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Nitrogen Fertilization and Sex Expression Affect Size Variability of Fibre Hemp (*Cannabis Sativa* L.)

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## ORIGINAL PAPER

H. M. G. van der Werf · W. van den Berg

**Nitrogen fertilization and sex expression affect size variability of fibre hemp (*Cannabis sativa* L.)**

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**Abstract** Mechanical harvesting and industrial processing of fibre hemp (*Cannabis sativa* L.) require uniformity of stem length and weight. In 1991 and 1992 we carried out field experiments to investigate the effects of soil nitrogen level (80 and 200 kg ha<sup>-1</sup> N) and row width (12.5, 25 and 50 cm) on the variability of weight and height in hemp plants. The crops were sampled 5 times between early June and early September. Row width did not affect size variability. At final harvest coefficients of variation (CV) of both weight and height were about 1.5 times higher at 200 than at 80 kg ha<sup>-1</sup> N. Distributions of dry weight were positively skewed at all sampling dates except the first, with skewness larger at 200 than at 80 kg ha<sup>-1</sup> N. Distributions of height were negatively skewed at all sampling dates except the first at 80 kg ha<sup>-1</sup> N. At 200 kg ha<sup>-1</sup> N they changed from negative skewness during the first part of the growing season to negative kurtosis in the second part of the growing season. More suppressed plants were present at 200 than at 80 kg ha<sup>-1</sup> N. Contrary to most published results, we did not find a reduction of CV of weight nor of CV of height at the onset of self-thinning. Suppressed hemp plants can survive relatively well in the low-light environment under the canopy. Sexual dimorphism contributed to variability of height and weight, but the effects were smaller than those of nitrogen fertilization. The ratio of female to male plants was higher at 200 than at 80 kg ha<sup>-1</sup> N, as a result of a shift in sex-ratio within the population of suppressed plants. As suppressed plants were much

more slender than dominating plants, self-thinning eliminated the most slender individuals in a hemp crop. However, the presence of many more heavy individuals of low slenderness at 200 than at 80 kg ha<sup>-1</sup> N was probably the major cause of the difference in slenderness between 200 and 80 kg ha<sup>-1</sup> N.

**Key words** *Cannabis sativa* L. · Allometry · Nitrogen fertilization · Competition · Sexual dimorphism

**Introduction**

Fibre hemp (*Cannabis sativa* L.) is grown for the production of stems, which are processed into textile or paper products. In hemp, the proportion of stem in the above-ground dry matter and the proportion of the valuable bast fibres in the stem dry matter increase with plant density (Van der Werf et al. 1995a), so a high density is desirable.

Uniformity of size is important for the mechanical harvesting and industrial processing of hemp stems (De Maeyer and Huisman 1995). The larger the range of plant heights in a hemp crop, the less efficient the measures for mechanical defoliation at harvest. In industrial processing, a wide range of stem weights and stem diameters is not desirable, as it hampers fine-tuning of decortication equipment, resulting in less efficient separation of bark and core. In dense plant stands inter-plant competition may generate a size hierarchy, i.e. increase variability in the size of individuals, with large plants suppressing smaller ones (Harper 1977). Eventually self-thinning may occur; suppressed plants may die. (Van der Werf et al. 1995a; Van der Werf et al. 1995b).

Differences in the size of individual plants may be determined by: age differences, genetic differences, environmental heterogeneity, maternal effects, effects of herbivores, parasites or pathogens, or competition

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(Weiner and Thomas 1986). In hemp, which is a dioecious species, sexual dimorphism may be an additional cause of size variability (Hoffmann 1957), but this has never been quantified.

The coefficient of variation (CV: standard deviation/mean) is a standard measure of relative variation and size variability (Weiner and Thomas 1986). In even-aged plant stands CVs of size parameters generally increase with time until the onset of self-thinning, and then decrease as suppressed plants die (Benjamin and Hardwick 1986; Weiner and Thomas 1986; Knox et al. 1989).

Size distributions often depart from normality; skewness and kurtosis measure the nature and amount of this departure (Sokal and Rohlf 1981). Skewness indicates the degree of asymmetry of the distribution, with negative skewness indicating a tail to the left, and positive skewness indicating a tail to the right. Kurtosis represents the pointedness of the distribution. A leptokurtic distribution (positive kurtosis) has more items near the mean and at the tails, with fewer items in the intermediate regions relative to a normal distribution with the same mean and variance. A platykurtic distribution (negative kurtosis) has fewer items at the mean and at the tails than the normal distribution but more in intermediate regions. Frequency distributions of plant mass generally become increasingly positively skewed as time passes, while distributions of plant height either remain symmetrical or become negatively skewed (Hara 1984; Geber 1989; Knox et al. 1989). Frequency distributions of both plant mass and plant height may become bimodal, i.e. two-peaked, an extreme platykurtic distribution (Huston and DeAngelis 1987). Once self-thinning has started, skewness generally decreases and bimodality tends to disappear (Hara 1984; Benjamin and Hardwick 1986).

Competition is a major cause of the development of size variability (Weiner and Thomas 1986; Bonan 1991). Weiner and Thomas (1986) suggested that competition for light is one-sided, i.e. large plants suppress small ones more than small plants suppress large ones, and that this effect is greater than would be expected from their relative sizes. In the most extreme form of "one-sided" competition, the growth of large plants would not be reduced at all by smaller individuals. In contrast, competition for below-ground resources would be two-sided, with shared resources being distributed in proportion to plant size. One-sided competition promotes size variability, whereas two-sided competition reduces it (Weiner and Thomas 1986). Reduced soil fertility may lead to earlier or more below-ground (two-sided) competition, and thus should reduce the rate at which size variability increases with time. Tests of this hypothesis were found in two studies only (Weiner 1985; Lieffers and Titus 1989), which reported on experiments which used extreme fertility treatments in a greenhouse. The effect of soil fertility, or of one of its major components such as soil nitro-

gen status, on size variability in a field situation has never been reported.

Because competition affects size variability, in a row crop we would expect rectangularity (the ratio of the between-row distance and the within-row distance) to influence size variability. At the same plant density, competition starts earlier, the more rectangularity exceeds 1:1. The effect of rectangularity on the occurrence of size variability has not been previously reported. The variability of seedling size may affect the variability of plant size later on in the growing season. The variability of seedling size may be influenced by the uniformity of sowing depth and of plant spacing within the row (Benjamin and Hardwick 1986), factors depending on the type of sowing implement. Reports on the effect of sowing-machine technology on size variability were not found.

The objective of our experiments was to investigate to what extent soil nitrogen level, rectangularity and type of sowing implement affect size variability in hemp. We also investigated to what extent sexual dimorphism contributes to size variability in hemp.

## Materials and methods

### Treatments and cultural methods

Field experiments were carried out in 1991 and 1992 in Lelystad, the Netherlands (52° 32' N, 5° 31' E, -5 m elevation), on a light marine clay soil. The experimental set-up was a randomized complete block design with ten treatments and two replications. The treatments involved a two-way factorial of two nitrogen levels (soil-N + fertilizer-N: 80 or 200 kg ha<sup>-1</sup>) and five plant arrangements. Plant arrangements were: (a) 12.5 cm row width ('12.5'), (b) 25 cm row width ('25'), (c) 50 cm row width ('50'), (d) 12.5 cm row width precision sown ('12.5p'), and (e) 25 cm row width thinned uniformly ('25u'). We used a precision seed drill to sow treatment '12.5p' and a studded roller seed drill for the other treatments. With the precision seed drill the distance between plants in the row and sowing depth are less variable than with the studded roller seed drill.

Stands in all treatments were thinned manually at the seedling stage (21 May 1991 and 26 May 1992) to obtain the desired plant density. The treatment '25u' was thinned to obtain a uniform crop: we removed tall and short plants and we tried to obtain a uniform distance between the plants in a row. To allow such extensive thinning, this treatment was over-sown with about twice the number of seeds required for the desired plant density. In 1991 all treatments were thinned to 160 plants m<sup>-2</sup>, while in 1992 plant emergence was less than expected and all treatments were thinned to 132 plants m<sup>-2</sup>.

P and K fertilizer were applied according to the recommendations for arable crop rotations in the Netherlands. Soil N was measured between 0 and 60 cm in March 1991 (25 kg ha<sup>-1</sup>) and between 0 and 90 cm in March 1992 (51 kg ha<sup>-1</sup>). In both years N fertilizer was applied shortly before sowing.

Hemp was sown on 18 April 1991 and on 8 May 1992, with 50% plant emergence on 5 May in 1991 and on 14 May in 1992, respectively. No herbicides were used, as weeds were adequately suppressed by the crop. The occurrence of *Botrytis cinerea* and other fungal diseases was prevented by spraying the crops with fungicides (alternating vinchlozolin at 167 g ha<sup>-1</sup> + chlorothalonil at 500 g ha<sup>-1</sup> and carbendazim at 87.5 g ha<sup>-1</sup> + iprodion at 175 g ha<sup>-1</sup>) during June, July and August at 14-day intervals.

### Data collection

The plots, which were 15 m long and 6 m wide, each contained five sample areas, 2 m apart. Four sample areas were 1 m × 1 m, while the sample area for the fifth (and final) harvest was 1 m × 2 m. The experiment was surrounded by a 3 m-wide buffer of hemp.

Harvest dates were 5 and 24 June, 22 July, 19 August and 9 September in 1991, and 2 and 22 June, 20 July, 17 August and 7 September in 1992. At each harvest 25 consecutive living plants per sample area were cut off at ground level. The length of each plant was measured, and all plants were dried individually at 105 °C until constant weight. At harvest 5 the sex expression of each of the 25 plants was determined (for method see Van der Werf et al. 1994). The remaining plants in the sample area were harvested similarly, and were used to determine plant densities, yield and its components as described in Van der Werf et al. (1995b).

### Data analysis

To characterize frequency distributions of plant height and plant weight the coefficient of variation (CV), and the skewness and kurtosis were calculated for each 25-plant sample (Sokal and Rohlf 1981). The CV was calculated as the standard deviation divided by the mean. Skewness was calculated as the third central moment divided by the cube of the standard deviation. Kurtosis was calculated as the fourth central moment divided by the fourth power of the standard deviation minus 3. Differences among treatments for CV, skewness and kurtosis were tested by analysis of variance. Tests for the departure from zero of the treatment means of skewness and kurtosis were based on the standard errors from the analysis of variance. As a statistical test for bimodality is not available, we evaluated bimodality by visual inspection of size distributions.

## Results

Nitrogen levels and plant arrangements did not significantly interact. Row width (treatments '12.5', '25' and '50'), type of sowing implement ('12.5p' versus '12.5') and manual thinning to obtain uniformity ('25u' versus '25') did not affect CV, skewness or kurtosis. The level of nitrogen fertilization strongly affected these size variability parameters, and the 2 years differed to some extent. Consequently, data are reported separately for the 2 years and averaged over the five plant arrangements.

### Development of size variability

The CV of plant dry weight was greater at 200 than at 80 kg ha<sup>-1</sup> N at harvests 3–5 in 1991 and at harvests 2–5 in 1992 (Table 1). CVs increased with time until harvest 4 or 5, and more rapidly at 200 than at 80 kg ha<sup>-1</sup> N. The distributions of plant dry weights were positively skewed at all harvests except the first in 1991, and skewness increased with time until harvest 3, 4 or 5 (Table 1). When skewness was affected by N level, it was larger at 200 than at 80 kg ha<sup>-1</sup> N. The distributions of plant dry weights were not kurtotic, except for those of harvests 4 and 5 of the 200 kg ha<sup>-1</sup> N crop in 1992, which showed positive kurtosis (Table 1).

**Table 1** Coefficient of variation, skewness and kurtosis of the dry weight of hemp plants grown at two soil nitrogen levels in 1991 and 1992. Data are means of five plant arrangements, see text for harvest (H) dates (NS not significant)

	1991			1992		
Parameter	Nitrogen (kg ha <sup>-1</sup> )			Nitrogen (kg ha <sup>-1</sup> )		
	80	200	<i>P</i>	80	200	<i>P</i>
Coefficient of variation						
H 1	35.6	31.1	NS <sup>a</sup>	36.9	36.0	NS
H 2	42.1	47.6	NS	49.1	70.0	<0.001
H 3	54.2	86.1	<0.001	57.8	107.1	<0.001
H 4	58.8	96.4	<0.001	77.6	110.6	<0.001
H 5	60.0	93.0	<0.001	70.3	110.3	<0.001
Skewness						
H 1	0.01	-0.17	NS	0.38*	0.41*	NS
H 2	0.41*	0.54*	NS	0.29	0.67*	NS
H 3	0.49*	1.02*	0.042	0.32*	1.20*	<0.001
H 4	0.61*	0.83*	NS	0.93*	1.52*	0.016
H 5	0.62*	0.97*	NS	0.67*	1.56*	<0.001
Kurtosis						
H 1	-0.47	-0.02	NS	-0.31	0.06	NS
H 2	0.07	0.62	NS	-0.33	-0.24	NS
H 3	0.56	0.42	NS	-0.62	0.85	NS
H 4	0.16	-0.50	NS	0.43	2.03*	NS
H 5	0.31	0.05	NS	-0.04	2.18*	<0.001

\* Skewness or kurtosis is significantly ( $P \leq 0.05$ ) different from zero

<sup>a</sup> NS:  $P > 0.05$

The CV of plant height was greater at 200 than at 80 kg ha<sup>-1</sup> N at harvests 3–5 in 1991 and at harvests 2–5 in 1992 (Table 2). CVs increased with time until harvest 3, 4 or 5, and more rapidly at 200 than at 80 kg ha<sup>-1</sup> N. At 80 kg ha<sup>-1</sup> N the distributions of plant heights were negatively skewed from harvest 2 to 5, while at 200 kg ha<sup>-1</sup> N they were negatively skewed at harvests 1–3 in 1991 and at harvest 2 in 1992 (Table 2). At all harvests except harvests 1 and 2 in 1992, skewness of the distribution of plant heights was more negative at 80 than at 200 kg ha<sup>-1</sup> N. At 80 kg ha<sup>-1</sup> N the distributions of plant heights showed positive kurtosis at harvests 2, 3 and 4 in 1991 and at harvest 3 in 1992. At 200 kg ha<sup>-1</sup> N they showed negative kurtosis from harvests 3 to 5 in 1991 and at harvests 4 and 5 in 1992.

### Size and sex expression

At harvest 5 the 200 kg ha<sup>-1</sup> N crop in both years comprised more very heavy plants and more very light plants than the 80 kg ha<sup>-1</sup> N crop (Fig. 1a). In both years and at both N levels heavy plants were mainly female (Fig. 1b–c). All non-flowering plants were very light and more were present at 200 than at 80 kg ha<sup>-1</sup> N (Fig. 1d).

At harvest 5 in both years the 200 kg ha<sup>-1</sup> N crop comprised more very tall and more short plants than the 80 kg ha<sup>-1</sup> N crop (Fig. 2a). In 1991 the frequency distribution of heights of the 200 kg ha<sup>-1</sup> N crop was

**Table 2** Coefficient of variation, skewness and kurtosis of the height of hemp plants grown at two soil nitrogen levels in 1991 and 1992. Data are means of five plant arrangements, see text for harvest (H) dates (NS not significant)

	1991			1992		
	Nitrogen (kg ha <sup>-1</sup> )			Nitrogen (kg ha <sup>-1</sup> )		
Parameter	80	200	<i>P</i>	80	200	<i>P</i>
Coefficient of variation						
H 1	13.9	12.0	NS <sup>a</sup>	16.5	14.8	NS
H 2	10.6	13.0	NS	13.5	23.3	0.004
H 3	17.9	28.5	<0.001	20.0	36.5	<0.001
H 4	18.3	35.3	<0.001	26.7	34.7	<0.001
H 5	22.2	32.9	<0.001	25.1	35.2	0.004
Skewness						
H 1	−0.08	−0.66*	0.017	0.00	−0.04	NS
H 2	−1.64*	−1.06*	0.017	−1.04*	−0.95*	NS
H 3	−1.27*	−0.48*	<0.001	−1.37*	−0.28	<0.001
H 4	−1.00*	−0.01	<0.001	−0.69*	−0.22	0.003
H 5	−0.71*	−0.18	0.015	−0.69*	−0.14	0.020
Kurtosis						
H 1	0.29	1.49*	NS	−0.17	0.18	NS
H 2	4.40*	0.68	0.009	0.68	0.26	NS
H 3	1.60*	−0.83*	<0.001	1.59*	−1.02	0.016
H 4	0.95*	−1.42*	<0.001	−0.27	−0.92*	0.009
H 5	−0.01	−1.20*	0.002	0.00	−0.96*	0.013

\* Skewness or kurtosis is significantly ( $P \leq 0.05$ ) different from zero  
<sup>a</sup>NS:  $P > 0.05$

clearly bimodal; in 1992 it was less so. In both years and at both N levels the tallest plants were mainly male (Fig. 2b–c). Plants of below-average stature were more often female than male (Fig. 2b–c), and, especially at 200 kg ha<sup>-1</sup> N, many of these short plants did not flower (Fig. 2d).

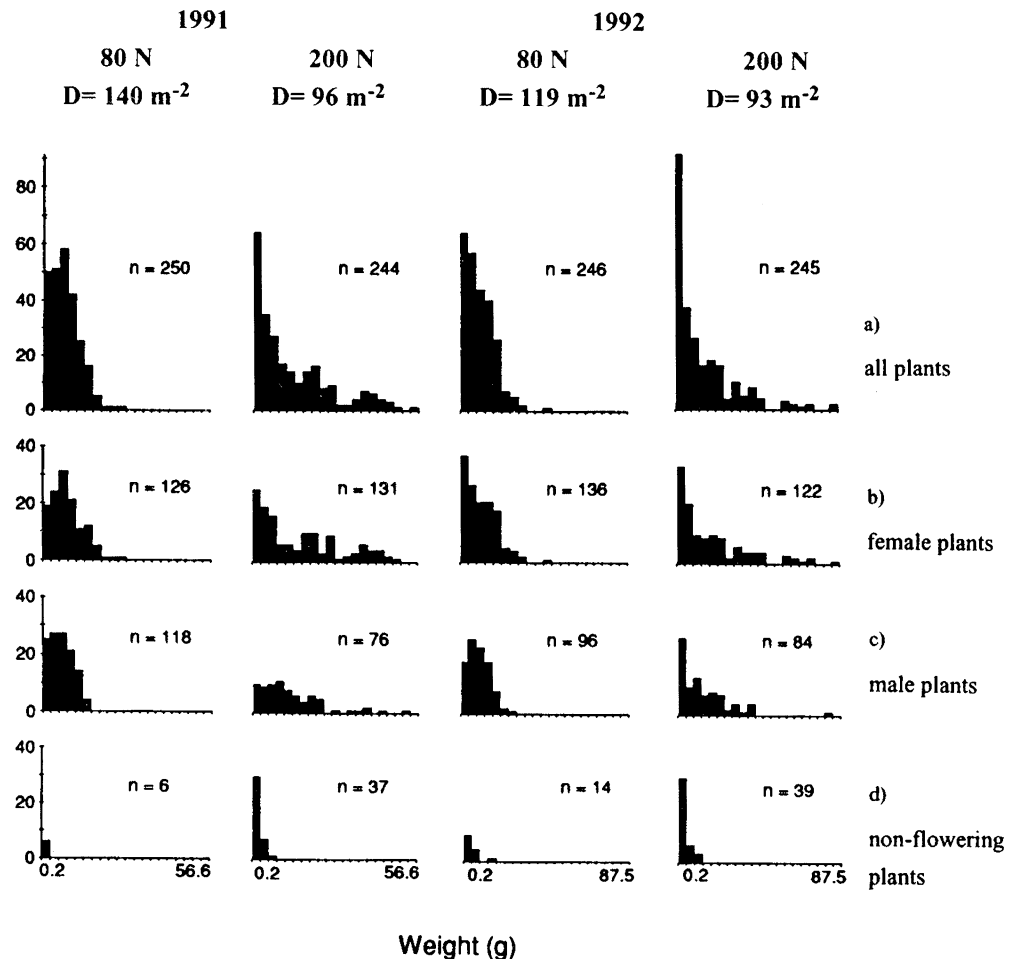
### Allometry

For convenience, changes in the relationship between height and weight of individual plants during the growing season are presented using the 1992 data only, as the results for 1991 were similar.

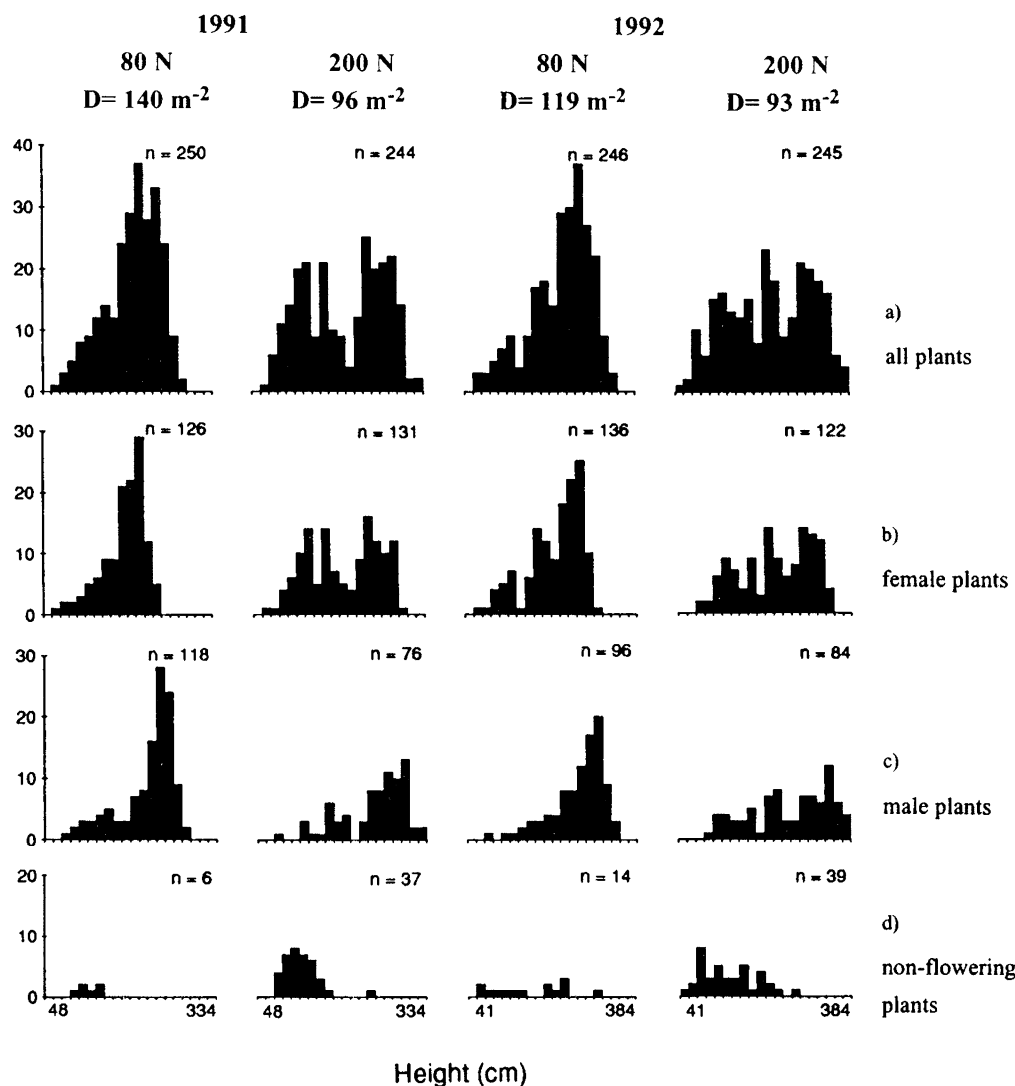
At harvest 1 plant height and plant weight were related, but the relationship was not close and the pattern was not affected by N fertilization level (Fig. 3). At harvest 2 the relationship between height and weight was closer than at harvest 1, and there were more short (< 60 cm), as well as more heavy (> 6 g), plants at 200 than at 80 kg ha<sup>-1</sup> N (Fig. 3).

At harvest 3, in spite of more severe self-thinning at 200 than at 80 kg ha<sup>-1</sup> N, the difference in the number of short (< 120 cm) plants at high versus low N had increased (Fig. 4). At 80 kg ha<sup>-1</sup> N maximum plant

**Fig. 1** Frequency distributions of dry weight of hemp plants grown at 80 and 200 kg ha<sup>-1</sup> of nitrogen at final harvest in 1991 and 1992. Density of survivors ( $D$ ) is given at the top of the figure; sample size ( $n$ ) is given for each histogram. Maximum and minimum values are beneath the histograms, at the bottom of the figure. There are 20 equal classes in each histogram



**Fig. 2** Frequency distributions of height of hemp plants grown at 80 and 200 kg ha<sup>-1</sup> of nitrogen at final harvest in 1991 and 1992. Density of survivors ( $D$ ) is given at the top of the figure; sample size ( $n$ ) is given for each histogram. Maximum and minimum values are beneath the histograms, at the bottom of the figure. There are 20 equal classes in each histogram



weight was 20 g, while at 200 kg ha<sup>-1</sup> N many plants of between 20 and 40 g were found. In the period between harvests 3 and 4 the plant density of the 200 kg ha<sup>-1</sup> N crop decreased by 21%, and this was associated with a large reduction in the number of very short (< 80 cm) plants (Fig. 4). However, at harvest 4, there were more short (< 120 cm) plants at 200 than at 80 kg ha<sup>-1</sup> N, and this trend persisted until harvest 5 (Fig. 2a). At harvest 4, as at harvests 2 and 3, more heavy (> 30 g) plants were present at 200 than at 80 kg ha<sup>-1</sup> N.

At all harvests except harvest 1, the range of plant weights was much wider than the range of plant heights, e.g. at harvest 4 in the 200 kg ha<sup>-1</sup> N crop (Fig. 4), heights spanned less than one order of magnitude (60–360 cm), whereas weights spanned about two orders of magnitude (0.6–60 g). This implies that the height/weight ratio ('slenderness': Van der Werf et al. 1995a) spanned more than one order of magnitude and that the slenderness of short and light (i.e. suppressed) plants was higher than that of tall and heavy (i.e. dom-

inating) plants. The heavy plants which were found at 200 but not at 80 kg ha<sup>-1</sup> N at harvests 2, 3 and 4, were of particularly low slenderness (Fig. 4).

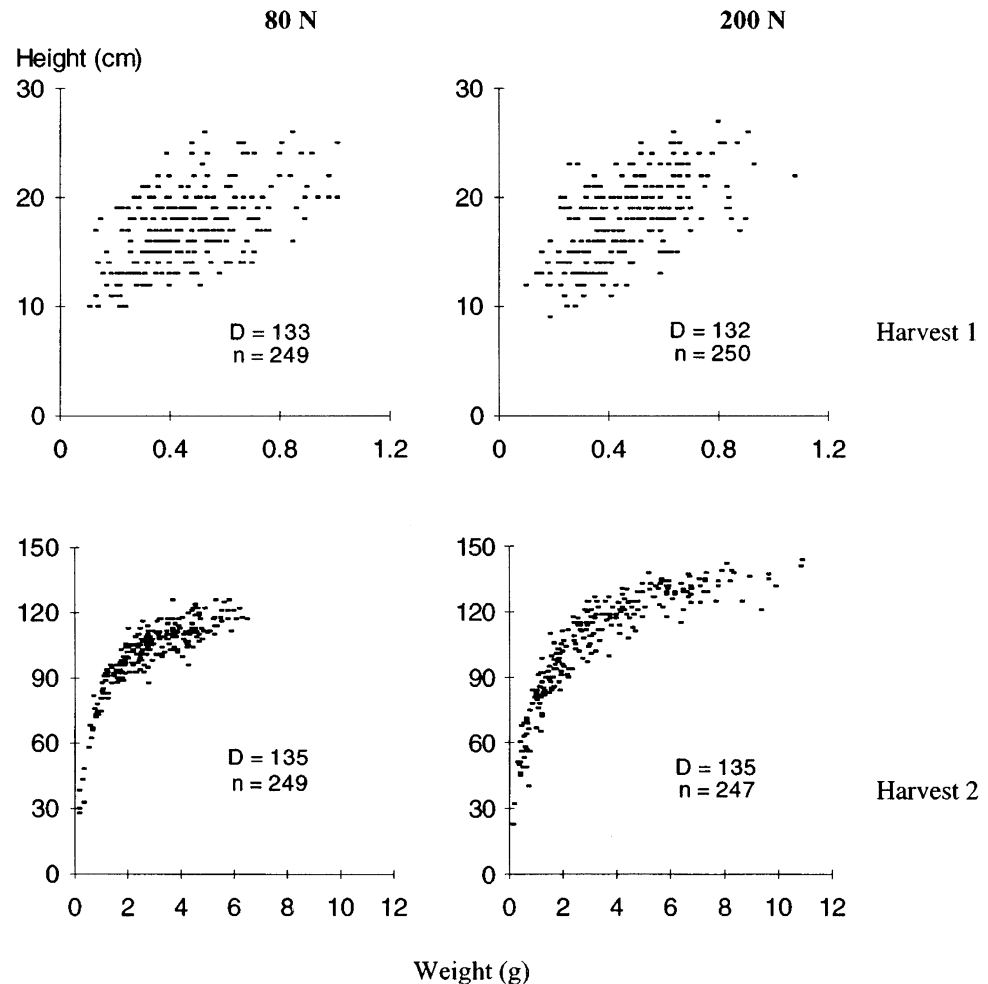
At harvest 5 results were similar to those at harvests 3 and 4, but slenderness was also affected by sex expression, since the male plants were more slender than the female (data not shown).

## Discussion

### Development of size variability

Although we investigated a fourfold range of row widths, corresponding to a 16-fold range of rectangularity, row width did not affect the distribution of weight and height in hemp plants. Apparently, the differences in the timing of onset of competition, as generated by differences in rectangularity, were insufficiently large to affect the development of size variability. The lack of response of size variability to a

**Fig. 3** The relationship between height and above-ground dry weight of hemp plants grown at 80 and 200 kg ha<sup>-1</sup> of nitrogen on 2 (Harvest 1) and 22 (Harvest 2) June 1992. Density of survivors ( $D$ , m<sup>-2</sup>) and sample size ( $n$ ) are indicated for each graph



fourfold range of row widths may also result from the height of the crop. Obviously the impact of row widths varying between 12.5 and 50 cm will be less in a hemp crop, which may exceed 3 m in height, than in most other annual crops which generally do not exceed 1 m in height. The treatments which aimed at reducing the variability of seedling size ('12.5p', precision sowing, and '25u', thinning to obtain uniformity) were not effective, as they did not affect the variability of seedling height or weight.

Nitrogen fertilization strongly affected size variability: at 80 kg ha<sup>-1</sup> N the CV of weight and the CV of height increased at a slower rate than at 200 kg ha<sup>-1</sup> N. At final harvest CVs of both size parameters were about 1.5 times higher at 200 than at 80 kg ha<sup>-1</sup> N, corroborating the hypothesis of Weiner and Thomas (1986), that competition for light is one-sided, whereas competition for below-ground resources is two-sided. At 80 kg ha<sup>-1</sup> N, nitrogen was scarcer than at 200 kg ha<sup>-1</sup> N, so below-ground competition was more important. Competition for light was probably less important at 80 than at 200 kg ha<sup>-1</sup> N, as the leaf area index and the fraction of light intercepted by the canopy were smaller at 80 than at 200 kg ha<sup>-1</sup> N (Van

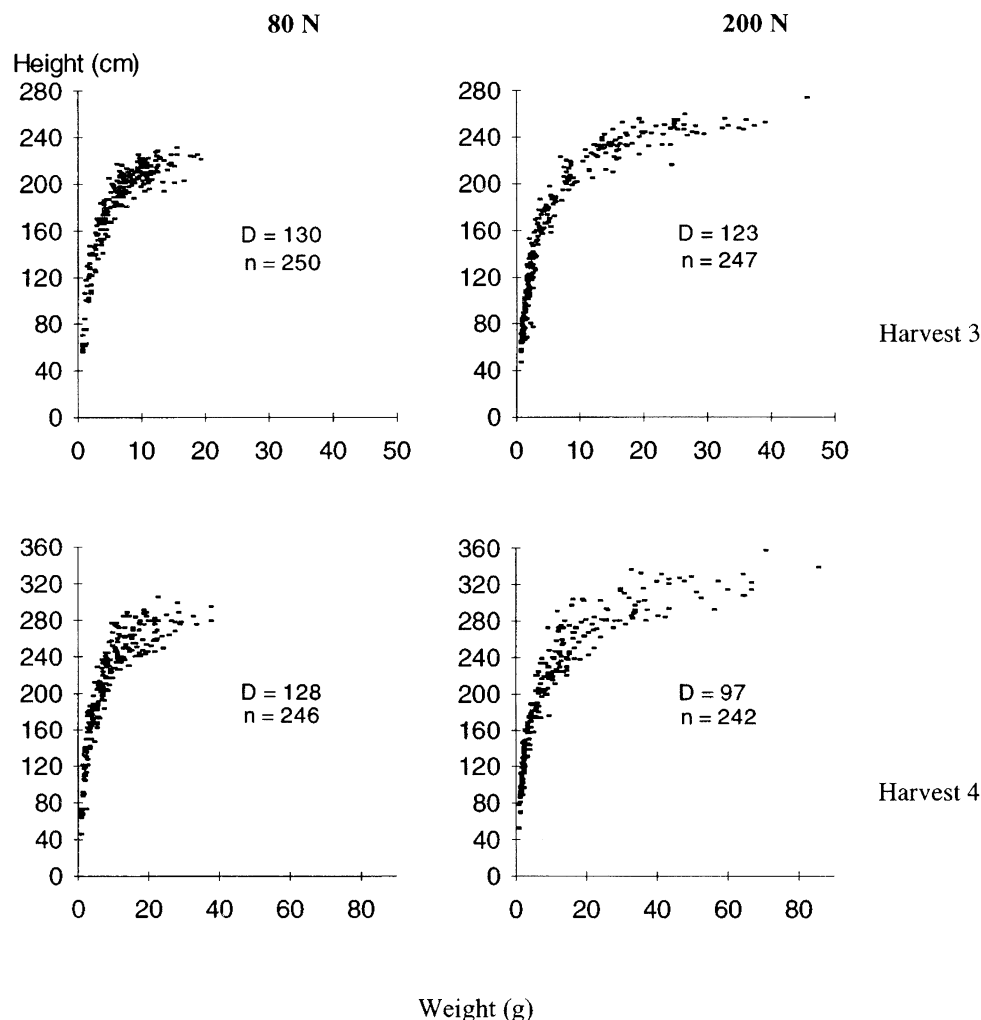
der Werf et al. 1995b). So, whereas at the high N level competition was mainly for light, at the low N level competition for nitrogen played a much larger role.

We found positive skewness of weight distributions and negative skewness of height distributions, confirming findings of Hara (1984), Geber (1989) and Knox et al. (1989) who reported that mass skewness was positive and height skewness was zero to negative.

In both years self-thinning first occurred in the period between harvests 2 and 3 and continued thereafter (Van der Werf et al. 1995b). Contrary to most earlier findings (Hara 1984; Weiner and Thomas 1986; Knox et al. 1989), we did not find a reduction of the CV of weight or of the CV of height at the onset of self-thinning. At 200 kg ha<sup>-1</sup> N, where self-thinning was most important, both CVs increased until harvest 3 (1992) or 4 (1991) and then stabilized.

Similarly, at 200 kg ha<sup>-1</sup> N, the skewness of weight did not decrease at the onset of self-thinning, but increased until harvest 3 and stabilized (1991), or increased until harvest 5 (1992). At 200 kg ha<sup>-1</sup> N, the height distributions changed from negative skewness to platykurtosis at the onset of self-thinning, and remained platykurtic until the final harvest. This

**Fig. 4** The relationship between height and above-ground dry weight of hemp plants grown at 80 and 200 kg ha<sup>-1</sup> of nitrogen on 20 July (Harvest 3) and 17 August (Harvest 4) 1992. Density of survivors ( $D$ , m<sup>-2</sup>) and sample size ( $n$ ) are indicated for each graph



contrasts with earlier findings, where self-thinning was found to remove the understorey, making the distribution unimodal and normal again (Benjamin and Hardwick 1986). On the other hand, however, Thomas and Weiner (1989) reported the survival of suppressed *Impatiens pallida* plants in spite of zero or negative growth rates for much of their lives, with size variability stabilizing rather than decreasing at the onset of self-thinning. Apparently, *Cannabis sativa* plants are similarly relatively tolerant to a low-light environment, as an understorey of short suppressed plants remained until the final harvest. There were more suppressed plants at 200 than at 80 kg ha<sup>-1</sup> N. More plants died at 200 than at 80 kg ha<sup>-1</sup> N, probably because light intensity below the canopy was lower at 200 than at 80 kg ha<sup>-1</sup> N (Van der Werf et al. 1995b).

#### Size and sex expression

In both years and at both N levels sexual dimorphism contributed to the variability of plant weight and height. The range of weights was much wider in female

than in male plants, and the shortest plants were mainly female, whereas the tallest plants were all male.

In 1991 the ratio of female to male plants was 1.07 at 80 kg ha<sup>-1</sup> N and 1.72 at 200 kg ha<sup>-1</sup> N; in 1992 it was 1.42 at 80 kg ha<sup>-1</sup> N and 1.45 at 200 kg ha<sup>-1</sup> N (Fig. 2). An increase in the proportion of female plants as a result of increased nitrogen fertilization as occurred in 1991 was found previously in hemp (Tibebu 1936) and in many other dioecious species (Freeman et al. 1980). From the literature on the effect of environmental factors on the sex expression of dioecious plants, Freeman et al. (1980) concluded that stresses (low soil nitrogen, dry soils, extreme temperatures, low light intensities) tend to reduce the ratio of female to male plants. They demonstrated that, as the cost of reproducing as a female exceeds that of reproducing as a male, a stress-induced reduction in the proportion of females has survival value, particularly in patchy or changing environments.

It is not clear why nitrogen fertilization affected the sex ratio in 1991 but not in 1992. The 1991 results, however, do shed some light on the mechanism which is involved. Freeman et al. (1980) attribute changes in



the sex ratio to alteration of the sexual state of the plants. In the 1991 experiment, the ratio of female to male plants was close to one in the plants of above-average stature, whereas in the suppressed plants, the individuals that did flower were more often female than male (Fig. 2). These results suggest that, in dense *Cannabis* stands, the shift towards femaleness associated with high soil nitrogen may result from the effect of nitrogen fertilization on size variability. Lack of nitrogen reduces growth rate, and thus delays the onset of competition and the appearance of a class of suppressed plants containing more female than male plants. This hypothesis can be further tested by investigating the effect of environmental stress on the sex expression of a *Cannabis* stand grown at low and high plant densities.

### Allometry

Dominating and suppressed plants differed not only in sex ratio, but also in shape: suppressed plants were more slender than dominating plants. Lack of light is the major cause of mortality in self-thinning stands and lodging was found to be instrumental in carrying the leaves into the low-light environment near the ground (Thomas and Weiner 1989). Obviously, the shortest plants suffer most from lack of light, and the most slender plants are most prone to buckle and lodge. In our hemp crop, the short suppressed plants were the most slender ones. Hence, in hemp, self-thinning eliminates the most slender individuals. Plant mortality from self-thinning was 5% at 80 kg ha<sup>-1</sup> N and 25% at 200 kg ha<sup>-1</sup> N (Van der Werf et al. 1995b). However, as self-thinning eliminates the lightest plants, a difference of this size in the mortality of suppressed plants may not have a major effect on the weighted mean of plant slenderness. Slenderness of the crop will be determined mainly by the heavy plants of above-average stature, and these were slightly taller, much heavier and, consequently, less slender at 200 than at 80 kg ha<sup>-1</sup> N. We found that the crop grown at 200 kg ha<sup>-1</sup> N was less slender than the crop grown at 80 kg ha<sup>-1</sup> N (Van der Werf et al. 1995b). This may have resulted in part from a larger number of slender plants dying from self-thinning at 200 than at 80 kg ha<sup>-1</sup> N, but the presence of many more heavy individuals of low slenderness at 200 than at 80 kg ha<sup>-1</sup> N was probably a more important cause.

### Conclusions

To the best of our knowledge, no other studies quantifying the effect of soil nitrogen level on size variability in a field-grown crop, or reports on the effect of sex expression on size variability in a dioecious crop, have been published.

In our experiments variability of both weight and height of hemp plants was higher at 200 than at 80 kg ha<sup>-1</sup> N. Contrary to most results obtained in other species, self-thinning was not associated with a reduction in size variability. Suppressed hemp plants can survive relatively well in the low-light environment near the ground.

Sexual dimorphism contributed to variability of height and weight. In 1 of the 2 years, the ratio of female to male plants was higher at 200 than at 80 kg ha<sup>-1</sup> N. In dense stands of *Cannabis*, the shift towards maleness induced by environmental stress may result from the delay in the appearance of a population of suppressed plants with a high ratio of female to male plants.

As suppressed plants were much more slender than dominating plants, self-thinning eliminated the most slender individuals in a hemp crop. The presence of many more heavy individuals of low slenderness at 200 than at 80 kg ha<sup>-1</sup> N was probably the major cause of the difference in slenderness of the crop between 200 and 80 kg ha<sup>-1</sup> N.

Our findings may help the fibre hemp industry to improve stem quality, as we show that a reduced N-fertilization leads to finer and less variable hemp stems.

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### References

- Benjamin LR, Hardwick RC (1986) Sources of variation and measures of variability in even-aged stands of plants. *Ann Bot* 58: 757–778
- Bonan GB (1991) Density effects on the size structure of annual plant populations: an indication of neighbourhood competition. *Ann Bot* 68: 341–347
- De Maeyer EAA, Huisman W (1995) Techniques for harvesting and storage of fibre hemp (in Dutch, with English summary). IMAG-DLO and WAU, Report 94–27, Wageningen
- Freeman DC, Harper KT, Charnow EL (1980) Sex change in plants: old and new observations and new hypotheses. *Oecologia* 47: 222–232
- Geber MA (1989) Interplay of morphology and development on size inequality: a *Polygonum* greenhouse study. *Ecol Monogr* 59: 276–288
- Hara T (1984) A stochastic model and the moment dynamics of the growth and size distribution in plant populations. *J Theor Biol* 109: 173–190
- Harper JL (1977) Population biology of plants. Academic Press, New York
- Hoffmann W (1957) Hanf, *Cannabis sativa*. Handbuch der Pflanzenzüchtung, part 5. Paul Parey, Berlin Hamburg, pp 204–263
- Huston MA, DeAngelis DL (1987) Size bimodality in monospecific populations: a critical review of potential mechanisms. *Am Nat* 129: 678–707

- Knox RG, Peet RK, Christensen NL (1989) Population dynamics in loblolly pine stands: changes in skewness and size inequality. *Ecology* 70: 1153–1166
- Lieffers VJ, Titus SJ (1989) The effects of stem density and nutrient status on size inequality and resource allocation in lodgepole pine and white spruce seedlings. *Can J Bot* 67: 2900–2903
- Sokal RR, Rohlf JE (1981) *Biometry*. Freeman, San Francisco
- Thomas SC, Weiner J (1989) Growth, death and size distribution change in an *Impatiens pallida* population. *J Ecol* 77: 524–536
- Tibbeau ME (1936) Time factors in utilization of mineral nutrients by hemp. *Plant Physiol* 11: 731–747
- Van der Werf HMG, Haasken HJ, Wijnhuizen M (1994) The effect of daylength on yield and quality of fibre hemp (*Cannabis sativa* L.). *Eur J Agron* 3: 117–123
- Van der Werf HMG, Wijnhuizen M, de Schutter J (1995a) Plant density and self-thinning affect yield and quality of fibre hemp (*Cannabis sativa* L.). *Field Crops Res* 40: 153–164
- Van der Werf HMG, van Geel WCA, van Gils LJC, Haverkort AJ (1995b) Nitrogen fertilization and row width affect self-thinning and productivity of fibre hemp (*Cannabis sativa* L.). *Field Crops Res* 42(1)
- Weiner J (1985) Size hierarchies in experimental populations of annual plants. *Ecology* 66: 743–752
- Weiner J, Thomas SC (1986) Size variability and competition in plant monocultures. *Oikos* 47: 211–222