Botany. — *On the Relation between Flower-Formation and Temperature. II. (Bulbous Irises).* By A. H. BLAAUW. (Contribution N⁰. 68 of the Laboratory for Plantphysiological Research, Wageningen).

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Basing ourselves on the series of experiments described in the first part and with reference to the communications Nos. 41 and 50 on the influence of the temperature in summer on flowering or non-flowering (Proceed. Vol. XXXVII and XXXIX), we can now outline *the relation between flower-formation and temperature* with these Irises as follows.

I. Bulbous plants in general, and among these the Bulbous Iris, must have reached a certain size before they can proceed to the formation of flowers. Under a certain limit the small bulbs can in no way, at least by no temperature-treatment, be induced to form flowers. It should be added that it is not known as yet whether e.g. by transplantation or by injection of some substance such young bulbs can be made to flower. Such bulbs however would not be in their natural state, which we are considering here.

A certain size and a certain weight must have been reached before, under definite conditions, generative organs can be produced. It is not age of which we are speaking here, but size or weight, for with the Hyacinth e.g. this flowering limit is not determined by the fact whether the bulb is already 3 years old and not 2; no, a two-year-old bulb, measuring 8 cm in circumference, will (with l'Innocence) under good condition usually be able to form a spike, but a three-year-old bulb of only 6 cm circumference will hardly ever do so. A tulip has a so-called one year bulb; if the bulbs (with Pride of Haarlem) weigh less than 8 g, they will pretty certainly originate no flowers, but a bulb of 12 g from the same mother-bulb, will in most cases start producing a flower: weight or circumference are decisive. Both these bulbs have not as yet themselves assimilated with green leaves of their own; both have been fed and grown by the mother-bulb. Only the bigger of the two has the power to originate a flower. The measure at which a bulb is or is not able to flower diverges widely for the different races and varieties of the same species. For the above-mentioned Darwin-tulip the limit lies at 8 to 10 g, but for certain early tulips it lies much lower, so that even small bulbs of 3 g can still form flowers. Now, with the Hyacinth and Tulip little attention has been paid to this flowering limit, it is an important factor however in the culture of the Bulbous Iris (see Comm. N⁰. 41, Proceed. XXXVII, 1934), and therefore every grower of Irises knows the limits for the different varieties well. For Imperator it lies at about 5—6 cm (2,4—4,0 g), with Wedgwood at 7—8 cm (7,4—

11 g), but with Yellow Queen already at $3\frac{1}{2}$—$4\frac{1}{2}$ cm (1,2—2,7 g). For closely related races this limit diverges very much and is a fixed characteristic of each race.

It should be remembered that the size of these bulbs, determining the flowering limit, can have been brought about in various ways: 1. from seed, about three years being required to reach the flowering stage; so here, barring the small reserve in the seed, it is only the assimilatory function of the own leaves (1 to 4) in three successive seasons, which in collaboration with the roots builds up the bulb; 2. the flowering or non-flowering mother-bulb produces a few smaller or bigger bulblets, which sometimes require 2 years, sometimes 1, to become able to flower; here the bulb has therefore grown to the flowering size partly by food-supply from the mother-bulb, partly by its own assimilation; 3. lastly, the full-grown bulb may have been entirely built up by the mother-bulb; this is the case e.g. with a flowering Iris plant, where the biggest of the new bulbs, though flattened and of little value for the trade, reaches the weight at which it has become able to flower by food-supply from the mother-bulb only.

Thus the flowering power can be brought about *by assimilation of the bulb itself, but also by food-supply and growth from the mother-bulb only.* In the latter case the new bulb must just as well reach a certain size in order to be able to flower: the smaller bulbs, though also in direct connection with the assimilating mother-bulb, cannot produce flowers. So by reaching the said limit something in the bulb has changed *qualitatively,* one might say *potentially.* This however may very well be the result of quantitative differences and a change in the relations caused by these.

II. The question may now be put: has the flowering power come into being gradually, or in a short time at (which, of course, does not mean "by") a definite size of the bulb? It seems probable for two reasons that the flowering power was already in preparation for a considerable time during growth, i.e. during the assimilation. In the first place the flowering limit is slightly different every year, which indicates that already the time before digging has a perceptible influence.

[Every year bulbs of Imperator are sorted in the beginning of August, directly after digging, at a circumference lying between 5 and 6 cm, with a weight of 2.4—4 g. Groups of 100 are then kept at different temperatures until planted at the end of October. In the following year the percentage of bloomers is counted in the field. After one year the number of bloomers is much greater than after another, as appears from the following example.

	5°	7°	9°	13°	17°	20°	23°	$25\frac{1}{2}$°	28°	31°
Weight per bulb 3.12 g 1934—35	22	39	60	87	65	63	80	—	88	94
Weight per bulb 3.40 g 1936—37	0	1	18	54	49	70	40	57	68	76

The bulbs that had been sorted in 1934 had in 1935 a very high percentage of bloomers as compared with other years; 1937 was an average blooming season. In the above series only after a treatment at 20° the bloom is about the same in both years.]

In the second place: with the size of the bulbs *also the flowering power steadily increases,* from ± 5 cm up to the biggest size of ± 10 cm. This is observed after various treatments: the bigger the bulb, with the more certainty the flower-origination will be successful. Therefore also below the limit a gradual approach to the flowering power is in any case more likely than a rather sudden development of such a condition.

So we suppose that during the growth of the bulb as well before as after the average size at which the flowering power begins has been reached, a process is active slowly increasing and passing at a certain point the size-limit above which the bulb is able to flower.

This limit means that below it *under no condition* flower-formation can occur, and that above it *under definite conditions* flowers are originated. The state below this limit we may provisionally denote as the *subflorigene state.*

[It is once more pointed out that in this article by flowering power only the ability is meant to form flower-organs, without regard to the process by which subsequently this flower-origination is brought into bloom].

III. Above this limit we cannot speak off-hand of a florigene state. being a state in which the flower will be formed. For with the Bulbous Irises at least three phases can be clearly distinguished above this limit. Although the bulbs above this size will *later on,* under definite conditions, produce flowers, still in the first months after digging even the heaviest bulbs are as yet unable to do so in any temperature, as contrasted with the Hyacinth e.g. So after digging the Iris-bulbs are still *undisposed* to form flowers, though *a predisposition to do so does exist.* This state may then be termed the *preflorigene phase.*

Numerous temperature-experiments revealed the following very characteristic properties with such bulbs kept in dark (IV—VIII).

IV. If after digging temperatures of 20° C and upwards are applied to the bulbs continuously flowers are never formed; the florigene phase leading to flower-formation is never reached.

[We have even kept bulbs for a whole year at 20° and upwards, e.g. first dry, afterwards planted and kept in dark; no flower-formation took place. By individual variation it may happen that in 20° an occasional bulb originates flower-primordia.]

V. On the other hand the temperatures of 20° C and upwards still strengthen the preflorigene phase.

[1. of the smaller bulbs a much greater percentage subsequently forms flowers if after digging first *a high temperature* has been given for *a couple of weeks.*

2. also with heavy bulbs flower-formation is brought about with greater certainty if previously heat has been given for a few weeks, e.g. 3 to 5 weeks 23° to 31° C.]

So the preflorigene state is not only promoted during the growth of the bulb, but also without growth by a high temperature.

VI. Temperatures below 17° C finally lead to flower-formation, i.e. they cause the preflorigene state to pass into the florigene phase. The stronger the preflorigene state, the stronger the florigene phase will become as the result of these low temperatures, and with the more certainty flower-formation is finally reached. Still the starting of the flower-origination with Imperator as a rule requires 2½ to 3 months in the most favourable temperature (at 9° C, also at 7° and 13° C).

VII. The same low temperatures that bring about the florigene phase at the same time weaken the preflorigene phase. This can be clearly proved with smaller bulbs of e.g. 5 to 7 cm; when after digging these are placed for some weeks in 5° to 9° C, the chance of flower-formation will be very much lessened and in most cases reduced to zero. Only temperatures of 20° and upwards can then restore the bulbs to the preflorigene phase. Of this we have numerous proofs: after 7 weeks at 5° the preflorigene state will generally have disappeared, but if then 23° is given for another 4 to 6 weeks or 20° for 6 to 8 weeks, afterwards a considerable percentage of the bulbs will again be able to form flowers in low temperatures.

VIII. About 17° C is the transitional temperature: part of the bulbs reach the flower-forming period in the long run, others never get so far and go on forming leaflets for a long time.

IX. Incidentally attention is here drawn to the leaf-formation. The requirements for it seem on the whole to be rather simpler: the newly germinated seed as well as the smallest bulb are able to form leaves. With the Bulbous Iris the optimum lies at about 13° C; leaves are however also formed at 20° and higher in dark, the upper limit lies at 25° to 28° C. So the relation to the temperature is very different from that for the flower-formation.

X. We know that the lower temperatures promote, or cause the florigene phase, with a simultaneous decline of the preflorigene phase. One might be inclined simply to say that the one state is directly transformed into the other. But the matter cannot be as simple as that. For 9° C makes the florigene phase appear sooner than 5° (see Fig. 1), but in 5° the preflorigene state disappears sooner than in 9° (see the experiments in the above mentioned communications). Secondly we saw that after the disappearance of the preflorigene phase in lower temperatures, it is possible to revive it by higher temperatures. This would suggest a reversible process, but it is also quite possible that the high temperature develops the preflorigene state afresh from the subflorigene state, and not by diminishing the florigene phase.

We hope that a few experiments will enable us to settle which conception is the true one. To this point we shall return later.

XI. Thus, during the growth of the bulb a subflorigene state passes into the preflorigene state and in high temperatures this latter is strengthened further. But only in temperatures below 17° the florigene phase develops, with a decline of the preflorigene phase. New experiments showed however, when this florigene state has advanced far enough, e.g.

by 9°, so that the flower-origination will begin within a few days (2d half of Oct. after 9°), that *then* the bulbs can nevertheless accomplish this flower-formation in 20° C, and even very smoothly. So there must still exist a distinct difference between the development of the florigene state and the flower-formation itself, for in 20° in dark the former can never come into being, whereas in 20° the flower may all the same be formed, provided the florigene condition has advanced far enough in the low temperature. Experiments on this point are being continued and may still considerably influence our conceptions.

XII. Summarizing we may state that the data up to now obtained about the relation between flower-formation and temperature with these Iris bulbs compel us to distinguish at least four different phases:

1. *The subflorigene phase:* as long as the bulbs remain under a certain weight no temperature-treatment can bring about flower-formation.

2. *The preflorigene phase*: the bulbs reach such a size that under definite conditions flower-formation will become possible. When dug, in August, bulbs of this size are in the preflorigene phase, which probably has been initiated in the soil for some time previously. A direct flower-origination cannot take place as yet in any temperature. Temperatures above 17° or 20° strengthen the preflorigene phase, but cannot lead to the florigene phase.

3. *The florigene phase*. Temperatures below 17° bring about the florigene phase and at the same time weaken the preflorigene phase. If the preflorigene phase is strong enough by size of bulb and by high temperature, the low temperature is able in the course of many weeks to raise the florigene phase so far that the organs of the flower can be formed.

4. *The flower-forming period* will now set in. The low temperatures which formed the florigene phase are also favourable for this flower-origination. These processes seem to be alike, but evidently are not, though. For if the low temperature has developed the florigene phase far enough, also in 20° the flower-origination can start and proceed very smoothly, whereas 20° is not able to give rise to the florigene phase (barring scarce individual exceptions).

The relation between these different phases is being more closely investigated by a number of experiments.

As no experiments were made by us, based on transplantations (see e.g. MELCHERS, Ber. d. D. B. G. 1939; HAMNER a. BONNER, Bot. Gaz. 100, 1938) or on the use of growth-substances, either by absorption or by injection, we are not qualified and have no occasion to speak in the above description more concretely of definite substances, in casu preflorigene and florigene (see e.g. CAJLACHJAN, C. R. Ac. Sci. U.R.S.S., 1936; KUYPER a. WIERSUM, Proc. Ac. Sci. Amst. 39, 1936; MELCHERS, Ber. D. B. G. 57, 1939). For simplicity one might also use them here, as a hypothesis; I have preferred, however, for the present to speak of "phase" or "state", since it is more likely that a whole complex of reactions is involved than a definite substance.

The relation here described between flower-formation and temperature holds for the bulbous plants from the *Xiphium*-section of the genus *Iris*, but not for the root-stock Irises or the bulbs from the *Reticulata*-section, which behave more like many other bulbous plants. A *comparison* of different investigated plants we hope to give later. The here described bulbous Irises with their characteristic low temperature-maximum for the flower-formation (at about 17° C) and with the opposite effect of low and high temperatures, at first seemed to be an exception. The plants investigated up to now, a.o. Hyacinth and Tulip, have a much higher temperature-optimum, form their flower over a much wider temperature-range and therefore do not show the same contrast between low and high temperatures. In some respects, however, the flower-formation of *Allium Cepa* appears to agree with that of the described Irises and it is probable that a large group of plants shows something similar. It is quite imaginable that the great difference in the relation between temperature and flower-formation with these Irises and e.g. the Hyacinth, signifies a characteristic difference between two large groups of plants.

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