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SUMMARY – The variability and heritability of bud location and distribution were studied in 14 families of the Zaragoza almond breeding programme involving 17 different parents. The traits studied included bud density, bud productivity, branching index, set and growing habit. Heritabilities by variance were more reliable than those from regression, probably due to the different growing conditions of the parents and the seedlings. Their values, however, were low, being 0.30 for bud density and 0.26 for bud productivity, probably related to the young age of the seedlings. Heritability was also low for branching index (0.19) and very low for fruit set (0.05), probably as a consequence of the great influence of the weather conditions on fruit set. Growth habit was very similar for all seedlings. The low heritabilities observed in these families could be due to the degree of closeness for these traits among the parents involved in these 14 progenies.

Key words: *Prunus amygdalus*, bud density, bud productivity, branching index, fruit set, growing habit.

RESUME – *"Héritabilité de la densité de bourgeons et des modes de branchaison chez l'amandier". La variabilité et l'héritabilité de la localisation et la distribution des bourgeons ont été étudiées chez 14 familles provenant de 17 parents différents du programme d'amélioration génétique de l'amandier de Saragosse. Les caractères étudiés ont été la densité de bourgeons, la floribondité, l'index de ramification, la nouaison et le port. Les héritabilités par variance ont été plus fiables que celles obtenues par régression, ce qui est dû probablement aux différentes conditions de conduite des parents et des semis. Leurs valeurs sont pourtant réduites, 0,30 pour la densité de bourgeons et 0,26 pour la floribondité, en relation probable avec le jeune âge des semis. L'héritabilité de l'index de ramification a été basse (0,19) et celle de la nouaison très basse (0,05), due probablement à la grande influence du climat sur la nouaison. Le port a été très semblable pour tous les semis. Les basses héritabilités obtenues chez ces familles peuvent être dues à la proximité pour ces caractères des parents produisant ces 14 familles.*

Mots-clés : Prunus amygdalus*, densité de bourgeons, floribondité, index de ramification, nouaison, port.*

Introduction

The introduction of a new almond (*Prunus amygdalus* Batsch) cultivar requires the right election of parents in order to apply an efficient screening among the offspring obtained and select a genotype as close as possible to the species ideotype (Socias i Company *et al*., 1998). The efficiency of this process will depend on the right definition of objectives, the availability of adequate plant material and the heritability of the trait for which selection has to be applied. The heritability of a number of traits is already known in almond, mostly for traits easily rated in the field or measured in the laboratory (Socias i Company, 1998; Arteaga and Socias i Company, 2002), but not for some traits requiring long measurements in the field.

One important breeding objective is a consistent productivity. This can only be attained with a high bloom density. Bud, and therefore bloom, density have usually been evaluated according to subjective observations and considered to be transmissible to the offspring (Grasselly, 1972; Kester and Asay, 1975), thus making selection for this character possible. However, these are only subjective appreciations and there has not been an estimation of its heritability, as only in a few cultivars (Socias i Company, 1988) and selections (Bernad and Socias i Company, 1998) have measurements been taken, not allowing a deeper approach to its genetic behaviour.

Tree structure is of primary importance in orchard management, as it reflects variations in size, shape, vigour, and growth habit (Gülcan, 1985). These characteristics affect productivity, the ability to train and prune the tree and its adaptation to management procedures, all of which determine the desirability of a cultivar as an orchard tree. Every growth habit requires a specific pruning technique

(Royo *et al*., 1990), and pruning is one of the most expensive operations in almond growing. Kester and Asay (1975) considered optimization of tree structure to be one of the 15 breeding objectives in almond, and pointed out that the morphological types of tree structure are polygenic in nature, transmitted to the offspring and highly heritable. However, again there is no information on the real value of the heritability of tree structure.

The almond breeding programme in Zaragoza (Felipe and Socias i Company, 1985) has placed self-compatibility and late bloom as its main priorities, but also paying attention to other objectives, including good productivity and easy training, traits conditioned by bloom density and branching habit. Thus, the objective of this work was to study the variability of these traits and to estimate their heritability in order to better choose the parents and design the crosses in the breeding programme.

Materials and methods

The study included 671 seedlings coming from 14 families, one of them placed in two different orchard conditions, among 17 parents: three traditional Spanish cultivars ('Marcona', 'Desmayo Largueta' and 'Vivot'), a Spanish local selection ('Bertina'), a release from the Zaragoza breeding programme ('Blanquerna') and 12 selections from the same programme. Ten selections come from the cross 'Felisia' x 'Bertina' (G-2-2, G-2-6, G-2-25, G-3-3, G-3-4, G-3-8, G-3-43, G-4-3, G-4-4 and I-3-27) and two from the cross 'Felisia' x 'Moncayo' (G-4-41 and G-5-2). All selections were chosen for their self-compatibility and very late bloom (Socias i Company *et al*., 2003) and were the original plants grown in a seedling plot close to the collection where the cultivars were grown. The seedlings were from crosses made in 1997 and planted in the field in early 1999. The number of seedlings in each family is shown in Table 1. Trees and seedlings received the same cultural practices according to the usual orchard management. Planting density was different for each group of genotypes: the five cultivars were at 5 x 5 m, the 12 selections at 1 x 5 m, the families 1 to 14 at 1 x 3 m, and family 15 at 0.2 x 3 m.

Table 1. Origin of the almond families studied and number of seedlings in each family

Family number	Cross	No. of seedlings
1	'Vivot' x 'Blanquerna' (P)	86
2	G-2-2 x 'Marcona'	12
3	G-2-2 x 'Desmayo Largueta'	9
4	G-5-2 x 'Bertina'	74
5	G-2-25 x 'Desmayo Largueta'	29
6	I-3-27 x 'Marcona'	48
7	G-3-43 x 'Marcona'	9
8	G-4-41 x 'Marcona'	11
9	G-3-3 x 'Marcona'	15
10	G-4-4 x 'Marcona'	18
11	G-3-8 x 'Marcona'	22
12	G-2-6 x 'Marcona'	29
13	G-3-4 x 'Desmayo Largueta'	49
14	G-4-3 x 'Marcona'	162
15	'Vivot' x 'Blanquerna' (O)	98

Two branches were selected for each tree at different directions, with homogeneous shape and position. The length of the main branch was measured, as well as that of all secondary branchings and their number and position noted. All the buds were also counted and positioned. The perimeter at the base of the branches was also measured to allow calculation of the cross sectional area, thus enabling the expression of bud density as the number of buds per unit length of shoots (Church and Williams, 1983) and also of bud productivity as the number of buds per unit of cross section of the branch sustaining all these shoots (Socias i Company, 1988). Sets were estimated after counting the fruits on the same branches in early June, after fruit fall.

The branching index was obtained by the relationship between the total length of the secondary and tertiary branches and the total length of the main branch. Growing habit was estimated according to the IBPGR (International Board for Plant Genetic Resources) descriptors (Gülcan, 1985).

Heritabilities were calculated by regression and by variance. Heritability by regression is a strict heritability (Falconer, 1970) and was obtained by:

$Y_i = B_o + B_1X_i + E_i$

where Y_i = mean of the progeny of the i family (i = 1,2,....., 14), B_o = mean of all the progenies studied, B_1 = regression coefficient, X_i = mean of the parents of the i family, E_i = experimental error.

Heritability by variance (Kearsey, 1965; Mather and Jinks, 1971) was obtained by:

$h^2 = 2S_f^2/(S_f^2+S_e^2)$

where S_f^2 = variance among families, S_e^2 = variance within families or error variance.

Results and discussion

A large variability was observed for all the traits studied with the only exception of growing habit, as shown in Table 2 for the average value of each trait for each family. In addition, to assess the homogeneity of the main branches used to measure the data, their length and the standard deviation of their values were also obtained (Table 3). The average length of the main branch ranged between 71 cm for family 15 and 99 cm for family 1, with standard deviations showing that the variability was consistent and enough for the traits of each family to proceed to estimate heritabilities. A clear environmental effect was also expressed, because families 1 and 15, showing the extreme values, have the same genetic origin but are planted in different conditions clearly affecting their growth. This environmental effect is also expressed for the other traits when considering the same families 1 and 15, although not always at the same level of significance than the main branch length.

Table 2. Average bud density, bud productivity, branching index, fruit set and growing habit for 15 almond families

Family number	Bud density (bud/cm)	Bud productivity (bud/cm^2)	Branching index	Fruit set (%)	Growing habit rate
1	0.21 fg[†]	59.86 cde	2.28 a	18.33 bcde	2.89 abc
2	0.29 defg	94.84 bc	2.31 a	24.38 b	2.82 abc
3	0.30 defg	57.43 de	1.44 bc	33.28 a	2.33 cd
4	0.29 defg	60.14 cde	1.01 c	23.82 bc	2.82 abc
5	0.24 efg	62.23 cde	1.72 b	23.01 bcd	3.07 a
6	0.30 defg	84.38 bcd	1.73 b	20.76 bcde	3.31 a
7	0.54 a	111.10 b	1.05 c	17.02 bcde	3.00 a
8	0.49 ab	155.50 a	1.57 bc	17.33 bcde	2.36 bcd
9	0.33 cdef	78.96 bcde	1.33 bc	23.58 bc	3.07 a
10	0.16 g	42.72 e	1.64 b	15.05 de	3.10 a
11	0.40 abcd	113.50 b	1.56 bc	14.08 e	3.13 a
12	0.36 bcdef	101.12 b	1.38 bc	16.12 cde	2.81 abc
13	0.25 defg	65.61 bcde	1.20 bc	18.41 bcde	2.80 abc
14	0.48 abc	116.43 b	1.28 bc	18.32 bcde	2.94 ab
15	0.39 bcde	81.82 bcde	1.18 bc	–	2.01 d

[†]Letters a, b, c, d, e, f, g stand for mean separation in columns by Duncan's LSD at P≥0.01.

Table 3. Average length and standard deviation of the main branch used for the measurement of the traits considered

Family number	Main branch average length (cm)	Standard deviation
1	99.34	13.58
2	97.33	14.89
3	93.06	13.28
4	90.95	22.45
5	87.22	18.84
6	86.56	10.56
7	79.61	16.41
8	86.18	13.12
9	79.17	10.84
10	89.33	15.18
11	87.59	16.88
12	78.05	12.35
13	83.52	13.60
14	80.40	14.21
15	71.29	15.06

Bud density

Average bud density ranged between 0.54 bud cm^{-1} for family 7 and 0.16 for family 10, values within the same range of variability already observed for some almond cultivars (Socias i Company, 1988) and selections (Bernad and Socias i Company, 1998), as well as for the parents of the families (data not shown). The heritabilities estimated for this trait are very divergent according to the method (Table 4). The heritability by variance was 0.30, a value within the range of values estimated for many traits in almond (Socias i Company, 1998) and confirming the previous suggestions that this trait is heritable and that selection for it is possible. The heritability by regression was very low, 0.05, a value which could discard considering this trait as heritable, but the very different growing conditions and the age of the parents and the seedlings made any correlation between them impossible. As in the case of fruit and kernel traits (Arteaga and Socias i Company, 2002), heritability by variance seems more reliable than that by regression.

Table 4. Heritabilities obtained for the traits considered

Trait	By variance	By regression
Bud density	0.30	0.05
Bud productivity	0.26	0.57
Branching index	0.19	0.26
Fruit set	0.05	–

Bud productivity

The same considerations than for the variance of bud density can be applied to bud productivity, which ranged from 155 for family 8 to 43 for family 10. Heritabilities, however, showed a very different pattern of values (Table 4). The heritability by variance was 0.26, a value close to that of bud density and other almond traits, but heritability by regression was 0.57, a value higher than the heritability of most traits in almond (Socias i Company, 1998). This could be due to the fact that, independently of the growth of trees of different age and in different growing conditions, as deduced by the total branch length, there is an important potential to induce flower buds in relation to the vigour of the branch, measured by its cross sectional area.

Branching index

The average branching index ranged between 2.31 for family 2 and 1.01 for family 4, with a more homogeneous behaviour for all the families than for the other traits, allowing only to distinguish three Duncan's groups, with families 1 and 2 much more branched than the others. The environmental effect was also important, as shown for families 1 and 15, with the first one showing a branching index double that of family 15, which grows in a much closer planting distance, thus probably reducing the ability of a plant to show of all its potential to grow and branch. Heritability by variance was low, 0.19 (Table 4), lower than for bud density and productivity, showing that selection for this trait may be more difficult than for the others. Heritability by regression was negative, probably as a consequence of the different age of the parents and the seedlings. Young plants grow more vigorously than old plants and branch more often. Only 4 of the 17 parents showed a branching index higher than 1 (data not shown), whereas all the families had an average branching index higher than 1.

Fruit set

Fruit set was not measured for the parents nor for family 15 in a different plot than the other families. The highest average set was 33.28% in family 3, close to the sets considered as normal for almond in California (Kester and Griggs, 1959). The lowest average set was 14.08% in family 11, low as compared to the previous ones, but giving a good commercial crop when flower density is high enough (Socias i Company and Felipe, 1987), which may be the case in this family, with good values of bud density and bud productivity (Table 2). As fruit set was not measured in the parents, only heritability by regression could be estimated, obtaining a very low value, 0.05, not really significant. This reflects the fact that fruit set depends on many physiological and environmental conditions (Socias i Company *et al.*, 2002) and that productivity estimation must be carried out in a further step of the breeding process.

Growing habit

Growing habit was only rated for the seedlings, not for the parents, due to their very different planting densities affecting growth. The average rates ranged from 2.01 for family 15 and 3.31 for family 6, all of them values of erect or very erect growing habit. This is due both to the young age of the seedlings and to the planting density of the plants, as evidenced by families 1 and 15, of identical origin: family 1 had an average rate of 2.89 and family 15 the significantly lowest one, as being the only family growing in the closest planting distance. Consequently, as plant age and planting distance affect growing habit more than the own plant pattern, heritabilities for this trait were not estimated.

Conclusions

Bud density, bud productivity and branching index show a wide variability in almond. Thus, selection for these traits is feasible in the breeding process. Although the heritabilities estimated for them are low, their values are in the range of many traits in almond, for which selection has been efficient (Socias i Company, 1998). As parents were selected for the breeding programme because of their good performance in some of these traits, their close values may produce a decrease of their variance and, consequently, of the covariance among the offspring and the value of their heritability (Falconer, 1970).

Heritabilities by variance, where only the families are considered, showed values more reliable than by regression, where the parents are also involved (Arteaga and Socias i Company, 2002). The difference observed between the two methods may be due to the different age of the parents and the families as well as to the growing conditions in different plots and planting distances.

As selection is based on individuals and not on families, the breeding strategies involve a two level consideration: families where many individuals show a high performance. Family 7, G-3-43 x 'Marcona' produced the two individuals with the highest bud density and bud productivity, although its average values were not the highest ones. However this family, as a whole, showed a high number of flowers and an adequate growth allowing canopy renewal with minimum pruning.

Set cannot be evaluated at this early stage, as it is largely influenced by the environment. However, it is interesting to point out that the same family 7, had the highest average set. Other families, such as number 8, G-4-41 x 'Marcona', even with a lower set, may be very interesting for their good bud density and productivity and an adequate branching index.

The results obtained show that these traits, very important for any new cultivar and for which no genetic information was available, can be efficiently selected applying the knowledge acquired in their variability and heritability.

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