BLISTER RUST RESISTANCE IN EASTERN WHITE PINE

R. F. Patton and A. J. Riker

Department of Plant Pathology, University of Wisconsin

A project aimed at the development of white pine trees resistant to blister rust was begun in 1938 by Professor A. J. Riker and his associates in collaboration with T. F. Kouba and other members of the Blister Rust Control unit. A long range view of the problem was adopted. The original aims were: (1) to determine whether resistance to blister rust existed in native eastern white pine; (2) once the existence of resistance was established, to determine the resistance of progeny of resistant individuals; and (3) to investigate means of propagation of resistant individuals and how they might be used in a reforestation program. The program included selection, testing, breeding, and vegetative propagation.

Selection and Testing

Initially, 163 white pines in severe rust infection centers were selected as possibly resistant. Crafts were made from all and seed collected from as many as possible. The grafts and open pollinated seedling progenies were then planted in a blister rust nursery established to test resistance to infection. In this first test, the material was divided among four replications, two of which were exposed to natural infection only, while the other two were given supplementary artificial inoculation. Inoculum for natural infection was assured by planting rows of ribes plants between the beds of white pine transplants. For artificial inoculation, telia-bearing ribes leaves were clipped to the top of each graft or seedling, the beds covered with cloth cages, and the proper humidity and temperature conditions for infection maintained by sprinkling periodically with water over a period of 3 days.

Resistance was measured by the response of the trees over a period of years. A summary of blister rust infection in grafts of the first selections and their wind-pollinated progeny appears in table 1. Infection in the replications given artificial inoculation was considerably higher than in the replications exposed only to natural infection. Artificial inoculation has been used in all subsequent tests of additional materials, supplemented by exposure to natural infection from interplanted ribes bushes.

Rating for resistance was based on amount of infection, vigor of the trees, and vigor and type of development of any resulting cankers. No selections were found which were completely immune to the disease, although widely different degrees of resistance appeared among the selections. Of the original 163 selections, 40 were rated as highly resistant to blister rust, and many of these have been used in the breeding program. one of the major factors in resistance was the ability to "cork-out" the infection through production of a wound periderm around the lesion, the tissues of which eventually became necrotic and were sloughed off with complete elimination of the invading pathogen. Additional selections have been, and others will be, made to encompass a wider range of climate and genotypes. Grafts of these additional selections are now undergoing testing.

Table 1.--Summary of blister rust infection to 1955 (killed or cankered trees) on trees of original selections under test for resistance at Blister Rust Nursery, Wisconsin Rapids.

Origin of Trees	Selections 1 - 63: Repl. no. and kind of inoculation	Selections 1 - 63: Total trees at beginning	Selections 1 - 63: Infected trees: 1942-55	Selections 101 - 200: Repl. no. and kind of inoculation	Selections 101 - 200: Total trees at beginning	Selections 101 - 200: Infected trees: 1944-55
		No.	Percent		No.	Percent
Control seedlings	1	156	99	5	318	99
Seedlings from selections	Natural +	686	99	Natural +	972	99
Grafts from selections	artificial (*Ribes cynosbati* 1941)	56	29	artificial (*R. nigrum* 1942 + 1943)	88	44
Control seedlings	4	237	100	8	297	98
Seedlings from selections	Natural +	827	99	Natural +	1004	98
Grafts from selections	artificial (*R. nigrum* 1941)	49	47	artificial (*R. nigrum* 1942 + 1943)	84	31
Control seedlings	2	157	95	6	335	74
Seedlings from selections	Natural only	669	94	Natural only	954	77
Grafts from selections		57	11		90	8
Control seedlings	3	238	94	7	265	70
Seedlings from selections	Natural only	851	91	Natural only	1060	62
Grafts from selections		49	14		82	4

Infection among the seedling progenies from the parent selections was high. The wind-pollinated seedlings exhibited no greater percentage of blister-rust--resistant individuals than ordinary seedlings from the nursery used as controls (table 2). Also, a comparison of infection in seedlings from resistant parents with that among seedlings of susceptible parents showed no difference between the groups (table 2).

Table 2.--Comparison of response of grafts and seedlings of resistant and susceptible selections to artificial inoculation and exposure to natural inoculation, 1942-1955.

Susceptibility Group	Grafts			Seedlings 1/	
	Total	Infected		Total	Infected
		Total	With resistance		
	No.	Percent	Percent	No.	Percent
Selections 1-63					
Resistant	119	26	19	344	97
Susceptible	319	39	3 2/	1859	97
Selections 101-200					
Resistant	165	18	12	928	90
Susceptible	453	57	2 2/	1953	94
All Selections					
Resistant	284	21	15	1272	92
Susceptible	772	50	2 2/	3812	95
Totals	1056	42	6	5084	94
Control Seedlings 3/	--	--	--	2003	91

1/ Seedlings were grown from wind-pollinated seed collected from the parent selections in the field.

2/ Cankers abnormal but amount of data insufficient to classify the selection as resistant; or, these trees may possess a lower degree of resistance than those classed as "resistant."

3/ Controls were ordinary commercial seedlings from the regular stock in Griffith State Forestry Nursery.

The amount of infection on the grafts was much less than that on either the seedling progenies of the selections or the control seedlings (tables 1 and 2). These and other tests in the blister rust nursery have shown that the physiological age of the material greatly influenced the susceptibility of white pine trees to blister rust. The longer incubation period of the rust fungus in older trees, before the appearance of visible bark discoloration, is well known. It appeared also, however, that grafts, even of susceptible trees, generally showed a much smaller total amount of infection than did seedlings (tables 1 and 2). For example, in tests of new material not represented in tables 1 and 2, 91 percent of 122 control seedlings were cankered after artificial inoculation. However, of 53 control grafts, representing 6 different susceptible selections, only 34 percent were cankered, with infection of individual selections ranging from 11 to 83 percent.

Resistance of the parent selections in the form of grafts is also being tested in outplantings in the field in a number of different places in this country and abroad. Grafts have been planted in areas favorable for severe blister rust infection, both in the open and in plots under a light overstory with some undercover. Poor survival and the abnormal growth habit of grafts have proved to be limiting factors in these field resistance studies. Grafts are usually grown in the Griffith State Nursery at Wisconsin Rapids for 2 or 3 years after grafting in order that a stocky, well-developed plant may be produced. However, after outplanting in the field the grafts put on little diameter growth. They develop a slender, leggy, sparsely-branched form. They are easily weighed down by the press of snow and surrounding grass, ferns, or other herbaceous vegetation and especially in the shade often assume a prostrate or semiprostrate form as a result of this constant suppression. The grafts rarely develop a bushy form, and of course make a poor target in the field for blister rust sporidia. Even in plots on open grassy areas, the grafts have not kept up with control seedlings. Their sparse branching and slow increase in diameter give them a markedly spindly appearance in the field. In the blister rust nursery under less rigorous conditions., some grafts show these effects, while others have produced trees indistinguishable in form and growth rate from trees which originated as seedlings.

Breeding

A breeding program was instituted to determine the inheritance pattern of resistance. Controlled cross- and self-pollinations have been made between resistant trees, and to date a total of 263 different successful crosses have been made. Recently, hybridization with related soft pines was added to the breeding program to introduce resistance factors from other species and to direct development of rust-resistant pine toward inclusion of other desirable characters.

The first successful crosses were made in 194.9. The resulting progenies were inoculated in 1953 as 3-year-old (2-1) transplants. Early results from the first crosses, in which 67 to 100 percent infection occurred, indicated that a rather low percentage of first-generation seedlings from crosses between resistant parents were resistant. However, some parents appeared to have a greater ability than others to pass their resistance on to their offspring. The single self-pollination included among these crosses was represented by somewhat smaller, stunted trees which had only 30 percent infection. Many of these appear to be corking-out the fungus. Observations are continuing on all these trees.

In 1954, progenies from controlled crosses made in 1950 were inoculated as 2-1 transplants. Both environmental conditions and inoculum were poor and it was realized that infection percentages might be low. Reinoculation was not possible in 1955 because of the constantly abnormal high temperatures in July and August which were unfavorable for proper rust development all over the State. In 1956, the 1380 seedlings under test were reinoculated under favorable conditions. These represent a total of 141 different crosses among 21 parent selections. In the fall of 1956, 2 years after the first inoculation, 59 percent of 215 control seedlings were cankered. When all progenies in which any one parent selection was represented were grouped together, the amount of infection ranged from 23 to 73 percent for the different progeny groups. The anticipated better success of the 1956 reinoculation may increase the overall percentage of infection, and also is likely to make more evident any significant differences among the various parents represented in degree of resistance or their ability to transmit resistance to their progeny. From these and other progenies now under test, selections of resistant F1 individuals will be made, with a view toward further screening and eventual production of F2 generations through Fl intercrosses, or backcrosses to the parents.

In 1956 also, some 7000 seedlings of additional progenies were inoculated, largely representing crosses between resistant eastern white pine selections, but including some of Bingham's controlled crosses between resistant western white pine selections, and between his western (Pinus monticola) and our eastern (P. strobus) white pine selections. Response of the seedlings to this and subsequent artificial inoculations will be observed over a period of several years.

More recently emphasis was placed on making interspecific crosses. Sound seed on P. strobus was obtained from controlled pollination with P. ayacahuite, P. griffithii, P. monticola, P. parviflora, and P. peuce. Failures resulted from crosses with pollen from P. armandii, P. cembra, P. flexilis, and P. koraiensis. In other crosses it exotics, pollen from P. cembra failed to give sound seed on P. peuce, and pollen from P. strobus yielded 17-37 percent sound seed on P. peace, but failed on P. parviflora and P. koraiensis. Seedlings from these successful crosses will be artificially inoculated.

Flower Induction

The induction of early flowering of first generation seedlings was attempted by grafting techniques. In 1953, 1954, and 1956, F1 seedlings were grafted onto branches of large flowering white pines with the hope of obtaining early flower production on representatives of some of our controlled crosses. Successful grafts, with entire tops of seedlings as the scions or with scions cut from larger seedlings, can be made with relative ease if plastic bags are used for protection of the scion during the period a graft is becoming established. As yet, however, pollen has not been produced on any of the scions even though an abundance of pollen has been produced on surrounding twigs. The oldest grafts have had four seasons of growth, plus the season in which they were grafted, but they still show juvenile characteristics in their growth in the old-tree crowns.

Vegetative Propagation

Propagation of resistant selections by grafting is employed commonly for multiplication of stock for experimental use. Difficulties encountered with the poor development of potted grafts planted in field test plots may be overcome, at least to a large extent, by top grafting on trees already well established in the field. Branches of the susceptible understock are gradually pruned off to prevent infection below the graft union.

Protection of scions in field grafting has proved most effective with polyethylene plus kraft paper bags. Success with the use of various antitranspirant dips such as latex or way emulsions has been variable and this technique has not been consistently as reliable as covering the grafts with polyethylene and kraft paper bags. On the other hand, the emulsions are simple and rapid to use, and sometimes have resulted in as many graft "takes" as with the plastic and paper bags. Field grafting will facilitate the establishment of seed orchards and possibly aid in speeding up the breeding program.

The rooting of cuttings offers promise of being much less expensive than grafting. Cuttings from 4- to 6-year-old white pine trees form roots readily, up to 90-100 percent, but those from older trees root with much more difficulty. Rooting trials were conducted in outdoor sand beds under an automatic intermittent sprinkler system, and involved various physical and chemical treatments of the cuttings. The use of plant growth regulators, primarily indolebutyric acid, was necessary as a standard procedure upon which other supplementary treatments were based. Standard treatments with IBA included a 21-hour basal soak in a water solution at a concentration of 50 ppm, or a one-second basal dip in a solution of IBA at 10 mg/ml in 50 percent alcohol. Results of treatment of cuttings from 15- to 60-year old trees have been extremely variable during the past 8 years. The best results with cuttings from older trees ranged between 20 and 35 percent rooting. No single treatment was found which consistently promoted a relatively high percentage of rooting from older-tree cuttings. The extreme variation encountered with similar treatments from year to year was one of the most conspicuous results of the rooting trials. Both "good" and "poor" rooting years were evident, resulting from inherent and environmental influences both while cuttings were still on the tree and after they had been placed in rooting beds.

Distinct differences in rooting ability among several clones appeared over a 4-year period. Several of the clones exhibited extreme up and down fluctuations in rooting ability in alternate years, though these did not correspond to the seasonal fluctuations in rooting as reflected in control cuttings from 1-year-old trees.

Further evidence on the influence of age on rooting was provided by the response of cuttings from trees which had originated as rooted cuttings. Rooting of cuttings from such trees was superior to that of cuttings from trees of seedling origin until the trees were 9 years old. AS the trees grew older rooting ability of cuttings from both types of trees declined, and from age 9 on, the difference between the two sources had equalized.

Air layering in limited trials on 60-year-old trees and on 15-year-old grafts from 60-year-old trees was not successful. Of 143 air layers made in July on the old trees, only 35 were still green 1 year later, and only 1 had produced a root 1/16 inch long, which later died. All 25 air layers in the second trial died before the end of the first summer.

The growth habit of rooted cuttings established in several plantations for as long as 12 years with seedlings for comparison has been normal and upright and could not be distinguished from that of trees of seedling origin. The root system of young rooted cuttings was dominated by the original main roots which had developed in the cutting bed. However, as the cuttings grew older their root systems tended to assume the characteristic form and development of a normal seedling-tree root system, with only minor differences in vertical and laterai root distribution.