and DAUBENMIRE, J. B.: Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Sta. Tech. Bull. No. 60 (1968). — KRIEBEL, H. B.: Parental and provenance effects on growth of red oak seedlings. Proc. 4th Cent. States For. Tree Imp. Conf. p. 19–25 (19664). — JENKINSON, J. L.: Ponderosa pine progenies: differential response to ultramafic and granitic soils. USDA Forest Service Res. Pap. PSW-101 (1974). — HERMANN, R. K. and LAVENDER, D. P.: Early growth of Douglas-fir from various altitudes and aspects in southern Oregon. Silvae Genet. 17: 143–151 (1968). — LANGLET, O.: TWO hundred years of genecology. Taxon 20 (56): 653–722 (1971). — LEVINS, R.: Theory of fitness in a heterogeneous environment. I. The Fitness set and adaptive function. Amer. Natur. 96: 361–373 (1962). — LEVINS, R.: Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. Amer. Natur. 97: 75–90 (1963). — LEVINS, R.: Theory of fitness in a heterogeneous environment. III. The response to selection. J. of Theoret. Biol. 7: 224–240 (1964). — LI, C. C.: Population Genetics. Univ. of Chigao Press, Chicago (1955). — LIBBY, W. J. and JUND, E.: Variance associated with Cloning. Heredity 17: 533–540. — LITTLE, E. L., JR.: Atlas of United States Trees. USDA Forest Service Misc. Pub. No. 1146 (1971). — MAYNARD SMITH, J.: Disruptive selection, polymorphism, and sympatric speciation. Nature. 195: 60–2 (1962). — MAYR, E.: Animal Species and Evolution. Harvard Univ. Press, Cambridge, Mass. (1963). — NAMKOONG, G., USANIS, R. A. and SILEN, R. R.: Age-related variation in genetic control of height growth in Douglas-fir. Theoret. and Appl. Gen. 42: 151–9 (1972). — PFISTER, R., KOVALCHIK, P. D. L., ARNO, A. F. and PRESBY, R. C.: Forest habitat types of Montana. Intermt. For. and Con. Exp. Sta. and Northern Region USFS. Misc. Pub. (1974). — REHFELDT, D. G.: Genetic variation of Douglas-fir in the northern Rocky Mountains, USDA Forest Service Res. Note INT-184 (1974). — REHFELDT, G. D. and LESTER, D. T.: Specialization and flexibility in genetic systems of forest trees. Silvae Genet. 18 (4): 118–123 (1969). — ROWE, K. E. and CHING, K. K.: Provenance study of Douglas-fir in the Pacific Northwest Region. II. Field performance at age nine. Silvae Genet. 22 (4): 115–119 (1973). — SILEN, R. R.: Personal communication (1976). — SNEDECOR, W. and COCHRAN, W. G.: Statistical Methods. The Iowa State University Press, Ames, Iowa (1968). — SQUILLACE, A. E.: Geographic variation in slash pine. For. Sci. Mono. 10 (1966). — SQUILLACE, A. E. and SILEN, R. R.: Racial variation in ponderosa pine. For. Sci. Monog. 2 (1962). — STEEL, R. G. D. and TORRIE, J. H.: Principles and Procedures of Statistics. McGraw Hill, N.Y. (1960). — STERN, K.: Herkunftsversuche für die Forstpflanzenzüchtung — erläutert am Beispiel zweier Herkunftsversuche mit Birken. Der Züchter 34: 181–219 (1964). — STERN, K. and ROCHE, L.: Genetics of Forest Ecosystems. Spring-Verlag, N.Y. (1974). — TOWNSEND, J. I.: Genetics of marginal populations of Drosophila willistoni. Evol. 6: 428–442 (1952). — VAN VALEN, L.: Morphological variation and width of ecological niche. Amer. Natur. 99: 377–390 (1965). — WANT., CH. W. and PATTEE, R. K.: Variation in seed characteristics and seedling growth of open-pollinated ponderosa pine progenies. FWR Exp. Sta., Univ. of Idaho Sta. Pap. No. 15 (1974). — VAN DEUSEN, J. L.: Five-year results of a ponderosa pine provenance study in the Black Hills. USDA Forest Service Res. Note RM-278 (1974). — WELLS, O. O.: Geographie variation in ponderosa pine. I. The ecotypes and their distribution. Silvae Genet. 13 (4): 89–103 (1964 a). — WELLS, O. O.: Geographic variation in ponderosa pine. II. Correlations between progeny performance and characteristics of the native habitat. Silvae Genet. 13 (5): 125–133 (1964 b). — WRIGHT, J. W.: Genetic variation among 140 half-sib Scotch pine families derived from 9 stands. Silvae Genet. 12: 83–9 (1963). — WRIGHT, J. W.: Introduction to Forest Genetics. Academic Press, N.Y. (1976).

An Intergrated Population of Abies grandis – Abies concolor in Central Idaho and its Relation to Decay[1])

By D. J. FREDERICK

Cooperative Tree Improvement and Hardwood Research Programs North Carolina State University Raleigh, North Carolina 27667 USA

(Received July 1976 / February 1977)

Introduction

Grand fir (Abies grandis [DOUGL. ex. D. DON] LINDL.) and white or concolor fir (Abies concolor [GORDON and GLEND.] LINDL. ex. HILDEBR.) are two important and widely distributed true firs in the Western United States. Grand fir occurs primarily in the Pacific Northwest and in the Rocky Mountains from central Idaho to southern British Columbia. White fir grows in the southern Cascade, Sierra Nevada, and Rocky Mountains south of the range of grand fir (LITTLE, 1971). The southern Rocky Mountains white fir is often referred to as A. concolor var. concolor and the Sierran to A. concolor var. lowiana. Presently grand fir and concolor fir are regarded as morphologically distinct (*Table* 1). Between the undisputed ranges of grand fir and white fir lies an area in northeastern Oregon and west central Idaho supporting fir populations that are morphologically intermediate and not easily assigned to either spccies.

Several authors recognize A. concolor as occurring in these two regions (DAVIS, 1952 and PECK, 1961). Many disclaim its occurrence (MCMINN and MAINO, 1947; FOWELLS, 1965; and E. L. LITTLE, personal communication, 1975).

These two species hybridize freely in areas of overlap in California and western Oregon (HAMRICK and LIBBY, 1972). There are no reports, however, of verified hybrids occurring in the northern Rocky Mountains.

In central Idaho, south of the Salmon River (approximately 46° 30' N. Lat.) an intergraded population apparently exists between concolor fir and grand fir. JOHNSON (1966) recognized this morphological complex in west-central Idaho and tentatively interpreted it as an intergraded population of A. *concolor*, var. lowiana, A. grandis and trees which exhibited characteristics of both species. DANIELS (1969) reported typical grand fir types, intermediate forms, and concolor-like individuals growing together near McCall, Idaho. He studied the phenotypic variability of the population and generally outlined its composition and extent using a hybrid index technique. Individuals in his

[1]) Supported by McIntire-Stennis, U.S. Department of Agriculture.

Table 1. — Morphological differences between grand and white firs, and grades (included in parentheses) used in computing hybrid indices.

Trait	Expression in	
	A. concolor	A. grandis
Stomatal bands on upper leaf surface	Present (= 0)	Absent (= 2)
Needle groove on upper leaf surface	Absent (= 0)	Present (= 2)
Needle tip	Not notched (= 0)	Notched (= 2)
Needle arrangement	Curve upward and outward (= 0)	2-ranked (= 2)
Periderm color	Yellow (= 0)	Red (= 2)
Bark thickness (not included in index)	10-15 cm on old trees	5 cm or less
Total index value for typical trees	0	10

sample were morphologically intermediate with no pure types even though the sampled trees were generally most similar to *A. grandis*.

Bark periderm color is a characteristic used to separate grand fir and white fir. The last-formed periderm of both species is known as necrophylactic periderm. This periderm in grand fir is reddish-purple while that of white fir is yellowish (CHANG, 1954; JOHNSON, 1966; DANIELS, 1969; MULLICK, 1969, 1971). Morphologically intermediate fir populations resulting from hybridization and subsequent back crossing to one or both parents such as apparently occur in central Idaho vary in periderm color, from red to yellow. Other intermediate populations have shown variation in the red color from deep reddish-purple to light pink (DANIELS, 1969; ZOBEL, 1973).

This paper reports the morphological variability in the *Abies grandis-Abies concolor* var. *lowiana* species complex in central Idaho. It also relates periderm color to incidence of decay.

Procedure

Stands were located on a variety of sites on the Payette and Boise National Forests, on State Forests, and private land in west central Idaho. Plot centers were randomly located within each selected stand. At each of 110 plots, 10 fir trees were randomly selected for evaluation of periderm color and incidence of decay by increment boring. Periderm color was examined and classified either red or yellow. The color variation in our sample was discret and all periderm could easily be classified into these two color classes.

The principle decay fungus associated with grand fir in central Idaho is the Indian paint fungus *(Echinodontium tinctorium* E. & E.). It causes a heartrot and its presence is readily detected by increment boring. Increment cores collected from all sample trees were cultured to isolate and identify fungi present.

At each of 28 randomly selected plots, two trees were randomly selected and felled. Branches for study were collected from the outside margin of the middle of the crown of each such tree. For each tree, four leaf and one bark characteristic were measured, and a hybrid index was computed according to the scheme outlined in *Table 1*. Total index values could vary from 0 (most similar to white fir) to 10 (most similar to grand fir).

Results and Discussion

Of the 1,100 trees studied, 475 = 43% had red periderm and 625 = 57% had yellow periderm characteristic of white fir.

Cores from 398 individual trees yielded positive cultures. *E. tinctorium* was the most common fungus found and appeared in more than 97 percent of the cores. Other fungi contributing a minor amount of decay included: *Armillaria mellea* (VAHL.) QUEL., *Fomes roseus* FR., *Hydnum abietus* WEIR., and *Stereum sulcatum* BURT in PECK. The proportion of yellow-periderm trees showing evidence of decay was lower (210 trees = 33.6%) than was the proportion of red-periderm trees showing evidence of decay (188 trees — 39.6%). This difference, while not large, was statistically significant at the 5% level: A Chi-square analysis gave a Chi-square value of 4.11, with 1 d. f. The basis for this may be genetic variability in the tree populations resistance to the heartrotting fungi, or, variability in susceptibility caused by microclimatic differences either favoring or restricting fungal development.

The mean hybrid index for the 56 felled trees was 5.9, indicating slightly greater phenotypic similarity to grand fir (index value = 10) than to white fir (index value = 0) *(Figure 1)*. Intermediacy in one character often is accompanied by intermediacy in others. The foliar traits varying together possibly are genetically linked polygenic characters but progeny testing would be necessary to validate this.

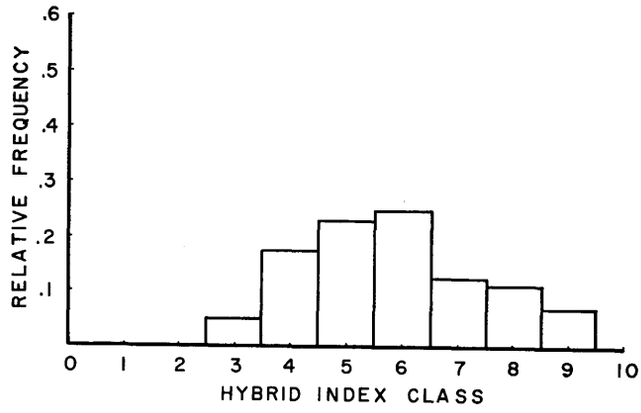

Fig. 1. — Relative frequency of 56 trees by hybrid index classes.

Periderm color does not seem to be linked with foliar characters. Individuals having *grandis*-like foliar characteristics often have yellow bark and those tending toward *concolor* foliar characteristics may be red barked.

In general this population tends to morphologically resemble *A. grandis* more than *A. concolor* var. *lowiana* suggesting a history of introgression with back crossing to parental grand fir. Fir populations sampled in eastern Oregon have shown similar results (HAMRICK and LIBBY, 1972).

Ecologically, true grand fir and concolor fir are quite dissimilar. Grand fir occurs most abundantly on cool, moist sites where it frequently has considerable heartrot. Concolor fir occurs on relatively xeric sites and generally has a lower incidence of heartrot. The hybrid in central Idaho seems intermediate in decay incidence and site moisture preference when compared to grand and concolor fir. These traits may be due to the presence of genes from white fir.

The hybrid obviously has selective advantage. Recognition and further study are essential to its understanding and proper management in this region of Idaho.

Acknowledgment

Thanks are extended to D. M. MULLICK, University of British Co-

lumbia and J. W. Wright, Michigan State University for their reviews and suggestions.

Summary

An intergraded population of *Abies* is reported in central Idaho between *Abies grandis* and *Abies concolor*. Its presence probably reflects a history of introgression and subsequent back crossing to parental grand fir. Analysis of 1100 trees for bark periderm color and decay by increment boring and 56 trees for foliar characteristics indicates an intermediate population. Periderm color tends to vary independently from foliar traits. Trees with yellow periderm have less incidence of decay than those with reddish periderm. The most common fungus isolated from decayed wood was *Echinodontium tinctorium* E. and E.

Key words: Abies grandis, Abies concolor, Echinodontium tinctorium, hybridization.

Zusammenfassung

Es wird über eine Hybridpopulation zwischen *Abies grandis* und *Abies concolor* in Zentral-Idaho berichtet. Ihre Existenz ist vermutlich auf Introgression mit nachfolgender Rückkreuzung zurückzuführen. Die Untersuchung von 1100 Individuen auf Peridermfarbe sowie andere Rinden- und Blattmerkmale hin läßt den Schluß auf eine Zwischenpopulation zu. Peridermfarbe und Blattmerkmale korrelieren nicht. Bäume mit gelbem Periderm sind gegenüber *Echinodontium tinctorium* E.a.E. resistenter als solche mit rötlichem Periderm.

Literature Cited

Chang, Y.-P.: Bark structure of North American conifers. U.S. Dep. Agr. Tech. Bull. 1095. 86 pp. (1954). — Daniels, J. D.: Variation and intergradation in the grand fir-white fir complex. Ph. D. Diss., Univ. of Idaho, Moscow. 235 pp. (1969). — Davis, R. L.: Flora of Idaho. Wm. C. Brown Company, Dubuque, Iowa. 828 pp. (1952. — Fowells, H. A.: Silvics of forest trees of the United States. U.S. Dep. Agr. For. Serv. Agr. Handbook No. 271. 762 pp. (1965). — Hamrick, J. L. III, and Libby, W. J.: Variation and selection in western U.S. montane species. I. White fir. Silvae Genet. 21: 29—35 (1972). — Johnson, F. D.: Native trees of Idaho. Idaho Agr. Ext. Serv. Bull. 289. 36 pp. (1966). — Little, E.: Atlas of United States trees. I. Conifers and important hardwoods. U.S. Dep. Agr. For. Serv. Misc. Publ. 1146. (1971). — McMinn, H. E., and Maino, E.: An illustrated manual of Pacific coast trees. Univ. California Press. Berkeley. 402 pp. (1947). — Mullick, D. B.: Studies on periderm. II. Anthocyanidins in secondary periderm tissue of amabilis fir, grand fir, western hemlock, and western red cedar. Can. J. Bot. 47: 1419—1422 (1969). — Mullick, D. B.: Natural pigment differences distinguish first and sequent periderms of conifers through a cryofixation and chemical techniques. Can. J. Bot. 49: 1703—1711 (1971). — Peck, M. E.: A manual of higher plants of Oregon. 2nd ed. Binfords and Mort., and Oregon State Univ. Press, Corvallis. 936 pp. (1961). — Zobel, D. B.: Local variation in intergrading *Abies grandis — Abies concolor* populations in the central Oregon Cascades: needle morphology and periderm color. Bot. Gaz. 134 (3): 209—220 (1973).

Isoenzyme Variation of Coastal Douglas-fir
I. A Study of Geographic Variation in Three Enzyme Systems[1]

By J.-Ch. Yang[2], T. M. Ching and K. K. Ching

(Received July/November 1976)

Introduction

Genetic polymorphism or individual variation in morphological, phenological, physiological, and biochemical characters in natural populations of Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) indicates fairly high heterozygosity in the gene pool of this species. By review of papers published by Ching *et al.* (1965) and others, Stern (1968) postulated the existence of genetic polymorphism of strobilus color as well as needle color in Douglas-fir. These characters were thought to be under the control of "complex loci" or "supergenes". The controlling mechanisms, however, could not be effectively explored and analyzed by traditional methods such as provenance trial, study of inheritable quantitative traits, investigation of rare recessive mutants, or cytogenetic studies.

Information on the distribution of allelic variation in natural populations can be obtained with the aid of electrophoretic analysis of isoenzymes. This is because enzymes are composed of polypeptides synthesized by the action of one or more structural genes. The electrophoretic variations of enzymes can be directly related to changes in gene structure or codon sequence and always follow Mendelian segregation in ideal populations. The objectives of this study were to reveal the existence and patterns of polymorphism in three enzyme systems, leucine aminopeptidase (LAP), esterase (EST), and glutamate oxaloacetate transaminase (GOT), and to analyze the extent of genetic differentiation among Douglas-fir provenances in terms of changes in allele frequency.

Literature Review

The applicability of electrophoretic separation of enzymes and proteins to the study of geographic variation in forest trees has been evidenced by several reports. Lewis and Cech (1969) found a high uniformity within a geographic area in acid phosphatase, leucine aminopeptidase, and peroxidase among trees of black cherry *(Prunus serotina* Ehrh.). Feret and Stairs (1971) indicated that, of the eight electrophoretic variants of peroxidase in *Ulmus pumila* L., three were seed-source specific and five exhibited varying frequencies in most seed sources.

Hare and Switzer (1969) reported that the electrophoretic patterns of seed proteins from western sources of loblolly pine *(Pinus taeda* L.) are more similar to those of shortleaf pine *(P. echinata* Mill.) than are the eastern sources. Esterase zymograms of needles of clonal grafts representing 16

[1] Research submitted as partial fulfillment of the Ph. D degree for Yang in Forest Management (Genetics) at Oregon State University, Corvallis, Oregon.

[2] The authors are Senior Research Fellow, Taiwan Forestry Institute, Taipei, Taiwan; Professor of Seed Physiology, Oregon State University; and Professor of Forest Genetics, Oregon State University. This is Paper 1,065 of the Forest Research Laboratory, School of Forestry, Oregon State University.