

Genotypic and Environmental Variation in Autumn-sown Onions

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Summary. Seven onion cultivars of Japanese and European origin were evaluated in autumn-sown trials, at six sites over two seasons. Within each season genotypic differences were detected for winter-kill, bolting, maturity time and yield. In general the Japanese cultivars showed consistently lower levels of bolting and winter-kill and earlier maturity relative to the European cultivars. Environmental effects were important with differences between seasons, sites and sowings recorded for most characters. It was concluded that the use of early and late August sowings would provide suitable screening environments for bolting and winter-kill respectively. There were also differences between genotypes in their linear response to environments as shown by joint regression analyses. 'Express Yellow O-X' (hybrid) showed least response to environments for bolting and winter-kill and 'Senshyu semi-globe Yellow' gave the most consistent time to maturity over environments.

Key words: Genotypic - Environmental - Variation - Autumn - Onions

Introduction

In the UK storage of spring-sown balb onions in ambient-cooled stores is effective until March (MAFF 1973) and from refrigerated stores until May, but from April until August supplies have always been dominated by imports. Recent experimental work has confirmed the potential of autumn-sown onions as a commercial method giving bulbs ready for harvest in the June/July period (Tucker and Hough 1973). Certain Japanese and European cultivars, when drilled in August, give acceptable yields in the following summer but the time of sowing has been shown to be critical (Salter and James 1975). Large plants entering the winter after an early August sowing react to a cold stimulus and may bolt during the following spring or summer. However, later sowing at the end of August or early September, may result in higher plant losses through winter-kill because of the smaller plant size. At the present time a mid-August sowing has been recommended for many production areas (Salter 1975) but this gives the grower very little flexibility in practice. Any genetic improvement for resistance to bolting and winter-kill is likely to be of value in extending the drilling period and should improve crop yields. In addition any new cultivars should have distinct and reliable maturity times to allow for sequential harvest throughout the June/July period.

As a preliminary to a breeding programme certain information about variation in the overwintered crop is desirable. The breeder will seek guidance on the selection of suitable parental material and of screening environments which maximise the expression of characters for improvement. The existence of any genotype x environment (GE) interactions will define whether special selection techniques are required to take account of them. To investigate the variation in winter-kill, bolting, maturity and yield data from a series of cultivar trials, originally designed to give agronomic information, were analysed and the variation partitioned into the respective genotypic, environmental and GE interaction components.

Materials and Methods

In the two seasons, 1973/73 and 1973/74, replicated trials of onion cultivars were conducted at several centres in the UK. The sites were selected according to their geographical and climatological position and upon the likely interest in the crop in the area.

Experimental variables

The site/year combinations are presented in Table 1. The sites were selected to cover a range of soil types including silts, sandy loams and fen-peat, all of which are representative of current onion growing practice. The sites differed also in their expected winter climate with lower temperatures anticipated in the north and east (Yorkshire and Cambridgeshire) and warmer conditions in the south-west (Cornwall).

Table 1. Location of the experimental sites for trials of autumn-sown onions in 1972/73 and 1973/74

Location	Symbol	Years of trials						
NVRS, Wellesbourne,								
Warks.	W	1972/73						
Stockbridge House								
EHS, Yorks.	S	1972/73	1973/74					
Luddington EHS,	_	1000/00						
Warks.	L	1972/73						
A. Rickwood EHF, Cambs.	AR	1972/73	1973/74					
Rosewarne EHS,		ŕ	,					
Cornwall	R	1972/73	1973/74					
Efford EHS, Hants.	E	1972/73	1973/74					

Six cultivars were grown at each site. In the first season these were 'Presto' (P), 'Express Yellow O-X' (EY), 'Senshyu semi-globe Yellow' (SY), 'Imai Yellow (IY), 'Hiberna' (H) and 'Rijnsburger Bola' (B). In the second season 'Extra Early Kaizuka' (K) replaced 'Hiberna'. 'Rijnsburger Bola' and 'Hiberna' are Dutch and Czechoslovakian cultivars respectively, with 16 hr daylength requirement for bulb initiation and the remainder are of Japanese origin with the intermediate daylength response (13-14 hr). 'Rijnsburger Bola' is usually grown from a spring-sowing in the UK and produces brown-skinned globe-shaped bulbs of the type required by the UK market. 'Hiberna' was bred for autumn-sowing in Czechoslovakia and produces brown-skinned bulbs. The Japanese cultivars have in previous trials shown a high degree of winter hardiness and resistance to bolting and in general have flat yellow-skinned bulbs. All the cultivars are open-pollinated except 'Express Yellow O-X', an F₁ hybrid. In addition, plots of cv. 'White Lisbon' were grown at each site as a control for comparison of susceptibility to winter-kill, this cultivar usually being overwintered in the UK for salad onion production. Fresh commercial seed was obtained each year for these trials.

Two sowings were made at each site, in mid-August and early September; because of land preparation requirements each sowing was made on a separate, but adjacent, section of land. To investigate the effect of plant density there were two sowing rates calculated to give stands of 108 and 216 plants/m² in the autumn. It was expected that these would be reduced by winter losses to approximately 86 and 130 plants/m² respectively. However, in 1972/73, these losses in plant stand were not consistent between plots and some thinning was necessary to achieve target densities in the spring. Modified drilling rates were used in the second year to give spring stands of 43 and 86 plants/m². There were three replicates at each site except Wellesbourne, where there were only two, and cultivar/density treatments were fully randomised within each replicate block for each sowing.

Cultural details

The land was prepared on a "bed-system" at all sites and a base dressing of 80 kg/ha of N, 96 of P and 186 of K was applied as a compound fertiliser followed by a top dressing of 168 kg/ha of N in early May. The use of herbicides varied between sites according to their indigenous weed floras. Plot size and row arrangement also varied between sites but at most sites each plot consisted of 4 row (0.3 m apart) on a 1.5 m (between wheel centres) wide bed. The minimum plot length was 3.7 m.

Table 2. Cultivar means for percentage winter-kill and bolting, maturity and

Cultivar	% winter-l [Angles in			% bolting [Angles in ()]			
	1972/73ª	1973/74°	2 years°	1972/73ª	1973/74°	2 years°	
P	14.9 (19.1)	17.1 (21.3)		1.0 (2.9)	10.1 (13.3)		
EY	7.3 (12.4)	11.7 (16.5)	10.8 (16.0)	0.5 (2.2)	2.3 (4.4)	1.4 (3.2)	
SY		15.7 (19.4)		3.5 (6.7)			
IY	10.2 (14.8)			1.8 (4.0)	5.2 (10.2)		
Н	9.4 (14.4)	-	-	19.9 (22.3)	-	-	
K	-	15.7 (19.5)	-	-	4.2 (7.3)	-	
В	25.0 (27.1)	30.0 (31.4)		assessed	at 85+ but	not counted	
sed ±	(1.15)	(1.88)	(1.17)	(0.35)	(0.72)	(0.37)	
'White Lisbon'	15.6	12.8	15.6				

a, b, c based upon 6, 5 and 4 sites respectively

Recording and analysis of data

Stand counts were made on the same two 1.3 m lengths of row per plot in both autumn and spring and from these counts percentage winter-kill was calculated. Counts of the total number of plants and of bolting plants were made on the whole plot prior to harvest. Percentages of the data for both characters were transformed to angles before analysis. Plant maturity was recorded as the date of 100% foliar die-down and expressed as days after 30 April. Plot yields were recorded after harvest.

Where possible analyses of variance were carried out on combined sites data for each year separately and for the two years overall. For winter-kill in 1972/73 data were available for six sites and six cultivars and at all six sites in this season data on bolting and yield were recorded for five cultivars. Maturity scores were not taken at Luddington EHS, therefore only a set of five sites × five cultivars were analysed for this variate. For the four sites in 1973/74 data were collected on five cultivars for all variates except winter-kill for which a sixth cultivar ('Bola') was included. Because 'Hiberna' was replaced in the 1973/74 trials by 'Extra Early Kaizuka' the combined analyses over years were only possible using data sets of two years × four sites × four cultivars for maturity and yield. Winter-kill data were available for five cultivars. The method of analysis was similar to that described by Dowker (1971). Sites, sowings, densities and genotypes were considered as fixed variables, being selected in advance, but years were treated as a random sample of all years. Variance components were calculated from expected mean squares using the method of Scheffe (1959) and were used to assess the relative magnitude of the main and interaction effects into which variation had been partitioned.

Where significant GE interactions were detected, further investigation was made using the joint-regression approach which is now widely used for such analyses (Perkins and Jinks 1968). The technique consists of regressing genotypic values on to environmental means and examining the differences between genotypes both in their regression coefficients and their deviations from linearity. The environmental scores are the mean value of all varieties grown in each environment. The linear proportion of the GE was estimated using the method of Fripp and Caten (1971) to assess the effectiveness of the technique. If GE is found to be represented as a linear function of the environment, it is possible to predict the performance of a genotype under given related environmental conditions. In addition the regression coefficient and deviation from linearity are measures of the sensitivity of a genotype to environmental change.

Results

Genotypic effects

The means of percentage winter-kill, percentage bolting, yield and maturity time for each cultivar are given in Table 2. Within each year the differences between cultivars for all variates were shown to be significant but from the combined analysis over two seasons genotypic differences were found only for percentage winter-kill. For bolting, yield and maturity, a year × genotype interaction was detected and be-

total yield

Maturity (100 % tops fallen) (Days after 30 April)		Total Yield (t/ha)			
1972/73 ^b	1973/74°	2 years°	1972/73ª	1973/74°	2 years°
43.4	54.4	49.5	28.1	30.4	29.6
42.0	46.3	44.5	36.7	31.4	33.9
55.9	56.0	55.4	46.4	38.7	41.9
47.3	50.4	48.6	37.7	32.6	34.6
74.4	-		34.4	-	
-	43.2		-	27.1	
0.7	1.0	0.6	0.9	3.2	0.9

Table 3. Variance components as a percentage for winter-kill, bolting, maturity and total yield calculated from 2 years combined analyses

Component	Winter- kill	Bolting	Maturity	Total Yield
GENOTYPIC (G)	1.5	0.8	6.2	5.5
ENVIRON-				
MENTAL (Total)	62.4	76.6	68.9	76.2
Years (Y)	0.2	10.1	3.7	1.4
Sites (S)	16.2	25.8	-	_
YS	2.6	9.8	27.2	34.2
Sowings (So)	19.6	14.2	17.3	11.3
SSo	9.9	4.8	_	4.8
YSSo	6.7	5.6	14.1	9.8
Densities (D)	-	_	2.1	8.0
YD	-	_	-	1.8
YSD	4.7	1.3	1.7	2.6
YSoD	-	1.2	0.5	1.7
YSSoD	-	3.0	2.0	0.7
Other	2.5	0.8	0.3	0.0
GE INTERACTIONS	3			
(Total)	14.9	17.5	16.3	8.8
YG	_	3.9	4.2	1.4
SoG	0.7	0.8	3.2	-
GD	-	-	_	0.7
YSG	5.8	2.8	1.9	1.3
YSoG	-	2.7	0.5	-
YSSoG	-	1.9	4.5	2.5
YSGD	-	1.1	-	-
SSoGD	6.9	_	-	-
YSSoGD	-	3.2	_	
Other	1.5	1.1	3.8	2.9
ERROR (Total)	21.1	5.0	8.6	9.4

came the correct error term for testing genotypic differences, as years were considered to be a random variable. As a result of reduced degrees of freedom, these tests were relatively insensitive and thus may have underestimated the importance of genotypic variation for each character which proved to be significant (P=0.001) when tested against the respective experimental errors. How much the change of seed stock between seasons contributed to the year \times genotype interactions cannot be determined but is must be considered when looking at combined years data.

In both years 'Express Yellow O-X' showed greatest winter survival and the lowest percentage of bolting plants. Conversely, 'Bola' showed the greatest winter losses and prevalence to bolting. 'Hiberna', grown only in the first season, had only 9% plant loss which was lower than some of the Japanese cultivars and the control cultivar 'White Lisbon'. The earliest maturing cultivars were 'Extra Early Kaizuka' and 'Expres Yellow O-X' followed, in order, by 'Imai

Yellow', 'Presto', 'Senshyu s.g. Yellow' and 'Hiberna'. Because of excessive levels of bolting the maturity time of 'Bola' could not be assessed accurately. The highest yields were produced by 'Senshyu s.g. Yellow' (42 t/ha), the latest maturing cultivar, and the lowest by 'Extra Early Kaizuka' (27 t/ha), the earliest (Table 2). The other cultivars produced intermediate yields and were similar to each other.

Environmental effects

The environmental influences were considerable, accounting for over 60 % of variation encountered for each variate (Table 3). For winter-kill and bolting, sites and sowings were the most important, but considerable variation between years was also detected for bolting. For maturity and yield, year × site, sowings and year × site × sowings were most important in that order. The environmental means for percentage winter-kill and percentage bolting are given in Table 4 and for maturity and yield in Table 5.

Winter losses were highest from the later sowing and percentage of bolters greatest from the earlier sowing at all sites. Winter losses were high at A. Rickwood EHF and Efford EHS and low at Rosewarne EHS (the site with the mildest winter climate) but a site × year interaction was also detected. When tested against the significant year × site × sowing interaction, which is the appropriate test when years are considered as random, the significance of a site × sowing interaction for winter-kill could not be shown. However, the deleterious effect of later sowing was very much greater at A. Rickwood EHF and Efford EHS than at the other sites.

For bolting the effects of site and sowing accounted for 26% and 14% of the overall variation respectively (Table 3) and year differences were detected, with higher numbers of bolting plants in the second season. At A. Rickwood EHS the percentage of bolters was low and at Rosewarne EHS high in both years. For maturity, differences were found between years and between sowings with later maturity in the second season and from later sowing. Site differences could not be shown because of the existence of a large site x year interaction but within each season site differences were significant (p = 0.001). Efford was the

Table 4. Environmental means for percentage winter-kill and bolting

	% winter-l [Angles in			% bolting [Angles in ()]		
Environment	1974/73°	1974/74ª	2 years ^b	1972/73 ^b	1973/74 ^b	2 years°
Site						
W	5.0 (11.4)	-	-	9.9 (12.2)	-	-
S	10.3 (15.1)	10.9 (16.5)	11.7 (17.0)	1.2 (2.7)	0.8 (3.1)	0.5 (1.9)
L	11.5 (15.3)	-	-	3.7 (7.1)	-	-
AR	27.3 (29.9)	30.8 (31.6)	29.3 (80.8)	0.3 (0.9)	0.9 (3.3)	0.5 (1.9)
R	3.4 (9.0)	11.5 (16.4)	7.9 (13.2)	12.4 (15.3)	18.4 (23.8)	12.8 (17.3)
E	20.2 (24.3)	18.1 (22.1)	20.1 (23.9)	4.6 (7.5)	2.8 (5.8)	1.9 (4.6)
sed ±	(1.78)	(1.48)	(1.17)	(0.56)	(1.54)	(0.71)
Sowing						
1	7.6 (13.1)	9.8 (15.8)	9.3 (15.3)	9.4 (12.6)	8.7 (13.2)	6.3 (10.1)
2	18.3 (21.9)	25.8 (27.4)	25.2 (27.2)	1.2 (2.6)	2.7 (4.8)	1.6 (2.9)
sed ±	(1.03)	(1.05)	(0.83)	(0.32)	(1.09)	(0.50)
Density						
Low	13.2 (17.3)	19.5 (22.5)	18.4 (21.7)	6.3 (8.5)	5.7 (9.2)	4.3 (8.9)
High	12.7 (17.7)	16.2 (20.7)	16.1 (20.7)	4.4 (6.7)	5.7 (8.9)	3.6 (8.0)
sed ±	(0.66)	(1.08)	(0.74)	(0.22)	(0.46)	(0.26)
Years						
1972/73	-	-	16.3 (20.4)	-	-	1.7 (3.5)
1973/74	-	-	18.2 (22.1)	-	-	6.1 (9.4)
sed ±			(0.83)			(0.50)

a, b, c based upon 6, 5 and 4 cultivars respectively

earliest site in 1973/74 (11 June) and also earliest when the results for two years were combined. A significant effect of sowing on yield was detected with higher yields from the first sowing. The largest environmental effect on yield was that of year × site with the sites ranked differently over the two seasons but the additional effects on yield of winter-kill and bolting appeared to be major factors at some sites. The highest yielding site in 1972/73 was Efford EHS (45 t/ha) but in 1973/74 the highest was A. Rickwood EHF (40 t/ha).

Maturity time was affected by plant density with slightly earlier maturity from the higher density plots. Densities did not significantly affect any of the other variates.

Genotype-environment (GE) interactions

Several important GE interactions were found for winter-kill, bolting and maturity accounting in total for 15%, 18% and 16% of the overall variation res-

	Maturity (days afte	(100 % tops er 30 April)	fallen)	Total yield (t/ha)			
Environment	1972/73 ^b	1973/74 ^b	2 years°	1972/73 ^b	1973/74 ^b	2 years	
Site							
w	52.4	_	_	41.7	-	-	
S	56.7	51.8	53.6	33.1	31.6	32.6	
L	-	_	-	31.9	-	-	
AR	56.3	45.4	48.7	28.4	39.7	33.4	
R	47.3	61.1	51.3	39.2	22.6	33.9	
E	50.3	41.9	44.4	45.4	34.4	40.2	
sed ±	0.9	1.5	1.0	1.6	2.8	1.2	
Sowing							
1	49.0	45.7	44.6	39.4	36.2	39.9	
2	56.2	54.4	54.4	33.6	27.9	30.1	
sed ±	0.6	1.1	0.6	0.8	2.0	0.9	
Density							
Low	54.5	52.2	51.2	33.9	25.6	30.6	
High	50.6	47.9	47.8	39.4	38.7	39.4	
sed ±	0.4	0.6	0.5	0.6	2.0	0.6	
Years							
1972/73		-	47.2	_	_	36.7	
1973/74	_	_	51.7	_	_	33.4	
sed ±			0.7			0.9	

b, c based upon 5 and 4 cultivars respectively

Table 6. Joint regression analyses of genotype \times environment interactions of autumnsown onions calculated from 2 years combined trials

	% winter-kill		% bolting		Maturity	Total Yield
<u>Item</u>	df	ms	df	ms	ms	ms
Replicates Genotypes Environment GE	2 4 31 124	50.6 2680.4° 1811.5° 9.50 ^b	2 3 31 93	8.9 490.2 ^b 978.1 ^c 47.9 ^c	50.9 1963.8° 1019.3° 85.9°	21.4° 404.4° 275.4° 12.3°
Heterogeneity of regression Remainder	4 120	374.8° 85.6	3 90	613.6° 29.1°	490.8° 72.4°	8.3 12.4°
Error	316(2)	67.3	253(1)	8.8	23.3	6.1
Linear proportion accounted for by regression		94 %		97 %	91%	_

a, b, c indicate p = 0.05, 0.01, 0.001 respectively

pectively (Table 3). For yield only 9% of the variation was attributable to GE effects, which was less than the error variation. For bolting the largest effect was that of year \times genotype and its implication regarding the test for genotypic differences in two years combined data has been mentioned.

Joint regression analyses (Table 6) were succesful in describing the GE variation in linear terms. Significant heterogeneities of regression were found for winter-kill, bolting and maturity accounting for 94%, 97% and 91% of the GE variation respectively. For bolting and maturity significant remainder items (non-linear portions) were also found.

The regression coefficients (b's) estimated for the cultivars grown over two seasons are given in Table 7. 'Express Yellow O-X' showed least response to environment for both winter-kill and bolting and 'Bola' was the most sensitive cultivar for winter-kill. For

Table 7. Regression coefficients $(\hat{b}'s)$ from 2 years combined joint regression analyses for winter-kill, bolting and maturity

	Regression coefficients					
Cultivar	Winter-kill	Bolting	Maturity			
'Presto' (P)	0.09	0.28	0.25			
'Express Yellow O-X' (EY)	-0.30	-0.40	0.07			
'Senshyu s.g. Yellow' (SY)	0.09	0.06	-0.35			
'Imai Yellow' (IY)	-0.05	0.06	0.04			
'Bola' (B)	0.16	-	_			

bolting 'Presto' appeared to be responsive to environmental change and also showed considerable variation in coefficients between years (-0.22 in 1972/73 and +0.38 in 1973/74). Because of the change in seed stock between years the conclusions drawn regarding this effect can only be tentative. 'Hiberna' (from one year's data) showed little response for winter-kill but was the most sensitive cultivar for bolting (b = 1.105). Additional research, however, (Dowker and Fennell 1975) has shown that there may be large seasonal fluctuation in winter losses for this cultivar related to conditions of soil waterlogging rather than temperature. For maturity 'Senshyu s.g. Yellow' was least sensitive to environment and 'Presto' the most sensitive. For winter-kill and bolting the cultivar means and regression coefficients appeared to be positively correlated.

Discussion

Some data from these trials have already been used for agronomic advice to prospective growers of this crop in the UK (Salter 1975). The combined analyses presented here has enabled the partitioning of variation into its respective genotypic, environmental and GE components and the results are useful for the effective planning of a breeding programme.

At all sites the effect of sowing was shown to be critical, leaving little flexibility for choice. Improvements made in the resistance to bolting should enable greater choice of sowing date and the opportunity of earlier sowing would improve yields at harvest by extension of the growing season and reduce plant loss through winter-kill and unmarketable loss through

bolting. Because of the uncertainty of magnitude of winter losses, plant stands in spring cannot be achieved with confidence but resistance to winter-kill would allow for precision drilling to a pre-determined plant density. Although it may be possible to improve yields without reducing the levels of winter-kill and bolting, the present unreliability of plant survival and the need for elimination of unmarketable plants at harvest would favour the resistance approach. At present the crop is primarily of value in providing mature bulbs during the early summer and is not suitable for storage, therefore it is also desirable to produce cultivars with distinct and reliable maturity times for sequential supply.

Knowledge of the effects induced by environmental conditions gives information to the breeder on suitable screening environments for important traits. The effect of years was shown to be considerable although change of seed stock may have introduced a GE effect here. In the early stages of a breeding programme the breeder may prefer to avoid evaluation of breeding lines over more than one season to reduce the time scale involved. During this time alternative environments within a season would be desirable but the effect of season must ultimately be known before the cultivar release stage. Site and sowing differences were shown and for winter-kill and bolting suitable screening could be achieved using combinations of these environments. The highest levels of winter-kill were found in the south and east of England and the lowest levels in the south-west, where air temperatures were generally higher. The south-west, however, produced higher levels of bolting possibly related to plant size (Salter 1975). Late sowing or choice of site (e.g. where winter plant losses are known to be high) would be suitable for winter-kill. assessment. Similarly, for bolting there were differences between sites and greater levels were induced be early sowing. Although the ranking of sites according to bolting and winter-kill is not a mirror image, the extreme sites were in reverse for these characters. Therefore in an environment providing effective selection for one character there may be insufficient selection pressure for the other. For practical purposes a suitable screening environment can be achieved using a single site and controlling the expression of winter-kill and bolting by the use of early and late

sowing dates. It is probable that an early and late August drilling would be adequate. Selection for maturity time is primarily an indirect selection for daylength response and the character should be satisfactorily expressed at all sites.

If a breeder is to use the cultivars studied as potential parental material the results obtained regarding their response to environment will be of value. When producing in improved cultivar for a specific environment, parental material would be selected on its mean performance in that environment regardless of its response over a range of environments. For this crop, however, there are several different environments, the sites in this study all being within the potential growing areas. Thus to accommodate all these environmental variables selection of parental material must include consideration of response to environment and mean performance.

The lowest levels of winter-kill and bolting were shown by 'Express Yellow O-X' and the regression coefficients indicate that this cultivar showed little variation in these characters over environments. This cultivar consistently gave early yields but as it is a hybrid (male-sterile), its use as a parent is limited. Of the open-pollinated cultivars, 'Extra Early Kaizuka' also showed early maturity but had lower yield potential. The joint regression analyses showed that it was consistent over environments for low bolting but it was responsive to environments for winter-kill. Thus its contribution to a breeding programme would be for its earliness and bolting resistance. 'Imai Yellow' was intermediate for bolting and winter-kill and relatively stable over environments. For maturity time it was approximately one week later than 'Extra Early Kaizuka' but showed superior yield potential.

The highest yielding cultivar, 'Senshyu s.g. Yellow', was later maturing but extremely consistent over the environments for all characters and must therefore be given consideration as a suitable source of valuable germplasm. For 'Presto' the two seed stocks appeared to differ and thus the overall performance was disappointing, particularly for bolting and maturity time. Likewise it has been shown that 'Hiberna' is variable with respect to winter plant loss. It would appear that the cultivar can withstand ex-

tremely low temperatures (Tronickova 1971) but not soil waterlogging.

The breeder, therefore, has material available for further development but the expected response to selection within these populations and the value of crosses between them have yet to be determined.

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