the foliage leaves first broke through their sheath until just before they withered.

(a) Galanthus nivalis.

Six times during the growth season experiments were carried out each with five or more plants, employing the methods described. The results obtained are given in Appendix 5 and shown graphically.

In Fig. 15 the total cross-sectional area of the xylem elements in the growing region of the two leaves of each individual plant, (conducting area) is represented as a rectangle.

It is seen that:-

- (1) plants of the same age vary considerably in the degree of development of their vascular tissue, particularly in the later part of the season.
- (2) in general the older the plant the greater is the "conducting area". At the beginning of January when the shoot has just appeared above the ground the area is very small and increases steadily until in mature plants examined in early April the area is about 100 times greater.

The average "conducting area" for plants of the same age is plotted against time in Figure 17; the curve rises through the season particularly in early February and again near the end of the season; the first increase corresponds with a rapid lignification of the metaxylem elements; the second marked increase may be attributed to the production

of large numbers of secondary tracheids. Since water passing through the xylem in the growing region is transpired from the whole leaf surface, it was thought that the "conducting area" might bear some definite relation to the area of the leaf, and hence to the amount of transpiration.

The ratio conducting area to leaf area was therefore calculated and the results obtained for individual plants shown graphically in Figure 16. The ratio is not constant in plants of the same age but a definite tendency may be recognised for it to increase with increasing age of the plant. If the average values for each experiment are considered (Figure 17) this increase is clearly marked. From the diagram it is seen that the "conducting area" and the leaf area increase with the age of the plant but not at the same rate so that their ratio varies. During the early part of the season the "conducting area" increases more quickly than the leaf area so that their ratio increases; in mid-season the "conducting area" and leaf area are increasing at the same rate so that their ratio is fairly constant. At the end of the season the "conducting area" is still increasing while expansion of the leaf surface has almost ceased so that the ratio increases suddenly.

Plants which had been planted in October were compared with those planted in December, in respect of the vascular supply; all the plants were grown under the same conditions and



differed only in that some were two months younger than others. In agreement with the results already described the older plants were found to have the better vascular system in the growing region of the leaf, Table XII illustrates this point.

Table XII.

"Conducting Area" and Conducting Area / Leaf Area Compared on March 9th 1935 in plants planted in December and October.

Galanthus nivalis.

Date of planting	C sq. mm.	C/L sq. mm. per sq. cm. leaf
Oct. 21st	.0262	.00072
	.0256	.00100
	.0219	.000700
	.0195	.000780
	.0159	.000480
Dec. 21st	.0087	.000410
	.0068	.000600

(b) Galanthus Elwesi.

Plants were examined at four periods in the season, (1935) namely 5th January, 2nd February, 23rd February and 9th March. At the last date the plants were already showing a tendency to wither so quantitative measurements of the "conducting area" were not made on older plants.

The data obtained are given in Appendix 7 and in Fig. 18 - 20 and the following points may be deduced from them:-

1. Individual plants of the same age vary very considerably in respect of both "conducting area" and "conducting area/leaf area."
2. The average value shows an increase through the season in "conducting area". This is particularly rapid in early February and this may be attributed to the lignification of the large metaxylem elements about this time.
3. The ratio of "conducting area" to leaf area does not increase constantly during the period of growth.

Comparison with the results obtained for Galanthus nivalis brings out the following differences.

1. "Conducting area" and "conducting area" / leaf area are both higher in Galanthus Elwesi than Galanthus nivalis.
2. "Conducting Area" / leaf area increases during the season much more markedly in Galanthus nivalis than in Galanthus Elwesi.
3. "Conducting Area" increases more rapidly in Galanthus Elwesi than Galanthus nivalis; this may be due to the fact that the former species reaches the flowering stage more quickly.

#### The Relationship between Transpiration and the Conducting Area.

It has been shown that in both Galanthus nivalis and Galanthus Elwesi the "relative transpiration ratio" increases with age and also that there is a progressive increase in the

degree of development of the vascular supply in the growing region of the leaf. All water passing to the transpiring leaf surface must traverse this region and it was thought that the increase in relative transpiration might be a direct outcome of the better developed vascular supply in that region. The data was therefore examined to determine what evidence exists for this point of view.

(a) Galanthus nivalis.

In Fig. 21 are shown the average values obtained at different times in the season for the "relative transpiration ratio" and the ratio of "conducting area" to leaf area. (See also Appendix 5).

Relative transpiration and the ratio of "conducting area" to leaf area show a striking general similarity, both curves are low at the beginning of the season and rise slowly at first and then very rapidly, becoming more constant in mid-season and rising again later. Between 5th January and 5th April the "relative transpiration ratio" increase fourfold while the ratio of "conducting area" to leaf area increases tenfold.

The similarity of the curves suggested that "the relative transpiration ratio" and the ratio of "conducting area" to leaf area are directly correlated. Accordingly a correlation diagram was made to test this correlation. In Fig. 22 "relative transpiration" and this ratio have been plotted against each other, 39 plants of 6 different ages being considered. The diagram is divided into four quadrats and if

positive correlation occurs most of the points should fall in the top left hand and bottom right hand quadrats. This is in fact what happens. Plants having a relatively small amount of xylem in their growing region and a high intensity of transpiration are rare, only 1 occurring in 39. A low intensity of transpiration and a well developed vascular system are more commonly associated (3 out of 39) but are not so common as low transpiration associated with a poorly developed vascular system (13 out of 39) or high transpiration with a well developed vascular supply (17 out of 39). It may therefore be concluded that there is a definite relationship between the "relative transpiration ratio" and the degree of development of the conducting strand in the growing region of the leaf.

The figures given in Appendix 5 show that no such close relationship is observed where the plants considered are all of the same age and the differences involved are small. So that of two plants of the same age that with the greater development of xylem in the growing region of its leaves will not necessarily have the greater rate of transpiration (under the same external conditions) or, conversely a plant will not necessarily transpire less intensely than another although its ratio of "conducting area" to leaf area may be lower,

The work of Yasuda on rice has already been mentioned (page 4). He found that a constant relationship existed between transpiration per unit area and the ratio of cross-

sectional area of the vascular portion at the base of the leaf to leaf area, provided external and internal conditions were the same. Of internal conditions the most important were differences in strains and cultivation.

A similar ratio has been calculated for plants of Galanthus nivalis namely:-

$$\frac{\text{Transpiration per unit area}}{\text{per unit time}} \bigg/ \frac{\text{Conducting area}}{\text{Leaf area}}$$

and the results obtained are given in Appendix 5. The ratio was not constant but was found to vary considerably.

The average values obtained for five plants of the same age are shown in Figure 24 for Galanthus nivalis and these fall continuously through the season. Transpiration is greatly affected by external conditions and as the experiments were carried out indoors these values would probably be quite different in the case of plants growing out of doors under natural conditions. It may be noted that in the earlier part of the season transpiration would probably be higher indoors than in a garden owing to a higher average temperature while later in the season the difference would become less and towards the end of March transpiration would possibly be greater outside than inside. In nature therefore it seems likely that the ratio would not be so markedly higher at the

beginning of the season than at the end, remaining more constant through the season.

(b) Galanthus Elwesi.

The average values obtained for relative transpiration and the ratio of conducting area to leaf area are given in Fig. 23 (see also Appendix 7). Both the relative transpiration ratio and the ratio of "conducting area" to leaf area increase slightly with age of the plants but the resemblance between the curves is much less striking than in Galanthus nivalis suggesting that there is less relation between them. This is borne out by a correlation diagram (Fig. 24b).

It has been found that ratio of "conducting area" to leaf area is higher in Galanthus Elwesi than in Galanthus nivalis while relative transpiration is lower, also the individual elements composing the wood of the former species are greater in length and diameter so that the leaf of Galanthus Elwesi appears to be much better supplied with conducting tissue in the growing region than that of Galanthus nivalis and this may account for the fact that the relationship between the relative transpiration ratio and the ratio of "conducting area" to leaf area is not so marked in Galanthus Elwesi.

The ratio of transpiration per unit area to "conducting area" / leaf area is not constant in individual plants of Galanthus Elwesi (c - f Appendix 7). The average values of the ratio for four plants of different ages is shown in Fig. 24 and these are very considerably lower than in Galanthus nivalis.

### Conclusion.

From the fore-going data it may be concluded that a close relationship exists between the relative transpiration ratio and the degree of development of the xylem in the growing region of the leaf of Galanthus nivalis. In Galanthus Elwesi there appears to be some relationship but it is not so evident as in Galanthus nivalis. The evidence does not however justify the view that the degree of development of the conducting strand controls transpiration, an increase in conducting tissue bringing about a corresponding increase in transpiration.

Recently Inandar and Shives<sup>5</sup>bava ( 9 ) have studied the specific conductivity of woods at different periods in the season and shown that a close relationship exists between the anatomical structure of the plant and its physiological requirement. Variations in the specific conductivity of the wood were correlated with the demand on the water supply made by the transpiring leaves: during the rainy season when transpiration is low specific conductivity is also low and begins to rise in the Summer months as transpiration increases, reaching a maximum when transpiration is at its height.

A relationship of this kind, may it is suggested be recognised in Galanthus between transpiration and the vascular supply of the leaf in that region where it is least developed. At the beginning of the season transpiration is low and the vascular supply is poorly developed. Later transpiration increases suddenly owing to the greater area of the leaf

surface, changing external conditions and possibly to internal factors and to meet this need an increase in the conducting tissue takes place in the growing region. The newly lignified elements are very much larger than the first formed protoxylem elements, thus meeting the need for a better water supply very rapidly. Transpiration goes on increasing through the season and the degree of development of the conducting strand also increases.

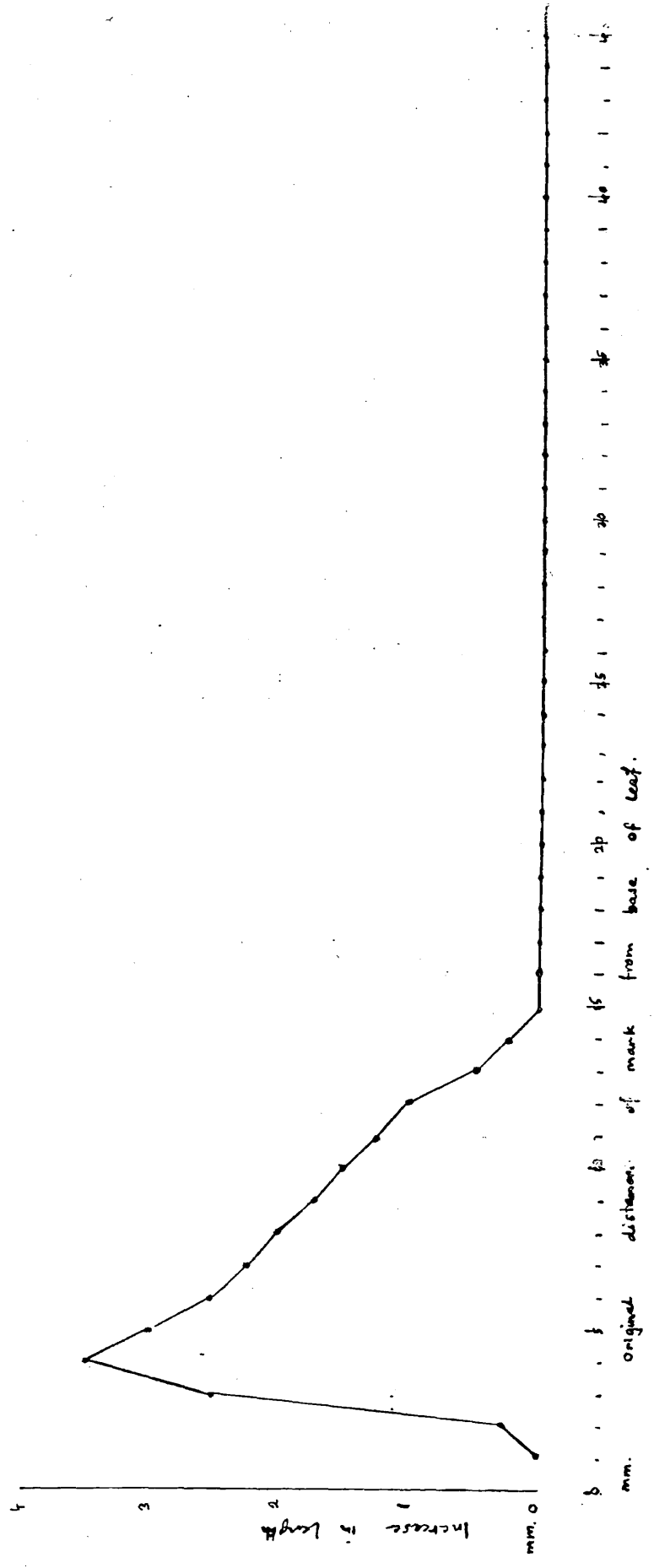
The relationship between transpiration and the degree of development of the vascular supply in the growing region of the leaf of Galanthus may be regarded as a further illustration of the theorem of Le Chatilvier which as stated by Maximov (12) says, "every change in enviromental condition influencing a body or system of bodies augments the resistance of the latter to a further increase of this influence". One may suggest that in transpiration and corresponding increased rate of flow of water in the conducting channels results in the development of further conducting elements, reducing the resistance shown to the water in its passage through the conducting channels to the leaf.



Fig. 14. *Galanthus nivalis* - Increase in Length taking place in successive lengths (1mm) of a leaf in 8 days

(15-23<sup>rd</sup> January 19<sup>th</sup>)

Length of leaf on Jan 15<sup>th</sup> = 47 mm  
 " " " " 23<sup>rd</sup> = 70 "  
 Increase in length = 27 "



0 . . . . . 5 . . . . . 10 . . . . . 15 . . . . . 20 . . . . . 25 . . . . . 30 . . . . . 35 . . . . . 40 . . . . . 45

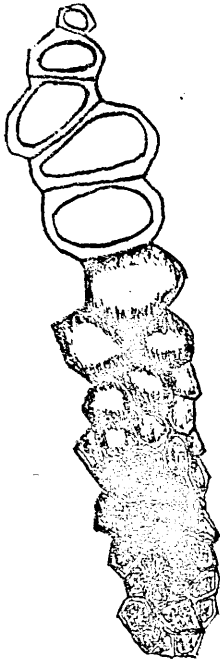
mm. original distance of mark from base of leaf.

Crataegus Elysi

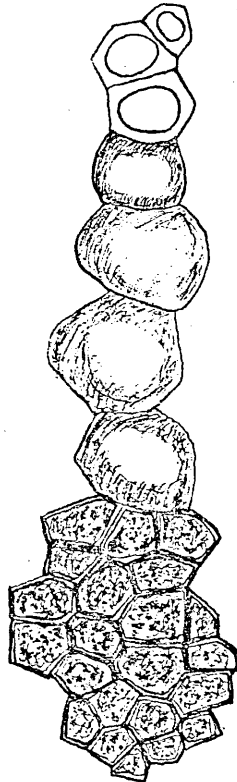
T.S Median bundle of dormant leaf (11<sup>th</sup> December 1934)  
in 3 regions of the leaf, showing variation in  
xylem development. (x540)

Fig. 28.

(a) 1cm below tip of leaf.



(b) 1.5 cm above base of leaf (growing region)



(c) 1mm above base of leaf



Galanthus Elvazi . Transverse Sections Through Median Bundle  
of Leaves of Different Ages, Cut in  
The Growing Region.

Fig 27 (a) 5<sup>th</sup> January

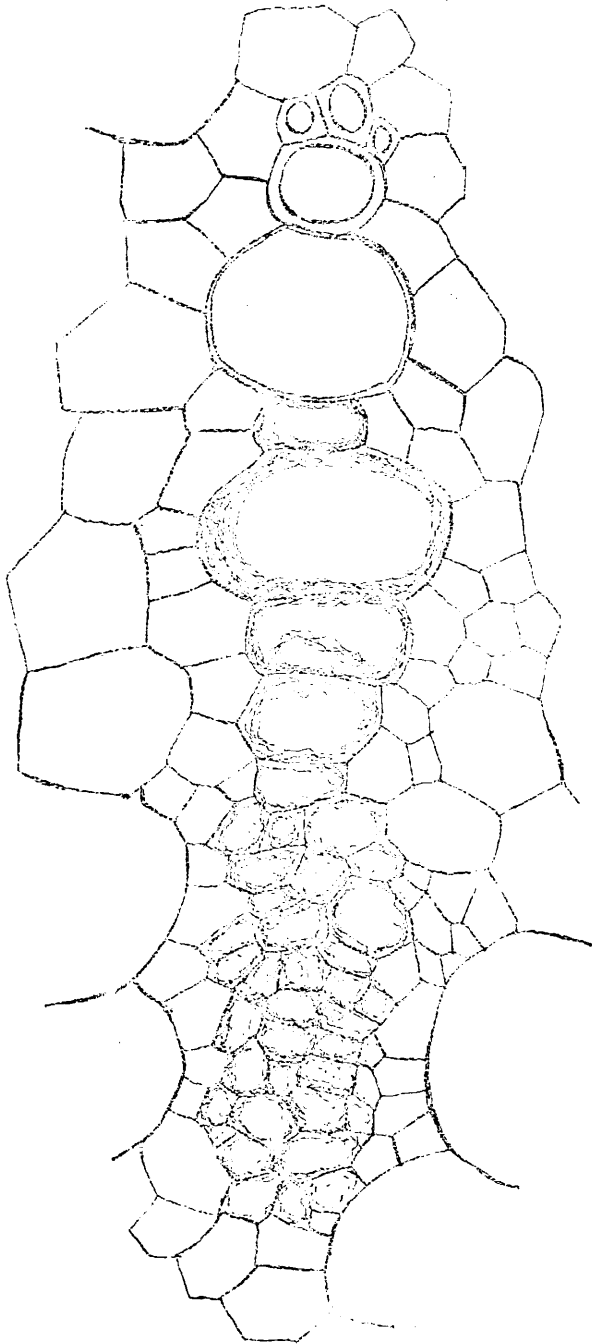
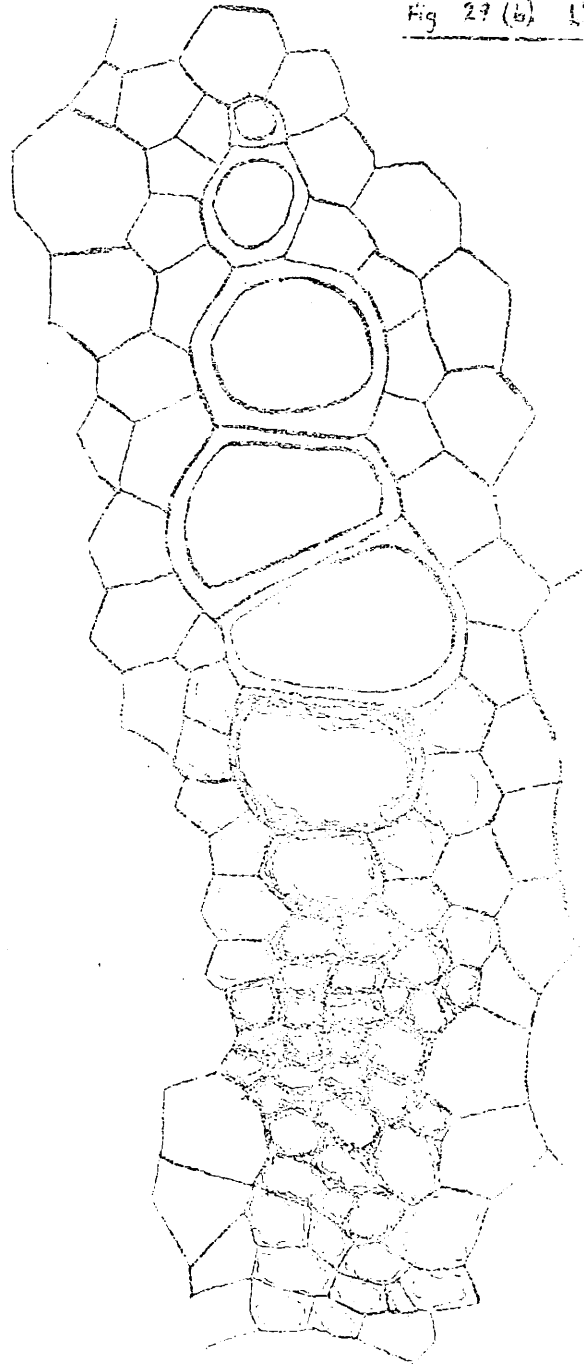


Fig 27 (b) 15<sup>th</sup> February



Galambias Elvosi.

Transverse Section Through the Median  
Bundle in the Growing Region of the Leaf

Fig. 29 (c)

22<sup>nd</sup> February.

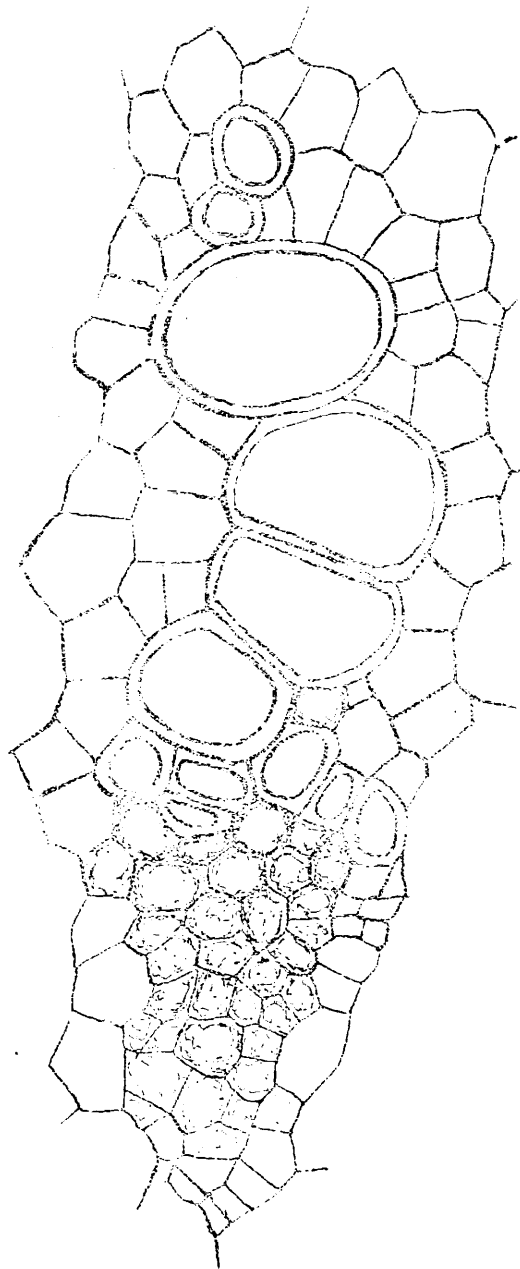
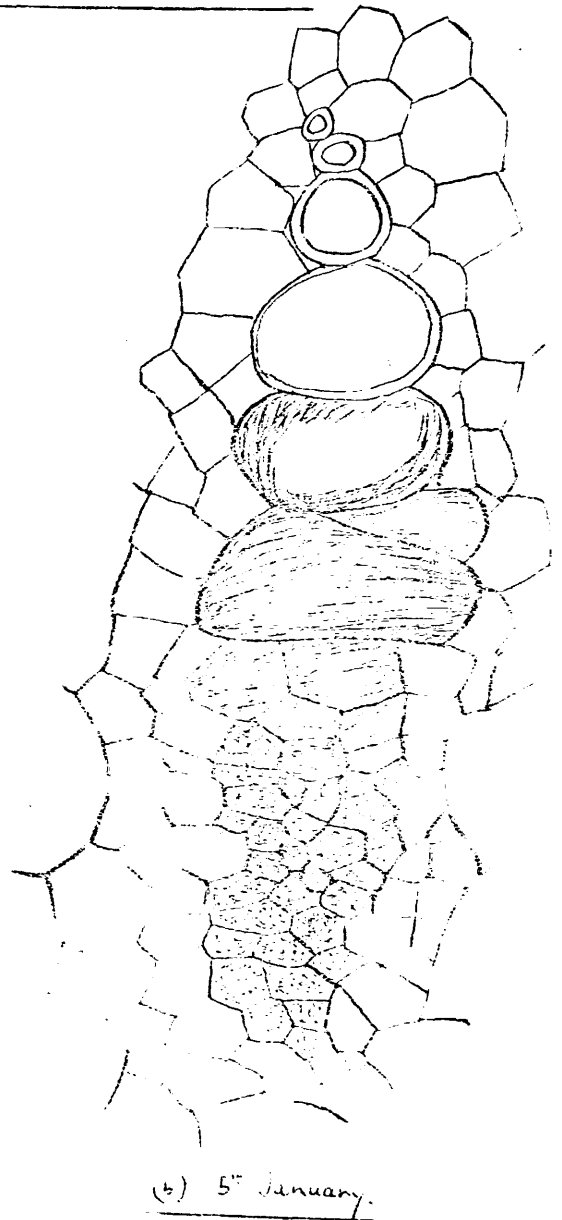
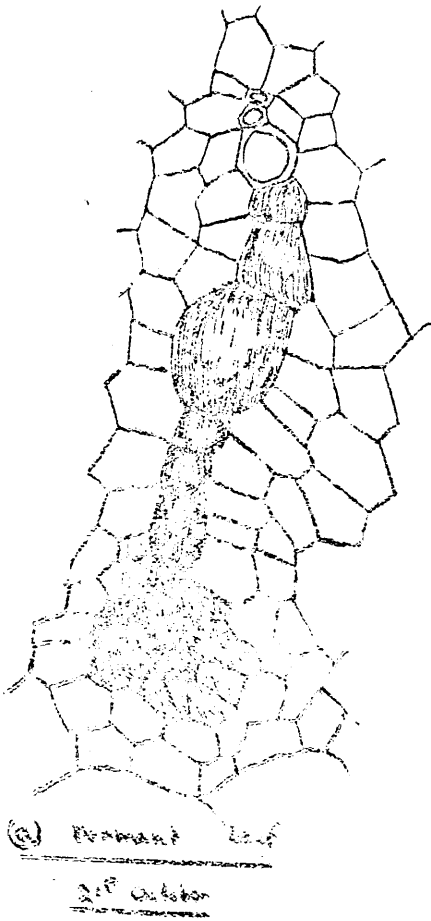


Fig. 30. Galanthus 'nivalis.

Transverse sections through growing  
region of leaves of different ages,  
showing median bundle.



Galanthus nivalis . Transverse Sections Through Growing Region of  
Leaves of Different Ages, Showing Median Bundles

Fig 30 (c) 3<sup>rd</sup> March.

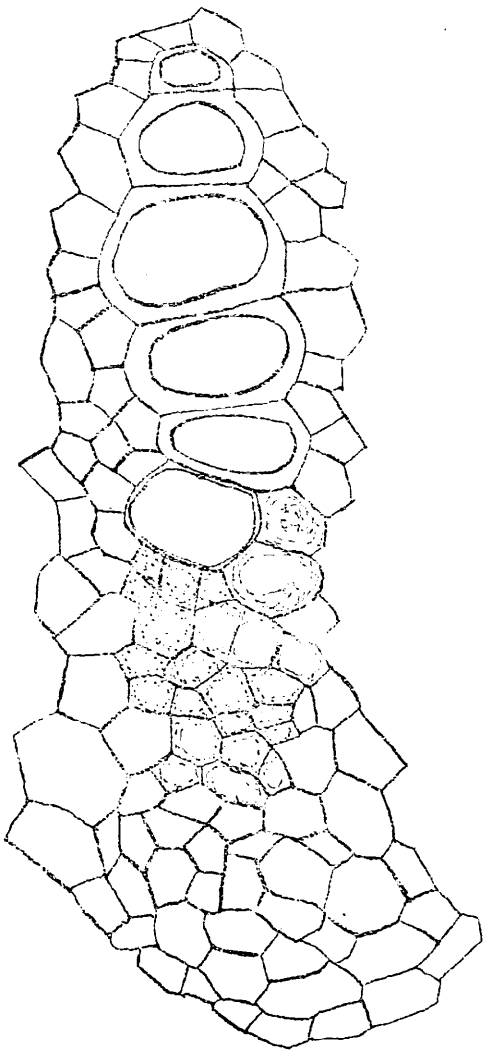
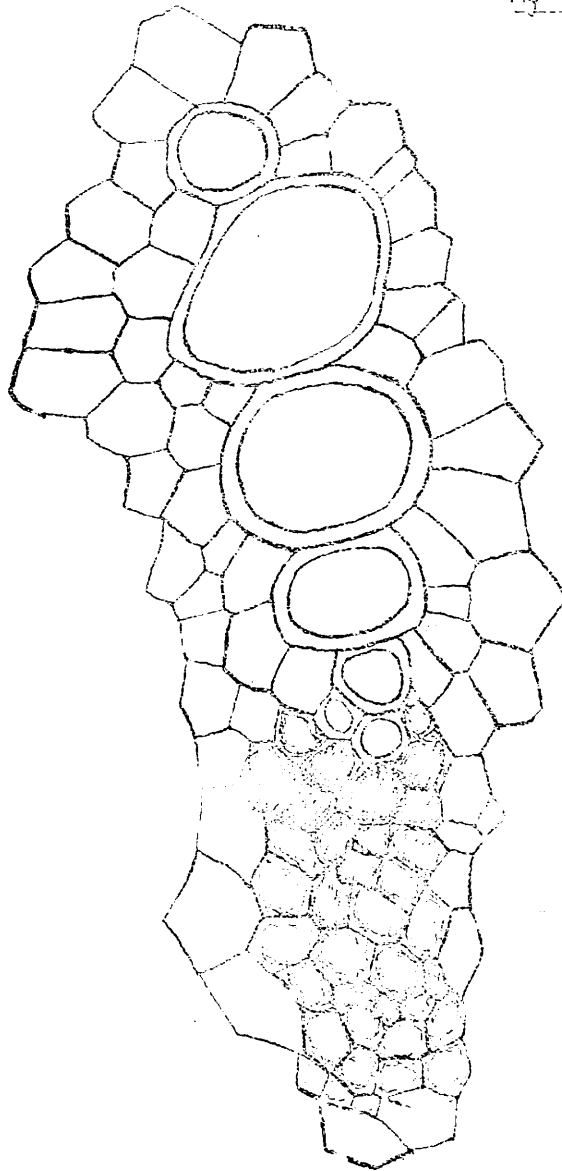
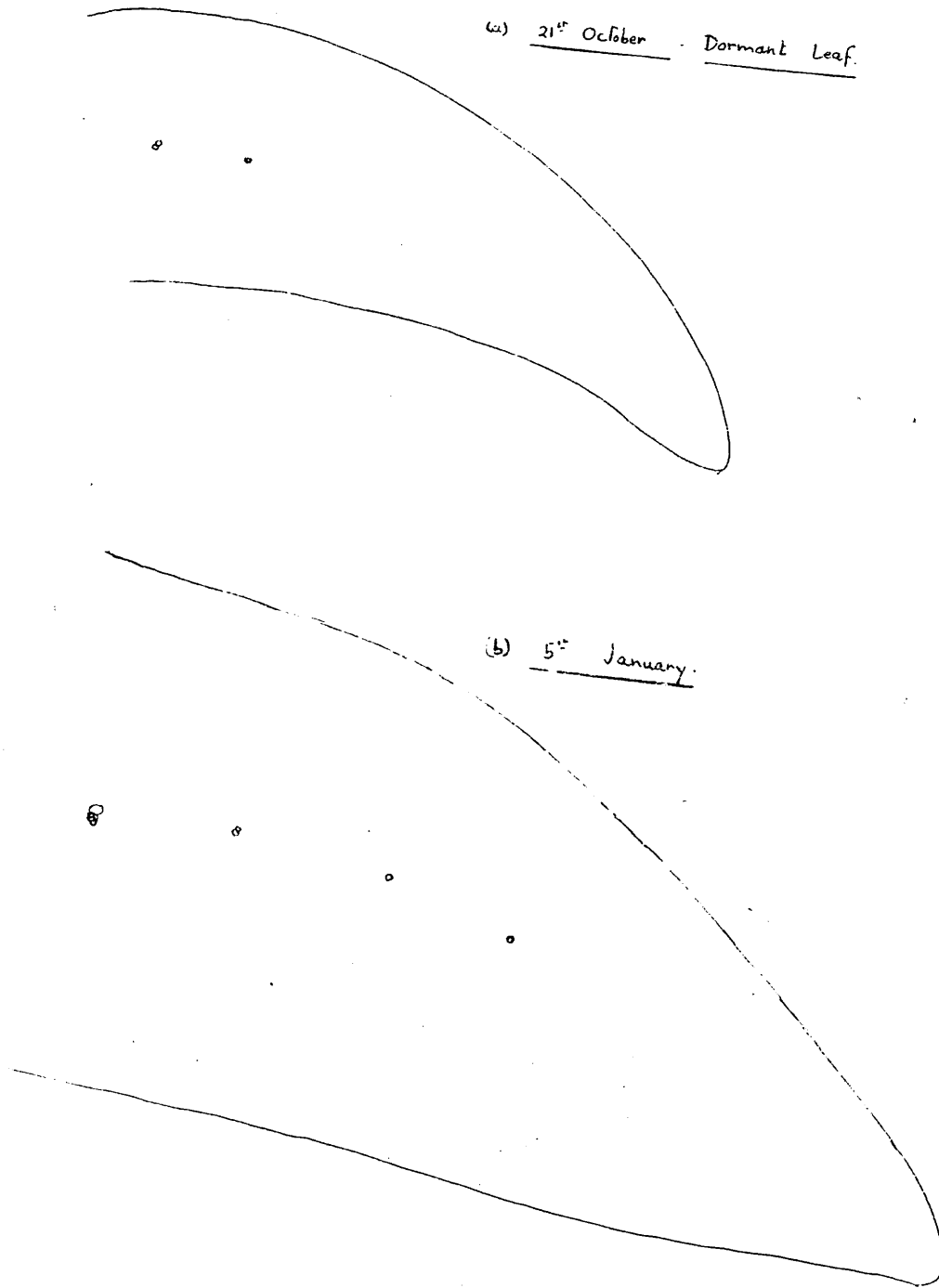


Fig 30 (d) 5<sup>th</sup> March.



Galanthus Elwesii. Transverse sections through the growing region of  
leaves of different ages (x50) showing xylem.

Fig. 31.

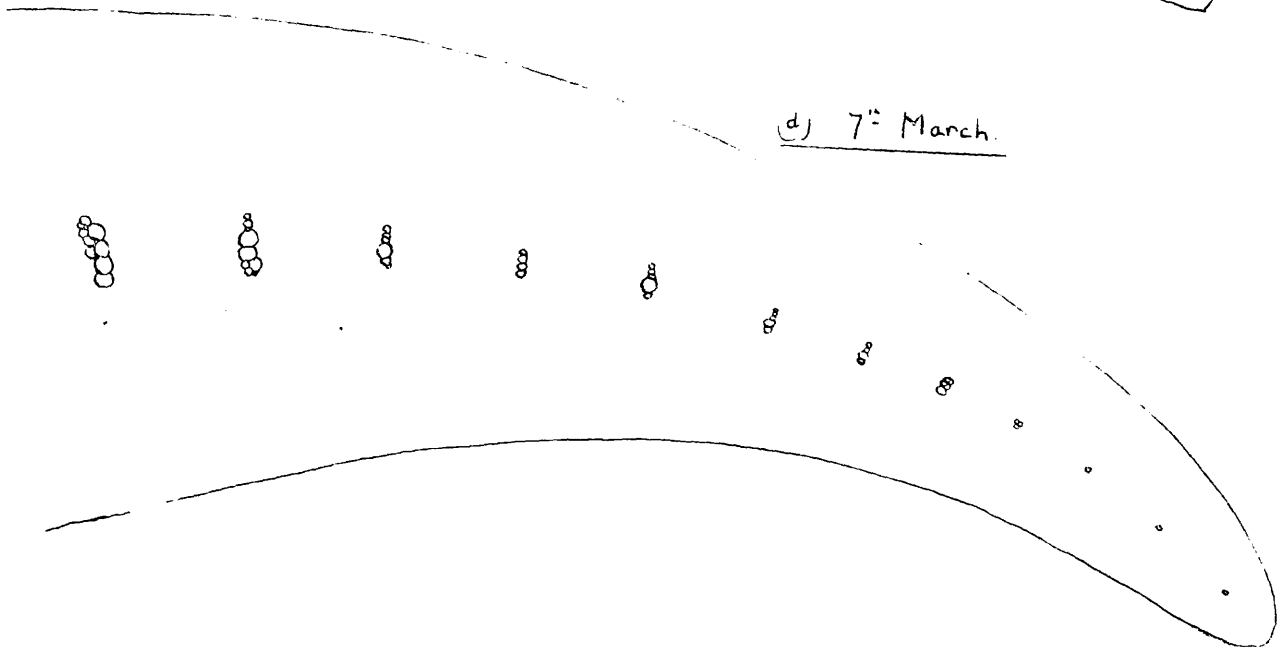
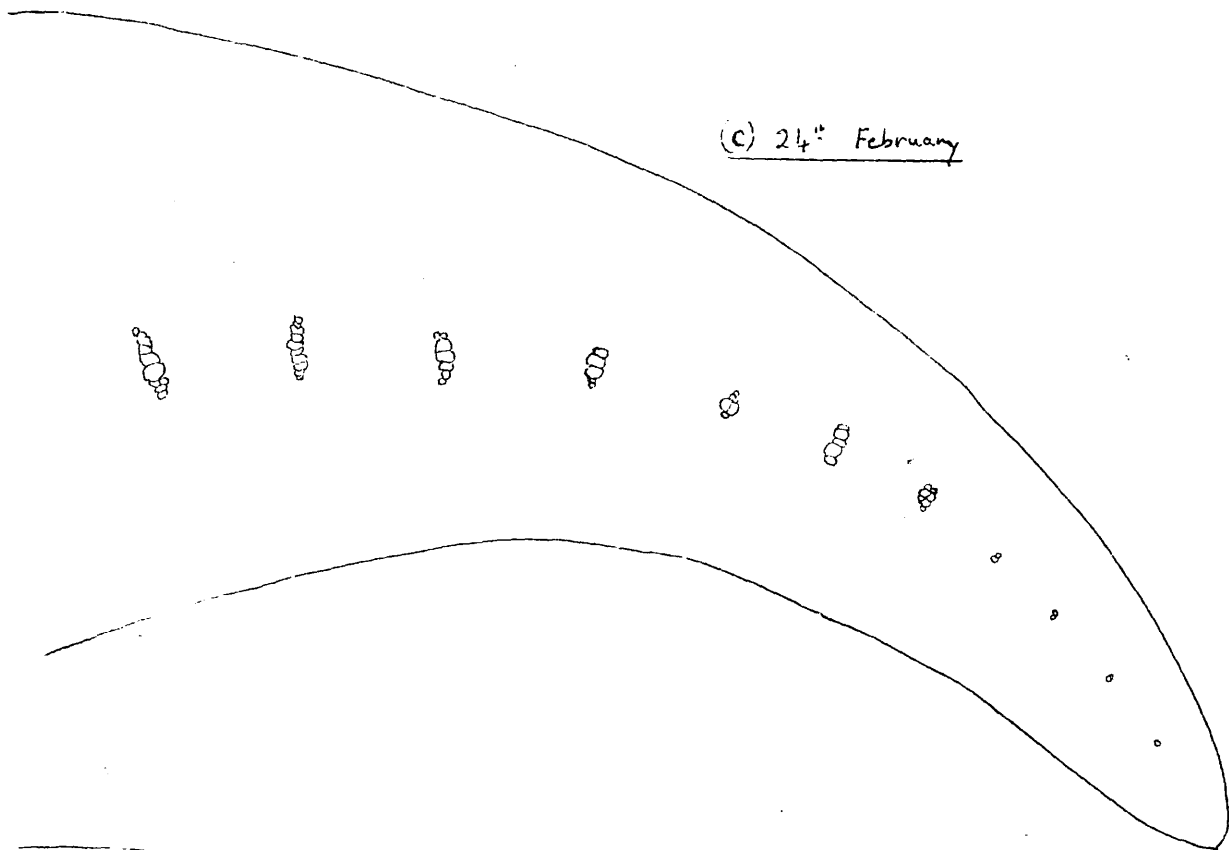


Galanthus Elwesii.

Transverse sections through the growing region of

Fig. 31.

Leaves of different ages, showing xylem elements (x50)





Galanthus nivalis.

Fig 32.

Transverse sections through the growing region  
of leaves of different ages. (x50)

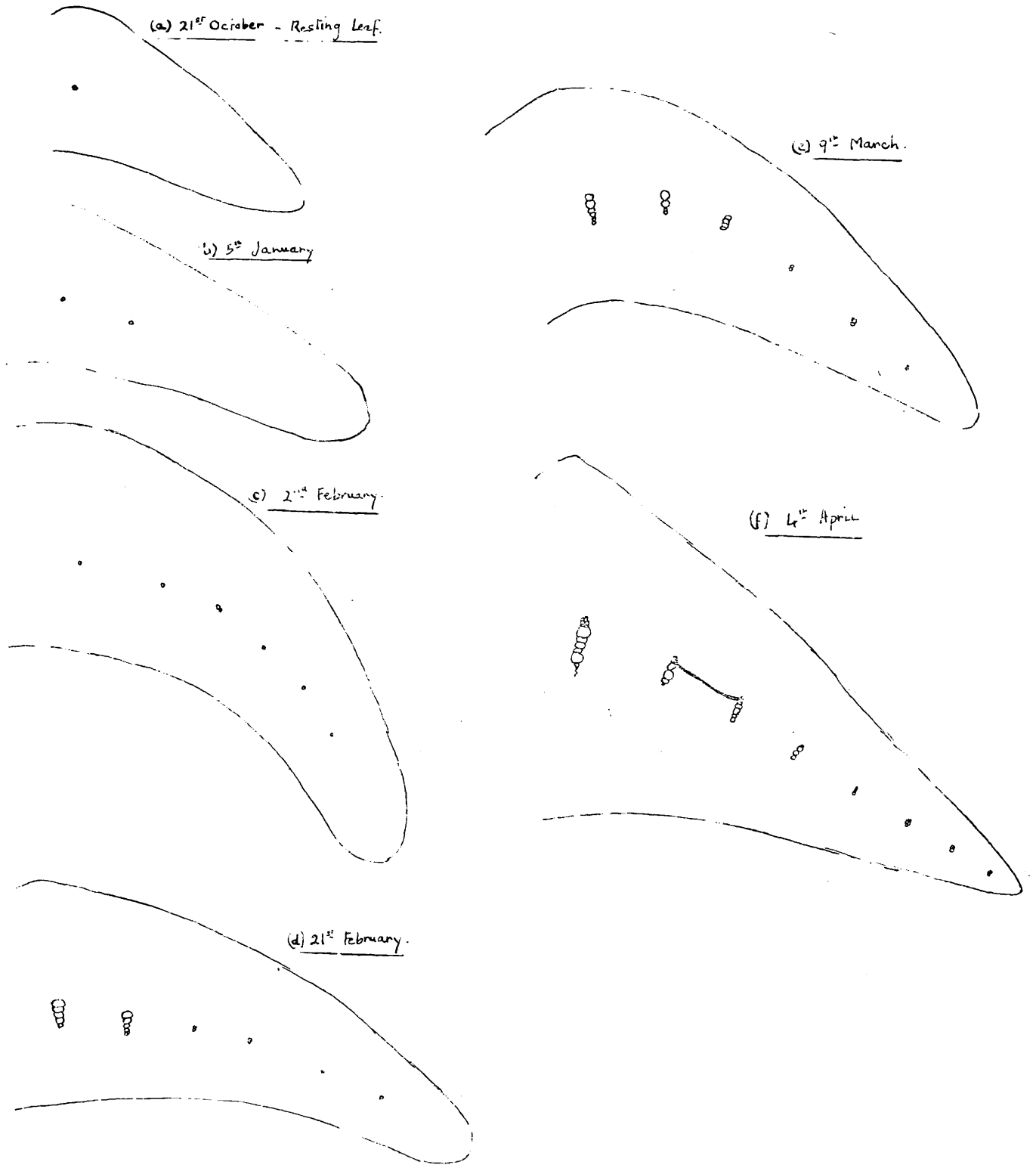
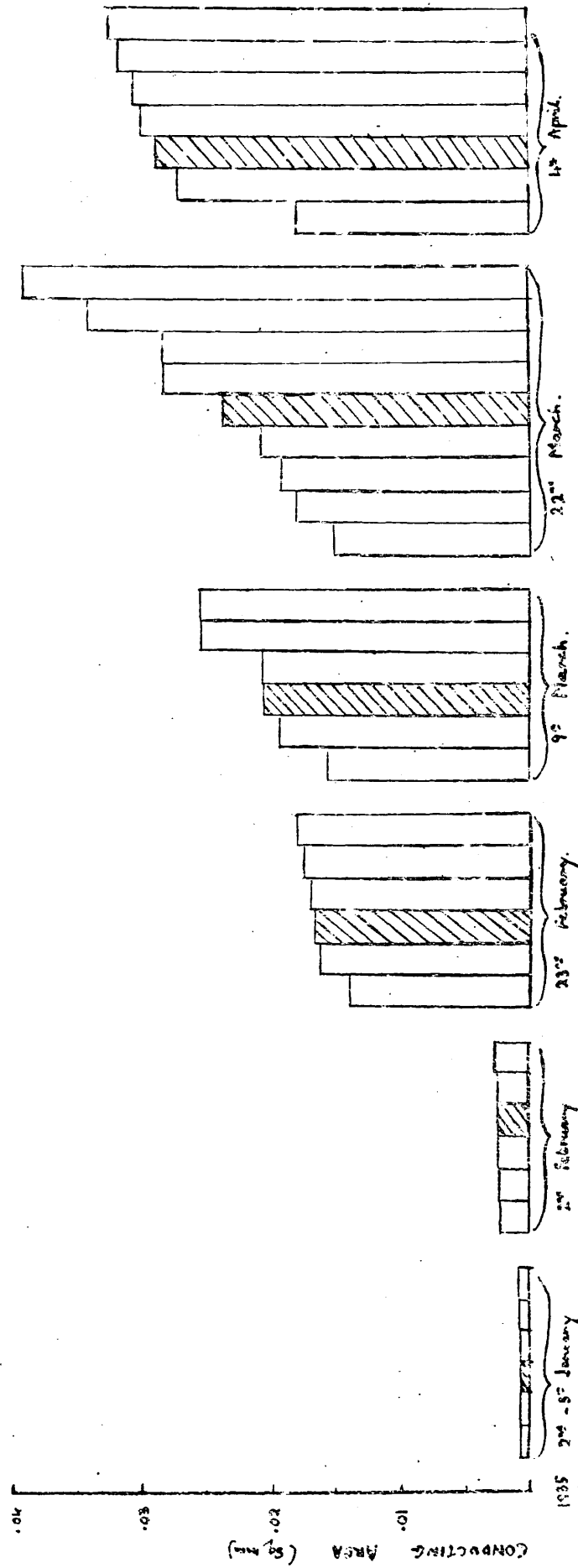


Fig. 15 *Galium aparine*.

Cross-sectioned Area of Tracheids in the Growing Region

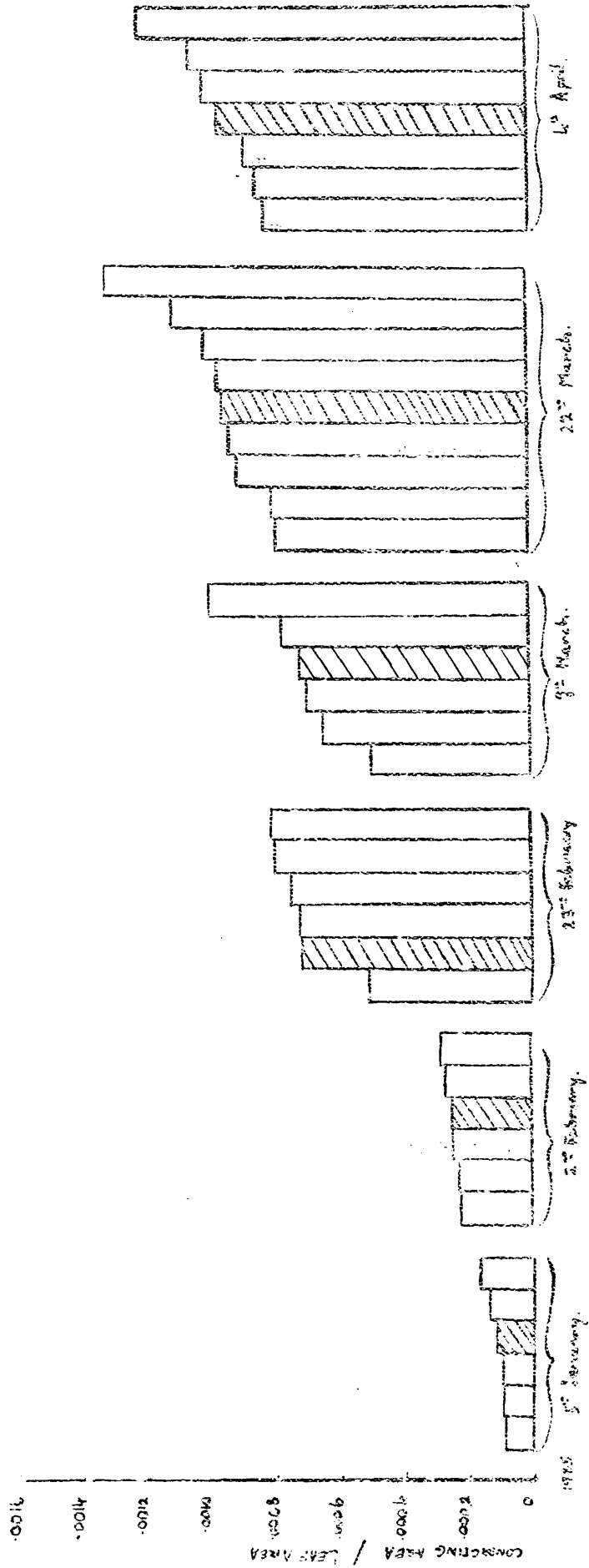
of the leaf in plants of different ages.



Each rectangle represents the conducting area in one plant, the average value for plants of the same age is shown.

Fig. 16 Gulabkhus mosablis Ratio of Cross. Sectional Area of Xylem Conductors in The Conducting

Region of The Leaf To Leaf Area in Plants of Different Ages.



Each rectangle represents the ratio of conducting area to leaf area in one plant. The average value of - the ratio in plants of the same age is shaded.

Fig. 17. *Solanum melintha*. Average Leaf Area, Gross Sectional Area of Xylem Located in the Growing Region of the Leaf (C = Conducting Area) and the Ratio of These in Plants of Different Ages.

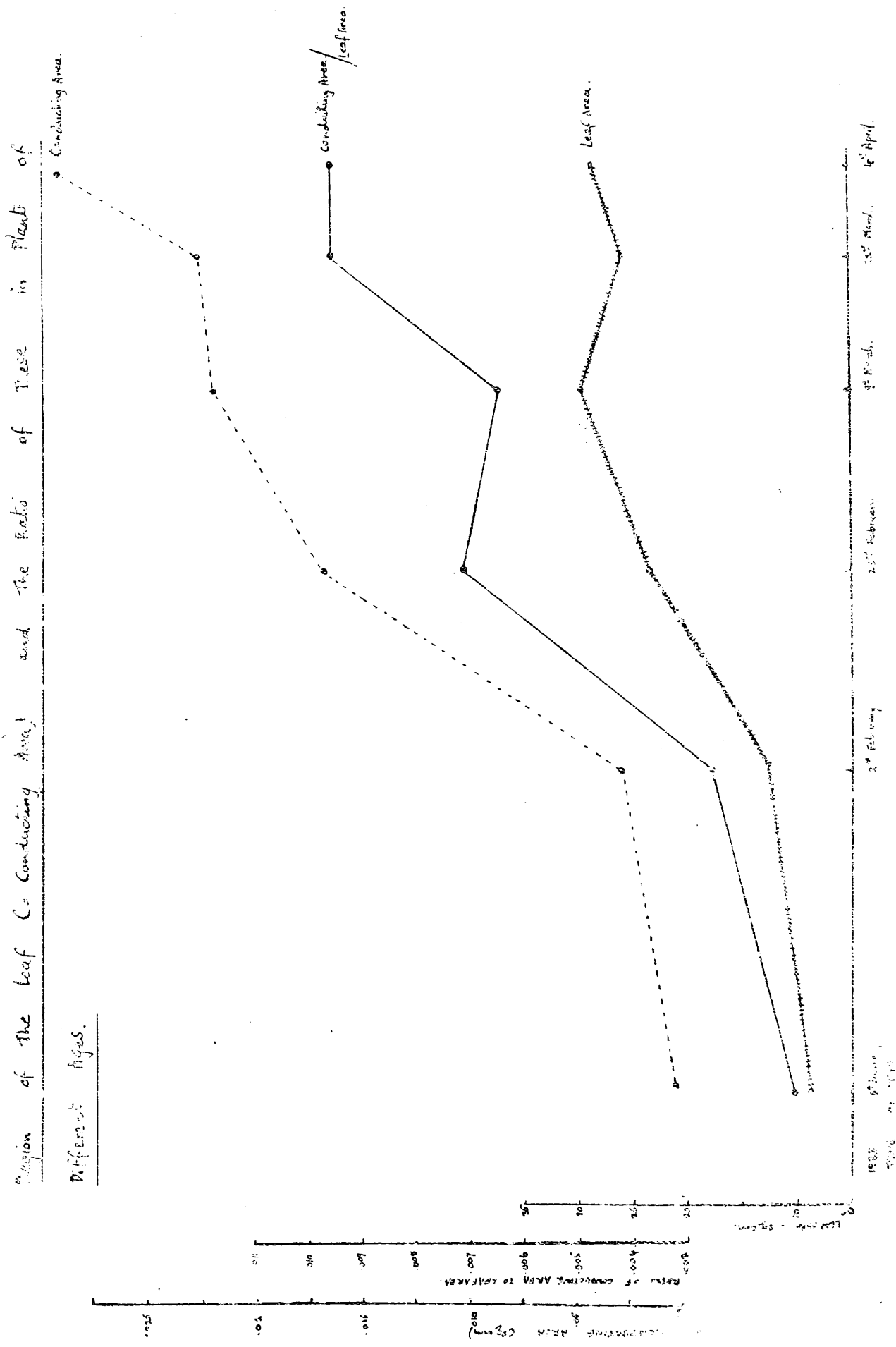
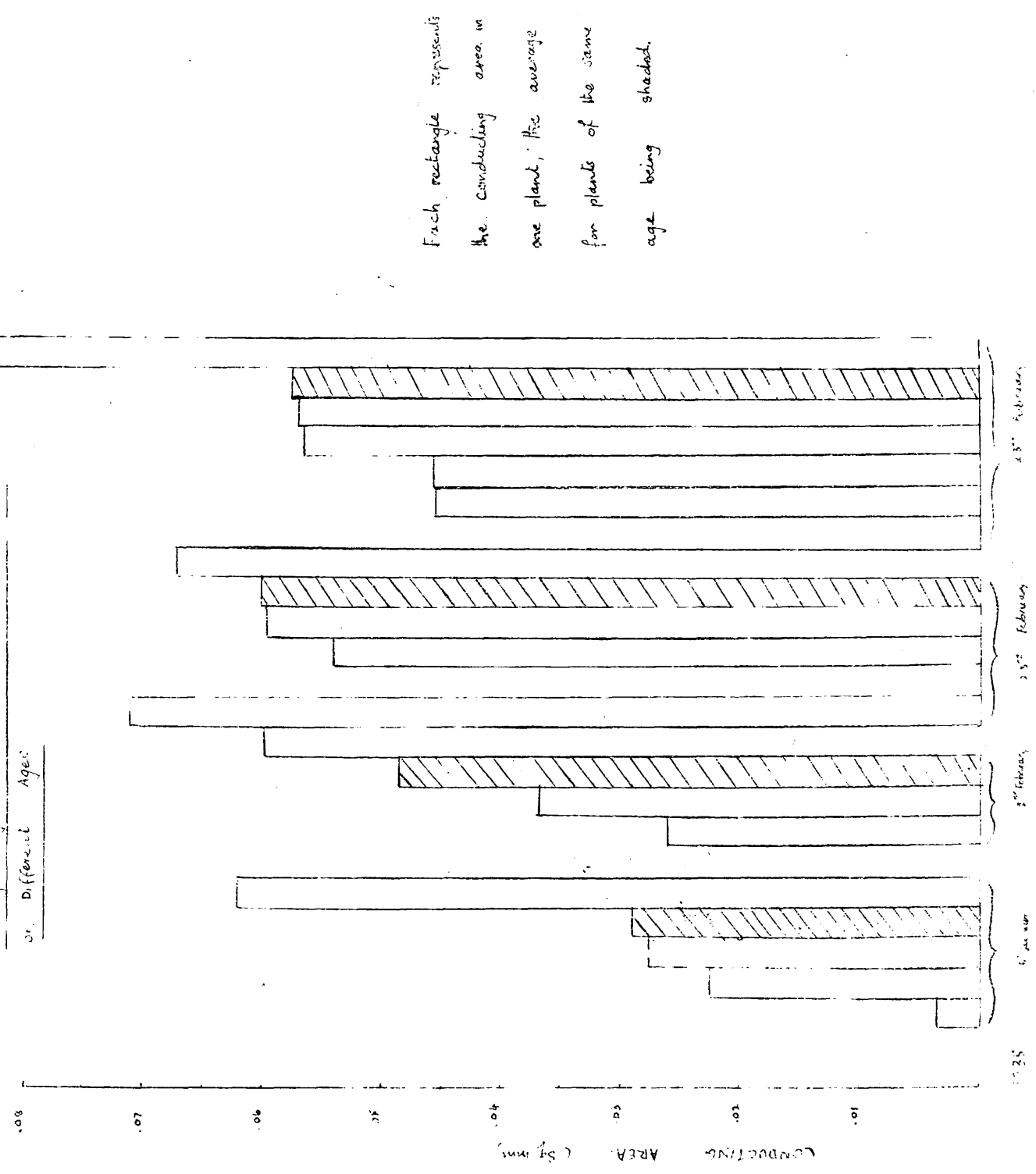


Fig 18 Galanthus Elvosi Cross Sectional Area of The Xylem Cavities in The Growing Region of The Leaves of Plants of Different Ages

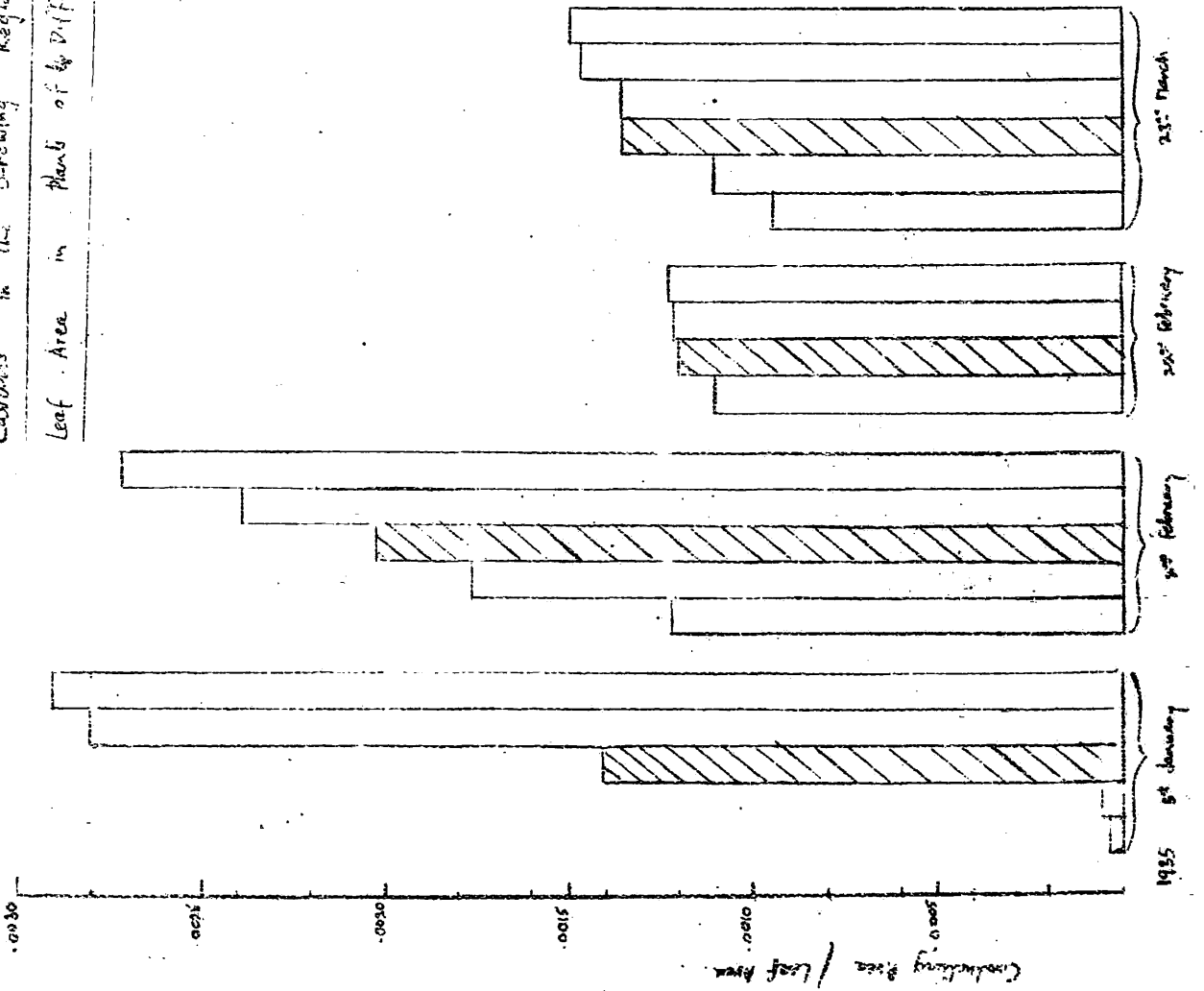


Each rectangle represents the conducting area in one plant, the average for plants of the same age being shaded.

Fig 19 *Crataegus Elmisi*

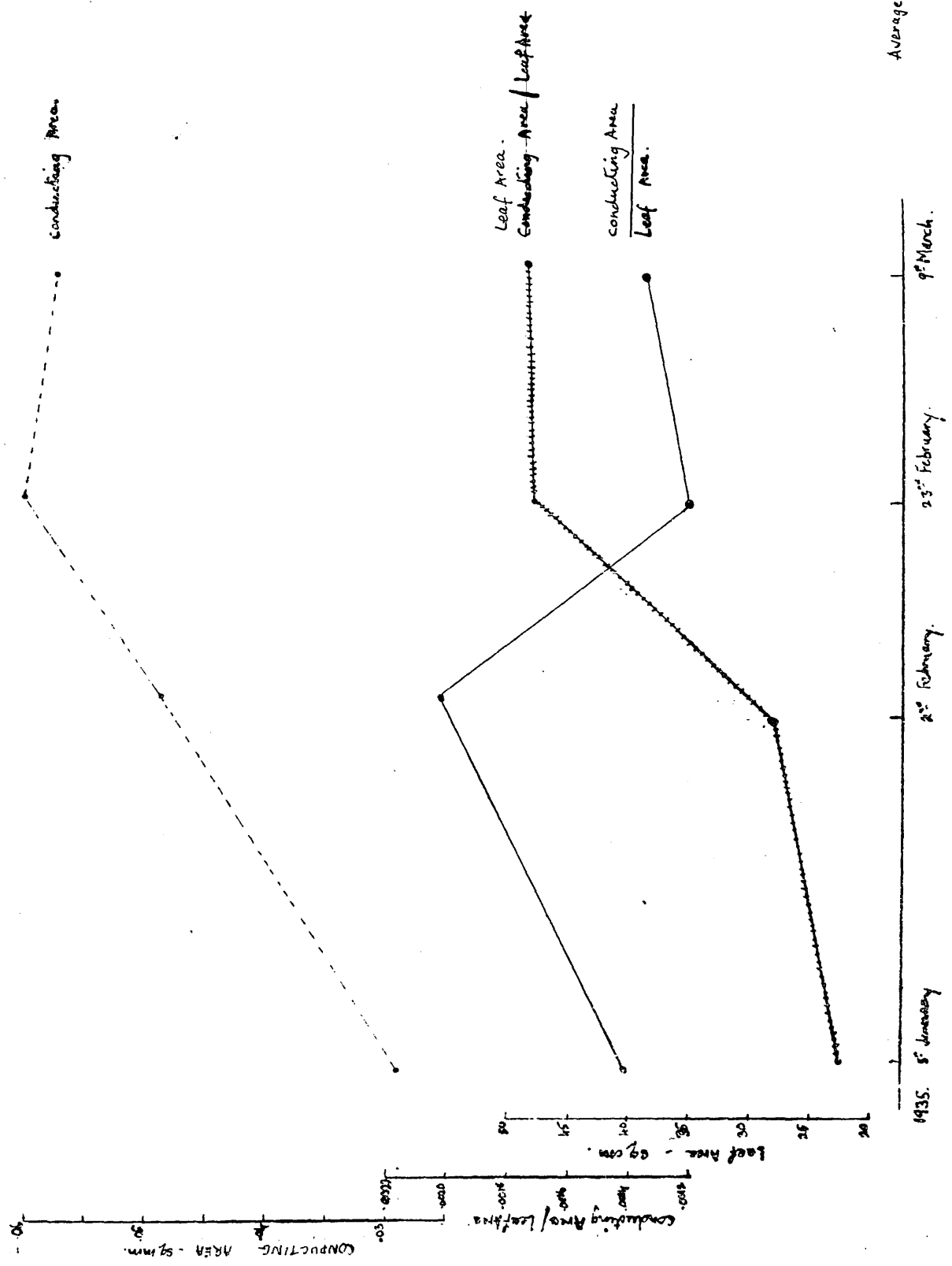
Average Ratio of Cross Sectional Area of Xylem

Cavities in the Growing Region of the Leaf to Leaf Area in Plants of Different Ages.



Each rectangle represents the ratio of Conducting Area to Leaf Area in one plant.

Fig 30 Galanthus Elvessi. Average Cross Sectional Area of the Xylem Cavities in the Growing Region of the Leaf, Leaf Area and The Ratio of These in Plants of Different Ages.



Average of 4 plants plotted

Fig 21. *Galaunthus nivalis*.

Average "Relative Transpiration" and Rate of Cross Sectional Area of Xylem Cavities in the Growing Region of the Leaf to Leaf Area at Different Periods in the Season.

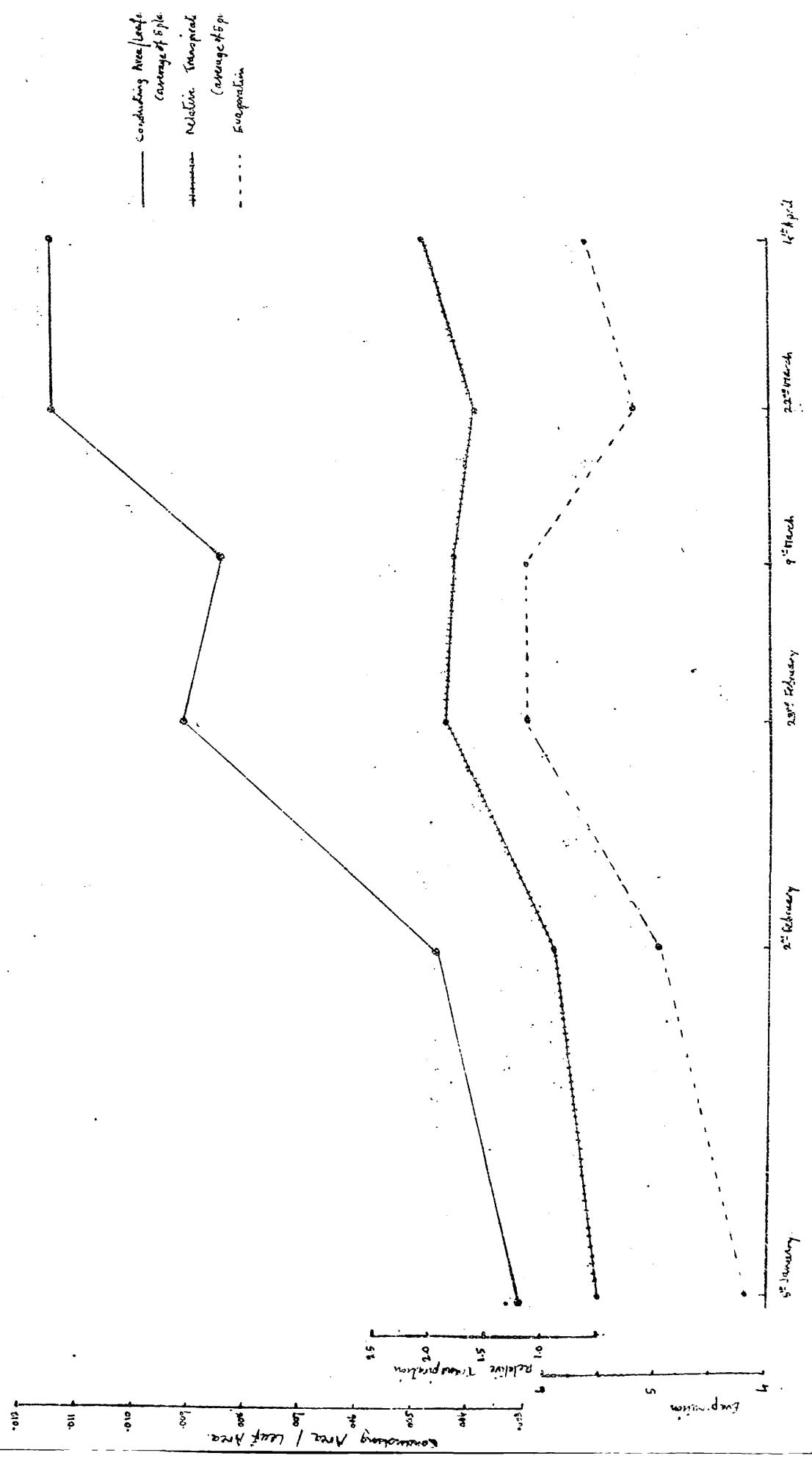
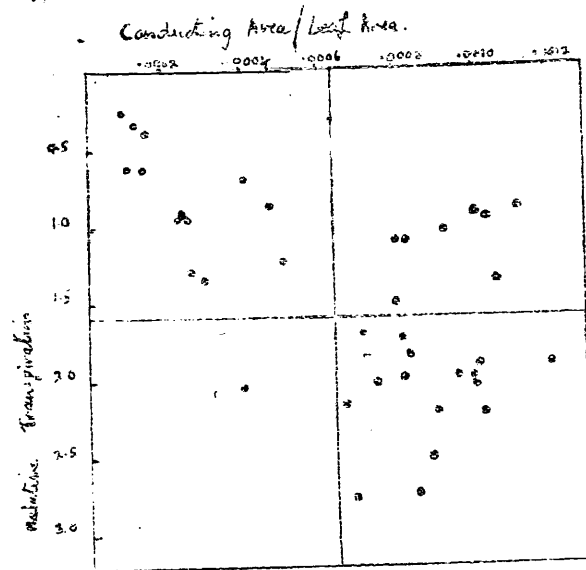




Fig 22

Correlation Diagrams to Show Relationship between  
 "Relative Transpiration" and the Area of the Conducting  
 Cavities in the growing Region of the Leaf  
 per. unit of Leaf Area.

(a) G. nivalis.



(b) G. Elwesii.

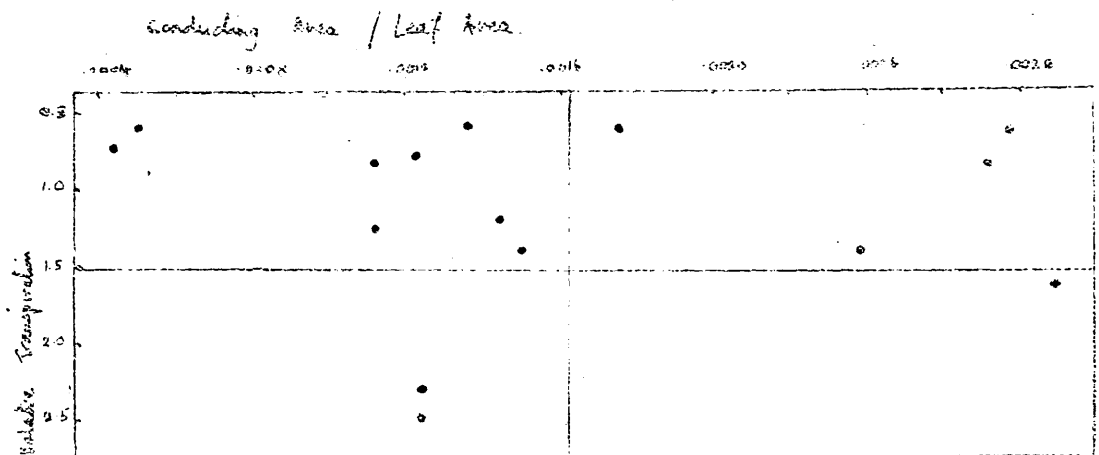


Fig 23. *Calanthe Eburn.* Average "Relative Transpiration" and Ratio of Cross Sectional Area of Xylem Cavities in the Curving Region of the Leaf (Conducting Area) to Leaf Area at Different Periods in This Season.

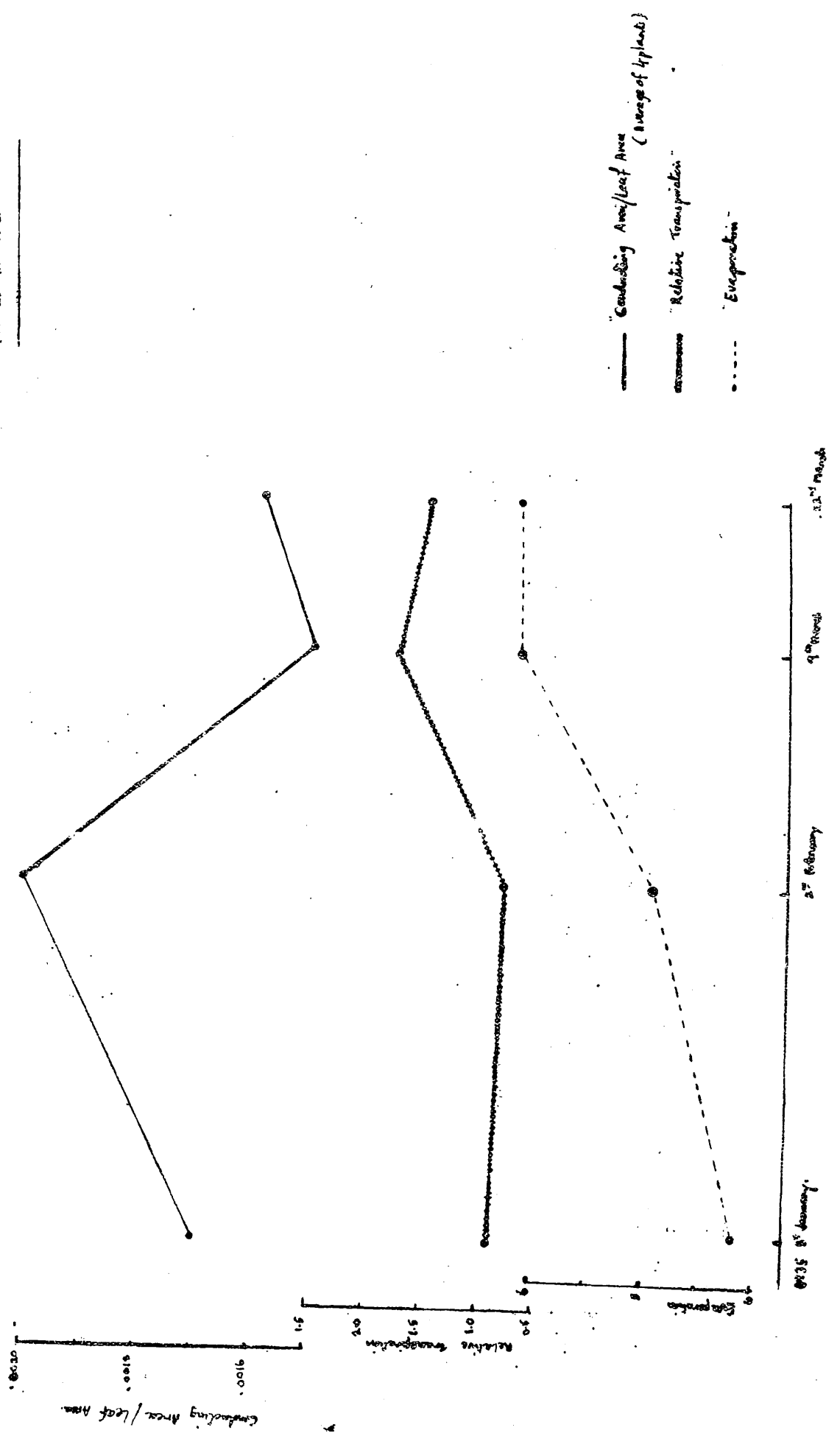
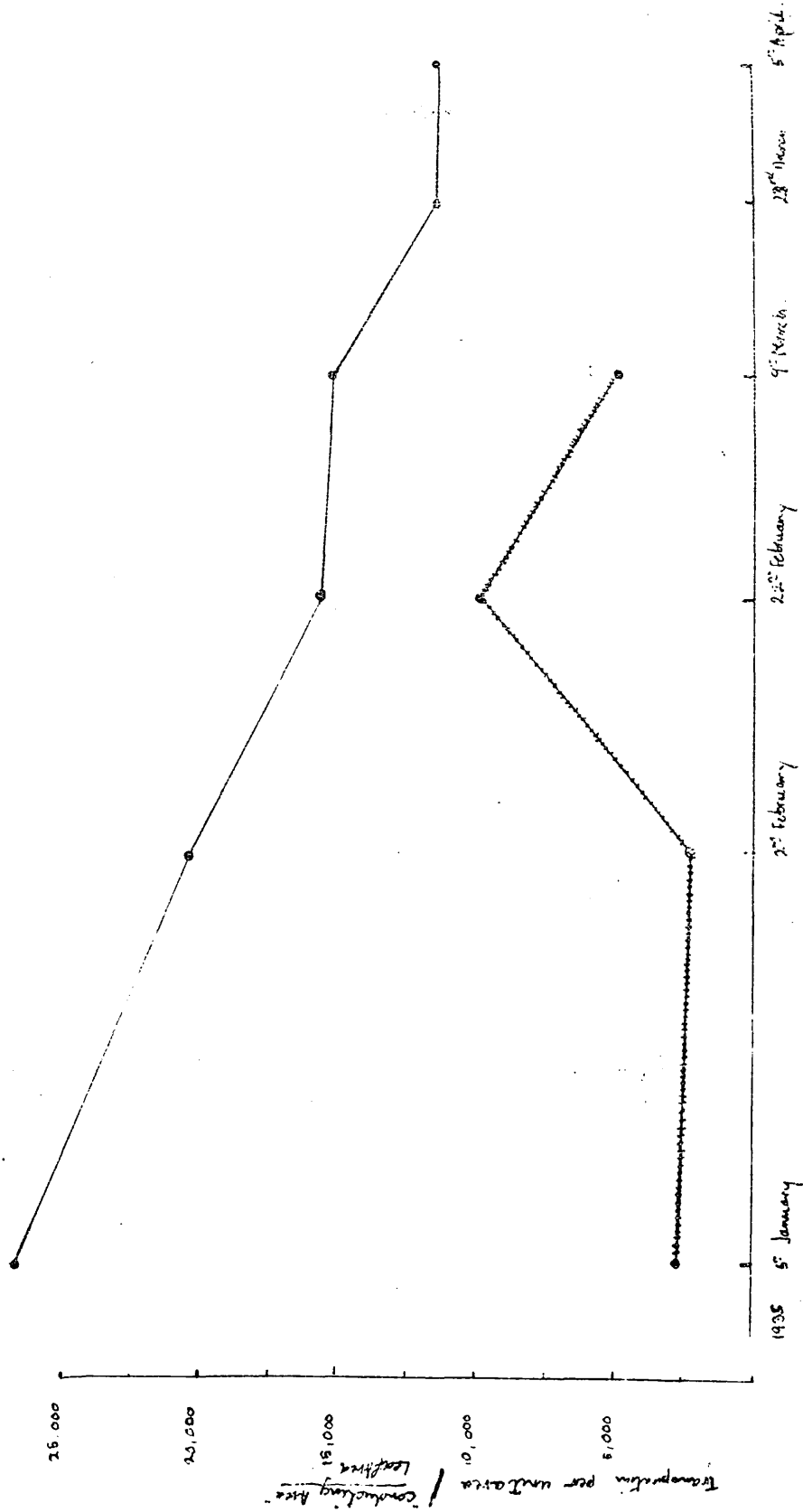


Fig. 24. Gelanthus niveus and G. Elwesii.

Ratio of Transpiration per unit Area Over a Period of 24 hours to Cross Sectional Area of Xylem Cavities / Leaf Area.

— Gelanthus niveus (average of 5 plants)

..... Elwesii ( " " " " )



## S E C T I O N VI.

### COMPARISON WITH OTHER PLANTS.

Some comparison of Galanthus has been made with other plants, particularly Senecio vulgaris in respect of:-

- (1) Transpiration
- (2) Vascular supply to the leaf
- (3) Absorption.

Senecio vulgaris was chosen in spite of the difficulty of estimating its leaf area, due to the form of its pinnatifid irregularly coarsely toothed leaves, because it grows well out of doors all through the winter and is of suitable size. The habit of this annual plant is of a very different type from that of the bulbous Snowdrop and leaf growth is not intercalary in Senecio vulgaris. It was thought therefore that a comparison between the two types of plant might be of interest.

Observations were also made on other dicotyledonous plants and certain monocotyledonous plants (for names of these see Table 13 and Figure 26).

#### 1. Transpiration.

The transpiration was estimated as before by (a) weighing, (b) cobalt chloride paper.

(a) Weighing.

In March (21 - 23rd) and May (20 - 25th) the transpiration of Galanthus and Senecio vulgaris was compared under the same conditions potted plants, wax sealed, were placed in the laboratory and their transpiration measured at intervals.

The plants of Galanthus and Senecio used at different dates were not the same. The plants of Senecio were of a approximately the same stage of growth at the two dates being 4 inches high and just beginning to flower, whereas the plants of Galanthus used in May were at a later stage of growth than those used in March.

Later in the year, after the Snowdrops had died down, transpiration in Senecio vulgaris and Gladiolus was compared since leaf growth in Gladiolus is intercalary as in Galanthus.

The results obtained are given in Appendix 25 and from these data it may be deduced that:-

(i) Transpiration per unit area is greater in Senecio vulgaris than in Galanthus especially early in the season.

Transpiration of one plant of Galanthus appeared to increase later in the season and to decrease in Senecio vulgaris so that the difference in intensity of transpiration apparently becomes less.

(ii) Transpiration per unit area is about equal under the same external conditions in plants of Gladiolus and Senecio vulgaris.

(iii) Plants of the same species show variation, under the same external conditions in intensity of transpiration as has been previously shown for Galanthus nivalis and Galanthus Elwesi.

(b) By means of Cobalt Chloride paper.

The transpiration of a number of plants growing in the garden of Bedford College was measured by means of cobalt chloride paper. The readings were taken during the middle of the day, two or more readings on the upper and lower leaf surfaces being made. The results obtained are given in Table 13 in the form of the length of time (average of readings) required to change the cobalt chloride paper from one standard tint to the other.

The first seven species given in the Table are Monocotyledons in which the growing region of the leaf is localised near the leaf-base. In the other species (Dicotyledons) leaf-growth is not intercalary.

The results given in Table 13 show that there is no marked difference in the intensity of transpiration in the Monocotyledons and mesophytic Dicotyledons studied and that a considerable range is observed among the species of each group. The transpiration of the evergreen types is definitely lower.

T A B L E XIII.

Comparison of Transpiration in certain Monocotyledonous types having Intercalary leaf growth with Dicotyledonous types, by means of cobalt chloride paper.

Monocotyledons	Date	18th Mar. 11½° C	19th Mar. 17° C	20th Mar. 18° C	21st Mar. 23° C
	Temperature	3mins18secs	2mins18secs	0mins58secs	0mins30secs
Galanthus nivalis		1 " 10 "	1 " 23 "	0 " 43 "	0 " 25 "
Leucojum					
Narcissus poeticus			1 " 6 "	0 " 50 "	0 " 30 "
Iris flavescens					0 " 17.5 "
" aphylla					0 " 27.5 "
" Germanica					0 " 19.5 "
Allium angustatum					0 " 47.5 "
Dicotyledons - Mesophytes.	Antirrhinum major	3 " 18 "	1 " 42 "	1 " 3 "	0 " 55 "
	Caltha polypetala	3 " 30 "	0 " 53 "	0 " 27 "	0 " 25 "
	Centranthus rubra	3 " 0 "	1 " 30 "	0 " 54 "	0 " 31 "
	Cherianthus Cheri	2 " 30 "	1 " 29 "	0 " 51 "	0 " 29 "
	Rumex hydropathum	1 " 20 "	0 " 29 "	0 " 16.5 "	0 " 13 "
Ever- Greens	Senecio <sup>Corymb</sup> Aeneii		3 " 2 "	2 " 8 "	
	Arbutus unedo		6 " 30 "	6 " 0 "	

The data given in Table 13 does not support Hales suggestion that Snowdrops, like evergreens, have a very low transpiration rate ( c - f page,1 ), but Hales was refering to the first months of the year. It has been shown previously that transpiration is then much lower in Galanthus (cf, Fig.7) and may therefore be more nearly equal in intensity to the transpiration of evergreen types with a low rate of transpiration as it is lower than that of mesophytic plants such as Senecio vulgaris (c.f. (Fig 25).

2. The degree of development of the vascular tissue at the Base of the leaf.

The cross-sectional area of the conducting cavities in the petiole was estimated in certain dicotyledonous plants, using the methods already described and the ratio of this area to leaf area calculated.

The results obtained are given in Appendix 14 and represented graphically in Fig. 26; the average ratios of "conducting area" to leaf area obtained at the beginning and end of the season in Galanthus nivalis and Galanthus Elwesi is also shown.

Of the plants examined those of Galanthus nivalis have the smallest development of conducting tissue in the leaf base, those of Galanthus Elwesi the next smallest while in all the dicotyledonous species the development of vascular tissue per unit of leaf surface is greater. In the two species of



Galanthus the vascular strands of the leaf pass through a region in which much of the vascular tissue is immature and useless for conduction and it is in this region that the area of the vascular tissues was estimated. In the Dicotyledons no such region occurs so that the vascular tissues are mature throughout the length of the vascular strand and there is a greater development of conducting tissue per unit of leaf surface.

Examination of other Monocotyledons in which leaf-growth is intercalary e.g. Narcissus, Leucojum, Iris, Gladiolus, suggested that the ratio of cross-sectional area of the xylem cavities in the growing region to leaf area was less than the ratio of the area of the xylem cavities at any point in the petiole or leaf base to the leaf surface in the dicotyledonous plants examined. Actual figures were not obtained for these monocotyledonous plants.

### 3. Absorption.

It was thought that it might be of interest to compare the volume of water absorbed by Snowdrop plants with that of other plants; under the same conditions. Young plants of Senecio vulgaris (about 4 inches high) and seedlings of Oat and Barley (each with one leaf expanded and the second leaf just appearing) were selected for comparison.

The methods employed were the same as those described on page 14. Only plants which had been growing in water for 7 days or more were used.

The results obtained at three different times in the season are given in Table 14, the volume of water absorbed over a period of several days being measured.

T A B L E XIV.

Volume of water absorbed by Galanthus nivalis, Galanthus Elwesi, Senecio vulgaris, Avena and Hordeum plants.

Plant (average of 3 plants)	Volume of water absorbed in c.c.		
	8-12th March	22-24th March	3-8th May
Galanthus Elwesi	2.0 c.c.	-	-
" nivalis	-	2.1 c.c.	6.5 c.c.
Senecio vulgaris	2.1 c.c.	8.6 c.c.	3.7 c.c.
Oat Seedlings	-	-	6.1 c.c.
Barley "	-	1.4 c.c.	-

The results obtained suggest that a Snowdrop plant requires about the same volume of water, under the same external conditions as a young groundsel plant or a seedling of oat.

Conclusion.

From the data given in the foregoing section it may be concluded that plants of Galanthus nivalis or Galanthus Elwesi, when approaching maturity, do not differ markedly from other plants such as Senecio vulgaris in respect of the volume of water absorbed or transpired but the conducting supply to the leaf is relatively less developed near the base of the leaf in the snowdrop plants.

Although water passing from the roots to the leaf of Galanthus must traverse the growing region in which there is a relatively small development of conducting tissue and in plants such as Senecio, Antirrhinum, Centranthus and Cherianthus the conducting strand is mature throughout its length, transpiration does not appear to be reduced in Galanthus.

This supports the conclusion that the intensity of transpiration is not directly affected by the degree of development of the conducting strand supplying the leaf. In this connection the following experiment may be mentioned as it shows that the size of a tube through which a transpiring lilac shoot obtained its water supply does not affect the rate at which water was absorbed.

Lilac shoots were cut under water and set up in an apparatus of the type figured in Fig. 27c. The cut end of the tube was passed through a hole in a rubber stopper into a tube filled with water, the lower end of the tube was filled with a rubber stopper and bent glass tubing to which was attached a capillary tube dipping into a measuring cylinder containing water. As the shoot absorbed water more water was drawn up through the capillary tube and the rate of absorption was measured by noting the change of volume in the measuring cylinder, evaporation was prevented from the water surface in the latter by a layer of oil. Capillary tubes of different sizes were used and their effect on absorption noted.

The results of the two experiments are given in Fig. 27.

In the first experiment (Fig. 27a) the absorption of three shoots was measured, each obtaining its water through a tube of different size. The capillary tubes were then interchanged and the volume of water absorbed in a given time was again measured. In each shoot an increase in absorption took place, irrespective of whether the bore of its capillary tube had been increased or decreased and this may perhaps be attributed to a slight increase in temperature and decrease in humidity.

In the second experiment (Fig. 27b) the absorption of two shoots was measured and the capillary tube of one was changed for a much larger one while the other was not changed. In both shoots a decrease in the rate of absorption took place and this may be attributed to the fact that temperature decreased and humidity increased during the latter half of the experiment.

The cross-sectional area of the smallest bored capillary tube was calculated and the leaf area of the shoot it supplied was measured and from these data it was deduced that a capillary tube of cross-sectional area 0.1184 sq.mm. was sufficient to supply a transpiring lilac shoot with a leaf area of 27700 sq.mm. at an average temperature of 69.5°F. It is interesting to compare the ratio of the tube to the leaf area (0.0004276) with the smallest ratio of "conducting

area" to leaf area observed in Galanthus, namely .00009, and to note that the latter is much the larger value.

In the absence of data as to the relative efficiency of glass capillary tubes and xylem elements for conducting purposes no great importance can be attached to the differences in the values.

Fig. 25. Average ratio of cross sectional area of xylem cavities at base of leaf to leaf surface in plants of Galanthus, and four species of Dicotyledons.

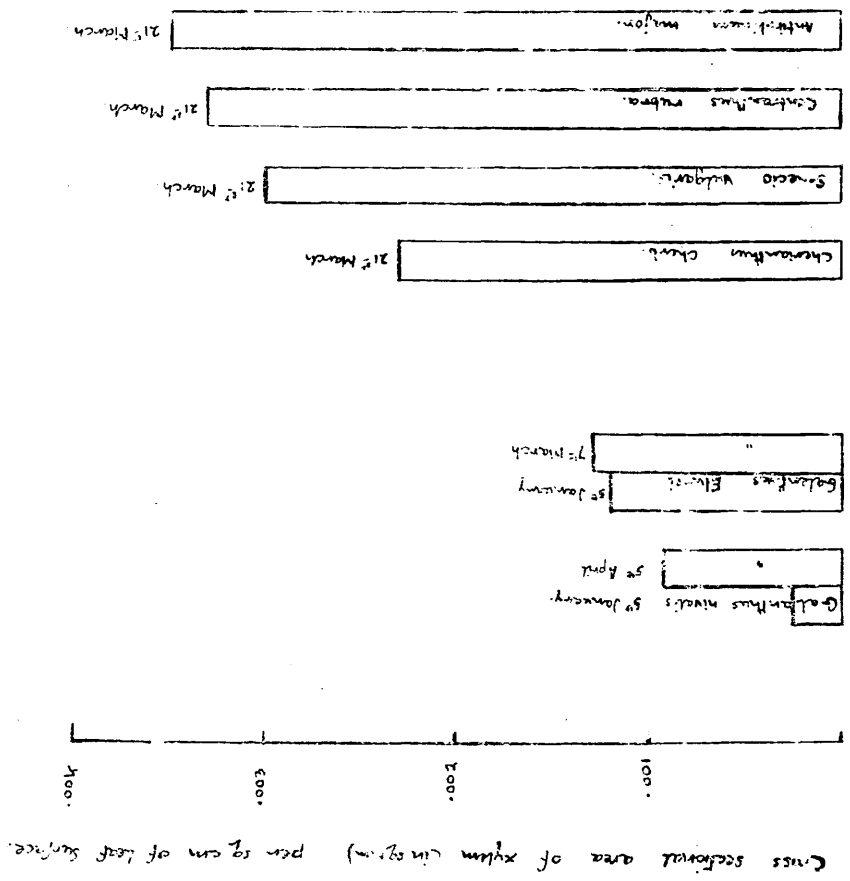
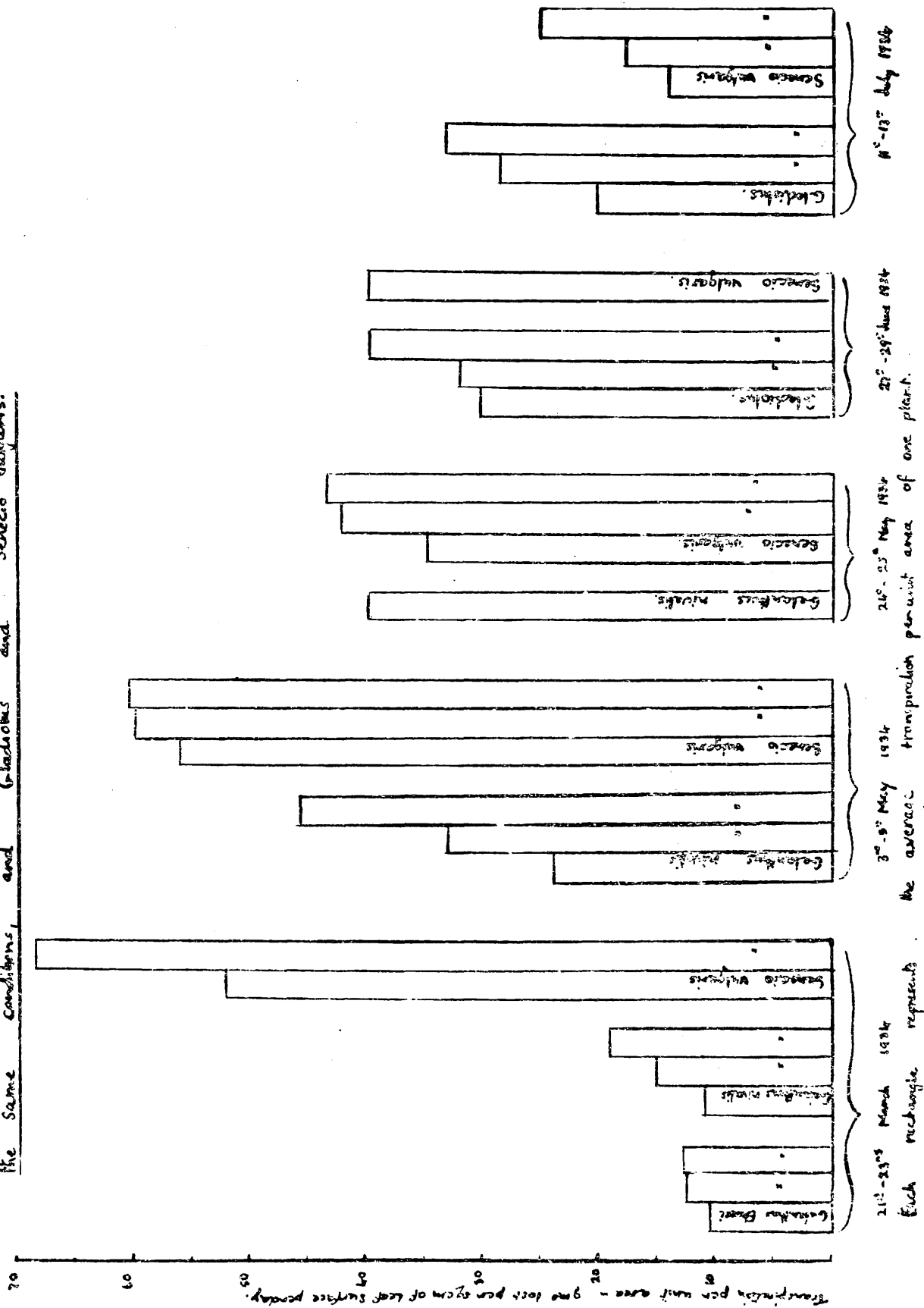


Fig. 26. Transpiration per unit area in plants of *Gadonhus* and *Senecio vulgaris* under

the same conditions, and *Gladolus* and *Senecio vulgaris*.



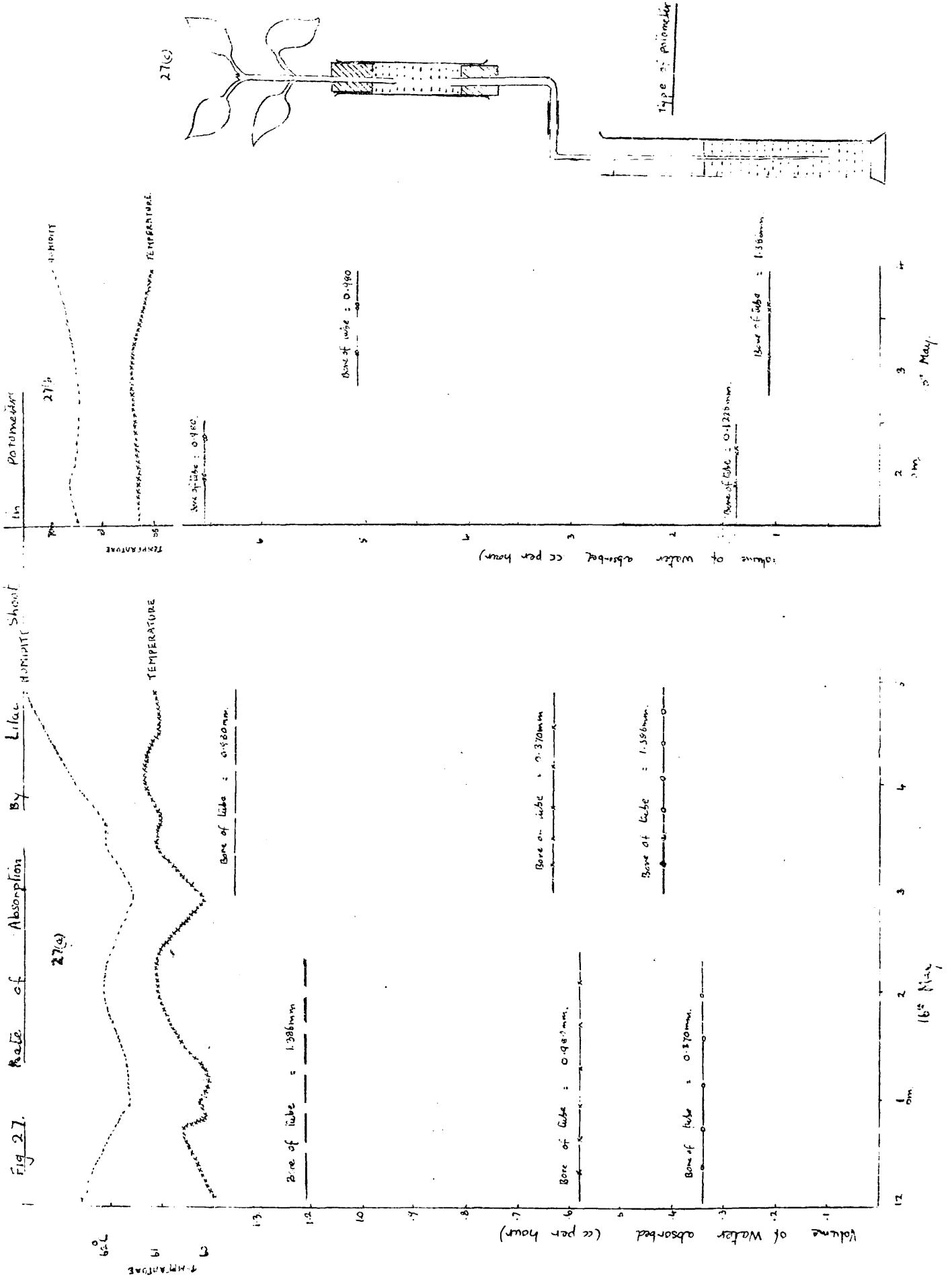
21-23 March 1934  
Each rectangle represents

3-5 May 1934  
the average transpiration per unit area of one plant.

26-28 May 1934

11-13 July 1936

Fig 27. Rate of Absorption By Lilac Humidate Shoot





S E C T I O N VII.OBSERVATIONS ON THE FOOD RESERVES IN GALANTHUS NIVALIS.

During the course of the work on "water relations" some observations were made on the storage leaves and on their starch reserves. Though these are incomplete it was thought that they are of sufficient interest to be included in this paper.

Plants of Galanthus nivalis were examined at different stages in the season and data collected on the following:-

- (a) Changes taking place within the storage cells.
- (b) Changes in thickness of the storage leaves and foliage leaf bases.
- (c) The dry weight of plants grown in soil and in water.

(a) Changes within the Storage Cells.

Halket (6) has followed the changes taking place in the storage cells of the tubercules of Ranunculus Ficaria from the time the starch is completely deposited until it is absorbed and an attempt was made to follow such changes in the bulb-scales of Galanthus nivalis. Hand sections were cut of fresh material and drawings made with aid of a camera lucida.

The food reserve consists chiefly of starch but according to Parkin (15) this is associated with an

amorphous form of Inulin. The starch occurs within the parenchymatous ground cells in the form of large grains, each with distinct striations and eccentric hilum. During the resting stage the cells are densely packed with starch grains which generally obscure the nucleus (Fig. 33a) but occasionally the nucleus was seen, and was observed to be of normal spherical type (Fig. 33b).

Soon after the leaves appear above ground etched grains were seen and vacuoles appear in the cells. (Fig. 33c). Etching begins in the region of the hilum and proceeds irregularly until the grain disappears. Hydrolysis takes place irregularly over the surface of the starch grains of barley and wheat also but in Ranunculus Ficaria it proceeds early so that the grains never appear etched. There is no matrix leaf after hydrolysis in Galanthus nivalis such as occurs in potato. Nuclei were rarely seen at this stage of growth but there is some evidence for believing that they may become lobed as in Ranunculus Ficaria.

The starch is gradually removed from the storage leaves until by the end of the season all starch and other cell contents have disappeared from the cells and the storage leaves collapse forming membranous scales.

Broadly speaking the starch is removed from the cells of the innermost scale leaf first and of the outermost last.

(b) Changes in thickness of the storage leaves and foliage leaf bases.

Transverse sections of plants grown in water were cut at a distance of 5mm. from the base of the bulb and drawings made with the aid of a camera lucida. A sketch of each plant cut was also made (see Fig. 34 a-f).

In the resting bulbs (Fig. 34a) the three storage leaf bases may be seen and the young shoot with its three leaves. The remains of last years flower stalk is also present and lateral shoots may occur . . . . .

By 2nd March the base of the sheathing leaf of the new shoot already perceptably thickened, due to the deposition of starch (Fig. 34b) and soon after (March 29th) the bases of the foliage leaves, also thicken (Fig. 34c).

The deposition of starch continues and the bases of the sheathing and foliage leaves become increasingly swollen while the storage leaves diminish in thickness. (Fig. 34d-f). The outermost storage leaf is depleted after the other two.

Finally the storage leaves collapse to form membranous scales protecting the new bulb. (Fig. 34f).

As the plants figured were grown in water the new bulbs formed were small.

The above observations were confirmed the following year in plants grown in soil and the only difference of note was that the storage leaves of the new bulb were slightly thicker.

(c) The Dry Weight of Plants at Different Periods of Growth.

The dry weight of plants was found as described in Part I, and the data obtained is given in Appendix 2. From these data the percentage dry weights of plants of different ages were calculated, and are shown graphically in Figure 35. One set of plants was grown in water, and one in culture solution (1933-4) and the other in garden soil (1934-5). It is seen that the percentage dry weight decreases steadily until near the end of the season when it increases; as the shoot and root wither, water is lost this causing the increase in percentage dry weight of the plants.

The plants were weighed before planting and from a knowledge of the average percentage dry weight of plants at that time (see Appendix 1 and page 9) the actual dry weight was calculated. The values so calculated were compared with those obtained at intervals in the season and the percentage changes found are shown in Fig. 36.

The actual dry weight of the plants growing in soil decreases in the early part of the season. This may be attributed to the fact that the plants were living on their food reserves and it is not until about February that the leaves are expanded and photosynthesis is possible. The dry weight begins to increase in late February and as the sheath and foliage leaf bases begin to thicken about this time (Fig. 34b) it may be concluded that the accumulation of food

reserve for the new bulb is taking place. Near the end of the season the increase in dry weight stops: this may be attributed to the fact that the withered shoot and root systems are being shed.

The dry weight of the plants was found to be actually less at the end of the season than at the beginning, probably as a result of the leaves withering unusually early.

The changes in dry weight follows a similar course for plants grown in water. At first the dry weight surprisingly increases slightly; this might be due to an error in calculating the original dry weight (c f Table I). The dry weight then decreases but becomes more constant in mid-season, suggesting that the formation of starch has began and is replacing that used. Finally the dry weight decreases as is the case with plants grown in soil and there is a net decrease in dry weight during the season.

Fig 33

*Galanthus nivalis*

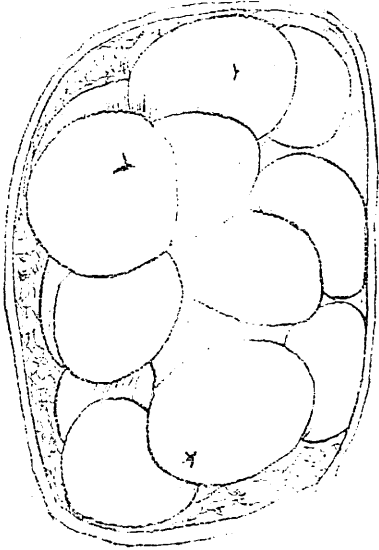
Cells from

storage layer of

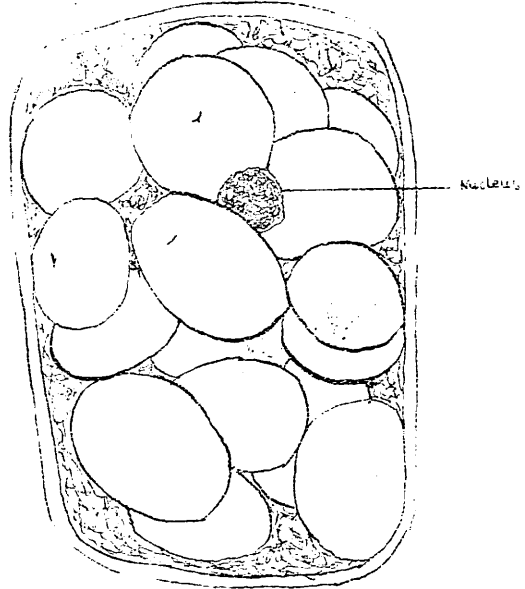
Bulbs

(x 20)

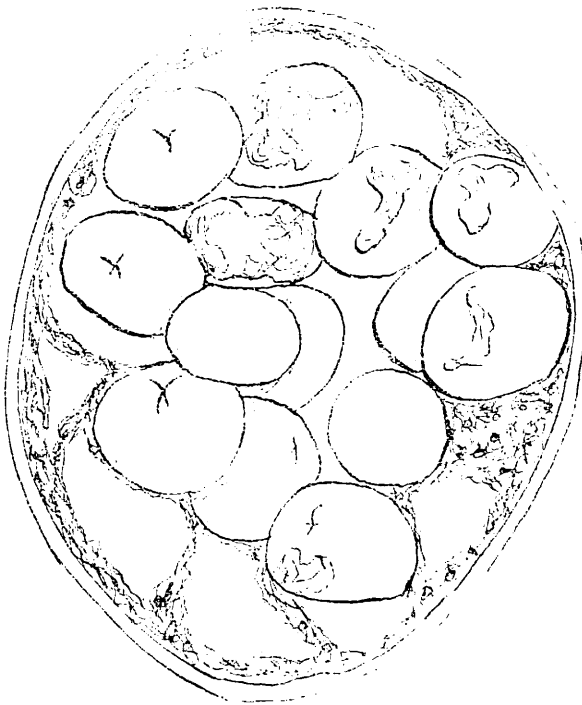
33 (a) 14 December 1933



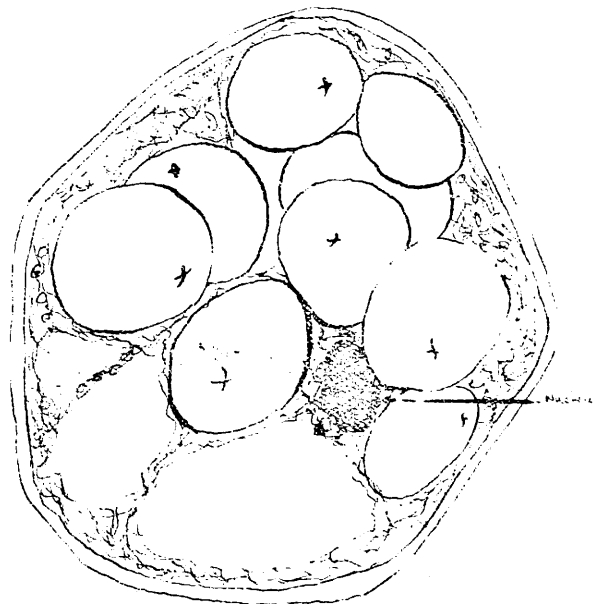
33 (b) 16 December 1933



(c) 19<sup>th</sup> February 1934

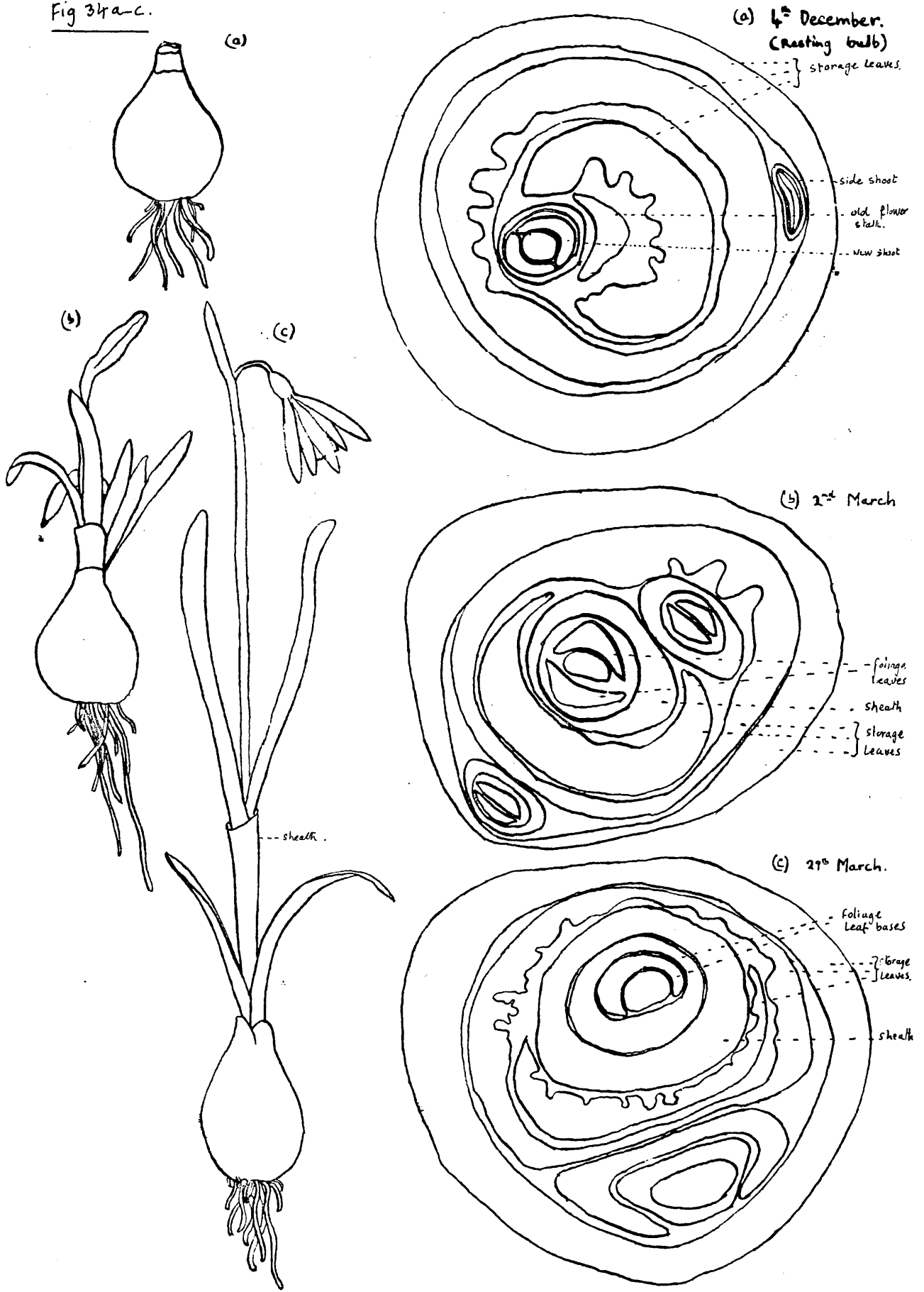


33 (d) 19 February 1934



*Galanthus nivalis* T.S. Bulbs of different ages 5mm above base ( $\times 4\frac{1}{2}$ )

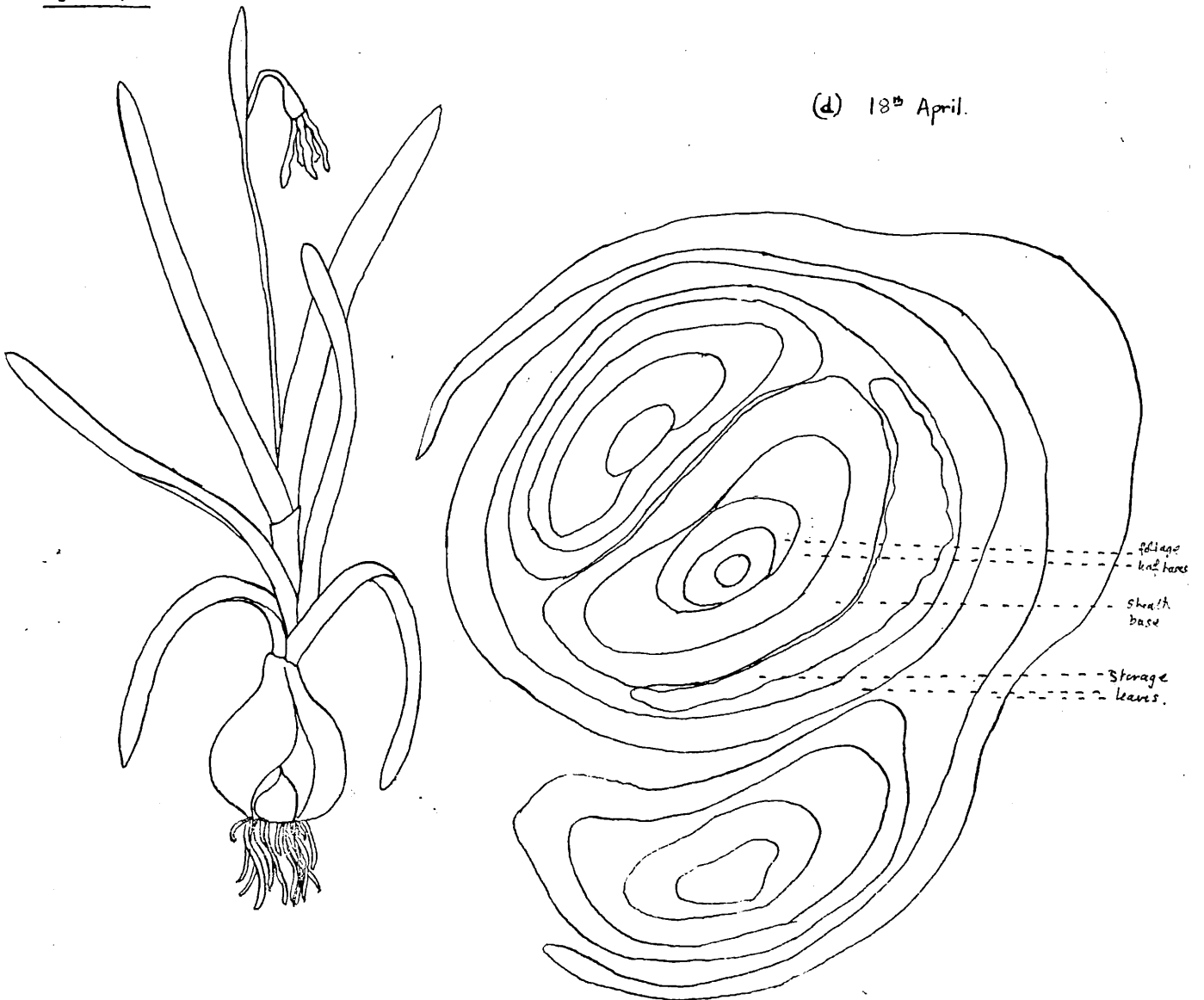
Fig 34a-c.



Galanthus nivalis - T.S. Bulb 5mm. above base (x42)

Fig 34 (d)

(d) 18<sup>th</sup> April.



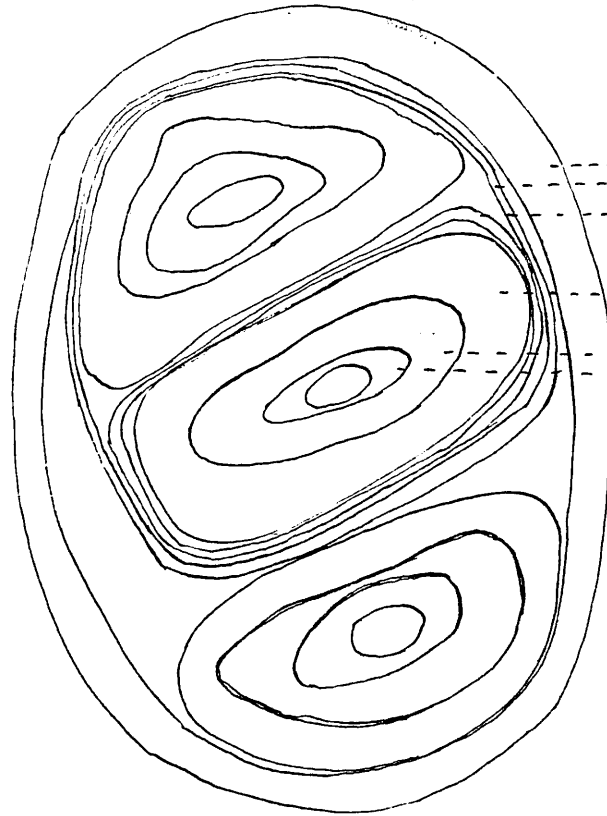
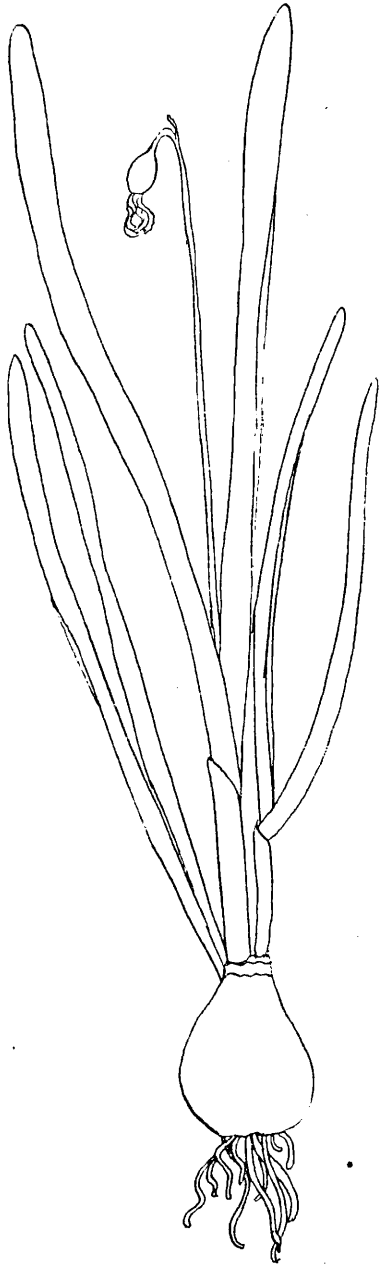


Galanthus nivalis - T.S. Bulbs of different ages 5mm above base (x4½)

(e)

Fig. 34 e-f.

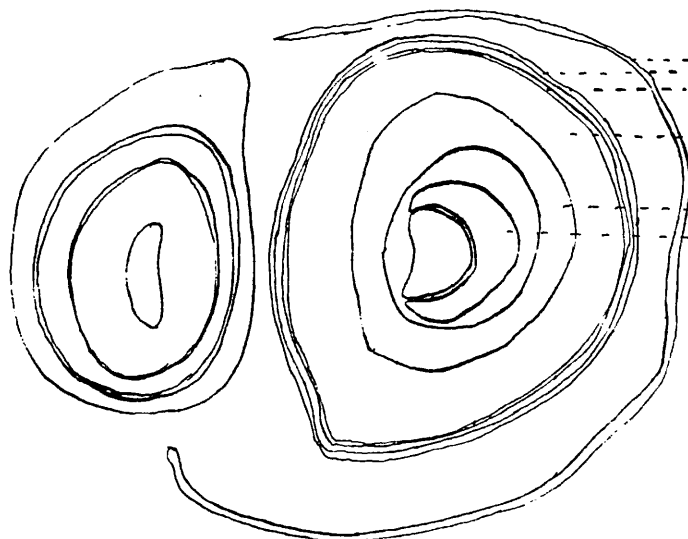
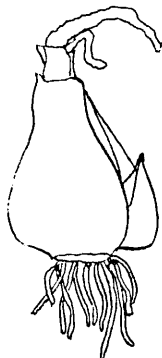
(e) 25<sup>th</sup> April.



storage leaves.  
base of sheath  
base of foliage leaves.

(f) 15<sup>th</sup> May.

(f)



depleted storage leaves.  
sheath base  
foliage leaf bases.

Fig 35 *Galanthus nivalis* - Percentage dry weight of plants at different stages of growth.

— Average of 10 plants grown in soil (1934-5)  
 —○— " " " " culture solution (1933-4)  
 —x— " " " " water (1933-4)

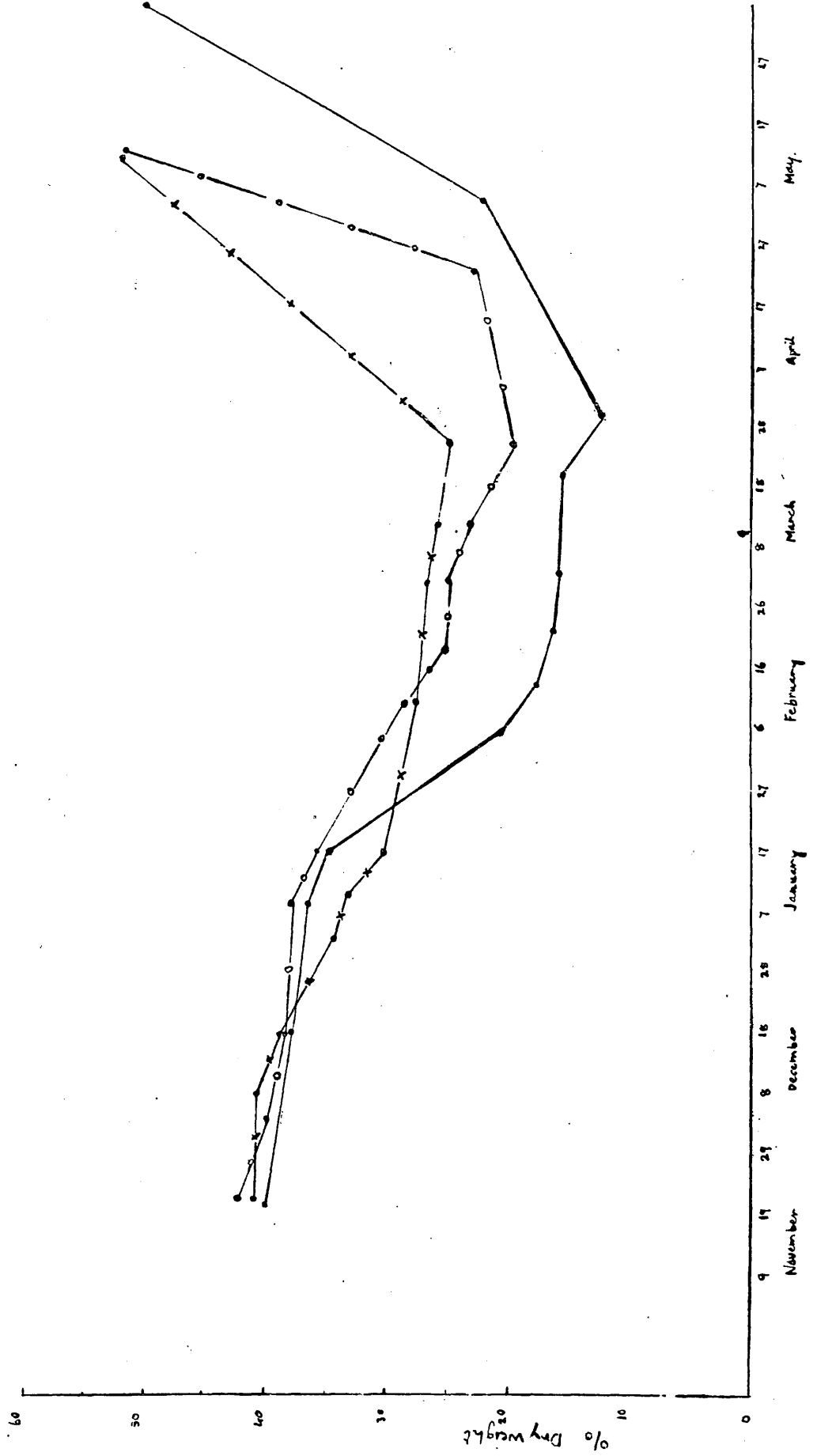
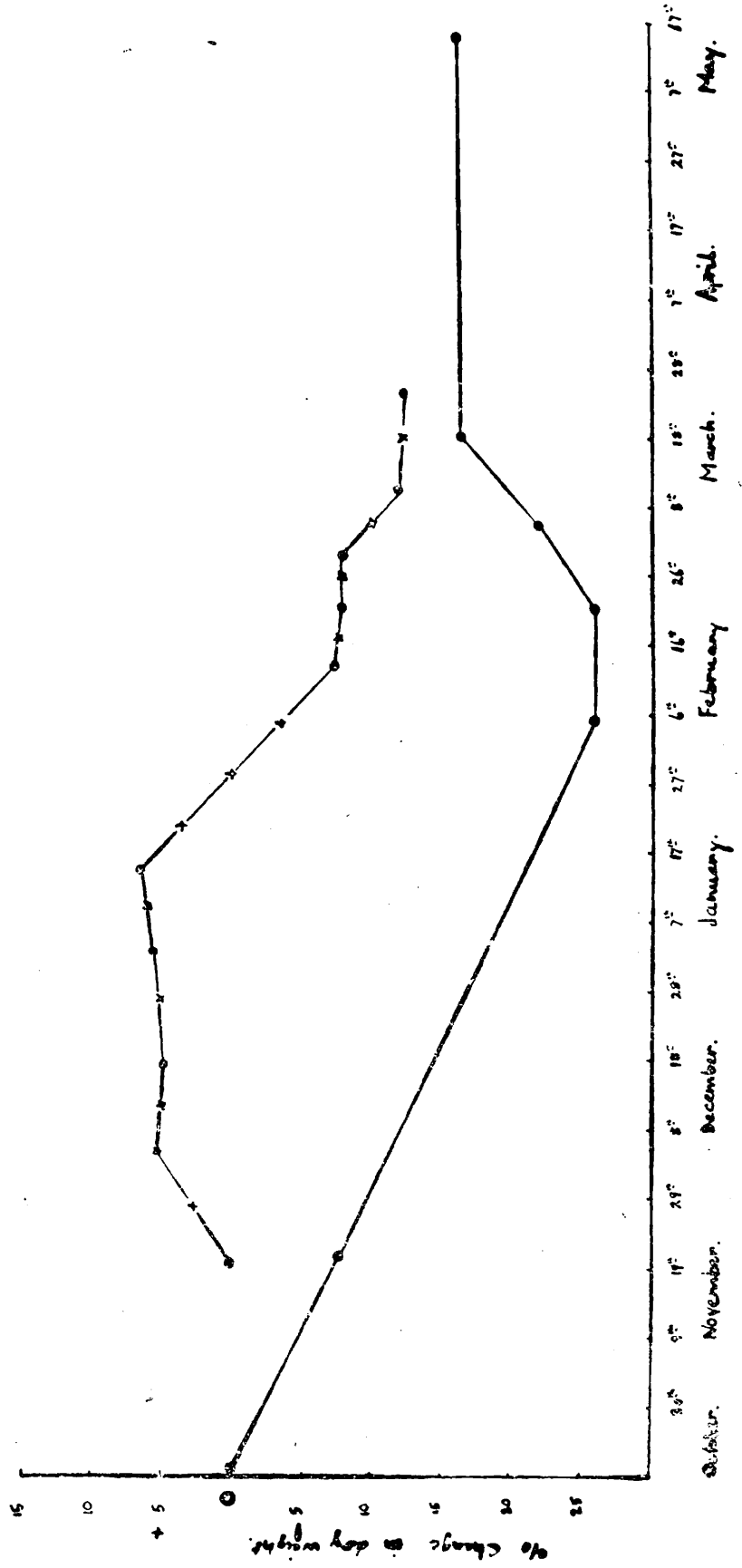


Fig 36 *Galium aparine* - Percentage change in dry weight of plants at different stages in growth compared with the dry weight (calculated) when planted the previous Autumn.

— Average of 10 plants grown in soil (1934-5)  
 -x- " " " " water or culture solution (1934)



S E C T I O N VIII.GENERAL CONCLUSION.

It may now be of interest to give a brief account of the season's growth cycle of Galanthus nivalis in the light of information already given regarding its water relations at different stages of growth.

Early in the Autumn numerous adventitious roots develop round the periphery of the basal part of the bulb and there absorb water so that the water content of the bulb begins to increase. Soon the young shoot, already formed within the bulb, begins to elongate and by the end of the year has pushed its way up through the ground. Eventually the leaves and flower are expanded. All this time the water content of the plant has been increasing, indicating that the volume of water absorbed is in excess of that given off in transpiration as has been shown by experiments.

As the leaves expand there naturally is a considerably increase in the area of the transpiring surface and in addition temperature tends to increase as the season proceeds so that the volume of water lost in transpiration also increases, to keep place with this the rate of absorption is accelerated.

It has been found that the 'relative transpiration ratio' increases through the season as the plants age.

It may be objected that the 'relative Transpiration ratio' does not give a measure of the intrinsic transpiring power of the plants and that the increase observed in the ratio is due to changes in external conditions affecting transpiration and evaporation unequally. However by planting bulbs late and thus retarding their growth it was possible to compare at the same time the rate of transpiration in plants of different ages when this was done it was found that the older plants transpired more intensely than the younger ones. The increase in 'relative transpiration Ratio' of plants as they age is therefore thought to be due to a change in the plant itself and not to be the result of changes in external atmospheric conditions.

The increase in the 'relative transpiration ratio' with age might be attributed to one of the following causes:-

1) Changes in the rate of absorption. Maximov (12) considers that transpiration is greatly affected by the rate at which water is taken in by the roots. Absorption is affected by

- (a) The degree of development of the root system. The root systems of older plants were observed to be not markedly better developed than those of the younger ones..
- (b) The water content of the soil. All plants used in the experiments described above were potted in glass tubes of the same size and watered about the same amount before

each experiment, so that differences in the water content of the pots of soil would be small.

- (c) The type of soil. The plants used were potted up at the same time in ordinary potting soil so that there is no reason to suppose that the soil of the plants used early in the season differed from that of the later plants.

It was thought therefore that the increase in the 'relative transpiration Ratio' was not due to a change in the rate of absorption.

2. Changes in the number of stomata per unit area of leaf surface. The data, described above, obtained by comparing the intensity of transpiration on the adaxial and abaxial surface of the leaf of Galanthus nivalis, Galanthus Elwesi and Narcissus poeticus and examining their stomatal distribution suggested that an increase in the number of stomata per unit area would result in an increase in transpiration. Wicks(20a) has shown however that the number of stomata per unit area decreases in each successive portion of the leaf interpolated by intercalary growth at the base of the leaf. The increase in the 'relative transpiration ratio' cannot there be attributed to changes in the number of stomata per unit area.

3). Changes in the degree of development and type of element composing the conducting strand which supplies the transpiring leaf surface. Water passing from the roots to the leaf surface must traverse the growing region of the leaf in which much of the conducting tissue is unligified. It has been shown above that the cross sectional area of the xylem in the growing region (the 'conducting area') increases as the plants age and also the ratio of 'conducting area' to leaf area increases through the season, so that the older the leaf the better is its water supply. By measuring transpiration and the conducting area in individual plants it was found that transpiration is not directly affected by the degree of development of the vascular system in the growing region and a plant in which the ratio of conducting area to leaf area is relatively high will not necessarily have a higher rate of transpiration than one in which the ratio is lower. The data suggests however that there is some relationship between transpiration and the degree of development of the conducting tissues in the growing region for as transpiration increases, making greater demands on the conducting system, a corresponding increase takes place in the amount of conducting tissue in the growing region of the leaf.

The transpiration of mature plants of Galanthus nivalis has been compared with that of certain mesophytic dicotyledonous plants and was found not to differ considerably from that of the latter although the conducting supply to the leaf is less developed in the snowdrop.

Earlier in the year the rate of transpiration of Galanthus nivalis is much lower than it is when the plants are mature so that the transpiration of young plants is probably much lower than that of the mesophytic dicotyledons and at that period would probably be about equal to that of evergreen plants. A point of interest in view of Hale's suggestion (page 1). Owing to the slow rate of transpiration and other experimental difficulties it was not possible to compare experimentally the rate of transpiration of Galanthus with that of evergreens.

The water relations of Galanthus Elwesi have not been investigated as fully as those of Galanthus nivalis but the data obtained suggest that they are similar to Galanthus nivalis. Transpiration increases through the season but plants of Galanthus Elwesi appear to transpire less per unit area than plants of Galanthus nivalis under the same conditions although the vascular supply to the leaf is better developed in the former.

The data already described relating to the intensity of transpiration in plants of Galanthus nivalis and Galanthus Elwesi at different ages and the amount of xylem in the growing region of the leaf are of interest as they are in agreement with the view held by Haberlandt, Kerner and others (c.f. p. 2-4) that the degree of development of the conducting strand varies according to the needs of the transpiring surface it supplies.



SECTION IX.SUMMARY.

1. The water content and fresh weight of plants of Galanthus nivalis grown in tap water and a Knop's Culture Solution (1933-4) and garden soil (1934-5) was found to increase from the time of planting until the shoots withered at the end of the season.
2. The volume of water absorbed during the season 1933-4 by plants of Galanthus nivalis grown in U-tubes (of the type shown in Fig.3) filled with water was measured by filling the U-tubes up at intervals from a burette. The volume of water absorbed by individual plants varied from 4 to 25 c.c.
3. In eight plants of Galanthus nivalis investigated absorption was found to increase as the season proceeded.
4. The relationship between absorption and transpiration was investigated by weighing plants of Galanthus nivalis and Galanthus Elwesii in U-tubes. It was found that absorption was equal to or very slightly in excess of transpiration over a period of about three days.

5. The daily march of transpiration in Galanthus nivalis was measured at three different stages of growth in 1934 by weighing potted plants. Evaporation was also measured and the 'relative transpiration ratio' calculated, this was found to:-
- a) increase through the season
  - b) be higher during the day than at night.
6. The 'relative transpiration ratio' of plants of Galanthus nivalis and Galanthus Elwesi was measured at different stages of growth in 1935 and it was found that the 'relative transpiration ratio':-
- a) increased through the season with the age of the plants investigated.
  - b) was not consistently higher during the day than at night.
7. The transpiration of plants of Galanthus nivalis retarded by planting two months late was compared with that of other plants which had been planted at the normal time. It was found that transpiration per unit area was more intense, under the same conditions, in the older plants.
8. Intensity of transpiration on the adaxial and abaxial leaf-surfaces has been compared by means of Cobalt Chloride paper in Galanthus nivalis, Galanthus Elwesi and Narcissus poeticus. It was found that transpiration was more intense on the abaxial surface than the adaxial surface in

Galanthus nivalis whereas in Galanthus Elwesi the adaxial surface transpired more intensely; in Narcissus poeticus transpiration was about equal on the two surfaces. It is suggested that these differences may be correlated with differences in the number of stomata per unit area on the two leaf surfaces, since in Galanthus nivalis the abaxial surface has the greater number of stomata per unit area, in Galanthus Elwesi the adaxial and Narcissus poeticus the two leaf surfaces differ little in the number of stomata per unit area.

9. By weighing potted plants of Galanthus nivalis and cut leaves supported with their ends in water a comparison was made of the rate of transpiration of cut leaves and leaves attached to growing plants. It was found that the latter transpired more intensely than cut leaves.
10. Plants of Galanthus nivalis and Galanthus Elwesi have been marked to confirm the fact that the growing region of their leaves, is situated within the bulb just above the base of the leaf.
11. The anatomy of the growing region of the leaf has been investigated in Galanthus nivalis and Galanthus Elwesi. Drawings to illustrate the changes taking place with age in the conducting tissue of that region are given for both species.

13. By placing plants of Galanthus nivalis and Galanthus Elwesi in dyes it was found that the unlignified elements in the growing region of the leaf were unable to conduct solutions of dyes, confirming Wicks(20a) observations on Narcissus.
14. The cross-sectional area of the lignified xylem elements in the growing region of the leaves of Galanthus nivalis and Galanthus Elwesi has been measured at different stages of growth. This area has been termed the 'conducting area' and was found to increase with the age of the plants examined.
15. The ratio of conducting area to leaf area has been calculated in individual plants of the two species of Galanthus. This ratio was found to increase markedly through the season with the age of the plants examined in Galanthus nivalis. In Galanthus Elwesi the increase observed was much smaller. In this species the ratio was consistently higher than in Galanthus nivalis.
16. The data obtained has been examined to see if any direct connection exists between the increase in the relative transpiration ratio and the increase in the ratio of conducting area to leaf area, since an increase in the latter will result in a better water supply to the leaf. The evidence suggests that the increase in the relative transpiration ratio is not a direct result of the better

developed vascular supply in the growing region. It is suggested that an increase in the amount of conducting tissue in the growing region takes place to meet the extra demands made on it by the transpiring leaf surface.

17. Comparison of the intensity of transpiration in Galanthus and other plants (by weighing and by means of cobalt chloride paper) showed that Galanthus transpires only slightly less intensely than mesophytic dicotyledons such as Senecio vulgaris and much more intensely than an evergreen such as Arbutus Unedo.
18. The area of the conducting tissue at the base of certain dicotyledonous leaves was measured and the ratio of leaf area calculated. This was found in each case to be greater than the ratio of 'conducting' area to leaf area obtained for Galanthus.
19. Details are given of an experiment which showed that the rate of absorption of a cut lilac shoot is not affected by the size of the capillary tube through which it obtains its water supply.
20. Observations on the food reserve in the bulb of Galanthus nivalis are given at different stages of growth. Changes taking place through the season within the storage cells and in the thickness of the storage leaves are illustrated and data obtained on the dry weights of plants at different stages of growth are given.

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Appendix 1.Galanthus nivalis Water Content of Resting bulbs.

Date	Bulb	Fresh weight in grams	Dry weight in grams	Water content in grams	% water content
8th Nov.1933	A B	2.5701	0.9314	1.6387	63.8
	A1	2.4036	0.9492	1.4544	60.5
	A4	2.3856	0.9596	1.4287	59.8
	A9	4.4244	1.7960	2.6280	59.4
	A10	2.4404	0.9910	1.4494	59.5
	A2	2.2737	0.9259	1.3478	59.3
	A7	2.5516	1.1077	1.4479	56.9
	A6	2.0691	0.9215	1.1476	55.6
	A5	2.2130	1.0150	1.1980	53.1
	A3	2.0802	0.9865	1.0937	53.1
	B10	1.7061	0.6055	1.1006	64.5
	B2	3.0949	1.2250	1.8699	62.2
	B1	3.4504	1.2250	2.2254	60.8
	B4	3.5756	1.4051	2.1705	59.4
	B7	3.4328	1.4226	2.0102	58.5
	B8	2.9212	1.2676	0.6576	57.7
	B6	2.2700	0.9383	1.3317	56.7
	B9	2.9044	1.2757	0.6297	56.1
	B5	1.7606	0.7963	0.9643	54.8
	20th Oct.1934	E10	1.275	0.4545	0.8205
E7		1.273	0.463	0.810	63.7
E3		1.262	0.475	0.787	62.4
E5		0.845	0.3255	0.5195	61.5
E2		1.4133	0.555	0.858	60.7
E1		1.645	0.6615	0.9835	59.8
E4		1.246	0.512	0.734	59.7
E9		1.392	0.585	0.807	58.0
F7		1.270	0.463	0.807	63.5
F5		0.833	0.3255	0.5125	61.0
F4		1.299	0.512	0.787	60.6
F-					59.1
F-					58.5
F10		1.0725	0.4545	0.6180	57.6
F6		0.872	0.463	0.409	56.1
F9	1.329	0.536	0.793	56.0	
8th Nov.1933	C1-10	25.1206	10.5798	14.5408	58.2
	D1-10	21.5097	10.4972	11.0125	56.4
20th Oct.1934	G1-10	14.143	5.264	8.879	63.6
	H1-10	11.821	4.5255	7.2955	61.7

Appendix 2(a).

Galanthus nivalis - Water content, and Increase Fresh and Dry Weight of Growing Bulbs.

Tap water - 1933 - 4. Sets of 3.

Date	Bulbs	Autumn Weight Fresh	Fresh Weight	Dry Weight	Water Content	Autumn Wt. calculated Dry	Increase Fresh Wt.	Change Dry Wt.	% water	% change Dry Wt.
4 Dec.	G1	6.5236	6.0555	2.0466	3.8820	2.544	0.4731	.103	59.3	4.05
4 "	G2	6.5940	6.1380	2.7003	3.8937	2.578	0.4560	.132	59.1	5.14
17 "	G3	7.3310	6.3163	2.9122	4.4188	2.653	1.0147	.259	60.3	9.76
17 "	G4	7.2645	6.7602	2.8784	4.3861	2.839	0.5043	.039	60.5	1.37
1 Jan.	G5	7.2233	6.0645	2.4713	4.7520	2.547	1.1588	-.076	65.8	2.98
1 "	G6	7.1918	5.9116	2.4991	4.6927	2.483	1.2756	.026	65.2	1.05
8 "	G7*			2.0742	3.2274				60.9	
8 "	G8	9.1374	6.7700	2.7229	6.4145	2.839	2.3674	-.117	70.2	3.93
15 "	G9	10.8882	8.3581	3.3810	7.5072	3.510	2.5601	-.139	68.5	3.96
15 "	G10	7.1169	5.9708	2.8724	4.2445	2.408	1.1461	.464	59.4	19.27
12 Feb.	G11	8.1118	5.9417	2.3794	5.7324	2.4955	2.2701	-.116	70.7	4.65
12 "	G12	7.1076		1.8205	5.2871				74.7	
19 "	G13	8.8172	5.5868	2.2459	6.5713	2.346	3.2314	-.100	74.5	4.274
19 "	G14*	6.2702		1.7897	4.4805				71.4	
28 "	G15†	3.000		0.8190	2.181	3.0295			72.8	
28 "	G16	8.9086	6.3939	2.4284	6.4802	2.685	2.5147	-.257	72.8	9.51
12 Mar.	G17	11.860	7.1487	2.525	9.335	3.002	4.7113	-.477	75.9	15.89
12 "	G18	11.405	6.5816	2.610	8.795	2.764	4.8234	-.134	77.6	5.37
27 "	G22	10.5865	6.1306	1.8508	8.7337	2.573	4.4542	-.724	82.5	18.10
27 "	G23	12.6919	6.0625	2.893	9.799	2.546	6.6294	.752	77.2	13.82
15 May	G30*	2.8916		1.6493	1.2423				43.1	
15 "	G27*	3.2351		1.6097	1.6254				50.2	

\* values refer to 2 bulbs only  
† " " " 1

Appendix 2(b).

Galanthus nivalis - Water content, and Increase Fresh and Dry Weight of Growing bulbs.

Culture solution 1933-4 Sets of 3 bulbs.

Date	Bulbs	Fresh Weight	Dry Weight	Water Content	Autumn Fresh Wt.	Autumn Dry Wt. Calculated	Increase Fresh Wt.	Change Dry Wt.	% water	% Increase Fresh Wt.	% change Dry Wt.
7 Dec.	H1	6.4056	2.8534	3.5522	6.4056	2.5735	0.2883	.2797	55.5	4.7	16.9
7 "	H2	6.1528	2.6522	3.7006	5.7809	2.3280	0.4719	.1242	60.1	8.2	5.3
17 "	H3	6.3992	2.6648	3.7344	5.9492	2.4986	0.4500	.1662	58.4	7.6	6.7
17 "	H4	7.0979	2.8075	4.2904	6.6220	2.7812	0.4759	.0263	60.5	7.2	.9
1 Jan.	H5	8.0883	2.9649	5.1234	6.7432	2.8321	1.3450	.1328	62.5	20.0	4.7
1 "	H6	7.0070	2.7901	4.2169	6.5084	2.7335	0.4986	.5566	60.2	7.7	20.4
8 "	H7*	4.9710	1.8616	3.1094		3.0691			62.6		
8 "	H8	8.4946	3.1212	5.3734	6.9264	2.9091	1.5682	.2121	60.3	22.6	7.3
15 "	H9	6.0371	3.0796	4.9595	7.3256	3.0768	0.7155	.0030	61.7	9.7	.9
15 "	H10*	4.2681	1.3806	2.8875					64.6		
12 "	H11	8.9994	2.6182	6.3812	6.9740	2.9291	2.0234	.3089	70.1	29.1	10.5
12 "	H12*	5.0895	1.2980	3.7915					74.5		
19 Feb.	H13	8.7942	2.2697	6.5245	6.3760	2.6779	2.4182	-.4082	74.2	37.9	-15.2
19 "	H14	9.0368	2.2475	6.7893	5.8202	2.4444	3.2166	-.1969	75.1	55.3	-8.1
28 "	H15	11.0618	2.7795	8.2223	6.7094	2.8179	4.2924	-.0384	74.7	64.0	-1.4
28 "	H16	9.5870	2.4965	7.0905	6.7812	2.8481	3.8058	-.3516	74.0	56.1	-12.3
12 Mar.	H17	10.4060	2.5250	7.8810	7.0657	2.9876	3.3403	-.4626	74.7	47.3	-15.5
12 "	H18	10.4360	2.3605	8.0755	6.1081	2.5634	3.2790	-.2049	77.4	53.7	-8.0
27 "	H19	12.6666	2.4224	10.462	6.8920	2.8946	5.7766	-.4722	80.9	83.8	-16.3
27 "	H20	12.0686	2.3372	9.3140	6.8474	2.8759	5.2212	-1.5387	80.5	76.3	-18.7
20 Apl.	H24*	7.3136	1.7182	5.5954	5.7380				76.4		
20 "	H27	11.0100	2.6208	8.2892	6.4673	2.7165	4.6427	-.0955	76.6	71.8	-3.6
15 May	H23	3.6616	2.0890	1.5726	6.4706				42.9		

\*2 bulbs only

Appendix 2(c).

Galanthus nivalis - Water content and Change in Fresh and Dry Weights of Growing Bulbs.

Soil 1934 - 5 Sets of 10.

Date	Bulbs	Fresh Weight	Dry Weight	Water Content	Autumn Fresh wt.	Autumn Dry wt. Calculated	Increase Fresh Wt.	Change Dry Wt.	% water	% Increase Fresh Wt.	% change Dry Wt.
4 Nov.	K5	17.853,	5.380	12.473	14.471	5.838	3.382	-.455	59.9	23.3	-7.8
14 Jan.	K3	23.297	8.408	14.889	14.627	5.850	8.670	2.558	63.9	59.7	
4 Feb.	K8	21.857	3.960	17.897	13.424	5.370	5.146	-1.413	77.7	62.8	-26.3
20 Feb.	K4	24.315	4.272	10.043	14.443	5.770	9.872	-1.50	82.4	68.4	-26.0
6 Mar.	K10	28.800	4.582	14.218	14.735	5.894	14.062	-1.312	84.4	95.4	-22.3
19 Mar.	K6	29.250	4.730	14.520	14.194	5.671	15.053	-0.944	83.9	100.6	-16.6
29 Mar.	K2	33.573	5.852	17.721	15.663	6.250	17.910	-1.983	87.3	114.4	-31.7
3 May	K1	27.590	6.168	14.220	15.355	6.142	12.243	-0.974	77.7	79.8	-15.9

Appendix 3.

Galanthus nivalis - Total amount of water absorbed at intervals during season by 8 individual plants grown in water. 1933 - 4.

Bulb J	2 Nov.-9 Feb.	9 Feb.-1 Mar.	1-13 Mar.	13-27 Mar.	Total c.c.
3	4.55c.c.	1.6c.c.	2.5c.c.	5.3c.c.	11.95
8	4.82 "	1.8 "	2.0 "	4.5 "	13.12
22	3.58 "	0.2 "	0.4 "	4.0 "	8.18
24	4.48 "	1.5 "	2.6 "	7.4 "	15.98
25	2.28 "	0.7 "	1.8 "	3.5 "	8.28
26	3.81 "	1.5 "	2.6 "	2.9 "	10.81
9	2.74 "	1.4 "	3.9 "	8.2 "	16.24
11	2.30 "	0.1 "	0.5 "	0.75 "	3.65
Average	3.65 "	1.10 "	2.04 "	4.18 "	10.74
Amount per day	0.05 "	0.055 "	0.17 "	0.30 "	

Appendix 4.

Galanthus nivalis. Change in dry weight and Total Volume of water absorbed during the season 1933-4(20 Nov-20 April) by individual plants grown in water and culture solution.

Bulb	Original dry weight (calculated)	Final dry weight (measured)	Volume of water absorbed (measured)
K24	0.9164 grms	0.7812 grms	25.3 c.c.
F 16	1.058	0.6560	16.2
K13	1.074	0.8814	16.0
K9	1.3920	1.2430	13.4
K23	1.303	0.9030	13.3
F9	1.046	0.9038	13.1
F2	0.8354	0.6500	12.9
K21	1.355	0.8042	12.0
K20	0.8808	0.7420	10.8
K18	1.053	0.8475	10.7
K15	1.360	0.8675	10.1
K26	0.9623	0.7554	9.4
K10	1.303	1.1636	9.0
K8	0.7947	0.5538	8.3
K1	1.377	1.1420	8.1
F12	0.8760	0.7444	7.2
K16	1.031	0.6250	6.6
K3	1.071	0.9115	6.5
K11	1.226	0.8220	6.2
F1	1.338	0.5384	5.8
K6	0.9804	0.7554	4.7
K12	1.066	0.9468	4.6
K29	0.9315	0.7038	4.5
K14	0.9143	0.6383	3.9

Abberrviation used in Appendix 5 7 and 9.

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Abbreviation		Unit
L	Leaf area	l sq. cm.
Ls	Loss in weight	l mg.
T	Transpiration per unit area	l mg. per sq.cm.
T/E	Relative transpiration ratio	
C	Conducting area	l sq. mm.
C/L	Conducting area/leaf area	
T-C/L	Transpiration per unit area divided by conducting area/ leaf area	
Ln	Length of Leaf.	lmm.

Appendix 5a.Experiment 1. 2nd - 5th January.

	Day of Expt.	N2	N7	N9	N3	N5	Average
L	1	4.8	4.3	4.1	4.8	5.3	48.5
	2	4.9	4.4	4.2	4.9	5.4	
	3	5.0	4.5	4.3	5.0	5.5	
Ls	1	10	2.5	10	7	5	11
	2	20	15	15	15	13	
	3	12.5	7.5	12.5	7	15	
T	1	2.04	0.57	2.38	1.31	1.01	21.7
	2	4.00	3.39	3.44	2.62	2.61	
	3	2.50	1.63	2.33	1.47	1.19	
T/E	1	0.532	0.148	0.621	0.329	0.276	.497
	2	1.051	0.876	0.916	0.675	0.683	
	3	0.457	0.224	0.462	0.290	0.322	
C	3	.0004814	.000728	.000629	.000500	.000495	.005867
c/L	3	.0000966	.0001648	.0001389	.0001000	.0000900	.0001181
T-C/L	3						287.7
Ln	1	10	9	7	9	12	
	2						
	3	20	19	23	21	25	



Appendix 5b.Experiments 2. 31st January - 2nd February 1935.

	Day of Expt.	PLANTS					Average
		N20	N11	N12	N13	N14	
L	1	11	12.5	16	11	9	12.4
	2	11.5	13	17.9	13	9.5	
Ls	1	58	58	90	52	83	61
	2	50	60	64	20	72	
T	1	5.27	4.68	5.62	4.73	9.22	5.29
	2	4.37	4.62	3.88	1.76	7.69	
T/E	1	.9078	.7988	.8138	.8138	1.1616	.9816
	2	1.075	1.141	.9590	.4360	.900	
C	2	.002675	.003075	.004150	.2338	.2775	.3005
C/L	2	.0002674	.002375	.0002500	.000231	.6002938	.0002503
T-C/L	2	20175	19195	1856	15895	2995	20755
Ln	1	55.5	50	57.5	52	44.5	
	2	62.5	61.5	82.5	61.5	51	

Appendix 5c.Experiment 3. 21st - 22nd February, 1934.

	Day of Expt.	PLANTS					Average
		N15	N16	N17	N18	N19	
L	1	19	19	25	22	20	23.5
	2	21.5	21.9	27.8	23.5	22.8	
Ls	1	223	298	198	251	245	236
	2	229	195	375	232	210	
T	1	12.27	12.68	7.92	11.41	12.26	10.83
	2	10.65	8.90	13.49	9.87	9.20	
T/E	1	2.105	2.693	1.360	1.959	2.103	18.25
	2	1.639	1.370	2.075	1.519	1.417	
C	2	.01760	.016425	.01411	.01695	.01816	.01665
C/L	2	.0008185	.0007501	.0005076	.0007211	.0008011	.0007193
T+C/L	2	13125	15015	20310	14200		15710
Ln	1	107	104	138.5	119	110	
	2	114	117	149	128.5	123.5	

Appendix 5e.

Experiment 4b. 7th - 9th March, 1934.  
(2 plants planted 2 months later).

	Day of Expt.	PLANTS		Average
		N24	N25	
L	1	15.8	10	11.0
	2	16.6	11.4	
Ls	1	36	73	76
	2	116	80	
T	1	2.28	7.30	5.70
	2	6.98	7.30	
T/E	1	04010	8106	829
	2	1040	1057	
C	2	.006834	.006456	.006645
C/L	2	.0004112	.0006033	.0005073
T-C/L	2	11650	11110	11480
Ln	1	80	69	
	2	90	75	

Appendix 5d.Experiment 4a. 7th - 9th March, 1934.

	Day of Expt.	PLANTS					Average
		N20	N21	N22	N23	N27	
L	1	23.5	31.7	24.3	29.7	34.2	29.9
	2	25.0	33.1	25.1	31.1	36.2	
Ls	1	171	272	346	567	368	
	2	165	266	276	311	414	
T	1	7.28	8.58	14.2	19.09	10.60	
	2	6.61	8.04	10.8	16.62	11.44	
T/E	1	1.280	1.409	2.393	3.359	1.866	18.05
	2	0.9934	1.210	1.625	2.198	1.719	
C	2	.01954	.01587	.02557	.02186	.02618	.02180
C/L	2	.0007830	.000498	.00100	.0007025	.0007313	.0006513
T-C/L	2	8500	20840	11700	22930	15720	15540
Ln	1	125	152	113	148	160	
	2	132.5	161	120.5	155	169	

Appendix 5f.

Experiment 5. 20th - 22nd March, 1934.

Day of Expt.	PLANTS										Average	
	N28	N29	N30	N31	N32	N33	N34	N35				
L	1	29.9	25.9	27.7	28.0	36.8	18.0	17.2	18.1			25.8
	2	30.2	26.1	28.0	29.0	37.5	19.0	17.5	19.1			
Ls	1	167	148	255	263	400	213	87	132			173
	2	158	142	304	294	465	192	83	160			
T	1	5.58	5.89	9.20	9.39	10.87	11.31	5.01	7.29			8.21
	2	5.23	15.44	10.86	10.31	12.41	10.14	4.74	8.38			
T/E	1	1058	1117	1744	1788	2059	2141	9571	1381			1582
	2	1020	1055	2106	1965	2407	1965	9201	1625			
C	2	.02841	.02094	.02841	.03830	.03423	.01837	.01937	.01523			.02386
C/L	2	.0009405	.0008026	.001015	.001320	.0009133	.0009694	.001108	.0007971			.0009582
T-C/L	2	91135	15865	15435	11685	19830	1687	4541	9800			1289
Ln	1	129	106	127	106	132.5	88.5	86	77.5			
	2	134	131	133	126	149	109	92	100.5			

Appendix 5g.

Experiment 6. 2nd - 4th April, 1934.

Day of Expt.	PLANTS								Average
	N37	N38	N39	N40	N41	N42	N43	N44	
L	1	29.4	36.2	19.2	24.0	26.0	37.8		28.7
	2	30.5	37.0	21.2	24.9	27.0	38.4		
Is	1	211	521	450	320	250	443		344
	2	235	556	201	394	352	411		
T	1	7.18	14.39	22.33	8.75	9.61	11.71		11.83
	2	8.03	15.05	9.49	11.62	13.02	10.70		
T/E	1	1.216	2.439	3.791	1.423	1.629	1.986		2.096
	2	1.490	2.794	1.762	2.169	2.415	1.986		
C	2	.03209	.03265	.01808	.03013	.02725	.03128		.02908
C/L	2	.001052	.0008237	.0008537	.001209	.001008	.0008143		.0009651
T-C/L	2	7107	16490	17460	8318	14520	13650		12920

Appendix 6a.Method of calculating 'Evaporation'.

In the present work evaporation has been measured by weighing two pairs of circular basins (diameter 55mm and 44mm respectively) filled with distilled water to within 0.5mm of the brim. Usually the differences in water loss from a pair of basins were small but it was thought that by using a pair instead of one only of a size errors to accidental variations would be reduced, the average loss from each pair of basins has therefore been calculated.

Thomas and Ferguson (19) state that evaporation from a circular free water surface may be represented by an equation of the type,

$$E = ka^n$$

where E is evaporation per unit time

a is radius of basin

n is constant varying according to certain factors, particularly depth of water surface from brim and rate of air movement.

Evaporation has been measured from vessels of two sizes so that two equations of the above type are obtained-

$$E_1 = k_1 a_1^{n_1}$$

$$E_2 = k_2 a_2^{n_2}$$

Taking logarithms and adding the equations:-

$$\text{Log } E_1 + \text{log } E_2 = n_1 (\text{log } k_1 + \text{log } a_1) + n_2 (\text{log } k_2 + \text{log } a_2)$$

It has been assumed that  $n_1$  and  $n_2$  are constant during the experiment so that:-

$$\frac{1}{2} [\text{log } E_1 + \text{log } E_2] \therefore \frac{1}{2} [\text{log } k_1 + \text{log } k_2]$$

$$E_1 + E_2 \therefore k_1 + k_2$$

It was thought that  $k_1 - k_2$  would give a true indication of the evaporating power of the air therefore to calculate evaporation the product of the average loss from the basins of each size has been found and the square root calculated. As in calculating transpiration 24 hours has been used as the unit of time. The values are referred to as 'Evaporation' and the figures are given in Appendix 6b.



Appendix 6b.Average - daily rate of evaporation during Transpiration expts.

Experiment	Date	Evaporation
Expt. 1	2 - 3 Jan.	3.836
	3 - 4 "	3.806
	4 - 5 "	5.039
	Average of Expt. 1	4.22
Expt. 2	31 Jan. - 1 Feb.	5.809
	1 - 2 Feb.	4.042
	Average of Expt. 2	4.926
Expt. 3	21 - 22 Feb.	5.824
	22 - 23 "	6.501
	Average of Expt. 3	6.163
Expt. 4	7 - 8 Mar.	5.682
	8 - 9 "	6.654
	Average of Expt. 4	6.165
Expt. 5	20 - 21 Mar.	5.289
	21 - 22 "	5.153
	Average of Expt. 5	5.22
Expt. 6	2 - 3 April	5.901
	3 - 4 "	5.387
	Average of Expt. 6	5.64

Appendix 7a.Experiment 1. 2nd - 5th January, 1934.

	Day of Expt.	PLANTS				Average
		E3	E5	E6	E7	
L	1	7.5	7.5	19.9	48	22.2
	2	7.9	7.8	20.6	49	
	3	8.3	8.0	21.3	50	
Ls	1	35	30	130	115	167.2
	2	70	45	260	130	
	3	45	25	100	120	
T	1	2.34	2.0	6.53	2.40	3.94
	2	4.43	2.87	12.6	2.65	
	3	2.71	1.50	4.090	2.40	
T/E	1	.609	0.521	.851	.646	.866
	2	1.164	.758	1.158	.6972	
	3	.538	.608	.406	.479	
C	3	.003615	.02259	.06189	.02754	.02891
C/L	3	.0004348	.002783	.002906	.0005508	.001419
T-C/L	3	1383	1470	2639	4460	279
Ln	1	12	23	62	50	47.4
	3	21	32	93	86	

Appendix 7b.Experiment 2. 31st January - 2nd February.

	Day of Expt.	PLANTS				Average
		E12	E9	E10	E11	
L	1	27	30	10	19.8	23.1
	2	30	33.2	13.5	21.2	
Ls	1	167	109	40	63	73
	2	123	101	45	90	
T	1	6.18	2.75	4.00	3.23	3.86
	2	4.10	3.035	3.32	4.24	
T/E	1	1.065	.4740	.6888	.5553	.8037
	2	1.015	.7502	.8206	1.049	
C	2	.07171	.05974	.03674	.02609	.04857
C/L	2	.002390	.001786	.002720	.001231	.002032
T-C/L	2	2022	1757	2721	2740	2310
Ln	1	77.5	93.5	47.5	77.5	66.1
	2	86.5	97.5	65	84	

Appendix 7c.Experiment 3. 21st - 23rd February.

	Day of Expt.	PLANTS			Average
		E1	E13	E14	
L	1	43.3	52.8	52.8	46.3
	2	43.3	53.3	54.1	
Ls	1	392	804	360	597
	2	291	508	1025	
T	1	9.06	15.23	6.82	11.06
	2	6.73	9.61	18.9	
T/E	1	1.555	2.614	1.170	1.811
	2	1.035	1.478	2.915	
C	2	.05408	.05969	.06711	.06029
C/L	2	.001120	.001240	.001256	.001205
T-C/L	2	63.08	11840	11040	9760
Ln	1	134.5	138	131	135.7
	2	134.5	141	133	

Appendix 7d.Experiment 4. 7th - 9th March 1935.

	Day of Expt.	PLANTS					Average
		E2	E8	E15	E16	E17	
L	1	46.4	48.1	49.5	31.0	61	47.2
	2	46.4	48.1	51.0	31.6	61.2	
Ls	1	705		212	99	223	373
	2	575		227	58	218	
T	1	15.20		4.23	3.12	3.66	6.18
	2	12.40		4.45	1.835	3.56	
T/E	1	2.577		.7537	.5619	.6434	1.0377
	2	2.302		.6684	.2758	.5351	
C	2	.05646	.04563	.05705	.04581	.08287	.05757
C/L	2	.001504	.000949	.001118	.001454	.001359	.001357
T-C/L	2	9563		3842	1714	3793	4728
Ln	1	140	127.5	113.5	83	164.5	118.4
	2	140	127.5	118.5	85	165	

Appendix 8.

Relative Transpiration of plants of Galanthus nivalis and Galanthus Elwesi

during day and night periods at different periods of the season.

	x		x		
	Galanthus Elwesi 10.45a.m.-4.45p.m.		Galanthus nivalis (Avg. of 5 plants) 4.45p.m.-10.45a.m. 10.45a.m.-4.45p.m.-10a.m. 10.45a.m.-4.45p.m. 4.45p.m.-10.45a.m.		
31st Jan. - 1st Feb.	0.446	0.912	0.909	9.912	2.811
1st Feb. - 2nd Feb.	0.650	0.851	0.807	6.416	1.850
21st - 22nd Feb.	2.326	1.561	1.200	6.600	3.188
22nd - 23rd "	1.926	1.652	0.948	7.536	3.200
7th - 8th Mar.	1.548	1.174	1.087	8.096	3.494
8th - 9th Mar.	0.934	0.685	0.889	9.272	3.265
22nd - 23rd Mar.		1.629	1.348	7.744	3.603
23rd - 24th "		1.1291	1.614	9.260	3.368
2nd - 3rd April		3.196	2.090	5.728	3.168
3rd - 4th "		2.159	2.306	8.140	2.862

x Same plants as those in Appendix 5 and 7.

## Appendix 9a.

Galanthus nivalis. Average daily transpiration per unit area and relative transpiration in four plants at different periods in the season.

Date	Transpiration per unit area (-T)						Relative Transpiration Ratio.					
	N1	N3	N4	N6	AVG.		N1	N3	N4	N6	AVG.	
2 - 5 Jan. 1935	2.44	1.72	2.12	2.30	2.27		.579	.419	.548	.697	.561	
31 Jan.-2 Feb.	5.15	4.43	5.75	6.12	5.36		1.073	0.855	1.139	1.326	1.098	
21 - 23 Feb.	6.07	10.94	11.99	13.79	10.93		0.988	1.521	1.971	2.264	1.686	
7 - 9 Mar.	9.29	11.56	11.33	10.72	11.72		1.530	1.914	1.878	1.375	1.674	
20 - 22 Mar.	13.89	26.83	8.50	14.13	15.79		2.799	5.135	1.689	2.713	3.112	
2 - 4 April.	20.52	19.62	12.32	12.93	16.35		3.627	3.480	2.185	3.278	2.890	

Appendix 9b.

Cross Sectional Area of Conducting Cavities etc. in  
these plants (on 4th April 1935).

	N1	N3	N4	N6	Average
L	39.9	33.8	45.5	40.2	39.85
C	.03540	.03454	.03007	.04082	.03523
C/L	.0008876	.001021	.0006609	.001015	.0008944
T-C/L	23050	19200	18640	12740	18660

For evaporation see Appendix 6.

Appendix 10.

Galanthus Elwesi. Average daily Transpiration per unit area  
and Relative Transpiration Ratio in 2 plants at different  
periods in the season.

Date	Trans unit area			Relative Trans.		
	E2	E4	Avg.	E2	E4	Avg.
2 - 5 Jan. 1935	4.00	2.707	3.35	1.191	0.685	0.938
31 Jan.-3 Feb.	5.31	4.280	4.80	1.079	0.882	0.981
21 - 23 Feb.	23.86	12.62	18.24	3.310	2.071	2.691
7 - 9 Mar.	13.81			2.440		

For evaporation see Appendix 6.



Appendix 11.Variation in weight of unit area of Graph paper.

	100sqcm.	AREA 25sqcm.	10sqcm.
Set 1	1.3960 grms	0.3368 grms	0.1394 grms
2	1.3983	0.3384	0.1402
3	1.4192	0.3417	0.1402
4	1.4202	0.3420	0.1404
5			0.1404
6			0.1414
7			0.1421
8			0.1424
Average	1.4035	0.3397	
Range	0.0042	0.0030	0.0030
% Variation	1.7%	1.3%	24%

Includes error due to variation in area/weight relationship and to cutting.

Appendix 12.

Variation in Weight of duplicate sets of drawings of  
cavities of conducting elements.

	N37	PLANT N4	N26
Set 1	1.5071 grms	1.3250 grms	0.5227
2	1.5141	1.3500	0.5177
Range	0.0070	0.0250	0.0050
% Variation	0.7%	1.8%	1%

Appendix 13.

Transpiration per unit area in Galanthus and Senecio vulgaris  
and Gladiolus and Senecio vulgaris under the same conditions.

Date	Transpiration per unit area			
	Galanthus nivalis	Galanthus Elwesi	Senecio vulgaris	Gladiolus
22 - 23 Mar. 1934	11.35	10.40	11.35	
"	15.27	12.60	68.41	
"	19.31	12.87		
3 - 5 May 1934	24.07		53.78	
"	32.99		60.00	
"	45.84		60.54	
24 - 25 May 1934	42.33		34.78	
"			39.89	
"			43.69	
27 - 29 June 1934			40.05	30.58
"				31.78
"				40.18
11 - 13 July 1934			14.4	38.5
			18.0	28.8
			25.2	20.4

Appendix 14.

Cross Sectional conducting area/leaf surface in four  
Dicotyledonous plants and in Galanthus.

Date	Name of plant.	xylem area/leaf area (In sqmm.xylem per sqcm. of leaf surface).
21st March, 1935	Antirrhinum major	.00350
"	Centranthus rubra	.00337
"	Senecio vulgaris	.00299
"	Cherianthus Cheri	.002325
7th March, 1935	Galanthus Elwesi	.00130
5th Jan.	" "	.00120
5th April	Galanthus nivalis	.00093
5th Jan.	" "	.00027