VERNALIZATION AND ITS RELATIONS TO DORMANCY[1]

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HISTORY AND DEFINITION OF VERNALIZATION

In temperate countries, the seed of winter cereals must be planted before the end of winter in order to fruit within 12 months of sowing. By contrast, spring cereals, which generally can not survive the winter cold, flower soon after a spring sowing. The very notion of vernalization originated from this early agricultural experience.

Systematic research was undertaken on this subject as early as 1857, by Klippart (128). He showed that among the various climatic factors of winter, the determining factor is the cold temperature to which the young plants are subjected for a few weeks; this makes the winter cereals capable of flowering soon after the return of a warmer temperature. This notion was extended to other plants by von Seelhorst in 1898 (237) and much more extensively by Gassner in 1918 (89), who showed the great variety of "cold requirements" (measured by minimal chilling time) displayed by numerous species known as "biennials" or "winter annuals" as opposed to "spring plants" or "summer annuals" which have no significant chilling requirement for flowering. Gassner also showed that in winter cereals the early swollen germinating seed is already sensitive to the specific cold effect. Finally, in 1928, Lysenko (155) established that slight imbibition (e.g., 50 parts water to 100 parts dry matter) makes the cereal seed susceptible to this action of cold without inducing the excessive germination that could prevent use of a sowing machine. It was Lysenko who gave a name to the phenomenon. As spring cereals are called Jarovoe in Russian (from "Jar": formerly fire, or the god of spring), he called the process which makes a winter cereal behave like a spring cereal "Jarovization," and translated the word in his own English, French, and German translations into "vernalization" (Latin *vernum* meaning spring). Some French authors use the word "printanisation" but vernalization is most commonly used. In the next 20 years, a tremendous number of studies were undertaken on vernalization, mostly by agronomists, to quantitize the data on the process in cereals and in numerous other cultivated plants, in order to facilitate growing a crop following late sowing.

From their study of vernalization, Lysenko and his followers built their famous phasic theory of the stadial development of plants (156, 157) and

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[1] The survey of literature pertaining to this review was concluded September 1959.

felt they had confirmed Mitchourin's theory of the transmissibility of certain characters acquired by adaptation. Two main groups have studied the physiology of vernalization on an accurate experimental basis: Gregory and Purvis (97 to 105, 206 to 215) in London using the winter rye Petkus; and Melchers, Lang *et al.* (139 to 146, 168 to 178) at Tübingen, with the biennial strain of henbane (*Hyoscyamus niger*). During all the development of that literature, "vernalization" was used with various meanings. Such disorder has to be clarified to prevent never-ending confusion. The original restricted meaning was: the substitution of chilling of a plant for the natural exposure to winter in order to make possible the initiation of flower primordia later. Vernalization induces or hastens the development of the capacity for flowering and although its action is not visible at first, it appears as an aftereffect. Chilling is the normal agent.

The derived meaning is: any physiological effect of chilling corresponding to the awakening of nature in spring. In this context any effect of chilling that has a forcing effect is called vernalization. A further derived meaning is: any physiological action stimulating the capacity for flowering, whatever the agent. In this sense vernalization was obtained by heat (e.g., 205) or by cold, by long days or short days, by light or dark, by nutrition, etc.

In this review, the original restricted meaning is used because it is the most precise and the nearest to the initial idea; this is implicitly admitted in the works of Gregory, Purvis, Melchers, and Lang, and is explicitly used by Wellensiek (274).

We reject the first derived meaning for it is expressed by the "breaking of dormancy." During dormancy, all organs or their primordia pre-exist, but either do not grow or grow slowly. The breaking of dormancy (often induced by chilling) removes growth inhibitions and allows an active growth as soon as favourable conditions return but does not directly cause the formation of new kinds of organs as does vernalization. The breaking of dormancy belongs to the physiology of growth or of vegetative development; vernalization belongs to the physiology of reproductive development. As an example, chilling potatoes to increase tuber yield, though commonly but wrongly named "vernalization," merely utilizes an aftereffect of cold on vegetative vigour and has nothing to do with the specific aim of vernalization which is to induce the capacity for flowering. Inducing this capacity in a non-dormant rosette of biennal black henbane is true vernalization. Inducing dormant flower buds of lilac to grow and expand is breaking dormancy—not vernalization. Chilling is used in both of the examples, and relations between these two distinct but related phenomena will be discussed later.

I also reject the second derived meaning for it covers very different physiological phenomena such as photoperiodism, nutrition, or normal acceleration of growth and ageing by temperature rise. These phenomena are not related to the primary process of vernalization; i.e., a transformation of a winter plant into a spring plant. For instance, I shall not discuss here the so-called "heat-vernalization" which, in practice, has referred to such various notions as normal growth acceleration by moderate heating, the phenomenon of thermoperiodicity, and sometimes experimental errors (241).

Another point to be emphasized concerning vernalization is that the process is revealed by an aftereffect. It is essentially a "preparatory process" to flowering, but is not the flower initiation process itself. In photoperiodism, the inductive photoperiod (or "euperiod") prepares for, as well as initiates, flower primordia. In bulbous Irises, subgenus *Xiphion,* studied by Blaauw (16), temperatures lower than 17° to 20°C. are necessary to initiate flower primordia, and this kind of chilling is not vernalization. During true vernalizing chilling, a sufficiently cold temperature is used, not to initiate flower primordia, but to create the capacity for subsequent flowering.

In summary, I will deal here with "vernalization" defined as follows: "The acquisition or acceleration of the ability to flower by a chilling treatment."

General reports or reviews on vernalization have been published during the last 20 years in Russian (157, 219), German (107, 139, 141, 172, 173, 177), French (36, 38, 41, 42, 63, 239, 274), Dutch (271, 277), and English (98, 140, 178, 183, 257, 279). In 1952 Lang published a general study on the physiology of flowering containing an excellent review of vernalization in the *Annual Review of Plant Physiology* (140). The story of vernalization of Petkus rye and henbane is so well described by Gregory (98) that no long description is necessary. The most commonly read book on this topic is probably *Vernalization and Photoperiodism* (183) published in 1948 by Murneek and Whyte; that fact explains why the present study deals mainly with investigations conducted between 1948 and 1959. Numerous important studies published before 1948 and here omitted appear in other references (140, 183, 279).

VARIOUS ASPECTS OF VERNALIZATION IN DIFFERENT SPECIES OF PLANTS

In order to work on a reliable basis I will first review the experimental data now available about vernalization in typical different species.

VERNALIZATION OF CEREAL GRAINS WITH SPECIAL REFERENCE TO THE RYE PETKUS

Cereals are monocarpic plants, growing initially as short rosettes but with elongated stems, the culms, when flower primordia have been formed. Nevertheless, they must be studied separately from other ordinary rosette plants like henbane because they have the peculiar ability to be vernalized in the seed stage, and the very large numbers of researches dealing with these plants have been conducted by trials using grain vernalization. The classical researches of Gregory and Purvis upon the rye Petkus are well known, so that only a short résumé is necessary.

"Petkus," a cultivated variety of *Secale cereale* consists of two races. The spring race is a typical annual rosette plant. When planted during the spring under long days, the primary axis produces seven leaf primordia and then forms the young ear, recognizable by double ridges on the sides of the apex. In short days, it produces about 25 leaves before earing and may be described as a quantitative long-day plant. The winter race is a typical biennial rosette plant. When planted during spring, under long-day conditions, the primary axis produces 25 leaf primordia before earing, and 16 under short-day conditions; but if the seed has been previously chilled, it grows exactly like the spring variety (205, 206). The vernalizing effect of chilling has been studied over long experimental periods in this plant. Ear primordia have been formed under long-day conditions after the seventh leaf, even sometimes after the sixth, when chilling has been extended up to 90 days (94). Thus, in both strains the first six or seven lateral primordia formed by the apex are pre-determined as leaves, and "ripeness to flowering" is reached at the sixth or seventh leaf. From the seventh to the twenty-fifth leaf level, primordia are "labile" and can either give leaves and tillers exclusively, according to the photoperiodic treatment in the spring race, or in the winter race, according to the degree of vernalization and the subsequent photoperiod in accordance with the above interactions. The "labile" character of the seventh to twenty-fifth primordia is evidenced by the pre-inflorescent structure observed in the apex during this period (204). It is to be noticed that short days can here replace part of vernalization (94, 161, 206, 207, 266) as if the plant was a "facultative short-day" plant in relation to flower initiation. This is true at least as long as the winter strain has not been chilled; many cereal species show the same behaviour but it has not been shown that this last point is universally true. In all winter cereals, however, after vernalization the plant is a quantitative long-day plant.

The effectiveness of the vernalizing treatment may be measured either as the inverse of the cold exposure necessary to obtain the same result, e.g., the level of complete vernalization defined by earing after the seventh leaf under long days; or by the reduced number of leaves formed before ear initiation (this reduction ranging from 25 to 7 leaves); or else by the "score" (206, 207, 210), a statistical evaluation of the results observed on earing and emerging.

The effectiveness of chilling depends on several conditions.

(*a*) There must be a sufficient imbibition of water not necessarily the maximum, but at least the minimum imbibition necessary to allow the vernalizing process while low enough to hinder seedling growth, according to Lysenko's and Tolmacev's method (156, 258). In cereals, the appropriate water content is about 45 to 50 per cent of the dry weight, which means that 30 parts of water are normally required for 100 parts of air-dried mature seeds, with some variations according to the species or variety (80, 84, 97, 99, 106, 152). The two methods, maximum or minimum imbibition, do not always give exactly the same results in vernalization (94).

(*b*) The vernalizing process cannot begin before a period of activation (the time necessary to induce the first apparent respiratory exchanges in the recently imbibed grain) of about 10 to 24 hr. at 15 to 18°C. after the beginning of soaking.

(*c*) The presence of air (oxygen) is absolutely required.

(*d*) An appropriate duration and temperature of chilling are needed. The effective low temperature is between +1 and 6 to 7°C. with a widespread optimum. It decreases from 0 to −4°C. and disappears completely below −6°C. It also decreases above +7°C. and disappears completely between 12 and 14°C. (89, 107, 108, 210, 220, 222, 223). Above 15 to 17°C. the devernalizing effect of warm temperatures begins (214, 219).

In immature embryos, as in mature seeds or seedlings, the time required for complete vernalization is about the same: about 40 to 45 days in the winter strain of Petkus rye. A longer vernalizing chilling does not greatly modify the result; however, if it exceeds three or four months it seems to become less effective (210). When the treatment is applied to an older plant the minimal exposure to vernalizing chilling that leads effectively to the immediate acquiring of the flowering ability, decreases with age (81).

Respiration inhibitors and growth inhibitors inhibit the vernalizing action when they are applied at concentrations that completely stop respiration and growth. But low hydration or imbibition with a highly osmotic solution greatly slows down growth without reducing anything in the vernalizing process (155, 258). From this fact originated Lysenko's absolute distinction between growth and development (156, 279). By contrast, some other inhibitors applied at moderate rates can inhibit vernalization without stopping growth significantly (28, 48) and can be called "anti-vernalizing" agents.

The age of the plant in which chilling can effectively induce vernalization is extremely precocious. The immature embyro within the milky caryopse can be vernalized, either because of the cold nights occurring during late summer maturation in subarctic countries (131, 288), or local chilling of the ear on stalk (100).

Gentle drying of the wet seeds during chilling stops the vernalizing process but does not delete the acquired stage of vernalization. Interruptions of chilling by mild temperatures around 14 to 15°C. do not markedly alter the stage already reached in the vernalizing process. Alternating temperatures do not reduce the minimum number of required chilling days. Interruptions at 20°C. partly throw back the characters acquired but strengthen them when prolonged (86, 233). Under natural conditions the various cereal races have different chilling-time requirements that correspond to their adaptation to their native climate and to the fact that resistance to death by cold decreases during earing (219).

Devernalization instigated numerous discussions. The Russian authors observed that hot temperatures partly offset the vernalization effects (8, 77, 95, 255); but under the influence of the development of all plants through successive irreversible stages (7, 157 to 159), devernalization was denied in various forms and nuances or interpreted as not being a real stage reversion (219, 248, 252). Purvis and Gregory have greatly enlightened the problem (101, 102, 214, 215). Two techniques ensure rapid devernalization: (*a*) exposure to about 20°C. in a damp atmosphere lacking oxygen (this exposure must not exceed about 1 to 5 days for it is most severe and would eventually kill the plants (102, 104); and (*b*) the exposure in ordinary damp atmosphere at about 35°C. for a longer period of about 8 to 12 days (101, 105, 213).

The effectiveness of both these treatments depends on the interval between the end of vernalizing chilling and the beginning of devernalization. When vernalization has been thoroughly achieved, a return to 15 to 20°C. fixes the vernalized state in a few days; at 4 to 5°C. the fixing requires several weeks. During the fixation process further devernalization loses its effectiveness (214). Revernalization may be achieved by another chilling.

The embryo itself directly perceives the chilling vernalizing effect (103, 207, 242), not the endosperm as was first thought (132, 165 to 167). Excised embryos and mere cauline fragments of the embryo, even when separated in the dry state before any diffusion of endosperm products, can be vernalized when imbibed (103, 113, 130, 190, 207). They must, however, be supplied with the sugars normally coming from endosperm. With their own metabolites, excised embryos can be but partly vernalized, even less when they have been starved in warm conditions without sugar before chilling. A sugar supply gives them back the complete ability of being vernalized (provided that starvation has not been excessive), but then a certain lag time will be observed which corresponds to the synthesis from sugar of some metabolites required for vernalization (99, 208 to 210). In winter cereals and some other perennials, minerals (3, 135, 185b) or vitamins (56) may enhance vernalizability, perhaps in relation to more active respiration. The meaning of the physico-chemical properties presented by vernalized meristems will be discussed later. The earlier emergence of the first leaves of cereals and most of all the smaller size of the first two leaves characterizes the vernalized state (108).

The vernalized state is not here transmitted by grafting, which is not generally successful in monocotyledons. But the vernalized state is communicated without reduction through cell divisions, i.e., in an autocatalytical way to all meristematic tissues originating at the apex of the embryo, e.g., to tillers even though they are formed after the vernalizing treatment (18, 108, 207).

In cereals the organs already formed (young leaves, young culms) are most responsive to the elongating effect of gibberellin, but this substance cannot cause them to flower and cannot therefore replace vernalization by chilling (154). On the contrary, soaking nonchilled winter-strain seeds in natural extracts from vernalized embryos of rye (215) or of vernalized peas (116, 117) seems to be able to replace part of the cold vernalizing effect.

But for slight quantitative differences, these fundamental rules of the vernalization of winter rye Petkus are the same for all cereals; especially for wheat (31, 82, 85, 147, 152, 161, 162, 229, 266, 282 to 284), barley (12, 70), oats (155 to 159, 202, 219, 239), rice (58, 244, 245) and different cereals (60, 89, 90, 155 to 159, 202, 219, 239, 252, 266).

VERNALIZATION OF BIENNIAL DICOTYLEDONS IN ROSETTES

The classical case of henbane.—Our classical information concerning vernalization was based on henbane as much as on Petkus rye, because of Melchers' and Lang's remarkable work (92, 139 to 146, 168 to 178, 228, 287). They worked together in Tübingen with other collaborators for a long time. In brief, I will only emphasize the differences observed between the behaviour of henbane and the cereals.

Here again the species, *Hyoscyamus niger* consists of two physiological races, the biennial and the annual strains. The important differences relative to the cereals follow below.

(*a*) Neither the seed nor the immature embryo have yet been vernalized; chilling is only effective on plants at least ten days old and in the rosette stage. The capacity for vernalization increases until the thirtieth day and then stays constant for a long time. That is to say, in the terms used by Wellensiek, this plant presents a "juvenile phase" for the first ten days of life after germination since the plant cannot feel the vernalizing effect of cold before the rosette is ten days old; or in my own terms, the plant reaches its "ripeness for vernalization" at that age.

(*b*) The leafy plant is strictly a long-day type.

(*c*) The winter strain has an obligate requirement for vernalization.

(*d*) Partial replacement of vernalization by previous exposure to short days is not possible.

(*e*) This plant shows a remarkable ability for grafting and for the transmission of vernalization from donor to receptor through grafts (168 to 172).

The effectiveness of vernalization can be estimated by the inverse of the number of days between the end of chilling and the beginning of shooting at 20 to 25°C. under long days. The optimum temperature for vernalization is lower and more widespread for the longer chilling periods. As an example of temperature and exposure period, it ranges between +3 and +6°C. for 42 days of treatment yielding complete vernalization and a short lag time before shooting of about ten days. Over-vernalization does not seem detrimental. Daily alternate temperatures have no increased effect (186b). During chilling, oxygen is indispensable and light is useful.

Henbane is also known as having a particular photoperiodic behaviour: its critical photoperiod ranges from 11.5 hr. at 20.5°C. to 8.5 hr. at 11.5°C. When plants are quite vigorous, with reserve food in the root, defoliation is followed by flowering even under short days. Suppressing respiration by anaerobiosis in the dark, or sugar infiltration into leaves, also induces flowering under short days. In the biennial variety, vernalization is acquired by chilling the vegetative point and not by chilling the leaves or roots only. Acquired vernalization is maintained for a long time even after more than 100 days under short-day conditions at 20°C. It can be acquired by split chilling periods interrupted by mild temperatures.

As in cereals, devernalization can be obtained either by anaerobiosis or more easily by raising the temperature to 35°C. for a few days, provided that the devernalization treatment be applied immediately after the end of chilling. An interval of 3 to 4 days at 20°C. is sufficient to fix the vernalized state definitively. After devernalization, revernalization is also possible.

Graft transmission of the vernalized state is one of the most extraordinary properties displayed by henbane (169 to 171, 176 to 178). A donor scion can be grafted generally by side-grafting onto the rosette; the scion either is a branch or a separate leaf from one of the numerous Solanaceous species among which all possible types of vernalization or photoperiodic requirements are found. By this means, Melchers succeeded in making a nonvernalized, biennial, black henbane receptor flower by grafting with a donor. The donor could be a fragment from an individual of the same strain previously vernalized and exposed to long days, or a fragment of the annual strain, or a fragment from the *Hyoscyamus albus* species which is indifferent to vernalization and photoperiodism, or from annual species, or from varieties that are photoperiodically insensitive (such as *Petunia hybrida, Nicotiana silvestris*), or even *Nicotiana tabacum* var. Maryland Mammoth, the famous short-day annual. Since a leaf of this latter plant exposed to long days cannot bring its own buds to flower, it is not a donor of the so-called flowering hormone or "florigen"; however, because it induces flowering in nonvernalized black henbane, it must contain another sort of hormone which is still only speculative, called "vernaline" by Melchers (172). Zeevaart (289) confirmed these facts and demonstrated the same results using a potato branch as donor. The potato donor is more active when defoliated. Tomato, on the other hand, does not transmit the flowering ability under these same conditions. Except for the tobacco, Maryland Mammoth, the donor must always be floriferous itself. Reciprocally, a nonvernalized, long-day, black henbane cannot be used as an effective donor to make a leafless Maryland Mammoth branch flower. The black henbane does act as a donor if previously vernalized. The theoretical concept concerning vernalization have been based mostly on these remarkably successful experiments on the graft transmission of the vernalized state. But, as has just been seen, their success is not general and in receptors other than henbane, such a transmission is only quite rarely successful.

Neither the serological properties (106) nor the measurements of respiratory intensity (112) have shown any significant differences between nonvernalized and vernalized plants.

Lang first successfully substituted treatment with gibberellin for vernalizing chilling using the biennial black henbane (142, 143). Whereas the formation of flower primordia precedes shooting in vernalization by chilling, shooting begins first and flowering follows later when gibberellin is used (263).

Other biennial plants in rosettes.—Studies with other species show that the classical data based on henbane need modification.

The industrial importance of beets resulted in numerous studies some time ago (12, 24, 51, 182, 192, 250, 251). Sugar beets, as well as mangelwurzel and other analogues, generally have an absolute vernalization requirement and their flowering depends absolutely on long days. Industrial sugar production utilizes these properties: plants must be sown late enough to suffer less cold than would vernalize them yet early enough to enjoy the longest possible period for vegetable growth and sugar accumulation in the tap-root. A sowing date can be fixed according to the variety and climate. By contrast, intentional vernalization yields flowers and seeds within the very year of sowing. Stout (251) showed that grafting a vernalized stock on a nonvernalized stock transmitted the flowering ability to the latter; this was confirmed by Margara (164).

More recent studies (275) show that vernalization can be achieved in very young plants and even in seeds, but responsiveness increases with age, beginning with the second month. Chilling rosettes deprived of most of their tap-roots did not give a vernalizing effect even though chilling only the root has no effect at all; therefore, in order to respond to the vernalization treatment, the vegetative point must receive what the root supplies to it (135).

Margara (164) extended his investigations to the various wild and cultivated *Beta* species that display the greatest variety in their physiological requirements. While the flowering of sugar beets and analogues generally requires absolute long days, the induction of shooting after vernalization can also occur in short days.

Short days show a quick and strong devernalizing effect which can act long after the end of chilling and when vernalization is already expressed by shooting or even by early flowering. The return to short days brings back the formation of perched rosettes and none of these plants reflower or grow if they are placed under long days again; everything must be revernalized by chilling. However, this revernalization is particularly difficult in more or less devernalized perched axillary rosettes. Gibberellin induces shooting but not flowering without chilling even for those perched rosettes about one metre high. In spite of prolonged gibberellin treatment, shooting finally stops, perched rosettes form again and now seem resistant to prolonged vernalization treatment.

In *Beta maritima,* which requires less vernalizing chilling, the terminal bud is somehow protected against initiation of flowers and the flowering that follows vernalization occurs much like that described later for *Geum,* by the shooting of axillary buds while the main rosette ensures a maintenance of the perennial state. In this species, gibberellin entirely replaces cold in inducing flowering as well as shooting.

The small crucifer, *Arabidopsis thaliana,* in rosette presents the advantages of quick growth and small dimensions, and displays all degrees of vernalization requirements from none at all to absolute (136, 138, 290). Napp-Zinn's investigations (184 to 186b) recently made the variety "Stockholm" of this carefully selected species a classical research material. This variety absolutely requires vernalization to be able to flower, but it shows successive possible periods for vernalization, devernalization, and anti-vernalization.

Normally, the treatment consists in soaking very small seeds for 24 hrs. at 20°C. followed by 9 to 15 weeks from —3.5° to +4 to 5°C. A long previous soaking of seeds delays flowering (anti-vernalizing effect), with the optimum vernalization obtained by 10 weeks at 2°C. Heat devernalization can be completely effected immediately after chilling no matter what chilling period is applied to the seeds. Heat treatment after germination can also delay flower formation, whether or not vernalization occurs later. The vernalized state is fixed by a stabilizing treatment at 20°C. for seven days. Revernalization is possible. The number of leaves on the main stem is related to the time of flowering: heat treatment before or after vernalization or after stabilization reduces the number of leaves by about 10 to 20 leaves compared to that of untreated plants flowering at the same age.

Gibberellic acid applied to the seeds of races that have low or facultative chilling requirements replaces the action of cold if the treated plants are grown under long days. Indoleacetic acid has a similar but weaker effect on plants grown under natural autumn days after the treatment, and a still weaker effect under long-day conditions. This action may sometimes be additive to that effected by gibberellin, whereas triiodobenzoic acid is antagonistic.

In contrast, true "winter"varieties that have an obligate chilling requirement do not respond to gibberellin. Young rosettes of nonvernalized plants of these varieties that are more resistant than older ones to vernalization by chilling, are more responsive to gibberellic acid, which induces them to shoot and flower. Then, as these rosettes grow and become susceptible once again to the vernalizing effect of cold, they grow less susceptible to gibberellic acid. Moreover, contrary to the situation in henbane, when cold and gibberellin cause shooting and flowering they simultaneously determine the initiation of the inflorescence and of shooting (228).

Salad lettuce (*Latuca sativa*), depending on the variety, responds in different degrees to vernalization, which is not, however, an absolute requirement for flowering (243, 267). They normally have a long vegetative growth period as a rosette, the leaves of which constitute the head. Under long warm days the axis shoots up, the head-leaves separate, and flowers appear. Head formation, followed by shooting, depends on light intensity, period, and colour, as well as the relative temperatures of day and night. The response to these factors, however, is modified by vernalization. The extent of this effect depends on the temperature to which the seeds (after soaking), or the seedlings, are exposed. Exposure of the Great Lakes variety for a minimum of 13 days, or better for 20 days, at about 3°C., followed by growth at a night temperature above 13°C. results in a rapid acceleration of shooting and flowering without head formation. At lower night temperatures a head is formed but flowering occurs sooner than in nonvernalized controls. Short interruptions of the cold treatment for a few hours per day with temperatures of 20° to 35°C. do not decrease the effectiveness of the vernalizing treatment (cf. mainly Rappaport and Wittwer (216, 217). Vernalized seeds release half as much indoleacetic acid as nonvernalized seeds when extracted with ethyl ether (87).

Other salad plants, like endive (*Cichorium endivia*), which respond quantitatively to vernalization and photoperiodism, are induced to bolt and flower by use of gibberellin (109).

Spinacia oleracea is considered to be a strictly annual, long-day plant with no vernalization requirement. Chilling the wet seeds of certain varieties however (e.g., Matador), between 0° and 5°C. for five days, causes plants to flower earlier under subsequent long days and to produce more flowers and seeds (126). The flowering of other varieties is generally accelerated by vernalization of wet seeds for two weeks at 3°C. (127, 187). Chilling treatments of 10 to 40 days speed up shooting, compared to the control, if shooting takes place under long 17-hour days preceeded by a short-day period of growth. Such acceleration is less marked, when compared to the control, if growth is entirely carried out under continuous days. Plants of the variety Nobel will flower under short days when the seeds have been vernalized (264).

Campanula medium was the object of a remarkable study by Wellensiek *et al.* (268, 270, 272). The seed is not vernalizable and rosettes maintained at a warm temperature under short or long days never flower. If such rosettes are exposed at the age of four months to cold temperature for at least four weeks and are then returned to a warm temperature combined with long days, they shoot and flower. If, upon the return to the warm temperature, they are subjected to short days, they remain in rosette. These results show this plant to be an absolute biennial that flowers only after vernalization followed by long days, similar to the biennial *Hyoscyamus niger*. *C. medium* differs from *H. niger* in that neither defoliation nor grafting can make it flower without previous chilling. On the contrary, if this plant is grown in rosette up to the age of three months in a warm temperature and under short days, and then exposed to the warm temperature again but in combination with long days, it shoots and flowers. Here the early growth under short days replaces the vernalization by chilling. This property may be called "Wellensiek's phenomenon."

Gibberellin causes most *C. medium* plants to shoot under long days but after a certain number of repeated applications, growth stops when the plants are about 20 to 30 cm. and perched rosettes form with no flowering (273). I personally obtained contrary results with certain individuals after the same treatment (43). This is not in contradiction to Wellensiek for I probably had plants from unselected horticultural strains, whereas Wellensiek's plants were selected genetically from ancestors that gave a variety of reactions to chilling. Among my own plants, some not only show "Wellensiek's phenomenon," but are also unable to flower under long days without vernalization in spite of gibberellin applications. In such cases, some of my plants, after they have formed the perched rosette, resume shooting when given repeated gibberellin applications and then after 20 to 30 cm. of elongation, set in rosette again for a few weeks and so on—until they are several metres high. This is of considerable interest since it demonstrates the different responses given by separate individuals that differ by slight genetical characteristics not evident under ordinary cultivation.

Oenothera biennis and other *Oenothera* constitute one of the most complex genera in relation to vernalization. The species must be determined most carefully. Mrs. Picard and I have observed (35, 39, 42, 43, 201, 202) that *Oenothera biennis* (in the pure race obtained from the Munich botanical garden) has an intense and obligate requirement for chilling followed by long days if it is to flower. Up to now, natural and complex winter chilling proved much more effective than attempts at artificial chilling and alternating temperatures appeared more effective than continuous cold. Seed vernalization has been ineffective. After natural vernalization, the plants exposed to short days remain in rosette but soon show that they have lost their vernalized state, for they do not react any more to long-day exposures. After a long devernalizing period under short days, their old rosettes even seem particularly difficult if not impossible to revernalize. Gibberellic acid repeatedly applied to nonvernalized rosettes causes shooting to a height of 20 to 30 cm., under long days, followed by another perched rosette which then seems almost fully resistant to further treatments.

With *Oenothera lamarckiana* (from the forest of Fontainebleau), and *O. parviflora* (from Hooge Weluve near Arnhem), on the other hand, even though the chilling and long-day requirements are also qualitatively obligate, they are much easier to satisfy quantitatively. Artificial chilling in a cold room under low illumination for 12 hr. per day at 3 to 4°C. for 1 to 2 months generally succeeds. A more effective treatment appears to be with temperatures alternating every week or half week at 3° and 10 to

12°C. successively. Late devernalization by short days is also evident and revernalization is possible. Repeated gibberellin applications to nonvernalized plants induce shooting and finally flowering quite rapidly under long days; and sometimes even under short days but then much more slowly. Neither Wellensiek's phenomenon, nor flowering after defoliation as in henbane, could be observed in any of these plants (42, 201).

In *Oenothera suaveolens, O. longiflora, O. stricta,* and others the chilling requirement is not obligate. After a long delay, flowering may occur under long days without previous chilling. Other species are annual without any vernalization requirement, but they do require long days; still others that are annual are almost day-neutral. Up to now, grafting has not succeeded in inducing flowering by nonchilled plants that have an obligate vernalization requirement.

Celery (*Apium*) requires vernalization for flowering; as a result, active leaf growth occurs during the first year of culture. Exposure of young plants to chilling at 4° to 10°C. for a few weeks, followed by a return to warm temperatures, causes flowering within the first year of culture. Long ago it was shown that when the collar alone is chilled, with the main root remaining at the warm temperature, vernalization was effected, whereas chilling the root alone had no effect at all. It was one of the first examples (1930) to demonstrate that vernalization is sensed by the vegetative growing point, not by leaves or roots (54).

Carrots require different degrees of vernalization depending upon the variety of carrot in question (132). Recent Russian studies (6; 133 to 135; 219, 221) indicate that:

(*a*) Varieties from southern U.S.S.R. (Armenia and Daghestan), after the wet seeds are chilled at 2°C. for 50 to 80 days, have about one-third of the individuals flowering the same year.

(*b*) In varieties from more northern countries, seed chilling first seemed totally ineffective; but the following winter, after storing the isolates in a cool cave and then setting out in a hot greenhouse to accelerate growth, the plants from chilled seeds started initiating flowers two weeks later, but the others did not, suggesting that seed chilling had achieved part of the vernalizing process which would have been completed during further storage at a cool temperature (219).

(*c*) Chilling carrot isolates from a first crop causes complete vernalization of whole plants as well as of those from which the bud has been separated from the tap root after chilling and then planted alone. By comparison, when the bud has been chilled after removal of four-fifths of the root, the plant is not vernalized. The sugar-supplying root seems to play the same part here as does endosperm in the vernalization of cereal caryopses. The same fact had been reported for beets (134).

(*d*) Nonvernalized carrots grafted to flowering carrots or to an annual umbellifer ready to flower under long days (the dill) flowered under these conditions (133, 135). Gibberellin may induce bolting and flowering without chilling (143).

Digitalis purpurea has long been recognized as requiring vernalization followed by long days to achieve flowering (5). The vernalization requirement still seems obligate; but the long-day requirement is less mandatory, at least in certain strains where I observed flowering after vernalization under short days. Wittwer, Bukovak *et al.* (280) showed that gibberellin causes these plants to shoot and flower without vernalization. I also observed this and showed that flowering is rapid in long days with frequent flower anomalies and the occurrence of perched rosettes on some axillary buds; but gibberellin also causes these plants to flower very late under short days (43). The other *Digitalis* species have various chilling requirements.

Scrofularia vernalis is a remarkable plant in many respects. It has a mandatory cold requirement. It is not seed vernalizable but natural chilling or artificial chilling, although less easily done, achieves vernalization of young rosettes as well as older ones, even those several years old. But after vernalization this plant is absolutely day neutral, proving that a long-day requirement is not necessarily linked with a mandatory vernalization requirement, as was often thought. Moreover, gibberellin causes considerable elongation of stems, even those of very young rosettes; this phenomenon is often associated with tumors issuing from cell proliferations in the medulla and cortex. Axillary shoots elongate too, but no evidence of flower initiation could ever be observed from such treatments. There appears here to be a sort of incompatibility between elongation caused by gibberellin and flower initiation whereas shooting after chilling is always followed by flowering (39, 41, 42, 43, 123).

Numerous other plants have been studied (38, 39, 43, 47). Many campanulaceous plants have a mandatory vernalization requirement, for example *Symphysandra, Campanula persicæfolia* [as was shown by Wellensiek (273)], *C. alliariæfolia, C. primulæfolia,* etc. In the last two, gibberellin has no effect either on shooting or on flowering. *Reseda luteola* requires extensive chilling, but gibberellin causes it to shoot and finally flower provided that it is injected into the stem at abnormally high concentrations (43). *Isatis tinctoria* absolutely requires vernalization and gibberellin injections can only make it shoot with difficulty. *Lunaria biennis* [studied by Wellensiek (271, 273)] has an absolute chilling requirement that diminishes with age, it is not seed vernalizable, and does not respond to gibberellin. This is also true for *Eryngium variifolium* (47) which, furthermore, doesn't grow at all when treated with gibberellin.

Several plants are remarkable because of the important modification exhibited by leaves after the chilling treatment. *Cichorium intybus* (274), the bitter Chicory, is seed-vernalizable (two weeks at 5°C.) [studied by Hartmann (111)]. After vernalization, the leaves are hairy and more serrated, they stand erect rather than spread out, and the plant flowers under long days with the new leaves sensing the photoperiod.

Crepis biennis and *Senecio jacobea,* which absolutely require vernalization, at least as rosettes, show similar modifications (39, 43, 47).

These examples could go on without end. The preceding are sufficient to show that the vernalization process is much more complex and varied than suggested by the comparison between classical winter rye and black henbane.

VERNALIZATION OF CAULESCENT BIENNIAL OR MONOCARPIC PLANTS

Contrary to rosette plants, caulescent plants form internodes of various lengths from the very beginning of growth. Their flowering is not associated, therefore, as in rosette plants, with the deep change which represents the shift of a brachyblast into a long stem. Several remarkable plants of this category require vernalization.

Euphorbia lathyris.—This species is remarkable for its regular elongation. It forms internodes about one-half cm. long under short days, and 1 to 2 cm. long under long days. As long as the plant has not been chilled, it keeps growing regularly producing stems that can reach two or three metres in length or more. Some individuals with different genetic factors finally flower under these conditions when quite old; but most of them do not flower except after chilling. Natural or artificial chilling, whether applied to young or old plants, causes vernalization. After returning to a warm temperature, there soon occurs the formation of one apex flower and, by the subterminal branching of the shoot, the inflorescence. After vernalization, flowering is strictly day neutral. Gibberellin applied to nonvernalized plants causes an initial rapid elongation of internodes, which then returns to normal a few weeks after the end of the treatment. This is repeated with every application of gibberellin, but no flowering is induced (43).

Various species of Iberis, particularly intermedia ssp. Durandii.—After the initial growth the nonvernalized plant branches into numerous very leafy shoots that never flower under long days until the plant is chilled. After chilling and returning to a warm temperature, flowering occurs equally soon under short days as under long days, but there are many more flowers formed under long-day conditions. If continuously grown under short days, without chilling, a few flowers appear after a long time. This is another example of those intriguing relations between short days and the vernalizing effect of chilling. Gibberellin has no effect on flowering even though it is very effective in increasing elongation (43).

Cabbages (Brassica).—Cabbages are botanically and physiologically highly variable. Their various chilling requirements have been extensively studied from an agricultural and horticultural point of view (52, 71, 78, 129, 180, 200, etc.). Certain species or varieties are rosette plants with tap-roots; for example, turnips, in which shooting and flowering are accelerated by seed vernalization, and "choux-navets" and rapes "rutabagas" which obligately require vernalization of leafy plants before initiating flowers. By contrast, other stay caulescent; such as the fodder strains of *Brassica oleracea,* or the oil-seed cabbages (*B. campestris*) "Colza" and "Navette" which are annual strains with no vernalization requirement, and strictly biennial strains which obligately require chilling of leafy plants. Others are caulescent first and then form perched rosettes with numerous leaves. Among these are the ordinary garden cabbages (*B. oleracea capitata*) that show various chilling requirements depending on the strain. Gibberellin is an effective substitute for chilling in certain strains, sometimes causing an extensive elongation and occasionally flowering, but it is ineffective in other cases. A natural gibberellin-like substance has been found in the young floriferous shoots of certain cabbages (153). There are biennial cabbages that flower without chilling after grafting on flowering cabbages (135) or on annual mustards or on annual *B. crenata* (55).

Brussel sprouts (*B. oleracea gemmifera*) were studied by Stokes and Verkerk (249, 260). They showed that if this plant cannot flower without chilling it is not because of a real vernalization requirement, but because flowering cannot occur in ordinary warm or mild conditions. Ripeness to flowering appears after a juvenile stage and requires 30 nodes. From then on, exposure to cold temperatures of 5 to 10°C. induces flowering. Exposures taking place at such temperatures therefore initiate flower primordia and are not a "preparatory" process as is vernalization. Chinese cabbage (or Pak-choi: *B. sinensis*) seems to be similar (286). White mustard (*Sinapis alba*) is an annual plant in which wet-seed chilling slightly speeds up flowering (59). Indian mustard (*B. juncea*) shows a higher vernalization requirement which may be satisfied by seed chilling; immediate heat devernalization is not effective (238) as is true of cereals.

Many other cases of vernalization requirements of various degrees have been reported for other crucifers and in particular for radishes (61), *Lunaria biennis* (271), stocks (*Matthiola incana*), *Erysimum perofskianum, Cheiranthus Allionii,* the Siberian wallflower, etc. (79, 203, 273, 274).

Tomatoes.—Tomatoes are considered typical annual plants with a remarkable responsiveness to daily photo-thermo-periods. However, they display some noticeable phenomena related to vernalization (93, 124): the stimulating effect of wet-seed chilling has been reported by Russian authors particularly e.g., 10 days at 0°C. or 14 days at alternating temperatures of 18°C. and 0°C. in relation to crop precocity and yield (253, 254, 265). In other cases, particularly in Ailsa Craig and Potentate, other authors (18, 281) showed that wet-seed chilling had no effect. After the cotyledons open, however, if the seedling is exposed to 8°C. for nine days instead of being maintained under warm conditions, the first inflorescence will be formed one or two nodes earlier. When chilling is extended for a few more days, this first inflorescence will contain more flowers. Then, by successive periods from week to week or more, similar chillings stimulate the earliness of further inflorescences. Nightly cold temperature is mostly effective during this kind of vernalization (13, 261), and for tomato growth generally.

Annual legumes.—Numerous cases of vernalization have been reported in caulescent annual legumes for example: sweet peas (125, 239), vetches (160, 239), lentils (130), chick peas (122, 194 to 196, 239), broad beans (240), etc. In many of these plants and particularly in vetches (239) the treatment increases the rapid growth of lower axillary buds, gives a more branched habit to plants, and makes them flower earlier.

Finally, the garden pea (*Pisum sativum*) reveals most interesting phenomena; the first flower is formed on a precise, genetically defined node for each variety (114). The next lower nodes bear aborted shoots that have a tendency to flower. Lower nodes later form the axillary leafy shoots. Often, dwarfed early varieties will generally present their first flower at a low node, the seventh for example, and are strictly indifferent to chilling (193). By comparison, late varieties that flower on higher nodes (the tenth or seventeenth for example) as Zelka, Unica, Greenfast. Alaska, Téléphone, etc. are markedly influenced by the chilling of recently soaked seed (62, 117, 121, 197). Exposing plants to a few days of 3° to 5°C. temperatures prior to growing them under normal conditions induces the appearance of the first flower 1, 2, or 3 nodes lower than in controls. Leopold & Guernsey (150) have shown that this effect is increased by soaking the seeds destined for chilling in an extremely diluted auxin and thiamine solution and that the effect increases with concentrations ranging from $10^{-7}M$ to $10^{-4}M$; but triiodobenzoic acid increases the vernalizing effect at a concentration of $10^{-7}M$, whereas at higher concentrations it reduces or inhibits the chilling vernalizating effect. After vernalization by chilling, even when enhanced by these chemicals, exposure to 39°C. for 18 to 24 hrs. totally removes the vernalizing effect. The same thing happens after a total lack of carbon dioxide for at least 1 hr. immediately after the vernalizing treatment. The carbon dioxide appears to be necessary to fix the vernalizing effect.

Highkin (117) showed that if seeds were exposed to 20°C. for some days after soaking and then subjected to chilling instead of being directly exposed to chilling immediately after imbibition, the vernalizing effect of chilling was completely prevented by a 5-day exposure to a warm temperature. He further showed that if the water used to soak pea seeds for 25 days at 4°C, was then used to soak other pea seeds which were immediately planted without chilling, it caused a significant reduction in the age of the appearance of the first flower (116). It was reported that this could also be obtained with the soaking water of chilled winter rye seeds and that these various soaking waters could speed up flowering not only in the pea, but also in other vernalization-requiring plants such as winter cereals. The active substance could be guanosine or something similar (118).

Gibberellin also effects the nodal placement of the first flower in peas. It greatly increases the internode elongation of dwarf varieties (this effect was sometimes called "vegetative vernalization," a possibly erroneous usage). More & Bonde (17, 181) showed that on late dwarf Téléphone peas, gibberellin applications delayed flowering slightly by bringing the first flower node to a somewhat higher rank. When seeds from this variety are chill-vernalized, the rank of the first flower node is lowered; but if gibberellin is applied at the same time as chilling in the soaking water, it prevents the chilling vernalizing effect. When it is applied immediately after chilling, it destroys the effect of chilling and corresponds to a "reproductive devernalization."

Paton & Barber (198) and Haupt (114) showed that grafting a late variety on an early one, or even on a flowering late variety, causes an accelerated scion flowering by lowering the rank of the first flowering node. This effect occurs even though the scion is set with its own cotyledons and leaves. However, the effect is stronger when the scion is defoliated. The stock used as donor is much more effective if it keeps its own leaves but it is still effective if set in interstock, the stock being from a late variety. These observations show that the fixing of the first flowering node in the pea depends mainly on a stimulating substance, but that an inhibiting substance may also occur, and that the final result may come from a balance between both effects.

VERNALIZATION OF PERENNIAL OR POLYCARPIC PLANTS

The vernalization requirement in perennials has often been cited incidentally (23, 188, 199). However, the association of perennial growth (= polycarpism) and a vernalization requirement appears contradictory. In a plant that requires vernalization, the effect of winter cold is transmitted to the buds arising from the treated bud; therefore, when spring arrives, all of the buds should ultimately produce flowers and the plant should be monocarpic. Since the plant is perennial, one of the following alterations of the normal vernalizing process is likely to have occurred (42): (*a*) some of the buds are devernalized during summer; (*b*) some of the buds are not vernalized during winter chilling; (*c*) vernalization is not indefinitely autocatalytic among the second generation of buds derived from adventitious buds arising in the tissues that were not meristematic at the time of vernalization. Let us see what is the result of studies, especially those of the English authors with *Chrysanthemum* and of the French authors with various genera such as *Geum, Scabiosa, Teucrium,* etc.

Perennial plants in rosettes.—In the vegetative stage, *Geum urbanum* and one other *Geum* form short rosettes consisting of leaves without stipules; flowers occur on long axillary stems bearing leaves with stipules. The plants remain perennial by a rosette main axis which seems absolutely protected against all possibilities of flower formation. We showed [Chouard (43, 47), Chouard & Weber (50), Lé (149), Weber (269)] that before the autumn cold, no axillary bud had yet been transformed into an inflorescence primordium. The normal chilling time for vernalization is at least five weeks, at + 1° to + 4°C. This chilling confers a flowering capacity to the buds located in the axil of the younger visible leaves and some of the still younger leaves. Everything occurs as if the youngest, barely differentiated buds were indifferent to chilling vernalization. They react to vernalization as they become more differentiated; finally, as they grow older, their state is definitively fixed, either in the vegetative stage if they have not been vernalized in time, or as inflorescences if they have been vernalized in time.

Older axillary buds on the outer part of the rosette generally stop growing because of the correlative inhibition exerted by the active terminal bud. If the latter is taken off, outer axillary buds start growing—but in rosette only. Then, if they have undergone chilling, those among their own axillary buds which were responsive at that time and were vernalized, flower.

When the vernalizing temperature is below 1°C. no initiation appears during the minimum chilling period, but then, after warming up to 4°C. to as high as 30 to 35°C, the evolution of vernalized buds into inflorescence primordia followed by the shooting of these inflorescences and their flowering occurs slowly. The process occurs more quickly at cool temperatures and at the normal rate at warm temperatures. Hot temperatures cause accelerated secondary branching. Vernalization occurs around 4°C. and is immediately followed by a slow tissue differentiation which goes on actively even at such a low temperature.

The most easily vernalizable buds are those which, at the time of the chilling treatment, consist of their own apex meristem with a few roughly differentiated leaf primordia. If the chilling time is extended to 10 to 15 weeks, more buds are vernalized, particularly those that were too young at the beginning of the treatment. If the treatment is prolonged for 30 to 50 weeks, a remarkable phenomenon occurs : the terminal apex itself, as well as the older outer buds of the rosette, is vernalized. It follows that all the existing buds become vernalized. They form inflorescences after a return to warm temperatures and also form a terminal inflorescence (which never occurs in any *Geum* in any natural climatic condition of the world). These polycarpic plants become monocarpic and die after complete flowering of all their buds.

By taking off a leaf with its axillary bud and planting it, the bud can be freed from correlative inhibition and reveal whether it is vernalized or not. Inflorescences then form several leaves with stipules before ending in a flower at their apex. Without exception all axillary buds of an inflorescence are vernalized and able to flower. In a few exceptional cases, we could obtain adventitious buds on the petiole of leaves with stipules on flowering shoots. These newly formed buds are not vernalized and only give rise to rosettes.

Flower initiation, growth, and flowering following vernalization are absolutely day-neutral. We could never obtain devernalization either by short-day treatment or by a high temperature (35°C.) even when applied immediately after chilling. The continuance of the vernalized state in an autocatalytic manner in all successive generations of buds of inflorescences is indefinite. Cutting young flower buds or treating them at a high temperature (30 to 35°C.) induces considerable axillary branching in the inflorescence yet all successive generations of buds still can flower. Shifting nonvernalized plants from short days to long days does not cause any flowering (that is to say this plant does not show Wellensiek's phenomenon).

Up to now, gibberellin has not caused *Geum* to flower. In the absence of chilling gibberellin induces the shooting of some axillary buds or even of the terminal bud, which then forms an erect leafy stem. Leaves take on some of the form of flowering shoot leaves but do not have stipules. In spite of repeated gibberellin treatments, these elongated shoots finally form perched rosettes.

Certain individuals 1 to 10 per 1000 at the most) in *Geum urbanum* show a reduced vernalization requirement. These individuals grow one or two inflorescences without chilling, after 1 to 3 years of growth in warm temperatures. They may sometimes be induced to flower by gibberellin. They seem to belong to physiological races which differ genetically from the common type. In *G. bulgaricum* and *G. intermedium* this situation is true of most individuals, whereas in such species as *G. canadense, G. album, G. macrophyllum,* etc. we have only observed up to now a mandatory vernalization requirement, similar to that generally found in *G. urbanum.*

In *Geum,* mature achenes are dormant due to tegument inhibitions. Excised mature embryos are not dormant. Neither achenes nor excised embryos have yet been chill-vernalized. But young seedlings having only two small leaves in addition to the cotyledons can respond to vernalization and can flower on a young axillary shoot.

Geum, and especially *Geum urbanum,* must be considered as a new type of vernalization-requiring plant groups, like Petkus rye and henbane, which were the first two classical types.

Scabiosa succisa (=*Succisa pratensis* = *S. praemorsa*) behaves much like *G. urbanum* particularly in relation to the permanent inability of the terminal bud rosette to flower. Normally, vernalizing chilling induces the ability for further growth into an inflorescence in the two main axillary buds at their very young responsive age. Here however, under long days, after a sufficient delay for differentiation, inflorescences grow rapidly with long internodes and then flower. Under short days, the phenomena are slower, internodes are shorter, and flowering occurs much later. After vernalization, this plant therefore is a "quantitative long-day plant."

We first used plants from the "forest of Breteuil," in Perche. All plants showed the following remarkable reactions. When grown under short days at a warm temperature up to the age of a vigorous rosette the plants, when placed under long days at warm temperature, soon flowered as if vernalized, thus reproducing "Wellensiek's phenomenon" as found in *Campanula medium.* Moreover, repeated gibberellin treatments induced the shooting of axillary buds as if they were vernalized. Under these conditions, they flowered either slowly with short days or faster with long days and finally attained about the same length. Experiments carried out on individuals from other countries, such as Burgundy and the forests of "Brie," showed much greater vernalization requirements. In these races, gibberellin induced temporary shooting as in *Geum,* but no flowering, and Wellensiek's phenomenon did not occur. We have separated different clones from different individuals of the same population: each one behaves consistently but may differ physiologically one from another. Again this example shows how different the behavior of different strains of the same Linnean species can be (35, 42, 45, 47, 115).

Perennial plants in rosettes with terminal inflorescence.—Contrary to both preceding types, the following plants normally flower after transformation of the main axis into an inflorescence. These perennials, which require vernalization of various degrees, are probably more numerous than formerly thought. Many perennial meadow Graminaceae, studied by Cepikova (23) and more recently by some others (53, 168, 199) but mainly by Wycherley (285) initiate inflorescences on main shoots after chilling. *Cynosurus cristatus* requires 15 to 30 days at 5°C. or less and active flower initiation may follow, even at such low temperatures. It is markedly speeded up by long days; returning to short days can force some of the inflorescences back into rosettes. *Lolium perenne* is easily vernalized by only 15 days at 5°C. *Dactylis glomerata* requires a much longer chilling period. *Poa pratensis, Dactylis glomerata,* as well as a strain of *Cynosurus* and probably *Agropyrum repens* seem to be vernalizable but on shoots brought into a state of short and stout shoots by a short-day treatment (53, 88, 188, 195, 199, 285). I also observed mandatory or substantial vernalization requirements in *Poa supina,* various *Festuca, Bromus,* etc. (47). Their behavior seems to display significant differences from clone to clone and will soon need careful investigation, especially the requirement for short days before or during chilling.

Saxifraga rotundifolia obligately requires vernalizing chilling; the subsequent flower initiation is photoperiodically day-neutral, but the length of the flowering shoots and the number of flowers are much greater with long than short days. Many perennial Crucifers behave similarly, except for certain rosette types, e.g., *Draba aizoides* and *D. hispanica,* which normally grow as small rosettes with numerous pointed leaves. These must be vernalized and then they initiate flowers even at relatively low temperatures and finally flower irrespective of the photoperiod. When maintained constantly in a warm temperature, the rosettes grow a short, sometimes flexible stem with numerous leaves, that never bears flowers. Here gibberellin increases elongation without inducing flowering. It does not appear that the axillary buds can be vernalized by chilling. In the genus *Erysimum,* numerous perennial species also require vernalization, either obligately, or almost so. Without chilling, certain species remain as mere rosettes while others, especially at warm temperatures, grow extensive leafy stems of various lengths. Gibberellin generally increases elongation without inducing the flowering that occurs normally after vernalization irrespective of the photoperiod. *Dianthus,* which we will refer to again, can be classified here. Various species of *Primula,* many of *Potentilla, Agrimonia, Lychnis coronaria, viscaria,* and *flos-cuculi, Cardamine amara,* various species of *Silene, Scrofularia alata,* etc. under observation for numerous years, proved to have mandatory vernalization requirements. In *Eryngium variifolium,* the vernalization requirement seems important and gibberellin has been totally ineffective in causing even the least elongation or modification of the plant habit (43, 46, 47).

In *Scrofularia alata,* a perennial absolutely requiring vernalization, gibberellin induces considerable elongation under either long or short days, but no flowering. However, after an insufficient period of chilling that has no apparent effect, gibberellin induces both elongation and flowering. The small seeds may be vernalized, contrary to those of henbane which cannot be (148). When fully studied, *Scrofularia alata* could become the other exemplifying type for perennial rosette plants requiring vernalization.

Scabiosa canescens (= *suaveolens*), after germination, produces simple obovate leaves that spread flat on the ground. After chilling, newly formed leaves are deeply pinnatisect into fine segments. The plant then grows and flowers quickly with long days, slowly under short days. Without vernalization, plants grown from seeds from an apparently homogeneous natural population display great genetic variability. Some plants of this category remain in rosettes for years with simple young leaves; others grow longer after a certain time lag but retain the simple leaves on a long stem for prolonged periods; others spontaneously form divided leaves quite early while growing either slightly or extensively and finally flower late. This plant, perennial according to the nonvernalized or devernalized shoots with simple leaves formed at the base, illustrates very well the leaf polymorphism that follows vernalization as was reported for bitter *Cichorium.* It also shows that the elongation and the different leaf forms that necessarily precede flowering, can either be linked or separate. Therefore, they are possibly independent phenomena (43, 47).

Caulescent perennial plants.—Before vernalization, certain of these have a short stem, differing little from an elongated rosette. *Dianthus* (carnation) (43, 47), displays all possible types of vernalization requirements: none in *D. superbus* which keeps flowering again and again under long days from bottom sprouts; low in *D. gallicus, seguieri, campestris,* etc. which elongate into creeping or stoliniferous stems and flower quite abundantly, but earlier and still more abundantly after vernalization; and important in *D. arenarius, attenuatus, geminiflorus,* and *caryophyllus,* which develop short stems of which the strongest shoots produce 1 or 2 flowers after 2 to 4 years of growth under warm conditions. In addition, the requirement is mandatory for numerous species with rare individual exceptions: *D. deltoides* forms long, very leafy shoots that never flower without vernalization or else flower very late and poorly; *D. coesius* and *D. carthusianorum,* remain as very short stems with heavy masses of leaves; *D. neglectus* and *graniticus* (with slightly longer stems) and *D. squarrosus,* with long stems, never flower without vernalization. *D. barbatus* (268, 271) forms stalks with very dense leaves and must be vernalized except for one strain that keeps flowering constantly and which, through a graft made by Waterschoot (268), induced a vernalization-requiring plant to flower. Gibberellin appears not to induce flowering in carnation in place of vernalization. Cultivated carnations (from *D. caryophyllus*) have more moderate requirements for flowering, e.g., everflowering carnation (14) must have formed 9 to 11 pairs of leaves before it can be vernalized. When chilling is then supplied, they can flower under long days at the fourteenth node. Flowering is markedly later under short days or without chilling.

Many *Leucanthemum,* mainly *L. cebennense* (= *monspeliense*) (43, 47), and probably *Pyrethrum cinerariaefolium* (91) form short bushy stems that only bear flowers on the terminal axis after vernalization under essentially day-neutral conditions. However, the pedicels are very short under short days and very long under long days. In these plants, as in carnation, very young or insufficiently robust shoots at the time of chilling are insensitive to vernalization and thus ensure the perennial condition.

We also find typically caulescent perennial species (42, 43, 47), *Teucrium scorodonia* is one of the best examples, forming suckers and leafy shoots. It never flowers unless previously vernalized. After vernalization it requires long days, although not always. The terminal shoots terminate in inflorescences. The secondary shoots, leafy lower sprouts, and subterranean stems or suckers maintain the perennial condition. Repeated applications of gibberellin can induce an elongation of several metres, but no flowering. *Teucrium scordium* continues in the form of creeping shoots without flowers when nonvernalized (47).

Many woody plants (bushes or even trees) have similar requirements (47), e.g., *Medicago arborea,* in which a chilled twig flowers without this ability being transmitted to the other nonchilled twigs of the same plant. Wellensiek also showed vernalization requirements for the woody crucifer *Cheiranthus cheiri,* the wallflower (273, 274). I found *Alyssoides* (= *Vesicaria*) *utriculatus* to also require vernalization. Obligate vernalization requirements are also found in various species of *Cistus,* in *Salvia* (*officinalis, triflora, lavanduldefolia*), in *Lavatera* (47), etc. It is also very likely that large trees such as the olive tree (*Olea europea*) have varying vernalization requirements depending on the variety (4, 110).

In other species, such as *Geum* and *Succisa,* the apical bud is protected against vernalization, but they are typically caulescent. An example is *Anagallis tenella,* which covers the ground with stoloniferous stems, mandatorily requires a long vernalization and then the axillary buds flower only under long days. Vernalization does not seem to extend to axillary buds other than those responsive at the time of treatment. Radicant *Lysimachia nemorum* and non-radicant *Saxifraga hypnoides* behave similarly (47).

Chrysanthemum hortorum or *morifolium,* the garden chrysanthemums (33, 49, 203) flower in short days more or less obligately (late varieties) or only prefer short days (early varieties). Some of them (22) flower irrespective of temperature; others are stimulated by warm temperatures (> 12°C.) and others by chilling (< 12°C.). Although short days induce flowering, chrysanthemums also require various degrees of preparation. I have already shown (33) that certain varieties respond to short days much earlier and more effectively when they have previously received a long-day treatment. Schwabe (230 to 232) showed that certain varieties require a preparatory chilling period of various extents which can be considered as vernalization. The treatment is more effective when given at night and for about three weeks around 4 to 6°C. These phenomena have also been carefully studied by Vince (262, 263) who showed in particular that only certain varieties may undergo the preparatory phase partly with cold temperature treatment and partly with long-day treatment. Many cold-requiring varieties grow in warm temperatures as creeping shoots, forming short sprouts with layered leaves, as in rosettes.

Removing the rosette terminal bud in certain of these releases axillary shoots that are then directly influenced by short days (233, 234, 263). Most often, axillary buds are vernalized simultaneously with the terminal bud, but not always down to the base of the stem. Moreover, exposure to high or low light intensities, or growth in the ground (suckers) causes devernalization, which ensures the perennial state. This is most effective at temperatures less than 18°C., even if the plants receive additional soluble sugars. However, heat does not devernalize in high light intensities. The vernalized state is not graft transmitted. Gibberellin often suppresses the branching stage, but the long shoots still develop flowers in a few varieties, even under short days. Picking the flower buds formed under short days sometimes induces flowers directly on young suckers, but this is not true for most varieties. The varietal responses are so varied that the interesting investigations recently completed are now giving rise to further studies [cf. recent works, Cathey (22), Chan (29), Doorenbos (72), Schwabe (230 to 236), Vince (262, 263)].

MECHANISMS OF VERNALIZATION

Up to now we have reviewed the main experimental work that determined the characteristics of vernalization in various species. We will now examine what processes were inferred in attempting to rationalize the mechanisms involved.

THE STADIAL DEVELOPMENT THEORY AND THE REVERSIBILITY OF VERNALIZATION

From embryogenesis to flowering, a plant grows through successive stages. The identification of these stages is useful in further analyzing every mechanism in their ontogeny. The "stadial theory" however, is exacting; it holds that the same stages occur in all plants and that they are fundamentally irreversible. For further information refer to Lysenko who proposed the theory (155 to 159) and to commentators on the theory (279). If these stages are believed to be ontogenetic natures or properties defined according to an *a priori* postulate and unaltered by experiment, they are to be considered as expressing a faith that does not fall within the scope of scientific experimental analysis. If we hold to mere facts that can be repeated in experiments we speak another language. We indeed recognize stages in plant development, but these are neither universal nor irreversible. For example, we cannot say that the vernalization process, or "thermostage," is universally imposed merely as a temperature-controlled period of development. *Bidens radiatus* reacts to photoperiods as soon as its cotyledons turn green, without any previous thermostage (37); also, the "photostage" is not always necessary for flowering. Flowering primordia exist in mature peanut seeds before any light treatment of the seedling. When a thermostage is required, it may be experimentaly reversible in certain cases, as we have seen for experimental successions of devernalization and revernalization. What is the obligate requirement for new vernalizing chilling if not the need for a new thermostage, the former having been fully eliminated? Bud regeneration returns the plant to most of its juvenile stages. In experiments with proliferating flowers (44) the partly differentiated floral apex is reversibly returned to a vegetative apex of a shoot which again will have to go through all the previous stages before flowering. As far as the words are concerned, we prefer to consider purely empirical stages as observed for each species in our experiments and their reversible or irreversible sequence, and to analyze the various regulating mechanisms, whether independent or correlated, that control the sequence of the development.

HEREDITARY TRANSMISSION OF DEVELOPMENTAL MECHANISMS

A requirement for vernalization is an hereditary property of certain species and concerns the transmission of a physiological characteristic. We have seen that a single species often includes several strains that display various kinds of vernalization requirements. We even found wild species that seem to have a simple vernalization requirement but in experiments reveal that they are a mixture of mutants with differing requirements. When hybrids can be obtained from plants with different vernalization requirements, the studies (169, 207) have shown that the vernalization characteristics are borne by a few Mendelian factors in which the various alleles are often selected by an adaptation to climate, e.g., one gene only in the case of the two black henbane strains. But vernalization was used as a stepping stone to demonstrate the transmissibility of acquired characters. Mitchourin's followers state that the growing of spring wheat in the autumn wipes out the inheritance of the "spring" character after a severe winter of growth; from the seeds of the few surviving individuals a second autumn crop would show a new "winter" heredity instead of the "spring" one (158, 159). In certain countries, vernalization is mostly studied from this point of view. Since such experiments have not been successfully repeated in any country where properly controlled experiments and pure strains were used, and since they do not concern the physiological processes involved in vernalization, there is no need to discuss them here.

However, the stadial theory led several physiologists to study so-called "lasting modifications" that were found to be reversible in a few generations. For example, Séchet (239) reports the "remanent effects of vernalization" in *Camelina sativa, Cicer arietinum, Vicia faba,* and in oats. Highkin (119) reported a nonidentical but related phenomenon in the training of peas for surviving detrimental thermal treatments.

DESCRIPTIVE FORMULATIONS OF VERNALIZATION

Several authors have established formulation of the facts observed. Lang & Melchers (144) express their observation on henbane as follows:

$$\begin{tikzcd}
\text{A (precursor)} \arrow[r, "\text{I}"] & \text{B (limiting substance)} \arrow[r, "\text{II}"] \arrow[d, "\text{III}"] & \text{C (floral initiation)} \\
& \text{D (loss)} &
\end{tikzcd}$$

I occurs in the cold, II takes place at normal temperatures and in the presence of oxygen, III is heat devernalization without oxygen, B is not necessarily the precursor substance of C, but may also be an agent involved in the synthesis of C.

Gott, Gregory & Purvis (94) and Purvis & Gregory (214) having corrected their previous formulation (212) of vernalization in rye Petkus now represent it as:

$$\begin{tikzcd}
\text{A (precursor)} \arrow[r, shift left] & \text{A}' \arrow[l, shift left, "\begin{array}{c}\text{(devernal-}\\\text{ization)}\\Q_{10}=2\text{–}3\end{array}"] \arrow[r, "\text{fixation}"] & \text{B} \arrow[r, shift left, "\text{short days}"] & \text{C} \arrow[l, shift left] \arrow[r, "\text{long days}"] & \text{D (flower promoting hormone)}
\end{tikzcd}$$

which contains in brief all the above-cited observations.

Van de Sande Bakhuyzen (9) expresses his findings by the following formulation:

$$\begin{tikzcd}
& \text{caulocaline} \arrow[dd] & {} \arrow[dr] & & \\
& & & \text{A} & \\
\text{phyllocaline} \arrow[r, shift left] & \text{protocaline} \arrow[l, shift left] \arrow[r, shift left, "\overset{\text{vernalase}}{\downarrow}"] \arrow[d] & \text{vernaline} \arrow[l, shift left] \arrow[r, shift left] & \text{B} \arrow[l, shift left] & \{\text{anthocaline} \\
& \text{rhyzocaline} & & &
\end{tikzcd}$$

A "thermophase" occurs under cold conditions releasing an enzyme "vernalase." Then during an "interphase" with warm temperatures and possibly short days, vernalase results in "vernaline" which, in a final "photophase," gives rise to "florigen" B; the latter, according to the proportions in which it combines with photosynthetic products A, either does or does not induce flowering. This diagram is meant primarilly to express simultaneously the mechanisms of short- and long-day plants.

Napp-Zinn (186) groups his studies on *Arabidopsis thaliana* "Stockholm" strain in the following diagram:

$$\begin{tikzcd}
A \arrow[r] & A_1 \arrow[r] \arrow[d] \arrow[rrrr, bend left] & A_2 \arrow[r] & A_3 \arrow[r] \arrow[d] & A' \arrow[r] \arrow[d] & B \\
 & X & & X' & Y &
\end{tikzcd}$$

in which A is a thermostable precursor; A_1 is the first thermolabile intermediate that can be shifted toward X by a heat treatment at 30°C. soon after sowing and causes anti-vernalization; A_2 is a thermostable intermediate demonstrated by the possibilities of revernalization after five days of devernalization; A_3 is the second thermolabile intermediate, demonstrated by the partial shifting towards X′ at 20°C.; A′ is the third thermolabile intermediate demonstrated by devernalization at 30°C., leading to Y, and corresponding to the thermolabile intermediate of Purvis and Gregory; and B is the final thermolabile intermediate of vernalization, leading to flowering. It may be directly attained from A by a shunt at 20°C.

These formulations are handy to memorize and thcy stimulate further investigations on hypothetical substances; but they provide no more clarification than the authors' descriptions of their own results. Further, they may require adjustmcnt for each ncw discovery and they also change for each plant type that behaves in a particular way and does not fit the particular representation.

REGULATORY MECHANISMS OF DEVELOPMENT

From a simpler point of view, I think that the experiments permit us to analyze separately some mechanisms found either naturally separated or interrelated. For example, the complex mechanism of vernalization is not always linked to that of photoperiodism. Table I shows that among the various species of plants there are all possible combinations of various vernalization and photoperiodic requirements (see Table I) (34, 36, 38, 39, 41, 42).

Before constructing a general theory of reproductive development—if one is possible—we have to analyze carefully one after the other, every elementary mechanism involved in it and choose the best possible example of each mechanism where it constitutes the limiting factor. Then we will consider the various relationships between these mechanisms. For example, as we have just seen, vernalization may bc either independent from or associ-

TABLE I

EXAMPLES OF THE DIFFERENT COMBINATIONS OF SEVERAL REGULATORY MECHANISMS OF DEVELOPMENT, INCLUDING VERNALIZATION

Requirement for vernalization by chilling / Photoperiodic requirement	Obligate (qualitative)	Partial (quantitative)		None or absent
		Great	Small	
Hemeroperiodism (long-day) Obligate (qualitative)	*Oenothera biennis, parviflora, lamarckiana* *Anagallis tenella* *Dianthus graniticus, coesius,* etc. *Hyoscyamus niger* (biennial strain) *Campanula medium* (Wellensiek strain) *Iberis intermedia*	*Oenothera suaveolens, stricta, longiflora* *Dianthus arenarius*	*Dianthus gallicus* Spinach (some varieties)	*Scabiosa ukranica* *Dianthus superbus* *Anagallis arvensis* *Hyoscyamus niger* (annual strain) *Lavauxia (Oenothera) acaulis* Spinach (some varieties)
Great	*Digitalis purpurea*	*Scabiosa canescens*		*Nigella damascena* *Scrofularia arguta* (apical stems with expanded leaves)
Partial (quantitative)	*Dianthus barbatus* *Teucrium scorodonia*	*Dianthus caryophyllus*	(depending on variety) *Agrostemma githago*	*Dianthus prolifer* *Dianthus barbatus* (one strain)
	Scabiosa succisa *Cheiranthus cheiri*	Winter wheats and cereals	Alternative wheats and cereals	*Oenothera rosea* Spring wheats and cereals
Small	*Leucanthemum cobennense*		*Sinapis alba*	*Nigella arvensis*
None or absent (day-neutral)	*Scrofularia vernalis* *Euphorbia lathyris* *Scrofularia alata* *Geum urbanum, macrophyllum, canadense* *Draba aizoides* *Saxifraga rotundifolia* *Lunaria biennis*	Several *Erysimum* *Geum intermedium* *G. bulgaricum*	*Pisum sativum* (some varieties)	*Scrofularia peregrina* *S. arguta* (basal aphyllous stems) *Senecio vulgaris* *Euphorbia peplus* *Lunaria annus* *Pisum sativum* (some varieties)
Nyctiperiodism (short-day)	Summer flowering, Autumn flowering } *Chrysanthemum ×hortorum (morifolium)* (depending on the variety)	*Chrysanthemum ×hortorum (=morifolium)* (depending on the variety)		*Chrysanthemum ×hortorum (morifolium)* (depending on the variety)

Many other examples could be given, but the above are sufficient to demonstrate that all the different combinations may be encountered. According to varietal or strain differences, some species may appear in several squares of this table.

ated with photoperiodism. The partial or total replacement of chilling by short days to achieve vernalization is illustrated by the rye Petkus, *Campanula medium* (Wellensiek's strain), and by one strain of *Scabiosa succisa* but not by most other plants. Partial or total replacement of vernalizing chilling by long days is exemplified by certain *Chrysanthemums* and not others. Heat devernalization, obtained by warm temperatures applied immediately after vernalizing chilling, although very common, is ineffective for Chinese mustard and *Geum.* Late devernalization after fixation of the vernalized state seems impossible with the rye Petkus, henbane, *Geum,* etc. but seems most readily attained with *Oenothera* and beets.

The analysis of the substitution of chemicals, particularly gibberellin, for chilling in order to achieve vernalization shows, as we will see later, that the vernalizing process probably consists of several stages; and some of them may be absent in related strains.

After the broad eco-physiological analysis of vernalization presented in the second part of this review, there remains the imposing task of interpreting each elementary process at the physico-chemical level.

COMMON PROPERTIES OF ALL VERNALIZATION PHENOMENA

The variety of elementary processes must not overshadow the characteristics common to all vernalization phenomena. Some of these are ecological, others physico-chemical.

Properties related to environmental conditions required for vernalization (42, 98, 173, 174, 273).—We have reviewed these in detail for the rye Petkus and for henbane; with reference to other plants we can summarize the results here. Chilling between the extreme limits of −6° and +12 to 14°C., normally from +1 to +5 or 6°C., is the fundamental agent of vernalization. It is only effective when applied for several days, weeks, or months in the presence of oxygen to moist enough tissues containing enough carbohydrate to support adequate respiration. Concomitant growth may be either moderate or very slow; if it stops completely, vernalization does not occur. Vernalization is directly perceived by stem or bud primary meristems; it is sensed at a certain age which is very early (immature embryo) or much later (leafy plant) according to the species. It is transitted by more or less stable or prolonged autocatalysis or self-perpetuation to the buds arising from the vernalized ones. It consists in the attainment of a new functional ability (the flowering ability) that is later "revealed" by flowering under special conditions (long or short days, various temperatures, etc.) which are characteristic for each species and variety.

Physico-chemical properties of vernalized tissues (76).—A great many investigations have been devoted to this question which consists essentially in comparing treated tissues at the end of the vernalizing treatment with nonchilled tissues, either to check on the completeness and effectiveness of the vernalizing process or to try to observe the intimate nature of the process. The second aim has not yet been fully attained, for in fact, we only observe either the ordinary consequences of growth in the cold or the metabolic consequences of vernalization itself, which are simply concomitant with the acquisition of the ability to flower and are not the agents conferring this ability (75, 76).

Thus, it is observed that carboyhdrates are depolymerized, resulting in an increase of soluble sugars, sometimes not very great (62, 63, 66, 75); depolymerisation of reserve proteins occurs with an increase in soluble nitrogen compounds (62, 65, 69); and there is a fall in the lipid content (64, 73 to 75). These are typical consequences of a low temperature metabolism and probably not specifically related to vernalization (38, 87). Moreover, during germination, a phase occurs in nonvernalized seeds in which the respiratory rate increases with a respiratory quotient approaching 1.0. In vernalized seeds, this phase is characterized by a low respiratory rate and the respiratory quotient only slowly increases to 1.0 (179).

Also observed are a reduction of the auxin level (57, 242), a shift of the isoelectric point of proteins toward acidity (283 to 286), a slight increase in the coagulability and permeability in the protoplasm (30, 83), and a modified pH of the cell liquids (214). After vernalization cells of the vegetative point are less readily coloured blue by ferric chloride and potassium ferrocyanide, showing, as well as by other colour reactions, a possible change of pH (11, 20). The serological properties of a vernalized plant do not seem modified compared to the control (1, 2). Cholodny's former theory (32), involving a transfer from endosperm of auxin and other hormones such as a blastanin, is no longer entertained (112, 242).

Enzyme activities are markedly modified (57, 69, 112, 120, 224, 225, 227, 242) e.g., relative increases in the activity of sugar hydrolases, in particular amylase and invertase (yet there are contradictory results), and of phosphatase, lipase, catalase, etc. Recent Russian authors (75, 246, 247) emphasize the alteration occurring in enzyme adsorption on protoplasmic surfaces, with tendencies toward depolymerization after chilling, following a loosening of the links between enzymes and protoplasm. There is also a reduced activity of cytochrome oxydase and succinic dehydrogenase and increased activity of ascorbic acid oxydase and of malic and citric dehydrogenases (247), even though, in general, the overall respiratory rate is not particularly changed at the end of vernalization. Changes in the vitamins C and B contents take place during (239) and after (189) vernalization.

When vernalization is complete, the ensuing metabolism is soon similar to that of the control. However, certain authors think that the above enzyme modifications persist after chilling and that they are like the enzyme characteristics attained directly by nonchilled annual strains (246).

In addition, it was reported that after vernalization certain plants (radish) show either increased resistance (240), or decreased (239). Chilling by itself is a process of training a plant to resist frost (259). Vernalized cereals respond more to water than do nonvernalized controls, but they also suffer more from drought (134). Their capacity for mineral and water absorption is changed (191) and the anatomical status looks more mature (25).

All these interesting facts still do not solve the problem: What is the biochemical nature of the process of vernalization?

HORMONAL TRANSMISSION OF VERNALIZATION

I emphasized that the autocatalytic transmission of vernalization is restricted entirely to those meristematic cells derived from actually vernalized ones. We should not overlook the fact, however, that vernalization may also be transmitted as if it were effected by some substance diffusing from cell to cell. The Melchers and Lang graft experiments on henbane (168 to 172, 178) elicited much enthusiasm and were interpreted as pointing to some general process. In actual fact, examples of vernalization induction from donor to receptor, by way of a graft union are few in number. Most of these are listed by Lang in his 1952 Review (140). These are: henbane as a receptor for several donors, beets, cabbage scion upon annual *Brassica* or upon mustard stock, carrot upon dill and, more recently, late peas upon early peas and grafts of different strains of sweet William, but almost nothing more. In other cases, vernalization is strictly localized to the chilled part of the stem (47, 289). An hypothesis based on a mobile vernaline holds only for a few special cases.

CHEMICAL OR BIOCHEMICAL VERNALIZATION

Many authors understand "chemical vernalization" to mean the more or less synergic effect of some substance acting conjointly with the chilling of seeds to promote vernalization. In *Brassica* and in peas (in as much as vernalization here is truly a vernalization as defined earlier) indole-3-acetic acid synergizes chilling whereas gibberellin and 2,3,5-triiodobenzoic acid antagonize chilling (27, 150). See also the several cases of synergism between different chemicals and chilling reported by Séchet (239).

The hypothetical vernaline has never been extracted from plants (176), but some reports indicated that vernalized seeds may yield undefined substances exerting a vernalizing effect when used to soak unvernalized seeds. Purvis and Gregory reported that extracts from cereal seeds being processed for vernalization could replace the effect of chilling, but they have not reported again since 1953 (215). More recently, Highkin showed that if late pea seeds are chilled for a long time they yield water extracts that replace chilling for the vernalization of other peas or even for winter cereals (116, 117). Guanosine may be involved (118).

The problem of vernalization by chemicals has had to be reinvestigated completely since Lang's discovery of the effect of the prolonged gibberellin treatment of henbane (biennial strain). In the green house under long-day conditions, such treatment induces elongation and then flowering (142). This report stimulated numerous experiments (15, 21, 43, 47, 153 to 156, 273, 280). The results are as follows. Most often gibberellin increases the elongation of the treated organ; caulescent stems become longer, "rosettes" elongate into leafy stems, etc. However, among plants requiring vernalization, few flower as a result of gibberellin treatment in the absence of chilling. Replacement of chilling by gibberellin is observed only among rosette plants mainly those flowering on elongating terminal buds such as: henbane, *Centaurium minus,* fox glove, *Oenothera lamarkiana* and *parviflora* (but not *biennis*), *Reseda luteola* (slightly), *Beta maritima* (but not several other *Beta*), some strains of *Scabiosa succisa* and *Campanula medium* (but not other strains), and a few species of *Geum* (*intermedium, etc.*). Likewise, gibberellin replaces the photoperiodic induction of flowering in some rosette plants *Samolus parviflorus* (146) and *Polemonium coeruleum* (43). In *Scabiosa ukranica,* under short-day conditions, gibberellin causes elongation and the formation of "inflorescence" primordia although not of "flower primordia." Usually, even repeated treatments will at most cause elongation from the rosette stage but without even initiation of inflorescence primordia (*Scrofularia vernalis, S. alata,* winter cereals). Frequently, elongation is restricted and results in either temporary or permanent "perched rosettes" (*Geum urbanum, Campanula medium,* sugar beets). In other plants gibberellin causes little (*Dianthus*) or no elongation (*Saxifraga rotundifolia, S. cotyledon, Eryngium variifolium,* etc.). Lastly, among caulescent plants, gibberellin has so far failed to replace the vernalization or photoperiodic requirements for flowering (*Euphorbia lathyris, Teucrium scorodonia,* etc.) (42, 43). Species vernalizable by seed chilling (*Brassica campestris, Cicer, Lens,* etc.) are not vernalizable by treatment of the seed with gibberellin (25).

Problems to be Solved

Having summarized what is already known about vernalization, we will now mention the many unsolved problems. The duration of the "juvenile period," i.e., the time elapsed before "ripeness to vernalization" is achieved must be determined in many cases. Most plants with an obligate vernalization requirement have embryos within the mature seed that cannot be vernalized (*Scrofularia alata* is an exception). This should be elucidated to find out whether chilling such seed effects a preliminary part of the vernalization process; also, a determination should be made as to when these plants actually become fully vernalizable.

Vernalization kinetics remain to be clarified. Further, the effects of overchilling should be investigated in as much as it may depress vernalization or conversely prolong the effectiveness unduly.

Anti-vernalization techniques should be elucidated in relation to the efficiency of chemicals (metabolic and growth inhibitors) about which we know very little (28, 48). In this regard, the efficiency of gibberellin as an anti-vernalizant of pea, the effect of metabolic agents, deficiency of food such as sugar (99, 208, 210), and the role of physical agents [heating or leaching previous to chilling (112)], remain to be studied in more detail.

Devernalization should be "explored" in a number of plants which have not yet been studied from this point of view. The effect of devernalization treatments should be studied not only immediately after the vernalization process but subsequently, for instance as in the effect of short days on beets (164) or *Oenothera* (201, 202). This kind of devernalization is probably very different from the classical devernalization by heat or by anaerobiosis immediately after chilling. Alternating temperatures should be investigated as to whether they delay or accelerate the vernalizing process.

Among plants bearing leaves, the roles of intensity, duration, and quality of light during chilling appear important and deserve further study. Is light necessary just to supply sugar or does it have specific effect? We do not know for sure whether leaves formed before vernalization are or are not photoperiodically receptive. Data is still scanty as to the role of the root, which when tuberized, intervenes as a sugar donor.

Some data suggest that vernalization may proceed by successive stages that may differ both as to requirements and results, e.g., short chilling, unable by itself to promote vernalization, may become effective by an additional treatment with gibberellin, which by itself would not have been effective. This should be checked (148, 201).

What has been termed "vernalization" in chrysanthemum, tomatoes, and peas, may differ from what is termed "vernalization" in henbane and *Oenothera*. Peas growing from nonchilled seeds produce, below the flowering nodes, axillary buds which tend to develop into abortive flowers. Had the seeds been chilled, flowers would differentiate; in that case, the "assumed vernalization" completes what otherwise would have only been initiated. Yet to be clarified is the chronological sequence of the initiation of inflorescence, the initiation of flowers, the various stages of elongation, and the possible interrelations among these events.

Perennial plants deserve special attention in relation to all the problems alluded to above as well as those peculiar to themselves. How can the perennial condition be preserved? The various alternative methods discussed above have been investigated only for a very few plants.

New researches are urgently needed on the total or partial replacement of "vernalizing chilling" by gibberellin, other chemical agents, extracts from vernalized plants, or by long or short days. The vernalizing effects of short days (apparently complete or partial) when followed by long days (Wellensiek's phenomenon) or in the absence of long days (Petkus rye, *Iberis durandii*) require more research. We know nothing about the possible similarity to the above of the different photoperiodic requirements in amphiperiodic plants.

Lastly, the biochemistry of vernalization should be investigated with increased vigor. Emphasis should be given to the identification of natural stimulating or inhibiting agents intervening in the various phases of vernalization, rather than to assays involving known, metabolically active substances. The exchange of material between the nucleus and the cytoplasm should be taken into consideration in terms of modern physiological genetics as discussed below.

VERNALIZATION AND DORMANCY

"Dormancy" coincides with a cessation of growth (or auxesis) caused by internal factors within the organism or organ. The growth of any developing organ is arrested since the mechanisms controlling the increase in size are inhibited. Among such mechanisms is production or effectiveness of auxin. Release from dormancy is evidenced by renewed growth, and implies a resumption of previous activities rather than the introduction of new activities. During dormancy the frequency of mitosis decreases correlatively with the inhibition of growth, e.g., a twig of *Salix repens* growing under long-day conditions forms leaves and internodes; when transferred to short-day conditions the twig forms short internodes, the leaves are reduced to the condition of scales, and the terminal bud goes into dormancy; when subjected to cold, the twig recovers its former activity (38, 40).

The shortening of internodes, termed "brachyblasty," and expressed by the "rosette" configuration, is related to dormancy since it results from a shortening of internodes, but it differs from dormancy in not interfering with the formation and expansion of leaves (43). What is affected is the mechanism of cell elongation in internodes and of cell formation in between leaf bases, but the ring of cells around the apex, from which leaves originate, retains its activity and the enlargement of leaf primordia remains unretarded.

The "nonvernalized state" may be defined as the inability to form flowers and affects the potential activity of the summit of the apex and of terminal or axillary vegetative points. These retain an "anticipating meristematic" condition that is completely independent of the production or nonproduction of leaves or internodes.

Dormancy may be broken by submitting buds to treatments apt to release inhibitions. Among external stimuli, cold is the common one, but similar effects may be achieved using heat (applied as a hot bath), drying, long days, anesthesics, glycol monochlorhydrin, thiourea, gibberellin, or an exogenous auxin. Brachyblasty, when released, is normally followed by the formation of long internodes. The release can be effected by exposure to cold or long days, or by treatment with gibberellin. Other agents that break dormancy are generally ineffective. The nonvernalized state is removed by cold or gibberellin, or rarely by either long or short days. The effectiveness of cold, and less often of gibberellin, is a feature common to the three phenomena: breaking of dormancy, releasing of brachyblasty, and vernalization.

These three phenomena, however, can be differentiated in terms of the response of each to other agents.

Dormancy may not coincide with the nonvernalized state and may intervene as flowers are being differentiated in the bud, which then ceases growth and forms leaves. The breaking of dormancy in this case has nothing to do with vernalization. The example of *Salix repens* is most illuminating (38, 47). Axillary catkins form following photosynthetic activity in the leaves. Transfer from long to short days may then be arranged to induce dormancy either before or after the catkins have differentiated. Thus, breaking dormancy may not be required for differentiation of catkins, and may therefore be confounded with vernalization or sharply separated from it. These alternatives clearly distinguish the breaking of dormancy from vernalization.

Likewise, dormancy in the seeds of *Geum* may be broken by low temperatures or by excising the integuments: neither of these treatments causes vernalization of the seeds.

Brachyblasty is closely related to the nonvernalized state, although not always. Most plants requiring vernalization are of the rosette type. Cold has a dual effect: elongation of internodes, and vernalization. Thus, vernalization can be confused with release of the inhibition of internode elongation. However, although they may be concomitant, the two phenomena are distinct, as shown by the following comparisons.

(*a*) Many plants that require vernalization are caulescent and never have a rosette phase; their vernalization is not related to the length of internodes [*Euphorbia lathyris, Teucrium scorodonia* (43, 47)].

(*b*) Gibberellin may shift the brachyblastic form to the caulescent type, without causing any vernalization [*Oenothera biennis* (201), *Scrophularia alata* (148)].

(*c*) Long days sometimes cause elongation of internodes from the rosette stage without effecting vernalization [*Salvia silvestris* (47)].

(*d*) Flowering does not necessarily depend on the elongation of the flower-bearing stem; thus, *Lavauxia* (*Oenothera*) *acaulis* develops flowers while it is a rosette, as does *Rudbeckia bicolor* (with high temperatures and short days) (226).

(*e*) Initiation of flowers may occur deep in the rosette with the flower stalk elongating later (*Spinacia oleracea*) (176), or the converse may occur [*Oenothera* sp., some strains of *Scabiosa ukranica* (47)].

(*f*) In henbane, cold-induced vernalization first entails inflorescence initiation and then elongation, whereas the situation is reversed when the inducing agent is gibberellin (228).

(*g*) In peach trees, seed dormancy is partially released with time if cold does not intervene, but the seedling can form only a rosette. Elongation is made possible following chilling or treatment with gibberellin (10). Later, in due time, flowering occurs and such a release of brachyblasty has been confused with vernalization. Flowering requires a proper equilibrium of mild temperature and nutrition such as can be obtained with properly developed leaves. Then flowering may occur either on long twigs or on rosette-like twigs ("bouquets de Mai"). Whenever a nonvernalized state is concomitant with brachyblasty or the rosette stage, it may be said that vernalization requires at least as much, and frequently more, cold (or gibberellin) as would be required to release brachyblasty.

Vernalization and brachyblasty have common features but must be considered as different phenomena unless we recognize various types or stages of vernalization. One such stage would be completely separate from the release of brachyblasty while the others might be strictly associated with its release. One or several stages would be needed according to the species, varieties, or even genotypes. Further research is needed to solve this problem.

ELUCIDATING THE INTIMATE PROCESS OF VERNALIZATION

Vernalization fundamentally implies: (*a*) an aftereffect resulting in active mitoses spreading to the very apex of the vegetative point, which then develops into the initial inflorescence or flower; and (*b*) irreversible, or reversible, autocatalytic preservation of the after effect.

Self-perpetuating new properties are expressed either through particulate release of DNA from the nucleus—to induce autocatalytic multiplication of cytoplasmic RNA particles as carriers of the new property—or through displacements of an equilibrium involving several pre-existing and self-perpetuating enzymes (68).

Cooling may control such a displacement of equilibrium while it slows down the rate of some enzymatic reactions and speeds up others; thereby triggering a cellular reaction which becomes autocatalytic. Cooling may even directly affect nuclear properties at the time it confers the capacity for the increased rate of mitoses. Gibberellin is endowed with properties similar in many respects to those of cold. It directly controls mitosis in primary meristems. This control is independent of that exerted on enlargement via auxins (216). Similar vernalizing properties of chilling and sometimes of gibberellin may be linked with similar properties affecting nuclear activity.

Assuming that flowering is induced by some interaction of nuclear DNA with an autocatalytic cytoplasmic system, flowering regulation would then be investigated either as a release of nuclear particles, or as an inhibition of stimulation of the proliferation of such particles once they had been released into the cytoplasm, or in the stimulation of inhibition of the activity of their products. Such effects might be, in some cases, mediated via mobile and diffusible hormonal compounds. Hereditary properties would be expected to intervene in forming stable or labile linkages between active particles and nuclei. The preceding discussion features vernalization as a self-perpetuating process involving certain "cellular lines" and focuses attention on some nucleo-cytoplasmic interrelationships.

Heretofore, biochemical investigations have concentrated on the consequences rather than the causes of vernalization. New lines of research are now possible on nucleo-cytoplasmic relations based on information from the ecophysiological studies reviewed here. The available information permits a screening to select the material most likely to yield valuable information on the fundamental problems of organogenesis.

(See the Addendum following Literature Cited section.)

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ADDENDUM

During the 9th International Botanical Congress, held in Montreal late in August of 1959, the problem of vernalization was dealt with during several sessions. We would like to report the data emphasized there and make some comments.

In winter cereals, the vernalization effect of chilling also acts on leafy plants as long as flower initiation has not occurred spontaneously without chilling (310).

The vernalization requirement appears quite variable in different races of red clover for example (311). As regards *Oenothera,* the differences between the author's findings and those of others resulted from the fact that, under the same name, they were speaking of different plants: the genetically controlled *O. biennis,* from the Munich Botanical Gardens (309) is not the same plant as the wild *O. biennis* from the Berlin area (307). Alternating temperatures have been confirmed as very effective and precise in the true *Oenothera biennis* (309).

Vernalization is effective on germinating seed of stock (301), endive (300), and chickory (297). In endive (302), after insufficient chilling, vernalization can be attained with short days, though the quickest flowering is caused by long days given as supplementary incandescent light.

The requirements for vernalization may vary according to the bud concerned: in *Limum alpinum* (293), the main shoot requires vernalization, but axilary shoots that appear after the head is removed have either low requirements or none at all.

Vernalizability varies with plant age; in *Lunaria biennis* (313), the seed does not seem vernalizable and yet it records a chilling effect that later appears in the smaller chilling requirement of the adult plant for vernalization. In the *Oenothera* of Berlin (307), vernalizability starts at 30 days of age and shows 2 maxima, one at 56 days and the other at 180 days. In *Arabidopsis thaliana* (308), a minimum vernalizability is observed at 45 days of age under low light, and at 7 days under intense light. Illumination during the vernalizing treatment increases the effectiveness of the treatment in plants less than 50 days old. When applied in that way, vernalization is nearly wholly fixed at the end of the treatment, whereas it requires a 4-day fixation at 20°C., with light, when it has been applied in the dark.

Several plants, mostly crucifers, show the same phenomenon as recorded in Brussels sprouts: for example, in stock (301), chilling is not only a "preparatory" condition, but is also required for the realization of the process of flowering. The first flower buds can only form in the cold; then later, the others can keep on blooming in a warm temperature. Something similar occurs in *Lunaria biennis* (313) at 6-8°C.

Whereas tubers are necessary for chilling efficiency in the beet and in carrot buds, leaves are useless, but they later become necessary for further flowering in a warm temperature even if tubers are present (303).

During germination of cereal embryos, indole-3-acetic acid increases the ascorbic acid production at the expense of sucrose, more so at a low temperature than at a high one, an observation supposedly related to the chilling vernalizing effect (292). However, when vernalization occurs below 0°C. (at −2°C., for example) mitoses completely stop (299).

The action of gibberellin has often been reported, extending or confirming what has been said above, either in general (295, 304, 306), in brachyblast shoots of a half-dormant peach tree (298), in *Oenothera* (309), in *Geum* (305), or in various seeds that are vernalized by cold and not by gibberellin (291). Gibberellin is certainly not the direct cause either of flowering or of the production of flowering ability, though it may restrain flowering in certain cases, when no elongating occurs during which it would act. The various factors in vernalization may result from an inability for elongation (necessary to flowering), or from an inability for flowering, or from both (295). Czajlahjan (296) thinks gibberellin is the growth factor that is lacking under short-day conditions in long-day plants, that "anthesine" is the flowering factor that is lacking under long-day conditions in short-day plants, and that they both constitute the proper florigen. This tempting hypothesis cannot be applied to long-day caulescent plants under short-day conditions nor to caulescent biennials before chilling, in which gibberellin cannot ever cause flowering (295).

A few more suggestions were made (294 to 312) concerning the above work schedule. It was supported in its general form and it seems likely that in about 10 years, through one or another of the suggested ways, that the study of vernalization will make considerable progress.

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