The Distribution of Plants.

BY

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IN examining the constituents of the flora of any country one is struck by the great variety of species, genera, and orders represented in it, and secondly, one notices that the species are not altogether those occurring in the nearest lands, though in most countries the greater number of the species have affinities or are identical with those of adjacent countries, even if these countries are separated now by considerable stretches of sea; there are besides a certain number—usually very local and generally consisting of one, or perhaps two, species of a genus—which have no affinity at present with anything else in the area, but with plants of far distant regions, and which are the relics of a long-lost flora. Besides these we have now in all parts of the world, wherever man has trod, a larger or smaller number of plants introduced accidentally or intentionally by man.

Ground bare of plants fills up very rapidly with vegetation brought to it in the form of seeds from the nearest land by various means of dispersal, and eventually becomes so densely covered that there is no room for additional species, and it remains in a state of equilibrium until one of the great factors of change comes again into play.

As a rule, the greatest variation is to be found where several distinct floras are, or have been in the past, sufficiently near to supply any given country with its flora.

In the British Isles we have a central European element, an Arctic element, a Portuguese element, and a North American element. In the Malay Peninsula a large percentage of the species is common to Sumatra or has close affinities with those of Sumatra; a number are represented in Borneo only; others are Javanese, Burmese, Indian, Cochin Chinese, and Siamese; while both in the British Isles and in the Malay Peninsula we have a number of established weeds, in the latter country chiefly from South America and the West Indies, which go to make the mixed floras as we find them to-day.

This mixture of plants in a country is due to the three great factors of change, which are—(1) change of climate, (2) change of the land surface, (3) change due to human agency.

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These three factors have all caused the destruction of large numbers of species, which have been replaced by invasions of others usually from the nearest lands; but in almost every case of which we have records of any of these catastrophes in the plant-world, there have remained survivors of the lost floras for a long time in suitable spots. Plants of these which have been sometimes modified so as to adapt themselves to the change of condition may form a distinct portion of the new flora.

The first two factors have been in action in one or other part of the world more or less continuously, probably from the foundation of the globe, and no part of the world has been free from their action, which has been repeated usually many times.

The third factor, human agency, almost certainly commenced to play its part in altering the vegetation of the world when the human race began its first migrations. The earliest record I know of dates from Neolithic times, when the immigrants from the East brought into western Europe many of our weeds mixed with their cereals and Flax seeds. But the greater effects began to be seen later, about four thousand years ago, and very much more extensively and rapidly within the last two hundred years.

Change of Climate.

This factor does not seem to have come into play in any part of the world, at least to any great extent, in historic times, but we have plenty of evidence of its having played a most important part in the past. We have had in England, since the first appearance of flowering plants, an extensive series of great changes of temperature, from the tropical or subtropical climates of the Eocene period to the milder one of the Miocene, to a temperate climate broken into by one or more Arctic periods and restored again later. Each change was accompanied by a corresponding change in the flora, the destruction of the old flora and the invasion of a fresh one.

In the equatorial regions we have no record of any Ice Age later than the Permian period, nor indeed, so far as I have been able to detect, any period of a temperate climate, but we have had fluctuations of humidity and dryness, alternations of a xerophytic period and of a hot, wet period, the latter causing the disappearance of the xerophytic flora except in a few still more or less dry spots on the higher mountains and on the sea-shore. Such island refuges of an otherwise lost xerophytic flora in the Malay Peninsula are the plateau of Gunong Tahan, 5,000 to 7,000 feet alt., where nearly all the plants are endemic, and the curious sandstone dyke, 1,400 feet high and only a few feet across in parts, which traverses the valley of the Klang river and is known as Klang Gates. Here, surrounded by mountains even higher and lowland jungle of entirely rain-forest species, I found several xerophytic endemic plants mixed with characteristic xerophytic plants occurring also on the dry mountain areas, very many miles away.

The name *endemic* has been used for two distinct classes of plants, and this has led to some confusion. It is used to cover any species confined to a given limited area. These may be either the relics of a lost flora just surviving in one spot, or species evolved in one locality which have spread no farther. It would be advisable to have different words to express these two utterly distinct classes of plants.

It is not at all difficult to distinguish to which class an endemic plant (in the double sense) belongs, for while the relic of a past flora has usually no affinity with any other in its area, the endemics of the second class evolved on the spot have affinities, often close, with abundance of other species in their locality.

Both of these classes are well represented in the Malay Peninsula, as they are in most countries.

A good example of the first class of endemic plants is that of the Gesneraceae of Europe, *Ramondia* and *Haberlea* occurring respectively in the Pyrenees and Balkan mountains. The nearest species of the order are the few occurring in the African mountains, but they have no affinities with the European species, nor have the species of northern India, but they are related to some Chinese and Japanese species; *Ramondia* is most closely allied to *Conandron* of Japan, not only in habit but in having four and sometimes five stamens, with lanceolate acuminate anthers, and also in the form of the fruit. *Haberlea* seems to be most nearly allied to *Ramondia* and *Oreocharis* of China.

Now Clement and Mrs. Reid have shown (Pliocene Floras of the Dutch-Prussian Borders, 'Mededeel. van de Rijksopsp. van Delfstoffen', and 'Quart. Journ. Geol.', lxxvi. 149) that South Europe in the Lower Pliocene period contained a number of forms of Chinese and Japanese affinities, i. e. plants now confined to these regions. It seems impossible to doubt that these European Gesneraceae are relics of this period, or to suggest any other cause for their occurrence here.

The second class of what are included popularly under the term 'endemics' may be exampled in the large numbers of species of Didymocarpi, Sonerilas, Argostemmas, and such-like big genera in the Malay Peninsula, evidently evolved on the spot and not spread farther than that area. I do not intend to offer suggestions to account for this evolution here, as it would lead away from the subject of distribution.

The Changes in Land-surface.

These are at present and most probably always have been slow, though very distinct. We know that in Europe, since the appearance of flowering plants, there have been great changes of land and sea, and we have distinct traces of a former land connexion between the British Islands and North America in the peculiar distribution of such plants as *Sisyrinchium*

bermudianum, Linn., *Eriocaulon septangulare*, With, and two species of *Spiranthes*, while a later land connexion between Portugal and south-west England and Ireland have given us *Pinguicula grandiflora*, Linn., *Erythraea Massoni*, Sweet., *Arbutus unedo*, Linn., *Saxifraga umbrosa*, Linn., *S. Geum*, Linn., and some other species.

The same fluctuation of land and sea has been going on in the Malay Peninsula. This area has been connected, I gather from its flora, with Borneo at one time, and then separated by sea; with Sumatra; with the Tenasserim region, and here, as I hope to show later, then broken off and joined again. Besides these land and sea changes, all of which altered to some extent the constituents of the flora, we have the constant and continuous denudation of the mountains, causing the disappearance or scarcity of many high mountain plants and the formation of plains of sand or mud, according to the constituents of the mountains denuded, and producing a lowland area soon invaded and covered by a flora quite distinct from that of the mountain area.

I give an instance of this factor in distribution from the Malay Peninsula. This region is now connected with Tenasserim by the Isthmus of Kra, and I have shown in a paper on the Flora of Lower Siam ('Journ. Roy. As. Soc. S. Br.' 59, p. 17) that the Isthmus of Kra contains a totally distinct flora from that of the Malay Peninsula, no less than forty genera occurring there which are absent from the Malay Peninsula, while sixty genera of the Malay Peninsula are missing altogether. The Isthmus of Kra is a sandy, flat area in which are scattered large islands of limestone, which, from the occurrence of sea-bird guano in their caves, shows that they were at no very distant period surrounded by sea. The climate is less wet than farther south, and there is a dry period in which most of the herbaceous plants wither.

The mountains of the centre and west of the Malay Peninsula are of granite, and by denudation form mud alluvium, and on the west coast none of this flora occurs, but on the east coast the mountains are of sandstone and have been washed down to form large areas of sandy heaths running down to the east corner of Singapore. All along this coast you may find plants of the Isthmus of Kra flora, and the farther north you go the more you will find.

Here we have a sample of the formation of a new sand-hill area being gradually invaded by a northern flora, since the land connexion was formed by the silting up of a shallow sea between the Burmese and Siamese regions and the Malay Peninsula, which was previously an island.

Changes due to Human Agency.

The alteration of a flora by human agency consists of the destruction of species, and the introduction of other species accidentally or intentionally.

This has probably been going on to some extent from the date of the first extensive migrations of man all over the world, but it was when the first great civilizations began that these changes commenced to seriously affect the floras. As long as the population is small, and the family system prevails, the wandering savage effects little alteration in the flora. It is when the families collect into tribes, settle on an extensive area, and cultivate on a large scale, that the great changes in the flora commence.

In England we do not find any species exterminated by the early immigrants, unless possibly *Trapa natans*, a valued food product, but in India, Ceylon, Java, and probably some other countries we may reckon that a very large portion, especially of the arboreous vegetation, was destroyed from two thousand to four thousand years ago. I have already called attention to this in the case of Ceylon in a paper on Endemism ('Ann. of Bot.', xxxv. 566). The civilization period in India probably dates from an earlier era, and it has been a much more persistently over-populated country. The great plains, nearly treeless, over which one travels in almost any part of peninsular India must, before the advent of man, have borne a totally different and much richer flora, but the great population required forest trees for the timber of their houses and temples, and for shipping and firewood, and the ground denuded of these trees was afterwards cleared for cultivation of materials for food and clothing. The original flora practically only persists now in a few mountainous tracts which were not suited for towns or cultivation areas. Apart from deductions made from the distribution of plants, I think that the fact of the plains of India being formerly afforested is at least strongly suggested by the occurrence all over them of the ape *Semnopithecus*, a genus of monkeys elsewhere exclusively occurring in the heart of tropical forests, and the peacock, a bird which elsewhere occurs only on the borders of heavily wooded country, though it is not, like the monkey, an inhabitant of the interior of lofty forests. Both of these animals have been preserved by man from religious motives, and seem now to have adapted themselves to the life of the villages of the plains.

Java was thickly populated in the twelfth century, and probably earlier. The Dutch commenced to trade there in the seventeenth century, and began to develop the country agriculturally early in the nineteenth century. This development entailed the destruction of the forests to such an extent that one may travel for days through much of the north part of the island and see nothing but rice and sugar plantations, so cleanly maintained that there is hardly a weed to be seen among the rice-plants.

We read in Raffles's 'History of Java' that in the eastern districts fifty to sixty thousand beams a year were delivered to the coast districts in about 1800, the timber of the coast area having been exhausted by then, and, besides this, large quantities of timber were used in local boat-building.

Thus in Java the original flora has almost entirely disappeared over large areas, and in the Tosari district there is hardly an indigenous tree to be seen. I found here but one native tree (*Helicia obovata*, Benn.), and the most conspicuous plants are the Radish of Europe and *Datura arborea*, Linn., of South America. The roadside banks are covered with a mixture of European weeds and indigenous Javanese herbs, which have been able to survive in these spots.

In the less accessible southern parts of Java, I am told, the original forest flora persists, as well as the larger mammalia which have long disappeared from northern Java. There are also some good forests left on the bigger volcanic mountains.

In dealing with questions of distribution and origin of floras, this destruction of the original vegetation must be taken into account, and it must be remembered that in such cases we are restricted to the investigation of the plants which occupy the ground at the present time, and not dealing with the original flora of a few centuries ago.

The fate of a forest flora when timber-felling is started is soon decided. Not only do the big trees with their epiphytic flora disappear, but, owing to the admission of light and heat into the jungle, all herbaceous, shade-loving plants for a long way through the still standing forest perish. Over the cleared land, if not put under cultivation, grows the Lalang Grass, *Imperata cylindrica*, Cyr., in the eastern tropics and other inflammable herbaceous plants elsewhere. These plants are often fired, accidentally or intentionally, and all the rest of the indigenous flora, herbs, and small shrubs, constantly burnt, soon disappear and all that remain are the few species of plants which can survive constant burning; such plants are those with subterranean rhizomes, like the *Imperata*, leguminous shrublets, and herbs whose seeds are uninjured by the passing fire, Macarangas (Euphorbiaceae), whose buds are protected from injury by resin, and trees like *Cinnamomum iners*, the resinous leaves of which burn with so great rapidity that the main buds and trunk are unharmed, as the fire passes too quickly by to really injure the tree.

Where land has got into this state after a few years, either by cultivation or by being cleared and overgrown with *Imperata* or such inflammable plants, it may be hundreds of years before any of the original vegetation comes back, and then only if big areas of original unhurt forest remain in the vicinity. In Province Wellesley, at Tasek Gelugur, was a flat, sandy plain covered with a dense growth of *Imperata*; possibly, as its name (Tasek, a lake) denotes, it was originally a swampy lake district: it had not been cultivated within the memory of man, and natives assured me it was in exactly the same state fifty years previously. Besides the grass, hardly any plants occur except a few shrublet Leguminosae. If the country becomes regularly settled by a large population or is extensively cultivated, all the

indigenous flora is destroyed. Big areas which in 1888 were covered with a trackless dense forest, such as the country lying along the railway between Klang and Kwala Lumpur, are now entirely covered with Pará rubber trees for many miles, and nothing at all is left of the indigenous flora, which has completely vanished, never to return. Already many local species collected by myself in 1899 to 1900 in such areas are now apparently quite extinct.

Where countries are thinly populated, as in the interior of the Malay Peninsula, tenanted only by the scattered wild tribes known as the Sakai, very little alteration in the flora is made by the people; they may fell the jungle round their huts, but they do not occupy one spot long; a death in the family or the shortage of game sooner or later causes them to leave, and the surrounding forest soon closes over these clearings again.

But where a village springs up and permanent cultivation is made, the indigenous flora soon vanishes. Sometimes plants of special economic value, such as rattans, rubber, gutta-percha, or wood-oil trees, are so extensively sought that they become rare, if not extinct.

I have visited an old Malay settlement on the Pahang river where I could only find one species of rattan, a valueless *Daemonorops*. As the rattan stems are cut before fruiting, the other species, valued for tying in house-building and for export, had been exterminated by not being allowed to fruit. Again, the wood-oil trees, *Dipterocarpus grandiflora*, Blanco, in all accessible parts round Malacca, were nearly exterminated (until more or less protected by Government), in the process of extracting the oil, by making large holes in the trees; and near Kuching, in Borneo, one could see hundreds of trees of *Dyera Lowii*, Hook. fil., standing dead from having been tapped to death for the Jelutong rubber. While in cases of complete destruction of the flora the trees, lianes, jungle herbs, and epiphytes disappear, there comes an invasion of open-country herbs and bushes, partly from surrounding areas, should there be any open country, heaths, or sandy plains to supply them, and partly plants introduced accidentally and occasionally intentionally by man. Curiously, plants introduced intentionally for use or ornament comparatively seldom establish themselves as part of the new flora—that is to say, reproduce themselves naturally and spread so as to form an all-important feature; but in the East Indies we may cite, as ornamental plants introduced and run wild, such examples as *Oxalis rosea*, Jacq., *Lantana mixta*, Linn., *Mimosa pudica*, Linn., *Lochnera rosea*, Rchb. fil., two species of *Turnera*, *Anacardium occidentale*, Linn., and the aquatics *Eichornia speciosa*, Kth., and *Limnocharis emarginata*, H. B. K., and in Africa Opuntias and *Argemone mexicana*, Linn. All these are tropical American plants mostly introduced originally for ornament, and now forming a conspicuous part of the flora. The larger number of weeds, however, are inconspicuous herbs: Grasses, Compositae, herbaceous Rubiaceae,

Amarantaceae, and such like introduced accidentally. All plants thus imported by man and run wild I class as weeds.

Weeds.

Weeds are usually identified by their being confined in their habitats to cultivated ground, or roads, or paths, as such classes of habitats did not occur previously to the advent of man, and it is clear that plants now confined to such spots in any given country must have been introduced by man. Some plants, however, like *Lochnera rosea*, the West Indian periwinkle, grow exclusively on sea-sand; others, like *Capsicum minimum*, Linn., establish themselves on limestone cliffs, or, like the Wallflower, on ruined walls, &c. In such cases their original habitat and place of origin can only be adduced by their history, if known, and otherwise by their affinities with other species allied to them.

All weeds must have been wild in some country, but may have been so long diffused over the surface of the globe that it is very difficult now to identify their original home.

A certain number of species of plants are only known in cultivation; of these some are derived from well-known wild forms, especially those of western Europe, whose history we know. In other cases we can only guess the origin by knowing where allied species are still actually to be met with in a wild state.

The greater number of the Malay fruit trees are not known in a wild state anywhere. They must have been wild somewhere in the Malay area, as they nearly all belong to local genera, but are specifically distinct from any species occurring in a wild state. The cause of this is, I think, that in very early days when a native found any of these trees in a forest he went and regularly gathered the fruit, taking it to his village, where the seeds thrown away germinated and formed an orchard. Often too, if a Malay finds an abandoned fruit tree in ripe fruit he fells it to save the trouble of climbing it. By persistently taking the fruit he prevents the tree reproducing itself by seed in its native haunts, so that the species eventually dies out. Or again, if he finds a number of these trees together, he will start a village round them and so bring them into cultivation. This, I believe, accounts for the absence in a wild state of the Durian (*Durio zibethinus*, Murr.), Mangosteen (*Garcinia mangostana*, Linn.), Rambutan (*Nephelium lappaceum*, Linn.), and Pulasan (*Nephelium mutabile*, Bl.), Betel-nut (*Areca catechu*, Linn.), and many other species which have never, so far as I have been able to ascertain, been found in a wild state.

We have two difficulties in tracing the migration of weeds; one is that our earliest herbaria are of so modern a date that we have little clue as to when the weeds first appeared, and secondly that, when botanists did begin

to form herbaria, they gave no information as to whether the specimens were obtained in altered or cultivated ground or not.

Weeds commonly follow the tracks of the largest migrations of man. The greater number of weeds in the Malay Peninsula are South American or more probably West Indian in origin.

In the sixteenth century the Jesuits brought useful plants from South America to Manila, their most important station in the East Indies. They brought the pineapple, Capsicums, Papaya, *Achras sapota*, Cashew-nut, and, apparently as a curiosity, the Sensitive plant. Most of these plants, the useful ones at least, were conveyed to Goa, and thence to Malacca, where Linschoten records them in 1583. It must have been in those days that most of our Malayan weeds came to Asia, but they appear to have come mainly to the Malay Peninsula through Java from the Philippines at a later date, for nearly all are abundant in Java and there are still a number of common weeds there which have not yet reached the Malay Peninsula, the stream of human migration to which has been strongest from Java.

We possess fewer weeds from India because, until the extensive introduction of Tamil labour, there was but slight migration from India. A few, chiefly medicinal plants, *Eryngium foetidum*, Linn., and *Leonurus sibiricus*, Linn., have been brought by the Chinese. Once in the country the area which one of these plants occupies depends on its adaptability to various classes of position and soil, or perhaps, more strictly speaking, to the extent of the area with suitable soils and conditions, and secondly to its means of dispersal.

Plants which thrive in made soil, or cultivated ground, will spread as far as there is any such ground ; those to which the sandy and gravelly drier roadsides are suitable will spread as far as such roads go.

Plants with adhesive fruits or seeds seem to travel fastest and farthest; such plants are *Paspalum conjugatum*, Berg., *Ageratum conyzoides*, Linn., and *Bidens*, and it is interesting to note that most of the tropical weed Compositae, and the most abundant, are those with adhesive fruits, not those with plumed achenes.

Weeds with berries, bird-dispersed, such as *Solanum oleraceum* and *Passiflora foetida*, Linn., also travel fast, and many small herbs with minute seeds, such as the herbaceous Rubiaceae, *Oldenlandia* and *Borreria*, the small Euphorbias like *E. thymifolia*, Linn., and very many Grasses ; mostly roadside weeds are quickly distributed by rainfall.

Some of these plants are now among the most widely distributed species in the world, and it can be readily shown that the duration of time in which the plant has been in its extended area plays practically no part in the wideness of its distribution. In other words, age has little or nothing to do with area.

It is unnecessary here to give a list of the weeds introduced into the

Malay Peninsula, but it may be interesting to point out that the greater part of the Compositae occurring here, twenty-six out of thirty-five species, and a large proportion of the Labiatae, Amarantaceae, and Grasses in the southern part of the peninsula have been undoubtedly introduced within a comparatively few years. Indeed, exclusive of the Bamboos, the forest region covering the greater part of the peninsula, where unaltered, contains only single species of *Leptaspis*, *Lophatherum*, and *Centotheca*, with one or two species of *Panicum* and *Isachne*.

The mountain Gunong Tahan, never visited by man until Mr. H. C. Robinson reached it in 1905, bore only a few Grasses, viz. one of these Panicums and a couple of rare Isachnes. A few indigenous Grasses grow on the tops of some of the other mountains and some on the sea-shores, but far the greater number are clearly recent introductions. The number of weeds in our area is still increasing, and is likely to continue so doing for very many years.

Methods of introduction of weeds.

Weeds are introduced into new countries by a variety of ways, and I give here some account of the chief ways in which they are introduced. Undoubtedly very many seeds of aliens are brought accidentally or intentionally into countries where they fail to make good or establish themselves. A study of Dunn's 'Alien Flora of Great Britain' illustrates this very well.

Weeds introduced in pot-plants.

A certain number of plants have been introduced casually in soil in pots of plants sent from other countries, and have been able to establish themselves in their new homes. Conspicuous among them are *Pilea muscosa*, Lindl. (Urticaceae), and *Peperomia exigua*, Miq. (Piperaceae), South American plants now established in the East Indies, and *Cardamine hirsuta*, Linn., probably of European origin but now spread over large areas of temperate or sub-tropical lands, though it does not seem to thrive in the tropics. The only time it appeared in Singapore it grew on rubbish heaps in the gardens, where the soil of pots of plants, sent, I believe, from Kew, had been emptied out. It failed to establish itself. *Drymaria cordata*, Willd. (Caryophyllaceae), a plant of unknown origin, is spreading all over the tropics in the same way, though it seems to confine itself to the highlands, about 5,000 ft. alt., in hot and wet regions. It appeared abundantly in the roadsides and gardens of the Semangkok Pass, Selangor, 4,000 ft. alt., in 1921, probably introduced with rose-trees from Java.

Weeds introduced in cereal or other seeds.

A very large number of plants have been introduced into alien

countries in seeds of rice plants in the tropics, and vegetable and corn seed in temperate climates. Clement Reid has shown that a considerable number, including the Fumitories, *Matricaria inodora*, Linn., *Centaurea cyanus*, Linn., *Euphorbia helioscopia*, Linn., &c., occur with the Flax introduced by Neolithic man, and Poppies, *Stachys arvensis*, Linn., &c., first appear in Roman times. The Neolithic weeds are the earliest we have any record of. Many European weeds occur in the vegetable grounds of Tosari in Java, obviously introduced in the vegetable seeds from Europe.

The rice-fields of the tropics contain also many species disseminated with rice-seed from other countries; such plants are *Scirpus grossus*, Linn. fil., and a number of other Cyperaceae and small Scrophularineae.

By transport of cattle.

Another method of introduction of weeds is by the transport of cattle. Large numbers of seeds of Grasses and other herbaceous plants are brought in the fodder, which with the dung is cleared out often on the foreshore on arrival at the port, and the seeds frequently germinate and soon establish themselves. Amaranthi, *Cleome viscosa*, Linn., and *Gynandropsis pentaphylla*, DC. (Capparidaceae), *Herpestes monniera*, H. B. K., and *Scoparia dulcis*, Linn. (Scrophulariaceae), *Panicum colonum*, *Paspalum conjugatum*, and *Imperata cylindrica* owe their wide distribution largely to this cause. An interesting case of a cattle-dispersed plant is that of *Clitoria cajanaefolia*, Benth. (Leguminosae), a shrub with showy, pale violet flowers, which is a native of eastern Brazil, but is now abundant in Singapore, south Johor, and Sarawak, in Borneo. The pods contain a number of very viscid seeds which become readily attached to the hair of cattle browsing among the bushes, and are so transported from place to place. It is often to be found along cart-tracks where cattle pass constantly, but more usually where they are grazed. The plant seems to have been first introduced into Java, probably as an ornamental shrub, and then, borne by cattle, imported thence to Singapore, and later to Johor. Mr. Larkin, a planter, told me that it did not appear on his estate on the Tebrau river in Johor until cattle were brought there from Singapore.

Another method of introduction is in the form of packing material, or by the attachment of the seeds or fruits to cargo, or in ballast on ships. An interesting example of this is the grass, *Chloris barbata*, Sw., probably indigenous in Africa, but now abundant in India, Ceylon, and South America. In Java and the Malay Peninsula it is quite confined to the regions of the docks and harbours, being abundant in these places in Singapore, Johor, and Province Wellesley, but it has not spread, so far as I have seen, 500 yards from these spots. The spikelets adhere by their awns to cloth. It occurs on sea-shores in Ceylon, and there seems no reason that it should not do so in the Straits Settlements, except that the soil in the neighbourhood of the

docks is clay, which apparently does not suit it, and the sandy area, though not far off, is barred by buildings and river-clay deposits.

Imperata cylindrica is also used for packing material, and is no doubt conveyed considerable distances in this way. I have picked up in the streets of Pernambuco, in Brazil, a fruiting spike of one of the African Pennisetums which had obviously been brought in packing for some goods from Africa.

Besides these ways in which plants get introduced there are many other cases of casual introduction, and, as some of the weeds are now among the most widely dispersed plants in the world, it is essential, in making any theories on 'Wides', as they are sometimes called, to know the history of each species included under this term. This requires a complete study of the ecology and past history of every species, so far as it is obtainable.

I give a few illustrations of the stories of weed distribution which I think are very instructive. A curious history attaches to *Glycosmis citrifolia*, Lindl. (Rutaceae), which is now apparently thoroughly established in St. Vincent, the Bahamas, Cuba, and French Guiana, where it appears to be abundant on the sandy sea-coasts. There is no other species of the genus occurring in the New World, all the others being confined to India, Malaya, and China. Griesbach, finding it apparently wild in the West Indies, actually described it as a new species under the name of *Glycosmis americana*.

The plant is an inconspicuous shrub with very small white flowers and small flesh-coloured pulpy berries, and it is neither attractive nor useful in any way. Its presence in the American region could never have been accounted for had it not been for a note on a specimen in Kew Herbarium, which states that, according to Dr. Broughton, it was introduced from England in 1788 to Jamaica under the name of the Mandarin Orange, by Henton East, Esq. The plant is a native of the Malay Peninsula, Java, and Hongkong, and the American plant agrees in all respects with the local form from Hongkong.

Cissampelos Pareira, Linn. (Menispermaceae), has a rather puzzling distribution. At one time a number of species had been made of the plant, but Diels, in his 'Monograph of Menispermaceae', has reduced them to one widely distributed and variable species. The plant occurs all over the tropics except apparently West Africa and Polynesia, is common in India, East Africa, and the Philippine Islands, scarce in the Malay Peninsula, and absent from Java. It is probably indigenous to South America.

It was mistaken at one time for the source of the true *Pareira brava* of South America (*Chondrodendron tomentosum*, Ruiz and Pavon), a drug highly valued by the Portuguese, and it seems very probable that the plant was introduced by them into the Philippines and India, as so many American plants were in the sixteenth century, and that it has run wild in Asia and Africa since. Its drupes are red and probably bird-dispersed, but that will not account for its wide distribution.

Scoparia dulcis, Linn. (Scrophulariaceae), is a bushy herb or shrublet

with very small white flowers, and small capsules of very small seeds. It was described by Linné from Jamaica specimens in 1753, and is undoubtedly a plant of South American origin. It is now abundant all over Africa, South America, and the Malay Peninsula and Archipelago. A note by J. Rotheram in a copy of Linné's 'Species Plantarum', ed. 2, 1762, states that it was used as a remedy for venereal disease in Africa. It is recorded for the Congo in Tuckey's voyage in 1816 by Christopher Smith. Loureiro met with it in Cochin China in 1773, and Robert Brown found it in Australia in 1802. It first appeared in India at Serampore in 1845, but it is very scarce there to the present day and has never been met with in Ceylon.

My earliest record in the Malay Peninsula is 1884, but it was probably there before. It has since travelled farther in Pahang and other parts than any South American weed except perhaps the grass, *Paspalum conjugatum*. Wherever buffaloes or cattle go, this plant follows, and it is frequently to be seen springing up from the dung of these animals, which readily feeds on it.

Besides a reputation as a drug in venereal disease, it is also considered beneficial in consumption. The Malaya call it Te'Macao (Macao Tea), which implies that they consider it as having been derived from China. I would suggest its having been carried about at first as a drug, probably dried whole, capsules and all, and by this means got from the West Indies to Africa and to the Philippines. There is nothing to show it was ever cultivated. From these places it has spread, mainly in cattle fodder, to the Malay Islands and Peninsula as far north as Siam, in fact wherever the Malay buffalo and cattle are sent. Its absence from Ceylon, and largely from India and Polynesia, is due to the fact that there has never been a cattle trade between these countries and the Malay or African regions.

This is a good sample of the wide distribution of a plant, extremely abundant in its area, which has obtained marked extension in a very short period of time, viz. about 200 years.

By way of comparison as to the difference in rapidity and wideness of distribution of species, I will give an illustration from two English weeds, both Compositae, *Galinsoga parviflora*, Cav., and *Matricaria discoidea*, DC. They are both herbs of American origin.

Galinsoga parviflora, Cav., occurred in Spain as early as 1794, and has since appeared in Holland, Germany (Berlin, 1812), Italy, and Austria, more or less sporadically and apparently chiefly as an escape from botanic gardens. In England the earliest record is at Twickenham, where it was collected by Rudge before 1809. It is now abundant in vegetable fields round Kew, being first reported in 1861. It has appeared at Guildford, and there is a specimen from Hertfordshire in the Natural History Museum, and in 1912 at the Tweedside with other aliens brought in wool. It has not spread very far from the Kew locality, though very

abundant there. Sowerby reports it as having been introduced into England as an ornamental annual in 1796, and I have seen a specimen, probably cultivated, from Chelsea in 1802. In other parts of the world the earliest dates I have procured are Peru, 1806; North America, apparently wild, 1893; India, 1845; Java, 1899; New Zealand, 1894; Africa, 1912.

Galinsoga possesses fruits with broad scales forming a pappus, and thus has a superior method of dispersal to those of the *Matricaria*, which possesses no scales or plumes at all on the achenes.

Matricaria discoidea, DC. (*M. suaveolens*, Buch.), is a much smaller, inconspicuous weed with small and light fruits quite unprovided with any particular means of dispersal. When ripe they become detached from the receptacle and are partially covered by the involucral bracts which curl over them. The plant is only about four to six inches tall. Holding the achenes on my hand, about two feet from the ground, I find that in a strong wind they are blown three or four yards before falling to the ground. At the normal height of the plant they would not, of course, travel so far.

The plant's first record in England that I can find is 1878, Kew (Druce), but I find specimens from Berlin, 1853; Königsberg, 1862; Dorpat, 1869. It now occurs on roadsides and paths all over England, from Surrey and Berkshire to Aberdeen, and probably farther, and is abundant everywhere.

Now here are two weeds, one of which (*Galinsoga*) has been over a century in the country, and though very abundant locally has not yet migrated more than a few miles from the spot in which it was first introduced, and another, the *Matricaria*, with poorer facilities for seed-dispersal, has in less than half a century spread over the whole of England and Scotland.

It is quite clear that in these cases the age of duration or time in which the two plants have been in the country is not commensurate with the extent of their distribution. The spread of the later introduction has been more rapid and wide than that of the earlier one.

Widely distributed Plants.

I intend in this section to deal mainly with Phanerogamous plants, but will make a few remarks about Cryptogams first, chiefly illustrating by Malayan species.

We know little at present about the cellular plants of the Malay Peninsula, as they have been little collected and still less worked out. They are, on the whole, much more widely distributed than flowering plants, or rather there are more widely distributed kinds than there are of flowering plants. This would give some colour to Dr. Willis's theory

of age and wide dispersal, as we may assume that the cellular plants were the earliest evolved, but we know that the spores of these plants are lighter and more easily dispersed than those of any Phanerogams, and that the plants are much less exigent in their requirements of suitable soils and climates. They are, too, the first vegetation to appear on exposed surfaces. Treub's investigations on Krakatau Island in 1886, three years after the total destruction of all vegetation by volcanic action, shows that the blue-green algae were the first colonists on the bare pumice and volcanic ash and exposed blocks of rock (Ernst, 'New Flora of Krakatau', p. 64). The same phenomenon appears on other exposed surfaces, such as a newly-built wall, as I have often observed in Singapore. First appears a coat of algae, then mosses, then ferns, and lastly, when these have made sufficient soil, come flowering plants.

A few Myxomycetes have been collected in Singapore, of which may be mentioned as of wide distribution :

Physarum nutans, Pers.: Europe, Australia, New Zealand, North America.

Physarum compressum, All.: with the same distribution, and the West Indies and South America.

Stemonitis fusca, Roth.: Europe, Ceylon, Java, Australasia, North and South America.

Lycogala miniatum, Pers.: Europe, Tropical Africa, North and South America.

Other Fungi are more local, especially of course the parasitic ones. We have in the Malay Peninsula :

Clavaria fusiformis, Sowerb.: also Europe and North America.

Agaricus campestris, Linn.: whole world.

Hygrophorus puniceus, Fries, as plentiful in Singapore as in Europe, and many others.

Of Lichens *Cladonia rangiferina*, Linn., is as abundant on the Malay mountains as it is in palaearctic regions.

Vascular Cryptogams.

Rhizocarpeae. We have an *Azolla* widely distributed over Africa and Asia, and undoubtedly carried about by man; and a *Marsilea* which occurs in rice-fields and roadside ditches in Penang and Province Wellesley, and is probably introduced also.

Selaginella.

We have thirty-seven species, of which twenty-one are endemic. *S. flabellata* occurs in all the tropics except Africa; and one or two other species go as far as China and one into Polynesia.

Of Lycopodiaceae, *Lycopodium* and *Psilotum*, there are no endemic

species. The epiphytic species have a smaller distribution than the terrestrial species, as the epiphytic area in the world is smaller than the non-epiphytic area. Of *Lycopodium*, three species, all terrestrial, occur in Asia, Africa, and America, and one, *L. complanatum*, over the palaearctic zone and into the tropic mountain regions, but our variety *thujoides* looks very different from palaearctic *complanatum* and may be specifically distinct. The remaining species range over India or Africa to Polynesia, except three confined to the Malay Isles.

Psilotum. Two species very readily propagated by bulbils as well as spores, growing on trees, rocks, and ruins freely, have a wide distribution all over the tropics and to Japan and New Zealand.

It will be noticed there is a very marked difference between the distribution of Selaginellaceae and Lycopodiaceae. According to the age and area hypothesis this would show that the Selaginellaceae were a very modern group and the Lycopodiaceae an ancient group, for which there is no further evidence.

The real cause, I think, is this: the Selaginellas are low-growing, often creeping, plants, producing comparatively few spores, and, growing in dense forests, have a comparatively slow dispersal, while the Lycopodiaceae are either high-borne epiphytes on the top of lofty trees or grow in dry open places, and produce great abundance of spores which are readily dispersed by wind. It is interesting to note that one of the earliest plants to reappear on Krakatau after the destruction of its flora was *Lycopodium cernuum*, of world-wide distribution, showing how rapidly this plant is dispersed by its light and abundant spores and its open-country habitat.

Ferns.

In the Malay Peninsula we have about four hundred species. A certain number, but not very many, are endemic, most extend over the Asiatic tropics, and many to Madagascar and Africa. Only about twenty also occur in America, and one or two of these may be escapes from cultivation. Only three species occur also in Europe, viz. *Pteris aquilina*, Linn., *Trichomanes radicans*, Sw., and *Lastraea thelypteris*, Desv.

Pteris aquilina, Linn., occurs nearly all over the world in temperate and tropical regions. It is quite absent from oceanic islands, and its earliest record is from late glacial or Neolithic deposits in Sweden (Gunnar Anderson, in Clement Reid, 'Origin of British Flora', p. 168). I have some evidence that it is occasionally, at least, transported by man, the spores attaching themselves to cloth, gunny-bags, &c. It is abundant in sandy soil in the Malay Peninsula, but was quite absent from the plateau of Gunong Tahan when the locality, hitherto unvisited by man, was explored by Mr. Robinson in 1906. In 1910 I visited the mountain, and beneath the floor of Robinson's old hut, and beneath one occupied by a surveyor a year or two

later than 1906, I found two or three plants of the Bracken, but no more occurred on the whole plateau. It is usual in camping here to put the rice-bags and such baggage under the raised floor of the huts, and there can be little doubt that the spores were brought in the baggage to these spots. Bracken is often used for packing and litter for animals, and it has probably largely at least made its way about the world in this way.

Trichomanes radicans, Sw., occurs over a wide area, but seems always to be scarce. It seems to be very variable, if all the plants included under its name are specifically identical, and is a plant of warm temperate regions which seems to have descended into the tropics along mountain chains. It is not known fossil, and is absent from oceanic islands.

Lastraea thelypteris, Desv., is widely distributed, though absent from America, but I have some doubt as to all the specimens recorded being of the same species.

Some others of the more widely distributed ferns are plants of great adaptability, such as *Litobrochia incisa*, Thunb., abundant in the dark, wet hill forests from 2,000 feet altitude and upwards, which I have found established in culverts by the roadside in the lowlands of Singapore, doubtless an escape from the Botanic Gardens, and as the highest ascending plant on the bare volcanic rocks of Sibayak Mountain in Sumatra with a low temperature and a full sun exposure.

Ceratopteris thalictroides, Linn., is an aquatic in ditches in the tropics, the spores perhaps borne about by water-fowl, and *Acrostichum aureum*, Linn., is a tidal-mud plant widely spread along the tidal rivers. Both these plants, by virtue of their peculiar habitats, have no fern competitors to contend with.

Ferns like some of the Adiantums and *Cheilanthes farinosa*, Kaulf., which have wide distributions, are popular garden plants, which have established themselves in many localities.

As ferns have an exceptionally favourable dispersal method in their minute spores and much less exigence in the matters of fertilization and habitats than flowering plants, it is extraordinary that species of an order of such undoubted antiquity should have such limited area of distribution as they do at present, if age was any qualification for extent of area.

The most widely distributed Flowering Plants.

I now deal with the most widely distributed Phanerogams exclusive of sea-borne species and weeds.

The most extensively distributed flowering plant in the world is, I believe, the Common Reed, *Phragmites communis*, Trin. I include under it *P. Karka* (*P. Roxburghii*), as I fail to see any real distinction between the plant of the temperate region and that of the tropics. The Reed ranges all over Europe, Asia, Africa, America, and Australia, but appears

to be absent from New Zealand and Polynesia. It is able to adapt itself to cold climates as far north as Finland, 69·40° N., and to the hot, wet lowlands of the Equator. It is known to reach an altitude of 10,000 feet in Tibet. It grows in wet, open spots, swamps, river banks, and watercourses, as well as on the sea-shore, on clay or sandy deposits with apparently equal facility. It is found fossil in the Cromer forest bed of the Preglacial Pliocene period.

The Reed is absent from oceanic islands such as Cocos, Christmas Island, and Fernando de Noronha, but there is hardly any suitable ground for it in any of these islands, which are over 200 miles from the nearest mainland, though it was one of the first plants to appear in Krakatau after the destruction of the flora by the eruption in 1883, Dr. Treub having found it there in 1886, where it was one of the first fourteen flowering plants to appear. Sumatra and Java, the nearest land from which it could come, are twenty-three to twenty-five miles away, and there is no doubt that the seeds were blown from there by the wind. Besides its dispersal by wind, the plumed fruits may perhaps be borne about by adhesion to the feathers of water-fowl or small birds nesting in the reed-brakes, many of which fly long distances. Like most grasses, the Reed is wind-fertilized and does not require the use of insect pollinators.

Here we have a plant possessing the greatest adaptability to soil and climate—only requiring sufficient moisture for its growth—and a good *dispersal mechanism*, though apparently for comparatively short distances, the two most important qualifications for wide dispersal. It does not appear as a fossil earlier than the Pliocene, though of course it may be older, and it is not by any means a primitive form of grass, but in the matter of dispersal throughout the world it has far outdistanced any of its contemporaries of the Pliocene beds.

Cynodon dactylon, Linn., is another grass of remarkably wide distribution. It ranges from Studland Bay, in Dorset, and Marazion, in Cornwall, all through southern Europe, as far north as North Germany, all over Africa and the warmer parts of Asia, Australasia and Polynesia, and North and South America. It has been suggested that it has been introduced to England in ship-ballast, but I see no evidence of this, as it does not occur with ballast plants in any other localities. I have seen it in both of its English habitats, one of which, Studland Bay, has never been a port and contains other Mediterranean plants, e. g. *Polypogon monspeliensis*, which do not grow on the beach. It may be to some extent a sea-dispersed plant, but it is difficult to see why it is confined to those two localities, and does not occur occasionally in other maritime spots. It prefers sandy ground, but is not a beach plant, and if planted in a clay soil soon disappears. In some localities it may have been introduced by man, possibly in foreign grass seed, as it has occasionally occurred temporarily as an

alien, e. g. on Kew Green. Against its being sea-dispersed is the fact that it is absent from the oceanic islands, Cocos, Christmas, Fernando de Noronha, &c., and did not appear on Krakatau after the eruption.

It is not known as a fossil at all, and its origin seems to have been Africa, as there are other species of the genus there.

Sanicula europaea, Linn. (Umbelliferae), is a plant of open woods in temperate regions, and the cooler parts of mountain forests in the tropics. It occurs in central and northern but not arctic Europe, the whole of Africa to the Cape, India, Ceylon, China, Japan, and in the mountains of the Malay Peninsula, Java, Sumatra, and Celebes. There are allied species apparently distinct in North America, but none in South America. The Malayan form has been considered distinct by some botanists, but it seems merely a warm country form. It does not appear to have been found fossil.

The fruit is armed with hooked bristles by which it can adhere to the fur of animals, and be so dispersed. Though the area covered by this plant is very large, it is mainly continental, and its occurrence in the islands mentioned shows a former land connexion with the mainland of Asia, corroborated by the presence of other palaearctic plants with it. It is absent from Borneo together with these palaearctic plants.

Anacardium occidentale, Linn., the Cashew-nut. This tree in the Malay Peninsula is commonly to be found in sandy spots along the coast and also on heaths, e.g. at Setul. It appears to be quite wild, and, though the natives do occasionally eat the kernels, I have never known them plant it, nor have I seen it near their houses. The form here appears to be the wild form which occurs in similar localities in Brazil, with a small, usually green, thickened peduncle to the fruits, not the cultivated form with a thick, reddish, fleshy peduncle. Seeds of it, apparently quite sound, occur in the sea, and I have little doubt that it is to some extent sea-borne. It is undoubtedly a native of Brazil, whence it was introduced, probably by the Jesuit Fathers, to Manila. Linschoten mentions it as occurring in Malacca in 1583, together with the Papaya, Chillis, and the pineapple, but it is only mentioned by Garcia in 1593 ('Historia Aromatum', ed. iv) as occurring in Brazil. There are several other species of the genus in tropical America, and it occurs now in the Seychelles and Madagascar and Ceylon, as it does in Singapore, on the sandy coasts. It still retains its original Brazilian name, Cashew, in the form of Gajus in Malay. It seems to be absent from Australia and Polynesia, and, except the cultivated form, inland from Africa. It seems certain that the original form introduced was the cultivated one with the large pear-like peduncle, and that it has established itself on our sea-shores, reverting to the small-fruited wild form, and been spread along our coasts by the sea.

Brasenia peltata, Pursh. This little water-lily was apparently common in Pliocene times in Russia, Germany, and Switzerland, but has entirely disappeared from Europe. It now persists in Manchuria, Khasiya, Japan, Australia, Angola, and North America. It is obvious that at one time it was very widely diffused over the world, but, like so many of the earlier plants, it has died out except in the palaearctic regions and in a few other isolated spots. The drying up or, what is more common, the silting up of lakes may account for the disappearance and isolation of these aquatics.

Naias. These water-weeds seem to be very easily dispersed, largely, I believe, by water-fowl, and some of them have a remarkably wide distribution; one may compare them in the matter of distribution and dispersal with the Characeae.

Naias marina, Linn., a brackish water and marine plant, practically occurs all over the world except tropical Africa and Malaya, but chiefly in temperate regions. It occurs in the Cromer forest bed.

N. minor, All., which occurs with it in the Cromer forest bed, is confined to Europe and temperate and tropical Asia as far east as Manchuria.

N. graminea, Del., occurs earliest in Britain in the interglacial period. It is widely spread over tropical and subtropical Asia. Its occurrence in a hot-water canal at Manchester shows how easily these plants get about the world.

N. flexilis, Rostk., known from interglacial deposits in Sweden and Germany and confined to northern Europe and North America.

Here we see that for four species of *Naias*, all of approximately the same geological antiquity and with very suitable dispersal mechanisms, we have very different areas of distribution.

The marine species, which can adapt itself apparently to sea, brackish, and fresh water, and can stand considerable variations of temperature, is the most widely distributed. The continuity of the sea largely ensures this, and is the reason why maritime plants, as will be shown, are more widely distributed than freshwater plants of streams and rivers which are not continuous.

N. minor, All., a freshwater species, has not reached America and does not seem to stand heat well.

N. flexilis, Rostk., is palaearctic and nearctic only, being a cold-climate species.

N. graminea, Del., is a warm-water species and cannot stand cold, so its area is limited.

It is quite clear that the area of distribution of *Naias* depends not on the age of the species at all, but on adaptability to climate and environment, the species with the largest continuous area, the sea, being the most widely distributed.

There are a few species of plants which occur in tropical Asia and South America which do not appear to be sea-borne, and as far as can be judged are not weeds. These are chiefly small-seeded Cyperaceae such as *Cyperus Haspan*, Linn., *Heleocharis capitata*, Br., and *H. chaetaria*, R. and S., *Fuirena umbellata*, Rothb., and *Rhynchospora aurea*, Vahl., all inhabiting damp, swampy, open spots or marshes, and *Scleria lithosperma*, Sw., which is an open-forest plant. All these plants occur all over Asia and Africa as well as South America (except the *Scleria* not recorded from Africa), but they are absent from oceanic islands. The swamp species are perhaps carried about by wading birds, as they have the habit of appearing very soon on the edges of artificial ponds where sandpipers constantly come. More research is required into this form of dispersal, but I cannot otherwise account for the appearance of these plants and some other swamp and aquatic plants in artificial lakes such as those in the Singapore Botanic Gardens. Wide as their distribution is, none are nearly as widely distributed as the Reed and *Cynodon dactylon*, as they are exclusively tropical, and cannot stand even a temperate climate. *Polygonum hydropiper*, Linn., and *P. minus*, Huds., are similarly widely distributed, though absent from South America, and probably dispersed by wading birds. They range from Europe, through India, the Malay Peninsula, and Java, to Australia, and *P. hydropiper* to North America. *P. minus* is absent from America and New Zealand. *P. hydropiper* first appears fossil in the Neolithic period, *P. minus* is found in the Tegham beds.

In a paper on the Cyperaceae of the Welwitsch Herbarium (' Trans. Linn. Soc.', ii, p. 122), I called attention to the extraordinarily large proportion of Cyperaceae common to Africa, chiefly the West Coast, and South America and the West Indies, and showed that these plants were largely forest plants. The proportion of species of other flowering plants common to the two continents is small, but I would add *Pothomorphe peltata*, Miq. (Piperaceae), and *Lophiocarpus guyanensis*, Mich. (Alismaceae), both of which range from South America, through Africa, into the Malay Islands ; neither of these species is likely to have been dispersed by man, nor could they be dispersed by birds. The *Pothomorphe* is not cultivated nor, so far as I am aware, used by man, and it does not produce drupaceous fruit like the Pipers. *Lophiocarpus* occurs in the Malay Peninsula in rice-fields only, and I had thought it might have been carried about in rice-seed, but the large size of its seeds makes this improbable, and prevents its being carried on the feet of birds.

Arldt, in ' Die Entwicklung der Kontinenten und ihre Lebenswelt ', gives a series of maps showing the distribution of land and water from early periods. Assuming that these are approximately correct geologically, a land connexion between Africa and Brazil appears in Silurian times and continues through the Chalk period to the Neocomian. This land area includes

eastern South America, Africa, the Mascarene Islands up to the western Himalayas—the Malay Peninsula, Ceylon, and Sumatra being submerged. This area, Sud-Atlantis, gets smaller in early Tertiary eras, but there is still a connexion between Guiana and North Brazil up to Cape Verde and south to Angola. In the Miocene period Sud-Atlantis is broken through and Africa and America are quite separated, and never reconnect.

If this disposition of sea and land is endorsed by other geologists, it would account for the large number of genera and some species common to both sides of the Atlantic, and especially would account for the forest Cyperaceae of Angola and Madagascar occurring in South America but being absent from tropical Asia, and the date of this flora would be before the Miocene period.

It might be suggested that the plants common to Africa and America had been transported by sea-currents or by birds, but against this there is the fact that hardly one of the African maritime or sea-shore plants dispersed by sea occurs in the New World, nor any of the New World species in the Old World, and, besides the fact that it does not appear that birds cross from the Old World into the New, the plants referred to are not such as are bird-borne.

Sea-dispersed Plants.

In deciding whether a plant comes into this class or not we have to take into account any special modification of the fruit or seed for dispersal by sea, such as the thick corky pericarp of *Barringtonia speciosa*, Forst., or the fibrous woody pericarp of *Cerbera*, or the enlarged bladder-like calyx of *Hernandia*, and it is further essential that the plant may be able to grow on the sandy beach or in tidal mud, as the case may be. A great deal has been written by Schimper, Hemsley, and others on the strand flora and its dispersal, and Guppy, 'Observations of a Naturalist in the Pacific', has summed up most of this work, and added so much that comparatively little has to be added. I cannot agree with many of the latter's deductions from the facts, but I do not intend to criticize them in this paper; I will merely content myself with a few remarks bearing on the strand flora of the Malay Peninsula which are not treated of by Schimper or others.

Mr. Guppy writes a good deal about the distribution of plants of the strand flora, i.e. sea-dispersed plants found inland, especially in the Polynesian Islands. This occurs, as is well known, in many parts of the world, the strand flora being met with often on the tops of mountains. I think it will be found that in all cases the strand flora in such spots is due to the sea having formerly reached these altitudes and left its flora there stranded. There are no such examples in the Malay Peninsula, so far as has yet been seen, as there is indeed no evidence of the sea having been

over or up to the ranges of hills in the interior, at least later than Mesozoic times, but there are a few cases of strand plants being found inland a long way from the present sea-coast. Thus at Kanga, in Perlis, at the base of the huge limestone islands now far off the sea in a great sandy plain, I found the little *Boerhaavia repanda*, Willd. (Nyctagineae), a typical sea-sand plant, while in the damper spots of the plains grew *Dolichandrone Rheedii*, Seem., a typical tidal-mud plant. Here the whole area, at no great distance of time submerged by the sea, had gradually silted up with the sand and gradually pushed the sea-coast far away, while these plants still remain and thrive stranded as they were by the departure of the sea. I have met with *Boerhaavia repens*, Linn., too, growing between the railway lines far inland in Java at Muntilan. Here I imagine it was brought in the ballast for the line. On a cart-track in Bukit Tangga, Negri Sembilan, thirty-six miles from the sea, and on railway banks in Kota Bharu, Kelantan, I have seen in sandy spots the sea-shore Convolvulus, *Ipomoea biloba*, well established though far away from its ordinary sea-sand habitat almost within the splash of the waves. Here again I have little doubt that it was brought in ballast from the sea-coast to which the railway ran, and contrived to establish itself on the sandy fields near the railway. But, except for these cases, it is remarkable to what a short distance the strand flora goes inland, even in such apparently favourable localities as the sandy heaths of Pekan, in Pahang, where the sandy country runs continuously to the strand-flora region.

As a rule, sea-shore plants and tidal-mud plants disappear altogether when, by deposit of silt or shifting of the tidal river, the ground they grow on ceases to be suitable for the strand flora. The Singapore river at Tanglin, from road-making, town-building, &c., has long ceased at this point, about four miles from the sea, to be tidal, and all the waste ground in the economic gardens near it was a low swampy patch covered with a wood of *Cinnamomum iners*, Bl., *Premna foetida*, Reinw., Macarangas, *Ficus*, &c., but when it was cleared a large clump of the tidal-mud fern *Acrostichum aureum* was found still growing there, and the ground was full of Nipa palm fruits, which last a very long time underground, showing that this must have been at one time a tidal-mud river. I once came across in Johor, near Gunong Pantai, a long way from any tidal mud and surrounded by dense forest, a large patch of the tidal-mud fern which must have marked a long-disappeared tidal river filled up and covered with heavy hill and lowland forest. These stranded sea-shore plants do not seem to spread at all, but remain, for the most part at least, in the same spot where they were left when abandoned by the salt water.

Dolichandrone Rheedii, Seem. (*D. spathacea*, Schum.), mentioned above, is rather an interesting plant from another point of view, as shown by Sprague's account of the genus in 'Kew Bulletin', 1919, p. 304. The genus,

belonging to the order Bignoniaceae, contains nine species, of which three are endemic in North Australia, one in Portuguese East Africa, three in the forests of southern India, one in the Irawaddy district, Burma, and one in Lower Siam. All these appear to be quite local plants in distribution. They are middle-sized trees with long-tubed, fragrant white flowers opening in the dusk and falling in early dawn, with long pods of winged seeds, the wings of the seed being thin and hyaline and longer than the body of the seed, so that they are easily dispersed by wind, as is the case in most plants of the order. But *D. Rheedii* is an inhabitant of tidal-river mud. Closely resembling the other Indian species in habit, foliage, and flowers, and most closely allied to the Burmese *D. serrulata*; it differs most remarkably in its seeds. Instead of having thin hyaline wings longer than the body of the seed at each end of it, the seed has at either end a short, oblong, corky prolongation, quite unsuited for wind dispersal and quite unlike any other Bignoniaceous seed. When dropped from a height it falls straight to the ground, while a winged seed of *D. serrulata* flutters, rotating as it goes, to a considerable distance. By the shortening and thickening of the wing of the seed it has been adapted for sea-dispersal.

As has been mentioned, the other species of the genus are confined to limited areas, but this species occurs in mangrove swamps and tidal rivers all round the Bay of Bengal as far as Ceylon, and to Travancore and Malabar on the west coast of the peninsula along the coasts of Burma, the Andamans and Nicobars, the Malay Peninsula and the Malay Islands from Sumatra to New Guinea, and the Philippines to New Caledonia and the Solomon Islands.

The distribution of this plant shows clearly the superiority of sea-dispersal, both in time and distance, over dispersal of winged seeds by wind, and, further, as all the other plants in the order have the peculiar thin-winged seeds possessed by the other species of *Dolichandrone*, we may certainly assume that *D. Rheedii* is derived from one of the thin-seeded species, probably *D. serrulata*, Seem., of the banks of the Irawaddy, as it so closely resembles it that specimens of the two plants have often been taken for each other. The seed-wings in *D. Rheedii* persist, but have been converted into shorter, thick corky floats. This species is therefore younger in time than the other winged-seed species, yet its distribution is far wider than that of any other species: it is in fact another case which militates strongly against the age and area hypothesis.

Most of the large orders of plants contain one or more species whose fruit is adapted especially for sea-dispersal; usually one species only occurs in a large order, the rest being inland plants having no such adaptation. In these cases it will be almost invariably found that the distribution of the sea-dispersed plant is very much wider than that of the inland species. Thus one may instance *Calophyllum* (Guttiferae), of which we have twenty-

four species in the Malay Peninsula, all inland plants and endemic, except one reaching to Cochin China, and one of rather dubious distribution to the Malay Islands, and the maritime *C. inophyllum*, Linn., ranging from Africa, through India, Ceylon, and the Malay region, including Christmas Island, to Australia and Polynesia.

Heritiera elata, Ridl. (Sterculiaceae), is a rare tree in Singapore forests only. *H. littoralis*, Dryand., inhabits tidal swamps and sea-shores, common over the whole of tropical Asia. *H. elata* has no means of dispersal except rolling of the fruits. A tree which fruited heavily was surrounded the following year with hundreds of seedlings, next year the number had largely diminished, till in three or four years hardly one had survived. *H. littoralis* has seeds modified for floating in the sea, and I have never seen it so heavily fruiting, yet it is far more widely distributed than the jungle tree.

Sophora (Leguminosae) is a genus of about fifty inland species ranging over the tropics and subtropics, all species local and of limited distribution, except *S. tomentosa*, Linn., a maritime species with sea-borne seeds, with a distribution over Florida, West Indies, Brazil, and the whole of Asia and Africa.

Scaevola (Goodenoviae) contains about fifty species confined to Australia, a few in New Zealand and Polynesia, one in China, and a few in the eastern Malay Archipelago. These are not sea-dispersed plants and are all very local. *S. Koenigii*, Vahl., a fleshy sea-shore shrub with fruits adapted for sea-dispersal, is common on the coasts of Mauritius, India, Ceylon, Siam, China, Formosa, Malay Peninsula and Archipelago, including Christmas Island, and Polynesia, a far wider distribution than all the rest of the genus put together.

Derris, Linn., is a genus of Leguminosae widely spread over Asia, but more or less local. Most of the species have thin, indehiscent, one-sided pods, drifted to a short distance by wind, and inhabit inland forests and plains.

Derris thyrsiflora, Benth., is found in low, open country; its pods are blown to about sixty yards from the plant by wind. It is confined to the Malay Peninsula as far north as Mergui, and Sumatra and Java. Closely allied to it is *D. sinuata*, Thw., a tidal-river plant with pods which bear several seeds and break up into joints and are sea-dispersed. It is distributed over Ceylon, Burma, the Malay Peninsula, and Borneo, a wider area than that of *D. thyrsiflora*. *D. uliginosa*, Benth., is a sea-shore species with pods specially adapted for sea-dispersal. It occurs from East Africa and the Mascarene Islands on all the Asiatic coasts to China and Japan, Formosa, Australia, and Polynesia. No other species of the genus has anything like this distribution, most being quite local. *D. scandens*, Benth., however, a sea-shore and river plant, occurs on most of the Asiatic coasts.

Pemphis acidula, Forst. (Lythrarieae), a monotypic genus, and *Tournefortia argentea*, Linn. fil. (Borragineae), have a distribution from the

Mascarene Islands along the coasts of India (*Tournefortia*, Ceylon and Andamans only), through the Malay region to Polynesia. Both are very scarce in the Malay Peninsula, though abundant in the Malay Islands, because they both grow on raised coral-reefs and there is practically no raised coral-reef in the peninsula.

The following maritime plants, besides the above mentioned, occur all over the tropics in both hemispheres: *Caesalpinia Bonduc*, Roxb., and *C. Bonducella*, Flem. (Leguminosae), *Ipomoea biloba*, Linn. (Convolvulaceae), *Hibiscus tiliaceus*, Linn., *Sida cordifolia*, Linn., *S. rhombifolia*, Linn., *S. carpinifolia*, Linn. (Malvaceae) (these Sidas are also weeds of cultivation), *Cassytha filiformis*, Linn. (Laurineae), *Fimbristylis spathacea*, Roth., *Remirea maritima*, Aubl. (monotypic Cyperaceae), *Paspalum vaginatum*, Sw. (Gramineae). All except *Remirea* and *Cassytha* belong to genera of many species of inland plants, none of which has anything like their distribution. Many other maritime plants have an area of the Mascarene Islands and all Asiatic coasts to Polynesia, but have not reached or settled in America. In all cases the story is the same; they are far more widely distributed than their inland non-maritime allies.

It is in the highest degree improbable that the inland species of these plants, numerous as they often are, can be derived from the few or solitary maritime species, but on the contrary the maritime species, retaining the general form of the fruit modified for sea-dispersal, must be derived from one or other species of the inland ones; consequently the widest distributed species must be later in time of evolution than the local and often endemic species.

Bird-carried Seeds.

There are a number of widely distributed plants which inhabit swampy ground and edges of ponds and open streams, but which do not appear to be weeds or to have been helped in any way by man. They chiefly consist of Cyperaceae. Such are *Rhynchospora aurea*, Vahl., *R. glauca*, Vahl., *Cyperus Haspan*, Linn., *C. radiatus*, Vahl., *C. digitatus*, Roxb., *Eleocharis fistulosa*, Schult., *E. variegata*, Kunth., *E. capitata*, Br., and *Polygonum hydropiper*, Linn. From the way in which most of these plants appear on the edges of artificial ponds, where the sandpipers often alight after their long migrant flights, I should suggest that these waders bring them in their feathers or possibly attached to their feet. Most have quite small seeds which could be easily carried in this way, but Guppy has shown that Cyperaceous seeds can be successfully carried by ducks in their intestines, and *Polygonum* seeds by various other birds in the same way. The Jussiaeas (Onagraceae) seem to be carried about largely by water-fowl, as they have the same habitat, but the American species, though closely allied to the Asiatic ones, appear to be specifically distinct.

The large artificial lake in the Botanic Gardens in Singapore contained a number of aquatic plants which were certainly not planted there, and which did not, as far as I know, occur in any spot whence they could have been drifted into the lake. They were *Enhydrias angustipetala*, Ridl., *Blyxa malayana*, Ridl. (Hydrocharideae), *Naias graminea*, Del., a *Chara*, and two Utricularias. I have little doubt that these were brought from considerable distances by wading birds or ducks. A lake like this in a country where ponds and pools are extremely scarce is always very attractive to birds on migration, and ducks, jacanas, sandpipers, and even cormorants have appeared from time to time on this pond.

It will be noticed that a considerable proportion of the most widely distributed species of plants are Cyperaceae and Gramineae, wind-fertilized plants which do not require pollination by insects, and I would suggest that this has a considerable bearing on the rapid distribution and the large number of plants of one species occurring together, often over considerable areas such as the extensive tracts of *Imperata arundinacea*, Cyr., *Chrysopogon aciculatus*, Trin., the dense masses of *Paspalum conjugatum*, Berg., along mountain paths, the large swamps almost entirely of *Eleocharis equisetina*, Presl., in Setul. I have never seen in the Malay Peninsula large areas of any single species of insect-fertilized plant, except the single-tree forests of *Dryobalanops* and of *Avicennia*, with which I will deal elsewhere.

Of the Wide Distribution of Orders of Plants.

In 'Journ. Linn. Soc.', xliv, p. 439, Mr. Guppy, in a paper entitled 'Plant Distribution from the Standpoint of an Idealist', suggested that orders were evolved first, then genera, then species. It is difficult to see how an order, an accumulation of species, could in the first instance be evolved before the species. The larger orders seem, from what we know of Eocene plants and from the story of distribution, to have appeared at an early date, such orders, that is, as Anonaceae, Laurineae, Leguminosae, and Myrtaceae, but that all orders, even large ones, were evolved before the genera is very easily disproved.

We have in tropical Asia a number of genera which are wanting in Australia and Polynesia, but which extend to Africa and are again well represented in South America. They have received no assistance from man, and are not widely dispersed by birds or by sea. Such genera are *Tetracera* (Dilleniaceae) and *Xylopia* (Anonaceae), and we have even one species, *Pothomorphe peltata*. Now the only way these plants could have crossed the ocean from Africa to South America is by a former land connexion such as is shown in Arldt's maps. This land connexion is believed to have broken down before the Pliocene period, and these plants must have crossed before that. Now in South America we have two big, besides several small, orders peculiar to that country which have even better means of dispersal

than these plants, viz. Bromeliaceae and Cactaceae.[1] Some at least of the species of these orders, notably the Opuntias, introduced into India and Africa have thriven remarkably, so that there is no reason to suppose that if they ever got across naturally we should not find traces of them, but there are none; the only possible deduction is that these orders were not evolved till after the connecting land had disappeared and the Tetraceras, Xylopias, &c., and *Pothomorphe peltata* had been evolved.

In the same way we may fairly decide that the Pandanaceae absent from the New World, though thriving when planted there, were evolved in Africa and Asia after the connective bridge was broken, and this is more remarkable in that structurally *Pandanus* appears to have been a very primitive plant. It has always struck me as remarkable that this genus of maritime and marsh habit, with leaves and fruits that preserve remarkably well, has not been found fossil in the European deposits at all.

Summary of widely distributed Plants.

I have dealt herein mainly with such widely distributed plants as occur in the Malay Peninsula, but this covers really the most widely distributed plants in the world of flowering plants. Those that are to be found over the large area of the world's surface fall into four groups:

1. The weeds, plants which have been accidentally or intentionally carried by man to various countries and there, finding suitable soil and climatic conditions, have spread themselves widely from the position to which they were first introduced. They belong to many different orders, but are chiefly herbaceous, and their area of distribution on arriving at their new position chiefly depends on their means of dispersion—adhesiveness of seeds or fruits, and wind dispersion, being the two most successful methods.

2. Plants dispersed by sea-currents. These all naturally grow on the sea-shore, either in sandy beaches or on tidal mud. The greater number of those of the Malay Peninsula cover an area from the Mascarene Islands over the Indian Ocean to North Australia and the Polynesian Islands in the Pacific Ocean; a smaller number occur also in South America and West Africa.

3. A small number of swamp plants, chiefly Cyperaceae, which appear to be dispersed by water-fowl, occurring in both hemispheres.

4. A few which are capable of thriving in temperate and tropical regions, such as *Phragmites communis* and *Cynodon dactylon*, with a few palaearctic forms which have descended along the mountain chains as far south as the equator. These latter, illustrated by *Sanicula europaea*, are very scanty in the Malay Peninsula and do not occur in America. They are more abundant in Sumatra and Java.

[1] *Rhipsalis Cassytha*, Gaertn. (Cactaceae), epiphyte, occurs in Ceylon as well as tropical Africa and tropical America. It is the only Cactacea wild in the Old World.

There is no evidence to show that all these various widely dispersed species are of specially great antiquity, or that the area occupied by them depends primarily on their age, as suggested by Dr. Willis. It is certainly not the case in the plants which I have called weeds, where we often know the date of the introduction of the plant into a given area. Their rapidity of dispersal depends on the area of suitable conditions for growth and their means of dispersal. On the other hand, we know that the Cycadeae are a very old group of plants now reduced to about eighty species, all remarkably local and confined to very limited areas, not one of which can be compared in extensive area-dispersal to the Reed, *Ipomoea biloba*, or *Paspalum conjugatum*, nor even to the Sanicle; while the Nipa palm inhabiting England in the Eocene period (for *Nipadites Burtini* is really hardly distinguishable from the Nipa of the present day) is now confined to the Indian Ocean from Ceylon and Bengal, down the Malay Peninsula to North Australia, and the Caroline and Solomon Islands, not having got so far as the Mascarene Islands, peninsular India, or Polynesia, in spite of its abundance as a drift plant both by seed and the large clumps of rhizome always to be seen drifting in Malayan seas. It is true it requires tidal mud for its growth, but there must be tidal-mud rivers in Samoa, Africa, and America quite suitable for this plant; we find, however, that, old as it is, it has a distribution now no wider than many of the doubtless more modern species which frequent the same area.

An examination of what is known of the early floras of the Eocene and Miocene periods serves to show how local now are many of the genera existing in those times; such instances are the genera *Sequoia*, *Thujopsis*, *Salisburia*, *Taxodium*, *Andromeda*, *Cinnamomum* (absent from America and Africa), *Liquidambar*, *Platanus*, *Hakea*, and many others.

Some of the older genera persist widely dispersed, as one might expect, occurring in both hemispheres, but many more have gradually disappeared and only persist now in a few isolated spots.

It would be quite natural to imagine that plants of great age would be more widely dispersed throughout the world than more modernly evolved species, as having had more time for their dispersal, but the changes which the world has undergone since their evolution have been accompanied by extensive changes in the flora, the old species disappearing or persisting as endemics or very local plants in different corners, where they have held their own in spite of the fluctuations of climate and changes in the earth's surface. The ecology, and especially the habitats and methods of dispersal, of each plant must be studied in the field before we can formulate any idea as to its history or the study of plant distribution in general.