GROWTH ANALYSIS OF PLANT AS AN ASSEMBLAGE OF INTERNOdal SEGMENTS
—A CASE OF SUNFLOWER PLANTS IN PURE STANDS—

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Synopsis

The growth of sunflower plants in experimental stands was analyzed in terms of the growth of every internodal segment consisting of a leaf and a piece of stem. The growth of a single leaf and an internodal stem length were both successfully approximated by the simple logistic curves having the same coefficient of growth in common. Daily rates of gross photosynthesis, surplus production and weight increase of each leaf were calculated with Kuroiwa's formula based on the logistic growth of leaf area and stem length in combination with the known light-photosynthesis curve and other properties of sunflower plants. The growth in weight of each stem segment was also calculated on the assumption that the daily surplus production in all leaves was distributed to all internodal stem segments in proportion to their current length. Results of the calculation agreed fairly well with the actually observed patterns of stem growth and their change with plant density.

Introduction
The structure of a plant community aboveground consists of two basic parts—leaf and stem. The community structure depends on how these organs are distributed three-dimensionally.

Since the pioneer work by MONSI & SAEKI (1953), many investigations have dealt with the distribution of leaves and the development of leaf canopy structure. SAEKI & KUROIWA (1959) pursued the development of the vertical distribution of phytoplankton cells in experimental culture and suggested its analogy to that of leaves in terrestrial plant communities. MONSI (1954) and SHINOZAKI (1961) tried to simulate the characteristic pattern of vertical leaf distribution on the assumption that a certain fraction of photosynthetic products in a leaf layer is successively transported to the upper layers to form new leaves. SAEKI (1961a, b) also proposed another interpretation based on the analysis of the distribution ratio of photosynthetic assimilates to newly produced leaves.

As referred to by SAEKI (1961a), however, the developmental process of leaf canopy is closely related to the elongation of the stems, although little is as yet known of the quantitative relationship between the growth of the leaves and that of the supporting organs except the pipe model theory of plant form proposed by SHINOZAKI et al. (1964). In the analysis of this very important relationship, special attention must be paid to the translocation of the assimilates from the leaves to the stems that support them, since the latter can not grow without the supply of matter from the former.

In an attempt to obtain a unified viewpoint on the development of community structure, the correlation between growth processes of the leaves and stems was studied in this experiment with a Russian strain of Helianthus annuus, sunflower plants. The plant is especially suited for such a study in that it seldom branches in a dense population and the whole plant can then be divided into a number of units each consisting of a leaf and an internodal
stem segment. Such simple make-up of the plants enabled analysis of community development in terms of the growth process of each component unit, which was expected to introduce a new viewpoint in this field of research.

**Material and Method**

A Russian strain of sunflower was used as the material in this experiment. To synchronize growth and promote germination, the seeds were sown after stripping the seed coat. The mean seed weight was 0.0763 g, d.w., and after stripping 0.0512 g, d.w.

The experiment was carried out on the campus of the Osaka City University from late April to middle August in 1973. The plants were grown at two levels of density, 4 plants/m² (ρ₁) and 25 plants/m² (ρ₂), or at the distances of 50 cm × 50 cm and 20 cm × 20 cm. The plot size was 1.5 m × 9 m and 1.5 m × 4 m respectively. Seedlings were thinned or transplanted immediately after the appearance of the first leaf to maintain the regularly arranged plant population of a given density. The experimental plots were fertilized with oil cake (400 g/m²) one month before sowing and ammonium sulphate (60 g/m²), calcium-superphosphate (120 g/m²) and potassium chloride (30 g/m²) one week before sowing. Sufficient water was sprinkled once every two days or in summer every day. The germination was completed about two weeks after sowing (31 April). Supplemental planting was made on 12 May and thinning on 14 May. Lower leaves began to shed 40 or 50 days after sowing, and about a half of all produced leaves was finally lost. Flower buds appeared around 2 July, and flowering had ceased and the seeds matured at the end of the experiment in late August.

Eight plants in ρ₁ stand and 15 plants in ρ₂ stand were chosen for continuous weekly measurements of plant height, number and order of nodes, height of nodes, length and width of leaf blade, and stem diameter at five or more height levels (at 5 cm intervals in the early period and at 10 cm intervals later). These plants were dug out and the dry weights of all leaves, internodal stem segments and roots were determined at the final measurement.

<table>
<thead>
<tr>
<th>Number of measurements</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Days after sowing</td>
<td>43</td>
<td>50</td>
<td>58</td>
<td>67</td>
<td>75</td>
<td>96–110</td>
</tr>
<tr>
<td>Date</td>
<td>June 8</td>
<td>15</td>
<td>23</td>
<td>July 2</td>
<td>10</td>
<td>Aug. 1–15</td>
</tr>
</tbody>
</table>

Three plants were sampled additionally from each density level on 8, 16, 23 May for similar measurements including dry weight determination. Dry weight was measured after drying for 7 days at 85°C. The area of a single leaf blade (u) was estimated with the following empirical relation between the area and length × width of blade obtained from the result of supplemental measurements.

\[ u = 0.687 \times \text{length} \times \text{width} \]  

The leaf area was further converted to the dry weight equivalent (w), using the equation,

\[ w = 0.0876u^{0.787} \]

The stem diameter at each node was estimated by the interpolation of the vertical distribution curve of the arithmetical mean of two-direction diameters. The internodal stem dry weight was calculated by multiplying the mean dry matter density at the last measurement by the volume of stem segment approximated to a truncated cone.

**Results**

1. **Rate of node appearance**

The node number increased at a fairly constant rate until 60 days after sowing, when the increase stopped (Fig. 1). The mean rate of new leaf emergence was therefore 0.74/day in ρ₁ and 0.52/day in ρ₂. The rate differed little among plants. The first node leaf began to unfold several days after germination. This corresponds approximately to the date when the node number began to increase in Fig. 1. Sunflower plants did not branch in this experiment, so that the leaf formation was stopped by the differentiation of flower bud at the top of the stem about 60 days after sowing. Flower buds tended to appear earlier in the low density plot, but the inter-plant difference at the time of flower bud formation was not so large at the same density level. The average of final node number differed

![Fig. 1. Increase of node number in a ρ₁ plant.](image.png)
considerably between the density levels, being 37 and 26 in \( \rho_1 \) and \( \rho_2 \) plots, respectively.

2. Growth of leaf area

a. Growth curve of single leaf

The area of a single leaf on the \( n \)th node \( (u_n(t)) \) is plotted against time \( t \) (days after its appearance estimated from Fig. 1 and similar curves for individual plants) in Fig. 2. When the area is expressed as the ratio to its final maximum value \( (u_{n,\text{max}}) \), the growth of all leaves can apparently be approximated by the same growth curve; the growth was completed in about 25 days. This growth curve can be fitted well by the simple logistic curve of Eq. (3).

\[
\begin{align*}
  u_n(t) &= u_{n,\text{max}} / [1 + 68 \exp(-0.40481t)] & \text{for } \rho_2 \text{ plants} \\
  u_n(t) &= u_{n,\text{max}} / [1 + 76 \exp(-0.41484t)] & \text{for } \rho_1 \text{ plants}
\end{align*}
\]

The coefficient of growth (0.41484 and 0.40481 d\(^{-1}\)) and the integration constant (76 and 68) differed little between the two plots with different plant densities. An example of the variation in area of the respective nodal leaves at each measurement is shown in Fig. 3. Not all leaves survived at the time of measurement owing to the shedding of the older leaves.

b. Variation of the maximum leaf area

An example of the nodal distribution of the maximum leaf area \( (u_{n,\text{max}}) \) is shown in Fig. 4. The final leaf area, when plotted against the order of node, gave a bell-shaped curve with the maximum value around the median node. Because of the constant rate of node appearance, the order of node in Fig. 4 may well correspond to the progress of plant growth. Therefore this curve shows that the leaves which appeared around the middle of the vegetative growth period tended to reach the largest final area. This pattern was almost the same in the sample plants grown at the same plant density, but differed between the two density levels. Fig. 5 shows the difference between the mean curves for \( \rho_2 \) and \( \rho_1 \) plants. In preparing the mean curves, the difference of final node number \( (N) \) between plants was eliminated by taking \( n/N \) on the abscissa instead of \( n \). \( u_{n,\text{max}} \) was averaged for 20 classes of \( n/N \), and the \( u_{n,\text{max}} = n/N \) curve was further converted to the case of a plant having the mean number of \( N \).

c. Loss of leaves

Lower leaves began to yellow at about 30 days after sowing and, at the time of the last measurement, the leaves were shed from 19.3 out of the total 37 nodes in \( \rho_1 \) plants and 15.3 out of 26 in \( \rho_2 \) plants, in average. The progress of leaf shedding was also approximated with the following simple logistic curve.


Fig. 5. Distribution of the maximum leaf area among different nodes of a plant, calculated as the averages of all sample plants in $\rho_1$ and $\rho_2$ plots.

\[ d = D/[1 + c \exp(-d t)] \] (4)

$\delta$; number of shed leaf
$D$; upper limit of $d$
$t$; time in days starting at the 15th day after germination in $\rho_1$, and from the 10th day after germination in $\rho_2$.
$c = 0.118 \, d^{-1} (\rho_1)$ and $0.109 \, (\rho_2)$
$c = 109$ ($\rho_1$) and 163 ($\rho_2$)

3. Growth of internodal stem

a. Elongation growth

The elongation growth of an internodal stem segment was also in good agreement with the simple logistic curve,

\[ l_n(t) = l_{n,\text{max}}[1 + 76 \exp(-0.41484t)](\rho_1) \] (5)
\[ l_n(t) = l_{n,\text{max}}[1 + 80 \exp(-0.38243t)](\rho_2) \) (5')

$l_n(t)$; length [cm] of internodal stem between the $n$th and $(n-1)$th nodes at time $t$

$l_{n,\text{max}}$; final maximum length of $l_n(t)$

$t$; time in days

Comparing the mean curve of internodal stem elongation with that of leaf area expansion (Fig. 2), it was found that the former started later than the latter with a lag of about 5 days. Therefore, the time $t$ in Eq. (5) was counted in days beginning on the 5th day after the appearance of the $n$th leaf. It is worthy of note that the coefficient of growth and the integration constant were nearly equal in both of the stem elongation (Eqs. (5) and (5')) and the leaf expansion (Eqs. (3) and (3')) in spite of the time lag. That is, the internodal stem began to elongate about 5 days after the beginning of leaf area growth and reached the maximum length ($l_{n,\text{max}}$) in about 25 days.

b. Variation of the maximum internodal stem length

The final maximum value of internodal length ($l_{n,\text{max}}$) was more variable than that of leaf area ($u_{n,\text{max}}$). As in $u_{n,\text{max}}$, the nodal distribution of $l_{n,\text{max}}$ varied with plant density. As shown by the mean curves in Fig. 6, which was drawn by the same procedure as in Fig. 5, all internodal lengths may be considered as nearly the same in $\rho_1$ plants, though a certain systematic trend was recognized. In $\rho_2$ plants, however, the internodes which appeared earlier tended to grow longer.

c. Weight growth

The dry weight of the internodal stem ($w_n$) was estimated from the mean dry matter density determined at the end of the experiment as stated before. The dry matter density increased systematically with the order of node except in a few basal nodes. Time trends of weight growth of the internodal stems in the average $\rho_1$ plant are shown in Fig. 7. These growth curves failed to fit the simple logistic equation, when examined by the
linearity between stem weight and current relative growth rate \( (dw_{n}/dt)/w_{n} \) (NISHIWAKI & SHINOZAKI, 1952). The nodal distributions of internodal stem weight and its daily increment in the average \( \rho_1 \) plant are given in Figs. 8 and 9. The weight increment was calculated on an exponential basis.

As obviously recognized in Fig. 9, the growth rate of internodal stem weight was larger in lower order internodes, but became almost constant toward the end of the experiment. The vertical distribution of actual internode length was similar to that of stem-weight growth rate at all stages of plant growth, so that the weight increment in an internodal stem segment seemed to be more or less proportional to its current length. The influence of plant density on the nodal distribution of stem weight at the last measurement is shown in Fig. 10, in which the distribution curves for the average \( \rho_1 \) and \( \rho_2 \) plants are compared. The internodal stem weight decreased generally toward the top of the plant, but at a greater rate in the lower density plot.

d. Leaf-stem relationship

According to the pipe-model theory (SHINOZAKI et al., 1964), the area of stem cross section at a given height is expected to be proportional to the total leaf mass existing above the height. This relationship was almost completely realized in the average \( \rho_1 \) and \( \rho_2 \) plants, except for several nodes near the base of stem (Fig. 11). The fact that the line did not pass the origin may be the effect of the flower which had already been fully developed at the top node.

Discussion

1. Growth of leaf area

It is well known that the leaf area per single leaf and individual plant are influenced by various environmental factors such as plant density, temperature, light intensity, inorganic nutrients, etc. (MILTHORPE & MOORBY, 1959; HOZUMI, 1961; HOZUMI et al., 1962; MILTHORPE & NEWTON, 1962; NEWTON, 1963; HOPKINSON, 1963; etc.). In this experiment as well, single leaves changed their area depending on plant density, growth stage and the order of leaf appearance. Each nodal leaf had apparently developed under different environmental conditions, but their growth curves were all approximated by the simple logistic curve having the same coefficient of growth. On the other hand, another parameter of logistic growth, or the maximum leaf area, varied with the order of node and plant density.

Fig. 8. Distributions of each internodal stem weight in the average \( \rho_1 \) plant at different stages of growth.

Fig. 9. Distributions of the daily rate of dry weight increase in internodal stem segments of the average \( \rho_1 \) plant.

Fig. 10. Distributions of mean internodal stem weight at the last measurement.

HOZUMI et al. (1961, 1962) pointed out that the growth of leaf area per plant was logistic and its coefficient of growth did not change with the
progress of time, but that the upper limit change
d with time and various environmental factors. The
growth of a single leaf in this experiment showed a
corresponding property, following the simple log-
istic curve almost completely, whereas the leaf
area per plant is known to have a more complex
nature and can only be fitted by a general logistic
curve. The simple logistic growth of single leaves
and the constancy of its growth coefficient seem to
be the most basic property in the growth of higher
plants. We may therefore guess that this property
of single leaves is the basis for the fundamentally
logistic nature of plant growth. In contrast to the
coefficient of growth, the upper limit of leaf size
seemed to be more sensitive to environmental
change, as indicated by its wider deviation from the
mean bell-shaped curve (cf. Figs. 4 and 5). The
characteristic nodal distribution of the maximum
leaf area (Figs. 4 and 5) may, however, be an
attribute specific to sunflower plants, as is the
constant rate of node appearance.

2. The growth of internodal stem

The elongation growth of all internodes was also
simple logistic as the growth of leaf area, and its
growth coefficient proved to be nearly equal to that
of leaf area, whereas the growth of the internodal
stem weight showed a more complex trend which
could not be fitted to a simple logistic curve. It is
interesting that the stem elongation was primarily
correlated with the leaf growth, while the growth of
steam weight seemed to depend on stem length
through the distribution of photosynthetic products
in proportion to internodal length.

The maximum internodal length (l_{n, max}) was
much more variable than the maximum leaf area
(u_{n, max}), showing that the internodal length was
very sensitive to environmental change. Further
analyses are necessary for examining the effects of
the environmental factors on stem elongation.

3. Simulation of the growth in average plants

An attempt is made to simulate the growth process
in an average plant by combining the simple
logistic nature of leaf and internodal stem growth
with the experimentally observed values of u_{n, max}
and l_{n, max}. The model is based on the following
assumptions.

[Assumption 1] Consider a stand of uniform-
sized average plants, each having the average values
of node number, u_{n, max} and l_{n, max}, for both \( \rho_1 \)
and \( \rho_2 \) plots.

[Assumption 2] The growth of a single leaf
follows the simple logistic curve of Eq. (3). The
maximum leaf area at each node (u_{n, max}) is given
by Fig. 5.

[Assumption 3] The growth of internodal length
follows the simple logistic curve of Eq. (5). The
maximum internodal length is given by Fig. 6.

[Assumption 4] The gross photosynthetic rate per
unit leaf area is calculated by the following equa-
tion (6) as the function of illuminance I on the
leaf surface.

\[
p = \frac{bI}{(1 + aI)}
\]

\( p \); [mg CO_2 dm^{-2} h^{-1}]
\( a = 7.692 \times 10^{-3}; [\text{lux}^{-1}] \)
\( b = 2.43 \times 10^{-2}; [\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1} \text{ lux}^{-1}] \)

(the constants \( a \) and \( b \) were determined from the
data of HIROI \& MONSI, 1966)

[Assumption 5] The daily gross photosynthetic rate
per unit leaf area is further calculated by
KUROWA (1966)'s equation (7).

\[
p_d = \frac{(8D/a)(1 - [1 + a_{\text{LOK}} \exp(-KF)])^{1/2}}{1}
\]

\( p_d \); [mg CO_2 dm^{-2} d^{-1}]
\( D \); day length (12 hrs, const.)
\( I_{\text{LOK}} \); midday illuminance on a horizontal plane
(6 \times 10^4 \text{ lux, const.})
\( K \); light extinction coefficient (0.8 LAI^{-1}, const.)
(\( K \) was obtained in a preliminary experiment in
1972)
\( F \); cumulative leaf area density above the node
concerned, calculated by multiplying the mean
leaf area per plant by \( \rho \).
[Assumption 6] The respiration rate of a leaf \(r_L\) is proportional to its gross photosynthetic rate, or \(r_L/r = 0.087\) (Hiroi & Monsi, 1966).

Based on these assumptions, the daily rates of gross photosynthesis, surplus production, and leaf area and weight increase are calculated. Daily net production rate is then calculated from the above results taking the mean respiration rate of the stems and roots (Hiroi & Monsi, 1966) into consideration. The calculated rates are in good agreement with the actually determined growth rates, thus suggesting that the parameter values of Eqs. (6) and (7) were properly specified. Fig. 12 shows the variation of midday relative illuminance on a horizontal plane at the height of each node through the growth period. The relative light intensity received by a leaf decreases with the growth of the overlying leaves, at first slowly and rapidly later, and tends to reach a certain constant value. The light intensity at the time of leaf shedding (shown by black dots in Fig. 12) is not constant, but mostly between 20% and 30% daylight except for the case of the first node leaf (50%). Obviously the deficiency of light is very important but not the only factor responsible for the shedding of lower leaves.

Time trends of daily gross photosynthetic rate corresponding to such light conditions are calculated as shown in Fig. 13. The daily gross photosynthetic production per single leaf (Fig. 14) reaches the maximum after about 18 days from leaf appearance, or at a week before the end of leaf growth. The decrease of production rate that follows is especially remarkable in the leaves which emerged earlier than the appearance of the \(\rho_{\max}\) node. That all such leaves are eventually shed suggests some relation between the decline of function in the lower leaves and their shedding.

Fig. 15 shows the variation of daily gross photosynthesis among the leaves of different node orders, while Fig. 16 shows the nodal distribution of daily leaf weight growth rate \((dw/dt)\). CO\(_2\)-dry weight conversion ratio was assumed to be 0.614. Subtracting leaf respiration and leaf weight increment from daily gross photosynthesis, the rate of translocation of the assimilate from the leaf can be estimated (Fig. 17). The stem grows on the supply of this translocated product, and the experimental result (Fig. 9) suggested that the supply to each internode was proportional to its length. The daily rate of the supply was therefore calculated on the assumption of this proportionality (Fig. 18).

The values in Fig. 18 are not directly comparable with those of internodal stem weight increase obtained by the experiment in Fig. 9, since the loss due to stem respiration is not considered in Fig. 18. However, the general trends of the curves corre-
The above calculation did not consider age-dependent change of photosynthetic activity, the supply of assimilates to roots and the respiration in stems and roots. Besides, the nodal variation of maximum leaf area (A_{max}) and maximum internodal length (L_{max}) were not treated theoretically. The model was therefore semi-empirical, but nevertheless could simulate the details of growth and reveal some interesting points not only qualitatively but also to a certain extent quantitatively.
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Fig. 20. The "pipe model" relationship calculated for the $\rho_1$ population. The size of stem cross section is tentatively substituted by the total amount of translocated dry matter supplied to an internode divided by its maximum length.

Summary

The spatial structure of a plant community plays an important role in determining the photosynthetic production of the community through its influence on the microclimate within leaf canopy. Many investigations have so far dealt with the spatial distribution of leaves as related to primary productivity, but few with the developmental process of canopy structure. Besides, more attention should be paid to the relationship between leaves and stems, which receive photosynthetic products from the leaves and in turn support them.

This study was intended to analyze the process of structural development in experimental stands of the sunflower with different plant densities, with special reference to the leaf-stem relationship during the process of development. The growth of a plant was analyzed in terms of the growth of every internodal segment consisting of a leaf and a piece of stem.

The results are summarized as follows.

1. The growth of the area of a single leaf and an internodal stem segment were both successfully approximated by the simple logistic curve. The final area of a fully grown leaf, when plotted against the order of nodes, gave a smooth bell-shaped curve with a maximum value around the median node. The largest leaf tended to appear on later nodes in more widely spaced plants.

2. The final length of the internodal stem was more variable than the final leaf area. It was almost the same in all internodes in plants grown at low density, but tended to become smaller with the progress of time in high-density plants.

3. Based on these patterns of growth of unit segments, and assuming a homogeneous stand of the same-sized plants, the growth of a whole plant was numerically simulated as the sum of such segments.

a. Daily rates of gross photosynthesis, surplus production and weight increase of each leaf were calculated with Kuroiwa's formula based on the logistic growth of leaf area and stem segment length in combination with the known light-photosynthesis curve and other properties of sunflower plants.

b. The growth in weight of each stem segment was also calculated on the assumption that the daily surplus production in all leaves was distributed to all segments in proportion to their current length.

c. Results of the calculation agreed fairly well with the actually observed patterns of stem growth and their change with plant density.

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摘 要

植物の成長過程で葉と茎の相互関係を解析するため、2段階の個体密度をもつヒマシの実験群落で、個体を1枚の葉と1節間の茎とからなる単位にわけてその成長を追跡調査した。その結果に基づいて、各節の葉の同化量および同化物質の基への分配をあたえる平均個体の成長モデルを組立て、数値計算によりその妥当性を検討した。得られた実験結果および結論の要点は、次の通りである。

1. 節は一定速度で出現した。
2. 各節位の葉の面積成長は、単純ロジスティック式でよく近似され、成長係数は、節位・個体・群落密度に関係なく、ほぼ一定であった。
3. 個々の葉が到達する最大葉面積は、中央付近の節で極大値を示し、上下の節で減少するようなか曲線をとがいて変化した。ただし、極大値を示す節は、高密度区では、仮密度区よりも早い時期に出現した。
4. 各節間の伸長は、葉と同じ成長係数をもつ、単純ロジスティック式でよく近似できた。
5. 各節間の到達する最大節間長は、低密度区では、節間位に関係なくほぼ一定であったが、高密度区では、初期に生じた節間ほど大きく、後期になるほど小さくなった。
6. 実測の各節最大葉面積・各節最大節間長を用い、葉面積および節間長の単純ロジスティック成長を仮定し、門司・佐伯・黒岩の群落光合成モデルを組合わせて、各密度区の平均個体の成長モデルを組立てた。各節の葉の各時期の光合成量・重量成長量・剰余生産量を計算し、転換した剰余生産量が、その時点での節間の長さに比例して各節間に配分されるものと仮定して数値計算すると、節間茎の重量成長の実測値の分布・時間的変化および密度区による相違を、細節までよく表現するパターンがえられた。