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Some aspects of sunflower crop physiology

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Summary:

The main traits of sunflower behavior related to crop physiology are developed here. They come expecially from the French group working on sunflower crop physiology and have been confirmed for plants growing under Europeans conditions. The author discribes first the growth characteristics of the plant (phenology, climatic requirements, dry matter accumulation and main growth stages and steps). The settlement of the captors (roots and leaves) is briefly described and illustrated by more recent finding. The optimum value for leaf area is close to 3 square meters of leaves per square meter of soil. More important than leaf establishment, the yield variations are explained by the leaf area duration and survival after flowering. Among all the physiological functions, special attention is given to the high level of photosynthesis observed in young leaves. The researches carried out on the Ribulose-Bi-Phosphate Carboxylase/Oxygenase allowed to understand such a behavior. The translocations of assimilates from the sources to the sinks is also discussed especially through the activity of enzymes responsible for saccharose translocations. On this special point, first results related to hormonal controls (ABA) are reported as a possible influence on the sink effect.

A part from the risk of deseases, the main limiting factor for sunflowers cultivation under European conditions is water. Special attention was given to the water status both under limiting and non-limiting conditions. Under high water availability, the water consumption increases considerably due mainly to the stomatal apparatus (large and numerous stomatas, low resistance to water flux). Nevertheless, when water stress occurs, mechanisms of drought adaptation can be switched on. The conditions for such behavior are described below.

In yield elaboration pathways, the importance of the number of seeds per square meter is developed. Depending on the level of this yield components, two growing stage must be checked carefully when attempting to optimize the quantity of seeds : the initiation period and the flowering time. Nitrogen and water have been established as the main factors acting on this component. Seed size can also vary, according to both genetic effect (about 40/50 % of variation), and environmental factors. Leaf area survival, which is strongly correlated to water availability during the ripening period, will optimize the second component. In such a case, oil content improves.

Introduction

Plant physiology interacts very much with environmental conditions. The presentation developed here will try to summarize some traits related to sunflower crop physiology derived from the results of the French Sunflower crop physiology group and highlighted by the literature. The main partners of such a group are INRA (Institut National de la Recherche Agronomique) from Toulouse-Auzeville, Clermont Ferrand and Montpellier, UPS (Université Paul Sabatier - Laboratoire de Physiologie végétale, Toulouse), ENSAT (Ecole Nationale Supérieure Agronomique de Toulouse) and CETIOM.

In order to improve the quality of plants, genetics is very helpful to correct problems in plant behavior. A great deal of success has been achieved (earlyness, yield levels, deseases tolerance or resistance, oil content and technological qualities.....). The new techniques of the genetic engeneering will certainly lead to further improvments. Nevertheless, progress has also been obtained in the field of the crop physiology. The better this knowledge is, the better the technical pathways will become, permitting more efficient and rational agricultural practices.

Those results have to be transfered from our laboratories into the field. Although this was essential in the past, it's becoming now essential for the survival of the European grower under the new EEC policy. To meet the requirents for lower costs interventions must become more scientific and accurate: the extension of Crop Physiology knowledge can make this more predictable.

1. Plant growth:

The whole growing cycle of the plant takes between 120 to 150 days from emergence until physiological maturity. In accordance with a temperature base for GDD (growing degrees days) of 6°C, the summations required vary from 1550°c.d (early cultivars) to 1700°c.d (late ones) - (CETIOM, 1986). Without important limiting factors, the biomass for sunflower crops reaches about 12 t per hectare. Until flowering, the stems (50%) and the leaves (25%) make up the main part of the dry matter. The root biomass is maximum at flowering (1 t/ha). As flowering and seed growth occurs, most of the assimilates are allocated to the capitulum. The lower the limiting factors (water...) are during the ripenning period, the higher the late assimilation which will lead to the best seed and oil yields. The harvest index varies from 0.25 to 0.35 and improvements are required.

The main climatic requirements can be summarized as following (Robinson, 1978):

- Seed germination can occur at 4°c, but the optimum to reach quick germination varies between 8 to 10° c.
- Young plants are resistant to frost. At the cotyledon stage, plants can survive temperatures of -5 to -7°c. Nevertheless, as soon as the first leaves appear, frost tolerance decreases. Under temperatures of below 0°c, the first leaves and terminal bud can be destroyed.
- Optimum value are also indicated for the net assimilation rate. The temperature base of 6°c is generally used for GDD summations, instead of an optimum at 7,2 °c. On the other hand, the photosynthetic level seems to reach a plateau between 27 and 28°c.

The growing cycle can be divided into 5 main stages according to the physiological processes occuring during the following periods (Merrien, 1992). - (Figure 1):

a. From sowing to emergence : soil humidity and temperature will explaine the duration of this stage. Emergence should be obtained under 7 days for optimun plant settlement and regularity.

b. From emergency to "4 leaves stage": the root system grows very rapidly and can reach 1 m. The differentiation of one leaf requires on average 20°c.d (base 6). 20 to 30 leaves will be obtained according to the genotypic variations.

c. From " 4 leaves stage" to bud of 15 mm of diameter: during this step, differentiation of the floret (1800 to 2000) is the principal physiological process. This number has two components on one hand the number of parastics, particulary influenced by the plant density and following the Fibonacci series (Hernandez and Palmer, 1988) and on the other hand by the number of florets per parastic, especially correlated to the plant's vigor (leaf area, dry matter, nitrogen absoption) at the budding stage (Steer and Hocking, 1983; Picq, 1986).

d. From bud at 15 mm to flowering : exponential growth of the plant and leaf area establishment are the main traits during this stage. Maximum values (2.5/2.8 g of dry matter/ MJ) for light convertion to biomass are obtained (Trapani et al., 1988). Plant adaptation to drought can occur.

e. Flowering period : very quick at the scale of the plant, this stage takes about 2 weeks in the fields. The seed set can be affected by water stress during this period (Robelin, 1967).

f. From the end of flowering to physiological maturity: the dry matter accumulation decreases. In the seeds, biosynthesis is very active in producing oil from late assimilation and in causing proteins synthesis from translocations.

2. The captors settlement:

2.1. The roots:

At the beginning of the growing cycle, root biomass represents 10 to 15 % of the total dry matter (Maertens et Bosc, 1981). Roots grow quickly and early (compared to the shoots) but are are very sensitive to soil structure problems (soil compaction, plow-sole...). The root system includes a taproot and lateral ones which appear following an acropete process (Aguirrezabal, 1989). Just under the collar (first 10cm), high concentrations of lateral roots can be observed, issued in many planes (Figure 2). 80 to 90 % of the total secondary roots are from this type. The nearer the secondary root is to the collar, the longer it is. It is possible to observe an area of inhibited root emission between this area witch is called the "crown" and the root cap. The first secondary root appears following the cotyledons and then the first leaf plane. Later, it is difficult to correlate the root appearance and the foliar plans. From the dynamical point of view, the taproot and the secondary roots from the crown have a more or less steady growth rate over time.

For the others ones, each time a new order root occurs (i.e. from III to IV type), the growth rate slow down for 2 or 3 days (Figure 3). The trophic relationships, the competion and allocation of carbon are actually studied. Steer (1988) suggest that root mass is influence by nitrogen supply before floret initiation. From all these primary results, the root architecture of the sunflowers which have been studied seem to be more a parallelipipedic in shape than conical. The results of nitrogen or water soil extraction by modelling is improved considerably by taking such a modification into account.

2.2. The leaf area:

The role of leaf area is crucial for the crops to enable them to intercept sufficient light. In the particular case of sunflower, we have demonstrated the excellent adjustment between leaf area and water availabilities (Merrien et al., 1981a). To a lesser extend, nitrogen nutrition can also interact. Usually, under European conditions, leaf establishment is not a limiting factor (sometimes excess of leaf area can be a source of complaint). More often, especially due to the occurence of drought, leaf area regression is very well correlated to the yield, and leaf area resistance to aging is a positive parameter for sunflowers grown under dry conditions (Merrien et al., 1981b).

a. leaf area establishment:

The leaf number is controlled in the early growth stage, during the initiation period. Among the climatic factors that can modify the leaf number, water and photoperiod are usely considered (Yegappan et al., 1980). The greater the water defict, the lower the number of leaves. Regarding the leaf settlement, 2 or 3 opposite leaves can be observed. Later, the phyllotaxy will alternate and the leaves will appear following a spiral. The modification in the rhythm of occurrence is due to the beginning of the floral initiation at the apex level. The maximum leaf area is obtained prior to anthesis. The value will fluctuate according to the plant settlement (between 4000 and 7000 cm2).

b. Contributions of the different levels in the canopy:

We observed not only that the largest leaves are at the 15th to 20th rank from the collar, but also that they have the best photosynthetic potential level (Figure 4). Experiences of leaf ablation allows to define the individual contribution of each leaf level precisely. In the case of ablation of the upper leaves in the canopy (18 to 25 numbered from the collar), leaf area is reduced by 22% and in the same way, production by 45 %.

c. Leaf area index and leaf area duration:

Like many crops, the maximum light interception is obtained as the leaf area index (LAI) value reaches 2.5 to 3. Maximum yields are obtained for such values at mid-flowering stage (Figure 5). In order to optimize the foliar apparatus functioning, some rules should to be respected.

- Exhuberation should be prevented during the establishment stage as this is source of increasing in water wastage, disease risks, lodging, and the occurence of early senescence due to self-shading of the lower leaves by the upper ones.
- Drought adaptation proccess can be promoted during the vegatative stage if natural water availabilities (soil contributions + rainfalls) is not excessive (Blanchet et al., 1990):

160 mm are enough to reach the minimun leaf area level (2.5/3). Irrigation prior to anthesis should be applied only if this level is not reached. This adaptation will affect the level of leaf area, the functionning of the captor and the assimilates redistribution during post anthesis stage. This will be described in detail in the next chapter.

Even more important than the LAI itself are the leaf area duration and survival which have to be taken in account. We have retained the leaf area duration parameter (LAD), which integrates the leaf establishment, the plateau and also the regression speed over time. For sunflowers crops, LAD values (expressed in square meters x days) varie from 100 to 250 m2.d. (Figure 6). Before anthesis, the leaf growth is mainly controlled by plant population and soil fertility (nitrogen and water). During the post-flowering period, this LAD could fluctuate considerably (from 30 to 100 m2.d) and is particularly related to water availabilities.

When drought occurs during the early stages, the leaf area development will be moderate, the number of leaf will be reduced (in case of early soil dessication), and each leaf will get a lower leaf area. In case of late water deficits, leaf area survival will be affected and the senescence processes will occur very quickly and suddently.

3. The mains physiological functions:

3.1. Photosynthesis:

Sunflower crops are characterized by a high photosynthetic level, especially in young plants. The enzymatic apparatus is a C3-type (assimilation of CO2 through the RUBISCO (= Ribulose 1-5 Bi-Phosphate Carboxilase/Oxygenase activity). The correlation between the enzyme content and the photosynthetic activity is high (Ranty and Cavalié, 1982). The gas exchanges are affected by photorespiration which can lead to CO2 losses approaching 10 mg/h/dm2. By taking in account the energetic costs for biosynthesis, it is possible to confirm that at the field level, the energy included in biomass is about the same for sunflower (C3) and maïze (C4) - (Figure 7). The energy accumulation looks even more rapid in sunflowers during the early stages (Blanchet et al., 1982a). Different factors can explain this behavior:

---> at the gas exchange level, stomata are numerous, and of large length. The stomatal resistance to surface CO2 reaching the photosynthetic site through the sub-stomatal chamber is lower.

---> at the carboxylation enzyme level, we can argue that protein is highly present in the leaves (60% of the total protein content or 10% of the dry matter), its specific activity is greater than the other C3 crops. In vivo, the RUBISCO activation level of wheat, peas stable. For this biochemical portion, changes are mainly limited to redistribution. Our experience has shown that 68% of the nitrogen stored in the seed comes from protein redistribution from the leaves (Merrien et al., 1988).

3.3. Water status :

Most of our results bear upon behavior of cultivated sunflower. Nevertheless, an important contribution is also expect from the findings on wild species to improve sunflower drought tolerance (Serieys, 1991; Vannozzi et al., 1992).

Concerning the cultivated sunflower, two different types of behaviors will be presented : the first discribes the traits of water consumptions without water stress and the second one will try to demonstrate that sunflower crops could be quite well adapted to drought conditions.

a. Behavior without water deficit:

The first observation to be reported bear upon the high water consumption for the crop: more than 600 mm are often observed (Morizet and Merrien, 1990). Among the main causes of this, we can indicate first the low resistance to water translocation from the root to the shoot, compared to maïze for exemple. The stomatal resistance, as indicated in Table 1 are among the lowest. So, the greater the water availability, the greater the consumption will be.

The leaf struture is also to be taken into account, and especially the stomatal apparatus: the stomatal resistance is low, the stomata are numerous, big in size (especially in length), with a high density on the lower face.

The main consequences are the wastage and the low efficiency of water (WUE). As climatic demand increases, photosynthesis reaches a plateau about 28°c, but transpiration continues to increase: the ratio (correlated with the instantaneous water efficiency) decreases. In such a case, the WUE will be close to 2.5 g of dry matter/liter .

b. Behavior under low water availability:

The mains differences that occur can be summarize has following:

- The osmotic adjustment:

The main reason why this criteria is important is because under water stress, the plant cells are able to maintain the minimum turgor pressure to allow functionning of the plant, especially gas exchanges. Until now, it had been accepted that for the normal cultivated sunflower, the adjustment was very low. Neverthelesss, genotypic variations exist (Chimenti and Hall, 1988). Planchon (1990) also demonstrate that when water stress occurs progessively at the budding stage, osmotic adjustment is observed (Figure 9).

- Effect on Photosystems

Under water stress, the photosynthetic apparatus is usually affected and photosynthesis declines. In the case of sunflowers, Blanchet and Merrien (1982) had demonstrated that transpiration was more affected than photosynthesis (Figure 10). Planchon (1990) indicate that the chloroplasts keep their exitation ability under low water stress. In case of progressive water stress occurence during the vegetative period, the difference between well watered plants, and stressed ones was very low. The restriction to assimilation by water shortage is dominated by the effect on the development and survival of leaf area rather than by its own activity (Blanchet et Merrien, 1982; Connor et Palta, 1985),

- Metabolism.

Three mains enzymes were checked under water deficits: Rubisco, Nitrate reductase (NR), and Saccharose Phosphate Syntase (SPS). Among the leaf activities, the potentials for CO2 fixation and for nitrate reduction are not affected under water stress as much. In the case of plant adaptation during the vegetative period, proteolytic activities seem to be less than when there is plant stress after flowering. Regarding saccharose translocations, an improvement can be obtained (Figure 11), well correlated with an improvement in the translocations to the seeds leading to an increase in the harvest index (Poeydomenge, 1992). The hormonal control can illustrate such a behavior: the ABA (Abscissic Acid) content is higher in the leaves of stressed plants.

c. Consequences on the whole plant :

As illustrated in Table 2, by creating drought adaptation or hardness during the vegetative period, the following characters have been obtained:

- water consumption was reduced, without any great effect on biomass. Leaf area index is moderate, and close to the optimum value

- stomatal resistances seem lower on plants previously adapted. There is no effect on gas exchanges.

- improvements in water use efficiency (i.e. increase in the ratio Photosynthesis/Transpiration).

In the light of these results the findings of the water managment in the fields network trials carried out by CETIOM can be summarize as following (Merrien and Grandin,1990) :

- it's desirable to promote the development of a moderate leaf area index (no more than 3) at anthesis. This could be obtained by water availabity (soil contribution + rainfall + irrigation if necessary) of 160 mm. The optimum level for the satisfaction ratio of the water requirements is 0.69. In this case, drought adaptation can occur. The question remains about what strategy to develop during rainy seasons or under conditions of deep soils with high water availability.

- leaf area duration from middle of anthesis to physiological maturity had to be maintained at 90 m2.d. (which represented a leaf area index of 2 during 45 days) - (Figure 12). Water requirements for such a goal are close to 180 mm under the French climate. Improvements in oil content will be obtained.
or soybean do not exceded 60%; in the case of sunflowers, the maximun value (100%) of this parameter can be checked early in the morning (Amiel, 1988). The saturation plateau is also greater than in the case of soybeans. Nevertheless, high fluctuations can be observed. Over time, the high level for photosynthesis observed for young leaves decreases rapidly. Among the mains causes, we can list:

+ Modifications in the "Source/Sink" ratio didn't significantly modify the regression (Merrien et al., 1983), as is the case with soybean behavior, where the occurence of pods can stimulate the photosynthetic apparatus. Nevertheless, in beheaded sunflowers (total suppression of the sink), the protein content (especially Rubico) does not decrease significantly.

+ As the foliar apparatus expands, the light interception by the lowest leaves of the canopy decreases and leaf aging increases (Danuso et al., 1988). In such leaves, if the chlorophyll content does not vary very much, the solub proteins do, especially the Rubisco. This process increases under water shortages. Succesive cycles of dehydratation and rehydratation of the plants leads to a break down of the carboxylase protein which seems to be more sensitive to the proteolitic mecanism (Amiel, 1988). In the same way, the turn-over of such proteins is low. 30 days after the beginning of flowering, sunflower leaves lost 80 % of the Rubisco content. The nitrogen coming from the breakdown of proteins is quite well allocated to the younger organs and especially to the seeds.

+ Adjustments can occur and in somes cases, a better activity can compensated a lower content. The proteolytic process can also be delayed, especially in the case of sunflowers growing under low water condition and nitrogen shortage during the vegetative stage and where adaptation processes have been switch on.

Taken together, these arguments lead to the conclusion that it is important to improve sunflower foliar resistance to aging. In the same fields, breeding varieties with moderate leaf area expansion but more resistance to senescence could benefit drought tolerance.

3.2. Translocations:

a. Repartition by organ:

At anthesis, biomass stored in stems and leaves reaches a peack. Translocations occur mainly from the leaves to the seeds (Blanchet et al., 1982b). They can fluctuate very much, according to the genotypic effect or to the water status. Hall et al., (1988) estimate that translocations of pre-anthesis assimilates to the seeds can represented 23 to 35 % of the total carbon stored in the seeds. The dry matter weight of the capitulum (without seed) does not increase as the maximum diameter is reached (end of flowering). At the level of the seeds the increase in dry matter is due on one hand to the direct translocations of assimilates coming from phoytosynthesis in the leaves which one still alive, but is also due to redistributions from senescent organs.

b. Repartition by nature:

The total quantities of glucides stored in the whole plant do not varie very much after anthesis (Figure 8). In some cases, it can decrease (due to the high cost of lipid biosynthesis). The accumulation of the nitrogen compounds takes place essentially during the vegetative period. After flowering, the total quantities of nitrogen stored in the plant is

- as the flowering period is the more sensitive stage to drought, water stress must be prevented at that time.

For the whole growing cycle, the optimization of the plant functionning and yields could be obtained with no more than 450 mm.

4. Yield elaboration:

Sunflower yield can be expressed as following:

Yield = number of capitulum/m2 x number of seeds/capitulum x weight of the seed

= number of seeds/m2 x weight of the seed.

The best yields will be obtained by the combination of the 2 components.

4.1. Optimisation of the number of seed per square meter:

It will depend especially on the number of seeds per head, according to the fact that sunflower yield does not vary very much with plant density (no significative differences between 4.5 to 7.5 plants/m2). Even more important than the number of plant per square meter, the distribution in the settlement had to be taken in account: the worse this repartition is, the worse the yield will be : sunflowers do not compensate for the lost.

Among the factors able to induce variations in the number of seed par capitulum, we can list:

- the number of parastics, following the Fibonacci serial and well corelated to plant density and stem diameter (Table 3) - (Cadéac, 1988).

- the potential number of florets, which is controlled during the initiatiation period. All parameters taking in account the early growth of the plant will be correlated to the number of florets (potentially between 1800 and 2000) : leaf area developed at the end of the floret differenciation (Figure 13) - (Picq, 1986), dry matter produced, or nitrogen absorption (Steer and Hocking, 1983; Steer and Hocking, 1984).

- this potential will actually be realised during the flowering period. Abortion of seeds can be observed under water stress during this period. 70% of the plant's requirements must be met during this stage (Figure 14).

- during the ripenning stages, competition for assimilates could induce late abortion of the seeds. In the case of water stress, plants with leaf area reduced by early senescence will presente a lower number of seeds. Picq (1986) shows that during this stage the plant requires 1.8 to 2 cm2 to produce one kernel.

4.2. Optimisation of the seed weight:

Two dimensions can be retained:

- the genetic one : for example, among the cultivars registered in France, the 1000 weight of the seed can vary from 50/60 to 30/40 g. In these cases, the oil content decreases with the big-seeded cultivars.

- the physiological one: this is particulary influenced by the capability of the plant to preserve living leaf area. The more the water plant requirements are satisfied, the better the weight of the seed (Table 4). In this case, an increase in seed weight will be associated with an increase in oil content. The position of the seed on the head also induces fluctuations: the kernels of the border will be heavier than the ones inside.

To conclude our observations regarding yield elaboration it should be remembered that the optimization will start with the seed sets of 10 000 to 12 000 seeds per square meter. In the case of limitation on the seeds number and instead of compensation occurance, the consequences on yield will persist.

Conclusions

By improving the knowledge of the plant behavior, we hope to improve the agronomical techniques for optimizing not only the functioning of the plant, but also yields and profits. To archive this, we believe that the following factors are crucial :

- More than plant density, the regularity of the plant settlement has to be improved (driller speed, seed quality, pests protection....)

- Until the end of the initiation period, the growth parameters of the plant will be well correlated to the number of seeds

- Luxurious development of leaf area before anthesis should be prevented : an LAI of 2.5/3 is enough. If nessessary, water and nitrogen could be use to increase the potential. By creating a moderate water deficit during this stage, drought adaptation process can be switch on. The question remains under deep soils, or under natural high water/nitrogen availabilities.

- Water stress should be prevented during flowering to optimize the seed number.

- All the agronomical pratices during the post flowering step should be directed at improving the resistance to aging of leaf area. The achievement of this objective will not only lead to an improvment of oil seed yield but also of oil yield.

Progress is still to be made in the field research of plant physiology: interaction between water and nitrogen in leaf establishment, regression, and also in the oil synthesis process. The high capability of the plant to extract water from the soil or sub-soil will only be well known when the root system is better understood. The hormonal control needs to be characterized, especially in case of drought adaptation. From all this research, plant indicators could be identified for the breeders: they can be completed by biochemical ones and the first preliminary findings are presented at this conference.

Modelling also will integrated all this knowledge and should help the advisers to define the agronomic potential of the crops and also the decision to be taken about somes agronomical practices (e.g. water management). Progress has been obtained in this a field by the adapatation of EPIC model to sunflowers by the French teams (Quinones et al., 1990; Texier et al., 1992) and of Ceres to sunflower by the Spanish and Argentine team (Villalobos et al., 1990).

Table 1 : Approximate size and distribution of stomata on mature leaves of different plants

Species	Average number of stomata/mm²		Average size of the stomata (lenght x width) in µm	Average distance on the lower face (µm)
	Upper face	Lower face		
Sunflower	85	156	38 x 7	91
Maize	53	68	19 x 5	137
Wheat	33	14	18 x 7	302

Table 2 : Gas exchanges according to different water treatments

Water treatment : - during the measurement period - prior	M. ET M. ET	0,5 M. ET Progressive adaptation	M. ET Stress during flowering
Water consumption (mm)	405	225	290
Total dry matter (g/plant)	111	120	96
Leaf area (dm²/plant)	55,0	36,6	21,9
Water potential (MPa) :			
- soil	- 0,3	- 1,0	- 0,3
- leaves	- 0,7	-1,1	-1,1
Relative water content (% max)	93,1	85,4	88,0
Stomatal resistance (s/cm) :			
- upper face	0,50	0,42	0,43
- lower face	1,15	0,72	0,82
Transpiration (g/dm²/h)	12,5 b	14,6 b	16,2 b
Net photosynthesis (mg CO2/dm²/h)	24,0 bc	45,1 a	30,3 b
Photosynthesis/transpiration (x10³)	1,9	3,1	1,9

Table 3 : Effect of the capitulum diameter and of the plant density on the parastic number

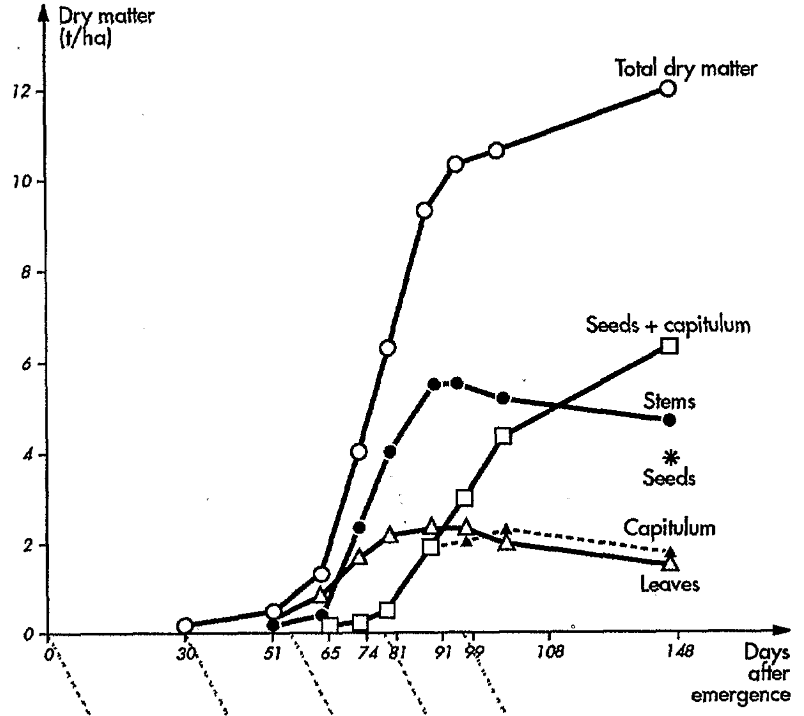
Plant density (/m²)	Capitulum diameter (cm)	Stem diameter (cm)	Number of parastics (max. frequency)
2-3	> 30	-	144
4-7	21 à 27	2,5 à 3,5	89
7-10	11 à 21	1,8 à 2,5	55
10-12	6 à 11	1,1 à 1,8	34

Table 4 : Effect of water limitation at different stages on the 1000 seeds weight

R. ET/M. ET Stage	0,3	0,4	0,5	0,6	0,7	0,8
1 = Emergency ➪ Flow.	nc	nc	- 20%	- 10%	-	-
2 = Flowering	nc	- 22%	- 22%	-15%	- 5%	-
3 = Flow. ➪ Maturity	- 50%	- 46%	- 28%	- 20%	-10%	- 5%

nc = no check

Figure 1 : Biomass accumulation in sunflower



Emergence B_8 E_2 F_1 F_4 M_3

Number of days	30	20 to 25	25 to 30	15 to 20	50
Dry matter accumulation (kg/ha/j)	10 to 15		200	100 to 150	30 to 40
Mains characters	Root growth and foliar initiation.	Floral initiation.	Increase in leaf area and active photosynthesis.	Flowering/Seed -Set.	Oil synthesis and translocations.

Figure 2 : Number of secondary roots by step of 2.5 cm on the tap root (each curve represente a sample date)

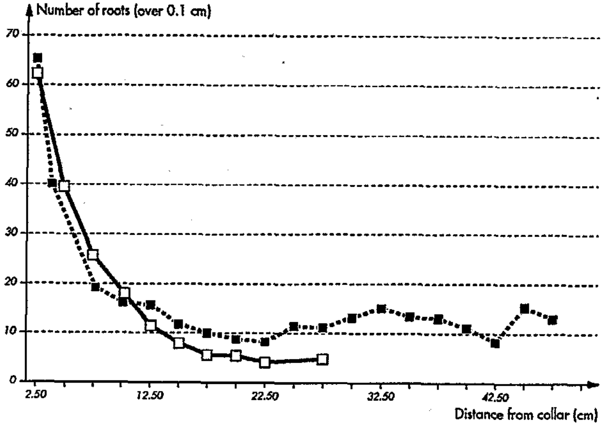


Figure 3 : Appearance speed of the secondary roots

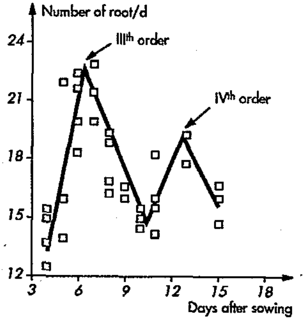


Figure 4 : Leaf area profil according to leaf position on the stem (0 = bottom)

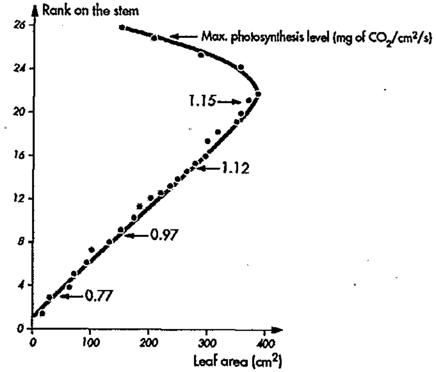


Figure 5 : Relationships between yield and Leaf Area Index (LAI) at flowering

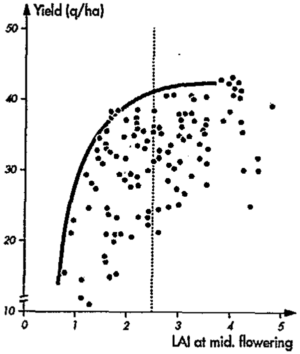


Figure 6 : Relationships between the final production and total leaf area duration

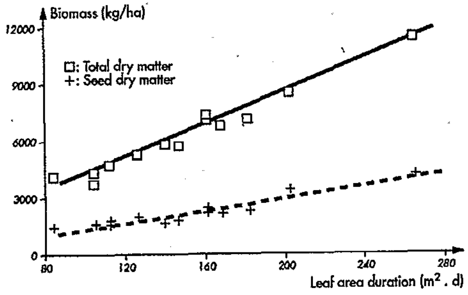


Figure 7 : Total dry matter production (a) and glucose-equivalents (b) through the time for sunflower, maïze and soybean

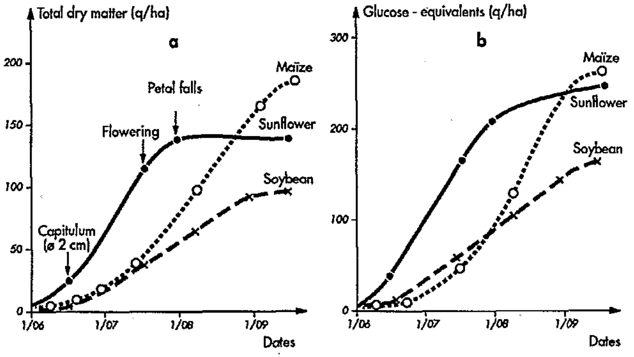


Figure 8 : Allocation of assimilates by nature through the time in sunflower

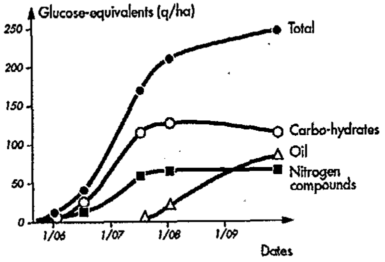


Figure 9 : Relationships between the osmotic potential (Ψo) and the leaf potential (Ψf) according to the water stress occurrence.

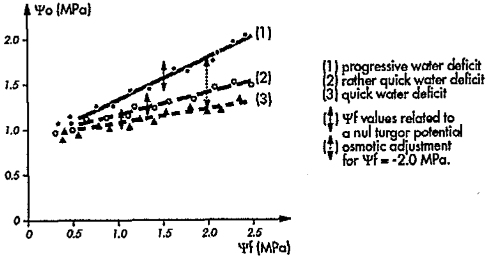
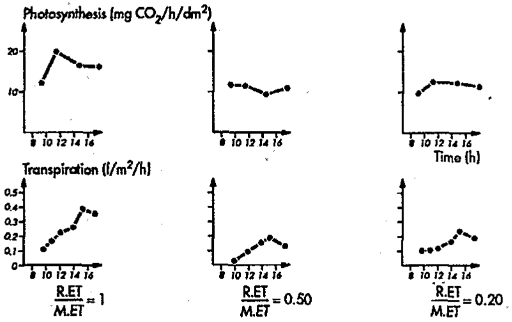


Figure 10 : Kinetics of photosynthesis and transpiration through the time, according with different water supplies.



R. ET = Real evapotranspiration M. ET = Max. evapotranspiration

Figure 11 : C^{14} allocation to saccharose and starch in sunflower submitted or not to drough

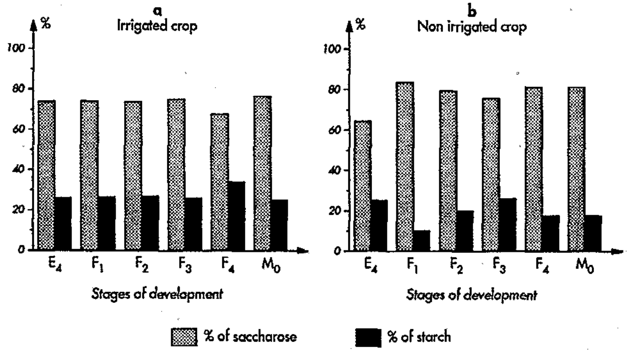
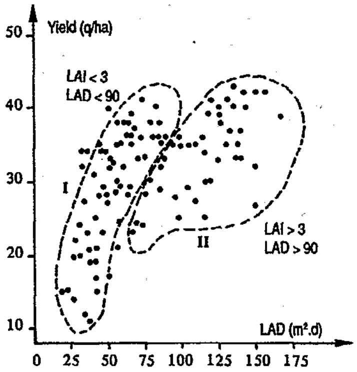


Fig. 12 : Relationship between leaf area duration after flowering and yield



LAI = Leaf Area Index
LAD = Leaf Area Duration

Figure 13 : Relationships between leaf area at the end of the initiation period (stage 3.2) and the number of florets

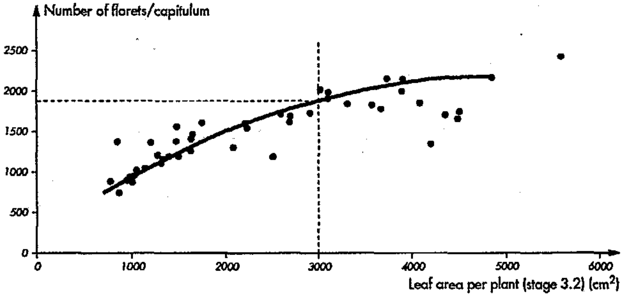
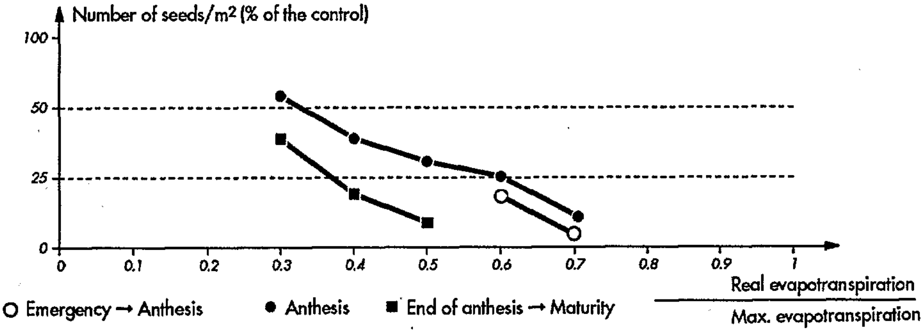


Figure 14 : Effect of water stress at different periods on the seed number



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