Chlorophyll Variegations due to Mutable Genes and Plastids

by

YOSHITAKA IMAI (Tokyo)

With 10 Text-figures

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Introduction

Our knowledge of chlorophyll variegations as the results of various causes has been greatly enriched by modern genetic investigators (cf. HAAN 1933). Although the mechanism of anthocyanin variegation has been cleared up to a great extent, that of chlorophyll variegation has not received the same amount of attention. Variegation is sometimes due to recurrent mutation of certain genes and plastids. After the conclusion in his paper regarding the behaviour of the apparently simple inheritance of variegation in *Polygonum*, IMAI (1934a), the author wrote: "I am of the opinion that, in view of the foregoing remarks concerning *Polygonum*, some cases of other plants that have been reported as being Mendelian in inheritance, should be checked by experiments." The present paper deals with the writer's further work in line with his previous opinion just quoted. Before listing and discussing a number of analogous cases, descriptions will be given of experiments made with the variegated forms of *Hordeum vulgare* and *Pharbitis Nil.*

Hordeum vulgare

The white-striated barley is due to recurrent exomutation of plastids (Sô 1921; IMAI 1928, 1935a). The progeny of variegated barley consisted of variegated, albinotic, and mosaic seedlings, no green ones being produced. The available data collected from 1931 to 1934 are

Num. of pedigrees	Variegated	Albinotic	Mosaic	Total
1595	335289	16989	659	352937
	95.0 %	4.8 %	0.2 %	

The frequency of the albinotic seedlings varies considerably from zero to nearly 30 per cent according to pedigree sampling (Imai 1935a). For separate ears, the percentage sometimes goes much higher. The highest record in the writer's culture is 86.4 per cent (6 variegated and 38 albinotic seedlings). The ear was very strongly variegated, the larger part of it being white.

The mosaic seedlings are belived to have been derived from those egg-cells that contained both white and green plastids, but not from the recurrent mutation that occurred in the development of embryos. The mutation is confined to the sporophytic generation, almost excluding embryonic development. Owing to the high constancy of the plastids in the promeristematic tissues, neither periclinal nor white shoots is hardly ever produced. The mosaic seedlings have white stripes, being sometimes sectorial, periclinal, or the positions of the white and green parts reversed. The contents of 141 mosaic seedlings taken at random were

Striped	Sectorial	Periclinal	Reversal	Total
90	28	19	4	141
63.8 %	19.9 %	13.5 %	2.8 %	

A striped seedling has generally one or two stripes, the variegation being very clear and simple, while the sectorial one is half-green and half-white. Such plants, when carefully cultivated, may produce white shoots and bear white ears. The seeds from the white ears gave rise to albinotic seedlings as was expected. Barley, being a dihistogenic plant, the periclinal seedlings have *albomarginata* leaves, while the reversals have *medioalbinata* foliage (Imai 1935c). Although the reversal seedlings are very weak owing to the lesser photosynthesis, the periclinal ones are rather strong and grow up to produce some ears. Five such ears gave 230 variegated and 5 albinotic seedlings, as expected. The result proves that the subepidermal tissue, which together with all inner tissues is derived from endohistogen, has ordinary genetic composition.

Pharbitis Nil

Three mutable genes that affect the chlorophyll content are known in this plant, namely, yellow-inconstant, yellowy, and xanthic (Imai 1934b). In these cases, the mutation occurs from the recessive genes to their prototypic alleles, the former resulting in deficient chlorophyll content. Its reverse however never occurs. The writer now places the other two genes, variegated and deficient, also in this category, the gene variegated-reduced working as a modifier for variegated. The variegated leaves have hitherto been supposed to be due to a pattern character manifested by a recessive gene, but this does not seem to be the case. The gene stimulates the mutation of the green plastids, as a consequence of which the green ones may alter frequently to albinotic, resulting in variegated leaves. The amount of variegation differs to a certain extent in the different strains and also according to environment as well as to ontogenical differences. The reason for the white leaves not generally appearing on the variegated stocks is due to absence of mutation in the earlier cell generations in the plant ontogeny. The mutated white plastids frequently change to green, giving fine green ticks in the whitish parts. The mutation therefore is reversible. Accepting this view, we should expect in the progeny of the variegated stocks some whitish seedlings with green ticks in the otherwise ordinary variegated ones. They have however hardly been observed. An investigation in order to check the correctness of this view is now under way.

The gene variegated-reduced, which lessens the extent of variegation, gives a characteristic mottling (IMAI 1925; MIYAKE and IMAI 1934). According to the new view, the gene modifies the extent of the plastid mutation caused by the so-called variegated gene.

The gene deficient results in imperfect tissues, causing deficiencies in certain parts of the foliage and the floral organs (IMAI 1925; MIYAKE and IMAI 1934). The new view holds that the gene stimulates the plastid mutation from normal to deficient. The cells containing the abnormal plastids do not develop normally, resulting in very shrinkled tissues that cause certain parts to be deficient. The mutation is strongly influenced by environment.

In 1934, a plant showed variegation with creamish white patches due to sporadic plastid mutation that occurred in early plant ontogeny. The whitish parts, in turn, contained yellow ticks or patches. Up to the present, there have been observed several cases of sporadic plastid mutations that occurred in normal pedigrees (MIYAKE and IMAI 1934, 1935), but the albinotic parts were monocoloured; in other words, the albinotic plastids had full constancy. In the present case, however, whitish plastids frequently alter to yellow.

The seeds collected from the variegated plant were sown immediately in a green-house, resulting in 33 green, 12 whitish with or without yellow ticks, and 5 yellow seedlings, the last-mentioned two forms being non-viable. The occurrence of the yellow seedlings is due to the plastid mutation that recurred from whitish to yellow. The flowers borne on the branchlets with yellow-ticked whitish leaves were pollinated by the pollen of the normal green plant, the seeds from which gave 6 whitish and 1 yellow seedlings. The reciprocal matings, however, produced 25 green seedlings. These crossings proved the maternal inheritance of the mutated plastids as also the plastid mutation from whitish to yellow. The occurrence of the whitish variegation on the normal plant therefore is due to sporadic plastid mutation from green to whitish and that of the yellow variegation to recurring plastid mutation from whitish to yellow; that is to say, the mutated whitish plastids are automutable to yellow, which, however, is highly constant, never changing to whitish. As expected, the yellow branchlets, when selfed, gave 3 yellow seedlings.

Analogous cases observed

The writer, who for some years past has been giving much attention to the mechanism of chlorophyll variegation, concludes that many of the cases that used to be regarded as simple Mendelian should be reconsidered from the new point of view that such variegations frequently result from mutable genes or plastids. His own experiments with several variegated plants have shown that it is due to the recurrent gene or plastid mutation. The following is a list of these cases, with breeding results, to which are added such cases as are regarded as being analogous according to the writer's judgement from his observations. The various species, together with short descriptions, are arranged according

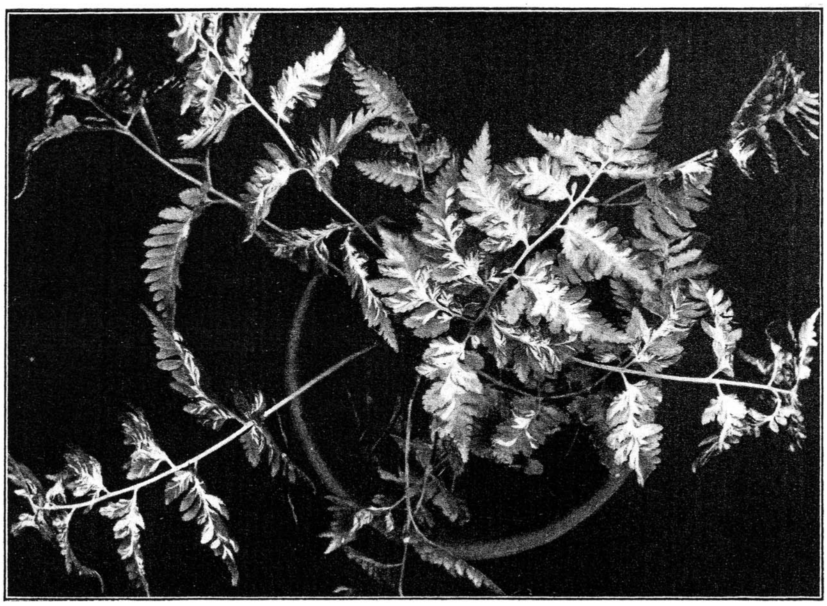


Fig. 1. Variegated form of *Athyrium nipponicum*.

to the alphabatical order of each plant group. As to the many other cases of Mendelian variegation (cf. Haan 1933), discussion is reserved for a future occasion when further investigations have been completed.

Pteridophyta

Adiantum cuneatum (Polypodiaceae): Wedge-like creamish white patches occur; sometimes small pinnae develop into white distorted. Andersson (1923) has made experiments with this variegation. Recurrent mutation occurs at gametogenesis and in sporophytes. Variegation is due to gene mutation, from dominant inconstant green to recessive white. The variegated stock itself is believed to be heterozygous (Imai 1934b).

Athyrium nipponicum (Polypodiaceae): White patches occur on leaves, especially in the central parts of the pinnae (Fig. 1). The white parts have fine green ticks, probably due to reverse mutation.

Gymnospermae

Chamaecyparis obtusa (Pinaceae): Variegation occurs in creamish yellow. The yellow branchlets are greatly contracted, owing to poor development of the albinotic tissues. In the variegated form of var. *breviramea*, creamish yellow variegation occurs also on the foliage. Rarely, pure green bud variation arises, due to reversion from variegated to green.

Chamaecyparis pisifera (Pinaceae): The variegated from of var. *breviramea* has yellow patches on the foliage. Sometimes pure green sports appear on the variegated stock. In var. *plumosa* are found two white-variegated forms. One of them at least bear green sports at intervals. In var. *filifera*, variegation occurs in the yellow. The albinotic branchlets of these forms never bear green ticks.

Juniperus chinensis (Pinaceae): Variegation occurs in both yellow and creamish white. Green sports arise at times on these variegated forms. White variegation also occurs in var. *procumbens*.

Thuja orientalis (Pinaceae): Golden yellow patches or branches arise in the variegated form. So far as the writer's oberservation went, no case of reverse mutation was found.

Monocotyledonae

Agapanthus africanus (Liliaceae): Variegated with creamish white and green stripes. Minute green ticks occur on the creamish background, mutation therefore being reversible. The central parts of the leaves have many green stripes.

Agave americana (Amaryllidaceae): Two periclinal types with mutable tissues were observed, the one having yellowish ectohistogen and variegated endohistogen, the other being *mediovariegata*. The striped parts of both forms are due to reversible recurrent mutation.

Alpinia formosana (Zingiberaceae): Finely variegated with cream and green colours, the cream parts being yellow at the young stage of the leaves. Mutation is reversible.

Angraecum falcatum (Orchidaceae): Fine green ticks occur on the yellowish leaves. Mutation is reversible.

Aspidistra elatior (Liliaceae): Fine creamish variegation occurs longitudinally on the leaves. The extent of variegation differs considerably. Mutation is only one way, from green to creamish.

Calathea Vandenheckei (Marantaceae): Creamish white variegation, but without any green patches, very frequently occur on the leaves.

Commelina communis (Commelinaceae): Variegated form has creamish white stripes, the degree of variegation varies markedly in different individuals as well as in different branches or leaves of the same individual, from nearly green to nearly creamish white. The creamish leaves have green stripes and fine ticks, due to reversible mutation. The variegated form is recessive in inheritance to green, but the exact nature of the variegated form is very complicated, owing to recurrent mutation into different grades of variegation (IMAI 1935b). Another variegated form in cultivation, however, has no green ticks on the creamish background, the variegation being merely due to mixture of stable green and albinotic plastids in the cells of the sporophytes.

Cyperus alternifolius (Cyperacea): Creamish stems bear cream leaves with green stripes and green leaves, due to recurrent mutation. Mutation here is probably not reversible, being only one way from cream to green. Very frequently green sports occur. The upper parts of the creamish umbels are apt to be green.

Dendrobium monile (Orchidaceae): The *mediovariegata* form is due to recurrent mutation of the creamish endohistogen.

Dracaena fragrans and *D. Deremensis* (Liliaceae): *D. fragrans* var. *Victoria* is a yellow-margined green form; that is, the form has yellow ectohistogen and green endohistogen. The yellow parts have a few green stripes, due to recurrent mutation. *D. Deremensis* var. *Bausei* bears leaves with green ectohistogen and white endohistogen, the latter being variegated with stripes, especially in its innermost parts.

Epipactis Thunbergii (Orchidaceae): Many green ticks occur on the yellowish leaves, due to reversible mutation.

Hakonechloa macra (Gramineae): Two types of variegation, yellow-variegated and creamish-variegated, were placed under observation. The former, though rarely, put out green sports. In both variegated forms, mutation is recurrent.

Hydrocleis nymphoides (Butomaceae): The stock (Fig. 2), which was introduced from an American nursery, shows at times variegation in creamish white. The plant, which probably has a mutable nature of low frequency, presents a few variegated leaves or sections of leaves.

Iris japonica (Iridaceae): White-over-green periclinal form has green patches on the creamish white parts due to reversion.

Liriope graminifolia (Liliaceae): Variegation occurs with green and yellowish flakes, the marginal parts being usually more yellowish and the central part more greenish.

Ophiopogon Jaburan (Liliaceae): Variegated with green and creamish stripes, due to reversible mutation.

Ophiopogon japonicus (Liliaceae): Variegated with green and creamish white stripes, due to recurrent mutation.

Oplismenus compositus (Gramineae): Variegation occurs in green and white, due to recurrent mutation from green to white.

Oryza sativa (Gramineae): Professor T. MORINAGA kindly sent to the writer seeds of a variegated strain, the variegation of which is transmitted as a simple recessive to normal green (MORINAGA 1932). The form exhibits white stripes with fine green ticks, due to reversible mutation. Other variegated forms of different non-Mendelian natures will be discussed later.

Pleioblastus argenteostriatus (Gramineae): Several forms of variegated bamboos are in cultivation. This species has green stripes on the yellowish green leaves. Mutation is recurrent.

Pleioblastus Fortunei (Gramineae): Variegation in stripes of green and cream, due to recurrent mutations.

Rohdea japonica (Liliaceae): A considerable number of horticultural strains are cultivated in Japan, including many variegated ones. In the recurrently mutating forms, green ticks occur very finely on the whitish background and *vice versa*. The degree of variegation varies to some extent in the different

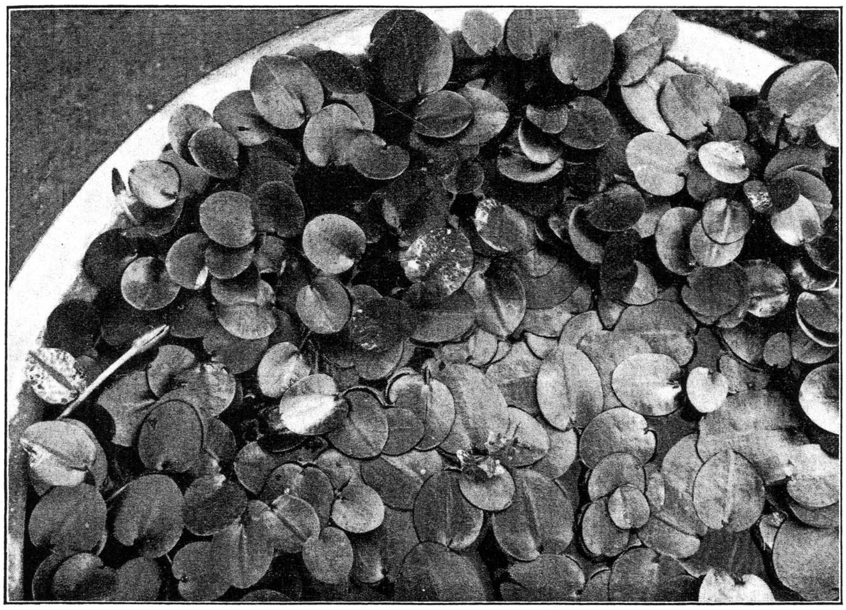


Fig. 2. *Hydrocleis nymphoides* bearing a few variegated leaves.

strains. Many periclinals also exist; in some strains one of the tissue components (the species is a dihistogenic plant) is of mutable nature, being finely mottled with green and whitish ticks running longitudinally, for instance, creamish-margined leaves with variegated centres and *mediovariegata* leaves. The former type, from the anatomical point of view, has creamish ectohistogen and mutable endohistogen, whereas the latter has green ectohistogen and mutable endohistogen.

Sansevieria cylindrica and *S. zeylanica* (Liliaceae): Cream or yellowish stripes occur in green leaves or *vice versa*. More frequent are the green stripes in the central parts of the leaves, probably due to more frequent mutation in those parts. Mutation is reversible.

Tradescantia fluminensis (Commelinaceae): Cream-variegated leaves are probably due to the mutable nature of the green tissues. Since the cream parts do not revert to green, pure cream branches occur. Green branches, though not often, also appear as bud variation from the variegated stock.

Zea Mays (Gramineae): A number of different variegated forms have been reported in American literature. A type called *japonica* has white and yellow stripes that appear on the leaves and sheaths, due to recurrent mutations.

Choripetalae

Acalypha Wilkesiana (Euphorbiaceae): Many whitish patches cause the leaves to be variegated. Mutation is reversible. Anthocyanin pigment frequently obscures the distribution of variegation.

Aucuba japonica (Cornaceae): Variegation with yellowish ticks varies remarkably in extent. The yellowish ticks have wholly albinotic tissues, not being covered by the usual green tissues, which condition is supposed to be due to surface affection by toxic substances that are secreted by the albinotic cells. The albinotic cells, however, slightly affect also the lateral and inner tissues. The strongly variegated forms at times produced yellow-over-green periclinal leaves or branches. The periclinal form has yellowish "skins" and green "cores" as usual, but its reversal, which forms *pseudo-medioalbinata*, has yellowish centres, without green "skins" at the central parts of the leaves.

Ampelopsis heterophylla (Vitaceae): Finely variegated with green and cream. Mutation takes place in reversible directions. Green sports occur at times.

Chaenomeles lagenaria (Rosaceae): Leaves finely variegated with whitish ticks. Mutation occurs in reversible ways.

Dianthus alpinus (Caryophyllaceae): Finely variegated with green and yellowish colours, due to reversible mutation. Green bud variation arises at times.

Dianthus chimensis var. *semperflorens* (Caryophyllaceae): Fine green ticks appear on the yellowish leaves. Mutation is reversible.

Dianthus superbus (Caryophyllaceae): Fine yellowish ticks occur on the otherwise green leaves, while reverse variegation also takes place, due to mutual mutation.

Distylium racemosum (Hamamelidaceae): Cream-over-green chimerical leaves exhibit at times green ticks on the cream margins, due to reversion. The cream branches, which are produced by the green inner component being left out, present more clearly the occurrence of the mutated green patches.

Firmiana platanifolia (Sterculiaceae): A variegated stock that frequently throws out green and white branches is cultivated in the Botanical Garden of the Institute. The sports, however, are due to sorting out of the mixed plastids in cell generation of plant development, but not to the mutable nature of the green tissues. Though not frequently, the sports, which bear white leaves, have green patches that may be attributed to the recurrent mutation of white plastids.

Hibiscus rosa-sinensis (Malvaceae): Mutation here being reversible, white variegation occurs finely on the green leaves and *vice versa*. The occurrence of anthocyanin frequently obscures the distribution of variegation.

Humulus japonicus (Moracea): A wild male plant, having yellow leaves mottled finely with green ticks, was found in a barren field at Meguro, Tokyo. The recurrent mutation is reversible between yellow and green, resulting in fine mottling. Green branches occur very frequently, due to reversion.

Hydrangea opuloides (Saxifragaceae): A white-over-green periclinal form is commonly found in our gardens, the white tissues usually having no green patches. Sometimes however periclinals are found with white "skins" having a few green patches. The occurrence of these patches is due to recurrent mutation from white to green. The quantity of the green patches is more marked in CHITTENDEN's form (1925). This investigator examined the offspring of the periclinal with green-lobed white "skins" and found 216 white and 383 green seedlings. The appearance of the green seedlings is probably due to recurrent mutation of white plastid to green. The form described above is analogous to CHITTENDEN's, though the frequency of the green patches differs considerably.

Kadsura japonica (Magnoliaceae): Very fine variegation occurs in green and cream mottling, the mutation being in reversible ways.

Lespedeza nipponica (Leguminosae): Creamish variegation appears on the green leaves, exhibiting fine mottling. Sometimes branches bearing creamish leaves with green variegation appear. The existence of these two forms of variegation is due to reversible mutation. The characteristic is transmitted from seed.

Opuntia elongata (Cactaceae): Some cultivated cactus have fleshy stems with mutable variegation. The mutation seems to occur reversibly between green and yellowish or creamish. Green sports occur at times.

Pelargonium zonale (Geraniaceae): Many variegated strains are found in cultivation. Besides the periclinal and reversal forms, are two types of variegation, one being due to sorting out of the once-mutated albinotic plastids in cell generation in foliage ontogeny and the other to recurring plastid mutation from green to albinotic. The latter type can maintain its characteristic through both sexual and asexual propagations, excepting however the sorting out of the albinotic and the reverted self-green branches or seedlings. Since the white sports that appeared on the variegated form have frequently green ticks, due to recurring mutation from creamish to green, the plastid mutation in this case occurs in two directions, from green to creamish and *vice versa*. When such inconstant albinotic plastids are distributed in the "skins" of periclinal leaves, the whitish "skins" have green ticks, this type being frequently observable.

Phyllanthus nivosus (Euphorbiaceae): Finely mottled in green and yellowish white. The upper leaves that appear in summer have more whitish (green-ticked white) than those that do so in spring. Mutation is reversible.

Polygonum Blumei (Polygonaceae): Variegated finely with green and creamish mottling. The degree of variegation varies to some extent in a single plant. Mutation is reversible. Breeding experiments are now in progress.

Polygonum orientale (Polygonaceae): The variegated form has fine creamish white patches. Sometimes creamish white branches appear, but never green sports. The creamish areas have no green ticks. The genetic nature of the variegated form has been elucidated by IMAI (1934a). The variegation is due to recurrent plastid mutation from green to white, the mutable nature being controlled by a recessive gene.

Polygonum virginianum var. *filiforme* (Polygonaceae): The green leaves have fine creamish white variegation, which appears at first to be cream in colour. The creamish areas have green ticks at times. According to personal information from Mr. Y. TERASAWA, the form bred true to type and when crossed transmitted as a simple recessive to green.

Punica Granatum (Punicaceae): Some strains have variegated leaves with fine whitish patches, the mutation being reversible. The variegated leaves are somewhat deformed and crumpled through poor development of the whitish tissues.

Rosa Luciae (Rosaceae): Finely variegated in green and cream, mutation being reversible.

Sedum Makinoi (Crassulaceae): White variegation occurs finely, frequently producing white or white-over-green periclinal branches.

Trifolium pratense (Leguminosae): The whitish variegation, which occurs very finely, seems to be due to recurrent mutation. In winter the variegation becomes less conspicuous, due probably to low mutability.

Veronica persica (Scrophulariaceae): A wild plant, found in Ômori, Tokyo, showed mosaics with branches bearing creamish leaves, the other branches being green. The creamish leaves and sepals have frequently green patches, the stems, peduncles, and young fruits being greenish. Seeds collected from the green branches germinated to green seedlings, while those from the creamish branches produced 38 cream and 2 green seedlings, the former dying before sending out any leaves. The appearance of the green seedlings are believed to be due to recurrent mutation from creamish to green, the somatic occurence of which gives green patches on the creamish leaves. The recurrent mutation, however, is not reversible, the occurrence of creamish branches on the original plant being due to sporadic mutation.

Vicia sativa var. *normalis* (Leguminosae): A wild green plant bore one abnormal branch, the leaves of which were creamish with fine green ticks, indicating reversible mutation. Found at a road-side in Ômori, Tokyo.

Gamopetalae

Ardisia crispa (Myrsinaceae): The observed specimen is variegated with white, especially on the margins of leaves.

Ardisia japonica (Myrsinaceae): The observed specimen is variegated with a cream colour, especially in the periphery of the leaves.

Ardisia punctata (Myrsinaceae): The variegated form that was placed under the writer's observation had cream patches. The mutation being reversible, the cream leaves bear green patches.

Capsicum annuum (Solanaceae): Whitish or white patches cause the leaves, young fruits, and other green parts to be variegated, the degree of variegation varying considerably. The variegated form is simple recessive to green, but it does not breed true to type when selfed. The offspring of the variegated fruits gave 7 green, 294 variegated, and 2 albinotic; the last-named, which was creamish white, died a few weeks after germination. The variegated offspring behaves in much the same way as the variegated mother, the green ones segregating monogenically green and variegated. These breeding aspects indicate that the variegation is controlled by a recessive gene, the effect of which frequently alters the green plastids into white. The mutated plastids revert to green at times, the mass effect of which forms fine green ticks on the whitish parts of leaves. Sometimes there occurs white branchlets with green ticks or patches. White-over-green periclinal leaves and branches also occur at times, the white tissues in this case having green ticks. The seeds from the white or white-over-green branches gave hardly any seedlings, except a few green and albinotic seedlings. The appearance of the green seedlings is due to reversion of the white plastids to the green. The white embryos germinate but a few of them. As already stated, the variegated fruits gave also a few albinotic seedlings besides variegated and green ones, differing somewhat from the variegated *Polygonum*, the white seeds of which never germinate. In this variegated form, therefore, recurrent mutation occurs in both gene and plastid. The recessive gene, which alters the green plastids to white, mutates at times to the normal allele; the variegated form thus resulting in a few green mutants to its offspring. The green plastids frequently change to white under the operation of the recessive gene, so that plastid mutation in this case is exomutable. The mutated white plastids, in turn, revert at times to green, the changes now being automutable. The reverted green plastids, then, coming under the control of the recessive gene in the variegated stock, may alter frequently into white.

Chrysanthemum lavandulaefolium (Compositae): Variegation occurs finely in green and creamish white, due to reversible mutation. Sometimes green sports occur.

Chrysanthemum Leucanthemum (Compositae): Cream ticks occur on the green leaves in the variegated form, while the cream sports, which are yellowish at their young stage, bear very fine green ticks, due to mutual mutations. Frequently green branches appear as bud variation.

Gentiana scabra var. *Buergeri* (Gentianaceae): Fine variegation occurs with green and yellowish colours, resulting in two types of yellowish-ticked green and green-ticked yellowish leaves. Mutation is reversible. The type is reproduced from seed.

Heliotropium peruvianum (Boraginaceae): Variegation in green and yellow (later becomes greenish yellow), being finely mottled. Mutation being reversible, yellow-ticked green and green-ticked forms are observable.

Hoya carnosa (Asclepiadaceae): Two types of white-over-green periclinals were observed, the one having a self-creamish "skin" and the other the same but with green patches. The specimen shown in Fig. 3 is of the latter type, the upper leaves becoming creamish with green patches, owing to exclusion of the green "core".

Ligustrum Ibota (Oleaceae): Whitish variegation occurs very finely, the mutation being in reversible ways.

Mirabilis Jalapa (Nyctaginaceae): The yellowish green (*chlorina*) form frequently bears green patches or branches, due to recurrent mutation of an inconstant gene which is recessive to green. The sported green tissues never revert to *chlorina*. CORRENS (1910) has made clear the mutable behaviour of this form.

Pharbitis purpurea (Convolvulaceae): Variegation in yellowish green, the patches being small. Mutation therefore seems to arise at later stages of leaf ontogeny.

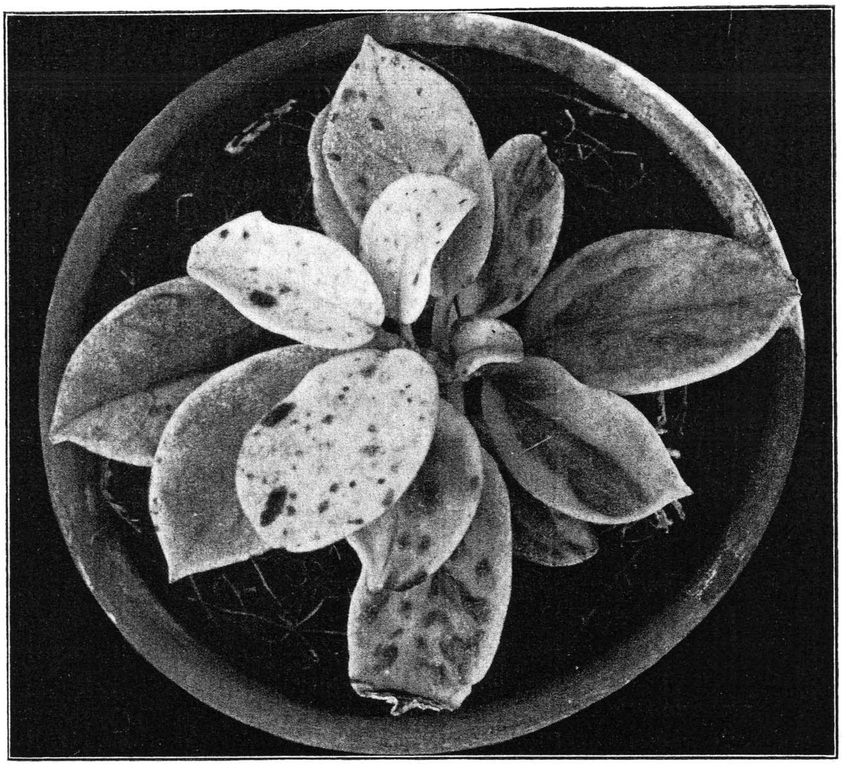


Fig. 3. *Hoya carnosa* with green-patched creamish "skins". Upper part has the green "cores" left out.

Plantago major var. *asiatica* (Plantaginaceae): Two variegated forms are observed. The common form has creamish white patches with green ticks. The variegation is believed to be due to recurrent mutation of plastid from green to white and *vice versa*. As the mutation from white to green is not frequent, the distinction of the two types, white-variegated green and green-variegated white, is quite clear. Sometimes periclinal leaves or individuals with green-variegated white "skins" and white-variegated green "skins" occur. The degree of variegation differs greatly with environment, indicating that the frequency in plastid mutation is variable. The variegated form apparently bred true to type. Five plants were completely isolated and selfed, the seeds thus produced resulting in 1555 variegated seedlings. The ears usually variegated. The size of the seeds collected from the ears vary, containing many that are small and imperfect. The seeds obtained by selfing the white parts of the ears gave no seedlings, indicating that the white seeds do not germinate in the manner as observed in the case of *Polygonum orientale*. Therefore, except in the mutability of the white plastids, the variegated form resembles *Polygonum*. In the variegated *Plantago*, plastid mutation is reversible, whereas in *Polygonum*, recurrent mutation is only in one direction. IKENO (1917) showed that the variegated form is dimeric recessive to green. The other variegated form, which is less commonly found in our gardens, has cream patches that sometimes extend to a large part of the leaf, and, in some cases, though not common, to the entire leaf. Such cream parts have very fine green ticks. The variegated form gives variegated seedlings, containing cream ones with fine green ticks. Their exact nature is now being investigated.

Platycodon grandiflorum (Campanulaceae): Creamish patches cause the leaves to be variegated. Mutation is reversible. This form is reproduced from seed.

Rhododendron indicum (Ericaceae): Two types of variegation were observed, one of them with fine greenish cream variegation or fine green ticks on a greenish cream background, due to reversible mutation. Green sports occur at times, but no purely creamish ones arise. The other form is finely mottled in three colours, green, creamish, and whitish. The creamish variegation occurs on otherwise green leaves and *vice versa*. Since the whitish parts neither revert to green nor change to creamish, the whitish sports grow to be pure whitish, but owing to its delicate nature, they cease to grow much further.

Rhododendron lateritium (Ericaceae): As far as the writer is aware, two types of mutable cases occur in the cultivated strains; the one being variegated in creamish and green, while the other has cream patches, both due to reversible mutation. In the latter case, cream branches, which usually have a few small green ticks, are of inferior growth on account of poor photosynthesis, hence unable to support themselves when they are isolated as cuttings. In both cases, green sports occur at times.

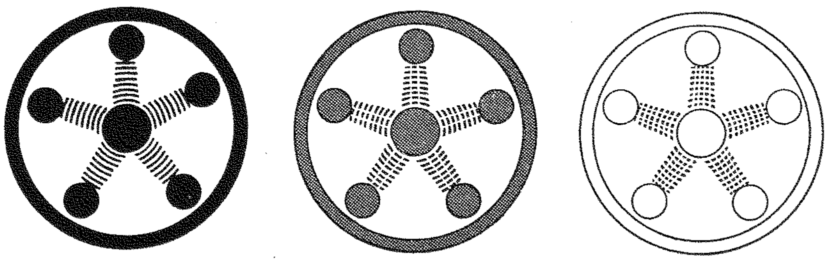
Trachelospermum jasminoides (Apocynaceae): Leaves are finely mottled with green and white, due to reversible mutation. The leaves that develop later, being usually either whitish or heavily variegated, generally attract much attention.

Discussion and conclusion

Although the causes of chlorophyll variegation are diverse, such as those due to pattern genes, sorting out of mixed plastids, mutable genes and plastids, plasmon action, chlorosis, and others, this paper deals especially with those due to mutable genes and plastids.

The manifestation of plastids is controlled by certain genes, as the result of which chlorophyll pigments are developed (Fig. 4 *A*). Some genes give partially chlorophyll-deficient forms (Fig. 4 *B*). The albinotic forms are due to some other genes that fail to produce the pigments (Fig. 4 *C*). Sometimes variegated forms are manifested by certain pattern genes. These forms are transmitted, simply, according to the Mendelian rule when crossed with normal.

The variegation due to recurrent gene mutation generally occurs from recessive albinotic or partially chlorophyll-deficient to dominant normal. In the yellow-inconstant, yellowy, and xanthic of *Pharbitis* (Imai 1934b), for example, the green patches or sports appear at times through recurrent mutation of the recessive genes to their dominant alleles (Fig. 5 *A*). Correns' *Mirabilis* (1910), and Kondô and Kasahara's *Oryza* (1933) are analogous cases. In



A *B* *C*

Fig. 4. Mendelian types of cells in which the characters of plastids are manifested under the control of the nuclear genotypes. *A*, normal green cell; *B*, partially chlorophyll-deficient cell; *C*, albinotic cell. The round frames indicate cell-walls and represent the cell characters; the larger circles in the middle are nuclei, and the smaller ones near the circumference the plastids. The solid ripple-like lines indicate action of the nucleus in producing ample chlorophyll pigments in plastids, the broken lines partial chlorophyll-deficient plastids, and the dotted lines failure to produce chlorophyll in the plastids. The dark part indicates green, the lighter part the partially chlorophyll-deficient, and the white the albinotic.

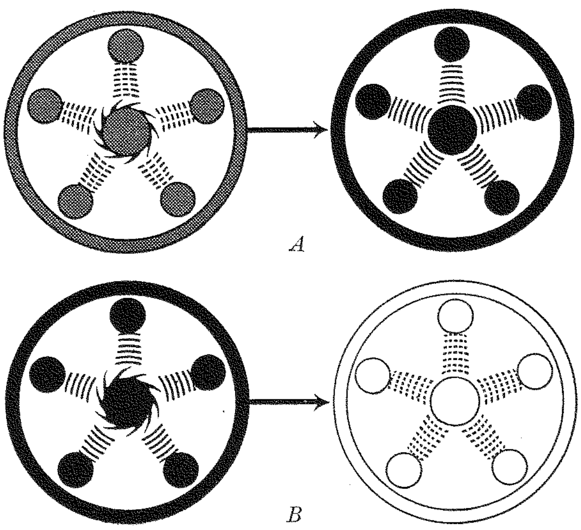
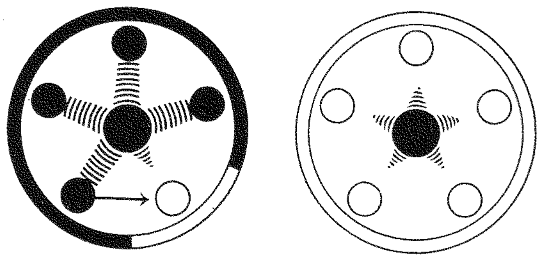


Fig. 5. The mechanism of mutable genes. *A*, automutable chlorina type, due to a partially chlorophyll-deficient gene that changes to the normal green genotype. In the child's toy pinwheel-like figure in the center, the vanes indicate the automutability of the gene. *B*, automutable gene altering to albinotic.

ANDERSSON's variegated *Adiantum* (1923), the process is reversed, that is, recurrent gene mutation arises from dominant green to its recessive white (Fig. 5 *B*). In both cases, the variegated plants carry automutable genes, which frequently alter to constant alleles. No exomutable case of chlorophyll genes has yet been observed.

The green plastid, although rarely, mutates sporadically by itself or automatically (Fig. 6 *A*). When such a mutated plastid is propagated in the course of cell generation a non-Mendelian variegated form may result. Although the white cells thus produced may apparently be similar to the Mendelian white cells, their white plastids manifest characteristics through properties of their own, quite apart from the influence of the gene (Fig. 6 *B*).



A *B*

Fig. 6. Ordinary non-Mendelian type of variegation with respect to plastid inheritance. *A*, shows the origin of variegation; one of the green plastids sporadically mutates to albinotic. The ripple-like marks that extend only a short distance out from the centre of the figure indicate the manner in which the plastid character manifests itself independent of the control of normal nuclear genotype. *B*, white cell containing the mutated, constant albinotic plastids, the inheritance of which is non-Mendelian. Compare with Fig. 4 *C*.

The white-variegated forms of *Hordeum* (SÔ 1921; IMAI 1928, 1935a) and *Polygonum* (IMAI 1934a) are due to recurrent exomutation of plastids. The mechanism of exomutation of plastids is as follows: A recessive gene contained in the variegated stock frequently alters the green plastids to white, so that plastid mutation occurs not automatically, but as the result of the gene (Fig. 7 *A*). The mutated white plastids being no longer controlled by the gene complex, the inheritance of the white plastids is non-Mendelian. The white plastids have high constancy. So far as the writer's observation went, no reversional mutation of these white plastids have occurred in the variegated forms of *Hordeum* and *Polygonum* here discussed.

The next case is seen in *Pelargonium* and other plants. Certain variegated forms of *Pelargonium* are inherited as apparently simple Mendelian recessives. Since this form carries a recessive gene, which frequently changes the green plastids to albinotic, the plastid mutation is also exomutable. This operation being similar to the cases just described, the present case is more complicated. The mutated albinotic plastids, which are automutable instead of being constant, mutate to normal green (Fig. 7 *B*). In their manifestations, the albinotic are free of control of the nuclear complex, while the green plastids, including the reverted ones, are under its control. Therefore when the change occurs from green to albinotic, the plastids exomutate, whereas when the reverse change occurs, they automutate. The variegated forms in *Commelina, Oryza, Rohdea,* *Polygonum* (*virginianum* var. *filiforme*), *Chrysanthemum*, *Pharbitis*, *Plantago*, etc. seem to be analogous cases. In *Commelina*, this type of variegation is more complicated, exhibiting a graded series in the extent of variegation. The variegated forms in the plants just mentioned, including possibly *Rohdea* and *Chrysanthemum*, are monogenic or digenic recessives, for which reason they have been regarded merely as ordinary Mendelian. Strictly speaking, however, Mendelian character is not variegation itself, but the ability to change the property of the plastids. Seeing that mutation is reversible, we may expect two types of seedlings, the one green variegated with white (or yellow, etc.) patches and the other white variegated with green ticks. Sometimes the latter seedlings do not germinate from seeds, when either no albinotic seedlings are obtained, or almost none. As the result of non-germination of the albinotic seedlings, the variegated seedlings apparently bred true to type, whence the variegation may be erroneously regarded as being due to pattern genes. In the variegated form of *Polygonum orientale*, in which some pure albinos may be expected, no such seedlings are produced. The mode of distribution of the variegation on the leaves, stems, and other parts accord with the ontogenical growth of these organs, showing that they are due to differentiation of the hereditary substances, but not to mere patterns.

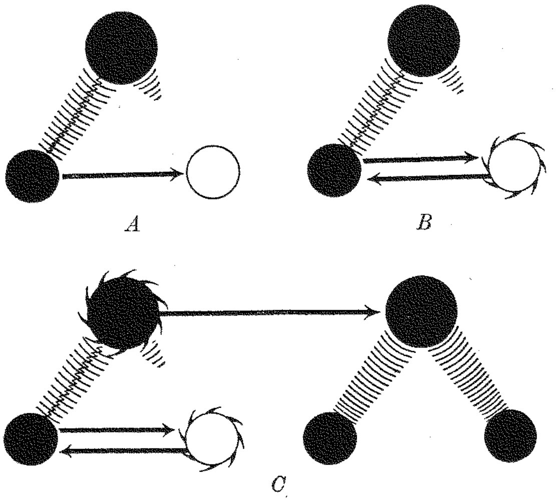


Fig. 7. The mechanism of variegation due to stimulant genes, which frequently alter green plastids into the albinotic (exomutation of plastids). *A*, the most simple case in which exomutation of plastid occurs in one way from green to constant albinotic. The zigzag line joining nucleus and plastid indicates the effects of the former in changing the property of the latter. *B*, the mutated albinotic plastid is automutable, frequently reverting to normal green, which then replaces itself under the control of the stimulant gene. *C*, further complication occurs through automutation of the stimulant gene itself to its dominant normal green allele. The vanes indicate the automutability of the gene and plastid.

The mutating behaviour in the variegated forms of *Pelargonium* and *Capsicum* is complicated still further, owing to recurrence of the green mutant individuals. The appearance of the green plants in the variegated pedigrees is due to gene mutation from recessive allele (resulting in variegation) to its dominant normal condition (Fig. 7 *C*). The green mutants are heterozygous for variegated, segregating in a monogenic ratio. The variegation results from stimulation of the recessive gene, the mutated white plastids altering automatically to normal green. The variegated form of *Capsicum*, therefore, carries an automutable gene which also alters green plastids into automutable white plastids. The seeds from the variegated plants gave only a small number of albinos in the variegated and green seedlings, though there were only a few of the last-named. Although the albinotic seedlings die before extending their leaves, had the leaves grown, they are expected to have green ticks due to recurrent plastid mutation.

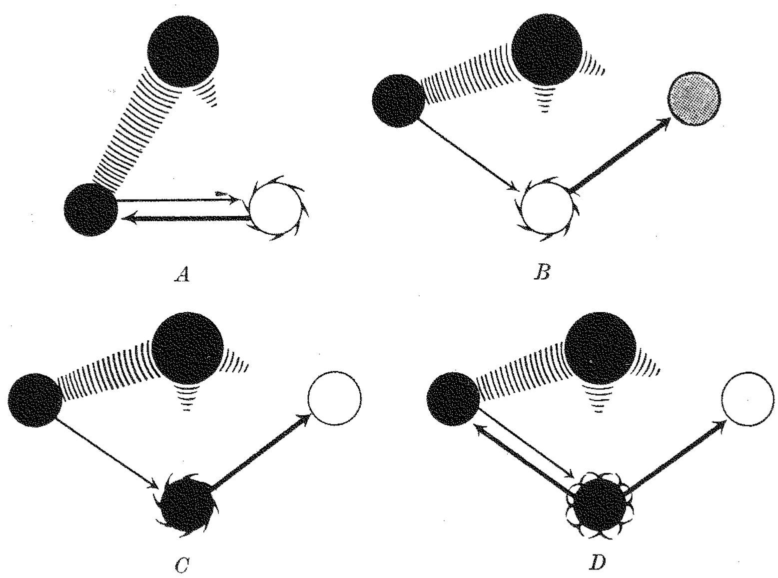


Fig. 8. Variegation that resulted from the automutation of the plastids. The thin arrow shows sporadic mutation and the thick, recurrent mutation. *A*, automutable white plastid that arose from green normal. *B*, automutable white plastid, which appeared by sporadic mutation from normal green, changing to constant yellow. *C*, the same, but differing in the colours of the automutable and its derivative plastids. *D*, the automutable green plastid changes its direction into two, constant green and albinotic. The pin-wheel figure with double vanes represents automutability in two directions.

Other mutable variegations are known in which plastid mutation occurs independently of the gene complex, that is, through the property of the plastids themselves. The periclinal *Hydrangea*, with green-lobed white "skins", gives white and green seedlings (CHITTENDEN 1925). The origin of the green seedlings is attributed to the presence of the green lobe that seems to appear by plastid mutation of white to green. If the unstable white plastid had mutated sporadically from green, the nature of the plastid that is contained in the white "skins" of the periclinal specimen should be as diagrammatically shown in Fig. 8 *A*, in which the automutable white plastid frequently changes to green, giving later green patches in the white "skin". In the case observed in *Pharbitis*, the white plastids, which made their appearance by sporadic mutation from normal green plastids, are automutable, frequently changing to a constant yellow condition (Fig. 8 *B*). The mutated white and yellow plastids therefore are inherited as non-Mendelian. CHITTENDEN (1925) gave breeding data for the periclinals with yellow-lobed white "skins" in *Hydrangea* and *Pelargonium*, the cases being analogous to that of *Pharbitis*.

MORINAGA's case (1932) of *Oryza* is essentially the same as that of *Pharbitis*, though the colour changes are quite different. In *Oryza*, unstable green plastid was derived from the ordinary stable green by sporadic mutation, the mutated plastid frequently changing to stable white (Fig. 8 *C*). TAKEZAKI's (1922) and KONDÔ and his collaborators' (1927) cases of *Oryza*, however, are a step more complicated through difference in the nature of the mutated automutable green plastids, which change themselves in two directions, green and white (Fig. 8 *D*). Plants containing such mutated green plastids recover their normal hereditary complex owing to stability of the plastids. One of KONDÔ's striated perenial

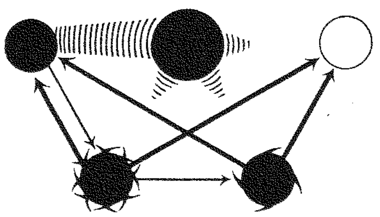


Fig. 9. The mechanism in the remutated variegation of rice. The pin-wheel figure with smaller number of vanes indicates low mutability.

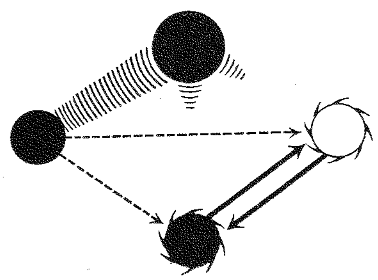


Fig. 10. Two automutable plastids, giving constant variegation. The dotted arrows indicate the possible ways of sporadic mutation in which the variegation originated.

stock later changed to such an extent as to bear leaves with slight degrees of variegation (KASAHARA 1934). The changed stock gave rise to 16.6—25.5 per cent white, 66.5—81.7 per cent variegated, and 0.2—8.2 per cent green seedlings in its progeny, while the controls produced 48.4—94.5 per cent, 1.9—42.4 per cent, and 1.0—48.0 per cent, respectively. The change is probably due to the unstable plastid having mutated to that with less automutability (Fig. 9).

According to WINGE (1917, 1919), the *albomaculata* form of *Humulus japonica* is transmitted maternally, and no segregation or sorting out of the green or white seedlings occurs in its progeny, it breeding true to form. WINGE regarded his *Humulus* and IKENO's *Capsicum* as rare cases of plasmic inheritance, which idea was popular for many years in genetic literature until IKENO (1930), after critical study of his material, found that this variegated form of *Capsicum* is due to infectious chlorosis, so that at present WINGE's *Humulus* is known only as an instance in which the variegation is believed to be due to cytoplasmic manifestation. From the descriptions as well as the drawings in WINGE's papers, the writer, however, is of the opinion that the variegated form of *Humulus*, instead of being a case of cytoplasmic inheritance, is due to the presence of two automutable plastids, green and white, the condition being shown diagrammatically in Fig. 10. The two automutable green and white plastids, one of which probably appeared by sporadic mutation from a constant green plastid, would retain the variegation in the course of sporophytic ontogeny as well as in sexual propagation; the character of plastids being manifested through properties of their own, is transmitted maternally without any influence of the male gametes. The foregoing solitary instance of supposed plasmic inheritance for chlorophyll variegation should perhaps be placed under such a different genetic group as just discussed. The writer, however, does not deny the possibility of cytoplasmic inheritance in certain cases in which abnormal plasms may play the rôle of inherited chlorophyll deficiency.

In the variegated leaves that resulted from the sorting out of the mixed plastids, the origin of the abnormal plastids is owing to sporadic mutation, through which a green plastid had altered into albinotic. In such cases the occurrence of green and albinotic branches is frequent, continuation of the variegated forms being rather difficult in both vegetative and seminal propagations. An example is the case observed in *Pelargonium*. The forms send out at times periclinal and reversal branches as well as green and albinotic ones. In contrast to this, another variegated type, which is due to exomutable plastids, easily continues its form through vegetative propagation, being also easily reproduced from seed. To the trained observer, mere inspection generally will suffice to distinguish the two types of variegation. In *Commelina* are found two types of variegation, the one due to mixture of the constant green and albinotic plastids and the other a very complicated form. The species being annual, their propagation is by seed. The former is of the ordinary non-Mendelian type. For instance, the variegated *Tradescantia*, which is probably due to recurrent mutation, resembles this form of variegation, but close inspection shows a difference between them, especially in their mode of vegetative continuation of the variegation in the course of sporophytic growth.

Mutable variegation may be one way or reversible. The cases observed in *Iris*, *Distylium*, *Firmiana*, *Hydrangea*, *Pelargonium*, *Veronica*, *Hoya*, *Mirabilis*, *Pharbitis*, and probably also *Cyperus*, are regarded as mutable in one direction from albinotic or partially chlorophyll-deficient to normal green, while those in *Adiantum*, *Chamaecyparis*, *Juniperus*, *Thuja*, *Aspidistra*, *Calathea*, *Hordeum*, *Oplismenus*, *Tradescantia*, *Zea*, *Aucuba*, *Polygonum* (*orientale*), and *Pharbitis* (*purpurea*) are also one way of recurrent mutation, but from green to albinotic. In the variegated leaves of *Athyrium*, *Agapanthus*, *Agave*, *Alpinia*, *Angraecum*, *Commelina*, *Epipactis*, *Ophiopogon*, *Oryza*, *Rohdea*, *Sansevieria*, *Acalypha*, *Ampelopsis*, *Chaenomeles*, *Dianthus*, *Hibiscus*, *Humulus*, *Kadsura*, *Lespedeza*, *Opuntia*, *Pelargonium*, *Phyllanthus*, *Polygonum* (*Blumei* and *virginianum* var. *filiforme*), *Punica*, *Rosa*, *Vicia*, *Ardisia*, *Capsicum*, *Chrysanthemum*, *Gentiana*, *Heliotropium*, *Ligustrum*, *Pharbitis*, *Plantago*, *Platycodon*, *Rhododendron*, and *Trachelospermum*, mutation occurs reversibly from green to albinotic (or partially chlorophyll-deficient) and *vice versa*.

In azaleas, three types of variegation were observed. Although the colours of the albinotic plastids in two of them differ from each other, the mutation is reversible between green and albinotic. The remaining one is more complicated.

In certain other variegated forms it is not clear whether the mutation occurs one way or reversibly. In the cases listed in an earlier part of this paper, except those in which the hereditary behaviour has been cleared up, it has not yet been determined whether the recurrent mutation is due to the nature of the genes or whether to that of the plastids. Microscopical examination of the plastids might show it in some cases, seeing that in recurrent plastid mutation, cells containing mixed plastids are found, while in recurrent gene mutation the cells invariably include the same plastids.

The degree or extent of variegation in a given plant is roughly definite in mutable variegation, unless further complications are involved, although in some cases we find great variation. The variegation exhibited in *Capsicum*, however, may roughly be divided into two forms, the one having white-variegated green leaves and the other green-variegated white leaves. In this plant, variegation occurs by the exomutation of plastids from green to white, the mutated white plastid, in turn, frequently reverting to green. The reverted green plastids, which result from the action of the stimulating gene that is contained in the variegated stock, frequently changes again to whitish, so that the two types can reversibly be altered, the one into the other. Since in *Capsicum*, the mode of the reversible mutations differs widely, the two types of variegation, the green-dominating and the white-dominating, can be definitely separated. The two types of variegation frequently occur as bud variation on one and the same plant. Bud variation with heterogeneous tissues is frequently observable, as in the white-variegated green "cores" covered with green-ticked white "skins". In *Commelina, Dianthus, Lespedeza, Pelargonium, Gentiana, Plantago, Heliotropium*, etc., we observe two types of leaves as in *Capsicum*. If however the frequency of reversible mutations is nearly the same, the two types may not be separable owing to their almost similar appearances. As the variegation pattern differs considerably with the time and frequency of mutation, very diverse types of variegation are seen in the different species.

Variegation, which as a rule is clearly shown, is sometimes not very apparent on account of the rare occurrence of mutated tissues. As examples, may be mentioned some albinotic leaves of the variegated *Pelargonium*, on which the green ticks are rather rare. The observed stock of *Hydrocleis* bore a few variegated leaves or parts of leaves in otherwise green foliage. In these cases, the mutation frequency is very low.

Green sports of a mutable nature sometimes or rarely occur on such variegated plants as *Chamaecyparis, Juniperus, Cyperus, Hakonechloa, Oryza, Tradescantia, Ampelopsis, Dianthus, Humulus, Chrysanthemum, Mirabilis, Pharbitis* and *Rhododendron*. In *Mirabilis* and *Pharbitis*, bud variation is due to gene mutation, while in *Oryza*, it arises through automutation of plastids. In other cases, the point is not very clear.

The periclinal plant body is induced by some such causes as mutation, sorting out of mixed plastids, grafting, etc. In nature, the two first-mentioned factors are largely responsible for the appearance of periclinal chimeras. As already stated, in *Agave*, *Dracaena*, *Iris*, *Rohdea*, *Distylium*, *Hydrangea*. *Pelargonium*, and *Hoya* are found some different periclinal forms with variegated tissues due to mutable causes. The forms are green-over-variegated, white-over-variegated, or variegated-over-green. The arrangement of the heterogeneous tissues differs with the number of histogens (IMAI 1935c). In *Capsicum* and also in *Plantago*, the two variegated tissues, white-patched green and green-ticked white, sometimes form periclinals, the cause of which is somatic mutation. In the yellow-inconstant and yellowy forms of *Pharbitis*, the green-over-yellow and its reversal chimeras arise at times, also through somatic mutation. From these facts, the origin of periclinal plants cited above, some of them at least, are attributed to mutation. The most common forms of chlorophyll periclinals is white-over-green and its reversal, with no variegated tissues. Since the variegated plants due to sorting out of the mixed plastids bear at times such periclinal branches, the sorting out of the mixed plastids also may contribute in part to the production of chimeras.

The extent of variegation changes somewhat through environment, particularly in *Aspidistra*, *Trifolium*, *Plantago*, etc. The variegated branches of *Phyllanthus* and *Trachelospermum* bear whitish leaves on their upper parts and greenish leaves on their lower nodes. This probably means that summer growth stimulates mutability, resulting in heavily variegated leaves. The changes in the degree of variegation is attributed to variation in mutability. Ontogeny also greatly affects it in certain cases. Variegation usually occurs on various parts of the leaves, but in *Athyrium*, white patches appear on the central parts of the pinnae. In *Iris*, *Hydrangea*, *Veronica*, and *Ardisia*, mutation arises more frequently, if not exclusively, in the marginal parts of leaves. In certain monocotyledons, such as *Agapanthus*, *Dracaena*, *Liriope*, *Ophiopogon*, and *Sansevieria*, the inner parts of leaves are more greenish, probably due to different mutability from that of the outer parts. The upper parts of the creamish umbels in *Cyperus* frequently bear green leaves, indicating a greater liklihood of changing to green. These facts collectively considered give some hints as to the rôle that environmental and ontogenical influences play on the mutability of chlorophyll variegation.

In concluding the present paper, the writer wishes to express his hearty thanks to the Foundation for the Promotion of Scientific and Industrial Research of Japan for the grant from which the expenses incurred in connection with the present investigation were partly defrayed.

Summary

1. The white-variegated barley due to recurrent exomutation of plastids produces 0.2 per cent of mosaic seedlings, the composition being 63.8 per cent striped, 19.9 per cent sectorial, 13.5 per cent periclinal, and 2.8 per cent reversla.

Their origination is attributed to the mixed plastids in the egg-cells from which they developed. The periclinal seedlings have *albomarginata* leaves, while the reversals have *medioalbinata* leaves.

2. In the white-and-yellow-variegated form of *Pharbitis Nil*, the whitish variegation is due to sporadic plastid mutation from green to whitish, while the yellow patches that occur on the whitish parts are caused, by recurrent automutation of the whitish plastids. The transmission of the whitish and yellow plastids are maternal.

3. A considerable number of chlorophyll variegations that are regarded as being due to recurrent mutable genes or plastids are listed with their diagnoses, together with breeding results from *Commelina*, *Veronica*, *Capsicum*, and *Plantago*. In some cases, mutation occurs in one direction and in others reversibly.

4. The mechanism of the mutable genes and plastids is discussed with the aid of diagrams (Figs. 4—10). Recurrent gene mutation takes place automatically, no case of exomutation being yet known. Recurrent plastid mutation, however, occurs in both ways. Exomutation of plastids is due to certain stimulant genes transmitted as recessives. Since the mutated plastids manifest their characteristics through certain properties of their own, transmission is non-Mendelian. Albinotic seedlings however frequently fail to germinate, as a consequence of which variegation is inherited as apparently simple Mendelian. The mutated albinotic plastids are either constant or automutable, reverting to green. In the automutation of plastids, which arises either in one or two directions, the changes occur independently of gene complex, whence it follows that the transmission of variegation is non-Mendelian. WINGE's variegated *Humulus* is probably not due to cytoplasmic inheritance, but to a mixture of the two automutable plastids.

5. In *Capsicum*, variegated leaves occur in two types, the one green with white variegation, and the other white with green ticks. The occurrence of these two types of variegation is due to differences in the mode of reversible mutations. Such a difference is also observed in *Commelina*, *Dianthus*, *Lespedeza*, *Pelargonium*, *Gentiana*, *Plantago*, *Heliotropium*, etc.

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