Photosynthesis and Pyllotactic Patterns of Herbaceous Plants — A Model Simulation[*]

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草本植物の葉序と光合成の関係についての一考察
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Spiral phyllotactic patterns of herbaceous plants are examined theoretically, based on three factors of pattern generation: photosynthesis, effective usage of resource, and mechanical balance. By using computer simulations of model plants, we find that the flux of solar radiation on leaves per unit leaf area per day is nearly constant for each phyllotactic pattern. We also deduce some results from the preceding finding and compare them with field observation data.

Keywords : Phyllotactic Pattern,Photosynthesis,Herbaceous Plant,Model Simulation

1. Introduction

This paper deals with the relation between photosynthesis and the geometry of leaf arrangement on stems(i.e.,phyllotactic pattern) of herbaceous plants. Leaf s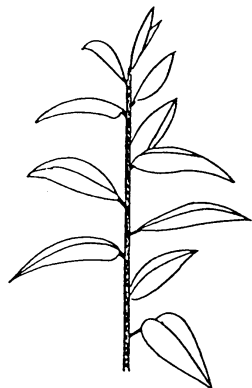hapes of different kinds of plants are also examined in relation to the leaf arrangement. The analysis is done by using computer simulations of model plants. Phyllotaxis is the ordered arrangement of leaf primordia on stems during plant growth. The spiral phyllotaxis is usually specified by the fraction derived from the Fibonacci numbers:$1/2, 1/3, 2/5, 3/8, 5/13,\ldots$. The ratio of integers n/m indcates that to follow the shortest path through the intermediate leaves between two leaves superposed,we have to turn n around the stem until we meet m leaves(see Fig.1).

In this paper,we present a model for generation of phyllotactic patterns. The model assumes three main factors of pattern generation: photosynthesis,resource usage,and mechanical balance. In the next section,we describe our basic asumptions for pattern generation. In section 3,we present a model for

Fig. 1 Sketch of a plant specified by the phyllotactic fraction 2/5

phyllotactic patterns briefly. In the last section,we show our results and we also discuss some related problems.

2. Basic Assumptions

1.Leaf arrangements on stems are designed to optimize three factors, i.e.,i)maximizing photosynthesis at leaves,ii)effective usage of resources between leaves and stems(in relation to photosynthesis) ,and iii)mechanical(or gravitational force) balance of leaves around the vertical stem.

2.Photosynthesis at the leaves is nearly proportional to the flux of incident solar radiation on leaves per unit time(e.g.,a day).

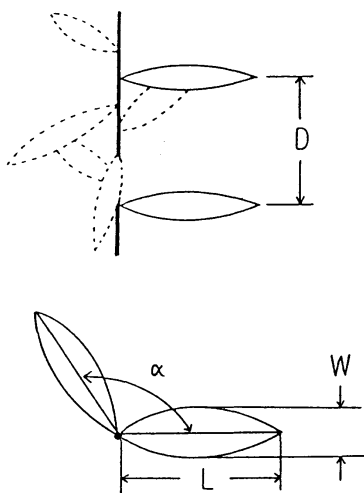3.Leaf surface area and internodal distance on stems(i.e.,distance between the nearest two

Fig. 2 Notation used to specify the geometry of leaf arrangement of a model plant:D = distance between two leaf lamina located at the same position;L = lamina length;W = lamina width;α = divergence angle between successive leaves in a phyllotactic pattern.

leaves) are determined by trade-offs of resources between leaves and stems, so as to maximize photosynthesis at the leaves.

3. Model for Phyllotactic Patterns

As noted in Section 2,we calculate the flux of incident solar radiation on leaves instead of photosynthesis. A model plant has a single vertical stem with horizontally oriented leaves. To specify the geometry of a plant with a spiral phyllotactic fraction n/m, we use following parameters: D is the distance on stem between two leaf lamina located at the same position; α is the phyllotactic divergence angle between successive leaves; L and W are leaf lamina length and lamina width,respectively(see Fig.2). We assume that leaf shape specified by L and W are generated by a certain mathematical function.

A stem of a model plant stands vertically with horizontally oriented leaves. The leaf arrangement on the stem is specified by the phyllotactic fraction n/m. The sun,from which solar radiation comes, is assumed to rise from the east and set in the west within certain timeframe(e.g.,12 hrs). In our present calculations,we are only taking into consideration that light interception for a leaf in question, comes only from the upper leaf located at the same phyllotactic position. In this way,we estimate the flux of incident solar radiation on every leaf(total fluxes of m leaves) during daylight hours. Total fluxes of m leaves are divided by the leaf number m, and then we get the flux per leaf per day.

4. Results and discussion

We calculated the flux of incident solar radiation per unit leaf area per day in a given phyllotactic fraction. The flux is calculated as a function of the variable D for a given leaf lamina length L and width W.

Fig.3 shows the flux for the phyllotactic fraction $2/5$. We can easily see that the flux equals zero at $D = 0$ and the flux approaches a constant value as the distance D goes to infinity, which is the flux on a non-shaded leaf. The three closed circles in Fig.3 are the flux values corresponding to observed data(i.e.,D, L, and W) of three kinds of plants,respectively. We find that these three values are almost the same(about 350(arbitrary unit)) as indicated by the broken line, whereas the extreme value is about 450. We have gotten almost the same
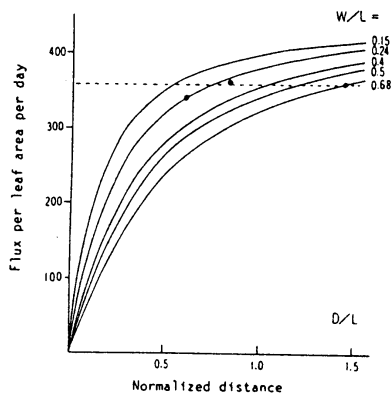

Fig. 3 The flux of incident solar radiation per leaf area per day for plants of the phyllotactic fraction $2/5$. The values of flux (arbitrary unit) are calculated as a function of the variable D/L for each normalized width W/L to lamina length (from 0.15 to 0.68). The closed circles are taken from observed data. The broken line indicates the expected constant value of the flux.

result for phyllotactic fractions $1/3, 3/8$ as for the fraction $2/5$ shown in Fig.3. This finding is true not only in the cases mentioned above,but also it proved to be true in the other cases.

From these findings mentioned above and Fig.3,we can easily deduce the following results. First,plants with narrow leaves(i.e.,small value of W/L) have short internodal distances on their stems(or short distance D/L). On the contrary,plants with wide leaves have long internodal distances on their stems. These results seem to be in accordance with field observations. This implies that there exist a variety of patterns that get the same flux even in a specific phyllotactic pattern. Second,If plants grow in a condition of weak solar radiation(e.g.,in forest),the distance D/L (or the internodal distance) becomes longer compared to plants growing in a field of strong solar radiation. In this case,of course,both plants growing in different conditions are supposed to have the same width W/L and phyllotactic fraction.

Our previous discussions have focused mainly on the relation between photosynthesis and leaf arrangement on stems for a given phyllotactic fraction. We have gotten the result that the flux of solar radiation on leaves becomes maximum for the phylotactic fraction derived from the Fibonacci numbers, which has also been shown in other papers [1, 2]. We would like to discuss the importance of other factors (i.e.,effective resource usage and mechanical balance) to phyllotaxis in another paper.

Photosynthesis and Phyllotactic Pattern

References

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