Yield and quality of sunflower as affected by row orientation, row spacing and plant density

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Ertrag und Qualität der Sonnenblume in Abhängigkeit von Reihenorientierung, Reihenabstand und Bestandesdichte

1. Introduction

Three primary variables in planting patterns may affect the growth, achene yield, and oil yield of sunflower (*Helianthus annuus* L.): row orientation, row spacing, and plant density. However, studies to test these variables singly or bi-combinedly have given inconsistent results. To the best of our knowledge, there is no study which considered all the three factors in the same experiment.

The effect of row orientation on yield is a debated point in sunflower crops, but sound information on this topic is still meager. ROBINSON (1975) reported that row orientation had no or only a slight effect on achene yield. Row spacing may affect the utilization of light (FLÉNET et al., 1996), water, and nutrients (GUBBELS and DEDIO, 1988) and, thus, the growth and achene yield of sunflower. METZ et al. (1984) suggested that the optimum achene yield might be obtained when intra- and inter-row spacings are about the same at any given plant density. A row spacing of about 50 cm is considered to be optimal under central European conditions (HUGGER, 1989). Studies on the effect of plant density on achene yield gave inconsistent results, suggesting that the optimum plant density for achene yield depends on the cultivar and environment (BLAMEY et al., 1997; PRUNTY, 1981). For instance,

Zusammenfassung

In den Jahren 1996, 1997 und 1998 wurden in Mitteldeutschland (51°24' N) Feldexperimente durchgeführt, in denen die Effekte von Reihenorientierung, Reihenabstand und Bestandesdichte auf den Ertrag und Qualitätsmerkmale der Sonnenblume (*Helianthus annuus* L.) untersucht wurden. Es gab zwei Reihenorientierungen (Ost-West, Nord-Süd), drei Reihenabstände (50, 75 und 100 cm) und drei Bestandesdichten (4, 8 und 12 Pflanzen m^{-2}). Bei Ost-West-Orientierung erzeugten die Sonnenblumen einen um durchschnittlich 12 % höheren Ölertrag als bei Nord-Süd-Orientierung. Die höheren Erträge bei Ost-West-Orientierung basierten auf einer höheren Achänenzahl m^{-2}; sowohl Biomasse als auch Ernteindex waren bei Ost-West-Orientierung höher als bei Nord-Süd-Orientierung. Die höchsten Erträge wurden in der Regel bei Ost-West-Reihenorientierung, 4 bis 8 Pflanzen m^{-2} und 75 bis 100 cm Reihenabstand erzielt.

Schlagworte: Sonnenblume, Reihenorientierung, Reihenabstand, Pflanzendichte, Ölkonzentration.

Summary

The responses of yield and quality traits of sunflower (*Helianthus annuus* L.) to row orientation, row spacing, and plant density were studied in a three year field experiment (1996, 1997, 1998) conducted at a high-latitude site (51°24' N) in central Germany. There were two row orientations (east-west; north-south), three row spacings (50, 75, and 100 cm), and three plant densities (four, eight, and 12 plants m^{-2}). Sunflower plants in east-west rows yielded on average 12% more oil than plants in north-south rows. The higher yield of plants in the east-west rows was mainly the result of a greater number of achenes m^{-2}; both aboveground biomass and the harvest index tended to be higher in the east-west rows than in the north-south rows. The maximum yield was produced in the east-west rows at four to eight plants m^{-2} and 75 to 100 cm row spacing.

Key words: sunflower (*Helianthus annus* L.), row orientation, row spacing, plant density, oil concentration.

WADE and FOREMAN (1988) found that the achene yield increased to a maximum with increasing plant density and remained constant at even higher plant densities under favourable environmental conditions. Under less favourable conditions, however, the achene yield started to decline at very high plant density. In central Europe, farmers use plant densities from 6 to 8.5 plants m^{-2} (SPERBER et al., 1988; HUGGER, 1989; HAMMANN et al., 1995; STOCK and DIEPENBROCK, 1999).

Lodging of plants can influence the achene yield. Some researchers investigated the relationships between lodging and the various planting patterns (e.g., ZUBRISKI and ZIMMERMAN, 1974; HOLT and ZENTNER, 1985). The probability of lodging increases with increasing row spacing (ZUBRISKI and ZIMMERMAN, 1974; HOLT and ZENTNER, 1985; HUGGER, 1989). ZUBRISKI and ZIMMERMAN (1974) concluded that excessive lodging was responsible for the lack of a positive correlation between plant density and achene yield. Thus, the effects of planting patterns on achene yield may simply reflect the variation in the extent of lodging.

The objective of the research reported here was to determine the yield and quality (concentrations of oil and nitrogen in the achenes) responses of sunflower to row orientation, row spacing, plant density, and their interactions at a high-latitude site.

2. Materials and Methods

2.1 Experimental field

Field experiments were conducted at Bad Lauchstädt (51°24' N, 11°53' E, 113 m asl) in central Germany on a loamy Haplic Chernozem in 1996, 1997, and 1998. This site is a border area for sunflower production. The short-season sunflower *(Helianthus annuus* L.) cultivar Eurosol was sown on 22 April 1996, 8 April 1997, and 14 April 1998. Nitrogen (N) fertilizer was applied at recommended rates (100 kg N ha^{-1} minus mineral N from 0 to 90 cm soil depth determined prior to planting) before sowing. Weeds were controlled by herbicides; no other pesticides were used. Harvest took place on 13 Sept. 1996, 9 Sept. 1997, and 31 Aug. 1998.

2.2 Parameters measured

Plant lodging was recorded shortly after flowering using lodging scores based on the average erectness of the stems: 1 = all plants erect; 3 = slight lodging at 30°; 5 = plants lodged at 45°; 7 = severe lodging at 60°; and 9 = all plants lodged flat. To determine achene yield and shoot dry matter, plant samples were taken at physiological maturity from an area of 9 m^2 in the center of each plot. Samples were dried at 60 °C to constant weight. The harvest index is the ratio of achene yield to aboveground biomass. A subsample of achenes was used to determine the 1000-achene weight (g). The number of achenes m^{-2} was calculated by dividing the achene yield by the 1000-achene weight and the ground area. The concentration of oil in the achenes was determined by means of a nuclear magnetic resonance analyzer (Oxford 4000, Oxford Instruments, Abingdon, UK) and a sunflower oil standard. The N concentration in the achenes was assessed by a modified Kjedahl procedure (HOFFMANN, 1991).

2.3 Experimental design and data analyis

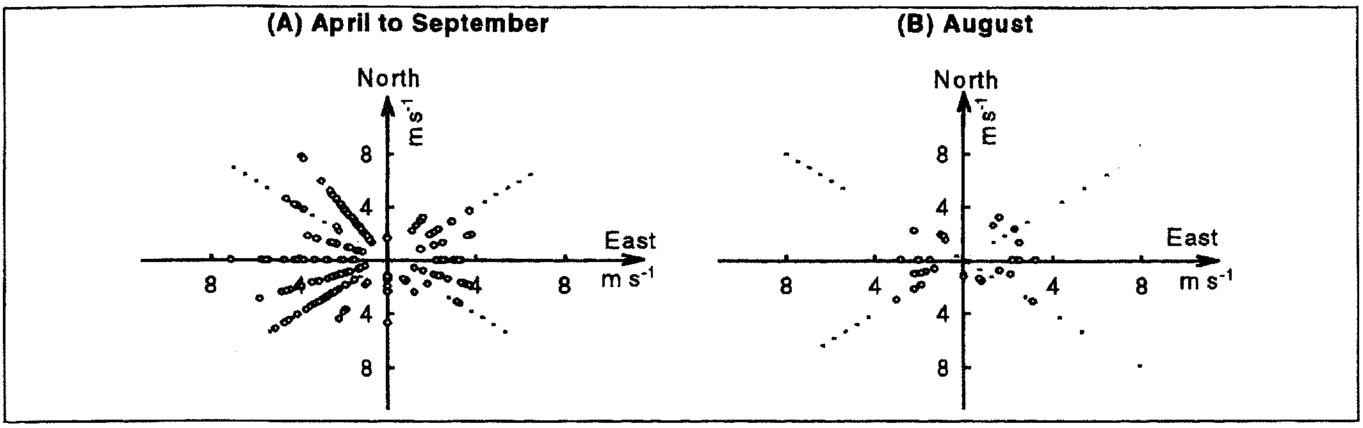
Plots (9 by 6 m) were arranged in a split-plot design with four replications. Row spacing (50, 75, and 100 cm) was the main plot and plant density (four, eight, and 12 plants m^{-2}) the subplot. This experimental unit was established for two row orientations, east-west and north-south. The analyses of variances were performed with the GLM procedure of SAS (SAS INSTITUTE, 1991). Comparisons of the means of the treatments were made using the least significant difference (LSD) test at the $P = 0.05$ level. LSD values are not shown when the differences between the measurements are not significant at $P = 0.05$ according to the F-test. Lodging scores were transformed into their logarithm; analyses of variance for original and transformed lodging scores showed the same significances.

3. Results

3.1 Weather conditions

The experimental years are characterized as follows: 1996 was relatively dry and cool; 1998 was comparatively wet and warm. Precipitation in July was much higher than the long-term average in all three years, indicating that the water supply was relatively high during the phase of rapid growth. In all years, solar radiation was relatively high throughout the growing season, especially in 1997 (LONG, 1999). The velocity and direction of the wind in 1997 are

Figure 1: Velocity and direction of wind from April to September (A) and in August (B) 1997. One dot = one day
Abbildung 1: Windgeschwindigkeit und -richtung von April bis September (A) und im August (B) 1997. Ein Punkt = 1 Tag



depicted in Figure 1. Data for the month of August are shown separately, because sunflower is especially susceptible to lodging during this month. The wind blew mainly from easterly and westerly directions.

3.2 Lodging

Figure 2 shows the scores of plant lodging for 1997 and 1998; there was no lodging in 1996. Lodging was more pronounced in the north-south rows than in the east-west rows, but the row orientation effect was significant in 1997 only. In both years, the lodging score increased significantly with increasing row spacing and plant density. Despite a significant row spacing – plant density effect in 1998, the ranking order of the plant densities was not affected by row spacing.

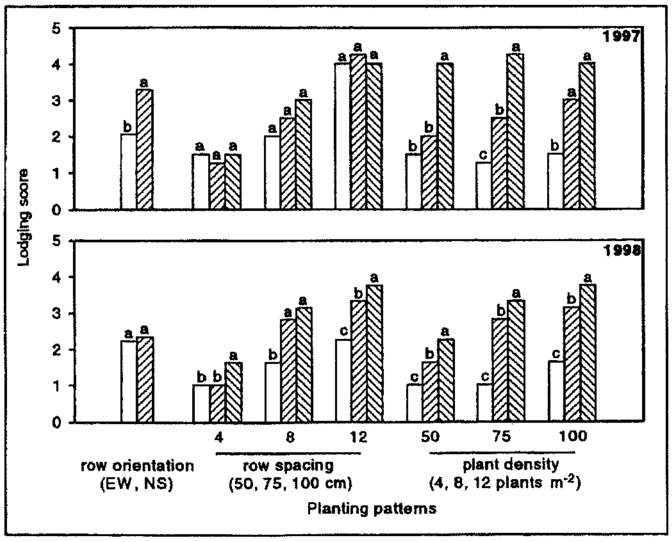


Figure 2: Plant lodging score as affected by row orientation, row spacing, and plant density. With a group of bars, letters above the bars indicate significant (P = 0.05) differences between the treatments
Abbildung 2: Lagerbonitur in Abhängigkeit von Reihenorientierung, Reihenabstand und Pflanzdichte. Die Buchstaben über den Balken zeigen signifikante (P = 0.05) Unterschiede zwischen den Behandlungen innerhalb einer Balkengruppe an

3.3 Achene yield, yield components, aboveground biomass, and harvest index

Averaged across the plant densities and the row spacings, the east-west row orientation produced higher achene yields than the north-south row orientation in all years. The effects, however, were significant in 1996 and 1998 only (Table 1). In 1998, the row orientation – plant density interaction was significant at P = 0.05. The row orientation effect was more pronounced at the high plant densities (12 and eight plants m^{-2}) than at four plants m^{-2} (data not shown). No such trend was observed in the remaining years. In 1996, the 1000-achene weight was higher in the east-west rows than in the north-south rows, while it was identical for both row orientations in 1997 and 1998. A greater number of achenes m^{-2} was produced in the east-west rows than in the north-south rows in all three years (Table 1). Although there were significant row orientation – row spacing, row orientation – plant density, and row spacing – plant density interactions, the row orientation effect on the number of achenes was not substantially altered by row spacing and plant density (data not shown). In 1996 and 1998, the achene yield increased with increasing row spacing. In 1997, when the row spacing effect was not significant, the row spacing of 50 cm still produced the lowest yield, but the 75 cm row spacing performed best (Table 1).

In 1997 and 1998, the highest achene yield was obtained with four plants m^{-2}. In 1998, the plant density effect was more pronounced in the north-south rows than in the east-west rows, resulting in a significant row orientation – plant density interaction. There was a significant row spacing – plant density interaction in 1996. The achene yield increased statistically significant with increasing plant density at 100 cm row spacing only; similar trends were found for the other row spacings, but the plant density effects were not significant (data not shown). The 1000-achene weight increased with increasing row spacing and decreased with increasing plant density (Table 1). The response of achene number m^{-2} to row spacing was inconsistent over the years, while the achene number always increased significantly with increasing plant density.

The east-west rows produced more biomass than the north-south rows in all years (Table 1). In 1996 and 1998, the aboveground biomass increased significantly with increasing row spacing. In 1997, however, the differences between the row spacings were small. The aboveground biomass increased with increasing plant density in 1996 and 1998, but the lowest biomass production was found at four plants m^{-2} in 1997. The interaction effects were inconsistent over the years. Only in 1996 there were significant row spacing – plant density and row orientation – row spacing – plant density interactions. We analyzed the three-way interaction and found that the row orientation had a significant effect on the aboveground biomass in the four plants m^{-2} / 100 cm row spacing treatment only and that differences in biomass production among the row spacings were significant at four plants m^{-2} in the east-west rows only (data not shown). The harvest index was consistently higher for the east-west row orientation than for the north-south row orientation (Table 1). The row spacing had a slight effect on harvest index, while the harvest index tended to decline with increasing plant density (Table 1). The means of all possible combinations of row orientation, row spacing, and plant density were used to calculate correlations (r; n = 18) among achene yield, biomass, and harvest index. In all years, achene yield was positively related to both biomass and harvest index (achene yield vs. biomass: r = 0.69^{**}, 0.64^{**}, and 0.37^{ns}; achene yield vs. harvest index: r = 0.24^{ns}, 0.39^{ns}, and 0.78^{***} for 1996, 1997, and 1998, respectively). Biomass and harvest index were always negatively correlated (r = -0.54^{*}, -0.46^{ns}, and -0.28^{ns} for 1996, 1997, and 1998, respectively).

Table 1: Achene yield, aboveground biomass, harvest index, achene number, and 1000-achene weight as affected by planting geometry
Tabelle 1: Achänenertrag, oberirdische Biomasse, Ernteindex, Achänenzahl und 1000-Achänengewicht in Abhängigkeit von der Pflanzgeometrie

Traits	Achene yield ($Mg\ ha^{-1}$)			Aboveground biomass ($Mg\ ha^{-1}$)			Harvest index			Achene number m^{-2} ($\times 10^3$)			1000-achene weight (g)		
Year	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1998
Row orientation (RO)															
East-west	3.31	3.59	3.67	12.27	10.68	12.50	0.27	0.34	0.29	7.58	7.47	8.68	44.5	49.2	43.3
North-south	2.93	3.50	3.20	11.72	10.65	11.84	0.25	0.33	0.27	7.15	7.31	7.52	41.9	49.4	43.4
$LSD_{0.05}$	0.19	-	0.49	1.17	-	-	0.01	-	0.03	-	-	1.27	1.7	-	-
Row spacing (RS)															
50 cm	2.92	3.43	3.23	11.25	10.47	11.58	0.26	0.33	0.28	7.37	7.56	8.09	40.5	47.3	40.6
75 cm	3.12	3.62	3.47	11.78	10.86	12.20	0.27	0.34	0.28	7.23	7.49	8.21	44.0	49.2	43.2
100 cm	3.32	3.59	3.61	12.94	10.66	12.72	0.26	0.34	0.28	7.50	7.12	8.00	45.0	51.3	46.0
$LSD_{0.05}$	0.32	-	0.24	1.30	-	0.57	0.01	-	-	-	0.69	-	0.9	1.3	1.2
Plant density (PD)															
4 plants m^{-2}	3.07	3.75	3.68	10.81	11.34	11.59	0.28	0.33	0.32	5.96	6.23	6.89	51.5	60.3	53.5
8 plants m^{-2}	3.16	3.43	3.34	12.14	9.85	12.15	0.26	0.35	0.27	7.64	7.45	8.31	41.3	46.2	40.2
12 plants m^{-2}	3.13	3.46	3.29	13.03	10.80	12.77	0.24	0.32	0.25	8.50	8.50	9.10	36.8	41.4	36.1
$LSD_{0.05}$	-	0.21	0.25	1.04	0.65	0.67	0.01	0.03	0.02	0.30	0.55	0.63	0.9	1.0	0.8
F-test															
RO	**	ns	*	*	ns	+	**	ns	*	+	ns	*	**	ns	ns
RS	**	+	*	***	ns	**	*	ns	ns	ns	***	ns	***	***	***
PD	ns	**	**	***	**	***	***	**	**	***	***	***	***	***	***
RO × RS	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	+	ns	ns
RO × PD	ns	ns	*	ns	ns	+	*	ns	*	ns	ns	*	ns	ns	ns
RS × PD	*	+	ns	*	ns	ns	ns	*	ns	ns	*	ns	ns	ns	ns
RO × RS × PD	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

+, *, **, *** significant at P = 0.10, 0.05, 0.01, and 0.001, respectively; ns not significant.

3.4 Oil yield and concentrations of oil and N

The east-west rows consistently produced higher oil yields than the north-south rows; the average yield advantage was about 12 % (Table 2). The lowest oil yield was observed in the 50 cm row spacing in all three years, whereas the plant density effect was different each year. The effects of the interactions on oil yield were similar to those on the yield of achenes (data not shown). Due to the latter and the fact that the effects were inconsistent over the years, they are not explained in detail. In 1996, the concentration of achene oil was significantly higher in the north-south rows than in the east-west rows. In 1997 and 1998, however, the reverse was true (Table 2). In all years, the lowest achene oil concentration was found at 100 cm row spacing and at a density of four plants m^{-2}. In 1996, plants in the east-west rows had a higher achene N concentration than those in the north-south rows. In 1997 and 1998, however, the opposite was found (Table 2). Plants in rows spaced 100 cm apart exhibited the highest achene N concentration in all three years; the differences between the 50 and 75 cm row spacings were small. The highest achene N concentration was always found at four plants m^{-2} (Table 2).

We pooled the means of the 18 treatments to calculate various correlations (r). It was found that the concentration of achene oil and the 1000-achene weight were always inversely correlated (r = -0.68**, -0.85***, and -0.40^{ns} for 1996, 1997, and 1998, respectively). Concentrations of oil and N also showed negative relationships (r = -0.43^{ns}, -0.70**, and -0.85*** for 1996, 1997, and 1998, respectively). The 1000-achene weight and the concentration of N were correlated at 0.41^{ns}, 0.52*, and 0.54* in 1996, 1997, and 1998, respectively. The correlation between achene yield and oil concentration was significant in 1997 only (r = -0.57*), that between achene yield and N concentration in 1996 only (r = 0.69**).

4. Discussion

4.1 The role of lodging

It may be hypothesized that the effects of the planting patterns on achene yield and other traits simply reflect varia-

Table 2: Oil yield and concentrations of oil and nitrogen (N) in the achenes as affected by row orientation, row spacing, and plant density
Tabelle 2: Ölertrag und Öl- und Stickstoffkonzentration in den Achänen in Abhängigkeit von Reihenorientierung, Reihenabstand und Pflanzdichte

Traits	Oil yield ($Mg\ ha^{-1}$)			Oil concentration ($g\ kg^{-1}$)			N concentration ($g\ kg^{-1}$)		
Year	1996	1997	1998	1996	1997	1998	1996	1997	1998
Row orientation (RO)									
East-west	1.47	1.65	1.59	443	460	465	22.7	21.6	24.8
North-south	1.31	1.59	1.31	448	455	443	19.3	23.8	26.5
$LSD_{0.05}$	0.08	-	0.27	5	-	22	1.0	0.6	1.4
Row spacing (RS)									
50 cm	1.29	1.59	1.42	443	464	454	20.6	22.5	25.2
75 cm	1.41	1.65	1.51	453	456	459	20.9	22.3	25.1
100 cm	1.46	1.62	1.43	440	452	450	21.4	23.3	26.5
$LSD_{0.05}$	0.07	-	-	3	5	-	-	0.7	0.7
Plant density (PD)									
4 plants m^{-2}	1.33	1.66	1.65	435	443	446	21.6	23.8	26.5
8 plants m^{-2}	1.42	1.60	1.45	450	467	458	20.4	21.9	25.3
12 plants m^{-2}	1.41	1.60	1.26	451	462	459	20.9	22.3	25.2
$LSD_{0.05}$	0.07	-	-	3	4	6	0.7	0.9	0.5
F-test									
RO	**	ns	*	**	ns	*	**	***	*
RS	**	ns	+	***	***	+	ns	*	**
PD	*	ns	+	***	***	***	*	***	***
RO × RS	ns	ns	ns	ns	ns	ns	ns	ns	ns
RO × PD	ns	ns	*	*	ns	ns	ns	ns	ns
RS × PD	+	*	ns	ns	ns	ns	ns	ns	ns
RO × RS × PD	ns	ns	ns	ns	ns	ns	ns	ns	ns

+, *, **, *** significant at P = 0.10, 0.05, 0.01, and 0.001, respectively; ns not significant.

tion in the extent of lodging. We will demonstrate that this is not true. There was no lodging in 1996 (Fig. 2). Nevertheless, the effects of row orientation and row spacing on achene yield were statistically significant (Table 1). This finding is in contrast to the above-mentioned hypothesis. However, in some cases, the absence or presence of achene yield responses to planting patterns may be due to differences in lodging. In 1996 and 1998, there was no row orientation effect on the lodging score. This may explain why the row orientation effects on achene yield were similar in these years. In 1997, however, there was significantly more lodging in the north-south rows than in the east-west rows. Consequently, the positive effect of the east-west rows on achene yield should have been even more pronounced in 1997 than in the other years. The opposite was true, however; surprisingly, the yield advantage of the east-west rows over the north-south rows was lowest just in 1997. It is even possible that, had there been no lodging, the plants in the north-south rows would have outyielded those in the east-west rows. These differences in lodging between the row orientations may be due to the following two reasons. First, plants grown at different row orientation may differ in morphological traits, such as plant height and leaf area, that determine susceptibility to lodging (MILLER et al., 1984). In our experiments, plants in the north-south rows were somewhat taller and had a greater leaf area than those in the east-west rows in all years (data not shown). It is suggested that both characteristics favored the occurrence of lodging. Second, the probability of lodging may increase when the plants are sown across the wind. Unfortunately, we have no information on the direction and the frequency of winds whose speed was sufficiently high to cause lodging. On the other hand, Figure 1 clearly shows that westerly and easterly winds prevailed in August, which may help to explain why lodging was more severe in the north-south rows than in the east-west rows in 1997. Earlier measurements, made from 1993 to 1996, indicate that the wind characteristics presented in Figure 1 are typical of our experimental site (LONG, 1999).

4.2 Row orientation

In contrast to previous report (ROBINSON, 1975), the yields of achenes and oil did respond to row orientation (Tables 1 and 2). Among other things, variations in the extent of lodging and in the radiation environment may explain these contradictory results (BANGE et al., 1997). Since the lodging effects were discussed above, this section will focus on the radiation environment. The radiation environment in stands is co-determined by latitude and the local weather conditions. Latitude affects the average and maximum light intensity as well as the angle of incoming radiation. At high latitudes, such as in our experiment (51°24' N), the total amount of solar radiation per day during the sunflower growing season is relatively large, but the quality of radiation is different from that at lower latitudes. The radiation environment of high latitudes is characterized by a long phase of light and a comparatively even distribution of radiation throughout the day. Due to the low elevation of the sun over the horizon, the portion of diffuse radiation is likely to be higher at high latitudes than at low latitudes. The fundamental effects of latitude are modified by clouds and the transparency of the atmosphere, which may be different for regions where sunflower is grown.

It is suggested that a positive achene yield response to a certain row orientation results from a better supply of light to the plants. In the present study, the intensity of solar radiation differed markedly among years. The highest radiation was recorded in 1997; radiation was markedly lower in the other two years (LONG, 1999). If the above hypothesis is true, then the effect of row orientation on achene yield should vary from year to year. In fact the row orientation effect on the yields of achenes and oil was clearly weaker in 1997 than in the other years (Tables 1 and 2). Solar radiation was above the long-term average in all years (LONG, 1999), suggesting that the row orientation effects are even more pronounced in years with average radiation. Precipitation during the period of rapid growth (July) was also markedly higher than the long-term average (LONG, 1999), indicating that water is probably more limiting for the productivity of a sunflower crop under average rainfall. Therefore, the optimum distribution of radiation within the stands and, thus, the choice of row orientation may be less relevant in years with average precipitation.

The yield advantage of the east-west rows over the north-south rows was based mainly on the greater number of achenes m^{-2}. The number of achenes is fixed in the period from 20 days before and 30 days after flowering (DIEPENBROCK and PASDA, 1995). Consequently, differences in light supply during this "critical period" may have caused the differences in achene number (CANTAGALLO et al., 1997). Measurements made in our experiments indicated that, during the supposed "critical period" for achene number, the amount of transmitted light is more or less independent of the row orientation (LONG, 1999). It may thus be concluded that the distribution of light within the canopy was more favorable in the east-west rows than in the north-south rows. The prevailing winds may influence the evapotranspiration and the temperature of the air and the soil; their effects depend on the row orienation (ANDA and STEPHENS, 1996). Consequently, apart from differences in lodging and solar radiation, variation in the availability of water may have contributed to the contrasting results of investigations on the row orientation effects on yield. In the present study, the upper soil layer (0 to 60 cm depth) tended to be drier in the east-west rows than in the north-south rows during the later stages of development in all years (LONG, 1999). It is possible that, as a result of effects on the microclimate in the stands, the prevailing westerly and easterly winds at our experimental site (Fig. 1) caused evapotranspiration to be higher in the east-west rows than in the north-south rows. However, the lower soil water content may also be attributed to the greater production of biomass in the east-west rows (Table 1).

4.3 Row spacing and plant density

Studies on the effect of increasing row spacing on achene yield gave inconsistent results (GUBBELS and DEDIO, 1988; METZ et al., 1984; ZAFFARONI and SCHNEITER, 1989). Wide rows may prevent the full exploitation of water in the inter-row subsoil where each sunflower plant is represented by only a single taproot (RADFORD, 1978). In the present study, achene yield was consistently higher at 75 cm rather than at 50 cm row spacing, while an even wider row spacing (100 cm) did not always result in a higher achene yield. This outcome is not in line with HUGGER's (1989) statement that a row spacing of about 50 cm is optimal. The reason for this discrepancy is unclear; the optimal row spacing may depend on the cultivar used.

Due to increasing interplant competition for light and other growth factors, the yields of achenes and oil of individual plants is expected to decrease with increasing plant densities. Studies on the effect of plant density on achene yield provided inconsistent results (BLAMEY et al., 1997; PRUNTY, 1981). This suggests that the optimum plant density depends on environmental conditions and on the cultivars used. In the present study, achene yield tended to be higher at four (1997 and 1998) or eight (1996) plants m^{-2} than at 12 plants m^{-2}. This agrees with recommendations in central Europe (SPERBER et al., 1988; HUGGER, 1989; HAMMANN et al., 1995; STOCK and DIEPENBROCK, 1999) and in the United States (PRUNTY, 1981; WADE and FOREMAN, 1988; BLAMEY et al., 1997). The responses of achene number m^{-2} and 1000-achene weight to increasing plant density are in line with results of previous studies (PRUNTY, 1981; WADE and FOREMAN, 1988).

4.4 Achene oil and N concentrations

To our knowledge, there is no published information on the effect of row orientation on achene oil concentration. ALESSI et al. (1977) reported that light intensity may affect the concentration of achene oil. Since it is possible that the light supply to the plants was affected by row orientation, variations in the light supply may explain the row orientation effect on achene oil concentration (Table 2). VILLALOBOS et al. (1994) reported that the amount of oil per achene is hardly affected by plant size; as a result, a low 1000-achene weight was always associated with a high oil concentration and vice versa. In line with this, we found negative correlations between the 1000-achene weight and oil concentration. Consequently, the effects of planting pattern on the 1000-achene weight in our experiments may account for some of their effects on oil concentration. The oil concentration in the achenes was higher in the east-west rows than in the north-south rows in 1997 and 1998, but lower in 1996 (Table 2). The different response to row orientation in 1996 may have been brought about by a "dilution effect" associated with the higher 1000-achene weight in the east-west rows (Table 1). In contrast to GUBBELS and DEDIO (1990), we found that the achene oil concentration was affected by row spacing. In our experiments, the achene weight increased and the oil concentration decreased with increasing row spacing. Thus, the response of oil concentration to row spacing may also be due to a "dilution effect". Our finding that the concentrations of oil and N are inversely related is in line with previous reports (SINGH et al., 1988).

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