SEROTINITY, GEOGRAPHY, AND FIRE IN THE PINE BARRENS OF NEW JERSEY

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In their study of clinal variation in *Pinus rigida*, Ledig and Fryer (1972) concluded that gene flow is a primary determinant of local levels of serotiny. In this paper I suggest that selection, rather than gene flow, is more important at most geographic scales. My data indicate that the incidence of serotiny reflects local fire history, and that there are clines in the selective forces favoring serotiny. Hypotheses are advanced to account for geographic patterns of fire frequency in the Pine Barrens; the position of the Pine Plains; and the low levels of serotiny found elsewhere on the northern Coastal Plain.

SEROTINITY

Serotiny in gymnosperms is marked by the retention of mature cones that open promptly only after exposure to high temperatures. The proximal cause of serotiny is the high melting point of the resin bond that seals the cone scales (Cameron, 1953). Serotiny is thought to be an adaptation to frequent fires, in that seeds are retained until fire opens suitable sites for seedlings. At the same time, serotiny should be a disadvantage where fires are less frequent or severe, since seeds would be dispersed infrequently to openings caused by disturbances other than fire.

*Pinus rigida*, or pitch pine, is a polymorphic species with individuals having either serotinous or non-serotinous cones; trees with both cone types are rare (Ledig and Fryer, 1972). Indirect evidence from *Pinus banksiana* and *P. contorta* suggests a simple genetic basis for this polymorphism, involving two alleles at a single locus (Teich, 1970; Sittman and Tyson, 1971). Pitch pine ranges from Maine to New Jersey along the New England Seaboard and Costal Plain, inland to Quebec and Ohio, and south to Georgia in the Appalachian Mountains (Critchfield and Little, 1966). Serotinous individuals are rare outside the Coastal Plain, and are most common in the Pine Barrens of New Jersey, a fireswept region of sandy soils dominated by forests of pitch pine, short-leaf pine, and several species of oaks (McCormick, 1970; Ledig and Fryer, 1972). Within the Pine Barrens, serotiny reaches a peak frequency of nearly 100% in the Pine Plains, three tracts of frequently burnt, genetically stunted vegetation (McCormick and Buell, 1968; Good et al., 1979). The Plains appear to burn every 6–8 years, on average, while the surrounding Pine Barrens burn every 16–26 years (Lutz, 1934).

Gene Flow Hypothesis

Ledig and Fryer (1972) envisioned the Plains as an environmental pocket favoring serotiny, surrounded by a less frequently burnt region in which serotiny has either a neutral or negative adaptive value. They documented an apparent cline in the frequency of serotiny with distance from the Plains (Fig. 1), and suggested that gene flow from the Plains was largely responsible for it. They reasoned that if selection, rather than gene flow, outside the Plains were responsible for local levels of serotiny, then a frequently burnt but distant area like the Albany glacial outwash plain should have a high incidence of serotiny, whereas in fact serotiny is rare there.

Ledig and Fryer's analysis can be questioned on several grounds. First, the number of trees in each of their samples is
small (8–12), so that the expected binomial sampling variance is large, with 95% confidence intervals up to ±34.6% in width (Fig. 1). Few of the 21 samples, based on a total of 216 trees, show significant differences from one another. The result of this is that the only trends that emerge above the sampling variance are that serotiny is most frequent in the Pine Plains, least frequent on Cape Cod, and of intermediate frequency elsewhere on the Coastal Plain.

Second, although serotiny in the “frequently burnt” Albany sand plain is reported as rare, no data are given regarding either the historical frequency of fires or the presence of at least some serotinous individuals upon which selection could act. Throughout its range, pitch pine occupies sites disturbed by fire to a greater or lesser degree (Little et al., 1970), yet serotiny is common only on the Coastal Plain. Ledig and Fryer’s argument concerning the Albany site is weakened by their data from a site in Clinton County, Pennsylvania. This site is more remote from the Pine Plains than the Albany site, yet has an estimated 100% incidence of serotiny, and a known history of severe fires.

Finally, Ledig and Fryer’s hypothesis seems to require an exceptionally high level of gene flow. On the one hand, pollen and/or seeds from less than 50 km² of Pine Plains is claimed to maintain a cline hundreds of kilometers long and several thousand square kilometers in extent. In the absence of favorable, large-scale selective clines, this would appear to require characteristic distances of pollen and/or seed movement on the order of tens or hundreds of kilometers (see May et al., 1975; Endler, 1977; and Appendix). On the other hand, if gene flow were really this massive it should swamp the Plains with pollen or seeds from non-serotinous trees elsewhere, since the Plains are only 0.8–5.6 km wide (McCormick and Buell, 1968). Available evidence indicates that the characteristic distance of pollen movement in conifers is actually on the order of tens or hundreds of meters, not kilometers (Colwell, 1951; Wright, 1952; Langner, 1953; Strand, 1957; Wang et al., 1960; Silen, 1962; Endler, 1977; Perry, 1978). Illick and Aughanbaugh (1930) report a characteristic distance of seed movement in *Pinus rigida* of less than 100 m.

**Selection Hypothesis**

To what extent does clinal variation in the incidence of serotiny reflect a cline of selection pressures rather than massive gene flow from the Pine Plains? I propose that local fire history is the selective agent that sets the local frequency of serotiny; that clines in the frequency of forest fires exist in the Pine Barrens and help generate clines in the frequency of serotiny; and that gene flow is unimportant in setting local frequencies of serotiny, except at scales less than a few kilometers over which pollen and seed movement has demonstrable importance (May et al., 1975; Endler, 1977; and references cited above). This is not to say that the occasional movement of pollen over tens of kilometers (Koski, 1967) is without evolutionary significance. However, such long-range gene flow should be more important in introducing genetic variability into a site.
than in determining the frequency of genetic variants there, simply because the few pollen grains so introduced, on average, must compete with millions produced locally.

I shall now outline a model for the maintenance of clines in fire frequency and produce evidence that such clines exist in the Pine Barrens. The presence of these clines suggests a number of tests of the relative importance of gene flow and selection. These tests are applied to data from the central Pine Barrens to determine the role of local fire history, physiography, and gene flow in setting geographic trends in serotiny and the position of the Pine Plains.

Clinal Variation in Fire Frequency

Clines in fire frequency, and thus in the selective forces favoring serotiny, should exist from the edge to the center of the Pine Barrens for the following reasons.

The Pine Barrens are nearly coincident with a geological unit that favors frequent fires. This unit, the Cohansey Formation, is a wedge of unconsolidated sands and gravels of Tertiary age, 45–75 m in thickness near the Atlantic Coast and becoming less thick to the west (Rhodehamel, 1979). In the highly permeable sand, water infiltrates rapidly, so that the soil surface in the uplands is usually arid (Rhodehamel, 1970). The soil is chemically unbuffered, so that it becomes highly acid as litter decomposes and this inhibits further breakdown. Finally, the droughty and acid soil helps prevent canopy closure in a humid climate (Whittaker, 1960), and favors a dense shrub layer. The buildup of dry litter and dense shrubbery is congenial to the initiation and spread of forest fires. Soils outside the Cohansey Formation contain more clay, are thus more retentive of moisture and better chemically buffered, and so are less likely to spawn fires.

Fires should be less frequent near the edge of the Cohansey Formation than at the center, because fires can burn into a given point from fewer directions and distances. Since fires are likely to start only within the Cohansey Formation, and since it is more likely that a fire will burn through a site than originate there, points near the edge should burn less frequently because they have fewer potential sources of ignition. Selection should thus favor serotiny more strongly near the center of the Pine Barrens than near the edge.

Direct historical evidence for this hypothesis is scanty, since accurate records of the position and extent of fires have been kept for only two or three interfering intervals (but see Lutz, 1934). Indirect evidence comes from the pattern of upland succession in the Pine Barrens. Arborescent oaks are less tolerant of fire than pitch pine, and predominate in sites that are less frequently or severely burnt (Burnham et al., 1946; Little, 1952, 1974; Buell and Canton, 1953; McCormick, 1970). This fact can be used with the detailed vegetation map of McCormick and Jones (1973) to infer the pattern of recent fire history in the Pine Barrens.

McCormick and Jones (1973) classify upland Barrens vegetation into two types: pine-oak forest, dominated by pitch pine; and oak-pine forest, dominated by arborescent oaks. These phases do not appear to differ substantially in depth of water table or parent soil material (McCormick, 1970; Givnish, pers. observ.). An indirect index of fire frequency over an area can be obtained by calculating the fraction of uplands covered by pine-dominated woodland. In this study, each 7½' × 7½' vegetation map was divided into quarters and scored for the incidence of pine-oak and oak-pine forest. These measurements were used to construct a contour map of the coverage by pine-oak forests, or the inferred frequency of fires, over the entire Pine Barrens (Fig. 2a).

As expected, the frequency of fires appears to increase from the edge of the Pine Barrens inwards, with the overall pattern being shifted slightly downwind along the predominantly west-to-east wind direction. The area of apparently most frequent fires lies in the widest gap between the firebreaks provided by major river and
swamp systems (Fig. 2b). The apparently low frequency of fires in the southern Pine Barrens may be due to the number of large rivers there (Cohansey, Maurice, Tuckahoe, Egg Harbor) and their general north-south orientation. The higher frequency of fires in the northern Pine Barrens may result from the width of the gap between the Mullica system and Toms River, and from the rivers' predominantly east-west orientation. Human activities that favor oak forests, such as fire-fighting and selective logging of pitch pine, may have been concentrated near the arable soil at the edge of the Cohanse Formation and could be partly responsible for the distribution of pine-dominated woodlands. These activities, however, are likely to promote the competitive ability of non-serotinous trees and so should have an effect qualitatively similar to that produced by a lower natural frequency of fires.

Tests of the Gene Flow and Selection Hypotheses

I propose three tests of the relative importance of local selection and gene flow, and the geographic scales at which they operate in pitch pine.

1. Does the incidence of serotiny decline uniformly in all directions as distance from the Pine Plains increases? If gene flow from the Plains is more important in setting local levels of serotiny, then the rate of decline should be uniform in all directions or, rather, should reflect the distribution of wind velocities during the breeding season (Fig. 3), assuming pine pollen moves much further than the seeds. If selection is more important, then the rate of decline with distance should depend on the pattern of fire history and the decline may not be monotonic. Therefore, the incidence of serotiny should parallel
the contours of inferred fire frequency if selection is more important, and should reflect May wind velocities if gene flow is more important.

2. What is the relation between the fire history of a site and its level of serotiny? If gene flow is significant, then two nearby sites with quite different fire histories should have similar levels of serotiny. If selection is important, then the incidence of serotiny should reflect local fire history. The scale at which selection and gene flow are significant can be estimated by comparing sites with different fire histories at various distances from the Plains.

3. How does the incidence of serotiny vary near watercourses and the edge of the Pine Barrens? If gene flow is the predominant effect, the incidence of serotiny should decline smoothly to the edge of the Barrens and the margin of large rivers. If selection is important, serotiny should decline sharply near the Barrens' edge and near the firebreaks provided by rivers.

**METHODS**

The region intensively sampled (Fig. 4) was chosen because it has the greatest variation in inferred fire frequency, contains the Pine Plains, and covers the gap between the apparently crucial firebreaks caused by the Toms River and the Mullica. It has been developed and disturbed by man relatively little, aside from the lowland cultivation of cranberries and local exploitation for firewood and pulpwood (McCormick, 1970; cf. Wacker, 1979). Much of this area is to be included in a National Biological Reserve mandated by Congress in 1978.

Census sites were chosen at regular intervals along transects, most of which radiate from the West, East, or Spring Hill Plains (Fig. 4). Most sites were located well away from sand roads, avoiding highway margins and recently logged areas. Such cleared areas favor trees with non-serotinous cones by providing openings in the absence of fire, and often had a higher fraction of individuals with open cones than adjacent forest.

Sites were censused from December 1978 to June 1979. At most sites, all trees greater than 1 m high and within 5 m of a straight line walked by the observer were tallied by species. Pitch pines were scored as being serotinous, non-serotinous, mixed, or non-reproductive. Serotinous individuals were those in which most cones of the current and preceding years' crops had remained closed. Non-serotinous trees were those in which most of the current and preceding years' crops had opened. Mixed individuals had an appreciable number of both closed and open cones in both the current and preceding years' crops. Individuals whose current crop of cones was closed, but whose crops of preceding years had opened, were classified as being non-serotinous since cone opening is occasionally delayed from October to April. Sites burnt in the recent past, as evidenced by charred bark and a disturbed shrub layer, were avoided to prevent mis-scoring serotinous cones that had opened after exposure to fire. Non-reproductives were individuals without mature cones. These assessments were made easier by the coloration of cones from November to June in New Jersey. The current year's crop, having ripened
in October, is a rich, nutty brown; previous years' crops are oxidized to a charcoal gray.

Individuals were tallied until a total of 50 serotinous and non-serotinous reproductives had been accumulated at each site. Although the sample size is modest, the census technique is designed to reduce possible error due to local patchiness by increasing the linear distance over which trees are tallied. Care was taken to census after at least three days of dry weather, since the scales of open cones close hygroscopically when wet (Shaw, 1914). During the study, 13 observers censused a total of 274 sites within the 1,900 km² study region, tallying about 13,700 reproductive pitch pines and more than 35,000 individual trees. Complete vegetation data were recorded at 168 sites and tallies only of serotinous and non-serotinous individuals at 106 sites. Average tree height was noted at all sites.

**RESULTS**

Geographic variation in the incidence of serotiny in the central Pine Barrens is shown in Figure 5. Each pie diagram represents a site, with the shaded portion corresponding to the fraction of serotinous reproductives. Mixed individuals were encountered rarely except near the Plains, and even there usually numbered fewer than five per site. Mixed and non-reproductive trees were ignored in calculating the incidence of serotiny.

With the exception of one aberrant sample with 88% serotiny, upland sites in the Plains average 98.8 ± 1.9% serotiny (n = 16) while lowland sites averaged 84.0 ± 5.3% serotiny (n = 3). The frequency of serotiny declines with distance in all directions from the Plains, but sites with 90–98% serotiny are found at distances of 3–19 km to the northeast, southeast, and west of the Plains.
Test 1.—How does the rate of decline in serotiny vary with direction from the Plains? Figure 5 shows there is a general tendency for serotiny to be more frequent downwind (east) of the Plains. To a certain extent, this is expected regardless of the relative importance of gene flow and selection, since both pollen and fire move downwind. However, analysis of transect data suggests that the decline of serotiny with distance from the Plains depends on fire history.

Figure 4 provides a key to the location of transects A through U into which the census sites are grouped. Three kinds of transect data will be examined. First, two paired transects that both run north of the West Plains, one through young pine-dominated forests and another through older, oak-dominated forests, are compared to assess the importance of inferred difference in fire history. Second, a transect from the West Plains through oak-dominated forests into pine-dominated forests is analyzed to assess whether oak forests affect the geographic pattern of serotiny indirectly by acting as partial barriers to gene flow. Third, data from several transects are compared with the specific predictions of the gene flow and selection hypotheses. More rigorous approaches to the role of fire history are then discussed in connection with Test 2.

Consider transects Q and R north of the
West Plains (Fig. 4 and 5). Both bear roughly the same orientation to the Plains and prevailing east-to-west winds. However, transect Q traverses oak-dominated forest while transect R cuts pine-dominated forests (McCormick and Jones, 1973). Along transect Q, the frequency of serotiny falls to 16% in 7.0 km from the Plains, or in 5.3 km from the oak-pine boundary near the Plains. In transect R, the frequency of serotiny remains higher at greater distances, and stands at 86% 8.3 km north of the West Plains and 1.3 km north of transect Q. Both transects cross upland areas essentially uninter rupted by streams and lowlands. Forests along transect R are considerably shorter and less heavily stocked than those along Q, and were largely devastated by wildfires in the summer of 1963 (N.J. Forestry Service Records, Trenton).

Although these results suggest the importance of local fire history in determining the frequency of serotiny over scales of 3–5 km, an indirect effect through gene flow cannot be ruled out. Pitch pine are uncommon in oak-dominated forests, and the penetration of serotiny into or through oak-rich areas may be hampered by poor gene flow. In particular, an area of low pine density could retard gene flow if it lies between two areas of high density (Endler, 1977). Although genes exported by an upwind area of high density could overwhelm the low density area, the low density area would export few pollen grains or seeds and be a poor transmitter of genes from the upwind to the downwind areas of high pine density.

 Transect F running east from the West Plains to the Atlantic Coast provides a test of this hypothetical effect of forest composition on serotiny through gene flow (Fig. 4 and 5). Serotiny declines moderately within 1.6 km of the Plains, from 100% to 72–96%, although one site with 58% serotiny is found just 300 m downwind of Plains sites that show 100% serotiny. An abrupt drop in serotiny occurs within the next 1.6 km, in old, apparently infrequently burnt, oak-dominated forests near Warren Grove. Protected from western fires by cedar swamps and bogs along the Oswego River, this area supports serotiny levels as low as 32% less than 3.2 km downwind of the Plains, and less than 1.6 km downwind of a site having 96% serotiny. Further downwind, 6–12 km from the West Plains, the forest becomes dominated by pitch pine and post oak, species of high fire tolerance (McCormick, 1970). Serotiny ranges from 55%–88% in these forests. The oak-pine forests near Warren Grove extend about 5.5 km from north to south, and about 3 km from east to west, and could be a formidable barrier to gene flow from both the West and East Plains. The high frequency of serotiny in pitch pine-post oak forests in the lee of this barrier strongly suggests that local fire history, and not gene flow moderated by pine density, sets the local level of serotiny.

The selection hypothesis predicts that, in parallel with the transition from pine- to oak-dominated woodlands, serotiny should decline least rapidly northeast of the West Plains, and most rapidly to the east, north, and northeast; and that serotiny should decline more rapidly to the east than to the west of the East Plains (Fig. 2). The gene flow hypothesis predicts that serotiny should decline least rapidly east of the Plains and most rapidly to the west and northwest (Fig. 3). These predictions are tested in this last portion of Test 1.

Serotiny remains at high levels, up to 94%, at distances of 4–19 km northeast of the West Plains along transect D (Figs. 4 and 5). This high level of serotiny corresponds to the long “peninsula” of most frequently burnt forests shown in Figure 4. The highest frequencies of serotiny observed in areas remote from the Plains are seen on this “peninsula,” which lies in one of the most extensive areas largely unbroken by swamps found in the central Pine Barrens, outside the Plains themselves (Fig. 12). As expected according to the selection hypothesis, serotiny is near its lowest level where the transect passes closest to the West Plains, in the oak woodlands near Warren Grove. This drop-off corresponds to the indentation at the base of
The "peninsula" of most frequent fires (Fig. 2), and is a direct contradiction of the gene flow hypothesis. Serotiny declines where the transect enters oak forest 20 km from the Plains, near the transect's terminus.

A similar pattern occurs on transect G (Figs. 4 and 5). Closest to the East Plains, transect G passes through oak-dominated forest to a forest dominated by pitch pine. The latter forest was burnt severely during the 1963 and 1971 wildfires, is short in stature, sparsely stocked with small-diameter boles, and possesses several shade-intolerant shrubs characteristic of the Plains (e.g., *Pyxidanthera barbulata*, *Arctostaphylos uva-ursi*). Arborescent oaks are completely absent. Serotiny increases rapidly from 62% near Warren Grove to 84–94% in the severely burnt area. One sample, an upland site partly protected from fire by an adjacent swamp, had several surviving older trees and a 68% incidence of serotiny. This level is significantly lower than that of neighboring sites closer to and further from the East Plains. It appears to reflect a lower incidence of serotiny in the pre-burn population, since 18 of 20 short reproductives are serotinous whereas only 16 of 30 tall reproductives are. This suggests that a single severe fire can have a profound effect on the local frequency of serotiny. Serotiny decreases to about 54% as transect G enters oak-dominated forest near the coast, and falls away to 18–20% at the coast.

Upwind of the West Plains serotiny declines rapidly (Figs. 4 and 5). Along transect O to Shoal Branch, serotiny decreases exponentially with distance, from 88%–20% in 6.4 km from the Plains (Fig. 6). The lowest frequencies of serotiny occur on necks of land near Shoal Branch, which are apparently somewhat protected from fire and support forests dominated by oaks. Other sites on transect O are dominated by *Pinus rigida*, *Quercus ilicifolia*, and *Quercus marilandica*.

Serotiny also decreases rapidly to the west of the West Plains on transect P (Figs. 4 and 5). In less than 250 m from the western edge of the Plains, serotiny declines from 98–100% to 68–82% in a transition zone between Plains and Barrens. Serotiny hovers near 50% between .4 and 3.2 km from the Plains, and drops to 16–25% 4.5–5.5 km from the Plains in oak-dominated forests. Several kilometers further away, serotiny decreases gradually from 30–36% to values of 18–20% at the Pine Barrens edge.

The rapid decrease in serotiny upwind of the Plains is not entirely due to a lack of gene flow against the prevailing winds. Transects J and N from the western edges of the East and Spring Hill Plains (Figs. 4 and 5) show that serotiny can remain quite common to the windward of the pygmy forests if selective conditions are favorable. Serotiny is about 94–98% at 2.4 km west of the East Plains on transect J, declining only to 84% at 3.7 km. Serotiny is 84–88% at 1.5 km west and southwest of the Spring Hill Plains on transect N, declining to 72% at 3.0 km. The less rapid decline in the frequency of serotiny along these transects, as opposed to those on the western edge of the West Plains, appears to reflect differences in topography. The West Plains borders on the massive lowlands of Shoal Branch and its tributaries, whereas both the East and Spring Hill Plains have several kilometers between their upwind edges and extensive lowlands to the west. Fires should thus de-
crease in frequency more rapidly to the windward of the West Plains than to the windward of the East and Spring Hill Plains. This interpretation is strengthened by the sudden decline in serotiny where transect J from the East Plains enters the lowlands surrounding the Oswego River (Figs. 4 and 5).

Taken as a whole, the transect data indicate the primary importance of fire history, rather than gene flow, in determining the frequency of serotiny near the Pine Plains. Serotiny declines least rapidly to the northeast of the West Plains, and most rapidly to the east, north, and northwest, contradicting the gene flow hypothesis and confirming the selection hypothesis. Serotiny declines most rapidly east-northeast of the East Plains and least rapidly to the west. Based on transects F, J, and P, it would appear that gene flow is important mainly over distances less than 3–5 km. Over smaller distances, isolating the role of gene flow requires a more detailed comparison of the fire history and serotiny level of closely spaced sites. The next section analyzes more directly the role of local fire history and the scale at which genetic differentiation can occur in pitch pine.

Test 2.—How does the frequency of serotiny vary with local fire history? In this section, comparisons are drawn between nearby upland and lowland sites, and among upland sites for which an index of fire frequency, based on forest composition, has been developed.

Upland/Lowland Comparisons

Fifteen pairs of upland sites and 11 paired sets of lowland and upland sites were sampled in this study. Each member of a given pair of sites is located within 100 m of the other. Upland pairs are located in locally uniform vegetation on well-drained soils; upland/lowland pairs are situated near the ecotone between well-drained and frequently inundated soils. Inundated or moist peat soils in the lowlands are not congenial to the spread of ground fires, and fire frequently burns to, but not through the edges of swamps (Little, 1950, 1974; McCormick, 1970).

Serotiny should thus be more common in upland sites than in nearby lowland areas.

Figure 7 shows that all lowland samples have a lower incidence of serotiny than their upland counterparts; the observed difference is significant in 9 of 11 cases. By comparison, the upland pairs show no statistically significant difference in 13 of 15 cases. These data show that marked genetic differentiation in pitch pine can occur within 100 m in the presence of a selection gradient. At the same time, the data suggest that gene flow may also be influential at this scale, since the frequencies of serotiny in paired upland and lowland sites are strongly correlated ($r^2 = .91, P < .01$). For example, lowland sites in the East Plains have 80–82% serotiny, whereas a lowland sample in the less frequently burnt area near the Mullica River (transect M, southwest end) displays 2% serotiny. Given current data, it is impossible to decide the extent to which this correlation results from gene flow or a comparatively similar fire history of nearby upland and lowland sites.

Although the data show consistent dif-
ferences in the selective environment posed by upland and lowland sites, and although uplands do burn more frequently than lowlands in the Pine Barrens, I have not shown that fire history is the selective agent responsible for the different levels of serotiny observed in upland and lowland sites. Other differences between upland and lowland sites, however, appear unlikely to favor reproduction of non-serotinous trees in the lowlands in ways unrelated to fire. For example, tree falls would favor non-serotinous individuals, but do not seem more common in swamp edges and are rare throughout the Pine Barrens; in any case, a higher rate of tree falls in swamps would presumably be related to lower rates of mortality due to fire. The collapse of beaver dams in lowland areas would also open space that would be most readily colonized by non-serotinous trees. However, beavers became extinct in the Pine Barrens around 1820 (Stone, 1908; McCormick, 1970) and have been reintroduced only locally. Finally, trees might grow more rapidly in moist lowland areas, favoring individuals that defer reproduction and allocate energy to competitive height growth. If serotinous individuals were to divert energy to reproduction earlier than non-serotinous trees, and this diversion had a significant impact on height growth, lowland environments might indirectly favor pines with open cones.

Serotiny in Relation to Inferred Fire Frequency of Uplands

McCormick (1970) states that oaks of the Pine Barrens can be classified according to their ecological tolerance of fire, or the ability of populations to compete successfully in areas frequently or severely burnt. Individuals in fire-tolerant species may themselves be fire-resistant, or may possess adaptations enabling their offspring to invade recently burnt areas successfully even if the adults are killed by fire. Scrub oak (Quercus ilicifolia) and blackjack oak (Q. marilandica), two shrubby species that occasionally reach tree size, are the most tolerant of fires and are the oaks usually encountered in the Pine Plains. At the other extreme, white oak (Q. alba), chestnut oak (Q. prinus), and scarlet oak (Q. coccinea) seem least adapted to frequent fires of the species found in the fireswept Pine Barrens. White, chestnut, and scarlet oaks are mostly found in tall, late successional forests 12–16 m in height, with 1,300–2,000 trees/hectare (McCormick, 1970). Post oak (Q. stellata) occurs occasionally in the Pine Plains and appears to be less tolerant of fire than blackjack oak, but slightly more so than black oak (Q. velutina). Black oak, in turn, is more tolerant of fire than white, chestnut, or scarlet oak; it occurs mainly in forests 8–12 m in height, with about 2,500 stems/hectare (McCormick, 1970). There are similar but less detailed rankings, based on sites with known or experimentally manipulated fire histories, given by Little (1946, 1952), Little and Moore (1949), Brown (1960), and Burnham et al. (1947).

The ranking of species by fire tolerance suggests a means of calculating an index of fire frequency or history for each sample site, which could then be related to its frequency of serotiny. Each species can be assigned a number between 0 and 100 that reflects its relative fire tolerance, even if little is known about its absolute tolerance. We can then use these numbers to calculate a weighted average score for each site. If fire-tolerant species are given high numbers, then sites with high scores can be inferred to have had a history of frequent or severe fires. The distribution of each species across sites with differing scores can then be used to calculate a new score for that species, weighted by its abundance at each site. After such new species scores are calculated and normalized so they range from 0 to 100, they can be used to calculate new site scores. This process continues iteratively until species and site scores approach equilibrium values.

This technique is called reciprocal averaging, and seems to be the most robust technique available for ordination, or the ordering of species samples along princi-
pal axes of variation in the sample set (Benzecri, 1969; Hill, 1973; Noy-Meir and Whittaker, 1978; Whittaker and Gauch, 1978). The final scores obtained by this method are independent of the original scores assigned (though they may run from 0–100 or 100–0), and reflect only the major directions of variation in the vegetational landscape sampled. To the extent that these scores correspond to what is known about the fire ecology of oaks, we can use the ordination both to rank all tree species by fire tolerance and to rank each site by fire history.

The 168 samples that include vegetation data were analyzed by reciprocal averaging, with the technique being applied directly to tree counts. The species scores obtained are shown in Figure 8. The ranking of oak species corresponds exactly to McCormick’s ranking by fire tolerance. Species highly tolerant of fires, such as scrub oak, blackjack oak, and pitch pine, received high scores; species of intermediate tolerance, such as post oak and black oak, received intermediate scores; and intolerant species, such as chestnut oak and white oak, received low scores. As expected, swamp species such as Atlantic white cedar (Chamaecyparis thyoides), sour gum (Nyssa sylvatica), and red maple (Acer rubrum var. trilobum) also received low scores. River birch (Betula nigra) occurs mainly in the ecotone between uplands and lowlands (Givnish, 1972), and appropriately received an intermediate score. Shortleaf pine (Pinus echinata) and sassafras (Sassafras albidum) were ranked as relatively fire intolerant, and are known as common invaders of old fields in the Pine Barrens (Little and Moore, 1949). American holly (Ilex opaca) ranks as the least tolerant species, and is largely confined to forests near the Atlantic Coast, to swamps along the Mullica River, and to chestnut oak/white oak forests. Scrub and blackjack oaks receive higher scores than pitch pine perhaps not because they better tolerate fire, but because they are less able to persist in the absence of fire. They become suppressed in closed vegetation and are less successful there than taller pitch pine, so their ecological amplitudes are included within the more frequently burnt portion of that of pitch pine.

The frequency of serotiny is correlated in a highly significant manner with the index of inferred fire frequency, with $r^2 = .341$ and $P < .001$ for 166 degrees of freedom (Fig. 9). A principal axis regression between the frequency of serotiny and ordination score, appropriate since the latter is only a correlate of the underlying causal factor of fire history (Sokal and Rohlf,
Fryer (1969), parallels 83.3% of the total variation in both variables.

Serotiny also shows a negative correlation with distance from the Pine Plains (Fig. 10). This pattern, like the Ledig and Fryer correlation, could arise mainly through gene flow or through a cline in selection pressures. To test between these ideas, the residuals from the principal axis regression were plotted against distance from the Pine Plains, pooling all 168 samples for which ordination scores are available. If distance has an independent effect through its influence on gene flow, sites close to the Plains should show higher levels, and those far from the Plains should show lower levels of serotiny than expected on the basis of their ordination scores. A least mean squares regression indicates no significant relation between the residuals and distance \( r^2 = 0.021, P > 0.05 \). Similar analyses for all points within various distances of the Pine Plains show a substantial residual effect of distance only within 2.5–3.0 km of the Plains (Table 1). Finally, sites grouped into “upwind” and “downwind” classes were analyzed to determine whether distance has a greater residual effect if direction is controlled. In one analysis, sites NW, W, and SW of the nearest Plains boundary were classed as upwind, while those to the NE, E, and SE were classed as downwind. In a second analysis the upwind directions were NW, W, SW, and S, with the remaining directions being downwind. In neither analysis was there a significant residual effect of distance in either the upwind \( r^2 = 0.001, 0.008 \) or downwind \( r^2 = 0.004, 0.031 \) directions. However, the slope of the principal axis regression between serotiny and ordination score was greater for the upwind class in both cases \( y = 3.02x - 153.01 \) and \( y = 2.77x - 133.17 \) vs. \( y = 1.14x - 7.51 \) and \( y = 1.43x - 30.13 \). Downwind sites, as a result, typically have a higher incidence of serotiny for a given ordination score less than 80.
This result may indicate either a cryptic effect of gene flow with no distance dependence over the range examined, or reflect subtle soil differences between the upwind and downwind directions that affect vegetation composition without influencing serotiny.

Test 3.—Does the frequency of serotiny decline markedly near the edge of the Pine Barrens, large rivers, and other massive firebreaks? Serotiny is much less common on the periphery of the study area than in the interior; the 18 sites found within 2 km of the lower Mullica, the western edge of the Pine Barrens, and the coastal marshes and swamps have an average score of 17.2% serotiny. The transition from periphery to interior is abrupt along transects A, B, D, and O and smooth along transects G, I, K, M, and P (Figs. 4 and 5). Serotiny decreases sharply within 1–3 km of the Wading and Batsto rivers along transect M; serotiny is relatively uncommon near and within lowland sites. Figure 11 shows how the frequency of serotiny increases with distance from fire-absorbing barriers; the width of the transition belt near these barriers is about 2–7 km. This is consistent with the findings of Heinselmann (1973) that fires in forests of Pinus banksiana in the Boundary Waters region occur much less frequently within a few kilometers of the firebreaks caused by large lakes. Olsvig et al. (1979) also report that oak forests predominate within 1–2 km of the coast in the Pine Barrens of Long Island. Finally, note that serotiny reaches moderately low levels of 26–30% on Long Beach Island, a sand spit cut off from the mainland and surrounded by Barnegat Bay and the Atlantic Ocean (Fig. 5). The data presented in Figure 11 suggest that sandy regions must be at least 15–20 km in diameter to support the natural frequency of fire and serotiny found in the central Pine Barrens.

**DISCUSSION**

Three lines of evidence suggest that fire history sets the local frequency of serotiny in pitch pine, and that gene flow is rather unimportant at scales of more than a few kilometers. In this section I discuss serotiny on the northern Coastal Plain and in the hybrid zone between pitch pine and pond pine (P. serotina); factors that bear on the geographic location of the Pine Plains; a model for the maintenance of serotinous and non-serotinous trees in populations of pitch pine; and the adaptive significance of serotiny in relation to the distribution of serotinous pines in the United States.

**Areas within the Coastal Plain where Serotiny Is Infrequent**

My analysis can help account for the low levels of serotiny seen on the northern fringes of the Coastal Plain and in the zone where pond and pitch pine hybridize. The hybrid zone fringes Delaware Bay in southern New Jersey, Delaware, and Maryland (Clausen, 1939; Little et al., 1967; Smouse, 1970). Serotiny is relatively infrequent in this area, even though pond pine is almost purely serotinous in the rest of its range (Ledig and Fryer, 1972). Since the hybrid zone is peripheral to the fire region defined by Coastal Plain sands and gravels, and thus should have a low frequency of fires, the infrequency of serotiny is expected. This conclusion is confirmed

<table>
<thead>
<tr>
<th>Distance of sites from Plains (km)</th>
<th>r</th>
<th>Number of sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;1</td>
<td>-.455**</td>
<td>30</td>
</tr>
<tr>
<td>&lt;1.5</td>
<td>-.521***</td>
<td>37</td>
</tr>
<tr>
<td>&lt;2</td>
<td>-.554***</td>
<td>40</td>
</tr>
<tr>
<td>&lt;2.5</td>
<td>-.386**</td>
<td>49</td>
</tr>
<tr>
<td>&lt;3</td>
<td>-.003</td>
<td>56</td>
</tr>
<tr>
<td>&lt;4</td>
<td>.000</td>
<td>65</td>
</tr>
<tr>
<td>&lt;5</td>
<td>-.084</td>
<td>75</td>
</tr>
<tr>
<td>&lt;10</td>
<td>+.164</td>
<td>99</td>
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<tr>
<td>&lt;15</td>
<td>.000</td>
<td>125</td>
</tr>
<tr>
<td>&lt;20</td>
<td>-.161*a</td>
<td>149</td>
</tr>
<tr>
<td>&lt;25</td>
<td>-.164*a</td>
<td>164</td>
</tr>
<tr>
<td>&lt;30</td>
<td>-.145</td>
<td>168</td>
</tr>
</tbody>
</table>

*Note that the correlations for all sites within 20 and 25 km of the Plains are barely significant and explain 2.6% and 2.7%, respectively, of the residual variance.*
by the low proportion of pine-dominated forests in the New Jersey portion of the hybrid zone (Fig. 2).

The infrequency of serotiny on the northern Coastal Plain can be understood in terms of similar considerations. Northward from New Jersey to eastern Massachusetts, the Coastal Plain becomes narrower in extent. The average frequency of fires should thus decrease to the north, because most forests are closer to the edge of sandy soils there. Scarlet oak is infrequent in the central Pine Barrens of New Jersey and is classified as fire-intolerant (McCormick, 1970), but is common in pine woodlands of Long Island and eastern Massachusetts (Jorgenson, 1978; Olsvig et al., 1979). Thus serotiny should be, and is, less frequent to the north.

Glacial history may also have favored this northward decline. During periods of glaciation, the range of pitch pine was probably pushed southward along the Coastal Plain, as was its border with pond pine. Frequent fires on the broad, southern Coastal Plain may have favored the introgression of genes for serotiny from pond pine into coastal populations of pitch pine. As the glaciers retreated, pitch pine extended its range northward again. Serotinous individuals would have been at a double disadvantage during this reinvansion. First, they are poor colonists because they can only disperse to openings caused by fires which affect them as well. Second, the narrowing of the Coastal Plain and consequent reduction in fire frequency northward would have impaired the migration of serotinous genes northward. The low level of serotiny in eastern Massachusetts may represent an equilibrium with current fire frequencies, or a transitory result of impaired migration across the discontinuities that prevail in the Coastal Plain northeast of western Connecticut. Serotinous individuals exist in at least some areas of eastern Massachusetts (Jorgenson, 1978), so that serotiny
ny could have spread locally if selection were favorable, and I therefore doubt the pattern is transitory. The infrequency of serotiny in certain glacial outwash plains (Ledig and Fryer, 1972) may result either from the infrequency of fires in sandy areas of limited extent, or from the selective disadvantage facing serotiny between the Coastal Plain and the outwash plain. If selection within the outwash plains is more important, then serotiny should be more common on larger outwash plains. If selection outside the outwash plains is more important, then serotiny should be absent more frequently in outwash plains more remote from the Coastal Plain.

**On the Location of the Pine Plains**

Several investigators have attempted to explain the geographic position of the Pine Plains, the stunted vegetation rich in serotiny (McCormick and Buell, 1968). They have raised one soil-related factor after another to account for the narrow confinement of Plains vegetation to a particular area, only to see the importance of each cast into doubt. Such factors include soil fertility (Cook, 1868; Redfield, 1889a, 1889b; Smock, 1892; Clute, 1914; vs. Gifford, 1895; Pinchot, 1899; Andresen, 1959); soil pH (Wherry, 1931; vs. Lutz, 1934; Andresen, 1959); soil toxicity (Joffe and Watson, 1934; Tedrow, 1952; vs. Andresen, 1959); soil aridity (Gifford, 1895; Pinchot, 1899; Harshberger, 1916, 1925; vs. Lutz, 1934; McCormick and Buell, 1968); soil microorganisms (Harshberger, 1916; Wherry, 1931; vs. Lutz, 1934; Andresen, 1959; McCormick and Buell, 1968); subsoil hardpan (Gifford, 1895; Pinchot, 1899; Harshberger, 1914a, 1914b, 1916, 1917, 1918, 1925; vs. Lutz, 1934; Andresen, 1959); and deep freezing of Plains soils (Harshberger, 1916; vs. Joffe and Watson, 1933).

Pinchot (1899), Harshberger (1916, 1925), and Seifritz (1953) believed that the Plains vegetation is dwarfed by strong desiccating winds, since it occurs on some of the highest ground in the Pine Barrens. Lutz (1934) showed that wind speeds are greater in the Plains than in Barrens forests, but he considered this a result, rather than a cause of stunted growth. Over 40% of the East Plains is less than 30 m in elevation and is lower than many areas supporting forests elsewhere in the Pine Barrens (McCormick and Buell, 1968; McCormick, 1970).

Biotic factors have also received attention. Certain insects attack pine stump sprouts (Gifford, 1900); tip moths damage some stunted pines (Stevens, 1940); and the collection of pine cones for sale at Christmas may add to the stunting pressures (Little, 1952). However, McCormick and Buell (1968) note that these effects apply only to pitch pine, not to blackjack and scrub oaks, which are also stunted in the Plains.

Most authors believe that frequent fires are responsible for the stunted nature of the Plains vegetation (Gifford, 1895; Gaskill, 1906; Lee et al., 1923; Lutz, 1934; Clements, 1934, 1936; Little, 1946, 1952; Little and Lentz, 1952; Andresen, 1959; McCormick and Buell, 1968; McCormick, 1970). Lutz (1934) estimated from newspaper accounts that fires sweep the Plains two to three times more frequently than nearby forests. Although a soil-related, edaphic factor would have had the advantage of accounting for the sharp boundaries of the Plains, an explanation based only on fire frequency does not. Why do the Plains burn more frequently than the Barrens? Why is this frequently burnt area found where it is?

Lutz (1934) and Andresen (1959) suggested that frequent fires and stunting of the vegetation may reinforce each other. Frequent fires tend to stunt plants if the fire damages the plant crowns. In such stunted vegetation, the more common but less damaging ground fires are more easily converted into devastating crown fires. Thus, once an area has become stunted, it has a greater tendency to remain so by favoring more frequent crown fires. Similarly, once an extensive area has grown into tall forest it should resist conversion into Plains vegetation by not favoring crown fires. The Barrens-fire and Plains-fire systems may thus be alternative equi-
libria in the interaction between fire and vegetation in the Coastal Plain. The Plains phase may be all the more stable because frequent fires favor the evolution of increased investment in belowground organs. Severely burnt saplings of pitch pine in the Plains lose their taproots, produce multiple stump sprouts, assume a shrubby habit, and form a woody stool of callous tissue where roots and sprouts meet. Consequently, they grow in height more slowly (Little, 1952; Little and Somes, 1956, 1964; McCormick and Buell, 1968) and remain capable of converting ground fires to crown fires longer after preceding fires.

This analysis partly explains the stability of the Plains once they were established, but not their origin and current location. I believe the position of the Plains is determined by local topography and its effects on fire frequency. The Plains occur on or near the highest ground in the Pine Barrens and are thus located on the watershed of many streams. As a result, there are no large, fire-absorbing swamps that bisect the West, East, or Spring Hill Plains; lowland areas in the Plains are of quite limited extent and end in cul-de-sacs, so that fires from many directions and distances can burn into the scrubby vegetation. Lutz (1934) has made a similar observation. Further, the West and Spring Hill Plains on the one hand and the East Plains on the other occupy the biggest pockets in the central Pine Barrens that have no streams with broad swamps; they occur in the widest gap between major river systems in the entire Pine Barrens, and are bordered by several other large areas free of riverine swamps (Fig. 12).

Fires should thus have been frequent on the site of the Plains even before a pygmy vegetation had been established. I therefore contend that the pattern of drainage and topography in the central Pine Barrens helped create and helps maintain the Pine Plains in their current location. The boundaries of the Plains, as delimited by Lee and Millen (1919) and recounted by McCormick and Buell (1968) closely parallel narrow swamps along Shoal Branch, Plains Branch, Papoose Branch, and a broader swamp along the Oswego River. Much of the boundary of the East Plains is nearly coincident with poorly defined depressions, inundated for only short intervals, that are dominated by scrubby pitch pines rather than swamp species, and appear to serve as modest barriers that stop but few fires (pers. observ.).

Although this explanation for the location and boundaries of the Plains is plausible, it is curious that a broad lowland along the Oswego River separates the West Plains from the East Plains. Forests there appear to burn frequently and have a high incidence of serotiny, though markedly less than that found in the Plains. In this regard the Plains may have a crucial effect on the fire ecology of the pitch pine lowlands near the Oswego. Several rare species of orchids, notably *Habenaria integrata*, find refuge in the relatively open,
moist pinelands there; for many species, this is one of the few stations or the only station now known in New Jersey (Thomas, 1967).

**Coexistence of Serotinous and Non-serotinous Forms**

*Within pitch pine.*—Since fires favor reproduction by serotinous trees, and since pitch pine usually occupies sites disturbed by fire, the question arises as to how non-serotinous forms are maintained in populations. The following model suggests how a polymorphism in cone behavior can be maintained if serotiny is recessive or dominant; if a distinct heterozygous phenotype exists, various overdominance effects might maintain the polymorphism (Haldane and Jayaker, 1963; Hartl and Cook, 1973; Karlin and Liebermann, 1974; Perry and Lotan, 1979).

In areas infrequently burnt, most patches will have few pitch pines since they are outcompeted by late-successional oaks and other hardwoods. When fire does create openings in a patch, the few serotinous individuals within the burnt patch may not release enough seed to saturate the available seedbed. In this case, non-serotinous trees in areas outside the patch may release most of the seed reaching the patch. An extreme situation would involve such a long interval between fires that all pitch pines in a patch would die before they reproduce within that patch; seeds would be provided by recently burnt, adjacent patches that have a high incidence of pitch pine. The stability of this system increases if there are permanent refuges for pitch pine locally, like highly xeric sites on talus or rock where, aridity and disturbance prevent dominance by mesic, late-successional species.

In areas frequently burnt, enough pitch pine may persist in each patch that a given proportion of serotinous trees releases enough seed that the seedbed is nearly saturated. The equilibrium frequency of serotiny should increase with the frequency and area of fires, since these increase the fraction of a tree’s potential reproduction that occurs in burnt patches where it, too, occurs. The frequency of serotiny should decrease in areas with infrequent, small fires since these favor reproduction by trees not themselves disturbed by a given fire.

If selection favors serotiny only in frequently burnt areas, it should also favor early and heavy allocation to reproduction in serotinous individuals. To the extent that such allocation impairs competitive ability in closed forests by diverting energy from height growth, serotinous trees may face an additional disadvantage in areas with infrequent fires. Frequent fires minimize this disadvantage by opening the canopy and releasing growth by short, suppressed trees. To the extent that serotinous and non-serotinous genotypes are differentially represented in the reproductive and non-reproductive tree pools, future studies should employ techniques that allow resolution of the genotype of non-reproductives.

*Among serotinous pines.*—Most serotinous species or geographic variants of *Pinus* in the United States overlap little, if at all, in range even though they belong to four different sections of the genus (see data of Critchfield and Little, 1966; Vogl et al., 1977). *Pinus clausa* occurs on upland sites where it overlaps the lowland *P. serotina* in Florida. Serotiny is common only in Coastal Plain populations of *P. rigida*, and is rare in the Appalachians where the species co-occurs with *P. pungens*. Pacific and Sierra Nevada populations of *P. contorta* generally are non-serotinous, with the exception of those found on the Mendocino Sand Plains in California (Critchfield, 1957). *Pinus muricata* overlaps *P. contorta* at Mendocino, but the species mainly segregate by substrate there. *Pinus radiata* co-occurs with *P. muricata* at one site on the Monterey Peninsula, and with *P. attenuata* at one site in the Santa Cruz Mountains (Vogl et al., 1977).

By the very nature of the resin seal underlying serotiny, two serotinous species in the same locality would be constrained to disperse their seeds to similar, open habitats at almost exactly the same time,
so that competition during the seedling stage could be severe. Countervailing adaptations in adult behavior and physiology may be insufficiently marked in closely related, wind-pollinated species of *Pinus* to allow coexistence of two serotinous species in the same habitat, and this may partly explain the nearly total allopatriy of serotinous pines. However, serotinous *Pinus contorta* var. *bolanderi* and *Cupressus pygmaea* do overlap almost entirely in the pygmy forests of the Mendocino Sand Plains in California (Westman, 1975; Westman and Whittaker, 1975; Vogl et al., 1977). These areas of extremely poor soils may favor serotiny both by dwarfing the vegetation and by increasing the advantage of seedling into an ashen seedbed. It is curious that most serotinous species of *Pinus* and *Cupressus* in California occur on highly sterile sites, frequently on serpentine (Vogl et al., 1977). The normally non-serotinous Pacific race of *P. contorta* is serotinous where it occurs on serpentine near Gasquet, California (Crichtfield, 1957). Finally, Olsvig et al. (1979) suggest that extremely poor and unretentive soils underly the Long Island Pine Plains, and may indirectly favor dwarf, serotinous *P. rigida* there by prolonging the periods when the litter is dry enough to burn. More research is needed on the synergistic effects of soil and fire on serotiny.

**Summary**

Evidence from 274 vegetation samples of pitch pine in the central Pine Barrens of New Jersey suggests that local fire frequency plays a predominant role in setting local levels of serotiny, contrary to an earlier suggestion by Ledig and Fryer (1972). Data from transect studies show that gene flow from the Pine Plains, an area of fire-swept pygmy forests with a high incidence of serotiny, is not important in setting the frequency of serotiny in other Barrens areas more than 3–5 km away. Significant differentiation occurs between frequently burnt upland sites and rarely burnt lowland sites less than 100 m apart. I analyze the relation between serotiny and fire frequency in upland forests by constructing an index of inferred fire frequency from an ordination of 168 vegetation samples and 14 tree species. Serotiny correlates in a highly significant manner with the inferred fire frequency. After using this relation to remove the effects of differential fire history across sites at various distances from the Plains, I found gene flow to have a significant effect on the frequency of serotiny only within 2.5–3.0 km of the Plains.

These data are related to a model that predicts fire frequency should increase from the edge to the center of the Pine Barrens, based on the premise that the sands underlying the Barrens are the ultimate cause of frequent fires there. This model is validated by an analysis of the geographic distribution of oak- and pine-dominated forests in the Pine Barrens, using the fact that arborescent oaks are less fire-tolerant than pitch pine. As expected, the inferred frequency of fires is greatest in the broadest gap between the firebreaks caused by large rivers and swamps in the Barrens. The Pine Plains occur in the largest area free of major barriers to fire. The rarity of serotiny on the northern Coastal Plain and in the hybrid zone between pitch pine and pond pine may also result from physiographic constraints on fire frequency, and appears to be a consequence of the low incidence of fires expected near the geographic limits of Coastal Plain soils.

**Table 2. Distance (meters) required to change frequency of an allele from 0.8 to 0.2, in terms of the selective advantage (*s*<sub>1</sub>) and disadvantage (*s*<sub>2</sub>) it confers on either side of an ecotone. RMS pollen movement equals 10 m.**

<table>
<thead>
<tr>
<th>s&lt;sub&gt;2&lt;/sub&gt;/s&lt;sub&gt;1&lt;/sub&gt;</th>
<th>Selective disadvantage outside Plains</th>
<th>Selective advantage inside Plains</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1.0</td>
<td>.1</td>
</tr>
<tr>
<td>0.5</td>
<td>33</td>
<td>211</td>
</tr>
<tr>
<td>0.1</td>
<td>99</td>
<td>471</td>
</tr>
<tr>
<td>0.01</td>
<td>312</td>
<td>1,493</td>
</tr>
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</table>
In light of data suggesting a selective advantage of serotinous trees following wildfires, I propose a model whereby serotinous and non-serotinous forms can be maintained in a population. This analysis relates fire frequency to the fraction of seeds dispersed to a burnt patch by trees within that patch; the lower the frequency of fires, the fewer are the number of patches with enough pitch pine to saturate the seedbed available after a fire within that patch, and the greater the reproduction within the patch by non-serotinous trees outside the patch. Highly similar patterns of seedling establishment may partly explain the high degree of non-overlap in the ranges of serotinous species or geographic variants of *Pinus*. The association of serotinous *Pinus* and *Cupressus* with highly infertile soils suggests that soil infertility may favor serotiny by dwarfing the vegetation and making it more arid, thus favoring fires, and by increasing the advantages of seeding into an ashen, fertilized seedbed. Throughout, the synergistic effects of fire, soil, and physiography on serotiny are emphasized.

**Acknowledgments**

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**Literature Cited**


**APPENDIX**

May et al. (1975) state that a cline involving two alleles at a single locus, located near a sharp spatial change in the environment, has a width given by:

\[ w = KL\sqrt{s}, \]

where \( w \) is the distance required to change the frequency of an allele from 0.2 to 0.8; \( L = \sqrt{\int f(x)^2dx} \) is the root-mean-square (RMS) distance of gene flow, with \( f(x) \) the probability that a pollen grain or seed will travel a distance \( x \) from its parent; \( s \) is the selective advantage or disadvantage of each homozygote on either side of the ecotone; and \( K \) is a constant of order unity. May et al. (1975) give a value for \( K \) equal to 1.47 for the following scheme involving symmetric fitness differentials on either side of the ecotone:

\[ F(A_1A_1) = 1 - s, \quad x < 0 \]
\[ F(A_1A_1) = 1 + s, \quad x > 0 \]

\[ F(A_2A_2) = 1, \quad \text{all } x \]

\[ F(A_3A_3) = 1 + s, \quad x > 0 \]
\[ F(A_3A_3) = 1 - s, \quad x < 0, \]

where the magnitude of \( x \) measures distance from the ecotone, and the sign of \( x \) indicates direction. The constant \( K \) has a value of 1.78 if one allele is dominant.

Equation (1) suggests that gene flow near an ecotone is unlikely to create a cline much wider than 2–20 times the RMS pollen movement in Pinus rigida, given any significant selection differentials (0.01 < \( s < 1.00 \)) near the ecotone. Endler (1977) uses the data of Colwell (1951) to calculate \( l = 7 \, \text{m} \) for Pinus pollen. Even if this figure underestimates gene flow by an order of magnitude, the maximum width of a cline near a supposed step change in the environment near the Plains is less than 2 km. If \( s > 0.1 \), then even a RMS pollen movement of 1 km would cause a cline less than 6 km in width. Therefore, except in the unlikely event that \( l > 50 \, \text{km} \), gene flow is unlikely to maintain a cline on the scale envisioned by Ledig and Fryer (1972), given the above fitness scheme.

However, a modest amount of gene flow might maintain a broad cline if the genotypic fitness differentials were *asymmetric* about the ecotone. If serotinous trees have a great advantage over non-serotinous within the Plains, but are only at a slight disadvantage outside, serotiny may decline slowly with distance from the Plains. In the limit as the advantage of non-serotinous trees outside the Plains goes to zero, the width of cline should increase without bound. Haldane (1948) has shown that the following fitness scheme leads to a cline whose width is easily calculated:

\[ F(A_1A_1) = 1 + s_1, \quad x < 0 \]
\[ F(A_1A_1) = 1 - s_2, \quad x > 0 \]

\[ F(A_2A_2) = 1, \quad \text{all } x \]

\[ F(A_3A_3) = 1 - s_1, \quad x < 0 \]
\[ F(A_3A_3) = 1 + s_2, \quad x > 0, \]

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The characteristic width of the cline resulting from this selection scheme for \( l = 10 \text{ m} \) is given in terms of \( s_1 \) and \( s_2 \) by Table 2. The expected width would vary in direct proportion to \( l \) for any other RMS distance of pollen movement. Table 2 shows that, even if selection outside the Pine Plains is only 1% as intense as it is within the Plains, moderate gene flow can only generate a cline with characteristic width of about 5.8 km. If we assume a modest level of selection for serotiny within the Plains \( (s_1 > 0.1) \), then a RMS pollen movement of 100 m would lead to a cline less than 18.5 km long; if selection against serotiny outside the Plains is at least 10% as intense as selection for it within the Plains, an \( l \) of 100 m would lead to a cline only 4.7 km long. Altering the selection scheme given by (3) to allow for a recessive allele for serotiny would slightly increase the widths of clines expected.

ANNOUNCEMENT OF THE THEODOSIUS DOBZHANSKY PRIZE

The Theodosius Dobzhansky Prize of the Society for the Study of Evolution is awarded to a young investigator to aid in the carrying out of research. Money for the prize was collected by a committee of Dobzhansky's friends and colleagues and turned over to the Society for administration. Because of his lifelong interest in young people and his efforts at helping them get started on a research career, it was decided that the proceeds should be used to help support the research of a young investigator. The prize will be awarded for the first time in the summer of 1981 and will be for a maximum of $1000. The intent is that the prize be awarded for research that could not be performed without the financial aid.

Eligibility.—Applicants should have received the Ph.D. degree no earlier than the summer of 1977. The prize may also be awarded to support research for the dissertation. Foreign applicants should be at an equivalent stage of their career.

Application.—The candidate should apply in writing to

Dr. Michael T. Clegg
Department of Botany
University of Georgia
Athens, Georgia 30602

The application should include a 500 word summary of the proposed research, a curriculum vitae and bibliography, and a proposed budget showing any other sources of support. If the candidate has performed any previous research, a 500 word summary should be included. The candidate should also request that two letters of recommendation be sent. If the candidate has a dissertation or any papers published or submitted to journals, it would be helpful but not essential to send copies. Three copies of application materials must be sent. No material can be returned. The deadline for receipt of all application materials is May 1, 1981.

It is possible that the prize will be divided between two or more recipients. The recipient will be notified immediately after the annual meeting of the Society.