Characterization of two major genetic factors controlling quantitative resistance to Melampsora larici-populina leaf rust in hybrid poplars : strain specificity, field expression, combined effects, and relationship with a defeated qualitative resistance gene

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Characterization of Two Major Genetic Factors Controlling Quantitative Resistance to *Melampsora larici-populina* Leaf Rust in Hybrid Poplars: Strain Specificity, Field Expression, Combined Effects, and Relationship with a Defeated Qualitative Resistance Gene

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Accepted for publication 2 August 2004.

ABSTRACT

Dowkiw, A., and Bastien, C. 2004. Characterization of two major genetic factors controlling quantitative resistance to *Melampsora larici-populina* leaf rust in hybrid poplars: Strain specificity, field expression, combined effects, and relationship with a defeated qualitative resistance gene. Phytopathology 94:1358-1367.

Two genetic factors explain a significant proportion of the variability for quantitative resistance to *Melampsora larici-populina* leaf rust in a *Populus deltoides* × *P. trichocarpa* F_1 progeny. One is inherited from *P. deltoides* and is associated with a defeated qualitative resistance gene R_1, and the other, R_{US}, is inherited from *P. trichocarpa*. To assess the potential contribution of these two factors for durable resistance breeding, 284 genotypes from this F_1 progeny were studied in laboratory experiments with three *M. larici-populina* strains and in a field experiment under natural inoculum pressure. Results confirmed that both factors can have strong beneficial effects in the laboratory. These effects were strain specific, thus impairing their chances for durability. However, association of both factors led to synergistic effects in most situations. In accordance with good field–laboratory relationships, especially those involving uredinia-size laboratory measurements, field effects of both resistance factors were significant. R_{US} led to a significant reduction of rust colonization on the most infected leaf in the field, and its effect was significant both in the presence and the absence of R_1. In contrast, the presence of R_1 was useful in the field only when R_{US} was absent. The nature of the genetic relationship between both factors remains unknown, but benefits from their association should be quantified over a longer period to evaluate potential adaptation of the pathogen.

Additional keyword: residual effect.

The foliar rust caused by *Melampsora larici-populina* Kleb. is the main disease affecting poplar stands in the northern part of France, and more generally in northern Europe. Although breeders developed several cultivars with qualitative *M. larici-populina* resistance inherited from *Populus deltoides,* especially *P. deltoides* × *P. nigra* and *P. deltoides* × *P. trichocarpa* hybrids, no cultivar remained free of *M. larici-populina* for more than 5 years after commercial release. New strains of the pathogen that were able to overcome the host resistance arose repeatedly (11).

Poplar breeding for *M. larici-populina* resistance now must develop a new selection strategy to improve resistance durability. A better understanding of *M. larici-populina*–poplar interactions and coevolution is needed, and one of the major issues is the relative advantage of breeding for quantitative compared with qualitative resistance.

Quantitative resistance is often regarded as durable because it is considered polygenic and horizontal (i.e., non-race-specific, uniform). In contrast, qualitative resistance generally is mono- or oligogenic and vertical (i.e., race-specific, differential) and, therefore, commonly supposed to be nondurable. Such generalization is misleading for at least four reasons. First, the term "polygenic" conjures an inappropriate impression of many minor genes, each of approximately equal effect on the phenotype. Results of quantitative trait loci (QTL) mapping indicate that quantitative resistance often is controlled by one or two QTL with large effects, in association with a few minor QTL (12,15,24,25,34,38,47,48). Second, race nonspecificity seems to be an exception rather than a rule (27) and demonstrating this phenomenon would require an exhaustive study of all variants of the pathogen (16). Third, resistance that is effective against a large spectrum of pathogen variants can result from the joint action of broad-spectrum and race-specific genes (4,21). Finally, even though the most widely cited examples of durable resistance against bacteria and fungal pathogens are quantitative traits, there are examples of durable monogenic qualitative resistances (19,30). As stated by Eenink (10), "The stability [of a resistance] is determined by the genetics of the host–parasite relationship and not by the genetics of resistance. Quantity as well as quality of resistance and pathogenicity genes may be important." Thus, the durability of a resistance gene cannot be predicted without taking the genetic adaptive potential of the pathogen into account. Assessing the strain specificity of a resistance allows insight into this potential.

Another question to address before negating the utility of *M. larici-populina* qualitative resistance is the potential genetic relationship between qualitative and quantitative resistance. A few years after Van der Plank's definitions of horizontal and vertical resistance (43), several authors argued that the possibility of close genetic relationships between these two forms of resistances should never be discarded. Nelson (27) made the hypothesis of common genes leading either to qualitative or to quantitative resistance, depending on their surrounding genetic background. Riley (35) wondered whether major genes whose effectiveness has been overcome by pathogen mutation to virulence contribute any further to resistance. Like Hayes (13), he stated that these genes

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Publication no. P-2004-1018-01R

might exhibit a "ghost" (i.e., residual) effect. Twelve years later, Robertson (36) generalized this concept by stating that qualitative and quantitative traits, not only resistance, may result from the expression of different alleles at the same locus. Since the early findings of Slesinski and Ellingboe (40) on the wheat–powdery mildew pathosystem, several reports have hypothesized such residual effects in different pathosystems (7,9,17,22,23,26,29, 31,41).

Lefèvre et al. (20) and then Dowkiw et al. (8) demonstrated how *M. larici-populina* quantitative resistance in a *P. deltoides* × *P. trichocarpa* F_1 progeny can disprove preconceived ideas. The variation they observed in that progeny for quantitative resistance to *M. larici-populina* strain 93CV1 in laboratory bioassays could be explained mainly by two segregating genetic factors. One is inherited from the *P. deltoides* parent and is related, either by linkage or because of a residual effect, to a defeated *M. larici-populina* qualitative resistance gene (designated here as R_1). The other factor (designated here as R_{US}) is inherited from the *P. trichocarpa* parent and produces dramatic effect on uredinia size. However, the presence of R_{US} could be detected only in the absence of R_1, from bimodal distributions of the genotypic values.

To further explore the implications of these two genetic factors for durable resistance breeding, the present study aimed at (i) quantifying their level of strain specificity using two other strains of the pathogen in laboratory experiments, (ii) studying their effectiveness under natural conditions in a field experiment where a mixture of strains of the pathogen was present, and (iii) measuring their relative and combined effects.

MATERIALS AND METHODS

Plant material. Poplar material consisted of 284 cloned F_1 genotypes from an interspecific *P. deltoides* × *P. trichocarpa* cross. The two parents used for hybridization are typical of the two parental species in terms of *M. larici-populina* resistance. The *P. deltoides* female parent (73-028-62) is a source of both qualitative and quantitative resistances, whereas quantitative resistance only has been identified in the *P. trichocarpa* male parent (101-74). Qualitative resistance is defined here as the absence of any sporulating uredinia, and does not necessarily involve hypersensitivity. This definition applies both to the *P. deltoides* female parent and to the F_1 progeny.

All data concerning compatibility and incompatibility of the F_1 progeny with *M. larici-populina* strain 93ID6 (i.e., absence and presence, respectively, of R_1) were obtained from previous studies that concluded the presence of a 1:1 segregation for qualitative resistance to this strain (20). The study material contained 122 compatible and 162 incompatible genotypes ($\chi^2 = 2.82$, $P > \chi^2 = 0.09$). In this article, these genotypes are referred to as r_1 and R_1 genotypes, respectively. The higher proportion of R_1 genotypes may have resulted from natural selection in the nursery under *M. larici-populina* pressure.

For the laboratory experiments, two ramets of each F_1 and parental clone were grown from cuttings in 3-liter pots (1 ramet/pot) containing 20% sand, 40% peat, and 40% ground bark mixture under rust-free glasshouse conditions. Natural daylight was supplemented for 16 h/day at 150 W m^{-2} minimum light intensity. The plants were watered and fertilized daily with a 15:10:15 solution (1 g/liter). Leaves were sampled from the fifth to the eighth unrolled leaf below the apex.

Fungal material. Variability within the *M. larici-populina* species is described in terms of virulences, a virulence being defined here as a qualitative attribute of the pathogen (i.e., the ability to infect a given host genotype). Eight virulences have been defined so far (32,33) based on a set of eight discriminant poplar genotypes. Each combination of these eight virulences is referred to as a pathotype. Analysis of a large number of *M. larici-populina* strains led to the conclusion that virulence 1 confers the ability to overcome the qualitative resistance that segregates 1:1 in the studied F_1 progeny. For this reason, we decided to name the corresponding qualitative resistance gene R_1.

The three inocula used for the laboratory experiments consisted of urediniospores from single-uredinial *M. larici-populina* strains 93CV1, 98AG69, and 98AR1. These three strains belong to pathotypes 1-3-4-5, 1-3-4-5-7, and 1-3-4-5-7-8, respectively, and, therefore, should be able to infect the entire F_1 progeny set of this study (except for a few probable recombinants). Inoculum of each strain was increased on *P. xeuramericana* highly susceptible cv. Robusta, as described elsewhere (8).

No attempt was made to influence the racial composition of the *M. larici-populina* inoculum that occurred naturally in the field experiment. However, the close proximity of *M. larici-populina*'s aecidial host, larch (*Larix*), should have promoted early infection and rapid epidemic build-up. The racial composition of the field inoculum was estimated twice during experimentation, in June and August, by the Institut National de la Recherche Agronomique (INRA) Forest Pathology Laboratory in Nancy, France. Each estimation was based on 100 uredinia isolated from leaves of cv. Robusta that was represented in the borders of the experimental plot. Robusta, a cultivar in which no qualitative *M. larici-populina* resistance has been detected so far, was considered an inoculum trap. These uredinia were multiplied on excised leaf disks from Robusta, then used to inoculate excised leaf disks of the eight discriminant poplar genotypes. The estimated field racial populations are shown in Table 1. The proportions of rust strains possessing virulence 1 and, hence, able to circumvent R_1 were very high: 81% in June and 89% in August. Thus, only a very small advantage was to be expected for R_1 genotypes over r_1 genotypes in the absence of another effect associated with the presence of R_1.

Quantitative resistance assessments in the laboratory. Protocols to study genetic variability for *M. larici-populina* quantitative resistance in inoculated excised leaf-disk bioassays have been presented and discussed elsewhere (8). All data concerning quantitative resistance to *M. larici-populina* strain 93CV1 in inoculated leaf-disk bioassay were obtained from this previous study. However, genetic parameters have been recalculated on the subset of host genotypes studied here to allow comparisons.

Inoculations were made by spraying suspensions of 30 mg of urediniospores per liter in five randomized complete-block designs using a hand atomizer. Each F_1 genotype was represented by one leaf disk per block while each of the two parents was represented three times per block. Temperature was set at 15°C. The number of urediniospores deposited per leaf disk has been estimated by scattering petri dishes containing solid water agar (20 g/liter) in the experiments before inoculation and by counting the number of deposited urediniospores using a microscope. The estimated values were 74 (SD = 19) for 93CV1, 93 (SD = 25) for 98AG69, and 46 (SD = 18) for 98AR1.

TABLE 1. Estimated proportions of *Melampsora larici-populina* pathotypes in the field experiment[a]

Pathotype	June 2000	August 2000
2-4	3	…
3-4	7	8
1-4-5	2	…
2-3-4	1	1
3-4-5	4	…
3-4-6	…	1
3-4-7	…	1
1-3-4-5	14	11
3-4-5-7	4	…
1-3-4-5-6	6	5
1-3-4-5-7	49	61
1-3-4-5-6-7	10	12

[a] All values are percentages calculated on 100 isolated uredinia.

Three quantitative resistance components have been measured: latent period measured on a half-day basis (LP), uredinia number at 13 days after inoculation (UN), and uredinial size at 14 days after inoculation (US). US was scored visually using a 1 (small) to 5 (large) ranking scale and was used as a surrogate estimate of uredinial spore production, Dowkiw et al. (8) having demonstrated the existence of a curvilinear relationship between both traits in the laboratory experiment involving rust strain 93CV1. By way of image analysis, this previous study also provides a quantification of the 1-to-5 ranking scale on an area basis (mm^2) for strain 93CV1. Despite a concern for consistency in the 1-to-5 ranking scale across experiments, these quantifications in terms of uredinial spore production and uredinial area may not be appropriate enough for strains 98AG69 and 98AR1, and they will not be used for these two strains.

Resistance assessment in the field. The field experimental design consisted of six randomized complete blocks, where each F_1 and parental genotype was represented by a single plant. Cuttings of the F_1 clones and the two parents were planted at a spacing of 0.5 m on plastic mulch in rows 1.5 m apart. The plants were allowed 1 year to establish, during which they were regularly treated with a systemic fungicide. All plants were cut down at ground level in spring of the year of measurement. After the clones started to produce new shoots, they were pruned to keep the dominant stem only. Herbicides were applied regularly between the rows and irrigation was provided by sprinklers from May to September in both establishment and measurement years. Susceptibility was estimated as the density of sporulating *M. larici-populina* uredinia on the most infected leaf using the 1-to-6 scale that is commonly used in several poplar breeding programs, where 1 = no uredinia, 2 = 1 to 10 uredinia, 3 = 11 uredinia to 25% of the leaf area, 4 = 25 to 50% of the leaf area, 5 = 50 to 75% of the leaf area, and 6 = >75% of the leaf area. We measured this trait three times during the growing season, in June (MAX1), July (MAX2), and August (MAX3).

Data analysis. Data were analyzed using S-plus (version 3.4 release 1 for Sun SPARC; Statistical Sciences, MathSoft Inc., Seattle, WA) and R.1.7.0 for Windows (The R Development Core Team).

Prior to analysis of variance, data were transformed using the Box-Cox procedure (2) to ensure homoscedasticity and normality of the residuals from the following model of analysis of variance: $Y_{ijk} = \mu + B_i + G_j + \varepsilon_{ijk}$, where μ is the grand mean, B is the block effect (fixed), and G is the genotype effect (random). LP, UN, and US were consequently transformed as LP^{-2}, $UN^{1/2}$, and $US^{1/2}$.

The block effects were significant ($P < 5\%$) for all data, both in the field and in the laboratory. Therefore, data were adjusted to account for the block effects before restricted maximum likelihood (REML) variance estimates σ^2_G and σ^2_ε were computed. Broad-sense heritabilities were calculated at and individual level as $H^2 = \sigma^2_G/(\sigma^2_G + \sigma^2_\varepsilon)$. Standard deviations of H^2 were derived from classical estimation of SD for a ratio x/y where $x = \sigma^2_G$ and $y = \sigma^2_G + \sigma^2_\varepsilon$.

Significance of the effect associated with any of the two resistance factors was estimated for each trait by comparing the means (untransformed data) of the groups of genotypes possessing versus lacking the studied factor. Variances sometimes were unequal in the two groups of genotypes; therefore, comparisons of means were based on the nonparametric Wilcoxon rank-sum test.

When significant, the relative difference between the means of R_1 (μ_{R1}) and r_1 (μ_{r1}) groups of genotypes was computed as $\Delta R_1 = (\mu_{R1} - \mu_{r1})/\mu_{r1}$. Similarly, we also computed ΔR_{US}, the relative difference between the means of R_{US} and r_{US} groups of genotypes. Interpretation of these two parameters was straightforward for LP and UN because these two traits were expressed on linear scales in biologically meaningful units (i.e., days after inoculation and number of uredinia, respectively). However, for categorical traits US, MAX1, MAX2, and MAX3 that were measured on arbitrary curvilinear scales, some data transformations were made for computation of more meaningful estimates of ΔR_1 and ΔR_{US}. For rust strain 93CV1, US individual values were converted into uredinial spore production values, using the relationship established by Dowkiw et al. (8) in the same experiment. US values of 1, 2, 3, 4, and 5 were converted into spore production values of 1,462, 2,593, 5,432, 10,504, and 16,174 urediniospores/uredinia, respectively. Linearization of MAX1, MAX2, and MAX3 individual values was obtained by converting MAX values of 1, 2, 3, 4, 5, and 6 into proportions of leaf area covered with uredinia of 0, 12.5, 12.5, 37.5, 62.5, and 87.5%, respectively.

TABLE 2. Broad-sense heritabilities at the individual level (H^2) for latent period (LP), number of uredinia (UN), and uredinia size (US) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny inoculated with three *Melampsora larici-populina* strains

	$H^2 \pm$ SD		
Strain	LP	UN	US
93CV1	0.71 ± 0.05	0.71 ± 0.04	0.73 ± 0.05
98AG69	0.62 ± 0.03	0.51 ± 0.02	0.80 ± 0.05
98AR1	0.46 ± 0.02	0.22 ± 0.03	0.62 ± 0.03

RESULTS

Quantitative resistance to three *M. larici-populina* strains in laboratory experiments. Significant genetic variability was observed with all three rust strains for the three measured traits even though heritability estimates often were higher for US than for LP and UN (Table 2). Overall ranking of the three strains was different from one trait to the other except for US, for which no significant difference was observed among strains (Table 3). However, the ranking based on UN certainly is not meaningful, given the contrasting inoculum pressures that were applied in each experiment. A previous study on the same F_1 progeny with strain 93CV1 in the laboratory showed how UN was unpredictably affected by a twofold change in the inoculum pressure, whereas LP and US were not significantly influenced (8). On the basis of LP, 98AR1 appeared to be the least aggressive strain.

TABLE 3. Summary statistics of latent period (LP), number of uredinia (UN), and uredinia size (US) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny inoculated with three *Melampsora larici-populina* strains

			LP (days)			UN			US		
Strain	Inoc. press.[a]	Uredinia-free[b]	Mean[c]	Q1–Q3[d]	Mean 101-74[e]	Mean[c]	Q1–Q3[d]	Mean 101-74[e]	Mean	Q1–Q3[d]	Mean 101-74[e]
93CV1	74 ± 19	33	9.6	8.1–10.8	8.8	5.7	0.8–9.5	7.1	2.3	1.6–2.8	2.4
98AG69	93 ± 25	1	9.6	8.8–10.0	9.6	*10.4	6.8–13.9	4.4	2.3	1.5–3.2	2.0
98AR1	46 ± 18	0	*9.9	9.3–10.4	10.2	5.8	3.8–7.4	4.3	2.4	1.8–3.0	2.2

[a] Inoculum pressure: estimated number of spores deposited per leaf disk, ± standard deviation.
[b] Genotypes with UN = 0 on each of the five leaf disks.
[c] An asterisk indicates a mean that is significantly different from each of the two other ones (Wilcoxon signed rank test, $P < 0.01$).
[d] First (Q1) and third (Q3) quartiles of mean values.
[e] Mean of the *P. trichocarpa* male parent 101-74.

The studied F_1 showed relatively high overall susceptibility to the three studied rust strains (Table 3). Mean values for each trait often were distributed widely on each side of the *P. trichocarpa* parental value, whereas the *P. deltoides* parent proved to be much more resistant, with infection frequencies too low for quantification (some sporulation occurred with strain 98AG69, but on only 4 of the 15 leaf disks) (Table 3).

Of the studied genotypes, 33 did not present any uredinia with strain 93CV1 (Table 3). These genotypes showed very high resistance levels with the two other rust strains: their interquartile range of variation always was disconnected from the mean of the whole population (Table 4). The susceptibility of 26 of these genotypes has been checked in a high inoculum pressure experiment, and only 3 of them clearly behaved as incompatible with strain 93CV1.

Effect of the resistance factor inherited from *P. deltoides* in the laboratory experiments. In accordance with previous findings on a slightly larger population (8), R_1 genotypes were significantly more resistant to strain 93CV1 than r_1 genotypes (Table 5). They exhibited longer LP, lower UN, and lower US. This effect remained significant for all three traits with strain 98AR1, even though its intensity was more than halved when compared with results with 93CV1 (Table 5). In contrast, no significant difference was observed between the means of R_1 and r_1 genotypes for LP and US with strain 98AG69; only UN exhibited a significant but tenuous difference (Table 5).

Relationships among the three studied traits for 98AG69 and 98AR1 were very similar to what was observed with 93CV1 in a previous study (8): all three traits were significantly correlated, UN and US were the less correlated traits, and the relationships between LP and the two other traits were left-triangular-shaped (Fig. 1). In most situations, the estimated correlation coefficients differed between R_1 and r_1 genotypes. These coefficients tended to be higher for R_1 genotypes because of a higher proportion of genotypes with very long LP, which may have limited the expression of US and UN.

Interstrain Spearman's rank correlation coefficients often were significant (Fig. 2). However, coefficients >0.5 were found only for US (Fig. 2).

Effect of the resistance factor inherited from *P. trichocarpa* in the laboratory experiments. In a previous study, bimodal distribution of the genotypic means of r_1 genotypes for US_{93CV1} led to the conclusion that a resistance factor inherited from *P. trichocarpa*, R_{US}, is segregating, which produces a major effect in absence of R_1. The results presented here clearly indicate that the presence of R_{US} imparts a major beneficial effect on US with 98AG69 and 98AR1 also, in both the absence and the presence of R_1. Distributions of the genotypic means for US_{98AG69} and US_{98AR1} were always bimodal (Fig. 3) and the composition of the two groups of genotypes with large versus small US was relatively stable across rust strains (Fig. 2).

TABLE 4. Summary statistics of latent period (LP), number of uredinia (UN), and uredinia size (US) following inoculation with *Melampsora larici-populina* strains 98AG69 and 98AR1 on 33 *Populus deltoides* × *P. trichocarpa* full-sib F_1 genotypes which did not present any uredinia when inoculated with strain 93CV1

	LP (days)		UN		US	
Strain	Mean	Q1–Q3[a]	Mean	Q1–Q3[a]	Mean	Q1–Q3[a]
98AG69	10.7	9.7–11.3	6.1	1.8–8.8	1.4	1.0–1.6
98AR1	10.6	10.0–11.3	4.0	2.6–5.2	1.7	1.3–2.0

[a] First (Q1) and third (Q3) quartiles of mean values.

TABLE 5. Relative advantage (ΔR_1) of the 162 R_1 genotypes over the 122 r_1 genotypes in terms of latent period (LP), number of uredinia (UN), and uredinia size (US) in 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny inoculated with three *Melampsora larici-populina* strains[a]

	LP (days)				UN				US			
Strain	Mean r_1	Mean R_1	P_w	ΔR_1 (%)	Mean r_1	Mean R_1	P_w	ΔR_1 (%)	Mean r_1	Mean R_1	P_w	ΔR_1 (%)[b]
93CV1	8.2	10.8	***	+32	10.0	2.4	***	–76	2.8	1.9	***	–34 (–51)
98AG69	9.4	9.7	0.66	ns	11.1	9.8	*	–12	2.3	2.4	0.35	ns
98AR1	9.6	10.2	***	+7	6.9	4.9	***	–27	2.6	2.3	**	–13

[a] P_w is the P value associated with the Wilcoxon rank-sum test of the significance of the difference between the means of R_1 and r_1 genotypes. P values below 5, 1, and 0.1% are represented by *, **, and ***, respectively; ns = nonsignificant.

[b] Value in parentheses indicated for US_{93CV1} was computed after conversion of individual US values into uredinial spore production values.

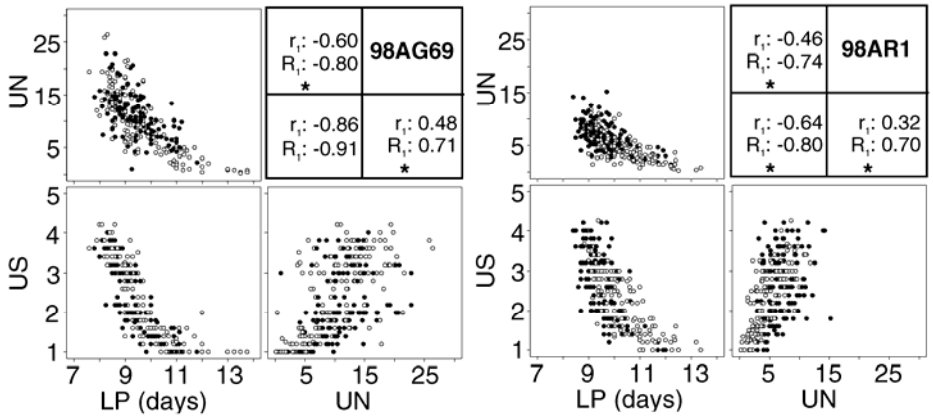

Fig. 1. Relationships between genotypic means for latent period (LP), uredinia number (UN), and uredinia size (US) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny inoculated with *Melampsora larici-populina* strains 98AG69 and 98AR1. The 122 r_1 genotypes appear as black dots and the 162 R_1 genotypes appear as open circles. Spearman rank correlation coefficients are indicated separately for r_1 and R_1 genotypes. Asterisks indicate situations where R_1 and r_1 genotypes have significantly different correlation coefficients (non-overlapping 95% confidence intervals).

Dowkiw et al. (8) hypothesized that a significant but less obvious effect of R_{US} on US_{93CV1} also occurs in the presence of R_1. Correlation coefficients >0.60 between US_{93CV1} and either US_{98AG69} or US_{98AR1} for R_1 genotypes (Fig. 2) support this hypothesis.

Presence or absence of R_{US} could be inferred from US_{98AG69} genotypic values, given the clear bimodal distributions for that trait; therefore, we were able to quantify the effect of R_{US}. We defined the 126 genotypes with $US_{98AG69} > 2.5$ as r_{US} genotypes and the 158 genotypes with $US_{98AG69} \leq 2.5$ as R_{US} genotypes, then estimated the significance of the differences between these two groups of genotypes.

When pooling R_1 and r_1 genotypes together, results showed that R_{US} imparted a beneficial effect not only on US but also on LP and UN, except on LP_{93CV1} (Table 6).

When distinguishing between R_1 and r_1 genotypes, results showed that R_1R_{US} genotypes always were significantly more resistant than genotypes possessing only one or the other of the two resistance factors (Fig. 4). This result indicates that apparent unimodality of the distribution of US_{93CV1} in the presence of R_1 was hiding a 52% relative advantage of R_1R_{US} genotypes over R_1r_{US} genotypes in terms of uredinial spore production (Fig. 4). Association of these two factors can have dramatic effects: R_1R_{US} genotypes had 42% longer LP, 93% less uredinia, and produced 85% less urediniospores per uredinia than r_1r_{US} genotypes with strain 93CV1 (Fig. 4). When these results are considered in more detail, it appears that the relative importance of R_1 and R_{US} is highly dependent on the trait–strain combination (Fig. 4). Both resistance factors produce dramatic effects on US_{93CV1}, LP_{98AR1}, and US_{98AR1}, both separately and in combination. In contrast, the presence of R_1 is beneficial for LP, UN, and US with strain 98AG69 only when associated with R_{US}, whereas the presence of R_{US} is beneficial for LP_{93CV1}, UN_{93CV1}, and UN_{98AR1} only when associated with R_1.

Field resistance. The studied F_1 exhibited very high susceptibility in the field compared with both parents: the interquartile ranges of variation for the three field-susceptibility measurements always were distinct from the parental mean values (Table 7). Both parents were equally infected at the end of field study, but the *P. deltoides* parent remained less infected than the *P. trichocarpa* parent until June.

Despite significant genetic effects, heritability estimates were lower than the ones obtained in the laboratory (Table 7). They were higher in July than in June and August. A lower mean infection level in July was related to the fall of the most infected leaves on some genotypes.

Effect of the resistance factor inherited from *P. deltoides* in the field. When considering the whole F_1, no significant effect was associated with the presence of R_1 in either June or July (Table 7). A tenuous effect was observed in August, which led to only 6% advantage for R_1 over r_1 genotypes in terms of rust colonization on the most infected leaf.

Effect of the resistance factor inherited from *P. trichocarpa* in the field. Significant relationships were evident between field and laboratory descriptors of resistance in both r_1 and R_1 groups of genotypes (Table 8). US is the only trait measured in the laboratory that was significantly linked to field susceptibility in all situations. Of the three *M. larici-populina* strains studied in the laboratory, significant field–laboratory relationships were most frequent with 98AG69.

Graphical display of the relationship between MAX1 and US_{98AG69} shows that the correlation was driven mostly by the difference between R_{US} and r_{US} genotypes, in both the absence and the presence of R_1 (Fig. 5). Indeed, presence of R_{US} produced a significant advantage for all three field descriptors: up to a 37% decrease of rust colonization on the most infected leaf in July

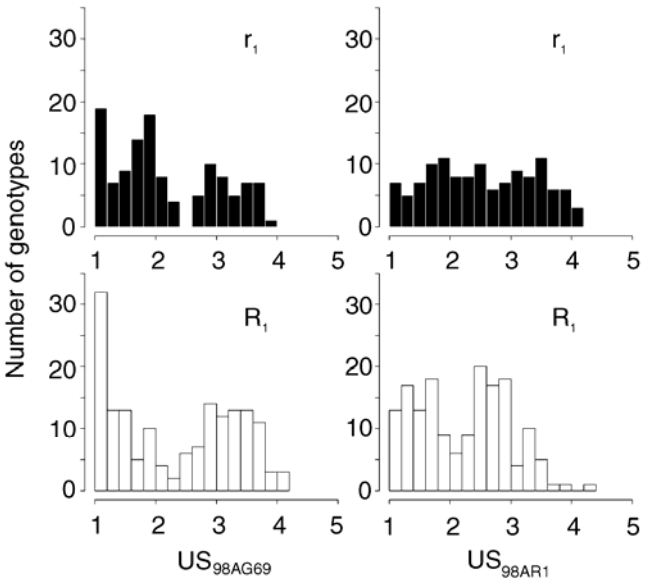

Fig. 3. Distribution of the genotypic means for uredinia size (US) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny inoculated with *Melampsora larici-populina* strains 98AG69 and 98AR1. Black and white histograms refer to the 122 r_1 and 162 R_1 genotypes, respectively.

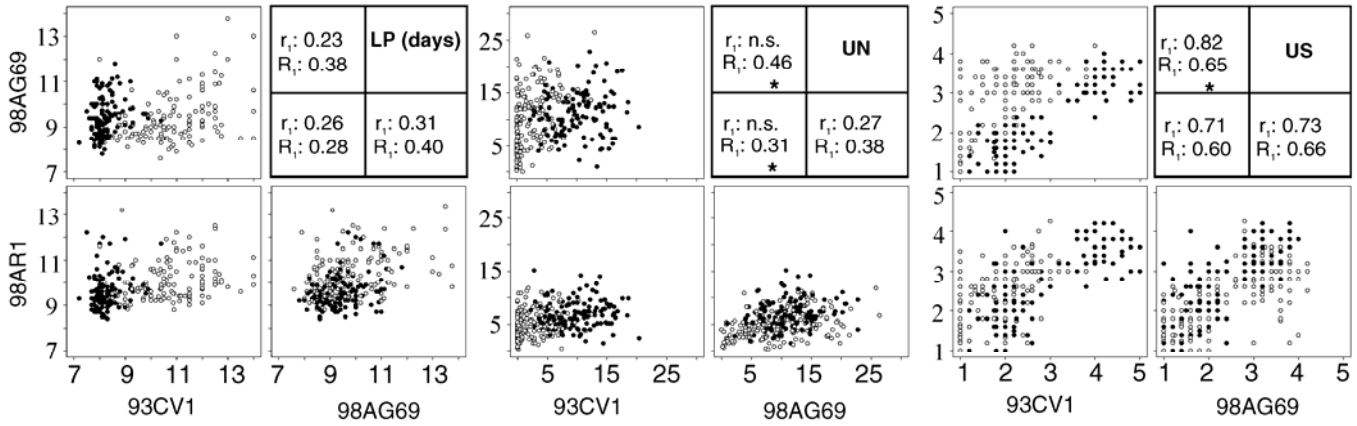

Fig. 2. Relationships between genotypic means for latent period (LP), uredinia number (UN) and uredinia size (US) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny inoculated with *Melampsora larici-populina* strains 93CV1, 98AG69, and 98AR1. The r_1 genotypes appear as black dots and R_1 genotypes appear as open circles. Spearman rank correlation coefficients are indicated separately for the 122 r_1 genotypes and the 162 R_1 genotypes. An asterisk indicates situations where r_1 and R_1 genotypes have significantly different correlation coefficients (non-overlapping 95% confidence intervals or presence of 0 in any confidence intervals); n.s. (nonsignificant) indicates a 95% confidence interval which includes zero.

(Table 9). Analysis of the relative advantage of R_1R_{US} genotypes over those possessing none or one of the two resistance factors shows that addition of R_1 was never useful in the field when R_{US} was already present, whereas R_1 always had significant beneficial effect in the absence of R_{US} (Fig. 6).

DISCUSSION

In previous studies using *M. larici-populina* strain 93CV1 in laboratory experiments, it was concluded that two resistance factors explain most of the observed variability for quantitative resis-

TABLE 6. Relative advantage (ΔR_{us}) of the 158 genotypes with $US_{98AG6} < 2.5$ (R_{us}) over the 126 genotypes with $US_{98AG69} > 2.5$ (r_{us}) in terms of latent period (LP), number of uredinia (UN), and uredinia size (US) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny inoculated with three *Melampsora larici-populina* strains[a]

	LP (days)				UN				US			
Strain	Mean r_{us}	Mean R_{us}	P_w	ΔR_{us} (%)	Mean R_{us}	Mean R_{us}	P_w	ΔR_{us} (%)	Mean r_{us}	Mean R_{us}	P_w	ΔR_{us} (%)[b]
93CV1	9.6	9.5	0.31	ns	6.1	5.5	*	–10	2.9	1.8	***	–38 (–60)
98AG69	8.7	10.2	***	+15	12.9	8.4	***	–35	3.3	1.6	***	–52
98AR1	9.7	10.2	***	+5	6.4	5.3	***	–17	3.1	1.9	***	–39

[a] P_w is the P value associated with the Wilcoxon rank-sum test of the significance of the difference between the means of R_{us} and r_{us} genotypes. P values below 5, 1, and 0.1% are represented by *, **, and ***, respectively; ns = nonsignificant.
[b] Value in parentheses indicated for US_{93CV1} was computed after conversion of individual US values into uredinial spore production values.

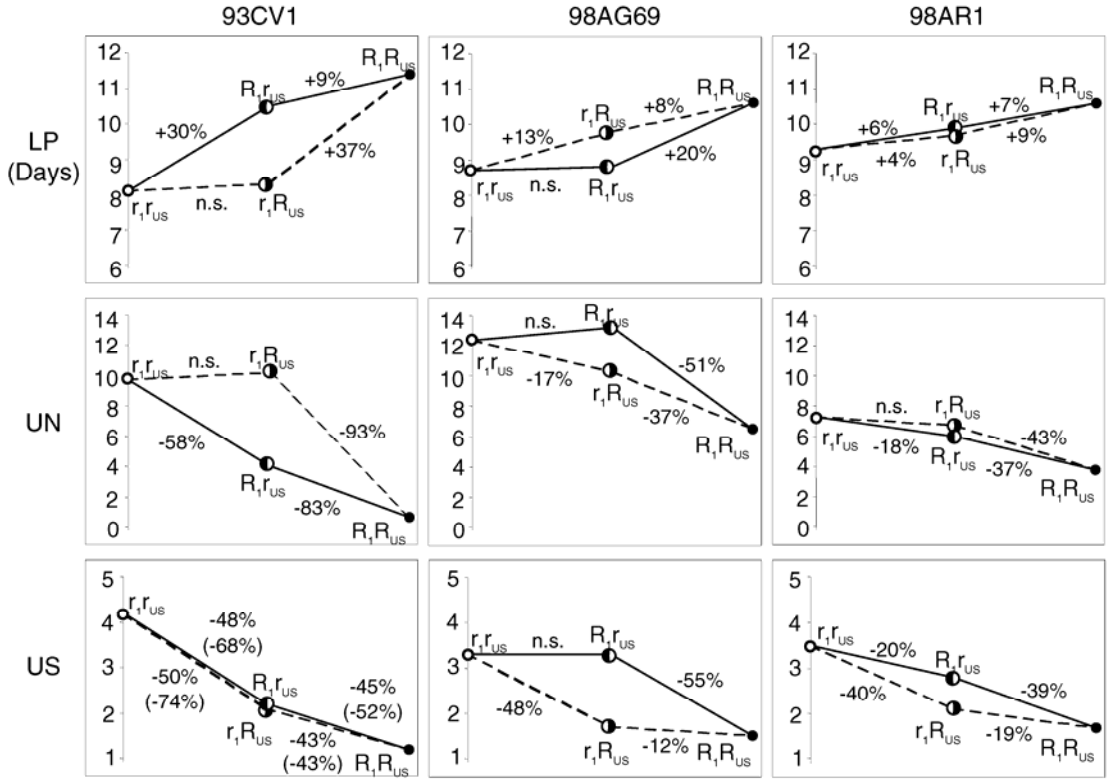

Fig. 4. Overall means of r_1r_{US}, R_1r_{US}, r_1R_{US}, and R_1R_{US} groups of genotypes for latent period (LP), uredinia number (UN), and uredinia size (US) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny inoculated with *Melampsora larici-populina* strains 93CV1, 98AG69, and 98AR1. n.s. = P value associated with the Wilcoxon rank-sum test of the significance of the difference between means of >5%. Values in parentheses indicated for US_{93CV1} were computed after transformation of individual US values into uredinial spore production values.

TABLE 7. Summary statistics and broad-sense heritabilities at the individual level (H^2) for three descriptors of field susceptibility to *Melampsora larici-populina* (MAX1, MAX2, and MAX3) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny, and relative advantage (ΔR_1) of the 162 R_1 genotypes over the 122 r_1 genotypes

	Mean	Q1–Q3[a]	Mean 101-74[b]	Mean 73028-62[c]	$H^2 \pm$ SD	Mean r_1	Mean R_1	P_w[d]	ΔR_1 (%)[e]
MAX1	4.4	4.0–4.7	3.2	2.5	0.33 ± 0.02	4.0	4.0	0.97	ns
MAX2	4.0	3.5–4.4	3.2	3.0	0.54 ± 0.02	4.1	4.0	0.29	ns
MAX3	4.8	4.5–5.2	3.2	3.3	0.38 ± 0.02	4.9	4.8	***	–3 (–6)

[a] First (Q1) and third (Q3) quartiles of mean values.
[b] Mean of the *P. trichocarpa* male parent 101-74.
[c] Mean of the *P. deltoides* female parent 73028-62.
[d] P_w is the P value associated with the Wilcoxon rank-sum test of the significance of the difference between the means of R_1 and r_1 genotypes. P values below 5, 1, and 0.1% are represented by *, **, and ***, respectively.
[e] ΔR_1 values in parentheses were computed after transformation of individual MAX values into percentages of leaf area covered with uredinia; ns = nonsignificant.

tance to that strain in a *P. deltoides* × *P. trichocarpa* F_1 progeny set (8,20). Even though these two factors appeared to have marked beneficial effects on several quantitative resistance components, the breeding potential of these factors for durable *M. larici-populina* resistance remained unknown. The present study explored this potential by addressing three important questions. (i) What are the respective levels of strain specificity of these two resistance factors? (ii) What is their influence on field resistance? (iii) Would breeding for durable resistance benefit from combining these resistance factors in a single genotype?

Reliability of the estimated effects. Biological significance of the estimated effects of both resistance factors is highly dependent on the measurement scales used to quantify *M. larici-populina* resistance. Effects computed for curvilinear traits US_{93CV1}, MAX1, MAX2, and MAX3 all were underestimating the effects computed after data transformation onto linear scales. Thus, the effects computed for US_{98AG69} and US_{98AR1}, two rust strains for which quantification of the relationship between US and uredinial spore production was not available, must be considered as lower limit values. Such distortions cannot be avoided when data are measured on arbitrary nonlinear ranking scales, or when data are transformed prior to statistical analysis (e.g., to comply with analysis of variance postulates).

It also must be considered that precision in the effects of both resistance factors depends on the quality of the two phenotypic predictors used to infer their presence or absence (i.e., R_1-mediated qualitative resistance for the one inherited from *P. deltoides*, and US_{98AG69} for R_{US} inherited from *P. trichocarpa*). Bimodality of the distribution of the genotypic means for US_{98AG69} was sufficiently clear to consider this phenotypic predictor as reliable. To evaluate the reliability of R_1 as an indicator of the quantitative resistance factor inherited from *P. deltoides*, a "residual" effect of R_1 itself must be considered. No evidence for such residual effect was observed, thereby supporting the hypothesis of a tight linkage between R_1 and a sensu stricto quantitative resistance factor. As Anderson previously cautioned (1), in many studies where authors claimed the presence of residual effects, the hypothesis that these effects may in fact result from quantitative resistance genes associated to the defeated gene by linkage or genetic drift cannot be excluded.

Strain specificity and field expression. This study confirmed that both resistance factors produce marked effects on some of the quantitative resistance components studied in the laboratory. However, this study highlighted significant levels of strain specificity for both factors, while their effectiveness in the field often was reduced compared with the laboratory observations.

The resistance factor inherited from *P. deltoides* and associated, either by linkage or pleiotropy, with qualitative resistance gene R_1 was known as having significant effect on LP, UN, and US with strain 93CV1 in the laboratory (8,20). When challenged by strain 98AR1, this factor showed significant but reduced effects on the three studied quantitative resistance components. Results obtained with strain 98AG69 were even more illustrative of the strong strain specificity of this resistance factor because a 12% decrease of UN was the only significant effect found. In the field, the only significant effect was a 6% benefit at the end of the study. This contrasts with previous results from Lefèvre et al. (20), who observed significant beneficial effects of the presence of R_1 on field resistance at two locations (R^2 = 82 and 77%) in a subset of 85 genotypes from the F_1 family studied here. However, at the time of that previous study, no data were available on the racial composition of the field inoculum and on the fact that virulence 1 was conferring the ability to overcome R_1. In this previous study, the proportion of strains lacking virulence 1 was potentially great enough for the observed effect to be due to a significant decrease in the proportion of the inoculum able to infect R_1 genotypes. Our results may indicate that the proportion of strains lacking virulence 1 needs to be much higher than 20% for R_1 qualitative resistance to influence field resistance. Absence of any effect associated with defeated qualitative resistance gene R_1 in the field is comparable with a recent report from Woo et al. (46) on the absence of a residual effect of a defeated resistance gene to *M. medusae* on field resistance of *P. trichocarpa* × *P. deltoides* hybrids infected with *Melampsora* × *columbiana*. Discrepancies between field and laboratory results possibly result from significant differences of host physiological status and environment characteristics between both experimental conditions. Pre- and postinoculation temperatures, leaf maturity, and shoot age, for example, have been identified as key parameters influencing quantitative resistance to *M. larici-populina* in poplars (5,6,39). Uncontrolled variability for these parameters certainly accounts for

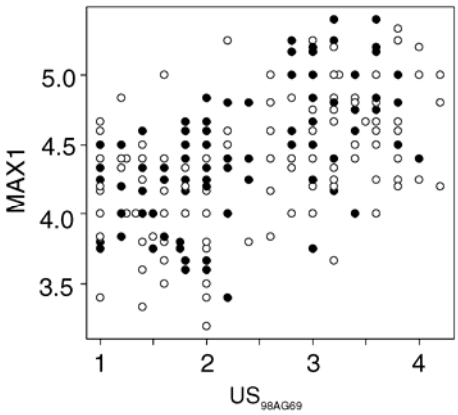

Fig. 5. Relationship between genotypic means for uredinia size with *Melampsora larici-populina* strain 98AG69 (US_{98AG69}) and field susceptibility (MAX1) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny. The 122 r_1 genotypes appear as black dots and the 162 R_1 genotypes appear as open circles.

TABLE 8. Spearman rank correlation coefficients between genotypic means for descriptors of susceptibility to *Melampsora larici-populina* in the field (MAX1, MAX2, and MAX3) and in the laboratory (latent period [LP], uredinia number [UN], and uredinia size [US] with three pathogenic strains: 93CV1, 98AG69, and 98AR1) for the 122 r_1 genotypes and the 162 R_1 genotypes in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny[a]

			LP			UN			US		
Field	MAX2	MAX3	93CV1	98AG69	98AR1	93CV1	98AG69	98AR1	93CV1	98AG69	98AR1
r_1											
MAX1	0.75	0.54	ns	–0.51	ns	ns	ns	ns	0.55	0.62	0.56
MAX2	…	0.67	ns	–0.57	ns	ns	0.31	ns	0.62	0.59	0.58
MAX3	…	…	ns	–0.39	ns	ns	ns	ns	0.49	0.61	0.42
R_1											
MAX1	*0.56	0.38	ns	–0.46	*–0.27	*0.36	*0.37	*0.32	0.45	0.53	0.48
MAX2	…	0.58	ns	*–0.38	*–0.31	*0.35	0.26	*0.36	*0.38	*0.45	0.47
MAX3	…	…	ns	–0.25	ns	ns	ns	ns	0.32	0.33	0.23

[a] An asterisk indicates a situation where r_1 and R_1 genotypes exhibit significantly different correlation coefficients (non-overlapping of the 95% confidence intervals or presence of 0 in any of these two confidence intervals); ns (nonsignificant) indicates a 95% confidence interval which includes zero.

the lower heritability estimates computed for field resistance. Newcombe (28) observed a similar reduction of clone-mean heritability for *M. medusae* from 0.91 to 0.64 when comparing uredinial size in a whole-plant growth-room bioassay and in a field experiment, respectively. Measuring other components of field resistance at broader observation scales (e.g., whole foliage) possibly would lead to different results. Moreover, analysis of the combined effects of both resistance factors, which is discussed below, showed that the situation is complex: the genetic background exerts a strong influence on the effectiveness of R_1.

The resistance factor inherited from *P. trichocarpa*, R_{US}, previously was shown to produce a sharp decrease of US with strain 93CV1 in the absence of R_1 (8). The present study showed that this factor exhibits a wider range of action. In the laboratory, it is effective against all three studied strains, in both the absence and the presence of R_1. In addition, it influences not only US but also LP and UN, despite significant levels of strain specificity. It is also effective in the field, where its maximum effect was a 37% decrease of rust colonization on the most infected leaf.

Combined effects. Genotypes possessing both resistance factors always were significantly more resistant than those possessing one or zero factors in the laboratory, even in situations where one of the two factors had no significant effect when alone. Such beneficial interactions warrant further analysis because they have strong implications for breeding. They support the idea of pyramiding "weak" resistance genes to achieve better levels of resistance. These synergistic effects, also referred to as quantitative complementation, have been observed on the rice–bacterial blight pathosystem when pyramiding several defeated qualitative resistance genes (14,22,23,37). More precisely, we are considering the possibility that some resistance factors may be effective only when associated with at least one other factor. Thus, it is crucial to take the genetic background into account when evaluating effectiveness of resistance factors. Mingeot et al. (26) discovered a similar situation when studying the residual effect of powdery mildew race-specific resistance gene *Pm4b* in two susceptible winter wheat genetic backgrounds. They detected no residual effect of *Pm4b* in one of the two backgrounds, whereas this gene produced a significant effect in the other background. Contributions of the genetic background to the efficiency of the resistance genes indicates that breeding programs would not have to involve exclusively parents with high levels of quantitative resistance. Importance of the genetic background on the effectiveness of resistance genes also is evident from the negative transgressions that are observed when comparing *M. larici-populina* resistance of the F_1 hybrid pedigree with that of its parents. Such negative transgressions have been observed when studying field resistance of *P. deltoides* × *P. trichocarpa* hybrids to *M. larici-populina* (20), and herbivore resistance of *P. angustifolia* × *P. fremontii* hybrids (45).

The situation was slightly different in the field, where the resistance factor associated with R_1 had significant effect only in the absence of R_{US}. The effect of R_{US} either negated or masked the effect of R_1.

One important issue is the genetic relationship between both resistance factors. Are they allelic versions of the same locus? Do they belong to different loci interacting in an epistatic manner? Ongoing genotyping will help answer these questions.

Poplar–*M. larici-populina* coevolution. US appeared as the best laboratory predictor of field resistance. Based on an experiment involving strain 93CV1, Dowkiw et al. (8) showed that sporulation intensity can vary from 500 to 20,000 urediniospores/uredinia in the studied F_1 progeny. Such range of variation should have more impact on the polycyclic progress of *M. larici-populina* field epidemics than a few-day variation in LP. Given its epidemiological significance, US could be used in coevolution experiments. We observed significant levels of strain specificity for both resistance factors, which means adaptation of the pathogen will occur, but how quickly? Several authors have reported field and laboratory techniques to measure pathogen adaptation to quantitative resistance in different pathosystems (3,18,44). Similar experiments could be conducted using genotypes with contrasting US_{98AG69} from this F_1 progeny set to study *M. larici-populina* adaptability to R_{US}. Combining r_1R_{US} and R_1R_{US} genotypes in such experiment would allow an assessment of whether R_1 can become beneficial once R_{US} is defeated.

The strain that was best correlated with field resistance, 98AG69, was isolated in a cultivated monoclonal stand of *P. deltoides* × *P. trichocarpa* cv. Beaupré, 300 km from Orléans, 2 years before the field study. Because this strain belongs to pathotype 1-3-4-5-7, which was predominant in the field experiment, questions are raised about the speed of diversification of this pathotype and of *M. larici-populina* populations in general.

Finally, the two resistance factors studied here originate from two North American *Populus* spp. which did not coevolve with *M. larici-populina*, identified in North America only 10 years ago. As discussed by Tabor et al. (42), a distinction should be made between such "exapted" resistances and those that are derived from continued host–pathogen coevolution. The latter can be found in the Eurasian *P. nigra* species; therefore, more emphasis is being put on that species and on Euramerican *P. deltoides* × *P. nigra* hybrids at INRA.

TABLE 9. Relative advantage (ΔR_{us}) of the 158 genotypes with $US_{98AG69} < 2.5$ (R_{us}) over the 126 genotypes with $US_{98AG69} > 2.5$ (r_{us}) in terms of field susceptibility to *Melampsora larici-populina* (MAX1, MAX2, and MAX3) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny[a]

	Mean r_{us}	Mean R_{us}	P_w	ΔR_{us} (%)[b]
MAX1	4.7	4.2	***	–11 (–23)
MAX2	4.4	3.7	***	–16 (–37)
MAX3	5.0	4.7	***	–6 (–13)

[a] P_w is the P value associated with the Wilcoxon rank-sum test of the significance of the difference between the means of R_{us} and r_{us} genotypes. P values below 5, 1, and 0.1% are represented by *, **, and ***, respectively.

[b] ΔR_{us} values in parentheses were computed after transformation of individual MAX values into percentages of leaf area covered with uredinia.

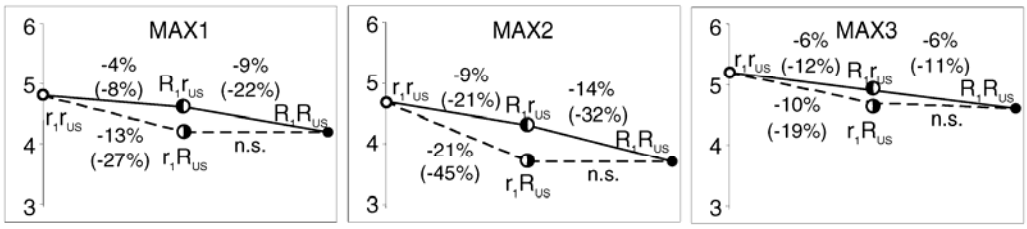

Fig. 6. Overall means of r_1r_{US}, R_1r_{US}, r_1R_{US}, and R_1R_{US} groups of genotypes for three field susceptibility descriptors (MAX1, MAX2, and MAX3) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny. n.s. = P value associated with the Wilcoxon rank-sum test of the significance of the difference between means of >5%. (There are two kinds of relative differences: the ones that are not parenthesized and the ones that are parenthesized.) Relative differences between the means of the four groups of genotypes were computed after transformation of individual MAX values into percentages of leaf area covered with uredinia.

ACKNOWLEDGMENTS

Financial support was provided by grants from INRA, Région Centre, and the French Ministry for Agriculture and Fisheries. We thank J. Pinon and the Forest Pathology Laboratory of INRA Nancy, who provided the inoculum used in the laboratory and who characterized the racial composition of the field inoculum; D. Lacan, P. Poursat, and their collaborators at the Unité Expérimentale of INRA Orléans, as well as F. Puel, for excellent technical assistance; and V. Jorge, A. Cruickshank, P. Frey, and two anonymous reviewers for their valuable comments on the manuscript.

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Erratum

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In the manuscript entitled "Characterization of Two Major Genetic Factors Controlling Quantitative Resistance to *Melampsora larici-populina* Leaf Rust in Hybrid Poplars: Strain Specificity, Field Expression, Combined Effects, and Relationship with a Defeated Qualitative Resistance Gene" by A. Dowkiw and C. Bastien (Phytopathology 94:1358-1367), the caption for Figure 6 is incorrect. The correct caption should read as follows. Overall means of r_1r_{US}, R_1r_{US}, r_1R_{US}, and R_1R_{US} groups of genotypes for three field susceptibility descriptors (MAX1, MAX2, and MAX3) in a 284 full-sib *Populus deltoides* × *P. trichocarpa* F_1 progeny. n.s. = *P* value associated with the Wilcoxon rank-sum test of the significance of the difference between means of >5%. Parenthesized relative differences between the means of the four groups of genotypes were computed after transformation of individual MAX values into percentages of leaf area covered with uredinia.