

Mechanics and form of the maize leaf: *in vivo* qualification of flexural behaviour

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An *in vivo* flexural test is designed and conducted on maize leaves. Data processing is based on a local structural definition of longitudinal leaf suppleness, which originates in the theory of pure plane bending of initially curved beams, in large displacements. A specific procedure for curvature and suppleness computation is methodologically discussed. The results presented concern only the elastic flexural behaviour of the leaf (which could be characterized in 59% of the tested leaves). A quasi-exponential increase in suppleness, from the base to the tip of the leaf, was always experienced. It is demonstrated that the midrib plays a major part in bending stiffness. Going up the longitudinal leaf form, it is shown that self weight related elastic bending strains only account for one-third of the actual curvature.

1. Introduction

Leaves are the major surfaces of light interception and gas exchange in plants. A study of their spatial display (their habit) is thus of interest in functional ecology. In particular, leaves must be stiff enough to stand their own weight without excessive bending [1, 2]. The maize leaf is not held by a stem like organ (petiole), but is a shell-shaped self-supporting structure (as are many monocotyledon leaves [1]), reinforced by a central midrib*. Dealing with such a complicated structure, there may be many putative phenomena that could *a priori* be addressed as implicated in its mechanical behaviour:

1. Is this behaviour mainly elastic, or do more complex rheologies have to be retained, as has been reported for other biological materials ([3] among others)?

2. Are shell structural effects dominant or does the midrib account for most of the rigidity?

3. Are there some active plant reactions [4]? Thus, as always the case in biomechanics [5], much of the challenge is the identification of the relevant phenomena for the particular problem under concern (i.e. the habit of the maize leaf). A way through, is to begin with an experimental study of the integrated structure (i.e. in this case, the whole leaf). Moreover, it is of particular interest to experiment on the plant *in vivo* because:

1. There are many experimental difficulties and possibilities of artifacts in the more classical testing procedures on specimens [6] (e.g. possible decay of the living material),

2. it allows assessment of possible plant reactions (e.g. [4, 7, 8]).

Although there are some reports of experimental mechanical studies on plant leaves [1, 2, 9–11], none of them deal with *in vivo* testing. The present paper is concerned with the design of such an *in vivo* bending test and its use for the analysis of the mechanical behaviour of plant leaves. Its results, and the insights they give about the mechanics of the maize leaf habit, are presented and discussed.

2. General morphology of the maize leaf

The maize leaf is a slender structure, with bilateral symmetry. Its size varies with leaf rank (and growing conditions). It is composed of a central thickened, curved midrib; and of a much thinner part, on both sides of the midrib, which will henceforth be referred to as the lamina (Fig. 1). Previous studies [12, 13] showed that the midrib usually lies within the vertical plane of symmetry. The shape of the curve made by the central line of the midrib in this vertical plane is often called, in botany, the leaf habit. It is the determination of this habit which is the ultimate goal of this study. Notice that the midrib has a strong taper and that the lamina is usually wavy, although the amount of waviness may vary with leaf rank and age.

Details about the internal material structure (anatomy) of gramineous (i.e. similar to maize) leaves can be found in [1, 10]. Just recall here that it is a composite cellular material.

3. Definition of bending suppleness and design of the test

From a mechanical point of view, the maize leaf is a complex three-dimensional structure. However, it is

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*Biological terms are defined in the Appendix.

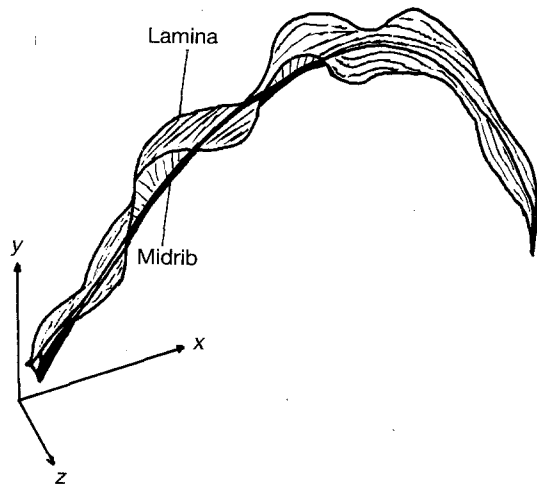


Figure 1 General morphology of the mature maize leaf (re-drawn from [16]).

a slender one; with its longitudinal dimension being much larger than the others. Moreover, investigations here are primarily interested in the longitudinal flexural behaviour, (as it is most likely to be related to leaf habit). Work has, thus, been focused on the bending behaviour of a particular line within the structure, the central line of the midrib. When the whole structure is vertically loaded, this line remains within the vertical x - y plane (as a consequence of symmetry). Thus, a very simple flexural plane test can be designed. Moreover, (structure related) bending suppleness [14] can be defined at a given material point within the central line as:

$$Sf = \frac{\delta(C)}{\delta(M_z)} \quad (1)$$

where Sf is the plane bending suppleness (its reciprocal being the stiffness), $\delta(C)$ and $\delta(M_z)$ are, respectively, the variation of curvature and the variation of the bending moment between the initial and final equilibrium states, at a given material point. Such formula applies to the case of initially pre-loaded and curved beams (with small curvatures[†]). It takes into account large displacements (as M_z in the final equilibrium state is determined in the final strained geometry). This is, of course, only one of the many criteria for structural suppleness that could be designed. It can be interpreted as the suppleness of an "equivalent homogeneous beam", in pure bending, in which case the construction of Sf from cross-sectional properties gives the classical equation:

$$Sf = (E_{eq} I_z)^{-1} \quad (2)$$

where E_{eq} is the longitudinal Young's modulus of the equivalent material and I_z is the second moment of inertia around the z axis. At this point, it might be a matter of surprise to note that Equation 1 differs from the classical strength of material formula for beams ($Sf = C/M_z$). However, the former is just a restriction of the latter, in problems of initially straight beams where, moreover, the influence of the initial

mass is negligible (i.e. either initially unloaded beams or small displacement cases). Lastly, it should be recalled here that the aim is somewhat different from that of usual mechanical tests. The usual purpose of mechanical tests is to obtain rheological equations of the constitutive material (independently of any geometry). In this case, however, the test is directly applied to the mechanical structure of interest, so that it is used here more for structural analysis than for real rheological testing.

4. Materials and methods

4.1. Plant material

Maize plants (*Zea mays* cv DEA) were raised from seeds during late spring and summer in Bordeaux, using outdoor pots. Care was taken to prevent water or mineral deficiency. To obtain a homogeneous material, the leaves were tested when they were mature (i.e. those no longer growing, and with at least three younger entire leaves above [15]), and when the plant had the same phenological age (male flowering). Moreover, to discard possible changes in the leaf-water status, all the plants were placed indoors in the morning before the tests, the pot liberally watered and the leaves sprayed several times. Thus, all the leaves were fully turgid. Forty leaves from three leaf ranks were studied (rank 8, 10, 11). Notice that these ranks correspond to the main leaves of the plants. Any leaf showing impairment of its bilateral symmetry was discarded. There was no effect of rank on leaf length under these conditions, within the studied rank range. The mean leaf length was 805 ± 48 mm. The typical ratio of maximum width to length was close to 10% (in accordance with data from [16]).

4.2. Mechanical test

The stem of the plant was carefully, but firmly, secured to a metallic framework, just beneath the leaf insertion, to avoid displacement. A pre-load was then applied as a small weight (2.4 g) hung on the midrib. Then, a known load was added (as an additional weight) and a new equilibrium shape was reached. The load was then removed, to test elastic recovery. Three or more loading cycles were achieved on each leaf tested, with increasing load level (+ 2, 5, 10 g, etc.). Each equilibrium shape was recorded by taking a photograph after a lag time of 1 min (preliminary studies showed that no apparent displacement was noticeable after 30 s). A plumb bob and a scale were included in each photograph, and particular care was taken to ensure that the leaf plane was parallel with the scale and the focus plane of the camera. Tests of more or less related designs have been reported in [17-19].

In order to study experimentally the role of the midrib in the overall behaviour of the structure, some of the leaves tested were submitted to a second set of loading cycles, after suppression of the lamina longitudinal cohesion by lacerating it transversally (on both

[†]In the case of large curvatures, the relationship between $\delta(C)$ and $\delta(M_z)$ is no longer linear [19], thus dismissing Equation 1 in the case of finite variations, as in our problem.

sides of the midrib) with a razor blade. Such operation (leaving 1 cm large strips) does not change the self weight distribution along the midrib, but allows for testing of the midrib alone. Care was taken to proceed as fast as possible in the second period, to prevent changes in the leaf water content related to enhanced evaporation through the cuts.

At the end of each experiment, the lamina and midrib self weight distributions were immediately measured by weighing cut segments using a precision balance.

4.3. Form recording

The positions of the midrib central line were obtained as a sequential set of points by digitizing the photograph (mean magnification rate of 0.33), using a two-dimensional digitizing tablet (0.01 mm accuracy). Care was taken to line up the plumb bob in the photograph with the ordinate axis. Approximately 50–80 points were recorded per leaf. The sharper the curvature, the larger the local density of points. The accuracy (which estimation is detailed in [13]) was 3.8 mm (at the real scale) on each point within view.

4.4. Data processing methods

A brief outline of these methods has been presented in [20], but a far more complete description, and check, is developed here.

4.4.1. Computational methods

4.4.1.1. Curvilinear abscissa. The curvilinear abscissa, s , was estimated for each point as the sum of the upstream inter-point segments:

$$s_i = \sum_{j=1}^i [(x_j - x_{j-1})^2 + (y_j - y_{j-1})^2]^{1/2} \quad (3)$$

where x_i, y_i are coordinates within the plane of symmetry of the i th point.

4.4.1.2. Curvature. The curvature on a line is a local value which can be analytically defined in smooth curves only, and thus obviously not in a discrete series of points. An immediate idea is to think of fitting a curve (e.g. polynomial). Unfortunately, no simple mathematical form is able to provide a convincing fit for a set of maize leaves. Usual smoothing methods from computer aided design (CAD), e.g. spline or Bezier curves [21, 22], are not suitable as they just perform interpolations, being very sensitive to local errors in point positioning (it should not be forgotten that curvature calculation requires second derivatives). Lastly, although adjusting smoothing procedures do exist (e.g. adjusting splines [21]), the choice of the sum of the square part of the functional to be minimized is rather arbitrary, in the sense that it has no immediate relation to the residual error term. Thus, a special calculation procedure, originating from a suggestion in [22], has been developed and tuned to estimate curvature, giving rise to computer software. For a given current point, a centred vicinity

is defined (the extent of which is input by the operator as a number of points). Then, the two principal axes of the set of points inside the vicinity are determined by diagonalization of its inertia matrix. The co-ordinates of all the points are recomputed in the local principal axes reference. Thereafter, a local fitted polynomial, P , is estimated by the least square method, and the order of the polynomial is incremented until the residual term (root mean square of the error) becomes less than an independent estimation of the mean digitizing error on a point position. The maximal order of the polynomial is constrained in order to leave at least six degrees of freedom to the residual. It should be noticed that the fitness criterion based on overall residual error, is only a global one and is not sufficient [23]. Therefore, the software forces the operator to a systematic graphical inspection of the residuals before validation. Note also that the change to local principal reference axes is very important, as polynomial fitting is very reference dependent. Then, the curvature is calculated in each point, i , as:

$$C_i = \frac{[d^2P(x_i)/dx^2]}{\{1 + [dP(x_i)/dx]^2\}^{3/2}} \quad (4)$$

The sign convention sets a positive curvature when the concavity is directed to the upper side of the leaf. Notice that the curvature calculations were limited to a subset of points, discarding the ones close to the edges of the interval to avoid border effects (a relationship between the safety margin and the size of the vicinity has been established empirically, which should of course be suitable only for conditions of curvature, digitizing point density and error, similar to these). When all these calculations are done, the current point is translated to the next point and the whole preceding procedure is reiterated. When the end of line has been reached, the mean and standard deviations are computed from the set of curvature estimates in each point. This last step restores the curvature “continuity”, this was by no means warranted in previous calculations. At the end of the computation, a file containing the curvilinear abscissa, s , and the corresponding mean curvature, $C(s)$, for all the points is generated.

4.4.1.3. Bending moment. The procedure for bending moment calculation involves the summation of discrete bending moments resulting from both the external load and the self weight (the former being distributed into point-wise equidistant loads)

$$M_{z_i} = \sum_{j=i+1}^n [(x_j - x_i) \times w_j] \quad (5)$$

where x is the point abscissa and w is the sum of the self weight and of an eventual additional weight acting on the current point. Anti-clockwise moments are set positive.

4.4.1.4. Flexural suppleness. The flexural suppleness was calculated according to Equation 1 for each transition between load levels. As the digitized points

in two successive configurations do not usually correspond (they have no relation with given material points), the variations of curvature and moment have been calculated at the same curvilinear abscissa (using linear local interpolations when necessary) generating a file of $[s, Sf(s)]$ pairs. Such a calculation is based on the assumption of pure bending (i.e. normal and shear strains are negligible). Since the hypothesis for negligible shear displacement is no longer valid close to the point of application of the external load, a safety zone of 15 cm in length was systematically excluded from analysis. Thus, the data presented here approximately concerns the basal first half of the leaf only.

4.4.2. Validation and estimation of accuracy

Preliminary studies were conducted to test the accuracy of the calculation program. As the *a priori* crucial point concerns the estimation of curvature, this is dealt with first. The first step is to check on the lack of bias. To do so, realistic sets of testing points, related to known curves, are required. To create them, several 3–5 order polynomials were fitted onto a set of digitized leaves. Although, as yet stated, such curves do not have satisfactory fitting power, they nevertheless provide curves with a realistic range of curvature changes along them. Moreover, a set of testing points can then be generated, as $[x, \hat{y}(x) + \varepsilon(x)]$, where x is the abscissa of the true set of digitized points, $\hat{y}(x)$ is the ordinate polynomial estimate, and $\varepsilon(x)$ is an error term. The program can then be run on this testing set (called the bias testing set) and its results compared to the analytical calculation of curvature on the polynomial. Such a comparison is given in Fig. 2, and reveals satisfactory behaviour of the curvature calculating program, as no bias can be detected. The second step is then to assess the error made when estimating curvatures from digitized leaves (including digitizing errors). The results of curvature calculations from ten independently digitized sets of points on the same leaf (making up the so-called repeatability testing set) are shown in Fig. 3. By a regression procedure, the mean error on the curvature (root mean square of the residual) can be estimated at $1.2 \times 10^{-4} \text{ mm}^{-1}$ (i.e. a radius of curvature of approximately 8 m). This represents a relative error (coefficient of variation) of approximately 2% at the peak of curvature and around 10% on the basal zone. Surprisingly, these results are very reasonable, taking into account the fact that curvature involves second derivatives.

Using the same procedure as for curvature, the moment calculation is shown to have no bias (data not shown) and the mean absolute error for moment calculation is 0.095 N mm^{-1} (i.e. from 0.5 to 1% of the moment within the studied range of moments).

The effects of point positioning errors and point density changes on length calculations (s) were also assessed on the aforementioned repeatability testing set. For the entire leaf, the standard deviation is 5.2 mm, which represents $< 0.6\%$ error.

The suppleness estimation error cannot be straightforwardly assessed from previous error estimations of curvature, moment and curvilinear abscissa. Actually,

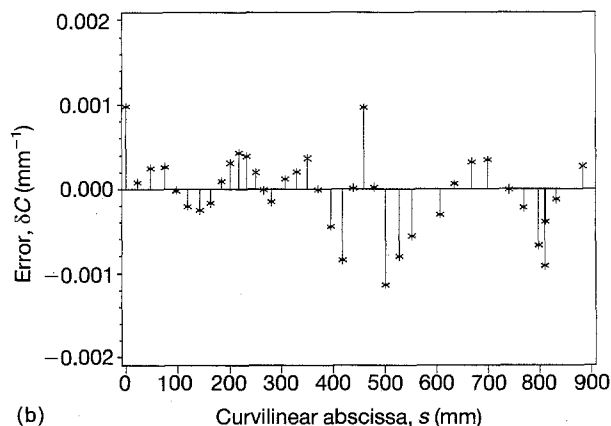
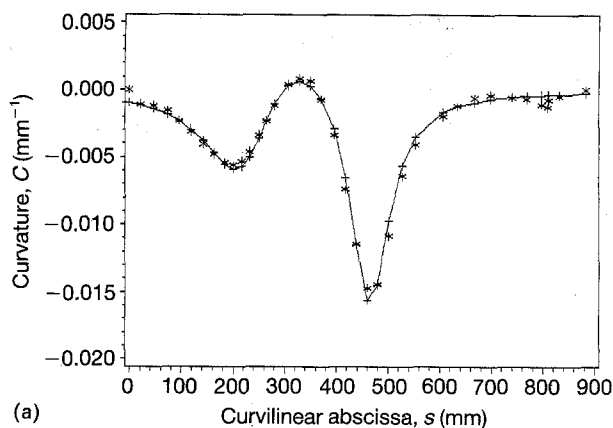


Figure 2 Comparison between analytical calculation and numerical computation of curvature for a realistic shape: (+ - +) analytical calculation, (*) numerical computation. (a) Curvature versus curvilinear abscissa, (b) numerical error versus curvilinear abscissa.

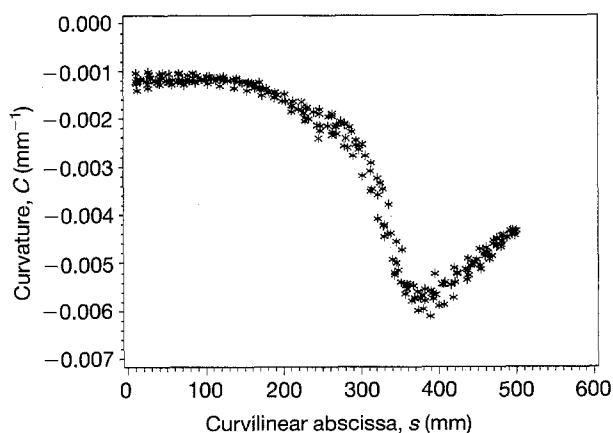


Figure 3 Repeatability of curvature computation (on the repeatability testing set).

it introduces an additional error term related to inter-photograph repeatability, which can be impaired for example by imperfect parallelism between the leaf and film planes, or slightly deviated bending. In fact, the error in length estimation (when calculated on the two first unloaded configurations for each leaf) is 4.2%, which is much higher than the one related to the point positioning error. Such an error level is not tolerable. It would include, for a typical curvature distribution as in Fig. 3, a maximal related error up to

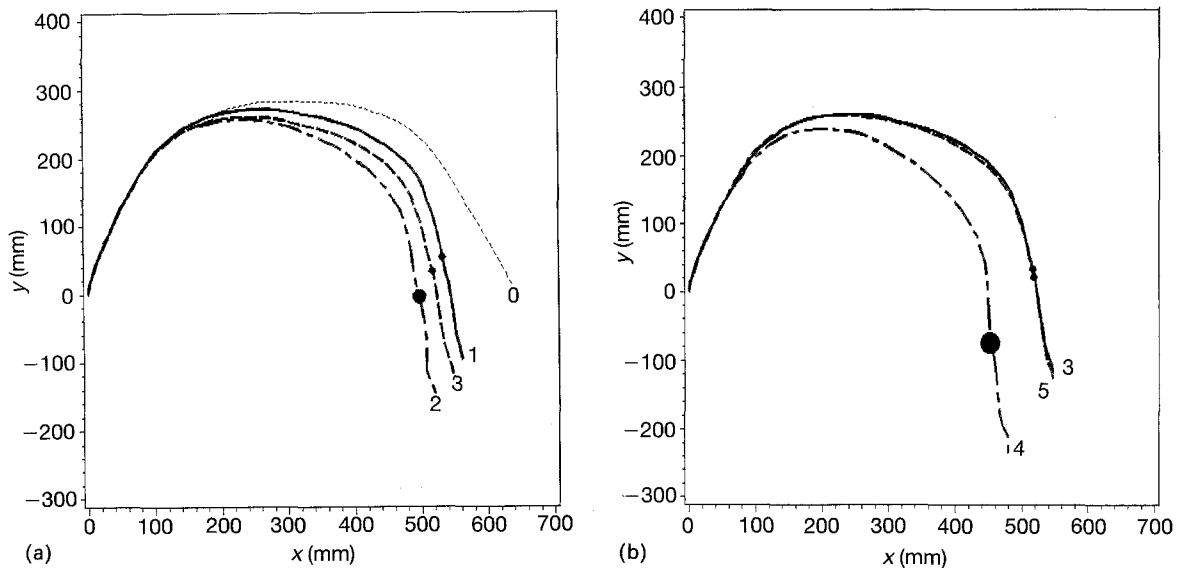


Figure 4 Successive leaf forms during two consecutive loading-unloading cycles. Each individual curve represents the equilibrium shape of the leaf, for a given point-wise load (●, position of additional weight). (a) First cycle, (b) second cycle. Loading conditions: (0) unloaded (self weight alone), (1) 2.4 g (pre-loading), (2) 4.4 g, (3) 2.4 g, (4) 7.4 g, (5) 2.4 g.

$2.10^{-3} \text{ mm}^{-1}$ (15%). Thus, for suppleness calculations, a subgroup of 60 loading cycles (representing 22 leaves) displaying a mean error length of 1% (and maximal related errors of $6.10^{-4} \text{ mm}^{-1}$ for curvature and of 1 Nmm^{-1} for bending moments) has been chosen. Moreover, minimal thresholds of $3.10^{-4} \text{ mm}^{-1}$ for curvature variations and of 0.5 Nmm^{-1} for bending moments were retained for the suppleness computation.

4.4.3. Statistical analysis

Statistical regression, variance and covariance analyses have been made using the general linear model (GLM) for SAS software [24]. The level of significance is usually explicitly specified as the probability of first type error (α) (when it is not, it means that $\alpha < 0.05$ at least).

5. Results

Two typical sets of leaf forms, during two consecutive loading and unloading cycles on the same leaf, are shown in Fig. 4. In one set of leaf form (Fig. 4b), there is good immediate recovery of the overall shape after unloading; a behaviour that can be called "global elasticity". For the other set (Fig. 4a), the cycle displays an important residual curvature.

Among the forty leaves tested, 59% displayed at least one globally elastic cycle. However, in 43% of these leaves, the "elastic" cycle is not the lower loading one; hence making the definition of a global limit of elasticity rather ambiguous (e.g. in Fig. 4, cycle (b) has an additional load 1.7 times higher than cycle (a), and nevertheless (b) displays global elasticity whereas (a) does not). Notice, lastly, that no obvious active plant reaction (such as for example righting movements or active drooping) can be established from the data. Such a conclusion was expected for such short term experiments, as the maize leaf (and especially the

mature one) is not known, among botanists, to be as quickly reacting as is for example the sensitive *Mimosa pudica* L [8].

Fig. 5a shows the characteristic profiles of bending moments, $M_z(s)$, along the midrib for three consecutive loading cycles within a test. Within the zone of interest, the bending moments are a roughly linear function of the curvilinear abscissa (deviations from linearity increase with increasing loads). This is also the case for the self weight related bending moment (Fig. 5a, curve 0). It is thus tempting to characterize the level of loading by the ratio of actual load to the self weight "natural load". This ratio is not constant along the leaf, as the linear regressions for the set of load levels do not cross one another at the moment origin. However, it varies very slowly within a major part of the studied range of s (the increase at $s = 300 \text{ mm}$ is less than 15%). Thus, the bending moment ratio at the leaf basis is a good characteristic of the "significance" of the load levels from the "leaf viewpoint". In these experiments, it ranges usually from 1.4 (pre-load) to 2.5. A few tests were brought up to higher loading, and breakage occurred for load levels around 6–7, so that the additional loadings in these experiments, ranged roughly from 6 to 30% of the ultimate breaking load.

It is of interest to assess the part played by self weight during the test (Fig. 5b). Do the large displacements induce significant variation in the self weight bending moments? In fact, leaf bending induces two crossed effects on the variation of the lever arms along s :

1. Increasing lever arms in the positively inclined basal part due to the increase in leaning;
2. Decreasing lever arms in the negatively inclined distal part due to drooping.

Therefore, for the loading conditions used, and within the first half of the leaf, variation in self weight moments increases the absolute value of δM_z in the

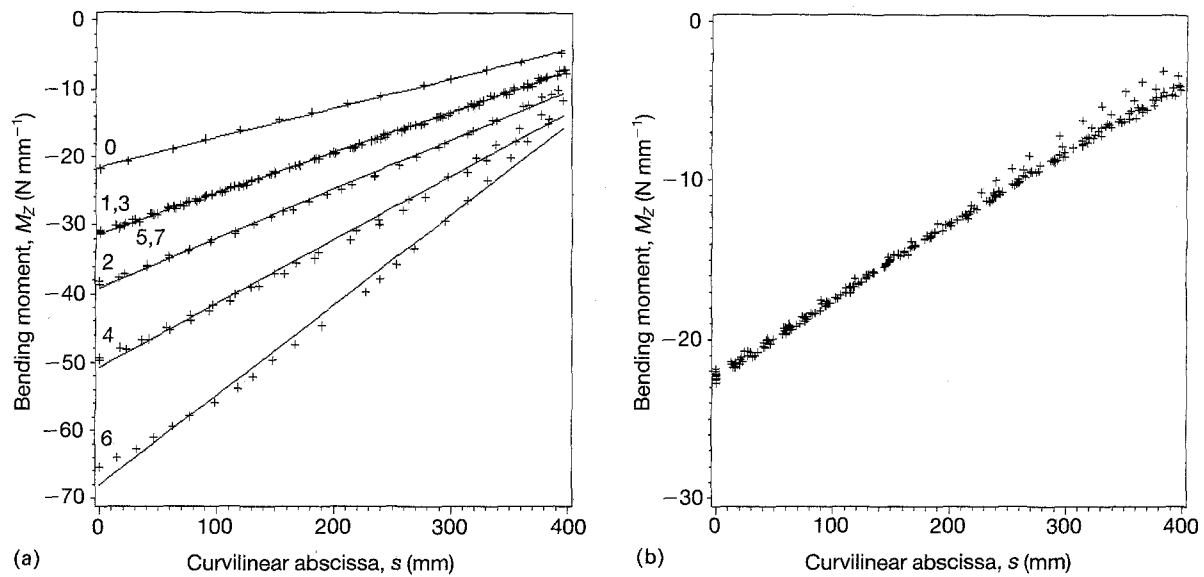


Figure 5 Changes in the bending moment distribution along the basal half of a leaf for three consecutive loading cycles, during a test. (a) Total bending moment, loading conditions: (0) unloaded (self weight alone), (1) 2.4 g (pre-loading), (2) 4.4 g, (3) 2.4 g, (4) 7.4 g, (5) 2.4 g, (6) 12.4 g (7) 2.4 g [bending moments are much less affected by possible departures from global elasticity; in this case the bending moments in the deloaded states (3, 5, 7) are perfectly superimposed on the ones in the first preloaded state (1)]. (b) Self weight related bending moments (in all the previous loading configurations).

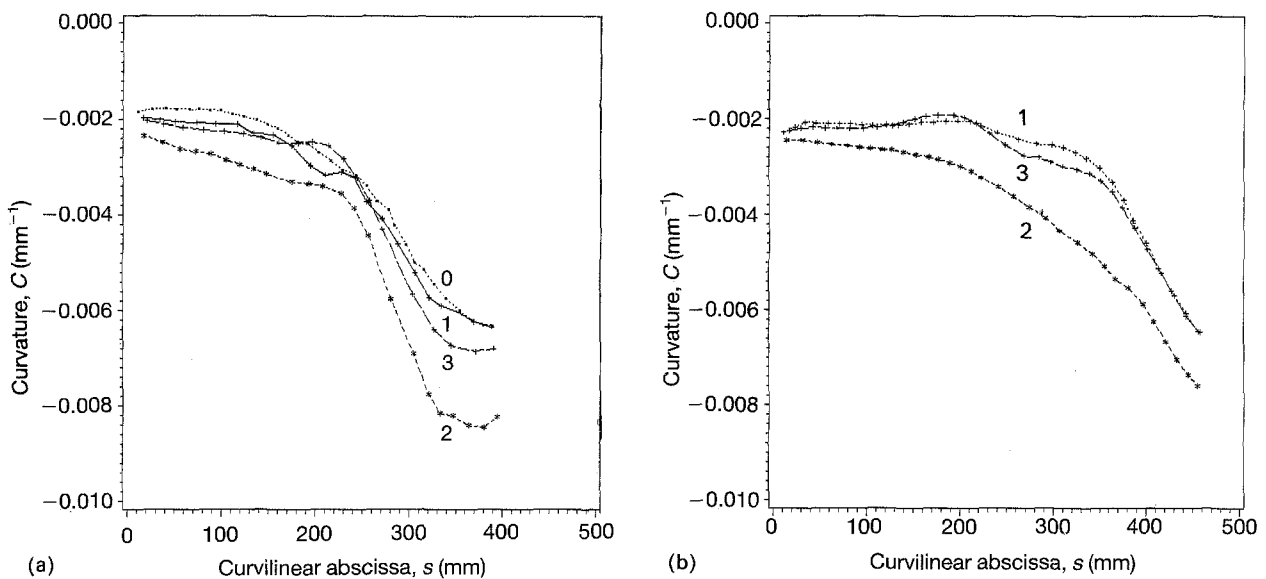


Figure 6 Two examples of changes in curvature along the basal half of a leaf during a test. Loading conditions: (0) self weight, (1) 2.4 g, (2) 12.4 g, (3) 2.4 g.

basal zone by less than 5%; whereas it decreases by up to 35% in the distal part. Thus, bearing in mind the above stated constraints about curvature accuracy, it seems safe to take into account the variation of self weight moments (although it is a rather time-consuming measurement).

Two typical plots of curvature versus curvilinear abscissa are shown in Fig. 6a and b. Although it is evident from leaf observation, attention should be paid here, first, to the fact that the initial form under self weight is far from being straight (Fig. 6a, curve 0), with typical radii of curvature ranging from approximately 50–60 cm near the leaf base, up to 10–20 cm at the peak of curvature. For all the tests, the measured radii of curvature always remain far greater than the characteristic midrib thickness (which tapers from 10 mm at the leaf base to less than 1 mm). This sup-

ports the hypothesis of small curvature, made while defining Equation 1.

Fig. 7 plots flexural suppleness versus curvilinear abscissa in the cases of "global elasticity". The overall shape of the suppleness curve is very stable, displaying a quasi-exponential increase in suppleness with s . However, when all the curves for all the "globally elastic" testing cycles for all the leaves tested, are put together, there is an important inter-leaf variability. The linear regression of the logarithm of suppleness against linear abscissa is significant ($\alpha = 0.0001$), and its r^2 is 0.83 (such log transformation of suppleness before regression is justified here as it stabilizes the residual variance, see Fig. 7). Through an analysis of slope homogeneity [24], no significant effect of the level of loading could be established. In opposition, there is significant difference in slopes between ranks

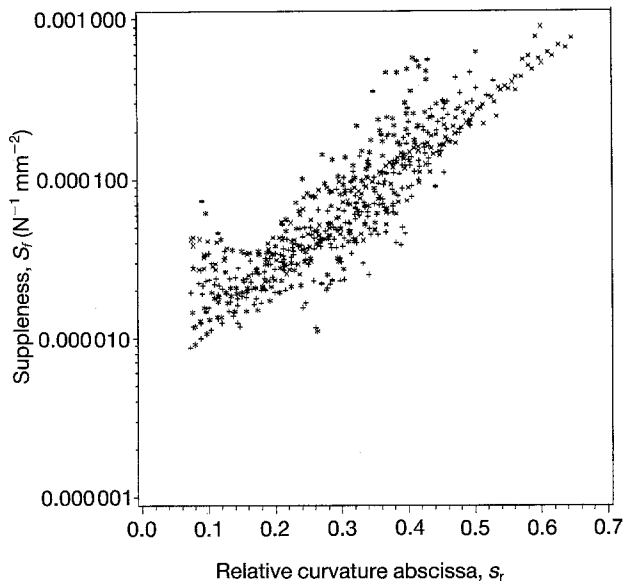


Figure 7 Relationship between suppleness and relative curvilinear abscissa for all the "globally elastic" tested leaves: (+) rank 8, (*) rank 10, (x) rank 11.

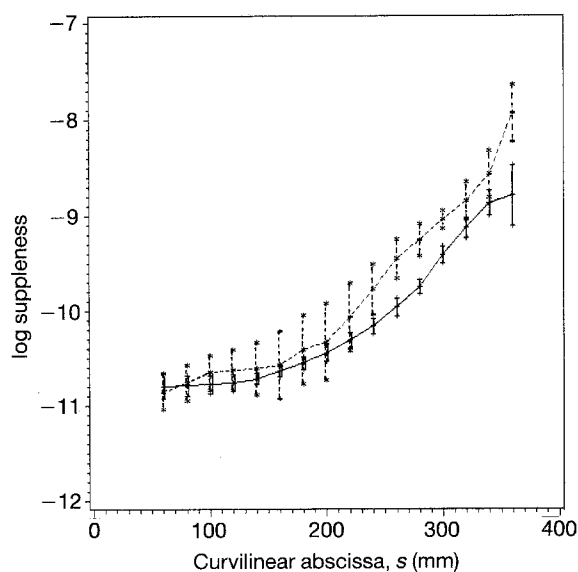


Figure 8 Effect of lamina disruption on the relationship between suppleness and curvilinear abscissa: (+, -) entire leaf, (*, ---) midrib alone (mean \pm standard error on a sample of seven leaves tested before and after lamina disruption and two reference undisturbed leaves tested twice).

($\alpha = 0.0001$), with rank 10 differing from the two others.

An interesting point is to assess the part of the midrib in supporting the overall leaf. As yet mentioned in the materials and methods, this has been characterized through sequential testing of:

1. The undisturbed leaf, and
2. The same leaf after suppression of lamina cohesion (in these tests the load levels were limited to the two least loading to prevent leaf damage). Fig. 8 shows the log transformed mean suppleness versus curvilinear abscissa for the seven leaves tested. The global trend is, as expected, that part of the lamina increases

from the base to the tip. However, within this subset of leaves, the linearity of the log transformed relation is no longer provided*. Thus slope analysis is no more suitable. A three way analysis of variance was, therefore, performed [with a model including leaf effect, lamina disruption effect, curvilinear abscissa effect, (leaf effect \times lamina disruption) and (lamina disruption \times curvilinear abscissa) first order interactions]. To do so, suppleness was interpolated at a given set of equidistant s in each individual curve (keeping the total number of degrees of freedom per test unchanged). The interaction between lamina disruption and curvilinear abscissa is statistically significant ($\alpha = 0.0375$). Moreover, a Tukey analysis of the means ([24]) reveals that the lamina part is not significant up to 200 mm, and then becomes significant. From the mean curves, the mean contribution of the midrib to the flexural behaviour of the whole leaf can also be quantified. It is more meaningful to express it in terms of part of the flexural rigidity (although there is some bias related to log transformations before averaging and taking the inverse values, the order of magnitude are correct). The midrib represents more than 87% of the leaf rigidity within the basal quarter of the leaf, and it reaches 50% only at the middle of the leaf. Thus, the midrib greatly stiffens the leaf, especially at the places where bending moments are high.

The last fact that can be extracted from the results goes back to the leaf form. Given the self weight loading (in equilibrium configuration) and the leaf suppleness, it is easy from Equation 1 to calculate the leaf curvature variation related to self weight. However, which part of the leaf curvature can be explained by the so calculated elastic curvature? From the data, the relative difference between real leaf curvatures and the calculated elastic ones can be estimated as 0.70 ± 0.15 (this ratio displays no evident relationship with s). This means that such elastic straining of the mature leaf under its self weight explains only one-third of the leaf habit. This conclusion is also supported by the common observation that, if a maize leaf is rotated 180° around its midrib, the leaf maintains a clear upward curvature, in spite of downward acting bending moments. The phenomena that determine such "natural" curvature are unknown. One may think of time-dependent mechanical effects such as creep. It is clear that the above-presented test can be applied perfectly to creep studies and, moreover, that *in vivo* tests are still advisable in such long term experiments. It should be added that other, more specifically biomechanical phenomena related to growth and anatomical maturation can also play a major part [4].

6. Conclusions

An *in vivo* flexural test has been designed and conducted on maize leaves. Data processing is based on local structural definition of the longitudinal suppleness of the leaf, which originates in the theory of pure plane bending of initially curved beams. It takes into ac-

*Such non-log linearity seems in contradiction with the aforesaid log linear relationship between suppleness and curvilinear abscissa for all the undisturbed leaves. In fact non-log linear suppleness distribution along the leaf is rather frequent. However, mixing of many curves from different leaves hides this effect, legitimating both the mean linear regression and the analysis of slopes for rank or load level effects.

count the large displacements that occur. A specific procedure for curvature and suppleness calculations has been designed and is methodologically discussed here. The crucial factor is the accuracy of point positioning for description of the leaf form. The use of a photographic and two-dimensional digitizing method, as done in this study, is limiting for accuracy, as it requires selection between numerous experiments, to retain only those with satisfactory precision. The use of a three-dimensional magnetic digitizer [13] to increase the accuracy of the form measurements is presently under development.

The results presented here only concern the elastic flexural behaviour of the leaf (which could be characterized in 59% of the tested leaves). There is always an almost exponential increase in suppleness, from the base to the tip of the leaf. It is demonstrated that the midrib plays a major part in the bending stiffness. Therefore, the next step in the study of maize leaf mechanics will concern the modelling of this midrib as a composite tapered beam. The leaf habit showed that self weight related elastic bending strains only account for one-third of the actual curvature. Thus, some time-dependent phenomena (either creep or biologically dependent mechanisms) have to be studied to account for curvature. Lastly, and in spite of sustained effort in leaf material standardization, it should be said that an important quantitative variability in leaf flexural characteristics is displayed.

Acknowledgements

We acknowledge Professor B. Taris and all the research team of the Chaire de Phytopathologie for their hospitality in their laboratory at E.N.I.T.A, Bordeaux. A special thanks to B. Chauvin for his very clever technical support. The present work is part of the senior author's thesis, who received a grant from the Département de Bioclimatologie, Institut National de la Recherche Agronomique (France).

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Received 16 February
and accepted 6 October 1993

Appendix: Definitions of the main biological terms used

Growth and anatomical maturation. The growth of a body means, in biology, irreversible strains related to a concomitant increase in its (dry) matter mass. At the end of the growth process, there are several changes in the internal structure (anatomy), particularly the spatially located deposition of a particular set of polymers called lignins [15]. This maturation has been shown in trees to cause internal stress fields which can be the mover of biologically controlled reorientation of growth axes [4].

Leaf rank. The number of the leaf within the sequence of leaf emergence (the first leaf to emerge has rank one).

Midrib. A central, thickened and "V-shaped" ridge (rib) within the leaf.

Phenological age. The main difficulty in assessing the age of a plant comes from the fact that its development kinetics can vary, first of all with temperature. Thus the "true" age of the plant is better assessed by morphological events like leaf appearance, flowering, etc.

Turgid. A plant organ is said to be turgid when the hydrostatic pressure inside its cells (called the turgor pressure) is positive. Such pressure is explained by elastic reaction of the cell wall to volumetric strains related to water flowing into the cell. Such water flow is driven by water potential differences between the cell content and the surrounding solution, and it stops when the turgor pressure equilibrates to the osmotic one. "Fully turgid" means that turgor pressure is maximal.