Fig. 6. *Nothofagus Solandri* (A), *N. truncata* (B) and 8 of the hybrids between them, with (C) a very small-leaved hybrid with toothed margins, and (D) of *Solandri* form, but with much larger leaves. All 0.85 life-size.

Photo by GIBSON.

SUCCESSION
IN THE VEGETATION OF MT. FUJI

BY

DR. BUNZÔ HAYATA

PROFESSOR OF BOTANY, IMPER. UNIV. OF TOKYO
I. INTRODUCTION.

In the commencement of my work, in March 1924, on the vegetation of Mt. Fuji, which I then took up for the second time, I was singularly struck with the fact that there was certainly some difference between the vegetation which I then had before my eyes and that which I had seen there nearly twenty years before. Although the difference was, of course, slight, as was only natural in a change that had taken place in a score of years, a short time when compared with the long age which the history of a plant-formation generally describes, yet it impressed me deeply and led me to think of the great changes that must have taken place in the vegetation during the long period of the past.

In the course of my study with this impression in mind, I became more and more convinced of the facts that successive changes are everywhere met with in the forest vegetation of the volcano, and that in these changes time plays a far more important rôle than mutual struggles for existence. It is only during a short period of time that the strong encroach upon the weak, and at last drive them out. In the long run, on the contrary, the strong become weaker and weaker, principally because of their having thriven too much, and begin to wane; then the weak, taking advantage of this opportunity, regain their former lands.

Now let me explain this matter with examples which we frequently meet with on Mt. Fuji. At an altitude of 2000 m., there are found pure stands of Tsuga diversifolia. Under the dark shade of these woods, we find generally a large number of the young trees of Abies Veitchii, but only a very few of the Tsuga. Also we frequently

1 The result of my first studies was published in 1911. (Hayata I.)
meet with cases where the forests of the latter species are about to be replaced by those of the former. This white fir lives a rather short life, and after some generations is replaced by some other plant, perhaps a larch. I have seen many cases of larches in their turn being driven out by *Picea ezoeën is* or *Tsuga diversifolia*. Thus, very roughly speaking, the spruce, fir and larch may be said to flourish turn and turn about. Attempts have been made in the past to explain this succession of plant formations according to different theories; but none of them has ever been considered to be satisfactory. No matter how different the theory may be, the fact always remains that a plant which occupies a certain place will in turn be replaced by another of a different kind.

To treat thoroughly these successive changes in the vegetation of Mt. Fuji, I have found it necessary to consider them such as have been taking place at all times from the beginning up to the present. Whether the vegetation under consideration is one newly formed or one restored is a point which is entirely beyond our ability to determine. It is nevertheless certain that the volcano in its early stage was entirely bare of any growth, and then, by and by, as it became cool, it received its inhabitants from both neighbouring and distant regions.

The present vegetation may, therefore, be said to have come, starting from its infancy and passing many stages in the course of its development, to its present state which is, in all probability, quite grown up, except in some few places such as monticules of a recent eruption. When it attained its present mature state, we do not know, as there exists no record concerning it. It is likely, however, although we cannot speak with any exactness owing to the want of records, that succession was as frequently taking place in every developmental stage, as it is doing in the mature state of the present day, the latter case being, of course, by far the most manifest.

Regarding the nature of succession we may, therefore, distinguish two kinds: — I, Succession in Developmental Stages; 2, Succession in Grown Up Stages. To study the first, we should have to trace it back to a remote antiquity, which is practically impossible. Yet there is something in the present which enables us to imagine what it was like, and that may be seen in the restoration of vegetation on some monticules of a recent eruption. One case showing this kind of restoration is treated in the first part of this paper, in the hope that it may throw some light on the chaos of successive changes which have been taking place in the past. It is, however, the second kind of succession that is most fully explained in the present paper.

In the latter case I have considered most deliberately just what interpretation the natural selection theory would give to the successive changes in general and have found that it has but little to do with those changes at least in the present case, as I have outlined immediately above.

Moreover, I have thought that the factors already pointed out by previous authors are not the things that have principally controlled succession, and have thus come to the conclusion that there must exist something essential which holds, as it were, the strings of dancing puppets at the back of the stage, where nothing but physiographical or biotic factors can be seen acting their parts in the play. This essential thing is what I propose to call provisionally, for want of a better name, the Innermost Factor.

With this assumption, I have proceeded to formulate the Succession Theory. According to my theory, every species, every formation should die its natural death owing to the Innermost Factor, ceding, as it were, its land to another species or formation, quite irrespective of what may follow it. The Succession Theory is, therefore, diametrically opposed to the natural selection theory.

This I now venture to make public, though I am aware that it will meet with a great deal of opposition. It is hoped that my new theory will be regarded as going hand in hand with the Participation Theory (Hayata pp. 101—105) which I published seven years ago, when I was engaged in erecting a dynamic system for the natural classification of plants.

July 1928.
II. RESTORATION OF VEGETATION ON THE HŌYE MONTICULE WITH REFERENCE TO THAT ON MT. KRAKATAU.

As I have stated in the Introduction to this paper, it is at this time almost impossible to trace back successive changes to remote antiquity in the early period of the development. Let us, therefore, consider the restoration of vegetation on one of the parasitic cones of recent eruption, say Hōye, that we may, perhaps, find some shadows of the changes which might have been taking place in former times. At the same time let us compare it with the vegetation on Mt. Krakatau in order to see how far the restoration on our monticule differs from that on the tropical mountain, which has several times been carefully studied as to the revival of vegetation. The Hōye monticule stands as the monument of a large explosion, which took place in the year 1707, on the eastern edge of a lateral crater of the south-eastern flank of Mt. Fuji at the altitude of about 2700 m. We shall first consider the vegetation of the present day on the parasitic cone in order to ascertain, how far restoration or development has been carried on since the day of the eruption which broke out more than two centuries ago to the total destruction of organic growths on the south-eastern side of the volcano. (fig. 1 and fig. 1—a). It seems that up to that time this same side had been clad with as dense forests as those on the other sides — with Larix-formation at 2300 m., evergreen conifers at 1800 m. and deciduous broad-leaved trees at 1500 m. altitudes. The explosion which took place at the 2700 m. altitude sent out a flow of ejectmenta consisting of ashes, sand and lapilli, which extended with the width of 3.1 km. as far as to the Hakone mountains. This extension of ejectmenta to the latter mountains can be seen clearly on the Ashigara-Pass, where the same kind of sand and lapilli are found deposited and consequently the same kind of vegetation as on the Hōye side. As the declivity of this track from 1100 m. downwards is very gentle, and at about 600 m. altitude is nearly level, we find there considerable deposits of soils.

This shows that the restoration had taken place pretty nearly as it is now, and that the lower parts of the track had already been turned to arable land. But on the regions upwards from that limit, the revival does not seem ever to have been carried out, except on a very small space at the marginal portions, as can be seen in the accompanying photograph.

Setting aside the lower regions, where cultivation is carried on and where consequently it is impossible to trace out the changes in the renovation of growths, let us consider the regions at about the 750 m. altitude. One place at that elevation on this track is called Ichirizuka (literally a mound marking a distance of nearly 4 km.), where are found pine clump consisting mainly of Pinus densiflora with a few P. Thunbergii. These are scattered intermittently up to the 850 m. line, one place being called Gohonmatsu (literally five stocks of pine). From this elevation upwards are found deciduous broad-leaved shrubs and trees with some evergreen conifers mostly of Picea or Abies, which make a forest in some parts, not very dense but rather thin. The middle of this track of ejectmenta at the altitude of 1100 m. is nearly treeless, and from 1200 m. upwards it lacks any kind of ligneous plants. We find there only patches of Polygonum cuspidatum or those of P. Savatieri, Calamagrostis Langsdorffii, Artemisia pedunculosa, and Astragalus adsurgens are also to be seen. Upwards from this elevation we find practically no vegetation in the central portions of the track. But it is quite different towards the margin, where restoration seems to have been carried on much earlier. Even at the altitude of 2300 m. we see at the margin of the track already several kinds of Alnus (A. alnobetula and A. Matsumurae) and a little outside of the margin some larches. The development of the larch forest is richest on the northern side of the track, and poorest on the southern side. Down at the elevation of 1300 m. or thereabouts there are no larches on the southern margin, but there are some on the northern. As we come down to the 1200 m. line, we see no larch on either side. Kinds of Alnus are found usually fringing the bare regions of the ejectmenta.
Now let us compare this vegetation which should as a whole be regarded as a very poor one, with that on another side of the volcano. There on the latter side we see, at the 2000 m. altitude, usually abundant patches of *Polygonum Savatieri* which are scattered like those of vegetables in a garden over acres of the sandy slope of the cone (figs. 2 and 3), and on the 2200 m. line there are already found dense forests of evergreen conifers. This difference between the two vegetations, one on the Höyé side and the other on another side, is, of course, due to the difference of the ages the ejectmenta. On the Höyé side they are only 220 years old, while on the other they are more than thousands. And yet the Höyé lava has already passed the period of 220 years since the time of eruption. That could never have been a period of time insufficient for restoration, had it been in a tropical country, where fifty years would have been quite enough as in the case of Mt. Krakatau near Java.

Now let us see what difference there is between the restoration of vegetation of the Malayan volcano and that on our monticule. Nothing could be more surprising than to note the great quickness of the recovery on Krakatau, when contrasted with the extreme slowness on our monticule. The violent explosion of Mt. Krakatau took place in 1883 to the total destruction of the vegetation which had densely clad the whole island. (Leeuwen II. p. 138). In 1886, three years after the eruption, the volcano was visited by Treub who found that the first indications of vegetation were being made by algae, mosses and ferns. He enumerates fifteen species of flowering plants in the shore regions; and in the interior eighteen species of vascular plants of which seven were of flowering plants and the rest, of ferns (Treub pp. 217—218). The principal species which made up the formation were the Pteridophyta, while flowering plants existed here and there in small numbers.

As to the vegetation of Höyé, we have no record of the earlier period of its recovery. As far as we can conjecture, the restoration must have commenced long after the eruption had ceased. The first stage can be but faintly inferred in a consideration of the plant associations at altitudes of 1600 m. — 1200 m. There vegetation commences with *Polygonum cuspidatum*, *P. Savatieri*, *Cirsium purpureatum*, *Calamagrostis Langsdorffii*, *Carex Doenitzii*, *Artemisia pedunculosa* and *Astragalus adsurgens*. Above the 1700 m. line there is no indication of vegetation on the middle portion of the ejectmenta track.

If we assume that the vegetation in the very beginning of restoration was such as we have just described, then we see that there was a great difference between the first state of recovery on Höyé and on Krakatau. The total absence of ferns on our monticule on the one hand, and the luxuriant growth of Pteridophyta on the Malayan volcano on the other, are facts that stand in striking contrast. Another point worthy of notice is the extreme smallness of the number of species on Höyé, as compared with those on Krakatau.

In 1897, fourteen years after the eruption, the latter volcano was visited by Penzig. He found that there had already been a wonderful change. There was in the lowland already a Pes-Caprea formation (Penzig p. 98), and in the interior a Barringtonia formation and a gramineous formation consisting principally of *Saccharum spontaneum* and *Imperata arundinacea*. Climbing plants were also found (Penzig p. 99). In the savannas and steppes, he saw mostly gramineous plants. Strand forests were not yet formed, there being only a few shrubs. At this stage of renovation, Penzig had already found 65 species of vascular plants, which number was nearly doubled twelve years later, as reported by Ernst.

This second stage, if it can be so called, in the restoration on the Malayan volcano may be roughly comparable with the marginal formation on the track of the ejectmenta of our monticule. There in Höyé we find a growth consisting of dwarf *Alnus* and *Larix* in which growth we meet for the first time with some ferns in the shade of the shrubbies. I have not counted the number of species found in these regions, yet it is quite certain that it is far smaller than that found on Krakatau.

The change observed in the latter volcano in 1919 by Leeuwen thirty-six years after the eruption is quite astonishing. He found
there a zone of Casuaria equisetifolia making a belt hand in hand with some Barringtonia formation around the shores (Leeuwen I. p. 107). He observed growing on the shore a large Cypas which had certainly not been there twelve years before. He was quite struck with the rapidity of the recovery of the vegetation (Leeuwen I. p. 104, II. p. 138) which showed five distinct formations according to altitudes, viz: 1, littoral formation; 2, Barringtonia formation; 3, Casuarina forest; 4, grassy formation with bushes; and 5, ravine forest.

Now turning our attention to the Hōyé monticule, let us take a place on the 1000 m. line where the vegetation is, so far as we can infer, most perfectly restored. There is in this part a mixed formation of evergreen conifers and deciduous broad-leaved trees, where they are not very large, nor are the forests very dense. Most of the trees are as yet young, some of them being 50—60 years old, with a very few above 100 years. Here we again observe that there is so great a difference in this stage of restoration that there can be no comparison between Hōyé and Krakatau. This difference is all the more striking, when we consider the fact that the vegetation of Krakatau was still young, as no more than thirty-six years had passed since the eruption, and yet it consisted of forests so dense that they were inhabited by big snakes fifteen feet in length. This richness of vegetation is mainly due to the abundant existence of microflora (Leeuwen I. p. 121), such as nitrogen tubercules in the roots of the Leguminosae which fertilize the soils.

There are on our monticule some species which may be taken as soil-fertilizers, such as several species of Alnus and Astragalus adsurgens, the former possessing mycorrhizas and the latter nitrogen bacteria, both in their roots. It seems that on Krakatau these micro-organisms are propagated so rapidly as to improve the soils within a few years, while on Hōyé the development of microflora in the soil is extremely slow owing to the cold climate. This scarcity of micro-organisms in the soil may be taken as one of the principal causes of the extreme tardiness in the recovery of vegetation on our monticule.

III. SUCCESSION IN THE VEGETATION OF MT. FUJI.

As I have remarked before, it seems that the vegetation of Mt. Fuji, generally speaking, has already passed the stage of development and has now come nearly to the stage of maturity — a maturity which means only a state of completeness, but does not denote anything fixed or settled. There has meanwhile been taking place another kind of alternation which may generally be called a succession. As far as I can judge from my actual observations on some parts of the mountain, the latter change, not of one kind, but of several different kinds, is taking place, though very slowly, in every corner of the vegetation. These successive changes are by no means directly met with everywhere, but in some limited places they are very distinctly observable. I shall give here just a few examples which are most clearly seen and which represent each a different kind of succession.

1) Birch-forest being replaced by Evergreen Conifers.

On the western side of Komitake, at the altitude of 2300 m. there is a fine broad-leaved forest principally composed of several kinds of Betula surrounded by an evergreen conifer, Tsuga diversifolia, constituting nearly pure stands. In this birch wood, neither sapling nor young tree is to be found to replace the forest, but there is abundant growth of young trees or saplings of Tsuga diversifolia, Abies Veitchii and Larix leptolepis. It is, therefore, evident that the present formation composed of birch will be replaced by conifers after some time, say fifty years.

2) Larch-forest being replaced by Spruce.

A little above the same place, at the altitude of 2,100 m. there is along a valley a fine nearly pure stand of Larix leptolepis. In the shade of this forest, we find no larch saplings, but a great number of young trees of Abies Veitchii and Tsuga diversifolia. Here, again, we see clearly that these larches will in time be succeeded by the evergreen conifers. Another case of succession of the same type is seen on the upper flank above Mizugatsuka, where Larix leptolepis is gradually being replaced by Picea exoënsis (fig. 4).
3) Hemlock-spruce giving way to White Fir.

On all sides of the volcano, at the altitude of 2000 m. there is found generally a wonderful growth of nearly pure stands of *Tsuga diversifolia*. Curiously enough, we find only a very few of the young trees of the same conifer, and those rarely; but very often and in large numbers, saplings of *Abies Veitchii* (fig. 5). What will become of the growth, wonderfully luxuriant at the present time, but without descendants for the future, we shall see presently. The natural life of this Hemlock-spruce is estimated to be as long as from two to three hundred years. When it attains to an advanced age, it presents evidences of senility. It comes to have shallower roots, and is likely to be blown down easily in a storm. I have seen, on the lower slope of Komitaké and on the upper flank on the Yamanaka side, several tracts, where a fine forest of the *Tsuga* had been totally destroyed by a whirlwind. Never have we seen even a single case where the forest, after suffering such a blow, has been directly restored with the same tree; but we often find that on such a site a new forest mainly consisting of *Abies Veitchii* has been established (fig. 6). What then will be the fate of the new stand thus formed?

4) White Fir being replaced by Larch.

*Abies Veitchii* (fig. 7) lives rather a short life and in keeping with this nature, it is most prolific. It is found everywhere forming new stands at altitudes of 2000 m. — 2300 m. In the forest of this white fir, we find in one case young trees of the same fir, but in another, saplings of *Larix leptolepis, Tsuga diversifolia* or *Picea exocénsis*. We may thus be justified in inferring that the stands of the *Abies* may be continued for some generations, and yet that sooner or later the time will come, when they will give way to some other kind of conifer. The most remarkable case, where the fir is about to be replaced by a larch, *Larix leptolepis*, is seen in a tract called «Kuroun» between the Takizawabori and the Namebori at an altitude of nearly 2300 m. There the firs already show symptoms of senility, and undoubtedly have come to their natural end. Most of them are dying a standing death, while under these old firs adolescent larches are growing vigor-

ously. The larch is, generally speaking, a comparatively light-loving plant, less able to endure shade than any other conifer. It is certain that the shade is more tolerable to the fir than to the larch. It is, therefore, quite natural that the former should invade the shade of the latter, and we find this to be usually the case on Mt. Fuji, and this in turn should be supplanted by another, more tolerant of shade than the fir itself. But here we see the case altogether reversed. It seems that tolerance of shade, with other conditions, has but little significance, if compared with the succession of formations, that is to say, that in time, when it must be replaced by another, it will be so replaced, irrespective of what the succeeding growth may be. Tolerance can never be absolute and at every time, but is a thing to be considered comparatively and to be asserted only in ordinary cases. (cf. LEE p. 166).

5) Broad-Leaved Trees being replaced by Evergreen Conifers.

The successive occurrence of broad-leaved trees and conifers is to be seen in the lower forest region at an altitude of nearly 1000 m. In the eleventh division in the region of broad-leaved trees on the western flank and also at a place near Akatsuka in the same region, there are several tracts, where broad-leaved trees are giving way to evergreen conifers, such as *Abies firma* or *A. homolepis*.

6) Alders giving way to Larch.

Moreover, there are many places, where clumps of alders commonly found along valleys are about to be replaced by forests of larches (fig. 8).

7) Cases Suggesting the Periodic Rise and Fall of Dwarf Bamboos.

A very interesting and everywhere well-known case is also to be seen in the formations of dwarf bamboos on Mt. Fuji (fig. 9). Their general distribution has already been considered and the probable relation which bamboos bear to rocks has been stated in my previous paper. (HAYATA II. 1926. p. 16). Yet there are many cases which seem entirely to ignore such a relation. I shall give here some of the most remarkable instances. As can be seen in the accompanying map (fig. 9—a), the abundant growth of dwarf bamboos, extending
from the southern flank to the western, forms a nearly semicircular belt (fig. 9—a). We find, however, a large gap measuring 3 km. in breadth in the south-western portion of the otherwise continuous band. The rocks and soils on both sides of the gap are very similar to those in the gap itself. When, in August, 1924, I passed these places, where I found the same kind of forest, I was greatly struck with this singular distribution. There, outside of the gap, my way was quite obstructed by dense impenetrable thickets of bamboos, but here in the gap I found none at all. I brought back a handful of each of the soils in- and out-side of the gap and had them analysed. They presented no distinction whatever either physically or chemically. To none of these controlling factors is this discrepancy to be attributed. Periodic rise and fall must, therefore, be taken into consideration.

The ejectmenta of sand or lapilli on all the parasitic cones seem very similar. Yet they are not clad alike with dwarf bamboos. Far from that, the vegetation on the monticules presents very different aspects with respect to the bamboos. On the one hand, Jiromonzuka, Hiratsuka, Asagizuka and Higashiusuzuka (all on the southern side); and Yumizuka, Katabutayama, Tenjinyama, Igdono and Futatsuyama (all on the north-western side), are all covered with sparse or dense thickets of several kinds of dwarf bamboo, mostly *Sasa borealis*; but on the other, Kofuji (on the eastern side); Maruyama and Komitake (both on the northern side); Nagaozama and Omurozama (both on the north-western side); and Nishiusutsuka and Shiratsuka (all on the south-western side), are entirely free of any kind of bamboo.

The periodic rise and fall of the bamboo is so well-known a fact that it is hardly necessary to discuss it here.

8) Alders being replaced by Hornbeam.

The replacement of alders by the hornbeam on a tertiary hill by the side of lake Yamanaka is well-known. Here, on this hill, if the land is left uncultivated, there is found a fine forest of an alder, *Alnus incisa*, quite spontaneously established in ten to twenty years, as this alder grows rapidly. Cut the forest down for fire-wood or other use and after a certain time we shall see unmistakably the formation of a new forest of a hornbeam, *Carpinus yedoensis*. What we shall find on the site of the latter forest, when it has been cleared, nobody knows exactly, as the hornbeams long outlive the man who would study them. Some say it is *Zelkova acuminata* that takes the place of *Carpinus yedoensis*, but others doubt this. I have never seen a wood of the *Zelkova* which would suggest its establishment after this fashion.

9) Abundant Growth of *Phellodendron Amurense* after Clearings.

On the southern flank at an altitude of nearly 1000 m. there are many clearings in deciduous broad-leaved forests, in which saplings of *Chamaecyparis obtusa* have been planted. There I have found a wonderful spontaneous growth of young trees of *Phellodendron amurense*. The latter tree may have existed in the former forests, but certainly only scattering, if at all. Presumably the seeds may have been abundantly conveyed by birds! crowding in the sunny places in the clearings, or they may have lain dormant for some years in the shade of the former forest and have been caused to germinate all at once by the direct sunshine, when the clearings were made. It is certain that there would have been bushes of the *Phellodendron*, had not the *Chamaecyparis* been planted there. But, if the latter be the case, it is quite problematical, whether they would grow up to make pure stands. Some saplings of the *Phellodendron* are now growing unassociated, but others in a mixed state. As the same species is a tree which affords an important timber, we are looking forward with much interest to see how the saplings there will thrive under the silviculturists.

10) Forest of *Picea Polita* Approaching its Natural End.

Finally, I may mention one more case in the grand pure stand of *Picea polita* on the Takamarubi. There the young trees of this species are rather rare, while those of *Tsuga Sieboldii* are abundant. One part of this forest was formerly destroyed by fire. On that part we

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1 The birds may, as I am kindly informed by Dr. N. Kuroda, be grey starlings, dusky ouzels, brown-eared bulbulis, or the like.
now see red pines making their way, but no new stand of the same spruce. The average age of the spruce is about two hundred years, as I have ascertained by counting the annual rings on the stumps left on the site of the former forest destroyed by fire. Although the trees in this forest do not as yet show any signs of senility, they already seem far past the prime of life and to be approaching their natural end. There, as I have said above, the young trees of the succeeding generation of Picea polita are rather rare. It is said that some time ago the people put on a layer of new soil over some parts of the forest in order to enable the falling seeds, which are here produced in profusion, to germinate and to produce seedlings. But this scheme failed entirely and we could not find more young trees on the new soil, than on the old ground. I have never made such an experiment; but, when I was told this story, the thought immediately occurred to me that, in that declining period, the seeds had lost all the power of germinating. Thus there seems to be no way of maintaining the same kind of forest through many generations. Should all forms of life share the same fate with this Picea polita, and prosper only to decline in the end, things should be greatly different from what we have been taught by the theory of natural selection due to the struggle for existence. To this matter I have repeatedly alluded in other places. (Hayata IV and V.)

IV. OUTLINE OF PREVIOUS STUDIES ON SUCCESSION, TOGETHER WITH REMARKS ON THEM IN CONNECTION WITH THE VEGETATION OF MT. FUJI.

Before entering upon the discussion of the successive changes to which I have just referred, I shall here devote a few pages to the general consideration of previous studies thus far made by several authors, which may have some bearing on the present subject.

Although it is since the publication of Lyell's Principle nearly a century ago, and that of Darwin's Origin of Species about thirty years after that time, that dynamics have come to be generally accepted, yet the first record of succession in vegetation dates back as early as 1685, when William King made his study on the bogs and boughs of Ireland. The latter work was, however, done only for one way of changing, i.e. from simple to complex but neither for the reverse nor for both (Cowles p. 163). Then follow, to mention only those whose names cross my mind, Buffon, Dureau de la Malle (1825), Warming (1891) Jaccard (1902), Cowles (1911) Clements (1916) Palmgren (1925), Cajander (1926) and especially for the vegetation of Japan, Terasaki (1924).

Upon considering the studies of these authors, I have found that in explaining plant successions some of them, such as Warming, lay great stress on the mutual struggle for existence, while Cowles, Wilson, Mayr, Willis, Clements and others regard physiographic or biotic factors as those principally controlling the changes, and pay but little or no attention to the mutual struggles.

Since the struggle for existence in the vegetable world was first pointed out by De Candolle (1820) and later by Darwin (1859), whose natural selection theory now has an undeniable influence upon every branch of botany, it has been regarded with more or less exaggeration by some scholars who have gone so far as to view the matter of vegetative dynamics in the light of the selection theory. In his monumental work "Ecologische Pflanzengeographie" (2-Auflage, 1918), Warming refers in several places to mutual struggles in plant life (pp. 896—941), regarding them as the principal causes of succession; for instance: the association of Calluna and Festuca (pp. 904, 908): the mixed formation of herbs and grasses, when the lands are left uncultivated, a formation which is succeeded in turn by shrubbery; and finally the latter by forests, — all these changes come, as he says, as a result of struggles for existence (p. 906). He also talks about the arming (Waffen) of plants for the struggle (p. 932). But all that he gives as the arms of the plants, such as want of nourishment, scarcity of heat and light, or the toxic action of some excrements from roots (p. 932) are in most cases not arms for defence nor those of attack, but rather those of self-destruction. Indeed, he recognises also the latter kind of arms, but he refers to them in only a very few places (p. 932), and regards them as a minor matter in controlling plant succession. Although he points out in a few places physiographic succession (p. 356), such as changes in climate (p. 915), accumulation of plant-roots, or changes of soils which are ascribable to other biotic factors (p. 933), yet he regards nearly all these as minor factors causing succession (p. 127). As to the alternation of steppes and forests, although he recognises to some extent changes in the chemical nature of soils and those in water conditions, he regards the struggle for
existence between steppe- and forest-plants (p. 915) as the principal factor controlling the succession. In my opinion this change in the vegetable growth is in the main, if we do not take into consideration the Innermost Factor which I shall explain later on, ascribable to the physiographical and biotic factors, and in the least degree to the struggle between the different groups of plants. He assumes a regular order in succession,—order from a simple formation to a complex one (p. 357), and says that the latter comes at last to an end-formation (Schlesiglidi der Entwicklung) (p. 928). To this I cannot agree. As far as I have observed in the vegetation of Mt. Fuji, whether we call a formation an end or an intermediate is but a matter of time, and is principally according to its being a long-lived or a short-lived formation, comparatively speaking.

NAGELI (1872) notes that he found in the Alps a case, where struggles were going on between Rhododendron ferrugineum and Rh. hirsutum. I have never seen anything like this in the vegetation of Mt. Fuji. On the other hand, I have found that a different species of Rhododendron predominates on each different lava-bed, different only with regard to its locality, but quite similar in respect of its structure, viz: R. sinensis on the Taka-marubilava; R. Kaempferi on the Tsurugi-marubilava; and R. dilatatum on the Aogigahara-marubilava. These three lavas being exactly the same in their structure, the above cases suggest that at one time one species prevails, and at another time another species. Here we cannot help thinking that the kinds of plant-associations are greater than those of life conditions, as the same statement is made regarding plant forms by Goebel (Goebel pp. 14, 18, 42, 70, 894).

CAJANDER (1926, p. 92), though he recognises that chance has some influence on the details of the floristic composition of plant associations, regards its influence as rather restricted. He thinks that the occurrence of the plant species is limited only by their respective capacity to thrive in the different localities.

JACCARD (1902, p. 375) mentions that the distribution of species on alpine meadows depends in the least degree upon the ability to thrive possessed by the plants themselves, and that each species can thrive equally well on the meadows. He considers that the countless varieties in plant associations in all different localities are ascribable to «outer factors» by which he means something different from the thriving ability possessed by the plants themselves. PAlmgren (1925, p. 138) states that JACCARD's «outer factors» cannot be those controlling the distribution of plants in this case, but it should be «chance» that should take the place of JACCARD's «factors». I quite agree with PALmGREN on this point.

Now let us turn our attention to another side of the matter and consider the opinions of previous authors who pay but little or no regard to struggles for existence. BLYTT, when explaining the alternation of moss- and forest vegetation, puts forward the theory that succession in the vegetation is due to physiographical change and especially to climatic change.

As to the succession in the vegetation of Japan, MAYR (1906) was, perhaps, the first who published in a language other than Japanese a note on the subject, although he did not use the term, succession. He mentions that prairie in Japan is not necessarily caused by human agency, as is usually thought, but may be a formation originally existing (p. 710). As to the causes of the existence of so extensive an area of a grass formation, whether it be original or secondary, he holds the opinion that it is mainly due to the nature of soils and the occurrence of dwarf bamboos, which are all but peculiar to Japan. As an argument in support of this opinion, he remarks that, even in cases where it may be well inferred that the existence of prairie might be ascribable to human agency, it may be equally reasonable to question why it has not been recovered in course of time in a country like Japan, where precipitations and moisture are so abundant that there should have been no difficulty in restoring it to its former vegetation. So far as I can judge from my own observations on the vegetation of Mt. Fuji, MAYR was right in his argument, and I cannot but hope to call to his opinion the attention of our Japanese foresters who are too apt to bring this vexed problem quickly to a conclusion by blindly sticking to the current opinion that our prairies are formed as a result of fires. As to the site of evergreen forests after cutting or fires, MAYR states that there come at the outset clumps of deciduous trees such as Rhus semialata, Rottlera japonica (= Mallotus japonicus), several kinds of Alnus, Aralia and others; then they in turn are driven out by evergreen trees, and thus the former forests are in the end restored.

DACHNOWSKI (1908) points out that decomposed remains of an earlier vegetation certainly cause mechanical and chemical changes in soils (I, p. 131). But he remarks also that, whether the injurious substance excreted by roots, to which attention had been called by WHITNEY and LIVINGSTON, should actually control succession in plant life, although it may be in part a cause of xerophily and decreased fertility (II. p. 404), he gives no more than a suggestion of that possibility (I. p. 142). The latter statement is true also for the theory of «Ilyachis», so generally accepted by Japanese agriculturists, — a theory which assumes the tendency of plants to come to dislike the same locality in course of time.

The most interesting paper, so far as I have read, is one by COWLES entitled «The Causes of Vegetation Cycless» (1911). According to his opinion, succession
is divided into three kinds: 1, regional succession; 2, topographic succession (p. 168); and 3, biotic succession. As to the present subject of the vegetation of Mt. Fuji, the first kind of succession seems to be too far remote a change, for the development of our volcano began probably during the early Pleistocene epoch. On the other hand, the two latter are clearly observable on the mountain, and, therefore, should be matters deserving careful consideration. Now the second class of succession is controlled by a physiographic factor, and the third, by a biotic factor. The latter is a very subtle thing and seems at first sight to be very insignificant as compared with a physiographic one, yet it is a thing which acts a most important rôle incessantly for a long period in a time of no sudden physiographic change. Cowles divides the biotic agencies into four, viz.: a) the humus complex; b) shade; c) plant invasion; and d) human agencies. I should like to add one more which is, in my opinion, by far the most important and which, as I have said, I propose to call the Innermost Factor. To this matter I shall return later on. Let me now refer to a few more points from Cowles which may have a more or less close relation to the present subject. He says that succession is carried out in humid regions in a shorter time than it is in arid districts (p. 163). A growth thriving all at once perishes also suddenly, while one having risen little by little falls very slowly (p. 167). Time plays a more important rôle than any other factor (p. 172). One vegetation in due time declines, leaving its place ready for the next plant to come (p. 174).

Harshberger (1916) gives diagramatic figures of succession after the destruction of pine forests (p. 100). He states that after the clearing of pine barrens, although there prevail different kinds of undershrubs for some generations following that time, the barrens are in due time restored to the state in which they were originally; but after burning, clumps of Quercus are found on the site of the barrens (p. 102).

Clements (1916) mentions that the developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity and therefore a formation, as an organic being, arises, grows, matures and dies (p. 1). Here I should like to dwell upon the meaning of the last word die. In my opinion, an organism may die, but leave behind it its posterity in the time of its rising phase, and the formation as a whole flourishes. But the case is quite different in the time of the falling phase. The organism then passes away, leaving no descendants, and thus causes the disappearance of the formation. The Succession Theory, which I aim to formulate in the present paper and to which I shall return later on, is principally based on the assumption that there is actually the death of the formation — a death comparable to an extinction of species.

Wilson (1918) states, regarding the forest regions of Korea, that in course of time after volcanic activity the first formation is that composed of birch, poplar and larch, and that the latter species by and by predominates and establishes a pure stand of its own. The latter formation then invites shade-loving trees such as the fir, spruce or Pinus koraiensis, and there is consequently found a forest of evergreen conifers. The forest thus formed, if only partially destroyed by fire due to lightning or human agency, gives way to birch, poplar and larch, and the latter in turn again to spruce or fir, thus completing a cycle of forest making. But in the case of total destruction, the forest is first turned into a prairie, then to bushes or shrubberies, and finally to a red pine forest (Pinus densiflora). These statements of Wilson come quite close to those I have made from my observations on the vegetation of Mt. Fuji.

Willis (1. 1922) holds an opinion which in many points agrees with my theory, and what he says about age is nearly the same as what I express by time. He discovered that the effects of mere age upon dispersal were so clear and unmistakable that they could be expressed by figures (1. p. 6), the result being that the older a species is, the greater is its range of distribution. An association of plants, occupying a given area of ground, passing its climax, opening its ground and leaving room for newcomers, tends to be succeeded by the latter (1. p. 20), the process being known as succession. Upon the consideration of endemic species in the flora of Ceylon, he states that they are, in all respects, formed by mutation, but not by survival of the fittest, there being no evidence of natural selection (111. p. 611). A limited species becomes first a wide ranging species usually of polymorphic character and then, as it grows older, gives rise to one or several new or endemic species, and finally dies away (111. p. 612). This statement of Willis's is quite in agreement with mine, in so far as an objection is concerned to the natural selection theory, and a recognition of inevitable rise and fall in organic growth, whether of an individual or of an association.

Lee (1924) says that there are in the vegetation of the United States three divisions of climax formations, viz.: 1) prairie, 2) coniferous forests, and 3) deciduous forests, all of which are mainly controlled by physiographic and especially by climatic factors, (pp. 129—135), as was already stated by Schimper (pp. 623—635). The edaphic factor does not, according to his opinion, determine the extent of the larger units of vegetation (p. 131), nor does the biotic, to which he gives but small significance. He mentions the replacement of Pinus Bankisiana by P. resinosa (p. 144) and then the latter by Acer saccharum or Pinus strobus, as the soils became gradually improved. This kind of succession caused by the improvement of soils occurs very often.
n the vegetation of Mt. Fuji, as is seen in the case of a site of clumps of *Ainus*. Soils in the latter case are made better by mycorrhizas which find their way into the roots of the *Ainus*, which then, at an altitude of 1,500 m. or upwards, is usually replaced by larch. Further improvement in the soil causes the larch to be succeeded by *Picea*, as may be seen at the foot of Nishihotatsuzuka. *Ainus* as a soil-fertilizer has since remote times been very well-known among farmers in Japan, and even now it is utilized as such in the province of Hida and in some other places. It is even known to the headhunters of Formosa and it is surprising to see them making use of the method with a much better device than that used by the farmers of Japan. Lee mentions that a slight fire kills the undergrowth and opens the resinous cones, thus stimulating germination. It is, therefore, somewhat favourable to forest making (p. 159). A nearly similar account of *Tectona grandis* was given me, when I was travelling in Siamese Indo-China. This may be altogether surprising to those who are apt to believe that fire is nothing but an enemy of the forest. He also says that the frequency of seed-reproduction aids in ensuring succession of the same species in the next generation (p. 167); but I think that seed-reproduction, however abundant and frequent, can do nothing for the continuation of generations, when the seeds do not germinate, as is the case on Mt. Fuji with *Tsuga diversifolia* at an elevation of 2,000 m. and *Picea polita* on the Taka-marubi.

TERASAKI (1924) remarks that, although cyclical changes in forest formations have long been known to Japanese foresters, they were never recorded nor applied to silviculture, and his paper is, as he says, the first in which the same subject has ever been treated systematically (p. 4). But I may add that MAYR had noticed successive changes nearly twenty years ago, as I have mentioned above.

PALMGREN (II. 1925, pp. 127—138) considers most deliberately what controls the distribution of plants and there in his paper he decidedly regards chance as a phytogeographical factor, to which matter he had already referred some years before. In his first paper (1922) he mentions that in an open land many species may live and thrive equally well, but whether this or that species first occupies the land or several species settle in together and form an association, depends mostly upon chance (I. 1922, pp. 98, 101 and 122). In his second work (II. 1925, p. 127) he regards chance as a true factor controlling the distribution of plants. He includes in the term, chance, a complex of causes — causes which in the present state of our knowledge can never be treated one by one independently, and which therefore we are obliged to regard collectively as one unit (I.c. p. 129).

V. THE SUCCESSION THEORY.

Thus far, I have endeavoured to give an outline of previous studies which may have more or less relation to the present subject. We shall now enter upon the discussion. To begin with the first stage of succession, let us assume that a vertical front plane represents the present state, and a vertical rear plane, the former state of vegetation (which can never actually be seen, but which can be imagined from data known to us) and the interspace between the two planes, the space of time between the two states of vegetation. Then the hexahedron bounded by the two planes, front and rear, should represent the vegetation displaying all the changes that have taken place from the former up to the present time, or in other words the succession of vegetation within the given space of time. Keeping this assumption in mind, we shall consider the vegetation thus to be compared to a hexahedron.

In one of my previous papers I have explained the vegetation at the present time as comparable, so to speak, to the front face of the hexahedron. Now, the question arises, what may the former vegetation, comparable to the rear, have been like? Imagine the very beginning of the vegetable world of Mt. Fuji. As it was formerly an active volcano, there can be no doubt but that it must have been in its earlier period, entirely destitute of plants. Then the mountain after some time became extinct and was given a vegetation, consisting, at first, of mosses and lichens\(^2\), and then, of grasses and herbs, somewhat similar to that shown in Fig. 9—a. How this poor vegetation gradually led up to the present luxuriant growth we do not clearly understand. Yet there is something in the present which enables us to thread our way through the chaos of the past. We see in one place that grassy or herbaceous formations have already been turned into shrubberies and in another that thickets are in their turn about

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2 Macroscopically, the first comers are species of *Polygonum or Carer.*
to be replaced by forests. So far as my observation extends, plant-formations do not remain constant through all time, but change from generation to generation as has been illustrated by a few examples given above.

While remarking in the foregoing pages on general studies on plant succession in connection with the present subject, I have considered most deliberately, what interpretation the natural selection theory bears to serial changes, and have found that it has but little or nothing at all to do with plant succession, at least in the present case, with a decided leaning towards the opinion of Willis and others.

Now what are the factors controlling succession? It is certain that they are not a few, a but are possibly numerous; some of them are essential, while others are accessory. Each succession should be ascribable to the same or different cause or causes. In a case where alder is succeeded by larch, or the latter, in its turn, by spruce, the change of soils due to a biotic factor may be taken as a direct cause. On the other hand, in another case where spruce is replaced by white fir, it is not conceivable that there must exist some change of soil or other like change. We would rather look for some change within the plants themselves which may, as it were, hold the strings of the marionettes behind the scenes, where nothing but physiographic or biotic factors seem to act their parts in the pay.

And again, upon considering the case of *Picea polita* approaching its natural end, or, to take up a matter arising in a much longer space of time, the case of the extinction of a wide spreading species, I cannot help suspecting the existence of some inner change due to a factor, which is what I should propose to call provisionally, for want of proper words, the Innermost Factor, and which is subject to outer factors and can never be conceivable as independent of the latter.

What this Innermost Factor is, it is rather difficult to explain in the concrete. Yet, I may here give two parallel cases which enable us to believe that such a factor must truly exist. It is a well-known fact that a living thing, when approaching an advanced age, dies its natural death, ceding, so to speak, all the things necessary for existence to its descendants. We explain this fact by saying that the cells are so exhausted through their work that they must come to the end of their activity. What the thing is which is supposed to have accumulated in the cells in the course of their life and which makes them unable to continue their work, we do not know exactly (Goldschmidt p. 3). Yet the fact is very clear that there exist some factors, within and without, that control the life and death of the individual. Now, let us consider the other analogous case of a species or a formation which after succeeding for some generations one after another and reaching its declining years dies its natural death, — a natural death not of an individual, but of a species as a whole, as is seen in the examples given in this paper — leaving, as it were, its land to other species or formations. Here in the latter case we cannot but think that something essential must truly exist which controls plant succession. This is what I have called the Innermost Factor. This factor belongs to the same group as the inner factor assumed by Goebel to exist (p. 1089), when explaining the cause of morphological difference. The Innermost Factor causes the innermost change in sexual cells, which change causes the extinction of a species or the total destruction of a plant formation. What the innermost change in sexual cells is, we do not understand exactly. Yet numerous facts shown by succession in plant life in recent as well as geological time are too clear to admit even the slightest shadow of doubt as to the existence of this same innermost change.

On this assumption I have proceeded to formulate a theory, the Succession Theory. The theory assumes the existence of the Innermost Factor which is subject to outer factors and which is inconceivable as independent of the latter. According to the theory every species, every formation, should die its natural death owing to the Innermost Factor, ceding, as it were, its land to another species or formation, irrespective of what follows it. The Succession Theory and the natural selection theory are, therefore, diametrically opposed.
Let us now examine these two theories by actual examples. There are on Mt. Fuji several lavas of recent origin named with the suffix smarubis to distinguish them from other lavas of much older eruptions. On the former lavas we sometimes find different plant associations, each consisting of a different kind of species. Thus we see a pure stand of *Picea polita* on the Taka-marubis, and a nearly pure stand of *Tsuga Sieboldii* on the Aokigahara-marubis. Under-shrubs growing on different lava-flows are also different. *Rhododendron sinenses* on the Taka-marubis, *Rh. Kaempferi* on the Tsurugi-marubis and *Rh. dilatatum* on the Aokigahara-marubis. At altitudes of 1600 m. or thereabout on the Hoyé lava consisting nearly uniformly of sand and lapilli, we find on the Gotemmba side an association of *Polygonum Sabatierii* growing extensively like radishes in a garden, while on the Suyama side is another association of *Cirsium purpuratum*. And again, in the shade of evergreen conifers we find in one place a pure association of *Cacalia adenosystylloides* (fig. 10), but in another, none at all. In like manner, in the shade of the deciduous broad-leaved forest, we find in one place an association of *Cirsium effusum* (fig. 11), while in another that of *Ligularia stenoecephala* (fig. 12) and in another *Osmunda cinnamomea*. In all these cases it is impossible to conceive of any difference which may have existed between the conditions, where we find one plant in one place, but another species in another place. Here I cannot but think that the manifoldness of plant-formations is greater than that of life-conditions. A single place is suited to several different plants, and it is, therefore, due to a mere chance, whether one plant or another is invited to occupy the site of the former species which at the end of their destiny passed away (Palmgren I. pp. 98, 101, 122; II. pp. 127—138). Plant formations take advantage of the land where they find themselves, but they do not strictly choose it, as we used to suppose that they did. The same statement is made by Goebel as to plant forms (pp. 14, 18, 42, 70, 894). Here I am forced to think, with much leaning towards Went, that we ought to drop all teleological explanation, and not consider nature as having any aim (cf. Willis and Went p. 270).

Upon considering all the cases so far given, I have come to the conclusion that species or formations are, after all, so formed as to be replaced by another, irrespective of what follows it, and that it is not the strongest that survive, but the one which is next in the ring, nor is it the weakest that perishes, but rather the one which has played its part and is in the order of falling out as necessarily follows from the Succession Theory.

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Fig. 1-a. View of the Hoyé monticule, seen from the very base, at the head of the Makuzawa valley; the top of Mt. Fuji is slightly visible just back of the monticule; the white patches in the foreground are stocks of 
Ceratium purpureum.
Phot. B. HAYATA, Aug. 21, 1936.

Fig. 2. Alpine stretches at an altitude of about 2400 m. on the Omiya (southern) side. Polygonum Sosatens, extending in patches over broad acres like vegetables in a garden. Carex 
Donnielli is also found here and there.
Phot. B. HAYATA, Aug. 11, 1936.
Fig. 3. One of the Polygonum patches on the same stretches. Phot. B. HAYATA, July 1924.

Fig. 4. Stands of Larix leptolepis at the altitude of 2800 m. on the western side at the head of the Hokuhuzawa valley near Mizugatsu. The Larix is about to be replaced by Picea hakusanis. The grayish white carpet in the foreground is a dense formation of Chamaecyparis obtusa Hoffm. Phot. B. HAYATA, July 1924.
Fig. 5. Pure stand of *Tsuga diversifolia*, at the altitude of about 2000 m by the side of the path up Mt. Fuji from Shōji. In the shade of the forest there are seen large numbers of young trees of *Abies Veitchii*.

Phot. B. HAYATA, May 1921.

Fig. 6. Young stands of *Abies Veitchii* on the site of *Tsuga diversifolia* blown down by a whirlwind, at the altitude of about 2000 m. on the Yanmazaka (northeastern) side.

Phot. B. HAYATA, Aug. 15, 1929.
Fig. 7. *Abies veitchii* at the altitude of about 1700 m. on the Yoshida (northern) side. One of the largest examples of the species, measuring roughly 75 cm. in diameter. A big hollow on the left side at the basal portion of the trunk is a symptom of senility and indicates that the tree will not survive many more storms.


Fig. 8. *Alnus* formation at the altitude of 1550 m. along the Ichibeiuzawa on the Omiya (southern) side. As the soil is improved by *Alnus*, *Larix* follows. In this picture the *Alnus* forest is seen in the foreground, while a few larches rise behind the alders.

Phot. B. HAYATA, Aug. 12, 1926.
Fig. 9. An association of *Sasa borealis* in a forest consisting mainly of *Quercus criippa* (= *Q. grosseserrata*) and *Fagus Sieboldii* at the altitude of 1200 m. on the eastern side of the Garanawa near Plantation No. 4, on the southern side of Mt. Fuji. The small tree with an inclined trunk and umbrella-shaped foliage is *Acer japonicum*.

Phot. B. HAYATA, July 19, 1924 (G. 1).

Fig. 9-a. Patches of *Polygamy Sessilis*, at an altitude of 2600 m. on the southern side, on the western edge of the depression, from the eastern side of which abruptly rises the *Hirye* monticule. The western flank of the monticule is seen in the background.

Phot. B. HAYATA, July, 1924.
Fig. 10. An association of Cacalia adenostyloides in the shade of a pure stand of Picea abies at a place called Oshino, at the altitude of 2300 m. on the Umaya (southern) side.

Phot. B. HAYATA, July 23, 1921 (n. VI.).

Fig. 11. An association of Cirsium effusum (in the foreground) in the shade of a deciduous broad-leaved forest at the altitude of about 1550 m. on the Umaya (southern) side. The principal trees to be observed in this picture are Picea obovata, Acer pictum and Carpinus japonica. Among the shrubs may be mentioned Lonicera japonica, Viburnum tircatum, Berberis floribunda, Fraxinus japonica and Ligustrum ibota.

Phot. B. HAYATA, July 22, 1921 (n. III.).
Fig. 12. An association of *Ligularia stenocephala* in the shade of a deciduous broad-leaved forest along the Dalhassen at an altitude of 1500 m. *Ligularia* in the foreground; the small tree with cordate leaves in the middle ground is *Tilia japonica*. *Prunus Maximowiczii* and *Acer pictum* with a climber, *Hydrangea anomala*, are the principal trees to be observed in this picture.

Phot. B. HAYATA, July 25, 1924 (N. II.).
Sketch map of Mt. Fuji
Showing the distribution of dwarf bamboo