VIRESCENCE AND PROLIFERATION IN HELENIUM AUTUMNALE AND THEIR CAUSE

by

H. DE HAAN (Groningen).

With 3 textfigures and tab. VI.

In his publication about an epidemic of virescences in the years 1893 and 1894, Hugo de Vries pointed out that some virescences are caused by parasites, whilst others must be caused by other agencies and there are many more cases about which we are still in the dark. Some can be multiplied in an unlimited quantity by cutting them, e.g. the wellknown vegetatively constant „green rose" (*Rosa indica*) and the green *Pelargonium zonale* where the flowers have turned into rosettes of green leaves. In these forms we occasionally come across a reversion to the normal type. Whereas these virescences are most probably hereditary, we should regard the abnormalities, caused by parasites as non-hereditary, as modifications.

De Vries examined many virescences a.o. in *Crepis biennis, Agrostemma Githago, Aster tripolium, Dipsacus sylvestris* and *Lysimachia vulgaris*. It was only in the case of *Lysimachia vulgaris* that de Vries succeeded in finding *Phytoptus* as the probable contaminator. The epidemic of virescences, however, left the impression that there was no doubt of a contagion. Moreover, sometime before, Peyritsch had succeeded in proving the contagion by artificial infection by means of Phytopts. Consequently it can be easily understood that in many cases where no

definite cause could be assigned, Phytopts were looked upon as the originators of the virescences.

Since de Vries' paper only few publications, enriching our knowledge of virescences, appeared. Worsdell thought that the Phytopts were to be regarded as the probable cause of the virescences in Helenium. Hus made an interesting observation of a fertile virescent specimen of *Oxalis stricta* which he found to be hereditarily constant. He intended to analyse its difference from the normal Oxalis by hybridisation. Up till now, however, I found no further communications about it in the literature. Virescences being as a rule sterile, such an analysis would be of high importance.

Magnus described flowers of *Anemone ranunculoides* attacked by the Uredineous fungus *Aecidium punctatum* in which the perianth-leaves had become foliaceous. Tubeuf described the fungus Cystopus in the Cruciferae and some more cases could be added (Cited from Worsdell 1915, Vol. II p. 127). All this, however, does not give us at all a general insight in the nature and causes of the virescences and so it is no wonder that the handbooks contain little information about it.

Important is Worsdell's publication, mentioned above. His paper about „Abnormal Flowers in *Helenium* appeared in the Journal of the Royal Hort. Soc. 1902—1903 pag. 940. It is well-written and elucidated as it is by many photos and drawings it has a most inspiring effect.

Abnormal flower-heads of *Helenium autumnale* had been sent to Worsdell, who traced the morphological value of the malformed capitula and formed an opinion about the cause of the abnormal flower-heads, which will be discussed below.

In the autumn of the year 1926 I perceived a number of similar malformed capitula in a Helenium plant in the Experimental Garden of the Genetic Institute at Groningen,

which I thought it worth while to investigate more closely. The comparison of my material both with the photos and the description of Worsdell gives me reason to consider them identical with those of Worsdell.

One of the first facts I found in the investigation was that all the variations were attached to one stem, whereas the normal capitula, standing between them, belonged to other stems.

This observation gives reason for the conclusion that it is not likely that an affection during the flower-phase originating with the various separate flower-heads is the case here. For if we imagine the plant with about 20 ramified stems, the flower-heads of which are growing in a confused mass and we notice that only one stem (with its branches spread over the whole plant) forms a variation, a contagion of each flower separately may be said to be out of the question. For in this case the other flower-heads would have been abnormal as well.

In nearly all the flower-heads Worsdell found eggs and established a certain relation between the abnormalities and the presence of eggs. In one observation Worsdell moreover found a larva in one of the ovaries, which he classified as being a Phytoptus. Apart from this one Worsdell did not find any more larvae though he observed a great number of eggs. Worsdell writes:

„These excessively minute animals probably entered the flowers during a very young condition of the bud stage. This must necessarily follow from what we know of the character of the various virescent organs of the flower for the profound nature of the metamorphosis and radical alteration of the ordinary character of so many of the organs could only have been incurred through the tendency to virescence and vegetative development generally, having supervened at a very early period, viz. when the organs were represented by very young and entirely undifferen-

tiated rudiments. This is a rather important point to remember. The eggs of the creature were observed in considerable quantity attached to the bracteoles between the disc-florets in a longitudinal section of one of the flower-heads (fig. 211, A)"

Fig. 1 is a reproduction of Worsdell's fig. 211 p. 946. If we compare this sketch with the real disc-florets, little resemblance is to be seen. Whereas Helenium has a very thin ovary-wall, we find in figs. C and B very thick ones. Fig. A moreover shows bracteoles to which the eggs are said to be attached. Up till now no bracteoles were discovered in Helenium.

When I examined in my own material a section like Fig. 1 A, I found egg-shaped parts which were stalked. It struck me that the proportions agreed with those of the Phytoptus eggs in Worsdell's figure. Upon closer examination they turned out, however, to be epidermal hairs. The hairs occurred especially at the inner side of the flower-tube. They have grown from one cell, whereas the division of the base-cell and the second lies somewhat about the level of the surrounding epidermis. (Fig. 2, b). The number of cells shows great fluctuations from 2—6, occasionnaly 12. The lower ones are thinner and shorter about 10 μ in length and 8 μ in breadth, the length increasing towards the top. The egg-shaped head-cell, mostly rising above the tubular disc-floret consists of a big oval cell, about 30 μ long and 15 μ broad.

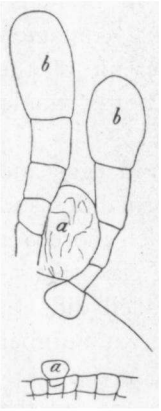

Fig. 2. Glandular hairs (a.) and epidermal hairs (b) of the modified disc-florets (×480)

In sectioning the hairs easily get detached, thus giving the whole the impression of an egg at first sight. (Fig. 3). Besides these, glandular hairs were to be seen among the appendages originating from 2 cells with a height of 3—6

layers of cells, each consisting of 2 cells. The top is surrounded by a typical cuticula-bladder.

As I have the impression that Worsdell's abnormal plants are identical with mine, I don't think that his interpretation is the right one. In the present case of Helenium we must not seek for the cause in the separate flowers, but in the stem itself, leaving it unsettled in what way the normal course was interfered with.

In the literature we find investigations where, in imitation of Worsdell, Phytopts were supposed to be the real cause but without containing observations of the authors themselves in support of Worsdell's opinions.

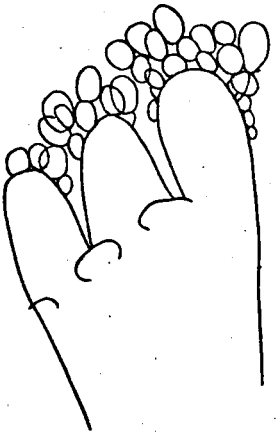

FIG. 3. Corolla-tube with a strong development of hairs. (× 200)

In the paper mentioned above Worsdell described the abnormal forms which occurred. Much of what he described I too was able to notice. I'm going however to mention some points which I think worth while. I observed the following abnormalities:

1. the rosette-shaped green flower-heads with virescent ray-florets and with disc-florets the calyx the styles and stigmata of which were virescent (fig. 4);
2. forms with young leafy shoots inserted in the ovary of the disc-florets;
3. forms with disc-florets proliferated into shoots and at the top of these a young secondary flower-head;
4. forms with trumpet-shaped disc-florets on a short or long stalk and each of them containing a secondary capitulum.

In short a great variety of modified forms attached to

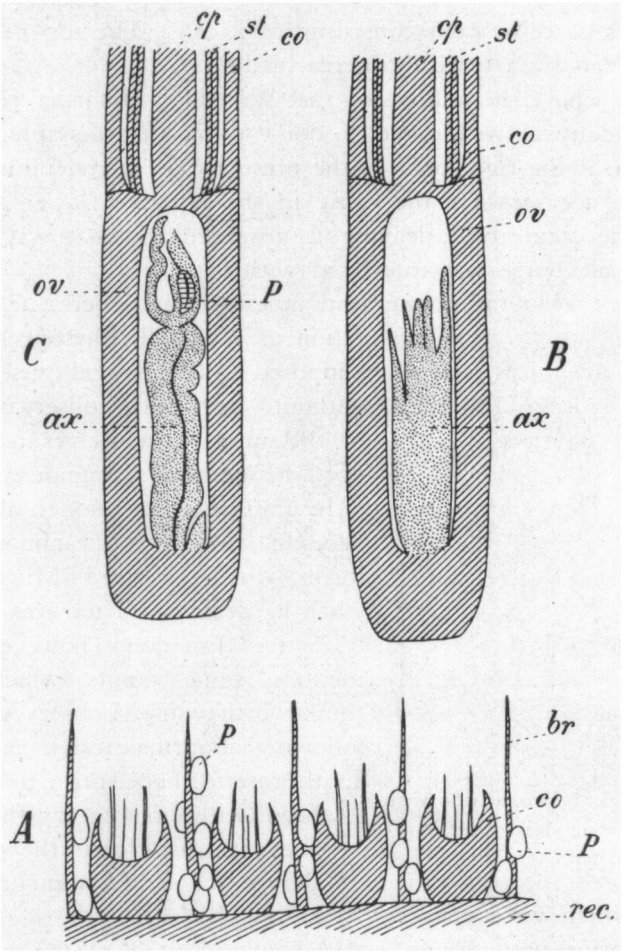

FIG. 1. A. Longitudinal section of the disc of a flower-head showing eggs of Phytoptus attached to bracteoles (× 360)
B.—C. Longitudinal section of an ovary of a slightly virescent disc-floret showing earliest stage of proliferation of the axis of the latter in form of an enclosed rudimentary shoot.
(After Worsdell).
ax. = proliferating axis of floret; br. = bracteole; co. = corolla; cp. = carpel; rec. = receptacle; st. = stamen; P, = Phytoptus.

one and the same stem occurred. In most cases the flower-head was only partly virescent the rest of the disc showing little development and containing short, partly developed disc-florets. On the latter no pappus was perceived, the corolla tube had at the innerside of its lobes numerous hairs, the stamens, more or less leafy, alternated with the flowerparts, no ovary was developed and the centre was formed by a secondary flower-head, probably as Worsdell points out the natural prolongation of the ordinary but usually suppressed axis of the floret, though it might be the adventious outgrowth at the base of the abortive ovule.

The leafy carpels of the rosettes about which Worsdell wrote that the upper portion should be regarded as representing the styles and the lower parts the ovary, must be interpreted differently since the ovary remained normal and only the style with the two stigmata virescent, which can also be seen in Worsdell's figures.

In the abnormal flowers the ovule does not occur in its full-grown form, whereas the degree of development it attains seems to depend on the stage at which the normal processes regulating the growth, are checked. In nearly all cases at the foot of the ovule a young shoot arose which in some cases remained contained in the ovary, in other cases showed a vigorous development, did burst the ovary-wall and grew right through it as a leafy shoot. Strasburger points out that in some cases the young shoot arises by the side of the ovule and that in other cases the latter seems to have proliferated into a shoot. Worsdell opposes this as he considers an actual proliferation into the shoot of the ovule itself impossible.

Though this last argument of Worsdell is not quite right, because an ovule, though being no stem, might be able to form an adventious bud, I don't think Strasburger was justified in concluding this from his observations. He observed many cases in Helenium Hoopesii, just as I did

in Helenium autumnale in which the growth of the ovule was checked at some stage so that the total obliteration of the ovule is much more probable than the conjecture that the shoot should have arisen from the ovule.

Three partly normal flower-heads were attached to our stem of Helenium (Fig. 5). The normal sectors made up ⅓ of the common disc. This seems very interesting to me and as much important as the abnormalities themselves. The question now arises: have the normal flowers on the disc not been influenced or must we regard them as reversions. At present it is impossible to choose between these possibilities.

Finally I would say that owing to the above, the causes of virescence and proliferation have become still more puzzling. But this will stimulate us the more to try and find an explanation of these questions.

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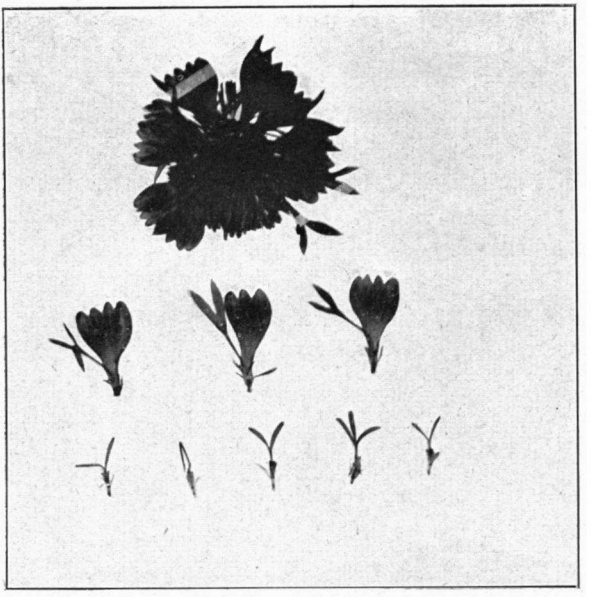

Fig. 4. Virescent, rosette-shaped Helenium flower-head and some of the virescent ray- and disc-flowers.

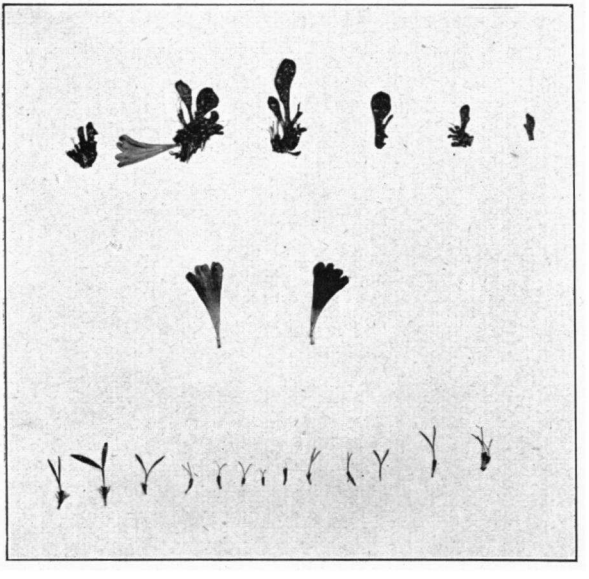

Fig. 5. Modified flowers of the partly normal flower-head, the leafy shoots (in the top row) are inserted on the bottom of the ovaries, the wall of which they burst.

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