# Association between Septoria tritici Blotch, Plant Height, and Heading Date in Wheat

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## ABSTRACT

**The relationship between resistance to Septoria tritici blotch with plant height and heading date has been in most cases attributed to genetic associations. More efficient selection for higher levels of quantitative resistance may result if the nature of the association between susceptibility with earliness and shortness can be determined. Genetic resistance to Septoria tritici blotch and its relationships with plant height and heading date were recorded in 50 Argentinean wheat (*Triticum aestivum* L.) cultivars in three environments (two in the field and one in the greenhouse) with one virulent isolate of *Mycosphaerella graminicola* (Fuckel) Schroeter, in Cohn (anamorph *Septoria tritici* Rob. ex Desm.). Furthermore, a set of 16 cultivars was tested with seven isolates of *M. graminicola* in the greenhouse at the adult stage. Cultivars varied greatly in resistance to the disease and plant material was identified with moderate to high levels of resistance to several isolates. The field and greenhouse experiments demonstrated no evidence of genetic associations between plant height, heading date, and resistance, indicating that selection of early and short lines with high levels of quantitative resistance is possible. The relationships between those traits were mainly caused by environmental and epidemiological factors, which indicates that management of cultivars should be optimized to minimize these associations.**

*Mycosphaerella graminicola* (Fuckel) Schroeter, in Cohn is an important disease in many wheat-producing areas of the world and causes significant yield losses (King et al., 1983; Eyal et al., 1985, 1987; Van Ginkel and Rajaram, 1993). It is a major problem in regions characterized by a temperate, wet environment during the growing season (Eyal et al., 1987). Breeding for resistance is the most economical approach to control the disease. Resistance controlled by one major gene was identified in some plant materials (Rillo and Caldwell, 1966; Rosielle and Brown, 1979; Wilson, 1979; Lee and Gough, 1984). Resistance based on several genes also was identified (Rosielle and Brown, 1979). Jlibene and El Bouami (1995) indicated that several components of the partial resistance to Septoria tritici blotch also may be controlled by only one or a few genes that could be combined into the same genetic background by crossing. Several quantitative studies have indicated the presence of general combining ability, although specific combining effects are also present (Van Ginkel and Scharen, 1987; Danon and Eyal, 1990; Jlibene et al., 1994; Simón and Cordo, 1997, 1998).

In Argentina, breeders classify most commercially grown cultivars in the range of moderately resistant to susceptible, suggesting the presence of quantitative, nonspecific resistance in some of them, although isolate-specific resistance also could be present. However, an accurate characterization is needed. Specific interaction between cultivars and isolates of *M. graminicola* has been reported (Van Ginkel and Scharen, 1987; Danon and Eyal, 1990; Jlibene et al., 1994; Kema et al., 1996a, 1996b, 1997; Simón and Cordo, 1997, 1998; Brown et al., 2001).

One of the most complicating factors in determining resistance to Septoria tritici blotch is the interaction between resistance, plant height, and heading date. Several scientists reported increased disease severity in earlier heading and shorter cultivars (Eyal et al., 1987; Van Beuningen and Kohli, 1990; Camacho Casas et al., 1995). Baltazar et al. (1990) suggested a genetic association between shortness and susceptibility, while Eyal (1981) and Rosielle and Boyd (1985) assumed a genetic association between earliness and susceptibility. Arama et al. (1999) reported no influence of heading date when cultivars were evaluated at the same development stage under similar weather conditions. From several investigations it is not clear if these associations are due to genetic or epidemiological factors.

The aims of this work were to determine (i) the resistance in a broad range of wheat cultivars grown in Argentina at the seedling and adult stages to one virulent isolate of *Mycosphaerella graminicola*; (ii) the relationship between resistance to *M. graminicola*, plant height and heading date in those cultivars; and (iii) the resistance in a set of wheat cultivars at the adult stage using several Argentinean isolates.

## MATERIALS AND METHODS

### Field Experiments

Fifty cultivars of wheat were tested in field experiments in 1998 and 2000 at the Estacion Experimental Facultad de Ciencias Agrarias y Forestales, Los Hornos, Argentina. The cultivars differed in plant height, heading date, and resistance to Septoria tritici blotch, and represented the range in these characteristics for cultivars grown in Argentina in 1998. 'Klein Toledo', an old cultivar, also was included because it is moderately resistant to Septoria tritici blotch (Gieco et al., 2004).

The field experiments were isolated 300 m from other wheat experiments in both years. For each experiment, cultivars were

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**Abbreviations:** AUDPC, area under disease progress curve; GS, growth stage; PDA, potato dextrose agar.

arranged in a randomized block design with three replicates separated by 3 m of oat (*Avena sativa* L.) to avoid interplot interference. Plots, also separated by two rows of oat, consisted of three 3 m long rows. The experiments were sown on 24 June 1998 (emergence on 5 July 1998) and 5 July 2000 (emergence on 23 July 2000). At sowing, both experiments were fertilized with 50 kg ha$^{-1}$ of P as ammonium diphosphate and 100 kg ha$^{-1}$ N as urea.

The Argentinean isolate of *M. graminicola* named IPO 99013 by the former IPO-DLO, now part of the Plant Research International, Wageningen, the Netherlands, was grown on Petri-dishes of potato dextrose agar (PDA) 2% (Plant Pathologist's Pocketbook, 1974) and transferred to malt extract agar (Plant Pathologist's Pocketbook, 1974) at 19°C with 12 h alternating light and dark cycles. The isolate was selected according to a previous greenhouse test with 5 cultivars and 10 isolates, where isolate 99013 showed contrasting results between cultivars (unpublished data). Inoculum was prepared by aseptically scraping sporulating colonies with a scalpel and suspending conidia in deionized water. The conidial suspension was adjusted for both years and both growth stages to 5 × 10$^6$ spores mL$^{-1}$. Tween 20 (Polyoxyethylene sorbitan monolaurate, Sigma-Aldrich) at 0.5 mL L$^{-1}$ was added as a surfactant. Plots were inoculated at two-leaf seedling stage (GS 12, Zadoks et al., 1974) and at tillering stage (GS 22) in both years with a hand pump. For each plot, 700 mL of inoculum were sprayed at each inoculation stage. After inoculations, plants were kept moist by spraying with water with a sprayer for applying pesticides, several times a day for 3 d. Plants were sprayed with Plantvax (oxycarboxin; 5,6 dihydro-2-methyl-*N*-phenyl-1, 4 oxathiin-3-carboxamide 4,4 dioxide; Dhanuka Group, New Dehli, India) when the first symptoms of leaf rust (caused by *Puccinia triticina* Eriks) appeared.

Percentage of necrosis and pycnidial coverage were visually estimated in seedlings on the second leaf at 26 d after the first inoculation at the same time for all cultivars. Evaluations started when Septoria tritici blotch was well expressed in the known susceptible cv. Buck Ombú, used as a control. Evaluations also were done at booting (GS 49), milk development (GS 70), and early dough (GS 83) stages. The three upper leaves of each plant (flag leaf, flag leaf-1, flag leaf-2) were evaluated at the latter three stages (adult stages). Twenty plants were rated in the central row of each plot at each growth stage. Plant height, measured from the soil to the flag leaf and heading date, the time from plant emergence to when 50% of the spikes emerged from the boot, also were recorded in each plot. Height to flag leaf was measured instead of tip of ear because Septoria tritici blotch usually progresses up to the flag leaf in the Argentina growing wheat area and it was not evaluated in the ears. An area under disease progress curve (AUDPC) for each cultivar and each treatment was calculated to summarize the progress of the disease, according to the formula of Shaner and Finney (1977). Cultivars were considered resistant when pycnidial coverage was up to 20%, moderately resistant between 21 and 40%, moderately susceptible between 41 and 60%, and susceptible with more than 60%.

Weather conditions (precipitation; minimum, maximum, and mean relative humidity; minimum, maximum, and mean daily temperature; and mean daily radiation) were recorded at a meteorological station situated 100 m from the experiments. In 1998, measurements of daily global radiation were not started until 3 September due to failure of the equipment. The first inoculation and the final evaluation were on 17 July and 22 Nov. 1998 and on 10 Aug. and 5 Dec. 2000, respectively. For these periods, mean daily temperatures were 13.9 and 14.4°C, mean relative humidity 85 and 83%, mean global radiation 4537 and 4100 W m$^{-2}$ d$^{-1}$, and total precipitation 198 and 388 mm for 1998 and 2000, respectively. Long-term averages mean temperatures for the period July–November and August–December are 14.3 and 16.8°C, respectively, and long-term precipitation for the same periods are 393 and 409 mm.

Data were transformed using arcsine square root and analyzed by a combined ANOVA for both years for a randomized block design. They were transformed to adjust them to a normal distribution and stabilize the residual variance. Cultivars and years were considered as fixed effects. Because of some significant cultivar × experiment interactions, a separate analysis for each year was also performed. Multiple linear and nonlinear regression analyses were performed with pycnidial coverage as the dependent variable and heading date and plant height as the independent variables. Models were generated with SAS (SAS Inst., 1989). Best models were those with the highest $R^2$, fewest number of parameters, and lowest Mallows Cp statistics. Data are presented in the tables as the backtransformed values.

## Greenhouse Experiments

### Experiment 1

The 50 wheat cultivars used in the field experiments were sown in a randomized block design with three replications in a growth chamber under controlled conditions at the Department of Plant Sciences, Wageningen University, the Netherlands, in 1999. Eight seeds per cultivar per replication were placed in 1-L plastic pots containing a sandy soil and fertilized with 100 kg N ha$^{-1}$ as urea and 50 kg P as ammonium diphosphate. Temperature was kept at 7 to 9°C, relative humidity at 70 to 75%, and photoperiod at 10 h. At tillering (GS 22), six to eight plants were transplanted to 10-L plastic pots with the same soil and fertilizer application and transferred to a greenhouse at 15 to 18°C, 70% relative humidity, and 13 to 14 h photoperiod, after an adaptation period of 3 d at 12°C to simulate similar conditions to those of the growing wheat area in Argentina. Pots were watered each 2 or 3 d with tap water as required to keep the soil wet.

At heading (GS 59) plants were inoculated with the same isolate (IPO 99013) as the one used in field experiments. Inoculation was done with a hand pump saturating the upper two leaves. Plants were inoculated in three groups according to their heading dates (from 80.5 to 88.5, 89 to 94.5, and 95 to 100 d to heading) and all were maintained in the same environmental conditions after inoculation. Plants were covered with a transparent plastic tent to maintain humidity at very high levels (>95%) for 72 h. After that, temperature was maintained between 17 and 22°C and relative humidity was kept between 75 and 85%. Two humidifiers were placed in the greenhouse to maintain those humidity levels. Although conditions were maintained as stable as possible, the control cultivars Klein Volcán (classified by breeders as moderately resistant) and Buck Ombú (susceptible) were planted at three different dates and inoculated in the three groups to detect if any environmental variation was influencing the results. Percentage of necrosis and pycnidial coverage were evaluated visually on the two upper leaves (flag leaf and flag leaf-1) of 10 to 15 main tillers per pot 24 d after inoculation (GS 83). Data were transformed using arcsine square root to adjust them to a normal distribution and to stabilize the residual variance and analyzed by ANOVA for randomized block designs. A preliminary ANOVA including the controls inoculated in the three groups differing in heading date was done. Controls did not show differences between the three inoculation groups. For that reason, values were not adjusted, and the final ANOVA was done without the controls. Multiple

**Table 1. Mean squares for the combined analysis of variance of pycnidial coverage percentage caused by *Mycosphaerella graminicola* at four growth stages, for the area under disease progress curve (AUDPC), plant height, and days to heading in 50 Argentinean wheat cultivars in two field experiments.**

| Source of variation | df | Seedlings | GS49‡ | GS70 | GS83 | AUDPC | Plant height | Days to heading |
|---|---|---|---|---|---|---|---|---|
| Cultivars | 49 | 378.4 ($P < 0.001$)† | 31.1 ($P < 0.001$) | 262.9 ($P < 0.001$) | 519.0 ($P < 0.001$) | 313 372 ($P < 0.001$) | 205.2 ($P < 0.001$) | 197.2 ($P < 0.001$) |
| Experiments | 1 | 646.3 ($P < 0.001$) | 1068 ($P < 0.001$) | 24 003 ($P < 0.001$) | 25 622 ($P < 0.001$) | 25 053 300 ($P < 0.001$) | 2775 ($P < 0.001$) | 1236 ($P < 0.001$) |
| Cultivars × Experiments | 49 | 126.2 ($P < 0.001$) | 24.16 ($P < 0.001$) | 190.2 ($P < 0.001$) | 216.1 ($P < 0.001$) | 168 245 ($P < 0.001$) | 25.6 ($P < 0.08$) | 16.0 ($P < 0.001$) |
| Error | 198 | 58.4 | 8.19 | 23.8 | 57.4 | 19 173 | 19.0 | 1.79 |

† $P > F$.
‡ GS 49, GS 70, GS 83 (growth stages; Zadoks et al., 1974).

linear and nonlinear regression analyses with pycnidial coverage as the dependent variable and heading date and plant height as the independent variables also were conducted. Data are presented in the tables as the backtransformed values.

### Experiment 2

Sixteen cultivars—chosen according to differences in resistance to Septoria tritici blotch, heading date, and plant height from the field experiments—were sown in a factorial randomized block design with two replications in a growth chamber under controlled conditions at the Department of Plant Science, Wageningen University, the Netherlands, in 1999. Factors were the 16 cultivars and 7 isolates of *M. graminicola*. Three isolates (IPO 92064, 92065, and 93014) were selected because they had shown differences in virulence with five genotypes in a previous screening (Simón et al., 2001) and four others (IPO 99013, 99014, 99015, and 99016) because they were new isolates to be tested. Eight seeds per treatment per replication were placed in 1-L pots with the same soil and fertilizer regimen as in the previous greenhouse experiment. Conditions in the growth chamber and after transplanting to the greenhouse were similar to Experiment 1. Pots were watered each 2 or 3 d.

At heading (GS 59), plants were inoculated with the seven Argentinean isolates. Isolates were grown on Petri dishes of Campbell V8 juice agar for 3 d and transferred to yeast–glucose liquid medium (glucose, 10 g $L^{-1}$ and yeast extract, 30 g $L^{-1}$). Flasks were shaken for 5 d at 18°C. Spores were resuspended in distilled water and the concentration adjusted to $1 \times 10^7$ spores $mL^{-1}$. Tween 20 (0.5 mL $L^{-1}$) was added as a surfactant. Plants were inoculated in three groups according to their heading date (from 84 to 88.5, 89 to 94.5, and 95 to 100 d to heading). The same cultivars as in the Experiment 1 were used as controls at each inoculation date and inoculated with each of the seven isolates. Plants were covered with a transparent plastic tent to maintain humidity at very high levels (>95%) for 72 h. After that, the temperature in the greenhouse was between 17 and 22°C and the relative humidity was kept between 75 and 85% using humidifiers.

Percentage of necrosis and pycnidial coverage were evaluated 24 d after inoculation (GS 83) on the two upper leaves of 10 to 15 main tillers per pot. Data were transformed using arcsine square root to adjust them to a normal distribution and stabilize the residual variance and analyzed by ANOVA for factorial experiments. Data are presented in the tables as the backtransformed values. Controls did not show significant differences between the three inoculation groups, and for that reason values were not adjusted.

## RESULTS

### Field Experiments

Because of greater precipitation, environmental conditions were more conducive to the development of the disease in 2000. The combined analysis of variance for both years showed that pycnidial coverage was significantly different ($P < 0.001$) for cultivars, experiments, and the cultivar × experiment interaction at all four growth stages. There were also significant differences between cultivars and experiments in AUDPC, days to heading and plant height. The cultivar × experiment interaction was significant for the AUDPC ($P < 0.001$) and days to heading ($P < 0.001$) but not for plant height ($P = 0.08$) (Table 1). Because of the significant experiment effects and cultivar × experiment interaction, a separate analysis was performed for each experiment (1998 and 2000). Cultivars were significant for all traits in both years ($P < 0.001$) (Table 2).

Percentage pycnidial coverage was higher in 2000 than in 1998 in the seedling stage (Table 1 and 3). Mean percentage of pycnidial coverage across cultivars with isolate IPO 99013 ranged from 2.13 to 77.5% in 1998 and from 19.5 to 78.8% in 2000 (i.e., from resistant to susceptible) (Table 3). In spite of some variation in cultivar behavior between experiments, 'Klein Estrella' and Klein Volcán showed relatively high levels of resistance in both years. Some other cultivars (Klein Dragón, Buck Chambergo, ProINTA Puntal, Klein Don Enrique, Buck

**Table 2. Mean squares for the separated analysis of variance for 2 yr of pycnidial coverage percentage caused by *Mycosphaerella graminicola* at four growth stages, for the area under disease progress curve (AUDPC), plant height, and days to heading in 50 Argentinean wheat cultivars in two field experiments.**

| | | Pycnidial coverage | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Seedlings | | GS49‡ | | GS70 | | GS83 | | AUDPC | | Plant height | | Days to heading | |
| Source of variation | df | 1998 | 2000 | 1998 | 2000 | 1998 | 2000 | 1998 | 2000 | 1998 | 2000 | 1998 | 2000 | 1998 | 2000 |
| | | % | | | | | | | | | | | | | |
| Cultivars† | 49 | 330.4 | 223.4 | 13.12 | 42.15 | 44.31 | 408.9 | 285.1 | 450.1 | 63 157 | 418 459 | 126.6 | 104.1 | 117.6 | 95.6 |
| Error | 98 | 60.0 | 35.0 | 4.14 | 11.80 | 10.08 | 35.63 | 57.13 | 58.60 | 11 320 | 27 094 | 14.5 | 17.5 | 1.63 | 1.80 |

† Cultivars were significant at $P < 0.001$ for all traits.
‡ GS 49, GS 70, GS 83 (growth stages; Zadoks et al., 1974).

Fogón, Buck Panadero) showed moderate level of resistance.

In all adult stages during which observations were made, average percentage of pycnidial coverage across cultivars was higher in 2000 than in 1998 (Table 4). The same difference between experiments was found for the AUDPC. However, some cultivars showed similar values for both experiments causing the cultivar × experiment interaction. For the AUDPC those cultivars were: Cooperación Calquín, Cooperación Millán, Granero INTA, Klein Don Enrique, Klein Dragón, Klein Estrella, Klein Pegaso, Klein Volcán, and ProINTA Federal. At GS 49 and GS 70, disease levels were very low in 1998. The means of the three upper leaves fluctuated between 0.0 and 2.58 in 1998 and 0.04 and 8.60 in 2000, 0.31 and 13.2 in 1998 and 0.76 and 53.5 in 2000, and 10.5 and 78.0 in 1998 and 22.3 and 94.0 in 2000 at GS 49, GS 70, and GS 83, respectively. The AUDPC values fluctuated between 123 and 718 and 274 and 1583 in 1998 and 2000, respectively.

Septoria tritici blotch always reached the flag leaf at GS 83, although Klein Dragón, Klein Estrella, Klein Volcán, Cooperación Millán, and Granero INTA showed very low values on that leaf in both years (data not shown). Those cultivars also showed moderate levels of resistance in both field experiments. The old cultivar Klein Toledo along with ProINTA Quintal also were moderately resistant to Septoria tritici blotch (Table 4).

Pycnidial coverage percentages at the seedling and adult stages were correlated. The correlation was higher in 2000 ($r = 0.68$, $P < 0.001$, $n = 50$) than in 1998 ($r = 0.26$, $P = 0.06$, $n = 50$). Klein Estrella, Klein Volcán, and Klein Dragón, which showed the best levels of resistance at the seedling stage, also showed low pycnidial coverage in the adult stage with isolate IPO 99013. Most susceptible cultivars in the seedling stage were also susceptible in the adult stage. Although statistically significant, the correlation coefficients were low because cultivars such as Cooperación Millán and Granero INTA showed moderate levels of resistance in the adult stage but were more susceptible in the seedling stage. Some other cultivars such as Buck Chambergo with moderate levels of resistance in seedlings were more susceptible in the adult stage, especially in 2000. Correlation coefficients between percentage necrosis and pycnidial coverage were 0.75, 0.70, 0.81, and 0.79 in 1998 and 0.78, 0.93, 0.86, and 0.81 for 2000 at seedling stage, GS 49, GS 70, and GS 83, respectively (significant at $P < 0.001$) (data not shown).

**Table 3. Pycnidial coverage percentage (backtransformed values) caused by *Mycosphaerella graminicola* in seedlings of 50 Argentinean wheat cultivars in two field experiments.**

| | Pycnidial coverage | | |
|---|---|---|---|
| Cultivars† | 1998 | 2000 | Avg. |
| | | % | |
| Klein Estrella | 2.13 | 25.0 | 13.6 |
| Klein Volcán | 2.47 | 28.2 | 15.3 |
| Klein Dragón | 36.0 | 19.5 | 27.7 |
| Buck Chambergo | 25.3 | 39.2 | 32.2 |
| ProINTA Puntal | 18.2 | 47.7 | 32.9 |
| Klein Don Enrique | 49.1 | 21.8 | 35.4 |
| Buck Fogón | 29.0 | 42.0 | 35.5 |
| Buck Panadero | 30.4 | 41.7 | 36.0 |
| Buck Poncho | 36.5 | 45.8 | 41.1 |
| Thomas Chapelco | 37.8 | 44.7 | 41.2 |
| Klein Cobre | 37.5 | 47.4 | 42.4 |
| ProINTA Pigüe | 35.5 | 50.6 | 43.0 |
| Klein Toledo | 33.1 | 55.0 | 44.0 |
| Cooperación Malambo | 41.3 | 47.2 | 44.2 |
| ProINTA Federal | 54.3 | 34.7 | 44.5 |
| ProINTA Imperial | 31.7 | 58.3 | 45.0 |
| Cooperación Calquín | 44.9 | 46.6 | 45.7 |
| Buck Charrúa | 39.6 | 54.4 | 47.0 |
| ProINTA Granar | 54.6 | 39.5 | 47.0 |
| Klein Pegaso | 53.7 | 41.1 | 47.4 |
| Buck Arrayán | 52.5 | 48.3 | 50.4 |
| Buck Candil | 50.9 | 50.1 | 50.5 |
| Thomas Aconcagua | 50.6 | 50.6 | 50.6 |
| Buck Pronto | 51.5 | 50.1 | 50.8 |
| Granero INTA | 62.0 | 40.3 | 51.1 |
| Bonaerense Pericón | 50.7 | 51.8 | 51.2 |
| Buck Ombú | 47.8 | 55.2 | 51.5 |
| ProINTA Super | 53.8 | 49.3 | 51.6 |
| ProINTA Cinco Cerros | 41.0 | 63.1 | 52.0 |
| ProINTA Quintal | 43.9 | 61.2 | 52.6 |
| Klein Brujo | 52.8 | 54.1 | 53.4 |
| Cooperación Millán | 64.9 | 43.3 | 54.1 |
| Cooperación Maipún | 47.7 | 62.2 | 54.9 |
| ProINTA Guazú | 55.9 | 55.0 | 55.4 |
| Cooperación Nahuel | 56.6 | 54.9 | 55.7 |
| Klein Cacique | 52.5 | 61.7 | 57.1 |
| Klein Granador | 56.0 | 59.0 | 57.5 |
| ProINTA Elite | 59.7 | 56.2 | 57.9 |
| Klein Centauro | 55.4 | 61.4 | 58.4 |
| ProINTA Bonaerense Cauquén | 59.8 | 57.0 | 58.4 |
| Klein Orión | 53.7 | 63.3 | 58.5 |
| Buck Catriel | 56.8 | 62.7 | 59.7 |
| ProINTA Real | 53.7 | 70.8 | 62.2 |
| ProINTA Bonaerense Redomón | 61.3 | 63.3 | 62.3 |
| Buck Guaraní | 56.5 | 70.1 | 63.3 |
| Buck Arriero | 65.8 | 64.5 | 65.1 |
| Thomas Nevado | 53.1 | 78.8 | 65.9 |
| ProINTA Oasis | 66.5 | 66.3 | 66.4 |
| Thomas Tupungato | 71.9 | 61.8 | 66.8 |
| Bonaerense Pasuco | 77.5 | 69.0 | 73.2 |
| Avg. | 47.6 | 51.7 | 49.6 |
| LSD(0.05)‡ | 12.5 | 9.6 | |

† Cultivars are placed in order according to the average of pycnidial coverage for both years.

‡ LSD test ($P < 0.05$) for comparison of pycnidial coverage percentage between cultivars within 2 yr.

For the average of both experiments, differences in extremes among cultivars were 20 d in heading date (from 89 to 112 d in 1998 and from 89 to 106 in 2000) and 30 cm in plant height (from 61 to 92 in 1998 and from 54 to 82 in 2000) (Table 5). Cultivars with high or moderate levels of resistance in seedling and adult stage to isolate IPO 99013 were found among those with early heading date and short stature. For example, Cooperación Millán and Granero INTA showed moderate levels of resistance in the adult stage and are early heading cultivars with short to intermediate plant stature. Klein Toledo was the earliest cultivar in the field experiments and has been considered for many years to be one of the most resistant cultivars in Argentina. This cultivar showed moderate levels of resistance in the adult stages in these experiments.

Multiple linear regression analysis between pycnidial coverage as the dependent variable and plant height and heading date as the independent variables yielded significant $R^2$ values in 1998 for the growth stages GS 49, GS 70, and GS 83 and for the AUDPC ($P = 0.06$), but not for the seedling stage. Regression coefficients were negative and significant for days to heading at GS 49 and GS 70 and for plant height at GS 83 and for the

Table 4. Pycnidial coverage percentage (backtransformed values) caused by *Mycosphaerella graminicola* in 50 Argentinean wheat cultivars at three adult growth stages and area under disease progress curve (AUDPC) in two field experiments.

| | GS49 | | | GS70 | | | GS83 | | | AUDPC | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cultivars† | 1998 | 2000 | Mean 1998–2000 | 1998 | 2000 | Mean 1998–2000 | 1998 | 2000 | Mean 1998–2000 | 1998 | 2000 | Mean 1998–2000 |
| Klein Dragón | 0.16 | 0.04 | 0.10 | 0.99 | 3.82 | 2.40 | 16.8 | 27.7 | 22.2 | 151 | 283 | 217 |
| Klein Estrella | 0.12 | 0.50 | 0.31 | 0.31 | 4.11 | 2.21 | 22.9 | 25.6 | 24.2 | 189 | 274 | 231 |
| Klein Volcán | 0.52 | 0.07 | 0.29 | 0.39 | 0.76 | 0.57 | 23.1 | 29.0 | 26.0 | 195 | 245 | 220 |
| Cooperación Millán | 0.37 | 0.09 | 0.23 | 1.53 | 10.6 | 6.06 | 29.9 | 22.3 | 26.1 | 267 | 349 | 308 |
| Granero INTA | 1.50 | 1.52 | 1.51 | 3.14 | 5.09 | 4.11 | 17.5 | 37.0 | 27.2 | 202 | 389 | 296 |
| ProINTA Quintal | 0.26 | 0.34 | 0.30 | 2.29 | 3.20 | 2.74 | 10.5 | 59.6 | 35.1 | 123 | 531 | 327 |
| Klein Toledo | 2.44 | 2.79 | 2.61 | 5.52 | 6.97 | 6.24 | 14.3 | 57.1 | 35.7 | 222 | 591 | 406 |
| ProINTA Elite | 2.58 | 2.25 | 2.41 | 6.48 | 33.7 | 20.1 | 32.7 | 54.9 | 43.8 | 386 | 997 | 691 |
| Buck Pronto | 0.38 | 2.09 | 1.23 | 3.99 | 3.96 | 3.97 | 29.9 | 60.4 | 45.1 | 306 | 564 | 435 |
| ProINTA Granar | 0.73 | 4.94 | 2.83 | 4.45 | 41.5 | 23.0 | 32.0 | 58.4 | 45.2 | 333 | 1171 | 523 |
| Klein Granador | 0.44 | 1.07 | 0.75 | 1.26 | 8.69 | 4.97 | 17.6 | 73.7 | 45.6 | 165 | 737 | 451 |
| Klein Don Enrique | 0.84 | 0.38 | 0.61 | 7.76 | 2.69 | 5.22 | 52.5 | 41.1 | 46.8 | 551 | 375 | 463 |
| Buck Panadero | 1.46 | 2.08 | 1.77 | 3.62 | 9.59 | 6.60 | 34.2 | 61.0 | 47.6 | 343 | 658 | 500 |
| Klein Brujo | 0.49 | 0.50 | 0.49 | 4.62 | 30.9 | 17.8 | 28.9 | 68.3 | 48.6 | 309 | 1045 | 677 |
| Klein Pegaso | 0.09 | 0.20 | 0.14 | 0.38 | 5.24 | 2.81 | 57.2 | 40.9 | 49.0 | 465 | 412 | 438 |
| ProINTA B. Redomón | 0.15 | 2.09 | 1.12 | 1.91 | 24.1 | 13.0 | 26.9 | 71.2 | 49.0 | 247 | 971 | 609 |
| Buck Poncho | 0.13 | 1.45 | 0.79 | 3.51 | 22.7 | 13.1 | 28.1 | 73.0 | 50.6 | 282 | 958 | 620 |
| Buck Charrúa | 1.12 | 1.79 | 1.45 | 7.70 | 20.4 | 14.0 | 30.2 | 72.5 | 51.3 | 373 | 921 | 647 |
| Bonaerense Pericón | 0.28 | 1.47 | 0.87 | 1.23 | 40.4 | 20.8 | 28.8 | 74.7 | 51.7 | 252 | 1256 | 754 |
| Cooperación Calquín | 0.41 | 0.91 | 0.66 | 2.07 | 5.93 | 4.00 | 50.0 | 54.7 | 52.3 | 437 | 539 | 488 |
| Buck Candil | 0.96 | 3.04 | 2.00 | 2.09 | 43.8 | 22.9 | 32.5 | 72.8 | 52.6 | 301 | 1307 | 804 |
| Klein Orión | 0.87 | 1.72 | 1.29 | 5.33 | 19.5 | 12.4 | 37.9 | 68.8 | 53.3 | 395 | 877 | 636 |
| Buck Catriel | 0.40 | 2.13 | 1.26 | 1.54 | 37.1 | 19.3 | 29.9 | 77.3 | 53.6 | 267 | 1229 | 748 |
| Klein Cobre | 0.53 | 2.56 | 1.54 | 2.42 | 18.7 | 10.6 | 36.7 | 70.7 | 53.7 | 337 | 885 | 611 |
| Thomas Aconcagua | 0.46 | 0.92 | 0.69 | 3.15 | 26.5 | 14.8 | 34.1 | 74.2 | 54.1 | 326 | 1024 | 675 |
| Thomas Chapelco | 0.31 | 2.22 | 1.26 | 1.04 | 30.3 | 15.7 | 51.2 | 60.9 | 56.1 | 428 | 990 | 709 |
| Buck Arrayán | 0.39 | 1.25 | 0.82 | 1.61 | 25.9 | 13.8 | 34.8 | 77.9 | 56.3 | 307 | 1048 | 678 |
| ProINTA Pigüe | 0.47 | 2.33 | 1.40 | 1.91 | 33.5 | 17.7 | 30.9 | 84.7 | 57.8 | 281 | 1232 | 756 |
| Buck Fogón | 0.88 | 4.28 | 2.58 | 2.51 | 25.5 | 14.0 | 44.3 | 72.4 | 58.3 | 402 | 1021 | 711 |
| Bonaerense Pasuco | 0.14 | 1.07 | 0.60 | 1.56 | 52.4 | 27.0 | 32.0 | 87.0 | 59.5 | 282 | 1543 | 913 |
| ProINTA Puntal | 0.00 | 0.19 | 0.09 | 1.75 | 13.2 | 7.47 | 52.4 | 67.5 | 59.9 | 447 | 753 | 600 |
| ProINTA Cinco Cerros | 0.19 | 2.63 | 1.41 | 3.79 | 34.0 | 18.9 | 36.9 | 83.0 | 60.0 | 357 | 1228 | 792 |
| ProINTA B. Cauquén | 0.29 | 6.11 | 3.20 | 2.32 | 23.5 | 12.9 | 32.8 | 87.5 | 60.1 | 302 | 1125 | 713 |
| Buck Arriero | 0.30 | 0.82 | 0.56 | 3.58 | 17.6 | 10.6 | 53.5 | 66.9 | 60.2 | 487 | 824 | 655 |
| Buck Chambergo | 1.84 | 4.34 | 3.09 | 4.54 | 18.0 | 11.3 | 32.8 | 90.3 | 61.6 | 350 | 1046 | 698 |
| Klein Centauro | 0.06 | 4.21 | 2.13 | 9.02 | 20.1 | 14.6 | 48.7 | 77.2 | 62.9 | 534 | 973 | 753 |
| Thomas Tupungato | 0.08 | 8.60 | 4.34 | 3.81 | 47.8 | 25.8 | 59.5 | 67.2 | 63.3 | 537 | 1372 | 954 |
| Buck Ombú | 1.19 | 6.21 | 3.70 | 4.30 | 17.0 | 10.6 | 42.9 | 84.1 | 63.5 | 422 | 994 | 708 |
| ProINTA Federal | 0.56 | 0.49 | 0.53 | 4.09 | 5.43 | 4.76 | 65.6 | 64.0 | 64.8 | 595 | 603 | 599 |
| Cooperación Maipún | 0.27 | 4.50 | 2.38 | 1.83 | 47.2 | 24.5 | 35.9 | 94.0 | 65.0 | 318 | 1543 | 931 |
| Buck Guaraní | 1.90 | 2.02 | 1.96 | 3.49 | 15.9 | 9.69 | 41.7 | 88.5 | 65.1 | 405 | 978 | 691 |
| ProINTA Oasis | 0.20 | 5.58 | 2.89 | 4.60 | 38.9 | 21.7 | 56.8 | 83.1 | 70.0 | 530 | 1332 | 931 |
| Cooperación Nahuel | 0.08 | 1.05 | 0.56 | 4.27 | 40.7 | 22.5 | 54.6 | 86.1 | 70.3 | 506 | 1349 | 927 |
| ProINTA Imperial | 1.02 | 2.43 | 1.72 | 4.10 | 29.9 | 17.0 | 55.9 | 84.8 | 70.3 | 521 | 1176 | 848 |
| Cooperación Malambo | 0.05 | 4.00 | 2.02 | 13.2 | 43.1 | 28.1 | 63.3 | 78.9 | 71.1 | 718 | 1353 | 1036 |
| ProINTA Real | 1.06 | 1.02 | 1.04 | 9.54 | 35.3 | 22.4 | 62.6 | 84.2 | 73.4 | 662 | 1247 | 954 |
| Klein Cacique | 0.36 | 3.65 | 2.00 | 5.85 | 50.1 | 28.0 | 60.5 | 88.5 | 74.5 | 580 | 1540 | 1060 |
| ProINTA Super | 0.24 | 0.84 | 0.54 | 1.40 | 27.4 | 14.4 | 64.9 | 85.4 | 75.1 | 544 | 1129 | 836 |
| ProINTA Guazú | 0.42 | 1.90 | 1.16 | 7.44 | 53.5 | 30.5 | 61.6 | 88.9 | 75.2 | 615 | 1583 | 1099 |
| Thomas Nevado | 0.24 | 5.40 | 2.82 | 2.31 | 47.6 | 25.0 | 78.0 | 93.1 | 85.6 | 663 | 1549 | 1106 |
| Avg. | 0.60 | 2.28 | 1.44 | 3.63 | 24.5 | 14.1 | 40.2 | 69.0 | 54.6 | 384 | 962 | 673 |
| LSD(0.05)‡ | 3.29 | 5.55 | | 5.13 | 9.65 | | 12.2 | 12.4 | | 172 | 266 | |

† Cultivars are placed in order according to the average of both years at GS 83.

‡ LSD test ($P < 0.05$) for comparisons of pycnidial coverage percentage and AUDPC between cultivars at three adult growth stages within 2 yr.

AUDPC (Table 6). However, the $R^2$ values were only significant at GS 70 and for the AUDPC in 2000. In those two cases, the regression coefficients were positive and significant for days to heading, but statistically not significant for plant height. We also tested a large set of multiple nonlinear regression models, with different numbers of predictors and different powers of these predictors. However, only for GS 83 and for the AUDPC in 1998 we were able to identify models with slightly higher probabilities of the $R^2$ value than for the multiple linear models. These models had an $R^2 = 0.24$ ($P = 0.014$) for GS 83 and $R^2 = 0.21$ ($P = 0.026$) for the AUDPC. The models indicated that plant height and heading date were negatively associated with pycnidial coverage and that the multiplicative coefficient ($x_1x_2$) was positively associated (due to the negative effects of plant height and heading date).

## Greenhouse Experiments

### Experiment 1

There was a high correlation between necrosis and pycnidial coverage percentage, mainly attributed to the appropriate conditions (temperature and humidity) for the development of Septoria tritici blotch (Table 7).

Cultivars differed for both resistance components. Necrosis percentage fluctuated between 17.6 and 76.3% and pycnidial coverage between 15.6 and 69.7% for all cultivars. The most resistant cultivars in the field also showed low disease values in this experiment. Klein

**Table 5. Days to heading and plant height of 50 Argentinean wheat cultivars in two field experiments.**

| | Days to heading | | | Plant height | | |
|---|---|---|---|---|---|---|
| Cultivars† | 1998 | 2000 | Avg. 1998–2000 | 1998 | 2000 | Avg. 1998–2000 |
| | d | | | cm | | |
| Cooperación Maipún | 106 | 99 | 102 | 62 | 56 | 59 |
| Klein Don Enrique | 97 | 90 | 93 | 67 | 54 | 60 |
| Buck Chambergo | 96 | 92 | 94 | 65 | 56 | 60 |
| Buck Ombú | 92 | 90 | 91 | 66 | 55 | 60 |
| ProINTA Real | 96 | 94 | 95 | 61 | 59 | 60 |
| Cooperación Malambo | 101 | 101 | 101 | 63 | 60 | 61 |
| Granero INTA | 91 | 91 | 91 | 64 | 60 | 62 |
| ProINTA Federal | 96 | 89 | 92 | 65 | 59 | 62 |
| Buck Candil | 110 | 105 | 107 | 63 | 61 | 62 |
| Buck Guaraní | 94 | 91 | 92 | 67 | 60 | 63 |
| ProINTA Oasis | 102 | 96 | 99 | 67 | 60 | 63 |
| Klein Cobre | 93 | 89 | 91 | 66 | 62 | 64 |
| Klein Estrella | 109 | 104 | 106 | 71 | 59 | 65 |
| Cooperación Millán | 99 | 94 | 96 | 66 | 65 | 65 |
| Buck Pronto | 91 | 90 | 90 | 70 | 61 | 65 |
| Cooperación Calquín | 96 | 90 | 93 | 66 | 59 | 65 |
| ProINTA Puntal | 111 | 95 | 103 | 66 | 65 | 65 |
| ProINTA Elite | 95 | 93 | 94 | 68 | 62 | 65 |
| ProINTA Granar | 96 | 93 | 94 | 68 | 62 | 65 |
| Thomas Tupungato | 103 | 102 | 102 | 68 | 65 | 66 |
| Buck Arrayán | 106 | 102 | 104 | 67 | 67 | 67 |
| Buck Poncho | 102 | 100 | 101 | 70 | 66 | 68 |
| Buck Arriero | 108 | 103 | 105 | 69 | 67 | 68 |
| Klein Brujo | 98 | 94 | 96 | 74 | 63 | 68 |
| ProINTA Super | 111 | 97 | 104 | 74 | 63 | 68 |
| ProINTA Guazú | 101 | 102 | 101 | 69 | 68 | 68 |
| Thomas Nevado | 100 | 98 | 99 | 73 | 64 | 68 |
| Klein Orión | 93 | 90 | 91 | 74 | 65 | 69 |
| Cooperación Nahuel | 105 | 102 | 103 | 71 | 67 | 69 |
| Thomas Aconcagua | 106 | 103 | 104 | 71 | 69 | 70 |
| Buck Fogón | 104 | 101 | 102 | 71 | 69 | 70 |
| ProINTA Bonaerense Cauquén | 105 | 101 | 103 | 73 | 68 | 70 |
| ProINTA Quintal | 94 | 90 | 92 | 75 | 67 | 71 |
| Buck Panadero | 103 | 100 | 101 | 71 | 71 | 71 |
| ProINTA Imperial | 95 | 90 | 92 | 74 | 68 | 71 |
| Bonaerense Pasuco | 103 | 103 | 103 | 73 | 70 | 71 |
| Klein Pegaso | 106 | 101 | 103 | 74 | 70 | 72 |
| ProINTA Pigüe | 105 | 101 | 103 | 77 | 68 | 72 |
| ProINTA Cinco Cerros | 107 | 105 | 106 | 77 | 68 | 72 |
| Klein Volcán | 101 | 94 | 97 | 81 | 65 | 73 |
| Bonaerense Pericón | 102 | 104 | 103 | 75 | 71 | 73 |
| ProINTA Bonaerense Redomón | 109 | 105 | 107 | 76 | 72 | 74 |
| Thomas Chapelco | 111 | 104 | 107 | 78 | 71 | 74 |
| Buck Charrúa | 111 | 103 | 107 | 75 | 75 | 75 |
| Buck Catriel | 112 | 106 | 109 | 78 | 73 | 75 |
| Klein Toledo | 89 | 89 | 89 | 82 | 70 | 76 |
| Klein Centauro | 103 | 100 | 101 | 80 | 76 | 78 |
| Klein Dragón | 97 | 92 | 94 | 84 | 74 | 79 |
| Klein Granador | 97 | 91 | 94 | 92 | 73 | 82 |
| Klein Cacique | 106 | 101 | 103 | 87 | 82 | 84 |
| Avg. | 101 | 97 | 99 | 72 | 66 | 69 |
| LSD(0.05)‡ | 2 | 2 | | 6 | 7 | |

† Cultivars are placed in order according to the average of plant height.
‡ LSD test ($P < 0.05$) for comparisons of days to heading and plant height between cultivars within 2 yr.

Dragón, Klein Volcán, and Klein Estrella showed the best resistance levels (Table 7). Multiple linear regression analysis showed no association between heading date and plant height with pycnidial coverage percentage ($R^2 = 0.0047$, $P = 0.89$). None of the nonlinear regression models were significant either.

### Experiment 2

Significant differences were found for both disease parameters between cultivars and isolates and for the cultivar × isolate interaction (Table 8). Percentages of necrosis and pycnidial coverage from the greenhouse experiment with several isolates are presented in Table 9. For necrosis percentage, Klein Dragón and Klein Volcán followed by ProINTA Quintal and 'Buck Poncho' showed the best levels of resistance for the average of the seven isolates. For Klein Dragón, necrosis percentage varied between 7.5 and 35.1% for all isolates and for Klein Volcán between 7.0 and 26.8%. For pycnidial coverage Klein Dragón, ProINTA Quintal, and Klein Volcán showed the lowest values for the average of the isolates. Considering each particular isolate, Klein Dragón varied between 0.5 and 32.6%; Klein Volcán between 0.9 and 23.7%, and ProINTA Quintal between 0.2 and 28.4% (Table 9).

For the whole set of cultivars and isolates, the correlation between necrosis and pycnidial coverage was 0.86 ($n = 112$, $P < 0.001$). Buck Panadero with isolates IPO 92064 and 92065 showed lower values for pycnidial coverage than expected based on the values for the percentage of necrosis. Moreover, some other combinations showed slightly higher pycnidial coverage values than expected based on necrosis percentage (Klein Estrella with isolate IPO 99015 and 'Buck Guaraní' with isolate IPO 99016).

## DISCUSSION

Pycnidial coverage percentages in seedlings and in adult plants were correlated in the field using the isolate IPO 99013, but the correlation was not high ($r = 0.26$ in 1998 and $r = 0.68$ in 2000). There were three cultivars with combined seedling and adult plant resistance, but others showed better levels of resistance either in the seedling or in the adult stage. That means that selection in both stages should be done in breeding programs to achieve acceptable levels of resistance throughout the entire growing period. Arama (1996) found similar results. Kema and Van Silfhout (1997) observed that in general adult plants were more susceptible than seedlings, although differences between isolates were found.

Pycnidial coverage was highly correlated with necrosis percentage in both field and greenhouse experiments. This is in agreement with previous findings for field experiments (Arama, 1996; Brown et al., 2001), although in some cultivar × isolate combinations, high percentages of necrosis with low pycnidial coverage have been found. In our research, there were also some cultivars that showed higher pycnidial coverage than necrosis due to the presence of pycnidia in green areas. In the greenhouse, sometimes the correlation between the two disease parameters was not high (Arama, 1996). In our greenhouse experiment, relative humidity was kept as high as possible during the period after inoculation by means of humidifiers. Measurement of pycnidial coverage is considered more accurate because senescence and other diseases do not interfere in the results. However, previous investigations indicate that especially in field conditions, necrosis percentage also can be a good predictor of resistance, and is easier to measure (Brown et al., 2001).

We found variation in genetic resistance—measured

Table 6. Multiple linear regression for pycnidial coverage caused by *Mycosphaerella graminicola* as dependent variable and with days to heading and plant height as independent variables for 50 Argentinean wheat cultivars at seedling stage, boot stage (GS 49), milk development (GS 70), and early dough stage (GS 83), and for the area under disease progress curve (AUDPC) in two field experiments.

| | Equation parameters ($P$ value) | | | |
|---|---|---|---|---|
| Growth stage/AUDPC | Constant ($P$ value) | Days to heading | Plant height | $R^2$ ($P$ value) |
| 1998 | | | | |
| Seedling | 62.7 ($P = 0.02$) | −0.06 ($P = 0.82$) | −0.19 ($P = 0.37$) | 0.02 ($P = 0.62$) |
| GS 49 | 24.8 ($P < 0.001$) | −0.19 ($P < 0.001$) | −0.03 ($P = 0.37$) | 0.33 ($P < 0.001$) |
| GS 70 | 37.9 ($P < 0.001$) | −0.18 ($P = 0.04$) | −0.14 ($P = 0.09$) | 0.15 ($P = 0.02$) |
| GS 83 | 35.3 ($P = 0.17$) | 0.38 ($P = 0.08$) | −0.48 ($P = 0.02$) | 0.14 ($P = 0.03$) |
| AUDPC | 636 ($P = 0.09$) | 2.68 ($P = 0.41$) | −7.30 ($P = 0.02$) | 0.11 ($P = 0.06$) |
| 2000 | | | | |
| Seedling | 14.6 ($P = 0.45$) | 0.22 ($P = 0.31$) | 0.16 ($P = 0.45$) | 0.06 ($P = 0.24$) |
| GS 49 | −0.55 ($P = 0.95$) | 0.15 ($P = 0.17$) | −0.10 ($P = 0.34$) | 0.04 ($P = 0.37$) |
| GS 70 | −76.6 ($P = 0.004$) | 1.24 ($P < 0.001$) | −0.25 ($P = 0.35$) | 0.31 ($P < 0.001$) |
| GS 83 | 4.04 ($P = 0.91$) | 0.73 ($P = 0.09$) | −0.09 ($P = 0.83$) | 0.07 ($P = 0.20$) |
| AUDPC | −2031 ($P = 0.03$) | 31.1 ($P = 0.0014$) | 0.04 ($P = 1.00$) | 0.22 ($P = 0.003$) |

Table 7. Necrosis and pycnidial coverage percentage (backtransformed values) caused by *Mycosphaerella graminicola*, days to heading, and plant height in 50 Argentinean wheat cultivars with isolate IPO 99013 at early dough stage (GS83) in the greenhouse (Experiment 1).

| Cultivars† | Days to heading | Plant height | Necrosis | Pycnidial coverage |
|---|---|---|---|---|
| | d | cm | % | |
| Klein Dragón | 87.0 | 74.5 | 17.6 | 15.6 |
| Klein Volcán | 89.5 | 72.0 | 25.1 | 20.5 |
| Klein Estrella | 97.5 | 60.0 | 26.0 | 22.7 |
| Granero INTA | 83.0 | 53.0 | 27.0 | 25.2 |
| Klein Toledo | 80.5 | 70.5 | 30.2 | 26.4 |
| ProINTA Quintal | 99.5 | 56.0 | 30.1 | 27.4 |
| Klein Brujo | 90.5 | 63.0 | 32.2 | 30.0 |
| Cooperación Millán | 88.5 | 56.0 | 32.4 | 30.1 |
| Buck Poncho | 90.0 | 59.0 | 35.1 | 30.9 |
| Buck Catriel | 100 | 66.5 | 35.9 | 31.4 |
| Klein Granador | 86.5 | 76.0 | 35.6 | 31.6 |
| Buck Chambergo | 85.5 | 54.5 | 40.1 | 32.7 |
| Buck Charrúa | 99.0 | 64.0 | 41.0 | 32.8 |
| Buck Pronto | 83.0 | 59.5 | 35.6 | 32.8 |
| Buck Panadero | 91.0 | 59.5 | 35.0 | 32.9 |
| ProINTA Granar | 95.0 | 65.5 | 35.0 | 33.1 |
| Bonaerense Pericón | 90.0 | 66.0 | 40.2 | 33.4 |
| Buck Candil | 98.5 | 51.5 | 40.1 | 34.3 |
| Buck Arriero | 95.5 | 60.0 | 44.7 | 34.4 |
| ProINTA Federal | 86.0 | 50.0 | 40.1 | 35.2 |
| ProINTA Elite | 90.5 | 57.5 | 40.1 | 35.6 |
| ProINTA Bonaerense Cauquén | 93.0 | 62.0 | 45.6 | 35.7 |
| ProINTA Bonaerense Redomón | 97.0 | 65.5 | 45.6 | 36.6 |
| Klein Cobre | 84.5 | 54.5 | 45.8 | 37.7 |
| ProINTA Puntal | 93.0 | 68.0 | 46.6 | 39.5 |
| ProINTA Cinco Cerros | 85.0 | 58.0 | 50.1 | 40.3 |
| Buck Arrayán | 94.0 | 56.0 | 55.6 | 40.4 |
| ProINTA Pigüe | 84.5 | 63.5 | 45.6 | 40.9 |
| Klein Don Enrique | 86.5 | 58.5 | 50.1 | 41.7 |
| Thomas Aconcagua | 94.5 | 60.0 | 45.6 | 41.7 |
| Bonaerense Pasuco | 92.0 | 64.0 | 50.2 | 41.8 |
| Cooperación Calquín | 84.5 | 56.5 | 50.1 | 42.7 |
| Klein Pegaso | 94.0 | 65.5 | 50.3 | 42.7 |
| Buck Fogón | 92.0 | 62.0 | 55.7 | 42.9 |
| Buck Guaraní | 84.5 | 58.5 | 52.5 | 42.9 |
| Buck Ombú | 84.5 | 58.0 | 52.8 | 43.0 |
| Klein Orión | 85.5 | 66.5 | 47.5 | 44.1 |
| Klein Centauro | 91.0 | 70.5 | 50.2 | 44.2 |
| Cooperación Maipún | 94.5 | 54.0 | 56.3 | 50.5 |
| Thomas Chapelco | 99.5 | 69.0 | 56.4 | 52.4 |
| Cooperación Nahuel | 94.0 | 61.0 | 60.1 | 52.9 |
| ProINTA Imperial | 86.0 | 59.0 | 60.2 | 53.4 |
| Klein Cacique | 94.0 | 77.5 | 60.4 | 57.2 |
| ProINTA Oasis | 89.0 | 60.5 | 68.4 | 58.9 |
| Cooperación Malambo | 89.0 | 53.5 | 70.0 | 60.6 |
| ProINTA Guazú | 86.0 | 55.0 | 70.0 | 61.8 |
| ProINTA Super | 99.0 | 65.0 | 70.1 | 63.3 |
| ProINTA Real | 84.0 | 65.5 | 72.5 | 64.0 |
| Thomas Nevado | 90.0 | 64.0 | 76.3 | 69.7 |
| Avg. | 90.4 | 61.7 | 46.8 | 39.8 |
| LSD(0.05)‡ | | | 14.7 | 0.98 |

† Cultivars are placed in order according to pycnidial coverage percentage.
‡ LSD test ($P = 0.05$) for comparison of necrosis and pycnidial coverage percentage between cultivars within 2 yr.

as percentage of pycnidial coverage—within a wide spectrum of cultivars grown in Argentina in 1998 and the old cultivar Klein Toledo. Cultivars can be classified from moderately resistant to susceptible in the adult stage with the Argentinean isolate IPO 99013 based on three experimental environments (two assays in the field and one in the greenhouse). A few cultivars also can be considered resistant in the seedling stage.

A cultivar × experiment interaction was found in the field experiments. Higher AUDPC values were generally observed in 2000 than in 1998, but a few cultivars showed similar values in both years. Some of the cultivars were the most resistant cultivars (Klein Volcán, Klein Estrella, Klein Dragón, Cooperación Millán, and Granero INTA). This indicates that the AUDPC of the most resistant cultivars was less influenced by environmental conditions compared with the susceptible cultivars.

Klein Volcán and Klein Dragón showed good levels of resistance to seven isolates in the adult stage. These two cultivars also showed a high level of resistance to IPO 99013 in the seedling stage. The level of resistance in the seedling stage was higher than in the adult stage and probably indicates that a gene for gene interaction is expressed at the seedling stage. Our findings suggests that nonisolate specific horizontal resistance may be present in these cultivars in the adult stage, but additional research with more isolates should be done to verify the results. Specific interactions have been reported by several researchers in seedlings (Eyal et al., 1985; Perelló et al., 1991; Ahmed et al., 1995; Ballantyne and Thomson, 1995; Kema et al., 1996a, 1996b). In the adult stage, Kema and Van Silfhout (1997) and Brown et al. (2001) reported cultivar × isolate interactions.

Results showed that resistance to Septoria tritici blotch is not genetically associated with heading date or plant height within a wide spectrum of cultivars grown in Argentina. In the seedling stage this is supported by the multiple linear regression analysis of heading date and plant height on pycnidial coverage, which showed no relationship between the resistance and any of the morphophysiological traits for either of the two field experiments. All cultivars reached GS 12 at the same time; thus, they were inoculated and scored at the same date and for that reason under the same weather conditions. In that way, no influence of weather conditions could

**Table 8. Analysis of variance for necrosis and pycnidial coverage percentage (backtransformed values) caused by *Mycosphaerella graminicola* in 16 wheat cultivars with seven isolates (Experiment 2).**

| Source of variation | df | Mean squares ($P > F$)<br>Necrosis percentage | Pycnidial coverage |
|---|---|---|---|
| Cultivars | 15 | 1307 ($P < 0.001$) | 935.8 ($P < 0.001$) |
| Isolates | 6 | 1213 ($P < 0.001$) | 2150 ($P < 0.001$) |
| Cultivars × Isolates | 90 | 251.4 ($P < 0.001$) | 193.1 ($P < 0.001$) |
| Error | 111 | 24.0 | 36.8 |

have affected the level of resistance and its association with the morphophysiological traits.

In the adult stage, the lack of genetic association is supported by the fact that associations between susceptibility and heading date in the field were positive or negative depending on how weather conditions predispose the development of the disease in late or early cultivars. Associations between plant height and resistance were also variable in the field. In addition, in 1999, the same experiment was performed under controlled conditions and the flag leaf was inoculated at heading (Experiment 1). In that way, effects of plant height and heading date on the development of the disease due to environment or epidemiological aspects were minimized. Conditions after inoculations in this experiment were similar for all cultivars independently of the date they reached the flag leaf stage. There was no influence of any of the morphological traits on the expression of the disease under the controlled conditions in this trial. For that reason, it is assumed that associations (negative or positive) found in the field experiments can be attributed to variation in weather conditions and not to genetic linkages among those traits.

Weather was more favorable for the expression of the disease in early cultivars because precipitation was higher and radiation lower for early cultivars than late ones in 1998. This was especially true when considering a period of 15 d before the beginning of the adult stage evaluations, which started on 28 Sept. and on 15 Oct. 1998 for the earliest and latest cultivars, respectively. Precipitation was 53.4 and 18.8 mm and radiation 3511 and 5127 W $m^{-2}$ $d^{-1}$ for the period of 15 d before evaluation for the earliest and the latest cultivars, respectively. Negative associations between pycnidial coverage and days to heading in 1998 can be attributed to these differences in weather variables.

In contrast, no negative associations were found between days to heading and the pycnidial coverage percentage in 2000. Some positive associations were found at GS 70 and for the AUDPC. Precipitation and temperatures were higher at the beginning of the infection for the latest cultivars. Adult stage evaluations started on 17 October and 2 November for the earliest and latest cultivars, respectively, in 2000. Considering a period of 15 d before those dates, mean temperatures were 14.2 and 16.8°C, precipitation 57.5 and 101.1 mm, and mean relative humidity 71.9 and 92.4% for early and late cultivars, causing the significant positive associations between pycnidial coverage and days to heading. Under greenhouse conditions, temperatures from 17 to 25°C are optimum for disease development (Hess and Shaner, 1987; Shaw, 1990; Wainshilbaum and Lipps, 1991; Magboul et al., 1992; Chungu et al., 2000). High humidity or precipitation and low radiation at time of infection also have been indicated as conditions conducive to the development of *Mycosphaerella graminicola* (Holmes

**Table 9. Means of necrosis (N) and pycnidial coverage percentage (P) caused by *Mycosphaerella gramicola* of 16 Argentinean wheat cultivars with seven Argentinean isolates in the greenhouse (Experiment 2).**

| | Isolate | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 92064 | | 92065 | | 93014 | | 99013 | | 99014 | | 99015 | | 99016 | | Avg.† | |
| Cultivar | N | P | N | P | N | P | N | P | N | P | N | P | N | P | N | P |
| | % | | | | | | | | | | | | | | | |
| Klein Dragón | 11.1 | 4.1 | 7.7 | 1.0 | 7.5 | 7.1 | 17.6 | 15.6 | 35.1 | 32.6 | 8.75 | 0.5 | 8.7 | 4.0 | 13.8 | 9.3 |
| ProINTA Quintal | 31.3 | 3.8 | 11.3 | 0.2 | 52.7 | 15.4 | 30.1 | 27.4 | 30.8 | 28.4 | 10.7 | 5.8 | 7.2 | 1.9 | 24.9 | 11.8 |
| Klein Volcán | 12.1 | 11.5 | 7.0 | 0.9 | 26.8 | 22.0 | 25.1 | 20.5 | 24.1 | 23.7 | 10.2 | 6.8 | 22.2 | 11.2 | 18.2 | 13.8 |
| Buck Arriero | 18.0 | 16.8 | 33.3 | 13.3 | 21.8 | 3.9 | 44.7 | 34.4 | 34.5 | 30.4 | 14.6 | 8.05 | 30.8 | 14.2 | 28.2 | 17.3 |
| Buck Charrúa | 51.3 | 20.2 | 45.7 | 28.6 | 22.6 | 14.8 | 41.0 | 32.8 | 33.0 | 32.4 | 10.3 | 5.8 | 33.2 | 16.3 | 33.9 | 21.5 |
| Buck Guaraní | 11.8 | 2.7 | 41.0 | 30.0 | 17.6 | 18.6 | 52.5 | 42.9 | 49.9 | 43.6 | 6.8 | 4.45 | 21.6 | 23.2 | 28.7 | 23.6 |
| Buck Poncho | 15.2 | 12.2 | 14.1 | 13.7 | 25.8 | 22.6 | 35.1 | 30.9 | 34.7 | 29.1 | 17.6 | 13.3 | 41.0 | 55.7 | 26.2 | 25.4 |
| ProINTA Oasis | 44.1 | 18.7 | 21.8 | 6.3 | 9.3 | 4.4 | 68.4 | 58.9 | 64.4 | 64.4 | 38.8 | 26.7 | 10.2 | 3.9 | 36.7 | 26.2 |
| Klein Estrella | 31.1 | 20.0 | 60.7 | 15.0 | 35.0 | 25.0 | 26.0 | 22.7 | 35.0 | 27.5 | 56.1 | 60.0 | 30.0 | 22.5 | 39.1 | 27.5 |
| Buck Panadero | 30.9 | 4.2 | 50.6 | 13.7 | 21.6 | 18.1 | 35.0 | 32.9 | 88.9 | 70.4 | 27.7 | 26.7 | 57.6 | 34.7 | 44.6 | 28.7 |
| Klein Orión | 45.6 | 25.0 | 24.0 | 17.2 | 16.8 | 5.4 | 47.5 | 44.1 | 86.6 | 67.1 | 45.0 | 30.0 | 35.0 | 30.0 | 43.1 | 31.3 |
| ProINTAReal | 43.4 | 27.1 | 9.7 | 8.02 | 57.6 | 34.7 | 72.5 | 64.0 | 63.0 | 47.2 | 35.0 | 30.0 | 35.0 | 22.2 | 45.2 | 33.3 |
| ProINTA Puntal | 37.5 | 25.0 | 50.0 | 25.0 | 68.5 | 50.0 | 46.6 | 39.5 | 42.5 | 32.5 | 50.0 | 40.0 | 37.5 | 32.5 | 47.5 | 34.9 |
| Buck Ombú | 83.7 | 61.6 | 28.3 | 12.2 | 36.7 | 11.4 | 52.8 | 43.0 | 89.1 | 70.0 | 46.7 | 23.0 | 91.4 | 59.4 | 61.2 | 40.1 |
| Thomas Tupungato | 17.0 | 7.8 | 36.6 | 23.6 | 55.1 | 20.0 | 60.2 | 53.4 | 67.6 | 66.6 | 51.6 | 32.4 | 89.4 | 83.5 | 53.9 | 41.0 |
| ProINTAGranar | 69.5 | 46.2 | 16.0 | 16.0 | 82.4 | 58.9 | 35.0 | 33.1 | 97.1 | 75.2 | 52.0 | 39.8 | 92.1 | 85.7 | 63.4 | 50.7 |
| Avg. | 34.7 | 19.2 | 28.6 | 14.0 | 34.9 | 20.8 | 43.1 | 37.3 | 54.8 | 46.3 | 30.1 | 22.1 | 40.2 | 31.3 | 38.0 | 28.9 |
| LSD(0.05) necrosis percentage‡ | | | | | | | | | | | | | | | | |
| Cultivars (C) | 3.7 | | | | | | | | | | | | | | | |
| Isolates (I) | 2.4 | | | | | | | | | | | | | | | |
| Interaction (C × I) | 9.7 | | | | | | | | | | | | | | | |
| LSD pycnidial coverage | | | | | | | | | | | | | | | | |
| Cultivars (C) | 4.5 | | | | | | | | | | | | | | | |
| Isolates (I) | 3.0 | | | | | | | | | | | | | | | |
| Interaction (C × I) | 12.0 | | | | | | | | | | | | | | | |

† Cultivars are placed in order according to the average of pycnidial coverage percentage.

‡ LSD test ($P = 0.05$) for comparisons of necrosis and pycnidial coverage percentage between cultivars, isolates, and for the interaction cultivars × isolates.

and Colhoun, 1974; Hess and Shaner, 1987; Shaw and Royle, 1989).

The lack of genetic associations between resistance and heading date agrees with research by Arama et al. (1999). As they mentioned, when one tries to assess true resistance of a range of cultivars, disease severity should be measured not at the same moment, but at the same stage of development. If, in our experiments, disease development had been measured at the same day in the adult stage for all cultivars, early cultivars would have been at GS 70 when late ones were at GS 49. That was demonstrated by the overlapping of the last date of evaluation for GS 49 and the first for GS 70 (data not shown). This would have caused high and significant negative associations between earliness and resistance due to differences in leaf age and because of differences in the duration of the period leaves were exposed to the disease.

Negative associations between shortness and resistance were mainly present in 1998 when weather conditions were less conducive to the development of the disease than in 2000. Unfavorable conditions and larger distances between leaves in tall cultivars could have reduced the rain–splash dispersal of pycnidiospores causing this negative association. Associations with plant height also could depend on the presence of the teleomorphic state and the importance of the ascospore release during the growth of the wheat crop. Air-borne dispersal of ascospores could reduce the effect of plant height in the expression of the disease. In Argentina, the presence of the teleomorphic state during the whole growing period has been reported (Cordo et al., 1990, 1999).

In Argentina, information about resistance levels of actual cultivars with different isolates is scarce. The results of this research showed specific interactions between cultivars and isolates, although some cultivars showed moderate levels of resistance toward several isolates. Even if these cultivars are susceptible to other isolates, higher levels of resistance could be achieved by intercrossing them. In this germplasm, no genetic associations between earliness, plant height, and resistance to Septoria tritici blotch are evident. The associations that were observed are likely caused by environmental and epidemiological factors.

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