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# Path coefficient analysis of the effects of stripe rust and cultivar mixtures on yield and yield components of winter wheat

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**Abstract** Four club wheat cultivars and three two-component cultivar mixtures, planted at five frequencies, were grown in three environments in both the presence and absence of stripe rust. The effect of stripe rust on wheat yield was through the yield components, with weight of individual seed being the component most affected by rust. In some cases, yield component compensation was indicated by the presence of negative correlations among the yield components. Path analysis of the yield components revealed that components with the highest correlations to yield also had the largest direct effects on yield. Of the yield components, number of heads per unit area exerted the largest direct influence on yield. The direct effects of number of seeds per head and weight of individual seed were similar, although number of seeds per head was more important in the absence of rust than in its presence. The pure stands and mixtures differed considerably with respect to correlation coefficients, but were very similar for direct effects of yield components on yield. Most of these discrepancies were due to opposing indirect effects, which were not evident from correlation coefficients alone.

**Key words** *Triticum aestivum* · *Puccinia striiformis* · Diversity · Competition · Path analysis

## Introduction

It has been suggested that plant genetic diversity provides significant protection from disease in both natural and agricultural ecosystems and may also contribute to increased yield and yield stability in the absence of disease (Mundt 1994; Mundt and Browning 1985; Wolfe 1985). Intraspecific genetic diversity can be attained by growing multiline varieties or simple cultivar mixtures. In recent years, however, more attention has been focused on cultivar mixtures (Mundt 1994; Wolfe 1985), which can be easily constituted from available commercial cultivars without any further breeding for agronomic uniformity.

The interrelationships between yield and yield components are rather complex in cultivar mixtures (Clay 1990; Finckh and Mundt 1992). This complexity increases in the presence of disease due to the influence of disease on plant-plant interactions and the interaction of disease with yield components (Alexander et al. 1986; Burdon and Chilvers 1977; Burdon et al. 1984; Finckh and Mundt 1992). Thus, it is of utmost importance to determine interrelationships among disease severity, yield and yield components in mixtures.

Path coefficient analysis is a very important statistical tool that can be used to obtain an indication of which variables (causes) exert on influence on other variables (effects), while recognizing the impacts of multicolinearity. A path coefficient is simply a standardized partial regression coefficient and, as such, estimates the direct influence of one variable upon another and permits the separation of correlation coefficients into components of direct and indirect effects (Bowers et al. 1990; Dewey and Lu 1959; Hampton 1975; Li 1975; Van Bruggen and Arneson 1986; Williams et al. 1990). The direct contribution of an independent variable to the variation observed in the dependent variable can be determined with reduced confounding influences caused by multicolinearity.

Path analysis has often been used in population genetics (Li 1975) and agronomy (Chung and Goulden 1971; Dewey and Lu 1959; Duarte and Adams 1972; Westermann and Crothers 1977). Grafius (1978) provided a conceptual basis in applying path coefficient analysis to yield components of annual crops. He proposed two corollaries to Sinnott's (1921) law, which states that "The size of an organ is directly proportional

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to the size of the meristem from which it develops". Grafius's (1978) first corollary is applicable to organs derived from the same meristem and states that "Plasticity is inversely proportional to ontogenetic proximity". The second corollary is applicable to organs derived from different meristems and states that "Numbers and size of organs tend to have an inverse relationship".

Path analysis has been used less frequently in plant pathology (Van Bruggen and Arneson 1986; Bowers et al. 1990; Calvero 1994; Hampton 1975; Torres and Teng 1993; Yang and Zeng 1989), and no attempt has yet been made to apply path coefficient analysis to cultivar mixtures. The purposes of the study presented here were to determine both the effect of stripe rust (*Puccinia striiformis*) on the yield components of wheat (*Triticum aestivum*) and the relative importance of the disease and yield components on yield, and to unravel opposing effects between variables along different paths of influence.

## Materials and methods

Our experiments were superimposed on studies designed to investigate changes in the frequency of wheat cultivars in mixtures, which will be reported in future papers. The effects of these wheat populations on stripe rust severity, yield and yield components have been described in detail (Akanda and Mundt 1996, in review). A summary of relevant materials and methods of those studies is provided below.

Field plots were established at Moro in central Oregon and at Pendleton in eastern Oregon, USA, in the fall of 1991, 1992 and 1993. The experiments planted at Pendleton in 1992 and 1993 and at Moro in 1992 were analyzed intensively for disease severity and yield, and only data from these three experiments are reported here. The experimental design was a split-plot, randomized complete block with four replications. The main plots were either inoculated with stripe rust or protected with two to three applications of triadimefon (as Bayleton), depending on the predisposing weather conditions. This fungicide treatment has been shown to have no significant effect on wheat yield (Mundt et al. 1995). Each cultivar was susceptible to only one pathogen race, except for 'Jacmar', which was susceptible to two races. Subplots within each mainplot consisted of four cultivars ('Faro', 'Jacmar', 'Tres' and 'Tyee') and three two-way mixtures among them ('Faro'-'Tyee', 'Faro'-Tres', and 'Jacmar'-'Tyee'), each grown in the proportions of 0.1:0.9, 0.25:0.75, 0.5:0.5, 0.75:0.25 and 0.9:0.1 in fall 1991, and seed was carried over for the following two seasons. Each subplot was four rows wide by 6.1 m long with a 36-cm spacing between the rows. Plots were planted at a seeding rate of 253 and 158 seeds/m$^2$ at Pendleton and Moro, respectively. To reduce the spread of spores and fungicide among plots, we sowed a subplot of the common soft white winter wheat cultivar 'Stephens', which is immune to the stripe rust races used for this study, between adjacent treatment subplots, in the narrow dimension, and a 6.1-m-long strip of 'Stephens' wheat separated the main plots. Fertilizer and weed control practices were those standardly accepted for commercial wheat production at each site. Inoculation was done by transplanting two peat pots in each inoculated subplot, each containing two rust-infected wheat seedlings.

Percent leaf area covered with stripe rust lesions was visibly quantified on the leaf below the flag leaf (F-1 leaf) on approximately 120 tillers. Miniplots containing approximately 120 head-bearing tillers, on average, were delineated from the center two rows of both inoculated and fungicide-treated subplots (same unit area for both inoculated and fungicide-treated subplots). These miniplots were hand-harvested with sickles, bagged and transported to the laboratory. Tillers were counted and then threshed with a stationary power thresher. Seeds were cleaned and weighed to determine total grain weight for each miniplot. Two replicates of 100 seeds each were weighed from each miniplot to calculate the mean individual seed weight.

### Data analyses

Data were analyzed with the General Linear Model procedure (PROC GLM) of the Statistical Analysis Systems (SAS Institute 1988). Simple correlation coefficients were calculated between pairs of all measured variables and were resolved into direct and indirect effects separately for the pure stands and mixtures. Logically, the direct path coefficient of disease on yield should be zero, as disease affects plant yield through its effect on yield components, and non-zero values can be considered to be experimental error (Dewey and Lu 1959; Yang and Zeng 1989).

## Results

### Correlations

For the inoculated pure stands, all of the yield components were positively correlated to yield, though not all correlations were significant (Table 1). The number of heads per unit area had the highest significant correlation with yield in all three environments, irrespective of rust, except at Pendleton in 1994 (Table 1, 2). The number of heads per unit area and the number of seeds per head were positively correlated to yield both in the presence and absence of stripe rust (Tables 1, 2). However, individual seed weight was positively correlated to yield in all three environments in the presence of disease (Table 1) and negatively correlated to yield at Moro in 1993 and at Pendleton in 1994 in the absence of rust (Table 2). The correlation between yield and individual seed weight was not significant in any of the three environments in the absence of rust (Table 2), but it was significant in all three environments in the presence of rust (Table 1).

For the rust-infected mixtures, yield was negatively correlated to rust in all of the environments, but the correlation was significant only at Pendleton in 1994 (Table 3). Irrespective of environment, the highest correlation was between yield and number of heads, followed by individual seed weight, with both correlations being significantly positive. The correlation between yield and number of seeds per head was significant and positive for Moro. At Pendleton, the correlations between yield and seed per head were nonsignificant in both years, and were positive in 1994 and negative in 1993. For the fungicide-treated mixtures, all of the yield components were significantly and positively correlated to yield, except for individual seed weight at Pendleton in 1994, which had an insignificant negative correlation (Table 4). The highest correlation was observed with number of heads per unit area, followed by number of seeds per head and weight of individual seed.

### Path analyses

For pure stands, variables with the highest correlations with yield (Tables 5, 6) also produced the largest direct

**Table 1** Correlations[a] among stripe rust, yield and yield components of four winter wheat cultivars in three environments

| Components | Head number | Yield | Seed/head | Seed wt. |
|---|---|---|---|---|
| Moro 1993 | | | | |
| Rust | −0.450* | −0.257 | 0.324 | −0.131 |
| Head number | – | 0.685*** | −0.265 | −0.103 |
| Yield | | – | 0.402 | 0.446* |
| Seed/head | | | – | 0.229 |
| Seed wt. | | | | – |
| Pendleton 1993 | | | | |
| Rust | 0.016 | −0.241 | −0.246 | −0.502** |
| Head number | – | 0.819*** | 0.093 | 0.086 |
| Yield | | – | 0.558** | 0.453* |
| Seed/head | | | – | 0.190 |
| Seed wt. | | | | – |
| Pendleton 1994 | | | | |
| Rust | −0.006 | −0.730*** | −0.554** | −0.738*** |
| Head number | – | 0.392 | −0.298 | −0.273 |
| Yield | | – | 0.558** | 0.693*** |
| Seed/head | | | – | 0.447* |

*,** and *** Correlation coefficients are significant at $P \leqslant 0.10$, $P \leqslant 0.05$ and $P \leqslant 0.01$, respectively
[a]For correlations, data were pooled from all pure stands

**Table 2** Correlations[a] between yield and yield components for four winter wheat cultivars in absence of stripe rust in three environments

| Components | Yield | Seed/head | Seed wt. |
|---|---|---|---|
| Moro 1993 | | | |
| Head number | 0.929*** | 0.374 | −0.550** |
| Yield | – | 0.580** | −0.369 |
| Seed/head | | – | −0.455* |
| Seed wt. | | | – |
| Pendleton 1993 | | | |
| Head number | 0.933*** | −0.066 | 0.204 |
| Yield | – | 0.185 | 0.354 |
| Seed/head | | – | −0.328 |
| Seed wt. | | | – |
| Pendleton 1994 | | | |
| Head number | 0.812*** | −0.218 | −0.428* |
| Yield | – | 0.236 | −0.164 |
| Seed/head | | – | −0.232 |
| Seed wt. | | | – |

*, ** and *** Correlation coefficients are significant at $P \leq 0.10$, $P \leq 0.05$ and $P \leq 0.01$, respectively
[a] For correlations, data were pooled from all pure stands

effects, irrespective of environment or presence of rust (Tables 5, 6). Under inoculated conditions, the direct contributions of yield components to total yield were similar in all three environments, except for seed weight at Pendleton in 1994, which was much higher than that observed in the other two environments (Table 5). Moreover, the indirect negative effect of rust was higher for individual seed weight than for the number of seeds per head at Pendleton in 1994. The indirect effect of rust in 1993 was mostly through number of heads per unit area at Moro, whereas it was through number of seeds per head and individual seed weight at Pendleton. The direct effect of rust on the yield of pure stands was nearly zero in all three environments (Table 5).

Path analyses of the contribution of yield components to overall yield revealed that the components with the highest correlation coefficients produced the largest direct effects on yield for both fungicide-treated and inoculated mixtures (Tables 7, 8). The direct effect of rust on yield was zero (Table 7). Among the variables correlated with yield of mixtures, number of heads per unit area always had the largest direct effect. Overall, the direct contribution of the number of heads per unit area and number of seeds per head were slightly greater for healthy plants than for infected ones, while the direct contribution of weight of individual seeds was greater for rust-infected plants (Tables 7, 8). The indirect effect of stripe rust through the yield components was generally substantial only through individual seed weight, though at Pendleton in 1994 two other yield variables were also moderately affected (Table 7).

Overall, when the correlation coefficients among the yield components were resolved into direct and indirect effects, direct effects were similar for all yield components both for pure stands and mixtures, irrespective of environment and disease (Tables 5–8).

## Discussion

As opposed to other rusts, stripe rust epidemics begin in the early phenological growth stages of wheat and affect all of the yield components, including number of heads per unit area and number of seeds per heat (Finckh and Mundt 1992; Hendrix and Fuchs 1970; Yang and Zeng 1989). Alexander et al. (1986), however, found that stem rust, which occurred in the later growth stages of wheat, affected only grain size and not number of heads or number of seeds per head. Though all of the yield components in our experiments were affected by disease, individual seed weight, which is determined last in the developmental sequence of the yield variables, was most consistently reduced by rust for both pure stands and mixtures and in all three environments. According to

**Table 3** Correlations[a] among stripe rust, yield, and yield components of winter wheat cultivar mixtures in three environments

| Components | Head number | Yield | Seed/head | Seed wt. |
|---|---|---|---|---|
| Moro/93 | | | | |
| Rust | −0.076 | −0.034 | 0.353*** | −0.292** |
| Head number | – | 0.824*** | 0.001 | −0.099 |
| Yield | | – | 0.371*** | 0.294** |
| Seed/head | | | – | −0.113 |
| Seed wt. | | | | – |
| Pendleton/93 | | | | |
| Rust | 0.246* | −0.143 | −0.025 | −0.617*** |
| Head number | – | 0.795*** | −0.450*** | 0.141 |
| Yield | | – | −0.113 | 0.592*** |
| Seed/head | | | – | −0.197 |
| Seed wt. | | | | – |
| Pendleton/94 | | | | |
| Rust | −0.242* | −0.576*** | −0.285** | −0.381*** |
| Head number | – | 0.735*** | −0.164 | 0.029 |
| Yield | | – | 0.147 | 0.528*** |
| Seed/head | | | – | −0.297** |
| Seed wt. | | | | – |

*,** and *** Correlation coefficients are significant at $P \leqslant 0.10$, $P \leqslant 0.05$ and $P \leqslant 0.01$, respectively
[a]For correlations, data were pooled from three mixtures, each planted at five proportions

**Table 4** Correlations[a] between yield and yield components for winter wheat cultivars in absence of stripe rust in three environments

| Components | Yield | Seed/head | Seed wt. |
|---|---|---|---|
| Moro/93 | | | |
| Head number | 0.784*** | −0.073 | −0.195 |
| Yield | – | 0.469*** | 0.292** |
| Seed/head | | – | 0.299** |
| Seed wt. | | | – |
| Pendleton/93 | | | |
| Head number | 0.887*** | 0.302** | 0.086 |
| Yield | – | 0.628*** | 0.233* |
| Seed/head | | – | −0.201 |
| Seed wt. | | | – |
| Pendleton/94 | | | |
| Head number | 0.766*** | 0.133 | −0.494*** |
| Yield | – | 0.533*** | −0.099 |
| Seed/head | | – | −0.320** |
| Seed wt. | | | – |

*,** and *** Correlations coefficients are significant at $P \leq 0.1$, $P \leq 0.05$ and $P \leq 0.01$, respectively
[a] For correlations, data were pooled from all the mixtures

Gaunt (1980), disease present at the time of determination of yield components may be responsible for loss incurred, though an earlier infection may have an indirect effect via leaf area reduction.

Negative correlations among the yield components, both in the pure stands and mixtures, indicated that there was some yield component compensation. However, these correlations were large and significant in only a few cases. Yield component compensation has also been reported in field bean (Adams 1967; Hampton 1975; Van Bruggen and Arneson 1986). Yang and Zeng (1989), however, found no evidence for significant yield component compensation with wheat infected with stripe rust.

Path analysis indicated that all yield components were negatively affected by rust. However, a positve effect between disease and number of heads was found at Pendleton in 1993. Subplots with higher tiller densities, perhaps caused by random differences in stand establishment among subplots, would be expected to yield higher, but might also provide a more favorable microenvironment for rust increase. A large degree of stand variability was observed at Pendleton in 1993 than in the other two experiments. A similar effect was found in the rice blast pathosystem, where leaf blast was positively correlated with the number of effective tillers (Torres and Teng 1993).

Irrespective of environment, path coefficients reveal that number of heads per unit area had the largest direct positive effect on yield in both the presence and absence of rust and for both pure stands and mixtures. For mixtures, number of seeds per head had the second largest direct positive effect on yield under fungicide-treated conditions, whereas under inoculated conditions, weight of individual seed had the second largest effect. A similar trend was found for pure stands, though in the presence of rust there was not much difference between the direct effects of number of seeds per head and weight of individual seed to yield. Number of seeds per head is expected to be greater in the absence than in the presence of disease, but increased seed number will increase competition between seeds, thus reducing seed weight. As a result, increased number of seeds per head would result in increased total yield. In the presence of rust, number of seeds per head is expected to be lower than in the absence of rust, which would reduce competition among the kernels and enable seed size to have a significant positive influence on yield.

A low correlation between variables can be the result of a balance between opposed paths of influence leading from common causes (Wright 1921). A nonsignificant correlation does not mean, however, that the individual paths would be unimportant. For example, under rust-free conditions, the correlation between yield and weight

**Table 5** Direct and indirect path coefficients of yield components and stripe rust severity to yield of four winter wheat cultivars in three environments

| Pathways of association | Environment | | |
|---|---|---|---|
| | Moro/93 | Pend./93 | Pend./94 |
| Stripe rust vs yield | | | |
| Direct effect | 0.021 | 0.009 | 0.058 |
| Indirect via head number | −0.396 | 0.012 | −0.004 |
| Indirect via seed/head | 0.173 | −0.106 | −0.259 |
| Indirect via seed wt. | −0.055 | −0.156 | −0.525 |
| Total correlation | −0.257 | −0.241 | −0.730*** |
| Head number vs yield | | | |
| Direct effect | 0.879 | 0.752 | 0.727 |
| Indirect via rust | −0.009 | 0.000 | −0.001 |
| Indirect via seed/head | −0.141 | 0.040 | −0.139 |
| Indirect via seed wt. | −0.043 | 0.027 | −0.195 |
| Total correlation | 0.686*** | 0.819*** | 0.392 |
| Seed/head vs yield | | | |
| Direct effect | 0.533 | 0.431 | 0.467 |
| Indirect via rust | 0.007 | −0.002 | −0.032 |
| Indirect via head number | −0.233 | 0.070 | −0.217 |
| Indirect via seed wt. | −0.095 | 0.059 | 0.342 |
| Total correlation | 0.402 | 0.558** | 0.560** |
| Seed weight vs yield | | | |
| Direct effect | 0.417 | 0.311 | 0.712 |
| Indirect via rust | −0.003 | −0.005 | −0.043 |
| Indirect via head number | −0.091 | 0.065 | −0.199 |
| Indirect via seed/head | 0.122 | 0.082 | 0.223 |
| Total correlation | 0.446* | 0.453* | 0.693*** |

*,** and *** Significant at $P \leqslant 0.1$, $P \leqslant 0.05$ and $P \leqslant 0.01$, respectively

**Table 6** Direct and indirect path coefficients of yield components to yield of four winter wheat cultivars in the absence of stripe rust in three environments

| Pathways of association | Environment | | |
|---|---|---|---|
| | Moro/93 | Pend./93 | Pend./94 |
| Head number vs yield | | | |
| Direct effect | 0.977 | 0.898 | 1.138 |
| Indirect via seed/head | 0.137 | −0.022 | −0.129 |
| Indirect via seed wt. | −0.185 | 0.057 | −0.197 |
| Total correlation | 0.929*** | 0.933*** | 0.812*** |
| Seed/head vs yield | | | |
| Direct effect | 0.367 | 0.337 | 0.591 |
| Indirect via head number | 0.365 | −0.059 | −0.248 |
| Indirect via seed wt. | −0.153 | −0.092 | −0.107 |
| Total correlation | 0.579** | 0.186 | 0.236 |
| Seed wt. vs yield | | | |
| Direct effect | 0.336 | 0.281 | 0.460 |
| Indirect via head number | −0.538 | 0.183 | −0.487 |
| Indirect via seed/head | −0.167 | −0.110 | −0.137 |
| Total correlation | −0.369 | 0.354 | −0.164 |

*,** and *** Significant at $P \leqslant 0.05$ and $P \leqslant 0.01$, respectively

of individual seed was found to be negative at Pendleton in 1994 for both the pure stands and mixtures, and at Moro for pure stands and for fungicide-treated mixtures. With path analysis, it was revealed that seed weight had a large and positive direct effect on yield. Hence, increased seed weight would ultimately increase total yield. However, the more subtle indirect negative effects through number of heads and number of seeds per head masked the direct effect of individual seed weight to overall yield in the correlation analyses.

There were considerable differences between mixtures and pure stands with respect to correlation coefficients. For example, disease had larger negative correlations with yield in pure stands than in mixtures. This would be expected, as mixtures reduce the overall level of stripe rust relative to pure stands (Akanda and Mundt 1996a). Moreover, in the presence of rust, number of seeds per head had a positive correlation with individual seed weight in pure stands but was negatively correlated in mixtures. The higher level of disease in pure

**Table 7** Direct and indirect path coefficients of yield components and stripe rust severity to yield of winter wheat cultivar mixtures in three environments

| Pathways of association | Environment | | |
|---|---|---|---|
| | Moro/93 | Pend./93 | Pend./94 |
| Stripe rust vs yield | | | |
| Direct effect | 0.011 | −0.035 | −0.010 |
| Indirect via head number | −0.066 | 0.223 | −0.191 |
| Indirect via seed/head | 0.147 | −0.010 | −0.132 |
| Indirect via seed wt. | −0.126 | −0.321 | −0.243 |
| Total correlation | −0.034 | −0.143 | −0.576*** |
| Head number vs yield | | | |
| Direct effect | 0.867 | 0.909 | 0.790 |
| Indirect via rust | −0.001 | −0.009 | 0.002 |
| Indirect via seed/head | 0.001 | −0.179 | −0.076 |
| Indirect via seed wt. | −0.043 | 0.074 | 0.019 |
| Total correlation | 0.824*** | 0.795*** | 0.735*** |
| Seed/head yield | | | |
| Direct effect | 0.415 | 0.398 | 0.464 |
| Indirect via rust | 0.004 | 0.001 | 0.003 |
| Indirect via head number | 0.001 | −0.409 | −0.130 |
| Indirect via seed wt. | −0.049 | −0.103 | −0.190 |
| Total correlation | 0.371*** | −0.113 | 0.147 |
| Seed weight vs yield | | | |
| Direct effect | 0.430 | 0.520 | 0.639 |
| Indirect via rust | −0.003 | 0.022 | 0.004 |
| Indirect via head number | −0.086 | 0.128 | 0.023 |
| Indirect via seed/head | −0.047 | −0.078 | −0.138 |
| Total correlation | 0.294** | 0.592*** | 0.528*** |

** and *** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively

**Table 8** Direct and indirect path coefficients of yield components to yield of winter wheat cultivar mixtures in the absence of stripe rust in three environments

| Pathways of association | Location/Year | | |
|---|---|---|---|
| | Moro/93 | Pend./93 | Pend./94 |
| Head number vs yield | | | |
| Direct effect | 0.881 | 0.725 | 0.968 |
| Indirect via seed/head | −0.032 | 0.140 | 0.078 |
| Indirect via wt./seed | −0.065 | 0.023 | −0.280 |
| The correlation | 0.784*** | 0.888*** | 0.7668*** |
| Seeds/head vs yield | | | |
| Direct effect | 0.434 | 0.462 | 0.585 |
| Indirect via head number | −0.065 | 0.219 | 0.129 |
| Indirect via wt./seed | 0.100 | −0.053 | −0.181 |
| Total correlation | 0.469*** | 0.628*** | 0.533*** |
| Weight/seed vs yield | | | |
| Direct effect | 0.334 | 0.264 | 0.567 |
| Indirect via head number | −0.171 | 0.062 | −0.478 |
| Indirect via seed/head | 0.129 | −0.093 | −0.188 |
| Total correlation | 0.292** | 0.233* | −0.099 |

*,** and *** Significant at $P \leqslant 0.1$, $P \leqslant 0.05$ and $P \leqslant 0.01$, respectively

stands compared to mixtures may have resulted in a reduction of number of seeds per head and, hence, reduced competition between seeds, resulting in higher seed weight and a positive correlation between number of seeds per head and individual seed weight. In contrast, the lower level of disease in mixtures would increase the number of seeds per head relative to pure stands, resulting in more competition between seeds and thus lowering the seed weight. Path analysis showed that most discrepancies between mixtures and pure stands were due predominately to indirect, opposing effects and that the mixtures and pure stands were very similar with respect to direct effects of yield components.

Plant–plant interactions or other complex interactions that occur in mixtures (Alexander et al. 1986; Burdon et al. 1984; Finckh and Mundt 1992) may have influenced correlations among yield components. Burdon et al. (1984) found that *Puccinia chondrilla* reversed the competitive abilities of *Chondrilla juncea* when grown in a mixture, the susceptible cultivar being the stronger competitor in the absence of disease, while the resistant one was the stronger competitor in the presence of rust. Finckh and Mundt (1992) found that wheat cultivars differed significantly in competitive ability in mixtures and that the presence of stripe rust influenced these differences by selecting for increased tillering of resistant or susceptible cultivars. It is unclear at this point how these complex competitive interactions may affect correlations among yield components.

In summary, our results suggest that number of heads per unit area was the most important yield component with the largest, absolute direct effect on yield, irrespective of disease, both for pure stands and mixtures. Number of seeds per head was the second most important yield component in the absence of rust, with positive effects on yield for both mixtures and pure stands. Under inoculated conditions, individual seed weight was the second most important yield component for mixtures, but for pure stands the contribution of number of seeds per head and individual seed weight to total yield was similar. It is also evident that the direct effects of yield components to yield were similar for both pure stands and mixtures and that most of the discrepancies between correlation coefficients and direct effects were due to indirect, opposing effects. Thus, path analysis uncovered relationships that would have otherwise remained confounded in correlation coefficients.

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