# Raindrops as Plant Dispersal Agents

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## Introduction

Among the characteristics of a plant likely to increase its capacity to survive, none is more important than an efficient means of dispersing its spores or its seeds. Dispersal is accomplished by plants through a variety of adaptations involving practically every natural force and agency. Although the facts about dispersal are generally well known, and have been for a long time, the importance of rain in this connection has been neglected or minimized. Yet, even where rainfall is sporadic, it represents a powerful natural force which many kinds of plants have "utilized" as one capable of bringing about the dispersal of their spores, seeds, pollen, and other propagative units.

The recognition of numerous small cup-shaped plant structures as specialized organs from which raindrops splash spores and seeds is a simple matter. Its very simplicity and obviousness may be the reason for the neglect of this concept by a considerable proportion of the modern textbooks of botany and of general biology. Since the first clear and complete account of the "splash-cups" of the fungi belonging to the family Nidulariaceae given by Buller (7) in 1942, the researches and observations of Brodie (1, 4) and others (7, 8, 9, 14, 15, 16) have revealed the existence of rain-operated dispersal mechanisms in thirty species representing almost all groups of land plants.

One of the most impressive features of the splash-cups of plants is their uniformity of size and structure. The fruit body of the fungus *Cyathus*, the rosette of the male plant of the moss *Polytrichum* and the open seed capsule of the angiosperm *Portulaca*, considered as splash-cups, have several characteristics in common: the shape is that of a crucible or of a vase, the sides of which make an angle of 60°-70° with the horizontal; the diameter of the circular mouth is between 5 and 8 mm.; the cup matures in a vertical position. It has been demonstrated by Brodie (1) that, in each of these plants, heavy raindrops falling into the cups splash the contents to a distance of three feet or more, and experiments suggest that the structural features of splash-cups are related to the way in which these organs function. The existence of rain-operated mechanisms in so many kinds of very different plants indicates that this type of dispersal has a powerful survival value. The similarity of the splash-cups in different groups of plants affords a striking example of parallelism in the evolutionary process.

Details of structure of various rain-operated mechanisms have been described elsewhere and the manner of their operation has been explained by experiment and observation (1, 2, 3, 4, 5, 7, 8). The purpose of this paper is to summarize the facts most recently brought to light and to review the phenomenon of splash dispersal in plants as a whole. To this end, five different ways in which rain facilitates reproduction and dispersal in plants are recognized.

### True Splash-cups

True splash-cups are now known in the fungi, lichens, liverworts, mosses, and seed plants (Brodie, 1, 4). In addition to the characteristics which the splash-cups of all these plants have in common, described above, true splash-cups operate in such a way that their spores or other reproductive structures are driven out by raindrops: in all examples, the cup is the producer as well as the dispenser of propagative units.

Splash-cups of fungi generally contain spores. The most elegant example of a fungus splash-cup is the fruit body of *Cyathus striatus* (Fig. 10). In this species and several other members of the Nidulariaceae, it has been demonstrated by Buller (7), Brodie (1, 5) and others that the lenticular peridioles containing basidiospores are ejected to distances up to seven feet. Adaptation to dispersal by rain has reached a remarkable degree of perfection: the little fruit body is firmly attached to the substrate by an emplacement of hyphae which prevents the cup from being dislodged by heavy raindrops; the inside surface of the cup is grooved or fluted and this feature is believed to break up the outgoing water drops, which occurrence results in the maximum lateral projection of the peridioles; the cup is highly resilient, a feature which prevents distortion by the battering of raindrops; and, perhaps most remarkable of all, the peridioles are provided with long cords by means of which they become attached to vegetation (Brodie 1, 5).

Spores smaller and more numerous than those of *Cyathus* are scattered by rain from the cups of *Polyporus conchifer.* The presence of cupulate structures on the upper side of the fruit body of this shelf-like polypore has long been known and recognized as a curious anomaly. It is now realized that the fungus begins its growth in the autumn as a cup developed on the upper side of a twig of elm (Brodie, 2). At this time, the inside of the cup produces minute spores or oidia embedded in a strongly hydrophilic gel which expands almost instantaneously when wetted. The cup is then filled with a concentrated suspension of oidia and the latter are splashed out by the first large raindrop landing in the fruit body (Fig. 6). Later in the season, hyphae grow from one side of the cup and form the typical bracket fruit body which bears pores on its lower side and liberates basidiospores (Fig. 7).

Two examples of fungi belonging to the Thelephoraceae are worthy of note. *Matula Rompelii* which is the asexual stage of *Cytidia habgallae* (Martin, 13) produces cups about 5 mm. in diameter, within which numerous chlamydospores are developed (Fig. 4). At the suggestion of Dr. G. W. Martin, this fungus was studied as a possible example of a splash mechanism. Although no living material was seen, and caution must be exercised in drawing conclusions from dead material, it was found that when the fungus was thoroughly wetted so that its rather matted contents became loosened, the contents were splashed from the cup by large water drops falling nine feet.

The ejection of a single projectile rather than of numerous spores is seen in *Aleurodiscus minnsiae* (Fig. 3). Each small, pink, hemispherical cup contains a single ball which is a sclerotium (Jackson, 11). The sclerotium, when planted on agar or on moist rotten wood, grows into mycelium. In nature, cups of *Aleurodiscus* grow only on the upper sides of hemlock twigs. When the cups are mature, heavy raindrops splash the sclerotium balls to a distance of about two feet.

Splash-cups in the lichens have not been studied extensively. However the striking resemblance between the vase-shaped podetia of *Cladonia* (Fig. 11) within which are borne soredia that serve for propagation and the vase-shaped fruit bodies of *Cyathus* (Fig. 10) is obvious. Soredia are, in fact, splashed from the cups of *Cladonia* (Brodie, 1) but rain is not the only natural force which disperses the soredia of this lichen. Brodie and Gregory (6) have shown that when the cup is dry it serves as a special organ from which wind scatters soredia. Clearly, the problem of the possible function of the various cupulate structures of lichens deserves more attention.

Among lower plants there are now recognized several in which gemmae are scattered by rain splash (Brodie, 1). The gemma cupules of *Marchantia polymorpha* are splash-cups from which the lenticular gemmae are readily disseminated by rain (Fig. 1, 2). Except for their small size, the gemma cupules resemble other splash-cups. Most textbooks of botany indicate that gemmae are "washed" away by rain. Few recount in detail that gemmae are thrown out forcibly as much as two feet as a result of their being developed in splash-cups, or that the gemmae themselves are coated with a hydrophilic colloid which doubtless enables them to withstand desiccation for some time and, by acting as a lubricant, facilitates their separation from one another and from the cupule.

The moss *Tetraphis* produces clustered gemmae partly enclosed within small leaf rosettes at the plant apices. Each leaf rosette is a splash-cup from which gemmae are dispersed by rain (Brodie, 1).

It is not surprising to find that gamete-producing structures of lower plants should occasionally represent adaptation to rain splash, especially in view of the importance of water in fertilization. Brodie (1) has shown that male gametes are thrown as much as two feet from the cupulate rosette of the male plant of the moss *Polytrichum* (Fig. 5). In the light of the notion that sperms are splashed upwards and outwards in a parabola to rain down upon the archegonia of female plants, the efficiency of reproduction of this moss becomes readily understood. Frequently sporophytes are found in great numbers on female plants two feet or more distant from male plants. If sperms had to swim down the male plants, along the ground for a distance of two feet and then up the female plants to the archegonia, it is doubtful that the females would develop sporophytes as regularly as observation shows they do.

Seed plants have developed splash-cups for seed dispersal to such an extent that it is difficult to understand why so little attention has been accorded to the subject. The fruits of the following plants vary somewhat in size of the cup and manner of operation, but all are efficient splash-cups: *Chrysoplenium spp., Mitella spp., Oenothera rosea* (Fig. 13), *Portulaca grandiflora* (Fig. 9), *P. oleracea, Sagina decumbens.* In each of these, seeds are thrown from the open fruits by raindrops. The capsule of *Oenothera rosea* remains closed when dry (Fig. 12) and opens by hygroscopic action when wet. The seeds can be dispersed only by rain unless the capsule should be broken open fortuitously by some animal or other agency.

These, in brief, are the true splash-cups of plants as we know them at present. There is little doubt that reflection and renewed observation will reveal many more when cup-shaped structures already well known are examined for evidence of rain splash mechanisms.

### Springboard Mechanisms

A rain-operated mechanism of still another type is found among flowering plants. In what has been called the "springboard" mechanism (now recognized in eight species of flowering plants) a cupulate structure is developed but seeds are not ejected directly from the cup which serves only to catch a raindrop. The blow received by the cup sets in motion a springboard from which seeds are thrown.

Springboard dispersal has been described recently by Saville (16) in *Tiarella* (Saxifragaceae) and by Brodie (4) in *Salvia* (Fig. 14) and *Ocimum* (Labiatae) and other genera. Actually, this kind of dispersal was reported as early as 1936 by Nordhagen (15) and by Müller (14), but the writings of these two botanists appear to have been overlooked.

A modification of the seed-dispersing springboard is found in some succulent plants. In *Kalanchoë tubiflora* (Fig. 17, 18) cup-like plantlets develop on narrow outgrowths from the edge of the parent leaf. When water drops fall into the cup formed by the leaves of the plantlet, the force of the downward blow depresses the springboard to which the plantlet is attached. As the springboard returns to its normal position, it hurls the plantlet as much as five feet away (Brodie, 4).

Dispersal of the bulbils of the clubmosses *Lycopodium selago* and *L. lucidulum* (Fig. 19, 20, 21) is effected by a similar rain-operated mechanism. In 1901, F. E. Lloyd (12) drew attention to the fact that the bulbils of these plants are projected to a distance of three or four feet when they are depressed with the finger and then released. No one appears to have recognized heretofore that the bulbils and the plant parts to which they are attached constitute a rain-operated mechanism. The bulbil of *L. lucidulum* is, at maurity, held between two sets of short stiff modified leaves (Fig. 19, *a*, *b*) comprising a receptacle. The lowermost leaf of the receptacle (Fig. 19, *a*) is especially important in that it fits over an elongated swollen piece (Fig. 20, *a*) on the lower side of the bulbil. The receptacle clasps the bulbil at its base under tension which, when released, serves to propel the bulbil. The most obvious naturally occurring force necessary to set off the mechanism is that of a large raindrop. The distal portion of the bulbil is a broad thin spatulate piece, hollowed out or depressed at the broad end (Fig. 19, *c*).

This extension catches a raindrop and the downward blow releases the bulbil from the stiff leaves that hold it, with the result that the bulbil springs from the parent plant. I had studied this apparatus carefully in 1953 and felt certain that it represented the first rain-operated device to be recognized among the clubmosses. Recently, Professor C. T. Ingold has reported observations which confirm my own entirely. With his permission, I quote from his letter to me (April 6, 1956):

"On allowing large drops of water to fall from a height of several feet on to *Lycopodium selago*, I found that when a drop registered a direct hit the bulbil was discharged to a distance of several inches."

Without undue emphasis, it is interesting to note the strong resemblance between the calyx tube and the pedicel of the angiosperm *Salvia lyrata* (Fig. 14) which together serve as a springboard mechanism for seed dispersal by rain, and the bulbil and receptacle of the clubmoss *Lycopodium lucidulum* (Fig. 19) !

### Rain-induced Puffing

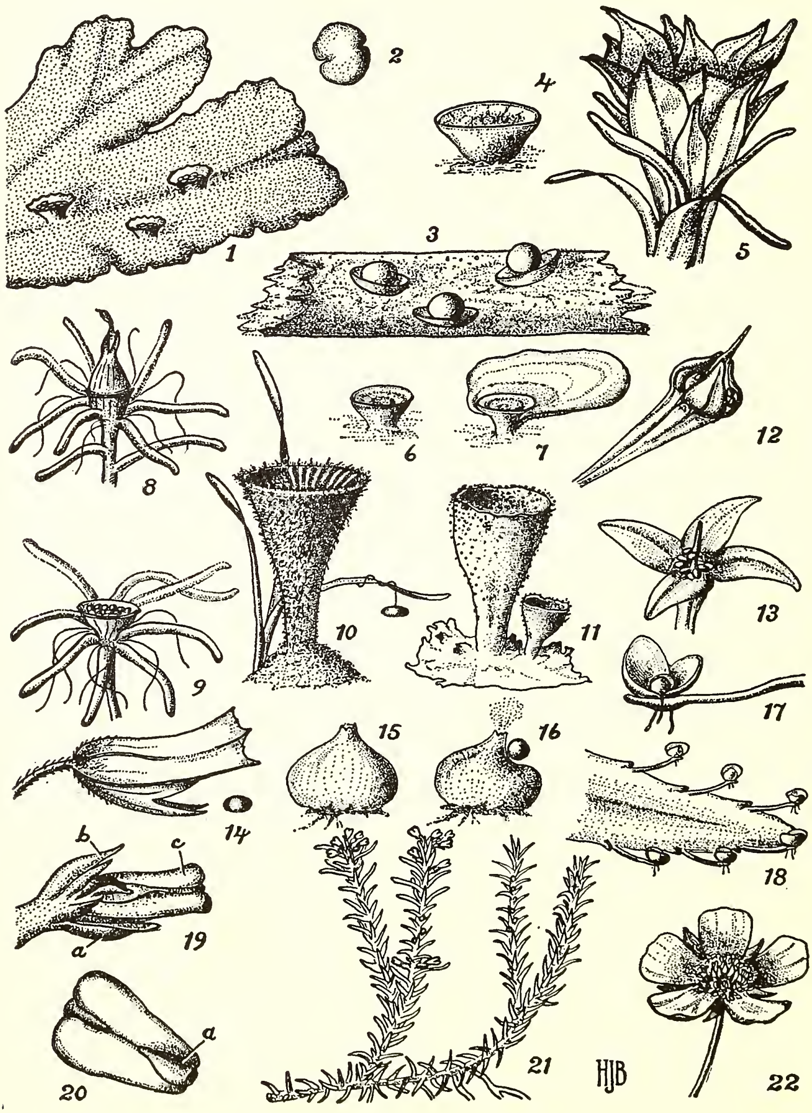
Puffballs, earthstars and similar fungi are generally supposed to discharge their powdery spores by the action of wind passing over the apical opening (ostiole) or entering the fruit body through holes in the side of the papery endoperidium and passing out through the ostiole as out of a chimney. In 1949 Gregory (8) proved that wind of ordinary speed is not effective in removing spores from puffballs. Spores can be discharged occasionally from puffballs as a result of blows received accidentally from the feet of large animals, but such occurrences cannot be very frequent. In a series of beautiful experiments, Gregory showed that the discharge of spores of *Lycoperdon perlatum* (Fig. 15, 16), *L. pyriforme* and *Geaster umbillicatus* is brought about by the impact of water drops with the papery top of the endoperidium. By means of high-speed photography, he demonstrated that when a raindrop depresses the endoperidium, air and spores are ejected through the ostiole of the fungus. To date, the fungi mentioned are the only examples of this kind of dispersal that have been studied. Careful examination of thin-walled ball-shaped structures in other plants might well prove profitable.

Grout's observation (Mosses with a Handlens, 1903, p. 71) that spores are puffed from the capsule of the moss *Diphyscium* by the battering of raindrops suggests the same kind of mechanism as that which operates in *Lycoperdon*.

### Rain-splash Pollination

Because of the common observation that pollen grains or the pollen tubes developed from them burst in water as a result of the concentration of the contents and consequent absorption of water, little thought has been given to the possible role of rain as an agency of pollination of land inhabiting plants. An objection to rain pollination often raised is that, in many plants, pollen is protected from contact with rain by floral structure.

True, the pollen of many plants is adversely affected by rain; the interesting facts remain, however, that the pollen of some plants at least germinates readily in rain water and that rain is the chief agency of pollination for some flowers. In 1950, Hagerup (10) showed that when raindrops land in the stiff cup-shaped flowers of some species of *Ranunculus* (Fig. 22), *Caltha* and *Narthecium*, splash action carries pollen from anthers to stigmas. In fact, Hagerup showed that seeds are not set by the plants he studied unless the flowers are subjected



### Description of Illustrations

Fig. 1. Gemma cupule on the thallus of *Marchantia polymorpha*. x 3.

Fig. 2. Gemma of *Marchantia polymorpha*. x 25.

Fig. 3. Splash-cups of *Aleurodiscus minnsiae* with sclerotial balls. x 12.

Fig. 4. Splash-cup of *Matula Rompelii*. x 4.

Fig. 5. Rosette of male plant of *Polytrichum juniperinum*. x 10.

Fig. 6. Young slash-cup of *Polyporus conchifer*. x 2.

Fig. 7. Mature fruit body of *Polyporus conchifer*. x 2.

Fig. 8. Unopened fruit of *Portulaca grandiflora*. x 1.5.

Fig. 9. Open fruit of *Portulaca grandiflora*, showing cupulate form and seeds within. x 1.5.

Fig. 10. Slash-cup of *Cyathus stiatus*. x 2.5.

Fig. 11. Podtium of the lichen *Cladonia pyxidata*. x 2.5.

Fig. 12. Capsule of *Oenothera rosea, dry*. x 2.

Fig. 13. Capsule of *Oenothera rosea* which has opened on being wetted. x 2.

Fig. 14. Calyx of *Salvia lyrata*, showing nutlet being ejected by springboard action. x 2.

Fig. 15. Puffball, *Lycoperdon perlatum*. x 1/5.

Fig. 16. Raindrop striking fruit body of *Lycoperdon perlatum* and spores being puffed out. x 1/5.

Fig. 17. Plantlet of *Kalanchoe tubiflora* attached to outgrowth from leaf x 2.5.

Fig. 18. Tip of leaf of *Kalanchoe tubiflora showing plantlets*. x 1.

Fig. 19. Bulbil of *Lycopodium lucidulum* showing attachment: *a,* lower modified leaf which clasps bulbil on lower side; *b,* upper clasping modified leaves; *c,* concave part of bulbil. x 3.5.

Fig. 20. Under side of bulbil of *Lycopodium lucidulum* showing projection *a* which fits into modified leaf shown in Fig. 19 *a*. x 4.

Fig. 21. *Lycopodium lucidulum* with bulbils. x 1/2.

Fig. 22. *Ranunculus sp.*, a cup from which pollen is splashed by rain. x 1.5.

to rain. Hagerup's observations become doubly important when it is realized not merely that rain effects self pollination of the flowers but also that, through splash action, pollen from one flower cup may be thrown out to land on another and thus ensure cross pollination. And it may be that rain is a more important agency of pollination that would be supposed on the basis of Hagerup's observations dealing with a small number of species of plants.

### Raindrops and the Dispersal of Curved Spores

The work of allergists and plant pathologists has produced a large amount of information concerning the dispersal of spores, pollen grains and other particles in the air. Students of aerobiology have a fairly accurate picture of what happens and may be expected to happen when dry spores and pollen grains are freed into the atmosphere to be carried by wind currents and scattered by air turbulence.

The distribution of certain kinds of spores remains anomalous. These exceptions are found mostly among fungi whose spores are developed in glutinous masses or, for some other reason, are not liberated except when wet. For these, there is some evidence (Gregory, 9) that the pattern of dispersal is different from that of most spores scattered in dry air. This may be because rain is the dispersal agent. Investigators who study the air flora by allowing microorganisms to collect on slides or in Petri plates exposed to the air often notice that minute water droplets (deposited from fog, mist, etc.) enclose fungus spores. Such spores are, more commonly than not, of the hyaline curved type, such as those of *Fusarium* and a number of other genera. The significance of this observation is not known with certainty. However, Gregory has suggested that many kinds of spores dispersed only during wet weather may be carried by very small water droplets. If droplets from mist or a drizzling rain bounce on to the surface of a leaf or other substrate on which spores like those of *Fusarium* are being developed, it is quite possible that the droplets may pick up spores and bounce away. Why curved spores would be more readily picked up by droplets than spores of other form, is unknown; it may be related to surface tension effects. Although no experimental work on this problem has been done, the evidence available suggests that raindrops may play a role as carriers of microorganisms the importance of which has been underestimated.

## Summary

1. Raindrops bring about the dispersal of gametes, spores, seeds, and other kinds of reproductive units in a great variety of plants. Over thirty rain-operated dispersal mechanisms are recognized, scattered throughout almost all groups of plants.

2. Special organs called "splash-cups" are produced by fungi, lichens, liverworts, mosses and seed plants. A typical splash-cup is 5-8 mm. wide at the mouth, is vase-shaped or crucible-shaped, has sides which make an angle of 60°-70° with the horizontal and matures in a vertical position. Raindrops splash peridioles from the fruit bodies of the fungus *Cyathus* and of other fungi, sperms from the cupulate male plant rosettes of the moss *Polytrichum* and of other mosses, and seeds from the open seed capsules of such angiosperms as *Portulaca.*

3. In certain flowering plants, such as *Salvia lyrata,* rain operates a "springboard" device. The calyx tube of *Salvia* produces a kind of cup which catches raindrops. The blow received by the cup depresses the calyx tube and, when the latter springs back into normal position, fruits are thrown from the calyx tube. The plantlets of *Kalanchoë tubiflora* are dispersed by a similar springboard action. The bulbils of *Lycopodium selago* and *L. lucidulum* are shown, for the first time, to be dispersed by a rain-operated mechanism of the springboard type.

4. The discharge of spores from puffballs is brought about by the impact of water drops with the papery top of the endoperidium.

5. The pollination of some cup-shaped flowers such as those of certain species of *Ranunculus*, *Caltha* and *Narthecium* is brought about by the splashing action of raindrops.

6. Many kinds of curved fungus spores, not ordinarily dispersed during dry weather, may be carried by minute water droplets which strike a spore-laden surface and bounce away taking spores with them.

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