SEX IN THE SALICACEÆ AND ITS MODIFICATION BY ERIOPHYID MITES AND OTHER INFLUENCES.

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I. Introductory.

During the past twenty years or so cytological research has demonstrated that, in many animals, the sexes are morphologically differentiated in respect to certain members of their chromosome complex, now familiarly known as the sex chromosomes. In general, we have a similar pair, the individual members of which are designated X chromosomes, in the female somatic cells, whilst the male possesses a dissimilar pair, one agreeing with those observed in the female (and hence an X chromosome) and the other, usually quite different, labelled for convenience' sake the Y chromosome. Rather unexpectedly, in the Lepidoptera amongst insects, and in the birds, the situation is reversed; in these groups the composition of the male must be regarded as XX, and the female XY—or perhaps better ZZ and ZW, respectively.

However, no matter what the position for any animal group, the orderly segregation of these chromosomes at the maturation divisions, and their subsequent recombinations on fertilisation, have led to the view that in them we have the veritable mechanism of sex determination. This, no doubt, in the main correctly represents the state of affairs, but, nevertheless, does not express the whole truth. Too many
cases are on record in which aberrant sex ratios arise in spite of presumed equality in the number of zygotes generated of the two types XX and XY (or ZW and ZZ). Reference need only be made to hybridisation experiments carried out in the Lepidopterous genera *Lymantria* and *Lycia* by Goldschmidt (1923) and myself (1919) to prove this. Both of us encountered zygotes of composition ZW (normally appearing as females in the Lepidoptera) which revealed themselves phenotypically as males or intersexes. Hence other influences than that of the mere possession of certain chromosomes must be regarded as playing a part in the matter of sex determination.

In the cases cited, primarily of course, the interfering cause was hybridity, but in pigeons, for instance, Riddle (1917) has demonstrated that reproductive overwork can likewise override the sex chromosome machinery and so, in other organisms, may diverse agencies, all apparently acting by influencing the general metabolism of the creature.

Naturally, with the recognition of this sex chromosome mechanism in animals, efforts were put forth to detect a parallel system in the dioecious plants, but the early investigations of Strasburger (1910) and Sykes (1909) seemed conclusive in demonstrating its absence. In 1917, however, Allen working with the liverwort *Sphærocarpus Donnellii* was able, for the first time, to correlate chromosomes and sex in plants—a result immediately confirmed by Schacke (1919) with *Sphærocarpus texanus*, an allied species of the same genus.

The next step occurred in 1922 when, as a result of our researches in the cytology of the Natural Order Salicaceae, we (Blackburn and Harrison) were able to announce at the Hull Meeting of the British Association, and to illustrate from our preparations, that the male plant of *Populus tremula* was endowed with a clearly marked unequal chromosome pair. Similarly, although the disparity in size between its two members was not so striking, a like pair was discovered in *Salix purpurea* and *S. viminalis* in the sister genus. On the contrary, in the female sex of all the species examined no such unequal pair was encountered.
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Presumably, therefore, *Populus* and *Salix*, as far as the diploid species are concerned, should possess 36 autosomes + 2X in female somatic cells, whilst similar cells in the male should display 36 + X + Y.

After this discovery events have moved rapidly for Santos (for *Elodea gigantea*, 1923), Kihara and Ono (for *Rumex Acetosa*, 1923), Blackburn (for the dioecious species of *Lychnis*, 1923), and Winge (for *Humulus Lupulus*, *H. japonicus*, *Vallisneria spiralis*, and *Lychnis Melandrium* spp., 1923) have demonstrated the presence of sex chromosomes, the plants named being in all cases dioecious. Thus it has been shown that the fundamental mechanism of sex determination in dioecious plants is substantially the same as in animals.

2. The Sex Ratios.

a. In the Pure Species. — Granting that this arrangement exists, and that its action proceeds smoothly without interference from outside agencies, then in the Willows one would expect the sexes to occur in approximately equal numbers. Curiously enough, this equality fails, not only in the present genera, but in most of the dioecious plants studied by Winge (1923) and others, both under experimental conditions and in a state of nature; almost uniformly an excess of females is developed. In contrast with this Nohara (1923) reports the sexes in his *Spinacia* cultures as occurring in the ratio of 495 ♀♀: 496 ♂♂.

To account for the marked preponderance of females, relying on the outcome of his work on *Melandrium* (Lychnis) and *Rumex Acetosa*, Correns (1922) urges the view that the explanation is to be sought in the slower growth of male determining pollen tubes as compared with those destined to produce females—an explanation accepted by Winge. Of course, if speed of growth is a function of chromatin content, this opinion cannot be gainsaid for the pollen grains carrying the Y in the plant *Melandrium* (Lychnis) album have distinctly less chromatin, as the most cursory examination of a heterotype spindle in profile will show.

Tempting as this explanation is, and at first sight in entire accord with the position in *Salix*, it seems to break down
immediately under rigid tests in the field in respect to certain
definite species when such grow free from admixture with other
species and hybrids; determined then the sex ratio becomes
practically normal although, as we shall see later, differential
growth of pollen tubes may even here have its effect. In
direct opposition to these observations, equally pure colonies
of other species regularly give rise to figures only serving to
accentuate the general excess of females in the genus.

The results of several determinations of this nature, with
other essential facts, are summarised in the following table. The
significance of the ratios there set out is enhanced
enormously (1) by the number of plants dealt with, which
varied from 137 in the case of Salix Andersoniana to 683
with S. phylicifolia; (2) by the steadiness of the ratio for any
given species as the count proceeded over great areas; and
(3) when the census was extended over more than one colony.

| TABLE I. |
| Showing Relation between Sex Ratio and Chromosome Complement. |

<table>
<thead>
<tr>
<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Salix Caprea, L.</td>
<td>Gibside</td>
<td>92-6</td>
<td>38</td>
<td>Diploid</td>
</tr>
<tr>
<td></td>
<td>Birtley and Lamesley</td>
<td>91-3</td>
<td>38</td>
<td>Diploid</td>
</tr>
<tr>
<td></td>
<td>Vigo</td>
<td>93-1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hexham</td>
<td>92-8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. purpurea, L.</td>
<td>Tyne Valley</td>
<td>92-4</td>
<td>38</td>
<td>Diploid</td>
</tr>
<tr>
<td>S. repens, L.</td>
<td>Birtley Fell</td>
<td>95-2</td>
<td>38</td>
<td>Diploid</td>
</tr>
<tr>
<td></td>
<td>Waldridge</td>
<td>41</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. aurita, L.</td>
<td>Upper Teesdale</td>
<td>43-6</td>
<td>76</td>
<td>Tetraploid</td>
</tr>
<tr>
<td></td>
<td>Team Valley</td>
<td>43-7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. cinerea, L.</td>
<td>Lamesley</td>
<td>32-3</td>
<td>76</td>
<td>Tetraploid</td>
</tr>
<tr>
<td>S. phylicifolia, L.</td>
<td>Upper Teesdale</td>
<td>33-9</td>
<td>88</td>
<td>Modified Tetraploid</td>
</tr>
<tr>
<td>S. Andersoniana, Sm.</td>
<td>Hexham</td>
<td>37-9</td>
<td>114</td>
<td>Hexaploid</td>
</tr>
</tbody>
</table>

Obviously, the species Salix Caprea, S. repens, and S.
purpurea, all diploids, give ratios not widely departing from
equality and, under certain circumstances, explicable as chance
variations from that ratio. For instance, the Gibside ratio,
allowing for the probable error, becomes 92.6 ± 9.35 and
approximates the normal. However, if we mass the figures
for the Gibside, Birtley, Vigo, and Hexham colonies of the
same species the excess of females, although relatively small
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compared with that seen in other Salices, becomes significant. This slight but constant preponderance of that sex arises, I think, as suggested by Correns through the more rapid growth of pollen tubes carrying female determining gametes. Allowance must be made for it in any consideration of the surplus of females, no matter what the Salix species under discussion, or what more powerful agencies assist its action.

On the other hand, the deficiency of males observed in Salix aurita, S. cinerea, S. Andersoniana, and S. phylicifolia, all polyploids, fall far beyond the limits allowable on the basis of pure chance, or on the supposition that parallel causes to those postulated in S. Caprea, S. purpurea, and S. repens are at work—unless the latter are infinitely more potent in their effects in the former group of species. Hence we must search further for explanations of the phenomena exhibited by them.

Now, just prior to our investigations in the cytology of the Salicaceae, we (Blackburn and Harrison, 1921) had pursued a parallel inquiry into the cytological position in Rosa. In that genus, as in Populus and Salix, there had been developed an orthoploid series, in this case on the base number seven, with diploid, triploid, tetraploid, pentaploid, and hexaploid members. Furthermore, castration work (Harrison, 1921) with guarded flowers had proved that, whilst the whole of the diploid and some of the tetraploid microgenes reproduced themselves sexually, the remainder of the tetraploids and the polyploids were facultatively apomictical. Here then was a hint as to the position of the polyploid Salices; if it were analogous to that obtaining in Rosa, the higher members of that series should be apomictical.

To test this possibility female catkins of the tetraploid Salix aurita, S. cinerea, S. phylicifolia, as well as of the diploid S. Caprea, S. viminalis, S. repens, and S. daphnoides, growing in my garden were enclosed in paper bags until no longer capable of receiving pollen. Not a single seed was obtained in the course of many attempts with the diploid group or with S. phylicifolia; S. cinerea, to a certain degree, compromised, for it proved to be feebly parthenocarpic, whilst S. aurita, so treated, gave rise to viable seeds although in no great numbers.
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Thus the tendency to apomixis in the polyploid Salices exists to a limited extent. Nor does its proof rest solely on the results of my work, for Ikeno (1922) had a similar experience with Salix multinervis in his experiments in crossing that willow with S. gracilistyla.

Next we ask ourselves the question; has this any bearing on the problem of the Salix sex ratio? Manifestly it has; for if Salix aurita is thelytokous, i.e. if it gives rise to purely female cultures from apomictical seeds, then the proportion of female plants would rapidly rise with an increased incidence of apomixis. And that Salix displays apomictical reproduction of the thelytokous type Ikeno conclusively proved in the species examined by him. As for Salix aurita, two lines of proof have served to demonstrate that the same holds there; (1) the apomictical seeds to which reference has been made above were grown and yielded seven females; (2) a wholly female colony of the species, existing in the Team Valley remote from other Salices, sets seeds sparingly and has maintained its female character during observations covering a fairly lengthy period.

However, even at its best, this seems inadequate as a complete explanation of the Salix sex ratio, for, as we have seen, several of the most vital species, submitted to rigorous examination under optimum conditions, have failed* to yield a single apomictical seed.

And an explanation, attractively simple in its possibilities, soon presents itself. No matter by what methods a tetraploid form arises, for present purposes they all amount to the same in the end; whether we invoke hybridity with a failure of the reduction in the hybrid owing to a lack of compatibility of the chromosomes derived from different species, or chromosome division in the fertilised egg followed by a suspended mitosis, or the like, in all there is involved a duplication of the chromosomes.

Admitting that this is so, then amongst the chromosomes so duplicated in dioecious genera, should such exhibit sex chromosomes, are those chromosomes themselves. Thus it

* In view of Ikeno's experiences they may be apomictical under environmental conditions differing from those obtaining during the years my experiments proceeded.
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appears likely that in *Salix aurita*, *S. cinerea*, *S. phylicifolia*, and *S. Andersoniana* we have anything but a simple XX, XY system. In the tetraploids the most regular arrangement possible is that the females should be represented as XXXX and the males as XXYY. Let us consider the possibilities when females and males of these respective types interbreed.

If mere chance decides what takes place when the homologous chromosomes pair in preparation for the reduction division then, in the female, all the gametes generated should be of type XX, whilst in the male three types XX, XY, and YY should appear, the XY form preponderating. Fertilisation, with subsequent successful development of the zygotes, should yield plants of composition XXXX, XXXY, and XXYY with an excess of those of composition XXXY. Thus the population, even if it commenced as XXXX in its females and XXYY in its males, would alter its composition at once.

Concerning the sex of these newly generated zygotes, assuming the truth of our original hypothesis, there can be no doubt as to those of constitution XXXX and XXYY; of a certainty they would be female and male respectively. But what is the position of the zygotes XXXY we ask? Attaching due weight to every fact produced in Bridges' (1916) *Drosophila* work which bears upon the point, and to the absence of intersexes in ordinary populations of *S. alba*, *S. fragilis*, *S. pentandra*, *S. aurita*, *S. cinerea*, etc., it seems almost certain that such plants would be females. Admitting that this is so, then immediately further complications ensue; we have the possibility of XXXY females being fertilised by XXYY males. This operation would produce, in addition to zygotes of composition just considered, those of type XYYY which, if viable, would almost certainly be males. Obviously, should the pollen from this novel type of male fall on the stigmas of the regular XXXX female, the outcome would be equality in the numbers of the sexes. On the other hand, if that pollen fertilises the irregular XXXY females, there would arise the zygotic series XXXY, XXYY, XXXY, and XYYY or 1 ☞ : 3 ♂ ♂ .

Therefore, we perceive that, although in the early history of the newly developed tetraploid *Salix* the females would
necessarily preponderate, almost at once, if all possible gametes and zygotes were equally viable, and all pollen tubes grew with equal speeds, a swing-back in the sex ratio would be initiated. This, if unchecked, would lead in the long run to practical equality in the sex figures.

Notwithstanding this, the numbers of females, as they grow in their natural habitats, completely disprove any theory as to a swing-back operating within the tetraploid and hexaploid populations studied. This observation makes it almost certain that there exists either selective elimination of certain gametes, a differential mortality amongst the zygotes, a preferential growth of pollen tubes, greater than that influencing the sex ratio in diploid species, or other similar disturbing agencies.

Here let us reconsider the arguments set out above; they all assume that in synapsis the attraction between an X and a Y chromosome is just as great as that tending to bring two X's or two Y's together; in other words, that homosynapsis and heterosynapsis are equally probable events. Such views fail to harmonise with Bridges' pronouncements in his work on non-disjunction in Drosophila; there he proves beyond cavil, that chromosome pairing was preferential in his XXY females, inasmuch as 86 per cent. homosynaptic unions against 14 per cent. of the reverse type took place. Should such a rule apply during sporogenesis in tetraploid Salices then, in the end, the gametes of the male would probably be in the bulk of cases, and possibly in all, of composition XY. These, on the one hand, say in the species S. cinerea, fertilising a female of type XXXX would yield a wholly female progeny and, on the other, pollinating a female of build XXXY would produce the sexes in equal numbers.

Nor is this occurrence of wholly female families a mere assumption; that they really do occur in tetraploid willows has definitely been proved experimentally by Heribert-Nilsson (1918) for Salix cinerea and by myself for S. aurita. But of these more will be said below.

Even if the synapses were not preferential there remain open further methods securing the functioning of XY gametes only in the case of the male. In the first place, the course
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of events during sporogenesis may be so disturbed that only selected chromosome combinations appear in the microspores and, secondly, even after the microspores have developed, they may prove to lack viability. That irregularities do arise during microspore formation we have pointed out elsewhere in the case of *S. aurita*, and these do end in gametic elimination. On the other hand, we detected no cytological disturbances with *S. cinerea*, yet five shrubs of that species in which the pollen grains were submitted to critical microscopic examination yielded respectively 18 per cent., 23 per cent., 16 per cent., 17 per cent., and 27 per cent. of aborted pollen. Should the gametes so disposed of in either *S. aurita* or *S. cinerea* be those of composition YY then the same results would be attained, as far as sex is concerned, as by a preferential mating of chromosomes during synapsis.

Tending to the same end, and an exaggeration of the point considered in seeking to explain the slight excess of females in the diploids, is the fact that, if Correns’ theory be on a firm foundation, the YY gametes should be even of slower growth than the XY fraternity. In such an event, granting the full viability of the YY gametes, the balance would fall on the female side. Thus, whether the greater powers of the XY gametes be explained by the elimination, or by the slowing down, of their male determining competitors, the result is invariably the same.

To return to the purely female families; there remains one possibility to be explored. Ikeno, in certain of his attempted crosses, obtained nothing but females which, although produced by applying *S. gracilistyla* pollen to *S. multinervis* stigmas, were entirely of maternal proclivities. Bringing this observation to bear on the present problem, if the pollen in the tetraploid willows acts occasionally by stimulating latent tendencies to apomixis, rather than by bringing about true fertilisation, then such species, being thelytokous when apomictical, should include a majority of females.

In the case of the hexaploid species, although further complicated by the hexaploidy, much the same set of forces can be pictured as acting and with the same effects, so no further analysis in that direction is required.
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Thus, to sum up, many factors contributing to the excess of females in the polyploid Salices may be at work: (1) a differential growth in pollen tubes favouring certain gametes; (2) the occurrence of thelytokous apomixis; (3) a combination of false fertilisation, acting by vivifying latent tendencies to apomixis, with thelytoky; (4) circumstances arising out of the necessary peculiarities in the sex chromosome complexes of polyploid dioecious plants.

b. In the Hybrids.—Nothing very definite seems to be known as to the sex ratios of recognised British willow hybrids; neither in hybridisation experiments deliberately carried out, nor under natural conditions, have great enough numbers been dealt with to warrant the fixing of any exact figure. Nevertheless many important facts in respect of them and certain other cultivated plants of similar origin, pertinent to the present inquiry, are indicated in the appended lists:—

(1) Hybrids, in which the male is known, involving only diploid species:—

<table>
<thead>
<tr>
<th>Triandra × viminalis.</th>
<th>Caprea × daphnoides.</th>
</tr>
</thead>
<tbody>
<tr>
<td>purpurea × repens.</td>
<td>Caprea × myrsinites.</td>
</tr>
<tr>
<td>purpurea × viminalis.</td>
<td>Caprea × repens.</td>
</tr>
<tr>
<td>purpurea × daphnoides.</td>
<td>viminalis × daphnoides.</td>
</tr>
<tr>
<td>Caprea × viminalis.</td>
<td>viminalis × repens.</td>
</tr>
<tr>
<td>Caprea × lanata.</td>
<td>repens × daphnoides.</td>
</tr>
</tbody>
</table>

(2) Hybrids, producing males, in which at least one parent is polyploid:—

<table>
<thead>
<tr>
<th>Fragilis × pentandra.</th>
<th>aurita × repens.</th>
</tr>
</thead>
<tbody>
<tr>
<td>fragilis × triandra.</td>
<td>cinerea × purpurea × Caprea</td>
</tr>
<tr>
<td>alba × fragilis.</td>
<td>(93 ♀ ♂ : 1 ♂).</td>
</tr>
<tr>
<td>alba × pentandra.</td>
<td>cinerea × purpurea.</td>
</tr>
<tr>
<td>babylonica × fragilis.</td>
<td>cinerea × viminalis.</td>
</tr>
<tr>
<td>aurita × purpurea.</td>
<td>cinerea × purpurea × viminalis.</td>
</tr>
<tr>
<td>aurita × Caprea.</td>
<td>cinerea × Caprea × viminalis.</td>
</tr>
<tr>
<td>aurita × cinerea.</td>
<td>cinerea × Caprea.</td>
</tr>
<tr>
<td>aurita × cinerea × Andersoniana.</td>
<td>cinerea × myrsinites.</td>
</tr>
<tr>
<td>aurita × lapponum.</td>
<td>phyllicifolia × purpurea.</td>
</tr>
<tr>
<td>aurita × myrsinites × Andersoniana.</td>
<td>phyllicifolia × myrsinites.</td>
</tr>
<tr>
<td>aurita × Andersoniana.</td>
<td>Andersoniana × Caprea.</td>
</tr>
<tr>
<td>aurita × phyllicifolia.</td>
<td>Andersoniana × myrsinites.</td>
</tr>
</tbody>
</table>
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(3) Hybrids, involving polyploids, in which only the female is known:—

<table>
<thead>
<tr>
<th>Female Species</th>
<th>Male Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alba</td>
<td>x triandra.</td>
</tr>
<tr>
<td>(cinerea × purpurea) × (purpurea x viminalis).</td>
<td>aurita × myrsinites.</td>
</tr>
<tr>
<td>cinerea × aurita × phyllicifolia.</td>
<td>phyllicifolia × viminalis.</td>
</tr>
<tr>
<td>cinerea × Caprea × phyllicifolia.</td>
<td>phyllicifolia × herbacea.</td>
</tr>
<tr>
<td>cinerea × Andersoniana.</td>
<td>phyllicifolia × repens.</td>
</tr>
<tr>
<td>cinerea × Andersoniana × phyllicifolia.</td>
<td>phyllicifolia × Caprea.</td>
</tr>
<tr>
<td>cinerea × phyllicifolia.</td>
<td>phyllicifolia × Andersoniana.</td>
</tr>
<tr>
<td>cinerea × repens.</td>
<td>phyllicifolia × arbuscula.</td>
</tr>
<tr>
<td>aurita × viminalis × Caprea.</td>
<td>Andersoniana × myrsinites × phyllicifolia.</td>
</tr>
<tr>
<td>aurita × repens × viminalis.</td>
<td>Andersoniana × repens.</td>
</tr>
<tr>
<td>aurita × herbacea.</td>
<td></td>
</tr>
</tbody>
</table>

(4) Miscellaneous hybrids built up from species in which the cytology has not been fully investigated:—

<table>
<thead>
<tr>
<th>Species combination</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Lapponum × herbacea.</td>
<td>lapponum × Caprea.</td>
<td></td>
</tr>
<tr>
<td>lapponum × arbuscula.</td>
<td>herbacea × lanata.</td>
<td></td>
</tr>
<tr>
<td>Arbuscula × herbacea.</td>
<td>herbacea × lapponum</td>
<td></td>
</tr>
<tr>
<td>herbacea × repens.</td>
<td>× myrsinites.</td>
<td></td>
</tr>
<tr>
<td>herbacea × reticulata.</td>
<td>herbacea × myrsinites.</td>
<td></td>
</tr>
<tr>
<td>lanata × reticulata.</td>
<td>myrsinites × arbuscula.</td>
<td></td>
</tr>
<tr>
<td>myrsinites × reticulata.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The first salient point to impress us here is that, whenever the hybrid is of purely diploid origin, the male is well known. Similarly, we are compelled to recognise that, in some crosses, males are either lacking, or occur so infrequently in the wild state, as to have escaped notice; in such crosses, when the cytology has been investigated, one, at least, of the parent species is a polyploid. On the other hand, we are assured that, in certain other crosses in which polyploids have participated, males are to be found; but this, of course, in the absence of exact figures, signifies little, the real value of the list in respect to polyploids lying in the preceding observation.

Inferentially, therefore, in such polyploid crosses males are, to say the least, of less frequent occurrence than the females—precisely the position in the pure polyploid species themselves. Similarly, although the mere presence of the male in the purely diploid crosses does not afford definite proof that the
position there harmonises with that within the limits of the pure diploid species, still, when the combined evidence of experimental work and of field observations points in the same direction, we are forced to admit that it seems probable. And such evidence can be adduced; Heribert-Nilsson, in his cross between *Caprea* ♀ and *viminalis* ♂ obtained 11 ♀♀ and 15 ♂♂ and so with his *repens-viminalis* crosses. So conclusive were these figures, and so markedly in contrast with the excess of females in his other crosses did they appear, that, in discussing the latter, he remarks: "Anderseits scheinen die *Caprea*- und *repens*-Verbindungen im allgemeinen eine normale Spaltung zu zeigen"—and I would add that his figures justify the inclusion of *S. viminalis* likewise.

Although the evidence drawn from the occurrence of natural hybrids between diploid forms is obscured by the fact that only rarely do they grow abundantly in one station still, in such crosses, one does, in the long run, encounter as many males as females. Further, in the one cross, *purpurea* × *viminalis* which occurs hereabouts in great numbers and provides ample material for judgment, the males are actually in excess.

From these observations we conclude that the sex ratio in hybrids between diploid *Salices* cannot depart widely from that revealed in those species themselves.

Wichura (1865), in his well-known work on hybrid willows, noting the superior numbers of females in certain crosses, assumed that only hybrids yielded such an excess, and that therefore the phenomenon was a sequel to hybridity. Clearly, he would not have been so sure of his opinions had he made a census of the *Salices* as to sex in their natural habitats, or grown the pure species as Heribert-Nilsson and I have done.

In spite of this, I regard it as extremely probable that an actual failure of males does take place in some instances and is an outcome of hybridity; the disappearance of the heterogametic sex under its influence would fall in line with Guyer's (1909) and Riddle's (1917) results with doves and pigeons, Goldschmidt's and mine with Lepidoptera, and with those of other workers so admirably summarised by Haldane (1922).

Remembering that both in Goldschmidt's and my work
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intersexes were encountered, we are brought naturally to a study of the so-called androgynous and _melamorphosans_ forms of _Salix_.

3. The Androgynous Forms.

In these androgynous plants, the catkins * instead of being purely male or female are endowed with a more or less irregularly arranged mixture of perfect male and female florets; in other words, the plant becomes monoecious. Such forms are known to systematists as "form" or "variety" _androgyne_, and they occur in hybrid _Salices_ of very diverse affinities as will be seen from the appended list †:

| Aurita × repens. | viminalis × triandra. |
| aurita × purpurea. | incana × daphnoides. |
| aurita × viminalis × repens. | fragilis × triandra. |
| aurita × phylicifolia × purpurea. | fragilis × alba. |
| cinerea × purpurea. | fragilis × babylonica. |
| viminalis × purpurea. | fragilis × pentandra. |
| viminalis × daphnoides. | t amygaloïdes × nigra. |

One fact stands out here in the most emphatic fashion, and that is the hybrid ‡ nature of the plants included; the phenomenon therefore is essentially one of hybridity.

Of the number given three, _fragilis × babylonica, viminalis × triandra, cinerea × purpurea_ have been submitted to more or less careful study; in particular, observations extending over a period of years have been made on the hybrid _fragilis × babylonica_ (fig. 1). In that plant, but little annual variation was detected in the distribution of the two sexes. Every year, in the majority of the catkins, there was a tendency for the female florets to be massed at the base, but, just as regularly, there existed catkins in which the two sexes alternated in zones; others, similarly, seemed to betray no hint of regularity in the disposition of the florets of either sex.

From a morphological standpoint, both types of florets

* Similar catkins have been described in _Betula_ (fig. 1) and _Alnus_ by Blackburn (1922) and by myself in _Corylus_.
† The forms listed produce males likewise.
‡ The last plant on the list is that called by Schaffner (1919) _Salix amygaloïdes_, Anders., but, acting on the indications of Camillo Schneider, and on the reluctance of Andersson and others to regard these androgynous forms as genuine _S. amygaloïdes_, I have ventured to assign to them the parentage stated.
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seemed functionally perfect, but no fruit was ever produced; the catkins demonstrated their fundamental maleness in the constancy with which they fell after they shed their pollen, but before fruit could be ripened. Even before this latter characteristic had given final confirmation to my surmise as to the original sex of the plant, critical examination, directed from many angles, had practically assured me on the point. Thus, there had taken place a definite switch-over from maleness to femaleness. Let it be noted, however, if this view is correct, the change from male to female must be effected every season.

![Diagram of plant parts](image)

FIG. 1.—A, androgynous form of *Betula* (N. Durham); B, androgynous form of *S. fragilis x S. babylonica* (Ravensworth, Co. Durham).

Wigand (1887), it is true, basing his opinion, I suppose, on the tolerable regularity with which the basal florets are female describes the change as occurring in the reverse order. Moreover, he refers to transitional florets; but these I have never had before me. Hibsch (1875), too, meeting with the same hybrid combination, both in its male and its androgynous guises, and knowing that only females of *Salix babylonica* were in cultivation in Europe expresses the same belief although, naturally enough, he assumes the sex transformation to occur within the limits of the species *S. babylonica*. That he, in reality, was dealing with the hybrid one can gather from the description of his alleged male and from Schneider's (1906) statements as to the status of that species in Europe.
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The other androgynous hybrids, *cinerea × purpurea* and *viminalis × triandra*, which came under my notice were, likewise, transformed males, the first-named yielding in the field all the indications provided by *fragilis × babylonica*, and the other such evidence as careful dissection in the laboratory could reveal.

The remainder of the plants on the list are apparently much of the same type and, generally, need no further discussion at this junction, for further details are obtainable from the works of Kerner, Wimmer, and other writers. Nevertheless, the cases of *viminalis × daphnoides* appearing in Heribert-Nilsson’s cultures, and of the so-called *S. amygdaloides* brought forward by Schaffner, must be considered for both speculated on the matter and advanced theories to account for the circumstances.

Necessarily, Heribert-Nilsson, as a consistent Mendelian invokes a factorial* explanation for his results; to quote his own words: “Durch eine ganz einfache faktorielle Annahme werden diese Spaltungen verständlich.” And the factor conjured up is a factor D for Dioeciousness for which both sexes are supposed to be heterozygous! On crossing *viminalis ♀* with *daphnoides ♂* he asserts that zygotes, homozygous recessives in respect to this gene, arise and, he declares, are the androgynous forms in question. I only ask, granting all this, what restrains the workings of the alleged gene in pure *Salix* and *Populus* species, all of which are dioecious?

To complicate matters he further states that the plants are sectorial chimaeras for sex; possibly they are but . . . !

Schaffner in his work deals with the White Mulberry, *Morus alba*, and the willow already mentioned, describing for both a state of affairs precisely the same as those given by Wigand for *babylonica × fragilis*. The chief interest here lies in his pronouncement that “a case of sex reversal can, and sometimes does, take place in old tissue whose cells are removed by thousands of vegetative divisions from the original zygote. It assures us that sex control is only a matter of finding out how to change the physiological state,” and in his conclusion

* In his symbolical presentation of his arguments, Heribert-Nilsson erroneously assumes the female to be the heterogametic sex.
that "sexuality is a condition not a character"—much the same opinions as those formulated by Hibsch forty-four years ago.

Above, it has been urged that possibly the absence of males in certain crosses, both under natural and artificial conditions, originates in hybridity. Further, the androgynous state has been indicated as marking the same condition. In point of fact I regard both features as links in the same chain.

In my introductory remarks I restated the current morphological views in the matter of sex determination. But it is well to make it clear that I regard the sex chromosomes (or the genes in them!) as acting as regulators of the physiological state of the organism, initiating when present in double dose the insignia of the one sex and when in single dose those of the other. To put it still more plainly, I recognise in the sex-chromosome mechanism one for setting up two opposed metabolic conditions, one translated as femaleness and the other as maleness.

But, as many converging lines of proof serve to show, external agencies like hybridity, parasitism, food, reproductive overwork, can all affect metabolism. Thus, theoretically, there seems nothing whatever against hybridity or other outside agencies affecting the sex of willow hybrids.

If the relation between the two states as they arise under the workings of the sex chromosomes are so delicately adjusted as to be characteristic for any given species, clearly enough hybridity, bringing together chromosomes of diverse origin, may throw the mechanism out of gear. Therefore, it seems well within the bounds of possibility that, in some hybrids, owing to overweighting on the part of the sex chromosomes derived from one side, uniformly one sex alone would be set up. In such a case one would anticipate, in harmony with my Lycia-Nyssia results, the disappearance of the heterogametic sex.

On the other hand, it appears equally possible that, whilst one sex should be determined normally, the physiological system set up by the other combination should be in a state of unstable equilibrium tending to swing in either direction as determined by environmental influences. Such influences operate in the rapid changes in light and heat intensities, in late summer and other periods when the catkins on certain
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trees are developing. That they acted effectively has been shown by Schaffner (1923) for Cannabis.

In this manner could be satisfactorily explained the periodic appearance of the normal sex, the annual swing over to the other and the local changes, hinting at temporary effects, observed in the regularly zoned distribution of the sexes in certain androgynous catkins.

However, it must be emphasised, it is not merely the catkins or portions thereof which pass into a condition of sex reversal; on the contrary, the general metabolism of the whole plant is temporarily disturbed, but only the susceptible structures, the developing sexual organs, can respond to the stimulus.

In much the same way, although hybridity plays no part, Davey and Gibson (1917) would seek to explain sex changes in Myrica Gale and Stout (1919) in Plantago* lanceolata.

4. The Metamorphosans Varieties.

In dealing with flowers of the metamorphosans type we are concerned with a wholly different phenomenon from that considered in the preceding section. Only rarely, and then only in the transitional zones, do androgynous catkins carry intersexual florets; on the contrary, the dominant characteristic of the metamorphosans inflorescence rests in the fact that the individual florets on any given catkin, independently of the course pursued by adjacent florets, or of other catkins (fig. 2) on the same tree are forced in varying degrees from maleness to the condition of the opposite sex, thereby generating a long chain of intersexes. As a culminating stage, a complete transformation occurs, and florets, which would normally have appeared as males, become perfect females. In fig. 3, including florets taken from the same twig, a practically perfect series of transitional forms, beginning with the male flower B and ending with the functional female flower A, is depicted.

Such metamorphosans varieties have been reported in the following plants:

*S. Caprca, L.*
*S. cinerea, L.*
*S. aurita, L.*
*S. grandifolia, Seringe.*

* S. silesiaca, Willd.
* S. Andersoniana, Sm.
* S. aurita × (S. repens × S. viminalis).

* I have seen wholly female plants of Plantago media.

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Of these species affected, examples of the first and third have been under observation for six years, and a specimen of *S. cinerea* for one season only. In addition, freshly gathered twigs from other *cinerea* plants, as well as from *S. Andersoniana* have been provided by my colleague Miss K. B. Blackburn. *Salix grandifolia* and *S. silesiaca*, being Continental forms not found in the British Islands, have not been studied at all,

![Figure 2. Twig from *Metamorphosans* var. of *Salix Caprea*, Birtley, Co. Durham.](image)

but, nevertheless, their abnormalities, as described by various authors, differ in no way from those occurring in the British species.

The phenomenon has been recognised for a considerable period, the earliest reference detected being the records of Host (1824). However, records covering the whole range of the affected species in Europe have been made by a series of authors, Schimper (1829), Moquin Tandon (1841), Wimmer (1853), Kerner (1860), Lundström (1875), Heinricher (1882),
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Buchanan White (1891), Burkill (1898), Velonovsky (1904), Worsdell (1916), Blackburn (1917), and so with others.

One very important difference between the list of androgynous forms and that presenting the *metamorphosans* group impresses us at once. As insisted above, the androgynous group comprises nothing but hybrids whilst, on the contrary, except in a single instance, one of Heribert-Nilsson’s cultivated plants, the *metamorphosans* varieties are confined to pure species; even the one exception appears as a derivative of *Salix aurita*, one of the same set, and therefore, apart from its hybridity, able to share in its peculiarities.

![Diagram of florets](image)

**Fig. 3.**—A, ♀ floret of *Salix Caprea*; B, ♂ floret; the remainder florets of the intersexual type. All taken from a *metamorphosans* bush of *Salix Caprea* growing at Birtley, Co. Durham.

Further, another remarkable feature stands out clearly, and that is that the *metamorphosans* list, save for *S. Andersoniana*, includes the whole of the European representatives of the genus *Salix* placed by competent salicologists in the *Caprea* (see Linton, 1913) Section. Even for *S. Andersoniana* reasons have been advanced elsewhere (Blackburn and Harrison, 1924) for regarding it as likewise of *Caprea* affinities. Hence the power of developing *metamorphosans* varieties characterises the *Caprea* group and its allies, and is, in the main, observable in its pure species.

The *Salix Caprea* colony kept under observation consists of 23 bushes. Twelve of these are uniformly quite ordinary females; one has always borne inflorescences with varying
proportions of intersexual flowers, whilst the other ten have
differed yearly, generally manifesting themselves as truly
male, but occasionally throwing a fair number of intersexes.
Although the colony is fairly compact, the environmental
conditions are far from being constant throughout. The
uniformly affected plant, accompanied by two or three others
more correctly described as males, and several females, grows
on a hot, sunny, somewhat dry sandy hollow forming the
southern slope of a deep well-wooded dene; the other trees
grow in a damp shaded spot with a clayey soil on the northern
slope. Thus, for the most part, the former contingent flower
first. Nevertheless, no correlation seems to exist between the
amount of intersexuality displayed by any particular plant and
its position in its habitat, except that the plant singled out for
special note, no matter how low its percentage of intersexual
florets in any given year, or to what degree the florets on the
other trees are transformed, always exhibits the phenomenon
in the highest degree.

In 1921, when the incidence of intersexuality attained a
medium level for the whole colony, an endeavour was made
to connect its actual degree on any special branch with its
position on the tree. At that time a lower branch, bearing
30 twigs and 188 catkins, had 19 of these twigs tipped with
catkins wholly male, but only three other catkins (two
penultimate) were in the same condition. On the other
hand, of catkins displaying nothing but female florets or
intersexes, there were three only, occurring on separate twigs
with totals of 6, 7, and 11 catkins respectively, of which the
topmost were male in two cases and in the other 90 per cent.
male. The rest of the catkins on the branch possessed an
average of 60 per cent. of female flowers or intersexes.

The highest branch of the same tree, during that season,
bore 27 twigs and 179 catkins; there the maleness was much
more pronounced, for over 60 per cent. of the catkins were
purely male, only one catkin being built up of females and
intersexes. The remainder of the catkins showed varying
proportions of male, female, and intersexual flowers, but with
an unmistakable surplus of the first.

Another tree, placed a few yards to the south-west, carried
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about 22 per cent. of females and intersexes on its lower branches, but such florets vanished higher up.

Later investigations, including the whole of the trees, yielded the same result, inasmuch as the tendency to sex reversal was distinctly greater on the lower branches.

Similarly, an attempt was made with but little hope of success, for reasons stated incidentally below, to link up the degree of intersexuality with the date of flowering of the species and the character of the preceding summer and winter; in this endeavour the observations appearing in Table II. were assembled.

TABLE II.

<table>
<thead>
<tr>
<th>Year</th>
<th>Date of Flowering of <em>Salix Caprea</em> Colony.</th>
<th>Description of Previous Summer and Autumn.</th>
<th>Description of Previous Winter.</th>
<th>Degree of Intersexuality.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1919</td>
<td>13th April</td>
<td>On the whole, warm and sunny</td>
<td>Harder earlier, open later</td>
<td>High</td>
</tr>
<tr>
<td>1920</td>
<td>13th March</td>
<td>Windy, cool, warmer later</td>
<td>Hard, little snow</td>
<td>Fairly high</td>
</tr>
<tr>
<td>1921</td>
<td>16th March</td>
<td>Fine and moderately warm</td>
<td>Open, little snow and frost</td>
<td>Moderate</td>
</tr>
<tr>
<td>1922</td>
<td>10th April</td>
<td>Hot and dry</td>
<td>Hard, much snow</td>
<td>Fairly low</td>
</tr>
<tr>
<td>1923</td>
<td>11th March</td>
<td>Cool, little sunshine</td>
<td>Open, mild</td>
<td>Moderate</td>
</tr>
<tr>
<td>1924</td>
<td>31st March</td>
<td>Cool, rather wet, windy</td>
<td>Hard, much frost, little snow</td>
<td>Low</td>
</tr>
</tbody>
</table>

However, no* relation in the way of cause and effect is discernible here. Curiously enough, Lundström (1875), early as his work appeared, had apparently, in his search for an explanation of the circumstances, theorised along much the same lines, for he developed a view that change in habitat was the inciting cause. The theory, of course, cannot be tenable when it is remembered that sex reversal of this type has been signalled for every species of the *Capreae* group throughout its geographical range, under climatic conditions varying from those of the most extreme Continental type to those typically oceanic.

Heribert-Nilsson, again adopting the usual Mendelian

* Unless the slight intersexuality in 1924 depends upon the unbroken series of frosty nights in January, February, and March; but see discussion on Eriophyid mites below.
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procedure in endeavouring to account for the intersexes, now casts his factor for diceousness, in spite of the occurrence of androgynous flowers both in his $F_1$ and his $F_2$ generations, and postulates a novel factor $M$ for the metamorphosans character. For this, he declares, the female is a homozygote and the male a heterozygote. On making his cross a new type of zygote of formula $wwMm$ arises and that, he asserts, although truly a male on his system, which reverses the actual composition of the sexes in deeming the male the homogametic sex, passes under the influence of the "Umwandlungsfaktor" into the metamorphosans state. If that be so, then the metamorphosans unit-character must be very peculiar in its geographical distribution, excessively variable in its intensity, and, moreover, to be quite exact, capable of failing to act at all. In his actual experiments true males did manifest themselves, but these he dismisses as only "scheinbar" male. This may, of course, be correct when cognisance is taken of the fluctuation, year by year, from pure maleness to intersexuality in my Birtley station, but hardly allows for the abundance of genuine males in *Salix Caprea* colonies not far away.

Again, to add to the complexity of his explanation, he states that these metamorphosans varieties, unlike the sectorial chimæras of the androgynous plants, are periclinal chimæras for sex.

To me these factorial elucidations fail in their sheer artificiality, and result from a failure to take broader possibilities into consideration.

In the present researches, since it was regarded as possible that hybridity might be responsible for both the androgynous and metamorphosans type of abnormality, cytological investigations were undertaken which made it absolutely certain that, whatever might be true of the former, it certainly did not apply to the latter. The only other species of *Salix* growing within a mile of my *S. Caprea*, with which the species is capable of crossing, are *S. cinerea* and *S. aurita*. Now, as we have seen previously, both of these species are tetraploid and possess a haploid chromosome count of 38 against 19 for pure *S. Caprea*. Any hybrid between *S. Caprea* on the one hand, and *cinerea* or *aurita* on the other, should have a somatic
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chromosome yield of $38 + 19 (= 57)$. This then should be the complement of the metamorphosans $S. \text{Caprea}$ had it originated in hybridity. Its actual condition was very far from supporting the view for, as will be gathered from fig. 4, its somatic and reduced counts agree with those determined from pure $S. \text{Caprea}$. The phenomenon, therefore, is not one of hybridity.

Next the possibilities of somatic non-disjunction were investigated, for changes in chromosome constitution, so

brought about, might result in a sex mosaic but, although the material was exceeding rich in somatic mitoses, at every point, whether in male, female, or intersexual somatic tissue the chromosome count was invariably 38 as shown in fig. 4. Non-disjunction thus cannot serve to interpret the position, and both cytological methods of attack have failed.

Now the Salices, except $S. \text{pentandra}$, supply hosts of tenants with food and shelter, flowers, leaves, stems, and roots all being subject to the attacks of various insects and mites. The possibility that parasitic castration in the Giardian sense might afford the solution could not be excluded. Hence

FIG. 4.—Heterotype, homotype, and somatic plates illustrating the conditions in the Caprea group. Plates from metamorphosans Caprea included: $S. \text{cinerea}$, Lamesley, Co. Durham; $S. \text{aurita}$, Waldridge, Co. Durham; $S. \text{Caprea}$, Bedfordshire; $S. \text{Caprea}$, N. Durham; metamorphosans $S. \text{Caprea}$, Birtley, Co. Durham.
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the organisms inhabiting Salix flowers were collected for
determination when those taken from Salix Caprea, S. cinerea,
and S. aurita included:—

1. Coleoptera: Dorytomus temnatus, Fab.
2. Lepidoptera: Xanthia fulvago, L., X. flavago, F.,
   X. circellaris, Huf., Eupithecia tenuiata, Hb.
4. Eriophyidæ: Eriophyes triradiatus, Nal., Phyllocopites
   phytoptoides, Nal., P. parvus, Nal., and Epitrimerus
   salicobius, Nal.

However, everyone of the species except the mites and
the Cecidomyid fly occurred in males and females alike. Not
only was this so, but the same held true of stations free from
metamorphosans plants. Rhabdophaga heterobia only affected
male catkins and terminal shoots, but no sex reversal
accompanied its presence. In every case, whether in the
Caprea or in Salix repens the effect was the same; a slight
swelling with a hoariness induced by hair development was
present.

There remained, therefore, for consideration the case of
the Eriophyid mites, and there the solution lay. Every
metamorphosans catkin in its early stages submitted to
examination, no matter to what species it belonged, harboured
a stock of mites chiefly of the more or less free living species
Epitrimerus salicobius, from which the unaffected plants were
quite clear.

These same mites are those to which the initiation of the
huge “Wirrzopf,” or Witches’ Brooms, most commonly seen
in the willows of the Pleiandrace supersection, and reported
for such by Houard (1908) and others abroad, and by Miller
Christy (1915) in England, is assigned. Apparently, therefore,
their action on the earlier flowering Salices is to determine
sex reversal in the males and in the later flowering sections,
proliferation.*

In my opinion, too, they act precisely as environmental
agencies do in generating the androgynous form, only in
the latter case I imagine the metabolic state of the whole

* This proliferation, occasionally, is determined by Aphis amenticola, Kaltenbach.

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plant is influenced temporarily. Here the change is local and its effects necessarily localised. That the amount of sex reversal varies from year to year has a ready explanation in the yearly fluctuation* in the quantities of mites present, and, similarly, the variation with the tree, and on portions of individual trees, depends on the degree of local infestation.

The phenomenon, therefore, may be compared with that seen in *Lynchnis dioica* and *L. alba* when, under the influence of the smut, *Ustilago antherarum*, male structures, anthers to wit, are produced in plants genotypically females. One difference, however, must be emphasised, and that is, that in the case of *Lynchnis* the castration is androgenous, *i.e.* male organs appear in female plants whilst in *Salix* it is thelygenous, *i.e.*, female structures arise on male plants.

In the matter of this parasitic castration (Giard, 1869, 1887, 1888) we are apt to look upon the case of *Lynchnis* as pre-eminent but, independently of Giard's work on *Lynchnis*, many important cases are known and attention is here directed to them. Roze (1888) shows how infection by *Ustilago caricis* induces the production of female flowers in the male spikes of the sedge *Carex praecox*; Kellerman and Swingle (1889) demonstrate a similar effect when *Buchloe dactyloides* is attacked by *Tilletia buchloëana*, Chifflot (1909) that *Ustilago Maydis* will produce female flowers in the male inflorescence of *Zea Mays*, var. *tunicata*, Magnin (1892), that the sterile flowers crowning the flower spike of the Grape Hyacinth, *Muscari comosum*, tend to become sexual under the influence of *Ustilago Vaillantii*—and many other examples could be adduced.

5. Summary.

1. The species of the two genera *Populus* and *Salix* are ordinarily dioecious.

2. In the whole of the British *Salix* species and hybrids examined a preponderance of female plants, slight in the diploid forms, but great in the polyploids, was discovered.

3. In the diploids this excess, if significant, probably arises from the slower growth of pollen tubes carrying the male determining gametes.

* Which may depend on meteorological conditions when the mites are dispersing.
4. In the polyploids that influence is assisted (a) by the occurrence of apomixis with thelytoky; (b) by pseudo-fertilisation with thelytoky; (c) by circumstances arising from peculiarities marking the chromosome complexes of polyploid dioecious plants.

5. Hybrid Salices, when combinations of diploid species, invariably possess males.

6. Other hybrids of which at least one parent is polyploid, are exclusively female as far as observation goes or, at best, produce but few males.

7. These latter features may arise from circumstances detailed in (4), or there may be a deliberate and permanent switch-over of the heterogametic sex as in my Lycia-Nyssia crosses.

8. Certain hybrids produce, in addition to plants of the normal male and female types, androgynous or monoeccious forms.

9. These are explained as arising through environmental influences temporarily switching the metabolism of a male plant over from its normal condition to that characteristic of the opposite sex.

10. If that be the correct view the switch-over must occur, with a subsequent reversal, annually.

11. In the Capreae group intersexual florets occur.

12. Such are induced by the attacks of parasites in the form of mites of the Eriophyid group, in particular of Epitrimerus salicobius.

13. They act by effecting local changes in the metabolism of the plant.

14. The phenomenon is thus one of parasitic castration.

15. Many similar cases are known, for which, for the most part, fungi are responsible.

6. References.


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Goldschmidt, R. (1923), The Mechanism and Physiology of Sex Determination.

Heinricher (1882), "Die Teratologie als Behif der phylogenetischen Forschung," Kosmos, Jahrgang 8.
Host (1824), Salix, 1.
Lundström, N. (1875), Studier över Slaglet Salix, Stockholm.
Moquin-Tandon (1841), Édin. de Tératologie Végétale, Paris.
J. W. Heslop Harrison


Schneider, K. C. (1906), Handbuch der Laubbholzkunde, 1, Jena.


Wichura, M. (1865), Die Bastardbefruchtung im Pflanzenreich erläutert an der Bastarden der Weiden, Breslau.


Wimmer, F. (1866), Salices Europae, Breslau.


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