

Prediction of the performance of inbred lines derived from a population cross in autumn-sown onions (*Allium cepa* L.)

C. P. Werner^{1,*}, M. J. Kearsey¹, T. C. Crowther² and B. D. Dowker²

¹ School of Biological Sciences, Birmingham University, P.O. Box 363, Birmingham B15 2TT, UK

² Institute of Horticultural Research, Wellesbourne, Warwick CV35 9EF, UK

Received September 6, 1989; Accepted November 2, 1989
Communicated by A. R. Hallauer

Summary. A design and model are presented to allow the prediction, in early generations, of the mean and distribution of recombinant inbred lines derived from a cross between two parental populations or partially inbred lines. The procedure has been tested in autumn-sown onions (in the UK) using a wide cross between the open-pollinated Japanese cultivar, Senshyu, and a partially inbred line derived from the European cultivar, Rawska. The early generations used for prediction included the first self-pollinated generation of the two parental populations and the F₃ generation produced from the hybrid population. The predictions were tested by reference to the field performance of a random array of inbred lines, which were produced by single-seed descent (SSD) and had been selfed for three generations. The early generations, used for prediction, and a sample of SSD lines were raised alongside each other in each of two seasons. Within each season, good agreement was found between the predicted and observed performance of the recombinant inbred lines for three characters – yield, quality and maturity. This is used as evidence of the validity of the genetical model and the assumptions made. The effects of genotype × environment interactions prevented predictions made in one season being reliably applied to those made in the other and, therefore, reduce the attraction of this type of prediction study to the plant breeder.

Key words: Genetic effects – Modelling – F₃ generation – Single-seed descent

Introduction

The prediction of inbred line performance from early generation trials was developed by Jinks and Pooni

(1976) using *Nicotiana rustica*, and has subsequently been used in many other species, such as barley (*Hordeum vulgare*) (Caligari et al. 1985) and Brussels sprouts (*Brassica oleracea* var. *gemmifera*) Rogers et al. 1987). These studies have substantiated the genetical theory and methods used. In each case they used crosses between two inbred parents, but in many naturally outcrossing crop species, the breeding stocks are maintained as populations. Breeding programmes often make use of crosses between populations because these have the advantage of providing a wide genetic base; however, it is particularly in these situations that it is difficult to judge the likely value of any inbred lines that may be produced, whether these be destined for use as cultivars per se or as the parents of hybrids. Under these circumstances it may be particularly valuable to predict the performance of inbred lines at as early a stage as possible.

The prediction methods of Jinks and Pooni (1976) include designs such as the triple test cross (TTC) or the F₃ generation augmented by the parents, F₁ and F₂. These designs are required to provide estimates both of the mean performance of F_∞ lines and the variation between them. However, Werner et al. (1988 b) suggested that the use of the TTC design for predictions involving population crosses may be very misleading. Likewise, the use of a standard F₃ trial may provide biased predictions of the mean performance of F_∞ lines. In each case the problems are caused by failing to account for the segregation of heterozygosity present within each population prior to crossing. In early generation predictions, it is necessary to utilise a design that incorporates either selfed generations of each parent and/or the selfed and randomly mated generations produced from the array of F₁ hybrids between the populations. The general model for genetic effects (Eberhart and Gardner 1966) provides the most appropriate theoretical scheme for the analysis

* Present address: Cambridge Plant Breeders Ltd., Church St., Thriplow, Royston, Herts, UK

of mean components of population crosses. This model allows for any number of alleles per locus, and assumes Hardy-Weinberg equilibrium in the parent populations and diploid inheritance. The model defines parameters for additive, dominance and additive \times additive epistatic effects. Table 1 summarizes the definitions of parameters and gives the model that may be derived for a selfing series produced from the hybrid population (referred to for convenience as the F_1), produced by randomly crossing two parental populations (π_1 and π_2).

The genetical expectations of variance components applicable to population crosses have been given by Griffing (1962) and Schnell (1982). It is, however, sufficient for prediction purposes to observe that, regardless of its origins, any group of material can be treated as a unique population in Hardy-Weinberg equilibrium after one generation of random mating. Following the restricted assumption of two alleles per locus (Kempthorne 1955), the additive-genetic variance of the random array of recombinant inbred lines derived from such a population is given by

$$\sigma_{A\infty}^2 = 4 \sum p_i q_i \alpha_i^2,$$

where p_i and q_i are the frequencies of the increasing and decreasing alleles, respectively. An estimate of $\sigma_{A\infty}^2$ may be obtained using the between-family mean square from the analysis of variance of the first selfed generation, which yields $r \sigma_b^2$, where r is the number of replicate plots,

$$\sigma_b^2 = \frac{1}{4} \sigma_{A\infty}^2 + \frac{1}{4} \sigma_A^2 + \frac{3}{16} \sigma_D^2 - \frac{1}{8} \sigma_{D1}^2,$$

$$\sigma_A^2 = 4 \sum p_i q_i (\alpha_i + (q_i - p_i) \delta_i)^2,$$

$$\sigma_D^2 = 16 \sum p_i^2 q_i^2 \delta_i^2$$

and

$$\sigma_{D1}^2 = 4 \sum p_i q_i \delta_i^2,$$

where α_i and δ_i are the additive and dominance effects at locus i , respectively. Assuming that σ_A^2 approximates to $\sigma_{A\infty}^2$ and that $\frac{3}{16} \sigma_D^2 - \frac{1}{8} \sigma_{D1}^2$ tends to be small, this source (σ_b^2) provides an estimate of $\frac{1}{2} \sigma_{A\infty}^2$. The situations under which these assumptions may not hold will be discussed later.

The available models, therefore, provide a method for obtaining unbiased estimates of the mean components involved in a population cross, regardless of the number of alleles segregating at each locus. The models and designs available for estimating variance components may lead to a bias in estimates of the additive-genetic variation between recombinant inbred lines owing to the effects of dominance.

Materials and methods

In an attempt to combine the favourable over-wintering characteristics of Japanese bulb onions with the superior bulb quality of European material, a cross was made between the cultivar

Table 1. Parameter definitions and model of gene effects for the selfing series

$m = \mu + \sum_i \sum_j (p_{1ij} + p_{2ij}) \alpha_{ij}$
$+ 2 \sum_{\substack{i,i' \\ i < i'}} \sum_j (p_{1ij} p_{1i'j} + p_{2ij} p_{2i'j}) \alpha \alpha_{ij,i'j} - aa$
$a = \sum_i \sum_j (p_{1ij} - p_{2ij}) \alpha_{ij} + 2 \sum_{\substack{i,i' \\ i < i'}} \sum_j (p_{1ij} p_{1i'j} - p_{2ij} p_{2i'j}) \alpha \alpha_{ij,i'j}$
$d_1 = 2 \sum_i \sum_{\substack{j,j' \\ j < j'}} p_{1ij} p_{1ij'} \delta_{ij,ij'}$
$d_2 = 2 \sum_i \sum_{\substack{j,j' \\ j < j'}} p_{2ij} p_{2ij'} \delta_{ij,ij'}$
$h = \sum_i \sum_{\substack{j,j' \\ j < j'}} (p_{1ij} - p_{2ij}) (p_{2ij'} - p_{1ij'}) \delta_{ij,ij'}$
$aa = \sum_{\substack{i,i' \\ i < i'}} \sum_j (p_{1ij} - p_{2ij}) (p_{1i'j} - p_{2i'j}) \alpha \alpha_{ij,i'j}$
$\pi_1 = m + a + d_1 + aa$
$\pi_{1s} = m + a + \frac{1}{2} d_1 + aa$
$\pi_2 = m - a + d_2 + aa$
$\pi_{2s} = m - a + \frac{1}{2} d_2 + aa$
$F_1 = m + \frac{1}{2} (d_1 + d_2) + h$
$F_{2s} = m + \frac{1}{4} (d_1 + d_2) + \frac{1}{2} h$
$F_{2r} = m + \frac{1}{2} (d_1 + d_2) + \frac{1}{2} h$
$F_{3r} = m + \frac{1}{4} (d_1 + d_2) + \frac{1}{4} h$
$F_{5r} = m + \frac{1}{16} (d_1 + d_2) + \frac{1}{16} h$
$F_{\infty r} = m$

Senshyu semi-globe yellow and a second generation inbred line derived from the Polish cultivar Rawska (selected for particularly good bulb quality). An F_2 population produced by mass pollination of the hybrid seed from a single (unselected) pair cross was used to initiate 1,400 single-seed descent (SSD) lines (Werner et al. 1988a). During the summer of 1986 seed was raised to provide the following genotypes: mass-pollinated seed of each parent population (π_1 = Senshyu and π_2 = Rawska) (produced in a cage of 24 plants); self seed of each parent (π_{1s} and π_{2s}) (from a random sample of ten plants); hand-emasculated F_1 seed, which was pooled together from five different pair crosses; F_{2r} seed produced by mass pollination and F_{2s} seed produced by self pollination of F_1 plants derived from four different pair crosses; F_{3r} seed produced from an F_2 seed lot, which originated from a single-pair cross that had been mass pollinated at the F_1 stage; and F_{5r} seed from 301 of the most advanced SSD lines. This last group included 53 lines that were represented by two F_{5r} families, which traced back to two full-sib F_{4r} plants; the remaining 248 lines were represented by a single F_{5r} family. In addition to this freshly produced seed, it was possible to include 60 'old' F_{3r} families that had been produced during 1983 as an interim stage of the SSD programme and kept in cold storage (germination potential was comparable to that of freshly produced seed). Commercial seed of the Senshyu parental population was included in the trial. This material was sown in the field in mid-August 1986 in a single block using completely randomised single-row plots (3 m long) and commercial densities (80 plants m^{-2}).

Fresh seed of all generations, with the exception of the F_1 and F_{3r} generations, was raised in 1987 and sown in the field for a comparable trial during the 1987/88 season. 'Old' F_{3r} seed was again available but not in sufficient quantities to permit replication. In this trial, 427 F_{5r} lines were included, of which 50 had been previously included in the 1986/87 trial. Table 2 shows the number of replicate plots sown with each generation in the two seasons.

The date for 50% foliage collapse (in days from 31 May) was used as an indicator of maturity. Yield was recorded as the whole-plot weight of marketable bulbs (bulbs less than 2.5 cm diameter, bolters, double bulbs and bull-necked bulbs were excluded) and is presented as the yield in tonnes per hectare. A five-point scale (1 = poor; 5 = very good) was used to assess overall bulb quality, which took into consideration skin colour, thickness and retention, together with bulb shape, bulb hardness and uniformity. These components of quality were also assessed separately but are not presented in this paper.

Table 2. Replication of generations raised in field trials during 1986/87 and 1987/88. See text for full descriptions of material

Material	1986/87			1987/88		
	Fami- lies	Sub- fami- lies	Repli- cates	Fami- lies	Sub- fami- lies	Repli- cates
π_1	1	1	8	1	1	8
π_{1s}	10	1	2	10	1	2
π_2	1	1	8	1	1	8
π_{2s}	10	1	2	10	1	2
F_1	1	1	2	—	—	—
F_{2r}	1	1	12	1	1	12
F_{2s}	4	3	2	6	3	2
F_{3r} 'new'	27	1	2	—	—	—
F_{3r}	60	1	1	60	1	1
F_{5r}						
replicated lines	53	2	2	50	1	2
remaining lines	248	1	1	377	1	1
Senshyu commercial	1	1	47	1	1	43

Results

The generation means are shown in Table 3. In both seasons there was a difference between the π_1 and π_{1s} scores for yield that was also reflected in the difference between F_{2r} and F_{2s} but not between the π_2 and π_{2s} generations. This suggests that substantial inbreeding depression occurs for yield when the Senshyu parent is selfed, but not the Rawska parent. For both yield and maturity there was a significant difference ($p < 0.01$ and $p < 0.05$, respectively) between the mean of the 'new' F_3 generation and that of the 'old' F_3 generation during 1986/87. There was also, for yield, a significant difference ($p < 0.05$) between the four selfed F_2 families, which could only be attributed to their origins from distinct pair crosses. The 'new' F_3 generation was derived from different pair crosses to those used to initiate the SSD lines; therefore, only the mean of the 'old' F_3 seed has been used to fit the model for these characters.

Regression parameters were fitted by weighted least squares to the data from each season using the model presented in Table 1; the estimates of the parameters required in the simplest adequate model for each character are shown in Table 4. There is a considerable difference between the models produced in the two seasons. Nevertheless, the consistencies permit some confident conclusions to be drawn with regard to the genetical control of these characters. For yield there was a highly significant ($p < 0.01$) level of dominance within the Senshyu parent (d_1) in both seasons; this confirmed the importance of heterozygosity in this population. For the overall quality character, there was significant dominance generated from the differences between parents (h), and there was also evidence of additive \times additive epistasis. For maturity date, the differences between the models fitted to the two seasons were particularly marked. It was observed that the period during which the plants reached maturity was very much shorter than normal in 1988. One of the

Table 3. Generation means and standard errors for three traits assessed in the two seasons 1986/87 and 1987/88

Generation	1986/87						1987/88					
	Yield (tons/ha)		Quality		Maturity (days)		Yield (tons/ha)		Quality		Maturity (days)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
π_1	43.6	2.92	3.13	0.16	12.1	3.0	59.2	2.73	3.13	0.15	13.7	0.82
π_{1s}	19.2	3.79	3.00	0.14	27.0	4.0	44.7	1.73	3.30	0.21	11.4	1.85
π_2	3.7	0.96	3.00	0.16	57.6	3.0	16.2	2.73	3.63	0.15	20.7	0.82
π_{2s}	5.9	2.01	3.06	0.12	50.6	2.0	13.1	1.78	3.47	0.12	22.7	1.65
F_1	29.3	5.86	3.00	0.32	32.0	6.0	—	—	—	—	—	—
F_{2r}	36.0	3.04	3.17	0.13	32.7	2.4	46.3	2.34	3.18	0.13	15.5	0.70
F_{2s}	17.4	4.10	3.21	0.12	33.0	1.9	35.7	1.29	3.25	0.07	18.6	1.00
F_{3r} 'new'	8.0	1.62	2.94	0.07	44.2	2.3	—	—	—	—	—	—
F_{3r}	17.3	1.37	2.80	0.07	38.4	1.7	29.6	1.26	2.74	0.08	19.4	0.77
F_{5r}	10.2	0.56	2.69	0.04	43.4	0.9	19.2	0.49	2.70	0.03	20.2	0.35

Table 4. Estimates (Est) of parameters (with standard errors; SE) and Chi-squared tests for the goodness of fit of the models used for three traits evaluated in two seasons

Parameter	1986/87						1987/88					
	Yield (tons/ha)		Quality		Maturity ^a (days)		Yield (tons/ha)		Quality		Maturity (days)	
	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
<i>m</i>	4.61	2.35	2.69	0.11	41.9	2.74	14.4	2.86	2.33	0.18	20.7	1.04
<i>a</i>	-7.39	3.25	-	-	-	-	6.5	1.86	-	-	-7.1	1.09
<i>d</i> ₁	53.82	6.83	-	-	-29.0	4.03	34.6	3.81	-0.49	0.11	-	-
<i>d</i> ₂	-	-	-	-	16.9	4.34	-	-	-	-	-8.0	2.43
<i>h</i>	-	-	0.79	0.30	-7.4	3.67	26.3	6.83	2.10	0.41	-	-
<i>aa</i>	-7.91	1.84	0.35	0.12	-	-	6.1	3.04	1.20	0.19	-	-
χ^2 (<i>df</i>)	4.57 (5)	<i>P</i> =0.47	6.64 (7)	<i>P</i> =0.47	2.55 (4)	<i>P</i> =0.64	2.30 (3)	<i>P</i> =0.51	1.10 (4)	<i>P</i> =0.89	7.06 (5)	<i>P</i> =0.22

^a The commercial Senshyu differed significantly from the π_1 generation and was excluded from the model

Table 5. Estimates (Est) and standard errors (SE) of the additive-genetic ($s_{A\infty}^2$) and environmental (s_w^2) variations from the F_3 generation for three traits evaluated in two seasons

Season - Trait	$s_{A\infty}^2$		s_w^2	
	Est	SE	Est	SE
1986/87				
Yield	163.0	30.02	23.2	6.83
Quality	0.0 ^a		0.2	0.03
Maturity	186.0	67.31	106.4	28.78
1987/88				
Yield	61.9	37.61	59.9	7.70
Quality	0.4	0.15	0.2	0.02
Maturity	61.2	13.66	5.4	0.69

^a The mean square between F_3 families gave a negative estimate of $s_{A\infty}^2 = -0.06$

consequences of this compression of the maturation was that the SSD lines, on average, matured only 6.5 days later than Senshyu in 1987/88 compared to 31.3 days later in 1986/87. The reduction in spread of maturity was not restricted to this trial or site, indeed, the effect was general throughout the UK during 1988 (NIAB 1988). This substantial seasonal difference was probably the basis for genotype \times environment interactions, which could account, particularly with regard to the maturity trait, for most of the discrepancy between the models.

The between-family item from the 'old' F_{3r} generation was used to supply estimates of $\sigma_w^2 + r\sigma_b^2$, where $r=1$ for each season and character. For the 1986/87 trial it was possible to estimate σ_w^2 from the replicate plots raised in the 'new' F_{3r} generation. For the 1987/88 trial, however, a pooled estimate of the variation between plots was obtained from the replicates grown in all generations. For the yield and maturity characters, Bartlett's tests (Snedecor and Cochran 1980) showed that the F_5 provided an estimate of s_w^2 that was heterogeneous to the re-

maining replicated generations. For these characters, the F_5 generation was omitted from the pool. The additive-genetic variances for the F_∞ lines ($\sigma_{A\infty}^2$) were, therefore, estimated as $2(MS_{b'old} - s_w^2)$ and are presented in Table 5.

The estimates of the gene effects were used to predict the mean performance of the SSD lines at F_5 relative to that of the over-wintered cultivar and parent, Senshyu. The distribution of the SSD lines was assumed to be normal with a variance equal to $\frac{7}{8}s_{A\infty}^2 + r_0s_w^2$. Owing to the unequal replication of the SSD lines, the coefficient r_0 takes the value $[1/(a-1)](N - \sum r_i^2/N)$, where a is the number of SSD lines, r_i is the number of replicate plots in the i^{th} line and N is the total number of plots. Predictions of the proportion of SSD lines expected to outperform Senshyu were made for each trait in each season. These are given in Table 6 together with the observed number of lines superior to Senshyu. In the case of the quality data (which was scored in categories 1-5), it was only possible for each SSD line to have a mean equal to a whole number (or to fractions of 1/2 or 1/4 for lines replicated in two and four plots, respectively). The expected Senshyu means were (by coincidence) 3.04 units in both seasons, therefore, for an SSD line (represented by a single plot) to outperform Senshyu it had to score 4, which was possible only if it had a latent value of 3.5 or greater. Allowing for lines replicated in two and four plots, the predictions presented for quality are based on the ability to exceed 3.37 and 3.47 on the underlying scale for the two seasons, respectively. Inspection of Table 6 shows that in each case the observed number of lines superior to Senshyu lies close to the expected number and is well within the 95% confidence interval.

Discussion

Eberhart and Gardner's (1966) model of gene effects was originally given for application to diallel crosses but has

Table 6. Predictions and observations (at F_3) of the number of lines outperforming Senshyu in 1986/87 and 1987/88 for three traits of autumn-sown onions

Character	Expected percentage of SSD lines > Senshyu	95% confidence interval (%)	Total no. of SSD lines	Expected no. of SSD lines > Senshyu	Observed no. of SSD lines > Senshyu	Observed percentage of SSD lines > Senshyu
1986/87						
Yield	0.11	0.01–0.90	301	0.34	1	0.33
Quality	5.53	1.66–14.55	262	14.49	19	7.25
Maturity ^a	2.96	0.59–10.47	271	8.01	6	2.21
1987/88						
Yield	0.00	0.00–0.08	385	0.00	0	0.00
Quality	5.34	1.09–15.44	375	20.01	31	8.27
Maturity ^a	17.46	10.16–27.43	381	66.53	80	21.00

^a Figures given are for lines which are earlier than Senshyu

been successfully used here, in the context of a single population cross, for the purposes of predicting the performance of recombinant inbred lines. Correct estimation of the components of mean performance is vital for prediction work and is, in turn, dependent upon the implicit assumptions of the model used. Yield showed it was important to estimate, or otherwise allow for, the effects of heterozygosity within the parental Senshyu population. This was not possible when this material was previously examined using a triple test cross (Werner et al. 1988 b). In this earlier study the assumption was made that the differences between the parental populations were greater than the variation within, but it is now clear that this assumption fails and leads to a substantial bias in the estimate of m , the mean of the recombinant inbred lines. The model presented incorporates additive, dominance and additive \times additive effects only. Dominance \times dominance nonallelic interactions were not included in the model, because insufficient generations were available to specify parameters for all the theoretical combinations of dominance \times dominance effects. This omission has not, in the material studied here, led to inadequacy in the model, but other sets of material may involve significant nonallelic interactions of this type. In this event the inclusion of the second selfed generation for each of the parent populations would be necessary. Additive \times dominance interactions are completely confounded with the dominance effects in a selfing series, and cannot be estimated unless backcross generations are also included. However, this effect does not introduce any bias to the prediction method based upon the F_3 . Linkage of interacting genes may lead to some bias in the predictions made from early generations but, given that the parental populations include little linkage disequilibrium, this will mainly be generated as a result of crossing and is likely to be of minor consequence. Finally, one or both of the parental sources may not be in Hardy-Weinberg equilibrium (as

may be the case for a partially inbred line). Had this been so, the model would have failed to fit the data, since the estimates of d_1 and/or d_2 obtained from the parental selfs would have been inconsistent with the combined estimate of $\frac{1}{4}(d_1 + d_2)$ from $F_{2r} - F_{2s}$.

In the presence of dominance, the use of the F_3 generation to estimate the additive-genetic variance is likely to lead to a biased estimator. The square root of this estimate ($s_{A\infty}$) is used to predict the distribution of recombinant inbred lines but, when obtained from the F_3 , may be biased either positively or negatively, depending upon the direction of dominance and the gene frequencies. However, even with a dominance ratio of 1 and unequal allele frequencies (i.e. as $p_i = 0$ or $p_i = 1$), the maximum theoretical bias in $s_{A\infty}$ is less than 50%. The average frequency of the increasing allele is very unlikely to approach either of these extremes, and the actual bias may be expected to be substantially less than 50%. The presence of more than two alleles at each locus would lead to a different theoretical partition of the variation to that used, but would make very little difference to the bias in the estimate of $s_{A\infty}$. Additional biases may occur as a result of linkage or epistasis; again, these may take either sign. Empirical studies using inbreeding crops suggest that the bias introduced by these last two effects is generally slight (Jinks and Pooni 1976). In general for prediction purposes, where the square root of the additive-genetic variance is used, it is unlikely that moderate biases will substantially affect the final prediction and will, in any case, be small compared to the inevitable sampling error associated with this statistic. The satisfactory predictions made indicate that the method used for estimating the additive-genetic variance may be adequate.

The augmented F_3 design used in this study successfully achieved the prediction of inbred lines in a relatively advanced generation. This leads to the conclusion that the genetical model was adequate for this set of material.

However, many of the problems of prediction exercises were deliberately avoided by testing SSD lines alongside the early generations, thereby eliminating the complications of genotype \times environment interactions. This is particularly apparent from the comparison of the maturity data across seasons. Whilst the predictions within each of the seasons were accurate, the expectations derived in 1986/87 were not borne out in 1987/88, or vice versa. Similar problems attributable to genotype \times environment interactions were also encountered by Caligari et al. (1985) and Werner et al. (1989). The application of a prediction technique such as the one used in this study to a commercial breeding programme must give due consideration to such problems.

Eberhart and Gardner (1966) emphasized that reasonably large sample sizes should be used when working with population crosses. Our observations with respect to the difference between F_3 generations derived from different pair crosses lead us to reiterate this warning, and suggest that when specific small samples have been enforced, perhaps because of other breeding constraints, then it is essential to relate all genetical work to that specific sample.

Acknowledgements. We would like to thank Mr. K. Lavery and Mrs. C. Vaux for their excellent technical assistance throughout the course of this work. The computing facilities of the University of Birmingham and the I.H.R., Wellesbourne were made available for this work. C.P.W. was supported by a fellowship from the AFRC.

References

- Caligari PDS, Powell W, Jinks JL (1985) The use of doubled haploids in barley breeding. 2. An assessment of univariate cross prediction methods. *Heredity* 54:353–358
- Eberhart SA, Gardner CO (1966) A general model for genetical effects. *Biometrics* 22:864–881
- Griffing B (1962) Prediction formulae for general combining ability selection methods utilizing one or two random mating populations. *Aust J Biol Sci* 15:650–665
- Jinks JL, Pooni HS (1976) Predicting the properties of recombinant inbred lines derived by single-seed descent. *Heredity* 36:253–266
- Kemphorne O (1955) The correlations between relatives in random mating populations. *Cold Spring Harbour Symp. Quant Biol* 20:60–78
- National Institute of Agricultural Botany (1988) Report of spring-sown onion trials. N.I.A.B., Cambridge
- Rogers WJ, Kearsley MJ, Smith BM (1987) The feasibility of producing inbred rather than F_1 hybrid cultivars in Brussels sprouts: Predictions from early generations. *Ann Appl Biol* 111:677–688
- Schnell FW (1982) A synoptic study of the methods and categories of plant breeding. *Z Pflanzenzuecht* 89:1–18
- Snedecor GW, Cochran WG (1980) *Statistical methods*. Iowa State University Press, Ames/IA
- Werner CP, Dowker BD, DeSouza DC, Crowther TC, Horobin JF, Kearsley MJ (1988 a) Trialling techniques in the breeding and prediction of recombinant inbred lines in onions (*Allium cepa* L.). *Ann Appl Biol* 112:515–524
- Werner CP, Dowker BD, DeSouza DC, Setter AP, Crowther TC, Horobin JF (1988 b) Triple test cross predictions of the performance of recombinant inbred lines from a wide cross in onions (*Allium cepa* L.). *Ann Appl Biol* 112:525–535
- Werner CP, Setter AP, Smith BM, Kubba J, Kearsley MJ (1989) Performance of recombinant inbred lines in Brussels sprouts (*Brassica oleracea* var. *gemmifera*). *Theor Appl Genet* 77:527–534