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Genetic Variability in Susceptibility of Pinus radiata to Western Gall Rust

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Summary

Western gall rust (WGR), caused by *Endocronartium harknessii* Hiratsuka, is a serious disease of *Pinus radiata* D. Don in California. The fungus presently exists only in western and northern North America, but it poses a threat to susceptible pines growing elsewhere. At a single experimental site, large differences in susceptibility to WGR were found between the five native populations of *P. radiata*. The two island populations, from Guadalupe and Cedros Islands, were least susceptible. Of the three mainland populations, Año Nuevo trees were substantially less susceptible than were trees from the Monterey and Cambria populations. New Zealand and Australian select families were intermediate in susceptibility between the Año Nuevo and the Monterey populations, from which the New Zealand and Australian land-races are derived. Components of variation between families within populations were significant in the native Monterey population, among the select families from New Zealand and Australia, and among inter-population hybrids. Heritability estimates and comparisons of full-sib families to half-sib or open-pollinated families indicate substantial levels of additive (narrow-sense) heritability with regard to susceptibility to WGR, and provide no evidence for non-additive genetic variance in this trait. The results suggest that breeding for resistance to the disease is likely to yield worthwhile changes in average susceptibility.

Key words: Endocronartium, Heritability, Population architecture, Radiata pine, Susceptibility.

Zusammenfassung

Rost, verursacht durch *Endocronartium harknessii* Hiratsuka, ist eine ernsthafte Krankheit von *Pinus radiata* D. Don in Kalifornien. Der Pilz existiert momentan nur im westlichen und nördlichen Nordamerika, stellt aber auch für empfindliche Kiefern, die woanders wachsen, eine Bedrohung dar. An einem einzelnen Versuchsstandort wurden große Unterschiede in der Empfindlichkeit gegenüber WGR bei den 5 autochthonen Populationen von *Pinus radiata* gefunden. Zwei Inselpopulationen von Guadeloupe und Cedros Islands waren am wenigsten empfindlich. Von den 3 Festlandpopulationen waren die Bäume der Año Nuevo Population beträchtlich weniger empfindlich als die Bäume der Monterey und Cambria Population. Selektierte Familien aus Neuseeland und Australien waren in ihrer Empfindlichkeit zwischen den Año Nuevo und Monterey Populationen intermediär, von denen die neuseeländischen und australischen Landrassen abstammen. Die Variationskomponenten zwischen Familien innerhalb von Populationen waren für die autochthone Monterey Population, innerhalb selektierter Familien aus Neuseeland und Australien, und innerhalb der Hybriden zwischen den Populationen signifikant. Heritabilitätsschätzwerte und Vergleiche von Voll- und Halbgeschwisterfamilien oder frei abgeblühten Familien zeigten beträchtliche Niveaus von additiver Heritabilität im engeren Sinne hinsichtlich ihrer Empfindlichkeit gegenüber WGR, und lieferten keinen Beweis für nicht additiv-genetische Varianz in diesem Merkmal. Die Ergebnisse legen nahe, daß die Züchtung auf Resistenz gegenüber dieser Krankheit wahrscheinlich zu erzielen ist, da die durchschnittliche Empfindlichkeit wechselt.

Introduction

Radiata pine *(Pinus radiata* D. Don) has become an important species for many purposes (commercial forests, parks, windbreaks, urban and amenity plantings, and Christmas trees) in many regions of the world. Western gall rust (WGR), caused by *Endocronartium harknessii* (Hiratsuka 1969) syn. *Peridermium harknessii* J. P. Moore, is a pathogen of many species of hard pines over much of northern and western North America (Peterson and Jewell 1968). It occurs on radiata pine in much of California. Damage is variable but can be severe, leading to stem-deforming galls and cankers and mainstem branching. WGR has not yet been reported outside of North America. Because of its wide host-range within the Diploxylon subgenus of *Pinus,* and because of its ability to spread from pine to pine without an intermediate stage on an alternate host, there is concern that WGR may spread rapidly and cause serious damage if it becomes established in other pine regions. Its possible introduction to the extensive plantations of pines in the Southern Hemisphere gives particular cause for concern (Old 1981; Parmeter and Newhook 1967).

Radiata pines at the University of California's Russell Reservation have been infected by WGR for over two decades, and there the disease has been at epidemic levels since about 1974. Repeated observations on its occurrence and spread have been made in *P. radiata* plantations installed at Russell Reservation for other purposes since 1969, and, since 1979, in a small clonal plantation designed

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specifically to test the relationship of WGR susceptibility to the maturation state (ZAGORY and LIBBY 1985) of *P. radiata*. By 1981, observations at Russell Reservation and elsewhere increasingly suggested that there is substantial and perhaps usable variation in susceptibility to WGR among populations, among clones, and among maturation states of radiata pine[1]).

Materials and Methods

Experimental Design

Each of the five native population-samples was composed of 20 families drawn approximately equally from 3—5 stands sampling the major different physiographic conditions in the population. Most of these were open-pollinated families, collected in 1978. The three mainland collections were made from parents judged to be of above-average phenotype with respect to size, form and general health (ELDRIDGE 1978, 1983), while the two island collections were mostly from randomly-selected trees (LIBBY 1978). Earlier collections had been made from the mainland stands in 1962 (LIBBY and CONKLE 1966) and from the islands in 1965 (LIBBY, BANNISTER and LINHART 1968), and breeding-orchards were established during 1963—68. By 1973, the breeding-orchard trees from these 1962 and 1965 samples were sexually mature and were then used as parents in various intra- and inter-population controlled crosses. Progeny from 20 of these inter-population hybrid crosses were included in the present experiment. At least one family of each possible inter-population combination was included (= 10 families) and the remaining 10 families were additional mainland × island combinations. The parents of seven of these hybrid families had also been succesfully used in a within-stand cross (for example, Año Nuevo 49 × Año Nuevo 47, Año Nuevo 47 × Guadalupe 15b, Guadalupe 14a × Guadalupe 15b), and these seven sets of related full-sib families were substituted for open-pollinated families of the same stand among the families sampling the native populations. In addition, 38 full-sib families were drawn from various combinations of trees selected in the New Zealand, Tasmanian, South Australian, Victorian, Australian Capital Territory, and New South Wales radiata breeding programmes. Finally four clones known to be moderately susceptible to WGR were included. Two were full-sibs from one of the New Zealand families and the other two were unpedigreed clones from the Monterey native population.

Details of tree propagation, location of the experimental site at the Russell Reservation and the arrangement of 5 replicate blocks in relation to a nearby source of inoculum of WGR are given elsewhere (OLD, LIBBY and RUSSELL 1985). The trees were planted in February 1982 at 2 m square spacing.

The plantation was designed to maximise sensitivity of the between- population comparisons. Each plot was com-

posed of ten randomly-arranged trees, as follows: one seedling from each of the five native populations; one seedling of an inter-population hybrid; one seedling from each of three different New Zealand-Australian select families: and one steckling (plantable rooted cutting) from one of the four clones. The four clones were systematically alternated among the 100 plots in the experiment, such that each clone sampled the environment of the entire plantation in a similar manner. Twenty-four of the 38 New Zealand-Australian (NZ-Aust) select families were organized in a hierarchical (18 families) or factorial (6 families) design, with half-sib relationships among them. Ten seedlings from each of these 24 families were included, with two seedlings being assigned to each replication. All other families contributed only 5 seedlings, one per replication. Thus, this 1000-tree plantation was composed of 100 seedlings from each native population, 100 inter-population hybrid seedlings, 300 seedlings from the 38 NZ-Aust select families, and 25 stecklings from each of four clones.

Data collection and analyses

Individual-tree observations and measurements were taken during February 1983 and again during January 1984. First-year data included numbers of branch- and stem-galls (recorded separately), height, crown density, and crown diameter as well as a number of other growth and form characteristics. Second-year data included the numbers of stem- and branch-galls, height, basal diameter and a form rating.
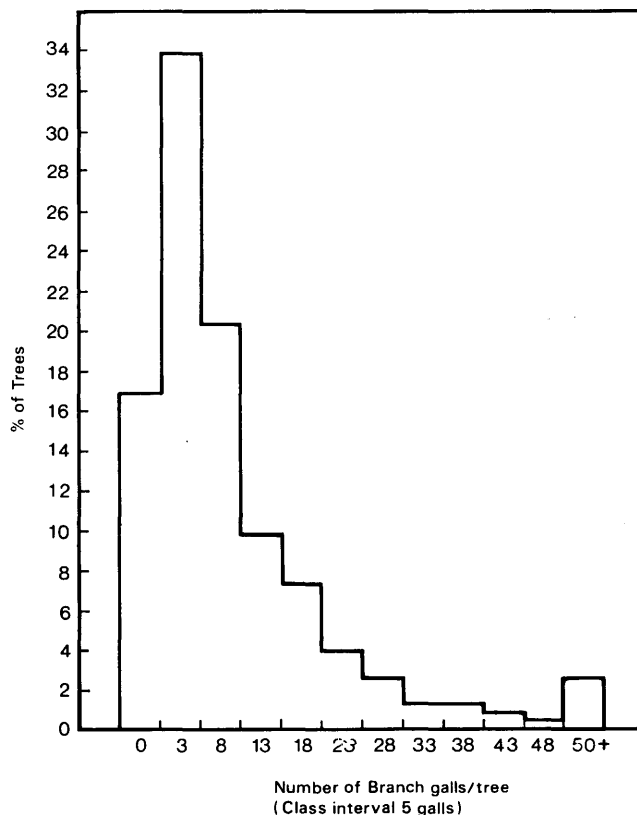

Figure 1. — Incidence of WGR on seedling-origin trees throughout the whole plantation, January 1984, following two growing seasons in the field, as indicated by the percentages of trees bearing zero to fifty or more branch galls. With the exception of trees having no observed branch galls (the zero class), or more than 50 (the 50 + class) the data are grouped in class intervals of 5 galls, with horizontal-axis numbers indicating the class midpoint.

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[1]) In 1981, a cooperative project was set up between U.C. Berkeley, CSIRO Australia, and private forestry interests in California and New Zealand, with the following primary objectives:
— to assess and rank the five native populations with respect to their susceptibility to WGR;
— to assess the WGR susceptibility of 38 pedigreed full-sib families from New Zealand and Australia (the parents of these families are members of extant seed-orchards, and their offspring are widely planted in New Zealand and Australia);
— to investigate the inheritance of WGR susceptibility, using interpopulation hybrids and heritability estimates within population samples.

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Table 1. — Radiata pine population-samples ranked by average numbers of stem-galls per tree after two years in the field.

Population Sampled	Average Numbers of Stem-galls per Tree	±95% Confidence Limits
Guadalupe Island	0.21	0.12
Año Nuevo	0.31	0.12
Cedros Island	0.55	0.23
Inter-Pop. Hybrids	0.61	0.29
NZ-Aus Selects	0.67	0.13
Monterey	0.80	0.22
Cambria	1.11	0.31

A two-way analysis of variance (ANOVA) was used to quantify differences between populations, differences between replications, and population $\times$ replication interactions for all populations (excluding the four clones). Two-way ANOVAs were similarly used to quantify differences between families, differences between replications, and family $\times$ replication interactions within each population. Families with missing trees were excluded from those analyses using all five replications. Additional ANOVAs were then performed using various combinations of only four and, if needed, only three replications, until every family was included at least once in an ANOVA. The variance components, significance levels, and heritability estimates derived from the various permutations of families and replications used in the ANOVAs were consistent within each population. In addition, Chi-square procedures were carried out for all important analyses where the normality assumption was suspect, as an independent check of significance levels of observed differences.

Results

Differences between Population Samples

In 1982 and 1983, long periods of unusually cool wet weather occurred during WGR sporulation. By January 1984, portions of the trial (especially replications 1, 2 and 5) were heavily infected by the fungus. Since stem-gall and branch-gall incidences were correlated in all populations ($r = .34$ to $.63$, $p < 0.001$), and the branch-gall data provide a wider range and thus better resolution of infection levels,

we have concentrated on branch-gall numbers as our main indicator of WGR susceptibility.

After 2 years in the field, 16.9% (see Fig. 1) of seedling origin trees were still free of observed branch galls and 2.5% bore more than 50 branch-galls. (By convention, we scored all trees with > 50 galls as having 51, even though some had over 100). The stem-gall data (Table 1) were even more skewed: 67.1% of these trees were still free of observed stem-galls in January 1984, and only 1.6% had five or more stem-galls.

Table 2 includes the mean numbers of branch-galls per tree for all seven population-samples (with associated 95% confidence limits), indicates the probability levels for statistically significant variation in gall incidence between the five replications, and gives estimates of narrow-sense heritability of WGR susceptibility for each population.

Statistically significant variation in branch galls per tree between the five replications occurred in six of the nine population-samples. (Note that full-sib and open-pollinated data are analyzed as separate samples of two of the populations in Table 2). This replication component of variation is clearly attributable to the location of the replication in relation to the nearby source of inoculum. The average numbers of branch-galls observed per tree (seedlings and stecklings) were 15.1 (rep 1), 10.8 (rep 2), 8.6 (rep 5), 4.4 (rep 4), and 4.3 (rep 3). In all analyses the population $\times$ replication interaction terms were near zero and none were statistically significant.

The average number of branch-galls per tree was significantly different between the seven population-samples at $p < .001$ (Table 2). Ranked means were from 2.0 galls per tree for the Guadalupe Island sample to 14.9 galls per tree for the Cambria sample. The 95% confidence limits in both Tables 1 and 2 indicate that the two island provenances were similarly of low susceptibility to WGR infection, whereas the Monterey provenance and (especially) the Cambria provenance contained many trees with high susceptibilities. The Año Nuevo provenance was significantly less susceptible to the disease than the other two mainland

Table 2. — Radiata pine population-samples ranked by their average number of branch-galls per tree after two years in the field, statistical significance of differences between replications and families, and estimates of narrow-sense heritability of susceptibility to WGR.

Population Sampled	Family Structure[1]	Number of Families	Mean Number of Branch-Galls/Tree[2]	±95% Confidence Limits	Statistical Significance[3] Between Replications	Statistical Significance[3] Between Families	Narrow-sense Heritability[4] %
Guadalupe Island	O-P	15)		1.1	NS	NS	30
	F-S	5)	2.0		*	NS	16
Cedros Island	O-P	20	3.1	1.2	*	NS	34
Ano Nuevo	O-P	14)		1.8	NS	NS	61
	F-S	6)	5.6		NS	NS	45
Inter-Pop. Hybrids	F-S	20	7.5	2.2	**	**	27
NZ-Aus Selects	F-S	38	10.5	1.4	***	***	61
Monterey	O-P	20	12.0	2.3	***	*	44
Cambria	O-P	20	14.9	2.5	***	NS	20

[1]) O-P = Open-pollinated families; F-S = Full-sib families.

[2]) Statistical significance of differences in mean number of branch-galls between populations is $p < .001$.

[3]) $* p < .05$ $** p < .01$ $*** p < .001$ NS $p > .05$.

[4]) narrow-sense heritability = (full-sib family variance component $\times$ 2)/(total variance)
= (open-pollinated family variance component $\times$ 3)/(total variance) (SQUILLACE 1974).

Data transformed to square roots before analyses.

provenances. The pattern of variation in branch-gall incidence among population samples was essentially the same regardless of replication.

Differences within population samples

Statistically significant between-family variation in branch gall incidence was detected (by ANOVA of square-root transformed data) only among the NZ-Aust selects, the interpopulation hybrids, and the Monterey families (Table 2). However, positive between-family variance components were obtained in every analysis performed, and the non-significant values reported in Table 2 have probability values of $< .10 > .05$ for the Cedros, Año Nuevo full-sib and Año Nuevo open-pollinated families, and probability values of $< .25 > .10$ for the Cambria, Guadalupe open-pollinated and Guadalupe full-sib families. Chi-square analyses of untransformed data indicate highly significant ($p < .001$) differences among families in each of the seven population-samples.

High heritability estimates (FALCONER 1981) of WGR susceptibility were obtained for the Año Nuevo and Monterey population-samples and for the NZ-Aust select families (Table 2). The high heritability estimates for the Año Nuevo population-samples, together with the nearly-significant difference between families, can be taken to mean that heritability is not zero for Año Nuevo, that it is not well estimated, and that it may be high. Lower heritability estimates were obtained for both island population-samples and for the inter-population hybrids, which had island parentage contributing to 17 of the 20 hybrid families. The Cambria population-sample, which was the most heavily infected, had an estimated heritability of only 20%. Of the 99 living Cambria seedlings, only five had no detected branch-galls, and none of its 20 families had more than one uninfected member. The least susceptible Cambria family averaged four branch-galls per tree, and the worst averaged 29.6. Thus, most or all Cambria trees were susceptible to WGR. The highly significant differences between replications and the low heritability estimates (Table 2) indicate a strong influence of environment on the degree of their susceptibility.

The presence of non-additive genetic variation may be inferred (FALCONER 1981) by comparing the two sets of variance components associated with open-pollinated and full-sib families (possible in the Guadalupe and Año Nuevo population-samples), one set of variance components associated with maternal and paternal families in the hierarchical design (possible with 18 NZ-Aust select families), and one set associated with maternal, paternal and full-sib families in the factorial design (possible with 6 NZ-Aust select families). The number of families being small, each test was of low power. In each of the four analyses, the component associated with non-additive genetic variation consistently had a negative point estimate. In those analyses with two seedlings per family per replication where the family $\times$ replication interaction term could be separated from the residual term, the interaction term proved to be near zero and non significant. Thus, these analyses provided no evidence for non-additive genetic variation in susceptibility to the WGR inoculum at Russell Reservation.

In general, analyses of the 20 inter-population hybrid families were not particularly informative with respect to mode of inheritance of WGR susceptibility (OLD, LIBBY and RUSSEL 1985), but Chi-square analysis of the untransformed data and ANOVA of square-root data (Table 2) both indicate a substantial family component to WGR susceptibility of the inter-population hybrids.

This study has provided no indication of the nature of susceptibility to E. harknessii in P. radiata. Statistically significant correlation values were obtained between susceptibility to the fungus and several growth and form characteristics, including plant height, crown diameter, and number of branches per whorl (OLD, LIBBY and RUSSELL 1985). These, however, accounted for only small percentages of the variation in WGR susceptibility. Larger significant correlations with 1983 crown density were found. This may reflect dense crowns providing a larger number of targets for spore infection during shoot elongation. In subsequent years crown density may be a composite of cause and effect as WGR infection commonly stimulates branch proliferation. Significant negative correlations to 1984 stem straightness were also obtained and are probably entirely the effect of WGR infection on stem form, and do not indicate any causal relationship of stem form to WGR infection.

Performance of the four clones

The four clones were included to provide information on spatial patterns of infection within the plantation. They failed in this assignment, for an interesting reason. In February 1983, when infection percentages of the seedling population-samples were from 7.1% to 18.1%, not one of the surviving 95 stecklings had a single gall. All four of these clones were known to be susceptible, and in fact eight stecklings of these four clones were among adjacent WGR-infected trees providing heavy inoculum loads to the experiment. By January 1984, some observable infection of the stecklings had occurred, but average numbers of branch-galls were only 1.3, 0.2, 1.2 and 1.0 for the four clones, and average numbers of stem-galls were 0.00, 0.04, 0.00 and 0.21 (compare to the averages for seedlings in Tables 1 and 2). Thus, although the clones were not infected to levels that allow spatial infection patterns to be accurately plotted, this experiment offers additional support to the findings of ZAGORY and LIBBY (1985) that WGR susceptibility is related to host maturation state. The seedlings were clearly in a more juvenile maturation state than the stecklings during 1982—83.

Comparison of parametric and non-parametric analyses

Because of the highly skewed nature of the gall-number data, not entirely corrected by square-root transformation, parametric analyses are suspect. In all cases, non-parametric Chi-square analyses indicated greater statistical significance (i.e. lower probability of differences being due to chance alone) for the main effects (populations, families, replications) than did the parametric ANOVAs. We have generally reported the more conservative parametric probabilities and confidence limits, but note here that most of the differences reported as NS ($p > .05$) in Table 2, for example, are statistically highly significant ($p < .01$ or $< .001$) in Chi-square analyses.

Discussion

Present knowledge of the patterns of susceptibility of P. radiata to WGR is restricted to the reaction of trees to the population of rust endemic at the Russell Reservation. There is a need to maintain the present trial in California for several years to see whether resistance of some families and genotypes persists at the high inoculum levels to be expected within the trial during future years. There is also

a need to investigate possible site × genotype interactions and to determine whether the relative resistance of the several populations, families and individual trees to WGR remains stable when exposed to collections of *E. harknessii* from a variety of geographical and host origins. Application of knowledge gained in this study to disease control in North America, and the assessment of tree breeding as a management option if WGR is accidentally introduced into other *P. radiata* - growing regions, will depend on the outcome of such research.

With the foregoing limitation, the main findings and implications for management of *P. radiata* are as follows:

This study has confirmed previous indications that the two island provenances of *P. radiata* are relatively resistant to infection by *E. harknessii* at the Russell Reservation (OLD 1981). Of the three mainland provenances, the Año Nuevo population ranked as the most resistant, and the Cambria population as the most susceptible. The lack of significant replication × population and replication × family interactions suggest that these differences exist at both high and low inoculum intensities, as replication 1 was undoubtedly subjected to a substantially greater inoculum load than were replications 3 and 4 (OLD, LIBBY and RUSSELL 1985).

There was substantial within-population variation in disease incidence and, for the select New Zealand and Australian families, highly significant between-family variation coupled with a high estimate of heritability. Analyses of limited numbers of families within the main NZ-Aust breeding design and within two of the population-samples, tested for the relative presence of additive and non-additive components of genetic variation. Although the available degrees of freedom are low the data suggest that inheritance of WGR susceptibility is largely additive.

These features of the inheritance of resistance and susceptibility to WGR indicate likely benefits from selection among tree genotypes already or concurrently selected for favourable silvicultural characteristics, and their inclusion in open-pollinated seed-orchards. Clonal selection of specific outstanding trees may remain an attractive option, particularly if sufficient additional maturation-related resistance can be added to the additive genetic gains obtained by mating selected individuals (ZAGORY and LIBBY 1985). The selection-plus-clonal option for the control of WGR runs a risk of breakdown of resistance to a variable pathogen population in the evvent of broadscale deployment of uniform radiata pine genotypes. However a proper deployment of enough unrelated clones may be no more dangerous than (or even preferable to) using seed-orchard seedlings (LIBBY 1982). Neither of these strategies is likely to achieve total resistance to the disease; however an attainable goal might be the reduction of average susceptibility of most plantations such that appropriate silvicultural practices could limit WGR-related damage to acceptable levels.

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The Effect of Crown Segment on the Mating System in a Douglas-Fir (Pseudotsuga menziesii (Mirb.) Franco) Seed Orchard

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Abstract

The mating system in a mixed clonal/seedling Douglas-fir [Pseudotsuga menziesii (MIRB.) FRANCO] seed orchard was studied with the aid of allozyme polymorphisms at six loci (EST-1, PGI-2, G6PD, 6PGD-1, PGM, and IDH). Trees were subjected to cooling treatment to retard bud development and compact the pollination period. The outcrossing rate of two crown levels (upper and lower) and aspects (northern and southern) were estimated and compared for clonal and seedling material separately using single and multilocus methods. Single locus estimates of t ranged

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