Chemical Evidence For Introgressive Hybridization in Picea

By J. W. HANOVER and R. C. WILKINSON

Department of Forestry, Michigan State University East Lansing, Michigan*)

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The genus *Picea* is composed of some forty species and presents problems in systematics that are unique among coniferous genera. The spruces are distributed throughout the northern hemisphere but of particular interest to forest biologists for many years have been the Northeastern and Northwestern complexes of North American species (WRIGHT, 1955). The Northeastern complex includes P. *rubens* and *P. mariana* and the Northwestern complex includes *P. glauca, P. engelmannii, P. pungcns, P. sitchcnsis.* and *P. breweriana.*

Within each complex the ranges of species overlap somewhat and the two complexes themselves are bridged by the vast, overlapping ranges of P. *glauca* and *P. mariana,* although these two species are not known to hybridize readily. Natural hybridization does occur between sympatric species to the extent that many local populations consist of phenotypes that exhibit all combinations of parental species characteristics. This has often led to confusion in identifying species for purposes of forest management, tree improvement, or systematic studies.

Several attempts have been made to construct phenotypic indicies on the basis of morphological traits as guides for differentiating one individual, population, or species from another. In areas where natural hybridization is believed to occur between species, character association analyes have supported the hypothesized patterns of introgression (MORGENSTERN and FARRAR, 1964, *[P. mariana* and *P. rubens];* ROCHE, 1966, *[P. glauca* and *P. engelmannii];* GARMAN, 1957, *[P. glauca* and *P. engelmannii];* DAUBENMIRE, 1968, *[P. sitchensis* and *P. glauca]).*

The use of biochemical criteria to distinguish species of *Picea* has been limited, and the results have been more indicative of potential than conclusive (BARTON and GARDNER, 1957; VON RUDLOFF, 1962, 1964, 1966, 1967 a; VON SCHANTZ and JUVONEN, 1966). However, VON RUDLOFF (1967 b) has found distinctive differences in the leaf oils of white spruce and black spruce which were consistent in samples from widely separated populations and ecological conditions.

The objective of our study was to examine the phenolic constituents in *P. sitchensis, P. glauca, P. engelmannii,* and putative natural hybrids to determine if the direction and degree of introgressive hybridization among these species could be distinguished chemically. The area in which hybrids were sampled is along the Skeena River of British Columbia. In this area natural hybridization and introgression are thought to have occurred between the coastal species, *P. sitchensis,* and the interior species, *P. glauca* (DAUBENMIRE, 1968).

Materials and Methods

Materials for the chromatographic analyses of phenolic compounds were collected and described by DAUBENMIRE (1968).

Foliage samples were air dried and stored in the laboratory at room temperature prior to extraction. The sources of the materials are as follows:

Species	Location	Lat. °N.	Long. °W.
Picea glauca	Whitehorse, Yukon Territory, Canada	60°	134°
Picaa engelmannzi	Emmonds Glacier, Washington, U. S. A.	47°	122°
	Blue Mountains, Oregon, U. S. A.	45°	118°
Picea *sitchensis*	Haines, Alaska, U. S. A.	59°	135°
	Hoquiam, Washington, U. S. A.	47°	124°
	Castle Rock, Washington, U. S. A.	46°	123°
	Big Lagoon, California, U. S. A.	41°	124°
Putative Hybrids			
Lower Skeena River, British Columbia, Canada		54°	129°
Upper Skeena River, British Columbia, Canada		55°	128°

Additional foliage samples of *P. glauca* were collected near Norfolk, Connecticut and Hillsboro, New Hampshire. These samples were dried at 70° C. prior to analysis.

Most of the analyses were done on 4 gm (dry weight) needle samples from 4 to 16 individual trees within each source. Composite samples of 10 grams representing 10 to 30 trees from each source were used for confirmatory analyses for the ether soluble phenolics.

Methods of extraction and chromatographic procedures are similar to those reported earlier (HANOVER and HOFF, 1966). Foliage samples were first extracted with hot water. The water extract was further extracted with ethyl ether followed by n-butanol to give two fractions of phenolic constituents free of tannins. Each fraction was taken to near-dryness on a rotary film evaporator and brought up to 1 ml with ethanol and butanol, respectively. Other methods of extraction were tried including one described by STAFFORD (1965) but were found unsuitable for spruce needle tissue.

Fifty microliters of an extract were spotted on a sheet of Whatman 3MM filter paper and irrigated in the first direction with either benzene, acetic acid, water (6 : 7 : 3) or n-butanol, acetic acid, water (4 : 1 : 5) for the ether soluble and butanol soluble fractions, respectively. Sodium formate, formic acid, water (10 : 1 : 200) was the solvent in the second direction for both fractions. Dried chromatograms were examined under ultraviolet radiation, exposed to ammonia. and reexamined in the ultraviolet. They were then sprayed with a solution of 0.4 gm of diazotized sulfanilic acid in 100 ml of water followed by 10 percent sodium hydroxide.

In order to provide marker compounds and also to tentatively identify a few of the spruce phenolics a number of known substances were chromatographed separately and in combination with the spruce extracts. Compounds consistently detected chromatographically were numbered, their R_f values were measured, and the spots were characterized by their reactions to the treatments. Each spot was visibly scored for intensity to give a rough estimate of relative amounts present in a sample.

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Results and Discussion

Data for all compounds in the foliage of the species and sources of spruce are given in *Tables 1 and 2*. Composite chromatograms of the ether soluble and butanol soluble fractions are illustrated in *Figure 1*. From the chromatographic results it is apparent that there exists a large

Table 1. — R_f values and color reactions of the n-butanol soluble phenolic compounds in spruce foliage.[1]

Compound no. (See Figure 1)	R_f		UV		Diazotized sulfanilic acid	10% NaOH
	n-butanol, acetic acid, water (4:1:5)	Sodium formate, formic acid, water (10:1:200)	Untreated	NH_3		
Catechin	.61	.33	-	Br	YB	YB
1	.82	.75	-	-	YB	R
2	.57	.80	-	-	R	O
3	.74	.53	-	-	YB	M
4	.74	.55	WP	-	YB	DY
5	.52	.73	-	-	-	M
6	.78	.37	Bl-P	-	-	-
7	.82	.39	-	-	Y	Pk
8	.72	.25	Bl	-	-	V
9	.70	.37	G	-	-	-
10	.51	.74	LBl-G	-	-	-
11	.45	.80	P	-	-	-
12	.56	.84	Y-W	-	-	-
13	.68	.65	P	-	YB	O
14	.56	.62	YG	-	YO	-
15	.83	.76	-	-	-	Pk
16	.52	.50	P	-	-	-
17	.70	.43	G	-	-	-
18	.52	.30	Y	-	-	-
19	.64	.14	DG	-	YB	YB
20	.59	.08	YG	-	YB	-
21	.52	.03	P	-	-	-
22	.49	.06	YO	-	B	-
23	.27	.00	BrBl	-	Pk-B	-
24	.40	.00	Bl	-	Pk-B	-
25	.85	.00	Pk-G	-	Pk-G	-
26	.26	.90	-	-	O	O
27	.34	.88	-	-	-	O
28	.40	.92	-	-	-	R
29	.33	.67	-	-	YB	-
30	.35	.37	-	-	YB	-
31	.36	.46	-	-	YB	-
32	.39	.34	-	-	YB	-
33	.46	.31	-	DB	YB	YB
34	.43	.26	-	-	YB	-
35	.09	.01	LBl	-	-	-
36	.61	.00	LBl	-	-	-
37	.58	.86	-	-	B	RO
38	.26	.36	Y-O	-	-	-
39	.62	.44	-	-	YB	O
40	.60	.77	P	-	-	-
41	.58	.47	BlG	-	-	-
42	.46	.47	-	-	YB	-
44	.36	.22	D	-	YB	-
45	.64	.73	Bl	-	-	-
46	.66	.79	-	-	YB	O
47	.45	.60	LBl	-	-	-
48	.57	.90	-	-	YB	R
49	.36	.68	P	-	-	-
50	.31	.59	Y-W	-	-	-
53	.51	.00	Pk-Y	-	-	-
54	.73	.15	G	-	-	-
55	.29	.32	D	-	YB	-
56	.58	.75	-	-	O	LO
57	.64	.83	-	D	-	-
58	.79	.65	-	-	YB	O
59	.50	.83	-	D	YB	O
60	.24	.16	Y	-	-	-
61	.27	.23	D	-	YB	-
62	.20	.32	-	-	YB	-
65	.84	.65	-	-	-	Y
67	.32	.07	DBl	-	-	-
72	.45	.56	LBl	-	-	-
74	.56	.61	Y	-	Pk	Y
78	.67	.54	BlG	-	-	-
80	.35	.53	LBl		Pk	-

1/ Color abbreviations: P=purple; Bl=blue; G=green; W=white; Y=yellow; B=brown; R=red; O=orange; Pk=pink; Bk=black; L=light; D=dark; M=magenta; Br=bright; V=violet; Gr=gray.

Table 2. — R_f values and color reactions of the ether soluble phenolic compounds in spruce foliage.[1])

Compound no. (See Figure 1B)	R_f		UV			
	Benzene, acetic acid, water (6:7:3)	Sodium formate formic acid, water (10:1:200)	Untreated	NH_3	Diazotized Sulfanilic acid	10% NaOH
1	.00	.09	YG	-	-	YB
2	.09	.00	YO	-	Y	-
3	.05	.54	L	-	YB	M
4	.14	.54	BlW	-	B	DY
5	.95	.00	Y	-	YB	OB
6	.29	.44	BrBl	-	-	-
7	.37	.38	Bl	-	Y	RPk
Ferulic acid	.66	.24	Bl	-	YB	V
9	.70	.35	G	-	-	-
Vanillic acid	.65	.57	-	-	YB	O
11	.76	.55	DBl	-	-	Pk
Vanillin	.75	.63	DP	-	-	OPk
13	.46	.68	P	-	YB	O
Para-hydroxy-benzoic acid	.31	.67	-	-	Y	DY
15	.41	.81	-	-	Y	Pk
16	.18	.06	L	-	Y	-
Caffeic acid	.07	.25	-	Bl	LB	PGr
18	.00	.87	LB	-	DY	RB
20	.00	.50	Bl	-	-	-
23	.81	.00	BlG	-	-	-
26	.46	.48	BlG	-	-	Y
27	.42	.70	D	-	-	-
28	.06	.66	-	O	LB	OPk
29	.10	.60	P	-	-	-
30	.57	.56	Y	-	-	-
31	.68	.59	Y	-	-	-
32	.64	.77	D	D	YB	-
33	.69	.74	LBl	-	YB	Pk
34	.72	.80	-	-	YB	RO
35	.65	.70	-	-	YB	Pk
36	.11	.14	BlG	-	-	-
37	.04	.22	-	-	Y	-
38	.06	.73	-	-	YB	OPk
39	.05	.00	BrBl	-	YB	-
40	.00	.72	P	-	-	-
41	.68	.44	-	-	YB	DPk
42	.44	.54	-	-	YB	Pk
43	.29	.34	Bl	-	-	-
44	.44	.54	DBl	-	-	LO
45	.24	.62	-	-	YB	DO
47	.81	.15	BlG	-	-	-
48	.58	.14	BlG	-	-	-
49	.21	.28	BlG	-	-	-
50	.15	.45	BlG	-	-	-
51	.42	.44	G	-	-	-
52	.04	.39	L	L	-	-
53	.58	.81	-	-	-	Pk
54	.13	.63	Bl	-	-	-
55	.86	.75	-	Y	YB	-
56	.49	.32	L	-	-	LY
57	.31	.74	Bl	-	-	-
58	.02	.28	Y	-	-	-
59	.10	.60	-	L	Y	-
60	.26	.39	Bl	-	-	-

1/ Color abbreviations: P=purple; Bl=blue; G=green; W=white; Y=yellow; B=brown; R=red; O=orange; Pk=pink; Bk=black; L=light; D=dark; M=Magenta; Br=bright; V=violet; Gr=gray.

potential source of both qualitative and quantitative variation in these chemical traits. Many of the phenolic compounds occurred in every sample analyzed and showed little quantitative variation. However, a number of other compounds did show patterns of variation associated with either species or source of origin. These compounds are of primary interest, and their distribution and relative concentrations in the tissue are presented in *Table 3 and 4.* Compounds 4 and 40 occurred in both fractions and have been designated by the same number in each fraction.

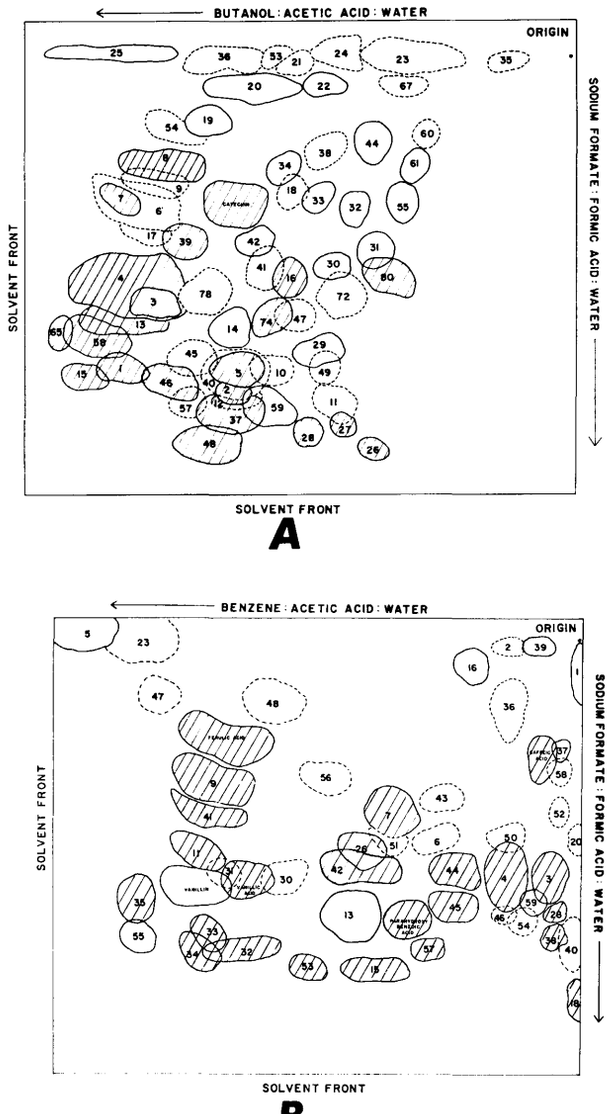

Figure 1. — Two-dimensional composite chromatogram of the n-butanol (A) and ether soluble (B) phenolic compounds in spruce foliage. A dashed outline indicates UV fluorescence, a solid outline indicates a reaction with sulfanilic acid and crosshatching indicates a reaction after treatment with both sulfanilic acid and sodium hydroxide.

Compound 40 has been tentatively identified as pungenin a glucoside found in *P. pungens* (Neish, 1957). Compound 4 has not been identified.

P. sitchensis can be unequivocally distinguished from *P. glauca* and *P. engelmannii* on the basis of compounds 4, 11, and 40. No sample of *P. sitchensis* contained these three substances which were consistently present in both *P. glauca* and *P. engelmannii*. The latter two species are very similar chemically. However, one consistent and potentially useful difference between these two species is the larger concentration of compound 4 in *P. glauca* than in *P. engelmannii*. This difference in concentration was consistent for all trees analyzed. Several other differences between the two species are evident in *Table 3 and 4*, but these differences were not consistent for all trees within a source. A possible genetic explanation of within source variation in a chemical is that the frequency of alleles controlling its synthesis may differ from source to source as well as between species, thus giving different frequencies of occurrence for the chemical. Supporting data for this hypothesis must be based upon much larger sample sizes before they can be validly applied to systematic investigations.

In general, there was little evidence for geographical variation within each species although the study was not designed to test this problem rigorously. Despite the diversity in origin of samples of *P. sitchensis*, i. e., Alaska to California, there was no chemical variation among the sources. This was also true for the more limited sources of *P. glauca* and *P. engelmannii*.

Daubenmire (1968) has presented morphological evidence from his observations on the same materials used in our chemical analyses that the Lower Skeena River and Upper Skeena River populations show the influence of natural hybridization between *P. glauca* and *P. sitchensis*. He concludes that the Lower Skeena trees are closely related to *P. sitchensis* and the Upper Skeena trees to *P. glauca*. Earlier Garman (1957) also reported that the Skeena River basin contained "variants of Engelmann and white spruce confounded with Sitka spruce". Our analyses of the phenolic compounds in these putative hybrid populations substantiate the conclusions of Daubenmire and possibly of Garman. The most clearcut evidence is found by comparing compounds 4 and 40 which are soluble in ether and butanol, respectively. Individual tree data for these two compounds are shown in *Table 5* in terms of frequency of occurrence. The data reveal a close chemical affinity between the Lower Skeena population and *P. sitchensis* and between the Upper Skeena population and *P. glauca*. This conclusion is substantiated by the presence of greater concentrations of compound 40 in Upper Skeena trees than Lower Skeena trees whenever this compound is found in trees from the Lower Skeena population, and by the lower concentration of compound 4 in trees from the Upper Skeena River when compared to *P. glauca*. This same pattern for compound 4 is borne out in composite chromatograms representing 22 additional trees of white spruce, 94 Sitka spruce, and 20 trees of each putative hybrid source. A limitation in our data is the fact that comparisons between species and hybrids involving those chemicals that may differentiate *P. glauca* from *P. engelmannii* (ether soluble compounds 34, 36, 52, and 58 and butanol soluble compounds 38, 53, 57, and 58) do not eliminate the possibility of introgression by *P. engelmannii* in the Skeena Basin populations. However, Roche (1969) reports that there are no extensive allopatric populations of *P. engelmannii* in this region.

Thus, in our limited chemotaxonomic study of one species complex in *Picea*, evidence is given for biochemical differentiation among four species. The phenolic compounds that distinguish the species have also been shown to provide a means for measuring the existence and possibly the degree of natural hybridization and introgression among the spruces. Further work is needed to characterize the chemical variation patterns of other species and species complexes of *Picea* and to identify the distinctive compounds so that genetic interpretations can be made. The results of the study also indicate the potential usefulness of phenolic constituents in helping to solve biosystematic problems in other tree species and genera.

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Table 3. — Distinctive phenolic compounds in the n-butanol soluble fraction extracted from foliage of *Picea* species.

Species and Source	Compounds															
	2	4	12	22	26	28	29	38	39	40	42	49	53	57	58	67
	Amount present[1])															
Picea glauca																
Whitehorse, Y. T.	+	++	+	+	+		+			++		+	+	+	+	
Northeast United States		++	+	+	+					++			+	+	+	
Picea engelmannii																
Emmonds Glacier, Wash.	+	+	+	+	+		+	+	+	++						+
Blue Mts., Ore.	+	+	+	+	+		+	+	+	++						
Picea sitchensis																
Haines, Alaska				+		+			+		+		+	+	+	
Hoquiam, Wash.				+				+			+		+	+	+	
Castle Rock, Wash.				+		+		+					+	+	+	
Big Lagoon, Calif.				+				+			+	+	+	+	+	
P. sitchensis × *P. glauca (?)*																
Lower Skeena Riv., B. C.	+			+	+	+				+			+	+	+	
Upper Skeena Riv., B. C.	+	+		+	+	+				++			+	+	+	

[1]) Amount present is based upon visual estimates of chromatogram spot intensity: + = Present. ++ = Present in relatively large amount. Compounds indicated as present in a source are not necessarily present in all trees in the source unless otherwise indicated in the text.

Table 4. — Distinctive phenolic compounds in the ether soluble fraction extracted from foliage of *Picea* species.

Species and source	Compounds															
	4	9	11	Vanillin	16	27	30	34	36	40	41	42	44	45	52	54	58
	Amount present[1])																
Picea glauca																	
Whitehorse, Y. T.	++	++	+	++	+					+					+		+
Northeast United States	++	++	+	++	+					+					+		+
Picea engelmannii																	
Emmonds Glacier, Wash.	+	++	+	++	+			+	+	+				+			
Blue Mts., Ore.	+	++	+	++	+			+	+								
Picea sitchensis																	
Haines, Alaska		+		+	+	+	+	+	+							+	+
Hoquiam, Wash.		+		+	+	+	+	+	+							+	+
Castle Rock, Wash.		+		+	+	+	+	+	+							+	+
Big Lagoon, Calif.		+		+	+	+		+	+							+	+
P. sitchensis × *P. glauca (?)*																	
Lower Skeena Riv., B. C.		++		++	+	+	+	+	+								+
Upper Skeena Riv., B. C.	+	++	+	++	+		+	+	+	+	+	+	+				

[1]) Amount present is based upon visual estimates of chromatogram spot intensity: + = Present. ++ = Present in relatively large amount. Compounds indicated as present in a source are not necessarily present in all trees in the source unless otherwise indicated in the text.

Table 5. — Occurrence of compounds 4 and 40 in *Picea sitchensis*, *Picea glauca*, and putative hybrids.

Species	Compound no. 4 (ether soluble)	Compound no. 40 (n-butanol soluble)
	Ratio of trees containing compound to trees analyzed	
Picea glauca (3 sources)	15/16	12/12
Picea sitchensis (4 sources)	0/21	0/20
Putative hybrids:		
Lower Skeena River	0/16	4/13
Upper Skeena River	14/16	12/12

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Summary

Chromatographic patterns of phenolic compounds in the foliage of *Picea sitchensis*, *P. glauca*, and *P. engelmannii*, were analyzed to determine qualitative and semi-quantitative variation patterns associated with individual trees, species, and geographic locations within species. Supposed hybrid populations located in the Skeena River Basin of British Columbia and involving *P. sitchensis* and *P. glauca* were analyzed to test for chemical variation among these trees and populations. The results show that several phenolic compounds among over 100 detected appear to be species-specific and vary little between individuals and geographic origins within species. Two of the distinctive phenolics provide a basis for determining the direction and possibly degree of natural hybridization occurring between *P. sitchensis* and *P. glauca*.

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Untersuchungen zur Konkurrenz zwischen verschiedenen Genotypen in Pflanzenbeständen

II. Darstellung des Untersuchungsmodells und Ableitung einiger Beziehungen über Konkurrenzvarianzen und Heritabilitäten

Von M. HÜHN*)

a) Einleitung

In einer ersten Arbeit (HÜHN 1969) wurde eine Modifikation der Methode von SAKAI zur Schätzung der genetischen-, Umwelt- und Konkurrenzvarianz einer Population theoretisch hergeleitet und diskutiert. Bei der Darstellung des Schätzverfahrens und der Ableitung der dazu notwendigen Formeln erwies sich eine ausführliche Beschreibung des zugrundeliegenden Konkurrenzmodells, seiner Eigenschaften und Anwendungsmöglichkeiten als nicht unbedingt erforderlich. Daher wurden dort auch nur die zum Verständnis der methodischen Überlegungen und Ansätze notwendigsten Voraussetzungen kurz beschrieben.

In dieser Arbeit soll nun auf das Konkurrenzmodell und die benutzten Parameter näher eingegangen werden. Dies um so mehr, als eine genaue Kenntnis des Modells und der Parameter für ein Verständnis der folgenden Arbeiten und auch für die praktische Anwendung der abgeleiteten theoretischen Ergebnisse unerläßlich ist.

Der erste Teil der vorliegenden Arbeit bringt also nicht so sehr neue wissenschaftliche Ergebnisse als Voraussetzungen, Definitionen und Grundlagen für die früheren und folgenden Konkurrenzuntersuchungen (HÜHN 1969; HÜHN 1970, Teile III, IV, V und VI). Im zweiten Teil *(Abschnitte e—g)* werden dann einige erste Folgerungen gezogen und Beziehungen über Konkurrenzvarianzen und Heritabilitäten abgeleitet.

In weiteren Arbeiten (HÜHN 1970, Teile III, IV, V und VI) folgt dann die Behandlung der folgenden Themen: 1) Das Konkurrenz-Korrelationsmuster eines Bestandes mit seinen Eigenschaften, Folgerungen und Anwendungsmöglichkeiten, 2) Probleme der optimalen Parzellengröße bei Feldversuchen und 3) Fragen der Phänotypenselektion.

*) Institut für Forstgenetik und Forstpflanzenzüchtung in Schmalenbeck der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Reinbek.

Über die Existenz von Konkurrenzeffekten in Pflanzenbeständen gibt es wohl keinen Zweifel, denn überall in der Natur, wo Organismen mit ähnlichen Ansprüchen an die Umwelt in Nachbarschaft zusammenleben, kommt es zu Konkurrenz zwischen ihnen um diejenigen Umweltfaktoren, in die sie sich teilen müssen. Die Nichtberücksichtigung dieser wechselseitigen Beeinflussung, deren Bedeutung für das Verständnis biologischer Zusammenhänge seit langem bekannt ist, dürfte bei vielen züchterischen Experimenten (Phänotypen-Selektion, Heritabilitätsschätzung) ein Grund für den oft nur so geringen erzielten Gewinn sein.

Man unterscheidet gewöhnlich zwischen einer intraspezifischen und einer interspezifischen Konkurrenz, das heißt einem Wettbewerb um die Wachstumsfaktoren innerhalb derselben Arten im Reinbestand und einem solchen zwischen verschiedenen Arten in Mischbeständen.

Wie in vielen Versuchen nachgewiesen werden konnte, führt intraspezifische Konkurrenz keineswegs zu Populationen, in denen ein Genotyp, nämlich der gegenüber Konkurrenz Bestgeeignete, erhalten bleibt, sondern intraspezifische Konkurrenz kann ein entscheidender Auslesefaktor sein und führt meistens zu balancierten Systemen mit hoher genetischer Variation. Die Untersuchungen von Mischbeständen aus verschiedenen Arten fanden früh das Interesse in der Pflanzenzüchtung — und schon DARWIN wies darauf hin, daß die Leistungen in Mischbeständen oft über den Leistungen von Reinbeständen der beteiligten Arten liegen.

Diese — besonders den Ökologen interessierende — Konkurrenz zwischen verschiedenen benachbart aufwachsenden Arten ist auch von großer Bedeutung für die Grundlagen der Pflanzensoziologie: „Man weiß, daß verschiedene Arten sich gegenseitig aus ihren physiologischen Optima verdrängen können, daß bestimmte Artgrenzen nicht Klimagrenzen, sondern Konkurrenzgrenzen sind, und Genökologen und Populationsgenetiker haben festgestellt, daß die Konkurrenzbedingungen, unter denen eine Population