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Genetic variability of productive and vegetative characters in *Asparagus officinalis* L. - Estimates of heritability and genetic correlations*

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ABSTRACT

Three asparagus populations (cultivar Argenteüil) from France and Denmark were evaluated in order to estimate broad sense heritability and determine genetic correlations between productive and vegetative characters. Significant differences were found between genotypes within populations for almost all characters. The heritability values for total and market yield, calculated on the basis of one repetition and one environment, were low (0.12 to 0.31); however this experimental unit permits, with the same effort, the evaluation of an increased number of plants, allowing the application of higher selection pressures. The vegetative characters "basal diameter of stalks" and "height to first ramification" presented, on average, the highest genetic correlations with total and market yield (0.84 and 0.87, respectively).

INTRODUCTION

Asparagus (*Asparagus officinalis* L.) is a dioecius vegetable, reproduced mainly by seed. Obligate cross-pollination between pistillate and staminate plants provides for considerable variation within populations (Huyskes, 1959; Ellison and Scheer, 1959; Moon, 1976). This variability has been studied at the isoenzymatic loci (Brettin and Sink, 1992; Geoffriau *et al.*, 1992; Lallemand *et al.*, 1994) and for productive and vegetative characters (Haber, 1932; Robb, 1936; Legg *et al.*, 1968; Bannerot *et al.*, 1969; Nikoloff *et al.*, 1986). Breeding programs in course since the beginning of the century first released improved populations and then double, clonal and simple hybrids, with an average yield increase of 75% (Ellison, 1986). However, information concerning genetic parameters and gene actions involved in the expression of characters of economic interest is scarce. Inbreeding and heterosis in a group of materials from different origins have been studied by Ito and Currence (1965) and the broad sense heritability for green asparagus by Legg *et al.* (1968).

The cultivar Argenteüil (blanched asparagus) has shown good adaptability and was widely cultivated in the recent past in Argentina. Therefore it is an adequate material to be considered in the search for elite genotypes for the production of double and clonal hybrids.

Estimates of genetic variance and heritabilities can be of value at all stages of a breeding program (Dudley and Moll, 1969). In the estimation of genetic parameters the reference unit, defined by the number of repetitions, years, localities, type of progeny or mate-

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rial, size of plots and cultural practices, would be the same as that used for selection. The reference population as well as the environmental population should be clearly defined, allowing the genetic parameters to be of value and devoid of genotype x environment interaction (Allard and Bradshaw, 1964; Dudley and Moll, 1969). The genotypic correlation coefficients give an idea of the secondary characters that would be useful as indicators of the more important ones under consideration (Johnson *et al.*, 1955). The estimates should come from unselected materials or populations, otherwise they could be due to fortuitously favorable gene combinations that would disappear if these materials were allowed to freely pollinate (Coyne, 1967). Nyquist (1991) considered that although there are few methods available to calculate heritability, there are many complexities introduced when one considers the variety of situations that exist in the plant kingdom. Since Burton and De Vane (1953) proposed the estimation of heritability using clonal propagules of each genotype of a population, this method has been used in several plant species (Keller and Likens, 1955; Legg *et al.*, 1968; Lee *et al.*, 1993; Shaw, 1993; Lin and Zsuffa, 1993).

MATERIAL AND METHODS

Three populations of cultivar Argenteüil from different origins were evaluated: P_1 and P_3 from France and P_2 from Denmark. In August 1992, two-year old plants were taken at random from each population. Each plant was cloned by crown division, obtaining four successful repetitions for 66, 61 and 38 plants of P_1, P_2 and P_3, respectively. Each cloned part of the crown was weighed (CRW) and disinfected with 100 g Benomyl/100 l water before planting. The field design was a randomized complete block with two repetitions in two localities of the Argentine humid plain (pampa): Zavalla (33°01′ SL; 60°53′ WL) and San Pedro (33°41′ SL; 59°41′ WL). These localities are 120 km apart. They have a temperate climate, with loamy soils, the soil being heavier in San Pedro. The planting grid had a distance of 210 cm between rows, 45 cm between plants in a row and a depth of 20 cm. One repetition of nine, seven and 16 plants of P_1, P_2 and P_3, respectively, and two repetitions of two plants of P_3 were lost due to failures in survival. In the first growing season, the "fern" was allowed to grow, and in the fall of 1993 the following vegetative characters were measured: number of stalks (NST), index of Ellison and Scheer (1959) or adjusted number of stalks (ANS), height of the tallest stalk (HTS), fresh weight of the fern cut at soil level (FWT), height to the first ramification (HFR), number of nodes to the first ramification (NNR) and basal diameter of stalks (BDS). The latter three characters were taken as a mean of the three largest stalks of each plant.

In August 1993, the rows were ridged and each plant was harvested individually during 40 days since the first cut. The harvests were made every two days, trimming the spears to 20 cm long. The following productive characters were evaluated in each plant: number of days since 12/4/93 (arbitrary date) to the first cut (NDC), total yield (TYD), market yield or yield of spears with a diameter over 12 mm (MYD), number of spears (NSP) and mean diameter of spears (DSP). These two latter characters are the yield components (considering the shape of a blanched spear as a cylinder and the specific weight as a constant, the yield of a plant will be a function of the number and diameter of the spears).

For each character an ANOVA was performed with the following linear model:

$$Y_{ijkr} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \tau_{k(j)} + \alpha\tau_{ik(j)} + \theta_{r(i)} + \varepsilon_{r(kij)}$$

where: i: $1 \rightarrow a$; j: $1 \rightarrow b$; k: $1 \rightarrow c_j$; r: $1 \rightarrow d$; Y_{ijkr} is the observation of the kth genotype or plant of the jth population in the rth block of the ith locality; μ is the general mean; α_i is the effect of the ith locality; β_j is the effect of the jth population; $\alpha\beta_{ij}$ is the interaction effect of the ith locality with the jth population; τ_k is the effect of the kth genotype nested in the jth population; $\alpha\tau_{ik}$ is the interaction effect of the ith locality with the kth genotype nested in the jth population; $\theta_{r(i)}$ is the effect of the rth block nested in the ith locality and $\varepsilon_{r(kij)}$ is the experimental error.

The expected mean squares were obtained considering the effects of locality and genotype as random, and the effect of populations fixed. In order to obtain variance components, the genotype and genotype x locality sources of variation were partitioned into the variation for each population. In the cases where the genotype x locality interaction was not significant, this source of variation was amalgamated with the error to test the genotype mean square. When no exact F-test was possible, the Satterthwaite (1946) methodology was used. The characters whose residuals did not show a satisfactory normal distribution were transformed: total yield and market yield by $(x + 0.5)^{1/2}$ and fern weight by log x.

The heritability in a broad sense was calculated as proposed by Hanson (1963):

$$h_a^2 = \frac{\sigma_\tau^2}{\sigma_\tau^2 + \sigma_{\tau\alpha}^2 + \sigma_\varepsilon^2}$$

where: α_τ^2, $\sigma_{\tau\alpha}^2$ and σ_ε^2 are, respectively, the genotype, genotype x locality and error component of variance.

The standard deviation of the heritability value was obtained following Vello and Vencovsky (1974):

$$SE(h_a^2)=\left(\frac{2}{n_1+2}+\frac{2}{n_2+2}\right)\cdot(1-h_a^2)$$

where n_1 and n_2 are the degrees of freedom of the genotype and error sources of variation.

The genetic correlation between the productive and vegetative characters were calculated as proposed by Searle (1961):

$$r_g=\frac{Cov_\tau xy}{\sigma_\tau x\cdot\sigma_\tau y}$$

where $Cov_\tau xy$ is the genetic covariance between characters x and y from the covariance analysis.

RESULTS AND DISCUSSION

The ANOVA for the productive and vegetative characters is presented in Tables I and II. A significant variation among populations was detected for all the productive characters, except days to first cut. Among the vegetative characters, this variation was significant for number and diameter of stalks, plant weight and height to the first ramification. The locality effect was significant for the majority of the characters, the mean values of Zavalla being superior (data not shown). However, except for plant height, the population x locality interaction was not significant in any case. The population mean values are presented in Table III. P_1 showed significantly higher values for total yield, market yield, diameter of spears and stalk diameter, whereas plant height was superior in P_2. The mean values revealed a clear differentiation between these populations. Cultivar Argenteüil originated in France in the XIX century, being introduced later to other European countries and America (Geoffriau *et al.*, 1992). During this period, it might have been subjected to different selection criteria: P_1 probably was selected mostly for spear size, an important quality factor in the French market. Genetic drift could also have been operating in this differentiation. Significant differences for total yield, spear number and spear diameter among 17 segregating populations of cultivar Argenteüil were also found by Thévenin (1967). Similar results were found by Nikoloff *et al.* (1986) in four populations of MW500w from different seed sources and by Ellison (1986) in populations of Mary Washington and Martha Washington. This was attributed, by the latter author, to the difficulties in maintaining the cultivar foundation stocks.

The source of variation of genotype within population was significant for all the characters except days to first cut (Tables I and II). When the variation was partitioned for each population, a different situation was observed. The variation was significant in the three populations for total and market yield, in P_2 and P_3 for spear diameter, and only in P_2 for spear number. For the vegetative characters, the genotype was a significant source of variation in the three populations for plant height and fern weight, in P_1 and P_2 for adjusted stalk

Table I - Means squares of the ANOVA for the productive characters total yield (TYD), market yield (MYD), number of spears (NSP), diameter of spears (DSP) and days to first cut (NDC) in asparagus.

S.V.	d.f.	Means squares				
		TYD	MYD	NSP	DSP	NDC
Locality	1	3615.56 **	5830.10 **	350.07 ns	2039.07 **	3050.71 ns
Rep/loc	2	32.44 ns	44.79 ns	10.18 ns	21.36 ns	366.52 *
Population	2	261.87 **	301.33 **	121.27 ns	118.50 **	49.52 ns
Popul x Loc	2	7.24 ns	4.82 ns	25.78 ns	25.93 ns	409.98 ns
Genotype/pop	163	18.67 **	28.45 **	10.13 **	15.59 **	117.08 ns
genot/pop 1	65	15.82 **	23.11 **	10.42 ns	13.52 ns	107.19 ns
genot/pop 2	60	15.27 *	24.96 **	11.09 *	12.85 **	124.17 ns
genot/pop 3	38	26.37 **	26.37 **	8.14 ns	20.44 **	113.35 ns
Genot/pop x Loc	161	8.09 ns	13.16 ns	7.43 ns	8.67 ns	96.82 ns
Error	295	10.96	16.14	8.34	9.11	111.77
Cv_e		26.87	36.99	50.90	21.40	6.20
R^2		0.74	0.75	0.60	0.71	0.57

**$P \leq 0.01$; *$P \leq 0.05$. ns, Nonsignificant.

Table II - Means squares of the ANOVA for the vegetative characters number of stalks (NST), adjusted number of stalks (ANS), basal diameter of stalks (BDS), height of the tallest stalk (HTS), fern weight (FWT), height to the first ramification (HFR) and number of nodes to the first ramification (NNR) in asparagus.

S.V.	d.f.	Means squares						
		NST	ANS	BDS	HTS	FWT	HFR	NNR
Locality	1	1062.5 **	662.39 ns	581.63 **	51716.7 **	36.4700 **	667.85 **	1.21 ns
Rep/loc	2	25.94 ns	69.64 **	4.97 ns	287.33 ns	0.2381 *	76.27 ns	49.39 **
Population	2	128.42 **	11.00 ns	402.89 **	8779.72 **	0.4006 *	4530.58 **	606.56 ns
Popul x Loc	2	10.54 ns	5.20 ns	36.87 ns	4692.19 *	0.0741 ns	267.33 ns	98.64 ns
Genotype/pop	163	27.41 **	7.67 **	9.24 **	1321.14 **	0.1153 **	77.71 **	13.12 **
genot/pop 1	65	20.84 ns	8.37 **	10.32 **	1085.87 **	0.1149 **	45.65 *	11.18 ns
genot/pop 2	60	36.18 **	8.02 **	7.69 **	1330.02 **	0.1265 **	145.38 **	19.46 **
genot/pop 3	38	24.45 *	6.16 ns	9.82 ns	1778.56 **	0.1035 **	29.99 ns	7.06 ns
Genot/pop x Loc	161	16.45 ns	3.96 ns	4.30 ns	1321.14 **	0.0237 ns	28.58 ns	7.05 ns
Error	295	17.47	3.78	5.07	583.12	0.0668	40.28	7.61
Cve		47.80	44.22	20.27	18.96	12.50	40.26	36.72
R^2		0.62	0.71	0.70	0.68	0.78	0.70	0.69

**P ≤ 0.01; *P ≤ 0.05. ns, Nonsignificant.

Table III - Population means for the productive and vegetative characters of asparagus over localities.

	Population 1	Population 2	Population 3
Productive characters			
TYD[1]	173.42 ± 0.80 *a*	150.07 ± 0.79 *b*	120.40 ± 1.04 *c*
MYD[1]	142.11 ± 0.93 *a*	109.28 ± 1.00 *b*	94.20 ± 1.04 *b*
NSP	6.02 ± 0.41 *a*	5.98 ± 0.39 *a*	4.55 ± 0.43 *b*
DSP[2]	14.81 ± 0.45 *a*	13.42 ± 0.46 *b*	14.01 ± 0.67 *b*
NDC	170.13 ± 1.30 *a*	171.11 ± 1.38 *a*	169.89 ± 1.99 *a*
Vegetative characters			
NST	8.01 ± 0.52 *a*	9.40 ± 0.65 *a*	8.55 ± 0.84 *b*
ANS	4.40 ± 0.31 *ab*	4.60 ± 0.32 *a*	4.05 ± 0.39 *b*
BDS[2]	12.22 ± 0.33 *a*	11.06 ± 0.31 *b*	9.20 ± 0.46 *c*
HTS[3]	126.13 ± 3.22 *b*	133.37 ± 3.71 *a*	119.40 ± 5.40 *c*
FWT[1]	114.81 ± 1.12 *ab*	128.82 ± 1.12 *a*	104.71 ± 1.14 *b*
HFR[3]	17.31 ± 0.74 *a*	18.42 ± 1.12 *a*	8.55 ± 0.84 *b*
NNR	8.51 ± 0.39 *a*	8.01 ± 0.43 *a*	4.89 ± 0.36 *b*

The values followed by the same letter are not different at the 5% level of the Tukey test.
For abbreviations see Tables I and II.
1, In grams; 2, in mm; 3, in cm.

number, stalk diameter and height to the first ramification, and in P_2 and P_3 for stalk number and nodes to the first ramification (Table II). The genotype/population x locality interaction was not significant in any case. The significant variation between plants found for the majority of the productive and vegetative characters was expected considering the type of plant material (populations originated from the obligatory cross pollination between staminate and pistillate plants). Legg *et al.* (1968) reported a significant variation among plants for stalk number, plant weight, total yield, spear number and spear diameter in some experimental crosses. Also in an Argenteüil population, Bannerot *et al.* (1969) reported a significant variation between plants for total yield. Pandita *et al.* (1988) presented a broad range of variation for plant height, stalk number and stalk diameter in four cultivars of the UC type, attributed to a great extent to genetic factors. The reduced genetic variation found for days to first cut could be explained by the selection practiced towards precocity, which has been one of the major objectives in the breeding programs of the European countries (Corriols, 1988; Rameau, 1990; Van den Broek and Boonen, 1990).

The heritabilities for one repetition and one locality are presented in Table IV. The values ranged from low to intermediate, being relatively higher for total and market yield in P_3 than in the other populations. Among the vegetative characters, plant height, adjusted number of stalks and stalk diameter in the three populations, and height and nodes number to the first ramification in P_2 were the ones with the higher values. Yield is a complex character that is a function of the number and size of buds formed in the preceding growing season by the photoassimilates that have been produced and stored (Tiedjens, 1924 and Robb, 1984); so this character is determined by a number of processes which are under genetic control but influenced by the micro and macroenvironment. This fact produces a

Table IV - Coefficient of heritability (broad sense) for asparagus productive and vegetative characters.

	Population 1	Population 2	Population 3
Productive characters			
TYD	0.16 ± 0.02	0.12 ± 0.03	0.31 ± 0.03
MYD	0.14 ± 0.03	0.14 ± 0.03	0.21 ± 0.03
NSP	0.07 ± 0.03	0.09 ± 0.03	0.07 ± 0.08
DSP	0.09 ± 0.03	0.17 ± 0.02	0.19 ± 0.06
NDC	0.03 ± 0.04	0.04 ± 0.04	0.01 ± 0.09
Vegetative characters			
NST	0.08 ± 0.04	0.17 ± 0.02	0.12 ± 0.07
ANS	0.21 ± 0.03	0.19 ± 0.03	0.12 ± 0.07
BDS	0.19 ± 0.02	0.19 ± 0.02	0.18 ± 0.06
HTS	0.23 ± 0.03	0.22 ±0.02	0.31 ± 0.06
FWT	0.18 ± 0.02	0.16 ± 0.03	0.14 ± 0.07
HFR	0.11 ± 0.03	0.31 ± 0.01	0.04 ± 0.09
NNR	0.01 ±0.06	0.27 ± 0.02	0.19 ± 0.04

reduction in the proportion of the phenotypic variation attributable to the genetic variation between plants. The variables stalk and spear number showed, in general, the lowest heritability values (Table IV), presenting the highest cv_e (Tables I and II). The heritability values presented by Legg *et al.* (1968) were: 0.30, 0.18, 0.24, 0.29 and 0.33 for total yield, spear diameter, days to first cut, stalk number and plant weight, respectively. They are a little higher than the values presented here, probably because they were obtained from a pool of four segregant populations. The heritabilities were calculated considering one repetition and one locality. Considering that the additive component of the genetic variance is the most important, even these intermediate to low values would be compatible with the results of the breeding programs in this species, where high intensity of selection has been applied in nonreplicated genotypes. Hanna (1952) mentioned that 400 acres of asparagus fields of cv. Mary Washington were evaluated in a search for elite plants; among approximately one million plants, 159 were selected for evaluation in crosses.

The genetic correlation values between the vegetative and productive characters are shown in Table V. Height to the first ramification in P_1 and stalk diameter in P_2 and P_3 presented the highest correlations with total and market yield. The yield component spear number was the most associated with height to the first ramification, stalk diameter, adjusted number of stalk and fern weight in P_1 and P_3, and with node number to the first ramification in P_2. Spear diameter presented a high and negative correlation with node number in P_1 and a high positive association with stalk diameter in P_2 and P_3, and with height to the first ramification in P_3.

Table V - Genetic correlation coefficients between productive and vegetative characters of asparagus.

		TYD	MYD	NSP	DSP
NST	P1	0.71**	0.83**	0.91**	0.15
	P2	0.32**	-0.06	0.64**	-0.33**
	P3	0.91**	0.81**	0.81**	0.58**
ANS	P1	0.63**	0.54**	0.95**	-0.24*
	P2	0.60**	0.30*	0.65**	-0.05
	P3	0.91**	0.94**	0.96**	0.86**
BDS	P1	0.70**	0.59**	0.98**	0.34**
	P2	0.87**	0.91**	0.11	0.90**
	P3	0.97**	0.94**	0.94**	0.98**
HTS	P1	0.51**	0.41**	0.90**	-0.31*
	P2	0.02	0.01	0.29*	-0.25*
	P3	0.61**	0.60**	0.77**	0.49**
FWT	P1	0.56**	0.47**	0.95**	-0.50**
	P2	0.33**	0.22	0.24	0.07
	P3	0.88**	0.86**	0.75**	0.37*
HFR	P1	0.92**	0.86**	0.98**	-0.61**
	P2	0.76**	0.57**	0.76**	0.17
	P3	0.94**	0.94**	0.80**	0.97**
NNR	P1	0.22	0.10	0.78**	-0.91**
	P2	0.82**	0.64**	0.84**	0.22
	P3	0.56**	0.54**	0.12	0.79**
CRW	P1	0.69**	0.71**	0.85**	0.62**
	P2	0.58**	0.35**	0.69**	-0.08
	P3	0.09	0.11	-0.31*	0.16

**P ≤ 0.01; *P ≤ 0.05. See Tables I and II for abbreviations.

The genetic correlation should be maximum for those vegetative characters that reflect the plant capacity to produce a given number of buds of adequate size. These buds will be the spears of the following season. The differences in mean values and genetic variances found explain the different roles that the vegetative characters presented among the populations in the determination of total yield and their components. In the cv. Raritan, Ellison *et al.* (1960) found that stalk number and stalk diameter presented a significant correlation with total yield. But for Thévenin (1967), in an Argenteüil population, this correlation was significant only for stalk number. Chen *et al.* (1987), studying the cvs. UC711 and UC309, showed that stalk number, stalk diameter and height to the first ramification presented a significant correlation with total yield. Silveira and Augustin (1993), in a set of cultivars, found a significant correlation between stalk diameter and total yield but not between the latter and stalk number. In P_2, the adjusted number of stalks presented higher correlation values with total and market yield than with stalk number (Table IV). This could be explained by a greater influence of stalk diameter in the adjusted number of stalks in this population. Ellison and Sheer (1959), in the cv. Raritan, and Wolyn (1993) obtained similar results in genotypes of various cultivars.

Height to the first ramification, which is a character associated with good quality of green spears, presented, in general, a high correlation with total yield. This reflects the possibility of obtaining a good yielding material for both types of production.

Plant weight, as a mean of the photosynthetic mass, was expected to present a higher correlation coefficient with the productive characters than that observed. The uneven senescence of the stalks that caused distortions in the weight of plants was probably the reason for the lack of a strong association between these characters. Also as Tiedjens (1924) said: "we can't expect that a stalk emerged in the beginning of the vegetative season photoassimilates the same as one emerged late in the season. In some cases this one could reduce the reserves, but both would contribute to the plant weight."

Finally, crown weight did not present a high correlation with total and market yield. This is in agreement with the works of Haber (1932), Currence and Richardson (1937), Thévenin (1967) and Williams and Garthwaite (1973). Ellison (1986) also stated that all the efforts for selecting superior plants on the basis of the vigor of plantlets and the crown weight had failed.

CONCLUSIONS

The populations presented a marked differentiation in the mean values and genetic parameters, between plant variation being significant for almost all the characters studied. The heritability values calculated on the basis of one repetition and one locality ranged from intermediate to low. However, this experimental unit permits, with the same effort, the evaluation of an increased number of plants, allowing the application of higher selection pressures. Population 1 of Argenteüil from France presented the highest values for the productive characters, and would be the most appropriate for use as a starting point in a breeding program. The vegetative characters height to the first ramification and stalk diameter presented the highest correlation coefficients with total and market yield and, on average, relatively high heritability values. These characters are easy to evaluate and appear to be the most appropriate for accomplishing yield selection.

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RESUMO

O presente trabalho pretende estimar a herdabilidade no sentido amplo e a correlação genética entre os caracteres produtivos e vegetativos em três populações originárias da França e Dinamarca do cv Argenteüil. Diferenças significativas foram encontradas entre genótipos dentro de populações para quase todos os caracteres. Para produção total e comercializável os valores das herdabilidades, calculadas com base em uma repetição e uma localidade, foram baixos (0.12-0.31), embora esta unidade experimental permita, com o mesmo esforço, a avaliação de um maior número de plantas possibilitando a aplicação de maiores intensidades de seleção. Os caracteres vegetativos diâmetro basal de hastes e altura até a primeira ramificação apresentaram as maiores correlações com produção total e comercializável (0.84-0.87), sendo os caracteres secundários mais apropriados para serem considerados em programas de melhoramento.

REFERENCES

Allard, R.W. and **Bradshaw, A.D.** (1964). Implications of genotype-environmental interactions in applied plant breeding. *Crop. Sci. 4*: 503-507.

Bannerot, H., Derieux, M., Thévenin, L. and **Arnoux, J.** (1969). Résultats d'un essai comparatif de populations d'asperge. *Ann. Amélior. Plant. 19*: 289-324.

Brettin, T.S. and **Sink, K.C.** (1992). Allozyme variation and genetics in Asparagus. *J. Hered. 83*: 383-386.

Burton, G.W. and **De Vane, E.H.** (1953). Estimating heritability in tall fescue (*Festuca arundinacea*) from replicated clonal material. *Agron. J. 45*: 478-481.

Chen, Y.W., Hung, L. and **Tu, C.C.** (1987). Use of economic characters as ideotypes in asparagus breeding. In: *The Breeding of Horticultural Crops*. FFTC Book Series No. 35, pp. 45-49.

Corriols, L. (1988). Selección y Mejora del Espárrago. Resúmenes de la II Jornadas Técnicas del espárrago. Pamplona, España, pp. 17-27.

Coyne, D.P. (1967). Correlation studies in asparagus in relation to cumulative season yield. *Hort. Res. 7*: 105-112.

Currence, T.M. and **Richardson, A.L.** (1937). Asparagus breeding studies. *Proc. Am. Soc. Hortic. Sci. 35*: 554-557.

Dudley, J.W. and **Moll, R.H.** (1969). Interpretation and use of estimates of heritability and genetic variance in plant breeding. *Crop. Sci. 9*: 257-262.

Ellison, J.H. (1986). Asparagus breeding. In: *Breeding Vegetable Crops* (Bassett, M.J., ed.). Avi Publisher Co., Westport, CT, pp. 521-569.

Ellison, J.H. and **Scheer, D.F.** (1959). Yield related to brush vigor in asparagus. *Proc. Am. Soc. Hortic. Sci. 73*: 339-344.

Ellison, J.H., Scheer, D.F. and **Wagner, J.J.** (1960). Asparagus yield as related to plant vigor, earliness and sex. *Proc. Am. Soc. Hortic. Sci. 75*: 411-415.

Geoffriau, E., Denoue, D. and **Rameau, C.** (1992). Assessment of genetic variation among asparagus (*Asparagus officinalis* L.) populations and cultivars: agro-morphological and isozymic data. *Euphytica 61*: 169-179.

Haber, E.S. (1932). Effect of size of crown and length of cutting season on yields of asparagus. *J. Agric. Res. 45*: 101-110.

Hanna, G.C. (1952). Asparagus plant breeding. *Calif. Agr. 6*: 6.

Hanson, W.D. (1963). Heritability. In: *Statistical Genetics and Plant Breeding* (Hanson, W.D. and Robinson, H.F., eds.). NAS-NRC Publ. 982. Washington, D.C., pp. 125-140.

Huyskes, J.A. (1959). The value of comparative tests of progenies from open-pollinated female asparagus plants. *Euphytica 8*: 141-144.

Ito, P.J. and **Currence, T.M.** (1965). Inbreeding and heterosis in asparagus. *Proc. Am. Soc. Hortic. Sci. 86*: 338-346.

Johnson, H.W., Robinson, H.F. and **Comstock, R.E.** (1955). Genotypic and phenotypic correlations in soybeans and their implications in selection. *Agron. J. 47*: 477-483.

Keller, K.R. and **Likens, S.T.** (1955). Estimates of heritability in hops, *Humulus lupulus* L. *Agron. J. 47*: 518-521.

Lallemand, J., Briand, F., Breuils, F., Denouse, D. and **Rameau, C.** (1994). Identification of asparagus varieties by isozyme patterns. *Euphytica 79*: 1-4.

Lee, C.K., Eagles, H.A., McFarlane, N.M. and **Kelly, K.B.** (1993). Genetic variation within white clover (*Trifolium repens* L.) populations from north-central Victoria. *Austr. J. Exp. Agric. 33*: 333-336.

Legg, P.D., Souther, R. and **Takatori, F.H.** (1968). Estimates of heritability in *Asparagus officinalis* from replicated clonal material. *Proc. Am. Soc. Hortic. Sci. 92*: 410-417.

Lin, J.Z. and **Zsuffa, L.** (1993). Quantitative genetic parameters for seven characters in a clonal test of *Salix eriocephala*. *Silvae Genet. 42*: 41-46.

Moon, D.M. (1976). Yield potential of *Asparagus officinalis* L. *N. Z. J. Expt. Agric. 4*: 435-438.

Nikoloff, A.S., Ensor, P., Palmer, T.P. and **Wallace, A.R.** (1986). Between plant variation of asparagus cultivars. *Agron. Soc. N. Z. Special Pub. 5*: 49-54.

Nyquist, W.E. (1991). Estimation of heritability and prediction of selection response in plant populations. *Crit. Rev. Plant Sci. 10*: 235-322.

Pandita, P.N., Bhan, M.K. and **Kaul, A.** (1988). Asparagus breeding in Kashmir. *Indian J. For. 11*: 238-240.

Rameau, C. (1990). Fifteen years of experiments on asparagus F_1 hybrids: synthesis, evaluation of homozygous parents and application to the French breeding programme. *Acta. Hortic. 271*: 47-54.

Robb, O.J. (1936). Some observations on individual asparagus plant records. *Sci. Agric. 17*: 144-145.

Robb, A.R. (1984). Physiology of asparagus (*Asparagus officinalis*) as related to the production of the crop. *N. Z. J. Expt. Agric. 12*: 251-260.

Satterthwaite, F.E. (1946). An approximate distribution of estimates of variance components. *Biometrics 2*: 110-112.

Searle, S.R. (1961). Phenotypic, genotypic and environmental correlations. *Biometrics 17*: 474-480.

Shaw, D.V. (1993). Genetic correlations between vegetative growth traits and productivity at different within-season intervals for strawberries (*Fragaria X ananassa*). *Theor. Appl. Genet. 85*: 1001-1009.

Silveira, R.F. and **Augustin, E.** (1993). Relações entre diâmetro e número de hastes, altura e vigor de plantas e produtividade de aspargo. *Pesq. Agropec. Bras. 28*: 129-133.

Thévenin, L. (1967). Les problèmes d'amélioration chez *Asparagus officinalis* L. I. Biologie et amélioration. *Ann. Amélior. Plant. 17*: 33-66.

Tiedjens, V.A. (1924). Some physiological aspects of *Asparagus officinalis*. *Proc. Am. Soc. Hortic. Sci. 21*: 129-140.

Van den Broek, J.H. and **Boonen, P.H.** (1990). Today's asparagus breeding in the Netherlands. *Acta. Hortic. 271*: 33-38.

Vello, N.A. and **Vencovsky, R.** (1974). Variâncias associadas às estimativas de variâncias genéticas e coeficientes de herdabilidade. *Rel. Cient. Inst. Genet.* (ESALQ-USP) *8*: 238-248.

Williams, J.B. and **Garthwaite, J.M.** (1973). The effects of seed and crown size and length of cutting period on the yield and quality of asparagus grown on ridges. *Exp. Hortic. 25*: 77-86.

Wolyn, D.J. (1993). Estimates of marketable yield in asparagus using fern vigor index and a minimum number of daily harvest records. *J. Am. Soc. Hortic. Sci. 118*: 558-561.

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