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Screening of Haploxylon Pines for Resistance to the White Pine Weevil

II. Pinus strobus and other species and hybrids grafted on white pine1)

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(Received June 1972)

Previously observations on weevil (Pissodes strobi Peck) resistance of Pinus peuce Griseb. and P. strobus L. field-grafted on P. *sylvestris* L. were considered (Heimburger and Sullivan, 1972). The present study reports on weevil resistance of additional white pine materials grafted on P. strobus.

Materials and Methods

A 3.3-acre (1.3 ha) plantation of P. strobus was established at 6 X 6 ft (1.83 \times 1.83 m) spacing in 1957, in Kirkwood

Township, Ontario. The trees were planted in north-south rows, and the plantation subdivided into 11 blocks by east-west lines. All grafting was done in the spring, with one scion on each stock tree. Series 1, 1961, utilized the five southern blocks, Series 2, 1962, blocks 6–10 and Series 3, 1963, block 11, at the north end (Table 1). The clones have been selected as resistant to blister rust (Cronartium *ribi*-cola Fischer).

The origin of the *P. strobus* clones 153, 154 and 157 is the same as that of the five unattacked *P. strobus* of the preceding study. They are one generation removed from a natural stand of good growth form and with a low weevil population. *P. peuce clones 700* and 709 have also been included in the preceding study. Within each block the ramets are distributed at random. Weevil attacks on tall

leaders were recorded on the basis of a target made avail-

Table 1. - Grafting record.

Species	Clone	Origin	Series1)
Pinus koraiensis Sieb. & Zucc.	362, 369	Orono, Ont.	2, 2
Pinus monticola Dougi.	346, 349, 350	Garibaldi, B. C.	1, 1, 1
Pinus peuce Griseb.	92, 94	Jamaica Plain, Mass.	1, 3
-	700, 709	Havelock, Ont.	1, 1
	229, 230, 196, 198	Rochester, N. Y.	2, 2, 3, 3
	740, 741	Ottawa, Ont.	2, 2
Pinus strobus L.	56, 60, 62, 56, 55	Pte. Platon, P. Q.	1, 1, 1, 2, 3
	153 154, 157	Midhurst, Ont.	1, 1, 1
	500, 512, 519, 539	Ottawa, Ont.	2, 2, 2, 2
	541, 546, 616, 622	Ottawa, Ont.	2, 2, 2, 2
	624, 625, 644, 645	Ottawa, Ont.	2, 2, 2, 2
	646, 683	Ottawa, Ont.	2, 2
	30	Kroglund, Denmark	3
	120	Wisconsin Rapids, Wis.	3
Pinus wallichiana A. B. Jackson	315	Jamaica Plain, Mass.	1
	326	Elmhurst, 111.	1
Pinus peuce X strobus	689, 691, 693	Petawawa F. E. S.	1, 1, 1
•	28	Charlottenlund, Denmark	3
	262, 263	St. Williams, Ont.	3, 3
Pinus strobus X himekornatsu			
Miyabe & Kudo	307, 308, 319	Wellesley, Mass.	1, 1, 1
Pinus wallichiana X strobus	739	Toronto, Ont.	1

¹⁾ In Series 1 and Series 2, 47-52 (mostly 50) scions of each clone were grafted, and 24-25 (mostly 25) in Series 3.

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able to the weevil by leader growth of the previous year.

In this study, leader length was considered to be "good"

In this study, leader length was considered to be "good" if it exceeded about 8 inches (20 cm) and "poor" if it did not reach this size. This discrimination is based on a comparison of the growth of graft terminals with the growth of ungrafted native *P. strobus* near the experimental area. Leader diameter was considered to be "good" if the upper diameter exceeded 5 mm and "poor" if it did not reach this size. This discrimination is based on the results of former studies (Sullivan, 1961) where a strong positive correlation was found between leader vigour, as expressed by an upper diameter up to this size, and frequency of weevil attack on *P. strobus*. Leaders were classified as attacked

and killed (girdled by weevil larvae), attacked but not killed, and not attacked, irrespective of the success of weevil attack and its influence on apical dominance. Grafts attacked by weevil and dead at the time of observation were classified as dead only.

During the annual observations in the fall of 1963 to 1967, multiple leaders and leaders killed by weevil attack or by other causes were removed by pruning. This greatly improved the comparability of the records but introduced an artifact into subsequent weevil attack and leader development.

The frequencies of attack in 1962 and 1963 of Series 1 and Series 2 and 1964 of Series 3 were far below average. There-

Table 2. - Weevil resistance of clones.

Clone	Species	Graft compatibility ¹)	Adaptation ²)	Frequency of attack	Recovery from attack	Resistance
		Ser	ies 1	<u> </u>		
56	s	74	66	8	9	8
60	s	92	74	15	14	13
62	S	90	86	11	5	10
92	P	94	88	29	73	8
153	s	96	86	5	37	3
154	s	81	73	17	12	15
157	s	94	50	10	18	8
307	SH	80	60	21	12	18
308	SH	82	56	26	0	26
315	\mathbf{w}	94	58	27	12	24
319	SH	66	30	28	12	25
326	w	98	48	39	10	35
346	M	82	8	6	0	6
349	M	76	32	18	8	17
350	M	90	45	31	17	26
689	PS	94	90	25	13	22
691	PS	100	88	19	6	18
693	PS	96	88	30	6	28
700	P	100	96	55	23	42
709	P	98	94	52	19	42
739	ws	78	8	39	14	33
100	***5	10	ŭ	00	11	30
		Ser	ies 2			
56	S	92	92	5	0	5
229	P	96	90	23	32	15
230	P	96	86	22	45	12
362	K	100	48	14	0	14
369	K	84	18	24	8	22
500	S	94	88	23	12	20
512	S	96	86	9	18	8
519	s	84	74	16	0	16
539	s	88	73	7	20	5
541	s	82	74	9	36	6
546	s	83	74	14	0	14
616	s	76	70	13	22	10
622	s	88	78	28	14	24
624	s	92	84	11	26	8
625	s	73	66	18	4	17
644	s	82	78	27	17	22
645	s	86	68	10	27	8
646	S	71	56	26	3	25
683	s	82	74	16	32	11
740	P	100	80	17	45	9
741	P	96	77	29	16	24
		Seri	ios 3			
28	PS	100	88	16	9	15
30	s	100	92	4	0	4
55	s	92	76	9	20	7
94	P	96	84	14	30	10
120	s	37	21	6	0	6
196	P	100	92	3	0	3
198	P	100	96	14	20	11
262	PS	100	92	26	6	25
263	PS	80	60	21	10	19

¹⁾ Per cent survival 1/2 year after grafting.

²⁾ Per cent survival 4 years after grafting.

 $^{^{3}}$) Per cent available leaders killed.

fore, this information was rejected from further processing. The remaining data were tested for homogeneity, yielding a combined χ^2 amounting to 134.8 which for 10 df is highly significant. The frequency of attack was greater in the southern part of the experimental area during the entire testing period. The bulk of the data contained in the field records was then transferred to IBM punch cards, one ramet to a card, and processed further by an IBM model 65 computer. This was essentially a scanning process. The printouts yielded information on mortality, leader size and weevil attack of clones, by years and blocks.

Results

Mortality

Survival 1/2 year after grafting is largely an expression of graft compatibility and survival 4 years after grafting also reflects the adaptation of a particular clone (Table 2). Some clones, such as P. strobus clone 120, were poor grafters but were reasonably well adapted by showing no marked increase in mortality after grafting. Other clones, mostly exotics and hybrids with exotics, such as P. monticola clone 346 and P. wallichiana × strobus clone 739, and P. koraiensis clones 362 and 369, were good grafters, but showed poor adaptation by steady attrition after grafting. Some clones showed an intermediate behaviour in this respect. For example, P. strobus clone 157 was a good grafter but later behaved as if were not well adapted. P. strobus clone 56 showed good grafting success and survival in Series 2, but somewhat lower values in these respects in Series 1. Thus, survival of grafts may also depend on local variation of the environment.

Leader size

Because leader size was regarded as an important indication of resistance to weevil attack in *P. strobus*, many such measurements were made during this study. The low overall frequency of attack precluded the use of replication in space (by blocks). Replication in time (by years), however, yielded some meaningful results. The influence of stock on leader size of the grafts is a source of error to be considered. At Maple, Ontario, several exotic white pines and their hybrids with *P. strobus* grew much better as grafts on *P. strobus* than on their own roots. This applies particularly to *P. peuce*, *P. monticola* and *P. himekomatsu*. These materials are thus expected to have produced larger proportions of leaders with "good" leader diameter and "good" leader length than they would have on their own roots.

A highly significant correlation (1% level) between leader diameter and frequency of weevil attack was found in *P. wallichiana* and *P. peuce* × strobus of Series 1 and in *P. strobus* of Series 2 (Table 3). However, interclonal variance did not reach a level of significance in *P. wallichiana* and was less significant than intraclonal variance, owing to years, in *P. peuce* × strobus (Table 4). In *P. strobus*, intraclonal variance was as significant as the variance owing to clones.

The correlation of leader length with frequency of weevil attack reached the 1% level of significance in P. peuce \times strobus of Series 1 and the 5% level in P. strobus of Series 2 (Table 3). In P. peuce \times strobus, interclonal variance, also in respect to leader length, was less significant than intraclonal variance (Table 4), while in P. strobus both kinds of variance reached the same level of significance

The low frequencies of weevil attack and lack of information on their success precluded much further study of recovery. In only *P. peuce* of Series 1, were leader length and recovery significantly correlated (*Table 3*). The variance in recovery owing to clones was more significant than intraclonal variance (*Table 4*). This makes leader length an important attribute, at least in *P. peuce*, for further consideration in breeding for resistance, even if in this case it may have been influenced by grafting.

Weevil resistance of clones

As pointed out by Heimburger and Sullivan (1972), weevil resistance is here defined as the combined effect of frequency of attack and recovery from attack. This information on the tested clones is presented in *Table 2*. Within each Series, the clones were arranged in an ascending order of severity of attack and screening for resistance could then be carried out. Good recovery from attack was given higher priority than low frequency of attack. Ten clones or about 20 per cent of all clones tested were retained as follows:

Series 1 — P. strobus clones 153 and 157, and P. peuce clone 92

Series 2 — P. strobus clones 512, 539, 541, 616, 624 and 645 Series 3 — P. strobus clone 55.

The selected clones were again examined in the summer of 1970, after the grafts had been allowed to develop in an unpruned condition for three growing seasons. This gave an indication of their recovery from attack without pruning and of inherent apical dominance. The average frequency of attack appeared to be greater than before 1967. By far the most grafts had more than one leader but their

Table 3	 Coefficients 	of	correlation.

Series	Species	Leader diameter vs Frequency of attack	Leader length vs Frequency of attack	Leader diameter vs Recovery from attack	Leader length vs Recovery from attack
1	Pinus peuce	0.37n.s.	0.46n.s.	0.20n.s.	0.66*
1	Pinus wallichiana	0.91**	0.62n.s.	_	_
1	Pinus peuce \times strobus	0.87**	0.78**	_	_
1	Pinus strobus X				
	himekomatsu	0.08n.s.	0.42n.s.		
2	Pinus strobus	0.40**	0.29*	_	
2	Pinus peuce	0.16n.s.	0.06n.s.	_	_
2	Pinus koraiensis	0.07n.s.	0.40n.s.		_
3	Pinus peuce	0.53n.s.	0.19n.s.	_	_
3	Pinus peuce × strobus	0.10n.s.	<.01n.s.		_

n.s. Not significant.

^{**} Significant at 1% level.

^{*} Significant at 5% level.

recovery from attack was apparently better than that of the unselected clones. However, they experienced about the same loss of apical dominance after attack as the unselected materials. Of the 10 clones selected for weevil resistance, only two, namely *P. strobus* clone 153 and *P. peuce* clone 92, were retained. Clone 153 still showed remarkably good recovery from attack and considerably above average retention of apical dominance. Clone 92 continued to show the outstanding recovery from attack and apical dominance observed earlier.

Weevil resistance of species and hybrids

The information on weevil resistance of species and hybrids has been compiled from data presented in *Table 2*.

Pinus strobus

The white pine materials used showed a relatively narrow range of reactions to weevil attack. The leaders of selected clones had average frequencies of attack of about 7 per cent in Series 1, 10 per cent in Series 2, and 9 per cent in Series 3. The leader survivals after attack were 92 per cent, 93 per cent and 93 per cent, respectively. Up to 17 per cent of the unselected clones were attacked in Series 1, 28 per cent in Series 2, and 9 per cent in Series 3. The corresponding leader survivals were 85, 75 and 92 per cent. Thus there are relatively limited opportunities for selection within most of the materials, and subsequent observations on reaction to attack under unpruned conditions also indicated this.

Pinus peuce

Most clones of *P. peuce* used showed rather high frequencies of attack, combined with good recoveries. This resulted in good resistance of clones 92, 94, 198, 230 and 740. Clones 229, 700 and 709 could not compensate for the high frequencies of attack with good recoveries and showed poor resistance. Clone 196 showed a non-preference reaction, combined with no recovery. Clone 741 had high frequencies of attack and poor recoveries.

It is remarkable that *P. peuce*, having a very restricted natural range since the last glaciation and otherwise very uniform morphologically, should show such a wide diversity of reactions against weevil attack. The very good recovery of clone 92 is of particular interest. The precocious flowering found in this species (Heimburger, 1972), could be applied in breeding.

Pinus peuce × strobus

Five of the six clones tested, namely clones 262, 263, 689, 691 and 693, are natural hybrids of P. peuce clone 740 with P. strobus. The P. strobus involved presumably belonged to the old-field type, subjected to high frequencies of attack and poor recoveries. The P. peuce parent showed good resistance, based on good recovery in spite of relatively high frequency of attack. The hybrids all showed relatively high frequencies of attack and poor recoveries, resulting in poor resistance. The same was true of clone 28, probably the result of a similar cross. The presumably poor recoveries of P. strobus were thus largely dominant over the good recoveries of P. peuce. It probably would be important, in breeding for high resistance in such crosses, to use P. strobus materials with good recoveries. The inheritance of the generally high susceptibility to attack of P. peuce could not be determined from these hybrids as the P. strobus parents are presumably also highly susceptible.

Pinus monticola

This species is known for its high resistance to Pissodes engelmanni Hopkins (Stevenson, 1967), based on a strong

			Table 4. — Significance levels of variance ratios (F values).	gnificance l	evels of vari	ance ratios (F values).				
Series	Species	Clones	Years	Leader diameter	der eter	Leader	der gth	Frequency of attack	equency of attack	Recovery from attack	very m ick
				Clone	year	Clone	year	Clone	year	Clone	year
1	Pinus strobus	9	4	2%	2%	1%	1%	1	.] 	
н	Pinus peuce	က	4	2%	2%	2%	n.s.	2%	5%	1%	2%
-	Pinus monticola	က	4	n.s.	n.s.	n.s.	n.s.	I	ļ	1	I
1	Pinus wallichiana	2	4	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	I	1
7	Pinus peuce \times strobus	က	4,	2%	1%	n.s.	2%	2%	2%	ļ	I
Т	Pinus strobus $ imes$										
	himekomatsu	က	4	n.s.	n.s.	n.s.	2%	n.s.	2%		I
7	Pinus strobus	15	4	1%	1%	1%	1%	1%	2%		1
2	Pinus peuce	4	4	1%	1%	1%	n.s.	n.s.	2%	1	I
2	Pinus koraiensis	2	4	n.s.	n.s.	n.s.	n.s.	2%	n.s.	1	1
က	Pinus strobus	က	က	n.s.	n.s.	n.s.	n.s.	ı	1	1	1
က	Pinus peuce	2	က	2%	n.s.	n.s.	n.s.	2%	1%	1	I
က	Pinus peuce $ imes$ strobus	က	က	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	l	1

non-preference reaction. Pissodes engelmanni has a life history similar to Pissodes strobi and the two weevils are very closely related, if not con-specific (Manna and Smith, 1959; Smith, 1962; Smith and Sugden, 1969). Wright and Gabriel (1959) found low frequencies of attack and good recoveries in Pinus monticola, mostly originating in northern Idaho, planted in New York State. The materials used here originated in the Coast Mountains in southern British Columbia. The three clones in question showed good grafting compatibility with P. strobus, but poor survival, indicating poor adaptation. Possibly for this reason they had relatively poor recoveries.

Pinus wallichiana

The information on the weevil resistance of *Pinus wallichiana* is conflicting. MacAloney (1930) and Wright and Gabriel (1959) state that it is rarely attacked in the eastern U. S., while Lemmien and Wright (1963) found it to be attacked about three times as much as *P. strobus* in Michigan. This is hardly surprising because of its great horizontal and vertical native range (Troup, 1921). The two clones tested were of arboretum origin. In spite of good grafting compatibility with *P. strobus*, survival after grafting was poor. Weevil resistance was also poor, because of high frequencies of attack and fairly poor recovery. The poor weevil resistance may be caused, at least partially, by poor adaptation.

Pinus wallichiana \times strobus

One natural hybrid clone was studied. Grafting compatibility with *P. strobus* and survival after grafting were rather poor. Weevil resistance was also poor, largely because of high frequencies of attack, whereas recovery is relatively good. Because of the expected, great diversity in weevil resistance of *P. wallichiana*, a direct comparison with the tested clones of this species is not meaningful.

Pinus strobus × himekomatsu

Scions of three natural hybrid clones were used. They showed only fair grafting compatibility with P. strobus and fair to poor survival after grafting, indicating poor adaptation. The weevil resistance was poor, with rather high frequencies of attack and poor recovery. As in the case of P. $peuce \times strobus$, the putative P. strobus parents of the hybrids presumably belonged to the old-field white pine type. According to Johnson (1952) the ortets of these hybrids are also heavily attacked by the weevil.

Pinus koraiensis

Two clones were used in the present study. They showed good grafting compatibility with *P. strobus*, but poor survival. Weevil resistance was poor, with fairly high frequencies of attack and poor recoveries. At Maple some clones showed good crossability with *P. lambertiana* Dougl. and may be of interest in the breeding of this species.

Discussion

Painter (1951; 1958) established three basic components of genetic resistance in plants to insects, namely, (1) tolerance, (2) non-preference, and (3) antibiosis. As a working hypothesis, the results of the present study were interpreted in terms of these three resistance categories.

The common old-field type of *P. strobus* is here regarded as being tolerant to the weevil. They have co-existed for a long time and are found together under natural conditions wherever white pine grows in open stands and in exposed

situations, such as on the rocky ridges in Algonquin Park, Ontario. Land use as practised by settlers in eastern North America created conditions favourable to the establishment and maintenance of open-grown white pine. The present abundance of a weevil-tolerant type of white pine is one of the long-term ecological consequences of such land use. Under such conditions, weevil attack does not interfere with the reproduction and survival of white pine. However, it is detrimental in forestry because of its influence on stem form. Old-field white pine is, therefore, classified as being susceptible for the purposes of this study. This type of white pine shows high relative frequency of attacks which cause some leader mortality and are mostly successful.

The non-preference reaction is elicited by the slender-leader type of white pine studied by Kriebel (1954), Belyea and Sullivan (1956), Sullivan (1961) and others. Under natural conditions, white pine of this type is usually found growing in closed pure stands or mixed with other pines on relatively poor sites, such as near Achray, Ontario. The non-preference reaction in the weevil causes low frequencies of attack. Relatively high population pressures by the weevil and growth in closed stands probably are the causes of the natural selection that favours this type of white pine. Most of the proposed breeding for weevil resistance in white pine is concerned with this type.

A white pine with an antibiosis reaction has good recoveries from largely unsuccessful attacks. Resin flow is usually given as the cause of weevil mortality after attack. Resin crystallization by weevil larvae (Santamour, 1965) may be a case of adaptation by the weevil to overcome the adverse effects of resin flow. This is being offset by noncrystallization of the resin(s) of certain white pines, perhaps as a further step in the natural evolution of weevil resistance. This type of white sine is at present rather rare. One known stand is in Norfolk County, Ontario. The unsuccessful attacks gradually reduce the weevil populations, resulting in a more or less self-regulating weevil resistance situation. This reaction is in the long run more desirable than resistance to attack only. For this reason, recovery from attack was given a higher priority than low frequency of attack in evaluating single clones.

There is possibly a successional trend in respect to these three general resistance mechanisms in white pine (and the weevil?) during the gradual replacement of open-grown white pine by closed stands. The most stable reaction type is again relatively open to attack with decreasing weevil population pressure, as this in the long run is of selective advantage.

Conclusions

According to the above hypothesis, breeding for weevil resistance is more promising than breeding for resistance to attack only. As recovery from attack cannot be observed without previous attack, high frequencies of attack are needed. These can be achieved in more heavily infested environments, through the use of "bait" clones of high susceptibility to attack, and by introducing weevils. The use of indirect indications of resistance, particularly leader length and recovery from attack in some P. peuce, also merits further investigation. Simulated weevil damage by pruning may also yield information on apical dominance, important in stem form. Santamour's (1965) findings, on resin crystallization in relation to resistance, and the high recoveries of some P. peuce also merit further study. The location of testing areas in southern Ontario, in a more favourable climate, should make an evaluation of exotic species and hybrids more meaningful. When more scions of certain clones become available in the future, it should be possible to field-graft a test area of three acres, such as the one used here, in one year and make the tested materials more intercomparable. The results already obtained should encourage further efforts in locating stands of native white pine with low weevil populations and others showing the antibiosis reaction.

Acknowledgements

The authors acknowledge the counsel of Dr. F. Raymond of the Research Branch, Ontario Ministry of Natural Resources, Maple, Ontario, in the statistical analysis of the data. Thanks are due to the Ontario Ministry of Natural Resources for valuable computer service in data processing, and to Dr. N. P. Badenhuizen, Chairman, Department of Botany, University of Toronto, for providing working facilities during preparation of the manuscript. Drs. D. P. Connola of Albany, N. Y., H. D. Gerhold of University Park, Penna and S. G. Smith of Sault Ste. Marie, Ontario, have kindly contributed their reviews.

Summary

A 3-acre plantation of Pinus strobus was established in 1957 and field-grafted in 1961, 1962 and 1963, in three Series, with 2320 scions of 51 clones of P. strobus and related species and hybrids, previously found resistant to Cronartium ribicola. Observations on weevil (Pissodes strobi) attack were made in 1963 to 1967, including annual determination of leader size, as a basis for weevil attack during the following year. The grafts were maintained in a one-leader condition by pruning, with an average annual frequency of weevil attack of 20 per cent. Screening for weevil resistance, based on combined low frequency of attack and good recovery, resulted in the selection of one clone of P. strobus and one clone of P. peuce. The results were interpreted by using Painter's three general resistance mechanisms tolerance, non-preference, and antibiosis — as a working hypothesis. It was concluded that old-field white pine is tolerant to the weevil and that its present abundance is a long-term ecological consequence of land use favouring the establishment and maintenance of open-grown stands. Examples of possible non-preference and antibiosis reactions were found in the more advanced succession stages from open-grown to closed stands. Some guidelines are presented favouring breeding for weevil resistance over breeding for resistance to weevil attack only. At present, clones combining the non-preference and antibiosis reactions are the most desirable for use in eastern Canada. At more advanced stages of succession and the use of the antibiosis type, weevil resistance could become self-regulating. Several exotic species and hybrids showed poor survival after grafting and poor weevil resistance, possibly because of poor adaptation.

Key words: Haploxylon clones, white pine weevil, blister rust, leader size, tolerance, non-preference, hybrids, grafting compatibility, resistance.

Zusammenfassung

1957 war eine Pinus strobus-Pflanzung begründet worden, von der man 1961, 1962 und 1963 Freilandpfropfungen herstellte. Es waren dabei insgesamt 2320 Reiser von 51 Klonen von Stroben und verwandten Arten und Hybriden genommen worden, die gegen Cronartium ribicola resistent gewesen waren. Von 1963 bis 1967 wurde der Befall mit Pissodes strobi beobachtet und die jährliche Größe des Leittriebes festgestellt, die gleichzeitig die Grundlage für den Pissodes-Angriff des folgenden Jahres bildet. Die Pfropflinge wurden eintriebig gehalten. Es bestand eine durchschnittliche jährliche Häufigkeit des Pissodes-Angriffs von 20%. - Unter der Voraussetzung von einer geringen Häufigkeit des Angriffs und von gutem Überstehen desselben konnten nur 1 Klon von P. strobus und 1 Klon von P. peuce ausgelesen werden. Bei der Interpretation der Ergebnisse werden als Arbeitshypothese die 3 allgemeinen Resistenzmechanismen (Toleranz, Nichtanfälligkeit und Antibiose) zugrundegelegt, die auch PAINTER verwendet hat, und Schlußfolgerungen für die weitere Arbeit ge-

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