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Genotypic and Environmental Effects on the Maturity Time of Autumn Cauliflowers

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Summary. Twelve genotypes representing a wide range of autumn cauliflower were grown in two seasons from six seedling propagation treatments in three sequential sowings. Genotypes differed in their mean time of maturity and spread of maturity, and in their sensitivity to environment for these characters. Those genotypes derived from self-incompatible stocks showed greater stability than those from self-compatible stocks. In particular, a National Vegetable Research Station breeding line 'KC' revealed outstanding stability and is thus a potential new variety. The best environments for discriminating between genotypes were those which gave the least check to early growth.

Introduction

Progressively better cauliflower cultivars for harvesting during the autumn period in the UK have become available during the last few decades. Previously, seed of Italian cultivars was used almost exclusively, but now cultivars bred in Australia and Holland have in general superseded the Italian types. Recent developments in the vegetative propagation of cauliflowers (Crisp and Lewthwaite 1974; Crisp and Walkey 1974; Crisp and Gray 1975) allow seed to be obtained reliably from autumn-maturing material in the UK, and raise prospects of breeding cultivars more suited to UK growing conditions than those bred primarily for other geographic regions. Thus, it is expected that breeding may further advance quality and yield, and that unpredictable variability in the time of maturity both within and between cultivars may be reduced.

As a preliminary to such breeding programmes, some genetic information is desirable. A number of studies have been reported on the genetics of the autumn cauliflower (Watts 1964, 1966a, 1966b; Crisp et al. 1975a, 1975b) and on the effects of different environments (Salter and Fradgley 1969a, 1969b; Whitwell and Crofts 1972). However, no investigations have been made into genotype × environment interactions (GE). The present investigation was aimed at estimating the magnitude and direction of genotypic, environmental, and GE effects for a range of characters in cultivars, and cultural practices representing those which are at present, or may later become commercially useful. This should lead to improved efficiency in the choice of parents for future breeding programmes, and to the determination of discriminating environments in which to carry out selection. It may also make possible the prediction of the performance of genotypes over a range of conditions.

This paper described the results obtained for maturity time. Other characters will be described in future papers.

Material and Methods

Genotypes and environments were chosen to represent commercial growing and plant breeding practices. Twelve genotypes were included, consisting of three cultivars from each of the three main types of autumn cauliflowers, and three selections made at the National Vegetable Research Station (NVRS), two of which represented the old Italian type (Table 1).

Normal commercial practice is to transplant autumn cauliflowers at the four to eight true-leaf stage from open or protected seed beds. More recently, direct drilling followed by thinning, and transplanting from paper pots or tubes has been introduced or investigated (Salter and Fradgley 1969a; Whitwell and Crofts 1972). Peat pots have also been used for this purpose at NVRS, as these allow the randomisation of experimental designs to be maintained from the time of sowing (Crisp and Pow 1971).

Thus, six methods were used to raise seedlings (Table 2). It was known that these would give different maturity dates if all seed was sown at the same time. Consequently, seeds were sown in sequence in order to give an approximate synchronisation of maturity times from all of the seedling treatments. Thus it was intended that plots representing each seedling treatment should have a common field environment during the post-seedling growth phase. Raising of seedlings by the six different methods was repeated to give three maturity groups in each of the years of the experiment, 1972 and 1973 (see Table 3).

Experimental details

The experiment consisted of two replicate blocks, each split into three main plots (planting groups). Each

Table 1. Genotypes of autumn cauliflower grown in the trials

Genotype	Origin/Seed Merchant	Type
cv. Le Cerf B Autumn	Asmer	Le Cerf (All the year Round)
cv. Lero	Asmer	
cv. Le Cerf Improved	Elsoms	
cv. South Pacific	Yates/Henderson	Australian
cv. Boomerang	Asmer	
cv. Kangaroo	Southern Cross	
cv. Clandonian	Asmer	Flora Blanca
cv. Hylite	Asmer	
cv. Autumn Glory	Elsoms	
KC	NVRS	Inbred line (S4) from a panmictic population of summer and winter stocks
YCM2	NVRS	Mass selection from an Italian stock
AGAQ	NVRS	Inbred line (S4) from an Italian stock

Table 2. Seedling treatments and sowing dates of autumn cauliflower used in the trial

Seedling treatment	Abbreviation used in text	Sowing date for each maturity group: 1		2		3	
		1972	1973	1972	1973	1972	1973
Sown direct in the field	DD	27 April	27 April	17 May	18 May	26 May	30 May
Sown direct in 50 × 50 mm peat pots* in the glasshouse; transferred to the field at 1 - 2 true leaf stage	J7	15 May	17 May	25 May	30 May	2 June	1 June
Sown in JI2 seed compost; pricked out into 50 × 50 mm paper pots** containing JI3 potting compost; pots maintained in frames and transferred to the field at 3 - 4 true leaf stage	PP	17 April	24 April	10 May	14 May	19 May	23 May
Sown in Dutch light seed beds to give 1 plant/75 mm of row; transplanted to the field at 4 - 5 true leaf stage	DLO	13 April	17 April	4 May	4 May	16 May	17 May
As above, at 1 plant/25 mm of row	DLN	13 April	17 April	4 May	4 May	16 May	17 May
As above, at 3 plants/25 mm of row	DLC	13 April	17 April	4 May	4 May	16 May	17 May

* Jiffy 7 peat pots, Jiffy Products, Ltd., Grorud, Norway

** V505 Paperpots, The Whalehide Co., Leigh on Sea, Essex, UK

Table 3. Spread of mean maturity time for seedling treatments *

Planting group	Genetic Type: Le Cerf		Australian		Flora Blanca		NVRS	
1	26 Aug - J7	3 Sept DLC	8 Sept - J7	22 Sept DLC	5 Sept - J7	9 Sept DLC	27 Sept - J7	9 Oct DLC
2	21 Aug - DD	23 Sept DLC	5 Sept - DD	17 Oct DLC	1 Sept - DD	5 Oct DLC	21 Sept - DD	28 Oct DLC=DLN
3	9 Sept - DD	18 Oct DLC	2 Oct - DD	6 Nov DLC	21 Sept - DD	28 Oct DLC	13 Oct - DD	15 Nov DLC

* Seedling treatments are indicated by abbreviations (see Table 2)

main plot was split into six randomised sub-plots (seedling treatments) consisting of ten fully randomised plants of each of the twelve genotypes, spaced at 0.6 × 0.6 m, with a peripheral guard row. In all seedling treatments except those from Dutch lights the individual plant randomisation was imposed at and maintained from sowing time. In the Dutch lights, however, seedlings were raised by drilling separate rows of each genotype, with the rows randomised.

The experiment was carried out at Wellesbourne, England, on a sandy loam. Irrigation was supplied at transplanting, and later if necessary. Chemical treatments (fertiliser, herbicide, insecticide) were applied according to normal practice.

The cauliflowers were harvested and recorded as they matured, the entire experiment being surveyed about five times a week during the August-December period.

Analysis of data

Means and variances of days to maturity from the date of seed sowing were calculated for each set of ten fully randomised plants of a particular genotype within a sub-plot. Preliminary analysis of these data showed that second and third order interactions were eliminated or reduced by a logarithmic transformation of the individual plant data. Also the positive correlation found between means and variances was removed by log transformation. Therefore the variates selected for full analysis were mean $\log_e$ days to maturity and variance $\log_e$ days to maturity, referred to hereafter as 'mean maturity time' and 'spread of maturity' respectively.

Analysis of variance

A combined analysis of variance was carried out on the two years' results assuming genotypes, plantings, seedling treatments and years to be fixed effects. Genotypic differences were partitioned into 'between types' and 'between cultivars or lines within types' for both main and interaction effects. The approach was essentially similar to that described by Dowker (1971) for carrot genotypes grown in a range of environments. In addition, single plant randomisation allowed the derivation of an error term from differences between individual plants within treatments and blocks. Expected mean squares were derived following the method of Scheffe (1959) and used in the estimation of variance components for all significant ($P < 0.05$) effects. The relative magnitudes of these variance components were taken as an indication of the importance of the corresponding main or interaction effects i.e. their proportional contribution to the overall variation.

Joint regression analysis

The regression approach to specify GE interactions, first proposed by Yates and Cochran (1938), has been modified and used by various workers (Freeman 1973). It has been shown that the magnitude of GE is frequently a linear function of environment where environment is measured by the mean performance of a number of genotypes in that environment. If this linear relationship accounts for most of the variation of a genotype over environments, it is possible to predict its performance under given related environmental conditions. In addition the regression coefficient and deviations from the regression mean square provide a measure of sensitivity of a genotype to change in environment. Alternative analytical methods like Principal Component Analysis may be of use (Freeman and Dowker 1973), but despite criticisms of non-orthogonality (Hardwick and Wood 1972), joint regression remains the most valuable approach to understanding GE. Hence, data were analysed as joint regressions by taking means over replicate blocks to give a set of twelve genotypes × thirty-six environments. Its effectiveness in describing GE was assessed by estimating the linear proportion of the variance accounted for by the heterogeneity of the regressions, as described by Fripp and Caten (1971).

Results

The staggering of the seedling treatments in order to synchronise the time of maturity within genotypes only succeeded adequately for the first planting group (Table 3). Spreads between the mean maturity times of the earliest and the latest of the seedling treatments in the second and third planting groups usually exceeded one month. Hence, seedling treatments were confounded with growing conditions in the field. However, the seedling treatments gave fairly consistent results over different planting groups, such that the seedling treatment × planting group interaction only accounted for 8 % and 7 % of the significant ($P < 0.05$) compo-

Table 4. Environmental means as $\log_e$ *

Environment		Days to maturity	Variance of days to maturity
Seedling treatments	DD	4.746 (116.9)	0.00851
	J7	4.787 (122.3)	0.01046
	PP	4.809 (124.2)	0.00790
	DLO	5.003 (151.3)	0.00938
	DLN	5.039 (156.4)	0.00731
	DLC	5.072 (161.7)	0.00877
	S.E.	± 0.0079	± 0.000965
Plantings	1	4.884 (134.9)	0.00842
	2	4.891 (136.5)	0.00954
	3	4.953 (145.0)	0.00820
	S.E.	± 0.0071	± 0.000724
Years	1972	4.893 (136.2)	0.00820
	1973	4.925 (141.5)	0.00924
	S.E.	± 0.0058	± 0.000591

* untransformed mean days to maturity in parentheses

nents of the variance for, respectively, mean maturity and spread of maturity for each plot. Therefore it seems reasonable to assume that the effect on maturity of the season during which the post-seedling stages were spent in the field was relatively unimportant, and that the confounding of seedling treatments with subsequent conditions in the field within each planting group can safely be ignored.

Environmental effects

Means over genotypes and replicates are presented in Table 4. Environmental effects (years, planting groups, seedling treatments and interactions between them) accounted for, respectively, 35 % and 16 % of the variance for mean maturity time and spread of maturity. For maturity time, 62 % of this environmental variance was due to the seedling treatments and most of the remainder (32 %) due to interactions of years with other environmental factors. In the case of spread of maturity, almost all (89 %) of the environmental variance was accounted for by years interacting with planting groups and seedling treatments, with none of the main factors having a significant effect except for the seedling treatments which contributed 3 % to the total environmental variance.

Genotypic effects

Differences between and within the four genetic types accounted for 54 % of the mean maturity time variance, and 12 % of the spread of maturity variance. The sequence of maturity to be expected from the work of Salter et al. (1972), that is, Le Cerf, Flora Blanca, Australian was observed, with the NVRS type maturing after the Australian type. These results conform with previous findings (J.D.C. Bowring, unpublished) that cultivars within the Le Cerf and Flora Blanca types are, respectively, very similar; and that the Australian cultivars cover a wide range of maturities and morphological types. Each NVRS breeding line was also of different origin and differences in performance were not unexpected.

For spread of maturity, significant differences were only apparent between types and between NVRS lines. Differences between types in spread of maturity have for long been a generally acknowledged feature of autumn cauliflowers. The belief was that as the season progressed, the later cultivars showed an extended spread of maturity. This dogma was not supported by a comparison of mean maturity time and spread of maturity of the twelve genotypes here (Table 5), which showed no overall correlation ($r = 0.001$). In

Table 5. Genotypic means as $\log_e$ *

Genotype	Days to maturity		Variance of days to maturity
Le Cerf B Autumn	4.799	(123.8)	0.00664
Lero	4.809	(124.7)	0.00557
Le Cerf Improved	4.748	(117.2)	0.00510
South Pacific	5.057	(159.7)	0.00831
Boomerang	4.789	(122.3)	0.00714
Kangaroo	4.982	(148.5)	0.00887
Clandonian	4.906	(137.3)	0.01203
Hylite	4.836	(128.2)	0.01256
Autumn Glory	4.893	(135.8)	0.01380
KC	5.166	(176.8)	0.00454
YCM2	4.889	(135.0)	0.00974
AGAQ	5.036	(156.5)	0.01033
	S.E. ± 0.0063		± 0.001111
Le Cerf type	4.786	(121.9)	0.00577
Australian type	4.942	(143.5)	0.00811
Flora Blanca type	4.878	(133.8)	0.01280
NVRS breeding lines	5.030	(156.1)	0.00820
	S.E. ± 0.0036		± 0.000641

* untransformed mean day to maturity in parentheses

particular, the latest genotype, KC, had the smallest variance - the opposite of the expected relationship! Consideration of the breeding systems, irrespective of the degree of inbreeding of the genotypes may account for this observation. The Le Cerf and Australian cultivars are all effectively selfcompatible; and each of the Flora Blanca cultivars and NVRS lines is either largely self-incompatible, or was derived recently from a stock which was of this type. A comparison of the twelve genotypes on this basis revealed two quite different relationships between mean maturity and spread of maturity. It appears that within the self-compatible types, the later genotypes had a longer spread of maturity than the early ones ($r = 0.851$, $P < 0.05$); and that within the self-imcompatible types ($r = -0.866$, $P < 0.05$) the converse was true.

Genotype × environment interactions

GE interactions contributed 10 % to the mean maturity time variance and 43 % to the spread of maturity variance. Only the third order interactions of the Flora Blanca cultivars × planting groups × seedling treatment × years contributed more than 1 % to the mean maturity time variance. Spread of maturity gave a different picture, with several first, second and third order interactions contributing between 1 and 4 % to the overall variance.

In both mean maturity time and spread of maturity, most of the GE variance (respectively 84 % and 83 %) was accounted for by heterogeneity of the joint regressions (Table 6). Only in the case of mean maturity time was the non-linear component significant within types.

A clear distinction could, again, be made between the self-incompatible and self-compatible types. When the individual values for each genotype were regressed on mean maturity time (Table 7) the self-incompatible types all showed negative slopes and the self-compatible types positive slopes, indicating that the former were more stable in the GE interactions under these conditions than the latter (Finlay and Wilkinson 1963).

No such pattern was apparent with the joint regressions of spread of maturity. Again, the highest negative regression coefficient (b) was given by the KC line

Table 6. Joint regression analysis of GE interaction for mean maturity time and spread of maturity

Source of variation		df	Mean $\log_e$ days to maturity	Variance $\log_e$ days to maturity
Genotypes		11	1.1620	0.000672
Environments		35	0.5504	0.000279
Genotypes x environments		385		
Heterogeneity of regressions between:	types	3	0.0350 * * *	0.000122 *
	Le Cerf cultivars	2	0.0030	0.000006
	Australian cultivars	2	0.0048 *	0.000057
	Flora Blanca cultivars	2	0.0011	0.000028
	NVRS lines	2	0.0411 * * *	0.000318 * * *
Deviations from regressions between:	types	102	0.0061 * * *	0.000080 * * *
	Le Cerf cultivars	68	0.0013	0.000029
	Australian cultivars	68	0.0039 * * *	0.000050
	Flora Blanca cultivars	68	0.0024 * * *	0.000064
	NVRS lines	68	0.0038 * * *	0.000054
Pooled error (replicate blocks × genotypes + replicate blocks × genotypes × environments)		396	0.0014	0.000044

Table 7. Regression coefficients for types, cultivars and lines, from the joint regression analysis

Genotype	Mean $\log_e$ days to maturity	Variance $\log_e$ days to maturity
Le Cerf B Autumn	0.112	-0.132
Lero	0.075	-0.294
Le Cerf Improved	0.027	-0.246
South Pacific	0.007	0.318
Boomerang	0.105	-0.213
Kangaroo	0.098	0.055
Clandonian	-0.067	0.491
Hylite	-0.014	0.133
Autumn Glory	-0.039	0.240
KC	-0.286	-0.748
YCM2	-0.004	-0.105
AGAQ	-0.013	0.501
Le Cerf type	0.071	0.224
Australian type	0.070	0.053
Flora Blanca type	-0.040	0.288
NVRS type	-0.101	-0.117

(Table 7) but the highest positive b values were shown by cv Clandonian and the AGAQ line, which both had negative b values in the mean maturity time regression.

Discussion

The high contribution of seedling treatments to variation in mean maturity was expected, as these treatments must have imposed quite different environmental regimes on the young plants. However, there were no appreciable interactions between seedling treatments and genotypes, and planting groups contributed little to the variation in mean maturity. This strongly suggests that a grower undertaking a planned programme of sequential cauliflower production should use one seedling propagation technique and use either a range of suitable genotypes, or one or a few genotypes planted sequentially.

Environmental factors contributed relatively little to the spread of maturity. It was, however, apparent that the self-incompatible types showed a fairly high degree of interaction with seedling treatments; but the Flora Blanca types exhibited a different pattern from the NVRS types. The lowest variance for the Flora Blanca types was achieved with transplants from paper pots (PP), but this treatment gave the highest variance for the NVRS types. Moreover, there was no consistent pattern over genotypes for the three treatments involving different spacings within the Dutch lights (DLO, DLN, DLC). These inconsistencies suggest that the only method by which substantial and reliable advances may be made in reducing the spread of maturity within the autumn cauliflower crop is by breeding. It is evident from the relatively consistent differences demonstrated between genotypes in this experiment that it is easy to shift the mean maturity time of a population by breeding. However, GE does occur and may upset a planned programme of sequential maturation of cauliflower cultivars throughout the growing season. Cultivars with low responsiveness to environment will be the most predictable and the results indicate that this feature can be bred for by using self-incompatible types.

It is clear that both the mean spread of maturity and the consistency of spread over environments are under genetical control. The experiment has demonstrated that KC, one of the NVRS breeding lines, has both the lowest, and the most consistently low spread of maturity and represents an important advance in breeding for these characters. The success of the trials procedure in identifying these features by variance partitioning, together with the analysis of GE interaction by joint regression is most encouraging, demonstrating yet again that this biometrical approach, such as was used by Perkins and Jinks (1968) on *Nicotiana rustica*, can with advantage be extended to the applied field. The breeder is restricted in his choice of genotypes and environments. It is necessary therefore to choose those environments which are likely to give the best discrimination between genotypes for the characters under selection. The "best" growing conditions for cauliflowers, i.e. those involving minimal check in growth (the direct drilling, the Jiffy seven and the paper pot treatments) gave the earliest maturity and the greatest variation between genotypes for mean maturity time and spread of maturity; whereas the "worst" growing conditions (the Dutch light, close spaced transplants) had the opposite effect. Thus the treatments giving the least check in growth appear to provide the best discriminating environments for both maturity characters.

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