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Optimisation of breeding for agronomic traits in fibre hemp (*Cannabis sativa* L.) by study of parent-offspring relationships

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Summary

In the framework of a comprehensive Dutch research project the feasibility of hemp cultivation for paper pulp production is being investigated. This project also includes a hemp breeding programme which was initiated at CPRO-DLO in 1990. Hemp breeding is primarily aimed at improving bast fibre production since bast fibre is qualitatively superior to woody core fibre for paper pulp production. The progress of the ongoing breeding programme is hampered by the lack of knowledge on the inheritance of agronomic traits.

The following traits were examined on 252 parental plants in 1991 and subsequently on their progenies in 1992: fibre content, plant height, date of flowering, stem diameter and cannabinoid contents. For each trait heritabilities were estimated and direct and indirect effects of artificial selection were studied.

The heritability of bast fibre content was high and mass selection proved to be an efficient method causing no undesirable influence on other characters. Characters not directly related to bast fibre yield such as date of flowering, plant height and stem diameter were shown to have disadvantages as selection criteria for the improvement of bast fibre yield.

The cannabinoids THC and CBD were studied, as the acceptance of hemp cultivation requires a low level. The content of THC, the psychoactive component can be successfully reduced by mass selection, but it is not certain that mass selection is the most efficient method.

Introduction

In the framework of a comprehensive Dutch research project the feasibility of hemp cultivation (*Cannabis sativa* L.) for paper pulp production is being investigated. This project also includes a hemp breeding programme which was initiated at CPRO-DLO in 1990. The progress of the ongoing breeding programme is hampered by the lack of knowledge on the inheritance of agronomic traits.

Traditionally only the bast fibre was used for rope and cloth production, while the woody core was considered as waste. When hemp is grown for fibre production, seed is sometimes considered a valuable by-product.

For paper production both bast fibre and woody core fibres can be utilized. The quality of paper made from bast fibre is superior to that from woody core fibre. Therefore, hemp breeding for paper production has primarily aimed at improved bast fibre production. The yielding (fibre) capacity can be improved directly by selection for yield components, i.e. stem yield and bast fibre content, or indirectly by selection for characters such as date of flowering, plant height or stem diameter (Hoffmann, 1957). Late flowering cultivars produce greater fibre yields than early flowering cultivars due to a longer vegetative growing period (van der Werf, 1993). For annual fibre crops a strong relationship between plant height and stem yield is often reported, for instance, in kenaf total dry matter yield is closely associated with plant height (Muchow, 1979).

Breeding of fibre hemp has been subject of many studies (Bredemann, 1938; Hoffmann, 1957; Bócsa, 1958; Bócsa, 1969). Since the 1920's bast fibre content has more than doubled from approximately 12–15% to 25–35% (Bredemann, 1922; Bredemann, 1938; Heimann, 1990). Breeders in Hungary and France discontinued selection for increase of bast fibre content, since further increase of bast fibre content is accompanied by an increase of secondary bast fibre. This would decrease quality for cloth and rope production (Bócsa, personal communication, 1991). In contrast high bast fibre levels have no negative effect on paper quality.

For political and social acceptance of large scale hemp cultivation, the content of cannabinoids, especially ▲9-Tetrahydrocannabinol (THC), should be minimal. Plants containing, at initial seed maturity, less then 0.3% THC in the dry matter of the female inflorescence are considered to have no psychoactive potency (De Meijer et al., 1992). In the former USSR a maximum THC content of 0.2% was tolerated. The tolerated level in France was 0.5%. Due to considerable inter-plant variation (De Meijer et al., 1992), individual plants can have THC levels above the tolerated maximum, although the overall population has an acceptable level.

A successful breeding programme for the reduction of cannabinoid contents was initiated in the former USSR in the 1970's. Cultivars completely lacking THC were obtained. In the 1980's breeders in France and Poland also started breeding for low cannabinoid contents. In France new selections of existing cultivars were released having a THC content less than 0.07% instead of the original content of 0.1–0.3% (van der Werf, 1992).

Mass selection is a common breeding method in hemp, indicating that the heritability of traits under selection are high. No studies have reported any estimates of realized or narrow-sense heritabilities. Evidently the maximisation of the response to selection is never considered.

The use of knowledge on relations among characters is also seldom considered. The relationship between narcotic components and other characteristics has been subject of some studies. De Meijer et al. (1992) found no apparent relation except for a weak correlation between leaflet width and THC content. Small et al. (1976) found only a weak association between a large set of characters and narcotic components using multivariate analyses. It is never reported that hemp breeding was hampered by unwanted relationships between characters.

In the present paper parent-offspring (HS-families) relationships for relevant agronomic traits are used to estimate genetic parameters such as narrow-sense heritability. With the aid of artificial selection the estimated genetic parameters are verified and relationships between characters assessed. The response to selection for the observed traits will be discussed in relation with the optimisation of yield capacity.

Materials and methods

Source population

To establish a broad-based experimental population, equal numbers of seeds from 36 accessions, of which 35 fibre types and one drug type, were mixed and multiplied in a greenhouse in autumn 1990. Each harvested female or monoecious plant contributed equally to the source population.

Performance of parents

In 1991 a field trial was established from the source population for the observation of individual plants. The trial was sown 24 April at Wageningen (The Netherlands) on a sandy soil. The distance between rows was 50 cm and that between plants within rows 10 cm. After seedling emergence 60 plants were marked in each of 20 rows. Plant heights were measured at 5 and 18 June (H1 & H2). Date of flowering (DF) of each plant was recorded when the sex could be determined. Male plants were harvested three weeks after start of flowering and female plants at seed maturity. After harvest, length of the vegetative (HV) and generative (HG) stem parts were measured. The leaves on the vegetative stem part are arranged oppositely and those on the generative stem part alternately. HV was measured from the stem basis to the last node with opposite leaves or leaf marks. Total plant height (HT) is the sum of HV and HG. The female inflorescences were separated into seeds, leaf parts and straw. The seeds were weighed (SY). The levels of THC (TC) and CBD (cannabidiol) (CB) were determined on the leaf parts (de Meijer et al., 1992).

The fibre content of each plant was determined using a stem segment of 20 cm, taken 1 m above soil level. The diameter (SD) of this segment was measured. Each segment was dried, 24 h at 105° C and then weighed. Each stem segment was boiled in 2% sodiumhydroxide solution in water for two hours. Bast fibre and woody core were separated and rinsed with water to remove the soluble parts. The bast fibre and woody core were dried for two days and then weighed. Bast fibre (FB) and woody core (FW) content (%) of the segments were calculated (de Meijer, 1994).

Performance of offspring

In total 252 seed bearing plants from the 1991 parental trial were selected randomly for the offspring trial. Their progenies were grown in an offspring trial. The trial was sown 22 April 1992. The field contained 252 plots, each containing one progeny (HS-family) of 40 seeds. The trial contained 42 rows spaced 50 cm apart. Each row was divided into 6 plots of 4 meters long. The whole trial was surrounded by borders of hemp cv 'Kompolti Hybrid TC'.

The same measurements were made as in 1991, to enable a comparison between parents and offspring. Plant height was measured on 9 June and 17 June (H1 & H2) using 15 plants per plot. During the growing season, date of flowering (DF) of a plot was scored when 50% of the plants flowered irrespective of sex. Unlike 1991 the entire field was harvested at once from 31 August till 2 September. After harvest the length of the vegetative and generative stem parts (HV & HG) of ten male and ten female plants from each plot were measured, and total plant height (HT) was calculated. The female inflorescences of the ten female plants were used to determine THC (TC) and CBD (CB) content. Seeds were not collected.

For the determination of fibre content, a sample of 20 stem segments per plot was used. The diameter (SD) of the segments was measured. Bast fibre and woody core contents (FB & FW) were determined as described for the parental trial.

Data from individual plant measurements of the offspring trial (HV, HG, HT and SD) were averaged per HS-family (plot) to enable comparison with the parents.

Estimation of genetic parameters

Narrow-sense heritability and additive genetic variance of each character were estimated by the regression (equation 1) of offspring (HS-families) on female parents (Falconer, 1981).

$$\beta_{P,HS} = \frac{\mathrm{cov}(p_P, p_{HS})}{\mathrm{var}(p_P)} = \frac{\frac{1}{2}\sigma_a^2}{\sigma_e^2 + \sigma_a^2} = \frac{1}{2}h_n^2 \qquad (1)$$

$\beta_{P,HS}$ = regression coefficient
p_P = phenotypic value of female parent
p_{HS} = phenotypic value of HS-family
${\sigma^2}_a$ = additive genetic variance
${\sigma^2}_e$ = error variance
${h^2}_n$ = narrow-sense heritability

Multiple linear regression on parental characters

Multiple linear regression of offspring characters was performed on all parental characters, using the procedure REGRESSION (FORWARD) of the statistical package SPSS-X (Anonymous, 1988). The maximum number of dependent variables (parental characters) allowed in the regression model was set at three. The parental characters and the linear combination of parental characters are compared for their relationship with offspring characters.

Artificial selection

Within the parental population selection was performed artificially for all characters. The number of selected plants was 227, 126 and 25 which equals approximately 90, 50 and 10 percent of the parental population. The direction of selection depended on the character, for example bast fibre content was selected for higher values and THC content for lower values. The direct and indirect effects of selection for each single character and selection intensity were calculated for all offspring characters. The response of selection was tested by comparing the average phenotypic value across the selected offspring with the average phenotypic value of the entire offspring population, using a *t*-test.

Based on selection differential (S) and response to selection (R) realized heritabilities (equation 2) were estimated for each of the three selection intensities and subsequently compared with the estimates of narrow-sense heritability (Bos, 1990).

$$h_r^2 = \frac{2R}{S} \qquad (2)$$

R = response to selection, being the average phenotypic value across the selected offspring minus the average phenotypic value of the entire offspring population
S = selection differential, being the average phenotypic value of the selected parental plants reduced with the average phenotypic value across all plants in the parental population

Table 1. Some statistics on the characters observed during the parental (1991) and offspring (1992) trials

Character		Statistic				
Code	Description	Mean	Minimum	Maximum	$\hat{\sigma}_P$	n
Parents						
FB	Bast fibre content (%)	19.5	10.5	32.9	4.7	252
FW	Woody core content (%)	65.0	43.0	83.2	6.9	252
H1	Plant height at 5 June (cm)	14.2	6	24	3.2	252
H2	Plant height at 18 June (cm)	57.3	35	83	8.9	252
HV	Vegetative stem length (cm)	256.1	158	344	42.4	252
HG	Generative stem length (cm)	119.5	0	263	45.3	252
HT	Total plant height (cm)	375.6	227	510	47.0	252
DF	Date of flowering (day number)	233.2	198	252	9.0	252
SD	Stem diameter (mm)	14.3	7.8	22.2	2.6	252
TC	THC content (%)	0.44	0.00	3.42	0.55	251
CB	CBD content (%)	0.83	0.00	2.56	0.52	251
SY	Seed yield (gr)	12.1	1.4	36.3	8.0	252
Offspring						
FB	Bast fibre content (%)	18.9	11.4	26.0	2.6	252
FW	Woody core content (%)	68.7	55.3	90.4	4.7	252
H1	Plant height at 9 June (cm)	87.7	52.7	106.5	9.7	252
H2	Plant height at 17 June (cm)	156.1	102.2	177.9	11.7	252
HV	Vegetative stem length (cm)	202.1	130.9	264.5	22.2	252
HG	Generative stem length (cm)	180.9	122.8	264.2	24.0	252
HT	Total plant height (cm)	383.0	296.4	435.8	25.0	252
DF	Date of flowering (day number)	200.6	170	238	18.1	252
SD	Stem diameter (mm)	15.7	11.6	22.8	1.7	252
TC	THC content (%)	0.18	0.01	0.65	0.12	242
CB	CBD content (%)	0.33	0.07	0.91	0.16	243

Results

Performance of parents and offspring

Table 1 summarizes the performance of parents and offspring for the observed characters. In June the plants were much taller (H1 & H2) in the offspring trial than in the parental trial. Flowering started more than 30 days earlier in the offspring trial. The contents of CBD and THC were much lower in the offspring trial than in the parental trial. For all other characters, parents and offspring differed very little.

The observed range (minimum-maximum) for most offspring characters was smaller than that for the corresponding parental characters (Table 1). The standard deviations of various characters (Table 1) was larger in the parental trial than in the offspring trial. It appeared that the ratio between σ_P and σ_{HS} was similar for most characters, i.e. approximately 1.8. Date of flowering (DF), plant height (H1 & H2) and THC content (TC) deviated from this ratio. The standard deviations for H1, H2 and DF in the offspring trial were relatively large, while the standard deviation for TC was relatively small.

Genetic parameters

The estimates for narrow-sense and realized heritabilities (Table 2) were very high for date of flowering (DF) and bast fibre content (FB), i.e. greater than 0.84. The estimated heritabilities for date of flowering exceed the theoretical maximum value 1.

The heritabilities for woody core content (FW), plant height (H2) and vegetative stem length (HV) were estimated fairly high to high, i.e. between 0.39 and 0.86. In contrast to the low estimate of narrow-sense

Table 2. Estimates of narrow-sense heritabilities (h^2_n), realized heritabilities (h^2_r) at three selection intensities (10, 50 and 90%) and additive standard deviation ($\hat{\sigma}_a$) for the observed characters

Character	h^2_n	$h^2_r(10)$	$h^2_r(50)$	$h^2_r(90)$	$\hat{\sigma}_a$
FB	0.89	0.84	0.90	0.98	4.5
FW	0.56	0.48	0.63	0.85	5.2
H1	0.47	- 0.41	1.17	- 0.02	2.2
H2	0.73	0.86	0.53	0.52	7.6
HV	0.47	0.49	0.46	0.39	28.9
HG	0.29	0.38	0.29	0.11	24.4
HT	0.28	0.77	0.30	0.28	24.7
DF	2.35	3.18	2.82	1.77	13.8
SD	0.22	0.33	0.22	0.15	1.2
TC	0.15	0.18	0.31	0.12	0.221
TC*	0.56				
CB	0.08	0.27	0.06	- 0.03	0.141

TC* is log(TC).

Table 3. Multiple linear equations of parental characters obtained by multiple regression of offspring on parental characters and the multiple correlation coefficient (r_m) and simple correlation coefficients of corresponding parental and offspring character (r_s)

Response variate	Multiple linear equations of parental characters	r_m	r_s
FB	10.23 + 0.469FB - 0.050H2 + 0.167SD	0.82	0.81
FW	62.94 - 0.484FB + 0.066DF	0.50	0.41
H1	110.14 + 0.264SY + 0.198H2 - 0.159DF	0.37	0.08
H2	198.82 + 0.213H2 - 0.285DF + 0.797SD	0.37	0.28
HV	- 11.67 + 0.189HV + 0.768DF - 0.947H1	0.57	0.44
HG	67.72 + 0.195HG + 0.409DF - 0.466SY	0.35	0.27
HT	36.76 + 1.285DF + 0.124HT	0.54	0.26
DF	- 80.40 + 1.206DF	0.60	0.59
SD	- 1.93 + 0.069DF + 0.105SD	0.40	0.16
TC	0.83 + 0.071TC - 0.003DF - 0.035CB	0.43	0.34
CB	1.92 - 0.007DF + 0.053CB + 0.005FB	0.45	0.12

heritability for total plant height (HT) being 0.28, the corresponding realized heritabilities were much higher, especially at a high selection intensity (0.77).

For generative stem length (HG), stem diameter (SD), THC content (TC) and CBD content (CB) both narrow-sense and realized heritabilities were low between - 0.03 and 0.38. Although heritabilities were estimated low for THC content, ranging from 0.15 to 0.31, the narrow-sense heritability based on the logarithmic value of THC content improved the value to 0.56. The realized heritabilities for plant height at 5 June (H1) were unpredictable.

In general realized heritabilities increased with increasing selection intensity.

Multiple linear regression on parental characters

The obtained linear combination of dependent variates (parental characters) are presented in Table 3. The major parental character in the equation were often identical to the response variate (FB, H2, DF, HV, HG and TC). Date of flowering (DF) is the major parental character in the equation of response variates HT, SD and CB. FB is the major parental character in the equation of response variate FW. It is striking that the parental characters FW and H1 did not appear in the equations for the response variates FW and H1 themselves.

The multiple correlation coefficients of H1, HT, SD and CB are much higher than the corresponding simple correlation coefficients (Table 3).

Artificial selection

Irrespective of the plant character, a selection intensity of 90% of the parental plants did not generally improve the offspring population (Table 4). In contrast, a selection intensity of 10 or 50% selection often gave a positive selection result and often caused correlated responses.

Selection for bast fibre content proved to be more effective for the improvement of bast fibre content than selection for decreased woody core content (Table 4), although both criteria are almost complementary.

Early selection for plant height, when plants were approximately 15 cm tall (H1), was not effective. Selection at a later stage, plants approximately 60 cm tall (H2), resulted in taller offspring, but it did not affect final plant height (HT). Selection for vegetative or generative plant height (HV & HG) was less effective than selection for total plant height with regard to the improvement of total plant height (HT). Selection for total plant height (HT) resulted in later flowering (DF), thicker stems (SD) and a slightly decreased bast fibre content (FB).

The population would have responded strongly to selection for date of flowering (DF): a selection inten-

Table 4. Mean direct and indirect response to selection for various traits in the parental population with selection intensities of 10, 50 or 90% of the plants (+ selection for higher values, - selection for lower values)

Parental selection			Mean of the selected offspring										
Criterion	Direction	Intensity	FB	FW	H1	H2	HV	HG	HT	DF	SD	TC	CB
FB	+	90	**19.3**	68.2	88.1	156.5	202.1	181.2	383.3	200.6	15.7	0.18	0.33
		50	**20.6***	67.1*	87.8	156.1	203.6	179.9	383.5	201.3	15.5	0.17	0.34
		10	**22.7***	65.1*	86.3	153.2	205.9	182.2	388.1	203.2	15.7	0.14*	0.33
FW	-	90	19.2	**68.2**	87.7	156.0	202.3	180.2	382.4	200.1	15.6	0.18	0.34
		50	20.3*	**67.0***	86.8	154.8	202.8	178.4	381.2	200.5	15.4	0.17	0.34
		10	21.2*	**65.7***	86.4	154.8	202.5	178.6	381.1	198.4	15.5	0.21	0.34
H1	+	90	18.9	68.9	**87.7**	156.1	202.5	181.2	383.7	201.1	15.7	0.17	0.32
		50	19.2	68.1	**89.2**	157.5	197.7	182.1	379.8	197.9	15.5	0.18	0.34
		10	18.8	69.4	**86.5**	155.0	193.3	190.3	383.7	200.4	15.7	0.18	0.36
H2	+	90	18.9	68.9	88.1	**156.5**	201.5	182.2	383.7	200.6	15.7	0.17	0.33
		50	19.0	68.6	89.3	**158.1**	199.9	181.2	381.1	198.0	15.6	0.18	0.35
		10	19.0	67.1	93.6*	**163.1***	198.7	175.2	373.8	193.6	15.2	0.20	0.42*
HV	+	90	19.1	68.5	87.9	156.3	**203.7**	180.0	383.7	201.2	15.7	0.18	0.33
		50	19.3	68.3	88.7	156.6	**210.4***	176.8	387.1	203.1	15.9	0.18	0.33
		10	19.2	68.5	87.8	154.9	**219.0***	172.4	391.4	205.6	16.5	0.17	0.30
HG	+	90	18.9	68.8	88.0	156.5	201.5	**181.3**	382.7	200.4	15.7	0.18	0.33
		50	18.8	68.8	89.8*	158.8*	196.5*	**186.1***	382.5	198.4	15.5	0.18	0.34
		10	18.4	71.0	87.0	156.0	194.6*	**197.4***	392.0	206.1	16.3	0.14	0.34
HT	+	90	19.0	68.7	88.2	156.7	202.6	181.9	**384.5**	201.0	15.7	0.17	0.33
		50	19.2	68.8	89.4	157.6	206.1	182.3	**388.4***	202.8	15.9	0.17	0.32
		10	18.3	72.0*	89.8	158.1	212.2*	192.8*	**404.9***	212.5*	17.2*	0.15	0.28
DF	+	90	19.0	68.7	87.6	155.8	204.4	180.9	385.2	**202.6**	15.8	0.17	0.32
		50	18.7	69.6	85.1*	152.9*	210.7*	181.6	392.3*	**209.2***	16.2*	0.14*	0.26*
		10	19.1	69.7	84.2*	152.2*	214.9*	178.5	393.4*	**215.8***	16.5*	0.13*	0.23*
SD	+	90	18.9	68.7	88.2	156.7	202.4	181.4	383.8	200.6	**15.7**	0.17	0.33
		50	18.9	68.8	89.5	158.1	206.0	181.1	387.1	203.6	**15.9**	0.18	0.32
		10	17.9	70.4	92.3*	161.4*	215.3*	178.9	394.2*	204.8	**16.5**	0.17	0.33
TC	-	90	19.0	68.7	87.5	156.1	201.5	181.4	382.8	200.2	15.7	**0.17**	0.34
		50	18.9	69.1	87.9	156.9	200.4	182.3	382.7	198.7	15.7	**0.12***	0.37
		10	18.7	69.0	89.0	159.2	193.1	179.1	372.2*	196.6	15.1	**0.12***	0.37
CB	-	90	18.9	68.7	87.7	156.1	201.5	180.8	382.3	199.9	15.6	0.18	**0.33**
		50	18.9	68.8	88.0	156.4	199.4	181.6	380.9	200.0	15.5	0.21*	**0.31**
		10	18.7	68.9	87.1	155.6	204.4	183.7	388.0	206.5	15.6	0.22*	**0.23***
SY	+	90	19.0	68.7	88.2	156.4	202.8	181.1	383.8	201.2	15.7	0.17	0.33
		50	19.1	68.4	90.5*	158.9*	204.1	180.4	384.6	200.6	15.8	0.17	0.34
		10	18.6	69.0	92.0*	160.4*	209.3	179.8	389.1	200.6	16.1	0.17	0.36
Population mean			18.9	68.7	87.7	156.1	202.1	180.8	383.0	200.6	15.7	0.18	0.33

* Significantly different from population mean ($P < 0.05$).

sity of 10% of the plants would have delayed flowering more than 14 days. Indirectly, plant height (HT) would have increased and cannabinoid contents (CB and TC) decreased.

Simulated selection for stem diameter (SD) had only little effect, but is strongly associated with plant height (HT) and slightly reduced bast fibre content (FB).

Although estimated heritabilities for THC and CBD content were low, a considerable decrease after selection was observed in simulation. For THC content the decrease was already considerable when 50% of the parental plants were selected.

Discussion

A major goal of breeding hemp for paper production is the increase of bast fibre yield, a trait determined by two yield components bast fibre content and stem yield. It was shown that in the used population yield increase can be achieved by simple mass selection for bast fibre content. The trait has a high heritability (Table 2) and mass selection had no undesirable influence on other characters (Table 4). A slight but significant reduction of THC content was found as an indirect response to selection for bast fibre content, although no significant correlation was found between THC and bast fibre content.

The determination of the bast fibre content is laborious. It would be more efficient to base selection on a character less awkward, but closely related to bast fibre yield, i.e. the second yield component stem yield, plant height, date of flowering or stem diameter. During this experiment the stem yield was not measured. Previous trials (unpublished) showed that the heritability of stem yield (0.55) is lower than that for bast fibre content (0.96).

The estimates for the heritability of plant height (Table 2) are low compared to those for bast fibre content. The multiple correlation coefficient (Table 3) of total plant height (0.54) is much higher than its simple correlation coefficient (0.26), indicating that plant height is influenced by other characters. The major character influencing plant height in this experiment was date of flowering (Table 3). Recent trials with fibre hemp (unpublished) showed that stem length accounted only for 36% of the total dry matter yield variance. The remaining variance is influenced by other characters such as date of flowering, stem diameter and stem filling. This is in contrast with other annual fibre crops where a close relationship between stem yield and plant height is often reported. For example, Muchow (1979) showed in kenaf that plant height accounted for 78% of the variance for total dry matter yield.

Average flowering date in the offspring was more than 30 days earlier than in the female parents (Table 1). Date of flowering in the offspring was mainly determined by date of male flowering, as male flowering starts earlier than female flowering. The average difference between male and female flowering in the parental population was 11.5 days. It is therefore not likely that the 30 day difference between generations, is solely due to the presence of male plants in the offspring population. Year effects due to differences in weather conditions may have been of influence as 1992 was much warmer than 1991. Moreover assortative mating within the parental population has likely caused a shift towards early flowering. The estimated heritabilities (Table 2) for date of flowering are beyond theoretical limits, but from the results of artificial selection (Table 4) it is clear that they are high. Tables 3 and 4 show that date of flowering has a relationship with many other characters (H2, HV, HG, HT and SD). Van der Werf (1993) reported a strong relationship between date of flowering and stem production; in general late flowering cultivars are more productive. The increased stem production of late-flowering cultivars is accompanied by a low seed production (Hoffmann, 1957; Mathieu, personal communication, 1992). Most cultivars are a compromise between seed and stem production.

The heritability of stem diameter is very low; selection resulted only in a positive correlated response of plant height. The relationship between stem diameter and yield was not clear.

Although year differences for CBD content are reported (de Meijer et al., 1992), it is likely that the large difference between parents and offspring for contents of both CBD and THC observed in this experiment (Table 1) have a methodological cause. The female parental plants were harvested during a period of several weeks when seeds were mature. The offspring was harvested in a period of three days. Some of the HS- families were not fully mature, within many HS-families some immature female plants were present. Since the contents of CBD and THC increase during the growing season, especially between start of flowering and seed maturity (Barni-Comparini et al., 1984), maximum contents of CBD and THC probably were not reached in the offspring generation.

Mass selection for THC and CBD content was successful despite low heritabilities (Table 4). The under-estimation of the THC and CBD content in the offspring probably masked differences between selected HS-families and the total population. The estimated heritabilities for the contents of THC and CBD are therefore probably underestimated.

Conclusions

Characters not directly related to bast fibre yield showed in the present study to have disadvantages as selection criteria for indirect improvement of bast fibre yield. Plant height had a weak relation with yield and its heritability is low. Date of flowering was highly heritable and had a significant relationship with stem yield. However this trait was negatively related with seed production. Stem diameter had a low heritability and the relation with yield is uncertain.

Bast fibre content was highly heritable and directly related to bast fibre yield. There was no undesirable influence on other characters as correlated response to selection. For the population under selection, mass selection for bast fibre content proved to an efficient selection method for the improvement of bast fibre yield. In general this will hold for all populations having sufficient genetic variation for bast fibre content. However, it is thought that simultaneous selection based on bast fibre content and stem yield is the best breeding strategy for improvement of bast fibre yield.

Since CBD is not a psychoactive substance, breeders can focus only on the reduction of THC content. This study confirmed the experience of breeders in the Ukraine and France that THC content can be reduced using mass selection. Although it is not certain that mass selection is the most efficient approach.

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References

Anonymous, 1988. SPSS-X User's guide, third edition, USA, 1072 p.

Barni-Comparini, I., S. Ferri & F. Centini, 1984. Cannabinoid level in the leaves as a tool for the early discrimination of *Cannabis* chemiovariants. Forensic Science International 24: 37–42.

Bócsa, I., 1958. Beiträge zur Züchtung eines ungarischen monözische Hanfes und zur Kenntnis der Inzuchterscheinungen beim Hanf (*Cannabis sativa* L.). Zeitschrift für Pflanzenzüchtung 39: 11–34.

Bócsa, I., B. Pozsár & Z. Majkó, 1969. Die Züchtung einer hellstengeligen, südlichen Hanfsorte. Zeitschrift für Pflanzenzüchtung 62: 231–240.

Bos, I., 1990. Selection methods part B: Quantitative genetical aspects. Department of plant breeding, Wageningen Agricultural University, pp. 70–71.

Bredemann, G., 1922. Die Bestimmung des Fasergehaltes in Bastfaserpflanzen bei züchterischen Untersuchungen. Faserforschung 4: 239–258.

Bredemann, G., 1938. Züchtung des Hanfes auf Fasergehalt. Die Ergebnisse des Jahres 1937. Faserforschung 8: 81–87.

Falconer, D.S., 1981. Introduction to quantitative genetics. Longman, London, p. 137.

Heimann, S., 1990. (Report of cultivar trails 1989, fibre flax, hemp) Synteza wyników doświadczeń odmianowych 1989, len wloknisty, konopie, (Issue 904) Zesty 904. (The research centre for agricultural crops cultivar testing). Centralny Osrodek Badania Odmian Roslin Uprawnych, Slupia Wielka, Poland.

Hoffmann, W., 1957. Hanf *Cannabis sativa* L. In: H. Kappert & W. Rudorf (Eds). Handbuch der Pflanzenzüchtung, Band V., Paul Parey, Berlin-Hamburg, pp. 204–263.

Meijer, E.P.M. de, H.J. van der Kamp & F.A. van Eeuwijk, 1992. Characterisation of *Cannabis* accessions with regard to cannabinoid content in relation to other plant characters. Euphytica 62: 187–200.

Meijer, E.P.M. de & H.M.G. van der Werf, 1994. Evaluation of current methods to estimate pulp yield of hemp. Industrial Crops and Products 2: 111–120.

Muchow, R.C., 1979. Effects of plant population and season on kenaf (*Hibiscus cannabinus* L.) grown under irrigation in tropical Australia II. Influence on growth parameters and yield prediction. Field Crops Research 2: 67–76.

Small, E., P.Y. Jui & L.P. Lefkovitch, 1976. A numerical taxonomic analysis of *Cannabis* with special reference to species delimitation. Systematic Botany 1: 67–84.

Werf, H.M.G., 1992. Fibre hemp in France: Report of a visit to the fédération nationale des producteurs de chanvre at Le Mans. Department of agronomy, Wageningen Agricultural University, The Netherlands.

Werf, H.M.G., H.J. Haasken & M. Wijlhuizen, 1993. The effect of daylength on yield and quality of fibre hemp. In preparation.