SHORTENING THE JUVENILE PHASE FOR FLOWERING

M. K. M. T. HIGAZY

THEOREMS

I

No fixed juvenile phase for flowering exists.

This thesis

II

Juvenility has no implication for Citrus propagation.

III

It is not possible to improve effectively the standard of living in U.A.R., Egypt with agriculture only.

IV

Rejuvenation can be an effective method of freeing Citrus of certain viruses

V

Hydroponic culture is something to be taken seriously for the benefit of horticulture in U.A.R., Egypt.

STEINER, A. A.: Advances Hort. Sci. & their Applications, 1, 1961: 112–117.

VI

There is no general rule with regard to the effect of gibberellin on flowering.

LANG, A.: Recent developments in the field of plant growth regulation. Scientia *53*, 1959: 9 pp.

M. K. M. T. HIGAZY, M. Sc.
Wageningen, October 1962

SHORTENING THE JUVENILE PHASE FOR FLOWERING

THESIS

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF AGRICULTURAL SCIENCES
AT THE STATE AGRICULTURAL UNIVERSITY,

WAGENINGEN, THE NETHERLANDS,
3 OCTOBER 1962

BY

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De Rector Magnificus der Landbouwhogeschool,

W. F. EIJSVOOGEL

Wageningen, 5 September 1962

SHORTENING THE JUVENILE PHASE FOR FLOWERING

Met een samenvatting:

VERKORTING VAN DE JEUGDFASE VOOR BLOEI

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWKUNDE
OP GEZAG VAN DE RECTOR MAGNIFICUS IR. W. F. EIJSVOOGEL,
HOOGLERAAR IN DE HYDRAULICA, DE BEVLOEIING,
DE WEG- EN WATERBOUWKUNDE EN DE BOSBOUWARCHITECTUUR,
TE VERDEDIGEN TEGEN DE BEDENKINGEN,
VAN EEN COMMISSIE UIT DE SENAAT
VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN
OP WOENSDAG 3 OCTOBER 1962 TE 16 UUR
DOOR

M. K. M. T. HIGAZY

H. VEENMAN EN ZONEN N.V. – WAGENINGEN – 1962

„But slowly comes the tree which thou has sown,
A canopy for grandsons of thine own."

(Virgil (80 B.C.), Georgics ii.)

TO

My MOTHER, WIFE and SON

KHALED

PROLOGUE

After a feeling of fulfilment and a sigh of relief for reaching the end of the manuscript, I am overtaken by a sentiment of gratitude for everyone from whom I have learned; for all the members of our family, and for the senate of the State Agricultural University, Wageningen, who had offered all the facilities at hand.

Professor WELLENSIEK, my promotor, I am grateful for the opportunity which you had offered me to work under your supervision. Your encouragement and interest always made me enthusiastic to reach the adult stage of my work. Your valuable guidance and constructive criticism were of paramount importance in reducing considerably the juvenile phase of the thesis. Your kindness, generosity and hospitality made us feel home and will never be forgotten. Indeed our words fall short of our feelings for what you have done for us.

Sincere appreciation is expressed to the staff members and personnel of the Horticultural Laboratory, especially Dr. GORTER and Dr. DOORENBOS, for the patient co-operation I received from them. Many obligations are due to Ir. WATERSCHOOT not only for preparing the Dutch summary but also for the care and interest shown for us. I feel greatly indebted to Dr. VERKERK and Ir. BARENDSE for their helpful suggestions in the statistical analyses. Miss WOLDA, hearty thanks for your sincere help which was not restricted only for the Laboratory hours, and for your careful checking of the proof. I am much obliged to JEANNE and JANSJE for their unlimited help in the administrative work.

Grateful acknowledgements and thanks are due to GIJS, SABARTE BELACORTU, ULTEE and co-workers, VAN WELIE and co-workers, WESSELS, MENKEN and ZEVENBERGEN for their considerable help, looking after the plants and assistance in recording the measurements; to Mr. v. d. PEPPEL and his colleagues for their great technical assistance; to REIJER and HENK for preparing the figures and photos very carefully; and to RIEKJE and CIS for typing the manuscript with devoted attention. The cordial atmosphere especially in the room with APTE, SYTSEMA and BARENDSE; and at the coffee club with Miss WOLDA, TONY, Miss v. d. PEPPEL, ERASMUS and ANKE will never be forgotten.

Particular thanks are due to the members of the main library and to all others, though not specifically mentioned, who helped in many ways to make this thesis possible.

Our stay in Wageningen, was made comfortable, enjoyable and profitable due to the efforts of many Dutch families and the Boards of the U.V.V. and the International Agricultural Centre.

Overdruk 581.145.1:631.547.47:635 9

MEDEDELINGEN VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN, NEDERLAND 62 (8), 1–53 (1962)

SHORTENING THE JUVENILE PHASE FOR FLOWERING

Met een samenvatting:
Verkorting van de jeugdfase voor bloei

by/*door*

M. K. M. T. HIGAZY

Publication No. 227, Laboratorium voor Tuinbouwplantenteelt, Landbouwhogeschool, Wageningen

(Received/Ontvangen 6.7.62)

CONTENTS

CHAPTER I

GENERAL INTRODUCTION ON JUVENILITY

1. DEFINITION OF JUVENILITY

Plants undergo a series of growth phases during their development from seeds. These phases are generally referred to as the juvenile, and mature or adult phases, with more or less gradual transitions. According to BLAIR *et al.* (8)* and O'ROURKE (89), GOEBEL (43) as early as 1900 observed the ready rooting of very young woody seedlings which at a later age did not root easily or not at all. He introduced the term juvenility to describe this physiological condition. Also with regard to flowering a juvenile phase can often be recognized. The juvenile phase with regard to vernalizing low temperature is a period from sowing in which low temperature is ineffective (121). WELLENSIEK *et al.* (129) defined the juvenile phase with regard to photoperiodism as a period from sowing during which the plant does not yet react to the relative length of day and night.In literature several indications, such as aging, a minimum vegetative size, wild stage, primary stage, sterile stage, and immature condition, point to this juve-

* These figures refer to literature references at the end.

nile phase. In general, the juvenile phase can be defined as a period from seed germination during which no flower initiation can take place under conditions which are favourable during a later stage.

2. Duration of the juvenile phase

The juvenile phase may vary even between varieties of the same species. In annuals it requires a few weeks or months after germination. In biennials a period of some months is required and in woody shrubs and trees usually a much greater period is necessary. The last also holds true for most bulb flowers.

Instances of juvenility in herbaceous plants are the following. Borthwick and Parker (9) stated, that no plants of Biloxi soybean responded to short day when treated one week after planting until the plants are at least six weeks old. Wellensiek (124) stated that the juvenile phase in *Campanula medium* normally lasts about 4 months for short day treatment and 5 months for vernalization.

In woody plants the following illustrations of juvenility can be mentioned. Knight (66) stated, that the raspberry requires 2 years, vine 3 or 4 years, plum and cherry 4 or 5 years, apple 5–12 or 13 years and pear from 12–18 years. Frost (37), in describing *Citrus* breeding work in California, stated that at least 5 or 6 years are required from seed to earliest fruiting. Furr *et al.* (38) stated that normally *Citrus* seedlings flower for the first time at 5–10 years of age. Savage (cf. 38) estimates that the time usually required for seedling trees on their own roots to flower is about as follows: tangerines 5–7 years, sweet orange 6–7 years, grapefruit 7–8 years, tangelo 5–8 years or may be longer. Fritzsche (34) pointed out that the juvenile stage for apple takes 5 years and for pear 6–7 years. Michurin (85) has found flowering in apple seedlings after 4 years, but mostly after 8–12 years. For pear he gives 10 years as the earliest. Seedlings of peach begin to flower in 2 or 3 years; seedlings of one variety of apple, namely 'Wealthy', may flower at the age of 3 or 4 years, but others such as of 'Northern Spy' may set flower as late as 15 or 20 years old (21, 69). According to Frank and Renner (33), English ivy, *Hedera helix*, requires 10 years or more from seed to adultness.

From the above literature citations it follows that the duration of the juvenile phase may vary considerably among different species, while in certain plants it may last several years.

3. Characteristics of juvenility

Juvenility may or may not be accompanied by differences from the mature individual such as leaf shape and size, leaf abscission, phyllotaxy, thorniness, ease of rooting of cuttings, growth habit and flowering. Stoutemyer (107) found that the juvenile form in apple is characterized by thin leaves and lack of pubescence. Romberg (98) described the juvenile stage in *Carya pecan* as sterile with reddish pubescent leaves. Passecker (90, 91) reported that the juvenile stage of apricot resembles the wild tree, while the mature form more closely resembles the cultivated types. Also, he concluded that apricot, peach, apple, pear and walnut have a juvenile phase in which both the form of the leaves and the anatomy of the branches differ from the adult stage. With apple and pear seedlings, Fritzsche (34) found further differences in mode of branching, bark, bud break, leaf surface, leaf serration and leaf size. He pointed out that young

seedlings of apple and pear have small leaves and horizontal thorny branches. O'ROURKE (89) assumed that the thorny condition of honey locust was associated with the juvenile growth phase and the relative ease of vegetative propagation. SAX (100) showed that the juvenile leaves of pecan are entire, while the adult form has compound leaves. In ivy, *Hedera helix*, these differences are well recognized, the juvenile stage has creeping or climbing shoots, lobed leaves, aerial roots, 2/2 phyllotaxy and somewhat flattened stems, while the adult form has entire leaves, no aerial roots, little or no pigment in stem or petioles, 2/5 phyllotaxy and rounded stems (29, 97). FROST (35) reported that *Citrus* seedlings produced either by gametic or apogamic means, are thorny in their earlier life but as they mature, the shoots upward and outward from the trunk gradually lose the thorny condition. SWINGLE (108) has discussed thorniness as a juvenile characteristic following seed reproduction, sexual or asexual, in *Citrus*. FROST (36), and HODGSON and CAMERON (55) have reported that young clones produced by apogamy (nucellar embryos) are more juvenile in appearance and characteristics than the old clones from which they arise. FURR *et al.* (38) pointed out that the juvenile seedling in *Citrus* is characterized by great vigor of growth, erect habit and numerous large thorns.

All these cases refer to woody plants. Although in herbaceous plants the juvenile phase may be morphologically different from the adult phase, no clear cases from the literature have come to my attention, besides Brussels sprouts. STOKES and VERKERK (106) stated that the seedlings pass through a juvenile phase during which the apex of the stem is somewhat flat and the growing point itself very small. At the time of the raising of the growing point, there is a very rapid change in the appearance of the plant, mainly due to an increase in the stem size. The stem of the young seedling gradually thickens as it grows up, so that the ratio of the dry weights of leaves and roots to the dry weight of stem gradually decreases, until it reaches a minimum at puberty. This ratio remains approximately constant in the adult vegetative stage and the plant can initiate flowers as soon as the environment permits.

We conclude that both in herbaceous and in woody plants the juvenile plants may differ morphologically and physiologically considerably from the adult ones, although thusfar relatively little attention has been paid to herbaceous plants.

4. INFLUENCING THE DURATION OF THE JUVENILE PHASE

SWINGLE (108) suggested that the cause of the juvenility of nucellar embryos in *Citrus* might be hormone-like substances located in the embryo-sac apparatus. STOUTEMYER (107) suggested that one or more hormones may be responsible for the change in growth phases and the occurrence of sexual maturity in plants. FRITZSCHE (34) also suggested that juvenility may be due to the influence of certain hormones. ROBBINS (97) stated that the origin of the juvenile and adult stages must be looked for in the activity of the apical meristem which changes or is changed with the age of the plant. WAREING (118) concluded that the juvenile and adult conditions involve different states of the cytoplasm which are transmitted from one cell generation to another.

From the above citations it is clear that the fundamental causes of juvenility are unknown and that the hypotheses on these causes remain vague. This implies that no clear insight into the possibility of influencing the duration of the juvenile phase exists and that conflicting ideas in the literature are found, also

because most of the experimental plants are woody and therefore are very difficult to work with.

Horticulturists are interested in the production of fruits, hence are interested in getting trees into flowering as early as possible. Also the plant breeders want to hasten the onset of the adult phase to obtain early flowering and by so doing reduce the length of the breeding cycle. On the other hand, plant propagators who apply vegetative reproduction, are interested in prolonging the juvenile phase in order to retain easy rooting.

The pioneer work of KLEBS (65), and GARNER and ALLARD (40, 41) was followed by many other investigators such as MURNEEK and WHYTE (87), and LANG (71) who have shown that flowering is conditioned by the environment and can be changed by modifying such factors as mineral nutrition, temperature and length of photoperiod. However, relatively little attention has been paid to the problem whether the length of the juvenile phase can be influenced.

Several authors do not think that the length of the juvenile phase can be influenced. As early as 1815 KNIGHT (66) expressed the opinion that the vegetative period of the seedling could not be shortened by any means. FURR *et al.* (38) found that the juvenile state in *Citrus* is not altered by a great variety of types of grafting to mature plants. Ringing was less effective in causing flowering in juvenile seedlings at 3 than at 7 years old. FRITZSCHE (34) showed that the juvenile stage of apples cannot be brought to bloom with any of the known treatments, whereas the adult stage can be hastened to flower by bark-ringing or grafting on Malling IX. FRITZSCHE agreed with the conclusion of FURR *et al.* that juvenile wood could not be made to flower before its normal time by grafting. GREGORY (44) stated that before ripeness to flower has been attained, no change in external factors can induce flower initiation. KOLOMIEC (67) found that fruiting of apple, apricot and other fruit tree seedlings may be hastened by applying measures which will ensure an increase in the concentration of nutrient materials in the growing point, but only after the phasic readiness for fruit bearing is achieved.

On the contrary, many investigators believe that the duration of the juvenile phase can be influenced, but there is no agreement on how this is achieved. CRANE (24), working with plum seedlings, found that such practices which restricted growth, shortened the juvenile period. TYDEMAN (112, 113), by working seedlings on the dwarfing rootstock M IX, was able to shorten the juvenile phase by approximately one year. KEMMER (59–62), the leading advocate of shortening the juvenile stage by checking the growth of the seedlings, presented evidence that no fixed juvenile form exists. He stated that the sterile period could be shortened by root pruning, girdling or grafting the seedlings on dwarfing stocks. LOOMIS (81) concluded that any factor, such as a deficient supply of water or nitrogen, which checks growth without correspondingly reducing photosynthesis will tend to increase any differentiation response. MURAVSKI (86) stated that juvenile branches reach the adult phase sooner when grafted on M IX. He also showed that scions from the tip of the seedling flower earlier than those taken from the base. Recently CAMPBELL (18) found that apple seedlings worked on apomictic seedling rootstocks from *Malus sikkimensis* have a shorter juvenile phase than when worked on M IX.

On the other hand, SPINKS (104) stated that any treatment which restricts growth, such as ringing, root pruning, working on dwarfing stocks or growing in pots did not induce earlier fruiting in very young seedlings. On the contrary, it

keeps the trees longer in a juvenile state and so delays fruiting. He thinks that application of optimal growth factors and increase of the periods of active growth may have a shortening influence on the duration of the juvenile phase. WELLENSIEK (121) has a similar view. PASSECKER (90, 92) found that all factors, such as high temperature and a generous supply of nutrients, promoting vigorous growth, appear to hasten the transition, whereas all factors which check growth seem to have a delaying effect. LANG (71) drew attention to the fact that the time of flower initiation depends on the rate of the preceding vegetative growth. SAX (99) stated that there is no evidence that knotting the stem of young apple seedlings will reduce the juvenile period.

From the above review the conclusion can be drawn that a number of investigators are of opinion that the length of the juvenile period cannot be influenced by external factors, while others have found evidence that this is possible. However, some representatives of the latter group believe that a restricted vegetative growth is favourable, while others hold the opposite view that all factors which promote vegetative growth tend to reduce the length of the vegetative period.

5. SCOPE OF THE PRESENT WORK

The present experiments have been conducted in the hope that they might throw some light on the relation between the length of the juvenile phase for flowering and certain external factors, in order to discover whether the duration of the juvenile phase is a fixed character or can be influenced by external factors. Evidence will be presented for the concept that the juvenile phase is subject to modification.

CHAPTER II

REVIEW OF LITERATURE

In this chapter the literature with regard to the various factors, used in my study of juvenility, will be discussed. First, some literature will be discussed on vernalization and photoperiodism, because my experimental plants depended on either vernalization or photoperiodism for flowering. From the bulk of the literature mainly illustrations will be presented on the existence of a juvenile phase. The literature on influencing the duration of the length of this juvenile phase is extremely scarce. Next, the growth factors light intensity, soil moisture, mineral nutrition and gibberellins will be discussed, because they have been used in my experiments.

1. VERNALIZATION

In 1858 KLIPPART (cf. WHYTE 131) described an empirical temperature treatment for winter cereals that would make them behave as spring cereals. GASSNER's investigation (42) concerning the origin of the differences existing between winter and spring cereals, represented the first scientific attempt to shorten the vegetative period of winter cereals. This phenomenon was rediscovered in Russia in 1928 by LYSENKO (cf. 131), who called it 'jarovizacija', the English translation of which is 'vernalization'. Many investigators indicate that induction of early flowering is one of the many effects of vernalization by reducing

the vegetative period (CHAKRAVARTI 20, KOREISHA *et al.* 68, PURVIS 95).

Not only in herbaceous plants, but also in large trees such as the olive tree *(Olea europea)*, flowering may depend on vernalization (ANAGNOSTOPOULOS 2, HARTMANN *et al.* 49).

CHOUARD (23) stated that if the chilling time in perennial plants in rosettes such as *Geum* sp., is extended to 10–15 weeks, more buds are vernalized, particularly those that were too young at the beginning of the treatment. This points to juvenility. It has already been cited (p. 4) that STOKES and VERKERK (106), working with Brussels sprouts, found the existence of a clear juvenile phase. WATERSCHOOT (120) indicated that low temperature for *Dianthus barbatus* does not promote flowering unless given to plants of a certain minimum size, reached about 12 weeks after sowing when growth conditions are favourable.

The last two cases are examples of the typically biennial plants with a juvenile phase, to which one of my experimental plants, *Lunaria biennis*, belongs. According to WELLENSIEK (121, 122) in this species the juvenile phase lasts at least 6 weeks, depending on the duration of vernalization, younger plants requiring relatively more cold than older ones.

DOORENBOS and WELLENSIEK (30) concluded that the photoperiod preceding the cold treatment may influence the effectiveness of the latter. TSUKAMOTO and KONISHI (111) found that the percentage of budding was higher in stock plants that received continuous lighting at the young stage prior to vernalization than those that received short-day length. WELLENSIEK and HIGAZY (130) have demonstrated that the duration of the juvenile phase in *Lunaria biennis* may be influenced by the light intensity. Details of these investigations will be presented in chapter IV.

2. PHOTOPERIODISM

The importance of the effects produced by the relative lengths of light and darkness per 24 hours upon the vegetative and reproductive activity of different species and varieties of plants has been emphasized by the classical work of GARNER and ALLARD (40). It is well known that, in addition to day-neutral plants, they distinguished long-day plants (LDP) and short-day plants (SDP). An example of the former is *Silene armeria* (79, 80), which according to LANG (74) and TAKIMOTO (109) remains vegetative for indefinite periods of time when grown in short days. An example of an SDP is *Salvia occidentalis* (82). These plants, *Silene armeria* and *Salvia occidentalis*, belong to my experimental plants. Also with regard to photoperiodism a juvenile phase can be distinguished. It has already been mentioned (p. 3) that *Campanula medium* has a clear juvenile phase for short-day treatment (WELLENSIEK 124). Through a combination of sulfuric acid treatment of the seed and short-day treatment of the seedlings of strawberry, the life cycle can be shortened from 18 or 24 months to 8 or 9 months. This treatment is only effective, when the seedlings have become sensitive to short days and this points to the existence of a juvenile phase (JONKERS 58).

The following publications point to a possibility of influencing the length of the juvenile phase. WITTENROOD (134) stated that in Jerusalem artichoke the juvenile stage appears to last longer, the shorter the photoperiod. BEST (7) stated that in rice short days during the early stages of growth, alone or in combination with factors such as transplanting, high night temperatures, excess of nitrogen, low light intensities, may cause less vigorous growth and, as a conse-

quence, later flowering. Conversely, long days may cause more vigorous growth and earlier flowering.

DOORENBOS (28) stated that growing *Rhododendron* seedlings in long day or continuous light, accelerates seedling growth and reduces the juvenile phase by as much as 50%. NIKITIN (cf. WAREING 117) exposed seedlings of oak to continuous illumination during the first five months following germination. The seedlings flowered and produced fruit in the eighth year of growth, whereas usually the duration of the juvenile period is 40–60 years.

3. LIGHT INTENSITY

The effect of light intensity on plant growth has been observed since very early times. Light intensity effects plant growth through its direct effects on photosynthesis, stomatal opening and chlorophyll synthesis. Photosynthesis is the process by which carbohydrates are manufactured from carbon dioxide and water in the chlorophyll-containing tissues of plants exposed to light. It undoubtedly is the most important physiological process occurring in plants, because their growth is dependent on the carbohydrates produced by photosynthesis.

According to GARDNER *et al.* (39) young non-bearing trees grow rapidly when exposed to full sunlight, come into bearing early and for several years produce heavier crops than those grown in partial shade. DE ZEEUW (27) indicated that light intensity effects the flowering of tomato plants.

MEYER *et al.* (84) indicate that the relation between intensity of light and flowering is not a simple one, because it is complicated by the influence of the photoperiod. The effect of an intensity which is adequate for flower induction can be completely nullified, in some species, if the photoperiod is too long, in other species, if it is too short. In general, however, assuming day length, temperature, and other conditions to be favourable for flowering, there is a minimum intensity for each species below which no blooming occurs. However, there are a few exceptions, namely in SDP. DE ZEEUW (27) found that in *Perilla* flowering could be obtained with a long-day treatment provided that the light intensity is very low. Even in continuous light *Perilla* will then flower. VAN DER VEEN and MEIJER (114) stated that *Salvia occidentalis* was induced to flower under long-day conditions (16 hours of light per day) with low intensity (250 uW/cm^2). WELLENSIEK (125) confirmed this and obtained flowering even under continuous light.

4. SOIL MOISTURE

It is an old concept that water is essential for plant growth. Water deficit is one of the most common factors limiting growth. HENDRICKSON and VEIHMEYER (51, 52) stated that the length of time during which the soil remains at or below the permanent wilting percentage is the most important factor effecting the plants. If the soil moisture is maintained between field capacity and permanent wilting percentage, plants do not suffer from lack of water, if not adversely effected by other limiting factors, such as lack of fertility, depredation of insects and diseases, lack of suitable pruning and thinning, or unfavourable weather conditions. They came to a general conclusion (115), namely that soil moisture is readily available between the field capacity and the permanent wilting percentage.

Other investigators have reported results purporting to show that soil moisture is not equally available throughout the range between the field capacity and the permanent wilting percentage (ALDRICH *et al.* 1, LEWIS *et al.* 76, 77, WORK *et al.* 137, KENWORTHY 63, HEINICKE *et al.* 50). They stated that photosynthesis, growth and other physiological functions were reduced before soil moisture reached the wilting range.

KRAUS and KRAYBILL (70) found that irrigation or moisture supply is effective in increasing growth or fruitfulness only when accompanied by an available nitrogen supply and vice versa. With soybean, GARNER *et al.* (40) concluded that a more favourable water supply during the period preceding the flowering stage resulted in a greater vegetative development. On the other hand, reduction of the water supply, even to the point where almost daily wilting of the plants occurred, did not change the time of flowering by a single day. GARDNER *et al.* (39) stated that a diminution of the water supply is well known to be frequently associated with fruitfulness. In this case, as in that of nitrate supply, there is probably a limit beyond which a further reduction results in unfruitfulness and stunted growth. HAGAN (46) shows that increased moisture stress retards the vegetative growth of guayule shrubs, and leads to a higher production of rubber.

5. MINERAL NUTRITION

Nitrogen. – KLEBS (65) in 1918 pronounced the postulation of a high ratio of carbohydrates to soil nutrients as causal factor for flowering, a concept which has been elaborated in terms of the C/N ratio by KRAUS and KRAYBILL (70). However, it becomes increasingly obvious that plants would flower over a wide range of C/N ratios. ARTHUR *et al.* (3) found that the percentages of C and N in general could be changed by varying light intensity and/or length of day. KHALIL (64) demonstrated that the transition from vegetative to reproductive growth can take place under a wide range of C/N ratios. DAVIS (26) and GREGORY (44) believed that a change in the C/N ratio is the result rather than the cause of flowering. HUSSEY *et al.* (57) found that the time to flower initiation is uneffected; this time depends only on the conditions of light and temperature. POST and HOWLAND (94) concluded that light intensity controls flower production and that nitrate fertilization cannot overcome this effect. SEELEY (103) and FLINT *et al.* (32) stated that mineral nutrient treatments had little or no effect on the time and initiation of flower primordia. WITHROW (133), working with long- and short-day plants, has concluded that nitrogen is not a determining factor in floral initiation, as are temperature and photoperiod, but that the time at which visible buds appear could be altered in some species by changing the nitrogen supply. In long-day plants, lack of nitrogen promotes and excess of nitrogen delays flowering. In short-day plants the effects of nitrogen metabolism are smaller and the reverse (WITHROW 133, MELCHERS 83, NEIDLE 88, CAJLACHJAN 16, 17). Also, BENSINK (5) stated that a low nitrate supply enhances flower initiation in lettuce, a long-day plant, apparently irrespective of light intensity.

On the contrary, AUCHTER (4) found that lack of nitrogen delayed blossoming of many plants decidedly in spite of the length of day. It was noted by WALLACE (116) that the actual time of blossoming was delayed with nitrogen deficiency. BROOKS (12) stated that when nitrogen is lacking, the time of flowering is retarded in chrysanthemums. EL HINNAWY (31) found that the deficiency of nitrogen had a great effect in retarding the initiation of floral buds in both *Perilla* and

dill, a short- and long-day plant respectively, but in mustard, a long-day plant, much earlier flowering occurred when nitrogen was supplied in low levels or when it was lacking.

Phosphorus. – HOWELL (56) found that there was little or no effect of the phosphorus level on the number of days to blooming in soybean. WALLACE (116) noted that the time of apple flowering was delayed with phosphorus deficiency. EL HINNAWY (31) stated that the deficiency of phosphorus had a great effect in retarding the initiation of flower buds in *Perilla*, a short-day plant. WILLIAMS (132) found that oat plants receiving high levels of phosphorus quickly exhausted their nitrogen supply and this hastened flowering. CHANDLER (22) found that phosphorus deficiency reduces flowering.

Potassium. – BERESFORD *et al.* (6) stated that plants of garden beet, receiving a complete solution and a solution deficient in potassium only, were similar in rate of growth and all plants started to flower at about the same time. MICHURIN (cf. 92) is quoted as achieving a rapid transformation of almond seedlings by supplying potassium permanganate. SCHWABE (101) indicates that reduction of light intensity is shown to have a beneficial effect under conditions of potassium deficiency. CHANDLER (22) found that potassium deficiency reduces flowering.

Conclusion. – In general, this mass of data cited above is very conflicting and moreover seems to concern largely the results of plants in comparatively late stages of development. Therefore, it is of very little value to our problem of juvenility. It may be concluded that the available literature does not indicate that the elements nitrogen, phosphorus and potassium are determining factors in juvenility.

6. GIBBERELLINS

In the early Japanese work on the bakanae disease of rice, which led to the discovery of the gibberellins, it was noticed that infected plants which reached maturity, had longer stems and flowered earlier than normal plants. An important characteristic of these gibberellins is that they apparently accelerate extension-growth in aerial organs. An extreme example of this response is shown by the dwarf bean, which can be induced to turn into a climbing bean (BUKOVAC *et al.* 14). Rosette plants, with very reduced stems, can be induced into a rapid stem elongation.

Gibberellin treatment can markedly modify the flowering behavior of many different species. In many biennial plants that require exposure to low temperature before they will flower, e.g. biennial *Hyoscyamus*, *Centaurium minus*, gibberellin treatment can replace the period of exposure to cold and will induce flowering in addition to the characteristic stem elongation (LANG 72, WITTWER *et al.* 135, LINDSTROM *et al.* 78, CARR *et al.* 19). It appears that a great number of long-day plants will flower under non-inductive conditions if treated with gibberellins. This is so for annual *Hyoscyamus*, *Silene* sp., *Samolus* sp. (LANG 73). In *Silene armeria*, LANG (73) stated that it needs considerably more gibberellin, more time and makes considerably more stem growth before it responds with flower formation. In short-day plants kept under long days, flowering has not been induced with gibberellin (HARDER *et al.* 47, LANG 74, HESLOP-HARRISON *et al.* 53). Moreover, it inhibits flowering of short-day plants in inductive short-day photoperiods (BRIAN 10, THOMPSON *et al.* 110). BRIAN (11) stated that gibberellic acid has little effect on the flowering of day-neutral plants, except to

delay or to accelerate the appearance of flowers slightly. The growth of grapefruit, sweet orange and rough lemon seedlings was greatly stimulated by leaf-spraying with gibberellic acid (STEWART *et al.* 105). BUKOVAC *et al.* (13) stated that in the seeded grape variety 'Delaware' flowering was accelerated from 2–4 days by pre-bloom application of 25–100 ppm of gibberellin. In other similar plants, however, the situation is not so clear-cut. In cabbage, beet and other biennials, BUKOVAC et al. (15) stated that stem elongation is promoted, but no flowering is induced unless plants are given a regular application of gibberellin and in addition are exposed to low temperature approaching those normally required for flower initiation. WELLENSIEK (122) concluded that gibberellin does not induce flower-formation in *Lunaria biennis* and therefore cannot replace low temperature.

BUKOVAC *et al.* (14) stated that many factors, including species, varieties, mineral nutrition, light, temperature, age of plant when treated and dosage, influence plant response to gibberellin. The results with *Silene armeria* indicated that gibberellin is only one of several factors in the photoinductive process (LANG 75). CARR *et al.* (19) found that long photoperiods were essential for gibberellin to be operative except with a few plants that had little or no photoperiodical requirement for flowering.

HARRINGTON *et al.* (48), LANG (74), WITTWER *et al.* (136) stated that responsive biennials must reach a certain stage of development before either cold or gibberellin is effective in promoting seedstalk elongation and flowering. This could mean that the length of the juvenile period is not influenced by gibberellin. However, PENNER (93) found that gibberellic acid is effective in reducing the juvenile phase of *Bryophyllum daigremontianum*, a long-short-day plant.

CHAPTER III

GENERAL REMARKS ON THE EXPERIMENTAL APPROACH

Since woody plants would take several years to give results, we have worked with herbaceous plants which can be handled more easily and which will give results much quicker. These plants are:

1. *Lunaria biennis*, a cold requiring biennial plant;
2. *Silene armeria*, a long-day plant;
3. *Salvia occidentalis*, a short-day plant.

Since the first mentioned species proved to be exceedingly suited to experiments on juvenility, most of the work was done with this plant.

In the original photoperiodism experiments of GARNER and ALLARD (40) the authors raised their plants in a non-inductive daylength and, using such a culture as standard material, investigations were made into the photoperiodic treatment which was required to bring the plants into flowering. This method was and still is used extensively by many of those undertaking experiments on photoperiodism and also on vernalization. In principle this method has been used in the present work.

In my experiments the plants mentioned above were periodically sown and potted under non-inductive conditions for flowering until an age-group was obtained differing from experiment to experiment and ranging from completely

juvenile to completely adult according to existing standards. All the plants were pretreated in various ways during non-inductive conditions. Then all were transferred to inductive conditions. In some experiments some plants were kept under non-inductive conditions as controls. In each experiment the dates of appearance of the first visible flower bud per plant was noted as the most important characteristic. Also, a growth analysis was made, in its complete form comprising number of leaves, length of petiole, length and width of lamina, height of plant (measured from the cotyledon node to the tip of the terminal bud or the growing point), diameter of stem, dry weight of leaves and of stems (determined by drying for some days in an electric oven thermostatically controlled at 85 °C), and seed weight. The percentage of the generative plants and the mean number of days to the appearance of the first visible flower bud per treatment were calculated.

CHAPTER IV

EXPERIMENTS WITH *LUNARIA BIENNIS*

1. LIGHT INTENSITY

1.1. *Methods*

An age-group of plants of 6, 7, 8, 9, 10, 11 or 12 weeks old was made. In the description of the experimental results, the indication "plants of ... weeks old" means the age of the plants when the vernalization started and not the real age at the date of observation. One half of each age-group was grown under the natural poor light conditions of the Dutch winter (-L), while the other half obtained a supplementary high intensity artificial illumination of fluorescent lamps during 16 hours per day from 8.00 to 24.00 (+L). The intensity of the supplementary light was between 2500 and 3000 μW/sec./cm^2 ⌀ sphere for the experiments 1 and 2, and was between 4500 and 5000 μW/sec./cm^2 ⌀ sphere for the experiments 3–8. The intensities of the light were measured by a spherical radiation meter (119). The temperature in the greenhouse averaged 20 °C, so that no vernalization could take place during the pretreatments. Vernalization was done at a temperature of 5 °C and fluorescent light of about 250 μW/sec./cm^2 ⌀ sphere for 16 hours per day. After vernalization part of the plants was put under natural out-door conditions (experiments 1, 3, 5 and 7), while other plants were kept permanently at the low temperature (experiment 2, 4, 6 and 8). To find out the effect of the different treatments statistically, the test of WILCOXON was used to analyse the data with regard to flowering.

1.2. *Experimental results.*

Experiment 1. – Vernalization during 12 weeks.

The main results with regard to flowering have been published before (130), but will be repeated for completeness sake in table 1.

These results clearly indicate that relatively young plants formed much more (columns 2 and 3) and much earlier (columns 4 and 5) flower buds after +L than after -L. This is the first, but already quite convincing proof that the length of the juvenile phase can be influenced by an external factor.

TABLE 1. Experiment 1.– The effect of a pretreatment with strong supplementary light (+L), compared with natural light only (–L), during different periods before vernalization, on the effect of vernalization (12 weeks 5 °C), judged by the percentages of generative plants and the mean numbers of days to budding under natural conditions after the vernalization. Twenty plants per treatment. None of the controls, 20 unvernalized plants per treatment, has turned generative. Data 147 days after the end of the vernalization at 21/4/60. From (130)

1	2	3	4	5
Pretreatment during ...weeks	% Generative plants		Days to budding	
	+L	–L	+L	–L
6	85	0	67.3	∾
7	100	25	38.5	99.0
8	100	35	26.5	89.5
9	100	45	25.0	69.8
10	100	95	20.5	63.1
11	100	95	19.0	34.3
12	100	100	17.5	29.9

Now we shall start in dealing with the growth analysis data which were collected in order to get an insight into the morphological effects of the differences in light intensity during various periods with regard to juvenility. Table 2 summarizes the results. The characters indicated as 1 to 7 have been determined during the cold treatment, those indicated as 8 to 11 represent data on the growing plants out-door.

All +L characters are higher than the corresponding –L ones, with the exception of the mean diameter of the stem (character 9) of the plants of the lower age-groups. We come back to this point, but leaving this exception out of discussion for the moment, it is clear how enormously great the influence of the light intensity has been. For striking illustrations compare characters 5, 6 and 7, left half of table (+L) with right half of table (–L). This means that the shift from juvenile to adult and from vegetative to generative runs parallel with an increase in the amount and size of all plant characters except stem diameter.

All values tend to increase from left to right within the +L and within the –L, which could be expected, but again the diameter of the stem forms an exception, which is more pronounced in the younger age-groups of +L and in the higher age-groups in –L. Hence the –L plants show the same trend as the +L plants, but at later ages.

There is a tendency to increase for the characters 1, 5, 6 and 7 during the cold period, while there is a tendency to decrease for the characters 2, 3 and 4.

The relatively low values for height of stem (character 8) after +L for plants of 11 or 12 weeks old is due to the fact that these plants were the first to initiate flower buds and hence stopped their stem-elongation.

The mean diameter of stem (character 9) could not be determined during the cold treatment, because at that time the plants were in rosette form. Measurements were made from two months after the cold treatment. Part of the data from table 2 have been presented in fig. 1.

If we follow the lines for +L first, they fall from 6 weeks old plants to 7 and to 8 weeks old plants, to rise up to 10 or 11 weeks old plants and to fall slightly

TABLE 2. Experiment 1.– Growth analysis data on plants of table 1. 27/1/60 = Start of cold treatment; 9/3/60 = Middle of cold treatment; 21/4/60 = End of cold treatment

		Pretreatment	+L												
		Age (weeks)	6	7	8	9	10	11	12	6	7	8	9	10	11	12
	Characters	Dates														
1.	Number of leaves	27/1/60	2.6	4.2	5.2	5.0	7.2	6.9	8.0	2.0	2.2	3.6	3.8	4.0	4.2	5.4
		9/3	4.4	4.0	5.2	6.0	6.8	7.6	10.0	2.0	4.0	4.0	4.0	4.0	6.0	6.8
		21/4/60	4.8	6.0	6.8	6.8	8.4	9.2	8.8	4.0	4.0	4.0	5.2	5.6	6.4	6.0
2.	Length of petiole in cm	27/1/60	4.6	6.5	7.9	8.0	10.0	11.0	11.5	2.6	3.3	2.9	2.9	3.3	3.5	3.7
		9/3	4.3	5.1	7.1	8.6	9.2	9.0	9.8	2.1	2.2	3.3	2.9	2.8	3.3	3.5
		21/4/60	4.1	4.2	6.8	7.3	8.6	9.8	9.9	2.0	2.8	2.9	3.0	2.8	3.1	3.9
3.	Length of lamina in cm	27/1/60	4.2	4.8	5.5	5.2	6.7	6.9	7.3	2.4	3.4	2.8	2.7	3.0	3.1	3.3
		9/3	3.7	3.8	4.8	5.8	6.2	5.7	6.4	2.1	2.1	2.9	2.7	2.4	2.8	3.0
		21/4/60	3.5	3.2	4.6	4.7	5.8	6.4	5.8	2.0	2.5	2.6	2.7	2.3	2.7	3.1
4.	Width of lamina in cm	27/1/60	4.5	5.3	6.1	5.8	7.5	7.9	8.1	2.5	3.3	2.9	2.8	3.0	3.2	3.4
		9/3	3.9	4.3	5.5	6.3	6.7	6.4	7.2	2.1	2.2	3.0	2.6	2.3	2.8	3.1
		21/4/60	3.8	3.6	4.9	5.1	6.5	7.0	6.4	2.0	2.7	2.6	2.8	2.4	2.7	3.3
5.	Dry weight of petiole in mg	27/1/60	16	57	112	114	305	350	456	5	11	15	13	15	22	34
		9/3	72	63	121	253	333	427	739	5	15	17	18	14	35	66
		21/4/60	54	95	167	254	402	717	625	19	28	23	33	27	37	52
6.	Dry weight of lamina in mg	27/1/60	66	166	289	275	718	809	1015	19	38	65	50	63	88	130
		9/3	251	207	305	621	795	913	1716	24	62	68	72	57	138	259
		21/4/60	238	477	425	537	1008	1486	1179	75	110	86	151	101	138	170
7.	Dry weight of stem in mg	27/1/60	3	7	13	12	35	45	54	2	1	1	2	2	2	5
		9/3	9	7	15	35	49	52	117	1	1	3	2	2	6	11
		21/4/60	9	14	26	35	60	119	107	4	5	3	6	5	5	7
8.	Height of stem in cm	22/6/60	14.1	54.7	69.5	85.4	96.9	94.1	86.1	7.8	9.7	9.6	12.7	18.0	62.1	66.2
		13/7	20.4	64.3	71.7	87.6	98.0	94.5	87.1	11.7	13.6	13.2	17.3	26.7	65.5	69.7
		3/8	28.0	69.4	73.2	88.0	98.0	94.9	87.7	14.8	16.9	16.4	24.9	32.7	67.4	71.5
		24/8	34.6	72.1	73.3	88.2	99.2	95.1	88.3	16.8	19.8	18.9	30.4	35.5	69.2	72.0
		14/9/60	35.6	72.8	73.7	88.3	99.4	95.3	88.4	17.7	21.0	19.9	31.6	37.1	69.3	72.2
9.	Diameter of stem in mm	22/6/60	10.4	9.0	8.0	9.1	10.0	10.1	9.4	12.0	11.0	9.6	11.1	9.5	7.3	7.4
		13/7	12.7	10.0	8.9	10.1	10.5	10.5	9.8	12.0	12.7	12.7	13.2	11.3	8.4	7.9
		3/8	12.8	9.8	8.9	10.4	10.5	10.6	9.9	12.1	13.6	13.8	13.7	12.1	8.5	7.8
		24/8	13.8	10.7	9.1	10.5	11.3	11.0	9.9	14.4	14.3	15.0	14.8	12.5	8.5	8.1
		14/9/60	13.9	10.8	9.2	10.6	11.3	11.1	10.0	14.6	14.5	15.0	14.9	12.6	8.5	8.2
10.	Number of lateral flowering branches	22/6/60	3.3	10.6	13.9	14.6	17.8	19.2	19.7	0	1.0	1.0	3.4	4.3	11.0	12.0
		13/7	3.4	12.8	15.4	15.4	18.7	20.8	21.7	0	1.0	1.0	4.1	6.9	11.5	12.6
		3/8	4.0	15.1	15.4	16.4	18.9	21.3	22.2	0	1.7	1.7	6.9	7.2	12.7	14.7
		24/8	5.4	16.7	16.9	18.2	21.3	21.9	23.2	0	1.6	2.0	7.9	8.1	14.4	16.8
		14/9/60	5.7	16.9	17.1	18.5	21.5	22.0	23.2	0	1.8	2.1	8.0	8.2	14.6	16.8
11.	Weight of seeds in g		3.6	16.7	20.9	22.3	33.6	33.9	33.9	0	0	0	2.4	3.1	18.9	30.1

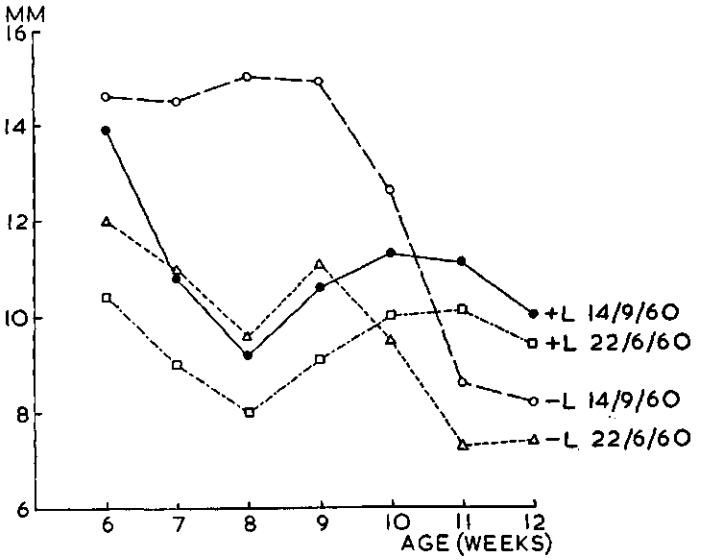

FIG. 1. Experiment 1.– Mean diameter of stem of *Lunaria biennis* (ordinate) of different age-groups (abscissa), grown + L or –L, 2 months (22/6/60) or about 5 months (14/9/60) after 12 weeks of vernalization. Part of the data from table 2.

afterwards. Combining these data with those of table 1, especially column 4, it seems that the more generative the plants are, the smaller the stem diameter is, until at rather complete flower bud formation the stem diameter increases. The fall in the lines of the older age-groups must be ascribed to maturation.

The trend in the –L lines is less regular than in the +L lines – especially 8 weeks old on 22/6/60 –, but in general they repeat the first part of the +L lines. This is in harmony with the fact that the –L plants turn generative at later ages.

Let us now return to table 2. The mean number of lateral flowering branches (character 10) was considerably higher after + L than after –L. For the rest, it is obvious that after –L, plants of 6 weeks old did not initiate any flower buds, consequently they did not form seeds (character 11). Also, plants of 7 or 8 weeks old did not form seeds or formed a few abnormal seeds only. The seed weight is another striking example of the enormous after-effect of the +L treatment, if we compare the ages of 9 or 10 weeks old; after +L the amount of seeds produced was roughly 10 times as much as after –L.

Referring to the results of STOKES and VERKERK (106), who found the ratio of dry weight of leaves to stem characteristic for the degree of adultness, it is worth while to determine the ratios of the mean dry weights of petiole + lamina (leaf) to stem. This has been done at the beginning, the middle and the end of the cold treatment. The data for the beginning and the end of the cold treatment have been presented in fig. 2, together with the data for the unvernalized controls. Those of the middle of the cold treatment are in between the extremes and have been omitted for the sake of simplicity.

Before discussing this figure, it should be remarked that the absolute values for the dry weights of stems are rather low for +L at 6 or 7 weeks old and for –L at all ages; see table 2, character 7. This means that the ratios in fig. 2 for

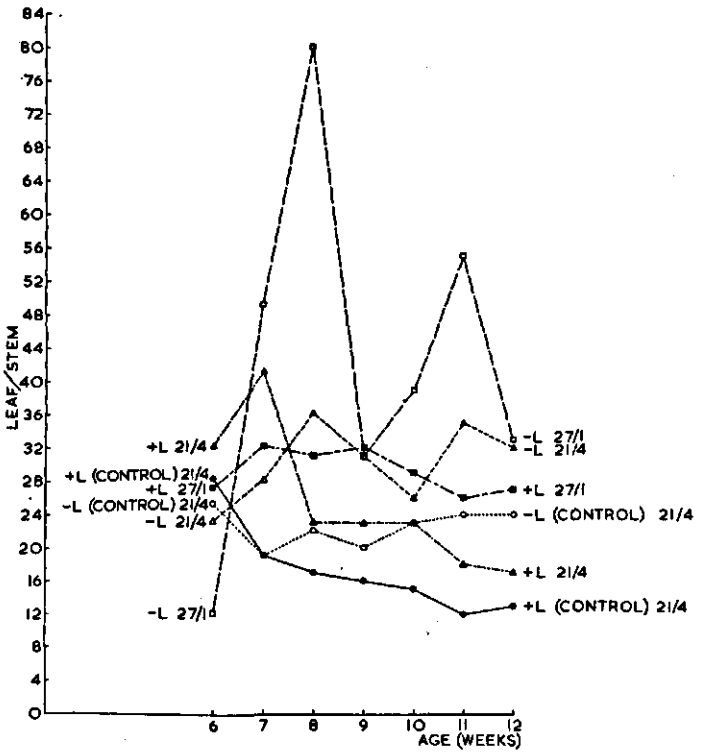

FIG. 2. Experiment 1.– The ratio of mean dry weight of petiole + lamina = leaf to mean dry weight of stem (ordinate) of plants of *Lunaria biennis* of 7 age-groups (abscissa), grown without (–L) or with supplementary strong light (+ L), determined at the beginning (27/1) and the end of the cold treatment (21/4), together with the ratios for unvernalized plants: –L (control) 21/4 and + L (control) 21/4/60

+L at 8 or more weeks old are reliable, but that for the rest great chance deviations may occur. Keeping this in mind, some trends in the graphs are clear:

(a) With the exception of 6 and/or 7 weeks old plants, –L gives higher ratios than the corresponding +L treatments.

(b) With the exception of 6 or 7 weeks old plants, + L at 21/4 gives lower ratios than the corresponding ones on 27/1. The +L controls at 21/4 are the lowest. All +L lines tend to slope down from 6 or 7 weeks old plants.

(c) The –L lines are rather irregular, doubtlessly for reasons mentioned above. It seems rather certain that the values on 21/4 tend to be smaller and sometimes very much smaller than those at 27/1, while again the controls are the lowest. However, a tendency to decrease as age increases is not clear.

All in all there are some indications that the ratio decreases as the degree of adultness increases, but the results can only be considered as a partial confirmation of STOKES and VERKERK's results with Brussels sprouts. Our data do not allow to indicate a certain ratio as marking the transition from juvenility to adultness. This must probably be due to the fact that young *Lunaria*-plants form more clear rosettes than Brussels sprouts and have practically no stems.

Experiment 2. – Results during a permanent cold treatment.
Table 3 mentions the data for the formation of flower buds.

TABLE 3. Experiment 2.– The effect of a pretreatment with strong supplementary light (+L), compared with natural light only (–L), during different periods before a permanent cold treatment (5 °C), judged by the percentages of generative plants *during* the cold treatment and the mean numbers of days to budding. Nine plants per treatment. Data 355 days after the beginning of the cold treatment at 27/1/60. From (130)

1	2	3	4	5
Pretreatment during ...weeks	% Generative plants		Days to budding	
	+L	–L	+L	–L
6	100	0	281.7	∞
7	100	11	197.0	355.0
8	100	33	184.2	334.0
9	100	89	184.2	296.3
10	100	100	181.0	216.0
11	100	100	176.3	203.0
12	100	100	174.0	179.2

These results are principally similar to those of table 1. Comparing the data in table 1 with those in table 3 shows two differences: *(a)* The values in table 3 column 3 tend to be larger than the corresponding ones in table 1, with the exception of the pretreatments during 7 or 8 weeks old. *(b)* The values in table 3 columns 4 and 5 are considerably larger than the corresponding ones in table 1, also if we subtract from the values in table 3 a period of 12 weeks = 84 days which is the duration of the cold treatment in table 1. Of course it is not surprising that the formation of flower buds at 5 °C takes place more slowly than at higher temperatures.

Some growth analyses data, determined during the cold at five different dates, have been summarized in table 4.

The mean height and diameter of stem are greater and often considerably greater after +L than after the corresponding –L treatments. Most values increase as the age-groups increase within the +L and within the –L. There is a tendency to increase during the cold period. In contradiction with the results during the limited period of 12 weeks cold (experiment 1), the mean diameter of stem is greater after +L than after –L for all the age-groups. This difference may be due to the effect of growing these plants in pots and in permanent cold treatment, while the plants in experiment 1 were grown only for 12 weeks in the cold, followed by natural out-door conditions in the soil.

1.3. *Further experimental results.*

In all following experiments, 3–8, a comparison between +L and –L was made in addition to other factors. In all cases the far better results of +L than of –L were confirmed. Photos 1 and 2 illustrate these results. We shall no longer point to the effect of light, but shall confine ourselves to the influence of minerals and water. Additional observations on the type of flowering will be mentioned in experiment 3.

TABLE 4. Experiment 2. – Growth analysis data on plants of table 3. Date of beginning of vernalization: 27/1/60

Pre-treatment	Measurements	Dates	Age (weeks)						
			6	7	8	9	10	11	12
+L	Height of stem in cm	1/8/60	1.9	2.3	2.5	2.5	3.0	5.4	7.2
		22/8	2.2	3.3	3.8	3.8	5.6	9.6	13.3
		12/9	2.9	4.5	6.0	5.6	9.4	17.1	21.9
		3/10	4.0	6.0	10.9	9.0	16.4	27.0	33.0
		17/1/61	11.4	26.7	34.8	35.7	51.3	63.7	63.3
	Diameter of stem in mm	22/8/60	2.3	2.1	2.5	2.9	3.5	3.8	4.2
		12/9	2.7	2.6	3.1	3.7	4.5	4.9	5.1
		3/10	3.0	2.7	3.2	3.9	4.8	5.0	5.0
		17/1/61	3.0	3.0	3.3	3.8	4.7	4.8	5.0
-L	Height of stem in cm	1/8/60	1.4	1.1	1.2	1.7	2.0	2.6	3.7
		22/8	1.8	1.5	1.7	2.1	2.5	3.2	5.1
		12/9	2.8	2.1	2.3	2.5	3.0	4.0	6.9
		3/10	3.2	2.4	2.7	3.1	3.4	5.2	10.2
		17/1/61	4.8	4.1	5.9	7.8	12.7	19.5	38.2
	Diameter of stem in mm	22/8/60	1.1	1.5	1.4	1.6	1.9	2.2	2.8
		12/9	1.6	2.2	2.1	2.3	2.4	2.5	3.4
		3/10	1.7	2.3	2.2	2.3	2.5	2.6	3.7
		17/1/61	1.9	2.2	2.4	2.5	2.5	2.9	3.8

2. NITROGEN AND WATER

2.1. *Methods.*

From 28th October 1960 five biweekly sowings took place, so that after 14 weeks an age-group of 6, 8, 10, 12 or 14 weeks old was available. The seeds were sown in wooden boxes 44½ × 37 × 15 cm which were filled with washed sand to 12 cm in height. The plants were grown under either +L or -L conditions. All the plants were treated with the complete nutrient solution number 1 according to HOAGLAND and ARNON (54) till they made the first pair of leaves which was 4 weeks after germination. Then the plants were treated with two different nutrient solutions and two different irrigation treatments as follows:

With nitrogen wet : +N+W
With nitrogen dry : +N-W
Without nitrogen wet: -N+W
Without nitrogen dry: -N-W

In the wet series, the +L plants were irrigated twice per week, the -L plants once per week, to maintain soil moisture at or near field capacity. In the dry series, both +L and -L plants were irrigated only when they began to wilt. All the plants were potted at 27/1/61 and irrigated with water one week before the cold treatment started at 3/2/61. Vernalization was done both during 12 weeks and permanently.

2.2. *Experimental results.*

Experiment 3. – Vernalization during 12 weeks.

Table 5 summarizes the results with regard to budding.

TABLE 5. Experiment 3. – The percentage of generative plants and the mean number of days to budding of *Lunaria biennis* plants, grown without (–L) or with supplementary strong light (+L), and pretreated with nitrogen wet (+N+W), with nitrogen dry (+N–W), without nitrogen wet (–N+W), and without nitrogen dry (–N–W) while vernalized during 12 weeks. Originally twelve plants per treatment. Data 150 days after the end of the vernalization at 28/4/61

1	2	3	4	5	6	7	8	9
Pretreatment / Age (weeks)	+L				–L			
	+N+W	+N–W	–N+W	–N–W	+N+W	+N–W	–N+W	–N–W
	% Generative plants							
6	16.7	16.7	41.7	16.7	0.0	0.0	0.0	0.0
8	75.0	58.3	83.3	83.3	8.3	8.3	33.3	8.3
10	100	100	100	100	100	100	83.3	83.3
12	100	100	100	100	100	100	100	75.0
14	100	100	100	100	100	100	100	100
	Days to budding							
6	99.5	78.5	84.8	101.0	∾	∾	∾	∾
8	63.8	64.7	65.6	54.9	84.0	125.0	113.2	117.0
10	27.1	27.5	21.8	23.7	61.7	41.3	51.2	55.3
12	20.6	21.5	20.4	23.5	34.3	31.5	42.9	58.3
14	17.5	17.7	17.7	16.9	15.8	18.7	18.5	19.7

After +L, the effect of nitrogen in the presence of water is presented in columns 2 and 4. The percentage of generative plants is greater with plants of 6 and 8 weeks old, which were treated only for a short time, in the absence of nitrogen (–N), while it is the same for all other age-groups. The mean number of days to budding is relatively small in the absence of nitrogen for plants of 6 or 10 weeks old. The effect of nitrogen in the absence of water is presented in columns 3 and 5. The percentage of generative plants is the same with all age-groups, except with plants of 8 weeks, where it is relatively high in the absence of nitrogen. The only significant difference for the mean number of days to budding was also found for plants of 8 weeks old with a rather low value in the absence of nitrogen.

After +L, the effect of water in the presence of nitrogen can be seen in columns 2 and 3. The percentage of generative plants is the same for plants of all age-groups, with the exception of plants of 8 weeks old. Also, the mean number of days to budding is about the same for all age-groups, with the exception of plants of 6 weeks old. The effect of water in the absence of nitrogen is presented in columns 4 and 5. The wet series, column 4, for plants of 6 weeks old gave a relatively high percentage of generative plants, which is the same for plants of 8 to 14 weeks old. Also, with regard to the mean number of days to budding, the wet series for plants of 6 weeks old consequently gave the lowest mean, which is about the same for plants of 10 to 14 weeks old.

Conclusion. – From these results after +L, it seems that nitrogen deficiency (–N), in the presence or absence of water (–N+W) or (–N–W) has little influence, but may reduce the duration of the juvenile phase. In general, the effect of water, in the presence or absence of nitrogen, is mathematically not significant for any age-group. Illustrations in photo 1.

After –L, plants of 6 weeks old did not initiate flower buds and remained juvenile. The effect of nitrogen in the presence of water is presented in columns 6 and 8. There is no significant difference between the presence or absence of nitrogen. The effect of nitrogen in the absence of water is presented in columns 7 and 9. With plants of 10 weeks old the presence of nitrogen (+N) has a significant reducing effect in the mean number of days, while with plants of 12 weeks old this effect is highly significant.

After –L, the effect of water in the presence of nitrogen is presented in columns 6 and 7. The percentage of generative plants is the same for all age-groups. There is no significant effect for the mean number of days to budding, except for plants of 14 weeks old in which the wet series (+W) gave a significant reducing effect. The effect of water in the absence of nitrogen is presented in columns 8 and 9. With plants of 12 weeks old, the wet series (+W) presents a higher percentage of generative plants and consequently a significantly lower mean number of days to budding.

Conclusion. – These results after –L indicate that the presence of nitrogen in the absence of water (+N–W) and the presence of water (+W) in the presence or absence of nitrogen (+N+W) or (–N+W), may have a favourable influence on the rapidity of flowering and hence tend to reduce juvenility. Photo 2 illustrates the results.

There was a striking difference in the type of flowering, especially between +L and —L for plants vernalized during 12 weeks, experiments 1, 3, 5 and 7. A normal type of flowering begins with a terminal inflorescence which is followed by lateral ones. Another type of flowering consists of lateral inflorescences only, in exceptional cases followed by terminal inflorescences in the younger age-groups after +L and in the relatively older plants after —L. Table 6 summarizes the observations on the type of flowering.

TABLE 6. Experiment 3.– Type of flowering of *Lunaria biennis* plants of table (5)

T = Terminal flower bud
LT = Lateral flower bud first and terminal flower bud later
L = Lateral flower bud

[N.B. In –L, 12 weeks, +N+W and +N–W, 6 and 2 plants respectively died prematurely]

Pretreatment ⟶		+N+W			+N–W			–N+W			–N–W		
↓	Type of flowering	T	LT	L	T	LT	L	T	LT	L	T	LT	L
	Age (weeks)												
+L	6	0	0	2	0	0	2	0	1	4	0	0	2
	8	1	1	7	1	1	5	4	1	5	2	2	6
	10	12	0	0	10	2	0	12	0	0	12	0	0
	12	12	0	0	12	0	0	12	0	0	12	0	0
	14	12	0	0	12	0	0	12	0	0	12	0	0
–L	6	0	0	0	0	0	0	0	0	0	0	0	0
	8	0	0	1	0	0	1	0	1	3	0	0	1
	10	4	5	3	6	2	4	3	2	5	4	1	5
	12	4	2	0	7	2	1	2	6	4	1	3	5
	14	12	0	0	12	0	0	12	0	0	12	0	0

The normal type of flowering was predominant in the +L, especially in the older plants which were completely vernalized. The lateral type of flowering was predominant in the -L, especially with the younger age-groups which were incompletely vernalized. There is no clear effect of nitrogen and water pretreatments on the type of flowering.

Let us now turn to the growth analysis data which were calculated three weeks after the end of the cold treatment at 28/4/61. Table 7 summarizes the results.

TABLE 7. Experiment 3.– Growth analysis data on plants of table 5, measured three weeks after the end of the vernalization at 28/4/61

1	2	3	4	5	6	7	8	9
Pretreatment / Age (weeks)	+L				-L			
	+N+W	+N-W	-N+W	-N-W	+N+W	+N-W	-N+W	-N-W
	Mean number of leaves							
6	6.0	6.8	8.8	8.8	8.0	8.0	8.0	7.6
8	8.5	9.6	9.5	8.8	10.0	8.0	8.0	8.4
10	12.8	13.0	10.0	10.5	11.0	10.0	9.3	10.0
12	14.8	12.0	11.3	9.0	-*)	8.8	8.0	8.8
14	17.5	14.0	10.3	11.3	14.0	-*)	12.0	10.7
	Mean dry weight of leaves in mg							
6	409	474	1020	1143	579	411	709	568
8	526	820	885	827	851	578	515	799
10	1678	1241	1025	1032	1099	688	664	1026
12	2231	1115	763	520	-*)	503	272	625
14	2338	1699	505	910	1544	-*)	732	512
	Mean dry weight of stem in mg							
6	23	33	61	68	33	27	39	35
8	44	56	73	54	51	34	39	42
10	146	120	72	75	74	42	45	52
12	215	142	72	45	-*)	47	22	39
14	315	241	100	133	261	-*)	140	104
	Mean weight of seeds in g							
6	0	0	4.5	6.5	0	0	0	0
8	5.8	7.2	7.6	12.4	0	0	0	0
10	22.7	24.6	31.3	30.2	14.6	11.1	9.7	8.5
12	28.7	32.9	36.6	30.2	21.5	18.1	14.5	8.5
14	18.8	24.8	25.2	17.7	43.6	26.0	27.7	10.2

*) Some plants died during the cold, so that no plants were left for the growth analysis.

The mean numbers of leaves after both +L and -L were, in general, larger after the presence of nitrogen in the presence or absence of water, especially for the older plants of 10, 12 or 14 weeks old after +L, columns 2 and 4, 6 and 8, and 3 and 5.

The mean dry weights of leaves after +L increase as the age of +N plants in-

creases, columns 2 and 3, while tend to decrease irregularly as the age of –N plants increases, columns 4 and 5. After +L, the presence of nitrogen in the presence or absence of water gave a larger mean dry weight of leaves for plants of 10, 12 or 14 weeks old, columns 2 and 4, and 3 and 5. After –L, the absence of nitrogen in the absence of water, columns 7 and 9, gave a larger mean dry weight of leaves. The mean dry weights of leaves were greater after the presence of water in the presence of nitrogen only for +L plants of 10, 12 or 14 weeks old, columns 2 and 3, and for –L plants of 6, 8 or 10 weeks old, columns 6 and 7 (12 and 14 weeks undetermined).

The mean dry weights of stem show the same trend as the mean dry weights of leaves mentioned above.

After +L, the +N plants of 6 weeks old, columns 2 and 3, and also after –L plants of 6 or 8 weeks old for all pretreatments, did not form seeds. The results of the mean weight of seeds strongly indicate that after +L, the absence of nitrogen in the presence of water, columns 2 and 4, or the absence of water in the presence of nitrogen, columns 2 and 3, had a good effect on the seed formation. On the contrary, after –L, the presence of nitrogen, columns 6 and 8, 7 and 9, or the presence of water, columns 6 and 7, 8 and 9, gave a good effect on the seed formation.

Measurements were also made of length of petiole, length and width of lamina, height and diameter of stem, and number of lateral flowering branches, but these results showed nothing of interest with regard to our scope.

Conclusion. – In general, these results after both + L and –L indicate that the presence of nitrogen in the presence of water (+N+W) is effective in increasing the growth analysis data.

Experiment 4. – Results during a permanent cold treatment.

The results with regard to the percentage of generative plants and to the rapidity of budding are given in table 8.

After +L, the presence of nitrogen in the presence of water, columns 2 and 4, tends to take a somewhat higher mean number of days, while in the absence of water, columns 3 and 5, tends to take a somewhat smaller mean number of days to budding. Also after +L, the presence of water in the presence of nitrogen, columns 2 and 3, tends to take a higher mean number of days to budding, while this effect is not clear in the absence of nitrogen, columns 4 and 5. Photo 3 illustrates the results.

After –L, the presence of nitrogen in the presence of water, columns 6 and 8, gave higher percentages of generative plants of 8 or 12 weeks old, while in the absence of water, columns 7 and 9, it gave lower percentages for plants of 8 or 10 weeks old, and tends in both cases to take lower mean numbers of days to budding. Also after –L, the presence of water in the presence of nitrogen gave higher percentages of generative plants, for plants of 8 or 10 weeks old, and tended to take lower mean numbers of days, columns 6 and 7. The presence of water in the absence of nitrogen gave lower percentages of generative plants for plants of 8 or 12 weeks old, and tended to take lower mean numbers of days to budding, columns 8 and 9. Photo 4 demonstrates the results.

Conclusion. – In general, the results after +L indicate that the absence of nitrogen in the presence of water (–N+W), and also the absence of water in the presence of nitrogen (+N–W), tend to take lower mean numbers of days to budding. After –L, the presence of nitrogen (+N) in the presence or absence of

TABLE 8. Experiment 4.– The percentage of generative plants and the mean number of days to budding of *Lunaria biennis* plants grown without (–L) or with supplementary strong light (+L), and pretreated with nitrogen wet (+N+W), with nitrogen dry (+N–W), without nitrogen wet (–N+W) and without nitrogen dry (–N–W), while treated with a permanent cold treatment. Originally ten plants per treatment. Data 360 days after the beginning of vernalization at 3/2/61

1	2	3	4	5	6	7	8	9
Pretreatment / Age (weeks)	+L				–L			
	+N+W	+N–W	–N+W	–N–W	+N+W	+N–W	–N+W	–N–W
	% Generative plants							
6	57.1	37.5	37.5	25.0	0.0	0.0	0.0	0.0
8	100	85.7	100	83.3	37.5	12.5	25.0	37.5
10	100	100	100	100	100	87.5	100	100
12	100	100	100	100	100	100	71.4	100
14	100	100	100	100	100	100	100	100
	Days to budding							
6	321.2	308.3	324.7	335.0	∞	∞	∞	∞
8	279.1	262.0	274.9	246.2	330.0	320.0	326.5	351.7
10	173.9	169.0	168.9	156.5	213.7	252.4	253.6	211.7
12	151.0	148.1	150.0	154.9	174.5	255.7	252.6	259.2
14	145.0	141.1	134.4	144.4	146.1	147.2	143.8	150.0

water (+N+W) or (+N–W), or the presence of water (+W) in the presence or absence of nitrogen (+N+W) or (–N+W), tend to take a lower mean number of days to budding. In general, these results are in agreement with those of experiment 3.

Some growth analysis data have been summarized in table 9.

After +L, the presence of nitrogen in the presence of water gave higher mean heights of stem for plants of 8 or 14 weeks old, columns 3 and 13, 6 and 16, while in the absence of water it tends to give higher means of height of stem for all age-groups, columns 7–11 and 17–21. Also after +L, the absence of water in the presence of nitrogen gave higher mean heights of stem for plants of 10, 12 or 14 weeks old, columns 4–6 and 9–11, while about the same holds true in the absence of nitrogen for plants of 10 or 14 weeks old, columns 14, 16 and 19, 21.

After –L, the presence of nitrogen in the presence of water gave higher mean heights of stem, columns 2–6 and 12–16, while in the absence of water it gave higher mean heights for all ages except for plants of 8 or 10 weeks old, columns 7–11 and 17–21. Also after –L the presence of water in the presence of nitrogen gave higher mean heights of stem, columns 2–6 and 7–11, while in the absence of nitrogen it gave higher mean heights only for plants of 14 weeks old, columns 12–16 and 17–21.

For the mean diameter of stem after +L the presence of nitrogen in the presence or absence of water tended to give higher means for plants of 10, 12 or 14 weeks old, columns 4–6, 14–16 or 9–11, 19–21. Also the presence of water in the presence or absence of nitrogen tended to give higher means of diameter of stem, columns 2–6, 7–11, or 12–16, 17–21.

After –L the results for the mean diameter of stem indicate that the presence of nitrogen or water in the presence or absence of water or nitrogen respectively

TABLE 9. Experiment 4.– Growth analysis data on plants of table 8. Date of beginning of vernalization: 3/2/61

1		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Pretreatment		+N+W					+N-W					-N+W					-N-W				
Age (weeks)		6	8	10	12	14	6	8	10	12	14	6	8	10	12	14	6	8	10	12	14
Characters	Dates																				
Height of stem in cm	21/7/61	3.0	4.2	4.5	5.0	5.5	2.4	3.1	4.2	4.9	5.6	3.2	3.7	3.2	3.4	4.5	2.6	2.3	2.9	3.0	4.4
	1/9	5.1	7.4	8.7	11.0	14.6	4.7	5.5	8.9	12.2	16.1	5.4	6.6	7.0	8.6	12.8	4.5	4.7	8.2	6.9	11.6
+L	13/10	5.9	8.2	10.4	13.6	21.3	5.6	6.5	11.6	18.7	23.2	6.5	7.9	13.0	14.7	17.5	5.2	6.4	14.1	10.1	20.3
	24/11	6.6	10.2	13.1	20.5	27.6	6.7	7.7	17.7	27.9	29.0	7.4	10.3	18.4	27.0	22.9	5.9	9.0	22.3	15.1	31.5
	5/1/62	7.9	13.6	21.8	27.7	32.6	7.4	9.8	31.2	33.9	34.4	8.3	12.8	27.7	34.2	25.7	6.6	12.2	26.8	18.9	34.4
	21/7/61	2.9	3.2	3.3	3.5	5.6	2.5	2.8	2.8	2.4	4.7	1.8	2.2	2.9	2.1	4.1	1.9	2.9	3.7	2.5	3.9
	1/9	5.7	5.5	5.5	7.8	12.8	4.7	4.7	5.3	4.7	10.8	3.5	4.4	5.3	3.7	9.6	3.6	5.5	7.1	4.4	9.9
-L	13/10	6.6	6.6	10.0	13.5	22.1	6.1	5.6	7.2	5.8	17.0	4.5	5.5	7.4	5.6	16.5	4.5	6.5	11.1	6.3	14.6
	24/11	7.5	7.3	15.5	21.5	33.3	6.7	6.3	10.8	9.4	27.3	4.9	6.3	10.7	9.1	29.3	5.0	7.4	16.4	7.7	19.4
	5/1/62	8.4	8.6	22.4	31.0	42.9	7.4	7.3	14.1	14.5	34.8	6.0	7.3	13.9	12.8	37.3	5.5	8.1	21.3	10.7	22.7
Diameter of stem in mm	21/7/61	1.8	1.9	3.5	3.8	4.3	1.3	1.8	2.8	2.9	4.0	2.1	2.4	2.6	2.3	3.2	1.9	2.0	2.3	1.7	3.0
	1/9	1.9	2.0	4.1	3.9	4.3	1.4	2.1	2.9	3.0	3.9	2.2	2.3	3.2	2.5	3.1	2.2	2.3	2.7	1.9	2.9
+L	13/10	2.0	2.0	4.0	3.7	4.3	1.6	2.3	3.2	3.1	4.1	2.4	2.5	3.1	2.3	2.9	2.3	2.3	2.7	1.9	3.1
	24/11	2.1	2.0	4.1	3.7	4.0	1.7	2.2	3.1	2.9	3.8	2.4	2.8	3.0	2.5	2.7	2.3	2.3	2.7	2.0	3.0
	5/1/62	2.2	2.1	4.5	3.9	4.0	1.9	2.3	3.4	3.1	4.0	2.4	2.5	3.1	2.7	3.0	2.4	2.4	2.8	2.0	3.2
	21/7/61	1.6	1.6	2.4	2.4	3.2	1.3	1.4	1.9	1.9	2.5	1.6	1.5	2.0	1.1	2.2	1.4	1.5	1.8	1.1	2.0
	1/9	1.8	1.8	2.3	2.5	3.4	1.5	1.6	2.0	2.0	2.7	1.9	1.7	2.1	1.2	2.5	1.7	1.6	2.1	1.4	2.2
-L	13/10	2.1	1.7	2.5	2.4	3.4	1.7	1.7	2.1	2.0	2.8	1.9	1.7	2.0	1.4	2.9	1.6	1.7	2.1	1.4	2.2
	24/11	2.1	1.8	2.5	2.5	3.5	1.7	1.7	2.1	2.0	2.7	2.0	1.9	2.2	1.6	2.5	1.5	1.8	2.2	1.5	2.2
	5/1/62	2.1	1.9	2.6	2.7	3.5	1.7	1.8	2.2	2.3	3.1	2.2	2.0	2.3	1.7	2.8	1.7	1.8	2.5	1.6	2.4

tend to give higher values, columns 2–6, 12–16, or 7–11, 17–21, or 2–6, 7–11, or 12–16–17–21.

Conclusion. – In general, these results after both +L and –L indicate that the presence of nitrogen (+N) or water (+W) tends to give higher values for the growth analysis data.

3. Nitrogen, phosphorus, and potassium

3.1. *Methods.*

From 25th November 1960 three biweekly sowings took place, so that after 10 weeks an age-group of 6, 8 or 10 weeks was available. The medium was perlite. The plants were grown under either +L or –L conditions. Four weeks after germination, when the plants had made the first pair of leaves, the plants were treated with four nutrient solutions, according to Hoagland and Arnon (54), as follows: a complete solution number 1 (NPK) and complete solutions without nitrogen, without phosphorus, and without potassium, –N, –P and –K respectively. The +L plants were irrigated twice per week, the –L plants once per week. All the plants were potted at 27/1/61 and irrigated with water one week before the vernalization started at 3/2/61. Again, vernalization was done both during 12 weeks and permanently.

3.2. *Experimental results.*

Experiment 5. – Vernalization during 12 weeks.

Table 10 summarizes the percentages of generative plants and the rapidity of budding.

Table 10. Experiment 5. – The percentage of generative plants and the mean number of days to budding of *Lunaria biennis* plants, grown without (–L) or with supplementary strong light (+L), and pretreated with complete nutrient solution (NPK), nutrient solutions without nitrogen (–N), without phosphorus (–P), without potassium (–K), while vernalized during 12 weeks. Originally twelve plants per treatment. Data 150 days after the end of vernalization at 28/4/61

1	2	3	4	5	6	7	8	9
Pretreatment	+L				–L			
Age (weeks)	NPK	–N	–P	–K	NPK	–N	–P	–K
	% Generative plants							
6	33.3	50.0	33.3	66.7	0	0	0	0
8	83.3	100	100	100	41.7	8.3	16.7	0
10	100	100	100	100	83.3	91.7	83.3	75.0
	Days to budding							
6	85.2	66.8	93.0	61.7	∾	∾	∾	∾
8	39.2	55.6	38.7	60.3	71.2	77.0	56.0	∾
10	25.0	29.1	21.7	27.1	33.5	40.6	39.7	56.1

After +L the following results were obtained:

1. With plants of 6 weeks old, the absence of potassium (–K), for a shorter time, gave higher percentage of generative plants, column 5, than the other pre-

treatments. Also it gave a significantly smaller mean number of days to budding than both NPK and –P pretreatments.
2. With plants of 8 weeks old, treated also for a relatively short time, the percentage of generative plants is the same for all pretreatments except for NPK, column 2. The absence of phosphorus (–P) gave a lower mean number of days to budding, column 4, than the other pretreatments. The only significant difference exists between –P and –K pretreatments, columns 4 and 5.
3. With plants of 10 weeks old, the percentage of generative plants was the same for all pretreatments. The absence of phosphorus (–P), column 4, gave a significantly lower mean number of days to budding than the other pretreatments.

After –L, plants of 6 weeks old did not form flower buds under the short influence of all the pretreatments. With plants of 8 weeks old, the plants did not form flower buds in the absence of potassium (–K), column 9. The absence of nitrogen (–N), column 7, gave the lowest percentage of generative plants. The absence of phosphorus (–P), column 8, gave the lowest mean number of days to budding. With plants of 10 weeks old also the absence of potassium (–K), column 9, gave the lowest percentage of generative plants, and the highest mean number of days.

Conclusion. – In general, the results after both +L and –L indicate that the absence of phosphorus (–P) may reduce the duration of the juvenile phase, especially with plants of 10 weeks old. On the other hand, after –L the absence of potassium (–K) may prolong the duration of the juvenile phase.

Some growth analysis data on plants of table 10 have been summarized in table 11.

In general, it may be concluded that there is no general rule with regard to the characters: After +L the absence of phosphorus (–P), columns 8–10, while after –L the complete solution (NPK), columns 14–16, gave the largest mean heights of stem. After +L the absence of potassium (–K) for plants of 8 or 10 weeks old, columns 12 and 13, and after –L also the complete solution (NPK), columns 14–16, gave the largest mean diameter of stem. After both +L and –L the complete solution (NPK) with plants of 8 weeks old, columns 3 and 15, gave the largest mean number of lateral flowering branches. After +L, the absence of phosphorus (–P), columns 8–10, gave the largest mean weight of seeds. After –L the absence of potassium (–K), columns 23–25, gave the smallest mean weight of seeds. Plants of 8 weeks old formed seeds only when pretreated with the complete solution (NPK), column 15.

Experiment 6. – Results during a permanent cold treatment.

The percentage of generative plants and the mean number of days to budding have been summarized in table 12.

After +L, with plants of 6 weeks old, the complete solution (NPK), column 2, gave a larger percentage of generative plants than the other pretreatments. The absence of nitrogen (–N), column 3, gave the lowest mean number of days to budding. With plants of 8 weeks old, the percentage of generative plants is the same for all pretreatments, and the absence of potassium (–K), column 5, gave a significantly lower mean number of days to budding. With plants of 10 weeks old, although the percentage of generative plants is the same for all pretreatments, the absence of phosphorus (–P), column 4, gave a significantly lower mean number of days to budding than both the absence of nitrogen (–N) or the

TABLE 11. Experiment 5.– Growth analysis data on plants of table 10, measured six weeks after the end of vernalization at 28/4/61

1		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Pretreatment		+L												−L											
		NPK			−N			−P			−K			NPK			−N			−P			−K		
Age (weeks)		6	8	10	6	8	10	6	8	10	6	8	10	6	8	10	6	8	10	6	8	10	6	8	10
Characters	Dates																								
Height of stem in cm	9/6/61	5.0	10.2	31.3	5.2	8.4	28.4	4.6	9.7	35.8	5.5	7.2	26.9	4.2	5.0	14.1	4.0	4.7	9.2	4.4	4.8	10.0	3.6	3.5	4.5
	30/6	7.2	28.9	56.6	8.7	28.6	61.1	9.7	34.0	71.2	9.8	21.3	58.2	8.0	8.7	30.1	7.4	7.8	27.0	6.5	7.1	23.8	4.8	5.2	10.2
	11/8	8.1	42.5	57.9	11.2	45.9	64.4	15.9	47.3	72.7	12.9	33.4	63.8	10.0	11.5	39.3	9.9	9.2	40.8	8.6	8.7	29.8	7.4	7.3	20.2
	22/9	9.0	46.1	58.1	13.4	47.7	65.9	17.6	52.9	73.1	16.2	45.9	66.2	13.2	15.2	41.4	12.4	11.0	46.7	10.0	10.2	31.1	8.2	8.5	21.7
Diameter of stem in mm	9/6/61	6.8	6.1	5.9	6.7	5.6	5.5	10.3	7.1	6.5	10.0	7.9	6.3	7.5	7.2	7.2	3.8	6.7	7.1	6.9	6.4	6.7	4.0	3.6	3.6
	30/6	8.7	8.6	6.7	10.3	9.3	7.0	10.4	9.6	7.3	10.4	10.8	7.8	11.4	10.8	9.2	10.3	9.8	9.4	9.0	9.7	8.4	6.4	6.0	4.3
	11/8	11.1	9.4	6.9	13.6	10.5	7.1	13.1	9.0	7.4	13.1	11.9	8.0	13.3	13.5	10.0	12.8	12.7	9.7	11.5	10.8	8.7	9.5	9.4	6.8
	22/9	12.9	9.0	6.4	14.4	11.0	6.8	12.2	9.2	7.3	14.5	12.5	7.8	15.3	14.2	10.5	14.5	14.0	9.6	13.8	13.9	10.1	11.5	11.7	6.9
Number of lateral flowering branches	9/6/61	0	5.0	6.6	0	4.0	4.9	0	5.0	5.7	0	5.0	5.9	0	0	6.0	0	0	3.0	0	0	4.0	0	0	0
	30/6	0	7.0	9.5	2.0	7.7	9.8	3.0	6.6	11.3	2.0	6.4	11.1	0	2.5	6.2	0	0	6.2	0	1.5	6.4	0	0	2.6
	11/8	1.0	10.9	10.7	1.7	10.5	10.7	11.5	8.2	11.6	2.2	9.1	12.7	0	2.5	9.8	0	1.0	12.9	0	1.5	7.7	0	0	4.7
	22/9	1.2	14.5	11.3	3.0	12.3	11.0	8.0	12.1	12.9	3.1	12.1	15.5	0	3.6	11.4	0	1.0	14.4	0	2.0	9.7	0	0	7.2
Mean weight of seeds in g		5.2	18.0	25.5	5.3	13.1	29.6	5.5	18.5	45.6	4.0	13.7	29.0	0	5.4	20.0	0	0	20.8	0	0	17.5	0	0	4.7

TABLE 12. Experiment 6. – The percentage of generative plants and the mean number of days to budding of *Lunaria biennis* plants, grown without (–L) or with supplementary strong light (+L), and pretreated with complete nutrient solution (NPK), and nutrient solutions without nitrogen (–N) without phosphorus (–P) without potassium (–K), while treated with a permanent cold treatment. Originally ten plants per treatment. Data 360 days after the beginning of vernalization at 3/2/61

1	2	3	4	5	6	7	8	9
Pretreatment	+L				–L			
Age (weeks)	NPK	–N	–P	–K	NPK	–N	–P	–K
	% Generative plants							
6	50.0	37.5	25.0	37.5	0	0	0	0
8	100	100	100	100	62.5	25.0	37.5	75.0
10	100	100	100	100	100	100	100	100
	Days to budding							
6	303.5	279.0	335.0	307.0	∞	∞	∞	∞
8	245.6	211.0	218.8	205.6	298.0	314.0	330.0	314.2
10	150.9	162.0	148.2	156.2	200.5	199.0	198.9	208.2

absence of potassium (–K). After –L, plants of 6 weeks old did not form flower buds. With plants of 8 weeks old, although the complete solution (NPK), column 6, did not give the largest percentage of generative plants, it gave a lower mean number of days to budding than the other pretreatments. With plants of 10 weeks old the percentage of generative plants is the same for all the pretreatments, and the absence of potassium (–K), column 9, gave the largest mean number of days to budding.

Measurements were also made of the height and diameter of stem, but these results showed nothing of interest with regard to our scope.

Conclusion. – The results after +L indicate that the absence of phosphorus (–P), in general, may reduce a little the duration of the juvenile phase for plants of 10 weeks old. After –L, the absence of potassium (–K) with plants of 10 weeks old may prolong the duration of the juvenile phase. These results after both +L and –L are in accordance with the results of experiment 5 (table 10).

4. GIBBERELLINS

4.1. *Methods.*

From 11th January 1961 four weekly sowings took place, so that after 9 weeks an age-group of 6, 7, 8 or 9 weeks was available. Four days after germination the seedlings were treated in both +L and –L conditions with gibberellic acid (GA), 500 ppm twice per week as a pretreatment before the cold treatment started at 15/3/61. The plants of 6, 7, 8 or 9 weeks old had 9, 11, 13 or 15 applications of GA respectively. The control plants (untreated plants, –GA), and the treated plants (+GA) were vernalized both during 12 weeks or permanently.

4.2. *Experimental results.*

Experiment 7. – Vernalization during 12 weeks.

Unfortunately, it happened that all –L plants had died within four weeks after

transferring to the open air. In itself this is a demonstration of the good effect of applying supplementary light, but no data are available for the –L plants and we shall deal only with +L plants.

Table 13 summarizes the results with regard to budding.

TABLE 13. *Experiment 7.*– The percentage of generative plants and the mean number of days to budding of *Lunaria biennis* plants pretreated with strong supplementary light (+L) and gibberellic acid 500 ppm twice per week, while vernalized during 12 weeks. Fifteen plants per treatment. Data 131 days after the end of the vernalization at 7/6/61

1	2	3	4	5
	% Generative plants		Days to budding	
Pretreatment / Age (weeks)	–GA	+GA	–GA	+GA
6	20.0	13.3	74.7	62.0
7	73.3	53.3	43.7	32.8
8	100	80.0	23.9	25.5
9	100	100	18.1	12.3

Comparing columns 2 and 3, it is obvious that GA reduced the percentage of generative plants in all the age-groups except 9 weeks old. Hence GA has a tendency to maintain juvenility judged by the percentage of generative plants. A comparison between columns 4 and 5 clearly demonstrates that GA has a reducing effect on the time for realization of flower bud formation, except with plants of 8 weeks old. Therefore GA may reduce juvenility decided by the mean days to budding. Hence the effect of GA is opposite to the rather general rule, found thusfar, that high percentages of generative plants are accompanied by low mean numbers of days to budding.

Some growth analysis data on plants of table 13, measured every three weeks after the end of the vernalization at 7/6/61, have been summarized in table 14.

According to expectation, GA increased the height of stem in every age-group, columns 6–9. At the three final measurements, treated plants of 8 or 9 weeks old, columns 8 and 9 had a smaller mean height than the untreated ones, columns 4 and 5.

GA reduced the diameter of stem (character 2) in every age-group and within all the measurements, columns 6–9. This may be due to its increasing effect on the height of stem. Also, GA tended to reduce the number of lateral flowering branches (character 3). It is clear that the treated plants of 6 weeks old, column 6, formed lateral flowering branches earlier than the untreated plants, column 2. Also, the results indicate that the mean dry weight of leaves (character 4) is greater with the untreated plants, columns 2–5, except with plants of 7 weeks old, columns 3 and 7. On the contrary, GA increased the dry weight of stem (character 5) in every age-group. This may be due to its increasing effect on stem-elongation. Illustrations in photo 5.

The results with the mean weight of seeds (character 6) indicate that GA reduced the weight of seeds in every age-group, columns 6–9. This may be due to its reducing effect on the number of lateral flowering branches (character 3), and the percentage of generative plants as mentioned in table 13.

TABLE 14. Experiment 7.– Growth analysis data on plants of table 13, measured every three weeks after the end of vernalization at 7/6/61

1		2	3	4	5	6	7	8	9
Pretreatment		–GA				+GA			
Age (weeks)		6	7	8	9	6	7	8	9
Characters	Dates								
1. Mean height of stem in cm	28/6/1961	4.6	4.4	4.6	8.4	13.7	18.7	23.4	30.5
	19/7	5.0	11.1	37.8	40.8	12.4	22.6	28.7	45.7
	9/8	5.5	20.9	55.7	57.6	13.4	24.9	32.7	52.1
	30/8	6.8	26.1	57.8	58.9	13.5	26.8	36.6	53.7
	20/9	8.7	28.0	58.4	59.2	14.3	26.8	37.7	54.1
2. Mean diameter of stem in mm	28/6/1961	6.1	6.3	6.2	5.3	3.3	3.6	3.6	3.3
	19/7	7.7	8.9	7.6	6.9	5.4	4.3	4.3	3.9
	9/8	9.5	10.5	8.2	7.3	7.6	5.6	5.6	5.4
	30/8	10.7	10.6	7.7	6.7	9.8	6.5	6.2	5.6
	20/9	12.1	11.0	7.6	6.5	11.0	6.7	7.0	5.8
3. Mean number of lateral flowering branches	19/7/1961	0	3.0	6.8	7.4	0	5.7	4.2	5.8
	9/8	0	6.3	10.1	10.9	1.0	4.7	4.2	8.9
	30/8	1.0	10.7	10.9	12.1	1.5	5.1	6.1	10.4
	20/9	1.3	10.8	11.3	12.5	1.5	5.5	6.7	10.5
4. Mean dry weight of leaves in mg		1483	1756	2084	2032	1343	2021	1720	1439
5. Mean dry weight of stem in mg		101	125	140	191	278	441	613	597
6. Mean weight of seeds in mg		0	8.0	10.1	11.8	0	2.3	2.6	5.2

Conclusion. – In general these results indicate that all the values for the untreated plants (-GA) tend to be higher than the corresponding values for the treated plants (+GA) with the exception of height of stem (character 1) and consequently the dry weight of stem (character 5).

Experiment 8. – Results during a permanent cold treatment.

The percentage of generative plants and the mean number of days to budding have been summarized in table 15.

A comparison between columns 4 and 5 for –L plants of 6 or 7 weeks old indicates that GA increased the percentage of generative plants. Therefore GA tends to reduce juvenility of –L plants judged by the percentage of generative plants. This effect is not clear for +L plants in which the percentage of generative plants is about the same, except for plants of 7 weeks old, columns 2 and 3.

After +L, the treated plants, column 7, need a smaller mean number of days to budding than the untreated ones, column 6, except for plants of 6 weeks old. Plants of 8 or 9 weeks old treated with GA need a highly significant lower mean number of days to budding. After –L, also the treated plants, column 9, need a lower mean number of days than the untreated ones, column 8. The treated plants of 7 or 9 weeks old need a highly significant lower mean number of days to budding. These results after +L and –L clearly indicate that GA has a shortening effect on the time for realization of flower bud formation. Hence GA

TABLE 15. Experiment 8.– The percentage of generative plants and the mean number of days to budding of *Lunaria biennis* plants pretreated with strong supplementary light (+L) compared with natural light only (–L), and with GA, 500 ppm twice per week (+GA) compared with untreated (–GA), while exposed to a permanent cold treatment. Originally ten plants per treatment. Data 327 days after the beginning of vernalization at 15/3/61

1	2	3	4	5	6	7	8	9
	% generative plants				Days to budding			
Pretreatment	+L		–L		+L		–L	
Age (weeks)	–GA	+GA	–GA	+GA	–GA	+GA	–GA	+GA
6	85.7	88.9	0	44.4	250.0	283.6	∾	264.2
7	100	83.3	90	100	223.4	219.6	277.2	234.9
8	100	100	100	100	195.4	149.3	217.7	202.5
9	100	100	100	100	155.3	137.8	174.6	140.1

tends to reduce juvenility decided by the number of days to budding. These results are in accordance with the same results shown in experiment 7 (table 13).

Table 16 summarizes some growth analysis data on plants of table 15.

TABLE 16. Experiment 8.– Growth analysis data on plants of table 15. The cold treatment started at 15/3/61

1		2	3	4	5	6	7	8	9
Pretreatment		–GA				+GA			
Age (weeks)		6	7	8	9	6	7	8	9
Characters	Dates								
Height of stem in cm									
	16/8/61	2.1	2.4	3.1	2.8	15.0	16.2	22.1	22.2
	6/9	3.4	3.7	5.0	5.2	18.0	20.3	30.7	30.7
+L	18/10	4.9	4.8	7.7	8.9	19.8	23.5	39.3	41.8
	29/11	6.6	7.4	12.2	17.1	21.6	26.0	50.7	53.7
	10/1/62	10.0	11.0	15.6	25.0	22.7	29.2	56.0	60.0
	16/8/61	3.0	3.7	3.0	2.9	13.6	18.0	18.5	20.8
	6/9	4.6	5.4	4.3	5.0	16.3	21.5	22.9	26.5
–L	18/10	5.5	6.4	6.3	6.9	18.4	24.4	27.7	33.9
	29/11	6.8	8.0	9.7	11.5	19.0	26.7	31.9	41.3
	10/1/62	8.0	10.1	14.1	17.5	19.6	29.0	36.3	47.2
Diameter of stem in mm									
	16/8/61	2.5	3.3	3.4	3.9	2.6	3.1	3.5	3.2
	6/9	2.6	3.1	3.4	3.3	2.8	3.2	3.5	3.0
+L	18/10	3.1	3.6	3.6	3.7	3.0	3.3	3.7	3.6
	29/11	3.1	3.5	3.7	3.6	3.1	3.1	3.5	3.2
	10/1/62	3.1	3.6	3.7	3.5	3.4	3.3	3.3	3.3
	16/8/61	2.8	3.0	2.9	3.1	2.8	2.8	3.0	3.2
	6/9	3.2	3.3	3.2	3.3	2.9	3.0	3.1	3.2
–L	18/10	3.2	3.3	3.7	3.5	2.9	3.2	3.1	3.5
	29/11	3.4	3.4	3.6	3.5	2.9	3.4	3.0	3.3
	10/1/62	3.5	3.6	3.8	3.5	3.2	3.2	3.0	3.4

The results indicate again that GA increased the height of the stem after both +L and –L for all the measurements, columns 6–9. Also, GA tended to reduce the diameter of the stem of +L plants of 7 or 9 weeks old, columns 7 and 9, and of –L plants of most age-groups, columns 6–9. This effect on the diameter of stem is not as clear cut as shown in experiment 7 (table 14). Photo 6 illustrates the results.

5. Conclusions

The foregoing results indicate that light intensity, subsidiary photosynthesis, has been a factor of paramount importance in the reduction of the duration of the juvenile phase. Much better flowering has occurred in the +L plants in all the experiments. This better flowering of +L plants is accompanied by an enormously great influence of the light intensity on the increase of the growth analysis data, except for the diameter of the stem. It seems that the more generative the plants are, the smaller the stem diameter is. Stress should be laid on the fact that the differences in the growth analysis data between +L and –L refer to limited periods between 6 or 8 and 12 or 14 weeks only, during which the differences in light intensity were applied. Furthermore, the results confirm the expectation that the formation of flower buds at 5 °C takes place more slowly than at higher natural summer temperatures.

It is difficult to draw general conclusions from the experiments with minerals and water. In so far as an effect could be observed, it was usually small and seemed to be rather incidental, especially with plants of 6 or 8 weeks old which were treated for a relatively short time. It seems reasonable to conclude that after +L, nitrogen deficiency (–N) in the presence or absence of water has a relatively good effect on flower and seed formation and may reduce the duration of the juvenile phase a little. On the contrary, after –L, the presence of nitrogen (+N) in the absence of water, and also the presence of water (+W) tend to have a favourable influence on the rapidity of flowering and hence tend to reduce juvenility.

After +L and –L, the results indicate, in general, that the absence of phosphorus (–P) gave a tendency to reduce the duration of the juvenile phase. After –L the absence of potassium (–K) gave smaller growth analysis data and hence tended to prolong the duration of the juvenile phase.

GA reduced the percentage of generative plants only with plants vernalized during 12 weeks (experiment 7). Hence GA has a tendency to maintain juvenility with a vernalization of a limited duration. After both +L and –L it is clear that GA has a hastening effect on the realization of flower bud formation. Therefore GA tends to reduce juvenility judged by the mean number of days to budding.

An interesting side-observation has been the difference in the type of flowering for plants vernalized during 12 weeks. Normal type (terminal and lateral inflorescences) was predominant in the older +L plants, especially after a complete vernalization. The lateral type was exclusive in the younger –L plants after an incomplete vernalization. For plants permanently treated with cold treatment the normal type was predominant in both +L and –L with all age-groups.

CHAPTER V

EXPERIMENTS WITH *SILENE ARMERIA*

1. Demonstration of juvenility

1.1. *Experiment 9. – Age-group of 6–12 weeks old.*

Methods. – By sowing every week from 5/11/59, a series of plants was obtained with ages of 6, 7, 8, 9, 10, 11 or 12 weeks old. After germination the plants were grown under short day (SD), which consists of 8 hours of natural light + additional fluorescent lamps from 8.30 a.m. to 16.30 p.m. On 29/1/60 when the plants reached their ages, twenty plants from SD were transferred to long day (LD), in which the plants received 16 hours of supplementary fluorescent light from 8.00 a.m. to 24.00 p.m. About 20 plants remained in SD as controls and were grown in an ordinary heated greenhouse.

In the description of the experimental results, the indication "plants of ... weeks or days old" means the age of the plants when the LD treatment started and not the real age at the date of observation.

Experimental results. – In this and in the following experiments *S. armeria* flowered for 100% in LD or CL which, of course, is according to expectation. The results of the experiments can only be judged by the mean number of days to budding. For experiment 9 this has been summarized in table 17.

Table 17. Experiment 9. – Mean number of days to budding of *Silene armeria* pretreated for 6, 7, 8, 9, 10, 11 or 12 weeks with short day (SD). The after-treatment was LD with SD as control. Twenty plants per treatment

Age (weeks) \ Treatment	SD → LD	SD → SD
6	71.2	∞
7	69.1	∞
8	65.7	∞
9	52.0	∞
10	48.5	∞
11	44.2	∞
12	45.3	∞

The results indicate that plants grown in SD remain in a purely vegetative condition forever. It is clear that the mean number of days to budding decreases as the age of the plants increases. It may be concluded that the longer the plants stayed in the non-inductive condition (SD), the lower is the mean number of days to budding in LD, and this points to juvenility.

1.2. *Experiment 10. – Age-group of 1–7 weeks old.*

Methods. – In this experiment an age-group with smaller ages was used. From 19th April 1960 seven weekly sowings took place, so that after 7 weeks an age-group of 1, 2, 3, 4, 5, 6 or 7 weeks was available. All the plants were grown under short day (SD), which consists of 8 hours of natural light from 8.30 a.m. to

6.30 p.m. On 7/6/60 all the plants were transferred from SD to continuous light (CL), in which the plants received 24 hours of additional fluorescent light.

Experimental results. – Table 18 summarizes the results with regard to rapidity of budding.

TABLE 18. Experiment 10. – Mean number of days to budding of *Silene armeria* pretreated during 1, 2, 3, 4, 5, 6 or 7 weeks with SD and treated with continuous light (CL). Twenty plants per treatment

Age (weeks)	Days to budding
1	47.8
2	43.5
3	41.7
4	40.3
5	38.6
6	33.6
7	32.3

The mean number of days to budding decreases as the age of the plants increases. In other words, the relatively young plants need a larger number of long days to budding than the relatively old plants. Again, this indicates juvenility.

2. LIGHT INTENSITY

2.1. *Experiment 11. – Age-group of 0, 3, 6, 9, 12, ... or 27 days old.*

Methods. – By sowing every three days from 26/8/60, a series of plants was obtained with ages of 0, 3, 6, 9, 12, 15, 18, 21, 24 or 27 days. The plants from each age-group were divided into two sets:

(a) SD(H)-groups: plants were grown under short day with a relatively high light intensity of 4773 μW/sec/cm^2 ⌀ sphere.

(b) SD(L)-group: plants were grown under a shed from cloth in the same SD, but with a relatively low light intensity of 942 μW/sec/cm^2 ⌀ sphere.

On 22/9/60 all the plants were transferred to long day (LD).

Experimental results. – The mean numbers of days to budding have been summarized in fig. 3.

The differences in number of days to budding between SD(H) and SD(L) are 2.2, 2.5, 0.9, —2.2, 4.1, 0.1, 17.6, 19.3, 34.1 or 33.9 days for plants of 0, 3, 6, 9, 12, 15, 18, 21, 24 or 27 days old respectively. The differences between plants of 0–15 days old are very small and not significant, while those between plants of 18–27 days old are significant. Illustrations in photos 7 and 8.

These results indicate that light intensity did not effect the plants of low ages such as 0–15 days, while as the age of the plants increases, the sensitivity to light intensity also increases.

Table 19 summarizes the growth analysis data on plants of experiment 11, which were collected in order to get an insight into the morphological effects of the differences in light intensity with regard to juvenility.

All the values tend to be greater after SD(H) than the corresponding ones after SD(L), especially with the older plants. The values tend to increase as the age of the plants increases.

Referring to fig. 3, it appears that the greater the growth analysis data are, the more generative the plants are.

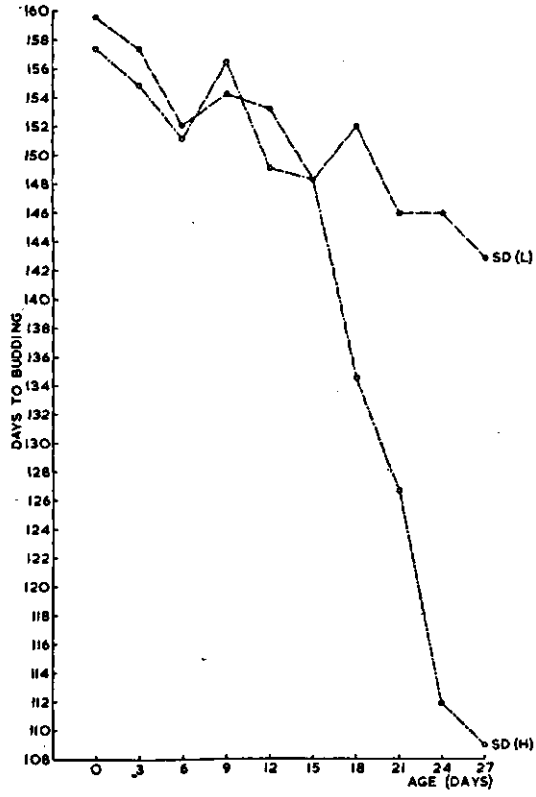

FIG. 3. Experiment 11.– Mean number of days to budding in LD of *Silene armeria* pretreated in short day (SD) with relatively high (H) or low (L) light intensity. Twenty plants per treatment

TABLE 19. Experiment 11.– Growth analysis data on plants of fig. 3, determined 18 weeks after transferring to LD treatment, when all plants of 21–27 days old flowered

	Mean number of leaves		Mean height of stem in cm		Mean diameter of stem in mm		Mean dry weight of leaves in mg		Mean dry weight of stem in mg	
Pretreatment / Age (days)	SD(H)	SD(L)	SD(H)	SD(L)	SD(H)	SD(L)	SD(H)	SD(L)	SD(H)	SD(L)
0	40.0	40.0	3.2	2.9	1.9	1.8	438	440	26	20
3	43.2	40.4	5.6	3.1	2.5	1.7	575	408	53	27
6	46.8	44.2	6.8	3.8	2.7	2.1	628	488	54	35
9	45.2	42.4	6.1	3.5	2.5	2.1	686	408	59	25
12	43.0	45.6	4.5	6.0	2.1	2.2	505	448	33	40
15	46.8	46.0	4.7	6.9	2.7	2.2	693	508	44	61
18	50.0	45.4	7.7	4.4	2.4	2.6	651	579	83	44
21	45.0	48.6	7.4	6.5	2.6	2.5	470	521	77	56
24	53.4	48.8	10.4	7.3	2.5	2.4	679	505	90	55
27	54.2	50.0	10.2	7.7	2.9	2.7	890	700	91	62

3. GIBBERELLINS

3.1. *Experiment 12. – Age-group of 2–5 weeks old.*

Methods. – By sowing every week from 18/1/61, a series of plants was obtained with ages of 2, 3, 4 or 5 weeks old. The plants from each age-group were divided into two sets:

(a) SD(H)-group: The plants were grown under SD with a relatively high light intensity of 3014 $\mu W/sec/cm^2$ ⌀ sphere.

(b) SD(L)-group: The plants were grown under a shed of cloth in the same SD, but with a relatively low light intensity of 1005 $\mu W/sec/cm^2$ ⌀ sphere.

Three days after germination, twenty plants from each age-group in both SD(H) and SD(L) were treated with gibberellic acid (GA), 50 ppm, repeated twice per week. This concentration was chosen on account of a preliminary experiment. On 22/2/61 all the treated plants (+GA) and the controls (–GA) were transferred to LD, and the GA treatment was ended, except for twenty plants of 2 weeks old where it was continued in LD (++GA). The number of applications, as a pretreatment, was 2, 4, 6 or 8 for plants of 2, 3, 4 or 5 weeks old respectively (+GA), while the number of ++GA applications was 16 for twenty plants of 2 weeks old.

Experimental results. – Table 20 summarizes the results with regard to the rapidity of budding.

TABLE 20. Experiment 12. – Mean number of days to budding of *Silene armeria* pretreated during 2, 3, 4 or 5 weeks in SD with high (H) or low (L) light intensity and treated with GA, 50 ppm twice per week during pretreatment (+GA) or permanently (++GA) after transferring to LD. Twenty plants per treatment

Treatment / Age (weeks)	SD(H)			SD(L)		
	–GA	+GA	++GA	–GA	+GA	++GA
2	54.5	51.2	51.6	55.5	57.8	58.9
3	53.7	50.9	–	58.5	58.4	–
4	50.3	49.4	–	56.6	58.3	–
5	49.3	49.5	–	57.4	60.8	–

In general, the –GA and +GA plants need a highly significant lower mean number of days to budding after SD(H) than the corresponding ones after SD(L) pretreatment. These results confirm the results of experiment 11. The results also indicate that GA hastened flower initiation under SD(H), while delayed it after SD(L). After SD(H) plants treated with GA need a lower mean number of days to budding than the untreated plants. The effect of GA on reducing the duration of the juvenile phase, associated with high light intensity as a pretreatment, was significant with plants of 2 weeks old treated as a pretreatment (+GA) or permanently (++GA). On the contrary, after low light intensity SD(L), the delaying effect of GA was especially clear with the older plants of 4 or 5 weeks old. The differences remain rather small, however.

The growth analysis data on plants of table 20 have been summarized in table 21.

Most values are greater after SD(H) than the corresponding ones after SD(L) for all the age-group. This confirms the data from table 19 and again shows the effect of high light intensity. Photos 9 and 10 illustrate the results.

TABLE 21. Experiment 12.– Growth analysis data on plants of table 20, determined 8 weeks after transferring to LD, when all plants of 5 weeks old flowered

Treatments / Age (weeks)	SD(H)			SD(L)		
	–GA	+GA	++GA	–GA	+GA	++GA
	Mean number of leaves					
2	30.8	28.0	29.2	24.8	26.0	24.4
3	32.0	28.4	–	27.2	26.8	–
4	31.6	35.6	–	28.0	26.8	–
5	40.4	34.8	–	26.8	26.4	–
	Mean height of stem in cm					
2	28.5	33.8	45.8	27.2	29.4	39.8
3	31.6	34.0	–	26.8	27.8	–
4	38.1	38.2	–	31.3	30.4	–
5	38.2	37.0	–	27.4	28.4	–
	Mean diameter of stem in mm					
2	3.1	2.8	2.6	3.2	3.0	2.6
3	3.1	2.8	–	3.0	2.7	–
4	3.2	3.1	–	2.8	2.7	–
5	3.6	3.2	–	2.9	2.8	–
	Mean dry weight of leaves in mg					
2	470	378	340	430	480	206
3	515	501	–	363	454	–
4	442	722	–	409	423	–
5	655	556	–	610	446	–
	Mean dry weight of stem in mg					
2	63	71	161	33	80	121
3	78	75	–	34	58	–
4	77	129	–	74	73	–
5	162	176	–	61	50	–

The effect of GA is especially clear after the permanent treatment (++GA): Mean number of leaves, mean diameter of stem and mean dry weight of leaves are decreased, mean height of stem and mean dry weight of stem are increased. The same tendency can be found for the GA treatments of limited duration (+GA), but the effects remain small.

4. CONCLUSIONS

The conclusions to be drawn from the experiments are that the duration of the juvenile phase is rather short. High light intensity reduced the length of the juvenile phase. The effect of GA was small; it reduced the duration of the juvenile phase especially after high light intensity and when frequently applied.

CHAPTER VI

EXPERIMENTS WITH *SALVIA OCCIDENTALIS*

1. Demonstration of juvenility in seedlings and cuttings

1.1. *Experiment 13. – Age-group of 6–12 weeks old.*

Methods. – From 5th November 1959 seven weekly sowings took place, so that after 7 weeks an age-group of 6, 7, 8, 9, 10, 11 or 12 weeks was available. These plants have been grown in an ordinary heated greenhouse under long day (LD), in which the plants received supplementary fluorescent light of 16 hours. On 29/1/60 all the plants were transferred to short day (SD).

In the description of the experimental results, the indication "plants of ... weeks or days old" means the age of the plants when the SD treatment started.

Experimental results. – After transferring the plants from LD to SD, all the plants of 6–12 weeks old initiated flower buds at the same time. The mean number of days to budding was 27 days for all the age-group. Hence no juvenile phase was demonstrated, probably because plants of 6 weeks old were already completely adult.

1.2. *Experiment 14. – Age-group of 1–8 weeks old.*

Methods. – Because there is no difference in the time of flower bud initiation within 6–12 weeks old (experiment 13), we took a lower age-group of 1–8 weeks old. By sowing every week from 27/4/60, a series of plants was obtained with ages of 1, 2, 3, 4, 5, 6, 7 or 8 weeks old. All the plants were grown under continuous light (CL). On 22/6/60 the plants were transferred to short day (SD).

Experimental results. – According to expectation all plants in SD in this and following experiment flowered for 100%. The experimental results will be judged by the mean numbers of days to budding.

Table 22 summarizes the results of experiment 14.

Table 22. Experiment 14. – Mean number of days to budding in SD of *Salvia occidentalis* plants grown in CL during 1, 2, 3, 4, 5, 6, 7 or 8 weeks. Twenty plants per treatment

Age (weeks)	Days to budding
1	34.6
2	32.0
3	30.2
4	29.2
5	28.6
6	28.6
7	28.4
8	28.0

These results indicate that the mean number of days to budding decreases as the age of plants of 1–3 weeks old increases; afterwards it tends to remain the same for all other age-group of 4–8 weeks old. It is evident that the younger plants need a higher number of days to budding than the older ones. From these

results it seems that a juvenile phase exists which lasts up to about three weeks. Experiments 16 and 17 will confirm these results.

1.3. *Experiment 15. – Cuttings with age-group of 0, 1, 2, 3, 4, ...* or *10 weeks old.*

Since *Salvia occidentalis* can be easily propagated vegetatively, it is worth while to study its relation to juvenility.

Methods. – Cuttings were made at 11/7/60. All the cuttings were grown under natural long day, except 25 cuttings which were grown directly under SD. All the cuttings were potted at 4/8/60. Every week after 11/7/60 about 25 plants were transferred to SD, so that a series of plants was obtained which had been exposed to LD for 0, 1, 2, 3, 4, 5, 6, 7, 8, 9 or 10 weeks, hence 11 groups.

Experimental results. – The mean numbers of days to budding in SD have been summarized in table 23.

TABLE 23. Experiment 15.– Mean number of days to budding in SD of *Salvia occidentalis* cuttings grown in natural long day (ND) during 0, 1, 2, 3, 4, 5, 6, 7, 8, 9 or 10 weeks. Twenty five plants per treatment

Age (weeks)	Days to budding
0	38.2
1	28.4
2	27.9
3	25.7
4	22.6
5	23.3
6	22.7
7	22.4
8	23.6
9	22.8
10	22.4

These results indicate that plants of 0–3 weeks old need more days to budding than plants of 4–10 weeks old. It is evident that the older plants need fewer days to budding than the younger plants, while in the plants of 0–3 weeks more days for budding are needed, the younger the plants are. These plants of 0–3 weeks old were less sensitive to SD treatment. From the results in table 22 and 23, it may be concluded that the growth of the plants after vegetative propagation has a favourable influence on the rapidity of flowering compared with seedlings of the same age, hence tends to reduce juvenility.

2. LIGHT INTENSITY

2.1. *Experiment 16. – Age-group of 0, 3, 6, 9, 12, ...* or *27 days old.*

Methods. – By sowing every three days from 26/8/60, a series of plants was obtained with ages of 0, 3, 6, 9, 12, 15, 18, 21, 24 or 27 days old, hence 10 groups. The plants from each age-group were divided into three sets:
(a) ND(H)-group: The plants were grown under natural long day with average light intensity of 5212 μW/sec/cm^2 ⌀ sphere.
(b) ND(L)-group: The plants were grown under a shed from cloth in natural long day with a light intensity of 1884 μW/sec/cm^2 ⌀ sphere.

(c) CL-group: The plants were grown under continuous light with an average intensity of 3768 μW/sec/cm² ⌀ sphere.

On 22/9/60 all the plants were transferred to SD.

Experimental results. – Table 24 summarizes the results with regard to rapidity of budding.

TABLE 24. Experiment 16.– Mean number of days to budding in SD of *Salvia occidentalis* plants grown during 0, 3, 6, 9, 12, 15, 18, 21, 24 or 27 days in different pretreatments: ND(H) – Natural long day with high light intensity
ND(L) – Natural long day with low light intensity
CL – Continuous light with relatively high intensity
Twenty plants per treatment

Age (days) \ Pretreatment	ND(H)	ND(L)	CL
0	38.5	37.7	38.9
3	37.3	37.0	40.3
6	34.1	32.9	38.4
9	32.9	31.9	37.3
12	29.8	29.9	37.3
15	29.9	29.1	34.7
18	28.1	27.6	34.0
21	27.6	27.2	31.1
24	26.9	27.7	31.4
27	27.3	26.8	31.9

There is no significant difference between ND(H) and ND(L) pretreatments for all the age-group except for 6 or 18 days old, where the high intensity gives slightly higher values. On the other hand, the differences between CL and ND(H) or ND(L) are highly significant. Evidently the difference between CL and ND with high or low light intensity is due to the inhibitive action on floral initiation which is stronger in CL than in ND.

From these results it may be concluded that light intensity cannot be demonstrated to influence the juvenile phase, because its eventual action is masked by the light inhibition. Photos 11, 12 and 13 illustrate the results.

3. GIBBERELLINS

3.1. *Experiment 17. – Age-group of 2–5 weeks old.*

Methods. – From 3rd February 1961 four weekly sowings took place, so that after 5 weeks an age-group of 2, 3, 4 or 5 weeks was available. All the plants were grown under long day (LD). Four days after germination 25 plants from each age-group were treated with 50 ppm GA, repeated twice per week. On 10/3/61 all the treated plants (+GA) and the controls (–GA) were transferred to SD, and the GA treatment was ended, except for 25 plants of 2 or 3 weeks old, where it was continued in SD (++GA). The number of applications of GA was, as a pretreatment (+GA), 2, 3, 5 or 7 for plants of 2, 3, 4 or 5 weeks old respectively, while as permanent treatment (++GA) it was 9 or 10 applications for plants of 2 or 3 weeks old respectively.

Experimental results. – Table 25 presents the results.

TABLE 25. Experiment 17.– Mean number of days to budding in SD of *Salvia occidentalis* plants, grown during 2, 3, 4 or 5 weeks in LD and treated with 50 ppm GA, repeated twice per week during pretreatment (+GA) or permanently (++GA). Twenty five plants per treatment

	Days to budding		
Age (weeks) \ Treatment	-GA	+GA	++GA
2	29.6	29.1	28.0
3	28.8	27.8	27.7
4	26.5	25.8	–
5	26.4	26.0	–

These results indicate that GA had a favourable, but small influence on the flower initiation. This effect of GA was highly significant for plants of 2 weeks old treated with GA as a pretreatment (+GA) and also treated permanently (++GA). The effect with the other age-groups of 3, 4 or 5 weeks old was not significant, except with plants of 4 weeks old.

TABLE 26. Experiment 17.– Growth analysis data on plants of table 25, determined four weeks after transferring to SD

Pretreatment during ... weeks	-GA	+GA	++GA
	Mean number of leaves		
2	8.4	7.6	7.6
3	15.6	11.2	11.6
4	26.0	18.4	–
5	30.4	21.6	–
	Mean height of stem cm		
2	3.6	8.6	14.3
3	5.6	17.9	18.9
4	11.0	24.7	–
5	15.1	38.5	–
	Mean diameter of stem mm		
2	1.1	1.0	1.0
3	1.3	1.2	1.4
4	1.6	1.4	–
5	1.8	1.7	–
	Mean dry weight of leaves mg		
2	45	33	27
3	77	65	41
4	186	100	–
5	242	170	–
	Mean dry weight of stem mg		
2	5	9	13
3	13	25	23
4	46	57	–
5	70	127	–

From these results it may be concluded that GA tends to reduce the duration of the juvenile phase a little, if used as a pretreatment in the non-inductive photoperiod, or even permanently (++GA) during the inductive photoperiod. Illustrations in photo 14.

The growth analysis data on plants of table 25 have been summarized in table 26.

The results indicate that GA reduces the mean number of leaves, mean diameter of stem and mean dry weight of leaves. The lowest mean dry weight of leaves occurred in plants treated permanently (++GA). On the contrary, GA increases the height of stem and consequently the dry weight of stem. Plants treated permanently (++GA) had the greatest height and dry weight of stem for plants of 2 weeks old.

These results indicate that while GA reduces the dry weight of leaves, due to the lower mean number of leaves, it increases the dry weight of stem, due to the greater height of stem, which had a somewhat favourable influence on the rapidity of flower bud initiation and hence tends to reduce juvenility.

4. Conclusions

The foregoing results indicate that the duration of the juvenile phase was very short and lasted up to 3 weeks. The growth of the plants after vegetative propagation has a favourable influence on the rapidity of flowering compared with seedlings of the same age, hence tends to reduce juvenility. Light intensity cannot be demonstrated to influence the duration of the juvenile phase on account of the light inhibition. GA tends to reduce juvenility a little.

CHAPTER VII

GENERAL DISCUSSION AND CONCLUSIONS

From the review of the literature in chapter I (p. 2) it was evident that there are two concepts about juvenility. The first one indicates that the duration of the juvenile phase cannot be influenced, and that it is a fixed character. The second concept claims that the duration of the juvenile phase can be influenced, although there is no agreement on how this is achieved. Several investigators stated that any treatment which restricts the vegetative growth, will hasten the transition to the adult phase. Other investigators are of opinion that all factors which promote or encourage vigorous vegetative growth, will reduce the length of the juvenile phase.

In the following, the experimental results will be discussed, especially with regard to the above stated problems.

1. *Vernalization.* – The results with *Lunaria biennis* confirm that the effect of low temperature may be direct: the formation of flowers may take place during a prolonged cold treatment (122). After high light intensity (+L) the young plants, such as 6 weeks old, already begin to react to low temperature, while after low light intensity (-L) they cannot be vernalized. These results indicate

that there is a correlation between the light intensity and the vernalizing effect of low temperature.

After both +L and –L, all the plants that flowered after a permanent cold treatment, formed the normal type of flowers, consisting of both terminal and lateral inflorescences. In case of plants which received only 12 weeks cold, there was an abnormal type of flowering, due to incomplete vernalization, depending on differences in age and light intensity. It seems that relatively old plants after high light intensity and a limited duration of cold, perceive the low temperature by the growing point – which is in accordance with most concepts in the literature (25, 45, 96, 102) – and the plants form the normal type of flowers. On the other hand, relatively young plants, after low light intensity and a limited duration of cold, perceive the low temperature by the leaves only (127) and the plants form the lateral flowering type. This is in harmony with recent results of WELLENSIEK (128) that vernalization takes place in dividing cells only. These results may support the second hypothesis of ROBBINS (97) that meristems themselves age and change during the life of the plant. There are juvenile and adult meristems.

2. *Light intensity.* – The results with *Lunaria biennis* show very convincingly that by applying strong supplementary light during the period which precedes vernalization, relatively young plants can be brought to flower bud formation or to a more rapid flower bud formation in comparison with plants which have been grown under poor light conditions. The results also indicate that the quantitative effect on several morphological characters may be great.

In *Silene armeria*, a long-day plant, the existence of a juvenile phase could be demonstrated. Also, the results clearly indicate that light intensity is very important in reducing the length of this juvenile phase.

Also in *Salvia occidentalis*, a short-day plant, the existence of a juvenile phase could be demonstrated but it lasts relatively very short. Light intensity, low or high, as a pretreatment during long days, did not significantly effect the time of flowering of plants of varying ages in short day. On the contrary, after continuous light as a pretreatment, the plants need more SD cycles for flower bud formation than after pretreatments with both high or low light intensity. These results support the work of WELLENSIEK (123) and others, who stated that light exerts an inhibitory action on floral initiation of short-day plants, while darkness removes this inhibition. This situation makes it impossible to demonstrate an eventual effect of light on juvenility.

The results on light intensity strongly support the second concept which claimed that the duration of the juvenile phase can be influenced and also support the hypothesis that products of photosynthesis play an important role in modifying the juvenile phase.

3. *Soil moisture.* – The results with *Lunaria biennis* illustrate that a good supply of water, in general, may reduce the length of the juvenile phase in comparison with deficiency of water. It is well known that water is essential for plant growth, while water deficit is one of the most common factors limiting growth. So these results support those of other investigators that factors promoting growth will reduce the duration of the juvenile phase.

4. *Mineral nutrition.* – With *Lunaria biennis* the results, in general, indicate that nitrogen deficiency after high light intensity (+L), but sufficient nitrogen after

low light intensity (–L), reduces the duration of the juvenile phase a little. These results confirm those of ARTHUR *et al.* (3), who found that the percentages of carbohydrate and nitrogen could be changed by varying light intensity and/or length of day.

The results of the N, P, K-experiment indicate that phosphorus deficiency, for +L plants of 8 or 10 weeks old, and also for –L plants of 8 weeks old, had a small influence on the reduction of juvenility. On the contrary, potassium deficiency prolongs the duration of the juvenile phase after both +L and –L.

The quantitative results indicate that nitrogen, phosphorus and potassium do not play an important part as determining factors in reducing juvenility. Our results with nitrogen are in accordance with the work of WITHROW (135) and others that nitrogen is not a determining factor in floral initiation, as are temperature and photoperiod.

5. *Gibberellins.* – With *Lunaria biennis* 500 ppm GA reduces the percentage of generative plants after vernalization during 12 weeks and hence tends to maintain juvenility. On the other hand, GA accelerates the realization of flower bud formation after both +L and –L. Therefore GA tends to reduce juvenility, decided by the mean number of days to budding.

With *Silene armeria* our results show that 50 ppm GA as a pretreatment in the non-inductive photoperiod reduces the juvenile period, especially with high light intensity, but prolongs it with low light intensity. These results point to the importance of light intensity in relation with gibberellic acid as factors in influencing the duration of the juvenile phase. They agree with the work of CARR *et al.* (19) and also with LANG (75), see p. 11.

With *Salvia occidentalis* 50 ppm GA reduces the duration of the juvenile phase when used as a pretreatment in the non-inductive photoperiod and even when used in both non-inductive and later in inductive photoperiods. These results disagree with the work of many authors that gibberellins do not influence the flowering of short-day plants (47, 53, 74) and even inhibit their flowering (10, 110). *S. occidentalis* forms one of the few cases of short-day plants that react to GA, as for instance *Perilla crispa* (126).

6. *Conclusions.* – Our results strongly support the second concept claiming that no fixed juvenile phase exists, but that it can be modified. Also, they support the results of the investigators, who stated that factors which promote vegetative growth, will reduce the duration of the juvenile phase, and that the adult phase is reached when a certain amount of energetic and/or building substances – products of photosynthesis – is available.

These results were obtained from experiments with herbaceous plants and cannot be applied as such to woody plants without special research. However these researches may be conducted on the main ideas, derived from the present work, as follows: In order to shorten the duration of the juvenile phase for flowering, we may subject the seedlings firstly to the optimal factors which promote or encourage vigorous vegetative growth and increase the periods of active growth, and secondly to the optimal environment for flower induction.

SUMMARY *

1. This work was carried out to determine whether the duration of the juvenile phase for flowering is a fixed character or whether it can be influenced by external growth factors. An attempt has been made to provide a wide review of most aspects and probabilities of influencing juvenility.

2. The literature concerning the effect of the individual environmental factors has been discussed in what is considered to be their logical order of importance. Vernalization, photoperiod, and light intensity are obviously the predominant factors in controlling flowering. They are always associated with other factors, such as soil moisture, mineral nutrition, and gibberellic acid, which may or may not be limiting.

3. We have worked with herbaceous plants which can be handled more easily and which will give results more quickly than woody plants. *Lunaria biennis* was chosen as a cold requiring biennial plant, *Silene armeria* as a long-day plant, and *Salvia occidentalis* as a short-day plant.

4. *Lunaria biennis.* – The duration of the juvenile phase can be strongly influenced. The photosynthesis is a factor of direct and great importance in reducing the length of the juvenile phase. The low temperature acts only on plants of a certain age, and photosynthesis preceding it may control this age. In general, the young plants cannot be vernalized, especially after low light intensity (–L) and are completely juvenile. Relatively old plants after both high light intensity (+L) and (–L) are in an adult stage and need relatively little cold. In between those two is a transitory stage, where more cold is required, the younger the plants are, especially after –L. Incomplete vernalization has resulted in the predominant formation of lateral flower buds, which could be explained by leaf vernalization.

Nitrogen deficiency after +L, but a sufficient amount of nitrogen after –L had a small influence on the reduction of juvenility. Soil moisture, nitrogen, phosphorus, and potassium do not play an important part as determining factors in reducing the duration of the juvenile phase.

Gibberellic acid (GA) lowers the percentage of generative plants in every age-group for +L plants after vernalization during 12 weeks, and hence tends to maintain juvenility. On the other hand, GA accelerates the realization of flower bud formation after both +L and –L. Therefore GA tends to reduce juvenility, judged by the number of days to budding.

5. *Silene armeria.* – The duration of the juvenile phase is rather short. Nevertheless, high light intensity reduces the duration of the juvenile phase for plants treated during 18 to 27 days; during shorter periods it is not effective yet. GA, when frequently applied, reduces the length of the juvenile phase a little, especially after high light intensity, while tends to prolong it after low light intensity.

6. *Salvia occidentalis.* – Plants of 4 weeks old or more are adult. The juvenile phase exists up to 3 weeks. The growth of the plants after vegetative propagation

* The Arabic figures in this summary refer to the corresponding chapters.

has a favourable influence on the rapidity of flowering compared with seedlings of the same age, hence tends to reduce juvenility. Light intensity cannot be demonstrated to influence the duration of the juvenile phase on account of the light inhibition. GA reduces the duration of the juvenile phase a little.

7. *Conclusions.* – In general, the results strongly indicate that no fixed juvenile phase exists and that the juvenile phase can be modified. The photosynthesis has been a determining factor of primary importance in the reduction of the duration of the juvenile phase, while soil moisture, mineral nutrition, and GA are not decisive factors, but nevertheless may influence the juvenile phase a little. In general, it may be concluded that factors, which promote vigorous vegetative growth and increase the periods of active growth, will reduce the duration of the juvenile phase. Our experiments do not give definite results with regard to the juvenile phase in woody plants, but they may be considered to give directions for future research with those plants.

Acknowledgements

I gratefully acknowledge my indebtedness to Professor Dr. Ir. S. J. Wellensiek for suggesting the problem, for his valuable advice, stimulating criticism and encouragement throughout the course of the work and the preparation of the manuscript.

I express my sincere gratitude to my Government of the U.A.R., Egypt for providing the opportunity and for the financial arrangements without which this study would have been impossible.

SAMENVATTING *

Verkorting van de jeugdfase voor bloei

1. Het onderzoek is uitgevoerd om na te gaan of de duur van de jeugdfase voor bloei een vaststaand iets is of beïnvloed kan worden door uitwendige groeifactoren. Gepoogd is een uitgebreid overzicht te verkrijgen van de meeste gezichtspunten en mogelijkheden bij het beïnvloeden van de jeugdfase.

2. De literatuur over de invloed van de afzonderlijke uitwendige factoren is nagegaan in de waarschijnlijke volgorde van belangrijkheid. Vernalisatie, fotoperiodiciteit en lichtintensiteit zijn blijkbaar de overheersende factoren voor het verkrijgen van bloei. Deze factoren zijn steeds gekoppeld aan factoren zoals vochtigheid van de grond, minerale voeding en gibberellazuur, welke al of niet beperkende factoren kunnen zijn.

3. Gewerkt is met kruidachtige gewassen, welke gemakkelijk geteeld kunnen worden en welke sneller resultaat geven dan houtachtige gewassen. *Lunaria biennis* is gekozen als een koudebehoeftige plant, *Silene armeria* als een langedag plant en *Salvia occidentalis* als een korte-dag plant.

* De arabische cijfers in dit hoofdstuk hebben betrekking op de overeenkomstige hoofdstukken.

4. *Lunaria biennis.* – De duur van de jeugdfase kan in hoge mate worden beinvloed. De fotosynthese is van direct en van groot belang voor het verminderen van de duur van de jeugdfase. De lage temperatuur is alleen werkzaam bij planten van een bepaalde leeftijd en de voorafgaande fotosynthese is bepalend voor deze leeftijd. Over het algemeen kunnen jonge planten niet gevernaliseerd worden, vooral niet na lage lichtintensiteit (–L); zij zijn volledig in de jeugdfase. Betrekkelijk oude planten, zowel na hoge- (+L), als na lage lichtintensiteit, zijn in een volwassen stadium en hebben betrekkelijk weinig koude nodig. Hiertussen ligt een overgangsstadium, waarin meer koude nodig is naarmate de planten jonger zijn, vooral na –L. Onvolledige vernalisatie resulteerde in de vorming van hoofdzakelijk laterale bloemknoppen, welke verklaard konden worden door bladvernalisatie.

Stikstofgebrek na +L en een voldoende hoeveelheid stikstof na –L hadden een geringe invloed op de verkorting van de jeugdfase. Bodemvochtigheid, stikstof, fosfor en kali zijn geen belangrijke factoren bij het verkorten van de duur van de jeugdfase.

Gibberellazuur (GA) vermindert het percentage generatieve planten in elke leeftijdsgroep bij +L planten na vernalisatie gedurende 12 weken; dit wijst er op, dat GA de jeugdfase verlengt. Van de andere kant versnelt GA de realisatie van de bloemknopvorming, zowel na +L als na –L. Daarom kan men zeggen, dat GA de jeugdfase bekort, wanneer deze beoordeeld wordt naar het aantal dagen tot aan de bloemknopvorming.

5. *Silene armeria.* – De duur van de jeugdfase is nogal kort. Toch verkort +L de duur van de jeugdfase bij planten, die gedurende 18 tot 27 dagen behandeld zijn; een behandeling gedurende kortere tijd is nog niet werkzaam. GA, herhaaldelijk toegediend, verkort de jeugdfase een weinig na +L; na –L zijn er aanwijzingen voor een verlenging.

6. *Salvia occidentalis.* – Planten van 4 weken of ouder zijn in de volwassen fase. De jeugdfase duurt 3 weken. Planten, die vegetatief vermeerderd worden, komen sneller in bloei dan zaailingen van dezelfde leeftijd; dit wijst in de richting van een verkorting van de jeugdfase. Er kon niet aangetoond worden, dat de lichtintensiteit invloed had op de duur van de jeugdfase, dit vanwege de lichtremming. GA verkort de duur van de jeugdfase een weinig.

7. *Conclusies.* – De resultaten tonen over het algemeen duidelijk aan, dat er geen bepaalde jeugdfase bestaat en dat deze gemodificeerd kan worden. De fotosynthese was van primair belang voor de verkorting van de duur van de jeugdfase, terwijl de vochtigheid van de grond, de minerale voeding en GA de duur van de jeugdfase een weinig beïnvloeden. Over het algemeen kan geconcludeerd worden, dat factoren, welke een sterke vegetatieve groei bevorderen en de perioden van actieve groei vermeerderen, de duur van de jeugdfase verkorten. De proeven geven geen uitsluitsel over de duur van de jeugdfase bij houtachtige gewassen, maar kunnen aanwijzingen geven voor toekomstig onderzoek bij deze gewassen.

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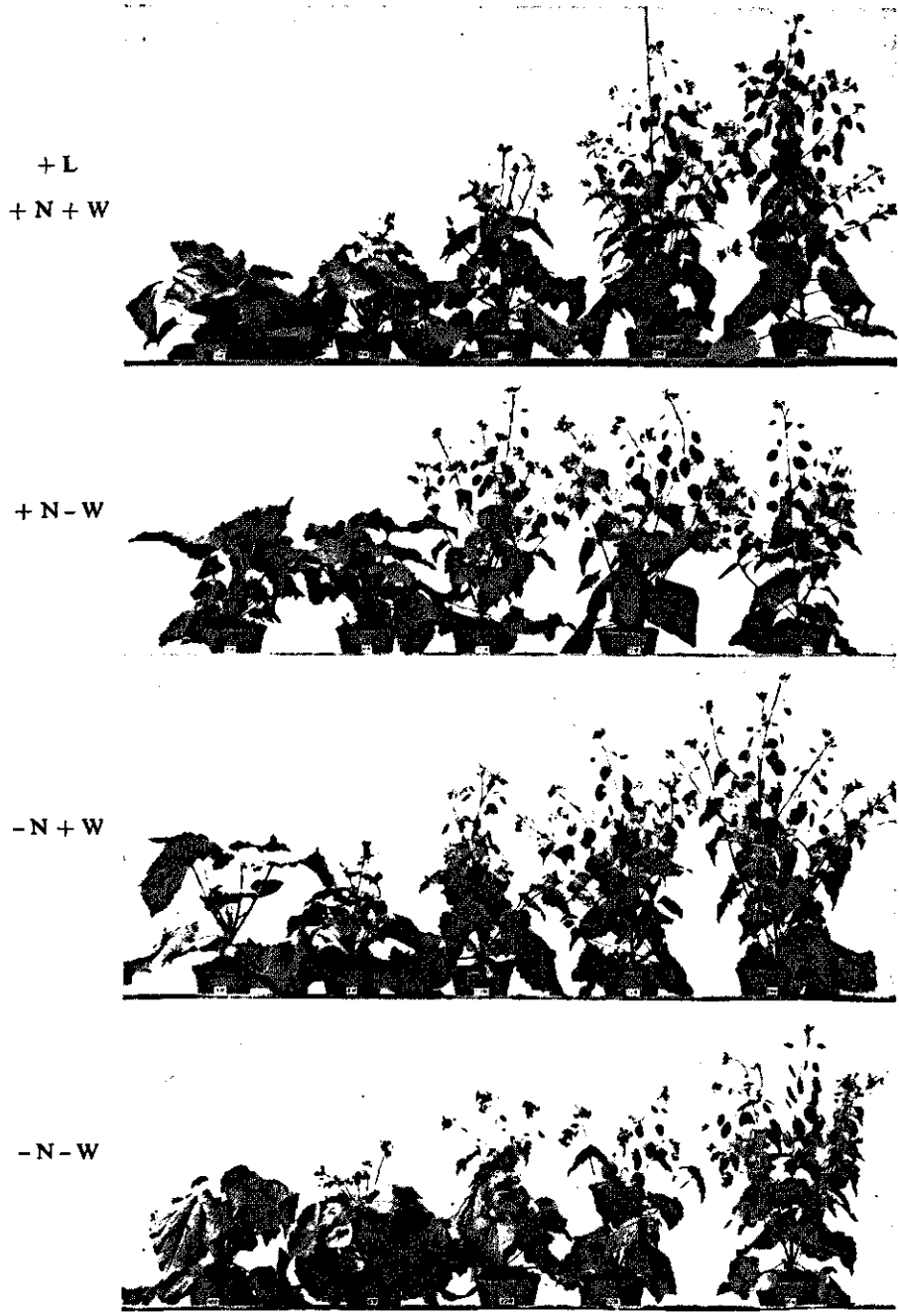

PHOTO 1. Experiment 3 – Representive plants grown under supplementary strong light (+ L),
from left to right: during 6, 8, 10, 12 or 14 weeks; from top to bottom, pretreated with:
+ N + W = with nitrogen, with water
+ N - W = with nitrogen, without water
- N + W = without nitrogen, with water
- N - W = without nitrogen, without water, before *vernalization during 12 weeks.*
Photo was taken 8 weeks after the end of the vernalization.

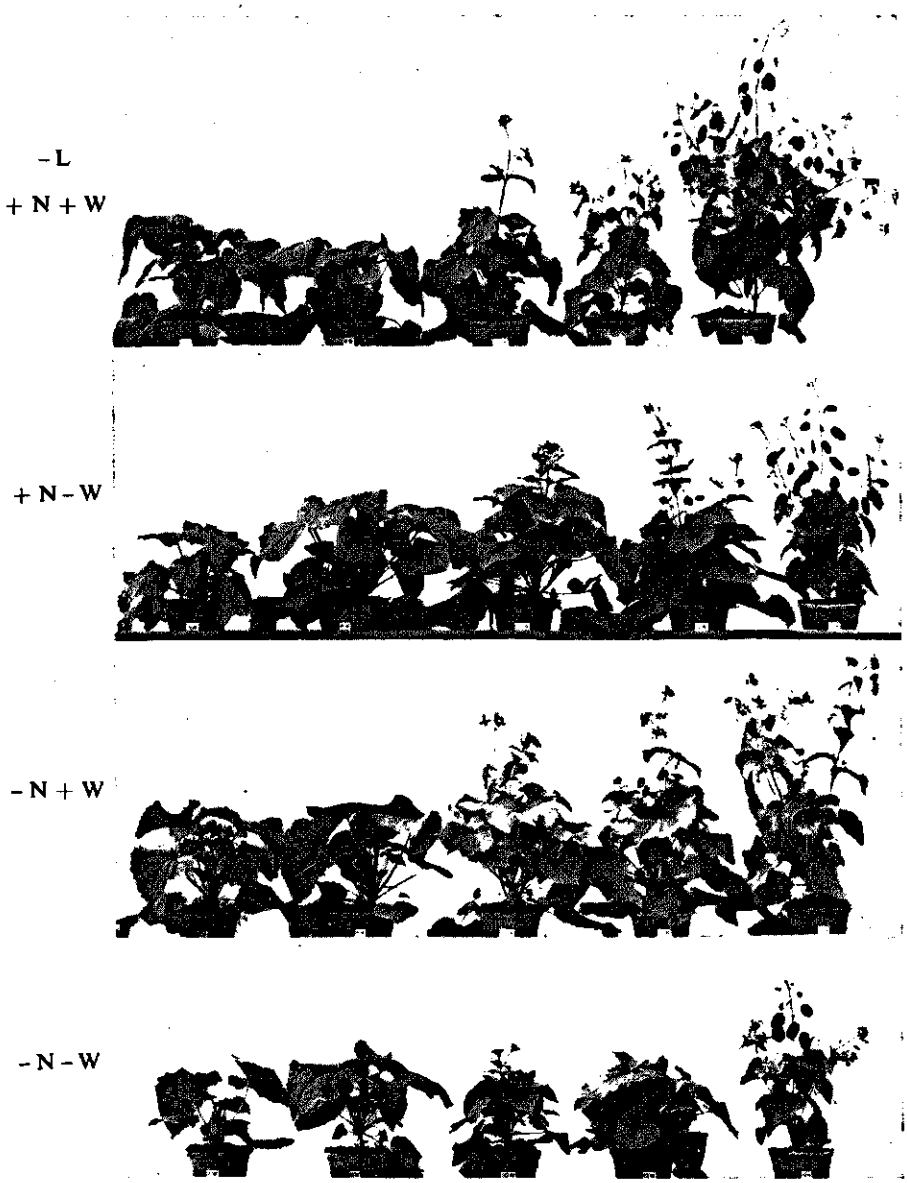

PHOTO 2. Experiment 3 – As photo 1, but with plants grown under poor natural light conditions (-L).

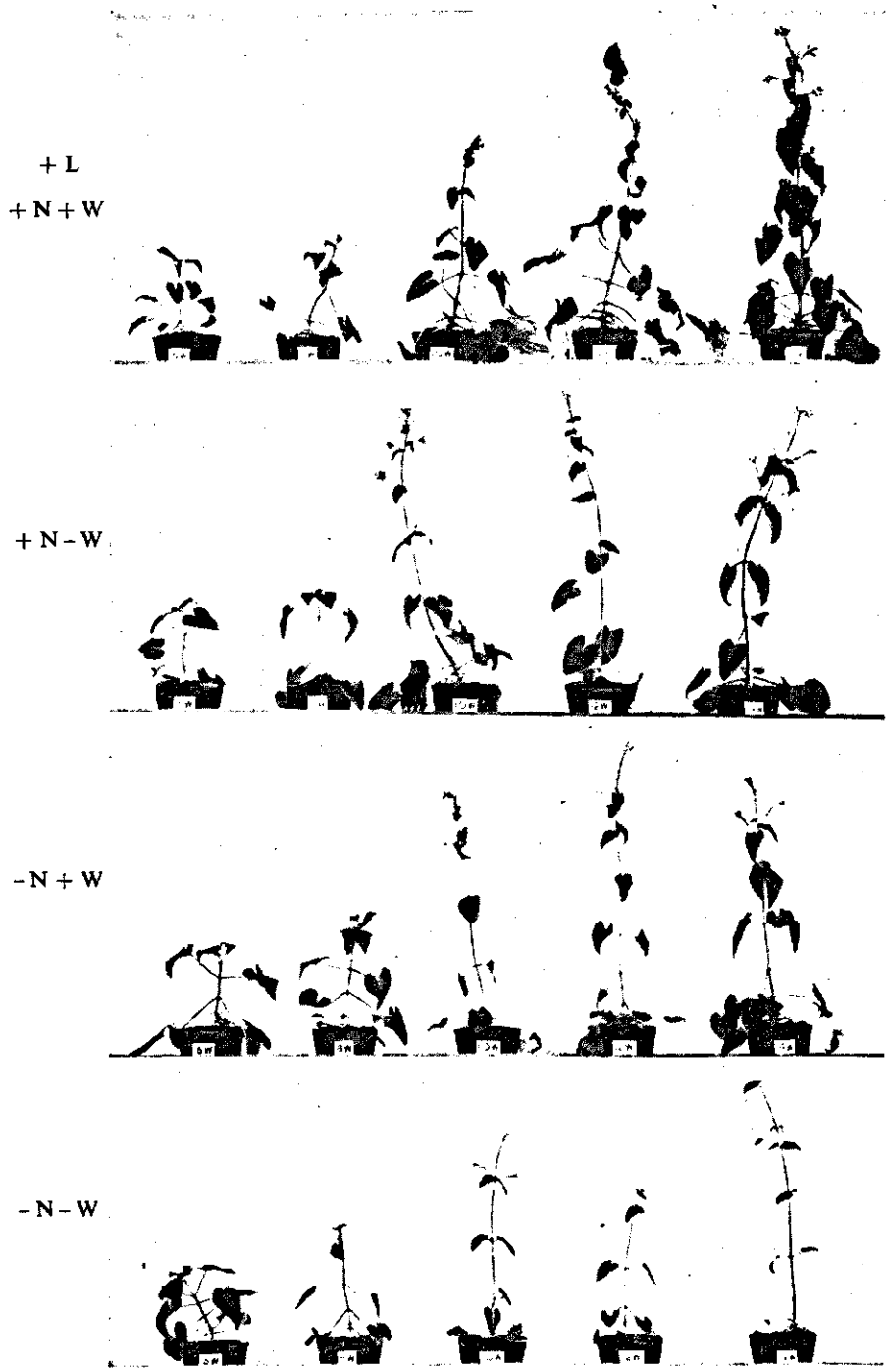

PHOTO 3. Experiment 4 – Representive plants grown under supplementary strong light (+ L),
from left to right: during 6, 8, 10, 12 or 14 weeks; from top to bottom, pretreated with:
+ N + W = with nitrogen, with water
+ N - W = with nitrogen, without water
- N + W = without nitrogen, with water
- N - W = without nitrogen, without water, before a *permanent cold treatment*.
Photo was taken after a cold treatment of 360 days.

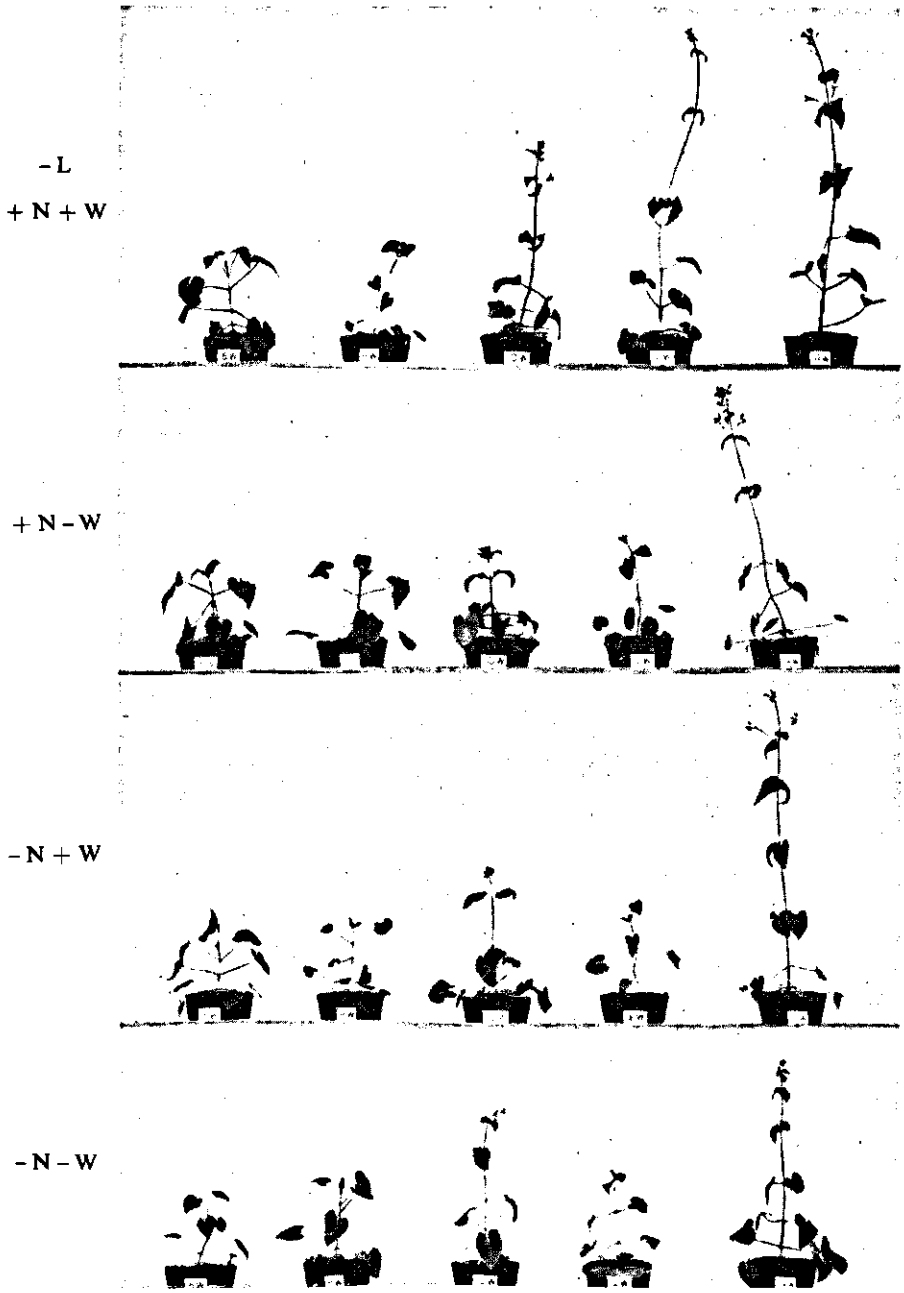

PHOTO 4. Experiment 4 – As photo 3, but with plants grown under poor natural light conditions (– L).

PHOTO 5. Experiment 7. – Representive plants grown under supplementary strong light (+ L),
left: during 6, 7, 8 or 9 weeks untreated plants (– GA);
right: plants treated with GA, 500 ppm twice per week as a pretreatment (+ GA), before *vernalization during 12 weeks*. Photo was taken 7 weeks after the end of the vernalization.

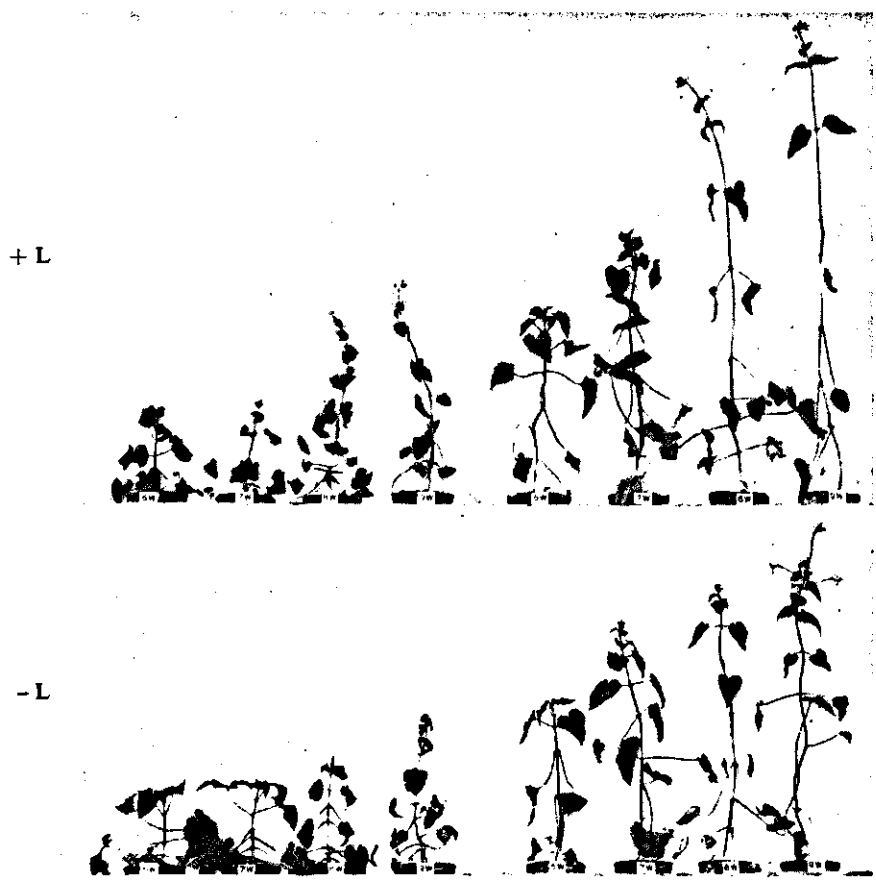

PHOTO 6. Experiment 8. – top: plants grown under supplementary strong light (+ L); bottom: plants grown under poor natural light condition (– L);
left: during 6, 7, 8 or 9 weeks untreated plants (– GA);
right: plants treated with GA, 500 ppm twice per week as a pretreatment (+GA), before a *permanent cold treatment*. Photo was taken after a cold treatment of 327 days.

PHOTO 7. Experiment 11. – Plants of *Silene armeria*, pretreated in short day with high light intensity, SD (H), during – from left to right – 27 days, 24 days,... 0 days, followed by long day (LD). Photo was taken 18 weeks after the beginning of the LD-treatment. Compare with photo 8.

PHOTO 8. Experiment 11. – As photo 7, but pretreated in short day with low light intensity, SD (L).

PHOTO 9. Experiment 12. – Plants of *Silene armeria*, pretreated in short day with high light intensity, SD (H), during 2, 3, 4 or 5 weeks, from left to right, and untreated (–) or treated (+) with 50 ppm GA twice per week, photographed 10 weeks after transferring to LD. Plants of 2 weeks old were also treated twice per week after transferring to LD (++). Compare photo 10.

PHOTO 10. Experiment 12. – As photo 9, but pretreated in short day with low intensity, SD (L).

PHOTO 11. Experiment 16. – Seedlings of *Salvia occidentalis*, pretreated during 27, 24, 21, ... 0 days (from left to right) in natural long day with high light intensity ND (H), photographed 6 weeks after transferring from ND (H) to SD.

PHOTO 12. Experiment 16. – As photo 11, but seedlings pretreated in natural long day with low light intensity ND (L).

PHOTO 13. Experiment 16. – As photo 11, but seedlings pretreated in continuous light (CL).

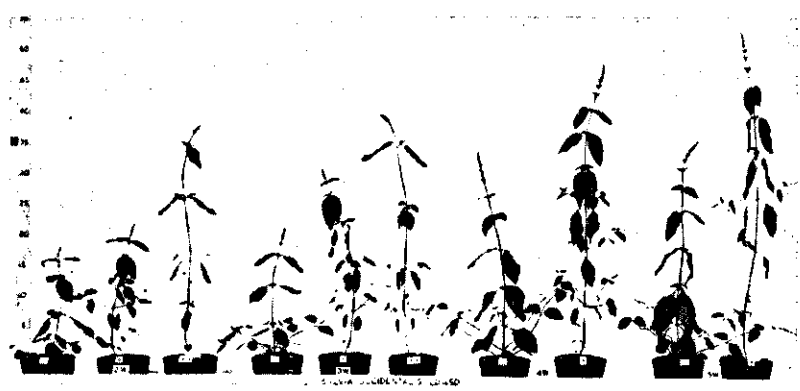

PHOTO 14. Experiment 17. – Plants of *Salvia occidentalis* grown in LD during 2, 3, 4 or 5 weeks (from left to right), untreated (–), treated during the LD period (+) or permanently (++) with 50 ppm GA twice per week, photographed 6 weeks after transferring from LD to SD.