I. Introduction

Flowering plants must attain a minimum size or age before they can reproduce. During the vegetative stages of growth and development, a plant is especially dependent upon nutrients. Energy is required for the transition from vegetative to reproductive phases and for the process of...
reproduction itself. Reserve foods supply this energy, and the plant, accordingly, must contain a sufficient reserve of foods to carry out the reproductive process. Reproductive organs, however, do not usually manufacture foods to any appreciable extent and seeds in particular are heterotrophic. In many species, especially those with an indeterminate growth habit, different parts of the same plant may simultaneously carry on vegetative and reproductive functions.

Light and temperature directly affect the initiation and development of floral primordia and the reproductive organs that develop later. Leaves, apical buds, and other vegetative organs are the receptors of these stimuli. Thus, the environment may determine whether anthesis begins, is retarded, or is suppressed. For example, sugar beets may flower prematurely in one environment or remain vegetative indefinitely in a humid environment. The course of reproduction may embrace more than a season, and, in biennials and woody plants, more than one year. Therefore, the plant is ordinarily subjected to wide variations in climate and nutrition during its life, factors that are critical to the over-all reproductive process.

Reproduction proceeds through stages of ripeness-to-flower, floral initiation, anthesis, fruit set, and maturation of fruit and seeds. As reproductive activity begins, the physiology of the plant is altered. Vegetative growth decreases and is continuously readjusted in accordance with the demands of reproduction. For a given plant and environment, the quantity of leaves, stems, and roots determines in a gross way the number of flowers formed and particularly the number of fruits that come to maturity. Especially in an unfavorable environment, there is a fluctuating competition between fruits and roots, leaves, or even other fruits on the same plant. As a consequence, reproduction slows down the vegetative growth but does not inhibit it entirely, and vegetative growth may proceed slower and then faster in succession in different stages of reproduction (Murneek, 1948). The complexity of these relationships is such that the plant as a whole must usually be considered in a discussion of the pathological aspects of reproduction.

Seeds and pericarp make very different substrates for pathogens. The heterogeneous nature of reproductive organs is evident on caryological examination. In addition, during the maturation of fruits, especially fleshy ones, seeds become dehydrated and show a marked increase in nitrogen content, and in condensation of reserve foods and finally appear isolated from the placenta, whereas in the pericarp, cell walls are hydrolyzed, simple sugars are formed, and water content increases.

Diseases of the pericarp have little influence on seeds unless there is premature fruit drop. Conversely, seeds may be killed by late frosts
whereas the pericarp is uninjured. When seeds are physiologically mature and firm, lysigenous breakdown of the pericarp begins adjacent to them and is intimately dependent upon their maturity (Naylor, 1952). On the other hand, the metabolic activities of the pericarp may produce physiologically active substances such as ethylene, which at appropriate concentrations may play a role in inhibiting seed germination. Thus, there is a correlation but no parallelism in the growth of the various parts of the fruit.

II. PARTHENOCARPCIC AND UNDERDEVELOPED FRUITS

Seedless and parthenocarpic fruits exemplify the correlation in development of the fruit parts. When parthenocarpy occurs naturally, it is assumed that the auxin content of the unfertilized ovule is sufficient to promote fruit development. The same results can be obtained by the application of auxin sprays to plants that do not undergo parthenocarpy naturally. These fruits are seedless, contain sterile pseudo-seeds, or, by partial reversal of the normal growth correlation, parthenogenetic embryos, *sensu lato*.

In fruits, the embryo, albumen, and pericarp are correlated in development. The embryo and albumen both arise through separate fertilizations on the part of the pollen nuclei. Therefore, in sterile seeds with an

![Fig. 1. Olive pseudodrupes (from Russo and Spina, 1952).](image-url)
abnormal, nongerminative embryo, the endosperm may be quite normal, e.g., in *Ruta graveolens* (Cappelletti, 1929). A similar situation occurs in Bartlett pears (Griggs and Iwakiri, 1954). In a favorable environment, the Bartlett pear matures fruits that arise from vegetative or pollen-induced parthenocarpy and are produced uniformly, abundantly, and of good shape. Unfortunately in other cases parthenocarpy is partially induced.

In the olive tree, very small, persistent pseudodrupes originate (Fig. 1) from pollinated flowers in which elongation of the pollen tubes ceases in stylar tissues (Russo and Spina, 1952). In these fruits, the useless pericarp is complete in all its parts, whereas the stone which consists of the hardened endocarp, contains pseudoseeds showing parenchymatous degeneration of the 4 ovules and no embryo (Messeri, 1947). Factors that lead to arresting of pollen tube growth and therefore to the formation of pseudodrupes in olives are incompatibility factors (Russo and Spina, 1952), and unfavorable environmental conditions such as high humidity (Morettini, 1950) and low temperature (Petri, 1942).

Parasites may cause similar responses. Thus, olive pseudodrupes may be the consequence of attack by insects, such as *Coccus oleae* and *Mytilococcus ulmi* (Petri, 1927). The same intrinsic or environmental causes are thought to be responsible for some types of "shot-berries" in other fruits, e.g., grapes.

### III. Nutritive Disturbances

Nutritive diseases act on the whole plant. Consequently, they influence the reproductive organs through the vegetative ones. El Hinnawy (1956), who recently studied this problem, concluded that the influence of minerals on the flowering response of long and short day plants is indirect and is exerted through their effect on the production of auxin, and therefore on growth and the production of material for flower bud formation.

#### A. The Carbohydrate: Nitrogen Ratio

In past decades, there was a prevalent belief that the relation between the life of the individual and the preservation of the species was largely dependent upon the C:N ratio, the influence of which on flower initiation was expressed in Kleb’s or Fischer’s rule. All the conditions that either favor an accumulation of assimilates or hinder the absorption of water and nitrogen salts increase the ratio of carbohydrate to inorganic nitrogen and consequently favor the transition of the plant to the reproductive stage. On the other hand, all conditions which cause the opposite effects favor vegetative growth.

After the discovery of photoperiodism, the importance of C:N ratio
was questioned and flower induction is now thought to be controlled by flowering hormones—the florigens. These have not as yet been isolated.

Floral initiation is not fundamentally dependent upon the C and N supplies (Naylor, 1952). Rather the proper photoperiod and other environmental factors as well as nutrition are necessary conditions to stimulate the formation of florigens. In healthy plants, the transition from vegetative to reproductive stages requires a level of light and nutrition exceeding the minimum needed by vegetative growth (Lona, 1953). With the onset of reproduction, vegetative growth is reduced. N and particularly C accumulate in the plant, and as a result the C:N ratio increases. However, this accumulation seems a consequence of flower induction and not a cause of it.

Once floral primordia are initiated, they as well as the blossoms and fruits are strongly influenced by the C and N supplies and their broad interrelationships are very important. A satisfactory understanding of these complex phenomena has not been gained as yet; coordinate studies on growth promoting substances and on food competition throughout the plant are badly needed.

B. Nutrient Excesses and Deficiencies Affecting Reproduction

The above discussion of floral induction refers to plants living within "the limits of health"; if the abundance or the deficiency of one nutrient in relation to another exceeds a certain range, the plant enters into a real pathological condition.

The supply of carbon directly influences flowering through its presence in a carbohydrate precursor of florigens and through the influence of carbohydrate translocation on the movement of the flowering stimulus (Lincoln et al., 1956).

Flower induction can be effected with very short exposures to illumination and with light intensities well below the compensation point. Later, a large supply of carbohydrates is necessary for reproductive growth and, at least in some cases, it has been found that carbohydrates directly influence the development of normal reproductive organs (Hartmann, 1955; Minessy and Schroeder, 1956).

The nitrogen nutrition of plants affects reproduction in a number of ways. Some plants seem to regulate nitrogen absorption regardless of the available supply (Crocker, 1948), but the response of different species to nitrogen is unpredictable. The assumption that nitrogen deficiency will promote flowering in long-day plants and slightly delay it in short-day plants proved to be erroneous (El Himawy, 1956); Murneek's conclusion (1948) still seems valid that nitrogen is one of the most crucial nutrient elements in the initiation of reproduction. Nitrogen
promotes growth in accordance with the principle that without nitrogen there is no growth hormone and consequently no growth (El Hinnawy, 1956). Therefore, an abundant nitrogen supply is usually required in the reproductive stages subsequent to floral induction. An excess or a deficiency of nitrogen can easily impair flowering or fruit set and the former condition frequently induces an increase in the number of members of flower verticillia, virescences, proliferations, and recrudescences of reproductive organs. Excessive nitrogen also increases the susceptibility of blossoms to low temperature (Boynton, 1954). During maturation of fruits, excessive nitrogen may excite more complex responses on the part of the plant as in "Baldwin spot" of apples (Garman and Mathis, 1956). Nitrogen deficiency may directly cause pistil abortion, affect pollen germination, and induce flower shedding and fruit drop. In dry climates, nitrogen deficiency is one of the most common causes of staminate flowers in the olive tree and nitrogen fertilization is, therefore, advocated so that otherwise symptomless trees will form normal flowers and set fruits (Petri, 1942). Biennial bearing in olives in dry climates is reduced by nitrogen dressings in April of the preceding year (Sommaini, 1954, 1955).

Although phosphorus does not affect flower initiation, according to El Hinnawy (1956), it accumulates in the developing primordia and flower buds. Phosphorus deficiency may lessen the fruit set and is a recognized factor affecting earliness of cereals and upland cotton, among other plants (Ergle and Eaton, 1957).

Phosphorus, however, does not seem highly important in some fruit crops. Thus, in peach, phosphorus can almost be considered a secondary nutrient, ranking below nitrogen, potassium, calcium, and magnesium (Bell and Childers, 1954). This behavior may be a result of the interaction of phosphorus with other elements, especially nitrogen.

Potassium plays an important role in carbohydrate metabolism; potassium deficiencies reduce set, size, sugar content, and color of fruits. An excess of available potassium, which is often related to high nitrogen levels, can indirectly damage reproduction because of its strong antagonism to calcium and, to a lesser extent, to magnesium, zinc, and other nutrients. Thus, an excess of potassium tends to accentuate the symptoms of blossom end-rot in tomatoes and of "Baldwin spot" in apples.

Boron deserves particular mention in regard to reproduction. In very low concentration (1 to 100 p.p.m.), it regulates the water absorption of certain pollens, prevents their bursting, and favors their germination. Also, it activates the development of the pollen tube. These functions of boron explain its presence in the nectar of the Nymphaeaceae and in the stigmatic secretions of tomato and other plants. The stimulation by boron of the elongation of pollen tubes is attributed to its influence on
oxygen uptake and sugar absorption, but it may also involve the synthesis of pectic materials in the cell walls of the elongating pollen tube (O'Kelley, 1957). In boron-deficient grapes, fruit set and yield are severely depressed, and fruits are seedless and undersized. Boron-deficient apples show internal and external corking. Preharvest drop and breakdown in late stored apples are also associated with the boron content.

A slight disturbance in boron nutrition sometimes affects a single stage of reproductive activity. Thus, an incipient boron deficiency in vigorously growing grapes and pears may cause failure of fruit set although there are no foliar symptoms. Sometimes this behavior is attributed to a high boron requirement of the plant when blossoming (Christ and Ulrich, 1954). In other cases it is attributed to the unavailability of boron in heavy, water-logged soils during the spring (Batjer et al., 1953), or to the dilution of boron induced by rapid development of vegetation following nitrogen fertilization (Boynton, 1954).

According to Brennan and Shive (1948), the influence of calcium on carbohydrate translocation is a result of the relationship of calcium to boron. Recently, Joham (1957) has judged the influence of calcium on carbohydrate translocation to be similar to, but independent of, boron.

Calcium deficiency per se exerts other, more direct, influences on reproduction. Thus, in cotton it affects the earliness of flowering, the number of flowers, and the weight of bolls (Joham, 1957). "Baldwin spot" of apples, often attributed to an excessive development of foliage, has been associated with calcium deficiency in the fruit (Garman and Mathis, 1956).

A zinc deficiency prevents the normal production of tryptophan, a precursor of indoleacetic acid, and results in an increase in blossom and fruit drop.

Recently, iron-deficient cocklebur has been studied during photoinduction treatment. Staminate flower primordia were delayed in appearance and developed more slowly. In pistillate inflorescences, mature burs developed abnormally or failed to be produced. The influence of iron during photoinduction was more pronounced than that of boron or magnesium (Smith et al., 1957).

Deficiency of magnesium seems especially effective in delaying flowering in such plants as mustard (El Hinnawy, 1956). It has also been repeatedly associated with fruit drop.

IV. WATER AND REPRODUCTION

When water in the soil or in the atmosphere is in excess or is deficient, or when the amount of water available undergoes sudden fluctuations, damage is likely to result. Unfavorable water relations in the soil...
do not always produce the same effect as unfavorable moisture relations in the atmosphere. For instance, an excess of humidity around flowers may prevent the access of oxygen and reduce abscission, whereas an excess of water in the soil increases abscission.

Excessive moisture generally interferes with the transition of the plant to the reproductive stage. When the atmosphere is too humid, flowering is delayed, fertilization is reduced because insect movement is reduced, stigmatic secretions are diluted, and pollen grains are not dispersed by wind and burst. Consequently fruit set is curtailed.

High atmospheric humidity may affect reproduction, even in fully developed fruits and embryos. Wheat embryos may germinate in the inflorescences still in the field. Intumescences of pod valves and of bean and pea seed are also attributed to high humidity (Hiltner, 1933).

Drought conditions, even if short in duration, may have profound effects upon pollen formation and vitality. At meiosis, drought may cause diploid and tetraploid microspores and pollen grains in Tradescantia. If some wilting occurs, the pollen may fail to develop (Naylor, 1952). During bloom, water inadequacy, therefore, reduces fruit set and causes blossom shedding.

Later on, a moderate moisture deficiency may increase firmness and keeping quality of apples and pears, but—especially in arid climates—it affects the leaf:root and leaf:fruit ratios and the competition among fruits. Sometimes, when fruits have attained their final size, competition between fruits and vegetative organs favors the fruit itself. Thus, in the San Marzano variety of tomato, the leaves—which have a thin cuticle—may wilt, whereas the fruits hold their moisture more efficiently by means of the mucilages and pectic substances they contain, and mature almost normally.

Usually, however, a water deficit causes a reduction in size, number, and quality of mature fruits. In mild cases, there is a partially reversible withdrawal of water from fruits, causing a shrinkage in olives, citrus fruits, etc. (Savastano, 1934). For this reason, late spring and summer irrigation increases the frequency of annual bearing in the olive tree, lessens fruit drop, and increases the size of individual drupes (Hartmann, 1953). In temperate fruit crops, such as apple and pear, the flower buds are laid down in the year preceding flowering. A mild water stress during the critical period may slow down vegetative growth and enhance flower initiation (Tubbs, 1955). Once induction has occurred, the subsequent stages of flower development require an adequate water supply.

In some tropical fruit trees, the dry season is the only rest period and the succession of dry and rainy periods is necessary for a normal periodical growth. In Litchi chinensis floral initiation and flowering occur
satisfactorily in Canton (Southern China), where the above conditions are found, but floral initiation is rare in Hawaii and there recourse is made to the use of such auxins as sodium naphthalene acetate (Nakata, 1955).

Drought can prevent after-ripening and induce "secondary dormancy" in seeds.

V. TEMPERATURE AND REPRODUCTION

In plants requiring a thermoperiod to go into the reproductive stage, temperature determines the initiation of flowering. The apical bud is the receptor of the stimulus and in the absence of a favorable thermoperiod, such plants either do not form floral primordia or fail to flower. If a favorable stimulus is received out of season, it can induce plants to flower at that time, e.g., the preflowering of sugar beets when winters are intermittently mild.

A minimum daily range of temperature is often necessary for good fruit set. Diurnal thermoperiodicity equilibrates photosynthesis and condensation reactions in daylight and respiration and growth at night. For the tomato, night temperatures should be at least 6° C. lower than daytime temperatures (Verkerk, 1955). The best temperatures for setting large crops of tomatoes in Texas, range from 13 to 20° C. at night and from 21 to 30° C. during the day (Young, 1957). Daily excursions of temperature are also needed for the after-ripening of some seed and can act as a substitute for light on light-sensitive seed.

Excursions of temperature on an annual basis are sometimes required. Thus, the annual periodicity of growth in subtropical trees is often impaired by the absence of a moderate winter chilling. Inflorescence development in olive and subsequent fruit production are generally proportional to the amount of chilling received (Hartmann and Porlingis, 1957). For this reason, olive yields poorly in the African highlands.

High temperatures are a common cause of blossom shedding and fruit drop. The most sensitive parts of flowers are pollen and stigmas. Thus, tomato pollen is inactivated when temperatures exceed 32° C. (Young, 1957) although the variety of the plant and its vigor affect this relation. Thus, the Hotset variety of tomato will set fruit at temperatures from 3 to 5° C. higher than the maxima that are usually tolerated.

Although high temperatures break dormancy of some seeds, they induce secondary dormancy in others and temperatures above 30° C. are not favorable to the germination of some species of seed (Toole et al., 1955).

The first effect of low temperatures may be shown by pollen. Temperatures below 15° C. at the time of dispersal may devitalize maize
pollen (Elitropi, 1958). Reproductive organs are highly susceptible to frost injury. According to Modlibowska (1956), the various parts of the flower are not equally susceptible. Petals may be harmed when male and female organs are still uninjured and vice versa. Often the filaments are damaged, whereas the gynoecium is still intact. Early autumn frost may harm the flesh of fruits that are low in sugar at maturity or that ripen late in the fall or during the winter. Thus, according to Azzi (1928), mature olives are injured by temperatures of $-0.4^\circ$ C. but even in these cases early frost causes little or no damage to reproduction.

Late spring frosts affect reproduction frequently. Modlibowska (1956) has shown that the economic consequences of late frost on the yield are less than is thought. Even when as many as 95% of the flowers are killed, the remaining ones produce a good crop if trees are well tended and pest and disease control is adequate. The effect of intense and repeated frosts on such early flowering trees as the almond may be so great, however, that the reproductive activities for the entire year may be suppressed.

The cold susceptibility of reproductive organs in different species varies widely. In apple and cherry the pistils are first injured at the base of the style. In pear the ovary is most susceptible. In cherry and plum the first lesions on the ovary are external. In apple and pear the centers of the flower and young fruit are injured earlier than the pericarp. Later the reverse is true. The susceptibility of flowers and fruits to frosts varies with the stage of growth, even in different varieties of a single species. Among apple varieties, “Belle de Boskoop” is equally sensitive at all stages; “Bramley’s seedling” is most sensitive at the green button and pink button stages, but becomes hardier later; the reverse is true in “Ellison’s orange” (Modlibowska, 1956).

The minimum temperature tolerated by flowers depends on their physiological condition, their nutrition, and the rapidity of growth. Thus rapid growth in a humid and warm environment predisposes flowers to frost injury.

Attack by pathogens may predispose flowers to frost injury. Thus, Modlibowska (1956) has shown that infection by *Stereum purpureum* increases susceptibility of plum flowers to low temperatures.

VI. LIGHT AND REPRODUCTION

The requirement of plants for a certain duration of daylight (in order to flower) is now well known. In order to flower many plants require—in addition to a low temperature period—a short photoperiod of 10 hours or less, and others require one of 14 hours or more. The light stimulus is perceived by the leaves and the interval over which the response to day length occurs is that of photoperiodic induction.
For short-day plants, the dark period is the critical one if it has been preceded by a light period. Long-day plants flower even in continuous light and then failure to flower is due to an excessively long dark period. Some plants require a succession of two different photoperiods. Thus *Cestrum nocturnum* flowers when subjected to long days followed by short days or continuous long or short days or short days before long days are ineffective.

The behavior of short- and long-day plants is presently explained in terms of flowering hormones. Florigens, formed in leaves, would be destroyed by high levels of auxins. But when florigens are translocated to buds, auxins contribute to their fixation and to the subsequent differentiation of floral primordia (Salisbury, 1955). In floral induction, according to Liverman (1955), there is a lowering of the auxin level during the dark period in both long- and short-day plants. In short-day plants, the dark period causes the auxin content to drop to a level where florigen synthesis can occur. In long-day plants, the auxin level is too low for flowering under short-day conditions and long days are thus required for floral induction.

When occurring late in the life of a plant, photoperiodic stimuli sometimes cause abnormal responses. Thus short-day conditions may cause the formation of embryo sacs in the anthers and of pollen in the pistils (Naylor, 1952).

Even plants indifferent to day length, such as tomato, fail to fruit when exposed to day lengths of 5 hours or less or of 24 hours or more. In the latter case, foliar injury often occurs.

Photoinduction occurs both in woody and herbaceous plants. *Poinsettia* and *Bougainvillaea* are short-day woody plants and *Hibiscus syriacus* is a long-day plant. Other species are day neutral. Although in herbaceous plants, photoperiods induce flowering, in woody plants they control dormancy primarily (Wareing, 1956). Sometimes, as in apple flowering, climatic conditions are less important than physiological conditions and the latter are modified by climatic conditions in ways which are still obscure (Gorter, 1955). In tropical and subtropical plants, dormancy or vegetative pause seems to depend upon chilling or dry spells.

A number of growth regulators interfere with floral initiation, and Salisbury (1957) has identified the steps in photoperiod induction of cocklebur that are blocked by some growth regulators. One mechanism determines the critical day length. Other stages of induction are synthesis of flowering hormone in the leaf and development of floral buds. Evidence for this reasoning is based on the ability of cobaltous ion to interfere with the mechanism controlling critical day length; the inhibition by 2,4-dinitrophenol of florigen synthesis; the action of 3-indolacetic acid,
naphthalene acetic acid, and 2,4-D to destroy the flowering hormone in the leaf; and the ability of maleic hydrazide, Dalapon, and 2,4-D to inhibit floral bud development.

Quite apart from photoperiodic effects, intense light absorbed by dark surfaces such as fruits and flowers is converted into heat and the exposed tissues can attain temperatures 8 to 9° C. above the temperature of the surrounding air. Blueberries in New Jersey attained temperatures of 40° C. when the air was 31° C. (Stevens and Wilcox, 1918).

Intense light prevents the germination of many seeds, e.g., most Liliaceae, and induces secondary dormancy in some of them, e.g., Nigella, which become light hard. In such cases their germination is hindered, even when they are put again in darkness. Dark hardness may be caused by low light on light-requiring seeds, as, for example, many grasses.

In insufficient light, leaf production takes place at the expense of roots (Shirley, 1929) and reproduction is impaired. Delayed flowering, reduction in the initial number of flowers, shedding of blossoms, and slow development of fruits are usually induced by low light intensities, either at high or low temperatures.

When plants receive the full spectrum of daylight, intensity is not very important. About 40 foot-candles seem sufficient for mere survival of many plants. In Guthrie's experiments (1929), flowering was impaired only when illumination was reduced to 8% of full summer sunlight. When harmful effects occur, they usually result from an incomplete spectrum, which lacks the shorter green, blue, and violet wavelengths, i.e., shorter than 5200 Å. Under glass that fails to transmit violet light, some plants differentiate few if any flowers.

The studies of Flint and associates (in Crocker, 1948) were among the first to present modern information on the influence of different rays on the life of plants. According to them, the region 5200 to 7000 Å (red, orange, and yellow light) stimulates the germination of lettuce seeds, whereas the regions from 4200 to 5200Å (green, blue, and violet) and 7000 to 8600 Å (mainly infrared) are inhibitive. The action spectrum for floral induction of short-day plants, such as Xanthium pennsylvanicum, is similar to that for germination of lettuce seed (Borthwick et al., 1952). Present data suggest that red and infrared rays generally participate in flower induction and elicit other morphological responses of higher plants; so that the action of light upon some seeds would be one aspect of a general phenomenon influencing living processes (Wassink and Stolwijk, 1956).

Red rays promote growth and flowering in barley, a long-day plant, whereas infrared rays inhibit growth and promote flowering in Xanthium,
a short-day plant. In flower initiation, the most effective red rays are in the region of 6500 Å and 7350 Å is the most effective region of the infrared. Red rays may repeatedly reverse the photoreactions induced by infrared and vice versa. These reactions appear to be independent of temperature. Their reversibility, however, is reduced by a dark period between the two irradiation periods. The effect of darkness depends upon temperature (Downs, 1957).

Infrared rays may also decrease fruit set, especially at high temperatures, in some neutral day plants, such as tomato (Young, 1957).

VII. INTERACTIONS OF NUTRITION AND CLIMATE ON REPRODUCTION

Although the effects of nutrition and climate on reproduction have been examined separately, their action on plants is sometimes inextricably interrelated and cumulative. Thus, long- and short-day plants do not respond to photoperiodic stimuli when temperatures are too low (1 to 4° C.) or too high (30 to 38° C.) (Liverman, 1955). In short-day plants, the night temperature is very important, and in long-short day plants, e.g., Cestrum nocturnum, the day temperature has a great effect upon long-day induction, whereas the night temperature has its effect upon short-day induction (Sachs, 1956). During part of the photoperiodic cycle, cool temperatures are required by Glycine max (Blaney and Hamner, 1957), perhaps indicating an “endogenous rhythm” of 24 hours’ duration (Bünning, 1956).

The behavior of seeds is altered by combinations of temperature and light. Lettuce seeds, kept for 24 hours at 25° C. in a dark germinator lose their sensitivity to light and do not respond to standard illumination. However, when stored in darkness at 5° C., they germinate normally. In a dry environment, seeds exposed to low temperatures do not after-ripen; but if allowed to imbibe water before exposure to red or infrared rays, the response of the seeds is different (Liverman, 1955).

The nature of the flowering response in cucurbits is altered by proper adjustment of temperature and light. Thus, cucurbits can be induced to form staminate, monoclinous, and pistillate flowers under appropriately controlled conditions, just as they do in nature (Nitsch et al., 1952).

High temperature in association with low light intensity, induces poor fruit set in tomato as well as dormancy of fertilized ovaries (Johnson, 1956). In some fruits, high temperatures, intense light, and deficient moisture, in combination, alter cell permeability with the result that cell sap fills the intercellular spaces, parenchymal cells become discolored, and a watery decay of tissues sets in, e.g., water core of apples. Blossom end rot of tomatoes is another example. It can be induced by intense daylight, by high night temperatures (Verkerk, 1955), by temporary
water shortage in a critical stage of the development of the fruit, or by
calcium deficiency in which the ratios of potassium to calcium and of
soluble calcium to total salts in the soil solution are important (Gerald-
son, 1955).

“Shrunken grain” of wheat is another complex disease induced by
moisture deficiency of the caryopses, which deficiency in turn is caused
by hot dry winds, by pathogens such as rust or Ophiobolus graminis, or
by malfunctioning of the vascular tissues, such as in lodging of wheat
(Baldacci and Ciferri, 1944). According to Mulder (1951), bitter pit of
apples is induced by inappropriate breeding and cultural methods, excess
nitrogen, relative lack of phosphates due to magnesium deficiency, and
adverse ratios of foliage to fruits.

VIII. IMPAIRED GROWTH CORRELATIONS OF REPRODUCTIVE ORGANS

The fulfilling of each stage of reproduction requires that the different
organs be in the right condition at the right time. Thus, for fertilization
to occur, pollen must be able to germinate, stigmas must be receptive;
water, inorganic nutrients, sugars, and growth factors must all be ade­
quate; and temperature and light must be within certain limits. If these
conditions are not fulfilled, fertilization may be impaired. In tomato, high
nitrogen levels, or low light, or high temperatures and high light intensity
may induce style exsertion before dehiscence of the anther sacs occurs
and, as a result, fruits fail to be set (Johnson, 1956; Leopold, 1955). In
maize, the environmental conditions may easily induce the opposite con­
dition, premature pollen dispersal, though this is usually not very harm­
ful (Elitropi, 1958).

IX. PREMATURE ABSISION OF REPRODUCTIVE ORGANS

Histologically, when flowers and fruits drop prematurely, a dissolu­
tion of the middle lamellae and adjacent layers of the primary cell walls
occurs in the abscission zone of the peduncle. Meristematic layers pro­
tect the stump of the peduncle, which remains on the plant, and the
lumens of vessels become occluded by gums and tyloses.

Abscission is now thought to be controlled by the relative auxin
concentration across the abscission zone. When the gradient of auxin
across the abscission zone—from the proximal to the distal side—is
steep, flowers and fruit are not shed; when the gradient is low, or dis­
appears, or is reversed as a result of an auxin spray on leaves, abscission
results (Addicott and Lynch, 1955). The “auxin gradient” hypothesis
may not be generally valid, since in Phaseolus vulgaris and Coleus
blumei the controlling factor in stimulation or inhibition of abscission
is the total amount of auxin applied and not the auxin gradient (Gaur
and Leopold, 1955).
In young flowers, auxin production is largely centered in the maturing stamens and ovaries (Leopold, 1955). When flowers are mature, their auxin content becomes very low, but upon pollination the ovary produces a new flush of auxin. This gradually diminishes until new auxin is produced by the endosperm and later by the embryo.

In the apple, there are four flushes of blossom and fruit abscission. The first drop is given by aborted and unfertilized flowers. The second appears associated with an insufficient activation of auxin-forming systems in the fertilized ovaries. These two can easily fuse one into another. The third (June drop) and the fourth (preharvest drop) occur in periods of lessened auxin production in endosperm and embryo. Auxin sprays satisfactorily control the first flushes of flower and fruit drop, when some environmental condition has temporarily interfered with pollination and limited fruit set.

Environmental conditions, however, can interfere with auxin action. Thus, Marglobe and Rutgers tomatoes do not respond to sprays of p-chlorophenoxyacetic acid under high temperatures and light intensities of summer, whereas summer setting varieties, sprayed with the same compound, nearly doubled their fruit production (Johnson and Hall, 1955). When there is a temporary lack of nutrients, as in the case of early tomatoes that may flower when there are still few leaves on the plant, auxin treatment can usefully delay fruit drop until nutrition becomes adequate, but auxins cannot indefinitely replace an adequate nutrient supply.

The competition for nutrients among reproductive organs may result in dropping of fruit shortly after fruit set. And, when the number of leaves is insufficient to supply the fertilized ovaries with the necessary food, the younger ovaries may become dormant because the fruit already set seems to have a priority upon the amount of nutrients and food available. In tomato and cotton, the dropping of young fruits is greater when older fruits have already been set on the plant. In cotton, for example, the dropping of fruits at the beginning of the fruit set period may be as low as 10%, whereas at the end of the flowering period, it may be over 90%. In this case, the abscission of younger fruits is stimulated by the auxin concentration of older fruits (Addicott and Lynch, 1955). Inasmuch as nutrients are translocated to and concentrated in regions high in auxin, young fruits receive fewer nutrients than older ones do.

The activity of auxins is, therefore, interrelated with and affected by nutrition as well as by light, temperature, respiration, and translocation (Hamner and Nanda, 1956; Biggs and Leopold, 1957). Furthermore, calcium is necessary for the formation of the insoluble pectins in middle lamellae and zinc is required for auxin synthesis. Carbohydrates are
specifically useful in the formation of cell wall material. Oxygen and carbon dioxide concentrations, insofar as they influence respiration at this stage, may influence abscission. The carbon:nitrogen ratio (a result of the processes of nutrition), photosynthesis, and respiration also provide information on the likelihood of abscission. Either a very high or a very low value of the carbon:nitrogen ratio indicates that fruit drop is likely.

Auxin sprays are a convenient method of preventing flower abscission, application being made to flowers or to the soil. A number of synthetic growth hormones are useful for this purpose. Esters of p-chlorophenoxyacetic acid, and of β-naphthoxyacetic acid are useful for improving fruit set of tomato. Very low concentrations of 2,4-D have proven effective on snap beans. Benzothiazole-2-oxycetic acid, a weak auxin, is preferred for use on figs because it causes development of seed coats as well, and this has improved the saleability of the parthenocarpic fruit.

For the control of preharvest fruit drop, auxins are applied as sprays or aerosols and treatment is repeated. The treatment tends to improve coloring of apple fruits and does not increase the percentage of defective fruits. The use of auxins in this way has some unfortunate side effects. Thus, the respiratory rate of the fruit is increased so that the useful storage life is shortened. To counteract this effect, maleic hydrazide can be incorporated into the auxin spray. Auxins also enhance radial cracking in apples and induce puffiness and other undesirable effects in tomatoes. Unless the concentration of 2,4-D on oranges is at the low level of 10 mg. per liter it tends to induce abnormally large navels or seeded fruits in the otherwise seedless Navel orange.

Olives fail to respond to auxins sprays, applied to prevent preharvest drop. Melis (1949) has pointed out, however, that both preharvest and summer fruit drop of olive is often caused by infestations of Prays oleellus, the importance of which had been overlooked.

Other auxins have been used for fruit thinning. It is thought that they may act by inducing incompatibility between pollen tubes and stylar tissue or by inhibiting pollen germination or tube elongation (Leopold, 1955).

X. PHYSIOLOGICAL DISORDERS FAVORING THE ESTABLISHMENT OF PARASITES ON REPRODUCTIVE ORGANS

Physiological disturbances sometimes make the plant more susceptible to attack by parasites. Thus, intumescences of peas and other legumes, induced by high humidity, have been attributed to Cladosporium pisi, which only colonizes them. Grape inflorescences, injured by low temperatures, are usually invaded by Botrytis cinerea. Olive pistils are often
infected by *Pseudomonas savastanoi* through wounds caused by late frosts. Sunburn or sunscald of tomato is readily infected by ubiquitous molds such as *Alternaria tenuis*, *Cladosporium herbarum*, etc.

The colonization of necrotic tissues by common molds is so inevitable that some physiological disorders have long been mistaken for infectious diseases. Blossom end rot of tomatoes is an example. In southern Italy, the damage caused by *Monilia laxa* to almond blossoms is so dependent upon cold and humid weather that farmers attribute the rot and shedding of blossoms directly to unfavorable weather. In some of these diseases, the action of the pathogen is primary in importance although secondary in order of time. Such diseases might, therefore, be classed as "consequential" or "concatenate" diseases ("Folgekrankheiten" or "Kettenwirkung verschiedenartiger Krankheitsprocesse"; Morstatt, 1933).

XI. Infectious Diseases

Whether infectious diseases are systemic or local, they affect the general physiology of the host and, when the infection exceeds a certain intensity, reproductive activities of the host become affected. The same pathogen can behave differently in regard to host reproduction, depending on the mode and amount of invasion of host tissue. *Kunkelia nitens* prevents flowering of blackberry (*Rubus* spp.) when mycelium is generalized in host tissues from the rootstock to the growing point, but does not interfere with blossoming except in the invaded nodes when infection is local (Dodge, 1923).

Some pathogens of flowers, fruits, and seeds limit their attack to accessory parts of reproductive organs and thus do not interfere with the preservation of the species. *Coryneum beijerinckii* behaves in this way because it injures the bulky or dry pericarp of stone fruits.

A. Seed-Borne Pathogens of the Vegetative Organs

Some parasites cause no injury to the seed but are simply carried on them and subsequently attack the plant developing from this seed. *Corynebacterium michiganense* plugs the micropyle and surrounds the embryo of tomato seeds, but may not interfere with the germination of the seed or with the life of the seedling. Thus, the disease is latent in the seed or seedling and becomes overt only in the vegetative organs of the adult plant. Similarly tomato plants, attacked by *Fusarium bulbigenum lycopersici*, often bear apparently normal fruits and viable seeds. In such cases, the reproductive organs act as carriers of a latent infection.

This situation is opposed to that of the parasite which generalizes in the green parts of the host plant and becomes pathogenic only in reproductive organs, e.g., many smuts.
B. Diseases of the Vegetative Parts Specifically Affecting Reproduction

It is well known that parasites may stimulate distant responses, useful or injurious, on the part of their host plant. There are orchids (Gastrodia elata) that do not flower unless infected by Armillaria mellea, and Rhizoctonia solani induces the formation of aerial tubers on stems of potato plants infected in the roots and stolons.

Occasionally, responses unfavorable to reproduction are elicited by mycorrhizae, the importance of which in the normal physiology of many plants is well known. Mycorrhizae of the olive tree may intercept the major part of nitrogen available in a nitrogen deficient soil. Pistil abortion and blossom shedding ensue (Petri, 1914). Sometimes this nitrogen deficiency results in morphologically abnormal staminate flowers, as Petri (1942) and others have found.

In northern Italy, the nitrogen starvation resulting from mycorrhizae of Ruta graveolens has prevented the development of the embryo in otherwise normal seeds so generally that extinction of the species seems inevitable. Plants lacking mycorrhizae produce germinable seeds (Cappeletti, 1929).

The indirect action of pathogens on reproduction is illustrated by Gibberella fujikuroi, which forms gibberellins in the plant. This fungus induces earliness in plants reaching adult size, but lowers yields. Generally, the gibberellins increase stem elongation and, in doing so, release a flowering response, especially evident in plants where the acceleration of vegetative growth eliminates mechanical barriers to flowering. The gibberellins may reduce germination time of seeds, but have no effect on total germination.

C. Pathogens Attacking Reproductive Organs Directly

1. Seed and Fruit Contaminants

Parasitic or saprophytic microorganisms may get into the flower and be borne on the surface of the seeds as external contaminants; or they may penetrate into its external layers, inducing “transitional infections,” “pseudoflower infections,” or “flower-seedling infections” (Gäumann, 1950). These microorganisms interfere with the viability of the embryo only when favored by particular environmental conditions. Among the genera of fungi acting in this manner are Alternaria, Cladosporium, Helminthosporium, Pullularia, and Stemphylium. “Heating” of moist grains is due to these fungi.

Most of the parasitic fungi that act in this way infect the seedling during preemergence or immediately thereafter. Some, e.g., Helminthosporium gramineum, are also harmful later in the life of the plant.
2. Fructicolous Infections

Some pathogens attack reproductive organs only. Thus the flower primordia of *Pennisetum* are attacked by *Tolyposporium penicillariae*, monoclinous flowers ready to blossom are attacked by *Claviceps purpurea*, and entire female flowers of *Ulmus* are attacked by *Taphrina* spp. Pistils are also attacked. Sometimes they are partially infected, as in "partial bunt" of wheat caused by *Tilletia indica*. In others they are entirely invaded, as in the case of mulberry ovaries attacked by *Ciboria caruncoloides*. The seeds of *Alnus* are attacked by *Helotium seminicola* and fruits may also be attacked as in the case of *Tilletia barclayana* of rice.

These parasites sometimes enter sexual organs through the accessory parts of the flower or fruit. In other cases they infect the pistils directly or are inoculated by insects into seeds or fruits, e.g., stigmatomycoses.

Many pathogens overwinter in the affected organs of the host, some in the soil by their own perennating structures, as in the case of *Claviceps purpurea* and many smuts; still others survive in ways that are not yet known (stigmatomycoses). These pathogens are not externally seed-borne, do not induce generalized infections of their hosts, and might be considered "fructicolous" sensu lato.

3. Generalized Parasites with Sporulation Restricted to Reproductive Organs

Other pathogens, perhaps the most interesting for students of diseases of reproduction, are more or less generalized through the green organs, where their parasitism is more or less indifferent to the host plant. They sporulate and, in doing so, induce overt disease in reproductive organs or in the accessory organs of flowers and fruits. Gäumann (1950) considers these as agents of "organotropic diseases."

In rare cases the infection begins from the embryo, which becomes infected at anthesis. *Ustilago nuda* and *U. tritici* provide examples of this condition. Gäumann (1950) has used the term "germinative transmission" to describe this situation and Fischer and Holton (1957) used the term "embryo infection." In other cases, infection may begin in the seed coat, e.g., *Botrytis anthophila*; in other instances, it arises from the pericarp and husks, e.g., *Ustilago avenae*, from the seedlings or from the shoots, as in *Ustilago violacea*. The period of incubation of shoot infections may last more than one year in plurennials. Parasites causing seedling infections and those causing seed coat, pericarp, and husk infections have seed-borne or soil-borne spores or mycelia. These situations correspond to Gäumann's (1950) terms "pseudoflower infection," "flower-seedling infection," and "adherent transmission." Such modes of infec-
tion may coexist in the same species. Thus, *U. violacea* can penetrate into the plant through flowers, buds, and excised stems (Spencer and White, 1951).

The chrysanthemum aspermy virus causes deformation of flowers but no symptoms or at most a slight mottling on leaves. The virus can be recovered from roots, stems, leaves, and flowers; sap from flowers is the most infective, that from roots the least. Leaf sap is said to contain an inhibitor, although little or none is present in the flowers (Hollings, 1955). Therefore, this is a case of "forced organotropism" (Gäumann, 1950).

The diseases discussed in Sections XI, C, 2 and 3 have been termed "venereal diseases" by Gäumann (1950). This is a suggestive term. Venereal diseases, however ("venereal" from Venus, the goddess of love) are not such simply because they affect the reproductive organs, but because they usually arise from sexual intercourse with an infected mate. Thus cancer of the reproductive organs is not a venereal disease. In the diseases considered above, the pathogens infect the reproductive organs but this is independent of the fertilization processes which are often prevented by the diseases caused by the pathogens.

In some cases, they effect also a "parasitic castration" (*Ustilago violacea*) or induce a "parasitic unfruitfulness" in a wider sense. Commonly, they do not penetrate into the host through the stigma and the stylar tissue. Even *U. tritici*, which shows so high an electivity for embryos, pierces the wall of the young ovary laterally (Batts, 1955; Batts and Jeater, 1958; Ohms, 1955).

It seems interesting to note that an apomictic progeny of a male sterile mutant of *Paspalum notatum* produced more than five times as many ergotized florets, infected by *Claviceps paspali*, as a similar progeny of a male fertile sister plant tested in comparison (Burton and Lefebvre, 1948). The sphacelial stage of *Claviceps purpurea* developed even on florets of wheat deprived of stamens and ovaries (Cherewick, 1953); *Tilletia buchloeana* and *Sorosporium Everhartii* may transform into bunt or smut balls the rudimentary ovaries of staminate spikelets, which normally would never produce seeds (Fischer and Holton, 1957). Therefore, these fungi are to a certain degree independent from the presence of mature sexual organs and from the nutritive environment including hormones and similar substances associated with the reproductive state.

A similarity to venereal diseases may be shown only by those diseases which are transmissible by way of the fertilization process. This is the case of bean mosaic virus (*Phaseolus* virus 1), which can be trans-
mitted through the agency of the pollen of infected plants. This virus
disease, however, is also transmitted in other ways and, when transmitted
through the pollen, does not particularly damage reproduction.

4. Reproduction Affected by Nonelective Parasites Entering the
   Plant through Reproductive Parts

Still other parasites (*Erwinia amylovora* and *Sclerotinia* spp., espe-
cially *S. laxa*) are capable of attacking tender vegetative organs, such as
unfolding buds and young leaves or twigs through natural openings and
through wounds, but they frequently penetrate the plant through floral
organs such as petals, stamens, and pistils. These structures are either
not cuticularized or little so, and offer conditions conducive to infec-
tion: high humidity and the presence of nectar and stigmatic secretions.
Ubiquitous organisms may also infect stigmas and enter fruits where
they usually remain ineffective, as, for example *Bacillus vulgatus* in
*Cucurbita pepo* (Marcus, 1942). High atmospheric humidity favors the
infection process. Thus, according to Weaver (1950), at 90% relative
humidity peach blossoms contract infection by *Sclerotinia fructicola*
through all floral organs; at 70 to 80% relative humidity, blight occurs
only from infected stigmas; while at 70% relative humidity, blight of
blossoms occurs only from stamen infections.

In the stone fruits, flower buds open before foliar buds do, and when
the season is most favorable to infection, floral infections are abundant.
In other cases, as with *Erwinia amylovora*, flowers attract the insect vec-
tors of the pathogens rather than the pathogens themselves.

Some pathogens may cause late infections on maturing fruits, enter-
ing through lenticels or by piercing the cuticle as, for example, *Sclero-
tinia* spp. In these fruits, which are changed into mummies, the perfect
stage of the pathogen is differentiated. Thus, fruits infected late act as
primary host organs and flowers and vegetative parts as secondary
host organs.

D. Undesirability of Sharp Discrimination between Vegetative and
   Reproductive Organs as Substrates for Pathogens

Gäumann (1950) rightly points out that sexual organs are the best
individualized organs of the plant body. This individuality refers not
only to the morphology and to the tissue characters of the reproductive
organs, but also to the microenvironment they offer, which is peculiar
and favorable to most pathogens, elective or not. Furthermore, in annual
plants and in cereals in particular, seeds are the organs which permit the
nonperennating structures of the parasites to survive best. Several exam-
pies have already been given to show that the suitability of reproductive organs for pathogens is not uniform through the flower and fruit.

Many pathogens affecting flowers, fruits, or seeds are able to sporulate on or to infect certain reproductive organs only, such as stamens and pistils. Among these pathogens are some of the least specialized which are provided with the grossest symbiotic adjustments. Electivity may be so strict that in some instances infection or sporulation can occur only on stamens, as, for example, *Ustilago violacea* and *Botrytis anthophila*, or on stigmas and filaments, e.g., *Peronospora stigmaticola*, or on peduncles, e.g., *Mycosyrinx cissi*. Others are restricted to petals, e.g., *Peronospora corollae*, seed funicles and placentae, as is the case for *Ustilago duriaeana* and *Schroeteria* spp. Viennot-Bourgin (1953) distinguished two types of floral galls induced by the Ustilaginales. In the first type, chlamydospores arise only in the stamens, the external flower verticillia not showing evident anomalies. In the second type, the whole of the floral organ, except stamens, participate in chlamydospore production.

Most parasites which overwinter as resting mycelium in viable seeds or fruits do not invade or injure the embryo, and *Ustilago tritici*, which invades the embryo, is elective for the scutellum and the growing point region and does not penetrate into the radicle (Batts and Jeater, 1958). As stated above, even parasites showing a less high degree of parasitism may not behave indiscriminately toward the different parts of the flowers and fruits. *Ustilaginoidea virens* does not affect stamens and pollen grains (Hashioka et al., 1951), and the filaments of the flowers of sour cherry are infected by *Sclerotinia laxa* (which displays poor electivity) only through wounds (Calavan and Keitt, 1948).

All the organs of the flower are affected by *Claviceps purpurea*, which parasitizes even the remnants of the glumes in heads invaded by *Ustilago tritici*, but *C. purpurea* tends to form sclerotia, and consequently ergotamine and related compounds, only in the presence of the ovary (Cherewick, 1953). This is detached from the receptacle and remains at the apex of the developing sclerotium (Ramstad and Gjerstad, 1955).

The foregoing examples suggest that many parasites are elective for single organs, and the activity of these pathogens is independent of the reproductive activity of the host. In some cases, however, infection is coordinated with the fertilization process. *Claviceps purpurea* commonly infects wheat before, and *Ustilago tritici* after the fertilization of the ovule.

That the activity of the pathogen is, in fact, independent of reproductive activity may be shown by experimentation or through field observation by demonstrating that green tissues, which are normally
not invaded or injured by the elective parasites considered here, are at least as subject to attack by these fungi as the reproductive organs. Some conditions favor such fungi as *Tilletia caries*, *T. foetida*, and *Ustilago tritici* to sporulate on vegetative organs (see Grasso, 1953 for literature), although these fungi usually manifest themselves in the inflorescence of wheat. The greenhouse environment, the amputation of the inflorescence (Flor, 1932), and the infection of lemmas by *Trichothecium roseum* or *Fusarium culmorum* (Viennot-Bourgin, 1953)—all favor this type of action. Viennot-Bourgin (1937), therefore, thinks that the parasitic action of *Ustilago nuda* f. sp. *tritici* makes it possible to approximate the Ustilaginales localized in vegetative organs to the naked smuts, usually considered specific for the inflorescences; and that a transition exists between the smuts sporulating on the ovaries, on the flower involucres, and on leaves (*Ustilago maydis*) (Viennot-Bourgin, 1953).

The best known fructicolous fungi show similar aspects and the conclusion of Cherewick (1953) about *Claviceps purpurea* is that ergot may develop not only on young ovaries but on any physiologically young tissue of the wheat and barley plant.

Sometimes the behavior of the pathogen is more complex. It changes, although the host organs and environmental conditions are equivalent. Maybe in these cases, the stage of the disease reveals its importance. Why do some Ustilaginales, e.g., *Tilletia barclayana* and *T. indica*, soon sporulate in ovaries on which their wind-borne conidia alight, whereas others, e.g., *Ustilago tritici*, sporulate only in the flowers they enter from adjacent vegetative tissues that are generally invaded? What changes does the host-parasite complex go through during the development of the infected wheat plant?

Many parasites affecting reproduction enter the plant through its vegetative organs and can be controlled by protective fungicides or by the natural defenses of the host during the process of infection. We might, therefore, conclude that the behavior of the green parts of the plant is of even more interest than that of the reproductive parts on which the pathogens usually manifest themselves.

**XII. The Influence of Reproduction on the Activity of Pathogens and Disease Expression**

The stimuli for the transition of the plant from the vegetative to the flowering condition excite responses throughout the plant, and influence the plant in its entirety. Therefore, even in diseases not especially related to reproduction and to the organs directly responsible for it, maturity and reproductive activity often upset the equilibrium between host and pathogen.
In some cases, the flowering plant overcomes its invaders, as in the case of root nodule bacteria on legumes. More often, the reverse is true. The attack of mature plants by rusts, the epidemic phase of *Phytophthora infestans* (Grainger, 1957), the leaf target spot stage of *Alternaria solani*, the *Oidia* as agents of "Alterskrankheiten," all afford examples of microorganisms more or less favored in this way. Genetic, seasonal, ecological, and nutritive factors, separately or in association, can also play a role in these changes of the physicochemical environment of host tissues. Recently, Grainger (1957) has proposed an index for the interpretation of the differences in susceptibility of new sprouts, young plants, and mature potato plants to *Phytophthora infestans*. This index indicates susceptibility or resistance according to its high or low value and consists of the ratio of the weight of total carbohydrates in the whole plant, \( C_p \), divided by the residual dry weight of the shoot, \( R_s \). The ratio \( C_p : R_s \) has been usefully adapted by Grainger for other diseases as well. The study of tissue factors, which are directly responsible for arresting the progress of infection or for allowing it to evolve into overt disease, is still in a most primitive state in animal and plant pathology (Dubos, 1954).

It is sufficient to conclude here that young vegetation may resist infection or keep it latent and be a "carrier" of disease, which becomes overt when the plant is mature. In such cases, the behavior of the young plant can be opposed to that of the same plant when adult. In these cases, therefore, the determinants of the pathological process are not the infectious agents, but the physiological changes of the host plant at maturity.

From a very different point of view, reproduction is a useful tool in checking the spread of and the economic effects of infectious diseases. Vegetative propagation results in genetic uniformity. Fertilization, and especially cross-fertilization, by contrast, makes for genetic heterogeneity. Stevens (1948), analyzing disease damages in clonal and pollinated crops, found that disease was more frequent on the former than on the latter and that losses were least in cross-fertilized plants.

XIII. REPRODUCTIVE ORGANS AS INJURIOUS AGENTS

Occasionally, pollen grains are harmful to human beings and injure vegetation, too. Valleau (1949) demonstrated that the leaf bleaching of tobacco growing near corn is caused by corn pollen on the tobacco plants. The reasons for this response are unknown.

REFERENCES


