

NOTES ON *RANUNCULUS FICARIA* L.
IN THE NETHERLANDS

I. INTRODUCTION. — REDUCTIONAL TRENDS AS A POSSIBLE INTERPRETATION OF
FLOWER TYPES

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One of the most striking features in *Ranunculus ficaria* is its way of reproduction, which is mainly vegetative and which is usually achieved by means of the well-known tubercles born in the axils of the leaves. Though the production of good or apparently good fruits and seeds is rather rare, a number of swollen achenes may be observed yet. However, we do not find seedlings too often, notwithstanding their being easily recognizable by the one single fanshaped cotyledon they possess. These facts have led to many investigations in the field of general biology, anatomy (seeds, tubercles, cotyledon), physiology, morphogenesis etc.

Flower structure and its variation and also diversity in vegetative parts (leaves) have been studied along taxonomic and phytogeographical lines; several botanists have conceived the lesser celandine as belonging to a separate genus, viz. *Ficaria*.¹

The area of distribution of the species or species-complex occupies the whole of Europe and adjacent regions of Asia and Africa.

Our knowledge of this plant has also been extended by field studies and cytological investigations and by crossing experiments.

H. WINKLER and co-workers published a series of papers under the title "Bausteine zu einer Monographie von *Ficaria*" in Beitr. z. Biol. d. Pflanzen in the years 1924–1933. Volume 21 (1933) procures a copious list of previous literature, which need not be repeated here.

The finding of a type of *Ranunculus ficaria* with aberrant flowers and new to the Netherlands led us to another investigation of this well-known plant along various lines. It was considered to be of importance to study the new type, already known from Italy (DELPINO 1897), Austria (BERG 1899) and probably from England (MARSDEN-JONES 1935), and also to establish whether data, obtained in the Netherlands, tally with those from other parts of Europe.

Ranunculus ficaria is a polymorphic species. In the introduction we

¹ In the present article we follow the nomenclature of the Dutch flora works.

mentioned already variation in characters of leaves and flowers. The flowers vary in number and shape of flower parts and also in size. Variation in number will not be treated here.

When studying populations in a certain and more or less restricted area, one gains a notion of the common width of variation,¹ so that divergent types can be discerned with ease.

In the Netherlands we find the bright yellow flowers of this species to be different in size within certain limits. Hence, some specimens with very small aberrant flowers and with badly developed stamens, occurring in the field together with the normal type, were rather striking.

The "normal" plants and the aberrant type, which will provisionally be called *micrantha*, were found in the Netherlands for the first time in the province of Groningen in a mixed population at the edge of a wood on the slope of a little ditch facing south. Later on we found *micrantha*-plants and specimens with transitional flower types in several other places in nature in the north of the Netherlands and in the botanic garden „De Wolf" in the village of Haren (near the town of Groningen). From herbarium studies and oral information, however, we got the impression that *micrantha* is not (yet) known in other parts of the country.

The original area did not occupy more than ca 20 square metres and apparently was uniform with regard to ecological conditions. There were but few *micrantha* specimens and they were scattered between the normal plants. No real differences in vegetative characters could be traced yet; perhaps in *micrantha* the plants and their leaves also are somewhat smaller in size than is the case in the normal type; tubercles are abundant in both of them. In some chromosome countings in roottips we found the somatic chromosome number to be $2n = (\pm) 32$, thus both types are (auto) tetraploids as is *Ranunculus ficaria* in the greater part of its area of distribution. A diploid and more or less fertile type, known from Great Britain (cf. MARSDEN-JONES 1935), Portugal (BARROS NEVES 1942), Sardinia (NEGODI 1930) and maybe from France (CLOS 1852) has $2n = 16$; in some places also the occurrence of triploids, pentaploids and hexaploids has been established.

Apart from variations the flower in *Ranunculus ficaria* usually is composed of 3 "sepals", 8 "petals" and a great number of stamens and pistils.

The petals of the normal type, as far as seen and measured by us, vary in length from 6–15.5 mm and in width from 2.5–6.8 mm. Also the petals of one flower show differences between them. The average length is 10.8 mm, the average width 4.4 mm, based on measuring of 131 petals and on frequencies in value classes of 1 mm each. Greater length of petals is not always correlated with greater width, so that the petals also may vary in shape. The petal indices,

¹ In this paper the term variation is used in its widest sense, denoting any kind of diversity irrespective the causes.

being length over width, are between 1.6 and 3.5 (once 4.5?); the average value for petal index is 2.6 (172 petals).

The figures found in *micrantha* are different from those in the normal type. We did not undertake statistical work, but at any rate the differences are so conspicuous that they can be used as a discerning character even in the field.

Length of petals in *micrantha* (102 petals measured) was 5.0–8.0 mm, average 7.1 mm; width of petals 1.8–3.8 mm, average 2.5 mm. The petal index of *micrantha* is obviously greater than in the normal type, viz. 2.1–4.3, average 3.0 (132 petals). Thus these petals not only are smaller in size but also relatively narrower and the flowers are strikingly different from the smaller flowers of the normal type.

On further observation we found that the small *micrantha*-flowers had badly developed stamens or even no stamens at all. In the first case these stamens were not more than thin and whitish threadlike organs with highly underdeveloped pollen or without any pollen. The flowers, instead of being hermaphrodite, have become functionally female by reduction of the androecium.

Differences in the expression of sex as well as self-sterility and apomixis to a certain degree are known from various species of the genus *Ranunculus* (MARSDEN-JONES and TURRILL 1929, 1935).

As the reduction of the androecium might be conceived as a barrier to the ineffective selfpollination at least and thus might mean a certain adaptation to crosspollination, a study of the relations between flower types and pollinating insects became necessary.

The chief pollinating insects on *Ranunculus ficaria* were species of *Meligethes* (Coleoptera), *Apis mellifica* (Hymenoptera) and *Scatophaga stercoraria* (Diptera). Species of *Bombus*, *Formica*, *Tubifera* and butterflies as pollinators were scarce; I observed *Vanessa urticae* as a visitor once or twice. (cf. MARSDEN-JONES 1937).

In the normal flowers the insects find pollen and nectar, nectar being secreted in small scales at the base of the petals. Even those insects that search for nectar only, get covered with pollen from the extrorse outer stamens unintendedly. Female *micrantha* flowers also excrete nectar, as can be concluded from the presence of glittering drops in the little scales on the base of the petals and from the behaviour of the visiting insects.

With regard to pollen transport on a longer distance *Apis* and *Scatophaga* will be most effective; *Meligethes* are much less mobile and thus less useful as pollinators. For they will often bring about pollination between neighbouring members of one clone only, which will be as ineffective as selfpollination in the selfsterile *Ranunculus ficaria*.

From the type of flower no windpollination could be expected. Indeed no pollen was "caught" on a sticky plate, placed vertically in the field near to a population of *Ranunculus ficaria*.¹

In the light of entomophily MARSDEN-JONES (1935) explained his

¹ Experiments by mr J. M. Bonga and mr L. M. Schoonhoven.

observations that seed development is better in sun plants than in shade plants. This also implies a great dependence upon the type of weather, in particular while *Ranunculus ficaria* flowers so early in spring.

For the purpose of investigating the possible biological sense of the little female flowers of the *micrantha* type we made a comparative study of insect visits both to the normal and the *micrantha* type. For these pollination studies it was necessary to select comparable habitats, which could easily be done because of the occurrence of the two types in mixed populations.

We studied insect visits to *Ranunculus ficaria* in such a mixed and limited population first on a sunny slope of a ditch facing south. On mere observation we noticed that bees, going from one plant to the other, passed over the female specimens without even touching them or paying any attention to them. This statement could be made repeatedly. Only the little black flower beetles of the genus *Meligethes* are to be seen rather often in the female flowers; as has been explained above, however, they may be little effective in crosspollination.

Countings were made to establish these differences in number of insect visits to both flower types more exactly. For that purpose we selected a little patch of ca $\frac{1}{2}$ -1 square metre in a mixed population, so that we were able to keep an eye on all the flowers. Results are listed in the following table:

Nr.	Insects	Nr of flowers		Nr of visits		"Inspection" Micrantha	Duration of observ.
		Norm.	Micr.	Norm.	Micr.		
1	Hymenoptera . . .	>	<	14	1	2	40 min.
2	Hymenoptera . . .	15	9	35	4	3?	75 "
	Diptera	15	9	23	1	—	75 "
	Coleoptera	15	9	4	—	—	75 "
3	Hymenoptera . . .	25	9	10	1	—	45 "
	Diptera	25	9	16	4	—	45 "
	Coleoptera	25	9	3	—	—	45 "
4	Hymenoptera . . .	12	7	7	3?-0	1(-4?)	60 "
	Diptera	12	7	11	1	—	60 "
	Coleoptera	12	7	1	5	—	60 "

In this table the term "inspection" indicates that the insects, when investigating the *micrantha*-flowers, either alight cursorily and without working or keep at a little distance.

The experimental area has always been chosen after careful introductory observation to ascertain that it was abundantly visited by insects. But the great abundance of normal flowers as compared with those of the *micrantha* type might have influenced the differentiation in the number of visits (cf. PERCIVAL 1947). For that reason we started another series of countings in the spring of 1954 in which we used two comparable small areas with ca equal numbers of

normal and *micrantha* flowers respectively, close to each other and somewhat distant from the remaining populations. However, results of one counting only can be given because the weather was too bad and flying insects too scanty to procure sufficient figures and more reliable data. It is hoped that inquiries of this kind can be continued.

In the first examination 11 normal and 9 *micrantha* flowers were involved. Time of observation 75 minutes. The results are presented in the following table:

Insects	Normal flowers	Micrantha
Hymenoptera (mostly <i>A. mellifica</i>).	18	3
Diptera	15	1
Coleoptera	3	0

The figures in the tables speak for themselves. They might have been even more evident had we counted the visits to every flower separately, instead of every visit as a whole. For the bees in particular visit several normal flowers in one flight, whereas in the case of *micrantha* they usually get through one single flower only.

Thus with regard to chances of pollination the facts are against *micrantha*. And as we hardly could yield any seeds judged to be more or less viable from a *micrantha* plant even after abundant artificial crosspollination with the normal type and never succeeded in raising progeny yet, we must conclude that in the case of *micrantha* reproduction is exclusively vegetative or very nearly so.

We cannot give details yet concerning the causes of unattractiveness of the *micrantha* flowers to insects. We mentioned the differences in number of the two types of plants. Moreover some properties at least are obvious in this respect, viz. the smallness and the sometimes slightly dull yellow colour of the flowers and the absence of stamens or functional stamens in *micrantha*.

In experiments with the normal type of *Ranunculus ficaria* we already gained some evidence that flowers without petals and also those from which the stamens had been taken away are less attractive than complete flowers. This holds true, as far as we can see now, particularly for bees. On the other hand it seems possible to stimulate insects, and again particularly bees, to visit *micrantha* by placing a cluster of normal stamens in the flowers. More experiments along these lines are desirable.

In conclusion we may state that the *micrantha* type of flower in *Ranunculus ficaria* prevents the ineffective selfpollination, it is true, but it cannot be considered as an adaptiveness to crosspollination, because it is hardly visited by mobile pollinating insects.

DISCUSSION

It is known from various plant species that apomixis goes together with selfsterility and with polyploidy (GUSTAFSSON 1946-'47; STEBBINS 1950).

Ranunculus ficaria is mainly known as an apomictic species. Its vegetative reproduction by means of axillary tubercles may be combined with a very poor development of but few seeds. Seed-formation may be achieved by agamospermy, but mostly is the result of crossfertilization, though the pollen is partly unviable (METCALFE 1939; BARROS NEVES 1942). The plants are highly selfsterile. Production of seeds, however, is not only checked by selfsterility, but it is also opposed by the presence of the axillary tubercles and probably by material influences of other vegetative parts (PERJE 1952). Development of the embryo is often disturbed in an early stage (METCALFE 1939).

Although there are some indications that in *Ranunculus ficaria* var. *ficaria* the result of the process of sexual reproduction in some degree depends on external conditions, it generally is very inconsiderable. The few apparently good seeds produce still fewer seedlings, which are liable to any kind of damage. (These facts hold for the tetraploid *Ranunculus ficaria* var. *ficaria*; the diploid fertile type, named var. *fertilis* Clapham (CLAPHAM, TUTIN and WARBURG 1952), will be left out of consideration here).

In the light of the present information we might consider the flower of *Ranunculus ficaria* as a rather functionless organ, the characters of which will have a low selective value in extensive parts of the area of distribution of the var. *ficaria*. Whether the flower is to be considered even as harmful and thus as being of negative selective value, will depend on the establishment of unfavourable influences of the flower on tubercle production.

With an organ which is practically functionless there is a good chance of survival for a series of its variants, which will hardly be subject to eradication by selection. By this also reductional types may continue to exist. And in tetraploid *Ranunculus ficaria*, under consideration here, even flowers with reductional trends in which the sexual organs are involved can maintain themselves, because in this plant such reductional processes are supported by ample vegetative reproduction.

As to the possible biological sense of the little female flowers of the *micrantha* type we might suggest that these flowers could be conceived as representing an advanced stage in a reduction process involving the flower of tetraploid *Ranunculus ficaria*. The existence of transitional types seems to confirm this idea. A similar process possibly leads to a type with male flowers by reduction of the pistils. However, no such completely male flowers have been seen by us, but they are known from Great Britain (MARSDEN-JONES 1935).

An other seemingly good interpretation—furtherance of cross-pollination—proved to be untenable in fact. The combined reduction in two different ways, leading to the occurrence of both male and female flowers and thus to dioecism might be conceived not only as a mere reduction but, on the other hand, as an improvement of the present situation. For it might also mean an escape from asexuality by exclusion of the ineffective selfing and by making crosspollination

and crossfertilization the only possible cause of sexual reproduction. This mechanism, however, as has been explained above in the case of the female flower, does not work because of lack of attractiveness to insects; it could function only when accompanied by the development of a type of insects adapted to those unisexual flowers. And even then success might be doubtful, because it is known that it is not only lack of sufficient crosspollination which prevents the production of viable seeds in the tetraploid; there are also factors inherent to the ovules themselves, disturbing their further development (METCALFE 1939; PERJE 1952), and to the pollen.

Although the tetraploid spreads abundantly by means of its tubercles its asexuality is detrimental in so far that it reduces variability. Thus sexual seed development would be important yet, for it is a process producing a quantity of different types from which selection makes a choice and which consequently may become particularly valuable when the species moves to new habitats or when ecological conditions change in an area already occupied by the species.

In the present stage of affairs the adaptive capacity will be low. On account of this fact and of the flower reduction one might consider the tetraploid *Ranunculus ficaria* var. *ficaria* even as a biotype being on its way to extinction.

It seems worth while at any rate to pay attention to flower development and flower reduction in *Ranunculus ficaria*, both in its diploid and tetraploid type and to see whether this species corroborates DARLINGTON's statement (1939): "apomixis is an escape from sterility, but it is an escape into a blind alley of evolution".

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