The Inheritance of Node Number and Rate of Node Production in Brussels Sprouts

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Summary. The total vegetative node number, rate of node production and number of sprouts over 13 mm diameter were recorded for 10 F_1 Brussels sprout cultivars and 45 progenies derived by intercrossing and selfing them. Significant differences, resulting from additive gene action, were found between the 10 cultivars and between their progenies for both characters. For total node number there was also evidence of dominant gene action. Total node number and rate of node production were closely correlated as were total node number and the number of harvested sprouts. The factors causing differences in rate of node production are indicated and the relationship of this character to other Brussels sprout yield components is outlined.

Key words: *Brassica oleracea* var. 'gemmifera' — Brussels sprouts — Nodes — Additive genes — Yield components

Introduction

Despite a number of major breeding programmes and considerable research on Brussels sprout F_1 cultivar production, there is little information on the inheritance of yield and its components in the crop. Rowlands (1962, 1964) investigated the inheritance of sprout number and weight in a small sample of lines, and other investigators (e.g. Thompson and Taylor 1973, 1974; Fisher 1974 a,b; Fisher and Milbourn 1974) have noted differences between cultivars for a number of yield related characters, but little other work has been published. However, plant breeders are continually selecting for improved crop yields and, in doing so, make assumptions about the inheritance of the characters they wish to manipulate. Since 1974, a series of experiments on the inheritance of Brussels sprout yield and its components has been conducted at the Scottisch Horticultural Research Institute in an attempt to provide breeders with useful information about such characters.

The enlarged axillary buds which constitute the sprouts of the Brussels sprout crop are produced singly in leaf axils of the plant. The number of such axils depends on the number of vegetative primordia cut off at the apex during the growing season, that is on the number of nodes produced by a plant. Not all nodes will give rise to harvestable sprouts, because a proportion of the axillary buds will be too small to be harvested, and near the base of the plant some nodes will not have axillary buds. In the first instance therefore sprout yield depends on the number of primordia formed and their subsequent growth. This paper describes the inheritance of the former character.

Materials and Methods

Plants from 10 F_1 cultivars ('Leonore', 'King Arthur', 'Peer Gynt', 'Parsifal', 'Jade E', 'Perfect Line', 'Achilles', 'Kadina', 'Gleneagles' and 'Nelson') were intercrossed in all combinations omitting reciprocals but including selfs. Sufficient seed was obtained from only 55 of the possible 65 lines (10 F_1 cultivars, 8 selfed and 37 cross-bred progenies) and these were sown during March 1976 into Jiffy 7 peat pots and transplanted in the third week of May at 60 × 46 cm spacing. The seedlings were individually randomised after germination into four blocks each of which contained twelve plants per line. Three whole plants from every line in each block were harvested at the end of October, when vegetative primordia production had effectively ceased, and the numbers of nodes present on each plant were counted, using a stereo microscope to count apical primordia. The number of sprouts over 13 mm was also recorded at this harvest and at harvests in November and December. For the experiment on node production rate three randomised blocks were used in which each plot was split for harvest date. Four whole plants from every line in each block were harvested on 24 June, 21 July and 13 August, node numbers being counted using the same procedures as in the other experiment. A preliminary analysis of variance showed that node production was linear form 24 June — 13 August, and the rate of node production was therefore calculated from plot means as: (nodes per plant at final harvest — nodes per plant at first harvest)/days between harvests.

Both final node number and the rate of node production were analysed using the procedure described by Gilbert (1967) which fits additive parental main effects or 'combining abilities' according to the model

$Y_{ij} = b_i + b_j + interaction.$

where b_i is the general combining ability (G.C.A.) of the ith parent plus one half of the general mean and b_j that of the jth parent plus one half of the general mean, and the interaction or specific combining ability (S.C.A.) includes all differences not ascribable to the parents. Each analysis was done twice, once with the parental cultivars omitted and once with the selfed progenies omitted.

Results

Final Node Number

Line means for final node number ranged form 104.5 for the selfed progeny of cv. 'Parsifal' to 161.3 for that of cv. 'Jade E' (Table 1). Both block and line differences were highly significant (P < 0.001, Table 2) but the interaction between them was not significant and was therefore pool-

ed with the within family variance. Block differences were considered to result from the siting of the experiment on a slope without irrigation during a growing season remarkable for a long dry spell from July to September. On blocks towards the bottom of the slope the plants were heavier and taller with higher node numbers than those further up the slope. The absence of a significant block × line interaction shows that this environmental variation did not differentially affect the lines with respect to node number.

In the Gilbert analysis in which the parents were included, all the line differences could be accounted for by G.C.A. effects (Table 2). However, when selfed progenies were substituted for the parents in the analysis, S.C.A. was also significant, a consequence of inbreeding depression in some of the selfed progenies. Selfed progenies from cvs. 'King Arthur', 'Peer Gynt', 'Parsifal' and 'Perfect Line' had 15-20 fewer nodes than their parents although there were no significant differences between the node numbers of the selfed progenies of cvs. 'Leonore',

Table 1. Mean final node number and parental constants for 10 F_1 Brussels sprout cultivars and their progenies

Parent		Node number											Parental constant[a]
		Parental Mean	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	
'Leonore'	(1)	134.5	133.4										135.2 (2.58)
'King Arthur'	(2)	126.5	129.5	110.4									117.6 (2.62)
'Peer Gynt'	(3)	124.3	130.6	123.8	110.0								126.5 (2.60)
'Parsifal'	(4)	128.9	132.1	127.6	130.5	104.5							133.0 (3.04)
'Jade E'	(5)	161.3	150.0	133.4	145.9	–	158.0						159.2 (2.85)
'Perfect Line'	(6)	127.6	129.6	120.3	123.5	136.0	–	110.9					128.1 (3.09)
'Achilles'	(7)	143.0	143.8	121.3	130.6	141.9	152.7	–	–				142.5 (2.69)
'Kadina'	(8)	129.6	126.6	116.4	129.8	129.7	132.4	130.8	140.7	128.8			127.4 (2.75)
'Gleneagles'	(9)	141.6	146.8	130.6	142.1	–	149.7	125.9	140.3	140.9	–		146.2 (3.03)
'Nelson'	(10)	121.2	120.3	119.2	121.3	–	143.9	–	129.7	–	–	119.0	119.8 (2.99)

[a] As calculated from the analysis which included parental cvs. and omitted their selfed progenies; figures in parenthesis are standard errors

Table 2. Analysis of variation for node number and node production of 10 Brussels sprout cultivars and their intercross progenies

Source of variation	Node number		Node production per day	
	d.f.	mean square	d.f.	mean square
Blocks	3	1496.3 ***	2	0.0460
Lines	46	1058.35***	46	0.0325**
G.C.A.	9	4474.89***	9	0.0901***
S.C.A.	37	227.30	37	0.0185
Within family residual	442 (60)[a]	217.48	92	0.0162

[a] Figure in parenthesis represents number of missing values

***, ** indicate significance at the 0.001 and 0.01 levels respectively

'Jade E', 'Kadina' and 'Nelson' and those of their parents (Table 1).

The parental constants (Table 1) show that cvs. 'Jade E', 'Gleneagles' and 'Achilles' conferred high node numbers on their progenies and cvs. 'King Arthur' and 'Nelson' low numbers. The rankings of the parental constants from both analyses were similar to those of the parent cultivars and no progeny had more nodes than cv. 'Jade E'.

The inheritance of final node number appeared to be controlled by genes acting additively and a high proportion of the total variation was due to the effect of such genes. Some evidence that dominant genes were also present may be inferred from the low node number of some of the selfed progenies and, from intercross progeny means, it seems probable that some genes dominant for low node number were present in cv. 'King Arthur'. The intercross progeny means of other cultivars with significant inbreeding depression (e.g. 'Parsifal', Table 1) were close to the mid-parent mean evidence that, in these cultivars, additive gene action predominated.

When final node numbers were compared with the sprout numbers obtained from all the harvests of the same experiment it was found that both the phenotypic and genotypic correlations were highly significant (r = 0.56 and 0.75 respectively, P < 0.001 for both) but the lower phenotypic correlation implies that independent within line variation occurred for sprout and node number.

Rate of Node Production

Progeny means for the number of nodes produced per day between 24 June and 13 August ranged from 0.820 for cv. 'King Arthur' to 1.310 for the selfed progeny of cv. 'Jade E', with an overall mean of 1.102 (Table 3). Differences

between lines were again highly significant, but although variation between blocks was quite large neither it nor the block × line interactions were significant.

In both Gilbert analyses (Table 2) only the G.C.A. effects were significant. All progeny means could be accounted for by reference to their parental means and there was no evidence of inbreeding depression in selfed progenies. This would suggest that the relatively low final node numbers of certain selfed progenies reflect an earlier cessation of node production in the autumn rather than a difference in rate of growth during the summer.

The parental constants show that the parents with the highest final node numbers were those with the highest node production rates (cvs. 'Jade E', 'Gleneagles' and 'Achilles', Table 3) and similarly for those with the lowest numbers and production rates (cvs. 'King Arthur' and 'Nelson', Table 3). It appeared that node production rate was also controlled by genes acting additively and there was little evidence of any dominant genes affecting the results. The two variates were significantly correlated genotypically (r = 0.60, P < 0.001) and the parental constants were even more closely correlated (r = 0.92, P < 0.001). This suggests that final node number depended largely on the rate of node production during their period of rapid production (June, July and August). Where differences were noted between the two variates it seemed likely that they resulted from differences between progenies in the slowing of node production rate during September and October.

Discussion

The number of vegetative nodes in Brussels sprouts depends on the number of primordia produced during the

Table 3. Mean rate of node production and parental constants for 10 F_1 Brussels sprout cultivars and their progenies

Parent		Nodes produced per day											Parental constant[a]
		Parental mean	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	
'Leonore'	(1)	1.090	1.260										1.133 (0.0464)
'King Arthur'	(2)	0.820	1.080	1.060									0.926 (0.0455)
'Peer Gynt'	(3)	1.065	1.223	1.030	0.963								1.105 (0.0477)
'Parsifal'	(4)	1.090	1.127	1.017	1.157	1.143							1.117 (0.0499)
'Jade E'	(5)	1.300	1.303	1.260	0.935	–	1.310						1.268 (0.0508)
'Perfect Line'	(6)	1.040	1.060	1.100	0.987	1.080	–	0.983					1.124 (0.0530)
'Achilles'	(7)	1.243	1.207	0.967	1.215	1.173	1.150	–	–				1.210 (0.0476)
'Kadina'	(8)	1.105	1.050	1.070	1.180	1.100	1.183	1.050	1.150	1.030			1.124 (0.0494)
'Gleneagles'	(9)	1.240	1.040	1.089	1.285	–	1.284	1.130	1.235	1.270	–		1.252 (0.0617)
'Nelson'	(10)	1.007	1.020	0.930	1.003	–	1.117	–	1.115	–	–	0.947	0.976 (0.0492)

[a] As calculated from the analysis which included parental cvs. and omitted selfed progenies; figures in parenthesis are standard errors

growing season prior to vernalisation. These primordia are cut off at the plant apex successively throughout the growing season. In preliminary experiments it was found that the arrangement of primordia on the apex was such that the mean angle between any two adjacent primordia and the centre of the apex was close to 137.5°. In their detailed description of the phyllotaxis of plants, Richards · and Schwabe (1969) refer to this angle as the Fibonacci angle, since it is the limiting angle of the Fibonacci series. This series can be identified on a Brussels sprout stem from examining the ordering of nodes. Richards and Schwabe (1969) also note that the period between the formation of two successive primordia, and hence the rate of primordia production will depend on the rate of cell division at the apex, the size and shape of the apex and the size of the primordia cut off (Richards and Schwabe 1969). In Brussels sprout the rate of node production increases until June when it reaches approx 1 per day and remains at this level until September. Subsequently the rate of production is much reduced until it is terminated by the production of floral primordia, (usually during November and December).

During the early phase of primordia production the apex gradually enlarges (Hodgkin, unpublished), and it may be that the large number of nodes on cv. 'Jade E' is the result of an earlier increase in apical size. However, for the other cultivars examined, differences in the rate of node production during the main growth period were sufficient to explain the differences found in the number present at maturity. Presumably these differences can ultimately be ascribed to variation in one or more of the characters cited by Richards and Schwabe, the inheritance of which must be controlled largely by additive genes.

The number of sprouts over 13 mm was found to be closely correlated genotypically with node number (r = 0.75), although only about half the nodes produced sprouts of sufficient size to be harvested. Since these nodes were all produced by mid-July a count at this time might well have been sufficient for early selection of the most productive progenies.

Rowlands (1962, 1964) found that sprout number showed additive variation with strong dominance for large numbers of sprouts. In this more extensive study, dominance did not appear to be of great importance for node number, but dominant genes did affect axillary bud growth, and thus the number of sprouts that were har-

vested. These aspects of sprout production will be the subject of future papers. However, the present study has shown clearly that the number of sites at which sprouts are produced can be manipulated by direct selection and that cultivars with high node producing potential are available for breeding purposes.

Acknowledgement

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