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Genetic Implications of Long-distance Pollen Transport

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Numerous published reports show that tree pollens can travel great distances. There is a possibility that a single pollen grain can travel 100 rniles from a distant population, arrive in a viable condition, effect fertilization in the local population, and give rise to a local X distant hybrid which is superior in vigor or adaptability to the local trees. Such a hybrid might then produce a superior selfed progeny to replace the local race in later generations. Or, the local X distant hybrid could give rise to a new race through backcrossing to the local population.

To determine the probability of such an occurrence in nature, it is necessary to consider the probability of the various steps in this sequence of events.

Duffield's (1954) studies show that pollen can live for long periods under the proper conditions but that high humidities are detrimental to pollen viability. Pollen that travels only 10 or 25 miles would probably not lose its viability. However, a journey of 100 miles or more would probably subject the pollen to at least one night of high humidity, which might cause a reduction in pollen viability. Longer journeys of several nights' duration would probably affect pollen viability seriousiy.

When the pollen grain arrives in a viable condition, it can effect fertilization if the local and distant populations belong to the same species, or in many cases, to closely related species.

If the local and distant populations belong to the same geographic race, the local X distant hybrid will have the same survival value as a local tree. If the two populations are separate races or species, the locsl X distant hybrid may have an advantage or disadvantage over the localstock. Such an advantage or disadvantage has to be calculated separately for each case.

Available data from F, hybrids in *Pinus* and Populus indicate that local X distant hybrids involving different species would not be at a reproductive disadvantage to local trees (Richter, 1946; Northeastern Forest Experiment Station, unpublished data).

It is improbable that a new race would result from the selfing of a single local X distant hybrid. Selfed progenies reported thus far in Pinus and Picea (Johnson, 1945; Gustafsson and Langlet, 1953; Northeastern Forest Experiment Station, unpublished data) have grown much slower than crosspollinated progenies, indicating that they would be incapable of surviving in nature. It is also improbable that a new race would result from crosses between two simultaneously produced neighboring hybrids. IP the probability is 10^{-6} that a single tree is a local X distant hybrid, the probability is 10^{-12} that two neighboring trees are local X distant hybrids. Thus the infiltration of genes into the local population would probably require backcrossing to the local population.

Sewall Wright's studies (1943 and earlier papers as quoted by Dobzhansky, 1937) provide a means of estimating the genetic consequences of long-distance hybridization. Following are some of the terms used in his calculations:

N_u = the number of breeding individuals in the random breeding unit (panmictic unit, the largest population within which crossing takes place at random).

N_i = the number of breeding individuals in the local population under consideration. This number is arbitrarily defined in continuous populations.

K_i = N_i/N_u, the number of random breeding units in the population under consideration.

m = long-distance migration rate or the proportion of local X distant hybrids to local trees in the population under consideration. Basing the rate on number of hybrids produced eliminates the need for considering differences in pollen viability or crossability.

s = selection pressure, defined as $(1-S_A)/S_a$ where S_A is the survival frequency of gene A and S_a is the survival frequency of its allele a. For example, there is a selection pressure of 0.001 in favor of gene a if for every 1,000 a genes that survive only 999 A genes survive (assuming equal numbers of a and A to start with).

Effects of Long-distance Migration between *Isolated Populations*

The calculations of Sewall Wright (quoted in Dobzhansky, 1937) for island models are applicable if the local and distant populations are isolated by a gap across which pollen does not usually travel. In the absence of selection, a migration rate of $m = \frac{1}{2} N_i$ (1 local X distant hybrid per two generations) is the critical value. Lower migration rates will' permit random genetic differentiation between the populations. Migration rates of m $= 4/N_i$ (4 hybrids per generation) or higher will cause the local and distant populations to become the same genetically.

Selection changes the picture, permitting more differentiation with given migration rates. With a selection pressure of s $= 2/N_i$ in favor of the local genes and a long-distance migration rate of m $= 2/N_i$ there will be little genetic differentiation between the local and distant populations. However, if there is selection pressure of $20/N_i$ or greater in favor of a local gene, that gene will remain almost fixed in spite of a long-distance migration rate of m $= 2/N_i$. Conversely, strong selection in favor of a distant gene would result in its replacing the local gene.

As a numerical example assume a local population and:

N_i = 100,000 breeding trees

m = 2/100,000 (2 local × distant hybrids per generation)

s = 1/50,000 in favor of the local gene.

There will be little genetic differentiation between the local and distant populations.

If other conditions remain the same, but s = 1/5,000 in favor of the local gene, the local gene tends to remain nearly fixed.

If other conditions remain the same, but m = 1/200,000 (1 local × distant hybrid each second generation), there is opportunity for genetic differentiation between populations if there is even slight selection pressure.

As shown later, the assumed migration rates of m = 1/50,000 and m = 1/200,000 used in the above example are probably high for populations isolated by as much as 25 miles. Hence, such populations probably could differentiate genetically even in the absence of selection. Since selection pressures as high as 0.1 may be common for genes or genomes (see estimates of selection pressure later), populations occupying different habitats and separated by gaps of 25 miles might become genetically differentiated in spite of higher-than-expected long-distance migration rates.

These calculations apply strictly only if the isolated population is limited to such a small area that there is random gene exchange between all parts of the population. Large isolated populations may be considered as isolated segments of continuous populations.

Effect of Long-distance Migration in Areally Continuous Populations

The mathematics of continuous populations is more complex and has not yet been worked out to include the effects of selection pressure. The following calculations are taken from SEWALL WRIGHT (1943).

If N_u is assumed to be 10, and K_i is less than $1/m$ (less than 1 local × distant hybrid per random breeding unit per generation), the genetic variability among random breeding units is about the same as if there were no long-distance migration.

If N_i is greater than $30/m$ (more than 30 local × distant hybrids in the local population under consideration per generation), there is virtually no random differentiation between the local population under consideration and the distant population.

If N_i = $1/m$, there is from 30 to 50 percent as much random differentiation between the local and distant populations as if there were no long-distance migration. ·

If N_i = $1/1000\ m$ (1 local × distant hybrid in the local population under consideration each 1,000 generations), there is virtually as much random genetic differentiation between the local and distant populations as if there were no long-distance migration.

The above calculations are approximately correct for populations with sizes of random breeding units other than N_u = 10, with the following exceptions. If the random breeding unit is so small (in rare trees) that K_i is more than $3/m$, there is little opportunity for random genetic differentiation between the local and distant populations. If the random breeding unit is very large, containing 1,000 or more trees, gene interchange between neighboring random breeding units is so rapid that there is little opportunity for random genetic differentiation whatever the long-distance migration rate.

A numerical example may clarify the interpretation of the calculations on continuous populations. If

N_i = 1,000,000 trees,

N_u = 50 trees in a random breeding unit,

K_i = 20,000,

$1/m$ = 100,00 (10 local × distant hybrids),

N_i = $10/m$ and there is about 30 percent as much random differentiation between the local and distant populations as if there were no long-distance migration.

If other conditions remain the same, but N_u = 1,000, there is little random genetic differentiation between random breeding units or between the local and distant populations.

If other conditions remain the same, but N_u = 100, and m = 1/1,000,000, then N_i = $1/m$ and there can be about 50 percent as much random genetic differentiation between the local and distant populations as if there were no long-distance migration.

If other conditions remain the same, but N_u = 2, and m = 1/100,000, then K_i = $5/m$ and there can be little random genetic differentiation between the local and distant populations.

Except for the case in which the random breeding unit contains 1,000 trees, these examples are of about equal validity for isolated populations and for segments of continuous populations.

Estimates of „N_u", „m" and „s" in forest Trees

The size of the random breeding unit is governed by population density and short-distance pollen dispersion. (Seed-dispersion distance may be taken as 0 except possibly in some light-seeded species.) There is constant interbreeding between one random breeding unit and its neighbors. According to J. WRIGHT (1952) the random breeding unit in wind-pollinated trees varies from 40 feet (*Pinus cembroides* ZUCC. var. *edulis* VOSS) to 200 feet (*Cedrus* spp.) and possibly to more than 1,000 feet (*Ulmus* and *Populus*) in radius, and contains from 12 (*Fraxinus americana* L.) to 200 trees (*Cedrus atlantica* MANETTI) or possibly more (*Ulmus* and *Populus*) trees. Estimates of 10 to 300 trees are probably valid for most common species growing to large size. The random breeding unit might contain only 2 or 3 trees in very rare or infrequent species.

Extrapolating from J. WRIGHT's actual data according to the curve $y = y_0 e^{-kD}$ (y_0 = source frequency, y = frequency at distance D, k is a constant) gives frequencies of 10^{-3}, 10^{-6} and 10^{-12} (one trillionth) of the source frequency at distances of ½ to 2½, 1 to 5, and 2 to 10 miles respectively from the source.

Unfortunately it is impossible to check the accuracy of the extrapolations from short-distance studies by using data from long-distance studies. In published reports on long-distance pollen dispersion the source has never been stated (nor could it be stated). Even if the source were known, the correct source frequency would be an incalculable number somewhere between the total number of pollen grains produced by all trees in a large area and the number of pollen grains trapped under a single tree. Also, the vacuum cleaners and moss polsters used in many long-distance dispersion studies are more efficient pollen collectors than the sticky slides used to determine source frequencies in short-distance studies.

An indirect estimate of the selection pressures likely to be encountered for some forest tree genes can be made in the following manner. Probably the most efficient way of

determining the amount of the genetic selection pressure against gene **a** would be to cross equal numbers of **AA** and **aa** plants. If this were done, it would be necessary to raise a progeny of at least 1,083 plants to detect a selection pressure of 0.1 or smaller against gene **a**. From this we can reason that we commonly encounter selection pressures of 0.01 or greater for those genes (for hardiness, growth rate, insect resistance, etc.) for which there are any experimental data regarding survival value. The same can be said of zygotic selection against a genome, for which a progeny test of about 400 trees would be needed to detect a selection pressure as low as 0.1.

With random breeding units of 50 to 200 trees, and with long-distance migration rates of the magnitude indicated by extrapolation of the short-distance dispersion data, it is probably safe to neglect occasional pollen transport between populations isolated by as much as 25 miles. This is especially true if there is any selection, because the smallest selection pressure detectable in ordinary forest tree experiments would be high enough to conteract the effects of relatively very high long-distance migration rates.

Fragmentary data on forest trees indicate the essential correctness of the conclusions drawn from SEWALL WRIGHT's calculations. For example, in *Picea* and series Sylvestres of *Pinus* there are 8 reported instances of natural hybrids between species with overlapping ranges, but no reported instances involving pollen transport between isolated species, many of which can be hybridized artificially (Northeastern Forest Experiment Station, unpublished data).

Summary

Whether or not long-distance pollen transport is effective in preventing the genetic differentiation of geographically separated populations depends on the frequency with which hybrids between the two populations are produced and on the selection pressure for or against such hybrids or their derivatives.

SEWALL WRIGHT's mathematical studies are useful in forecasting the amount of genetic differentiation that will take place with different frequencies of hybrid production and selection pressures. Estimates of long-distance pollen migration rates obtained by extrapolation from short-distance dispersion data (the only estimates possible so far) are very small for distances of more than 10 miles, indicating that pollen transport over greater distances is relatively ineffective in preventing genetic differentiation. Indirect estimates of selection pressures operative on forest tree genes are relatively high, indicating that the effectiveness of long-distance pollen transport will be further reduced by selection.

Zusammenfassung

Titel der Arbeit: *Genetische Auswirkungen von Fernpollen.* —

Ob von weit herangetragener Pollen verhindernd auf die genetische Differenzierung geographisch getrennter Populationen wirkt oder nicht, hängt von der Häufigkeit ab, mit der Hybriden zwischen den beiden Populationen erzeugt werden und davon, ob der Selektionsdruck solche Hybriden oder ihre Nachkommen begünstigt oder nicht.

Für eine Voraussage des Ausmaßes der genetischen Differenzierung bei verschieden starker Hybridenbildung und verschiedenem Selektionsdruck sind SEWALL WRIGHTS mathematische Untersuchungen anwendbar. Auf Grund von Schätzungen der Pollenausbreitung über weitere Strecken, die durch Extrapolierung von Ausbreitungswerten auf kurze Entfernungen erhalten wurden (der einzig mögliche Weg), ergibt sich, daß die Ausbreitung über mehr als 10 Meilen (1 Meile = 1,609 km) sehr geringfügig ist, und daß somit über größere Entfernungen herangetragener Pollen relativ bedeutungslos für die Verhinderung einer genetischen Differenzierung ist. Da außerdem der auf die Gene der Forstpflanzen wirksame Selektionsdruck nach indirekten Schätzungen verhältnismäßig hoch angenommen werden muß, ergibt sich, daß die Wirksamkeit eines solchen Fernpollens durch Selektion noch weiter vermindert wird.

Résumé

Titre de l'article: *Considérations d'ordre génétique sur le transport du pollen à longue distance.* —

La question se pose de savoir si le transport du pollen à longue distance peut être ou non un obstacle à la différenciation génétique de populations séparées géographiquement; cette possibilité dépend d'une part de la fréquence avec laquelle les hybrides entre les deux populations sont produits, et d'autre part de la pression de sélection pour ou contre ces hybrides ou leurs descendants.

Les études mathématiques de SEWALL WRIGHT peuvent servir à prévoir et à calculer la différenciation génétique qui peut se produire en fonction de la fréquence de production d'hybrides et de la pression de sélection.

Les estimations des taux de migration du pollen à longue distance, obtenues par exrapolation à partir des données acquises pour la dispersion à courte distance (seules estimations possibles jusqu'ici) sont très faibles pour des distances supérieures à 10 miles, ce qui indiquerait que le transport de pollen sur de longues distances ne constitue pas un obstacle sérieux à la différenciation génétique. Les estimations indirectes des pressions de sélection agissant sur les gênes des arbres forestiers sont assez élevées, ce qui semble montrer que les effects du transport du pollen à longue distance pourraient être ultérieurement réduits par l'action de la sélection.

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