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Otto L. Stein
University of Minnesota

Ernst C. Abbe
University of Minnesota

APPLICATION OF SCHÜEPP'S METHOD TO FORM ANALYSIS OF THE SHOOT APEX IN MAIZE

OTTO L. STEIN AND ERNST C. ABBE
University of Minnesota, Minneapolis

The purpose of this study is to evaluate periodic form changes in the shoot apex of *Zea mays*, by describing form in terms of the angle included within the shoot apex. This is an application of one of Schüepp's (1938) techniques as developed by him in a study of *Lathyrus odoratus*. Schüepp's results are compared with those obtained here for *Zea mays*.

MATERIALS AND METHODS

A. *Schüepp's method*

Schüepp (1938) reports the following procedure in obtaining materials for analysis: buds of *Lathyrus odoratus* were hand-sectioned with a razor to provide median sections. These sections were "fairly thick." After clearing, these sections furnished well-defined and complete outlines of the apical meristems. Median sections were enlarged 400 diameters and drawn. The resulting drawings were arranged in order according to the configurations of the apical meristem and of the youngest leaves, thus furnishing a succession of substages through several plastochrons. The shoot apex during each plastochron (Askenasy, 1880) was thus subdivided into nine substages. This permitted not only the observation of the total growth of the apical meristem but also its behavior within any one plastochron. On this basis Schüepp (1938, p. 35) was led to observe (as translated), that "there exists a continuous progression in the segmentation of the outlines and the entire surface. It appears that a shoot apex and a leaf apex, as long as they retain their meristematic character, cannot grow without changing their form continuously and dividing perpetually." Schüepp aptly points out that the apical meristem behaves somewhat like a drop on the end of a leaky faucet. It swells steadily in size and periodically segments off droplets, is reduced to a minimum size and again increases in size until another droplet separates from it. This periodic process is repeated. The analogy to the behavior of the shoot apex is clear. The shoot apex increases gradually in size as does the drop on the end of the faucet; when a maximum size has been reached a segment of the growing material becomes morphologically distinct (as a leaf primordium plus the associated stem unit) leaving a shoot apex of minimum size; the process then repeats itself again, periodically.

Schüepp (1938) devised a number of quantitative measurements of the form of the shoot apex. Since these deal with various interrelated angles erected upon the apical dome, they are obviously functions of each other. The present study restricts itself to the angle α measured by two straight lines which intersect at the mid-point of the distal portion of the shoot apex. One leg intersects the axil of the youngest leaf, the other intersects the axil of the next oldest leaf. (The angle α is illustrated as applied to *Zea mays* in Fig. 1). The angle α decreases, with some fluctuations, from 110 degrees when first measurable during a given plastochron to 60 degrees at the end of the following plastochron in *Lathyrus odoratus*. Schüepp (1938, p. 66) observes that the measurements of these angles merely serve to "strengthen the impression that the change in form of the shoot apex is a continous process during which a definite moment for the initiation of leaf formation could only be designated arbitrarily."

It is perhaps worth calling attention to the fact that Schüepp (1938) has not attempted to establish a correlation between two linear dimensions (such as length and width) which would serve to define form changes in ontogeny on the basis of absolute size. He thus avoids the necessity of dealing with regression coefficients or other measures of the inter-relation between two interdependent variables; instead he utilizes the measurement of a single angle which is a function of these. Because absolute dimensions are not directly concerned with the objectives of the problem, his method is definitely advantageous.

B. *Methods used in this study*

Material used for this study was planted in the summer of 1940 as normal sibs of a line back-crossed to a University of Minnesota Agricultural Experiment Station inbred. The population was segregating for d_1d_1. There was no external means of differentiating between D_1D_1 and D_1d_1. The plants were grown in the field and harvested at intervals by removing them in their entirety from the soil. They were then taken to the laboratory, fixed in Randolph's "Craf," imbedded in paraffin, sectioned sagittally through the shoot apex and stained according to the usual procedures. In classifying the material according to plastochrons the first primordium formed above the coleoptile was designated as having been formed during plastochron 1.

It was promptly recognized upon the examination of the sections made according to the procedure outlined above that only in a few cases did they represent mathematically precise median sections. It became necessary to take this fact into account, in applying the method of microprojection to the preparation of the outline drawings used subsequently in this study. The section which apparently was most nearly median for the shoot apex proper was first outlined along with its associated leaf primordia. By comparison with this outline, adjacent sections were checked to permit identification of the most median section of the leaf primordia themselves.

In occasional sections some lateral distortion had been introduced by the pressure of the microtome knife. Correction was made for this distortion although the most serious cases were discarded. There was finally thus obtained a composite outline for each shoot apex showing maximum sectioned area of the shoot apex and its associated leaf primordia. These composite drawings provided the basis for measurement of the angle α (Fig. 1).

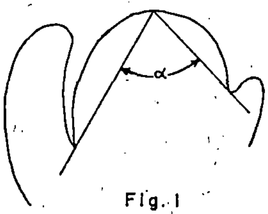

Fig. 1

Diagram of median section of shoot apex of *Zea mays*, with two associated leaf primordia. The angle α describes the form of the shoot apex.

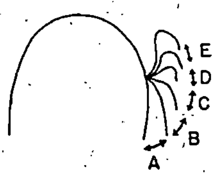

Fig. 2

Diagram to illustrate criteria used for identifying substages A through E in plastochrons 7 through 9.

The projection system was checked for linear distortion by calibration with a stage micrometer, and corrected by readjusting the alignment of the prism and microprojector.

The drawings were arranged within each plastochron according to their respective stages. Schüepp's (1938) method was used in measuring and graphing the angles.

C. *Supplementary methods used in this study*

In order to minimize variability due to limited sampling each plastochron was subdivided into five substages (Fig. 2). These substages were established on the basis of the extent to which the uppermost leaf primordium had developed. The data for each substage were averaged and plotted on graph paper. The maximum and minimum values in each substage are indicated when possible, since the sampling was too limited to justify the computation of measures of statistical error.

Data for five substages in *Lathyrus odoratus* corresponding to those described above were obtained from Schüepp's graph (1938, p. 5) by averaging the values for H and C, E and G, D and A, F and I, (represented by a, b, d, and e respectively in Fig. 4) — B (c in Fig. 4) still representing a single value.

OBSERVATIONS AND DISCUSSIONS

Figure 3 shows representative shoot apices of *Zea mays* arranged according to substages within the plastochron, with the youngest shoot apex, in plastochron 7, at the bottom. There occurs an increase in volume of the apical dome throughout each of these plas-

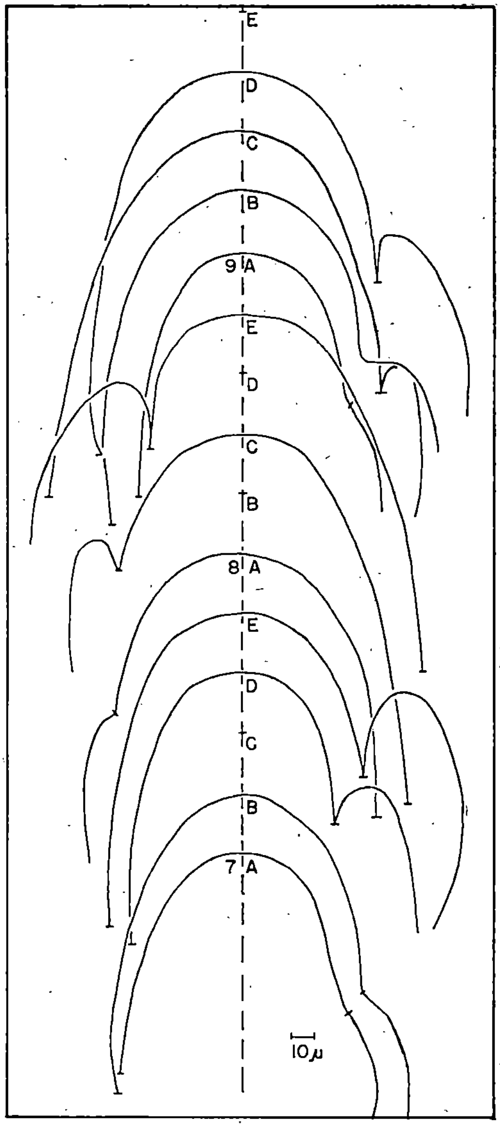

FIG. 3

Camera lucida diagrams of median sections of representative shoot apices in successive substages within plastochrons 7 through 9 in *Zea mays*.

tochrons. At the transition from one plastochron to the next there is a drop to a smaller shoot apex size. The apical dome assumes larger final dimensions toward the end of each successive plastochron. This aspect has been discussed at length by Abbe, Randolph, and Einset (1941). Thus in *Zea mays* there is an increase in size of the apical dome during the individual plastochron.

A comparison with Schüepp's diagram (1938, p. 65, Fig. 3a) of *Lathyrus odoratus* bud sections shows a definite contrast in the development of the shoot apex in a plant of indefinite growth. Here, throughout the two plastochrons shown, there is a continuous increase in the length of the apical dome with very little increase in width. Thus, Schüepp (1938) states, that there is no clear delimitation of successive plastochrons as observable from the general configurations of the apical meristems.

Figure 4 shows graphically data for *Lathyrus odoratus* adapted from Schüepp (1938) compared with data for *Zea mays* as obtained in this study. The ordinate is the magnitude of the angle α, measured as described above.

In Schüepp's (1938) data there is a steady downward trend of the magnitude of the angle. Thus the angle decreases from 110 degrees to 60 degrees in two successive plastochrons. For some unknown reason no further measurements were recorded, although other angular measurements had been graphed through at least a third plastochron. In this curve (Fig. 4, continuous line) a marked transition from one plastochron to the next can be observed, although Schüepp does not recognize its existence in his treatment of the material.

The curve representing the data for *Zea mays* (Fig. 4, broken line) shows a lesser range in size of the angle α, the maximum and minimum values obtained being 68 degrees and 45.5 degrees respectively. Here too, a general downward trend can be observed during each plastochron. The significant difference however is shown by the sharp increase of the angle between the last stage of a younger plastochron and the first stage of the next older plastochron.

SUMMARY

A method proposed by Schüepp (1938) for the description of changes in form in the apical meristem of *Lathyrus odoratus* was applied to *Zea mays*. Bud sections were arranged in developmental order within a plastochron. The shape of the shoot apex in median section is described in terms of the magnitude of the included angle. Schüepp's graphs imply that the shoot apex in *Lathyrus odoratus* is characterized by continuous growth, changing the form of its apical meristem continuously through the transition from one plastochron to the next. This is not supported by the re-analysis of his data as presented in Figure 4. A sharp break appears when the tran-

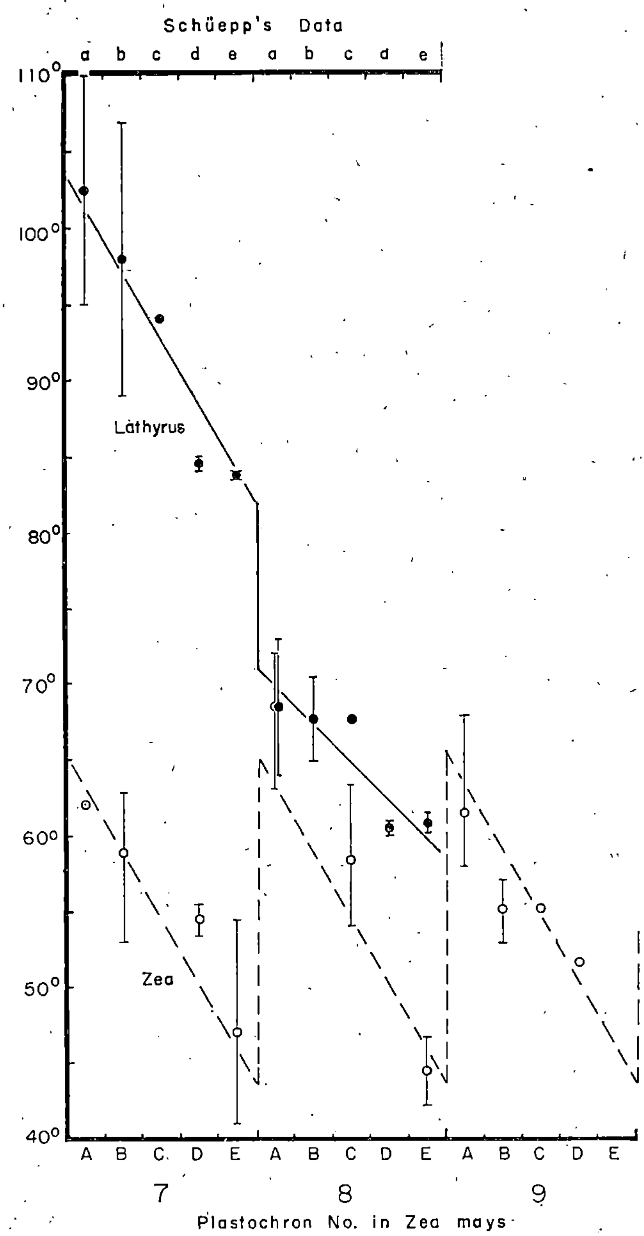

Fig. 4

Comparison of Schüepp's data for *Lathyrus odoratus* (cf. text) with analogous observations on *Zea mays*; ordinate is in degrees subtended by angle a (cf. Fig. 1), lower abscissa represents substages (cf. Fig. 2) of plastochrons 7 through 9 in *Zea mays*, upper abscissa substages of two plastochrons in *Lathyrus odoratus*.

sition is made. In *Zea mays* the overall change in form of the shoot apex as it goes through a succession of plastochrons was repeated in detail within each plastochron. Thus the apical meristem is of small size at the beginning of the plastochron and increases to a maximum at the end of the plastochron. The following plastochron begins at a somewhat larger initial size of the apical meristem and also terminates with a somewhat larger maximum. The periodic form change of the shoot apex is thus clearly evident.

For a more accurate representation of the actual behavior of the apical meristem, a modification of Schüepp's (1938) method was used. As shown in Figure 4, distinct groupings representing plastochrons were obtained, each having a similar decrease in magnitude of angle α. When applied to Schüepp's (1938) data on *Lathyrus odoratus* two similar groupings resulted. A definite break between plastochrons was observable. Under the assumption that the material used by Schüepp (1938) was genetically uniform, this break must be considered biologically significant, and to have been obscured from Schüepp's attention by his method of analysis. However in contrast to the data for *Zea mays*, a plant of definitive growth, in *Lathyrus odoratus* the following plastochron was initiated by an apical meristem with lesser angular magnitude than that of the last stage of the preceding plastochron. This apparently is attributable to the indefinite type of growth, characteristic of *Lathyrus odoratus*.

In conclusion, then, it is evident from the very limited data at present available that the sequence of form changes in the ontogeny of the shoot apex follows at least two very different patterns, —a *Lathyrus* pattern and a *Zea* pattern.

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PLANT SUCCESSION ON A SUBALPINE EARTHFLOW IN COLORADO

JEAN H. LANGENHEIM
University of Minnesota, Minneapolis

ABSTRACT

An investigation was made of the physiographic and vegetational