BIOLOGIA PLANTARUM (PRAHA)

14 (3) : 213—218, 1972

Vegetative Propagation in *Scirpus lacustris* L.

J. P. ONDOK

Institute of Botany, Czechoslovak Academy of Sciences, Praha-Průhonice, Czechoslovakia*

Received April 26, 1971

Abstract. Growth measurements on individual polycormones of *Scirpus lacustris* L. cultivated in hydroponic sand cultures from single rhizome cuttings enabled us to analyse the process of offshoot formation. The time interval in the growth of individual subsequent shoots of one polycormone (plastochron), the final length of the shoot and the number of shoots formed during the growth period are suitable parameters for describing the rhythm of offshoot formation. The interdependence of these parameters and the effect of cutting or shading of individual shoots characterize the translocation of assimilates produced by individual shoots, and their use for the growth of subsequent shoots.

From the physiological standpoint, an analogy exists between the formation of successive shoots growing from a parent perennial plant and the formation of successive leaves on a shoot. The rhythm of development of individual successive shoots may be described, as in leaf development, in terms of plastochrons, which are widely used as a measure of the rate of leaf development (ERICKSON and MICHELINI 1944, SAEKI 1960, WHALEY 1961, DORMER 1965, *etc.*) A plastochron is conventionally defined as the time interval between corresponding stages of the development of successive leaves. Any stage (initiation, maturity *etc.*) may be chosen as a reference stage. The main theme of our experiments was the analysis of offshoot formation as a developmental process defined by certain parameters, the interdependence of these parameters or their relation to the production aspect of offshoot formation and to the translocation of assimilates.

Materials and Methods

Scirpus lacustris L. was chosen for experiments on offshoot formation for its simple morphology of both aerial and underground parts. The cylindrical aerial shoots bear several small leaves only in the early stage of shoot development. Later on, these leaves die off. The rhizomes growing from the parent plant form one or several branches, and only few shoots sprout from the base of mature shoots at right angles to the original direction of propagation.

The planted material originated from the littoral stands of *Scirpus lecustris* growing in the surroundings of Třeboň (South Bohemia). The plants were cultivated in hydroponic installations

* *Present address:* Dukelská 145, Třeboň, Czechoslovakia.

in sand irrigated with a nutrient solution (composition is given in Dykyjová *et al.* 1971) from January to July in the years 1968—1970, in Třeboň (South Bohemia), mean day temperature about 20 °C. Each year, 50 cuttings of rhizomes bearing one terminal bud were planted. Only few of them showed an extremely abnormal growth and were therefore discarded. The relatively high variation in growth rate enabled us to compare the parameters of offshoot formation on a larger scale than would have been possible with a homogeneous material.

The length of the individual shoots was measured at three day intervals and their growth curves were constructed. In 1969 and 1970 the cutting off and total shading of individual shoots were applied to clarify the translocation of assimilates from one shoot to another. The individual shoots were cut at their bases at different stages of development or in succession (cutting the first, second *etc.* shoots). The period of total shading with polyethylenous foils was one week in all cases.

Results

The development of individual shoots forms a regular succession resembling that of a plastochron scheme for successive leaves on a shoot. The length of the shoots increases with their order, reaching an approximately constant value after a certain period. If we apply the term plastochron to the time distance between the growth of two successive shoots, we obtain a time scale for the development of shoots from a parent bud. A plastochron may be defined in different ways (see discussion in Ondok 1968). We defined the plastochron for the process of offshoot formation as the time interval of two successive growth stages of the shoot (height 20 cm).

The plastochron scale in offshoot formation has a different character from that of leaf development: Firstly, one or more branches of successive offshoots are formed, each having different orientation (for examples see Fig. 1), and a different plastochron scale. Secondly, in leaf development the successive plastochrons become longer with the age of the plant (Fig. 2b), whereas, in offshoot formation of *Scirpus lacustris* the successive plastochrons become shorter (Fig. 2a). The growth scheme of offshoot formation in a linear succession on a single branch (obtained on the basis of shoot length measurements) has its own regular rhythm different from that of the formation of lateral offshoots growing at right angles to the orientation of this branch (Fig. 2c). The growth scheme and plastochron scale are different in individual branches growing from one parent bud (full and dashed line in Figs. 2d and 3a).

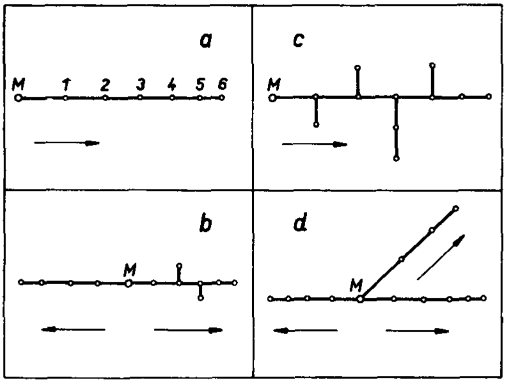

Fig. 1. Schematical illustration of offshoot formation in *Scirpus lacustris* cultivated in hydroponical conditions. M — planted cutting of the rhizome.

The plastochron scale (when considering only the main succession of offshoots) generally has the following rhythm: At the initial phase the plastochron becomes shorter, and the length of successive shoots increases. From a certain time point of development the final length of shoots and plastochrons remain approximately constant. Finally, the reverse process may

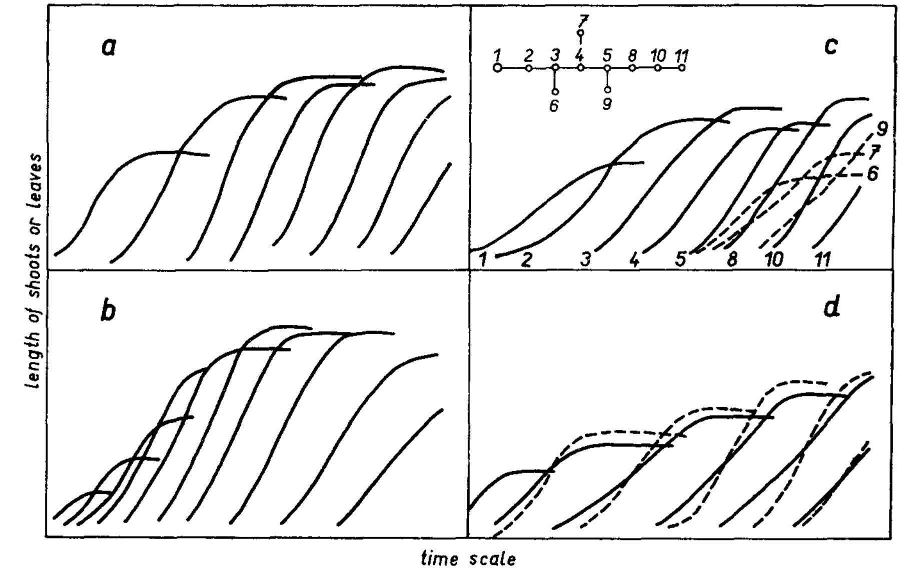

Fig. 2. Some examples of growth schemes: *a*, *c*, *d* — plastochron scale of offshoot formation in *Scirpus lacustris*, *b* — plastochron scale of leaf development in *Typha latifolia*. — In *c*, the figures mark the order of shoots in succession, the dashed line lateral offshoots; in *d* offshoot formation in two directions is represented by a full and a dashed line.

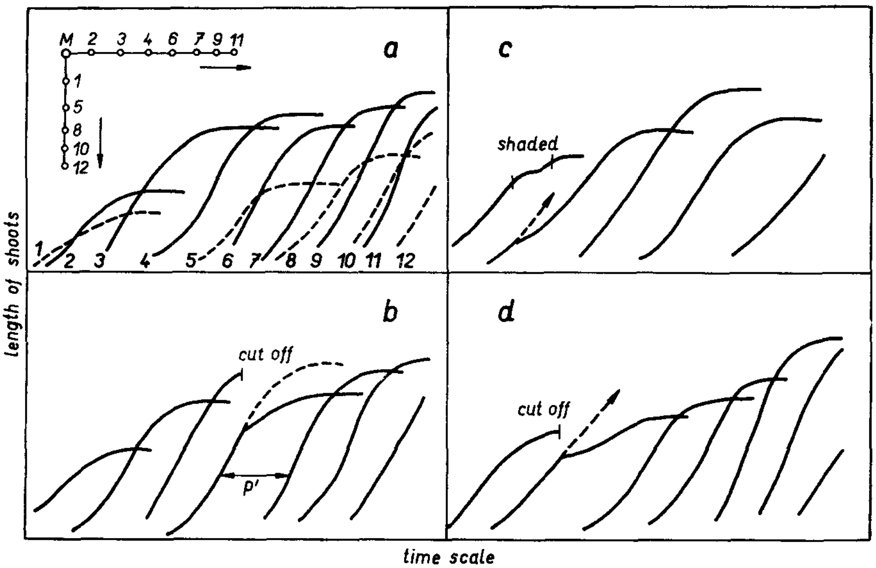

Fig. 3. Scheme of offshoot formation in two directions (*a*) and the effect of cutting or shading on the rhythm of offshoot formation (*b*, *c*, *d*) in three polycormones. The dashed line shows the expected values, *p*' — plastochron.

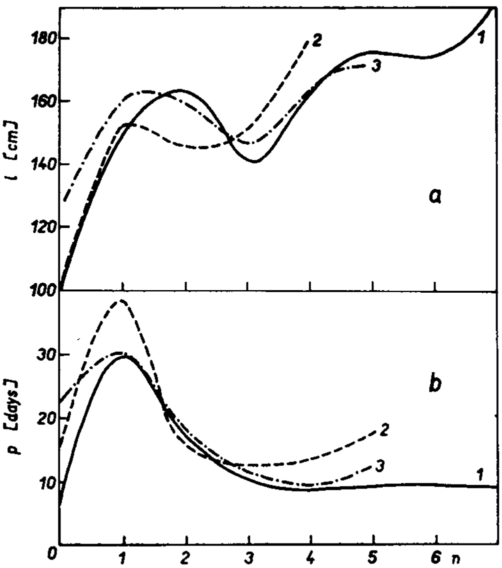

Fig. 4. Gradient of final shoot length (l) and of plastochrons (p) in subsequent shoots (n — order of the shoot) for three polycormones.

be observed — the plastochrons become longer and the final length decreases. This general rhythm of offshoot formation was observed in all polycormones with some exceptions: (1) A very small value for the first plastochron in many cases (Fig. 4). This is easy to interpret, as the growth of the second shoot may be dependent not only on the photosynthetic capacity of the first shoot but also on the translocation of reserves from the original rhizome cutting, whereas all the subsequent shoots presumably make use of assimilates produced by the previous shoots. — (2) Deviations in values of the plastochron and in shoot length (*e.g.*, one or two tillers were shorter than the previous ones). This deviation is explained by the formation of lateral offshoots affecting just those shoots to which they are attached (Fig. 2c).

We may consider three quantities as parameters of offshoot formation: the total number of shoots formed during the growth period (n), the mean plastochron value ($\bar{p}$) and the mean final shoot length ($\bar{l}$) per 1 polycormone. In our experiments n was most variable ($V = 31.6\%$), the smallest variation was assessed in $\bar{l}$ ($V = 17.7\%$), while the variability of $\bar{p}$ was intermediate ($V = 27.1\%$). The distribution of the variability did not change when cutting or shading had been applied. The parameters n, $\bar{l}$ and $\bar{p}$ are not independent but show a mutual correlation. The negative correlations of an approximately linear

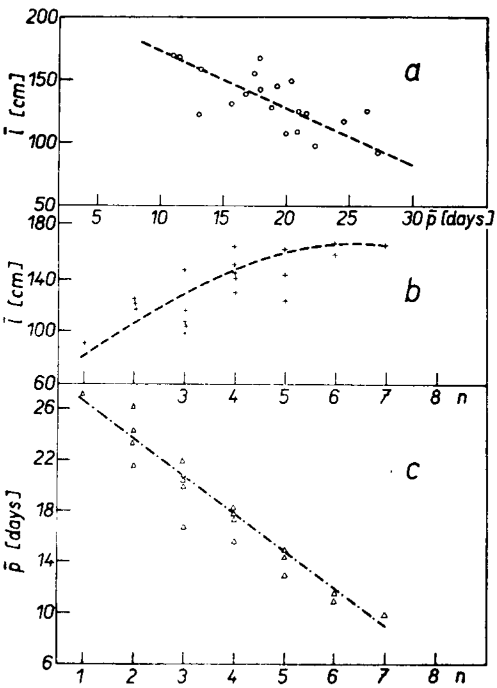

Fig. 5. Correlation between single parameters of offshoot formation: n — number of shoots formed from one bud during the season, $\bar{p}$ — mean plastochron value for 1 polycormone, $\bar{l}$ — mean final length of shoots in 1 polycormone.

form between $\bar{l}$ and $\bar{p}$, and between $\bar{p}$ and n are illustrated in Figs. 5a and 5b, respectively. The correlation between $\bar{l}$ and n is positive, but slighter than in the two previous cases (Fig. 5c).

The rhythm of offshoot formation may be interpreted as a result of two factors: (a) of the production capacity (size of assimilation apparatus) and photosynthetic efficiency (given prevailingly by climatic conditions) of individual shoots, and (b) of a morphological trend on the other hand. The interaction of these factors influences the growth of a shoot in dependence on the growth of the previous shoots. The rhythm of offshoot formation may be disturbed by removing one or more shoots or by shading them over a chosen interval. Cutting off (or shading) a shoot should affect all the subsequent shoots that were supplied with assimilates from this cut-off (shaded) shoot. Such a study of translocation, of course, offers only qualitative data.

The Effects of Cutting off or Shading May be Summarized as Follows:

(1) They induce a decrease in the final length in subsequent shoots, the lengthening of subsequent plastochrons, and an immediate deviation from the expected growth curve in some of the immediately subsequent shoots (Figs. 3b, 3d).

(2) Their effect on any of the parameters n, $\bar{l}$, $\bar{p}$ was of the same strength.

(3) An immediate deviation from the expected growth curve was observed in the first and sometimes in the second subsequent shoot.

(4) The effect on the parameters n, $\bar{l}$, $\bar{p}$ and on the immediate deviation from the growth curve was dependent on the order of the shoot cut off or shaded and was most pronounced in the first shoot.

(5) The intensity of the effect was dependent on the growth rate of a polycormone. It was more conspicuous in individual shoots, which attain relatively smaller final lengths and whose plastochrons are longer.

Discussion

The immediate deviation from the expected growth curve observed in the first subsequent shoot suggests that assimilates are translocated from any single shoot only to the two subsequent offshoots. Later offshoots seem to depend prevailingly or entirely on the parent shoot only. The rate of formation of lateral offshoots depends on the vigour of individual shoots. If the growth is favourable and the offshoots sprouting at short intervals form a large assimilation apparatus which produces more material than is required by the internal rhythm of the growth, some shoots begin to form lateral offshoots. However, even in considering this, the interpretation of the translocation mechanism is by no means simple. In some instances, the growth of new lateral offshoots because of parent shoots was observed (Fig. 2c). These parent shoots did not attain the expected final length. We may distinguish between three cases: (a) the production capacity is over-sufficient to supply the growth of the main succession of shoots and lateral offshoots are formed; (b) the production capacity is just sufficient to supply the growth of the main succession and no lateral offshoots are formed; (c) the production capacity is sufficient to supply the growth of the main succession of shoots and lateral offshoots are formed because of the growth of their parent shoots.

The effect reported in (4) of Results may be explained if it is assumed that the cutting off or shading of the first offshoot means a complete destruction of the photosynthetic apparatus. The new shoots must grow from underground reserves. In cutting off (shading) any further subsequent shoot, this apparatus is only partially destroyed and, with mature shoots left, the effect may be fully compensated, and only the number of lateral offshoots is limited, so that no change is observed.

From point (4) it follows that the translocation of assimilates may be better understood as a fully coordinated process in which materials formed by a growing shoot are partly used for its own growth and, at the same time, partly translocated to the subsequent shoots that start growing.

The picture of the mechanism of vegetative propagation as given in our results of experiments represents a simplified model. The material under investigation in our experiments were single polycormones cultivated in artificial conditions. In natural conditions some additional factors play a role, which could not be involved in our experiments, *e.g.* the competitive ability, variation in soil conditions, density pattern *etc.* Nevertheless these experiments enable us to understand to some extent the rhythm of offshoot formation and to analyse the hypothetical mechanism of translocation of photosynthates although in qualitative terms only.

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J. P. ONDOK, Botanický ústav Československé akademie věd, Průhonice: **Vegetativní rozrůstání u *Scirpus lacustris* L.** — Biol. Plant. **14** : 213—218, 1972.

Růstová měření na jednotlivých polycormonech druhu *Scirpus lacustris* L. pěstovaných v hydroponních kulturách z oddenkových řízků umožnila analyzovat proces odnožování. Časový interval růstu dvou následných prýtů (plastochron), konečná délka prýtu a počet prýtů vytvořených během sezony jsou vhodnými parametry pro popis rytmu vegetativního rozrůstání polykormu. Vzájemná závislost těchto parametrů a vliv odřezání, resp. úplného zastínění jednotlivých prýtů charakterizují translokaci asimilátů vytvořených jednotlivými prýty i jejich využití pro růst dalších následných prýtů.