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INTROGRESSIVE HYBRIDIZATION

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I. INTRODUCTION

There are in these days two basic ways of studying the species problem and the dynamics of natural populations. One may amplify the known facts of genetics regarding mutation rates and factor segregation, with a few likely assumptions, and then by exact mathematical computation work out the evolutionary roles of selection, mutation, population size, migration, etc. Outstanding examples of this approach are the works of Sewall Wright (1931) and R. A. Fisher (1936). Their results have been applied to general evolutionary problems by numerous biologists, as, for instance, Dobzhansky (1937), Mayr (1942), Stebbins (1950) and Simpson (1944). These investigators have, so to speak, brought genetics to the service of taxonomy. During the last two decades this integration of cytogenetics with systematics and palaeontology in the general study of evolution has been one of the most fruitful fields of modern biology.

A much less popular approach has been the attempt to bring taxonomy to the service of genetics, to study species differences and population differences so effectively and so exactly that the effects of the evolutionary forces actually at work could be measured in natural populations. This was, in essence, the aim of Karl Pearson and the biometricians. This entire school made the tacit assumption that species vary at random, one means of measuring species differences being as good as another, provided the measure be an exact one and the resulting statistics be dealt with expertly. It is unfortunately true that this assumption is without any biological basis. Species differences are *not* expressed at random (Anderson & Whitaker, 1934; Anderson, 1952*b*; Cousin, 1948). Species differ in various ways,

some of them very subtle. An exact measure of a species difference is not necessarily an effective one (Anderson, 1952*b*). The measurement of species differences is a problem which must be thoroughly analysed on the biological level before we can begin to approach it on the purely statistical level. The morphological analysis of interspecific differences and intraspecific differences brings what are essentially taxonomic data to bear upon fundamental questions in genetics. Many of those primarily interested in the application of genetics to natural history have employed this method in part, as, for instance, Turrill (1940), Mayr (1942), Gregor (1938, 1939), and others. However, taking the efficient measurement of species differences as a definite goal is a concern which has been almost wholly my own in the last twenty-five years (Anderson, 1928, 1929, 1933, 1936*b*, 1937, 1944, 1948, 1950, 1952*b*; Anderson & Abbe, 1934; Anderson & Turrill, 1935; Anderson & Hubricht, 1938*a, b*, 1943; Anderson & Ownbey, 1939; Anderson & Schregardus, 1944).

The contrast between the two approaches is clearly shown by Baker's excellent review on 'Hybridization and gene flow' (1951) as compared with this article on 'Introgressive hybridization'. His review answers the question, 'From the standpoint of modern genetics, what is the importance and what are the evolutionary effects of hybridization?' This article, on the other hand, seeks to answer the question, 'From an examination of the variation patterns of plant and animal populations, what is the relative importance of hybridization and mutation in evolution?' Though both draw in part on the same literature, the two articles reflect fundamentally different (but not necessarily antagonistic) approaches to the same basic biological problem. Each complements the other.

Our understanding of the biological nature of individual differences is still too imperfect to allow us to analyse variation effectively in natural populations by purely mathematical methods, though several mathematical devices (as, for instance, Fisher's multiple discriminate function (1936), particularly in its developments by Rao (1948) and others) hold promise of ultimate usefulness. As a stop-gap, and as a means of exploring the field, a number of semi-graphical, semi-mathematical devices have been developed. These have been listed and discussed in *Introgressive hybridization* (Anderson, 1949, pp. 81-101). Originally rather crude, they have been slightly improved. They should ultimately be supplanted by more mathematically elegant methods. They present to the eye the extent to which the varying characters of a natural population are or are not associated with one another, in such a way that by carefully studying the diagrams the relations between the variables can at length be grasped by the mind, and precise comparisons made with other populations.

The devices were developed in the hope of demonstrating the operation of mutation in natural populations, and the studies of variation in *Iris* (Anderson, 1928, 1936*b*) and in *Clematis* (Erickson, 1945) do approach the fringes of that subject. As the methods became extended and improved, however, the studies of variation in which they were employed showed with increasing clarity the important role of hybridization among the higher plants. Taken as a whole, together with similar

work by others, they now constitute a body of codified information on the importance of hybridization in population dynamics. It needs to be specifically pointed out, therefore, that the methods were originally developed to detect the role of mutation or any other primary source of variation and that they can be (and have been) used quite as readily to show the comparative unimportance of hybridization, given natural populations in which hybridization is not an important factor.

II. HISTORY

The term 'introgressive hybridization' was first used by Anderson & Hubricht in 1938 to denote the gradual infiltration of the germplasm of one species into that of another as a consequence of hybridization and repeated backcrossing. The phenomenon itself had previously been described and its probable significance discussed in a series of papers (the genera concerned are shown in *italics* after each reference): Anderson & Woodson, 1935, p. 37 (*Tradescantia*); Anderson, 1936*b* (*Iris*); Anderson & Sax, 1936, p. 456 (*Tradescantia*); Anderson, 1936*c* (*Tradescantia*); Anderson, 1936*a* (*Apocynum*). It was concluded that the chief result of hybridization in the latter genus was the enrichment of variation in the parental species, a conclusion foreshadowed by such work as that of Ostenfeld (1928). I had also been collaborating informally with Goodwin in his studies on introgression in *Solidago* (1937*a, b*), with Wetmore & Delisle (1939) in their work with *Aster*, and with Riley on his studies of hybridization in *Iris* (1938, 1939).

By 1938 (Anderson & Turrill) it had been shown pragmatically that character association in hybridizing populations could be used as a criterion of hybridity. The criterion was valid only when built upon as many of the multiple factor characters of the organism as possible. Its successful use, therefore, involved a long probationary period of learning how to measure such characters effectively. The technical tricks of this technique can be acquired by reading and persistent application, but they are still in the exploratory stage (and are most readily acquired through association). Though they are beginning to be widely used, they have been mastered by only a half-dozen investigators. For that reason the example in the following section of this article is presented in more detail than would otherwise be appropriate in a review. In 1939 the theoretical basis of this criterion was specifically pointed out (Anderson, p. 162). In 1949 the process of using character association in not only reporting but in analysing variation in natural populations was described in detail and named 'the method of extrapolated correlates' (Anderson, 1949, pp. 92-9). A similar exposition is presented in the following section of this article. The method being a powerful one, it was so rapidly adopted that Baker (1947) protested against the increasing imputation of hybridity without experimental proof. He was apparently unaware of the criterion of character association, nor could he then readily have ascertained (the relevant literature never yet having been assembled in any one publication) that my own work had been preceded by rigidly experimental methods, for *Iris* (1928, 1936*b*) and for *Tradescantia* (1936*c*, 1937; Anderson & Diehl, 1932; Anderson & Sax, 1934, 1936; Anderson & Woodson,

1935). In addition to these papers the importance of introgression has been demonstrated for *Helianthus* by Heiser (1947*a, b*) and for *Parthenium* by Rollins (1944, 1945, 1946), and for *Gilia capitata* by Verne Grant (1950), in each case with detailed experimental data. Dansereau (1938, 1939*a, b*, 1940, 1941, 1943) has presented evidence for its evolutionary role in *Cistus*, and he and Desmarais (1947) have studied its effects in *Acer*. It has been shown to be at the basis of the population variability which is characteristic of the genus *Phlox* (Anderson & Gage, 1952). It is a phenomenon of much economic significance in *Cinchona*, according to Camp (1948), and in *Hevea* according to Baldwin (1947) and Seibert (1947). The subject has been briefly monographed (Anderson, 1949), particular attention being given to the theoretical background and to techniques for analysing introgression in natural or artificial populations. An inclusive bibliography designed to supplement this volume was published at about the same time (Heiser, 1949). The general evolutionary significance of introgression has been critically considered by Stebbins (1950, pp. 262–78). A popular account, using the minimum of technical language, has been presented in a book designed for general reading (Anderson, 1952*a*). A discussion of the basic mathematical problems was presented to the Biostatistics Conference at Ames, Iowa, in 1952, and is to be included in the published volume summarizing the programme.

III. EXAMPLE: *OXYTROPIS*

The dynamics of introgression in natural populations and the validity of the methods used in analysing such populations are best understood by reference to an actual example. The introgression of *Oxytropis albiflorus* by *O. Lambertii*, previously unpublished, serves as a particularly convenient instance for demonstration and discussion because (1) the specific differences are easily measured and easily demonstrable, (2) for technical reasons the analysis is equally facile in the field or in the herbarium, and (3) the analysis has been partially confirmed by breeding techniques.

Oxytropis albiflorus, a perennial legume, is a common and conspicuous plant in the Rocky Mountains of Colorado where it grows in aspen groves at eight to ten thousand feet. While ordinarily white-flowered, it is customarily quite variable, and pale blue and pale pink-flowered plants are so numerous as to outnumber the white-flowered ones in some populations. A preliminary sample of such a population was studied carefully with the naked eye and under the dissecting microscope. It was soon apparent that in addition to flower colour, the population was varying widely as follows: (1) Racemes condensed to open. (2) Peduncles exceeding the leaves, to much shorter. (3) Outer microscopic pubescence from appressed to woolly. (4) Inner microscopic pubescence of tiny black hairs varying from (a) none at all to (b) lines or blotches on the calyx to (c) covering the calyx. (5) The colour of the corolla followed a fairly simple variation pattern. The apparently white-flowered plants had small eye-spots of deep blue. Those with the barest tinge of ground colour were pale blue. Pinks varied from pale pink to, very rarely, an intense rose pink. (6) The colour of the corolla was frequently enhanced by bright flushes of

anthocyanin in the epidermal cells of the calyx. While coloured calyces tended to accompany coloured corollas, there were exceptional plants which had the corolla colour without the calyx colour and vice versa.

A random collection was then carefully made from a variable population, a flowering peduncle with a subtending leaf being selected on each plant. In making the collection great care was taken to see that the sample was typical of the particular plant. *Oxytropis* characteristically has several inflorescences in bloom at one time, and it was a comparatively simple matter to select one which in form and colour was representative of that particular plant and had undergone no obvious developmental accidents due to grazing, insect attack, and the like.

Two of the variable characters proved easy to score: the openness of the raceme, and the extent to which the peduncle did or did not exceed the leaves. Inflorescence exertion was measured to the nearest centimetre and gave values from a minus 4 to a plus 3, the first of these values indicating that the tip of the leaf was 4 cm. above the base of the raceme, the latter extreme indicating that the base of the raceme was 3 cm. above the tip of the leaf. The denseness of the raceme was difficult to score in such a way that the measured grades corresponded with subjective judgements as to comparative densities. Finally, it was found that scoring the number of flowers in the lowest 2 cm. of the raceme gave biologically accurate as well as a mathematically exact measure of comparative density.

A scatter diagram was then prepared to show the relation between density and exertion of the peduncle. The correlation was slight and negative, that is, the densest racemes were least exerted; the more open the racemes, on the average, the more they tended to extend beyond the leaves. The correlation being just barely perceptible in this small sample, the original population was restudied carefully to see if the correlation held. The following four tests were made. (1) The densest heads in the entire population were examined for their average exertion. It was found to be low. (2) The most open heads in the entire population were examined for their average exertion. It was found to be high. (3) The least exerted plants were examined for density. It was found to be high on the average. (4) The most exerted were examined for average density, which proved to be low.

For this population it had, therefore, been established that there was a slight but perceptible association between laxness of the raceme and the extent to which it was exerted above the leaves and of the denseness of the raceme and the extent to which it was included within the leaves. This was checked in other local populations nearby and found to hold. The two extreme types, low-dense and tall-open, were then examined for the other variables. It was found that the low-dense extremes tended to be white-flowered, woolly and without microscopic hairs under the other pubescence. These were all scored in such a way that the extreme values associated with tall-open were represented by long bars appended to the dots of the scatter diagram (Fig. 1). To be more specific, coloured calyx, coloured corolla, appressed pubescence, and unrestricted microscopic hairs were all represented by long rays, each of these four additional characters being scored at a particular position on each

dot of the diagram, as shown in Fig. 1. Rays of intermediate length indicate an intermediate expression of this character in the plant represented by that dot. Complete absence of a ray indicates the opposite extreme, so that those dots in Fig. 1 which are completely rayless represent white-flowered plants with a green calyx, very curly pubescence, and no short underlying hairs.

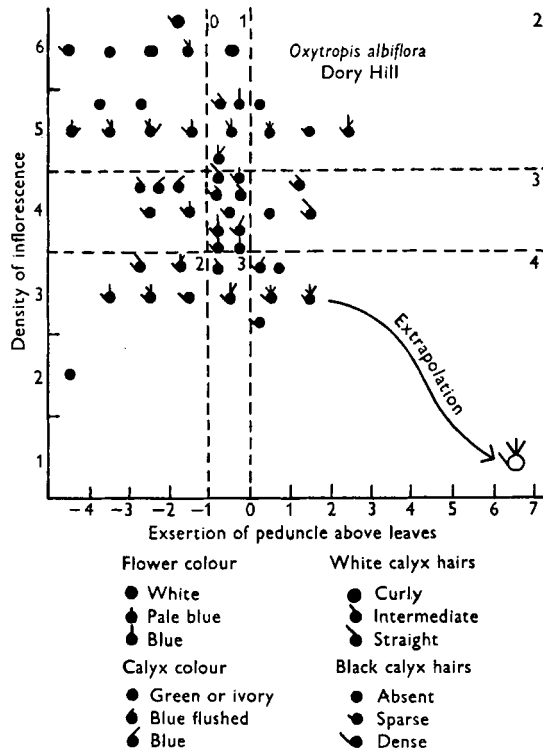


Fig. 1. Pictorial scatter diagram showing interrelationships of six variables in a population of fifty plants of *Oxytropis*.

The most important use of such pictorial scatter diagrams is for analysis, rather than for exposition. Fig. 1 is a summary of six kinds of facts concerning forty plants arranged in such a way that the main relationships between these six variables may be considered as one. The human mind is poor at grasping the exact relationship of anything beyond two variables. In these diagrams the trained eye can assist the mind, but it cannot do the whole job; the diagram has to be studied. In this way it is possible, from a careful and prolonged study of Fig. 1, to ascertain that all six of the variables tend to be loosely associated, but not even any two of them are so directly associated that an increase in one is always accompanied by an increase in the other. This loose, non-random association of various characters is critical evidence for hybridization. Species are separated from each other by barriers of various kinds working together in various ways. When species hybridize, these

barriers continue to work, gradually being lessened, generation after generation, in the mongrel populations. The forces of specific coherence are so strong that for many generations after hybridization the characters which went into the cross together still have a measurable tendency to stay together, though this coherence ordinarily becomes less with each succeeding generation. This has been proved on theoretical grounds (Anderson, 1939; Dempster, 1949), in various artificial crosses (Anderson, 1939, and unpublished), and in all the natural populations of hybrids which have been analysed to date. For *Zea Mays* it has been demonstrated (Brown, 1949; Anderson & Brown, 1952) that after 50–100 generations of selective breeding, all the multiple-factor differences which distinguished two interfertile races are still perceptibly associated. Certainly one of the cohesive forces which tends to keep together the germ elements which went in together is natural selection. Effective gene combinations which had been evolved through natural selection might well continue to be at a selective advantage even after having been partially broken up after hybridization.

With a little study of Fig. 1, one can see that the characters represented by long rays tend to be associated with the tall-open extremes, and those represented by no rays with the low-dense. For instance, if we divide the scatter diagram roughly into thirds on each axis, putting the modal class in the middle third (as shown by the broken lines), then we can study the average length and number of rays in each of the nine sections into which the diagram has been divided. We find that the section in the upper left-hand corner averages less than two-thirds of a ray per dot, and that this average increases fairly regularly until we reach the lower right-hand extremes with an average of one and one-third rays per dot.

To sort out the extremes in the population the scores for the six characters were turned into a hybrid index (Anderson, 1936c). Each character was scored in three grades, low, modal and high, the scoring being adjusted so that characters associated with the low-dense complex had the lowest and those associated with the tall-open complex the highest scores. For each character 'low' was rated at zero, 'modal' at 1, and 'high' at 2. In practice the index is made directly from the pictorialized scatter diagram. The characters on the two axes are scored 0, 1 and 2, so that the upper left-hand compartment (0, 0) has a 'ground value' of 0, the next one to the right (0, 1) a ground value of 1, and so on until one reaches the lower right-hand compartment (2, 2) which has a value of 4. To find the index value of any dot on the diagram, one takes the ground value of that compartment and adds two points for each long ray and one point for each short ray, giving an index running from 0 to 12. The frequency distribution of the sample for this index is shown in Fig. 2. As soon as it had been calculated, the three plants representing the greatest extremes of the low-dense complex were compared with the three which were at the other extreme. Outline drawings of these individuals are shown in Figs. 3 and 4. The low-dense extremes proved to be very much alike, not only in the characters for which they had been scored, but for many others as well. The open-tall extremes were unlike one another. It was therefore assumed that the low-dense extremes represented

more or less the original population before it had undergone introgression and that the tall-open extremes were three out of a potentially large number of mongrels which might result from extensive introgression from another species. Had they

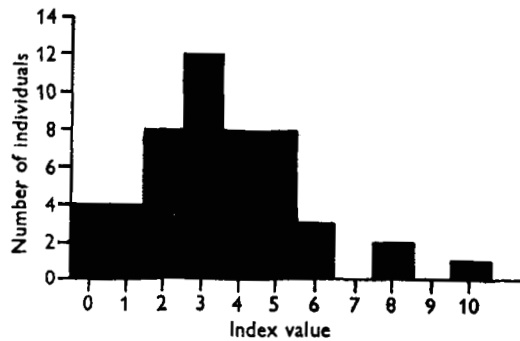


Fig. 2. Frequency distribution of the fifty plants of Fig. 1 on a hybrid index with values of 0 for 'pure' *albiflora* and of 12 for the opposite extreme.

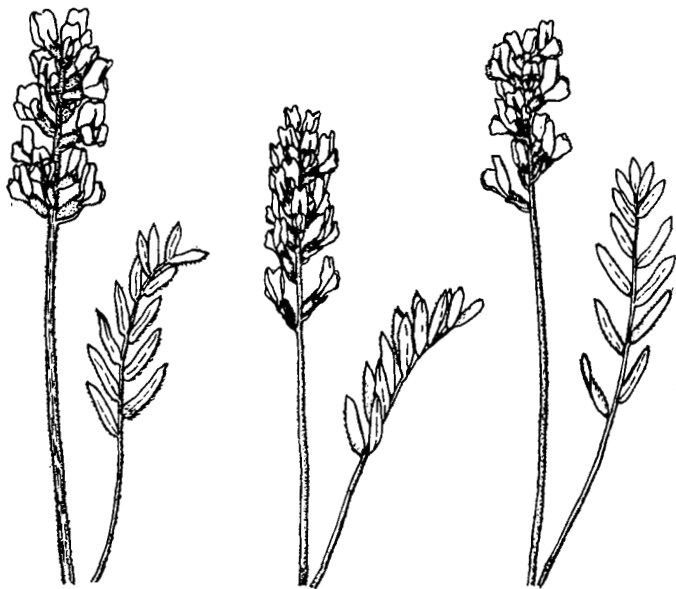


Fig. 3. The white low-dense extremes from Figs. 1 and 2.

been due to independent mutations it is difficult, if not impossible, to suggest any mechanism by which variations toward more colour should tend to be accompanied by variations of greater exertion, more open inflorescence and a more appressed pubescence. The probable introgressing species was then apprehended by the method of extrapolated correlates (Anderson, 1949, pp. 93-9). The argument was as follows: If these three introgressants are so different from each other and on the whole so similar to the putative originals, then they must carry a good deal of the

original germplasm. To produce their more open inflorescence the original dense inflorescence must have been crossed with a species which had an extremely open inflorescence. Extrapolating this way, character by character, a hypothetical description was drawn up of a species of *Oxytropis* with a long narrow inflorescence, greatly exserted above the leaves, covered with a highly appressed pubescence and

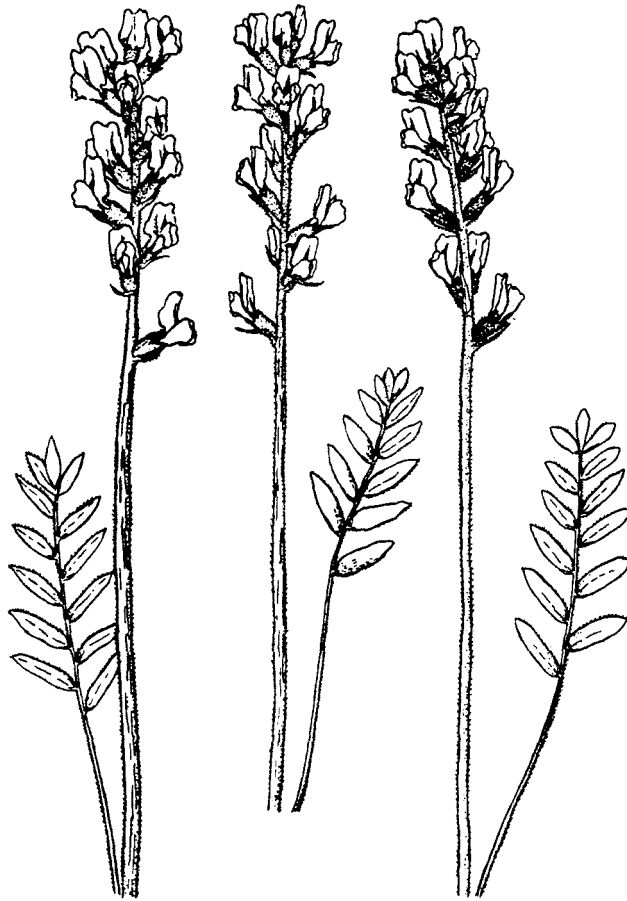


Fig. 4. The coloured tall-open extremes from Figs. 1 and 2.

bearing brilliant dark magenta flowers. By comparing the two sets of extremes, a few more characters were associated with the two complexes. By extrapolation they were added to the description. It was predicted in this way that the standards of the introgressing species should be apiculate, the peduncles slender, and the leaflets long and narrow. This description was detailed enough, so that although this species was not yet known to me, the description could be run down in Nelson's *Flora of the Rocky Mountains* (1898-1904), and the unknown, unseen species identified. It proved to be *Oxytropis Lambertii*, common at slightly lower elevations. It was

subsequently collected and found to answer the description exactly, including the apiculation of the standard.

Mass collections were made of these and other populations of *Oxytropis*, and from time to time have been assigned to various advanced students as an exercise. These students, using the same general method (but making their own choices of characters to study and means of measuring them), have succeeded in drawing up similarly effective descriptions of *O. Lambertii*. When two different people can in this way make independent predictions of a species unknown to either of them and then, out of all the conceivable species which might exist, predict exactly that one, correct even to technical details, then the method of extrapolated correlates is as valid as any we have in biology. The first test of a scientific method is its ability to make predictions. The second test is the ability of different observers, working independently, to make virtually the same predictions from the same data.

There has also been some experimental confirmation of these results. Because of their importance as stock poisons these two species have been investigated by students of range management. Artificial hybrids have been produced resembling some of those described above, but detailed reports of these experiments have not yet appeared in print. This was the first really critical test of the method of extrapolated correlates. It has since been repeatedly used with floras with which the operator was not familiar and has produced similarly verifiable predictions.

IV. INTROGRESSION AND EXTERNAL BARRIERS

The dependence upon suitable ecological niches, if hybridization is to have any important evolutionary consequence, has been demonstrated repeatedly in various field studies. The pertinent literature was reviewed in *Hybridization of the habitat* (Anderson, 1940) and a detailed exposition of the hybridizing irises studied by Riley (1938, 1939) and Viosca (1935) was presented in *Introgressive hybridization*, pp. 1-11 and 94-8. All of the evidence from sympatric introgression shows that such species are kept apart by ecological and internal barriers of various kinds. In old, well-established floras, until the ecological barriers are broken down, there will be little or no introgression no matter how weak the internal barriers because there are few intermediate niches for the first generation hybrids and virtually no niches for the various new recombinations produced in the second generation and in backcrosses. When man 'hybridizes the habitat', as by burning, ditching, pasturing, tilling the soil, he produces new, and frequently relatively unoccupied, niches in which introgressants are at a selective advantage. It is significant that most of the earlier field studies of hybridization were made at places where the ecological pattern of the environment had been grossly disturbed by man and his domesticated animals. This is particularly true of New Zealand, where the frequency of hybridization is so high as to have led to extensive studies by various naturalists (see Allan, 1937, for a review of the literature). The situation there may be briefly interpreted as follows: New Zealand had essentially an island flora which had evolved not only in the absence of man, but essentially in the absence of any

higher vertebrates. The arrival of the Maori in the fourteenth century brought in fire, which they used deliberately in clearing fields for cultivation. These burns were usually deserted after a few years and abandoned to the native vegetation which moved in. White colonists arrived five hundred years later, bringing with them pigs, horses, chickens, cattle and sheep, and increasingly intensive methods of cultivation. Whenever a pig first rooted in the forest, whenever a piece of forest land was first burned over by the Maori, whenever a herd of cattle were loosed in a semi-wooded area, they were attacking a flora which not only had had no association with such marauders throughout its history, but had even had no experience of much milder vertebrates. When pigs rooted in the turf, when cattle browsed upon vegetation, when trees were felled, new ecological niches were created which were outside the evolutionary experience of the entire New Zealand flora. Hybrids which had previously been spawned with a low frequency now had strange new habitats in which they and their variable backcrosses could grow without intense competition. As I have suggested elsewhere (1951) the fact that New Zealand's agriculture was largely pastoral greatly furthered these developments. Had New Zealand gone in for modern large-scale production of cotton or wheat, with her native vegetation wiped clean from thousands of square miles, there would not have been a varied native flora to seed into the disturbed area, nor would there have been, as in old pastures, a continuing readjustment of native and weed floras decade after decade.

V. INTROGRESSION AND INTERNAL BARRIERS

The experimental field studies of the last two decades have shown with increasing force that there is no very evident association between the strength of the internal barriers between species and the degree to which the species introgress in nature. Given a selective advantage strong enough to encourage introgression it is surprising how extensive it can be in spite of very strong internal barriers, as Heiser demonstrated (1949) for the California sunflowers.

The relation between the strength of the internal barriers and the pattern of introgression is of quite another sort. The results of introgression with and without strong internal barriers are shown diagrammatically in Fig. 5. With weak internal barriers, as in the genus *Aquilegia*, introgression produces subspecies or varieties which grade imperceptibly and smoothly into the parental species. With strong internal barriers, introgression tends to bring these barriers into the populations of the recurrent parent. *Elymus glaucus*, for instance, hybridizes with species of *Sitanion*, in spite of strong internal barriers between these genera, as has been demonstrated by Stebbins and his students (Stebbins, Valencia & Valencia, 1946; Snyder, 1950, 1951). Within the populations of *Elymus glaucus* these barriers continue to segregate, so that morphologically similar plants of *E. glaucus* may be separated by cross-sterilities virtually as strong as those which separate *Elymus* and *Sitanion*. If one thinks of all the types of internal barriers which have so far been discovered, it is clear that in backcrosses they will either segregate entire, like a single gene, or produce a set of multiple but weaker barriers. Let us take, for

instance, an inherent difference in flowering period due to two sets of genes, AAB being early flowering and $A'A'B'B'$ being late flowering. Introgression between the early- and late- flowering races may eventually produce a whole set of intermediates all the way from $AA'BB'$ to $A'A'BB'$, including the true-breeding, intermediate flowering sorts $AAB'B'$ and $A'A'BB$.

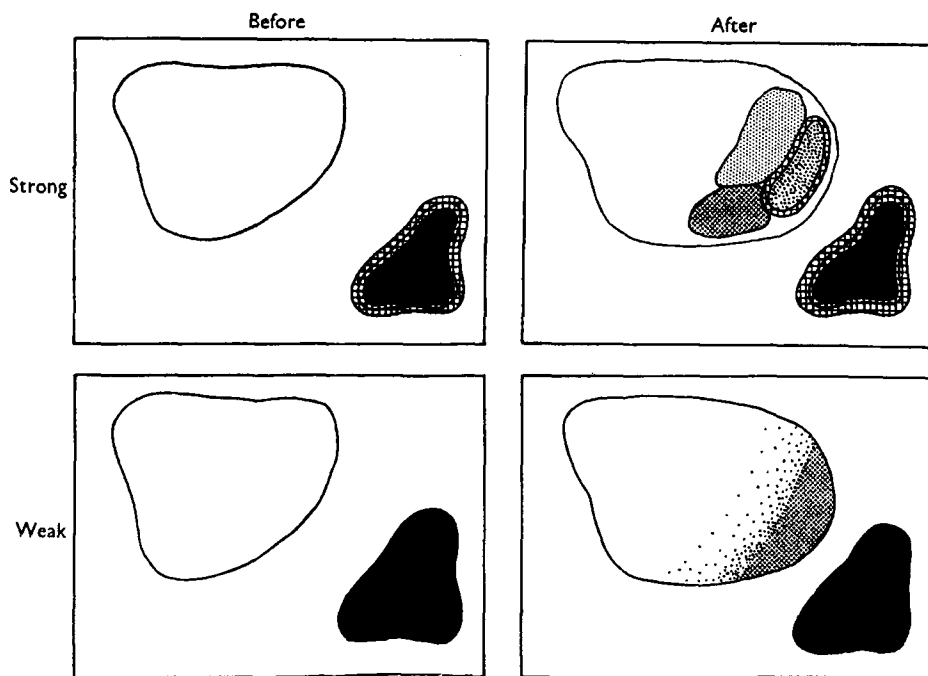


Fig. 5. Diagram showing the results of introgression with and without strong internal barriers. In each case there is introgression of the black species into the white. With strong internal barriers, parts of the barrier system are carried into the introgressed species and form semi-isolated subspecies or races within it.

In advance of any general comprehensive surveys of sterility barriers, a number of biologists, by logical processes of deduction, concluded that sterility must be of special significance as a criterion of species relationships. Such results as those of Heiser with *Helianthus* and those of Stebbins with *Elymus glaucus* raise grave doubts as to the truth of these generalizations about the special significance of sterility. The facts do not seem to bear out the generalizations. Until we have vastly more information on the subject of barriers than we have at present it would seem wiser to admit that species barriers are of various kinds working together in various ways. When adequate sampling has shown us what the average condition may be in various groups of plants and animals, then we may be able to make more precise generalizations. This conservative point of view receives additional force from Kinsey's discovery in 1948 that the notion that species ought not to cross is a folk idea widely held in north European and American cultures. As he has also shown,

scientists are not themselves immune from prejudices derived from the folk ideas of their early associates.

In all the literature concerning the evolutionary importance of sterility there is a need for more precise mathematical thinking. Sterility and fertility are not absolute attributes; they are comparative terms. When in a scientific paper the statement is made that two species are intersterile, one would like to know whether it means that half a dozen plants of one species were cross-pollinated with half a dozen of the other in one experimental plot as many as ten or twenty times, or whether it means that several hundred plants of many different strains were repeatedly cross-pollinated with each other under varying field conditions. Such precise information as we have on wide crosses gives no indication that interfertility has any definite limit beyond which one might not find a still lower degree of fertility with even wider experimentation. Few experimenters have even considered the possibility of estimating whether in their material there might be fertilities of one in a million or one in several million. Fertilities of such low frequencies are of little direct importance in laboratory experiments. In evolution under natural conditions where populations of hundreds of thousands, if not millions, of individuals are exposed to hybridization over millions of years, fertilities no higher than one in a hundred million might be of great theoretical importance. This is a field in which though there are many opinions on record there is little or no exact evidence critically assembled. The success of Mangelsdorf & Reeves (1939), Venkatraman (1938), and Janaki-Ammal (1941) in producing crosses previously considered impossible, by the use of mass-production methods, demonstrates that such evidence could be obtained if its importance were realized.

VI. INTROGRESSION IN DIFFERENT GROUPS OF ORGANISMS

An even greater lacuna in the body of scientific knowledge relating to hybridization concerns the comparative frequency of hybridization in different groups of organisms. Detailed studies of introgression have revealed the importance of a fact thoroughly demonstrated by such early hybridizers as Koelreuter and Von Gärtner, but whose importance was soon forgotten; hybridization under natural conditions is cryptic. Hybridization under natural conditions is largely backcrossing, and backcrossing leads immediately to forms so closely resembling the recurrent parent that though they have greater variability, to the ordinary biologist or field naturalist there usually is no suggestion of hybrid ancestry. When the studies reported above had shown the surprising frequency of hybridization under natural conditions, I began the investigation of several genera with notoriously variable populations, to ascertain the degree to which this variability, very generally considered as typical of such species, might be due to introgression. In each case which has so far been investigated, introgression was indicated, and in some of them this hypothesis has been experimentally confirmed. The first of these studies to be published, that on *Phlox bifida* (Anderson & Gage, 1952), demonstrated such evident introgression from *P. amoena* that students given the data have been able independently to

predict the characteristics of *P. amoena*, even though that species was unknown to them.

We shall know little about the possible frequencies of introgression in various groups of plants and animals, therefore, until careful tests have been made of variation patterns of natural populations. In birds, for instance, closely related species usually have fairly similar plumage patterns. Introgression, even if fairly frequent, would not generally have been perceived by the methods currently in vogue among avian systematists. Only in those cases where closely related species have strikingly different plumage patterns would there be enough conspicuous differences between backcrosses and their recurrent parents to force the phenomenon upon the attention of systematists trained (as any good systematist must be) to see resemblances and therefore get the maximum number of specimens sorted with the minimum amount of effort. It is significant that the few cases of introgression in birds already reported in the literature deal with species with strikingly different plumage patterns. Chapin's case of African flycatchers (1948) concerned two species with brilliant and utterly different plumages. Sibley's detailed report on introgression in Mexican towhees (1950) involved a black-plumaged species with white spots in the tail and an olive-green species with a chestnut crown and no tail spots. Had these two species been even more different morphologically but with similar coloration, it is doubtful if the fact that each species varies in the direction of the other would have been noticed or, having been noticed, that its significance for introgression would have been seized upon.

VII. SYMPATRIC VERSUS ALLOPATRIC INTROGRESSION

Most of the examples of introgression which have been most carefully analysed involve two species with much the same general geographical distribution separated by ecological barriers. For *Oxytropis* one of the chief barriers was altitude; for the *Iris* species of Viosca (1935) and Riley (1938) it was the amount of shell lime in the soil; for the two species of *Tradescantia* for which the term 'introgression' was originally coined the chief barrier seems to have been sunlight and shade. It is convenient to extend Ernst Mayr's terminology (1942) and classify all these examples as sympatric introgression; that is, introgression between sympatric species. Such species tend to be isolated, among other things, by differences in ecological preference. Sympatric introgression, therefore, is commonest at those spots where man (or other powerful natural catastrophes such as floods or hurricanes) has broken down the exterior barrier system and provided new ecological niches in which hybrids and backcrosses may survive.

Sympatric introgression will occur more or less sporadically wherever the habitat has been greatly disturbed. If it is frequent, the results may be well known to observant local naturalists (as, for instance, in the case of the stemless blue violets in eastern North America). While it may be responsible for the bulk of the variation within the contributing species, it may give no evidence of its importance by ordinary taxonomic methods. If it is so common as to interfere with the identification of

specimens and their sorting in herbaria, it will be of concern to taxonomists. If it is so slight that no taxonomic pigeonholes are required, though it is the source of genic vitality which keeps the species from drifting into a backwater, it may be generally ignored.

Allopatric introgression, on the other hand, will by definition occur, if it occurs at all, between species which are native to different areas. In either of these regions at their centres, the genes of the other will generally be at a disadvantage, but in the intermediate zones there will be sites and perhaps subregions where the genes of one species will be at an advantage in the germplasm of the other. Introgression will present rich material for natural selection to work upon in these intervening zones. Once these widely separated species are able to mingle, every backcross will be the equivalent of scores or perhaps hundreds of gene mutations. They will have a rapid action in population dynamics because they bring in not only new genes, but whole gene systems which work well together. Evolution will be speeded up, and in the intermediate tension zone there may be a whole series of intermediates. In genuine allopatric introgression this tension zone is wide; one cannot study the phenomenon effectively in any one locality, and may have to go hundreds or even thousands of miles. The mere demonstration that allopatric introgression might occur will require careful study of variation patterns over a considerable region. In contrast to sympatric introgression it can be quite common and still outside the range of vision of local naturalists, who see only one part of the pattern. Only where it leads to taxonomic difficulties will it be perceived by most monographers. It could be well nigh universal and still remain largely unrecognized.

Though most of the introgression readily observed by local naturalists is sympatric, allopatric introgression is quite as common and equally important. Since by definition it involves species of different geographical regions, its demonstration and analysis will ordinarily require extensive collection and travel. It can be intense without producing conspicuous results in any one area. However, a number of examples of allopatric introgression have been analysed and discussed. Before the term 'introgression' had been coined, Anderson & Woodson (1935, pp. 33-9) described the introgression of the common *Tradescantia Ohlensis* (= *T. reflexa*) of the middle-western United States into *T. occidentalis* of the Great Plains. This analysis had been preceded by experimental hybridization. The most detailed study of allopatric introgression which has as yet been published is Hall's analysis of the interaction between *Juniperus Ashei* and *J. virginiana* (1952). *J. virginiana* is a characteristic member of the mesophytic flora of eastern North America, in its purest form a tall forest tree. *J. Ashei* is a low bushy xerophyte from dry dolomitic outcrops in Texas and Oklahoma. In a series of papers (1952, various papers in press) Hall demonstrated that the area of intergradation between these two species (from Texas to Indiana) was indeed an area of introgression. Throughout that area perceptible tree to tree variation was exclusively confined to partial recombinations of the differences between these two highly differentiated species. There was a general overall tendency for the characters which came in from one species to be

associated with one another much more closely than if all these various characters (size of fruit, bushiness of tree, density of foliage, colour of heartwood, shape of leaf glands, etc.) were each varying at random. Though at first sight *Juniperus* would seem to be poorly suited to experimental work, Hall was able to use various widely planted horticultural clones of *Juniperus* introgressants to demonstrate experimentally the comparative stability of these variables under widely different environments.

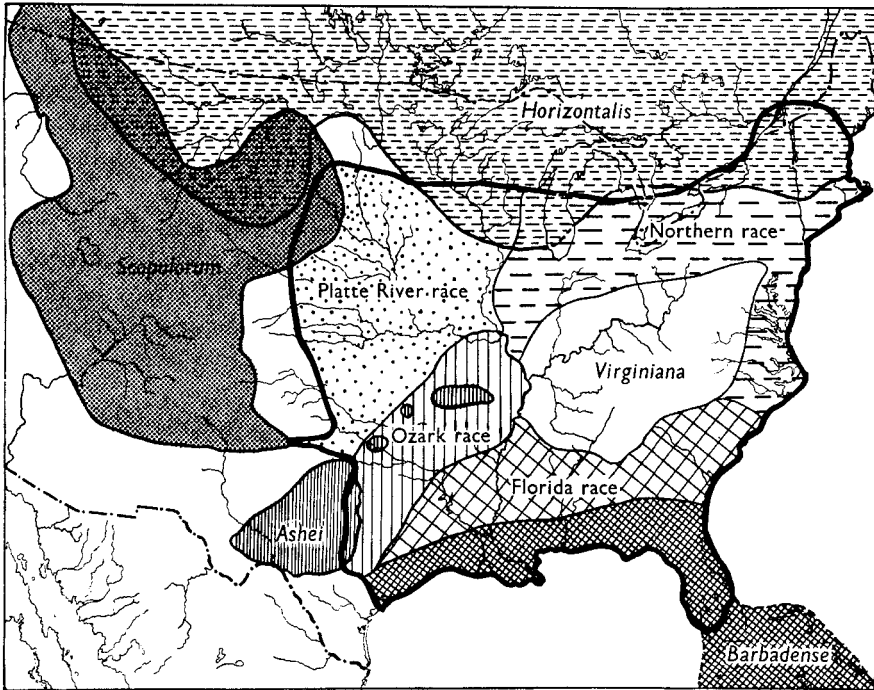


Fig. 6. The effect of introgression in forming geographical subspecies within *Juniperus virginiana*. Modified from the original diagram of M. T. Hall. The broadest line indicates the distribution of *J. virginiana* in the eastern United States. Introgression from *J. ashei* has produced the Ozark race; from *J. barbadense* the Florida race; from *J. horizontalis* the northern race; and from *J. scopulorum* the Platte River race.

Hall then proceeded (Fig. 6) to consider variation in *J. virginiana* as a whole. It is a species centred upon ancient low plateaus in Kentucky and Tennessee which have been continuously habitable for land plants since the Cretaceous, an area of notorious physiographic and floristic stability (Fernald, 1931). Within this core area Hall reports minimal differentiation within *J. virginiana*, and little plant to plant variation beyond age differences. Towards the south-west from this core stretches an increasingly well-marked geographical subspecies due to the introgression from *J. Ashei* already described. To the north and west are similar areas of introgression from *J. scopulorum* of the Rocky Mountains, and *J. horizontalis*. The analysis of

their introgression had been the subject of previous studies by Fassett (1944, 1945) and is being continued by Hall. To the east and south are similar geographical subspecies due to allopatric introgression, with whose analysis in the field Hall has just begun to work. Hall's picture of the ancient relatively undifferentiated core surrounded by a series of peripheral areas of allopatric introgression is of particular interest because it is so close to the variation pattern reported by Woodson in his studies of variation in *Asclepias tuberosa* (1947), and which he referred to as the 'peripheral effect'. In *Asclepias* the undifferentiated core was based upon the ancient Ozark Plateau. Before the publication of Hall's paper, Woodson had already interpreted variation eastward and southward from this centre as introgression from subspecies in the east and south. Woodson, however, had not ascribed the variation westward and south-westward from the Ozark centre to introgression, though there is, indeed, another element in *A. tuberosa* which is native to the south-west, and which might be responsible for differentiation in that direction.

Allopatric introgression has been reported in *Helianthus* by Heiser and its experimental analysis is under way. In combination with sympatric introgression, allopatric introgression has been studied experimentally by Grant in the *Gilia capitata* complex (1950). Its importance in *Quercus* has been indicated by Muller (1952) and Tucker (1952), and for Mexican towhees (two species of birds) by Sibley (1950).

Allopatric introgression in the red-eyed towhees is of particular interest because the geographical pattern of differentiation is similar to that reported for many subspecies of the vertebrates, and common, though not so universal, among the higher plants. Well-differentiated and more or less uniform taxa are separated by areas in which there are morphologically more variable intermediates. It has frequently been assumed that these variable intermediates represent the ancestral stock from which the extremes were differentiated. With the arrival of the evidence for introgressive hybridization this hypothesis of variable intermediates as the ultimate source of differentiated extremes has frequently been revived, though so far as I am aware it has never been given a formal name, being variously referred to as 'a store of variability', 'a genetic pool' and the like.

VIII. INTROGRESSION VERSUS THE 'GENETIC POOL' HYPOTHESIS

There are a number of tests which can be applied to distinguish between these two hypotheses. In the first place, the loose association of most of the variables into complexes demonstrable in pictorialized scatter diagrams is exactly what would have been predicted on the hypothesis of introgression, since this matches the variation pattern in artificially produced backcrosses and hybrids. There is no other known genetic mechanism by which loose associations of variables might arise. Secondly, on the hypothesis of allopatric introgression we should find the relatively uncorrupted species in the older areas, the introgressants in floristically newer areas. On the alternate hypothesis the variable intermediates should be in the floristically older areas. All evidence yet reported on this point favours the hypo-

thesis of introgression. Thirdly, on the hypothesis of introgression, the higher fertilities should be among the original species; the sterility, if any, should show up among the introgressants. Here again the published evidence is all on the side of the hypothesis of introgression. In the fourth place the ability to predict, down to technical details, as in the method of extrapolated correlates, a taxon with which the observer is unacquainted, indicates remarkable validity for the hypothesis involved. Finally, in a fair proportion of the cases, hybrids and backcrosses have been experimentally produced, matching the putative backcrosses and hybrids found in the field. Since the hypothesis has met all these tests in every instance for which the data were available, and since no detailed evidence favouring the alternative hypothesis has yet been put forward, the latter may be disregarded until definite evidence for such an hypothesis has been put on record.

IX. AREAS OF INTROGRESSION

Allopatric introgression, by definition, is introgression between species geographically separated. It will occur most actively at those times and places where previously separated faunas and floras are brought together, as when islands are tied to a mainland or when climatic changes make widespread alterations in barrier patterns. In the American south-west, for instance, mesophytic floras and faunas are to-day isolated on the various mountains and mountain systems of that region. During the Pleistocene each pluvial period, with its widely prevailing mesophytic conditions and its glaciation of the higher peaks, would have brought many of these isolated floras and faunas together. Each interpluvial period would have found them isolated again, much as they are now. During the Pleistocene, therefore, in the south-west there have been repeated opportunities for floras previously separated to come together and undergo introgression, for these consequently more variable introgressed species to be reisolated and become differentiated, and again to come together, all this not once but again and again and again through the various pluvials and interpluvials. As a result, the floras and faunas of the south-west are not only rich in species and subspecies, as has been generally recognized, but their populations show higher average frequencies of introgressive variation than any which have yet been analysed.

In eastern North America, on the other hand, while continental glaciation displaced the pre-Glacial and inter-Glacial floras, the region was generally mesophytic; pluvial periods in the south-east seldom brought together species previously isolated by intervening deserts. Towards the south-west, however, pluvial conditions *did* allow previously isolated mesophytic elements in northern Mexico and Texas to meet their eastern relatives at the very time when the latter had retreated the farthest southwards. As a result all the widespread eastern species which have so far been analysed exhibit introgression along the Ozark-Texas axis, if they have a related taxon in that direction (*Juniperus*, Hall, 1952; *Acer*, Desmarais, 1947; *Asclepias*, unpublished; *Cercis*, see below; *Asclepias*, Woodson, 1947).

In a region as floristically simple as the eastern United States it is easy to demon-

strate that virtually all the allopatric introgression follows a few simple patterns. In addition to Pleistocene glaciation the only outstanding floristic event since the late Cretaceous was the gradual building up of the coastal plain during the Tertiary, during which time Florida appeared as an island or an archipelago and was gradually linked with the mainland, to undergo at least partial isolation again during the heights of the inter-Glacial periods when the sea-level was higher than now. The whole wide sub-continental area of eastern North America is mostly a region of

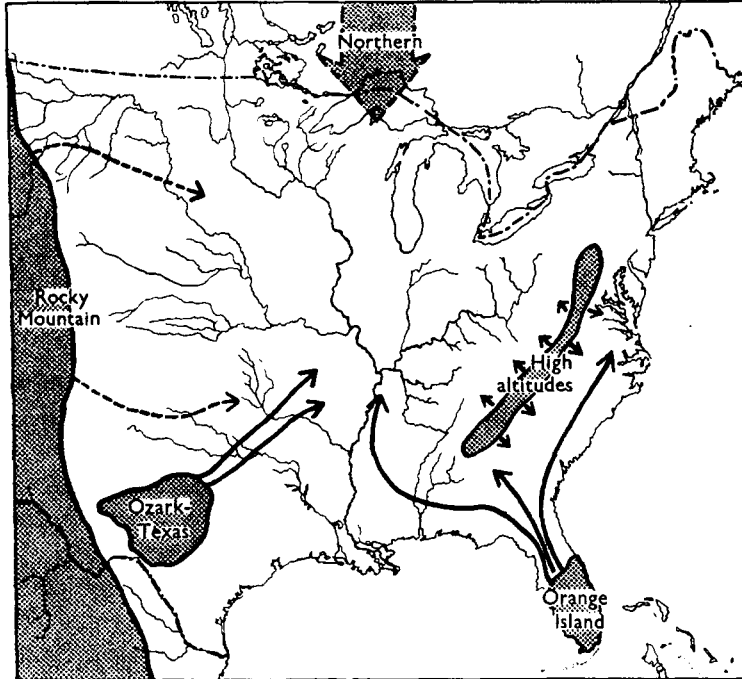


Fig. 7. The five centres from which species in the eastern United States received allopatric introgression.

low plateaus. There are no desert barriers, though periods of increasing mid-continental dryness drove the more purely mesophytical species farther east and periods of greatly increased mid-continental rainfall narrowed the gap between the mesophytes of the east and those of the Rockies.

As a result of this simple floristic history all the cases of allopatric introgression which have yet been investigated in the eastern states fall into a few simple patterns as shown by the map in Fig. 7. Introgression may stem from related taxa in Florida, in the Rockies, in Texas or Mexico, in the north, or (very rarely) from higher altitudes in the eastern mountains. If, like *Juniperus virginiana*, eastern species possess relatives in most of these centres, they have a complex pattern of differentiation; if, like *Cercis* and *Phytolacca*, they possess relatives in only one centre, then they are differentiated in that direction and in no other.

The introgressive patterns of these species are particularly instructive (Fig. 8). They were chosen for detailed analysis because each of them has no other close

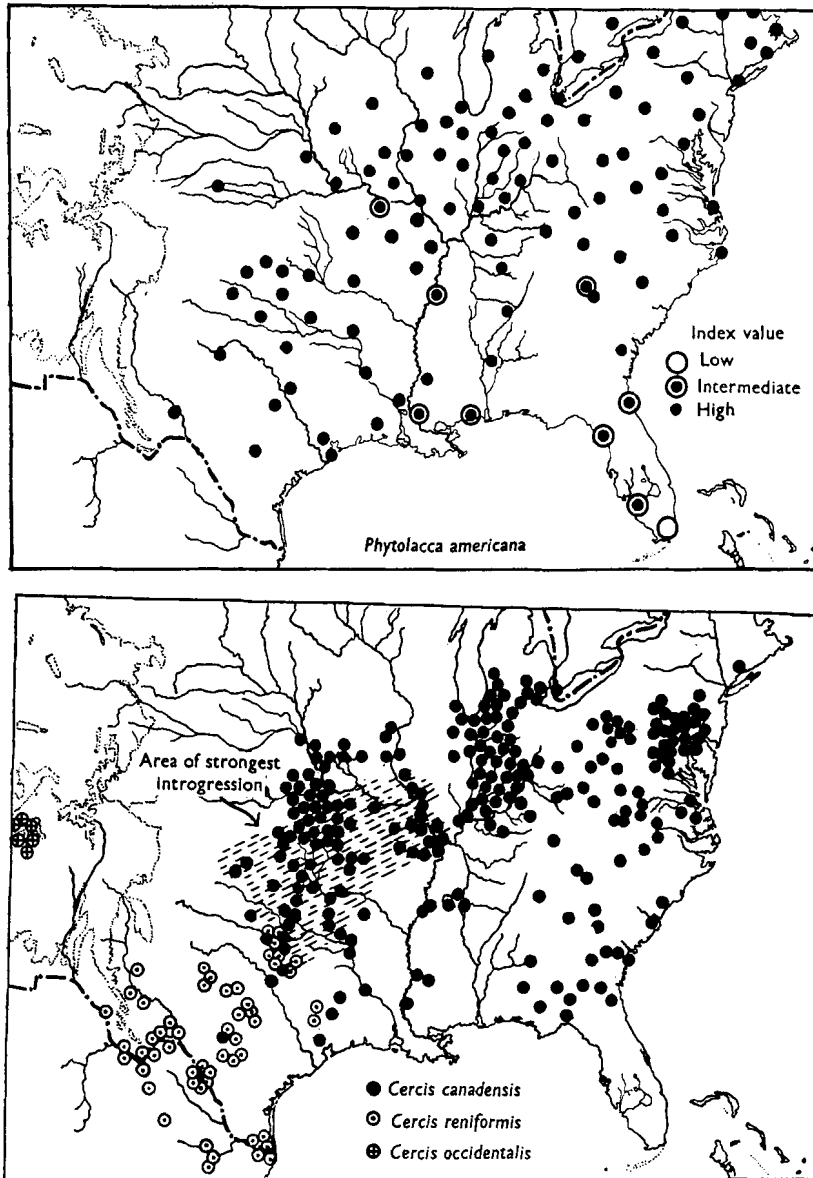


Fig. 8. *Phytolacca americana* and *Cercis canadensis*, two wide-spread species in eastern North America. The former has a related species to the south-east and is differentiated in that direction; the latter has a related species in the south-west with which it hybridizes and introgresses.

relative over most of its range. Any pronounced plant-to-plant variation in that area could not be due to introgression, unless it was obviously spreading in from

the direction of its nearest relative. The distributions of the two species are in general similar, and both are widely distributed and commonly found throughout wide areas in the eastern United States. *Phytolacca americana* has a related tropical species, *P. octandra*, in the Caribbean. In southern Florida there is a poorly marked variety (var. *rigida* of Small) intermediate in all its characters between *P. americana* and *P. octandra*, and evidently the result of introgression between the mainland and the Caribbean species at one of those times when the Floridean archipelago ('Orange Island') was reunited with the mainland. The introgression of the *rigida* complex into *americana* can be measured as far north as the Carolinas along the Coastal Plain and up the Mississippi Valley to Saint Louis. Beyond that area, *P. americana* is phenotypically undifferentiated. In a broad belt from Oklahoma to Iowa to Ohio to New York there are neither demonstrable differences from plant to plant nor from place to place. *Cercis canadensis* shows the reverse picture. It has no relatives in Florida, but in Texas and Oklahoma there is a xerophytic shrub, *C. reniformis*, which forms hybrid swarms with *C. canadensis* in the Arbuckle mountains and perhaps in other parts of the south-west, producing vigorous introgression which can easily be measured as far east as southern Indiana and Ohio. In the region outside this influence, from the Gulf States to Pennsylvania, it is a notoriously uniform species, differing little or not at all from plant to plant, and obviously filling the same ecological niche throughout a wide area. In other words, for these two critical genera all the plant-to-plant and place-to-place variation is of the sort expected by introgression; furthermore, this variation is confined to exactly those areas in which introgression could have occurred. Outside of these areas both species are morphologically and ecologically of phenomenal stability.

The variation of some thirty genera of the flowering plants has now been examined (important papers by Desmarais, Camp and Anderson are still to be published) in the sub-continental area between the Great Plains and the Atlantic. For each of these genera, all the readily detectable variation can be ascribed to introgression. With sympatric species the variability is largely concentrated in ecologically disturbed areas. In allopatric species it is concentrated in such floristically active areas as northern Florida and eastern Oklahoma; it is least perceptible in such floristically stabilized areas as the central interior plateaus of Kentucky and Tennessee. For critical genera such as *Cercis* and *Phytolacca* which have no close relatives over much of the area, there is plant-to-plant and place-to-place ecological and morphological uniformity except in those sectors of their distributions which abut on the area of a related species. Variation, in other words, is strictly proportional to the opportunity for introgression. From a consideration of all the evidence we are forced to the conclusion that introgressive hybridization is certainly more important than all other factors combined in providing raw material for natural selection to work upon. It must be one of the chief immediate causes of variability if not the chief one. These conclusions as to the relative unimportance of mutation as the immediate cause of population variability, force us to consider critically the hypothesis of gene

mutation as the chief raw material for evolution. This is a question which is virtually outside the scope of a review article, since aside from certain rather general objections (see, for instance, Goldschmidt, 1940) there are practically no modern critiques of the evidence.

X. INTROGRESSION AND MUTATION

One facet of the discussion may rightly be anticipated in this article, since it is in the field of introgressive hybridization. In so far as we have any knowledge of their ultimate origins, the plants and animals used as materials for genetic research are themselves the products of extensive introgression (see Anderson, 1952*a*, for a critical outline of the evidence relating to cultivated plants). The extreme variability which made them particularly favourable material for genetic investigation is founded in part at least upon introgressive segments of foreign germplasm. Their germplasms are not typical for germplasms in general. It has not been generally recognized that in such material it is difficult and sometimes impossible to distinguish critically between crossing-over and mutation. Let us represent corresponding segments of the chromosomes of two species as *a-b-c-d-e-f-g-h-i-j-k* and *A-B-C-D-E-F-G-H-I-J-K*, using each letter to denote merely a very small portion of the chromosome. We will assume that this entire segment is one in which there is ordinarily one crossover. In so far as can be ascertained from the published cytological evidence, crossing-over is never at random in the true mathematical sense. It tends to occur with high frequencies in certain parts of the chromosome and very low frequencies in others (see, for instance, the extensive literature on the relation between chromosome maps and crossing-over maps in *Drosophila*). Therefore in our diagram if the species represented by capital letters is introgressing into the species represented by small letters, in a few generations we shall find such chromosomes as *a-b-c-D-E-F-G-H-i-j-k* segregating in a population which is predominantly of the formula *a-b-c-d-e-f-g-h-i-j-k* for this segment. Unless the introgressive segment *D-E-F-G-H* is at a region of high chiasma frequency it will only occasionally be still further divided by a cross-over. Until that occurs it will segregate in the population like a giant gene, as Darlington has termed it, with ratios of 1:2:1 or 1:1, depending upon the particular cross. Very rarely and in frequencies nearly as low as the known frequencies for mutation it will, by crossing-over, produce such new combinations as *D-E-f-g-h-* and *d-e-F-G-H*. Each of these in turn will segregate like genes and with frequencies approaching still more closely to those for gene mutations. After a few generations there will, in material of this sort, ordinarily be no way of distinguishing critically between a genuine mutation and a new recombination in an introgressive segment. Much of the supposed mutation in genetic material therefore may well be crossing-over in an introgressive segment, rather than true mutation. In the last decade a series of critical studies with both plant and animal material have demonstrated with increasing clarity the difficulties of distinguishing between crossing-over and mutation. Stephens (1948) for cotton, the Greens (1949) for *Drosophila*, Laughnan (1949) for maize, and

Lewis (1946) for *Oenothera* have demonstrated that what had been supposed to be mutation was indeed crossing-over when more critical tests were applied to the phenomenon. In relatively homogeneous germplasms such crossing-over would produce little morphological effect unless it were unequal and formed repetitive segments. In introgressive populations where widely different germplasms were mingling, cross-overs which involved introgressive segments would produce new combinations of two widely different reaction systems. Most of these should produce morphological and ecological variability and a few might be expected to be spectacularly different.

The problem is made much more difficult by the fact that the two hypotheses (introgression and mutation) are by no means mutually exclusive. It may be that mutation is ultimately responsible for the differentiation of the germplasm, but that introgression is the immediate cause of much of the population variability. It might be that germplasms differentiate in ways not yet understood by geneticists, and that true mutations, though of great ontogenetic significance, are of little importance in evolution. There is need for much more accurate work in pure genetics and with much more critical material. As genetics has advanced it has gradually acquired the mathematical and biochemical accuracies necessary for really critical experiments in certain areas. If it is to draw critical conclusions as to the phylogenetic importance of mutation, then it will have to acquire phylogenetic accuracy as well. It will have to perform critical experiments with phylogenetically accurate germplasms, that is, with species such as *Phytolacca americana*, the purity of whose germplasm is beyond reasonable doubt.

XI. SUMMARY

1. The work summarized in this article is in a sense a return to the attempts of the early biometricians to measure evolution directly by its effects on populations.

2. Differences between and within species have been examined morphologically and mathematically. It was found that species differences are multiple and are not at random, hence ordinary biometrical techniques are ineffective in studying them. Semi-graphical methods were therefore set up for analysing population patterns. Pictorial scatter diagrams have been found to be effective and adaptable. Though most of the studies in which they were used have demonstrated the importance of hybridization in evolution, these diagrams are equally efficient for demonstrating the relative unimportance of hybridization, in populations where it is not an important factor.

3. Introgressive hybridization is defined as the gradual infiltration of the germplasm of one species into that of another as a consequence of hybridization and repeated backcrossing. The concept is briefly outlined.

4. The use of pictorial scatter diagrams is illustrated step by step with a variable population of *Oxytropis* from the Rocky Mountains. The *method of extrapolated correlates*, an extension of this technique, is illustrated in this material. By its use a description is drawn up of the hypothetical introgressing species responsible for

the variation, a description so detailed that it can be identified in monographs and manuals. The description fits a species of *Oxytropis* which is native to the same region. Pressed material from the same population given to students trained in these techniques led to independent predictions of the same species. The method therefore satisfies two fundamental scientific tests: (1) the ability to make successful predictions, (2) the ability of independent observers to make identical predictions from the same data.

5. The importance of external barriers in preventing and restricting introgression is illustrated by examples. It is shown that the effects of hybridization are more conspicuous where man has 'hybridized the habitat'. New Zealand, with a demonstrably high frequency of hybridization, is interpreted as an island flora evolved in the absence of vertebrates, including man. The arrival of man and his domestic animals produced various new ecological niches in which hybrids might survive. Furthermore, a pastoral agriculture brought native and weed floras together under conditions conducive to introgression.

6. Introgression is proportional to the selective advantage conferred by the foreign germplasm and within wide limits is independent of the strength of internal barriers to hybridization.

7. The effect of strong internal barriers is for the barrier apparatus, in part at least, to be carried into the introgressed species, where it produces partially isolated varieties and subvarieties.

8. Sterile and fertile are comparative rather than absolute terms. Fertilities of one in a million, though of little significance in laboratory experiments, may be of great importance in natural populations of hundreds of thousands of plants or animals which exist (as populations) for millions of years.

9. The effects of hybridization under natural conditions are cryptic. Backcrosses tend to resemble the recurrent parent so strongly as to pass unnoticed by naturalists and monographers. Only when the hybridizing species have conspicuous colour or colour pattern differences will introgression readily be apparent by ordinary methods of study. It is probably significant that the two examples of introgression in birds which have recently been reported involve conspicuous colour and pattern differences.

10. Introgression is classified as sympatric or allopatric, depending upon whether it is between species of similar distributions which are kept separate largely by ecological barriers or between species which occupy different geographical areas. Allopatric introgression will be restricted to those times and places where floras and faunas previously separated are brought into contact (removal of desert barriers during a pluvial period, islands united to a continent, etc.). Under these conditions it may produce variation patterns which are sub-continental in scale and therefore difficult of interpretation without extensive travel and experiment.

11. The hypothesis that the intermediates between two well-marked species, or varieties, represent not introgressants, but the original undifferentiated pool out of which both entities have emerged, is discussed. Five critical tests are applied to

this hypothesis. There is no evidence for such a genetic pool, and each of the five tests favours the hypothesis of introgression. It should be used as a general working hypothesis until there is definite evidence favouring the 'genetic pool' concept or some other alternative explanation.

12. Allopatric introgression will be common in regions (such as the south-western United States) where faunas and floras were united, separated, and reunited during the Tertiary and the Pleistocene periods by changes in shore line, advance and retreat of desert areas, etc. Allopatric introgression will be at a minimum in areas such as the eastern United States, where such physiographic changes have been at a minimum during the Tertiary and the Pleistocene. In this conservative area it is possible to demonstrate that all the instances of allopatric introgression fit the following readily defined patterns: Orange Island, Ozark-Texas, high altitude, northern, and Rocky Mountain.

13. Analysis of population variability within this critical eastern area produces no evidence for mutation as the immediate source of variability for natural selection. The basic questions raised by this discovery are mostly outside the scope of this article. One is discussed briefly, since it is directly concerned with introgression. From Mendel's peas to Beadle's *Neurospora* the plants used for genetic research have been weeds and cultivated plants. Their origin, where known, is a consequence of introgression, frequently multiple introgression. In such material crossing-over in short heterozygous introgressive segments could be distinguished from gene mutation with great difficulty or not at all. Attention is called to the need for a study of mutation frequencies in phylogenetically critical material, i.e. with species the purity of whose germplasm is beyond reasonable doubt.

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ADDENDUM

During the interval since this article was written the literature on introgression has increased so rapidly that I shall cite only those papers having a distinct bearing on the issues here presented. Desmarais's exhaustive study of introgression in sugar maples has at length (1952) appeared in print. Grant (1952*a*) and Hall (1952) have amplified their previous reports on *Gilia* and on *Juniperus*. Grant has also analysed (1952*b*) one example of natural hybridization in *Aquilegia* and discussed the role of hybridity in the evolution of the genus. Fassett & Calhoun (1952) have given a detailed report on introgression in *Typha*. Their data are effectively presented by a new graphical method. My colleague, Dr R. E. Woodson, Jr. (whose insistence on the evolutionary importance of hybridization first led me to study it experimentally) has presented (1952) still further evidence on introgression in *Asclepias*, and has discussed its general importance in evolution. Increasing experience in counselling workers in other laboratories has led me to publish (1953) a detailed account of elementary techniques for apprehending the fundamental morphological variables of natural populations.

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