

SEED DISPERSAL

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The dispersal of ^{man} plants by means of seeds and fruits, has ~~been~~ ^{been} ~~studied~~ ^{studied} and has been dealt with at length by many botanists from the time of Darwin to the present. In most parts of the world observations have been made in the field on plants growing under natural conditions; in the universities the causes and physiology of the various adaptations have been studied; and at the farms of the agricultural colleges extensive experiments have been carried on. The reason for so much attention lies in the interest of the subject from both the theoretical and the practical sides of science. Its bearing on the evolution of plant life and on the relation of the flora of different regions has given it great theoretical importance, while its relation to the agricultural industries has led to careful study of the means of dissemination of all these plants which are weeds in any country, with a view to their prevention or eradication.

Examples of the rapid spread of plants injurious to human industry are numerous. Darwin says of the cardoon, *Cynara cardunculus*, in Argentina; "Very many, probably several hundred, square miles are covered by one mass of these prickly plants and are unpenetrable by man and beast. Over the undulating plains where these beds occur nothing else can now live. Before their introduction, however, the surface must have supported as in other parts, a rank herbage." (1) Almost equally striking has been the spread of the Russian Thistle, *Salsola Tragus*, in parts of the States of North and South Dakota.

In this account of Seed Dispersal an attempt will be made to review the various general methods by which dispersal is accomplished, with reference to plants which exemplify

(1) Darwin, Journal of Researches, Chap. VI.

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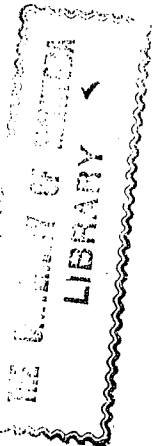
THE DISPERSAL OF SEEDS.

The dispersal of seeds, or rather the dispersal of plants by means of seeds and fruits, has received careful study and has been dealt with at length by many botanists from the time of Darwin to the present. In most parts of the world observations have been made in the field on plants growing under natural conditions; in the universities the causes and physiology of the various adaptations have been studied; and at the farms of the agricultural colleges extensive experiments have been carried on. The reason for so much attention lies in the interest of the subject from both the theoretical and the practical sides of science. Its bearing on the evolution of plant life and on the relation of the flora of different regions has given it great theoretical importance, while its relation to the agricultural industries has led to careful study of the means of dissemination of all those plants which are weeds in any country, with a view to their prevention or eradication.

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these methods, and then to consider the conditions prevailing in Western Canada and the means chiefly employed by the characteristic plants of this region to meet these conditions.

Many plants have no special adaptation of their seeds or fruit for securing a wide distribution. These depend upon the number of seeds produced and often upon the lightness of them to secure from ordinary conditions an opportunity to grow in sufficient numbers to perpetuate and even to spread the species such forms as the grains of many species of *Poa* and *Panicularia* among grasses, the seeds of most of the *Orobanchaceae*, the small utricles of the *Chenopodiaceae* and *Amarantaceae*, the seeds of *Portulacaceae* and *Caryophyllaceae*, the mericarps of *Sisya* and *Cicuta*, among the *Umbelliferae*, the Achenes of *Melianthus* and *Achillea* among the *Compositae*, and many others in various families are examples of prevalent types without special modifications to secure dispersal. A reasonably wide scattering of their numerous seeds is obtained by means of the wind which detaching them by shaking the plant send them over a circle whose radius depends of the height of the plant, and the strength of the wind. Such plants as grow on ground in the least unequal will have the rains and melting snow to wash them to the lower levels, even a small shower sufficing to roll many seeds over considerable distances, without injury to the least protected. Animals may brush against plants and entangle light seeds in their coats so that they will be carried for distances, greater or less. Still more seeds will be contained in the earth adhering to the feet of animals moving about in wet weather, or feeding or watering in low places. Darwin found seeds in little cakes of earth attached to the feet and legs of birds, and these seeds germinated. In one case six and a half ounces of earth from

the leg of a wounded bird yielded eighty-two plants. (2) Great numbers of seeds would thus be carried in the large lumps of earth adhering to the hoofs and legs of cattle and other animals, and this is a frequent source of the infection of cultivated fields with the seeds of such weeds as French weed, *Thlaspi arvense*. Thus even without any special adaptations there is a fair chance for the dispersal of seeds that are not of very large size.

But many plants have made some special provision for dispersal. Of these provisions the simplest are those providing for the flotation of fruits and the preventing of injury to them by soaking, thus providing for their dispersal by water. Darwin found that a large number of seeds could bear immersion in salt water for periods varying from twenty-eight to one hundred and thirty-seven days and still germinate. He also found that their powers of flotation varied greatly and were often assisted by their remaining attached to dried branches. (3)

Both flotation and resistance to injury by immersion will depend largely upon the thickness and structure of the outer coat of the seed or fruit and upon the attachment of other parts to this. Many seeds which sink in water at once, if clean will be floated for a long time by the withered and wrinkled skin of the dried up fruit in which they were enclosed, as is seen in the case of the wild grape where the few grapes which have adhered to the vines until spring are wrinkled into balls light enough to float. (4) This is a secondary resource for dispersal adopted by various berries. Other seeds are provided from maturity with corky coverings or air-filled sacs. Corky coverings are found in the fruits of *Alisma* and *Plantago*, by means of which the seeds are floated to all parts

(2) Origin of Species, Chap. XII.

(3) Darwin, Origin of Species, Chap. XII.

(4) W. J. Beal, Seed Dispersal, Chap. IV.

of the surface of the body of water where the parent plants grow. Air sacs are found in the perigynia of the marsh growing species of *Carex*, though the upland growing species lack them. The bladder-nut, *Staphylea triloba*, has three papery cells which float it high out of the water and even if one or ^{two} of these be broken the remainder gives sufficient buoyancy.

(5) Most nuts with their woody coverings are light enough to float, and many of them contain much air space. The cocconut has outside its hard shell a thick husk which serves it so well that it is the most widely dispersed plant of tropical seas. Darwin found the islands at the mouth of the Parana covered with orange and peach trees springing from seeds carried by the river (6).

Naturally more seeds fall during a wind than during a time of calm, and being acted upon by the breeze they are carried away from directly under their place of origin. This is especially effective in the case of very light seeds. Some plants are so arranged that it is only in a wind that their seeds can fall. This is achieved in the case of the Poppy by a series of openings near the top of the capsule when ripe, out of which the seeds are one by one shaken when the plant is swung by the wind. A similar arrangement prevails among the Campanulaceae, but here some species have the capsules erect, others have them pendent, and it is found that in those with erect capsules the openings are near the top, while in those with pendent capsules the openings are near the base, clearly showing that the purpose is to have the seeds scattered only in a wind. (7).

In a gale dried herbs, and sometimes branches of shrubs and trees, bearing fruits are broken off and carried or rolled along knocking off the fruits as they strike obstacles, or are rubbed over the ground. The lighter and more rounded such part

(5) W. J. Beal, Seed Dispersal, Chap. IV.

(6) Darwin, Journal of Researches, Chap. VI.

(7) Lubbock, Flowers, Fruits and Leaves, Chap. III

of a plant is the more easily will it be transported, and the more numerous its seeds the more widely will they be scattered. This condition has given rise to the large group of tumbleweeds, examples of which are to be found in almost all the open regions of the earth's surface. *Hubbock* mentions an Australian grass, *Spinifex squarrosus*, in which "the mass of inflorescence, forming a large round head is thus driven for miles" and the Rose of Jericho, *Anastatica hierochuntica*, "which, when dry, curls itself up into a ball or round cushion and is thus driven by the wind until it finds a damp place when it uncurls, the pods open and sow the seed." (8)

Other plants have parts of their fruit thin and large giving a surface to the wind especially for drifting over the snow. "The common locust tree, *Robinia Pseudacacia*, produces large numbers of thin flat pods. They become dry and slowly split apart, each half of the pod usually carrying every other seed. Each half pod as it comes off is slightly bent and twisted --- like an ice-boat, it has a sail always spread to the breeze. In this way there is nothing to hinder some of the seeds from going a mile or two in a few minutes, now and then striking some hard object which jars off a seed or two." (9).

In most plants the adaptation for wind carrying of the seeds is in the nature of a wing-like attachment to the seed or fruit. This takes many forms; in some plants it is a membranous wing, in others a single plumose tail, in a bunch of bristles forming a parachute, in still others a cobwebby mass.

As examples of fruits having wings may be mentioned the maple, ash, elm, birch, American hornbeam, basswood, dock in many species, parsnip, many crucifers and some leguminous plants. In maple, ash, elm, birch, dock and parsnip the wing

(8) *Hubbock*, Flowers, Fruits and Leaves, Chap. III.

(9) *W. J. Beal*, Seed Dispersal, Chap. V.

is an extension of the pericarp and takes various shapes and sizes. In the maples one long wing projects from each of the twin fruits; in the ash a long straight wing projects from the single fruit; the elm has a thin membrane stretched completely round the fruit; in the birch there are wings at the two sides; the dock is winged usually along three angles; and the parsnip is flat and extended sideways. In the horn-beam and hop the fruiting bract is persistent and attached closely to the achenes. In the basswood a large twisted bract is attached to the stem of a cluster of nuts. In the crucifers Zubcock instances the genus *Thysanocarpus*, where in *T. radians* and *T. elegans* there is a very broad wing. (10)

Winged seeds are found in many of the Coniferae, e.g. in the genera *Pinus*, *Larix*, *Picea*, *Taxus*, etc. In these a single wing extends from the seed. The seeds of several genera of the trumpet creeper family, *Bignoniaceae*, are broadly winged on both sides. Those of the genus *Catalpa* are several inches in breadth and divided at the ends into capillary processes. (11)

A plumose tail, sometimes of considerable length, is attached to the fruit in the plants of the genera *Clematis* and *Pulsatilla* of *Ranunculaceae* and German *Dryas* of *Rosaceae*. In these cases the style is persistent elongated and hairy. There are also some grasses where the awn is plumose as in *Stipa pennata*, figured by Zubcock. (12)

A very large number of species have hairs or bristles attached to their fruits or seeds, in the form of a tuft or ring. These are very various as to size, length, surface, quantity and are produced by different parts. In a very great number of composites a bristly pappus representing the calyx is present. This varies from the short hairs of

(10) Zubcock, Flowers, Fruits and Leaves, Chap. III.

(11) Britton and Brown, Illustrated Flora of the Northern United States, Canada, etc. Vol. III, p. 198-200.

(12) Zubcock, Flowers, Fruits and Leaves, Chap. IV.

Brachy^{ch}seta or Arctium, to the long ones of Antennaria or Carduus; from the copious tufts of Sonchus or Hieracium to the few bristles of Boltonia or Chaetopappa; from naked bristles as in Erigeron to plumose ones as in *Miatris* or roughened ones as in Vernonia, or barbed ones as in Trilisa; and from a tuft borne right on the achene as in all these species to one raised on a long beak as in Taraxacum and Lactuca^{ca}. Other families have^{ng} hairy fruits are Graminae, Cyperaceae and Platanaceae. In the grasses Erianthus has a ring of hairs at the base of the spikelet; Andropogon has the rachis below the empty spikelet, hairy and remaining attached to the fertile one in fruit; and various species of Festuca, Bromus and Elymus, besides many other genera, have numerous spikelets with hairy arms grouped into a spike. In Cyperaceae the genus Eriophorum has the perianth represented by soft bristles which project much beyond the scales of the mature chene. Platanus, the buttonwood, has the nutlets with a ring of bristles around the base.

Of plants having the hairs on the seeds instead of the fruits the most conspicuous examples are the Poplars and Willows of the order Salicaceae and the genus Epilobium of the Onagraceae. The seeds of these plants have a coma of silky hairs which, when the capsules split open, permit of wide distribution by the wind. "In the Cotton plant the whole outer surface of the seed is clothed with long hairs." (13)

By these various means plants in such situations and of such heights as to be exposed to the wind have become adapted to secure wide dispersal of their seeds. But there are numerous plants to which such means are not suited. With many of these the desired result has been most conveniently attained by taking advantage of the movements of animals.

Two chief systems of dispersal by means of animal movement have been developed; in the one the appetite of the animal is made the ally of the plant, and the seeds are dis-
(13) *Hubbock, Flowers, Fruits and Leaves, Chap. lll.*

persed either by being taken into the alimentary canal and afterwards ejected, or are scattered during the process of securing other edible parts with which the seeds are connected; the other is by means of mechanical attachment to the bodies of passing animals by means of hooked, braced, or stick parts. In these adaptations we see most clearly the interdependence of the various forms of life. The habits of animals have largely been formed by their relation to plants as a means of sustenance and in turn plants have developed features in consequence of which animals have become one of the chief means of dispersal..

In order that a species may be scattered by animal agency in connection with the feeding process it must either, (a) attract animals by the possession of edible parts usually of a pulpy and brightly colored character surrounding the seeds, but sometimes in the seeds themselves, and attractive by their size and position, or, (b), have its seeds either (1), capable of being swallowed and passing through the intestines of animals without the destruction of their germinating power, or (2) having some provision against being eaten when the fruit in which they are situated is devoured.

Fleshy edible fruits are found in all situations; close to the ground, as with the strawberry or dewberry; raised on erect herbs and low scrubs as in *Physalis*, *Smilax*, the raspberry or the currant; or on trees of varying size as in the cherry, plum, apple, orange and many others. Such fruits are brightly colored in order to attract animals, and it is noteworthy that the color is not present in the unripe fruit, which is of an inconspicuous green, usually, but is developed rapidly at maturity. (14) The range of color is from white, as in *Actaea alba*, *Cornus Stolonifera*, etc. to black, as in *Rubus villosus*, with all shades of red, orange, yellow, blue and

(14) *Subbeck, Flowers, Fruits and Leaves, Chap. IV.*

purple. The edible part may be in the seed itself, as is the case with all nuts, as cocconut, acorn, walnut, hazelnut, etc. These are usually the fruit of trees conspicuous in the situation in which they grow, and the nuts are commonly borne conspicuously on the branches.

Fruits of which the seeds are likely to be swallowed when the pulp is eaten, usually have them either small and hard or covered with a very hard endocarp. Darwin says "Hard seeds of fruit pass uninjured through even the digestive organs of a turkey. In the course of two months, I picked up in my garden twelve kinds of seeds out of the excrement of small birds, and these seemed perfect, and some of them which were tried germinated." (15) Waterton records an instance of a fig tree growing in the crotch of a mora in Guiana, which had sprung from the excrement of a fig eating bird. (16) Kerner von Marilaun found that very few seeds came through the horse or pig with germinating power, none through the turkey, hen, pigeon, duck and several other birds; 75 per cent. through the European blackbird; 80 per cent. through the European robin; and 85 per cent through the thrush. (17) Examples of fruits with small hard seeds are the fig, strawberry, raspberry, currant, cranberry; and of seeds covered with a hard endocarp the cherry, plum, peach, *Viburnum* of different species.

Other fruits make provision against the swallowing of their seeds by enclosing them in a stringy or cartilaginous core, as in the case of the apple and pear; by making them dry, hard and hairy as in the rose, or by making them of a bitter or unpleasant taste, as in the orange. Other plants have a fleshy caruncle on the seed, as in bloodroot, *Cyclamen*, *Trillium*, and *Cucullaria*. This is used in transporting the seed by insects such as ants, which eat the fleshy portion but leave the hard smooth seed. (18)

(15) Darwin, Origin of Species, Chap. XII.

(16) Waterton, Wanderings in South America.

(17) W. J. Beal, Seed Dispersal, Chap. VII.

(18) W. J. Beal, Seed Dispersal, Chap. VII.

In addition to such fleshy fruits and seeds, nuts are largely dispersed by animal agency. They form the chief winter food of squirrels, which lay up large stores of them in holes and other hiding places. Frequently such stores are in excess of the winter requirements and some hoards are left to grow, or it may happen that the hoarder perishes and his stores are left unvisited. Stores are also laid up by some species of jays and the magpies, and in carrying nuts for these some must fall if the bird be frightened or encounter too high a wind. I have observed the blue jay carrying hazelnuts to the limb of a maple beside my house, and cracking them on the limb, picking out and eating the meat. On examining the ground beneath the tree after he had been at this for an hour or two, I found a heap of husks, the broken shells of many nuts and several uninjured ones, which had evidently slipped away in the unhusking process.

A large number of species, however, make use of the movements of animals without their consent, by attaching their fruits by means of hooked or barbed processes or sticky portions. Such hooked or barbed processes take many forms, but in all they are adapted for taking hold of the hairy or woolly coats of animals. In some cases they are modifications of parts outside the ovary as in the burdock, *Arcium minus*, in which the involucre is globular with many rows of scales each terminated by a hooked bristle the whole forming a most effective bur. In the buffalo bur, *Solanum rostratum*, and its close relative *Solanum heterodoxum* the calyx is prickly and persists about the fruit. In various species of *Agrimonia* a row of hooked bristles springs from the rim of the calyx; these are very numerous in the agrimony of this region, *A. hirsuta*, forming a girdle which enables the fruit to lay hold of any hairy body which comes into contact with it. In *Myosotis arvensis* the calyx is covered with slender hooked bristles. In the Russian Thistle, *Salsola Fragus*, the prickly bracts along the flowering branches are slightly reflexed in

bodies of animals.

In most fruits, however, the hooks are an outgrowth of the ovary, and vary in number from one to thousands, and in size from several inches in length to a fraction of a line. The genus *Ceanothus* has the styles in some species, as in *C. strictum*, forming the fruit a long beak with a hook at the end. In such species the style in the young pistil has a joint or bend near the centre and as the fruit ripens the part below this enlarges and grows stiff, while the part above withers and falls away leaving the bend as a strong hook terminating the beaked achene. By this device the hook is rendered harmless while the seed is immature but becomes ready for assisting in dispersal as soon as the seed matures. (19) In *Martynia proboscidea* the fruit is prolonged into two long, stout, recurved processes which are of hard texture and with sharp ends. Along the side of the fruit toward these are stout bristles which serve to hold anything that has got below the hooks. The whole is beautifully adapted to lay hold of the divided hoofs of ruminants. (20) The fruit of the cocklebur, *Xanthium Canadense*, has usually two stout hooked beaks, and in addition has its surface covered with more slender hooked spines. The *Borraginaceae* furnish many examples of fruit provided with hooked prickles. In *Cynoglossum* the entire upper surface of the nutlets is covered with short barbed prickles; in *Lappula* the prickles, barbed at the summit, vary from a single row round the margin of the nutlet in *L. floribunda* to a complete covering of the upper surface in *L. virginiana* in *Myosotis* as already mentioned, and in several other genera the hooks are the hairs of the calyx. In the *Umbelliferae* the carrot, *Daucus Carota*, and Bur Parsley *Canalis nodosa* have bristles along the ribs of the fruit, and *Sanicula* in several species has the whole surface covered with hooked bristles. Of the *Leguminosae*

(19) W. J. Beal, Seed Dispersal, Chap. VII.

(20) Tubbock, Flowers, Fruits and Leaves, Chap. IV.

Glycyrrhiza lepidota has the surface of the pod covered with rather large hooked prickles; some species of *Medicago* have the edges of their spiral pods armed with small hooks; many species of *Meibomia* have the whole surface of their jointed pods covered with very small hooks; and some species of *Tespedeza* have a hooked beak.

Of fruits equipped with barbed processes the most striking are those of the genus *Bidens* in many of which from two to six stiff arms are sharp pointed and barbed, in most cases downward. The long awns of various grasses are usually minutely barbed, and in a few cases the barbs are large enough to be visible to the naked eye, as in the cultivated barley. Genera having some or most of their species with barbed awns are *Avena*, *Bromus*, *Elymus*, *Agropyronand* and *Hordeum*.

Sticky surfaces are usually found in seeds, but a few plants have a gummy portion on the fruit. Some have viscid glands on the fruit or fruit bearing branches. (21) These are found in several species of *Silene*, especially *Silene noctiflora*, *Alychnis* and *Cerastium*. A gummy secretion covers the involucre of *Grindelia squarrosa*, the Gum-weed. Many seeds are quite mucilaginous and especially upon being wetted will adhere to whatever touches them; such are flax, plantain, and pepper-grass. "The berries of some plants when fully ripe burst very easily when touched, and some of the seeds are then likely to adhere to animals and be carried away. Berries of several plants belonging to the night shade family have this peculiarity, as well as some of the cucurbits. When the outer covering of seeds of water lilies, arums and others are broken the gummy secretion is very likely to adhere to the feathers or fur or feet of animals." (22)

(21) W. J. Beal, Seed Dispersal, Chap. VII.

(22) W. J. Beal, Seed Dispersal, Chap. VII.

Certain plants secure a limited dispersal of their seeds by mechanical action on the part of the parent plant. This is usually due to stresses set up in the fruit by the drying process attendant upon maturity, but in a few cases to other causes. A number of plants produce or ripen their seeds in the soil in which they are to grow, and others have seeds which are able to move through a short space or to bury themselves in the earth, generally by means of a hygroscopic action of some part.

Fruits which scatter their seeds by the application of pressure or by a sudden jerk are common among the dry dehiscent varieties and among those with a central axis to which the carpels are attached. In many of the Leguminosae the pods split at maturity and each half coils spirally owing to the woody fibres lying inclined to the direction of the pod. (23) In most cases the coiling is done suddenly as the pod opens, and the seeds are thrown with a jerk which scatters them quite widely. This is seen in many species of *Vicia* and *Lathyrus* and is quite easily observed in our *Lathyrus venosus*. In *Impatiens* the valves of the capsule separate, especially if touched, and coil suddenly scattering the seeds on all sides. In the violet the capsule splits into three valves, which in drying shrink together and press against the seeds which are finally ejected with sufficient force to scatter them some distance. Of the witch hazel, *Hamamelis Virginiana*, Beal says, "The witch hazel bears a hard woody nut-like fruit, as large as a hazelnut; when ripe the apex gaps open more and more, the sides pressing harder against each smooth seed, till finally it is shot, sometimes for a distance of thirty feet." (24)

In the geraniums the carpels are attached around a central axis, which elongates as the fruit matures, the single-seeded capsules having red-like portions which are attached along the axis. When ripe these red-like portions curve up-

(23) Tubbock, Flowers, Fruits and Leaves, Chap. 111.
(24) W. J. Beal, Seed Dispersal, Chap. VI.

ward, tearing loose with a jerk and either throwing the seed from the capsule as in *G. dissectum*, or projecting the whole capsule as in *G. Robertianum*. Lubbock found that some of the latter which he had observed threw the seeds more than twenty feet. (25)

In the Squinting Cucumber the result is attained through the tension arising from the gorging of the fruit with fluid. In this state a touch is sufficient to break it from its stem, and the contents are then forced out through the opening thus made. (26). *Muracrepitans*, the sand-box tree, the ripe fruit bursts with a loud noise and scatters the seed all about. (27)

Various plants, especially of the Leguminosae, either produce subterranean flowers or bury them when the pistil has been fertilized. Of the latter the peanut, *Arachis hypogaea*, and *Trifolium subterraneum*, a clover described by Lubbock, are examples. Of the former a species of *Vicia*, *V. amphicarpa* and a *Lathyrus*, *L. amphicarpos*, both of which produce aerial as well as subterranean pods are mentioned by Lubbock. (28) One of our native plants, *Falcata comosa*, has the same peculiarity. One or more species of each of several other families have developed the same peculiar method of insuring the success of their seeds. In all such cases the number of seeds in each of the underground pods or capsules is small as they are assured a suitable soil of growth, and the presence of many would not only mean a waste of productive energy but be detrimental to the growth of all after germination.

Other plants, especially species of the Graminae, and of the genus *Erodium* in Geraniaceae have an awn which twists or untwists according to the scarcity or abundance of moisture in its surroundings. In this way they move over the surface

(25) Lubbock, Flowers, Fruits and Leaves, Chap. III.

(26) Lubbock, Flowers, Fruits and Leaves, Chap. III.

(27) Coulter, Plant Relations.

(28) Lubbock, Flowers, Fruits and Leaves, Chap. IV.

of the soil as the wild oat, *Avena fatua*, has been observed to do, or they bury the seed in the ground by pressing against blades of grass or other obstructions as they unroll. The pulling back of the seed as the awn coils again is prevented by the stiff hairs with which its beak is armed. This action has been observed in various *Erodiums* and also in various species of the genus *Stipa*. When the seed is forced to a sufficient depth the awn will be broken off by further pushing, or will remain to decay while the seed germinates.

It may be well now to consider the conditions under which each of the different modes of dispersal will prevail. Of course in all situations there are many plants which produce numerous small seeds with no special adaptations and leave their distribution to the chances of wind-borne branches, animals, muddy feet, and rills of rain water or melting snow. Such are the upland sedges, *Carex*, the puccoons, *Eithospernum*, and the prairie mallow, *Malvastrum coccinea*, of our prairies and open hill sides; such, the *Chenopodiums*, the buttercups and the common anemone, *A. Canadensis*, of the lower and moister grounds; such also the showy Lady's Slipper, *Cypripedium spectabile*, and the different species of *Ren* *Ochis*, *Habenaria*, of our woodlands. Besides these there are many varieties of grasses and other plants with small seeds, which, growing in the open, are by position adapted to the winter drifting which prevails on the prairies. In this way, seeds are carried along with the snow which is continually driven onward and onward until it is piled up at the edge of some thicket, fence or hollow.

Plants adapted to the water dispersal will necessarily be found only in streams, lakes or marsh regions, or growing along the margin of such. Of this nature are the numerous grasses, sedges, water knot-weeds, and water lilies found in our slow flowing streams, our lakes, sloughs and the large marshes about lakes Winnipeg and Manitoba. Such

also are the wild grape, basswood, and red osier dogwood, growing beside the prairie rivers.

Where animal transportation is depended upon, the plants will grow in such places as would be the haunt of the wild beasts and birds and the methods provided for will be determined by the character of the animals likely to frequent such spots. Edible pulpy fruits are found in all situations; lying on the ground, as the strawberry; at the height of a few inches, as the ground cherry, *Physalis*; up a foot or two, as the raspberry; on taller shrubs as *Viburnum Opulus*, or *V. Pentago*, on small trees, as the wild red cherry, *Prunus Pennsylvanica*, choke-cherry, *P. Virginiana*, or wild plum, *P. Americana*; or on lofty trees as the wild black cherry, *Prunus serotina*. In all such situations they are exposed to birds, which are probably the best distributors of seeds from edible fruits. Many of them fall from the tree when perfectly ripe, and are then exposed to the appetite of mammals; others stay on the plant until spring, if not disturbed before; in this way the high bush cranberry, *Viburnum Opulus*, and the wolfberry, *Symphoricarpos occidentalis*, furnish food for the birds and secure dispersal throughout the winter. Nuts on the other hand are almost restricted to fairly tall scrubs and trees, where they grow, out of reach of grazing animals and unattractive to birds until ripe, when many of them fall within reach of the ground squirrels, and others are secured from the place of growth by tree squirrels, jays, woodpeckers and other nut-eaters. Both pulpy and nut-like fruits are found in the greatest number in plants growing in thickets and especially in the neighborhood of streams, where birds particularly haunt.

Fruits having hooked or barbed processes are suited to catch the wool and soft hair of passing animals mammals, and will be found in the places where such mammals move about, and at such heights as to be not above the backs of woolly or

furry creatures. They are found particularly about the edges of thickets and openings in the woods, as with the stickseeds, genus *Lappula*; along the sandy shores of lakes as with cockle bur, *Xanthium Canadense*; by the side of marshy water holes, as with *Bidens frondosa*, or *B. connata*; on the grassy sides of hills and ravines as with *Glycyrrhiza lepidota* and *Stipa spartea*, or in the low level meadows as with *Hordeum jubatum*. As to the heights at which such fruits grow Labbock found that of thirty three British genera of trees and shrubs over eight feet in height not one had hooked fruits, and also that of about thirty English plants with hooked fruits not one was aquatic and not one was ever four feet high. (29) Pretty much the same is true of our native species, the tallest being *Bidens frondosa*, which reaches but little above the height of the backs of the buffaloes which would frequent its habitat. Moreover, almost all plants with hooked fruits retain these until the following year, unless they are detached by animal agency before that.

Plants depending on wind dispersal will be either those of open regions or the loftier plants of wooded districts if they are to secure effective breezes to scatter their fruits abroad. We would naturally expect then to find this mode of distribution common among the plants of the world's great plains and among the large forest trees, and that is precisely where we do find it; plants growing at the edge of forest glades, beside lakes or along streams are also in some cases adapted to the same means. Labbock found that nearly all the taller British forest trees had winged or hairy seeds or fruit. (30) Of our own, the poplars have hairy seeds, the pine, spruce and tamarac have winged seeds, and maple, ash, elm, birch and basswood have winged

(29) Labbock, Flowers, Fruits and Leaves, Chap. IV.
(30) Labbock, Flowers, Fruits and Leaves, Chap. IV.

or bracted fruits. Among plants of the open plains and great marshes are found the great numbers of Compositae with parachutes of bristles, many species of grasses with tufted seeds, hairy seeded members of the Rosaceae, the Ranunculaceae and other families and all the tumbleweeds of many distinct families. There are very few with simple dilated wings as these appendages, though very useful as a sail to a fruit falling from a height, are too small in proportion to the weight of the fruit to be effective in lifting it from on or near the ground in a wind, and besides would usually lie so on the ground as to present no hold for a wind after they had once fallen.

As the whole southern and western part of Manitoba is of a prairie character, and as it is a region of high winds, one would naturally expect to find adaptation for wind dispersal in many of its plants, and an examination will show the prevalence of this type. The chief orders of the prairie flora are Gramineae and Compositae, these being conspicuous both by the number of species and of individuals. In addition are found large numbers of Leguminosae, especially of the genera Astragalus and Spiesia; Ranunculaceae, especially the genus Anemone; Rosaceae, particularly Potentilla and Geum; Cruciferae, the native Arabis and Lesquerella and many introduced weeds; various species of Chenopodium, Artiflex and Amaranthus, especially in alkaline soil; Galium boreale and Campanula rotundifolia of the Rubiaceae and Campanulaceae; Eragrostis, of the Melanthaceae; Allium and Liliium of the Liliaceae; and a few upland willows, Salix. These constitute the greater part of the prairie plants, and of the remainder most, as the strawberry, the rose, the wolfberry and the silverberry have edible fruit, and in the case of the shrubs form low thickets where the ground is unequal. It may be worth while to consider the methods of dispersal provided in these prairie species.

The upland willows have the typical hairy willow seed. The geum of the prairies, *G. ciliatum* is remarkable for its long plumose style, while all other Manitoba Geums have the style hooked or naked. One of the Potentillas, *P. fruticosa* which grows on the sandy ridges of the prairie region shows a tendency to the development of a hairy chene though chiefly dependent on the shaking of its branches for scattering. Of Ranunculaceae the most striking Manitoba examples are *Anemone cylindrica* and *A. multifida*, both of which have densely wool achenes, while all our woodland anemones have naked achenes.

Various members of the *Astragalus* and *Spiesia* genera have their spike or head of pods raised on the top of a fairly tall stiff stalk; when the plant is ripe the pods split open from the upper end for about one-third of their length, and then when the wind drives the head to and fro the seeds are shaken out and scattered to a considerable distance. A similar result is obtained in *Campanula rotundifolia* by the little doors in its capsule which were mentioned before. The most widely prevalent of the prairie Potentillas is *P. arguta*, which is the tallest and stoutest of our species and so is suited to the scattering of its seeds as it sways in the wind.

Of the tumbleweeds the best known and most typical are two introduced plants, *Salsola Tragus*, and *Sisymbrium altissimum*, which have become, especially the latter, very prevalent. But there are numerous other plants which when dry are apt to be broken off and driven by the wind across the dry prairie or the snow. Such are *Galium boreale*, several species of *Chenopodium* and *Amarantus*, and many grasses and Compositae, several of which will be referred to later.

Of the very numerous Compositae growing on the prairies the majority have a hairy or bristly pappus which serves as a parachute. Of the Cichoriaceae or *Liguliflorae*

such are *Lygodesmia juncea*, the very common *Agoseris glauca* and *Nabalus racemosus*. The large number of the *Cichoriaceae* however, other than introduced plants, appear to belong to the woods and thickets. Of the *Compositae* proper the following genera with hairy pappus have from one to many species very common on the prairies; *Laminaria*, *Chrysopsis*, *Eriocarpum*, *Solidago*, *Aster*, *Erigeron*, *Antennaria*, *Gnaphalium*, *Senecio* and *Carduus*. Of these *Chrysopsis villosa* and *Eriocarpum spinulosum* in particular have the tumbling habit well developed, and when they dry up in the autumn, break off close to the ground and are whirled along by the winds, gradually losing their achenes which set off on independent journeys through the air. Of the genera having achenes without numerous bristles, the most frequent on the prairie are *Rudbeckia*, *Ratibida*, *Helianthus*, *Gaillardia* and *Artemisia*; all the species of the first four are strong tallish plants, which, standing stiffly are widely swayed by the wind. Their achenes also are more or less flat and in some cases attached to chaff of the receptacle so that they yield a fair surface to the wind when shaken out of the swaying head. Of *Artemisia* some species are tall and stout and the achenes shake off in a wind; others grow more or less diffusely and become tumbleweeds when loosened from the dry soil or broken off close to the ground.

The very numerous grasses of the prairies have also developed adaptations of the various types for wind dispersal, to which they have added in many instances the power of using the coat of animals that would feed among them. Many of them grow to a height of from two to four feet with a slender culm capable of being swayed by a very slight breeze. At the top of this is the spike or panicle in which the grains are surrounded by the dry glumes and paleas which give them a bulk very large for their weight, and sometimes form a wing-

like expansion to them. Such are *Bouteloua oligostachya*, *Coeleria cristata* and *Elymus Macoumi* besides many others growing on the open prairie or by the ponds and sloughs of the prairie region. Others grow with a branching habit, and, breaking off when dry, are driven for long distances by the wind, being extremely light. Such are *Sporobolus asperifolius*, *Poa pratensis*, *P. flava*, *Agrostis hyemalis* and various species of *Banicum* and *Panicularia*. A few species have hairy attachments to the grains, as *Andropogon scoparius*, with the rachis hairy below its sterile spikelet and the common seed of our prairie marshes, *Phragmites Phragmites*, with its rachilla long hairy giving the grain the appearance of a tuft of down..

Two other grasses are specially interesting as having more than one form of adaptation for their dispersal, through which advantage they have become about the most wide spread and general plants of the prairie flora. *Hordeum jubatum* is found especially in the alkaline meadows of the whole Western Canadian region. Its spikelets are arranged usually in threes, the central fertile, the two lateral sterile; the empty scales of all three spikelets become slender awns, and the flowering scale of the fertile spikelet bears a long awn. Thus the grain has the appearance, beside being awned, of being surrounded by an involucre of six slender bristles, by the aid of which, in a high wind, it can rise into the air and sail for great distances. These awns besides are rough and when examined under the microscope are found to have the edges barbed downward, enabling them to lay hold of the woolly coats of animals and thus to be spread as burrs. The barbed awns also serve to hold together grains which come in contact when driving along the ground before the wind, in which way masses are formed which roll along in

true tumbleweed fashion.

The other grass referred to, *Stipa spartea*, is the porcupine grass found in almost all dry parts of the prairie region. Its culm is from two to four feet tall, and the weight of the grains usually bends the top to a drooping posture. In this position it sways in the wind and the grains on being shaken out are jerked to a distance of a yard or more on each side. Owing to the weight of the grain it falls with the sharp point downwards, and the awn, from three to six inches long, upwards. This awn is somewhat four-sided and has in its outer covering two strips of a lighter color and finer texture than the remainder, which in the upper half almost completely cover the surface. Owing to the difference in texture of these parts of the surface the lower half of the awn, as it becomes dry, twists in a tight spiral and the upper half goes off at an abrupt angle. In a large number of fallen grains which I observed, over half were found to have coiled about blades of grass, and the upper half of the awn was pressing in most cases, against other blades. In uncoiling, in the presence of moisture the awn drove the grain into the ground; the rough edges of awn and the backward pointing barbs of the grain both prevented it being pulled up again when the awn in drying coiled up once more, so that in two or three days the grains were buried an inch or more in the soil. The sharp barbed point of the grain serves, however, another purpose, as it makes the fruit of this grass one of the most effective burs in existence, and by the aid of the spiral awn often drives it not merely into the wool or long hair of sheep, cattle and dogs, but, in the case of sheep at least, into their flesh and even

their very vitals.

There are numerous other plants of the prairies interesting and well worthy of study in connection with the dispersal of their seeds, but they belong to the types of either animal or of wind dispersal that have been described. Their effectiveness is proved by the rapidity with which a cultivated field returns to the original prairie condition if allowed to lie idle. For a year or two the introduced weeds predominate, then the native *Artemisias*, *anemones*, roses, lilies and grasses take hold, and in four or five years it is almost impossible to find a plant whose presence is due to former cultivation. That this is not true to the same extent of more sheltered situations is proved by the presence in one woodland clearing which I know of *Hesperis* after fifteen years or more of absence of cultivation. On the prairies dozens of deserted homesteads in the years of frost and drouth gave opportunity for observing the return of the native flora in the short time mentioned above, a return which was due to the wind carriage of the seeds of so many of the prairie plants.

Note:-

In giving the names of plants within its range the nomenclature adopted in Britton and Brown's *Illustrated Flora of the Northern United States and Canada* has been followed.