Hybridization Between Juniperus Ashei Buchholz and Juniperus Pinchoti Sudworth in Southwestern Texas

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The Botany Department attracted many notable faculty members and students. Distinguished faculty, in addition to Cain and Friesner , included John E. Potzger, a forest ecologist and palynologist, Willard Nelson Clute, co-founder of the American Fern Society, Marion T. Hall, former director of the Morton Arboretum, C. Mervin Palmer, Rex Webster, and John Pelton. Some of the former undergraduate and master's students who made active contributions to the fields of botany and ecology include Dwight. W. Billings, Fay Kenoyer Daily, William A. Daily, Rexford Daudenmire, Francis Hueber, Frank McCormick, Scott McCoy, Robert Petty, Potzger, Helene Starcs, and Theodore Sperry. Cain, Daubenmire, Potzger, and Billings served as Presidents of the Ecological Society of America.

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HYBRIDIZATION BETWEEN *JUNIPERUS ASHEI* BUCHHOLZ AND *JUNIPERUS PINCHOTI* SUDWORTH IN SOUTHWESTERN TEXAS[1]

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INTRODUCTION

This paper presents an analysis of the interactions of two processes, hybridization and differential selection, in the diversification of *Juniperus* where *Juniperus Ashei* Buchholz and *Juniperus Pinchoti* Sudw.[3] occur together. An attempt is made to show man's influence toward accelerating these interactions.

Since the taxonomist is rarely blessed with a natural population which is undifferentiated and the time to watch it go through the throes of evolutionary processes, he must usually work with messy, complex populations and speculate upon historical factors to visualize simpler patterns. In the meantime he must untangle the mosaic of forces and events which have determined the population currently under study. While much has been said about the importance of this factor or that factor in speciation, most naturalists sense that populations of races or species result from the interaction of mosaics of forces and events acting in different combinations and different degrees throughout the various taxonomic groups.

Three major processes, distinct in both operation and result, which may act on a population either simultaneously or successively are inbreeding, differential selection, and hybridization.

Inbreeding, an event producing divergence following spatial isolation, is an important cause of abrupt isolation of segments of an originally undifferentiated population. The separation may be of great magnitude as in those species showing discontinuous distributions in Japan and North America (Asiatic-American disjuncts, Asa Gray, 1846, 1859; A. J. Sharp;

[3] *Juniperus Pinchoti* Sudw. This name is used here in the sense that it is the southern facies or "variety" of *Juniperus monosperma* Sarg. The origin and significance of *J. Pinchoti* is complex and will be presented elsewhere.

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1952); or a matter of a few feet either horizontally or vertically as in the snails, *Achatinella* (J. T. Gulick, 1905) and *Partula* (H. E. Crampton, 1916, 1932) in the Pacific; and the synusial isolation of mosquitos in Trinidad (C. S. Pittendrigh, 1948). Isolated colonies may result from numerous agents: for instance, climatic and topographic changes; disoperations by man such as overgrazing, clearing, and fire; successional mosaics moving toward a climax association; or disjunct dissemination. Gene interchange is restricted with the possible consequent random fixation of non-adaptive characters in small colonies. *Iris setosa* Pall. var. *canadensis* Foster, endemic to eastern Canada, was derived from a small colony of plants isolated from the main body of *Iris setosa* by continental glaciation (E. Anderson, 1936a). Similarly, random fixation has effected pigment genes in the South Sea island bird, *Pachycephala pectoralis* (E. Mayr, 1932). Differential selection seems to be another important force acting on isolated colonies but to produce divergent evolution of adaptive characters, a seemingly acceptable explanation of the odd behavior of sectional characters in *Vernonia* (H. A. Gleason, 1923) where adaptive diversity is great though apparently unrelated to ecologic or physiologic factors. The *Vernonia* pattern is surely the result of the isolation of colonies after expansion by migration. The patterns of racial or even specific differentiation resulting from inbreeding, while not uncommon in other plants, are not evident in *Juniperus*.

The second factor, differential selection, produces divergence consequent to environmental adaptation. Where genotypes persist in the face of the production of abundant hybrid progeny, it is by the selective advantage of the adapted genotypes and the elimination of the hybrids. Numerous ecotypes, races, and species are able to proliferate and evolve because of their tight adaptation to a particular habitat. In *Tradescantia* many species are interfertile and remain distinct because of differences in ecological adaptations (E. Anderson and K. Sax, 1936, and E. Anderson, 1936b). *Tradescantia ohiensis* Raf. is found on open sunny cliff tops among prairie species while *T. subaspera* Ker grows in shady, moist woods at the cliff bases. They may come in contact occasionally along talus breaks where they freely mix. *Juniperus Ashei* Buchholz and *J. virginiana* L. are confined to specific rock strata in the stony lands of the Arbuckle Mountains in Oklahoma, but hybridize freely where the rubble of these strata mix (Hall, 1952a). The leopard frog, *Rana pipiens,* forms a cline correlated with temperature gradients in eastern North America where the terminal forms are so diverged as to have lost interfertility, (J. A. Moore, 1944, 1947). Whether distribution is clinal or discontinuous depends on the pattern of the limiting environmental factors. Species may show clines for one character and ecotypic discontinuities for another. The "niche effect" demonstrates similar complex variability factor by factor.

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Adaptive divergence may result in isolation of populations within species. Where isolating mechanisms are active, clines may eventually be replaced by discontinuities.

The third factor, antithetic to differential selection, is hybridization. It may result in swamping partial discontinuities between divergent populations through the resumption of gene interchange. This return of gene flow is usually the result of a rather catastrophic change in the environment, most frequently man induced. After hybridization between adapted races or species there is further elimination of hybrid genotypes poorly adapted to habitat conditions and increase for those hybrids suited to the disturbed habitat. Populations seem to go through states of tightening up from the effects of differential selection to a loosening from hybridization. Thus evolution both conserves efficiency and produces new trials for achieving new efficiency as changes occur in the environment.

THE HABITAT

The distribution of *Juniperus Ashei* (Hall, 1954) was shown to be a narrow ellipse about 1,000 miles long roughly running from southwestern Missouri to central Coahuila along a northeast, southwest axis. In the northeast the species is disjunct and shows strong introgression from *J. virginiana;* in Coahuila it is again disjunct. The main body of the species, *J. Ashei,* occurs in the Central Texas Section and the Edwards Plateau[4] of Texas. Along the western margin of the range of *J. Ashei* from Saltillo, Mexico, north to the Pecos River and east to about Abilene, Texas, there is abundant evidence of introgression into *J. Ashei* of genes from *J. Pinchoti.* Population samples were made along a curving transect from Dryden, Terrell County, north to Big Spring, Howard County, and east to Abilene, Taylor County, and northwestward to the Palo Duro Canyon, Texas. Further samples of *J. Pinchoti* were collected west across the Trans-Pecos of Texas to determine the extent of introgression in that direction of genes from *J. Ashei.* The massive limestones of the Comanche series[5] from the Cretaceous have been essentially exposed to plant colonization since their seas were drained and their formations were uplifted. The Upper Cretaceous Woodbine merely licked at the northern edge of these massive strata and the recent Gulf invasions likewise never reached as far north as the Balcones fault. These massive aquifers were probably covered with the uniform

[4] The physiographic provinces after N. M. Fenneman, Physiography of Western United States, McGraw Hill, New York, 1931.

[5] The geologic formations referred to in this paper are described in The Geology of Texas, Vol. 1, Stratigraphy by E. H. Sellards, W. S. Adkins, and F. B. Plummer, Un. of Tex. Bull. 3232, 1932.

vegetation characteristic of the Tertiary and developed the more arid modern aspect as a consequence of the changes wrought by the Laramide Revolution which culminated in the Pliocene. The evidence suggests that while the Edwards Plateau was at its highest, *J. Ashei* may have been well isolated from other juniper species. The first species to have contacted *J. Ashei* seems to have been *J. virginiana* from the north and east (Hall, 1952b). Much later, apparently post-settlement, contact was made between *J. Ashei* and *J. Pinchoti* from the west. A wealth of supporting evidence is available from early landholders of the region.

Typical *J. Ashei* is restricted to the thick limestone aquifers from the Balcones Escarpment on the east to the western edge of the high cap from Ranger to Abilene to a few miles south of Barnhart and Rankin to Sheffield and the eastern breaks of the lower Pecos River. *J. Pinchoti* is most abundant on the Permian clays and sands above and below the Callahan Divide and on the clayey conglomeritic or caliche Cretaceous lowlands from San Angelo to Rankin and westward. The two species occur in mixed stands and produce hybrid swarms on the talus of the high escarpment and in limy washes of the lower Pecos breaks from Sheffield to Del Rio. Their habitat requirements are quite distinct. Ashe's juniper requires a good supply of soil moisture, freedom from grazing or browsing damage, a limy substrate, and low competition pressures from grasses. *J. Pinchoti* requires less soil moisture and withstands grazing or browsing pressure easily because of its bud crown. It grows in sand or clay, and competes well with grasses. Like buffalo grass and mesquite, *J. Pinchoti* may occur in playa lakes where its roots survive low oxygen tension.

REVIEW OF MORPHOLOGY

Juniperus Ashei and *J. Pinchoti* are not only in the Sabina section (fleshy berry-cones and scale leaves) but in the same species group (*occidentalis*). Thus one expects rather slight differences in at least several characters. Both species are monospermous with denticulate leaf margins. Both are multi-stemmed xerophytes with *J. Pinchoti* expressing the extreme form in both characters. However, the differences are greater than meet the eye on casual inspection or from studies of only herbarium materials. By contrast these two species are very different in their ecology. *J. Ashei* grows mostly in calcareous soils over aquifers or limy rock talus while *J. Pinchoti* grows in a variety of soil types from sands to heavy clays where it may compete with grasses once germination has been accomplished. Essentially, all junipers require exposed soil for effective germination and seedling survival.

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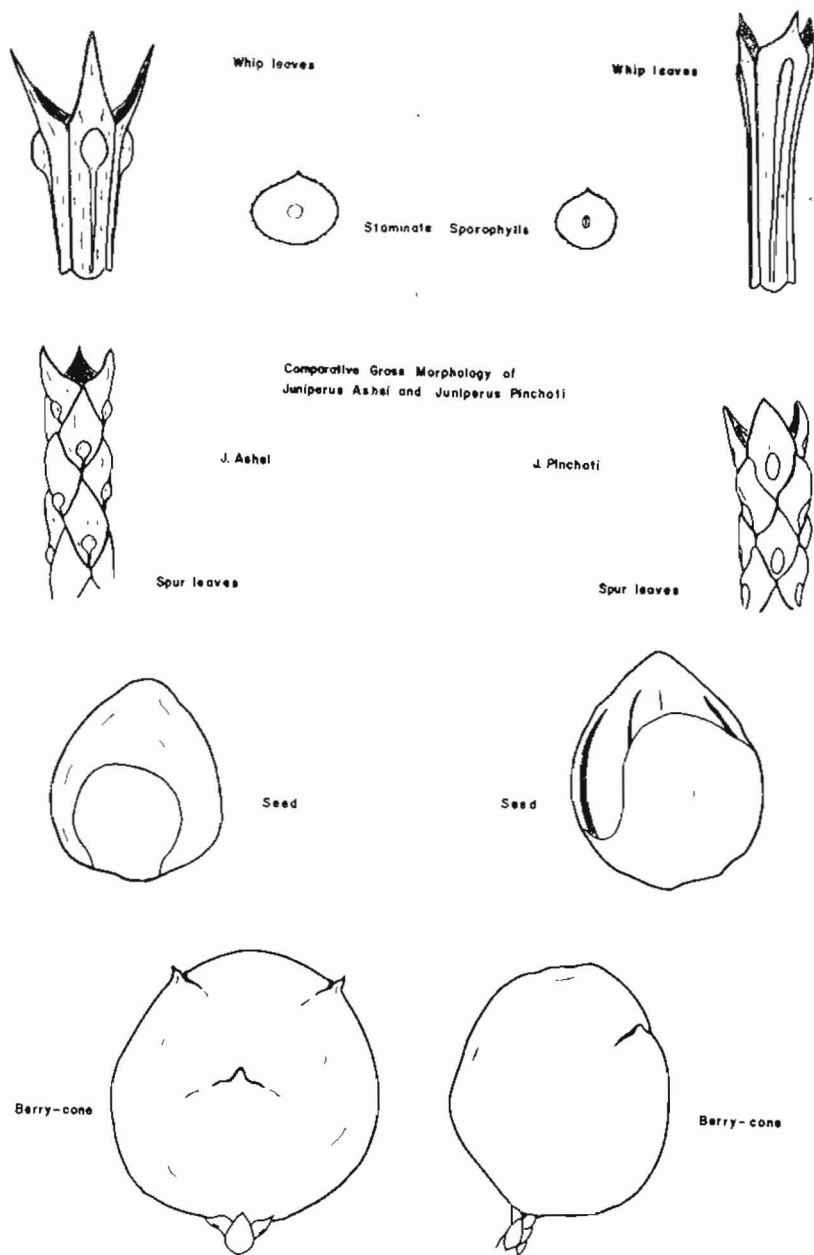FIG. 1 shows the comparative gross morphology of *Juniperus Ashei* and *J. Pinchoti.*

FIG. 1. Comparative gross morphology of *Juniperus Ashei* and *J. Pinchoti.*

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TABLE 1 summarizes the major morphological differences between the two species:

JUNIPERUS ASHEI	JUNIPERUS PINCHOTI
1. Trunk more or less branched above the base, typically a foot or more above the ground level; without bud crown; aspect generally bush-like, often as tall as or taller than wide; height to 35 feet.	1. Trunk branched at or below the ground level; with bud crown; aspect a spreading dwarf, wider than tall; height to 15 feet.
2. Angle of branching of laterals obtuse; branches numerous and uniformly increasing in length back from the tip giving a rounded effect.	2. Angle of branching of laterals acute; branches less numerous and uniformly short back to an occasionally quite long lateral giving a strict wand-like aspect.
3. Foliage dense, mostly ternate, even on ultimate branches. but finer textured than *J. Pinchoti*.	3. Foliage dense, ternate, more coarse in texture.
4. Foliage olive-green, young woody whip bright rust-brown at base changing to dull tan to olive-green at tip.	4. Foliage a lighter, brighter yellow-green. Young woody whip pinkish-red at base changing to orange to yellow-green at tip.
5. Whip leaves average 7 mm. long with a circular raised gland (about ½ mm. in diameter), and a keel extending from the gland to the base of the sheath.	5. Whip leaves average 8 mm. long with a flat, very long, knifeline gland usually the entire length of the leaf, frequently lateral glands 1 to 3 mm. long result in a leaf with triple glands, no keel.
6. Spur leaves 1½ to 2 mm. long. with round gland or frequently eglandular, a slight hinge where blade joins sheath, occasionally a keel.	6. Spur leaves 2 to 2½ mm. long, with flat elliptic or almost round obscure gland or eglandular, no hinge, no keel.
7. Fruit large (6-8 mm. in diameter), resinously aromatic - pungent, azure-blue, slightly bloomy, with slightly resinous juicy pulp. which is black when fresh and rust-brown when dry, fruiting branchlets straight.	7. Fruit slightly smaller (4-7 mm. in diameter), with a mild raw pumpkin odor, rust-brown to rust-red, with thin dry fibrous pulp, greenish when fresh, pale tan when dry, fruiting branchlets straight.
8. Seed chocolate-brown, 5 mm. in length, 1, rarely 2 per berry-cone, sharply pointed conical tip, no pits, occasionally a very narrow longitudinal groove, smooth white hilum covering at least one-fourth the length of the seed.	8. Seed medium tan, 5-6 mm. long filling the fruit tightly, 1, occasionally 2 per berry-cone, blunt to slightly shovel-like tip usually with several narrow longitudinal grooves to the tip, smooth elliptic less distinct hilum covering one-half to two-thirds the length of the seed.

FIG. 2 shows the diagrammatic growth habit and branching pattern in these two junipers. From the axis to the ultimate branchlets, branching achieves the seventh degree in *J. Ashei* and the eighth degree in *J. Pinchoti,* which is the greatest degree known in *Juniperus.* In *J. Ashei* the arrangement of the ultimate branchlets is fairly uniform about the twigs giving a full-rounded aspect, while in *J. Pinchoti* the ultimates tend to branch predominately in one plane producing a fan-like aspect. In the eastern part of the range of *J. Pinchoti,* especially near the edges of the Cretaceous escarp-
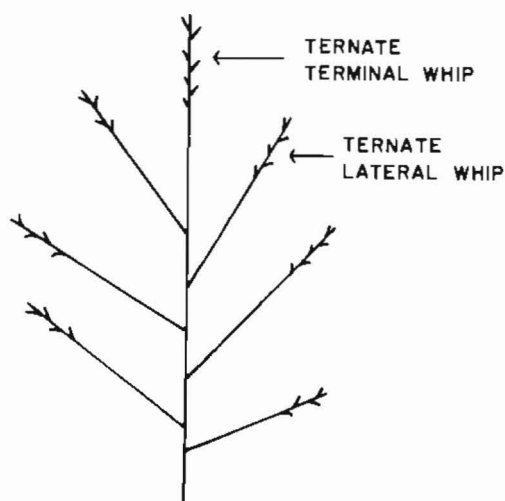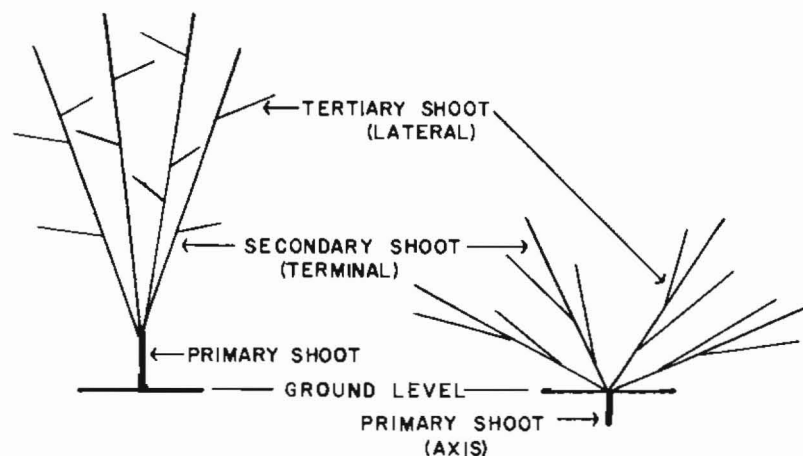

FIG. 2. Above, a diagrammatic representation of growth habit and branching pattern in *Juniperus Ashei* and *J. Pinchoti.* Below, a secondary shoot (terminal) enlarged, for identifying terminology.

ments, the branching tends to resemble that of *J. Ashei*. This is the area where hybrids between the two junipers are common. Farther westward the branching of *J. Pinchoti* becomes more and more fan-like, resembling that of *J. Deppeana* Steud.

The secondary shoot of FIG. 2 shows its morphology and identifies the terminology used with respect to it in this paper. Terminal whip is the long shoot growth which is characterized by long type leaves and borne at the apex of the secondary shoot (second degree of branching). Lateral whip is long-shoot growth at the apex of the tertiary shoot (third degree of branching). The whip is apparently wholly ternate in these two species. The leaves shown in FIG. 1 represent those from typical specimens of *J. Ashei* and *J. Pinchoti*. The long leaves are whip-leaves characteristic of long-shoot growth which occurs terminally on secondary and tertiary shoots. The short leaves are spur-leaves characteristic of short-shoots. While recombinations of leaf characters in the hybrids suggest moderate linkage, they are so distinct as to be readily observed among mixed populations. Again, *J. Ashei* exhibits slightly greater apical dominance with its suppression of lateral long-shoots even though the mass of tissue produced per unit is nearly the same. One may distinguish between the two junipers by the greater terminal and lateral whip of *J. Pinchoti* over *J. Ashei*. There are several variable quantitative characters which differentiate these junipers even though no single key character is dependable.

METHODS

The Population Samples. Analyses of variability for *Juniperus Ashei* have been presented elsewhere (Hall, 1952a, 1952b, 1955). This species shows introgression with *J. virginiana* at the eastern edge of its range along the Balcones Escarpment and northeastward into the Ozark Plateau. Hundreds of population samples have been taken and measured throughout the range of *J. Ashei*. Population 1 of FIG. 3 shows variability of *Juniperus Ashei* from the Central Texas Section and the Edwards Plateau contrasted with the variability of *J. Pinchoti* (Population 13) from the Pecos Valley and High Plains sections of the Great Plains Province. Both species, *Juniperus Ashei* and *J. Pinchoti,* have been sampled and six characters measured throughout the species ranges. This paper is concerned with the region where the two species clearly influence one another. The area of mutual influence is between the 98° and 105° longitude, 29° N to 36° N latitude. This region was covered thoroughly and samples taken wherever juniper populations were substantial. Where plants were sparse, transects over several miles were made. Sample size varied from eight specimens to one hundred specimens with an average of thirty specimens per stand. Even though

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each stand was studied as a whole only healthy plants of the same age class were measured. Collections were made by a wandering L- transect to sample sites varying in topography.

The secondary shoot (FIG. 2) was selected as the most useful material for characterizing variability. Shoots were selected with similar orientation and for their value in characterizing the whole plant. A length of 45 cm. from the tip was chosen as most suitable to give an accurate measure of branching pattern as shown by the angles, lengths, and amount of whip of the tertiary branches. The reliability of the secondary shoot characters was thoroughly discussed in previous papers (Hall, 1952a, 1952b).

Character Analysis. In the stands sampled standardized photographs (to scale) were taken to show variation in habit. The sex was recorded since these are dioecious species. Site factors for each sample were noted in the field books. The following characters were measured for use in scatter diagrams and for further statistical treatment: 1. gland length-width ratio for whip leaves, 2. distance from tip of gland to tip of leaf, 3. length of whip leaf, 4. length of terminal whip (secondary shoot), 5. length of lateral whip (sum of whip on tertiary shoots 45 cm. from the tip of the secondary), 6. berry-cone diameter.

Four of these characters were selected to construct scatter diagrams and population indices: gland length-width ratio, lateral whip length, terminal whip length, whip leaf length. Thirteen populations were selected to show the distribution of variation involving *J. Ashei* and *J. Pinchoti*. These populations are diagrammed in FIGURES 3, 4, and 5.

In woody plants, aspect or habit is frequently a capricious character. However, branching pattern, the relative lengths, positions, and angles of the lateral branches and the branching degree are excellent characters of diagnostic value even in hybrid swarms. Edgar Anderson and Marion T. Hall have made numerous analyses of branching pattern in woody plants: sweetgum, red, sugar, and black maples, hackberry and sugarberry, and several of the shrubby dogwoods. My students and I have analysed branching pattern in *Juniperus* and *Pinus.* These analyses are very useful in showing affinities and recombinations among species groups. They are also easily and accurately accomplished. FIG. 4 shows selected specimens from a hybrid swarm between *J. Ashei* and *J. Pinchoti* in the Pecos watershed between Dryden and Sheffield, Texas. These diagrams are scale drawings of secondary shoots (see FIG. 2) collected from comparable branches of plants of the same age class. The branching patterns of juniper species were carefully studied first to determine what unit would characterize most species. Intra-individual as well as inter-individual variability was determined. A secondary shoot no less than 45 cm. in length was determined to be adequate to characterize the southwestern species. For *Juniperus* these branch-
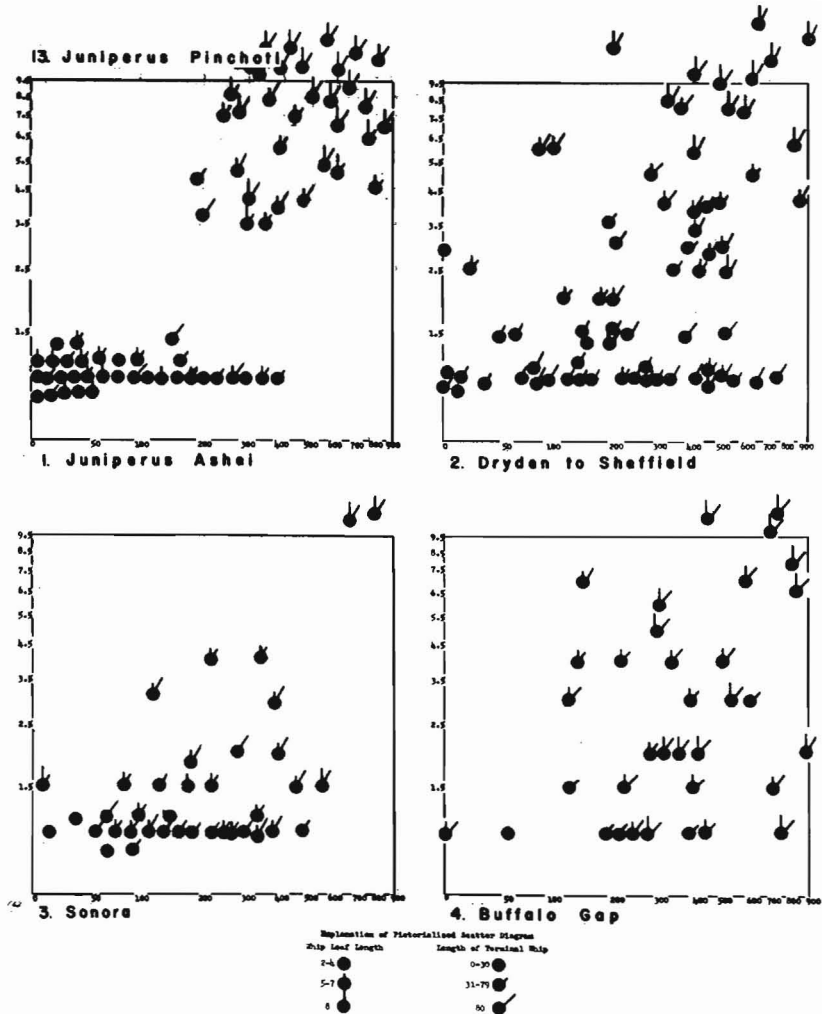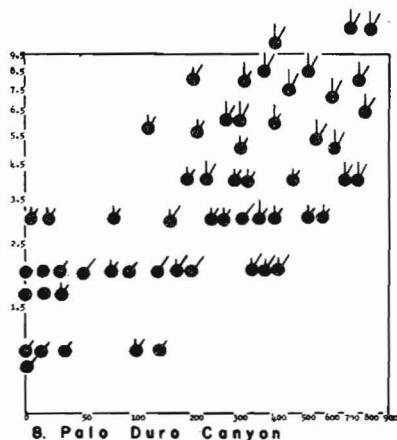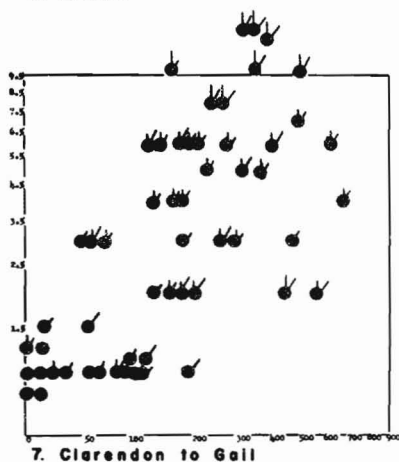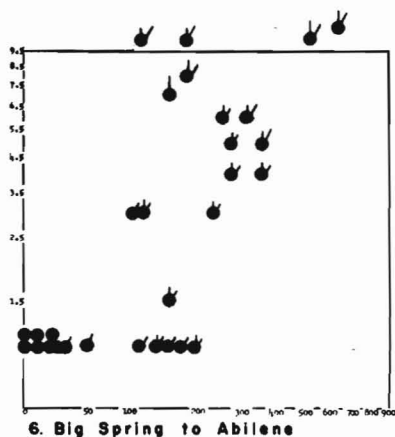
FIG. 3. Pictorialized scatter diagrams of selected populations of *Juniperus Pinchoti* introgressed by *J. Ashei* in central and west Texas. Populations 2, Dryden, Terrell County; 3, Sonora, Sutton County; 4, Buffalo Gap, Taylor County, Texas.
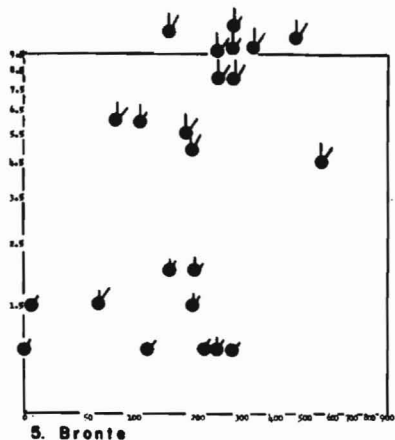
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FIG. 4. Pictorialized scatter diagrams of selected populations of *Juniperus Pinchoti* introgressed by *J. Ashei* in central and west Texas. Populations 5, Bronte, Coke County; 6, Big Spring, Howard County; 7, Clarendon, Donley County; 8, Palo Duro Canyon, Randall County, Texas.
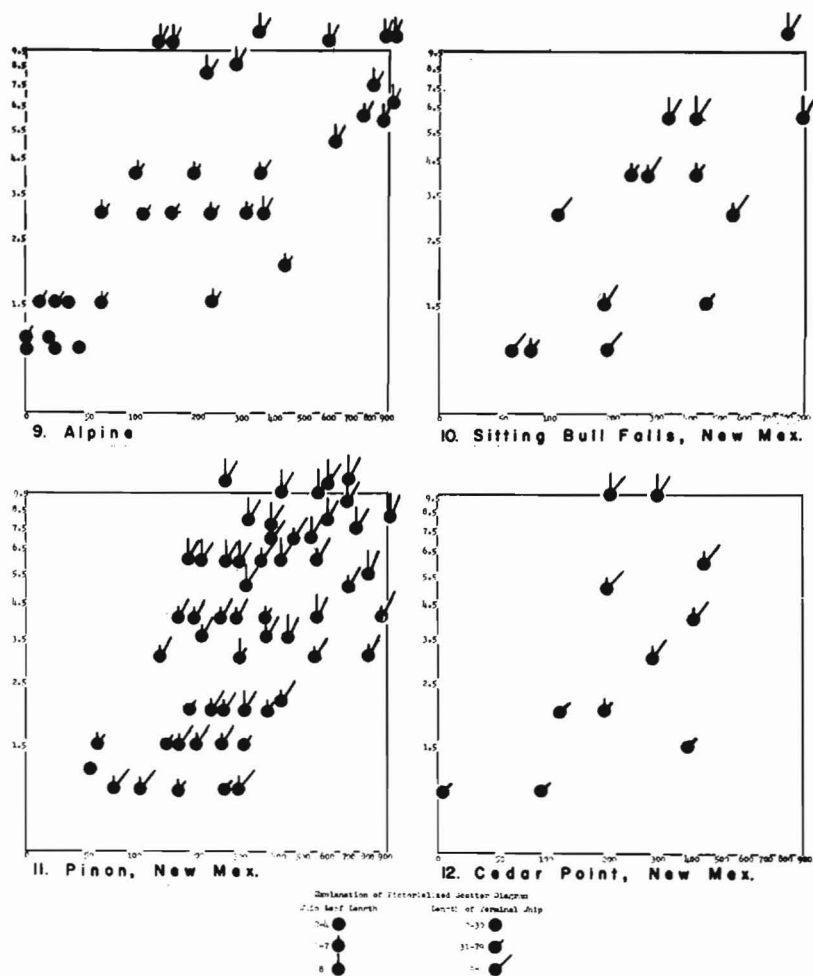
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FIG. 5. Pictorialized scatter diagrams of selected populations of *Juniperus Pinchoti* introgressed by *J. Ashei* in west Texas and southeastern New Mexico. Populations 9, Alpine, Brewster County, Texas; 10, Sitting Bull Falls, Eddy County, New Mexico; 11, Pinon, Otero County, New Mexico; 12, Cedar Point, Chaves County, New Mexico.
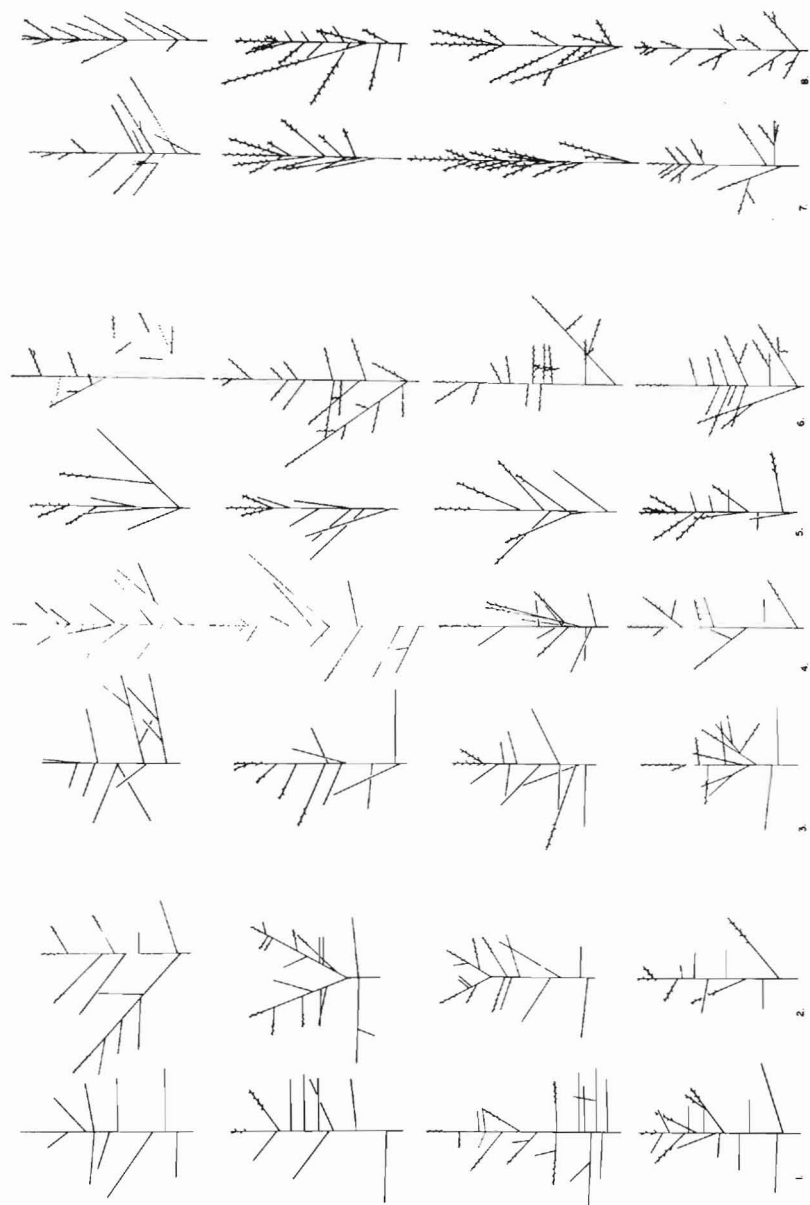
FIG. 6. These diagrams represent the terminal 45 cms. of secondary shoots (see Fig. 2) of *Juniperus Ashei* and *J. Pinchoti*. The two lower rows, 1 and 2, are *J. Ashei;* the two upper rows, 7 and 8, are *J. Pinchoti;* the four middle rows, 3, 4, 5, 6, are hybrids of the two species.

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ing pattern diagrams show six characters: length of tertiary branches, relative spacing of tertiaries, angles of tertiaries, amount of long shoot growth on secondaries, amount of long shoot growth on tertiaries, arrangement of leaves (decussate vs. ternate) on secondaries and tertiaries. Where these characters differ between species, they show such clearly marked recombination patterns in the hybrids to be powerful indicators of affinity to the hybridizing species. Wide recombinations also suggest weak linkage of multiple factors, an impression supported by the spread of characters in the scatter diagrams. The branches of rows 1 and 2, FIG. 6, are to be referred to *J. Ashei,* even though when compared with *J. Ashei* farther east on the Edward's Plateau, these Pecos River specimens suggest some introgression from *J. Pinchoti.* The four middle rows (3, 4, 5, 6) are from hybrid individuals, the third row are individuals resembling *J. Ashei* in these characters, while the sixth row are those closer to *J. Pinchoti.* Branches of rows 7 and 8 are specimens to be referred to *J. Pinchoti,* even though they show quite strong introgression from *J. Ashei* in the lower Pecos breaks.

RESULTS

The pictorialized scatter diagrams (FIGS. 3, 4, 5) show that hybrid swarms between *J. Ashei* and *J. Pinchoti* are well developed from the lower Pecos to Abilene and the Callahan Divide in Texas. Introgression of genes of *J. Pinchoti* are not evident eastward on the summit of the Comanche and Edward's Plateaus where *J. Ashei* is quite homogeneous. However, the introgression of genes of *J. Ashei* westward is another story. The variation spectrum shows some measurable *J. Ashei* influence as far west as the Davis Mountains of Texas north through the Guadaloupe to the flanks of the Sacramento Mountains of New Mexico. However, actual *J. Ashei*-like specimens are rarely found so far westward. Farther north introgression of *J. Ashei* genes are measurable only east of the Pecos Valley along the breaks of the Llano Estacado until they disappear north of Caprock, New Mexico. well south of the Canadian River watershed.

Populations 5, 6 (FIG. 4) show that differential selection is powerfully working on these hybrid populations. The habitats vary with almost knife-line discontinuities, and the populations they support are equally discontinuous though highly variable. Even as far southwest as the Glass Mountains of west Texas, limy moist habitats support hybrids of *J. Ashei* and *J. Pinchoti* very close to the former species while tight, dry clay soils support more typical *J. Pinchoti.* Wherever the habitats are clearly mixed or possess more gradual ecotones, whether at the base of the Comanche Plateau or in the foothills of the Sacramento Mountains over three hundred miles westward, the whole hybrid spectrum between *J. Ashei* and *J. Pinchoti*

occurs with large numbers of intermediates. These two species and their hybrids present a beautifully clear example of the effects of differential selection by the habitat on a complex gene pool.

Analysis of the population behavior of the six characters diagrammed in Fig. 6 likewise supports the results stated above.

The map, Fig. 7, shows the extent of this mutual influence between *Juniperus Ashei* and *J. Pinchoti*. Populations 1, *Ashei* and 13, *Pinchoti* are as "pure" stands of the species as may be found. Populations 2 through 12 show varying amounts of introgression between the species.

A more detailed examination of each population in Figs. 3, 4, 5 clearly show certain significant features concerning the interactions of the two species.

Numerous hybrid swarms at the commissures of the ranges, introgression of Ashe's juniper into Pinchot's juniper clearly measurable as far west as the Palo Duro Canyon and Alpine, Texas, weakly measurable to the Sacramento Mountains of New Mexico, are evidences that there are at most only slight barriers to hybridization between these species. Recombinations are wide and yet linkage is sufficient to show a strong tendency for the characters of the species to stay together. Hybrids, close to Ashe's juniper, with
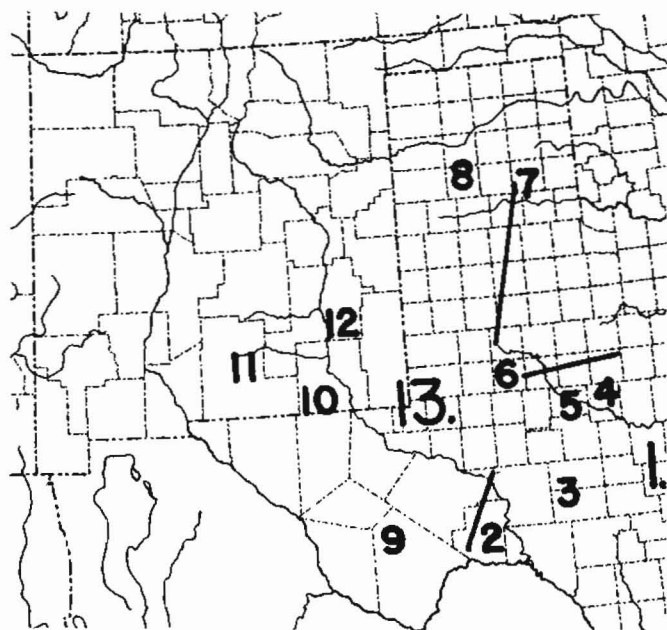

FIG. 7. Distributions of Populations 1 through 13 of Figs. 3, 4, and 5. The inked line represents transect collections. Population 1 is *Juniperus Ashei*; 13 is *J. Pinchoti*; 2 through 12 are populations of *J. Pinchoti* introgressed by genes from *J. Ashei*.

wide angles of branching, also show reduced whip, with few long lateral branches, a tendency for keeled leaves and rounded raised glands while hybrids closer to Pinchot's juniper have acute branching, much whip, numerous long but widely spaced lateral branches, flattened leaves with long narrow ruptured glands. The best developed hybrid swarms are in regions where the species meet with the most favorable soil, moisture relationships. The largest colonies of hybrids are in the breaks on talus and alluvium of the lower Pecos River from Sheffield to Dryden. The talus and alluvium are not only fine reservoirs but are also heavily calcareous in this area. The breaks of the upper Devils River have similar stands but with fewer numbers of *J. Pinchoti* variants. Hybrid swarms are numerous along the talus of the north slopes of the Cretaceous cap to San Saba and the Llano uplift. Hybrid swarms are missing in the Permian from San Angelo, Ballinger, and Paint Rock but develop extensively again about the Callahan Divide from Blackwell to Cross Plains. Here again the Cretaceous talus mixes with the Permian clays and presents a hybrid habitat which supports a broad spectrum of recombinants. Populations 2 (Dryden on the breaks of the lower Pecos,) 3 (Sonora on the breaks of the upper Devils River), and 4 (Buffalo Gap on the Callahan Divide) are seen to be well developed hybrid swarms in well "mixed" habitats. The best development of the *J. Pinchoti* element in the hybrid swarms is in the areas where the rainfall is low enough for the soil factors and topography to become limiting to *J. Ashei*. The Dryden stands (Population 2, FIG. 3) have an 18 inch rainfall with rugged terrain going from hilly talus to rocky limestone streambeds to fairly level clay hardpan areas. Here *J. Ashei* and close recombinants occupy the talus, the limestone washes and streambanks where moisture is normally plentiful. *J. Pinchoti* and recombinants occupy the clayey flats while mixing where the habitats intergrade. This is a very easily observed differentiation after one has learned the junipers. Westward from the lower Pecos the rainfall drops off rapidly so that these areas, such as the Glass Mountains near Alpine (Population 9, FIG. 5) where good talus accumulations are too dry (14 inches) for typical *J. Ashei*, support close recombinants of that species in rocky limestone creekbeds and banks. In dryer areas westward from Alpine (10 to 12 inches) *J. Pinchoti* shows little influence from *J. Ashei* except in more mesic canyons or mountain talus in localized situations (Populations 10, 11, 12 of FIG. 5).

Near Sonora, Texas, the Comanche limestones (Fredericksburg group) form the cap and slopes of the uplands overlooking narrow clayey valleys formed from the Walnut group of rocks. Permian clays are some fifty miles to the north. At Sonora in the Devils River breaks we have a well developed population of *J. Ashei* and introgressants with *J. Pinchoti*. Habitats suitable for more extreme forms of *J. Pinchoti* are restricted, and there are very few

such specimens (Population 3, FIG. 3). This area supports an average annual rainfall of 22-23 inches.

The Callahan Divide supports large numbers of hybrids. *J. Ashei* grows on the mesa tops in Cretaceous limestone soils and on the slopes and colluvial limy material near the bases of the dissected plateau. Farther out, to the north or the south, in the Permian clays, *J. Ashei* disappears and *J. Pinchoti* becomes abundant. At the edges of the divide where the habitats are mixed the hybrids are very numerous. The stand discussed in this paper from the Divide is labelled Buffalo Gap (Population 4, FIG 3). The average annual rainfall at the Buffalo Gap is 24 inches, the most mesic habitat presented in this paper. There is a vigorous growth of *J. Ashei* where the individuals are closely spaced and show well developed whip. *J. Pinchoti* is likewise vigorous, and the hybrids are numerous showing a full spectrum of recombinations.

Where habitats are sharply contrasting the intermediates between *J. Ashei* and *J. Pinchoti* are missing or infrequent. At Bronte in Permian clays of the rough lands of the Colorado River watershed, *J. Pinchoti* is abundant. Where intermittent streambeds drain from the nearby Cretaceous knolls *J. Ashei* recombinants are found. The distribution of juniper in such a site is weakly bimodal with the intermediate spectrum of hybrids poorly developed or missing. The habitat differences, from limy streambed to clayey valley floor, are almost knifeline, and these junipers segregate accordingly (Population 5, FIG. 4). In areas where "parental" habitats do not mix, selection is a powerful force tending to keep the species distinct, yet allowing some introgression.

The stands occurring in Triassic and Permian but close to the Cretaceous cap, from Big Spring to Trent to Abilene, (Population 6, FIG. 4) show a similar pattern as those in the Permian at Bronte. *J. Ashei* recombinants are found in limy streambeds while *J. Pinchoti* recombinants are found on the clayey valley slopes. The average annual rainfall varies from 20 inches at Big Spring to 24 inches at Abilene, enough to support *J. Ashei* where other conditions are suitable.

Farther west in the Glass Mountains northeast of Alpine where the whole landscape is formed from Permian limestones and conglomerates, there are again fairly well developed intermediates between *J. Ashei* and *J. Pinchoti.* Habitat selection is not favoring only the recombinants close to the species. Even here the specimens close to *J. Ashei* are found in the streambeds and those close to *J. Pinchoti* on the rough uplands, a moisture response. Intermediates are relatively numerous. Westward from Alpine, *J. Pinchoti* shows little influence from *J. Ashei.*

To the northwest of the Callahan Divide, hybrid swarms occur along the caprock where limy Cretaceous talus mixes with the calcareous and gypseous Dockum group (Triassic) or where the talus rubble is well charged with

water drained from the caprock as in the upper Palo Duro Canyon. The average annual rainfall varies along the caprock from the head of the Palo Duro where it is 24 inches to Big Spring where it is 20 inches. A transect study of junipers along this caprock (Clarendon, Population 7, FIG. 4) shows *J. Ashei* introgressants in the more mesic areas and numerous intermediates in the area as a whole. However, when one collects westward on the Cenozoic above the caprock little influence from *J. Ashei* is evident in the occasional specimens of *J. Pinchoti.* The major differences in the stands below the caprock from those of the Callahan Divide is the lower vigor and wider spacing of individuals in the more western stands and the lack of quite typical specimens of *J. Ashei* even though close introgressants are not difficult to find.

The upper Palo Duro Canyon (State Park area, Population 8, FIG 4) shows introgression of *J. Ashei* into *J. Pinchoti,* but the juniper populations are much more complex here because of the presence of genes of *J. virginiana* and *J. scopulorum.* A more detailed analysis of variability in *Juniperus* in the Palo Duro Canyon will be reported elsewhere.

Populations 10, 11, FIG. 5 show slight influences from *J. Ashei* genes. These are stands from low summits or mountain talus where soil moisture is more favorable for *Ashei* genes than the intervening desert scrub and grasslands. These stands are further complicated by genes from *J. Deppeana* and will be given a more detailed discussion elsewhere. Population 12 represents the farthest northwest that *Ashei* influence is descernible in stands of *J. Pinchoti.*

Study of these populations (FIGS. 3, 4, 5) show that hybridization and differential selection have played a dynamic role in the development of the southwestern junipers. Unpublished data of the authors' for other southwestern and Mexican species of *Juniperus* suggest the same point.

DISCUSSION

Where internal barriers are weak which is usually the situation where allopatric species are concerned, introgression results in races which grade imperceptibly and smoothly into the parent species (but does not show clinal gradients for different characters); i.e., the closer one approaches the parent species the less easily can morphological evidence of introgression be observed. But where differential selection is strong these dispersed introgressant genotypes "clump together" to form discontinuous ecotypes and sympatric speciation becomes incipient, and internal differentiation within that species is given new impetus. The degree of discontinuity of these ecotypes is a function of the discontinuities of the operational environment which is great in arid areas, less so in mesic areas.

The examples from this paper suggest the complexity which may arise from divergence consequent to environmental adaptation through the agency of hybridization. This is certainly a very general phenomenon able to stamp its influence in whatever degree over great distances.

Indeed, our general experience leads us to the conclusion that racial or specific differentiation in response to selection pressure, i.e., ecotype differentiation, is indeed widespread. Perhaps most natural populations of species undergo this type of stimulation at some stage of their existence. It seems evident that the development of a vigorous gene pool is the experience of most species which are situated in open, rapidly changing habitats. As communities close and the efficiency of the utilization of environmental resources increases the population tends to become either depauperate of biotypes, or perhaps more generally biotypically stabilized. Although adapted and efficient in its own time, a species may depend on its close relatives for rejuvenation, through hybridization, at a future time of radically changing environmental conditions.

SUMMARY

1. *Juniperus Ashei* of central Texas and *J. Pinchoti* in western Texas hybridize where they meet to form hybrid swarms and introgress as far west as the Palo Duro Canyon, and Alpine, Texas.

2. *J. Ashei* is the more mesic species occupying aquiferous limestones; *J. Pinchoti* occupies dry clayey lowlands where it may successfully compete with grasses.

3. Hybrid swarms are best developed in intermediate habitats where the species meet, e.g., Dryden, Sheffield, Texas, upper Devils River, and at the Callahan Divide from Blackwell to Cross Plains, Texas.

4. Introgression of genes of *J. Ashei* into *J. Pinchoti* is measurable from the western Edward's Plateau becoming progressively lower in intensity to the western slopes of the Sacramento Mountains of New Mexico.

5. Bimodal variation is typical of stands growing in habitats where nearly knifeline differences are observed. Where limestone washes (intermittent) with clayey banks sloping to clayey talus support junipers, variants close to *J. Ashei* occupy the limy creekbed, while those close to *J. Pinchoti* occur on the clay slopes. Differential selection in these habitats is quite strong.

6. The results of hybridization and differential selection between these species are marked ecotypic differentiation, enhancement of variability, and increase in survival value as evidenced by recent expansions of stands of introgressants.

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