

Interpretation of performances of hybrids obtained from 43 asparagus parent genotypes

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Summary — The data used were the yields of 231 distinct hybrids grown in long-term multi-site trials (10 yr, 4 sites), resulting from the crossing of 43 genotypes. Genotype–environment interaction was taken into account by means of a factorial regression model previously defined through the varieties used as controls in the trials. Two environmental covariates were used: the latitude of the site, and the type of production (green or white asparagus). It is shown in this paper that most of main effects and genotype–environment interactions could be explained by additive and symmetrical parental influences. The pseudo-diallel structure was therefore reduced to the values of 3 parameters associated with each parent (main effect and 2 regression coefficients) and could thus be easily interpreted. The model was used to evaluate yields of all 816 possible hybrids within chosen environmental conditions.

***Asparagus officinalis* / genotype–environment interaction / diallel / series of experiments / parental effect**

Résumé — **Interprétation des performances d'hybrides issus de 43 génotypes d'asperge.** *Les rendements de 231 hybrides différents constituent l'ensemble des données utilisées, provenant d'un réseau d'expérimentation comprenant 10 années et 4 lieux. Les interactions génotype-milieu sont prises en compte par le biais d'un modèle de régression factorielle établi dans un travail antérieur à partir des variétés utilisées comme témoin dans le dispositif. Deux covariables du milieu sont utilisées : la latitude du lieu et le type de production (asperge blanche ou verte) dans le lieu et l'année. On arrive à la conclusion que les effets principaux et les interactions génotype-milieu peuvent être décrites par des effets parentaux additifs et symétriques. L'interprétation du pseudo-diallel peut donc être facilement établie grâce aux valeurs de 3 paramètres (effet principal et 2 coefficients de régression) caractérisant chacun des 43 génotypes parentaux. Enfin la valeur hypothétique des hybrides est prédite (y compris pour les hybrides non expérimentés) grâce au modèle retenu pour des conditions d'un milieu déterminé.*

***Asparagus officinalis* / interaction génotype-milieu / diallel / réseau d'essai / effets parentaux**

INTRODUCTION

During the past 30 years, asparagus breeders have developed several types of hybrids (Corriols and Doré, 1989) ranging from highly heterogeneous populations (Bannerot *et al*, 1969) to genetically homogeneous F1 hybrids (Corriols *et*

al, 1989). Many characteristics of asparagus make experimentation difficult and lengthy; the species is a perennial and hybrids cannot be obtained or tested simultaneously in large numbers. Indeed the yield varies greatly from year to year. In the French (INRA) breeding program, it is suggested that at least 4 years' observation is

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necessary to have a reliable estimate of yield; the experiments began in 1969, the main objective being to produce homogeneous F1 hybrids with high yield, an early production and thick spears (the edible portion of young stems) with a good shape.

There are 2 types of asparagus produced in the world: (i) white asparagus in which the spears are harvested from raised beds just as the tip of the spear emerges through the soil; and (ii) green asparagus in which the spears are harvested at ground level once elongated to about 20–30 cm. Any cultivar can be used for white or green asparagus. Nevertheless, in different countries, specific cultivars have been bred for each type of cultivation. In France we used to cultivate only white asparagus, which predominates in Europe, while green asparagus is common in both the United States and Italy.

During the selection process, plant breeders are faced with difficult choices. First of all, the genotype–environment interaction must be taken into account by introducing soil and climatic variability corresponding to the target regions of cultivation. This can be done by performing experiments in different environments (years and sites). When the cultivars to be produced are hybrids, however, these difficulties are increased by the enormous multiplication of possibilities from only a few potential parents. This is of course impossible and some drastic reduction must be applied.

The large quantity of heterogeneous information analysed in this study has been gathered over the last 15 years in the French (INRA) breeding program in a 4-location multisite experiment in France; it represents an exceptional set of data. An initial interpretation of these data (Corriols and Doré, 1989) based on a ranking index was used for comparing different types of hybrids. Their synthesis took into account 4 characters (total yield, early yield, spear diameter and spear appearance). The novelties introduced in this paper concern the modelling of the genotype–environment interaction and the parental effects on total yield.

In this study we examine the available data on hybrids in order to assess the values of the parents. The aim is also to know which parents can be used to produce hybrids for cultivation both in the south and north of France and/or for both white and green production. To reach these objectives, we used a simplified model leading to 3 parameters for each of the parental genotypes. They could be used as additional help for recommending future hybrid creations.

MATERIALS AND METHODS

Biology of asparagus

Asparagus is a dioecious species (with separate male and female plants). Sex determinism is monogenic; the male plants are heterogametic (Mm) and the female plants are homogametic recessive (mm) (Rick and Hanna, 1943). Homozygous genotypes were obtained by 1 of 2 different methods.

The search for haploid genotypes from polyembryonic seeds

After chromosome doubling this method leads to female plants homozygous for all loci (Thévenin, 1968; Doré, 1977). This is the case for parents L1 to L24, which are homozygous lines composed of 50% female (mm) and 50% male (Mm) isogenic plants and have been produced by crossing a homozygous female plant to a male plant and back-crossing to the female recurrent parent for 5–6 generations (Thévenin and Doré, 1976). These pure lines can be used either as the male or the female parent (tables I and II).

In vitro anther culture

This method (Doré, 1974) gives either female or male homozygous plants. M1 to M10 are male genotypes obtained by this method. These genotypes are homogametic (MM) and are called super-males because of their all male progeny.

Data

Data were issued from the French (INRA) asparagus breeding program; their detailed environmental characteristics have been described previously by Rameau and Denis (1992). About 40 new hybrids and standard varieties were planted each year generally in 4 testing sites: 2 in the north of France, 1 in Central France and 1 in the south. Hybrids were grown in a randomized complete block design with 4 replications and 15 plants per plot. One of the northern locations and the central location produce white asparagus; the other 2 produce green asparagus. The difference to the first study is that all the hybrids are now included in the statistical analysis. There were 231 hybrids which can be presented in a pseudo-diallel scheme (table I), as some parents cannot be or were not used in both directions. The total number of parent genotypes was 43 but they were used non-randomly according to their genetic structure, their fertility and the date when they were obtained within the breeding program.

Genotypes f1 to f7 are heterozygous female plants and were used only as female parents. Genotype m11 and m12 are heterozygous male plants used only as male parents. The other 34 parents are homozygous

Table I. Number of yields for each of the 231 hybrids. Rows (columns) correspond to female (male) parents.

	MMMMMMMMmm											LLLLLLLLLLLLLLLLLLLLLLLLLLLLLLLLLLLL											
	1	2	3	4	5	6	7	8	9	11	12	1	2	3	4	6	7	8	9	11	12		
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0		
f1	3	3	3	3	4																3	*	
f2	4	3		3	3	3	3	4															*
f3						3																	
f4	4	3	4				3				*												
f5	4	4	3		4	4	3	3			*												
f6	3	4				4	3																
f7	3	3	3	3	3	3	5	3	4														
L1								4													6		4
L2									4												3		4
L4	3	3	4																		7	7	4
L5																					4	3	3
L6																					4		4
L7																					3		3
L8	4																				3	3	3
L9	3	3																			4	4	3
L10		3																			3	3	3
L11	4	3	3	4																	5	3	4
L12																					4		4
L13																							
L14	3	3																			3	3	4
L15		3																			4	4	4
L16																					3	3	3
L17																					4	4	3
L18																					3		3
L19																					4	4	4
L20																					3	3	3
L21																					3		
L22																							
L23	5																				4	4	4
L24																					3	4	3

Empty cells indicate that there was no hybrid; stars indicate > 9 replications.

genotypes; super-males (M1 to M10) can only be used as male (see above); pure lines (L1 to L24) were generally used as male and female (due to sterility problems L3 was used only as male and L5 and L11 were used only as female).

As in the previous study, the yield was estimated by the weight of harvested spears during the 4th year after planting, *ie* the second harvest season. Among the 7 standard varieties used to select the factorial regression model (Rameau and Denis, 1992), 5 had their parents among the 43 genotypes: 'Andréas' is an F1 hybrid between L19 and the super-male M8 (Corriols *et al*, 1989); 'Stéline' is a clonal hybrid between f5 and m12; and 'Aneto', 'Cito' and 'Desto' are clonal hybrids between m11 and the female plants

f1, f2 and f4, respectively. A clonal hybrid results from crossing between 2 (heterozygous) plants, 1 male and 1 female, multiplied by *in vitro* culture.

Statistical methods

Even with incomplete data, the major features of variability must be introduced in the statistical model to give an unbiased and accurate interpretation of genotype behavior. This has been done in 2 ways. First the genotype-environment interaction was modelled with the model selected by Rameau and Denis (1992), in the same series of experiments, analysing yields of

Table II. Summary of the data set for lines with male or female parents.

<i>Female</i>						<i>Male</i>					
-1-	-2-	-3-	-4-	-5-	-6-	-1-	-2-	-3-	-4-	-5-	-6-
M1	0					M1	7	24	3.49	1.37	4.88
M2	0					M2	12	42	4.38	3.10	7.27
M3	0					M3	7	21	2.83	2.15	3.39
M4	0					M4	8	27	4.09	2.15	4.98
M5	0					M5	2	6	6.45	6.31	6.60
M6	0					M6	6	20	3.89	3.73	4.11
M7	0					M7	8	29	5.12	2.87	6.26
M8	0					M8	11	55	4.92	2.98	6.19
M9	0					M9	15	60	3.89	0.93	6.25
M10	0					M10	4	14	3.23	2.51	3.69
m11	0					m11	3	75	3.69	3.07	4.14
m12	0					m12	1	25	3.30	3.30	3.30
f1	9	51	3.89	2.87	6.60	f1	0				
f2	9	55	4.25	3.54	6.06	f2	0				
f3	1	3	5.36	5.36	5.36	f3	0				
f4	5	34	3.47	3.07	4.98	f4	0				
f5	8	50	3.65	2.98	5.24	f5	0				
f6	4	14	3.99	2.17	5.64	f6	0				
f7	11	37	4.34	3.39	6.31	f7	0				
L1	4	20	3.39	2.90	3.70	L1	2	8	3.71	3.69	3.72
L2	7	25	3.27	1.95	4.59	L2	2	6	3.90	3.85	3.95
L3	0					L3	2	7	3.75	3.50	4.09
L4	21	118	4.02	2.51	6.06	L4	17	68	3.85	2.38	5.22
L5	6	21	2.21	0.76	3.33	L5	0				
L6	2	8	2.52	1.95	3.09	L6	2	7	3.44	2.63	4.05
L7	8	28	2.19	1.36	3.80	L7	5	17	2.87	2.04	4.32
L8	13	45	3.27	2.03	4.96	L8	9	39	3.19	2.46	3.97
L9	21	112	4.36	2.15	7.27	L9	13	55	3.60	2.40	4.82
L10	8	29	3.35	1.62	4.49	L10	5	18	3.31	2.38	4.23
L11	17	63	3.12	0.76	4.48	L11	0				
L12	1	4	3.22	3.22	3.22	L12	5	20	3.33	3.02	3.84
L13	1	3	2.43	2.43	2.43	L13	3	11	3.20	1.83	4.38
L14	14	49	2.80	0.93	4.09	L14	12	50	2.90	1.73	4.19
L15	17	64	3.37	2.21	6.39	L15	11	42	2.65	0.76	4.61
L16	5	16	3.00	2.12	4.42	L16	3	11	3.10	1.95	3.64
L17	4	17	4.63	3.90	5.22	L17	9	40	4.30	2.98	5.40
L18	4	12	4.37	2.96	6.19	L18	8	33	2.98	0.76	3.70
L19	13	49	3.30	2.08	4.83	L19	6	22	3.46	1.36	5.11
L20	2	6	2.82	2.45	3.18	L20	4	14	2.65	2.12	3.44
L21	1	3	4.69	4.69	4.69	L21	8	32	3.28	2.08	4.27
L22	1	3	2.28	2.28	2.28	L22	4	12	2.48	1.67	3.13
L23	10	37	3.32	1.67	5.40	L23	10	48	2.96	1.40	4.65
L24	4	14	2.99	1.83	4.68	L24	7	32	3.23	2.03	3.57

(-1-) Identification; (-2-) number of distinct crossings; (-3-) number of yields; (-4-) mean; (-5-) minimum; and (-6-) maximum of the yields.

control varieties which were more systematically experimented. Secondly genotype effects, main effects and interactions were simplified by retaining only the main effects associated with the parental lines of the hybrids.

Following the model selected in Rameau and Denis (1992) some more specific models using the diallel structure were fitted. Only the general model [GEN] and the model retained according to the ANOVA [RET] are reported here. Let $E(Y_{(f,m),(s,y)})$ be the expectation of the yield of hybrid (f,m) , crossing female f with male m , grown in environment (s,y) , defined by site s in year y . Two models similar to those proposed by Lin *et al* (1977) can then be written:

$$E(Y_{(f,m),(s,y)}) = \mu + e_{(s,y)} + v_{(f,m)} + c_{(f,m)} \cdot \text{Lat}_{(s)} + d_{(f,m)} \cdot \text{Prod}_{(s,y)} \quad [\text{GEN}]$$

$$E(Y_{(f,m),(s,y)}) = \mu + e1_{(s)} + e2_{(y)} + v_{(f)} + v_{(m)} + e3_{(s,y)} + c_{(f)} \cdot \text{Lat}_{(s)} + c_{(m)} \cdot \text{Lat}_{(s)} + d_{(f)} \cdot \text{Prod}_{(s,y)} + d_{(m)} \cdot \text{Prod}_{(s,y)} \quad [\text{RET}]$$

$\text{Lat}_{(s)}$ and $\text{Prod}_{(s,y)}$ are, respectively, the latitude of the experimental site s and the type of production (1 for green asparagus, 0 for white asparagus) used in site s year y ; μ is the general constant; $e_{(s,y)}$, $v_{(f,m)}$, $e1_{(s)}$, $e2_{(y)}$, $v_{(p)}$ are main effects; $e3_{(s,y)}$ is the interaction between site and year; $c_{(f,m)}$, $d_{(f,m)}$, $c_{(p)}$ and $d_{(p)}$ are regression coefficients depending on various factors. These parameters are unknown and were estimated from the data; here subscript p is used for parent and can be f or m in model [RET]. Both models are similar for environmental effects because the interaction term between site and year has been retained, as well as the regression terms for latitude (Lat) and type of production (Prod). The difference is in the simplification of the parameters for the hybrids. For main effect and regression coefficients, only additive and identical mother/father effects are retained, eg, $v_{(f,m)}$ is turned into $v_{(f)} + v_{(m)}$. Incidentally, 2 problematic effects vanished: (i) the specific combining ability, which was not completely inspected because of the numerous missing crossings (table I); and (ii) the maternal effect at the level of main effects, which could have been different for male and female parents $v1_{(f)} + v2_{(m)}$.

The models considered are linear fixed-effect models, ie the observations are assumed to be non-correlated, and to have identical unknown variance; they belong to the factorial regression models described by Denis (1980, 1988, 1991). Therefore, they do not take into account the genetic relationship existing between the genotypes or the genetical heterogeneity of the types of hybrids; they must be used as approximate models. The statistical process was performed by means of Intera (Decoux and Denis, 1991) and Modii (Modulad, 1987), 2 statistical packages allowing analysis of such models with many missing values.

Finally the model [RET] was applied to predict yields of all possible hybrids even when they were not

observed in a given year and in particular conditions (latitude and type of production). In fact the influence of the year was not important for comparing genotypes because both factors interact only through the type of production; we chose 1985. Southern site and green asparagus production were chosen because no specifically adapted variety was really available for these conditions. In France, traditional asparagus production is white and not located in the South. Such predictions must be used cautiously due to the fact that the model is approximate and it was not possible to calculate confidence intervals for the predictions.

RESULTS

The 990 yields that make up the data are summarized in table II. There were large differences between the lines both for the number of crossings or replications and for the yields.

Table III displays the ANOVA table of the 2 embedded models [GEN] and [RET] described above. As there were only 6 true replications (reciprocal hybrids grown twice in the same environment), these were eliminated from the sum-of-squares decomposition and the last remainder term was used as the error term.

The results obtained here are consistent with those obtained by Rameau and Denis (1992). At the hybrid level the mean squares for genotype-environment interaction have the same order of magnitude: 0.57 (vs 0.42 in Rameau and Denis (1992)) while the MS remainder is 0.38 (vs 0.23). Some reduction can be noted for the MS associated with the 2 covariates: 0.72 and 0.67 (against 2.36 and 1.88) but this is understandable because in the previous study the covariates were chosen as maximizing the mean squares. On the contrary, it is worth noting that they are still highly significant and explain a substantial part of the interaction. The new result given by the retained model [RET] is that most genotype effects can be explained by additive and symmetrical parent effects.

Parameters of this model concerning genotypes are given in table IV. As in Rameau and Denis (1992), these parameters correspond to previously centered covariates in order to interpret the main effect $v_{(p)}$ independently of the other 2 regression coefficients.

From the 816 potential hybrids, the best 30 were selected to assess the best parents for green asparagus production (Prod = 1; 0.486 after centering) in the south (Lat = 43.83; -1.286 after centering).

Table III. Analysis of variance combining the general model [GEN] and the retained model [RET].

Source of variation	DF	MS
Environment main effect	34	35.82 ***
Site main effect	3	121.04 ***
Year main effect / site main effect	9	38.44 ***
Site x year interaction	22	23.12 ***
Hybrid main effect / environment main effect	230	3.47 ***
Additive symmetrical parent effect / (site + year) main effects	42	14.70 ***
Environment x hybrid interaction	719	0.57 (**)
Hybrid x latitude	230	0.72 ***
Additive symmetrical parent x latitude	42	2.22 ***
Remainder	188	0.38
Hybrid x production	230	0.67 ***
Additive symmetrical parent x production	42	2.01 ***
Remainder	188	0.37
Remainder	259	0.38

Sources of variation of the general model are decomposed according to their selected part in the retained model inducing with the remaining part a *f* test justifying the retained model if not significant. /: adjusted for; *** significant at the 0.1% level, the last remainder term being taken as the error term.

DISCUSSION

The main parental effect $v_{(p)}$ (table IV) confirmed the advantage of the super-male in asparagus. The values for 5 of the super-males (out of 10) were greater than 1. This advantage was highlighted when we compared the main parental effect of the pure line L9 (0.520) and the main parental effect of the super-male M7 (1.164) obtained from this pure line by androgenesis. The same tendency was observed when we compared the main parental effects of the super-male M9 (0.232) obtained by androgenesis from the pure line L14 (-0.564) with the main effect of the pure line itself. These genotypes are both homozygous (with a residual heterozygosity for the pure line); the main difference is that the super-male gives an all-male hybrid progeny whereas the pure line gives 50% female and 50% male progeny. The agronomic advantage of male plants over female plants is well known in asparagus: male plants produce more spears per plant than female plants and consequently have a higher yield (Robbins and Jones, 1926; Thévenin, 1967). Consequently, the use of super-males as the male parent is a direct way of increasing the yield and also the homogeneity of the hybrids.

The regression term $(c_{(p)} \cdot \text{Lat}_{(s)})$ for the latitude of the experimental site is particularly interesting

for the continuation of the breeding program (table IV). Development of hybrids for specific sites is more and more frequent in plant breeding. Low negative values indicate the parents that give hybrids with good behavior in the south of France. This is particularly true for M3, m12, L5, L6, L13 and L24. Three of these (m12, L6 and L24) are lines known to give hybrids with a relatively good early yield especially in the south of France (data not published); early yield, which is the yield cumulated in the first 6–8 harvests within a season is positively correlated with total yield. These results and empirical observations could be interpreted by the hypothesis that these hybrids do not need cold temperatures for starting growth and consequently start earlier and behave better in the south than hybrids that have high cold temperature requirements to start and to have a good yield. In previous work (Rameau and Denis, 1992), we gave examples of the well-known varieties 'Andréas', whose superiority shows up better in the north of France, and 'Stéline' which yields as much as 'Andréas' in the south and which is a particularly early yielding hybrid. The parents of 'Andréas' (L9 and M8) have a positive regression coefficient for the latitude whereas one of the parents of 'Stéline' (f5 and m12) has a low negative value for this parameter. These hypotheses, suggested by the sta-

Table IV. Estimated parameters of the retained model [RET] with centered covariates for each parent line.

	<i>Main</i> *	<i>Latitude</i> *	<i>ToProd</i> *
M1	0.590	0.300	0.790
M2	1.141	0.153	0.422
M3	-0.101	-0.742	-0.938
M4	1.084	0.362	0.955
M5	1.044	1.212	-1.665
M6	0.516	0.173	-0.670
M7	1.164	-0.015	-1.268
M8	1.331	0.510	0.709
M9	0.232	-0.173	-0.414
M10	-0.701	0.159	0.360
m11	0.309	-0.127	-0.183
m12	-0.022	-0.702	-0.003
f1	-0.100	-0.045	0.151
f2	0.447	0.310	0.915
f3	0.921	0.803	-0.520
f4	-0.430	-0.143	0.022
f5	-0.193	0.294	0.346
f6	-0.716	0.027	0.287
f7	0.099	0.265	0.816
L1	-0.278	0.248	0.253
L2	0.024	0.081	0.987
L3	0.422	-0.084	-0.370
L4	0.386	0.306	0.573
L5	-1.397	-0.562	-0.741
L6	0.778	-0.480	-0.322
L7	-1.045	-0.347	0.345
L8	-0.193	-0.470	-0.391
L9	0.520	0.495	0.368
L10	0.202	0.401	0.205
L11	-0.658	0.368	0.664
L12	-0.547	-0.123	0.215
L13	-0.950	-0.738	-0.246
L14	-0.564	-0.200	-0.122
L15	-0.565	-0.143	0.050
L16	-0.631	-0.111	-0.066
L17	0.757	-0.266	-0.701
L18	-0.401	0.205	0.031
L19	-0.331	-0.170	-0.084
L20	-0.335	-0.170	-0.038
L21	-0.312	0.029	-0.228
L22	-0.459	0.263	0.436
L23	-0.482	-0.274	-0.205
L24	-0.567	-0.882	-0.742

* Main, latitude and ToProd correspond to $v_{(p)}$, $c_{(p)}$ and $d_{(p)}$ respectively in model [RET].

tistical interpretation, would require further physiological studies to be confirmed; on the other hand, early yields should be analysed more precisely.

When the parameter associated with the type of production ($d_{(p)}$; table IV, col 'ToProd') is positive, the yield was greater for the green production than for the white. This parameter is to be interpreted while keeping in mind that, in the data analysed, the type of production depends on the site; fortunately, the confounding with latitude is not important because green asparagus production was represented in both the northernmost and the southernmost sites. An interesting feature is the positive covariation of $d_{(p)}$ with $c_{(p)}$ for all the parents except 3 (M7, f3 and particularly M5). This general trend may explain why no variety specially adapted for green asparagus production (positive regression coefficient for the type of production) and for the south of France (negative regression coefficient for the latitude) has been commercialized from this genetic material from a relatively narrow range of sources (Geoffriau *et al*, 1992).

Predicted yields for the conditions chosen (the year 1985, southern site and green asparagus), vary from 0.14 (L5 x M5) to 4.89 T/ha (L6 x M2). Among the best 30 predicted hybrids, the most frequent parents are L6, M2, M4, M8 and m12, which occur 9, 7, 6, 5 and 4 times, respectively. These results give additional support to the current breeding program for constructing new populations that are improved for different characters of breeding importance as stem number, stem diameter and early yield. Taking into account the genealogy of the parents (when known), M8 was used (with L4 and L17) to construct the population improved for stem number and consequently total yield. The 2 lines L6 and M2 with L24 are involved in the construction of the population improved for early yield and specially adapted to the south of France. M4 has not been used because it is genetically close to M2.

In the same way it would be worth analysing the determinism of early yield as well as other characters of breeding importance which have been observed in these experiments. We have made the hypothesis that early yield is certainly influenced by temperature during the rest period of the plant in winter. This is also true for spear diameter and spear number, which are yield components influenced by the type of production; green production gives thinner and more numerous spears than white production.

Despite of the poorly filled genotype x environment table of data, we were able to evidence important genotype x environment interactions. This was only possible by using the pseudo-diallel structure of the genotype factor, which led us to applied considerations. Once more, it must be recognized that genotype x environment interactions cannot be neglected in breeding programs and that specifically adapted cultivars must be obtained.

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