BOTANY

1929 M.Sc.

Lockyer

SEED DISPERSAL FROM THE HYGROSCOPIC FRUITS OF MESEMBRIANTHEMUM POMERIDIANUM LINN. (Carpanthea N. E. Br.).

by

S. Garside

and S. Lockyer.

Thesis submitted for M.Sc. Degree (Internal) by Miss S. Lockyer & in October 1929

Contents.

I. Introduction.

The capsules of *Mesembrianthemum*, the valves of which open only when wetted, have long been objects of interest to botanists, though very little precise information, either of the anatomy of the capsule or of its mechanism has been available.

In an early reference to the hygroscopic fruits of *Mesembrianthemum* Steinbrinck (10), in 1888, suggested that the capsule valves protect the seeds from the dessicating influence of the sun; as they remain closed except when wetted by rain. The boss projecting from the wall of the ovary and partially closing the aperture of each compartment in *M. linguaeforme* Haw, he regards as an additional device to prevent the seeds from escaping too readily from the projecting capsule.

Kerner and Oliver (8) in 1895 give two figures of the fruits of *Mesembrianthemum*. The first *M. annuum* has the five valved type of capsule which on opening leaves the seeds completely exposed. The second capsule figured *M. candolleanum* (Candollii Haw - pomeridianum Linn.) having 17 valves is that of *Carpanthea pomeridiana* N. E. Br. which forms the subject of this paper. Kerner merely remarks that the seeds are washed out by the rain.

More recent observations have been made by Berger (1). He allowed drops of water to fall from a height of 2 metres on to an open capsule and obtained a radial distribution of seeds of 50cm. Schmid (9), in an account of M. pseudotruncatellum Berger suggested that it is the weight of the falling drops of rain which ejects the seeds from their compartments, and distributes them in a circle in the zone covered by the water splashing from the capsule.

Recent work by N. E. Brown (5) led him to suggest that the structure of the capsule of Mesembrianthemum prevents the seeds from escaping too rapidly. In cases where membranous wings covering the loculi are absent, the seeds can, doubtless, be readily washed out by the rain, since they are uncovered when the capsule valves are open; where the loculi are covered in the open capsule, however, the escape of the seeds is more difficult to explain, and Brown regards the problem as being still unsolved, although he considers the washing out of the seeds by rain to be likely. This view agrees with that of Huber (7) who suggests that after the open capsule has become filled with water the seeds are torn away from the funiculi by the falling drops. On account of the flow of the water through the inner chambers of the capsule some seeds are washed on to the upper side of the open fruit, from whence they are splashed away by the falling drops of water.

H. M. L. Bolus (2) is probably of the same opinion as N. E. Brown i.e. that the seeds do not escape readily, for she describes a case where two young plants of *Carpanthea pomeridiana* N. E. Br. were found flowering but still attached to the capsule; the seeds having germinated *in situ* in the loculi. The capsule of *C. pomeridiana* N. E. Br. has been used in the present investigation of the anatomy and seed dispersal mechanism. It is one of the most complicated types of fruit and a casual examination gives the impression that it is almost impossible for the seeds to escape, except by decay of the capsule wall; a condition which might have arisen owing to over specialisation. However, a critical examination in the laboratory, using carefully divised experimental methods, has shown this capsule to be a most efficient mechanism for the dispersal of the seeds by rain.

II. Description of Plant.

Brown's (4) observations on the fruits and flowers of Mesembrianthemum led him to split up the very large genus into a number of new genera, of which the monotypic genus Carpanthea is one.

Carpanthea pomeridiana N. E. Br. is a freely flowering annual which occurs on sandy areas and cultivated lands on the Cape Peninsula and adjoining mainland. The leaves, which are mostly radical, are opposite, flat, and somewhat succulent. The large (5·5cms. diameter) lemon-yellow coloured flowers are born on erect pedicels which are much longer than the leaves, but which become prostrate in the fruiting stage. The green, five lobed perianth ("calyx") surrounds and supports several rows of very numerous slender lemon-yellow staminodes ("petals"), within which are several rows of yellow stamens, the outer stamens being filiform and without anthers. In the centre of the flower are 10 - 20 threadlike pointed stigmas, the number being the same as the number of loculi in the large inferior ovary. The stamens are at first inflexed to the centre of the flower, and cover the stigmas, later they spread outwards and expose the latter. The ovary, which is much broader than deep, increases considerably in size after fertilisation and matures to form a capsule with 10 to 20 valves, and as many loculi. The details of the structure of this fruit will be given later. Each loculus contains from 5 to 7 D shaped black seeds, with minutely tuberculated testa.

III. Morphology of the fruit.

The number of valves in the fruits of Carpanthea is very variable, as can be seen from the following table which gives the figures for 79 fruits that were examined.

Variation in No. of valves of fruit.										
No. of valves	10	11	12	13	14	15	16	17	18	19
No. of fruits with above No. of valves.	4	5	19	12	7	17	6	7	1	1

The table shows that fruits with 12 valves are the most common, but 15 and 13 are also very frequent numbers. There is no correlation between the size of the fruit and the number of the valves.

When the fruit is mature and dry the withered remains of the calyx are visible round the outside of the fruit, and remains of stigmas are often to be seen on the tips of the valves (Plate I Fig. 1). The valves do not correspond to carpels, although they equal these in number, for each rests over a septum and not over a loculus; hence the halves of each valve are formed from adjacent carpels.

Plate I fig. 2 shows the same fruit after it has been expanded in water. Each valve (Fig. 1 C) has opened outwards exposing on its under side two fan shaped keels (B) ending in long awns (D). Each keel is attached to the top of a septum between two loculi, starting approximately midway between the central axis of the fruit and its outer wall, and runs from thence outwards along the under side of a valve for about half its length, after which it is prolonged to form a free awn. The two keels of each valve are attached some distance apart, but their inner faces converge, so that the free edges are in contact for part of their length (Fig.1)

The seeds are not easily seen when the fruit opens, for each septum (Fig. II L) is split vertically and the halves which are of a cartilaginous nature, diverge and so arch over the loculi (M).

The septa are split to the base towards the centre of the fruit, but only through about half their height where they join the ovary wall. As the two keels of each pair are attached to the two halves of each septum they are necessarily some distance apart at their attached edges. (Fig. 2) The halves of each septum are joined by a narrow arch (Fig. I A) situated approximately midway between the centre of the fruit and the ovary wall. In the figure an arrow has been drawn passing under this. The arch is of a horny texture and serves to keep the two halves of each septum apart, so that they diverge and arch over the loculi. The elasticity of the arch forces the septa to meet above the loculus (H), but a narrow space is left towards the centre of the capsule (F) and between the bases of the valves (G). Seeds may often be seen through the former opening (F).

As the loculi have no roofs (Fig. 2) the seeds would be completely exposed when the valves are reflexed (Fig.1) were it not for the fact that the split septa arch over the loculi (Fig. 2 M). Although there is a narrow opening above each loculus (Fig 1 F) the aperture is not wide enough to allow the seeds to escape unless force is used, as can easily be seen if one attempts to displace the seeds with a needle.

Brown found that when capsules of certain types were repeatedly opened by wetting, on each occasion a few seeds fell out of them into the saucer in which they were placed. He suggests that probably, under natural conditions, a few seeds only are liberated each time the capsule opens; this he considers to be an adaptation to the dry climate "for if all the seeds were shed at once and the subsequent rainfall insufficient to enable the seedlings to establish themselves the effort of the plant would be wasted for that year". (3 Vol. 70 p. 173).

If a closed fruit be cut vertically and radially between two valves, a loculus is seen in section (Fig. III). When the fruit is mature the hardened walls of the carpels separate from the central conical axis or columella of the fruit (Fig. 1 and 4), and also to a great extent from each other, because the septa are split to their bases in the region of the columella.

The free follicle-like tip of each carpel rests upon the corky columella, and the base of each carpel is also to a great extent detached from the corky floor of the ovary. The placenta is situated on the floor of the carpel towards the periphery of the fruit; and attached to it are numerous very long funiculi, often twisted together, some bearing ripe seeds, others unfertilized withered ovules. As many as 7 ripe seeds may occur in a single loculus. The funiculi are so delicate that the relatively heavy seeds are easily broken away, and it is scarcely possible to remove a seed with its funiculus attached.

In the dry fruit the keels are hard and woody and compactly folded under the closed valve (Fig. 3). The arch (A) joining the halves of the septum extends just beyond the point of attachment of the keels.

When the fruit is wetted the keels absorb water and expand rapidly. They unfold like a fan, and force the valve upwards and outwards until the fruit is fully open (Plate I Fig. 2). On drying the keels contract, and the valves close again but are ready to reopen under sutiable conditions. (Plate I Fig. 1)

IV. Structure of the Expanding Keels.

An expanding keel with its awn can be easily torn off from the valve, and its structure examined after mounting in water.

The keel is one cell in thickness (Fig. ix) except along the line of its attachment to the valve, where it is several cells thick (Fig. xi). The free edge of the keel is serrated, as the marginal cells have free tips which project irregularly (Fig. V). In surface view the keel is seen to be composed of cells, the free surfaces of which are rhomboidal in shape, and arranged so that the long axis of each cell-face is parallel to a line joining the point of attachment of the keel to the free margin (Fig.V). 150 μ is an average length for the longer axis, the shorter axis being approximately 50 μ. The cells therefore appear to radiate from a basal line of attachment and give the impression of an open fan.

The free surfaces of the cells are somewhat convex, and overlap slightly like the scales of a fish, the free tips of each cell being prolonged into a small spinous process (Fig. V P).

Each cell composing the keel, in the region in which it is one cell in thickness. has the shape of an oblique prism, with two free rhomboidal faces (already described) and four faces in contact with adjoining cells. The latter faces are comparatively thin and lignified and all are densely pitted over about half their area (Fig 6 and 7), thus facilitating the rapid passage of water from cell to cell, whereas the two free rhomboidal faces are without pits. In addition to the lignified walls, every cell has a thick secondary deposit of lamellated mucilage entirely covering its inner face, and almost completely occluding the lumen, but with the remains of the protoplast still occupying the centre of the cell. The mucilage very readily imbibes water thus causing the expansion of the keel. It becomes blue in colour when treated with chlor-zinc iodide, indicating that it is of a cellulose nature.

The anatomical structure of these cells is in agreement with that described by Von Guttenberg (6) for Mesembrianthemum rhomboideum Salm Dyck, and by Huber (7) for M. linguaeforme. The figures (Fig. 5,6,7) of cell structure of the keel were made from fully imbibed cells. When dry and contracted the tissue is thrown into folds and wrinkles and it is difficult to distinguish individual cells. As a result, it is impossible to give comparative measurements of single cells in the dry and in the imbibed condition, but some idea of the degree of expansion may be obtained by comparing the width of a piece of keel tissue in the dry and in the imbibed state. Fig. 8 illustrates the comparative sizes of a piece of the keel mounted in (a) water, (b) 50% alcohol and (c) pure glycerine. In the fully imbibed condition the keel tissue is approximately 4 times the length of the same piece when dry. It can be seen from the figure that increase in size takes place almost entirely in a direction parallel to the margin of the keel i.e. in the best direction for bringing about the opening of the capsule valves.

Each of the two keels is separately attached to the valve by a specialised colourless basal tissue which is several cells in thickness (Fig.9 N). The keel cells resting upon this colourless tissue are smaller, with thicker walls and are darker brown in colour than the normal cells of the keel. Towards the apex of the valve, these modified cells of the keel are prolonged to form a free awn composed of very elongated cells of the same type.

The superficial cells of the basal region are irregularly lobed and their colourless thick walls have well marked pits. (Fig. 10); below this layer, the more deeply seated cells are less lobed but have similar pits (Fig. 11).

V. The Seed.

The campylotropous seeds are D shaped and compressed with a rough very resistant testa. Plate I Fig. 3. There is no obvious external trace of the micropyle but the seed shows a tubercle on its straight margin which marks the point of attachment of the funiculus. (Fig. 12 V).

The oil containing embryo (Fig 13 T) is curved round a starch containing parenchyma U, interpreted by Huber (7) as perisperm. In section the epidermis of the seed consists of cells approximately 85μ long by 80μ high, whose outer walls are strongly convex. This outer wall of the epidermal cell is three layered; externally there is a thin colourless cuticular skin, then a dark brown region approximately 12μ thick, while the innermost yellowish brown layer is also 12μ thick. The lumen of the cell is completely filled with a reddish brown substance.

The subepidermal layer (Fig. 14 X) is composed of rectangular cells in section 24μ long by 10μ high. These cells are completely filled with small crystals of calcium oxalate. The third layer shows cells of similar size and form but their walls are thicker and their contents dark brown in colour.

The walls of all three layers are strongly suberised and are unaffected by concentrated sulphuric acid; their colour shows them to be strongly impregnated with tannin.

According to Huber (7) the two outer layers of the testa are derived from the outer integument, while the third layer is derived from the inner integument.

VI. Experimental Results.

A knowledge of the structure of the fruit of <u>Carpanthea</u> gives little or no indication as to the mode of seed dispersal. In fact, a more intimate knowledge of the morphology of the fruit completely justifies N. E. Brown's statement that "they would seem to be specially designed to prevent the seed from escaping". (3 Vol. 70 p. 151). Experiments were therefore made to determine whether falling water drops would cause ejection of the seeds.

<u>Experiment I.</u>

A dry capsule was fixed by its stalk into a small dish of paraffin wax, and drops of water were allowed to fall on to it from a height of 1·75m. The capsule valves opened, and as the drops struck the interior of the capsule, seeds were forced out and carried to a distance by the splashing water. Each seed was ejected so quickly that it was not possible to tell whether it was forced from the loculus through slit F (Fig. 1), or whether the drops falling on the centre forced the seeds out laterally through slit G. The drop of water which displaces the seed from its loculus also, on splashing, carries the seed to some distance from the capsule. All the seeds (about 30) were dispersed within 20 mins. of the drops beginning to fall. Each loculus was afterwards explored with the point of a needle in order to make certain that the capsule had been completely emptied of seeds. This experiment shows in a simple way that drops of water falling from a height are most efficient in seed ejection.

Experiment II.

A capsule was opened by soaking in water, so that its seeds were not displaced, and after the surface water had been removed, melted wax was run into the central depression of the fruit, around and above the columella. Fig. 1. This has the effect of closing those openings of the follicles (F) which are directed towards the centre of the fruit.

In this particular capsule 9 seeds were visible lodged at the outer openings of the follicles when the fruit was first opened. When the open capsule was put under the falling water drops these 9 seeds were immediately splashed out, but although the experiment was continued 20 mins. no other seeds were removed. On removal of the wax, however, seeds immediately began to come out and the capsule was completely empty in 26 mins. from the time that the inner openings to the follicles had been freed. This result indicated that the seeds normally escape towards the centre of the capsule, and a further experiment was therefore devised to prove this.

Experiment III.

A small circle of transparent celluloid was cut to form a cover fitting excatly the central depression of a fruit. This cover was held in place, over the depression, by a pin passing through its centre and inserted in the columella. A small piece of sealing wax was applied, to prevent the celluloid cover from slipping down the pin. The cover was adjusted so that sufficient room was left for the seeds to escape from their carpels into the cup-like centre of the fruit through the slits at F, but it prevented the ejected seeds from being carried away by splashing water drops.

A capsule treated in this manner was placed under the dripping water. After three minutes the cover was removed and many ejected seeds were found lodged underneath it.

These experiments (II and III) lead to the conclusion that the seeds are forced out through the slits opening towards the centre of the fruit. A large drop, falling with some force into the loculus through the opening G (Fig. I), drives the seeds through the valve-like aperture F and ejects them towards the centre of the capsule.

Experiment IV.

The height from which the drops fell was varied in order to see whether there was a limiting height below which the energy of the falling drop was insufficient to bring out the seeds. i.e. to force them through the elastic valve-like aperture F. No exact limit was found, for drops falling from only ·5m. could eject one or two seeds from a capsule. It is obvious, however, that there may be a few seeds loosely placed near the openings of the follicles and these would need far less energy to disperse them than those more firmly lodged at the base of the compartments. For each height a few seeds were displaced but only when the drops fell from a height of 1·75m or more was the mechanism really effective.

With drops falling from this height 4 seeds were shot to a distance of over 1m. With drops falling from 2m. the furthest distance a seed was observed to travel was ·88m. It is interesting to note here that Berger (1) when allowing drops to fall from a height of 2m. obtained a radial distribution of ·5m. and Huber obtained a distribution of over 1 metre, but these distances were obtained with other types of fruits.

Dissection of the capsule which had been used for the above tests showed 3 seeds still lodged at the bases of the follicles It is probable that in nature 2 or 3 seeds in each capsule may fail to be ejected by rain in much the same way. They may be so tightly lodged at the base of the deep follicles that the falling rain has insufficient energy to move them. Probably it was seeds such as these that gave rise to the two plants that Bolus (2) found flowering but still attached by their roots to a capsule. Although this may happen as an exception, the experiments already described show that the fruit of Carpanthea pomeridiana is an extraodinarily effective mechanism for seed dispersal.

These experiments also disprove the idea that only one or two seeds are dispersed each time the capsule opens, as N. E. Brown (3) suggested. Drops falling at the rate of 20 a minute will open a capsule and disperse all its seeds in 20 mins. so that a heavy thunderstorm could accomplish this in a much shorter time. It is obvious that a fine or drizzly rain will be ineffective, for although it will cause the capsule to open it will not necessarily disperse its seeds.

Although a very few drops of water falling directly on to one of these capsules will bring about its opening, a saturated atmosphere even when maintained for 3 or 4 hours, has been shown experimentally to be unable to bring about any opening.

Some calculations have been made in connection with the above experiments. In the laboratory drops of ·269cm. radius falling from a height of 175 cm. were effective for seed dispersal. By means of these data the limiting velocity of a drop of this size was calculated, and also its velocity after falling through the distance 175cm. Hence knowing the mass and velocity of a drop which had been shown experimentally to be effective for seed dispersal, the smallest drop capable of bringing about the same effect, when travelling at its limiting velocity was calculated. (on the assumption that the energy of the drop is the determining factor in the ejection of the seeds). Actually the viscosity of the air is so small that it is unlikely that any drops attain their limiting velocity before reaching the earth. Consequently the smallest drop which would be effective for seed dispersal is larger than that calculated.

The following data were used in the calculation:-

V_o = limiting velocity of experimental drop.

r = radius of expt. drop = ·269 cms.

m = mass of " " = ·0813 grm.

g = acceleration due to gravity = 982

η = viscosity of air = 181×10^{-6}

s = distance fallen by expt. drop = 175 cms.

v = velocity attained by expt drop after falling distance of 175 cm.

R = radius of smallest drop capable of producing same result when falling at its limiting velocity.

m' = mass of drop of radius R

v_o' = limiting velocity of drop of radius R

ρ = density of water

σ = " " air

Stokes formula was applied to determine the limiting velocity of the experimental drop, and in so doing $(\rho - \sigma)$ was taken as unity so that

$$1) \quad V_0 = \frac{2}{9} g \frac{r^2}{\eta} (\rho - \sigma)$$

$$= \frac{2}{9} g \frac{r^2}{\eta}$$

$$= \frac{2}{9} \times \frac{.269^2 \times 982}{181 \times 10^{-6}}$$

$$= 87260 \text{ cms per sec.}$$

As η is very small we may get the velocity of the experimental drops by

$$2) \quad v^2 = 2gs$$

$$v = 586.2$$

A more accurate formula taking viscosity into account is

$$3) \quad \frac{gs}{V_0^2} = \log \frac{1}{\varepsilon} + \varepsilon - 1$$

$$\text{where } \varepsilon = \frac{V_0 - V}{V_0}$$

deduced on the assumption that the mass of the drop is all the mass in motion i.e. ~~and~~ neglecting the mass of the air carried along with the drop.

$$\frac{g\,s}{V_0^2} = \frac{(1-\varepsilon)^2}{2} \text{ neglecting higher powers of } (1-\varepsilon)$$

$$\sqrt{\frac{g\,s}{V_0^2} \times 2} = 1-\varepsilon$$

$$\frac{\sqrt{982 \times 175 \times 2}}{87260} = 1-\varepsilon$$

$$\cdot 006719 = 1-\varepsilon$$

$$\frac{V_0 - V}{V_0} = \varepsilon$$

$$1-\varepsilon = \frac{V}{V_0}$$

$$V = \cdot 006719 \times 87260$$

$$V = 586 \cdot 2$$

which agrees with the result obtained with formula 2) and therefore shows that the viscosity of the air is a negligible factor when dealing with such a short distance.

Then since,

$$m V^2 = m' v'^2$$

$$= \frac{4}{3} \pi R^3 \left(\frac{2}{9} \frac{R^2 g}{\eta}\right)^2$$

$$R = \sqrt[7]{\frac{m v^2}{g^2} \cdot \frac{243}{\pi} \cdot \frac{\eta^2}{16}}$$

$$= \cdot 06439 \text{ cm.}$$

Meteorologists (5) divide rain drops into the 3 following classes,

fine rain	·0125 cm. radius	
medium "	·15 " "	
heavy "	·3 " "	

According to the calculation made above ·0644 cms. radius is the smallest size drop that will be effective. Comparing the effective size of rain drop, found by calculation, with the above figures we find that it accords with the suggestion made previously - namely that "a fine or drizzly rain will be ineffective, for although it will cause the capsule to open it will not necessarily disperse its seeds". Thus "medium" rain if falling from a great height, or "heavy" rain falling only a short distance will bring about ejection of the seeds from the capsules.

Among other experiments designed to throw light on the nature of the valve mechanism were some in which the rate of movement of the valves was studied. For this purpose capsules were cut up and portions of carpels and attached valve and keels used separately. A fine capillary glass pointer was attached to the tip of a valve and the tissues fixed above a protractor by means of a pin inserted through the base of the septa. Wax was used to prevent the valve from slipping round on the pin. The dry valve was arranged so that the glass pointer lay along the o° line.

The apparatus was then covered with water when the keel expanded and rotated the valve so that the pointer passed over the scale until it came to rest approximately over the 180° line. Most valves were found to move through 180°, although variations slightly above or below this valve occurred.

The distance which the pointer moved was measured every half minute, and in this way the rates for different valves were compared. Valves from the same capsule were found to behave in like manner, but differences were found in the behaviour of valves from different capsules. As a general rule the rate of movement increases until an approximately vertical position is reached, after which a gradual slowing off occurs until about 175°. After this point the rate is often so slow as to be almost imperceptible.

The rate of movement was found to increase with rise of temperature. Fig 14 shows a graph illustrating the behaviour of the same valve at different temperatures. At 10·5°C. the valve took 16 mins to move through 180°, while at 37°C the time taken was only 7·5 mins. At high temperatures the rate is not only higher but is more uniform than at lower temperatures; a graph of the former shows a smooth steep curve, while a curve of the latter is very irregular as well as being much flatter (Fig.14)

Perhaps the most striking result of this investigation is the practical demonstration of the extent to which the capsule of _Carpanthea_ is fitted for a type of seed dispersal brought about by falling rain. Almost all previous writers have commented upon the manner in which the seeds are enclosed by the carpels, and have suggested a slow and gradual emptying of the capsule by successive rainstorms, or even liberation of seeds by decay of the capsule wall. If it is born in mind that the plant is an annual, it will be readily seen that such a slow mode of dispersal would not be favourable. The plant, represented only by seeds during the dry Cape summer, must take full advantage of the rainy winter season for its vegetative and reproductive activities; and sufficient seed for the continuation of the species must be formed before the dry season again approaches. As the capsule matures the peduncle becomes prostrate, bringing the broad flat base of the capsule to rest upon the ground, the capsule valves thus being directed upwards. Usually the capsule remains in this position, attached to the withered remains of the parent plant, and it is only thus that it can function properly. If the capsules became detached and blown about by the wind, many of them would settle with the upper portion of the capsule towards the soil, in which case the seeds could not escape. Normally, however, the first rainstorms find the capsules still favourably orientated, with their broad bases firmly bedded on the soil, and their valves directed towards the clouds, ~~in which position the energy of the falling drops will completely empty them in a few minutes.~~

In this position the whole energy of the falling drops is available for seed ejection, for the capsules being on a firm base do not give way or become knocked over by the force of impact, and they therefore stand every chance of becoming completely empty in a few minutes.

SUMMARY.

1. The Carpanthea fruit has from 10 to 20 carpels, 15 and 13 being the most frequent numbers.

2. The valves equal the carpels in number and are over the septa, not over the loculi.

3. The septa are split, the halves diverging and so roofing the loculi, so that the seeds are almost invisible when the valves are open.

4. Two slits are left, one between each pair of valves, and one towards the central axis of the fruit. Experiments show that the seeds escape by the latter aperture only.

5. All the seeds in a capsule are readily dispersed in a short time (10 to 20 minutes) by falling rain drops, contrary to previous supposition.

6. Radial distribution of seeds, to about 1 metre from the capsule, is caused by drops of water approximately the size of the drops falling during heavy rain.

7. A calculation has been made to determine the size of the smallest rain drop in nature capable of causing efficient ejection. This was found to be a drop of ·06 cm. radius, and corresponds to "medium" rain in nature. Fine rain fails to eject seeds, but causes the capsule to open. The capsule remains closed in damp air.

8. Each capsule valve has 2 hygroscopic keels composed of mucilage containing cells, which imbibe water readily and thus bring about the rapid opening of the valve. The time required for the complete opening of the valves decreased with rise of temperature.

9 The rate of opening of the valve increases until the valve is half open, beyond this the rate decreases until the fully opened condition is attained.

The material used for this investigation was collected by one of the authors from Stellenbosch Flats, South Africa, in December, 1920.

In conclusion we wish to thank Prof. W. Wilson, of Bedford College, for his help with the mathematical section.

LITERATURE.

1. BERGER, A.: Mesembrianthemum and Portulacaceen 1908.
2. BOLUS, H. M. L.: Notes on Mesembrianthemum and some allied genera. 1928.
3. BROWN, N. E.: "Mesembrianthemum and some new genera separated from it". Gardener's Chronicle, Vol. 70, 1921.
4. BROWN, N. E.: Vol. 78 1925
5. GEDDES, A. E. M.: "Meteorology".
6. VON GUTTENBERG, HERRMANN.: Die Bewegungsgewebe.
7. ÜBER, J. A.: "Zur Morphologie von Mesembrianthemum" Botanisches Archiv. 1924.
8. KERNER AND OLIVER ; 1895. "The Natural History of Plants."
9. SCHMID, WERNER.: Morphologische, anatomische und entwicklungsgeschichtliche Untersuchungen an Mesembrianthemum pseudotruncatellum Berger. Viertel J. Naturf. Gesells Zurich 70, 1925.
10. STEINBRINCK.: Über einige Früchtgehäuse, die ihre Samen infolge von Benetzung freilegen. Ber. d. dentsch bot. Ges Bd. 1, 1883.

FIGURES.

Fig. I (x 4).

Surface view of an open fruit showing two valves.

A. Horny arch which keeps the two halves of the septum apart.

B. Hygroscopic keel.

C. Valve.

D. Awn.

E. Space between the two halves of a split septum.

F. Space above loculus, towards the centre of the capsule, through which the seeds are ejected.

G. Space above loculus between the bases of the valves.

H. Point where the septa are forced together above the loculus.

I. Central column.

Fig. II. (x 5).

Tangential section of open fruit.

J. Funiculus.

K. Seed.

L. Septum.

M. Loculus.

Fig. III (x 4).

Vertical and radial section through closed fruit, showing a loculus in section.

Fig. IV. (x 4).

Vertical and radial section through open fruit.

Fig. V. (x 200).

Surface view of cells of hygroscopic keel in the fully expanded condition.

P. Spine.

Fig. VI. (x 200).

Vertical section of a cell of a fully expanded keel - showing the pitted walls. (the cell contents are omitted).

Fig. VII. (x 200).

Horizontal section of expanded keel.

R. Pits in the vertical walls.

Q. Lamellated mucilage.

Fig. VIII. (x 15).

Outline drawings of the same piece of keel tissue in :-

a) water

b) 50% alcohol

c) pure glycerine.

Fig. IX. (x 15).

T. S. of a valve to show the attachment of the keels.

N. Specialised colourless basal tissue.

O. Tissue of valve.

Fig. X. (x 250).

Surface view of basal tissue of keel showing the irregularly lobed walls and well marked pits.

Fig. XI. (x 250).

Vertical section through the specialised basal tissue of the keel.

Fig. XII. (x 7.5).

Surface view of seed showing its rough testa.

V. Tubercle which marks the point of attachment of the funiculus.

Fig. XIII. (x 7.5).

Vertical section through the seed.

S. Testa.

T. Curved embryo.

U. Starch containing parenchyma.

Fig. XIV. (x 250).

Section of testa.

W. Epidermis of testa.

X. Sub-epidermis whose cells contain crystals of calcium oxalate.

Y. Third layer of testa.

Fig. XV.

Graph of the rate of movement of the same valve at

a) 10·5°C. b) 37°C.

Plate I.

Fig. I. x

Closed fruit.

Fig. II.

Open fruit.

Fig. III.

Seeds.

Plate I.

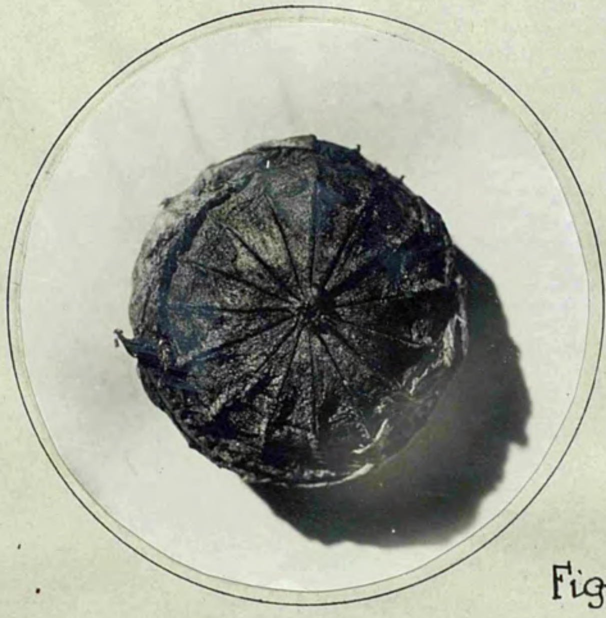


Fig: I.

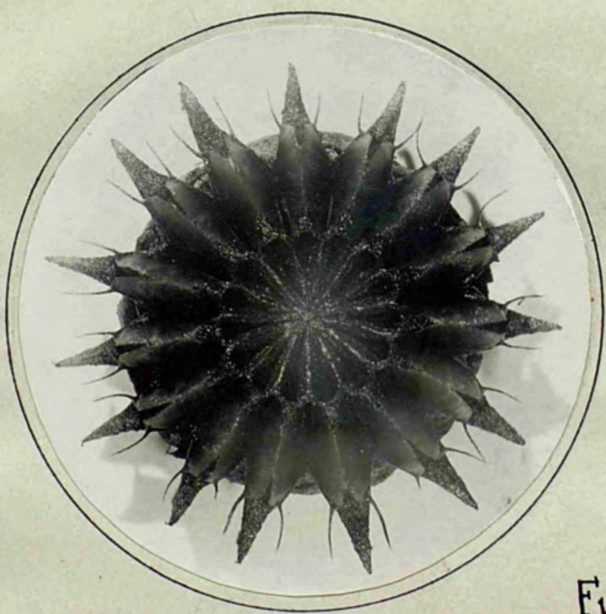


Fig: II.

Fig: III.

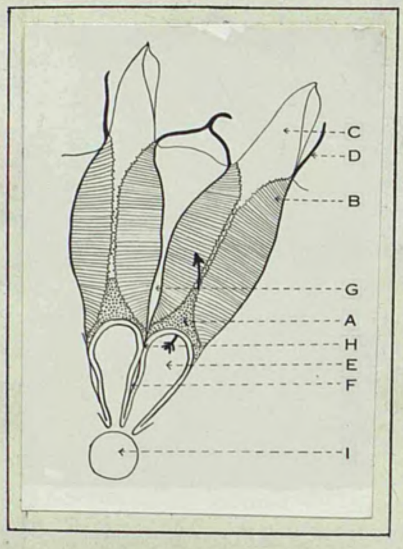


Fig: I

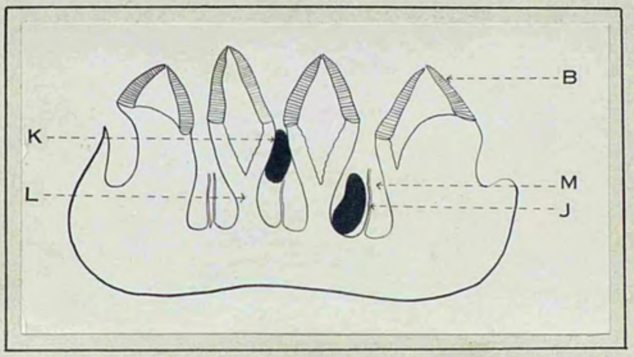


Fig: II

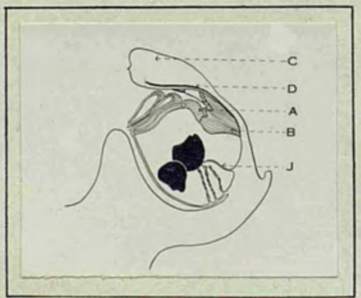


Fig III

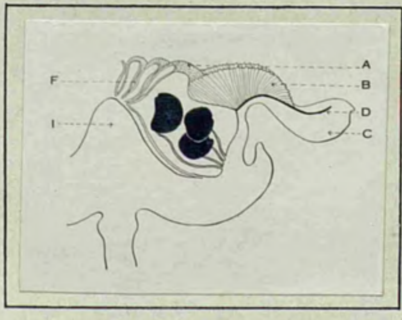
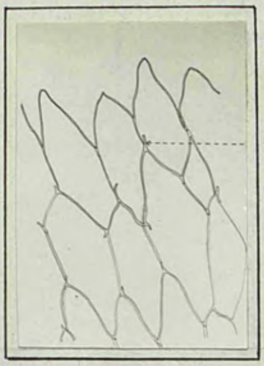
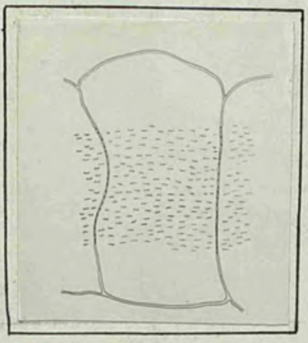


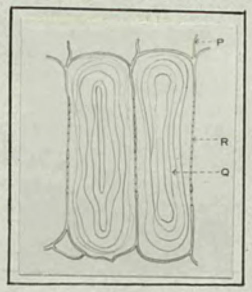
Fig: IV



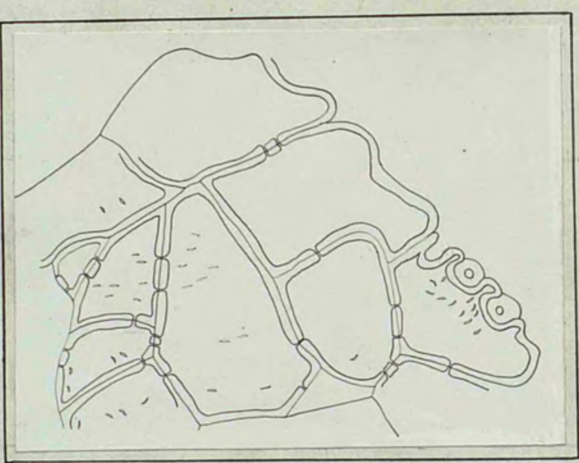
V



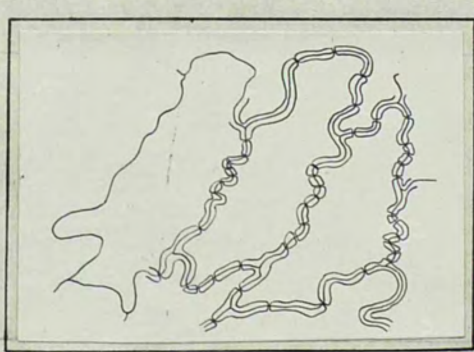
VI



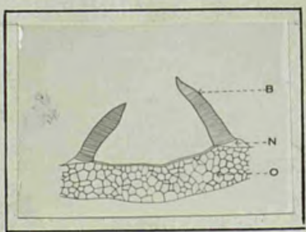
VII



XI

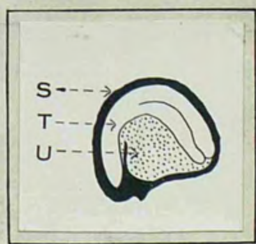


X

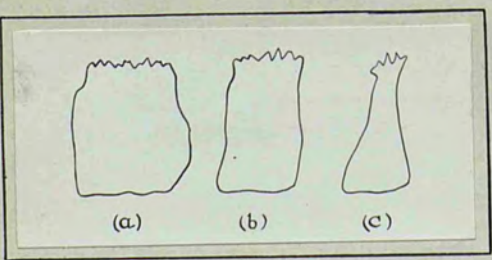


IX

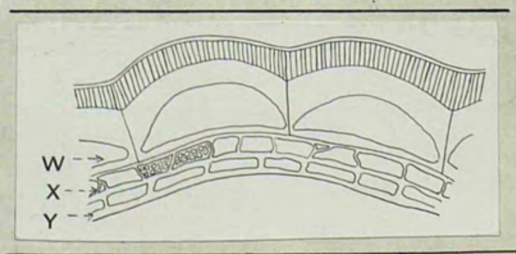
XII



XIII



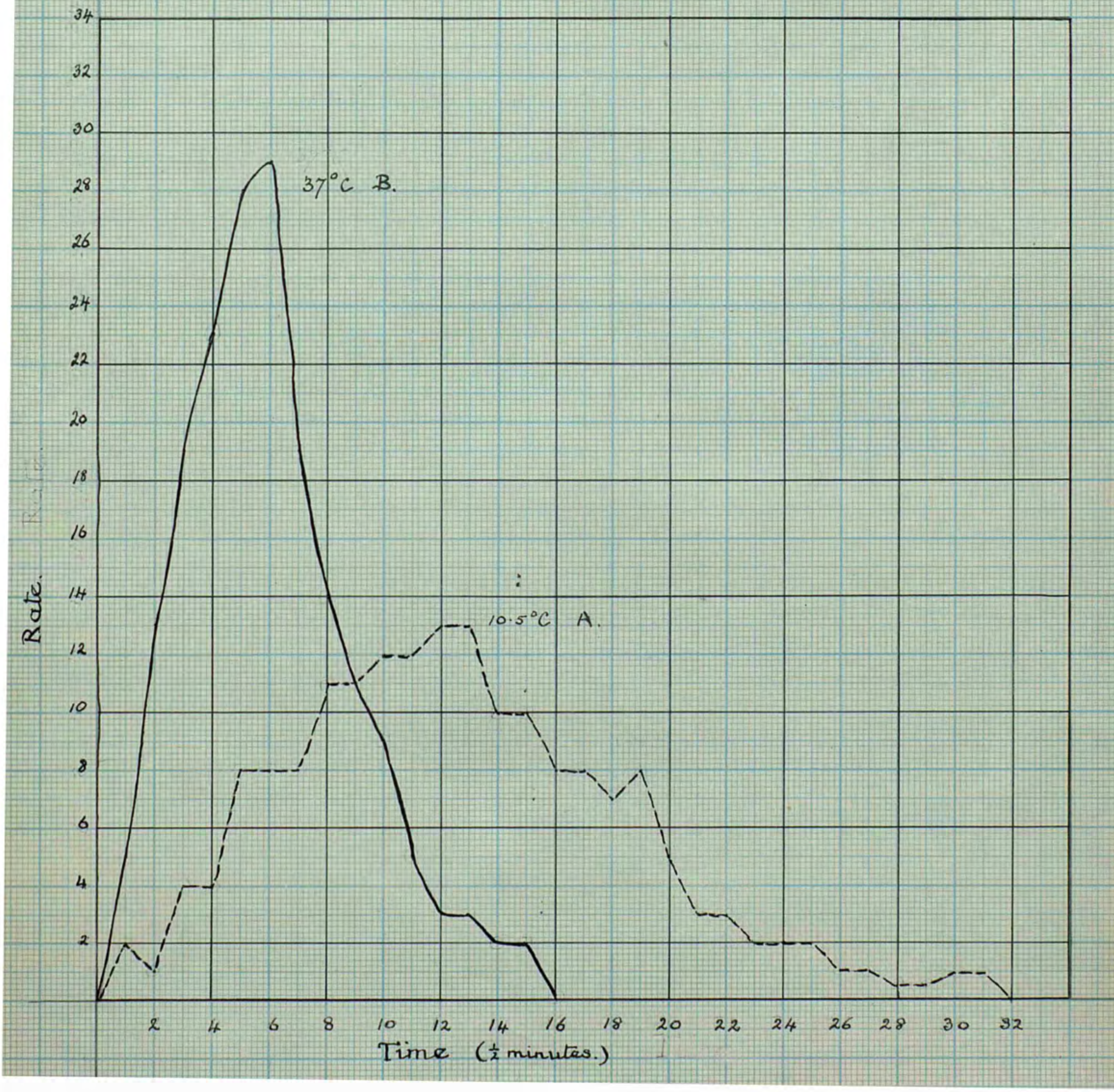
VIII



XIV

Fig: XV.

XIV.


37°C B.
10.5°C A.
Rate.
Time (½ minutes.)
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32