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Resistance of *Glycine tomentella* to soybean leaf rust *Phakopsora pachyrhizi* in relation to ploidy level and geographic distribution

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Summary. Accessions of five diploid and five tetraploid isozymically defined groups of *Glycine tomentella* collected from throughout the species range in Australasia were scored for resistance to three separate isolates of *Phakopsora pachyrhizi*, the causal agent of soybean leaf rust. Resistance levels were found to be high (>75%) in most of the groups. While resistance levels differed among groups, the overall levels in polyploids were similar to those in diploids. Geographical patterns of resistance and susceptibility to *P. pachyrhizi* indicate that two regions of susceptibility exist. The highest proportion of susceptible accessions occurs in the Kimberley Plateau region of Western Australia and the Northern Territory, while another region of susceptibility is found in the Townsville/Cairns region of Queensland. Results from genetic crosses between accessions within two forms of the tetraploids indicate that in the aneuploid form (2n=78), resistance to *P. pachyrhizi* was under the control of a single dominant gene, whereas in a second group of tetraploids (2n=80), resistance was controlled by two or three gene loci.

Key words: *Glycine tomentella* – *Phakopsora pachyrhizi* – Pathogen resistance – Polyploidy – Soybean leaf rust

Introduction

The switch from diploidy to tetraploidy has often been linked to evolutionary and ecological change in plants (Darlington 1939; Stebbins 1950, 1971; Levin 1983). While it is known that polyploidy can alter the physiological and ecological properties of organisms, one poorly understood consequence of polyploidy is the effect it has on pest and pathogen resistance. In this regard, Levin (1983) pointed out that chromosome doubling within a race or species (or autopolyploidy) should result in higher levels of plant resistance to pests and pathogens, due to higher production levels of the chemical products known to play a role in plant defense. Apart from the quantitative changes in plant defense compounds resulting from autopolyploidy, it might also be expected that the process of allopolyploidization (or polyploidy involving separate taxa) would lead to qualitatively new kinds of defense properties in the resulting hybrid derivatives. This notion follows from observations that allopolyploids possess more gene loci than their diploid relatives, and have higher levels of genetic diversity compared with the diploid progenitors (Roose and Gottlieb 1976; Hancock and Bringhurst 1981). With the potential for increased diversity of genes coding for pathogen resistance, it is possible that allotetraploid derivatives may show resistance to a greater range of pathogen types compared with their diploid progenitors.

Glycine tomentella Hayata is one of 15 species recognized as belonging to the perennial subgenus *Glycine*. It is a perennial legume with a wide distribution in Australia, New Guinea, The Philippines, and Taiwan. Cytologically it is diverse, consisting of diploids (2n=40), tetraploids (2n=80), and aneuploids (2n=38, 78) (Newell and Hymowitz 1982; Grant et al. 1984; Singh and Hymowitz 1985). It is heterogeneous for isozyme genotypes, 5S nuclear ribosomal RNA genes, 18S–25S ribosomal RNA genes, and chloroplast DNA restriction sites (Doyle and Brown 1985, 1989; Doyle et al. 1990). Cytological and isozyme marker data, as well as crossing studies, have revealed that the species consists of at least

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five diploid and six tetraploid groups, referred to as D1 through D5 (diploids) and T1 through T6 (tetraploids). With the exception of crosses between groups D1 and D2, all other crosses between accessions of different groups produce sterile hybrids (Doyle et al. 1986, A.H.D. Brown, unpublished data). The cytological and molecular data support the hypothesis that the tetraploid groups T1, T2, T4, T5, and T6 are allopolyploids, being derived from a number of separate hybridization events (Doyle and Brown 1989).

Phakopsora pachyrhizi Syd. is the causal agent of soybean leaf rust and is found on a range of legumes occurring in Australia and Southeast Asia (Keogh 1976; Sinclair 1982; Burdon and Lenné 1989). In Australia, the fungus has a wide geographic distribution. Race-specific resistance to this rust has been reported from a number of species in the subgenus *Glycine*, including *G. tomentella* (Burdon and Marshall 1981; Burdon and Speer 1984; Burdon 1987, 1988; Jarosz and Burdon 1990).

Here we report the results of an investigation of resistance and susceptibility in the diploid and tetraploid groups of *G. tomentella* to the leaf rust disease caused by *P. pachyrhizi*. The study encompassed the entire known geographic range of *G. tomentella*, as well as three separate isolates of *P. pachyrhizi* collected from different locations in eastern Australia (Burdon and Speer 1984). We also test the genetic control of resistance to leaf rust in the tetraploid groups of *G. tomentella*. There have now been four reports of successful attempts to hybridize tetraploid *Glycine tomentella* with *G. max* (Newell and Hymowitz 1982; Singh and Hymowitz 1985; Newell et al. 1987; Chung and Kim 1990). Knowledge of the distribution and range of resistance to *Phakopsora pachyrhizi* in *G. tomentella*, as well as its the mode of inheritance, is needed to introduce genes for soybean leaf rust resistance into *G. max*.

Materials and methods

The plants used in this study include 78 diploid and 85 tetraploid accessions of *Glycine tomentella* from all known groups of the species, except group T6. Each accession represents a collection from one naturally occurring population of *G. tomentella*. Five to 15 plants from each accession were grown in 5 cm diameter × 7 cm deep pots filled with sandy loam (two or three seeds per pot) and placed in a heated glasshouse. Approximately 6 weeks after seedling emergence, these plants possessed sufficient young leaves to allow screening for rust resistance.

The three isolates of *Phakopsora pachyrhizi* used in this study were collected from either soybean or wild perennial species of *Glycine* growing within the major region of geographic distribution of this pathogen. One was from Redland Bay (Queensland), one from Taree (New South Wales), and one from Jackadgery (New South Wales). These isolates are referred to as R1, R3, and R4, respectively (Burdon and Speer 1984). The pathogenicity of these isolates was shown to differ by assessment of the reaction they induced on a set of wild *Glycine* hosts carrying different genes for resistance to *P. pachyrhizi* (Burdon and Speer 1984).

Seedlings of each *G. tomentella* accession included in this study were inoculated with each isolate of *Phakopsora pachyrhizi*. A different set of seedlings of each accession was used to assess infection type responses to each pathogen isolate. This procedure ensured that plant material of the same age was used in screening for rust resistance. Seedlings were inoculated by dusting leaves with dry spores borne on infected soybean plants. Inoculated seedlings were then sprayed with a fine mist of water and stored overnight at 100% relative humidity before being placed in a naturally lit glasshouse. Infection type responses of these seedlings were apparent 14–21 days later.

Infection types responses were scored using the following scale (Burdon 1987):

Infection type	Symptoms
;	Necrotic flecks or spots only; no sporulation
1	Minute uredia surrounded by large regions of chlorotic or necrotic tissue
2	Small uredia associated with chlorotic or necrotic tissue
3	Large, profusely sporulating uredia, with little or no associated chlorotic or necrotic tissue

Minor variations within infection types were noted and scored as "−" or "+"; e.g., "1−" or "1+". Infection type responses (;) and (1) were classed as resistant; (2+) and (3) were considered susceptible.

An investigation of the genetic control of disease resistance in *Glycine tomentella* was made using accessions of the tetraploid groups T1 and T2. Within each group, F_1 hybrids were produced by crossing plants from separate accessions. The cytology of the crosses used here was reported by Grant et al. (1984) and Doyle et al. (1986). In all but one case, one of the two accessions in each cross was known to be susceptible to the rust isolate of interest, whereas in one case (cross of accessions 1400 and 1408), one accession was susceptible (accession 1400) and the other was segregating (accession 1408) for susceptibility and resistance. As the F_2 progeny segregated for resistance, it was assumed that the parent plant was resistant.

Results

Host resistance and ploidy level

Patterns of resistance to *Phakopsora pachyrhizi* among the various isozymically defined groups of *Glycine tomentella* are summarized in Table 1. Of the diploid groups of *G. tomentella*, accessions of group D3 exhibited the highest frequency of resistance (88% resistant to all three isolates of *P. pachyrhizi*). In contrast, accessions of group D5 showed the lowest level (42% resistant). Among the tetraploid groups, group T1 had the highest proportion of resistant accessions (77% resistant to all three isolates of *P. pachyrhizi*), while accessions of group T2 had the lowest (42% resistant). Despite such variation among both the five diploid and five tetraploid groups,

Table 1. Pattern of resistance and susceptibility of diploid and tetraploid accessions of *Glycine tomentella* to the rust disease caused by isolates of *Phakopsora pachyrhizi*

Isozyme group of *G. tomentella*	Proportion of accessions resistant to single rust isolates or to combinations of isolates								
	2n[a]	N[b]	R1	R3	R4	R1 and R3	R1 and R4	R3 and R4	R1, R3 and R4
Diploid races									
D1	38	17	0.82	1.0	0.94	0.82	0.82	0.94	0.82
D2	38	9	0.89	1.0	0.78	0.89	0.67	0.78	0.67
D3	40	16	0.94	1.0	0.88	0.94	0.88	0.88	0.88
D4	40	10	0.80	0.80	0.60	0.80	0.60	0.60	0.60
D5	40	26	0.77	0.69	0.65	0.65	0.50	0.46	0.42
All five races		78	0.83	0.87	0.77	0.79	0.68	0.71	0.65
Tetraploid races									
T1	78	35	0.77	0.91	0.77	0.77	0.77	0.77	0.77
T2	80	12	0.50	0.50	0.83	0.42	0.42	0.50	0.42
T3	80	14	0.86	0.71	0.71	0.71	0.64	0.64	0.64
T4	80	14	0.93	1.0	0.79	0.93	0.71	0.79	0.71
T5	78	10	0.80	0.70	0.80	0.70	0.70	0.70	0.70
All five races		85	0.78	0.81	0.78	0.73	0.68	0.71	0.68

[a] Chromosome number
[b] Number of accessions tested

the overall frequency of resistance in diploids was remarkably similar to that in tetraploid accessions (Table 1).

The three isolates of *Phakopsora pachyrhizi* differed in their pathogenicity on the accessions of *G. tomentella*. Isolate R4 was the most virulent, inducing susceptible responses in 23% of the diploid accessions and 22% of the tetraploid accessions, while isolate R3 was the least virulent, causing disease in only 13% of the diploid accessions and in 19% of the tetraploid accessions.

Geographic patterns of host resistance

Considerable spatial structuring of resistance and susceptibility is apparent from the geographic distribution maps (Fig. 1 a–d). In the diploid aneuploids, D1 and D2, all accessions from drier, inland south-central Queensland were resistant, whereas six susceptible accessions were from the Great Dividing Range and the coast (Fig. 1 a). Susceptibility to any of the isolates R1, R3, or R4 of the rust was too rare in D3 to exhibit any pattern. Although susceptibility is more common in group D4 than in D3, group D4 itself is relatively localized and thus cannot show any broad geographical pattern of resistance (Fig. 1 b). The susceptible accessions in group D5 were concentrated in the central (northwestern Northern Territory) or western (Kimberley district) parts of its distribution, while resistant accessions were widespread (Fig. 1 c).

Among the tetraploid accessions, group T1 exhibited the clearest pattern, in which all accessions from southeastern Queensland and northern New South Wales were resistant, and susceptibility was common north of latitude 21 °S in northeastern Queensland and in Papua New Guinea (Fig. 1 d). The geographically restricted groups T2 and T5 showed no pattern of resistance (Fig. 1 b and 1 d). All the widespread accessions of the groups T3 and T4 from north Queensland were resistant, whereas many accessions from the western portions of their ranges (the Kimberley Plateau, northwestern Northern Territory, and the island of Timor) were susceptible (Fig. 1 c).

The latitude, longitude, and average annual rainfall of the collection sites of resistant and susceptible accessions in each of the widespread *G. tomentella* groups were compared using *t*-tests. The greater likelihood of susceptible accessions of group T1 to be found in the tropics compared with the subtropics was significant ($t=4.98$, $P<0.01$; Table 2). Also significant was the trend for susceptibility to be more frequent towards the western end of the ranges of groups with pan-Australian tropical distribution (D5, T3, and T4). Neither of the broad geographic patterns in latitude or longitude could be clearly related to rainfall.

Genetic basis of host resistance

The segregation patterns of resistance to *Phakopsora pachyrhizi* in F_2 progeny of *Glycine tomentella* were tested for crosses within groups T1 and T2 (Table 3). Depending upon the cross, infection type responses were readily classified into two, three, or four distinct categories. Mendelian analyses were carried out on the ratios obtained by pooling all resistant phenotypes into one category.

In the two crosses involving T1 parents, 3:1 ratios of resistant to susceptible F_2 progeny were found, indicating the presence of one dominant resistance gene. In the

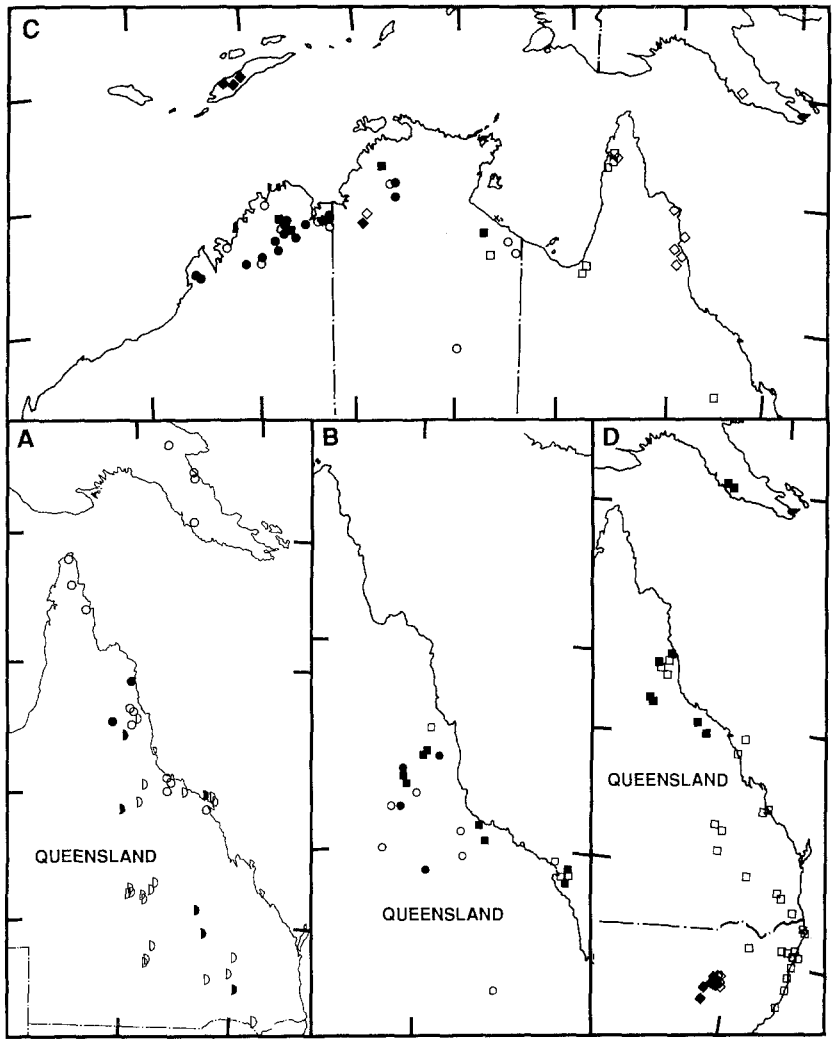

Fig. 1 A–D. The geographical pattern of resistance to *Phakopsora pachyrhizi* in *Glycine tomentella*. **a** Resistance in diploid groups D1, D2, and D3. *Open semi-circles* = groups D1 and D2 (resistant); *closed semi-circles* = groups D1 and D2 (susceptible); *open circles* = group D3 (resistant); *closed circles* = group D3 (susceptible). **b** Resistance in diploid group D4 and tetraploid group T2. *Open circles* = group D4 (resistant); *closed circles* = group D4 (susceptible); *open squares* = group T2 (resistant); *closed squares* = group T2 (susceptible). **c** Resistance in diploid group D5 and tetraploid groups T3. *Open circles* = group D5 (resistant); *closed circles* = group D5 (susceptible); *open diamonds* = group T3 (resistant); *closed diamonds* = group T3 (susceptible). *Open squares* = group T4 (resistant); *closed squares* = group T4 (susceptible). **d** Resistance in tetraploid groups T1 and T5. *Open squares* = group T1 (resistant); *closed squares* = group T1 (susceptible). *Open diamonds* = group T5 (resistant); *closed diamonds* = group T5 (susceptible)

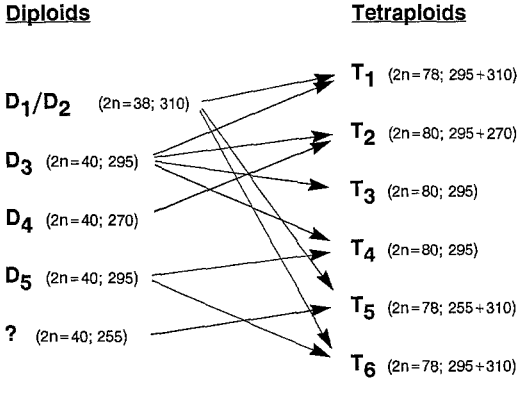

Fig. 2. Hypothesized origins of tetraploid races of *Glycine tomentella* modified from Doyle and Brown (1989). Designations (D1, T1, etc.) are groups discussed in the text. For each group, chromosome number and size of the 5S ribosomal gene (in bp) are given

three crosses that involved T2 parents, segregation ratios suggested the presence of more than one resistance gene (ratios of 15:1 and 63:1, Table 3). In accession G1188, the same segregation ratio of 15:1 was found using either rust isolate R1 or R3. Reciprocal crosses of this accession with the susceptible accession G1146 detected no maternal effects. The ratio for the cross involving accession G1402 was in agreement with that for three dominant genes.

Discussion

High levels of resistance to *Phakopsora pachyrhizi* were apparent in both diploid and tetraploid groups of *Glycine tomentella*. The overall levels of resistance in the diploids were similar to those in the tetraploids. Hence, we found

no general trend that polyploidy per se leads to greater levels of resistance.

This conclusion can be examined more precisely by taking the phylogenetic origin of the tetraploid groups into account. Figure 2 summarizes the postulated relationships among the diploid and tetraploid groups, based on cytological and isozyme data, 5S ribosomal genes (Grant et al. 1984; Doyle et al. 1986; Singh et al. 1987, 1989, Doyle and Brown 1989). The tetraploids T1, T2, T4, and presumably T3 are allotetraploids, apparently possessing in common one diploid genome that is related to the diploid group D3. The final tetraploid race studied here, T5, is also of allotetraploid origin, but as one of its putative diploid progenitors remains unknown, it is not considered further. The T1 aneutetraploids (2n=78) have an average proportion of fully resistant accessions of 0.77. Their putative diploid donors D1/D2 and D3 had 0.77 and 0.88, respectively. The T2 tetraploids (2n=80) had a minority of fully resistant accessions (0.42) that possibly related to the lower resistance of its diploid donor D4 (0.60).

The tetraploid group T4 was the only one with a higher resistance level (0.71) than might be expected from the level in its distinctive diploid donor (D5). Yet its resistance was still lower than that found in D3. Thus, there is no evidence of increased resistance to combinations of rust isolates in these tetraploid races compared with the hypothesized diploid parental races, D1, D2, D3, and D4 (Table 1).

However, the results highlight the complexities of a simple comparison between taxa of different ploidy level where variations in geographic ranges, the heterogeneous nature of the origin of the allotetraploid groups, and differences in the pathogenicity of pathogen isolates may all affect the potential outcome. Further, even if the proposed phylogeny of the diploid and tetraploid races (Fig. 2) is correct, the particular diploid populations that gave rise to the tetraploids have yet to be identified. For example, the hypothesis is that T1 is a polyploid of D1/2 × D3. These diploid groups overlap in the northern portion of the D1/2 range, where the susceptible accessions of D1/2 were found.

Table 2. Means of latitude, longitude, and annual rainfall and *t*-tests of significance for resistant and susceptible accessions from each of the widespread groups of diploid (D1, D2, and D5) and tetraploid (T1, T3, and T4) *Glycine tomentella*

Group	Rust reaction	N	Mean and *t*-value		
			Latitude (°S)	Longitude (°E)	Rainfall (mm)
D1D2	Resistant	20	23° 34′	147° 05′	640
	Susceptible	6	22° 43′	147° 35′	730
	t		0.56	0.56	0.73
D5	Resistant	12	16° 26′	129° 54′	730
	Susceptible	15	16° 16′	126° 48′	780
	t		0.31	2.12*	0.69
T1	Resistant	27	25° 46′	150° 50′	1,080
	Susceptible	8	16° 25′	145° 59′	1,230
	t		4.98**	4.18**	0.96
T3T4[a]	Resistant	16	15° 24′	141° 51′	1,190
	Susceptible	6	15° 33′	129° 52′	830
	t		0.11	5.13**	1.74

[a] Excluding three T3 accessions from Timor (susceptible) and three T4 accessions from Taiwan (resistant)
* $P<0.05$
** $P<0.01$

Table 3. Segregation of resistance and susceptibility in F_2 progeny of *Glycine tomentella* crosses

Cross	Rust isolate used	Infection type response					Ratio of best fit	χ^2
		Resistant			Susceptible			
		–;	1	1+	3	3+		
Between T1 (2n=78) accessions								
1400[a] × 1408	R1	89	–	15	–	29	3:1	0.72 NS*
1468 × *1392*	R1	78	–	5	–	17	3:1	3.41 NS
Between T2 (2n=80) accessions								
1146 × 1188	R1	80	5	1	3	–	15:1	1.26 NS
1188 × *1146*	R1	79	9	1	3	–	15:1	1.32 NS
1146 × 1188	R3	67	–	4	2	–	15:1	1.53 NS
1188 × *1146*	R3	108	–	8	10	–	15:1	0.61 NS
1402 × *1146*	R1	156	45	–	4	–	63:1	0.20 NS

[a] Italics indicate the accession number that is susceptible to the rust isolate used
* $P>0.05$
Origin of accessions. T1: 1400, 1408, north Queensland; 1468, south Queensland; 1392, Papua New Guinea. T2: 1146, 1188, 1402, north Queensland

The genetic analysis in Table 2 revealed a further complication to testing this hypothesis. It was unexpected that the resistant accessions of the more susceptible polyploid (T2) should have *more* resistance genes (2 or 3) than the resistant accessions of the more resistant polyploid (T1).

Finally, this study used only three rust isolates from the southeast portion of the *G. tomentella* distribution for disease resistance screening. Screening with a larger range of pathogen isolates would have increased the probability of detecting further susceptible host-pathogen combinations and potentially provided a more rigorous test of the allopolyploidy hypothesis.

For the reasons detailed above, it is not surprising that no single pattern points to a role for polyploidy in accounting for variation in rust resistance patterns in *Glycine tomentella*. What does emerge from the screening results is a markedly nonrandom distribution of rust resistance among the different diploid and tetraploid groups, as well as among different geographic locations (Figs. 1 a–d). The accessions from two distinct geographic areas appear to have high levels of susceptibility to isolates of the rust. One of these is the Kimberley region, where susceptible accessions were frequent in both the tetraploid group T4 and the cytogenetically related diploid group D5 (Fig. 1 c). Similarly, in the north Queensland region the susceptible accessions of tetraploid group T2 overlapped with those of its unique donor D4.

A number of studies have detailed the presence of a wide range of resistance genes in the perennial wild relatives of *G. max* (Burdon 1987, 1988; Jarosz and Burdon 1990). A number of hybrids have been generated between *G. max* and *G. tomentella*, with particular success centering on the use of the tetraploid *G. tomentella* group T1 (Newell and Hymowitz 1982; Newell et al. 1987). The *G. tomentella* parents of these crosses, G1133 and G1855, were both resistant to all three of the isolates of *P. pachyrhizi* used in this study. This indicates the potential of *Glycine tomentella* germ plasm pool to contribute to the genetic improvement of cultivated soybean.

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