

STUDIES OF THE *PINUS RIGIDA-SEROTINA* COMPLEX II.
NATURAL HYBRIDIZATION AMONG THE *PINUS RIGIDA-SEROTINA* COMPLEX, *P. TAEDA* AND *P. ECHINATA*¹

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ABSTRACT

Patterns of hybridization were studied among *Pinus taeda*, *P. echinata* and the *P. rigida-serotina* complex. Efforts were made to determine the relationships of these taxa to help clarify the taxonomic status of members of the *P. rigida-serotina* complex.

Hybridization between *Pinus taeda* and the *P. rigida-serotina* complex was common, and genetic exchange occurred in both directions. Hybridization between *P. echinata* and the *P. rigida-serotina* complex was more restricted, as was hybridization between *P. taeda* and *P. echinata*. All three of these entities (*P. taeda*, *P. echinata*, and the *P. rigida-serotina* complex) were found to maintain their separate integrities in sympatric populations, in spite of the hybridization.

The aforementioned species distinctions were contrasted with the cohesiveness of the types within the *Pinus rigida-serotina* complex, to explain further the decision by Smouse and Saylor (1973) to denote the components of the complex as subspecies: *P. rigida* subsp. *rigida* and *P. rigida* subsp. *serotina*.

The subsection *Australes* Loud. of the genus *Pinus* L. consists of a geographically cohesive assemblage of species which inhabit the eastern United States and the Caribbean. Individual species extend into Canada (*P. rigida* Mill.) and into Central America (*P. caribaea* Morelet). The geographic ranges of various species within this group overlap considerably, and it is common to find two or more species in intimate contact. Natural hybridization is not uncommon in sympatric populations, and genetic exchange is sometimes extensive enough to create taxonomic problems.

Natural hybridization between the *Pinus rigida-serotina* complex and *P. taeda* is one example. Hybridization between *P. taeda* L. and *P. rigida* Mill. subsp. *rigida* has been reported by Little *et al.* (1967), while similar hybridization between *P. taeda* and *P. rigida* subsp. *serotina* (Michx.) Clausen has been reported by Kang (1966)⁴. Preliminary field observations for the present study indicated the existence of considerable hybridization between *P. taeda* and the transitional type of the *P. rigida-serotina* complex. In addition, hybridization between *P. echinata* Mill. and *P. rigida* subsp. *rigida* has been reported (Austin, 1928).

Because of these complex hybridization patterns and because of previous

¹ Paper number 3679 of the Journal Series of the North Carolina State University Agricultural Experiment Station, Raleigh, North Carolina, U.S.A. This study was supported, in part, by McIntire-Stennis funds (Project 4016) and by the National Aeronautics and Space Administration and the National Science Foundation, which provided fellowship support for the senior author.

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⁴ The classification used in this paper for members of the *P. rigida-serotina* complex follows that proposed by Smouse and Saylor (1973).

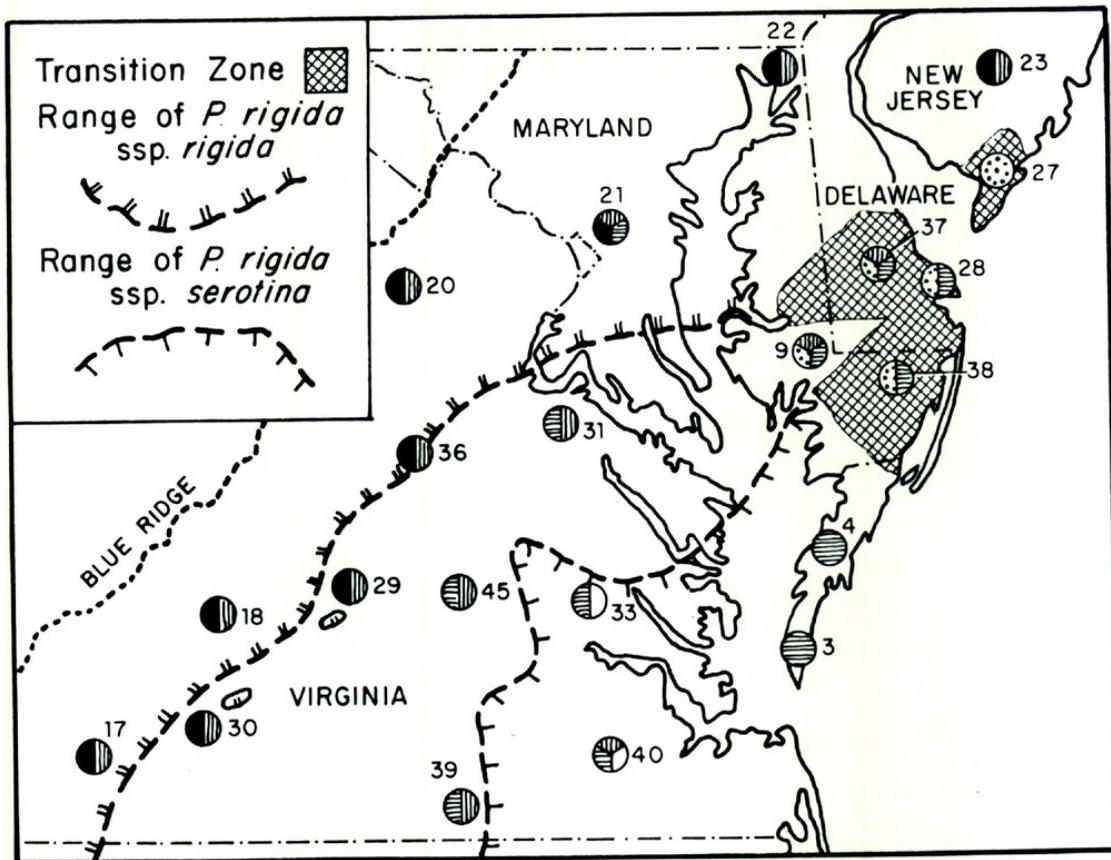


FIGURE 1. Population map of the study area, showing sample locations and taxa present. Solid shading, *Pinus rigida* subsp. *rigida*; no shading, *P. rigida* subsp. *serotina*; dotted shading, transitional type; horizontal shading, *P. taeda*; vertical shading, *P. echinata*.

taxonomic problems associated with members of the *P. rigida-serotina* complex, the present study was proposed to better determine existing relationships among all of these taxa. The specific objective of this paper is to describe the patterns of natural hybridization among the *P. rigida-serotina* complex, *P. taeda*, and *P. echinata* in and near the area of maximum sympatry of all three taxa.

SAMPLING AND MEASUREMENT PROCEDURES

A number of populations located within and near the geographic ranges of *Pinus rigida* subsp. *rigida* and *P. rigida* subsp. *serotina* and within the transition zone between them were chosen for sampling (Fig. 1). The geographic ranges of both subspecies, as well as those of *P. taeda* and *P. echinata*, extend considerably beyond the region sampled; this area was chosen because it represented the zone of maximum sympatry of all three components of the *P. rigida-serotina* complex with both *P. taeda* and *P. echinata*.

An attempt was made to obtain a representative sample of the trees growing at each location. Within each population, a square grid was superimposed upon the ground, utilizing a random starting point; distance between parallel lines of the grid was 50 feet. The nearest cone bearing tree to each grid intersection was selected for sampling. The number of trees sampled was determined by the following schedule:

1 species present	15 trees
2 species present	30 trees
2 species and hybrid suspects present	45 trees
3 species present	45 trees
3 species and hybrid suspects present	60 trees

The location and probable taxonomic identity of each tree sampled was recorded on a map. Populations with two or three species were seldom balanced as to representation in the sample, so an adjustment was necessary to insure an adequate sample of the rarer taxon or taxa. The trees of the most numerous taxon were assigned numbers which were drawn out at random without replacement until only 15 trees remained. The trees whose number had been drawn were deleted from the sample, and areas at the grid intersections represented by the deleted trees were resampled. The nearest tree not of the species deleted was then added to the sample.

In addition to natural hybrids, it was possible to obtain samples from artificial F_1 hybrids of the following crosses: *Pinus rigida* subsp. *rigida* \times *P. taeda* (located at the Wicomico State Forest, Maryland), and *P. rigida* subsp. *serotina* \times *P. taeda* (located at the Westvaco Experimental Forest, Georgetown, South Carolina).

Seven morphological characters were utilized in this study. These traits were: needle length, fascicle sheath diameter, peduncle length, cone length, closed cone diameter, seed wing length, and seed thickness. The traits were chosen on the basis of: (1) accuracy of measurement, (2) availability from the largest number of trees sampled, (3) utility in separating the taxa under consideration, and (4) intermediacy of the values in F_1 hybrids.

ANALYSIS AND RESULTS

The analysis proceeded in two stages. The first step was to adjust each taxon to the location in question by removing morphological variation associated with environmental differences. The second step was to determine which of the possible taxa constituted the most likely parents of each putative hybrid specimen and to determine the pattern of hybridization. These two operations are described in sections on *Geographic Variation* and *Canonical Analysis*.

Geographic Variation: Each of the four taxa exhibited morphological variation from population to population. Since it was desirable to analyze hybridization at each location separately, it was necessary to construct taxonomic standards of comparison which allowed for such geographic variation. While it was clear that each of the taxa actually growing at the location should be represented, it was also clear that a taxon need not be currently present to have been involved in hybridization.

For locations in and near the range of *Pinus rigida* subsp. *rigida*, putative hybrids were compared with *P. rigida* subsp. *rigida*, *P. taeda*, and *P. echinata*; whereas for those locations in and near the range of *P. rigida* subsp. *serotina*, putative hybrids were compared with *P. rigida* subsp. *serotina*, *P. taeda*, and *P. echinata*. For locations within the *P. rigida-serotina* transition zone, putative hybrids were compared with the transitional type, *P. taeda*, and *P. echinata*. The

threeway division of the locations into those with *P. rigida* subsp. *rigida*, those with *P. rigida* subsp. *serotina*, and those with the transitional type was based on the finding that the three taxa constituted a single geographically variable complex, in which only one type occurred at any given location (Smouse & Saylor, 1973).

Each taxonomic standard (an array of seven character means and a covariance matrix describing the variation) was constructed in one of two manners. If a taxon were actually present at the location, the character means for that population were used. The measure of variation employed was the average within population covariance matrix for that taxon.

If a taxon were not present, it was necessary to construct an abstract image of what it would look like if it had been present. Before this could be done, however, it was necessary to describe the association of the seven morphological variables with the geographic and environmental variation within each taxon. To accomplish this, information was used from a companion study (Smouse & Saylor, 1973) for *Pinus rigida* subsp. *rigida* and *P. rigida* subsp. *serotina* from populations to the north and south of the transition zone. The only samples of *P. taeda* and *P. echinata* available were those shown in Figure 1. The description of the association between morphological appearance and geographic location was accomplished by means of unweighted multiple regression analyses of the seven character variables on four environmental measures—(1) latitude, (2) elevation, (3) a measure of potential annual incident solar radiation, and (4) a measure of site productivity. The first two were used in logarithmic form, because a better description of geographic patterns was possible using the two variables in this form. The second two variables are defined in Smouse (1970) as are the computational details of the regression analyses.

The final result of this operation was a set of regression equations describing the association of morphological and environmental factors within each taxon. With this set of equations, it was possible to predict by standard multivariate regression procedures the seven character means and the corresponding covariance matrix for each of the taxa at any given location. (The estimated means and variances for all locations are given in Table 1.)

Canonical Analysis: Once the taxonomic standards for the three taxa were constructed at each location, it was possible to determine which taxa were the most likely ancestors of a particular hybrid specimen. The method employed was a canonical rotation of axes, details of which are described by Smouse (1972). This technique gives rise to a two dimensional, equilateral triangle of three species, which in turn can be divided into three hybrid regions (corresponding to three types of two-taxon hybrids) by bisecting the angles of the triangle (Figs. 2–4).

For the present study, the coordinates of each putative hybrid specimen at each location were plotted, along with those of artificial F_1 hybrids of *Pinus rigida* subsp. *rigida* \times *P. taeda* and *P. rigida* subsp. *serotina* \times *P. taeda* (Figs. 2–4). Preliminary laboratory designations were attached to each putative hybrid on the basis of a thorough visual examination.

It can be seen from the figures that the *a priori* and *a posteriori* designations

TABLE 1. Estimated population means and variances for the various taxa.

Population	Taxon ^a	Character means and variances ^b						
		Y ₁	Y ₂	Y ₃	Y ₄	Y ₅	Y ₆	Y ₇
(03)	T	193(351)	213(443)	1(5)	86(105)	34(10)	24(11)	243(431)
	S+	176(527)	247(507)	11(11)	61(53)	41(21)	22(9)	164(221)
	E+	91(187)	162(307)	5(3)	47(30)	21(5)	18(4)	191(265)
(04)	T	177(351)	197(443)	0(5)	87(105)	33(10)	26(11)	255(431)
	S+	178(562)	252(541)	11(12)	63(56)	41(23)	21(10)	162(236)
	E+	92(192)	165(315)	6(3)	51(31)	23(5)	18(4)	187(272)
(33)	T	195(351)	247(443)	1(5)	82(105)	31(10)	24(11)	248(431)
	S	167(404)	248(445)	10(10)	60(46)	37(16)	22(9)	158(190)
	E+	86(175)	157(288)	6(3)	47(29)	21(4)	17(4)	187(248)
(39)	T	180(351)	231(443)	1(5)	81(105)	32(10)	24(11)	251(431)
	S+	185(583)	256(560)	13(13)	54(58)	35(23)	22(10)	167(244)
	E	82(117)	142(262)	6(2)	44(25)	20(4)	16(3)	189(244)
(40)	T	189(351)	233(443)	1(5)	84(105)	35(10)	27(11)	255(431)
	S	183(404)	256(445)	14(10)	58(46)	40(16)	22(9)	171(190)
	E	87(117)	156(262)	6(2)	44(25)	19(4)	16(3)	181(244)
(09)	T	189(351)	224(443)	1(5)	87(105)	36(10)	29(11)	254(431)
	RS	156(271)	259(273)	13(6)	64(33)	36(12)	25(5)	155(214)
	E	83(117)	157(262)	4(2)	45(25)	22(4)	17(3)	192(244)
(27)	T+	181(412)	232(583)	3(5)	85(117)	35(13)	27(13)	234(493)
	RS	129(271)	230(273)	5(6)	66(33)	40(12)	24(5)	165(214)
	E+	80(177)	163(290)	5(3)	44(29)	21(4)	16(4)	183(251)
(28)	T	187(391)	218(443)	4(5)	92(105)	38(10)	26(11)	224(431)
	RS	133(271)	250(273)	9(6)	67(33)	39(12)	23(5)	177(214)
	E+	84(190)	167(312)	4(3)	42(31)	20(5)	17(4)	190(270)
(37)	T	185(351)	227(443)	1(5)	88(105)	37(10)	26(11)	232(431)
	RS	151(271)	239(273)	8(6)	61(33)	38(12)	22(5)	170(214)
	E	78(117)	170(262)	7(2)	50(25)	22(4)	15(3)	180(244)
(38)	T	172(351)	231(443)	1(5)	78(105)	32(10)	24(11)	224(431)
	RS	148(271)	237(273)	8(6)	56(33)	34(12)	21(5)	153(214)
	E+	80(172)	157(282)	5(3)	44(28)	20(4)	16(3)	186(243)
(17)	T+	181(528)	231(748)	4(7)	71(150)	32(17)	23(17)	222(632)
	R	124(188)	255(403)	6(5)	55(44)	35(10)	20(7)	180(198)
	E	73(117)	145(262)	5(2)	42(25)	19(4)	15(3)	198(244)
(18)	T+	182(516)	266(732)	2(7)	83(147)	34(17)	25(17)	250(619)
	R	113(188)	230(403)	8(5)	56(44)	34(10)	22(7)	173(198)
	E	70(117)	139(262)	7(2)	44(25)	19(4)	15(3)	181(244)
(20)	T+	160(449)	217(567)	5(6)	69(134)	32(13)	25(14)	217(552)
	R	132(188)	243(403)	7(5)	56(44)	36(10)	21(7)	188(198)
	E	70(117)	145(262)	5(2)	41(25)	19(4)	14(3)	182(244)
(21)	T	171(351)	227(443)	3(5)	77(105)	32(10)	25(11)	233(431)
	R	129(188)	239(403)	8(5)	57(44)	35(10)	22(7)	176(198)
	E	75(117)	160(262)	5(2)	42(25)	20(4)	16(3)	182(244)

^a R = *P. rigida* subsp. *rigida*
 S = *P. rigida* subsp. *serotina*
 RS = *P. rigida-serotina* transitional type
 T = *P. taeda*
 E = *P. echinata*
 + = estimated by regression

^b The characters are:
 Y₁ = needle length (mm)
 Y₂ = needle fascicle diameter (.01 mm)
 Y₃ = peduncle length (mm)
 Y₄ = cone length (mm)
 Y₅ = cone diameter (mm)
 Y₆ = seed wing length (mm)
 Y₇ = seed thickness (.01 mm)
 A(B): A = mean; B = variance.

TABLE 1. (continued)

Population	Taxon ^a	Character means and variances ^b						
		Y ₁	Y ₂	Y ₃	Y ₄	Y ₅	Y ₆	Y ₇
(22)	T+	174(453)	246(642)	4(6)	80(129)	35(14)	26(15)	222(543)
	R	116(188)	236(403)	7(5)	56(44)	33(10)	21(7)	162(198)
	E	72(117)	154(262)	4(2)	40(25)	19(4)	14(3)	183(244)
(23)	T+	172(412)	225(583)	4(5)	78(117)	35(13)	26(13)	218(493)
	R	103(188)	216(403)	3(5)	58(44)	35(10)	22(7)	158(198)
	E	71(117)	158(262)	5(2)	44(25)	20(4)	16(3)	181(244)
(20)	T+	179(400)	246(567)	3(5)	78(114)	33(13)	25(13)	238(480)
	R	105(188)	247(403)	9(5)	69(44)	41(10)	25(7)	193(198)
	E	76(173)	145(285)	6(3)	43(28)	19(4)	16(4)	186(246)
(30)	T+	181(550)	260(780)	0(7)	86(156)	33(18)	26(18)	269(659)
	R	134(188)	239(403)	9(5)	62(44)	39(10)	23(7)	178(198)
	E	86(117)	158(262)	6(2)	47(25)	22(4)	17(3)	186(244)
(31)	T	169(351)	213(443)	3(5)	76(105)	33(10)	26(11)	238(431)
	R+	131(291)	240(463)	8(7)	59(50)	37(12)	22(8)	175(218)
	E	88(117)	152(262)	7(2)	46(25)	20(4)	16(3)	183(244)
(36)	T+	172(389)	236(552)	3(5)	77(110)	33(12)	25(13)	238(466)
	R	135(188)	249(403)	10(5)	55(44)	35(10)	21(7)	173(198)
	E	79(117)	147(262)	7(2)	45(25)	20(4)	16(3)	180(244)
(45)	T	157(351)	220(443)	2(5)	85(105)	34(10)	26(11)	255(431)
	R+	150(317)	241(504)	10(8)	60(55)	38(13)	23(8)	184(238)
	E	71(117)	139(262)	6(2)	51(25)	21(4)	16(3)	182(244)

are generally compatible. Almost all of the specimens which are "misclassified" fall within the confidence limits of one or the other of the parental taxa; these had been designated in the laboratory as likely advanced generation segregants. It would be difficult in most such cases to be sure of the donor parent, but the laboratory designations were felt to be reliable.

It is possible to construct a central region for specimens derived from genetic exchange involving all three taxa, but the fact that known F_1 hybrids between pairs of taxa sometimes occupied a rather central position suggested that the technique was not sensitive enough to detect such specimens with any precision. In addition, there was no visual evidence of complex hybridization in these populations, and the possibility was therefore ignored.

It is readily apparent from Figures 2-4 that there is no difficulty in distinguishing among *Pinus taeda*, *P. echinata*, and the *P. rigida-serotina* complex in sympatric populations. The morphological variations encountered within each of these taxa, as indicated by the confidence ellipses of the three figures, show no overlap, and separation is complete. The various taxa therefore are separately recognizable entities in sympatric populations, in spite of natural hybridization.

In the case where the covariance matrices of the three taxa are identical, the three sides of the triangle correspond exactly to the two-taxon discriminant functions often employed in hybridization analysis. In that case, two-taxon hybridization patterns can be described by simply projecting the hybrids perpendicularly onto the appropriate side of the triangle. As pointed out by Smouse (1972), the position along the line can be used as an estimate of the relative proportions of ancestry contributed by the two parental taxa. For example,

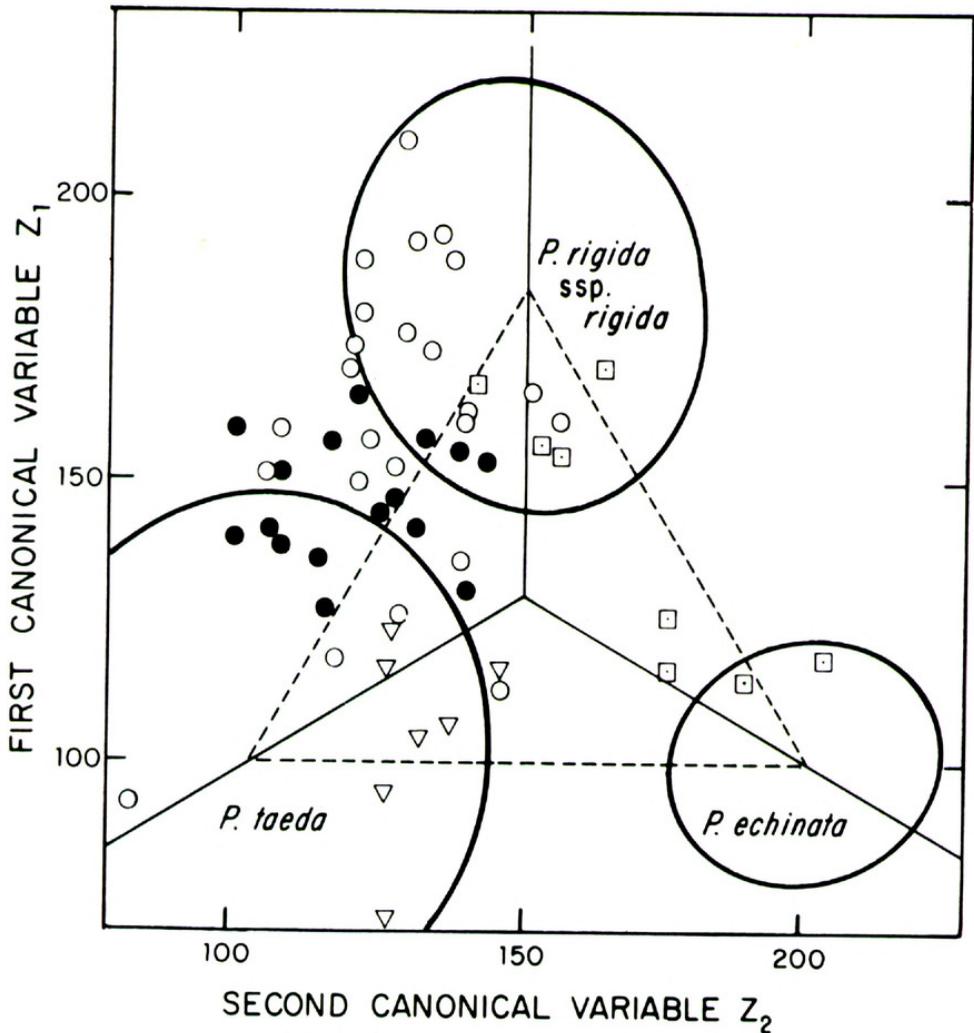


FIGURE 2. Canonical analysis of populations in and near the range of *Pinus rigida* subsp. *rigida*. Solid circles, experimental F_1 hybrid of *P. rigida* subsp. *rigida* \times *P. taeda*; open circles, putative natural hybrid of *P. rigida* subsp. *rigida* \times *P. taeda*; squares, putative natural hybrid of *P. rigida* subsp. *rigida* \times *P. echinata*; inverted triangles, putative natural hybrid of *P. taeda* \times *P. echinata*; large ellipses denote 95% confidence contours.

backcross derivatives are closer to the recurrent parent. Although the covariance matrices of the various taxa are not completely identical, separate two-species analyses were made, and these showed patterns of hybridization very similar to those illustrated in Figures 2-4.

The artificial *Pinus rigida* subsp. *rigida* \times *P. taeda* F_1 hybrids occupy the center of the corresponding side of the triangle, as expected. Genetic exchange, as indicated by the direction of backcrossing, occurs in both directions (Fig. 2). Separate analysis of individual locations showed that backcrossing was primarily in the direction of the more abundant parental taxon for a given location. A similar situation exists for *P. rigida* subsp. *serotina* and *P. taeda* (Fig. 3). Although genetic exchange between *P. taeda* and the *P. rigida-serotina* transitional type occurred in both directions, the transitional type served as the primary recipient of genetic material.

Hybridization between *Pinus echinata* and *P. taeda* resulted in backcrossing

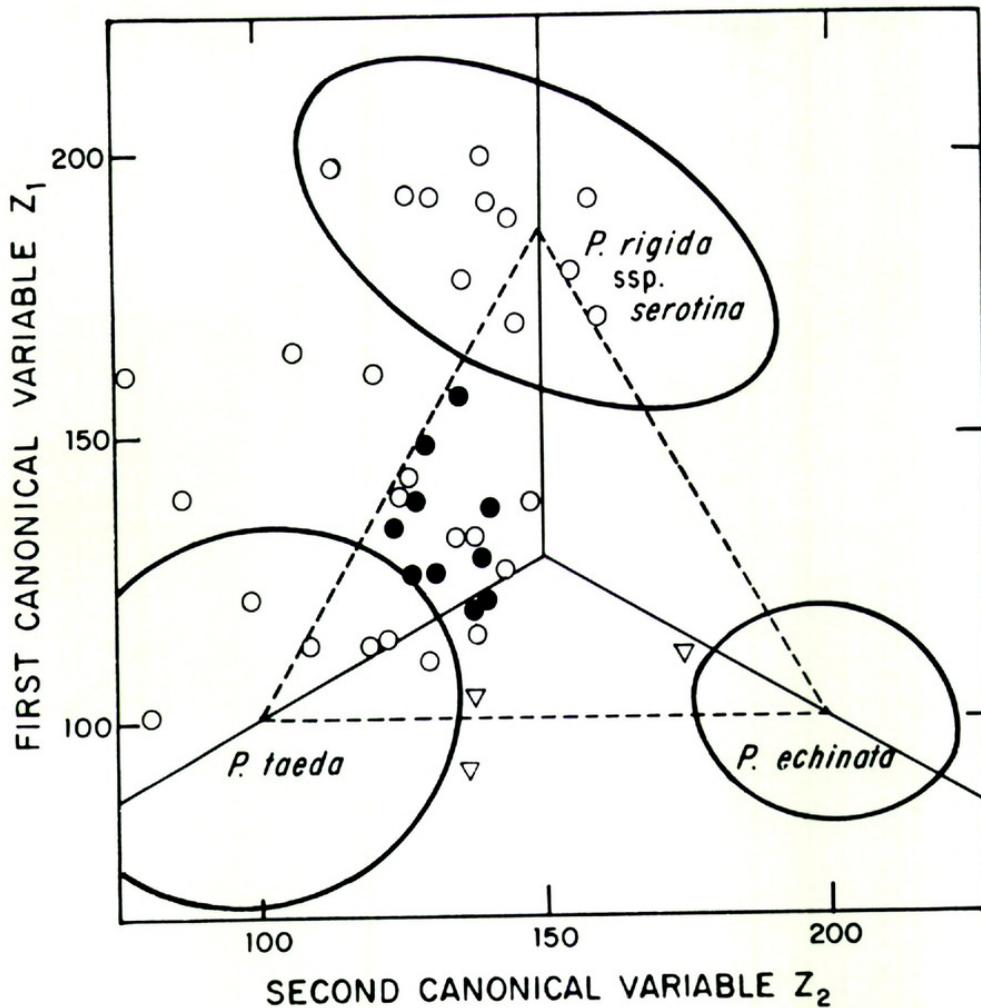


FIGURE 3. Canonical analysis of populations in and near the range of *Pinus rigida* subsp. *serotina*. Solid circles, experimental F_1 hybrid of *P. rigida* subsp. *serotina* \times *P. taeda*; open circles, putative natural hybrid of *P. rigida* subsp. *serotina* \times *P. taeda*; inverted triangles, putative natural hybrid of *P. taeda* \times *P. echinata*; large ellipses denote 95% confidence contours.

primarily in the direction of *P. taeda* (Figs. 2-4), while genetic exchange between *P. echinata* and *P. rigida* subsp. *rigida* occurred in both directions (Fig. 2). Hybridization between *P. echinata* and the transitional type was too rare to adequately categorize (Fig. 4), and no hybridization was detected between *P. echinata* and *P. rigida* subsp. *serotina* (Fig. 3). It should be pointed out that sympatric occurrence of *P. echinata* with both of the latter was rather limited.

DISCUSSION AND CONCLUSIONS

Whether or not the "advanced generation segregants" were possibly species representatives was a matter of some concern in this study. If their classifications were altered arbitrarily, it is possible that the patterns of hybridization illustrated in Figures 2-4 would change. To check this possibility, all putative hybrid specimens within each of the confidence contours were reclassified as species representatives, and the analyses were repeated. The results were negligibly different for the putative hybrid specimens not inside the confidence contours.

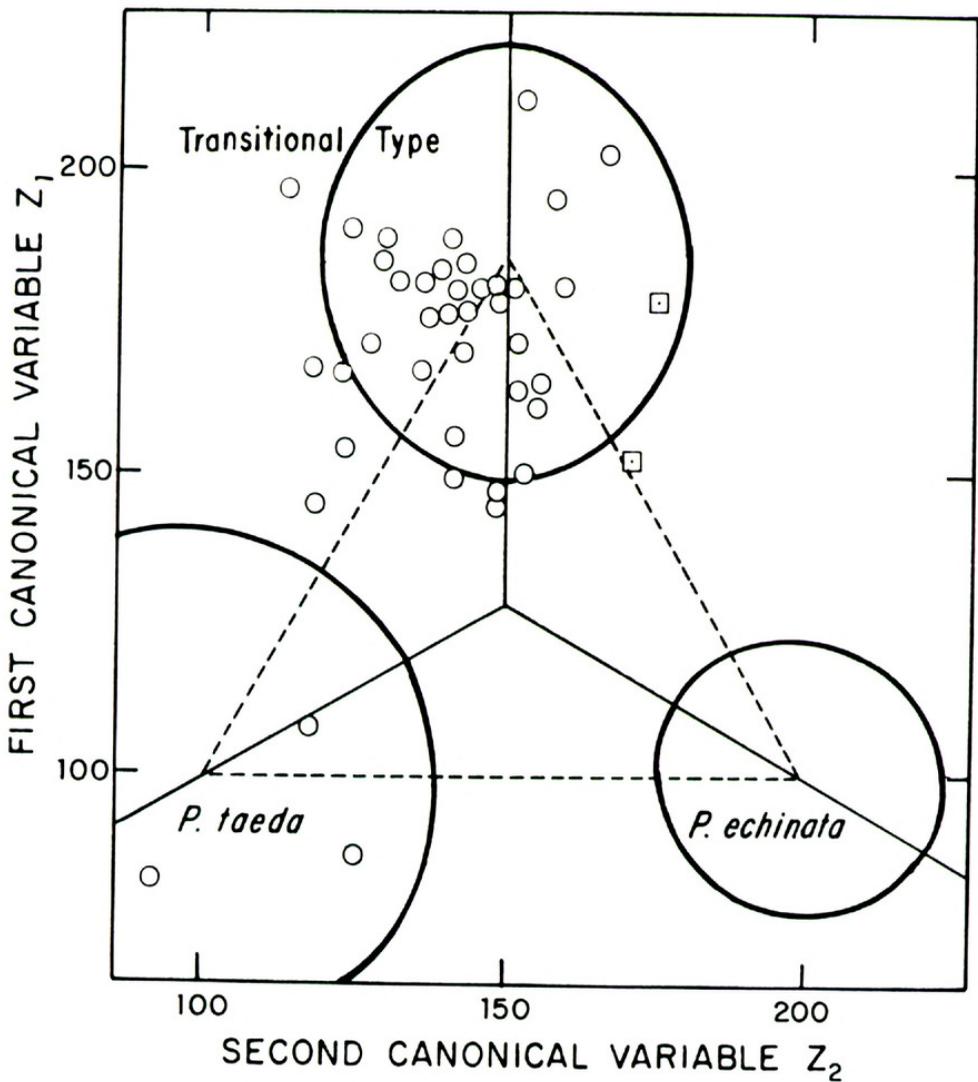


FIGURE 4. Canonical analysis of populations in and near transitional zone. Open circles, putative natural hybrid of transitional type \times *Pinus taeda*; squares, putative natural hybrid of transitional type \times *P. echinata*; large ellipses denote 95% confidence contours.

It is of interest to compare the pattern of hybridization encountered between *Pinus rigida* subsp. *serotina* and *P. taeda* in the present study with that found by Kang (1966), who found no evidence for backcrossing with the former. Most of the populations in that study were very much dominated by *P. taeda*, whereas a range of species frequencies was sampled in the present study. It may be that the difference in the results of the two studies reflect this difference in the types of populations sampled. It would seem reasonable that populations dominated by *P. taeda* would show a preponderance of *P. taeda*-like hybrid derivatives.

Interpretation of the hybridization between the transitional type and *Pinus taeda* rests very heavily on the treatment of the transitional type as a clinal intermediate between the two subspecies of *P. rigida* (Smouse & Saylor, 1973). In view of the amount of hybridization occurring between *P. taeda* and the transitional type, however, the question might well be raised as to whether the structure of the transitional type can be adequately resolved without reference to

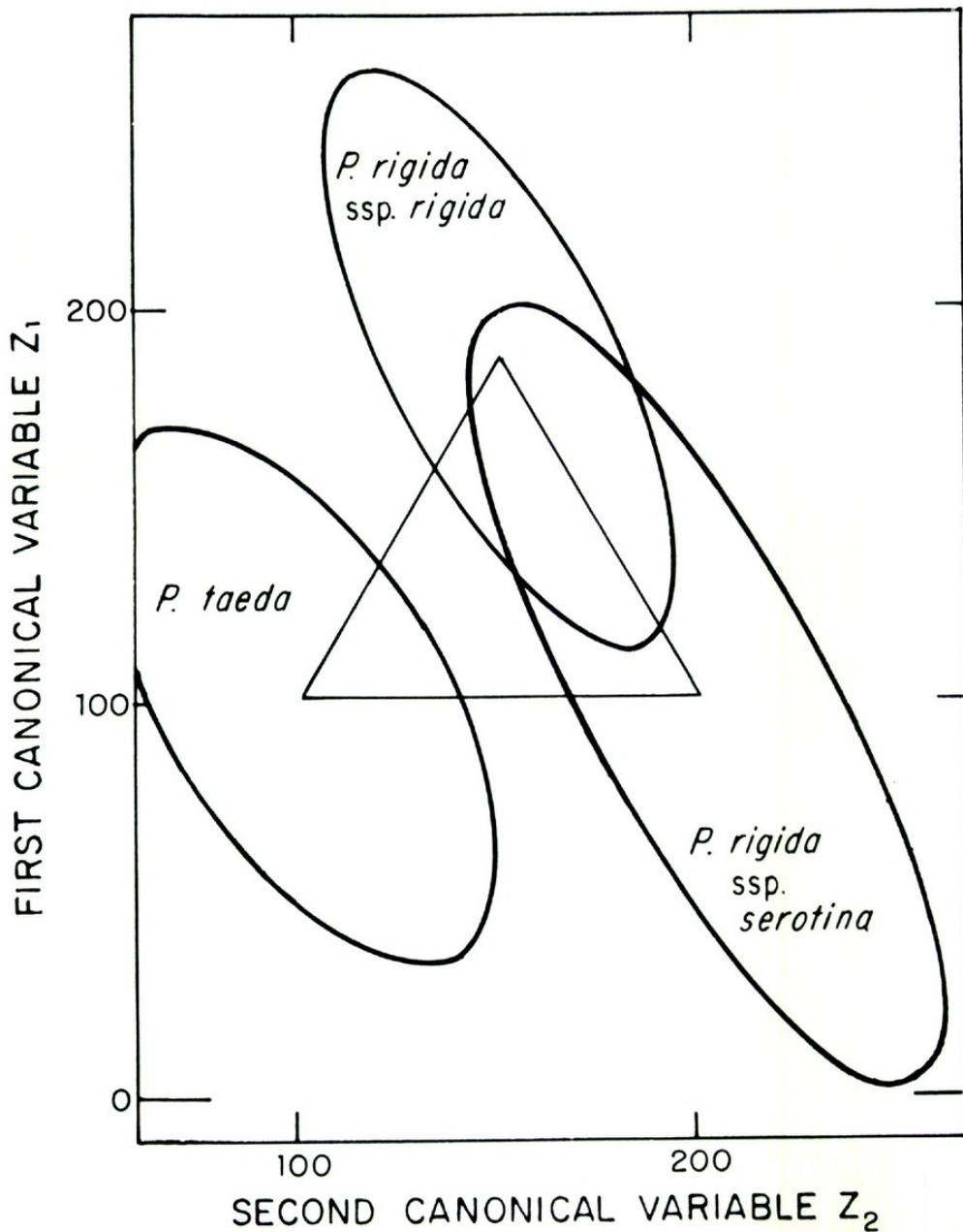


FIGURE 5. Canonical triangle of *Pinus rigida* subsp. *rigida*, *P. rigida* subsp. *serotina*, and *P. taeda*. Large ellipses denote 95% confidence contours.

P. taeda. The relationships among the three taxa and the transitional type can be portrayed by recourse to the canonical technique employed earlier; in this case the taxa were placed at the corners of the triangle, and 95% confidence contours were computed for each (Fig. 5).

The attenuated shape of the confidence ellipses resulted from the considerable stretching of scales necessary to separate the subspecies of *Pinus rigida*. The overlap between them was still considerable, as was expected on the basis of similar results reported by Smouse and Saylor (1973). The transitional type was intermediate between the subspecies of *P. rigida*, and it showed a slight tendency

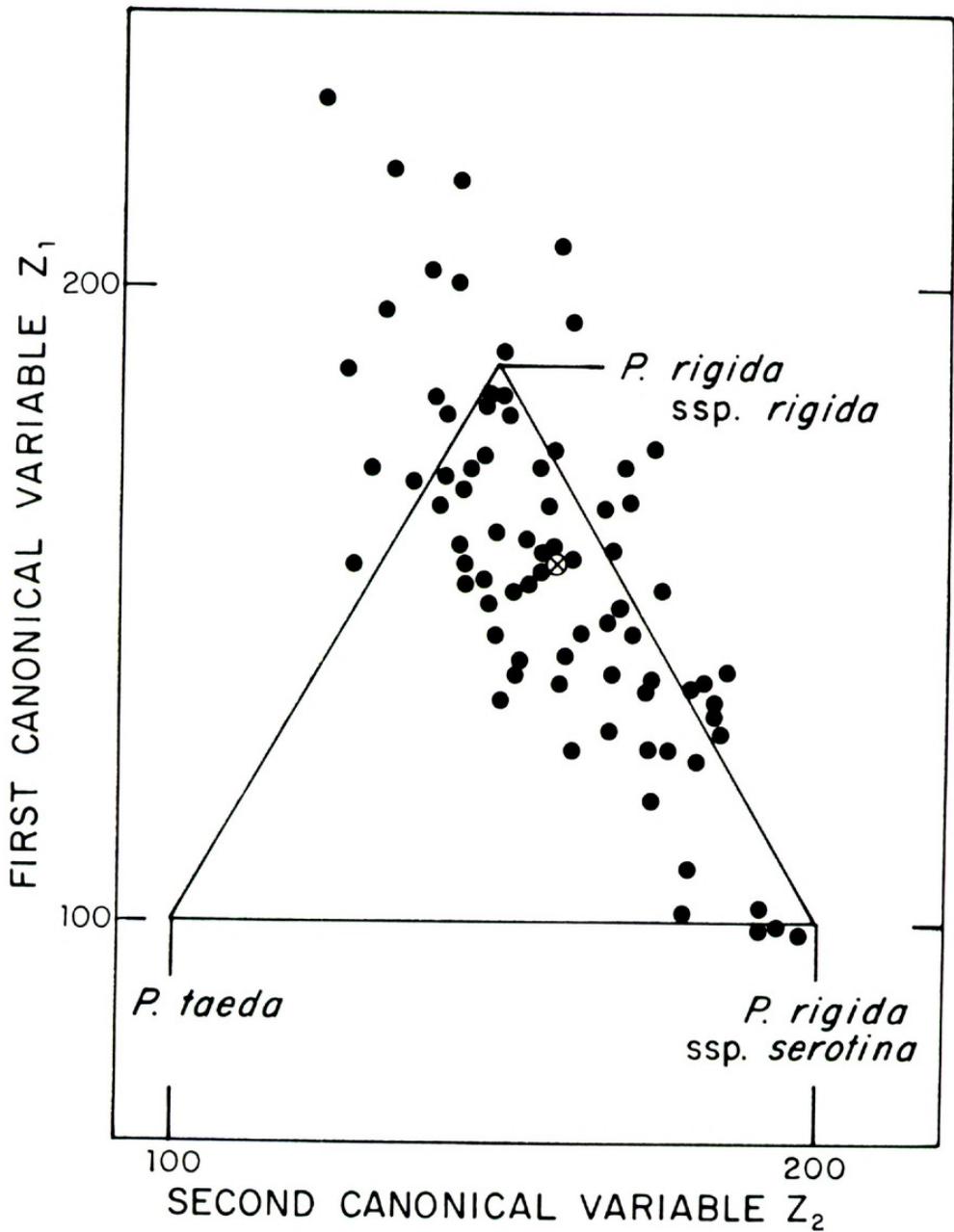


FIGURE 6. Canonical analysis of transitional type. Solid circles, transitional specimens; X-ed circle, average of the transitional type.

to cluster on the *P. taeda* side of the *P. rigida-serotina* axis (Fig. 6). This tendency was only slightly exaggerated by adding the *P. taeda* × transitional type hybrids to the transitional type, which should be evident from Figure 4. It therefore appears that there has been a pervasive, but minor contribution of *P. taeda* to the gene pool of the transitional type.

Based on the results of this and other related studies, several conclusions were considered valid regarding crossing patterns and taxonomic status. Hybridization between *Pinus taeda* and the *P. rigida-serotina* complex has been common, and genetic exchange, as indicated by the pattern of backcrossing, occurs in



Smouse, Peter E and Saylor, Leroy C. 1973. "Studies of the *Pinus rigida*-*Serotina* Complex II. Natural Hybridization Among the *Pinus rigida*-*Serotina* Complex, *P. taeda* and *P. echinata*." *Annals of the Missouri Botanical Garden* 60, 192–203. <https://doi.org/10.2307/2395085>.

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