that in going to classes in the morning, his path often crossed that of Dr. Thurston and that he grew to look forward to these meetings with anticipation; that Dr. Thurston's manner of saying "Good morning" would always make the day seem brighter and fairer for him.

In physical frame, Dr. Thurston was moderate in stature, rather spare of build, erect in carriage and mien. His hair with full beard and moustache were in early and middle life black, becoming gray with the passing years. His eyes were dark and piercing, often with something kind and quizzical shining through. His gait was rapid and firm, with figure trim and erect, a characteristic tracing back, perhaps, to his naval training, but none the less a natural expression of his personal energy and normal outlook on the world about him. This daily walk between his house and office, with black portfolio of lecture notes under his arm, body erect, shoulders back, head up and eyes to the front, formed a picture of personal dignity and of purpose toward an intended goal which will surely long be remembered by those who saw this as a familiar sight during the years of his life at Cornell.

I wish that there were time for some of the anecdotes which illustrate his kindly nature, his intense human sympathy, his resourcefulness in adapting himself to the unexpected, all combined with his optimistic outlook on his environment, his abiding faith in the ultimate working out of the great enterprise in which he was embarked, but time presses and I must close.

The fall of 1903 found Dr. Thurston in seeming good health, in the midst of interesting and important work and apparently with many years of fruitful activity before him. On the occasion of his birthday, thirty-six years ago to-day, Mrs. Thurston had arranged for a small dinner party of intimate friends. Sitting quietly in his home waiting for the arrival of these friends, the final summons came—apparently through an aneurism of the heart. Peacefully and with hardly a movement he passed on, and so out of the busy life in which he had wrought so long, so courageously and so well.

In the shuffling of human characteristics by the Fates, only too rarely do the combinations give us a man such as was Dr. Robert Henry Thurston. We shall not soon look upon his like again.

# PHOTOPERIODIC ASPECTS OF PHASIC DEVELOPMENT

By Professor W. F. LOEHWING

THE STATE UNIVERSITY OF IOWA

THE concept of phasic development of plants has, in less than a decade, profoundly influenced the fundamental philosophy of plant growth as well as theory and practice in plant physiology, ecology, agronomy and genetics. This theory emphasizes especially the differences between the thermo- and photo-phases of plant growth. In view of the fact that recent advances in our knowledge of photoperiodism show variable effects of a given light period upon the different processes involved in sexual reproduction, it now seems desirable to evaluate this evidence to determine the possible desirability of subdividing the photophase of plant development into (*a*) an initial flowering phase as distinguished from a subsequent (*b*) gametogenic phase concerned with the formation of viable gametes.

When the photoperiodic concept was first clearly enunciated by Garner and Allard (1920), formation of macroscopic flowers in known periods of diurnal illumination was taken as a criterion of photoperiodic response. It was soon learned, however, that plants receiving minimal periods of photo-induction frequently produce flowers of anomalous shape and marked sterility. *Xanthium* of one short photoperiod, for example, exhibits marked pollen sterility (Hamner and Bonner, 1938; Neidle, 1939). Kirichenko and his associates (1934–36) had also previously observed that though flowers developed in *Triticum erythrospermum* when exposed for several weeks to a daily two-hour photoperiod, pollen when present was invariably sterile. The data of Kirichenko and other investigators indicate that the development of viable pollen requires (*a*) a longer period (6 hours or over) of photo-induction, consisting both of more days and longer daily light periods than necessary for the differentiation of pistil and ear. In conformity with other light-induced, formative processes, once the requisite period of photo-induction has been supplied, *Triticum erythrospermum* then continues to produce viable pollen indefinitely in all ranges of illumination from continuous day to continuous night. Oleson (1938) observed similar conditions in *Fuchsia* and *Begonia*.

The work of Rosenbaum (1937) on 18 varieties of soybean indicates that not only stamen but also perianth and ovule development can be suppressed by extremely short day length (8 hours or less), thus reducing the fruits to parthenocarpic, seedless pods. A 13-hour day, on the other hand, results in normal flowers producing pods with the usual complement of viable seeds (Hamner, 1938). Earlier still, Schaffner (1927–30), Richey and Sprague (1932) noted the absence of tassels in corn grown during very short photoperiods, especially in low intensities of light, and that ears formed normally, or sometimes apically in place of tassels. Short day thus rendered corn dioecious. In cucumbers, it has been known for many years that short day of low intensity results in a preponderance of pistillate flowers (Edmond, 1930; McCollum, 1934; Miller, 1938; Zukova, 1938). The production of staminate flowers requires longer days and higher light intensity. Allard (1938) found that the flower habit of the hog peanut changed from hypogeic to cleistogamous and finally to anthesitic as the photoperiod increased. Aerial flowers required a $13\frac{1}{2}$ hour day for their formation, but hypogeic forms developed in as little as a five-hour light period.

It is evident from the foregoing data that the photoperiod exerts a variable effect on the different parts of the flower, just as it does upon different vegetative structures. Thus, if flower fertility is to be made the criterion of photoperiodicity, the conditions will be somewhat different from those necessary to cause the inception of primordia alone.

The contrast in the photoperiodic demands of staminate and pistillate tissues is a manifestation of sex, and it is to be expected that these organs will differ as much in metabolism and composition as in mode of origin. In fact, as the evidence on flower physiology accumulates, it shows increasingly that the most profound compositional and developmental changes in the plant's entire existence occur in the brief period of floral differentiation, a condition as yet inadequately appreciated, probably due to the rapidity, extreme localization and inconspicuousness of the changes involved. The technical and analytical difficulties in physiological studies of this sort are obvious, and they constitute a further reason for the meagerness of quantitative data on reproduction. Once the importance of such information is generally recognized, it is to be expected that adequate techniques and increased investigation will follow. It would be helpful, however, if some consensus could be reached as to precisely what constitutes flowering. If inception of floral primordia is to be the criterion, then there is definite need of distinguishing gametogenesis from the origin of the other floral parts, since inception of primordia and perianth development are no absolute guarantee of the production of viable gametes.

The common denominators of flowering, in both long- and short-day species, such as the non-specific character of the florigenic hormone, suggested by the researches of Cailachian, Murneek, Loehwing, Hamner and Bonner and many others, as well as similarity in stem anatomy of all flowering types as worked out by Roberts and his associates, are all valuable inventories of the various attributes of normal flowering. They still leave much unanswered, however, as to the physiological nature of sporogenesis and the differentiation of the sex organs. In addition to those features which are common to all plants in the flowering phase, we must identify the physiological stimuli responsible for differences between pistils and stamens.

More than a decade of research by the writer and his students upon dioecious species suggests that, among the most important physiological differences of the sexes, are the oxidation-reduction enzymes, marked quantitative if not qualitative differences in soluble carbohydrates and qualitative contrasts in proteins. Mild hydrolysis of proteins in sexually differentiated hemp plants discloses arginine and lysine but no proline or histidine in staminate individuals, while pistillate plants are the exact converse. Tests for these amino acids in foliar tissues of vegetative plants without flower primordia enable one to forecast the eventual sex of the mature plant (Kiesel and Pachewitsch, 1938; Loehwing, 1939). Inception of staminate organs seems to be characterized by a preponderance of soluble sugars and presence of oxidase. Pistillate loci have a preponderance of nitrogen and marked reducase activity (Loehwing, 1937; Stanfield, 1937). Though the foregoing appear to be significant physico-chemical differences between the sexes, we have not as yet successfully distinguished cause and effect, nor have we the desired degree of voluntary control over carpo- and andro-genesis.

Not only are the photoperiodic requirements for development of pollen and embryo sac different from one another, but they in turn also differ from the post-fertilization processes of fruit enlargement. Fertilization marks the inception of the new sporophyte phase and as such, essentially the recommencement of vegetative activity, temporarily of a parasitic sort with a high food demand. In many plants, it seems that the photoperiodic conditions favorable for fruit development are more similar to those for vegetative growth than for flowering. In brief, the optimal photoperiodic conditions change as the plant progresses from inception of primordia to differentiation of floral parts and finally to fruiting.

This fact has been recognized in varying degrees by many investigators, but has recently been well formulated by Eguchi (1937), who suggests a double photoperiodic classification for plants. Eguchi's system not only recognizes but definitely emphasizes the difference in the light optima of flowering and fruiting. Following Garner and Allard's classification, he postulates three fundamental types of plants, namely, long day, short day and photoperiodically indifferent. With respect to flowering, the plant may have a short optimal period but a long or indifferent light requirement with respect to fruiting. There are, then, nine possible permutations of these three classes as given in Table 1:

This synoptic classification is perhaps a bit extreme

TABLE I

| Optimal photoperiods for: Flowering | Fruiting | Representative species |
|---|---|---|
| Short | Long | Strawberry, Cineraria |
| Long | Long | Oxeye Daisy, Spring Barley |
| Long | Short | *Physostegia virginiana, Boltonia latisquama* |
| Short | Short | Soybeans, *Cosmos bipinnatus* |
| Long | Indifferent | *Phlox paniculata* |
| Short | Indifferent | Late rice varieties |
| Indifferent | Short | *Chrysanthemum articum* |
| Indifferent | Long | Spinach, Many wheats |
| Indifferent | Indifferent | Pepper, Early rices, *Stellaria media, Poa annua* (Tincker, 1924) Buckwheat (Arthur, 1930) |

and as a result not wholly clear. A plant may be long day with reference both to flowering and fruiting, yet nevertheless have a shorter optimum by several hours for fruiting than for flowering. It will be noted that this classification of Eguchi controverts the original suggestion of Lysenko that long-day species are at their optimum in continuous-day and short-day species in continuous-night. Even with reference to flowering alone, we already have abundant evidence that this interpretation by Lysenko is too extreme (Singh, 1937; Allard, 1938; Borthwick and Parker, 1938; Murneek, 1937; Celjadinova, 1937).

The fact that the optimal photoperiod for fruiting is different than for flowering in some species, often causes delay in the enlargement and even abscission of the earliest fruits. Oleson (1938) noted that after the first crop of *Begonia* and *Fuchsia* fruits appeared in early spring, about four to six weeks elapsed before these began to enlarge under conditions of normal day-length. Many fruits abscissed during the period from late February to late April. Neither pollination with viable pollen nor stimulation with indole acetic, indole butyric or phenyl acetic acids was capable of inducing ovary growth until late April or early May. These earliest successful fruits, both natural and parthenocarpic, were seedless. As the days became longer, ovules filled out in both naturally and artificially stimulated fruits. In cucumbers, a similar favorable effect of long day was noted in setting of natural and parthenocarpic fruits by Miller (1938). Whyte (1939) has recently suggested that in fruit growth, temperature plays a somewhat more important role, along with the photoperiod, than it does in the pre-fertilization processes.

The period of embryo development is preceded by extensive mobilization of food reserves, so profound that the entire plant is involved. Renewed root growth and absorption is a concomitant of this phase, making the applications of soil nutrients peculiarly effective at this time (Polster, 1938; Kraus and Kraybill, 1918; Hamner, 1938; Borodin, 1931; Auchter, 1924; Combes, 1935; Howlett, 1934–36; Murneek, 1937; Dobrunov, 1938).

If we consider photoperiodic responses as one stage of phasic development in the sense of Lysenko's concept, a number of open questions still remain. Though Lysenko originally considered the thermal and light phases qualitatively distinct, there is now evidence of overlap between them as shown by the ability to complete a portion or all the essential photoperiodic induction in swollen seeds and seedlings undergoing low temperature vernalization (Wöber, 1936). Harder (1937) has shown this to be true in *Sinapsis, Agrostemma* and winter rye. If the thermo- and photophases are wholly separate, we as yet possess neither readily recognizable criteria of the completion of the former nor inception of the latter. Though the transitions are functional rather than structural, they should be identifiable nevertheless. Changes in permeability, oxidase enzymes and protein iso-electric point have been suggested, but the data are thus far too meager to be conclusive (Bassaraskoja, 1936; Richter, 1936). There also remains the question as to why morning light is more effective than evening light in a long-day species as shown by Fabian (1938) for *Ullucus* and contrariwise for short-day forms as shown by Bünning (1936) for *Phaseolus*.

Lysenko and Whyte (1939) have also postulated the irreversibility of phases. Yet it is possible to rejuvenate a reproductive plant photoperiodically, making it again vegetative. While in some cases a shift from reproductive to vegetative photoperiod leads to the death of the apical meristem and initiation of subsequent vegetative growth from previously dormant lateral buds well down on the stem, as in hemp, there are, however, also cases of vegetative proliferation of the apical meristem of flowering plants, as in the *Compositae*. Whether such rejuvenation is possible only in plants on the threshold of reproduction but not in those which have been exposed for a considerable length of time to an optimal reproductive photoperiod is not yet definitely settled. It seems likely, however, that the rigidity of Lysenko's concept as to irreversibility in the light phase may, on the basis of recent data, undergo modification as already has the previous belief in irreversibility of the vernalization phase. Instances of devernalization with age and unduly prolonged low temperature treatment appear to be well established (Gregory and Purvis, 1937–38).

When a rejuvenated plant is shifted from a vegetative to a slightly reproductive photoperiod, certain anomalous yet progressive transitional intergrades from vegetative to reproductive structures are often obtained. Older portions of the stem produce green and leafy perianth segments devoid of stamens and pistils. Younger regions near the tip of the main axis produce increasingly perfect flowers until normal, functional flowers appear at the apex. This response often occurs in ornamentals of the *Solanaceae,* such as *Petunia*. Another aspect of reversion is the effect of change in temperature by means of which a short-day type such as *Xanthium* can be induced to exhibit long-day response (Gilbert, 1926, 1934).

The recent observation by Melchers (1939) that a vegetative scion of tobacco is able to induce flowering in a vegetative stock in the first year of the biennial species, *Hyoscyamus niger,* presages an early and profound revision of the current form of the florigen concept. Melchers' painstaking experiments were conclusive and clearly significant statistically. With reference to the normal flowering of biennials, Melchers postulates the formation of a new hormone, tentatively designated "vernalin," at low temperatures at the end of the first season. Upon this "vernalin" in turn depends the ability to produce florigen in the reproductive photoperiod of the second year. Melchers points out that our knowledge of the reproductive physiology of biennials, such as *Hyoscyamus niger* with which he worked, is almost as nebulous as our understanding of the day-neutral group of plants. Melchers' results also contradict the suggestion previously made by Cailachian that the photoperiodic effect is proportional to the area of foliage. Melchers noted no such quantitative relationships. Recent temperature studies suggest that radical revisions are also imminent in regard to the supposed indispensability of light for inception of flowering in the so-called photophase (Roberts, 1936–37–38–39; Thompson, 1933–36; Chroboczek, 1934).

In conclusion, it would seem, on the basis of recent evidence, that the thermo- and photo-phases are not as rigidly set apart nor as irreversible as originally suggested by Lsyenko. Further, it may prove desirable and conducive to a better understanding of reproduction if the photophase is subdivided into a flowering and gametogenic stage. If the profound and rapid transformations occurring between inception of flower primordia and fertilization, namely, the phenomena of sex, are studied as intensively as vernalization and photoperiodism, they promise to contribute fully as much as the former to our understanding of reproduction. If speed and magnitude of transformation be criteria of vital significance, the gametogenic or sexual phase *per se* represents the stage of most profound alterations in the ontogeny of the higher plants.

# OBITUARY

## MARGARET FLOY WASHBURN
### 1871–1939

MARGARET FLOY WASHBURN, emeritus professor of psychology at Vassar College since June, 1937, and a member of the Vassar faculty for thirty-six years, died after a long illness at Poughkeepsie, N. Y., on the afternoon of October 29, 1939. Her illness dated from a cerebral hemorrhage suffered on March 18, 1937—on the eve of the meeting of the Eastern Psychological Association, which was held at Vassar College in observance of her approaching retirement. She was at the time of her death in her sixty-ninth year, having been born in Harlem, New York City, on July 25, 1871, the only child of Rev. Francis and Elizabeth Floy (Davis) Washburn.

Professor Washburn was one of the foremost women in American science and was long recognized as a leader in her field. Her services and contributions to psychology were many and outstanding, and she received in recognition of them the highest honors and awards at the disposal of her confrères.

In 1919–1920, when the Division of Psychology and Anthropology of the National Research Council was formed, she acted as a representative of psychology, and again in 1925–1928. In 1921, she was president of the American Psychological Association. That same year she was awarded the prize of $500 by the Edison Phonograph Company for the best research on the effects of music, an investigation, done in collaboration with a colleague in the Vassar Department of Music, on "The Emotional Effects of Instrumental Music." In 1927, she was vice-president of Section I (Psychology) of the American Association for the Advancement of Science and was the recipient of a *Festschrift* and of an honorary degree of D.Sc. The *Festschrift,* volume 39 of *The American Journal of Psychology,* was dedicated to her by its authors, thirty-two colleagues from the various editorial boards upon which she had served, "in recognition of thirty-three years of distinguished service to psychology." The degree, *honoris causa,* was conferred upon her by Wittenberg College during the International Symposium on Feeling and Emotion that was held there at the dedication of the new psychological laboratory. She was elected, in 1929, to the International Committee on Psychology (the governing body of the International Congresses) and to the Society of Experimental Psychologists; and, in 1931, to fellowship in the National Academy of Sciences (the second woman to receive that honor, Dr. Florence Sabin having been elected before her in 1925). She was president, in 1931, of the New York Branch of the American Psychological Association (now the Eastern Psychological Association) and chairman of the Society of Experimental Psychologists. In 1932, she was the U. S. delegate to the International Congress of Psychology in Copenhagen. Professor Washburn was also a member of the National Institute of Psychology, the American Philosophical Society, the New York Academy of Sciences, the American Association of University Professors and Sigma Xi.

Besides publishing nearly 200 scientific articles and