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# Inheritance of Partial Resistance to two Races of Leaf Rust, Melampsora medusae in Eastern Cottonwood, Populus deltoides

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## Summary

The $F_1$ progenies of a cross of eastern cottonwood, *Populus deltoides* (Bartr.) were analysed for inheritance of partial resistance (three traits-latent period, uredial infection frequency and sporulation capacity) to two Australien races of leaf rust, *Melampsora medusae* (Thüm.), employing leaf disks excised from the plants. All three traits appeared to be under polygenic control (continuous distribution was observed) and both additive and non-additive interactions were detected. Considerable transgressive segregation and racespecificity was observed for all three traits. Based on the direction of skewness, higher resistance appeared to be partially recessive to lower resistance. We conclude that, although it is possible to select for trees with high partial resistance combined with a hypersensitive-type resistance against specific races of the pathogen, the apparent race-specificity of the partial- resistance traits suggest that this type of resistance may also be vulnerable to pathogen adaptation. These results are discussed in terms of their relevance to the management of the poplar-leaf rust pathosystem.

*Key words:* Disease Resistance, Genetics, Host-parasite interaction, inheritance, leaf rust, *Melampsora medusae*, partial resistance, poplars, *Populus deltoides*, slow rusting.

## 1. Introduction

Host resistance is the most popular approach to managing a plant disease because it is economical, efficient and environmentally benign. Thus breeding for resistance to diseases assumes high priority in most tree breeding programs (Zobel, 1982; Heybroek *et al.*, 1982), as diseases cause considerable reduction in growth and in harvestable wood volume. Various resistance patterns may be observed in plants but complete resistance, characterized by a hypersensitive reaction, is the type of resistance preferred by most breeders as a defense against many foliar pathogens (in both annual and perennial plants) (Day, 1974; Barrett, 1985). This is understandable as hypersensitive resistance is easily recognizable in the plant population, is usually under simple genetic control (Day, 1974) and, hence is easier to incorporate into breeding programs.

However, at the population level complete resistance has an aspect of vulnerability. It is relatively easy for most pathogens to negate the effects of a resistance gene by a simple mutation from avirulence to virulence (Prakash and Heather, 1986a). The short life cycle and large population size of most pathogens also ensures rapid selection of rare but virulent alleles (Person *et al.*, 1976). Several authors have suggested employing partial resistance (also called rate-reducing or incomplete resistance) which is characterized by slower disease progress, reduced infection frequency and restricted sporulation, as a safer alternative to complete resistance in annual crops (Parlevliet, 1979; Wilcoxson, 1981; Eskes, 1983). The rationale is that partial resistance may be race-non-specific and, as it allows a limited development of the disease, it may not exert strong selection pressure on the pathogen population. Stable or durable resistance is highly desirable in tree crops as forest systems are composed of relatively static host genotypes maintained exclusively over space and time, and they are thus more volnerable to large-scale shifts in the pathogen population.

Leaf rust caused by *Melampsora medusae* (Thüm.) is a serious disease of eastern cottonwood, *Populus deltoides* (Bartr. ex Marsh.) in Australia and United States, where active breeding programs strive to maintain disease incidence below the economic threshold (Jokela and Mohn, 1977; Pryor and Willing, 1982; Heather and Chandrashekar, 1982; Thielges, 1985; Prakash and Thielges, 1987).

In an earlier paper (Prakash and Heather, 1986b), we reported that complete, hypersensitive-type resistance in cv. T-173 of *P. deltoides* to five races of *M. medusae* was simply inherited and mostly under single gene control. Further studies showed that this cultivar was susceptible, at reduced levels, to some races of the leaf rust pathogen (Prakash and Heather, 1986c). In this study, we report the analysis of inheritance for three partial resistance traits in this cultivar to two virulent, compatible races of *M. medusae* and also examine the usefulness of partial-resistance in the management of leaf rust disease of poplars. An assessment of race specificity of partial resistance and of the association between complete and partial resistance

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in the progeny is also made, We are not aware of other reports on the inheritance of traits of partial or rate-reducing resistance to foliar pathogens in forest trees.

## 2. Materials and Methods

A leaf disk method, which permits independent but simultaneous analysis of the disease reaction of single plants in a non-destructive manner to a number of the physiologic races of the pathogen, was employed. Both parents ($P_1$-cv. 60/122 - female; $P_2$-cv. T-173 - male) are susceptible to the two pathogen races used in this study, but the level of susceptibility to disease (all traits) of cv. 60/122 is greater than that of cv. T-173. The hybridisation and culture of hybrid plants is fully described elsewhere (PRAKASH and HEATHER, 1986b). Briefly, crosses were performed employing pollen of cv. T-173 on bottle grafted branches of cv. 60/122 in isolated greenhouses at Canberra (Australia) as described by KNOX *et al.* (1972). Seeds were collected 60 to 70 days after pollination and individually labeled plants, raised in perlite-vermiculite (1:1 v/v) medium, were maintained in a rust-proof greenhouse under controlled conditions (22° C and 16 h photoperiod) with a weekly supplement of complete liquid fertilizer. The parents were propagated as clonal cuttings and cultured with the $F_1$ seedlings. Uniformity in maturity of parents and seedlings was achieved by delayed planting of the parents. Rust inoculation tests were conducted on leaves of 20-month-old $F_1$ plants and approximate uniformity in leaf maturity of all plants was ensured by harvesting only-3-month-old shoots.

Pathogen races 5M and 7A of *M. medusae* are of single-urediospore origin and were identified as separate races by their reaction on a set of differential cultivars of *Populus* spp. Race 5 M was isolated as a radiation-induced mutant of race 5A, selected for its virulence on cv. T-173 at Australia (PRAKASH and HEATHER, 1986a), while race 7A is a natural isolate collected on cv. 60/122 in a field near Canberra. The urediospores (which are asexual spores) were multiplied (6—8 cycles) on *Populus* × *euramericana* (DODE) GUINIER cv. I-488, (a unioersal suscept) to produce sufficient inoculum for the study.

Disease reaction to each race was assessed using five replicate leaf disks (1.70 cm$^2$) from each $F_1$ plant and ten leaf disks from each of the parents. Fresh, dry urediospores (4 mg) of each race (5M and 7A) were deposited separately in a spore settling tower (SHARMA *et al.*, 1980) on replicate leaf disks of the parental cultivar, 61 $F_1$ plants of the cross cvs. 60/122 and T-173 and on a few cover glasses. Uniformity in deposition of inoculum ($< 10\%$ variation) and in germination of urediospores ($> 95\%$ for both races) was determined using the coverglasses as a control.

Inoculated replicate leaf disks were placed on plastic foam disks soaked in gibberellic acid solution (10 mg/l), separated by glass rods, placed in sterile Petri dishes and incubated in growth chambers at 16° C, 100 micro Einsteins per metre per second light intensity (400 to 700 nm PAR) and 16 h photoperiod.

Partial resistance was assessed by three parameters — (1) Latent period to production of first uredium (LP1) which is indicative of the timing of disease expression; (2) Uredia produced per leaf disk (ULD), a measure of infection frequency recorded when the number of uredia assumes a plateau (usually at or after 14 days); (3) Urediospores produced per mm$^2$ of the leaf area (USM), a measure of sporulation potential assessed immediately after recording ULD. USM was estimated by agitating replicate leaf disks in a suspension of 0.1% agar solution with several drops per litre of Tween 20 detergent and then counting urediospores in a Haemocytometer (PRAKASH and HEATHER, 1986c). High values for LP1 and low values for ULD and USM are indicative of a high degree of partial resistance to leaf rust.

The data were tested for homoscedasticity and normality of error variance (NETER and WASSERMAN, 1976) and the values for ULD and USM were transformed by square-root and $\log_e (x + 1)$, respectively to satisfy these requirements. The transformed data were used for all subsequent analyses including the analysis of variance (2 races X 61 plants) and for constructing $F_1$ distribution frequency

*Table 1.* — Reactions to leaf rust induced by *M. medusae* races 5M and 7A in parental cultivars and $F_1$ seedling progenies of the cross *P. deltoides* cv. 60/122 and T-173.

| Disease Trait | Parental Cultivar[b] | | Mid Parent Values[b] | $F_1$ Mean[b] | Range of $F_1$ Values[c] | S.D.[d] for $F_1$ | Skewness[e] | Kurtosis | Sign. of fit to normal (P) | L.S.D. (0.05)[f] |
|---|---|---|---|---|---|---|---|---|---|---|
| | 60/122 | T-173 | | | | | | | | |
| | | | | | Reaction with race 5M | | | | | |
| LP1[f] | 8.60 | 10.80 | 9.70 | 9.74 | 7.40-15.40 | 1.47 | 1.25 | 2.16 | 0.01 | 0.504 |
| ULD | 6.56 | 5.95 | 6.25 | 6.43 | 1.89-8.79 | 1.55 | -1.57 | 3.85 | 0.25-0.75 | 0.748 |
| USM | 6.81 | 6.33 | 6.57 | 6.33 | 2.55-7.31 | 1.08 | -3.95 | 18.62 | 0.01 | 0.313 |
| | | | | | Reaction with race 7A | | | | | |
| LP1 | 8.00 | 12.20 | 10.10 | 9.94 | 7.60-15.40 | 1.61 | 1.19 | 1.48 | 0.01 | 0.504 |
| ULD | 7.67 | 5.48 | 6.58 | 6.59 | 3.31-9.70 | 1.62 | -1.01 | 3.01 | 0.1-0.25 | 0.748 |
| USM | 7.15 | 6.14 | 6.65 | 6.41 | 4.61-7.51 | 1.01 | -4.25 | 24.01 | 0.05 | 0.313 |

a) LPI — Latent period to production of first uredium (days).
ULD — uredia produced per leaf disk (number); square-root transformed values.
USM — urediospores produced per sq. mm (number); $\log_e + 1$ transformed values.
b) Each value is a mean of ten replicates for parents and five replicates for $F_1$ seedlings.
c) $F_1$ seedling which was completely resistant was ignored in computing the range.
d) Standard deviation of mean of the population.
e) Skewness of distribution of all five traits with both races are significant ($P < 0.05$).
f) Least Significant Differences (LSD) computed with the interaction component of both races on the $F_1$ plants, and thus the same values for both races.

graphs. Most statistical computations were performed employing a GENSTAT package (Alvey *et al.*, 1982). However, the test for goodness of fit (employing Chi-square values) of the distribution of progeny means to the normal distribution was conducted using the MPL package (Ross, 1980). Skewness and kurtosis for observed distribution of the F1 plants were also estimated using the MPL package. Significance of skewness was tested by dividing the means of standard error and comparing with Z values at the 0.05 level. Correlation coefficients between traits were computed employing the GENSTAT package using the $F_1$ mean values.

## 3. Results

The female parent (cv. 60/122) was more susceptible than the male parent (cv. T-173) to both races 5M and 7A of *M. medusae*. That is, the rate of disease development was slower (longer LP1) and disease severity lower (smaller ULD and USM) on cv. T-173 than cv. 60/122, irrespective of the pathogen race employed (*Table 1*). However, there were significant differences ($P < 0.05$) in the ranking of the pathogen races on the parents for particular traits of the disease; race 5M was more aggressive than race 7A on cv. T-173, while on cv. 60/122 the reverse was true (*Table*

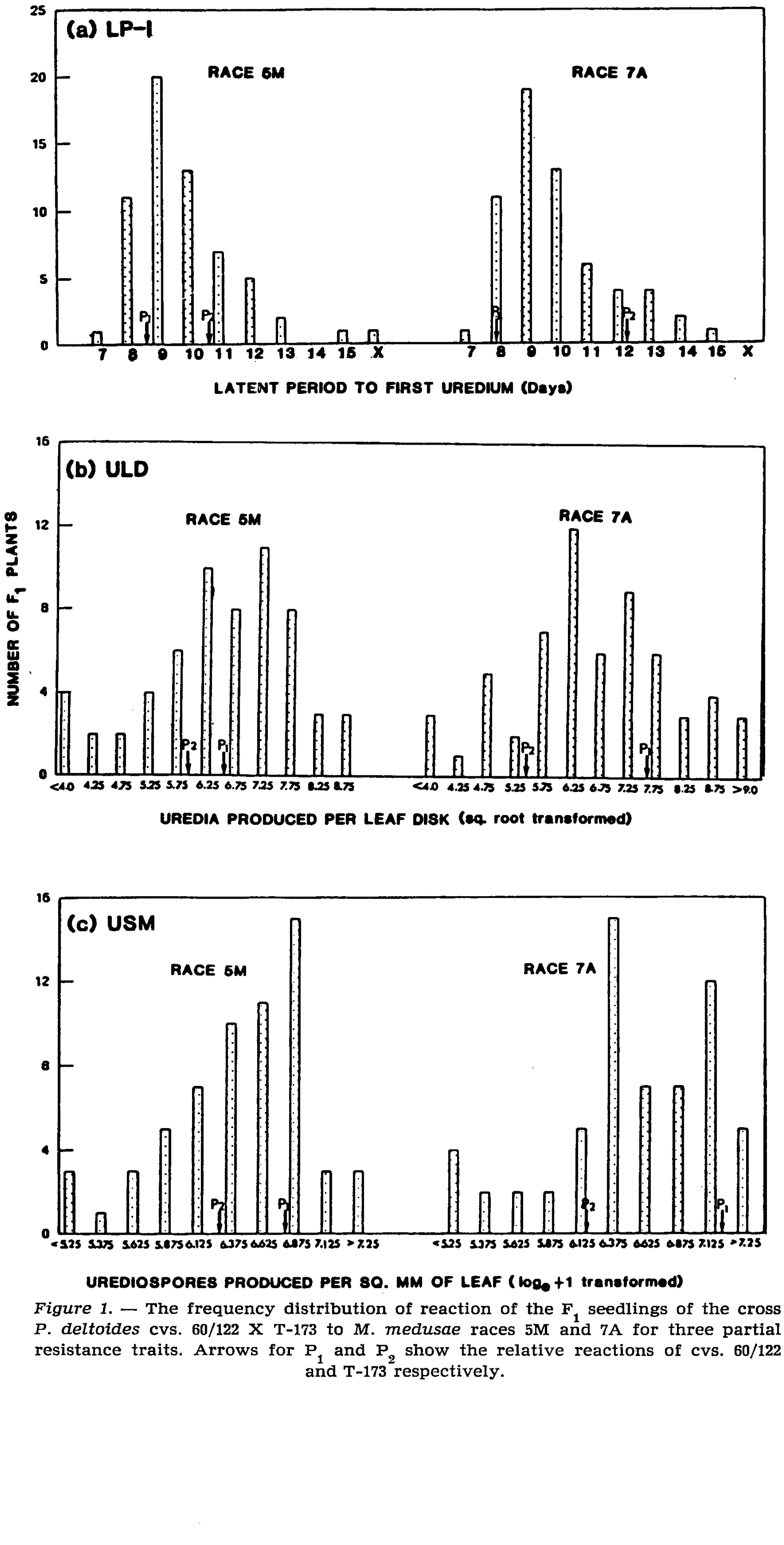

*Figure 1.* — The frequency distribution of reaction of the $F_1$ seedlings of the cross *P. deltoides* cvs. 60/122 X T-173 to *M. medusae* races 5M and 7A for three partial resistance traits. Arrows for $P_1$ and $P_2$ show the relative reactions of cvs. 60/122 and T-173 respectively.

Table 2. — Analysis of variance a) for three disease traits b) by the $F_1$ progeny of the *P. deltoides* cross cvs. 60/122 X T-173 with two races of *M. medusae*.

| Source | D F | LP1 | ULD | USM |
|---|---|---|---|---|
| $F_1$ Plant | 60 | 20.97 | 21.24 | 10.10 |
| Pathogen Race | 1 | 6.47 | 4.25 | 1.47 |
| $F_1$ Plant X Race | 60 | 5.62 | 3.76 | 1.04 |
| Residual | 483 | 0.16 | 0.36 | 0.06 |
| Total | 609 | 2.76 | 2.76 | 1.15 |

a) Mean sum of squares presented; all values are highly significant ($P < 0.001$).

b) The three traits are latent period to production of first uredium (LP1), uredia produced per leaf disk (ULD; square root transformed) and urediospores produced per sq. mm (USM; $\log_e+1$ transformed).

*1*). For all three traits, differences in the parental reactions were greater for race 7A than for race 5M (*Table 1* and *Figure 1*.) The $F_1$ mean values were similar for both races and approximated the mid-parent values for all three traits (*Table 1*). Since transformed values for ULD and USM have been presented throughout, the differences between treatments, particularly for higher values, appear smaller than those actually observed.

A clear segregation of the $F_1$ plants for all three disease traits was observed (*Figure 1*) indicating the heterozygosity of the parents employed in the study. The frequency distribution of the $F_1$ plants appears continuous for disease reaction to both races and thus indicates polygenic control of the traits of partial resistance in the parents (*Figure 1*). The range of mean values for $F_1$ plants exceeded the means of both parents (for all 3 traits with both races), indicating the occurrence of transgressive segregation in the progeny of this cross. For all three traits, the fit of the frequency distribution of progeny means to a normal distribution was low to moderate (P, 0.01 to 0.75). Skewness was statistically significant ($P < 0.05$), although positive for LP1 and negative for ULD and USM. This indicates the partial dominance of lower resistance (higher susceptibility) over higher resistance.

The distribution of the $F_1$ seedlings for latent period (LP1) was continuous for both races (*Figure 1a*). The modal class was closer to the susceptible (shorter LP1) parent cv. 60/122 but the tail toward cv. T-173 was pronounced (longer LP1) and extended beyond the value of this parent (*Figure 1*). Those plants which exhibited a very long LP1 were re-tested and the results were reproduced. The frequency distribution of the $F_1$ plants for uredia produced per leaf disk (ULD) was closer to a normal distribution than for the other two traits (*Table 1*; *Figure 1b*). The response of the $F_1$ plants as measured by urediospores per square mm of leaf (USM) was also characterized by continuity in distribution and transgressive segregation, but was markedly skewed towards the susceptible parent and, hence, the high kurtosis values (*Table 1; Figure 1c*). Similar continuous distribution of the $F_1$ plants was also observed for another trait, urediospores produced per uredium, with an high approximation to normal distribution but with a low degree of skewness (data not shown).

Although there was a similarity in the trends of disease reaction of the $F_1$ seedlings to both races, significant differences in the racial specificity of individual seedlings were observed. Some seedlings which were moderately resistant to race 5M exhibited high susceptibility to race 7A and *vice versa*. Such racial specificity was also apparent in the analysis of variance where the $F_1$ plant X race interaction was highly significant ($P < 0.001$) source of variation (*Table 2*). In the ANOVA (*Table 2*), the $F_1$ plant was by far the largest contributor to the variation followed by pathogen race and the $F_1$ plant x race interaction ($P < 0.001$) for the three disease traits studied. This further supports the observation that $F_1$ plants studied here exhibit considerable variation to partial resistance, and that the level of resistance was contignent on the type of pathogen race employed.

Although there was some inconsistency, the ranking of the 61 $F_1$ clones for the three traits was largely similar. When correlation coefficients between the three disease traits as measured on the $F_1$ seedlings, were estimated, trends of association among traits were generally similar for both races (*Table 3*). LP1 was significantly but negatively correlated with ULD and USM, while ULD and USM were significantly and positively correlated ($P < 0.001$; *Table 3*).

## 4. Discussion

Poplars are dioceious and a high degree of heterozygosity in the parental cultivars was expected; thus, the segregation for disease resistance observed in the $F_1$ plants is not surprising. In a separate study employing the same cross, similar but discrete segregation for qualitative (complete or hypersensitive) resistance occurred against many races of the *Melampsora* leaf rust (Prakash and Heather, 1986b). The nature of the experimental technique employed here, enables strict control of the environmental variables (both pre- and post-inoculation conditions of plant culture, and uniformity of leaf maturity and inoculum), which resulted in the uniformity of disease expression in the replicate leaf disks of an individual plant and

*Table 3.* — Matrix of correlation coefficients (r) between the three disease traits of induced by races 5M and 7A of *M. medusae* on $F_1$ seedlings of the cross *P. deltoides* cvs, 60/122 X T-173 (D F = 60).

a) WITH RACE 5M

| | Disease Trait ab | | |
|---|---|---|---|
| | LP1 | ULD | USM |
| LP1 | 1.00 | | |
| ULD | -0.68 | 1.00 | |
| USM | -0.71 | 0.65 | 1.00 |

b) WITH RACE 7A

| | Disease Trait a | | |
|---|---|---|---|
| | LP1 | ULD | USM |
| LP1 | 1.00 | | |
| ULD | -0.67 | 1.00 | |
| USM | -0.79 | 0.59 | 1.00 |

a) LP1 — Latent period to production of first uredium in days.
ULD — Uredia produced per leaf disk.
USM — Urediospores produced per sq. mm.

b) All values are highly significant ($P < 0.001$).

ensured that variation in disease reaction was largely genetically based.

In this study, cultivar T-173 exhibited relatively high partial resistance to both races of *M. medusae* while cv. 60/122 was relatively more susceptible. However it appears that cv. 60/122 may also carry some genes for partial resistance because of the occurrence in the $F_1$ progeny of a few seedlings which were more susceptible than this parent.

The continuous, rather than discrete, distribution of $F_1$ plants for all three traits of partial resistance is indicative of polygenic control (genes with minor effects) with additive ($F_1$ mean values approximate mid-parent values) and non-additive (skewed distribution) interactions. The apparent recessiveness of higher partial resistance to a lower partial resistance (based on skewness; *Table 1*) is similar to those results observed in cereals for rust resistance (Luke *et al.*, 1975; Parlevliet, 1976; Skovmand *et al.*. 1978; Wilcoxson, 1981), but differs in terms of the genetic control of a hypersensitive-type resistance which is usually (but not always) inherited as a dominant trait (Day, 1974).

The occurrence of many seedlings in the $F_1$ progeny exhibiting a long latent period, fewer uredia and reduced sporulation, due to transgressive segregation (*Figure 1*), is significant for breeding and selection of "slow-rusting" plants. Such plants are expected to contribute to an overall reduction of the disease in the field due to a slower progress of the disease and a consequent reduction in the inoculum available for further infection. The parameter LP1, which can be estimated with relative ease and accuracy, can be employed as a selection criterion to identify slow-rusting plants because of its high inverse correlation with uredial number and sporulation (ULD and USM in *Table 3*). Similar correlations have been observed in many cereal crops for resistance to rust riseases (Parlevliet, 1979).

Whilst the $F_1$ seedlings exhibited varying degrees of susceptibility/resistance to either of the races, one $F_1$ seedling was completely resistant to both races. This suggests that despite their wide virulence spectrum, both races of the pathogen may carry an avirulent gene (or genes) corresponding to the resistance gene(s) in this plant. This particular seedling was, however, susceptible to other races of *M. medusae* (Prakash and Heather, 1986b). Hence high resistance in this plant to races 5M and 7A is unlikely to result from the cumulative effect of additive resistance genes. This observation conflicts with the theory of the role of "defeated" resistance genes in contributing to partial or rate-reducing resistance (Nelson, 1979).

The observed race-specificity of the plants in this study for traits of partial resistance (*Table 2*) exemplifies the need to employ many, pure races with broad virulence spectrum in selecting resistant cultivars. However, this also suggests that partial-resistance (or slow-rusting) by itself may not confer long-term protection against all races and may indeed enforce selection on the pathogen to adapt to such resistance. In serial culture studies, an increase in aggressiveness of the pathogen to some cultivars of *P. deltoides* was observed (Prakash and Heather, in preparation) and an increased in aggressiveness due to host selection has also been noted in other pathogens (Alexander *et al.*, 1985; Kolmer and Leonard, 1986).

To achieve stability in the pathosystem and thus, to effectively manage poplar leaf rust, we suggest the selection of many host genotypes encompassing a high degree of partial resistance and also a broad spectrum of hypersensitive-type resistance against many prevalent races of the pathogen, and the deployment of these as mixtures or mosaics. While such a system may not completely eliminate the disease, the variable host population may serve to buffer rapid shifts to virulence in the pathogen population and, by promoting pathogen polymorphism, a great degree of pathosystem stability may be obtained.

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