THE GROWTH AND DEVELOPMENT OF HELIANTHUS ANNUUS L. cv INRA 6501 AT THREE IRRADIANCE LEVELS.

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SUMMARY
Seedlings of sunflower (INRA 6501) were grown at 15,30 and 60 $W.m^{-2}$,at 16 h per day, 22°C and 70% relative humidity in subirrigated gravel culture. High irradiance level (IL) accelerates development in a constant way from germination to anthesis. This acceleration is the consequence of a light dependent increase of relative growth rate (RGR) together with a proportional decrease of the duration of growth. In the linear phase of growth RGR decreases with leaf number independent of IL : this patternised retardation of growth may be related to flower induction. The volume of the growing shoot (GS) may be defined as the summation of volumes of successive internodes growing in length. The increase of this volume plays an important role in the adaptation of absolute growth rate of the plant to IL, because this volume is an important determinant of leaf initiation rate and of the size of the initiated primordia. At constant conditions the initiated primordia grow out according to a growth pattern depending on leaf number and IL. The size of GS reflects the size,architecture and phyllotactic order of the vascular system : the larger the number and diameter of the individual vascular sympodia the larger the diameter of GS, the larger the length of the orthostichy the longer GS. The rate of increase of GS depends on IL. One orthostichy below the leaf primordium, neighbouring leaf vascular bundles (direct bundles) merge and form together the socalled synthetic bundles. This special cambial system expands tangentially in the also expanding medullary rays with a rate proportional to IL and this development is related to the diameter the ripe flower head will reach. The unequally distributed tangential growth in the vascular cylinder causes the stem to be ultimately hollow.

INTRODUCTION.

The morphology of young plants growing at high irradiance level in the open or in the phytotron is often characterised by an increase in length and width of successive mature leaves, indicating an increasing absolute growth rate (Pieters 1974,1983). The mature length of successive internodes, however tends to be constant, although also the main axis is steadily increasing in absolute growth rate. This morphology suggests that there is a correlation between the mature size a leaf reaches, leaf initiation rate and the absolute growth rate of the axis. Sunflower and poplar conform to this morphology.

Analysis of the growth of poplar has shown that the cause of this correlation lies in the significance of the volume of the growing shoot (GS) in adapting absolute growth rate of a plant to the prevailing irradiance level (IL). The volume of GS may be defined as the summation of volumes of successive internodes growing in length. The volume of GS is also reflected in the architecture of the vascular system (Larson 1975,1977,1980, Pieters 1983) by a proportional increase of (1) the number of vascular sympodia composing the vascular cylinder and (2) the length of the orthostichy. The initiation rate of primordia and their size at initiation is correlated with the length or diameter of GS. The initiated primordium of poplar grows according to an autonomous growth pattern independent of IL. This growth pattern can be characterised as a specific relation between relative growth rate (RGR = growth rate in % per unit time) and the age of the organ. In the individual primordia of leaves and internodes of poplar RGR decreases steadily during their growth until RGR equals zero and growth stops. This means that also mature length (L_m) and width of the leaves are coupled to the

length of GS. Consequently, total leaf area production per branch per unit time, which is proportional to leaf initiation rate * length * width of the youngest mature leaf, is linearly related to the cube of the length of the youngest mature leaf (L_{my}^3) and to the volume of GS, as is experimentally shown (Pieters 1974, 1983). The rate of growth of stem length is coupled to the length of GS.

The increasing size of the vascular system is correlated with an increasing phyllotactic order, which is, according to anatomical literature, coupled to an increasing growth vigour. This indicates that the increase of GS as an adaptation to IL can be generalised. Poplar adapts its production to energy supply by investing cellular capital in GS, the average interest (RGR) remaining constant. With this organisation of growth poplar optimises its growth in height and leaf area to the prevailing light conditions and enhances the chance for survival in the course of years. The objectives of sunflower are different, because it is an annual herb with determinate growth forming a flower head: its has to optimise the chance for survival by the formation of an optimal amount of seed.

The objectives of growth analysis of sunflower are to establish (a) whether GS plays a role in the adaptation of growth rate to irradiance level, (b) wether the leaves grow according to a fixed growth pattern independent of irradiance level and (c) how sunflower adapts the size of its flower head.

MATERIALS AND METHODS
Plant materials and growth conditions
Helianthus annuus L. cv INRA 6501 was cultivated in gravel culture in polyethylene containers (250x250x300 mm^3) at three irradiance levels. The plants were subirrigated every 30 min with Hoagland A-Z nutrient solution modified after Steiner (1968). Three containers with one plant each were placed on a trolley in a light room for each treatment. The plants were irradiated from above and from two sides to ensure even irradiation. The irradiance levels were 15, 30 and 60 W.m^{-2}, 400-700 nm (Philips TLM/F 30 fluorescent tubes, 120 W). The day length was 16 h and night length 8 h. Room temperature was maintained at 20°C and relative humidity at 60 %.

Measurements
Length and width of every second leaf and plant height were measured 3 times per week from appearance to maturation. The date at which the flower bud became visible and the day of anthesis was recorded. The dates at which the first, the 19th and the last leaf reached 95 % of their mature length was read from curves of relative length against time. Relative leaf length is actual length of an individual leaf divided by its mature length (L/L_m). The diameter of the inflorescence at anthesis was measured.

RESULTS

Table I Phenological data and some plant dimensions of sunflower INRA 6501 grown at 15, 30 and 60 W.m^{-2}. Time to several stages given in the number of days after the opening of the cotyledons and (in brackets) as % of the number of days required to reach anthesis.

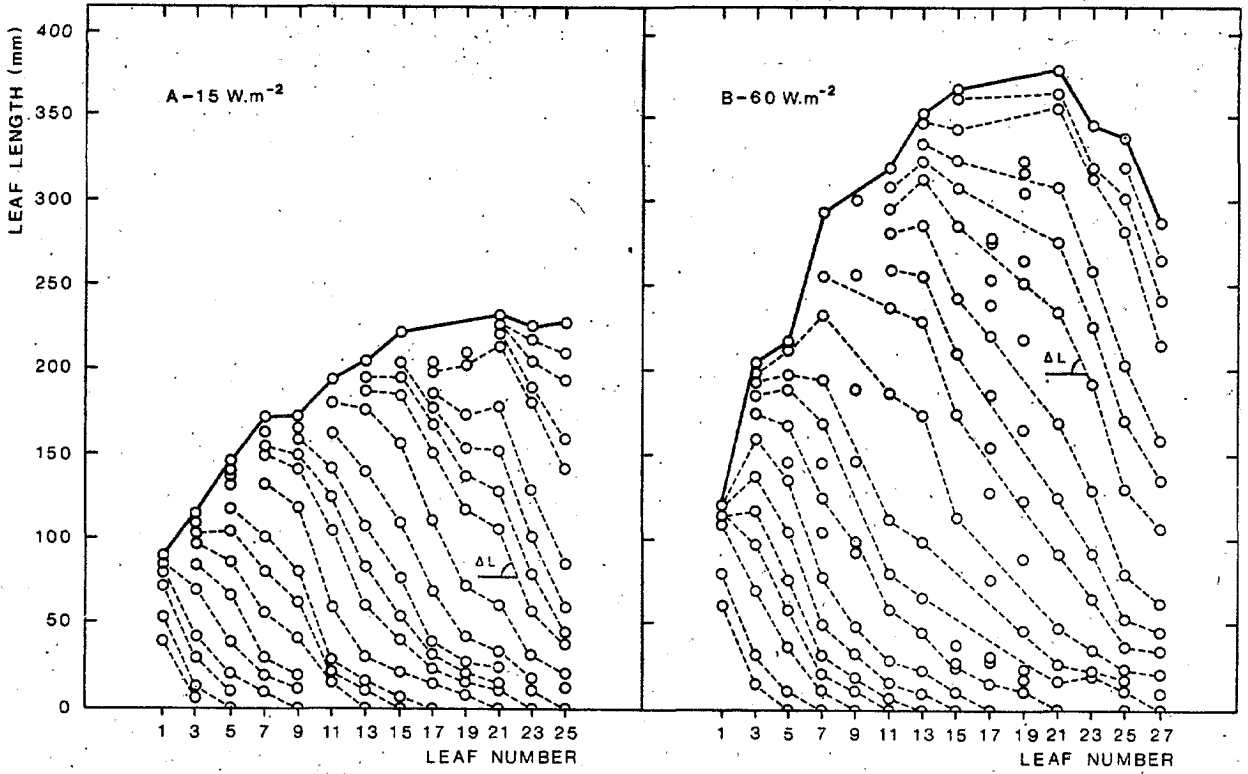| irradiance level W.m^{-2} | begin increase diam.shoot | appearance of flower bud | days from opening of cotyledons to | | | | anthesis | number of leaves | stem height mm |
			maturation of the						
			first leaf	19th leaf	last leaf	stem length			
15	7	37 (42)	19 (22)	73 (83)	82 (93)	79 (89)	88 (100)	27	1050
30	7	31 (44)	16 (23)	59 (83)	66 (93)	64 (90)	71 (100)	27	1050
60	7	25 (40)	15 (25)	51 (81)	54 (86)	57 (90)	63 (100)	27	1100

Fig. 1 Mature length (L_m) of successive leaves (solid line) and the decreasing length of successive growing leaves, measured at successive ages of the same plant (dashed line) vs leaf number. The tangent $\Delta L/\Delta N$ is the difference in length of successive leaves at about half mature length (ΔL). Plants grown at 15 $W.m^{-2}$ (A) and at 60 $W.m^{-2}$ (B).
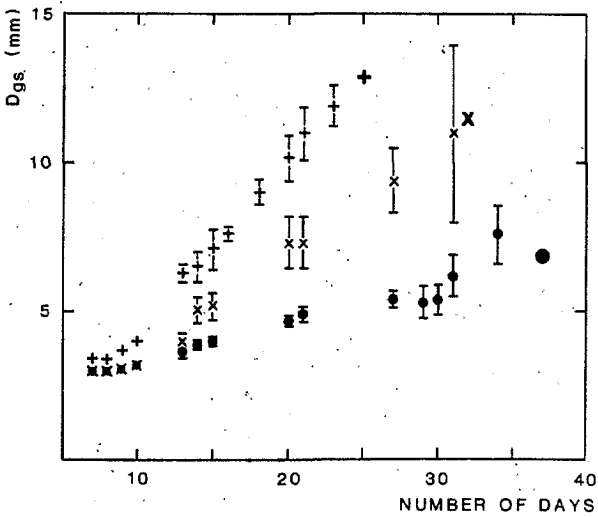

Fig. 2 The increase of the diameter of the growing shoot (D_{gs}) of sunflower grown at 15 ($\bullet$), 30 (x) and 60 (+) $W.m^{-2}$. Standard errors smaller than 0.3 mm are not shown.
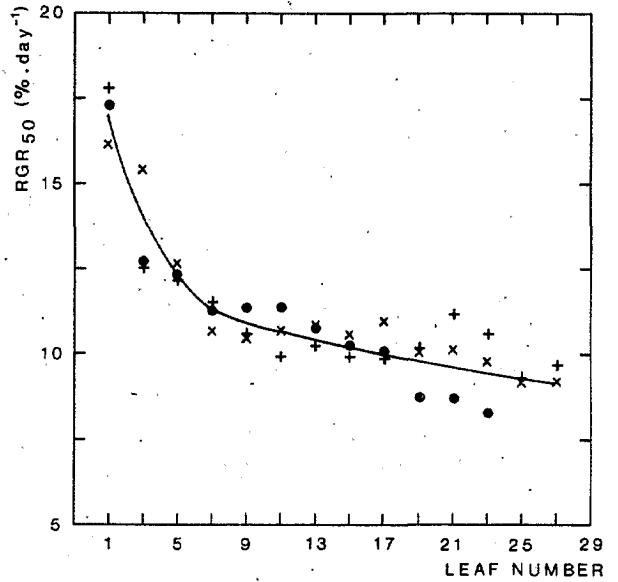
Fig. 3 The constant relationship between relative growth rate of leaves at half mature length (RGR_{50}) and leaf number of plants grown at 15 ($\bullet$), 30 (x) and 60 (+) $W.m^{-2}$. Bold symbols indicate the appearance of the flower bud.

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Table I summarises some phenological data and dimensions of plants grown at 15, 30 and 60 $W.m^{-2}$. High irradiance level accelerates developmental rate in a constant way throughout plant growth, as appears from the duration needed to reach a certain stage expressed in % of the number of days to reach anthesis (in brackets). The same holds for floral induction. It is clear that the average RGR is increased by high irradiance level, because it increases growth rate and maximum mature size of the leaves (Fig 1,solid line) and the diameter of the stem (Fig 2) and flower. The number of leaves nor the mature plant height,however, is influenced by IL. Fig 3 shows that relative growth rate of leaves at half mature length (RGR_{50}) is independent of IL, but depends on leaf number. The rate of the increase of mature leaf length ($\Delta L_m/\Delta t$) depends on IL (Fig 1,Table II). The slopes of the dashed lines in Fig 1 are a measure of $\Delta L/\Delta N$, which is the difference in length of successive leaves in the linear phase of growth (ΔL). ΔL at about half mature length is given in Table II and is about constant within each treatment and only slightly dependent on IL. The growth of the diameter of the growing shoot proceeds linearly with time and its rate is linearly related to IL (Fig 2, Table III).

Table II The rate of increase of mature length of successive leaves ($\Delta L_m/\Delta t$),its correlation coefficient (R) and the difference in length of successive leaves at about half mature length (ΔL) in plants grown at irradiance levels of 15, 30 and 60 $W.m^{-2}$.

irradiance level	$\Delta L_m/\Delta t$		ΔL
$W.m^{-2}$	$cm.day^{-1}$	R	cm
15	?.43	0.992	2.28±0.13
30	?.63	0.979	1.97±0.17
60	6.83	0.977	1.85±0.13

Table III Regression coefficient a, intercept b and correlation coefficient R for the relation between the diameter of the growing shoot (D_{gs}) and time in sunflower grown at irradiance levels of 15, 30 and 60 $W.m^{-2}$.

irradiance level			
$W.m^{-2}$	a	b	R
15	0.142	2.891	0.931
30	0.365	2.610	0.996
60	0.601	2.982	0.998

DISCUSSION

High irradiance level accelerates the development of sunflower (Table I) and thus increases the average RGR. In the linear phase, however, light does not have any influence on RGR of the leaves (Fig 3) and consequently also not on the absolute growth rate of epidermal cells (Pieters 1974). The increase of RGR by high irradiance level thus is confined to the primordial phase of growth : the potential growth rate of these cells is higher than the actual growth rate, which is limited by assimilate supply. During the growth of an organ the potential growth rate of the cells decreases and at a certain developmental stage assimilate level is saturating and the cells continue to grow with their potential growth rate until RGR is 0. The decrease of RGR with leaf number (retardation) in the linear phase of growth does not depend on IL and is therefore not due to competition for assimilates, but is physiologically determined, possibly by the increasing influence of the growing flower head. The retardation of growth with leaf number is also found in the growth of the internodes (Philippe and Dubouchet 1983).

The difference in length of successive growing leaves at about half mature length, ΔL, tends to be constant (Table II). Considering that this difference equals absolute growth rate, m_{50}, times the time difference (P) in appearing at 1/2 mature length (1/2 L_m), we get

$$m_{50} * P = \Delta L$$

P is plastochron duration (day/leaf) and its inverse (N) the rate of leaf appearance (leaf/day). Absolute growth rate $m_{50}= 1/2*L_m*RGR_{50}$, thus:

$$RGR_{50} * L_m / 2N = \Delta L$$

Leaf appearance in sunflower is correlated with RGR_{50} and L_m. It is obvious that the decrease of RGR with leaf number (Fig 3) correlates with the rate of leaf

appearance, but also that the constancy of ΔL (Table II) compels to assume that leaf initiation and RGR are generally correlated. The correlation between leaf initiation rate and mature leaf length suggests, that the size of the growing shoot (GS) is an important determinant of leaf initiation rate as well as of the mature length a leaf will reach. This idea is corroborated by the observations of Thoday (1922) and Priestley (1935) that high irradiance level increases phyllotactic order and that the size of the vascular bundle increases with mature leaf length. In sunflower, as in poplar, the size of GS and its vascular system plays an important role in the adaptation of absolute growth rate of the plant to IL. While in poplar, at constant conditions, the form of the relative growth curves (ln L versus time) of successive leaves are identical, in sunflower the form of the relative growth curves depend on IL and on the developmental stage of the plant. The growth model developed implicates that, at the constant conditions used, the increase of mean RGR by IL is compensated for by a proportional decrease of the duration of growth. This accounts for the acceleration of development by high IL.

The increase of the size of GS with time is reflected in the change of mature leaf length with time ($\Delta L_m/\Delta T$). In this way Table II illustrates indirectly that high IL accelerates the rate of increase of GS of sunflower, but the duration of its growth diminishes (Table I). The increase of the diameter of GS (D_{gs}) is also measured directly and appears to be linear with time (Fig 2). The rate of increase is proportional to IL (Table III). The duration of growth can be read from Table I and is 81, 64 and 56 days respectively. Using the linear regression, D_{gs} at anthesis can be calculated and is 14, 26 and 37 mm respectively. The measured mature diameters of the sunflower heads are 132, 238 and 356 mm. The ratios of mature diameter of head and neck are 9.2, 9.2 and 9.7. The development of both parts is clearly related.
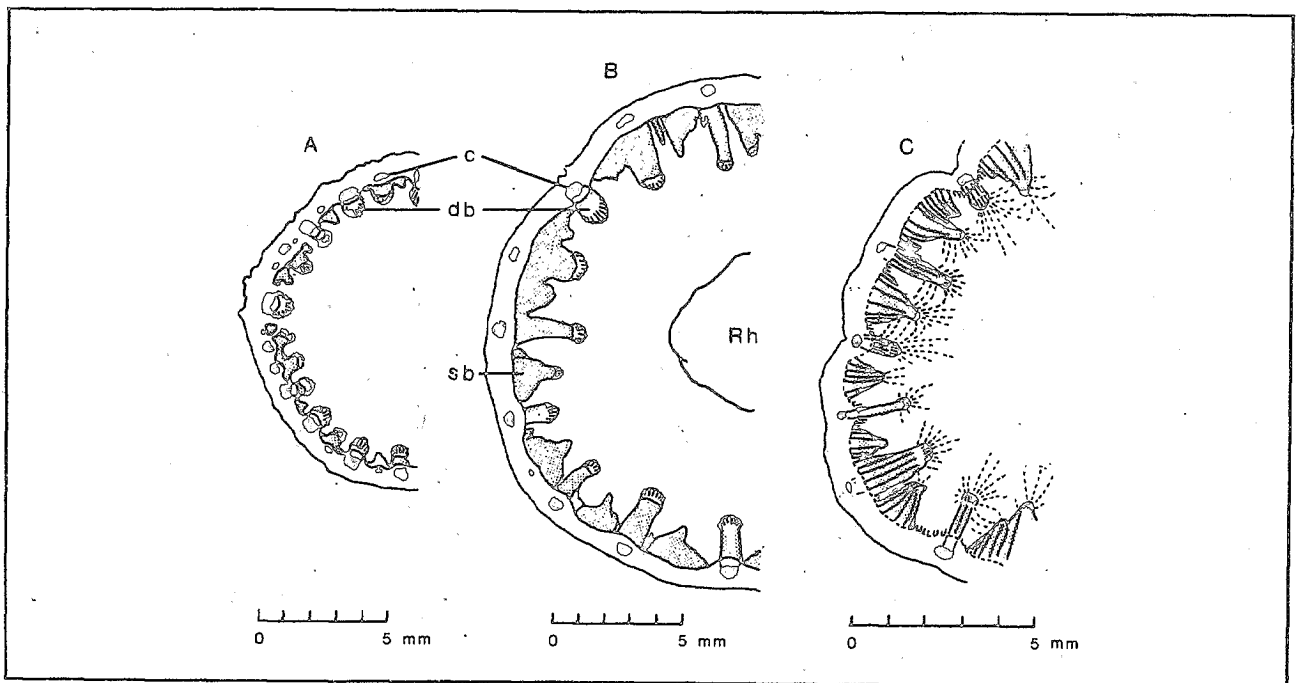

Fig. 4 Structure of the vascular cylinder in the growing shoot at different stages of development. A: young plant, B: older plant. The direct bundles (db) are recognisable by sclerenchyma caps (c, in black). Synthetic bundles (sb) are well developed in B ; their tangential growth is demonstrated by their wedge shape. Rh is rhexigeneous cavity. C: detail of B ; the radial lines in the secondary xylem show the direction of the individual elements formed by the cambial cells. The broken lines in the pith represent lines of strain by the arrangement, shape and dimension of the cells (after Thoday 1922).

The structural elements of the anatomy of a sunflower stem are (Fig 4a, b and c) a vascular cylinder with parenchymateous pith tissue at its centre surrounded by some layers parenchymateous cells, two layers collenchyma and a one-layered epidermis (Knowles 1978). It is clear that the light dependent increase of the diameter of the growing shoot of sunflower (Fig. 2, Table III) has to accomodate a changing size of the vascular cylinder. Thoday (1922) and Priestley (1936) describe in a classical study the anatomy of the sunflower stem and how the diameter of the vascular cylinder enlarges during development. The vascular bundles serving a leaf (direct bundles,db) are connected to the vascular bundle of the leaf one orthos ichy below (according to the phyllotactic order, 1, 2, 3, 5, 8 or sometimes 13 internodes downward). Further down these vascular bundles merge with neighbouring vascular bundles and form the socalled 'synthetic bundles' (Fig 4b). The cambium in the synthetic bundles continuously expands tangentially in the also expanding medullary rays. The irradiance dependent increase of the diameter of the growing shoot can be ascribed to the tangential growth activity of the synthetic bundles. This unequal distribution of tangential growth in the vascular cylinder between the leaf trace bundles (db), widens the vascular cylinder throughout from top to base. This accounts for the continual increase in diameter of the pith tissue, which yields passively by division under the tension exerted on it by the expanding vascular cylinder (Fig 4c) In the older parts of the stem the pith tissue tears apart to form the hollow stem.

As in poplar, the morphogenesis of leaves, stem and inflorescence of Helianthus annuus L.seems to be directed by the development of the vascular system. While in poplar the organisation of the development of the vascular system supports the strategy of outgrowing its neighbour by optimation of growth in height and leaf area, in sunflower it supports optimal flower size by the 'composite' character of its vascular system.

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