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Leaf azimuth in maize canopies

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Abstract

The canopy structure of maize can be an important determinant of light and water interception. Leaf orientation is determined by two parameters, angle and azimuth. The first variable has been extensively investigated, whereas data concerning leaf azimuth are virtually non-existent. Studies were therefore undertaken to answer the following questions : (i) are the plants randomly oriented in azimuth within a maize crop ; and, (ii) are the leaves in the same vertical plane on a maize plant ? Two hybrids were used for the experiment : P3902 and DEA, a European hybrid with more upright leaves than P3902.

The five first leaves developed in the same vertical plane, but not all the later leaves formed were in this plane. From the 6th leaf to the ear leaf the leaves tended to be oriented more and more perpendicularly to the row. This was more obvious for the upper leaves : the 9th leaf under these experimental conditions (70.000 plants ha⁻¹) was already non randomly oriented. This suggests that the competition for light, which occurs at this time, influenced leaf azimuth. The continuous shift of leaf azimuth during plant growth was particularly evident when plants whose 6th and 7th leaves were aligned in the same orientation as the row, were investigated : only 13 per cent of their 14th and 15th leaves were still oriented row-wise. There was a developmental adaptation to light competition which consisted of a shift of the azimuth of upper leaves towards a direction perpendicular to the row. This may partly explain the insensitivity of maize yield to narrow row spacing and to the orientation in the row at sowing.

Key-words : competition, Leaf development, leaf orientation, row spacing, seed placement.

INTRODUCTION

Duncan (1958) showed that ear weight per plant in maize declined linearly with an increase in plant density while yield per hectare increased. The main factor causing this decrease in grain yield per plant is believed to be competition for light resulting from mutual shading of individual plants. To improve light interception, and to develop higher yielding crop varieties, research focused on altering plant morphology, particularly by breeding for plants with upright leaves (Moss and Musgrave, 1971). This has involved analyzing aspects of the geometry of the foliage in maize canopies and its relationship to light interception and photosynthesis (Pearce *et al.*, 1967 ; Pendelton, 1968 ; Duncan, 1971 ; Russell, 1972).

Some twenty years later, relatively few of the recently commercialized maize hybrids have upright leaves, although they can tolerate higher plant densities, mainly because of their better resistance to lodging. Perhaps this means that leaf-angle changes did not alter the competition for light, and/or that light was not the main limiting factor. However, for the maize grain crop, plant density was limited technically to around 120.000 plants ha⁻¹ because of the closeness of the plants within the row. Experiments on narrow row spacing have received renewed attention in recent years (Allesl and Power, 1976 ; Camp *et al.*, 1985). However, the results are inconsistent,

and have not shown the superiority of narrow row spacing (0.4-0.5 m) compared to conventional spacing (0.7-0.8 m). Intuitively, it may be expected that interception may be greater at narrow row spacing and mutual shading reduced, although current evidence does not support this expectation.

One reason for this may be that, even with conventional row spacing, the mutual shading of leaves within a maize canopy is not greater than with narrow-row spacing. This may be due to progressive adaptive changes in leaf azimuth of the successive leaves of the plants. In other words, at least the upper leaves of the plants will not be in the same plane as the earlier formed leaves. Little scientific information is available on this topic for maize, compared to the massive literature dealing with leaf angle, even though Anderson (1970) emphasized the importance of studies on leaf azimuthal distribution. There are few relevant studies on other crops. From a study on a wheat canopy, Kirkham (1982) found that, « as expected » leaf orientation became more random later in plant development than at early stages, although the data were not evaluated statistically. Ledent (1974) concluded that the leaves in a wheat canopy has a random azimuthal distribution. Blad and Baker (1972) reported the same conclusion for soybean. Lugg *et al.* (1981) studied leaf azimuthal orientation in a sorghum crop. These authors concluded that leaf orientation was not random, but they found, as did

Ledent (1974) for wheat, that wind direction may influence leaf orientation. Concerning maize crops Lemeur (1973) pointed out a marked preference of maize leaves to be perpendicular to the row. These data confirmed previous observations (Ross and Nilson, 1967) concerning a slight orientation perpendicular to the row in the middle layers of the maize canopy, but according to Ross (1981) this azimuthal orientation did not occur before stand closure. The objective of the present study was to test the hypothesis of the randomness of leaf azimuth in two maize hybrids.

MATERIALS AND METHODS

Initial observations were made at Colmar (Alsace-France, 48° 3' N 7° 2' E, 200 m elevation) in 1991. The hybrid DEA was planted at double density on 25 April, and thinned at 6-leaf stage at a plant density of 86 000 plants ha⁻¹ (0.16 m within the row and 0.75 m between rows). Thirty-five plants were randomly chosen for measurements. Weeds were controlled by an application of pyridate after sowing. fertilizer was applied before planting at rates of 140 kg ha⁻¹ of P₂O₅ and 140 kg ha⁻¹ of K₂O and 140 kg ha⁻¹ of N as ammonium nitrate was applied as a side dressing at the 6-leaf stage.

The experiment was carried out at Elora Research Station (Ontario, Canada, 43° 7' N, 380 m elevation) in 1991). Two hybrids were used : DEA, a European cultivar, and P3902, grown in Ontario. They were chosen because of their difference in leaf orientation, DEA having more erect leaves than P3902. The experiment was of a randomized complete block design with four replications. The plots consisted of 5 rows 12 m long and 0.7 m apart and oriented 16° eastward. The experiment was planted in May 1991 and thinned by hand at the 4.5 leaf stage to obtain a stand of 70.000 plants ha⁻¹. The plots were kept weed free by hand during the whole growing period. Fertilizers were applied before planting at rates of 150 kg ha⁻¹ of N, 150 kg ha⁻¹ P₂O₅ and 150 kg ha⁻¹ K₂O. Ten plants per plot were used for measurement. The 6th was systematically marked after it was fully expanded, and leaf azimuths were determined 23 days after silking. The midrib azimuths, called leaf azimuths hereafter, were estimated placing on the ground around the bottom of the stem, a board with an azimuthal circle with 16 sectors (22° 30' per sector). The 0-360° line was always oriented in the row direction. The sector number where the projection of the midrib occurred was recorded for each leaf directly or with a plumb line to indicate the vertical. The azimuth of the ear leaf was not taken in to account because the measurements were made after silking when the orientation of this leaf was affected by ear growth.

RESULTS

In the two locations the hybrid DEA had 16 or 17 leaves. The 17th leaf was not taken into account because of its small size and because it was not pre-

sent in all plants. For the same reason only the azimuths of the first 16 leaves of P3902 hybrid were recorded at Guelph.

The azimuths of the first leaf of 35 maize plants grown in Colmar are presented in Figure 1. A chi-square test indicated that the leaves were randomly distributed. This means that the sowing technique used in this field plot gave a random orientation of the seeds, and also gave a random orientation of the first leaves. Considering the orientation for the first five leaves, there was no azimuthal shift. About 40 per cent of leaves 2 to 6 were in the same vertical plane ($\pm \pi/8$ radians) as the first leaves (Table 1). For 74 per cent of these leaves, the angular shift was less than $\pi/4$. However, when all the leaves of plants grown at Guelph were considered (Figure 2), some orientations were more frequent than others. Very few leaves had a row-wise direction. Nevertheless, after combining the azimuths into four classes ($00-\pi/2$, $\pi/2-\pi$, $\pi-3\pi/2$ and $3\pi/2-2\pi$), the chi-square test was no longer significant, (i.e. the distribution of leaf azimuth was random) as in Nichiporovich's (1961) study where four classes of azimuth were considered.

As the first five leaves tended to be oriented in the same vertical plane, the other leaves were split into two classes ; leaves 6 to 10 (those below the ear) and leaves 12 to 16 (those above the ear). For both hybrids, 78 per cent of the ears were in the axil of the 11th leaf. For P3902, for the leaves of the first class, there were two frequency maxima (around $2\pi/3$ and 5.1 radians) (120° and 290°) and two minima (0.17 and 2π radians) (10° and 180°) (Figure 3). The azimuthal distribution of leaves 6 to 10 was not ran-

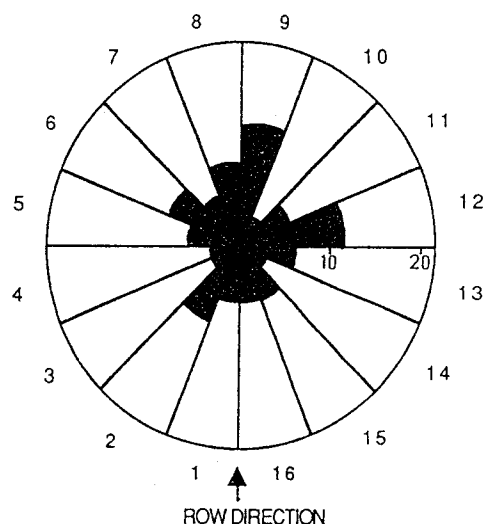


Figure 1. — Azimuths of the first leaf of 35 maize plants (Colmar 1991). The length of the sector is proportional to the frequency of the leaf azimuth in the sector. χ^2 observed = 8.5, d.f. = 15 : the distribution was not statistically different from a random distribution at $P \leq 0.01$.

Table 1. — Frequency (per cent) of the difference between azimuths of the 1st leaf and the four following leaves of 35 maize plants (Colmar, 1991).

Leaf number	Classes of differences in azimuth (radians)												
	$-\frac{3\pi}{4}$	$-\frac{5\pi}{8}$	$-\frac{\pi}{2}$	$-\frac{3\pi}{8}$	$-\frac{\pi}{4}$	$-\frac{\pi}{8}$	0	$+\frac{\pi}{8}$	$+\frac{\pi}{4}$	$+\frac{3\pi}{8}$	$+\frac{\pi}{2}$	$+\frac{5\pi}{8}$	$+\frac{3\pi}{4}$
2	0	0	5.7	4.3	30.0	14.3		11.4	8.6	14.3	2.9	2.9	0
3	0	0	2.9	8.6	11.4	22.9		28.6	12.9	4.3	0	8.6	0
4	0	2.9	2.9	10.0	18.6	12.9		24.3	20.0	2.9	5.7	0	0
5	0	0	0	10.0	12.9	24.3		18.6	21.4	10.0	0	0	2.9
Mean	0	0.7	2.9	8.3	18.3	18.6		20.8	15.7	7.9	2.2	2.9	0.7

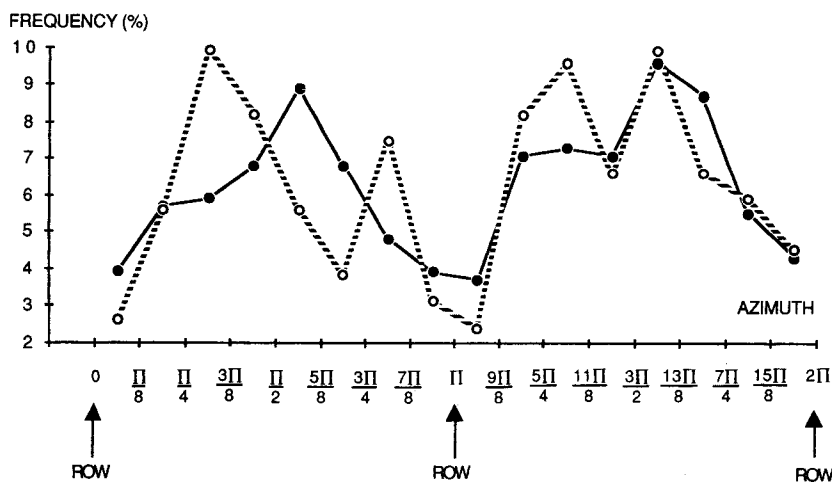


Figure 2. — Frequency distribution of azimuths of leaves 6 to 16 of 40 plants of each hybrid: DEA (○) and P3902 (●). There are 16 classes of azimuth (intervals of $\pi/8$ radians). χ^2 observed were 103 and 133 respectively for DEA and P3902, d.f. = 15: the distribution was statistically different from a random distribution at $P \leq 0.01$.

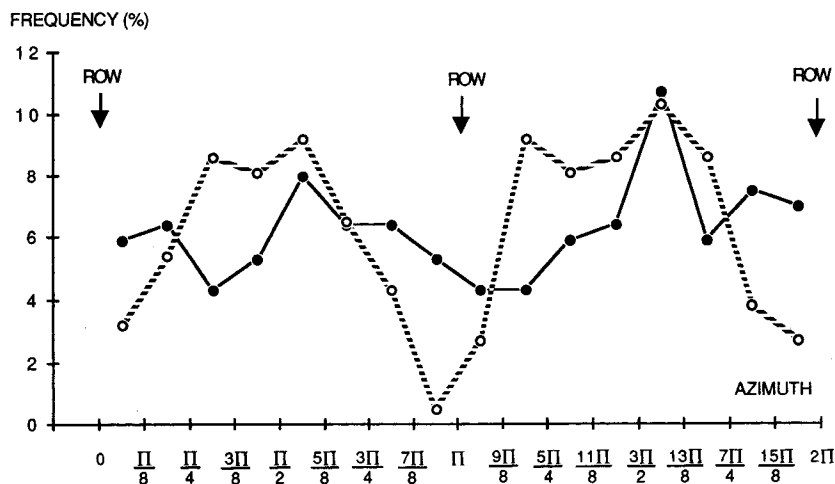


Figure 3. — Frequency distribution of azimuths of leaves 6 to 10 (●), and 12 to 16 (○) from 40 plants of P3902 (Elora 1991).

dom for either hybrid (χ^2 observed = 40.2 and 37.7 respectively for DEA and P3902, with d.f. = 15 ; $P \leq 0.01$).

In contrast, hardly any of the upper leaves (level 12 to 16) were oriented in a row-rise direction and the more frequent orientation was perpendicular to the row.

For plants whose leaves were oriented parallel to the row, only 13 per cent of the 14th and 15th leaves were oriented in the same direction, and for the majority of the upper leaves an azimuthal shift was observed (Figure 4). The higher the leaves were on the stem, the more perpendicular to the row they were. Consequently, the leaves of a plant were not all in the same plane. Therefore, there was a shift in

azimuth from leaf n to leaf $n + 2$, particularly when the lower leaves were oriented parallel to the row. The mean shifts in azimuth from 6th and 7th to 14th and 15th leaves were 1.17 and 1.12 radians (67° and 64°) respectively for P3902 and DEA. Where the 6th and 7th leaves were perpendicular to the row, the 14th and 15th leaves were never oriented parallel to the row (Figure 5). To ascertain whether or not there was a preferential azimuthal orientation, the frequency of leaves positioned perpendicularly and parallel to the row was plotted for each leaf level (Figure 6). Under these experimental conditions (7 plants m^{-2}), the 9th and upper leaves were no longer randomly oriented.

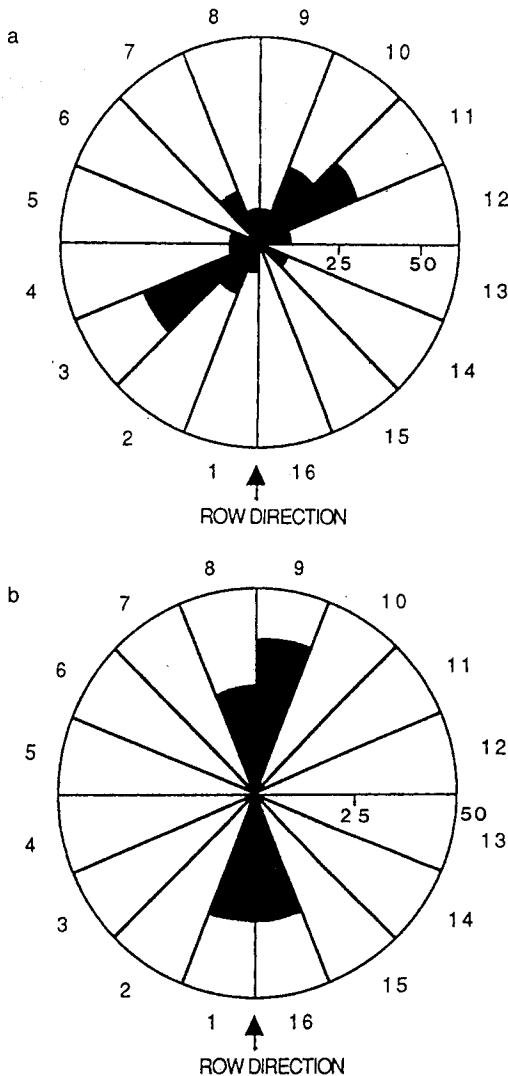


Figure 4. — Azimuth of (a) the 14th and 15th leaves of 20 P3902 plants and (b) the azimuths of the 6th and 7th leaves of the same plants, all of which were oriented parallel to the row. The length of the sector is proportional to the frequency of the leaf azimuth.

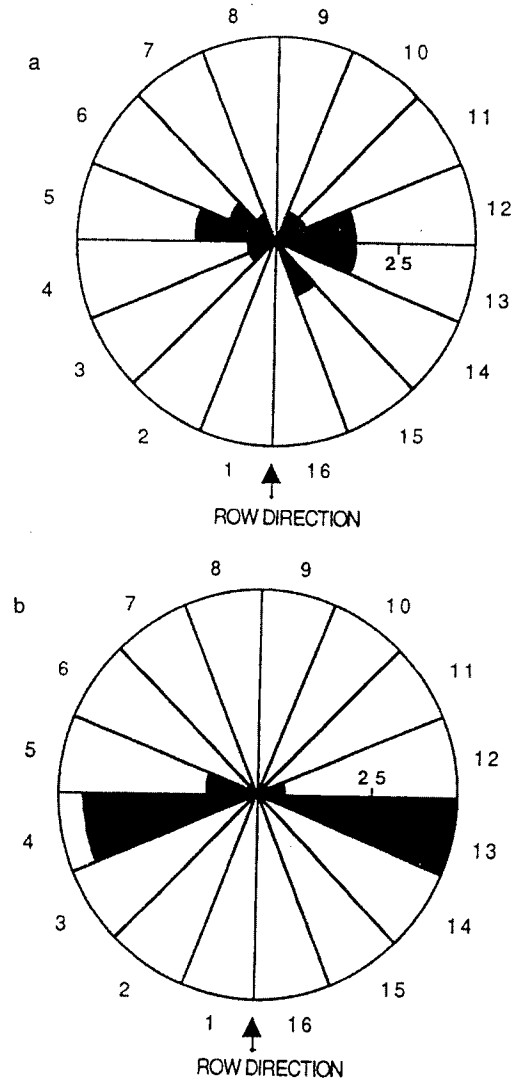


Figure 5. — Azimuth of (a) the 14-15th leaves of 18 DEA plants and (b) the azimuths of the 6th and 7th leaves of the same plants, all of which were oriented perpendicularly to the row. The length of the sector is proportional to the frequency of leaf azimuth in this sector.

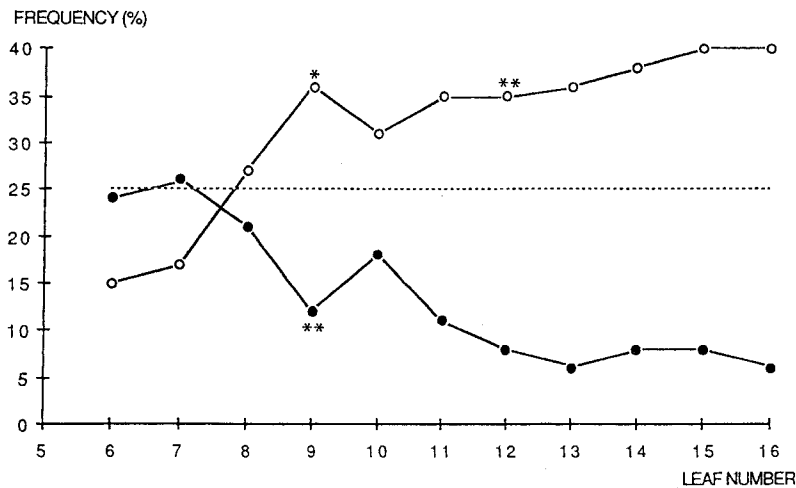


Figure 6. — Frequency per cent of leaves oriented perpendicularly (○) or parallel (●) to the row for each leaf level (all the data together from both hybrids DEA and P3902). From the point marked by (*) or (**), the azimuthal orientations are statistically different (χ^2 respectively at $P = 0.005$ and 0.01 level) from a random orientation.

DISCUSSION

Because it is easier for calculation of light interception, crop modellers (i.e. : Monsi and Saeki, 1953, Chartier, 1966 ; Ross, 1981 ; Sinoquet 1989) generally assume that within a maize canopy the leaves are randomly oriented. This assumption is based on the fact that all the leaves of the same plant are roughly in the same vertical plane, and that the plants are randomly oriented in a field because the seeds are randomly positioned by the sowing machine. The data presented in Figure 1 show that the plants are indeed randomly oriented within a maize crop. However, the second assumption seems to be true only for the first five leaves (Table 1).

The orientation of the first leaves of the maize plants in the same vertical plane does not correspond with the general leaf pattern of the Gramineae (Gallais, 1968). This author found that the azimuth angle between two successive leaf primordia is about 150° instead of 180° as generally expected. However, when the data presented by Kiesselbach (1949) are considered, it seems that maize leaf primordia are not positioned like those of the leaf primordia of other gramineae. If the upper leaves (6 to 16) are considered, there was a preferential orientation perpendicularly to the row (Figure 3). If this phenomenon has not been noted previously (Nichiporovich, 1961), it may be because the recording of the leaf azimuth was not precise enough (only four classes of azimuth). As shown by Girardin and Tollenaar *in press*), the azimuthal shift from the 6th leaf to the top leaf is the result of a twisting of the internodes caused by the orientation of the leaf blade of the same phytomer.

This is probably why Bui and Box (1992) described the leaf pattern of maize as helicoidal. Even when the lower leaves were oriented perpendicularly to the row, the orientation of upper leaves shifted a little, since only about 50 per cent of them kept the same orientation as the 6th and 7th leaves (Figure 5). This was confirmed by Girardin and Tollenaar (*in press*) who found that the middle leaves (7 to 11) of the plants initially perpendicular to the row, explore a relatively large range of azimuths during their unfolding. This behaviour minimizes the overlapping and the intraplant competition and, like the overall azimuthal shift, minimizes interplant competition. Under the present experimental conditions (7 plants m^{-2}) early light effects were evident since the 9th leaf was already no longer randomly oriented (Figure 6). Intercrop competition occurring at the 5 to 6-leaf stage presumably induces the azimuthal shift of the 9th leaf. The first variable which is influenced by light competition is leaf growth (Blaise and Girardin, 1990). It would be interesting to know whether leaf azimuth is affected by light competition induced by a high density earlier than leaf growth. The shift of leaf azimuth could be an indicator of light competition. It could be a particularly useful tool in study of crop-weed and crop-intercrop competition.

The data presented here cast doubt on the assumption made in most of the crop architecture analyses, as pointed out by Ross (1981), that there is no preferred azimuthal leaf orientation in a maize crop. This assumption is also implied in the estimation of leaf area index indirectly with a new instrument using a radiation interception method (Welles and Norman, 1991). As a mathematical expression of the distribu-

tion function of foliage area orientation has been developed (Ross and Nilson, 1967), the calculation of the integral of the distribution function G is only possible by ignoring the azimuthal dependence of leaf orientation. However, a mathematical solution was obtained by Ross (1981), assuming a uniform distribution of leaf inclination, which has been shown to be invalid for maize by Ross himself. In fact, the penetration function of direct solar radiation, A depends on G. Almost all crop models assume a constant angle of leaf inclination and a uniform azimuthal distribution, by using a simplified expression for A ;

$$A = \exp(-KL)$$

where L is the leaf area index and K is the extinction coefficient which is assumed to be independent of solar elevation, leaf angle and azimuthal distribution.

Although Ross (1981) asserts that « all geometric characteristics of an individual plant vary, therefore, they should be treated as random values », we have insufficient data to be sure that the assumption of random azimuthal distribution is always true for a row crop like maize.

CONCLUSION

The orientation of upper leaves perpendicular to the row as a reaction to a light competition probably explains the insensitivity of corn dry matter production to narrow row spacing. Indeed, with conventional row spacing, the plant is able to make optimal use of solar radiation since its upper leaves are mainly directed to the inter-row where there is less light competition than within the row. To develop good models of light interception, it is important to know the azimuth of different leaves, and to predict the azimuth of a new expanded leaf if the azimuths of the lower leaves are already known. Almost all light interception models are based on a relationship between L and PAR (photosynthetic active radiation) interception and do not take into account the orientation (angle and azimuth) of individual leaves. With increased knowledge of these last two parameters more accurate light interception models could be devised. Because of the preferential azimuth of the upper leaves of a maize plant documented here, the question of the seed positioning in the row (Prine, 1973, 1977 ; Yadav and Gupta, 1987), particularly at high densities, becomes unimportant, since, whatever the initial azimuths of the first leaves, the upper leaves tend to be orientated perpendicularly to the row.

Finally, these data concerning leaf azimuth permit a better understanding of the « funnel effect » the so-called « biological water harvesting » (Yadav *et al.*, 1983 ; Kumar *et al.*, 1977). Leaf azimuth may influence not only light interception but also, water interception. Nevertheless, some questions remain

unanswered, in particular : what are the effects of genotype and the effects of density on leaf azimuth ? This will be investigated in further experiments.

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