

FLOWER COLOURS AND THEIR FREQUENCY

BY

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Flower pigments are among the easiest recognisable chemical characteristics of plants, although it is unfortunately not possible to analyse them by sight. The former circumstance induced me to study the frequency of flower colours in a number of widely different countries. It was my intention to take into consideration as many species as possible also those from the tropics. Consequently I was not able to give biochemical or genetical surveys such as those of ROSE SCOTT-MONCRIEFF (15) or of T. WIT (19) and could only take into account the colour data mentioned in the standard flora's in question. The adoption of this method involved certain difficulties since the problem is not so simple as was formerly supposed when it was customary to speak of one single pigment, anthocyan, which when dissolved in cell-sap at a low p_H would be red and at a high p_H blue. Things are by no means so simple, as we shall see later on.

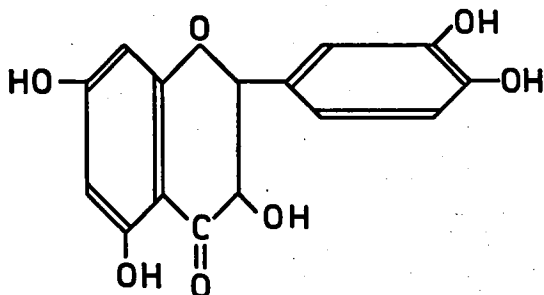
The following colours were distinguished: (1) green, (2) white, (3) yellow-orange, (4) pink-red in different tones, (5) purple, (6) violet-lilac, (7) blue.

Green parts of plants, also the young flowerbuds contain the same pigments as the leaf, viz. two green pigments, chlorophyll A & B, besides two yellow-orange ones, carotene ($C_{40}H_{56}$) and xanthophyll, 3,3-dioxy- α carotene ($C_{40}H_{56}O_2$). These green and yellow pigments are not soluble in water but carried by plastids.

The white parts of the flowers contain no pigments whose solution in the cell-sap is perceptible to the human eye. The total reflection caused specially by air-containing intercellulars of the corolla brings about a white colour. The restriction, perceptible to the human eye, must be added because most or perhaps even all those flowers which we call white contain a kind of anthoxanthins, compounds which when solved in water absorb in the near ultraviolet only. To bees whose eyes are insensitive to red radiation but sensitive to that in the near ultraviolet the presence or absence of such anthoxanthins must be perceptible. HALDANE (2) maintains that this kind of anthoxanthins is present in all white flowers. The fact that red poppies are visited by bees is due to the presence of these compounds.

Yellow or orange flowers contain carotenoids as was proved long ago by T. TAMMES (16). In tomato fruits an isomere of β -carotene, called lycopene is to be found, in yellow flowers e.d. *Viola* spec. different epoxides which are also insoluble in water. In flowers some-

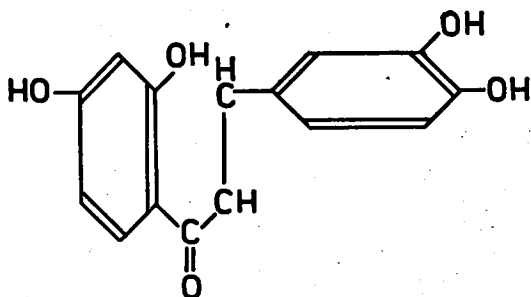
times yellow water-soluble pigments of a totally different chemical constitution however, are met with which are anthoxanthins. These compounds, flavones and flavonols



FLAVONOL (QUERCETINE)

are usually present in glycosidic form, in combination with one or two molecules of a sugar. First studied by PERKINS (11) they were later on an object of special study by P. KARRER (3) as well as by the ROBINSON's (14) and by PRICE (13).

The chemical relation of anthoxanthins and anthocyanins will be dealt with later, here however I will mention that PRICE isolated the chalcone butein from the yellow flowers of *Dahlia variabilis*.

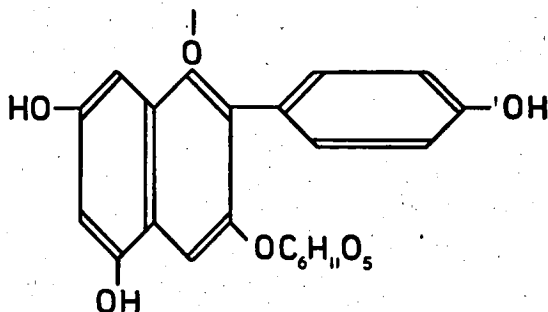


CHALCONE (BUTEIN)

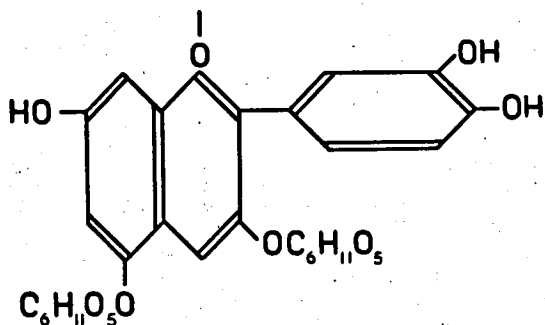
The red and blue colours of flowers are caused by anthocyanins which are also glycosides, the aglycone anthocyanidin being combined with one or two sugar molecules. If this sugar is a monose the glycoside is in the former case called a monoside, in the latter a dimonoside. The anthocyanidins are to be derived from the hydroxyflavilium compounds pelargonidin, cyanidin and delphinidin which differ in number of hydroxylgroups.

Pelargonidin has only one, cyanidin two and delphinidin three hydroxyl groups in the 2- phenyl nucleus. The hydroxylgroups can be methylated, so there is one methylated derivative of cyanidin called peonidin and three of delphinidin called petunidin, malvidin

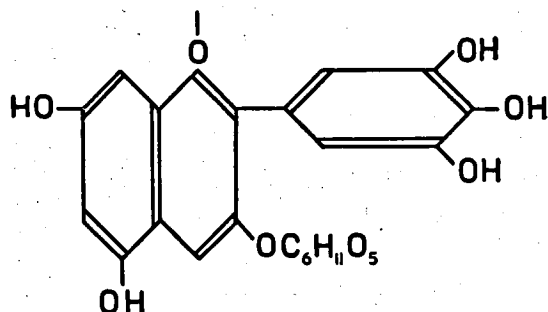
and hirsutidin. Some twenty anthocyanins are isolated from the higher plants and some of them e.g. hirsutidin, trimethyldelphinidin seem to be characteristic of special genera.



PELARGONIDIN 3 MONOSIDE



CYANIDIN 3,5 DIMONOSIDE



DELPHINIDIN 3 MONOSIDE

Combinations of these anthocyanins may be even characteristics of families of the Phanerogams. In this respect I refer to my publication (18) on the relation between taxonomy and chemistry in plants.

The number of these hydroxylgroups is one of the factors upon

which variation in colour from bright red to purple depends; an increase of this number causes an increasing tinge of blueness. On the contrary methylated anthocyanins are redder than the corresponding unmethylated ones, whilst dimonosides are bluer than monosides of the same anthocyanidins.

Variation in colour also depends upon changes in p_H of cell-sap, an increase in p_H causes increase in blueness. In the opinion of LAWRENCE and PRICE (7) the influence of the latter factor however, is not so dominating as was formerly supposed. The cell-sap of blue corn-flowers turns blue-litmus red and is more acid than that of red roses which contains the same anthocyanin. If this opinion of LAWRENCE and PRICE holds good there must be yet another factor which causes the purely blue colour to arise. The difference in colour e.g. between young flowers of *Anchusa italica* and full-grown ones of the same species is not caused by a different p_H -value. In most Boraginaceae the blue-flowering species have red flowerbuds, in the Scrophulariaceae *Polycarena discolor* the young flowers are blue, the adult ones rosy. The studies of the ROBINSONS' (14) have shown on the one hand the influence of the colloidal condition of the cell-sap, on the other hand the significance of so-called co-pigments. These substances, colourless anthoxanthins or tannins effect the colour of anthocyanin-solutions, making them pure blue by the formation of loose compounds. Even with a p_H 4,9 the colour may then be a pure blue one, e.g. the blue colour of cornflowers, caused by the diglycoside of cyanidin. In 1939 the ROBINSONS' suggest absorption of the cyanin to colloidal polysaccharids.

From a chemical point of view the anthocyanins and anthoxanthins are closely related and several authors have argued in favour of a synthetical interrelation. Formerly WHELDALÉ ONSLOW (9) supposed that anthocyanins were oxidation products of flavones and flavonols, but later on when their chemical constitution was better known this theory was discarded in favour of a reduction process. The ROBINSONS' who have given us the most important contribution in this matter suggest that both kinds of substances, anthocyanins as well as anthoxanthins may be derived from the same intermediate. The latter might be built up from two hexose-units and one aldose unit by a series of aldol-condensations. This theory can be supported by general observations of competition in development between these compounds, particularly in flowers of *Dahlia variabilis*, although the yellow substance here is not a real anthoxanthin but a closely related compound a chalcone (s. formula). This theory might also give the explanation of a fact observed by WHELDALÉ ONSLOW & BASSETT (10), who showed that crossing of an ivory-yellow variety of *Antirrhinum majus* and a white-coloured one produced a magenta-red offspring. The genetic side of the question can not be dealt with here.

In the following table only the colours of the corolla, perianth or coloured calyx are taken into account, not those of the bractae. When the stamens or their filaments are responsible for the colour, as is often the case in Myrtaceae, these colours were also taken into

account. Species with flowers without a well developed corolla and calyx, such as those of Gramineae, Cyperaceae, or Cupuliferae were not recorded. On the other hand it was necessary to record species with two or more colours in their flowers under several heads. I have adopted the same course with Compositae, having differently coloured ray- and disk florets, or with species frequently giving colour varieties. The number of recorded cases was thus always greater than that of the species concerned, mostly in the ratio of appr. 125 : 100. Tints such as violet-blue were recorded as blue, whilst blue-violet was recorded as violet. The data are percentages from each total number of cases:

The examined flora's were those of the following countries:

- (1) the Netherlands. by Heukels and Wachter
- (2) France by Bonnier and de Layens
- (3) Switzerland by Gremli
- (4) Sweden by Lindman
- (5) Victoria (Australia) by Ewart
- (6) Tropical Africa by Oliver
- (7) Cape Colony by Thiselton Dyer
- (8) Java by Backer

TABLE 1

colour	Average	Scandi- navia	Nether- lands	France	Switzer- land	Sweden	Victoria	Trop. Africa.	Cape Col.	Java
green	71½	0,8	71½	61½	61½	8	9	8	7	7
white	26½	1,4	26½	26½	26	26	27	26	25	30
yellow	31	1,8	32	31	31	33	33	27	32	30
red-pink	15	1,4	15	18	16	13	15	15	16	15
purple	7	2,8	7	4	6	4	7	12	11	5
violet	7	2,4	7	8	7	11	4	6	4	10
blue	5½	1,1	5½	6	7	6	5	6	5	3
total species ¹	22850		1000	2375	1825	1350	1750	5500	7150	1900
cases	28150		1200	3000	2200	1530	2270	6600	8900	2450
percent.	123		120	126	121	114	130	120	124	129

¹ appr. 18000 different species

A drawback was that in the flora of Tropical Africa colours of flowers often were not mentioned, whilst BACKERS' Flora of Java is not yet wholly completed. The species introduced in Java by man are not recorded.

On examining the table one is struck by the fact that there is such a large measure of agreement between the data of widely different parts of the world. The low values of the standard deviations are evidence of of this fact. Not only are the differences between the countries of Western Europe inconsiderable but the same is true as

regards the data of Tropical Africa, Cape Colony and Victoria. Java is somewhat an exception, but the incompleteness of the flora may be the cause of this. It is especially the standard deviations for white, yellow, green and blue, that are small, those for purple and violet are greater. One of the causes of this fact is that the same species are in one flora recorded as having red flowers, in another as having purple ones. If we take red, purple and violet together the agreement is closer, (Average 29, Standard Deviation 1.9).

If there are differences in colour frequency between countries and climates they cannot be so great as has often been maintained.

With respect to red and blue colours the question of differences in connection with the surroundings will be entered into later. First however, it is necessary to point out that the predominance of yellow and white colours in parts of Western Europe, e.g. in our Dutch meadow-landscape is only partly to be ascribed to the greater number of species with flowers of these colours. For the yellow colour this amounts to 31 %, for the white colour to 26½ %, together not more than 57½ %. Next to this the fact is to be observed that some of the yellow- or white-flowering species have by far the greatest number of individuals. As a matter of fact we must not forget that on the moors and bogs of Western Europe the dominating flower-colour is a whitish pink or violet.

We are coming now to a discussion of the red and blue flower-colour and it is obvious that the vegetative parts also must be discussed in this connection. Blue colours are not frequent in vegetative parts and are only to be met with in bracteae of the floral region e.g. *Ajuga*, *Bartsia*, *Bromeliaceae*. On the contrary red colours are very often present in vegetative parts, leaves, stems etc. and the connection of these pigments with those in the flowers was accentuated by LAWRENCE and PRICE (7). The authors proved that in vegetative parts the same anthocyanins are met with as are mentioned above for the flowers. There is only one remarkable difference viz. the marked preponderance of cyanidin. Of the plants examined the number of genera containing cyanidine-derivatives expressed as a percentage of the total number of genera examined is: in autumn leaves 95 %, young leaves 93 %, permanently pigmented leaves 76 %, fruits 69 % and flowers 50 %. The authors come to the conclusion — which might be supported by the chemical structure of the compounds in question — that cyanidin is the anthocyanidin originally formed, which by mutation might give pelargonidin or delphinidin, the former by reduction, the latter by oxidation. The opinion of LAWRENCE and PRICE l.c. is, that selection has been an eliminating factor, as in the tropics by far the greater part of the flowers which contain pelargonidin is to be found.

Pollination by bees dominates in temperate regions, whilst in the tropics birds and butterflies are of preponderant influence. Nor should it be forgotten that VAN DER PIJL (12) has shown that purple flowers with a definite odor have a special attraction for bats, which

are then the pollinating agents. The selective influence might be understood by consideration that pelargonidin-derivatives are more reddish, delphinidin-derivatives more blueish and that bees are sensitive to blue and ultraviolet rays whilst on the contrary birds, butterflies and bats are sensitive to red and purple. The supposed selective value of these facts however, is rarely proved and sometimes rather exaggerated. The data of the preceding table are not very convincing in this respect. The flora of Java — apart from the species introduced by man — does not show preponderance of red flowering species in general, only of the violet-lilac ones. It should also be borne in mind that without co-pigments the colours of the anthocyanins in living tissue vary from bright red to purple, not to blue.

It has been pointed out frequently that the temperature of environment directly influences the production of colour in flowers, especially of the blue colour. KLEBS (5) observed a change in flowers of *Campanula Trachelium* from white in the hothouse to blue in a cold environment. He ascribed this fact to a more rapid growth in the former case which would lead to insufficient material for anthocyan-production. This explanation does not tally with observations by KUILMAN (6) with germinating plants of *Fagopyrum esculentum*. At a temperature of 25° C. production of the anthocyanidin—cyanidin.³ according to KARSTENS (4) — takes place more quickly but the total quantity is smaller than at 5° C. In KUILMAN's opinion this process consists of two separate ones, a purely chemical and a photochemical one. By illumination a chromogen is formed from a prochromogen and this process takes place the more quickly as temperatures are higher. In other words the photochemical reaction is accompanied by a chemical one with less velocity. The second part of the anthocyanin production — change of the chromogen into anthocyanin — is an ordinary dark-reaction but there temperature has the peculiar effect which was mentioned above. At a lower temperature the total production is higher, a fact which might be explained by assuming that at high temperature this chromogen is changed into a different compound. In young leaves as well as in autumn leaves an explanation of the production of anthocyanin might be found in this manner. NOACK (8) associated this anthocyanin production with flavones and flavonols (s. above). He suggested that changes in the intensity of photosynthesis influenced the equilibrium flavonol \rightleftharpoons anthocyanidin by means of the changing oxygen tension. His views however, were not confirmed by KUILMAN's experiments.

This discussion was mainly concerned with anthocyanin production in vegetative parts. Whether the same reasoning is valid with respect to the production of these pigments in flowers is another question. Many observations e.g. by BONNIER (1) suggest that by stronger ultra-violet radiance at a higher level the formation of blue pigment in the flowers of mountain regions is intensified. A possible influence of the greater changes in day- and night temperature is almost entirely neglected in spite of the observations of KLEBS l.c. VAN DER PIJL (12a)

in these respects mentions an *Ageratum* species in Java. Besides the white coloured flowers also blue coloured ones are to be found in the low lying plains but only very seldom. As appears from an observation by E. NIJLAND both forms grew side by side at appr. 1000 m on the Pangerango but here the pure white ones are rare and have disappeared at appr. 1800 m. At a height of appr. 2400 m only deep blue flowers are to be met with.

These facts can be explained either by postulating the existence of two genetically different forms, a blue- and a white flowering one, of which the former predominates by selection especially at a higher altitude, or by accepting a direct physical-chemical influence on the colourproduction of one single form in connection with the altitude. Heredity experiments might settle the matter but the presence of white and blue coloured flowers side by side points towards the former alternative. In deed both explanations might be true.

What, generally speaking, are the flower colours of species on higher mountains? Are they different from those in the lower regions around them? In table II is compared: (1) the flora of Switzerland as a whole with the species of the Swiss Alpine mountain region above 1100 m (Alpen & Voralpen), both from the flora of Gremlí. (2) the flora of Java as a whole (Flora of BACKER, but without the species introduced by man) and the mountain flora of Java above 1500 m (Flora of KOORDERS).

The flora of BACKER, as already was said, is not complete, but the missing families are not very important in connection with the question of blue and red flower colours in which we are mainly interested here.

TABLE 2

Colour	Switzerland GREMLI		Java	
	total	above 1100 m	BACKER total	KOORDERS above 1500 m
green	6½	5	7	9
white	26	23	30	36
yellow-orange	31	31	30	24
red-pink	16	15	15	14
purple	6 } 29	4 } 29	5 } 30	4 } 26
violet-lilac	7	10	10	8
blue	7	11	3	6
species	1830	380	1900	275
cases	2200	460	2450	320
percentage	120	121	129	116

In both cases, in Switzerland as well as in Java the differences in the frequency of red and blue-flowering species are obvious. We observe a kind of shift from red to blue. In Switzerland the percentage of blue-flowering species rises from 7 % to 11 %. In Java where the percentage for the total island is extraordinarily low (3 %) it rises to the double value in the mountain region above 1500 m.

It is possible to put this fact differently. There are especially among the Sympetals genera with many species, the great majority of which possess blue coloured flowers e.g. *Campanula*, *Gentiana*, *Myosotis*,

Veronica. It is a remarkable fact that many of these genera are to be found especially in mountain regions and cause the high percentage of blue-flowering species.

It seems extremely doubtful whether direct influence of light and temperature might have caused this preponderance of blue-flowering species. Seeing that modifications are not hereditary, the development in question must have been due to mutation caused by climatic factors. Experimental evidence is almost entirely lacking however, although Russian authors as N. I. VAVILOV, claim that stronger radiation at high altitude promotes the mutability of species. Just as in other questions of evolution and descent the time factor places these developments beyond the range of experimental evidence.

The main point in the question of flower colours however, is the fact proved above that in totally different parts of the world the percentages of white-, yellow-, or red-flowering species are about 5 times as high as those of the blue-flowering ones. It is evident that the originating of all these species did not take place in the same circumstances and this fact in my opinion leads to the assumption that in the course of ages evolution of pigment in flowers has, generally speaking, been an autonomous genetic process. The process may be slightly influenced by environment, this word taken in the widest sense and including the pollinating agents. Though environment varied greatly in different parts of the world yet in this matter of flower colour the result of evolution has been almost the same. Only the mountain flora seems to be an exception.

I will wind up with a further discussion of this fact that the percentage of species with blue flowers is everywhere so low, $5\frac{1}{2}\%$ — 7% ; the only observed exceptions being the mountain flora of the Alps, 11% and that of Java 3% .

Many years ago HUGO DE VRIES (17) gave the following suggestion: the yellow flowers might have arisen by loss of green pigment in the corolla whilst loss of both green and yellow pigments might have given a white corolla or perianth. Both were cases of retrogression, of the well known and common phenomenon of loss of character through mutation. Red pigments are present in almost every group of Phanerogams and formation of blue pigment might have taken place by mutations which in the opinion of DE VRIES were nothing but a change of the acid cell-sap into an alkaline one. This mutation was supposed to be a progressive one and as such much rarer than the retrogressive loss of green and yellow pigment.

This rather simple way of representing the facts cannot be maintained. In the first place because mutations which control formation of these pigments are usually much more complicated. In *Zea Mays* at least 11 different dominant genes must be present for the production of chlorophyll and carotinoids; in *Lathyrus odoratus* there are at least 13 genes affecting flower colour. In other cases the latter process is more simple as is proved by crossing experiments. These instances will suffice to show the intricacy of the question. But there is more to be said in this connection. An important group of yellow flowers

contain anthoxanthins, the yellow, water soluble pigments which bear no relation at all to the carotinoids. Moreover a change of the p_H of the cell-sap although of importance with respect to the colour of anthocyanins is not the decisive factor in living tissues of plants. As was already said above the colloidal condition of cell-sap and the presence of co-pigments are said to be more decisive in the changing of red into blue.

According to HALDANE (2) we cannot in general say that blueing genes are either dominant or recessive. This author distinguishes the following genes which cause blueing: (1) genes controlling acidity. This acidity is dominant of alkalinity, the blueing effect is recessive. (2) genes favouring co-pigment formation, generally at the expense of anthocyanin. In this case the blueing effect is dominant and sometimes accompanied by dilution of the anthocyanin, due to competition from the common source (s. above). (3) genes substituting a more oxidised and thus more blueish anthocyanin for a less oxidised and more reddish one; her blueing is always dominant.

It is generally known that there are many wild growing species with blue flowers which often give reddish or pink varieties e.g. *Aquilegia vulgaris*, *Delphinium consolida*, *Polygala vulgaris*, *Ajuga reptans*, *Salvia pratensis*, *Endymion nutans*. On the other hand there is perhaps only a single case in which a wild growing species with red flowers has a blue coloured variety. *Anagallis arvensis* s.sp. *coerulea* Voll. (forma *femina* Nills) might be an example but an equally possible view is the following. The genus *Anagallis* might be considered as having in general blue flowering species, e.g. *Anagallis Monelli* Clus., *Anagallis latifolia* L., *Anagallis grandiflora* Andr. so that the red-flowering species *Anagallis arvensis* is an exception, formed by a recessive mutation as in the cases mentioned above. *Anagallis arvensis* s.sp. *coerulea* might then be a case of degression or regression, the reassuming of activity by a latent character s. DE VRIES l.c.. Be this as it may, the numerous red or pink varieties of blue flowering species prove that we have here a case of recessive mutation, a so-called factor mutation in which a dominant factor changes into a recessive one. Even in vegetative varieties this can happen as was observed by BATESON in *Lathyrus odoratus* when an individual with violet flowers produced a branch with red ones.

According to these facts it appears likely that in the arising of red flowering varieties from blue-flowering ancestors it is the co-pigment factor which from dominant changes into recessive. Consequently the mutations which gave blue-flowering mutants from red-flowering species must have been progressive mutations in the sense of HUGO DE VRIES and very rare as such. Here in my opinion lies the explanation of the low percentage of blue-flowering species in all parts of the world, the same explanation as was suggested by DE VRIES, but argued in a different way.

Perhaps it is worth while to note the following facts compiled from the work of A. KARSCH, called *Vademecum botanicum*. This book contains the species of the higher plants of Germany, Western and

Central Europe besides the best known species of other countries of the world, in total some 9000 species. If we select from this Vademecum the genera in which blue-flowering species are to be found we get a number of appr. 180 genera with appr. 1170 species. Of these species 41 % have blue flowers, 11 % white-, 15 % yellow-, 10 % red-, 8 % purple- and 15 % violet ones. That this percentage of yellow flowering species is as high as that of the violet ones might give occasion for the suggestion that blue pigment can as well be formed in connection with a yellow as with a red pigment. Remembering what was said above about the chemical relation of anthocyanins and anthoxanthins we might suppose the yellow pigment in this case to be an anthoxanthin, which by progressive mutation might give the blue pigment.

SUMMARY

After a short survey of the chemical structure of flower pigments the relative frequency of the various flower colours is examined on the basis of an analysis of standard flora's of different parts of the world: The Netherlands, France, Switzerland, Sweden, Tropical Africa, Cape Colony, Java and Victoria (Australia). The following colours were distinguished: green, white, yellow-orange, red-pink, purple, violet-lilac and blue. In the flora's thus analysed the percentages of species with these flower-colours do not vary greatly, as is proved by the small standard deviation. The data are: green 7 $\frac{1}{2}$ % (St.D. 0,8), white 26 $\frac{1}{2}$ % (St.D. 1,4), yellow-orange 31 % (St.D. 1,8), red-pink 15 % (St.D. 1,4), purple 7 % (St.D. 2,8), violet-lilac 7 % (St.D. 2,4), blue 5 $\frac{1}{2}$ % (St.D. 1,1) Red, purple and violet taken together 29 % (St.D. 1,9).

The dominance of species with red flowers in the tropics, often supposed to be founded on selective action by birds, bats and butterflies is less pronounced in the table than usually claimed, whilst in the flora of Java it is lacking. A higher percentage of blue-flowering species in temperate regions is not borne out by the analysis either. But there is a marked difference as regards percentages of blue-flowering species between the flora of Switzerland as a whole and that of the Swiss Alpine mountain region above 1100 m. The respective percentages are 7 % and 11 %. In the flora of Java which as a whole has a very low percentage of blue flowering species (3 %), this percentage in the mountain region above 1500 m is 6 %.

In connection with the experiments of KLEBS and others the idea of a direct influence of radiation cannot be ruled out entirely although its significance for the originating of new species is very problematic. Russian authors (N. I. VAVILOV) have claimed an influence of more intense radiation in high altitude on mutation processes. The possibility of selection by pollinating agents (2a) deserves consideration, decisive experiments in this matter however, are almost lacking.

The main point in the question of flower colour is the fact established by an examination of some 18000 different species from

various parts of the world, that in these countries the percentages of white-, yellow-, or red-flowering species are almost everywhere about 5 times as high as that of the blue-flowering species. The mountain-flora is the only exception. This fact leads us to the assumption that in the course of ages the evolution of blue pigment in flowers has been an autonomous genetic process only slightly influenced by environment and by the selective action of pollinating agents.

This genetical problem of colour evolution in flowers is discussed and the conclusion, corresponding with DE VRIES' suggestion, is that whilst yellow flowering as well as white flowering species may be originated by retrogression, the arising of blue-flowering species from red flowering ancestors must have taken place by progressive mutations, in casu of the co-pigment factor. In the fact that these progressive mutations are much rarer than retrogressive ones lies in my opinion the explanation of the low percentage of blue flowering species in all parts of the world. The frequently observed phenomenon of wild blue species giving pink coloured variants is a case of factor mutation in which a dominant factor, probably the co-pigment factor, changes from dominant into recessive.

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