A TAXONOMIC ANALYSIS OF JUNIPERUS IN THE CENTRAL AND NORTHERN GREAT PLAINS

by

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The junipers constitute one of the most widely used and economically important groups of coniferous plants in Great Plains forestry and horticulture. The extensive use of juniper in shelterbelts, windbreaks, and wildlife and recreational plantings is well known—one has only to look out the window to see some form of *Juniperus* in the landscape plantings around most homes and buildings. The junipers, the third largest genus in the *Coniferales,* are one of the most difficult and confusing groups of plants to identify, however, with over 40 recognized species and perhaps as many as 60 described species (Hall 1961).

The junipers also hybridize freely. Hybrid swarms between eastern redcedar *(Juniperus virginiana* L.) and Rocky Mountain juniper *(J. scopulorum* Sarg.) have been reported (Fassett 1944); between eastern redcedar and horizontal juniper *(J. horizontalis* Moench.) (Fassett 1945b); and possibly between Rocky Mountain juniper and horizontal juniper (Fassett 1945a). Hall *et al.* (1961) reported hybridization between *Juniperus ashei* Buchholz and *Juniperus pinchoti* Sudworth.

Hall (1961) stated that in the New World there are many close relations between species of juniper, which suggests much introgression and possibly occasional swamping of genetic differences whenever species ranges meet and hybrid swarms develop. These hybrid swarms may be extensive and exist in nature for a long time.

Also, man has selected and propagated vegetatively as clones every conceivable kind of juniper from the vast storehouse of variation existing in nature. Many of these variants are, in fact, themselves hybrids containing genes from three or four "species." Frequently, these horticultural forms are grown in such quantities that mutants are occasionally found, and these are then propagated as cultivars. Thus, as the result of man's economic and esthetic interest in the junipers, he has further complicated the variation patterns of many species.

Hall (1961) concluded that the taxonomy of the junipers is not adequately known, and probably will not be known until someone is able to look at our "wild" species as a whole and then fit the cultivated types into a realistic pattern. It would seem that when the taxonomy is worked out there will be fewer named species, more synonyms, more descriptions of the complex variation patterns, and more analyses of the factors responsible for them.

This paper reports on a taxonomic analysis of the *Juniperus* population in the Missouri River Basin, a region encompassing most of the northern half of the Great Plains (fig. 1). This region includes the reported ranges of two arborescent species of juniper important to Plains forestry and to horticulture—Rocky Mountain juniper in the western part of the Great Plains, and eastern redcedar in the eastern part. Fassett (1944), as mentioned above, reported hybrid swarms between these two species within this region.

Nurserymen have found many valuable types for landscaping by selecting and reproducing these plants of mixed lineage. Some well-known horticultural clones selected from Rocky Mountain juniper include Hill Silver juniper, Moonlight, Blue Moon, North Star, Silver Queen, Hill Weeping juniper, Blue Haven, and Montana Green. The Platte River Valley of western Nebraska, the Dakota Badlands, and parts of Wyoming and Montana are rich sources of these variants. Some of the important selections from eastern redcedar include the Canaert juniper, Silver Cedar, Dundee juniper, Cupressifolia juniper, Glauca juniper, Grey Owl, and Nova juniper.

While there are many kinds of junipers available on the commercial market, even the better-established named varieties are often known only by catalog names. Many are difficult, if not impossible, to identify unless the name tags are on the plants. The origin and degree of hybridity of most is, at best, obscure. Undoubtedly, some plants that are called by different varietal names are, in fact, identical. Hall (1961) stressed that selection of junipers to receive horticultural names should be accompanied by careful analysis of their origins.

It is also from this portion of the Great Plains that juniper seed collections are made to supply the millions of seedlings distributed annually through the Clarke-McNary program for shelterbelts and windbreaks. Despite the long use of juniper in Great Plains forestry, much speculation and misunderstanding still exists among experienced foresters about Rocky Mountain juniper and eastern redcedar and their interrelations. It would thus be helpful from both a horticultural and forestry point of view to better understand the nature, extent, and basis of the variation in the *Juniperus* population within this region—as it exists in nature.

MATERIALS AND METHODS

In the fall of 1965, 72 native stands of *Juniperus* were sampled throughout the Missouri River Basin (fig. 1). A minimum of 10 trees old enough to bear reproductive structures and to possess mature foliage were sampled at each collection site. Since the Basin includes a relatively smaller portion of the natural range of eastern redcedar, additional samples were collected through the eastern redcedar range to the Atlantic Coast to gain some insight as to the nature of the more extreme type of eastern redcedar.

A total of 43 characters, including gross morphological, foliage, cone and seed, and biochemical characters, were measured and analyzed to characterize the population. A total of about 700 trees, both ovulate and staminate, were included in the analyses. The population was analyzed by plotting frequency distributions of character values, computing correlation coefficients for all possible combinations of characters, constructing hybrid indices, and arraying hybrid index values and germ plasm percentages geographically. Computers were used in the analysis. Details of sampling procedures and analytical techniques are outlined in a recent publication' entitled "A Population Analysis of *Juniperus* in the Missouri River Basin" (Van Haverbeke 1968).

RESULTS AND INTERPRETATIONS

Frequency Distributions

Frequency distributions of character values indicate the nature of the characters and of population relationships. For instance, when the distribution of the values of a given character shows incomplete bimodality—that is, the occurrence of two interlocking or overlapping curves on the same frequency distribution—the presence of two different but not completely separable germ plasms is suggested. This condition was illustrated by a substantial number of the characters, including percent leaf overlap, branch angle, and optical density of lipid extracts from cone pulp at wavenumber 1735 cm^{-1}.

When the plotted values of a given character produce a normal or nearly normal distribution, as in the character cone width, the variation of this character may be distributed at random throughout the population. However, if all or most character data should result in a series of normal distributions, it would suggest the sample represents members of an interbreeding population. Whether this interbreeding represents a single variable species or a hybrid swarm depends upon whether the characters are correlated. If there is no correlation among characters, a single variable intrabreeding population is indicated as in a variable species. If correlations are established, however, a hybrid swarm is suggested as an explanation as to why these characters tend to occur together.

In this study, the presence of bimodality in the frequency distributions of a substantial number of the characters suggests the presence of two germ plasm systems. Thus hybridization is indicated between Rocky Mountain juniper and eastern redcedar.

Correlations

Correlation coefficients *(r)* were computed for all possible combinations among the 43 characters. A large series of significant relations between characters was demonstrated. For example, a significant relation was established between the biochemical character, optical density of lipid extract from cone pulp at wavenumber 2915 cm^{-1}, and the morphological character, leaf resin gland length (fig. 2). Thus, as the length of the leaf resin gland tended to become longer—from the range of eastern redcedar to and into the range of Rocky Mountain juniper—the absorption of infrared by the longchain hydrocarbons present in the lipid extracts from cones also tended to increase.

The essence of a taxonomic evaluation of any given population is the establishment of the presence or absence of groups of characters that are associated, or correlated, within segments of the population—thus indicating genetic relations. As Ownbey and Aase stated (Benson 1962, p. 276) "The chances of a large series of correlated resemblances coming about by any other pathway than by common ancestry are exceedingly improbable statistically." Thus, the correlation of an eastern redcedar character with any other eastern redcedar character, and the contrasting occurrence of any Rocky Mountain juniper character with any other Rocky Mountain juniper c..aracter, would appear to indicate relations tending toward the parental types.

Hybrid Indices

Hybrid indices, after the method of Anderson (1949), indicated that no trees sampled had the minimum or maximum value for all characters evaluated; thus, neither extreme parental type was sampled (fig. 3). Minimum and maximum hybrid values of only 22 and 81 were attained—as opposed to theoretical values of 0 and 96 for the extreme parental types. These data suggest that the entire population within the Basin is of hybrid origin.

There was a strong tendency toward bimodality, however. This indicates that one segment of the population was characterized by a pattern of associated characters that tended to set it apart from the remainder of the population; the latter segment also had a set of character associations expressing a common pattern among its members. These data can logically be interpreted as indicating the presence of two different, although not completely separated, germ plasm systems (or species) within the Basin—namely, Rocky Mountain juniper (maximal values on the right) and eastern redcedar (minimal values on the left). Hybrid index values in the range of 45 to 50 would be comparable to an F type.

While the hybrid values for trees collected outside the Basin (white bars) tended to be arrayed toward the minimal side of the eastern redcedar portion of the frequency distribution, again the theoretical extreme type was not sampled. The lowest values were recorded in Tennessee, however, where environmental conditions are most unlike those found within the reported range of Rocky Mountain juniper.

The geographic array of hybrid values derived from trees within the Basin showed a bilateral introgressive trend between southeast and northwest over the Basin from the reported range of eastern redcedar into that of Rocky Mountain juniper (fig. 4). This introgressive trend can be followed nicely out the Platte River Valley of central Nebraska, where values of 32, 36, 42, 46, 52, and 60 were recorded.

A zone of hybrid values comparable to an F_1 type was demonstrated along and adjacent to a line extending from extreme eastern Colorado, northward into western Nebraska, diagonally northeastward through southwestern South Dakota and the Badlands, then northward into central North Dakota. These F1 -like values (in the magnitude of 50+ or -) correspond closely to the values in the region of overlap between the two population curves indicated on the preceding hybrid index frequency distribution. However, the trend toward Rocky Mountain juniper on the west side of this zone is much more rapid than is the trend toward eastern redcedar on the east side of the zone. This trend difference is to be expected, since the Ft zone closely parallels the region of more rapid topographic change from a gradual rise in elevation westward across the Great Plains to a more abrupt rise into the Black Hills and the Rocky Mountains. Hence, the total of all the environmental conditions—not just elevation alone—apparently becomes more rigorous in its selection of genotypes tending toward Rocky Mountain juniper on the west side of this zone.

The variability in hybrid indices, as indicated by the plus or minus value following each hybrid index number is generally higher in and near the F1 zone between the two populations. Values of plus or minus 6 or more are common along this zone. Anderson (1949) stated that variation between individuals lessens as parental character combinations are approached.

Variation in other portions of the study area can be explained largely on the basis of: (1) differential selection due to unique environments in isolated habitats, (2) probable introgression with a third species of juniper, and (3) the action of wind, birds, and water in the transport of pollen and seed-bearing cones.

Interpretation

The next logical step in this analysis might be to re-evaluate distribution maps portraying the species ranges of the two major plant populations and their sub-divisions (fig. 5). Although this investigation has confirmed the existence of two basically different groups of junipers within this area of hybridity, and has indicated a zone where the groups might logically be separated, it has also revealed a situation that would be masked by the erection of such arbitrarily established boundary lines —that is, the existence of directional trends strongly indicating interchange of germ plasm between the two species. Definite delineations of species ranges would tend to cause one to again think of all junipers within the confines of the Rocky Mountain juniper range as being entirely Rocky Mountain juniper, and all junipers within the eastern redcedar range as being all eastern redcedar. In reality this is not the case, since these data indicate the presence of some germ plasm from both species throughout the entire population.

We recognize species in terms of pattern perception; that is, certain individuals or groups of individuals are put into this or that species category because they have certain characters in common. Davidson (1952) stressed that uniformity is rare within a given taxon, however, and that one should expect to find variation until constancy has been established.

There is a gradual change in environmental conditions from southeast to northwest throughout the Great Plains. Average annual precipitation decreases, elevation and latitude increase, average annual minimum temperatures decrease, and climatic types change from moist humid to semiarid (Fowells 1965). Since species differ in their genetic constitution, this difference is manifested in their physiological, morphological, and biochemical characters. For an individual to survive, the range of variation in environmental factors must fall within the range of tolerance of the genotype (Callaham 1962). Thus, in the junipers studied, it would be expected that there would be a range of intermediate genetic constitutions viable only in the corresponding ranges of intermediate environmental conditions. Hence, the trees would exhibit a corresponding range of intermediate physiological, morphological, and biochemical characters—each tree having arrived at its balance with its environment on the merits of its own genetic base (Callaham 1962).

Evolution

The preceding data can certainly be interpreted as evidence for introgressive hybridization between Rocky Mountain juniper and eastern redcedar. There is another possible interpretation, however, which is perhaps even more tenable.

As an alternative interpretation, it would seem that, because of the greater diversity of the junipers in the mountains of western North America, eastern redcedar was at some time derived from this region. It seems possible that, with the inherent variability in the germ plasm ancestral to both Rocky Mountain juniper and eastern redcedar, propagules could flourish in sites toward the east. This could have initiated an eastward migration—propagule by propagule—which, through mutation and selection, eventually became what we now recognize as eastern redcedar.

The present study area thus could represent the remnants of one such migration route—along the Missouri and Platte River drainages. Since these propagules still carry a moderate amount of Rocky Mountain juniper germ plasm, recombination would permit offspring to again inhabit a more Rocky Mountain juniper type environment. This would explain the higher hybrid indices found in the more rugged Appalachian areas as contrasted with those of the lower Missouri and Mississippi Valleys. Thus, rather than being considered as an introgressive series, this juniper population can alternately be interpreted as a divergent evolutionary series which has not yet completely separated.

APPLICATION TO TREE BREEDING AND HORTICULTURE

The selection pressures exerted by the environment over long periods of time are exceedingly brutal—only the locally adapted individuals survive. The survival ratio in nature is estimated to be something on the order of one in a million. The survivors are the individuals that have, indeed, passed the test of the "survival of the fit", and thus, accurately portray adapted germ plasm at a given locality.

From the tree breeder's point of view, analyses of plant populations can increase the efficiency of tree improvement programs in that they can quickly show the nature, extent, and basis of geographic variation. Such analyses enable germ plasm of known location and composition to be identified and readily obtained for improved seed source selections or recombination in breeding programs. For instance, if a seed source other than the local source was desired—with a high probability of being adapted at the local site—it would seem prudent to collect seed from sites where the trees have hybrid index values within the range of those found within the local source. In short, the chances of HI 90 or HI 20 material being adapted in an HI 55 locale would not be very promising. If, on the other hand, no local seed source was available to serve as a comparison, then collection of seed from areas with environmental conditions as similar to those at the planting site as possible would be most likely to insure success.

For breeding purposes, hybrid index values can be utilized to achieve new gene combinations with a high probability of being adapted. For example, improvement over a local seed source carrying a hybrid index value of, say, 50 might be achieved by crossing individuals of hybrid index 75 with those of hybrid index 25. The resultant progenies would represent fresh recombinations of germ plasm of approximately HI 50 composition. Many of these individuals should have an excellent chance of being adapted at the local site.

It is appreciated that what we see and describe in the "wild" is a result of the interaction of two influences, heredity and environment. Therefore, the genetic capabilities of an individual or of a population can best be determined—or estimated—by analyzing the effects of environment and genotype in the progeny test under an appropriate set of environmental conditions. In view of the limitations of conventional seed source tests, however, which tend to restrict their fact-finding efficiency and completeness, the analysis of geographic variation should come first (Callaham 1961). Priorities for growing trees under field conditions can then be assigned, favoring those sources or individuals—as revealed through prior taxonomic and biosystematic analyses of the natural population—that are the most likely to be adapted to a particular environment.

Taxonomic analysis of natural plant populations can also serve a useful role to the horticulturist. While *Juniperus* is apparently a very plastic taxon and, thus has a wide range of adaptability, knowledge of the variational patterns in nature can aid in selecting clonal material that will be best adapted under given site conditions. These analyses also make possible the establishment of "standards," to which popular and widely propagated horticultural clones of doubtful origin and composition can be compared taxonomically, and thus be characterized more accurately.

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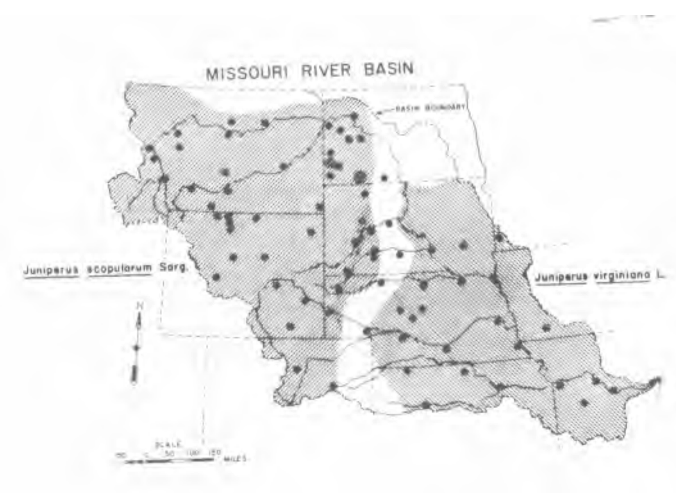

Figure 1—Missouri River Basin, with reported species ranges of *Juniperus scopulorum* Sarg. and I *virginiana* L., major river drainages, and locations of collection sites.

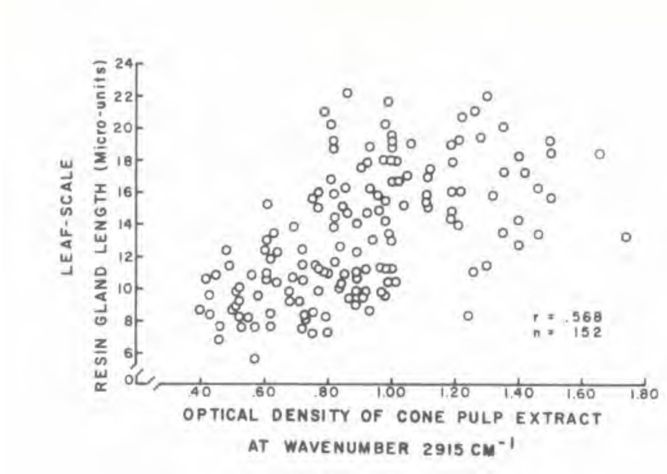

Figure 2—Relationship between optical density of cone pulp extract at wavenumber 2915 cm-/ and length of leaf-scale resin gland for juniper trees sampled throughout the Missouri River Basin (correlation coefficient significant at 1% level; 30 micro-units = 1 mm.).

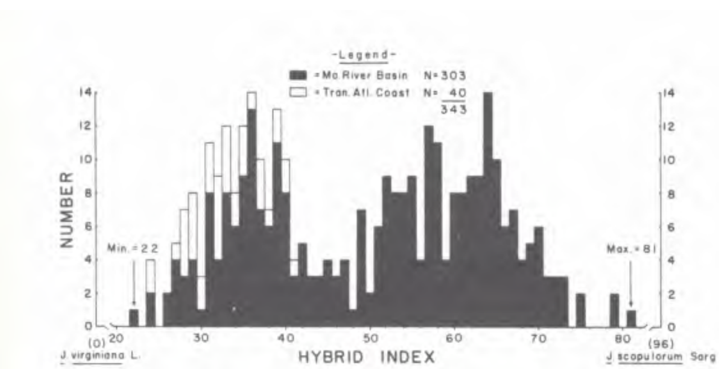

Figure 3—Hybrid index frequency distribution of 343 *Juniperus* trees, based on 24 gross morphological, foliage, and cone and seed characters.

Figure 4—Geographic array of hybrid index values derived from 303 *Juniperus* trees and based on 24 gross morphological, foliage, and cone and seed characters.

Figure 5—Geographic array of percent *J. scopulorum* germ plasm in *Juniperus* throughout the Missouri River Basin.

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