

## Biometrical analysis of alternative plot types for selection in rye

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### Summary

Maximizing the efficiency of selection for yield and baking quality of winter rye (*Secale cereale* L.) requires reliable knowledge on the pertinent population parameters. This study reports estimates of variances, heritabilities and genetic correlations from a) large ( $\approx 5 \text{ m}^2$ ) drilled (LD) plots, b) micro drilled (MD) plots, and c) one-row plots of 4 spaced plants (SP). Thirty eight single crosses of rye were grown at two locations for two years in LD, MD and SP plots replicated 2, 4, and 6 times, respectively. Genotypic differences were significant in all plot types for all agronomic and quality traits, although estimates of genetic variances were smaller in LD than MD or SP plots for grain yield, 32-spike weight, and kernels per spike. Heritabilities on an entry mean basis (0.62 to 0.95) were similar among plot types, but on a single plot basis estimates were lower for SP than for MD or LD plots. Genetic correlations were high between all three plot types, with correlations between LD and SP plots being approximately 1.0 for falling number, thousand-kernel weight, and bloom date, 0.90 for grain yield, kernels per spike, test weight and height, and 0.70 for tiller number. Based on the high heritabilities achieved in small plots and the close agreement between MD- or SP- with LD-plot performance we conclude that greater use should be made of small plot types when selecting for yield and quality in winter rye.

### Introduction

The goals of selection in rye (*Secale cereale* L.) are to increase grain yield, baking quality, and resistances to lodging and diseases of populations and of hybrids formed from superior inbreds. Selection as practised at the University of Hohenheim (Geiger, 1982; Geiger, 1988) relies on evaluating line *per se* or testcross performance in plot types ranging from cloned plants spaced at 25 cm intervals to 4–5 m<sup>2</sup> plots with rows drilled at optimal field densities (180 to 300 plants m<sup>-2</sup>). Typically one to three plot types are used for evaluation within each cycle of multistage selection, with grain quality and agron-

omic traits observed on smaller plots whereas grain yield determinations are made on larger plots (Wilde & Geiger, 1984; Wilde, 1987).

Optimum plot size for evaluation in a single environment was determined from statistics of plot to plot variability (Koch & Rigney, 1951; Hatheway & Williams, 1958; Durner, 1989; Frey & Baten, 1953) primarily using an index of soil variability proposed by Smith (1938). Utility of plots differing in size and form for selection in small-grains was assessed by estimation of heritabilities in, and genetic correlations among the alternative plot types (Frey, 1965; Kramer et al., 1982; Spitters, 1984). Results vary with crop species and trait under selec-

tion (Weber, 1984). For example, interactions of genotypes with plot types were greater in barley (*Hordeum vulgare*) than in oat (*Avena sativa* L.) (Ross & Miller, 1955). In the latter species these interactions were greater for lodging than for grain yield (Frey, 1965).

An effort was made in rye to identify optimal resource allocation for multistage recurrent selection using an array of plot types (Wilde, 1987). Lacking, however, were estimates of variance components from the different plot types based on identical genetic entries grown in the same environments. Also lacking were estimates of the genetic correlation between the alternative plots used for evaluation and the target environment (drilled stand with minimized border effects). The purpose of this study is to provide those biometric estimates that are needed to maximize the gain from selection in rye. Estimates of (a) heritabilities on an entry mean-, plot- and single plant basis, (b) components of variance, and (c) genotypic correlations between plot types are to be computed for 4–5 m<sup>2</sup> and ≈ 1 m<sup>2</sup> drilled plots, as well as for space-planted plots. Implications of these results for ongoing recurrent selection programs will be discussed.

## Materials and methods

### *Genetic materials*

Forty-eight single crosses were formed by crossing 18 self-fertile inbred lines from the Petkus gene pool in an incomplete diallel. The lines represent a broad sample of the elite seed parent materials developed in the hybrid breeding programs at the University of Hohenheim and the seed firm Hybro GbR, Bad Schönborn, Germany. Cytoplasmic male sterile (CMS) A lines were open-pollinated in isolated plots by a male-fertile B line. As both parents were lacking fertility restorer alleles the resulting single crosses were male sterile and fertilization in the evaluation trials was assured by pollen from plots of the male-fertile population variety Halo, sown on the perimeter of each experiment, and from fertile plants in adjacent experiments. Both A and B lines were practically homozygous.

Each single cross was therefore considered to represent one genotype.

### *Field trials*

The single crosses were evaluated in field trials conducted for two seasons (1987/1988 and 1988/1989) at Hohenheim and Oberer Lindenhof in southern Germany. Hohenheim (350 m altitude) and Oberer Lindenhof (705 m) differ considerably in mean annual temperature (8.5°C and 6.4°C, respectively) and mean annual precipitation (685 mm, 912 mm). The single crosses were tested in the three plot types described below, with each plot type occurring in a separate but adjacent block in the same field.

Space-planted (SP) plots: Seeds of each single cross were planted in pots and the seedlings were transplanted to the field at approximately 6 weeks after sowing. Four plants per single cross were transplanted in a row which constituted one space-planted plot. Distances between plants within rows and between rows were 20 cm at Hohenheim (HOH) and 27 cm at Oberer Lindenhof (OLI) resulting in plot sizes of 0.16 m<sup>2</sup> at HOH and 0.29 m<sup>2</sup> at OLI. Alleys of 50 cm separated ranges of plots.

Micro drilled (MD) plots: Four-row plots of 1.2 m (HOH) and 1.5 m length (OLI) were drilled with 18 cm between rows and 70 cm separating outer rows of adjacent plots. These micro drilled plots of approximately 1 m<sup>2</sup> (0.86 m<sup>2</sup> HOH, 1.08 m<sup>2</sup> OLI) correspond to the smallest plots currently used for yield evaluation in rye (Wilde, 1987).

Large drilled (LD) plots: Large drilled, 1.25 m wide plots with 8 rows, 13 cm between inner and 34 cm between outer rows, and 3.8 m row length (HOH) or 6 rows, 18 cm between inner and 35 cm between outer rows, and 4.0 m row length (OLI) provided plots of 4.75 m<sup>2</sup> and 5.0 m<sup>2</sup>, respectively.

Seeding rates of MD and LD plots were adjusted to give 300 plants m<sup>-2</sup> on the basis of the germinability and thousand-kernel weight of each entry.

Assignments of genotypes to plots within each experiment were according to randomizations of a 7 × 7 lattice in 1987/1988 and a 6 × 7 lattice in 1988/1989. In the first test year one cross was in-

cluded twice to complete the lattice. In the second test year 10 single crosses had to be excluded due to insufficient seed supply and 4 crosses were entered twice. Experiments had 6, 4 or 2 replications per environment for the SP, MD and LD plots, respectively, taking into consideration the larger errors of the smaller plots.

### Traits

Bloom date was recorded as the date in May that the primary spikes headed (OLI) or exhibited anthesis (HOH) on 50% of the plants. Plant height was observed on a whole plot basis. The number of tillers bearing spikes was counted in entire SP plots but only in a 1 m length of a bordered row of MD and LD plots. A plot combine was used to harvest all rows of the MD and LD plots whereas the SP plots were hand harvested and threshed in a head thresher. The grain was dried with forced air (35°C). Thousand-kernel weight was determined twice per plot on samples of 100 seeds. The 32-spike weight was measured from 32 random primary spikes per LD plot and from the 8 largest spikes per plant in SP plots. The number of kernels per spike in LD and SP plots was computed from the mean grain weight per spike and the mean 1000-kernel weight. The straw of space-planted plots was harvested, dried and weighed at both locations in 1989. Grain yield and straw yield were summed to estimate biomass. Harvest index was calculated by dividing grain yield by biomass and multiplying by 100. Test weight was assessed once per MD and LD plot using a standard 250 ml cylinder and twice per SP plot by pouring seed through a funnel into a 25 ml graduated cylinder up to the 25 ml graduation. Falling number (Hagberg, 1960; Doerre, 1979), was determined by milling 80 to 100 gram samples of grain in a Cyclotec 1093 Tecator mill, and using 7 g of flour in the Falling Number 1600 machine.

### Statistical analysis

Analyses of variance and covariance in each ex-

periment (plot type-year-location combination) were conducted according to their respective lattice designs. Combined analyses over environments for each plot type were computed with the lattice adjusted means of 38 genotypes common to both years of testing. The combined analyses were performed twice; once with the four environments structured into locations and years and once with the environments considered as an unstructured set. All effects were assumed to be random.

Components of variance were estimated by setting the mean squares equal to their expectations. Heritabilities ( $h^2$ ) were computed based on entry means, single plots, or single plants (only in SP plots) according to the following formulae (Fehr, 1987):

$$\text{Entry mean } h^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{ge}^2/E + \sigma^2/ER)$$

$$\text{Plot } h^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{ge}^2 + \sigma^2)$$

$$\text{Individual plant } h^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{ge}^2 + \sigma_r^2 + \sigma_w^2)$$

where

- $\sigma_g^2$  = genetic component of variance
- $\sigma_{ge}^2$  = genotype  $\times$  environment interaction
- $\sigma_r^2$  = residual variance between plots
- $\sigma_w^2$  = within-plot variance (only in SP plots)
- $\sigma^2 = \sigma_r^2 + \sigma_w^2/N$  = error variance
- E = number of environments
- R = number of replications
- N = number of plants per plot

The within-SP-plot variances were estimated from single plant data collected for five genotypes in each test environment for all traits besides harvest index and biomass. Variance components from the analysis of unstructured environments were used to estimate heritabilities so as to avoid too large sampling errors of the interaction terms arising from the limited number of locations and years. Computation of the confidence intervals for the entry-mean heritabilities were according to Knapp et al. (1987) and the standard errors for plot- and single-plant heritabilities were based on the approximate method of Dickerson (1969).

The genetic correlation of traits X and Y ( $r_g$ ), where X and Y are different traits or the same trait evaluated in different plot types, was computed from estimates of the genetic covariance of X and Y [ $Cov_g(X, Y)$ ] and the genetic standard deviations of X and Y ( $\sigma_{gX}$  and  $\sigma_{gY}$ , respectively) according to the following formula:

$$r_g = Cov_g(X, Y) / (\sigma_{gX} \times \sigma_{gY})$$

The standard errors for the variance components and for the genetic correlations were computed according to Mode & Robinson (1959). All statistical analysis were performed with the PLABSTAT computer program (Utz, 1988).

Table 1. Heritability estimates on entry-mean, single-plot and single-plant basis for traits measured on 38 rye single crosses in large drilled (LD), micro drilled (MD) and space-planted (SP) plots in four environments

Character and plot type	Entry mean		Single plot	Single plant
Falling number				
LD	0.90	0.84–0.94 <sup>a</sup>	0.63 ± 0.16 <sup>b</sup>	
MD	0.88	0.80–0.93	0.55 ± 0.14	
SP	0.89	0.83–0.94	0.47 ± 0.12	0.33 ± 0.08 <sup>b</sup>
Test weight <sup>c</sup>				
LD	0.80	0.61–0.89	0.61 ± 0.18	
MD-bordered	0.71	0.44–0.85	0.38 ± 0.17	
MD-unbordered	0.88	0.76–0.94	0.67 ± 0.13	
SP	0.89	0.78–0.94	0.61 ± 0.16	0.32 ± 0.08
Grain yield				
LD	0.77	0.63–0.87	0.42 ± 0.12	
MD	0.84	0.73–0.91	0.46 ± 0.13	
SP	0.79	0.65–0.88	0.19 ± 0.06	0.10 ± 0.03
32-spike weight				
LD	0.91	0.85–0.95	0.60 ± 0.15	
SP	0.92	0.87–0.95	0.43 ± 0.11	0.30 ± 0.07
Kernels per spike				
LD	0.91	0.86–0.95	0.62 ± 0.15	
SP	0.90	0.83–0.94	0.40 ± 0.10	0.24 ± 0.06
Tiller number				
LD	0.64	0.41–0.79	0.20 ± 0.07	
MD	0.62	0.37–0.78	0.12 ± 0.05	
SP	0.71	0.52–0.83	0.12 ± 0.04	0.06 ± 0.02
Thousand-kernel weight				
LD	0.88	0.81–0.93	0.60 ± 0.15	
MD	0.93	0.89–0.96	0.63 ± 0.15	
SP	0.93	0.89–0.96	0.55 ± 0.13	0.37 ± 0.09
Plant height				
LD	0.89	0.82–0.94	0.61 ± 0.16	
MD	0.94	0.89–0.96	0.64 ± 0.16	
SP	0.95	0.91–0.97	0.46 ± 0.11	0.32 ± 0.08
Bloom date				
LD	0.74	0.58–0.85	0.36 ± 0.11	
MD	0.77	0.62–0.87	0.37 ± 0.11	
SP	0.82	0.70–0.90	0.29 ± 0.08	0.18 ± 0.05
Harvest index <sup>c</sup>				
SP	0.31	– 0.32–0.64	0.19 ± 0.16	–
Biomass <sup>c</sup>				
SP	0.62	0.27–0.80	0.45 ± 0.18	–

<sup>a</sup>Confidence intervals (Knapp, 1987), where  $1-\alpha = 0.95$ . <sup>b</sup>Standard error. <sup>c</sup>Data from one year, two locations only.

## Results

Heritabilities on an entry-mean basis were very similar between the large-drilled (LD), micro-drilled (MD) and the space-planted (SP) plots for all of the agronomic traits evaluated (Table 1). The traits showing the highest heritability (around 0.9) were falling number, 32-spike weight, kernels per spike, thousand-kernel weight and plant height. Heritabilities of approximately 0.8 were observed for grain yield, test weight, and bloom date. Tiller number showed the lowest heritability (0.62 to 0.71).

Estimates of heritability on a single-plot basis tended to be lower for the SP plots than the drilled plots, although the difference was only large for grain yield (Table 1). Despite the MD plots being five times smaller than the LD plots, they had single-plot heritabilities similar to LD plots for thousand-kernel weight, plant height and days to bloom as well as for grain yield.

The heritabilities estimated on a single-plant basis for grain yield and tiller number were near zero and very low for other characters including quality traits (0.18 to 0.37).

The plot type means across genotypes and environments were in the same order magnitude for most of the traits measured (Table 2). Estimates of genetic variance were highly significant ( $P < 0.01$ ) for all traits in each plot type evaluated with the exceptions of grain yield ( $P < 0.05$ ) and tiller number ( $P < 0.10$ ) in the LD plots (Table 2). The magnitudes of genetic variances estimates were similar in the different plot types for falling number, 1000-kernel weight, plant height, and bloom date. For grain yield and most yield components, however, there was less genetic variation expressed in the LD plots than in the smaller plots. As measured by the genetic coefficient of variation, a reduced variability in the LD-plot experiments was mainly observed for grain yield.

The components of genotype  $\times$  location and genotype  $\times$  year interaction were most often small and nonsignificant ( $P > 0.05$ ), particularly in the SP plots. Significant interactions of genotypes with locations in LD plots and with years in LD and MD plots were frequently observed for grain yield,

plant height, and bloom date. The genotype  $\times$  location  $\times$  year interaction was significant ( $P < 0.05$ ) for falling number and 1000-kernel weight in all three plot types and for bloom date in all but the SP plots.

Error variances decreased as the plot size became larger. The differences between plot types were relatively large for most traits. Small differences between LD and MD plots occurred for falling number, tiller number, plant height, and bloom date.

The genetic correlations among all three types of plots were near 1.0 for falling number, 1000-kernel weight, and bloom date (Table 3). Grain yield, test weight and plant height had genetic correlations near 1.0 between LD and MD and around 0.8 to 0.9 between the drilled plots and the SP plots. A similarly good agreement between LD and SP plots existed for 32-spike weight and kernels per spike. The weakest correlations (near 0.7) between SP and drilled plots were found for tiller number.

The cross correlations of yield components measured on space-planted plots with grain yield in drilled plots do not surpass the correlation SP grain yield as such, and are mostly much weaker (Table 4). The only SP plot trait whose correlation approached that of SP plot grain yield was that of total biomass.

## Discussion

Genetic differentiation for major agronomic traits of rye was found to be feasible using any of the three plot types examined. Large and micro drilled plots as well as space-planted plots provided high heritabilities on an entry-mean basis. Selection in MD and SP plots was encouraged by the high genetic correlations between the smaller plot types and the LD plots which best represent the target of selection. The entries in this study were genetically uniform and highly heterozygous. It remains to be determined, if such strong correlations between plot types would also apply to the more inbred or heterogeneous entries frequently occurring in early testing or recurrent selection programs.

Very low phenotypic correlations ( $r = 0.03$  to

Table 2. Variance component estimates and their standard errors, means and genetic coefficients of variation for 38 rye single crosses grown in large drilled (LD), micro drilled (MD) and space-planted (SP) plots for two years at two locations

Character Source of variation, and statistic, resp.	LD	MD	SP
<b>Falling number (seconds)</b>			
Genotype	1096 ± 276	976 ± 256	1187 ± 313
Genot × location	-46 ± 75	25 ± 92	89 ± 89
Genot × year	2 ± 82	-38 ± 83	93 ± 93
Genot × lc × yr	355 ± 117	463 ± 125	363 ± 119
Pooled error	311 ± 38	356 ± 25	978 ± 51
Mean	185.3	194.9	215.4
Genetic cv %	17.9	16.0	16.0
<b>Test weight<sup>a</sup> (kg hl<sup>-1</sup>)</b>			
Genotype	1.68 ± 1.20	1.02 ± 0.88	2.88 ± 0.20
Genot × location	0.66 ± 0.52	0.59 ± 0.68	0.48 ± 0.08
Pooled error	0.40 ± 0.20	1.07 ± 0.28	1.44 ± 0.04
Mean	73.2	72.8	70.0
Genetic cv %	1.8	1.4	2.4
<b>Grain yield (dt ha<sup>-1</sup> in LD and MD; g plant<sup>-1</sup> in SP plots)</b>			
Genotype	22.9 ± 12.3	49.2 ± 16.1	12.9 ± 4.4
Genot × location	13.8 ± 5.0	-3.3 ± 4.3	2.7 ± 2.7
Genot × year	32.2 ± 9.0	24.8 ± 9.6	1.6 ± 1.6
Genot × lc × yr	5.7 ± 3.4	22.9 ± 6.8	4.0 ± 2.9
Pooled error	17.0 ± 2.1	28.0 ± 1.9	53.5 ± 2.7
Mean	62.4	65.1	34.0
Genetic cv %	7.7	10.8	10.6
<b>32-spike weight (g)</b>			
Genotype	41.3 ± 11.0	- -	73.7 ± 18.8
Genot × location	3.9 ± 2.8	- -	4.2 ± 4.3
Genot × year	3.2 ± 2.6	- -	1.9 ± 3.9
Genot × lc × yr	1.5 ± 3.2	- -	7.6 ± 5.1
Pooled error	22.2 ± 2.7	- -	87.4 ± 4.5
Mean	70.1	- -	76.4
Genetic cv %	9.2	- -	11.2
<b>Kernels per spike</b>			
Genotype	19.3 ± 5.1	- -	29.1 ± 7.7
Genot × location	2.6 ± 1.4	- -	3.2 ± 2.4
Genot × year	0.6 ± 1.0	- -	-0.6 ± 1.8
Genot × lc × yr	0.6 ± 1.4	- -	5.3 ± 2.7
Pooled error	9.7 ± 1.2	- -	38.3 ± 2.0
Mean	53.6	- -	58.9
Genetic cv %	8.2	- -	9.2
<b>Tiller number (no. m<sup>-2</sup> in LD and MD, no. plant<sup>-1</sup> in SP plots)</b>			
Genotype	1175 ± 656	892 ± 408	1.2 ± 0.6
Genot × location	696 ± 563	171 ± 387	0.6 ± 0.4
Genot × year	473 ± 522	-79 ± 346	0.4 ± 0.4
Genot × lc × yr	142 ± 701	807 ± 517	0.2 ± 0.5
Pooled error	5217 ± 642	5734 ± 398	10.5 ± 0.5
Mean	426	474	16.6
Genetic cv %	8.0	6.3	6.7

Table 2. Continued.

Character	LD	MD	SP
Source of variation, and statistic, resp.			
<b>Thousand-kernel weight (g)</b>			
Genotype	5.5 ± 1.6	6.3 ± 1.6	7.4 ± 1.9
Genot × location	0.7 ± 0.5	0.4 ± 0.3	0.7 ± 0.4
Genot × year	0.8 ± 0.5	0.0 ± 0.3	0.2 ± 0.3
Genot × lc × yr	1.3 ± 0.5	1.0 ± 0.4	0.9 ± 0.4
Pooled error	1.7 ± 0.2	2.5 ± 0.2	4.8 ± 0.3
Mean	40.0	37.5	40.6
Genetic cv %	6.3	6.7	6.7
<b>Plant height (cm)</b>			
Genotype	21.3 ± 6.1	23.1 ± 5.9	21.5 ± 5.1
Genot × location	3.2 ± 1.6	0.0 ± 0.8	-0.8 ± 0.7
Genot × year	4.2 ± 1.8	2.9 ± 1.3	0.7 ± 0.9
Genot × lc × yr	2.8 ± 1.5	2.5 ± 1.1	0.7 ± 1.1
Pooled error	7.3 ± 0.9	8.8 ± 0.6	24.5 ± 1.3
Mean	119.3	119.0	108.1
Genetic cv %	3.9	4.0	4.3
<b>Bloom date (days in May)</b>			
Genotype	0.81 ± 0.37	0.80 ± 0.31	0.50 ± 0.17
Genot × location	0.57 ± 0.26	0.17 ± 0.16	0.19 ± 0.09
Genot × year	0.28 ± 0.20	0.37 ± 0.20	0.09 ± 0.07
Genot × lc × yr	0.49 ± 0.22	0.66 ± 0.19	0.15 ± 0.08
Pooled error	0.94 ± 0.12	0.66 ± 0.05	1.13 ± 0.06
Mean	27.1	26.9	28.7
Genetic cv %	3.3	3.3	2.5
<b>Harvest index<sup>a</sup></b>			
Genotype	-	-	1.15 ± 1.02
Genot × location	-	-	2.89 ± 1.17
Pooled error	-	-	2.20 ± 0.19
Mean			41.1
Genetic cv %			2.6
<b>Biomass<sup>a</sup> (g plot<sup>-1</sup>)</b>			
Genotype	-	-	65.21 ± 25.40
Genot × location	-	-	23.02 ± 18.58
Pooled error	-	-	56.40 ± 4.86
Mean			87.9
Genetic cv %			9.2

<sup>a</sup> Data from one year, two locations; MD values from two bordered rows presented, MD values from two unbordered rows resemble those of LD.

0.15) for grain yield of rye were found between spaced plants and their open pollinated progenies in four-row drilled plots (Wolski et al., 1972). Considering the low heritabilities of individual spaced plants (Table 1), such low phenotypic correlations may well occur despite high genetic correlations (Falconer, 1989). Frey (1965) estimated a genetic

correlation of  $r = 0.98$  for grain yield of oats (*Avena sativa* L.) from hill plots (30 plants) with that from single-row drilled plots (400 plants). Spitters (1984) reported estimates of 0.24 and 0.83 for yields of single-plant and three-row drilled plots, respectively, with 10 m<sup>2</sup> drilled plots, based on re-

sults from wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare*) trials.

The heritabilities estimated on an entry-mean basis represented the maximum levels achievable in recurrent selection as the extent of testing was greater than is practised in current programs (see below). Furthermore, the numerators include non-additive components of genetic variance as they are broad sense estimates. Upward bias due to partial confounding of genotype  $\times$  location and genotype  $\times$  year interactions with the genetic effects was possible because estimates from an analysis of unstructured environments were used (Hanson, 1964). This type of bias was negligible except for grain yield, tiller number and bloom date, primarily in LD plots, as determined by comparing heritabilities computed for the different models.

A typical recurrent selection (RS) scheme for improving grain yield and quality in rye is based on a three year cycle (Geiger, 1982):

1st year:

Each  $S_0$  genotype is testcrossed to a CMS single cross tester. The  $S_0$  plant is cloned into 4 parts which are transplanted next to the tester genotype and serve as its pollinator as well as for production of  $S_1$  seed.

2nd year:

Testcross progenies and  $S_1$ -lines are evaluated; Seed quantities are sufficient for 4 to 6 LD or 16 to 24 MD plots of each testcross progeny and of 1 LD or about 4 MD plots of each  $S_1$  line.

3rd year:

Selected  $S_1$  lines are intercrossed to form the improved population.

The population of single crosses used in this study possess the same genetic structure as the population of random  $S_0$  clones serving as selection units in the above RS scheme. Our results demonstrate that selecting on  $S_0$  space-planted clones in the first year of each RS-cycle is indeed effective. The gain from selection ( $G(y)$ ) on the mean of 4  $S_0$  cloned plants for performance in the target environment is predicted as (Falconer, 1989):

$$G(y) = i h_x r_G \sigma_y$$

where  $i$  is the selection intensity,  $h_x$  the square root of the heritability of the selection criterion, i.e. the performance of a single SP plot,  $r_G$  the genetic correlation of the performance in SP plots with the performance in LD plots, and  $\sigma_y$  the genetic standard deviation of the entries for the desired trait in LD plots. The predicted gains in LD-plot performance from selection in SP plots, assuming a selected fraction of 0.5 ( $i = 0.8$ ), were for grain yield 148 kg ha<sup>-1</sup>, for falling number 18 seconds, for plant height 2.2 cm, and for 1000-kernel weight 1.4 g. Similar gains in grain yield were predicted for selecting directly on grain yield, and indirectly on 32-spike weight, 1000-kernel weight, and biomass (Table 4). In contrast, selection on tiller number or kernels per spike was much less effective.

Table 3. Estimates of genetic correlations, their standard errors, and phenotypic correlations between large drilled (LD), micro drilled (MD) and space-planted (SP) plots for agronomic characters measured on 38 rye single crosses in four environments

Trait	Genetic correlation			Phenotypic correlation <sup>a</sup>		
	LD-MD	LD-SP	MD-SP	LD-MD	LD-SP	MD-SP
Falling no.	1.01 $\pm$ 0.02	0.98 $\pm$ 0.02	0.99 $\pm$ 0.02	0.95	0.94	0.95
Test wt.	1.07 $\pm$ 0.07	0.87 $\pm$ 0.07	0.90 $\pm$ 0.08	0.87	0.79	0.77
Grain yld.	1.01 $\pm$ 0.02	0.89 $\pm$ 0.07	0.82 $\pm$ 0.08	0.93	0.79	0.73
32-spike wt.	–	0.96 $\pm$ 0.03	–	–	0.90	–
Kernels per sp.	–	0.91 $\pm$ 0.04	–	–	0.86	–
Tiller no.	0.91 $\pm$ 0.15	0.71 $\pm$ 0.16	0.69 $\pm$ 0.16	0.63	0.54	0.54
1000-K. wt.	0.97 $\pm$ 0.02	0.97 $\pm$ 0.02	0.98 $\pm$ 0.02	0.93	0.92	0.95
Plant ht.	1.00 $\pm$ 0.01	0.88 $\pm$ 0.05	0.85 $\pm$ 0.05	0.96	0.84	0.82
Bloom date	0.97 $\pm$ 0.03	0.95 $\pm$ 0.06	0.95 $\pm$ 0.05	0.91	0.81	0.85

<sup>a</sup> All significant at  $P < 0.01$ .



The predicted responses encourage direct and indirect selection on the basis of  $S_0$  clone performance. However, as the objective in recurrent selection is the improvement of general combining ability (GCA) more realistic predictions of gains would be obtained by multiplying the computed responses by the genetic correlations between the GCA and the genotypic value of the  $S_0$  genotypes under selection. Further research is necessary to estimate this correlation.

Syme (1972) and Fischer & Kertesz (1976) working with spring wheat (*Triticum aestivum*) concluded from their data that the harvest index of spaced plants offers a better criterion for improving grain yield under dense stands than grain yield itself or yield components. Our study, however, found harvest index to be a poor criterion for improving grain yield (Table 4). Biomass of space-planted material provided a better selection criterion, although no better than grain yield *per se*.

The quantities of testcross seed and selfed seed produced in the first year of a RS cycle are sufficient for testing in either LD or MD plots. Based on our results we expect considerable advantage in using MD rather than LD plots as the heritability levels were similar, even on a single plot basis, and the genetic correlations between the two plot types

were high for all traits. The much lower seed requirement per MD plot would enable significant increase in the numbers of locations and replications relative to testing in LD plots. Use of plots with even smaller seed requirements than MD plots, for example hill plots of 0.1 m<sup>2</sup>, have already been shown to be feasible in recurrent selection for grain yield and quality in small grains (Frey, et al., 1988).

The expression of larger genetic variation for grain yield in MD relative to LD plots was previously reported in rye by Wilde (1987), although those differences were not as pronounced as in this study. The MD and SP plots have a much larger proportion of unbordered plants than LD plots. Greater access to growth resources by plants in MD and SP plots, particularly in periods of insufficient rainfall, may enable better expression of genetic differences for grain yield. This is substantiated by the greater genetic coefficients of variation for grain yield in the two unbordered (outer) rows as compared to the two bordered (inner) rows in the 1989 MD plots, these being 21.0% and 16.1% at Oberer Lindenhof, and 9.8% and 5.7% at Hohenheim, respectively. Fasoulas (1984) suggested that competition between plants can reduce genetic differences for yield in small grains. Spitters (1984) reported genetic coefficients of variation generalized from barley and spring wheat yields of 21% for single spaced plants, 11% for single rows, and 5% for 10 m<sup>2</sup> plots.

The expression of grain yield in SP, MD, and LD plots of rye seem to be basically the same despite the differences in competition experienced. Not only were there high genotypic correlations between the small plot types and LD plots, but there were equally high genetic correlations of yield in LD plots with yield in both the unbordered ( $r_g = 0.97 \pm 0.04$ ) and the bordered MD rows ( $r_g = 1.04 \pm 0.07$ ) over two locations in 1989. Additional research is necessary to verify these findings in other populations and environments.

Table 4. Estimates of genetic correlations ( $r_g$ ), their standard errors, and phenotypic correlations ( $r_p$ ) of traits assessed in space-planted (SP) plots to grain yield in large drilled (LD) plots and the predicted gain in grain yield in LD plots from selection on various traits in SP plots (selected fraction = 0.5; for further explanations see Discussion)

Traits in SP plots	Corr. to LD gr.yd.		Exp. gain	
	$r_g$	$r_p$	kg ha <sup>-1</sup>	rel. <sup>a</sup>
Grain yield	0.89 ± 0.07	0.79**	148	2.4
32-spike wt.	0.58 ± 0.13	0.55**	145	2.3
Kernels per sp.	0.29 ± 0.18	0.29	70	1.1
Tiller no.	0.30 ± 0.20	0.29	40	0.6
1000-K. wt.	0.58 ± 0.13	0.53**	164	2.6
Harvest index <sup>b</sup>	0.28 ± 0.31	0.27	30	0.5
Biomass <sup>b</sup>	0.84 ± 0.12	0.69**	140	2.2

<sup>a</sup>Percent of mean yield in LD plots. <sup>b</sup>Two locations in 1989.

\*\* Significant at  $P < 0.01$ .

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