PHOSPHORUS AND THE EARLY MATURITY OF PLANTS

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INTRODUCTION

Ever since the Earl of Dundonald found that alkaline phosphates were of importance in the nutrition of plants, the element phosphorus has been considered necessary for plant growth. All subsequent research has confirmed the view that phosphorus is essential to the complete nutrition of plants, and for a long time phosphorus has been included among the elements needed for a complete fertilizer in improving soil fertility. In summarizing the value of phosphates in plant growth, Russell calls attention to the increased growth of the root system in lateral and fibrous roots, and the better storage of food in root crops provided with an abundance of soluble phosphates. He mentions the influence of this element in increasing both straw and grain production, its connection with nuclear processes in cell division, its relation to the normal transformations of starch, and its importance in determining the quality and feeding value of crops grown on the soil.

In addition to these effects, it has been observed that phosphates hasten the maturing processes, thereby hastening the harvest of cereal grains by a few days. Nothing is said as to whether the grains develop bloom primordia at an earlier date in the presence of abundant phosphate supplies, and no observations are recorded as to whether the blooming time, or sexual maturity, comes on earlier due to phosphorus abundance. The hastening of maturity is said to be obvious only when a control plot is near by. The grain supplied with phosphates is then seen to turn golden yellow while the untreated plots are still green. The effect is likened to that of water deficiency which also hastens the coloring of ripening grains.

In some of the grains it seems that phosphorus is closely connected with the flowering processes. Thus Eckerson has shown for wheat that there are only traces of phosphates in the very young spike, but that when sporogenous tissue begins to develop in the flower primordia, phosphate begins to enter the stamens and pistils in considerable quantity, mainly in the form of magnesium phosphate. The phosphates continue to enter the spore producing tissues until pollen grains and eggs have been formed. As the megaspore mother cell divides, and the functioning megaspore increases in size, the phosphate becomes very abundant in the embyro sac. With the development of the egg, maximum phosphate content of the embryo sac tissue is attained. Hooker has found an increase of phosphates in fruit spurs of apples at the blooming time, so that it is apparent that the use of phosphates in the building of nucleins, nucleo-proteins, phospholipines, hexosephosphates, etc. is most rapid during the development of sex organs.

These interesting observations, however, do not show whether the presence of phosphorus in the form of soluble phosphates leads to an earlier formation of the primordia of the flower, or earlier attainment of sexual maturity (blooming) than in plants grown with deficient supplies of this element. It would be of considerable interest to know whether the earlier ripening of grains with phosphate supply is correlated with an earlier date of sexual maturity.

Some recent experiments at the University of Chicago with one of our lower plants, Marchantia polymorpha, indicate that this plant can be hastened through its life history to sexual maturity by strong applications of soluble phosphates. This paper gives a brief account of the experiments in which this effect was noted.

THE METHOD USED

Soils were obtained from the margin of the Forest Preserve at Thornton, Ill., in an area that had been burned over some years ago, and upon which Marchantia had been growing abundantly for some time. The free growth indicated that this soil was well adapted to the needs of Marchantia. At the same time, similar soil from unburned areas was obtained for control studies. The unburned soil differed in no essential respect from the burned soil, but was occupied by trees and shrubs under which no liverworts were growing.

The burned soils were used in fertilizer tests to determine the effects of added nutrients on the rate of growth of Marchantia. A triangular series of pots was arranged, containing 21 cultures. To these pots varying amounts of phosphates, potash, and nitrogen fertilizers were added.

The pot at one apex of the triangle received enough sodium dihydrogen phosphate solution to give it the equivalent of 80 ppm of P_2O_5. The succeeding rows received 64, 48, 32, and 16 ppm, and the row opposite the high phosphorus apex received no phosphate addition.

At another corner of the triangle, one of the pots that received no phosphorus was given potassium chloride solution equivalent to 80 ppm K_2O, and the succeeding rows 64, 48, 32, and 16 ppm, while the last row opposite the high potash apex received no potash.

Similarly the third corner pot received an addition of sodium nitrate solution equivalent to 80 ppm of NH_3. The succeeding rows received 64, 48, 32, and 16 ppm, and the final row opposite the high nitrogen apex received no addition of nitrate fertilizer. This arrangement permitted observation of the effects of a single nutrient, of combinations of any two, and of various proportions of all three, upon growth, on the production of cupules, and upon the rate of attainment of sexual maturity.

RESULTS

The pots, including duplicate controls of burned and unburned soils, were sowed with gemmae of approximately the same age, and in about equal numbers, on April 20, 1922. The observations were extended over a period of a few weeks until sexual maturity had been attained by a number of the cultures.

(a) *Growth of thalli.*

The effects of the addition of the salt solutions soon became evident in the growth of the thalli. When the young plants were nine days old, it was evident that R_1S_6, the pot which received 80 ppm sodium nitrate only, was the poorest culture in the entire triangle. The row of pots forming the right side of the triangle, in Figs. 1 and 2, showed a regular gradation in size of thalli from pot 6 to pot 21 at the apex, the latter being the best in the row, judging by size of thalli. As nitrogen supply decreased, and phosphate increased, the growth was very noticeably better.

Along the base of the triangle from pot 6 to pot 1, there was a larger difference between number six and number five than at any other point in the row; but pots 4, 3, 2, 1, seemed to be increasingly good, with rather small gradations.

On May 1 the best culture in the entire set was R_2S_1, or pot number seven, which had received 64 ppm K_2O, and 16 ppm P_2O_5. The best region of vegetative growth was represented by pots 7, 8, 9, 12, and 13, at the left end of the second and third rows from the bottom of the triangle.

(b) *Production of cupules.*

Cupules began to develop on certain cultures soon after the first of May, and observations were continued until May 22. The diagram shown in Fig. 1 indicates the order of appearance of gemmae in all of the pots where asexual budding occurred. The general region of the triangle to show cupule development was the potash corner, where four of the six pots with these organs are clustered. The first cupules to appear were on the plants receiving 80 ppm potash, without any other nutrients. The results suggest the possibility that potash may be specially advantageous to the plant in this asexual reproductive phase of its life history.

(c) *Attainment of sexual maturity.*

About May 10 it became evident that some of the plants were beginning to produce gametophores. As the receptacles developed their disks it was noted that all of them were antheridial. No females were developed

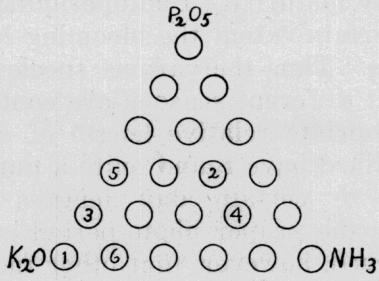

FIG. I. Order of development of cupules in Marchantia polymorpha.

during the course of these observations. Observations were made from day to day until May 22, at which time all but four of the pots showed at least the beginnings of gametophore development. The results on May 22 are shown in Fig. 2, in which the oldest receptacles are numbered 1, and succeeding stages with younger disks, 2, 3, 4, and 5. Those marked 5 were just visibly entering the period of gametophore development, and those marked 0 did not yet show the beginnings of sexual development. They were almost ready, however, as traces of such growth became visible on May 25. At this later date, ten of the cultures had full size mature receptacles, and of these eight were at the phosphorus corner of the triangle, pots 21 to 14, inclusive. The other two were pots number 7 and 9.

At the same time the controls, both on the burned over and unburned soils, showed the merest traces of sexual development in one pot of each duplicate, and the other pot of each control showed no sexual tendencies.

The results show very clearly the acceleration of the life history by means of soluble phosphate application, and the strong tendency toward development of sexual maturity, even in plants that did not show the most rapid vegetative growth.

DISCUSSION

The factors which cause plants to blossom and fruit are receiving much attention from plant physiologists at present. Appropriate carbohydrate-nitrogen ratios are thought to be favorable to fruitfulness, and high ratios to lead to early maturity. Photoperiodism is known to control to a certain extent the blooming habits of many kinds of plants. Thus the various species of Xanthium which bloom at different seasons are controllable if one uses the appropriate relative length of day and night. Garner and Allard have found quite a number of plants that respond to certain day lengths by blooming promptly when the proper photo-period is provided. It has been observed, however, that other factors may sub-

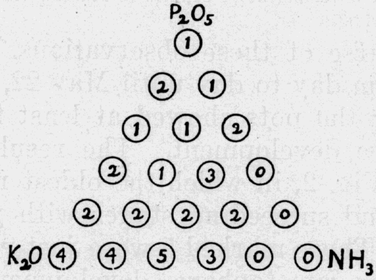

FIG. II. Phosphorus and sexual maturity in Marchantia polymorpha.

stitute for photoperiodic stimulation. Thus Gilbert has recently found that temperature greatly modifies the photoperiodic response of the Xanthiums. During the short day period of winter, Xanthium plants may be blossomed in three weeks from the seed if a temperature of about 25° C. is employed, but at 18° to 20° C., it will require several months to reach sexual maturity. During the long day period of summer, high temperatures will not cause blooming, but a shortening of the day does induce flowering.

Some of the lower plants have been found to be photoperiodic also; thus among the algae, Chara is known to fruit when it has the proper day length. And Marchantia has shown responses to different photoperiods, indicating that sexual maturity may depend in part upon conditions controlled by illumination.

Kraybill and Smith have noted that phosphorus supply has some influence upon the carbohydrate and nitrogen metabolism of the tomato, and it certainly has a greatly accelerating effect upon the development of sexual maturity of Marchantia.

It is evident that the control of blooming is not simple, and as yet cannot be expressed in terms of some common factor. However, a study of metabolism in all of these cases should throw much light on the causes which induce sexual development. It would also be valuable to know whether phosphorus will bring about earlier blooming in our common crop plants. In regions where length of growing season is a limiting factor on the kinds and varieties of crops produced, a difference of a few days in the time of blooming would be very important from the agricultural standpoint.