Studies on the Occurrence and Reproduction of British Freshwater Algae in Nature.

I. Preliminary Observations on Spirogyra.

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With Eleven Figures in the Text.

A. Introductory.

IN the course of extensive investigation of periodical samples of Algae from various ponds, situated mainly in the south of England, a considerable number of facts regarding the occurrence and reproduction of *Spirogyra* have come to light. Certain data dealing with the biology of this genus have already been published,[1] but we believe that the subject has not yet been approached from exactly the same point of view as that adopted in the present paper. A general preliminary account of the results so far obtained may thus be of some value. It is proposed in subsequent papers of this series to deal with other genera of freshwater Algae in the same way.

The materials on which our observations are based have been collected by the method already described in some detail by one of us,[2] and it

[1] See especially Messrs. W. and G. S. West, Observations on the Conjugatae. Annals of Botany, vol. xii, No. xlv, 1898, p. 29 et seq. J. Comère, Observations sur la périodicité du développement de la flore algologique dans la région toulousaine. Bull. Soc. Bot. de France, t. liii, 1906, p. 390 et seq. G. Klebs, Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen. Jena, 1896, p. 229 et seq.

[2] Cf. Fritsch, Problems in Aquatic Biology, &c. New Phytologist, vol. v, No. 7, 1906, p. 149 et seq.

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is unnecessary to say much more about it here. We are glad, however, to have this opportunity of expressing our sense of obligation to a number of botanists, who have with such kind perseverance and care considerably furthered these investigations. We are fully aware of the objections that can be raised against observations based on the collection of isolated monthly or fortnightly samples by individuals who are not in direct touch with the work. But apart from the fact that most of those who have collected for us have evidently done so conscientiously, we may point out that in dealing with small pieces of water like those to which we have confined our attention, it is very unlikely that a form, which is at all common, will have escaped observation ; and we have been careful not to draw many conclusions as to relative amounts of an Alga present without the existence of overwhelming evidence. Much labour has been bestowed on a thorough examination of each sample of Algae, particularly where a negative conclusion was concerned.

The conditions, which lead to and modify the process of reproduction in *Spirogyra* (and other Algae) have been investigated by Klebs, and are published in his 'Bedingungen der Fortpflanzung, etc.' (Jena, 1896). Klebs's results are of great interest, and we shall have frequent occasion to refer to them in recounting our own observations, but there is one objection to which a large number of his experiments are open. It is doubtless of some value to know how diverse reagents and changes in external factors affect the reproduction of an algal genus, but unless they are such as are realized in nature, they do not contribute materially towards an understanding of its biology. To our thinking work of this kind is best started from the other side ; that is to say, we should commence by undertaking careful observations on the Alga in nature, and endeavour to correlate any changes it shows with variations in the natural conditions of its habitat. The Alga in this method of investigation is left to react under the play of nature's forces, and it is the work of the investigator to interpret such reaction in terms of external factors. When that is accomplished we must resort to experiment, which must ultimately settle whether the inference from direct observation is correct or not.

B. The Occurrence of Spirogyra in Nature.

In dealing with the occurrence of *Spirogyra* in nature we must distinguish between a vernal and an autumnal phase, which are more or less sharply marked. It is in the vernal phase that reproduction mainly takes place, although, as we shall see, this is not without exception. Some species of *Spirogyra* (e. g. *S. varians* (Hass.), Kütz., *S. quadrata* (Hass.), Petit) would appear to be (ordinarily) confined to the vernal phase and not to reappear again in the autumn, while others (e. g. *S. rivularis*, Rabh., *S. affinis* (Hass.), Petit, *S. jugalis* (Dillw.), Kütz.) are present both in spring

and autumn. Between the vernal and the autumnal phase, however, there is always a very marked decrease in quantity, amounting in very many cases to complete disappearance (in July and August, cf. *S. affinis*, *S. jugalis*, *S. rivularis*). There is some evidence also to show that between the autumnal phase and the ensuing vernal phase some species of *Spirogyra* again practically disappear, being absent in midwinter (cf. *S. jugalis* (Dillw.), Kütz., *S. Weberi*, Kütz., *S. rivularis*, Rabh., in 1905). Since zygospores (except in a few cases) are not formed during the autumnal phase, the reappearance of the Alga in the following spring must take place at the expense of the zygospores formed in the preceding vernal phase. The Alga never appears in autumn in such quantity as to warrant the supposition that all the zygospores formed in the previous spring have germinated ; in all probability the conditions which lead to the autumnal appearance of these *Spirogyras* are only sufficient to stimulate a small number of zygospores to germination, and the main mass of them remains dormant till the spring.[1] We shall return to this subject below.

Before passing on to further considerations we may briefly discuss some of the data in the literature bearing on this subject. Comère (loc. cit., p. 405) records the occurrence of Zygnemaceae in the waters examined by him as follows : In the ' eaux stagnantes ' they are found in his second vernal, aestival, and autumnal periods (i. e. from the middle of April to the first frosts), while in the ' milieux passagers ' they are present only in the first and second vernal periods (i. e. from the end of February to the end of June).[2] While we have been unable to recognize any marked differences in the occurrence of *Spirogyra* in permanent waters and in those which dry up in summer, Comère's observations agree with ours in the prevalence of this genus in the spring. The waters examined by Comère do not apparently show any marked decrease of *Spirogyra* in midsummer, while its absence in winter is much more marked. Petit [3] in his valuable treatise on the *Spirogyras* of the neighbourhood of Paris mentions March—July as the period of occurrence of most of the species described, although many of them have a much more limited period ; *S. orthospira* (Naeg.), Kütz., *S. bellis* (Hass.), Cleve, and *S. orbicularis* (Hass.), Kütz., are the only species found by him also in the autumn. Petit's observations are particularly valuable, as they are the results of investigations extending over many years. According to Klebs (loc. cit., p. 229), species of *Spirogyra* are found ' zu

[1] It is not quite impossible that the disappearance of *Spirogyra* in summer and midwinter may be only apparent, and that a certain number of filaments may sink to the bottom and remain there in a dormant condition. In view of the fact that our knowledge of algal reproduction is so scanty, it is just worth while keeping this in mind, although there are no data to support it.

[2] The pieces of water with which we are concerned in the present paper belong only to Comère's ' eaux stagnantes ' and ' milieux passagers.'

[3] Paul Petit, *Spirogyra* des environs de Paris. Paris, 1880, 39 pp. Unfortunately, Petit does not definitely state whether the months mentioned by him after each species refer to period of occurrence or period of reproduction, but it seems probable that they refer to the former.

allen Jahreszeiten in Sümpfen und Teichen,' although his own subsequent remarks do not point to an occurrence at *all* times of the year. Regarding *S. inflata*, Vauch. (p. 233), he states that he found it (in the sterile condition) in spring, 1894 (apparently present already in February), and that the first indications of conjugation were observed at the beginning of May. *S. Weberi*, Kütz. (p. 241), appeared regularly in a pond in the Botanic Gardens at Basle in March and attained an abundant development in the course of April; at the end of April or the beginning of May conjugation took place, after which the Alga disappeared. Klebs found this species again in the autumn, and remarks upon it as follows: 'Erst im Herbst, sei es aus überlebenden, einzelnen Fäden, sei es aus Zygoten, entwickelt sich die Alge noch einmal, kommt aber nicht mehr zur Konjugation.' This is in complete accord with the observations we have made on some species of *Spirogyra*, although in the case of *S. Weberi* our data testifying to an autumnal occurrence are rather meagre. These few statements quoted from the literature indicate that the general occurrence of *Spirogyra* is much as we have described it in the preceding paragraph, but that minor modifications of the ordinary scheme are frequent (as indeed our own observations show). It is not at all likely that the periodicity of *Spirogyra* (or of any other Alga) will be quite the same even in the same latitudes as numerous modifying climatic factors must come into play.

The different species of *Spirogyra* certainly as a rule attain their maximum development in the vernal phase. The autumnal phase is on the whole quite subsidiary to the vernal phase—a fact which is already evidenced by the lack of reproduction in the autumn. The reappearance of species of *Spirogyra* in the autumn probably depends on the realization of certain external conditions which stimulate a certain number of the zygospores to germination. In the absence of the necessary conditions the autumnal phase may be far less evident, or even completely suppressed, and species which are ordinarily present both in spring and autumn may appear to have a vernal phase only (cf. *S. jugalis*, present in Abbot's Pool in autumn, 1905, but absent in autumn, 1906; see also *S. affinis*). On the other hand, it is quite possible that those species, which we have been led to regard as purely vernal ones (e.g. *S. varians*), do under exceptional circumstances exhibit an autumnal phase as well. We have no data at present in support of this latter view, but they may be forthcoming in the course of further investigation. All species of *Spirogyra* would then have the tendency to be present both in spring and autumn, but in the case of some of them, the necessary conditions for an autumnal appearance would only very rarely be realized. The causes for the disappearance of *Spirogyras* after the vernal phase will probably be found in some or all of the factors connected with the advent of summer. These factors may be enumerated as follows:—

(*a*) The increase in the intensity and duration of the light.

(*b*) The increase in the temperature of the water and the consequent diminution in the amount of dissolved gases in the water.

(*c*) The gradual concentration of the salts dissolved in the water owing to the heat, and lack of rainfall in a normal summer.

(*d*) ? The increase in the amount of the higher (Phanerogamic) vegetation present.

At the end of a normal summer all these factors undergo modification in the reverse direction, and in this way conditions may become favourable for the reappearance of *Spirogyra*. We may point out, however, that certain definite combinations of these external factors are probably necessary for the reappearance of any given species, and that these combinations will vary for each individual species. From observations made last autumn it would seem as though dilution of the water back to its ordinary degree of concentration were one of the essential factors for an autumnal phase, but that if this dilution is delayed too long it may take place at a time when the average daily temperature or light-intensity is not high enough to allow of the appearance of *Spirogyra*. Thus in the autumn of last year (1906), in which after a very dry and hot summer rain only set in at a late date, *Spirogyras* were practically wanting in all the ponds examined, whilst in 1905, in which the rain commenced early and was rather equally distributed over the autumn months, many of the *Spirogyras* showed a very well-marked autumnal phase (cf. the table). In the case of one pond (Barton's pond at Harpenden), in which *Spirogyras* were very common in the spring, the water in 1906 only attained its ordinary level after the summer shrinkage at the end of October, i. e. at a time when the average daily temperature was 10·9° C. (on November 7th the average for the previous fortnight was only 6·8° C.); there was practically no autumnal *Spirogyra*.

The above suggestion that the occurrence and especially the extent of the autumnal phase depend on certain combinations of external factors is supported by a number of data, which may be briefly referred to; they are mainly derived from Abbot's Pool, near Bristol, from which we have three years' consecutive observations. *S. rivularis* was fairly abundant in this pond in the autumn of 1904, but much rarer, though always present in some quantity, in the autumn of 1905 and 1906. *S. jugalis* was quite a common form in the autumn of 1905, but absent at this time of the year both in 1904 and 1906. The special conditions, which led to the non-development of *S. jugalis* in autumn, 1904 and 1906, did not, therefore cause the disappearance of *S. rivularis*, which even flourished in 1904.

The disappearance of *Spirogyras* in midwinter between the autumnal and the vernal phase, which is not quite certainly established, can only be related to temperature and light-conditions. It would be premature to discuss the matter further at the present moment.

The ordinary curve of frequency of *Spirogyra* would thus either be a single one (with vernal phase only) or a double one (with both vernal and autumnal phase) with two maxima, one of which (in spring) would be much higher than the other (in autumn). *Spirogyras* are, however, occasionally found flourishing at other times of the year, and we must now notice a few cases of this kind. In the aquatics' tank near the Jodrell Laboratory at Kew, *S. crassa* is present in quantity practically all the year round, although it has not been found reproducing; *S. condensata* and *S. longata*, however, are ordinarily only common in the same piece of water from June to August. This tank belongs to Comère's 'milieux mixtes,' and the period of occurrence of the two *Spirogyras* last-named roughly agrees with Comère's observations on such pieces of water (loc. cit., p. 405).[1] In a pond at Telscombe, near Newhaven, *S. insignis* (Hass.), Kütz., was present in very large amount (but did not reproduce), in December, 1902, and January, 1903, although it disappeared totally after that, and did not occur again in the following winter.[2] *S. affinis* (Hass.), Petit, and *S. cataeniformis* (Hass.), Kütz., were very abundant from September to December, 1904, in the same pond (cf. table). *S. communis* (Hass.), Kütz., is frequently very abundant in midwinter in one of the ponds on Sheen Common, Richmond. We cannot do more than merely mention these cases, which no doubt any one of our readers could multiply. Further observation and experiment will no doubt bring an adequate explanation of these apparently abnormal phenomena.

It still remains to consider a few examples of the reverse state of affairs, i. e. absence of a species of *Spirogyra* at a time when one would expect it to be present. One of the most striking cases of this kind is the complete absence of all species of *Spirogyra* in the first half of 1904[3] in Abbot's Pool, although in 1905, 1906, and 1907 they were present in great amount. We are indebted to Dr. H. R. Mill for data as to the rainfall in the early part of 1904 and in the latter half of 1903. In October, 1903, the rainfall at Clifton was very much in excess of the average (= 4·01 in. for the last thirty years), viz. 8·03 in.; December also had a high rainfall, viz. 3·13 in. The total rainfall from September to December, 1903, amounted to 16·4 in., as against 7·35 in. in 1904, 7·51 in. in 1905, and 11·13 in. in 1906. With reference to the sunshine, Dr. Mill writes: 'I cannot speak positively about the sunshine, as I have no statistics of it, but I think you may safely take it that the last three months of 1903, and the earlier months of 1904, were decidedly deficient in sunshine.' There is thus good evidence to show

[1] Cf. Fritsch, Algological Notes. IV. Remarks on the Periodical Development of the Algae in the artificial waters at Kew. Annals of Botany, vol. xvii, 1903, p. 277; cf. also occurrence of *Spirogyra* in the lake at Kew.

[2] Fritsch, Problems in Aquatic Biology, &c., loc. cit., pp. 164, 165.

[3] Unfortunately, we have no samples from this pond before January, 1904, so that we are unable to say how long previously this state of affairs had obtained.

that prior to the abnormal absence of *Spirogyra* in Abbot's Pool in the spring of 1904 the state of the weather was not at all normal (very excessive rainfall and lack of sunshine). That these conditions have something to do with the vernal appearance of *Spirogyra* is also exemplified by the remarkably late appearance of this genus in Abbot's Pool (and other ponds) in the spring of this year (1907). Ordinarily, *Spirogyra* is quite abundant already in March; this year, however, it did not occur in any amount before April (cf. the table).[1] As above shown, the rainfall in the autumn of 1906, although not as great as in 1903, was considerably above that of 1904 and 1905; this may again have something to do with the late appearance of *Spirogyra* this spring. There has, however, been a general dearth of *Spirogyra*[2] this spring, and we should not like it to be imagined that we consider the rainfall of the previous autumn solely responsible. The last year had a very long and hot summer, during which many of the smaller pieces of water dried up, and we have already pointed out that the ordinary water-level was probably regained too late for the proper development of an autumnal phase in any *Spirogyra*; this may have acted as a check on these forms, which may be connected with their late appearance this spring. The spring of this year has moreover also been abnormal, and may be partly accountable.

C. The Reproduction of Spirogyra in Nature.

The fact that in most cases the species of *Spirogyra* reproduce during the vernal phase is a very marked feature in the biology of the genus (cf. the table on p. 436). The conditions which lead to reproduction at this time of the year must be very complicated ones, and we may quote the following examples in illustration of this. In the case of Abbot's Pool, near Bristol, *S. varians* (Hass.), Kütz., has been found reproducing abundantly in the spring of 1905, 1906, and 1907; *S. Weberi*, Kütz., and *S. affinis* (Hass.), Petit, although present in all three years, formed zygospores only in 1906; *S. nitida* (Dillw.), Link, was present both in 1905 and 1906, but reproduced only in 1905; while *S. neglecta* (Hass.), Kütz., formed zygospores in both years. In all three years *S. varians* was found with zygospores in two other ponds during the vernal phase (cf. the table). In the case of this species, therefore, the conditions necessary for reproduction appear to be realized every spring; while in the case of the other species mentioned above, the factors which lead to conjugation only occasionally obtain. Similar observations were made on the *Spirogyras* in Barton's Pond, near Harpenden; *S. tenuissima* (Hass.), Kütz., was reproductive in both 1906

[1] Reproduction also set in considerably later than usual.

[2] In some ponds, which ordinarily have a good deal of *Spirogyra* in spring, it has scarcely put in an appearance up to the time of writing (June 3), e.g. Hendon Pond.

and 1907; *S. quadrata* (Hass.), Petit, and *S. cataeniformis* (Hass.), Kütz., formed zygospores only in 1906, *S. Hassallii* (Jenn.), Petit, only in 1907.

Although the period of reproduction may be roughly limited to April–June, reproduction takes place at different times in the individual species during this period (cf. the table). Thus in Barton's Pond a considerable amount of sterile *Spirogyra* was present on April 9, 1906; on April 21, *S. quadrata* (Hass.), Petit, and *S. tenuissima* (Hass.), Kütz., were observed with zygospores, while *S. cataeniformis* (Hass.), Kütz., was beginning to conjugate; on May 5 matters were unaltered, and *S. cataeniformis* was only observed with zygospores on May 19. By June 18 all *Spirogyras* had disappeared. Similarly, in Abbot's Pool in 1905, *S. varians* and *S. jugalis* were found in the reproductive condition in April; while *S. neglecta* and *S. nitida*, although previously present, did not begin to reproduce before May. In some species the period of reproduction is remarkably long (e. g. *S. affinis* (Hass.), Petit, *S. neglecta* (Hass.), Kütz.), in others short (e. g. *S. varians* (Hass.), Kütz., *S. Weberi*, Kütz., *S. jugalis* (Dillw.), Kütz.).

As a rule, if the same species is found in two or more ponds, and is reproductive in one of them, it is found to reproduce in all of them, though not always at exactly the same time (e. g. *S. varians*, *S. neglecta* var. *ternata*, *S. quadrata*, *S. jugalis* in 1905); this is, however, not without exception (cf. *S. Weberi*, *S. jugalis* in 1906). In the case of some species (e. g. *S. varians*, *S. tenuissima*, *S. condensata*, *S. affinis*) the conditions causing reproduction affect nearly all the filaments, and with the formation of zygospores the species disappears; in other cases, however (e. g. *S. neglecta* var. *ternata*, *S. nitida*, *S. Weberi*), by no means all the filaments become involved in conjugation, and these sterile filaments may persist for some time after zygospore-formation. This phenomenon is no doubt also dependent on the degree of development of the external factors influencing reproduction in *Spirogyra*, and one and the same species may in some cases disappear completely after reproduction, in other cases still persist for a time (cf. *S. affinis*, *S. neglecta*, &c.). Another feature illustrating the varying effect of external conditions on reproduction in *Spirogyra*, is the occasional conjugation of a species without the process coming to an end (i. e. without formation of zygospores), cf. *S. jugalis* (Dillw.), Kütz., in Abbot's Pool in 1905, and at Tiltham's Pond in 1906.

The facts detailed in the preceding paragraphs suffice to show the complexity of the conditions influencing vernal reproduction in *Spirogyra*. The prevalent occurrence of reproduction in the vernal phase may be due to an inherent tendency, or to certain combinations of external conditions, which occur more or less regularly every spring (seasonal factors). If vernal reproduction is the result of inherent tendency, then it is difficult to understand why a species reproduces in the spring of one year and not (although present) in the spring of another year (cf. the data given above); moreover,

the occasional reproduction of *Spirogyra* at other times of the year is incomprehensible. With regard to the former point we cannot deny the possibility of some of the *Spirogyras* being biennial as far as reproduction is concerned; one or two years' further observations will show whether there is any truth in this. But from all we know about algal reproduction it seems very unlikely, and it is far more probable that reproduction in *Spirogyra* depends on the presence of certain combinations of factors, which probably differ for each individual species. The most important changes that take place in spring are on the whole the same as those which have been enumerated on p. 427; it does not seem likely, however, that there is any marked annual concentration or dilution of the water during the early part of the vernal phase (March and April), although this factor will in many years come into play during May and June. All the factors concerned, it will be noted, undergo a gradual intensification as the summer approaches, and this intensification reaches its maximum somewhere during the summer months, after which there is again a gradual diminution. At some time in the autumn, therefore, each factor must be present in the same degree as in spring, and it might be argued that autumnal reproduction should for this reason be as common as vernal reproduction. In the case of the autumn, however, each factor is undergoing change in the reverse direction (intensity and duration of light decreasing, temperature decreasing, &c.) to that which obtains in the spring, and this difference probably accounts for the absence of autumnal reproduction—even though combinations of factors, similar to those found in spring, must sometimes occur. The direction of change of a factor or of a group of factors, is no doubt of great importance, and it probably makes all the difference whether, for instance, an Alga after being exposed to a low temperature is subjected to a higher one, or vice versa. The response in the two cases may be quite different.

The reproduction of the different species of *Spirogyra* in the vernal phase is thus most probably dependent on the seasonal occurrence of certain external conditions, particularly on an increase in intensity of the factors liable to change in spring. For each particular species certain intensities of the different factors will probably be necessary, and it depends on the realization of these intensities as to whether the given species will reproduce or not. That these intensities vary for different species, is shown by the fact that in the same pond different *Spirogyras* begin to reproduce at different times during the vernal phase, and that the same species reproduces at different times in different ponds and in different years (cf. the table). The general *modus operandi* of these factors is illustrated by Klebs's work. He has shown (loc. cit., pp. 233, 237, and 241) that in the case of a number of species of *Spirogyra* zygospore-formation can be induced by placing the Alga in water in bright sunlight for a few days. If we substitute a weak nutritive solution for the water, it will, unless very dilute, absolutely work

against the effect of strong sunlight, and no conjugation will take place. Temperature has very little effect on the process except to accelerate it. We have no data as to the possible effect of the smaller amount of dissolved gases except that those species of *Spirogyra*, which grow in running (well-aerated) water, practically never show sexual reproduction. The preceding facts give us an insight into the causes leading to reproduction in the vernal phase; these are the increased intensity of the light, the small percentage of dissolved salts in the water, the rising temperature, and (?) the decrease in amount of dissolved gases. Light is probably the most important, but its effect will be qualified by the increasing concentration of the water as the vernal period passes on; and in the case of a dull spring (without much rainfall), the water may have attained such a degree of concentration by the time the light-intensity becomes adequate, that the latter is no longer able to stimulate the Alga in the direction of reproduction. In fact everything probably depends on each factor acquiring the proper degree of development at the proper time, and in co-ordination with the other influencing factors. It seems very likely that F. F. Blackman's doctrine of limiting factors [1] can be applied to algal reproduction as to other physiological phenomena, and that in the event of the non-reproduction of a species of *Spirogyra* in the spring, one or more of the complex of influencing factors is limiting the process. In the case of a species like *S. varians* (Hass.), Kütz., the combination of factors necessary for reproduction is usually realized in nature, but in other species the reverse is the case (cf. *S. rivularis*, Rabh., in our table; see also Petit, loc. cit., p. 27 (*S. fluviatilis*, Hilse), and Klebs, loc. cit., p. 239).

Our data, as will be seen by a glance at the table, give overwhelming evidence of the reproduction of *Spirogyra* in the vernal phase, and we are only able to mention one example to the contrary. From Comère's and Petit's observations (quoted on p. 425) we gather that matters are very much the same in the districts they investigated. Klebs, however (loc. cit., p. 244), gives a rather different account; he says: 'In der freien Natur pflegen viele Spirogyren im Früjahr und Frühsommer zu kopulieren, doch ohne irgend welche bestimmte Regel; man findet Zygotenbildung ebenso im Sommer, bisweilen sogar im Frühherbst bei sehr sonnigem Wetter.' This statement is not directly contrary to what we have found, but we think it unlikely that reproduction of *Spirogyra* in Germany is not just as predominant in the vernal phase as it is with us; Klebs's own observations, in fact (quoted on p. 428), point in that direction. The phrase 'ohne irgend welche bestimmte Regel' is perhaps therefore not quite exact. That zygospore-formation does go on occasionally in the height of summer and

[1] F. F. Blackman, Optima and Limiting Factors. Ann. of Bot., vol. xix, No. lxxiv, April, 1905, pp. 281–295.

autumn or even in midwinter,[1] is undoubted, and it is quite possible that in some regions owing to certain climatic combinations such phenomena are more abundant than we have found them to be. If reproduction in *Spirogyra* is a result of intensification of certain factors, it is comprehensible that such intensification may occasionally occur at other times of the year than in spring, and that we may consequently find a species reproducing in the autumn or winter.

We may briefly consider the one exceptional case we have observed; this was in a pond at Telscombe, near Newhaven, in which *S. cataeniformis* (Hass.), Kütz., and *S. affinis* (Hass.), Petit,[2] were found reproducing abundantly from September to November, 1904. The following data as to the nature of the weather at this time of the year are taken from Brighton,[3] which is sufficiently near to Telscombe to justify the assumption that there were no marked differences. August and September, 1904, had a good deal more bright sunshine than is their wont (August had 249·26 hours, while the average for the last twenty-seven years was 205·66 hours; September had 192·50 hours, the average for the last twenty-seven years being 163·35). The mean temperature for September, 1904, was 58·1° F., which is about the average (58·4° F.); the extreme temperatures for this month were, however, much less than the average, the range being 44·1° F. to 70·6° F. (as against 35·9° F. to 83·2° F. for the last twenty-seven years). The rainfall was as follows:—July, 1904 = 0·52 in. (average 2·33 in.); August, 1904 = 1·71 in. (average 2·44 in.); September, 1904 = 1·64 in. (average 2·39 in.); October, 1904 = 2·47 in. (average 3·87 in.). The rainfall was therefore considerably below the average. August and September, 1904, were certainly abnormal months meteorologically, and hence possibly the abnormal reproduction of the two species of *Spirogyra*. The very considerably larger number of hours of bright sunshine was probably one of the most important factors.

D. Points of Systematic Interest.

The determination of species of *Spirogyra*, even in the reproductive condition, is combined with so many difficulties that we have thought it best to figure a number of the species examined, so as to leave a permanent record. The following systematic details may also be of some interest.

S. ternata, Ripart, is now usually regarded as a variety of *S. neglecta* (Hass.), Kütz.,[4] and our observations certainly support this view. In a pond in Sydenham Wells Park (July 2, 1906) filaments answering to Petit's

[1] Cf. W. and G. S. West, loc. cit., p. 33.

[2] Cf. Fritsch, Problems in Aquatic Biology, &c., loc. cit., pp. 164-7. The two species are here referred to as '*S. gracilis*.' Renewed investigation of the sample has shown that this determination was incorrect.

[3] Cf. Brighton and Hove Nat. Hist. and Phil. Soc. Annual Report for 1905.

[4] Cf. also Petit, loc. cit., p. 27.

description (loc. cit.) were found. In some filaments zygospores were present in every cell, while in others cells containing zygospores alternated with vegetative cells (cf. Fig. 10); in the latter case the zygospores had their long axes at right angles to the direction of the filament, and the cells containing them were abbreviated and deformed. The vegetative cells were slightly inflated on both sides (Fig. 10) or only on one side (Fig. 11), and had prominent pyrenoids in their chloroplasts. Other filaments of *Spirogyra*, present in the same sample (July 2, 1906) undoubtedly belonged to *S. neglecta*; they were also in the reproductive

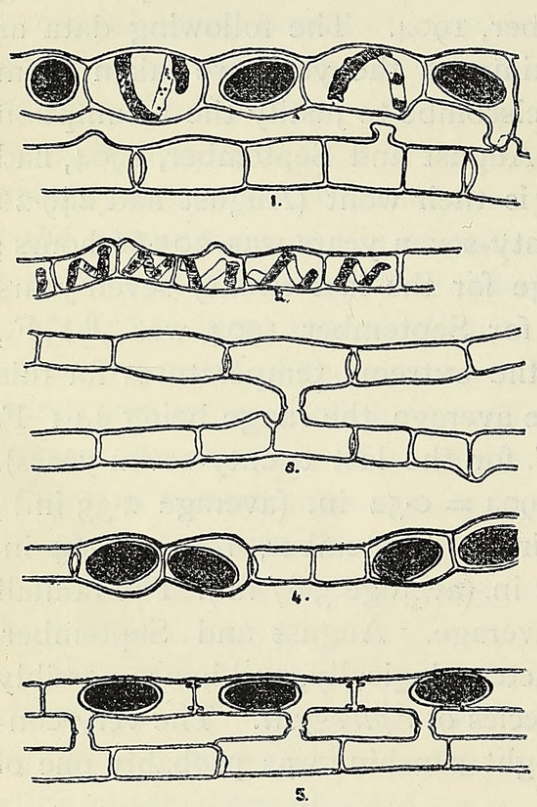

FIG. 1. *Spirogyra varians*. From Tiltham's Pond.
,, 2, 3, 4. *S. affinis*. From Abbot's Pool.
,, 5. *S. Weberi* (Abbot's), magnified 240 times.

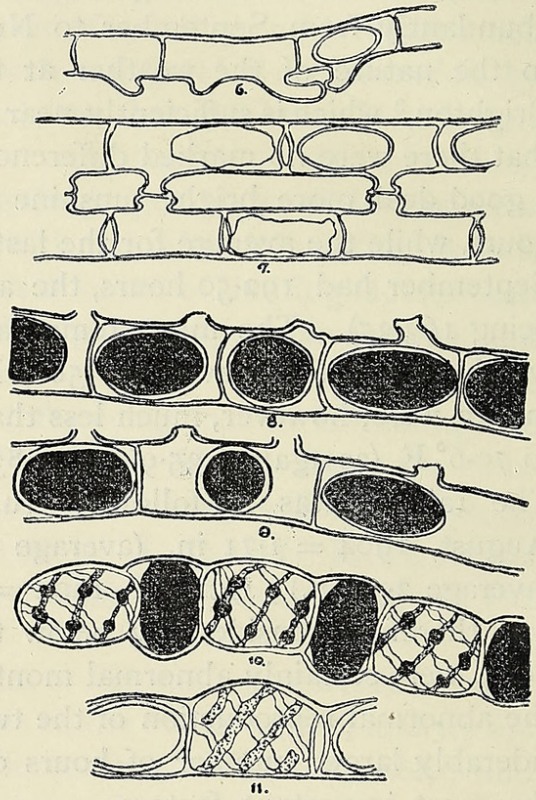

FIG. 6. *Spirogyra longata* from Epsom.
,, 7. ,, ,, from Hendon.
,, 8, 9. *S. neglecta forma* from Abbot's Pool.
,, 10, 11. *S. ternata* from Sydenham Wells.

condition. Earlier samples from the same pond contained abundant *S. neglecta*, but it was almost impossible to identify any of the *Spirogyra* as *S. ternata*.

S. neglecta (Hass.), Kütz., can thus exhibit considerable variation, and we met with another example of this in Abbot's Pool. We were much puzzled in examining samples from this pond to find two *Spirogyras* of the same width, one of which was undoubtedly *S. neglecta*, while the other answered to no description we could find. It differed from *S. neglecta* in having rather broader chloroplasts with larger, better-marked pyrenoids, and in the absence of what Petit calls a 'nervure centrale.' Figs. 8 and 9

give some idea of the different appearance of the zygospores according to their position in the cell ; in some cases the ends of the spores were quite pointed, at other times blunt and almost square. For a time we were inclined to regard this form as a distinct species, but we found so many transitions between it and the typical *S. neglecta* that we have come to the conclusion that it cannot be separated from that species ; it may possibly prove to be a definite variety.

We may add a few notes regarding other species. *S. varians* (Hass.), Kütz. (Fig. 1), is mentioned by G. S. West[1] as frequently exhibiting lateral conjugation. Although, as will be seen by a glance at the table, we have often found this species in the reproductive condition, we have noticed only scalariform conjugation. In a pond at Hendon, near London (sample collected on April 25, 1905), a long filament of *S. varians* was observed, which was doubled back and conjugating with itself. In Fig. 3 *S. affinis* is shown with both scalariform and lateral conjugation in the same filament. Figs. 6 and 7 show the two types of conjugation in *S. longata.*

E. Summary.

The species of *Spirogyra*, which we have examined, are either purely vernal or exhibit both a vernal and an autumnal phase with an intervening period of scarcity or complete disappearance ; it seems possible that there is also a period of disappearance in midwinter, but this is not certainly established. The autumnal reappearance of certain species of *Spirogyra* is no doubt due to the influence of certain combinations of external factors causing a small number of zygospores to germinate ; in the absence of these conditions there may be no autumnal phase. Abnormal meteorological conditions may bring about abnormal absence or occurrence of *Spirogyra.*

Reproduction takes place ordinarily in the vernal phase, and is most probably the result of certain periodically recurring combinations of factors, which vary for different species. A considerable number of data are advanced in support of this view. The nature of the stimulus causing vernal reproduction is probably an intensification of those conditions, which are liable to change in spring. Such intensification may exceptionally take place at other times of the year and lead to reproduction at other times than in spring.

[1] A treatise on the British Freshwater Algae. Cambridge, 1904, p. 125.

Spirogyra	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
affinis (Hass.), Petit	'04 I	R, I	I	R	—	—	—	—	**I!**	**I**	**I**	I, R
	'05 A	A	A	A	A	A	A	—	A	A	A	A
	'06 A	A	A	**A**	**A**	**A**	**A**	—	—	—	—	A
	'07 A	A	A	A	..	..	..	..	..	..	..	..
bellis (Hass.), Cleve	'04 ..	..	..	R	R	**R**	..	..	..	..	..	..
	'07 ..	..	..	**S**	..	..	..	..	..	..	..	..
cataeniformis (Hass.), Kütz.	'04 ..	..	..	..	..	..	..	..	**I!**	**I**	**I**	I
	'06 ..	..	B	B	**B**	B	—	—	—	—	—	—
	'07 —	—	—	—	B	..	..	..	..	..	..	..
condensata (Vauch.), Kütz.	'04 —	—	—	I	**I**	**I**	—	—	—	—	—	—
Hassallii (Jenn.), Petit	'05 ..	..	..	H	..	..	..	..	..	..	..	..
	'06 ..	..	..	—	—	B	—	—	—	—	—	—
	'07 —	—	—	—	**B**	..	..	..	..	..	..	..
jugalis (Dillw.), Kütz.	'05 A	A	A	**A!**	A, **O**	—	—	A	A	A	A	—
	'06 —	A	A	**T** ! A	A	A	A	—	—	—	—	—
	'07 —	—	—	—	..	..	..	..	..	..	..	..
longata (Vauch.), Kütz.	'02 ..	..	..	..	..	**K**	..	..	..	..	..	..
	'05 ..	..	..	**H**	..	..	..	..	..	..	..	..
	'06 ..	..	..	**E**	..	..	..	..	..	..	..	..
neglecta (Hass.), Kütz.	'05 —	—	—	A	**A**	**A**	**A**	**A**	A	—	—	—
	'06 —	—	—	**A**	**A**	**A**	**A**	—	—	—	—	—
	'07 —	—	—	—	..	..	..	..	..	..	..	..
neglecta (Hass.), Kütz., var. *ternata*, Ripart.	'05 ..	..	..	..	..	..	..	..	..	..	..	..
	'06 ..	..	T, W	**T**, W	**T**, W	T, W	**T, W**	—	—	—	—	—
nitida (Dillw.), Link	'02 ..	..	..	..	..	**K**	..	..	..	..	..	..
	'05 A	A	A	A	**A**	A	—	—	—	—	—	—
	'06 ..	..	..	A	A, R	A, R	A, R	R	—	—	—	—
	'07 —	—	—	—	..	..	..	..	..	..	..	..
quadrata (Hass.), Petit	'06 —	—	T	**B, T**	**B**	**B**	—	—	—	—	—	—
	'07 —	—	—	—	B	..	..	..	..	..	..	..
rivularis, Rabh. ?	'04 —	—	—	—	—	A	—	—	A	A	A	A
	'05 A	A	A	A	A	A	A	—	A	A	—	—
	'06 A	A	A	A	—	—	—	—	—	—	A	A
	'07 A	A	A	A	A	..	..	..	..	..	..	..
tenuissima (Hass.), Kütz.	'06 ..	..	..	**B**	**B**	**B**	—	—	—	—	—	—
	'07 —	—	—	—	**B**	..	..	..	..	..	..	..
varians (Hass.), Kütz.	'05 —	—	A, H	**A, H**	**A, O**	—	—	—	—	—	—	—
	'06 —	—	A	**A, T, E**	—	—	—	—	—	—	—	—
	'07 —	—	—	**Q, A**	**B, A**	..	..	..	..	..	..	..
Weberi, Kütz.	'02 ..	..	..	..	..	**K**	..	..	..	..	N	—
	'03 —	—	N	N	N	G	..	..	..	..	..	..
	'04 ..	..	..	N	..	..	..	..	..	..	..	..
	'05 A	A	A	A	A, **O**	A	—	—	A	—	—	—
	'06 A	A	A, W?	**A**, W ?	**C, A**, W?	A	A	—	—	—	—	—
	'07 A	A	A	A, **S**	..	..	..	..	..	..	..	..

Ordinary type indicates sterile, Clarendon type reproductive condition; where an exclamation mark is added, conjugation only was observed and no zygospores were seen. Wherever a species of *Sp.* is recorded in a pond from which a consecutive series was available its absence is indicated in other months by means of a dash. The letters refer to the different ponds, which are as follows:—

A = Abbot's Pool (series).
B = Barton's Pond (series).
C = Coalville.
E = Chessington.
G = Reigate
H = Hendon.
K = Kew (cf. Fritsch, in Kew Bulletin, Addit. Ser. v, 1906, p. 187, et seq.).
I = Telscombe Pond (series).
N = Penn Ponds (series).
O = Portishead Pond (series).
Q = Pond at Erquy (Brittany).
R = Sheen Common Pond.
S = Pond at Silverdale.
T = Tiltham's Pond (series).
W = Sydenham Wells Pond (series).