BOTANISKA NOTISER 1960 · VOL. 113 · FASC. 1 · LUND

Studies on Carex stenophylla Wg in Europe

By TYCHO NORLINDH

(Meddelande från Lunds Botaniska Museum, Nr 139)

During my studies of collections of *Carex* from Central Asia, particularly from Mongolia, I have met with numerous difficulties in the taxonomic treatment of the *Carex stenophylla* complex. As the species was described from Austria I considered it necessary first to revise the herbarium material from this and adjacent countries. The species then proved to be fairly variable even in this westernmost part of its area of distribution. Many of the taxa which have been distinguished within this complex are only slightly delimited from each other and the view as to whether these taxa should be considered as valid species, subspecies or varieties, has changed considerably during the course of time.

In Kükenthal, 1909, pp. 120—122, in Engler, Das Pflanzenreich, *Cyperaceae-Caricoideae* one finds *C. stenophylla* in its widest sense. Kükenthal has treated quite a large number of earlier described species as synonyms of *C. stenophylla*. However, in some cases he went to extremes in uniting species, for instance, when he included in *C. stenophylla sensu lato* such taxa as *C. enervis* C. E. Mey. and *C. pachystylis* Gay. But broadly speaking his conception of the limits of *C. stenophylla* will probably be accepted by future botanists. According to his statements, this species extends from the central and south-eastern part of Europe, Asia Minor, Syria and Mesopotamia eastward through Asia as far as Lena in Eastern Siberia, Manchuria, Korea and North China. It also occurs in the North American prairie regions and in the Rocky Mountains. It appears mainly in arid areas, particularly in grass steppes and in semideserts. Meusel designates (Vergl. Arealkunde, 1943) *C. stenophylla* as "amphiboreo-meridional-(sub)montan-kontinental".

Kreczetowicz went to the other extreme in delimiting *C. stenophylla*. In this species he wanted to include only the isolated populations of

C. stenophylla which occur in Austria and Hungary, particularly in the Danube area, in Czechoslovakia and Romania (Transsilvania), and in a few localities in northernmost Italy, in northwestern Jugoslavia and in Trieste (See map by Kreczetowicz in Ianiszevski, Sovietskaia Botanica, n:r 4, fig. 1). In his large work on *Carex* in Flora URSS III (1935) Kreczetowicz, therefore, has not included *C. stenophylla* itself among the species of the Soviet Union. However, he has regarded the populations of *C. stenophylla sensu lato,* which occur in the European part of Russia, as belonging to *C. uralensis* C. B. Clarke.

One might say that in Kükenthal the amalgamation of species, and in Kreczetowicz the splitting of species, have been exaggerations in the treatment of the so-called *Carex stenophylla* complex.

Carex stenophylla sensu lato contains a great wealth of biotypes in Central Asia, and the species might be said to have its gene centre there. The nomenclatorial type of the species comes from the westernmost part of its vast area of distribution. The type locality of *C. stenophylla* has hitherto been considered as unknown, because Wahlenberg himself did not give any information concerning its occurrence. However, when reviewing the literature which Wahlenberg cited in his description of the species, and when studying the records of localities in the type material I came to the conclusion that the description of *C. stenophylla* is founded on specimens from Austria.

My primary intention in this investigation has been to search for a type specimen or select a "lectotypus" of *C. stenophylla*; to try to establish the type locality; to revise its synonymy regarding the European material; to study the variation amplitude of the species in Europe and especially in the area of its type locality; and to determine whether there really are any constant characteristics by which it is possible to distinguish *C. uralensis* from *C. stenophylla.* Since no such new localities have been added, which in any essential respect alter the above mentioned map (Kreczetowicz apud Ianiszevski 1937) of the distribution of *C. stenophylla* in Europe, I refrain from publishing a new map of it at the present time.

The following abbreviations according to Index Herbariorum I, ed. 4 (1959, pp. 188—209) are used for herbaria from which specimens have been seen: HAL = Botanische Anstalten der Martin-Luther-Universität, Halle (Saale); K = The Herbarium, Royal Botanic Gardens, Kew; LD = Botanical Museum of the University, Lund; S = Botanical Department, Naturhistoriska Riksmuseum, Stockholm; UPS = Botanical Museum of the University, Uppsala; WU = Botanisches Institut der Universität, Vienna.

I would like to thank the Directors and Curators of those herbaria from which I have received material on loan. I am particularly indebted to Dipl. Biol. K. Werner of the University of Halle for his kind consideration in interpreting and typing the text on the cover and labels of the *C. stenophylla* Wg ("*C. juncifolia*") material, etc. in Schkuhr's herbarium. I also wish to thank Mrs Patricia Frithiof and Dr Robert F. Scagel for revising my English translation.

Earlier treatment. Synonymy

There are at least two specimens which bear the name *Carex stenophylla* in Wahlenberg's handwriting. One is preserved in the Botanical Museum of the University of Uppsala, the other in the Botanical Department of the Naturhistoriska Riksmuseum in Stockholm. The former specimen with the locality reported as "in moeniis Vindobonensibus", is dated 1813, the year that Wahlenberg made his exploratory trip to the Carpathians. It can not possibly be regarded as a type specimen, because it was collected by Wahlenberg ten years after he described the species. The latter specimen which bears the statement "Wiennae ad munimenta", lacks a date. Thus it is impossible to decide whether Wahlenberg's diagnosis of the species was founded on this latter specimen or not. I have refrained from chosing this specimen as the type of *C. stenophylla,* partly because it lacks mature utricles, and partly because its leaves are somewhat damaged and badly developed. There is one more possibility (See p. 5) of designating a type for *C. stenophylla.*

In his short, comprehensive description of the species Wahlenberg has indicated several important characteristics, viz. the spikelets being male at the top and together forming an ovoid cluster, the utricles being plane-convex, veined and provided with serrulate margins, etc. In addition to his diagnosis he added "C. juncifolia Host. Schkuhr Car. n. 18. Tab. G. & Ii. fig. 32". From the text it is not clear if Wahlenberg founded his *C. stenophylla* solely on Schkuhr's above mentioned description and the two illustrations of "*C. juncifolia*" (1801) or whether he also had herbarium specimens at his disposal when he made the description. The name *C. juncifolia,* used by Schkuhr, is invalid, because it was used earlier, viz. by Allioni in 1785, for quite a different species, now called *C. maritima* Gunn. (syn. *C. incurva* Lightf.).

Schkuhr wrote that he had received the plant under the name *C. juncifolia* Host and cited Host's work, Fl. austriaca p. 503, but with the addition "exclus. synonym". With the latter he alluded to the following three synonyms given by Host:

"Gramen cyperoides, juncifolium . . ." Scheuchzer (1719), p. 492, tab. XI, fig. 7.

"Carex spica unica subrotunda . . ." Haller (1768), n. 1354, p. 183.

Carex juncifolia Allioni (1785), tab. 92, fig. 4.

These plants have turned out to belong to the form series of *Carex maritima* Gunn. and thus Schkuhr was right when he pointed out that they were not identical with the plant which he called *C. juncifolia.* Strangely enough Host did not include a description of his own for "*C. juncifolia*" in 1797, but he was content to cite the three above mentioned descriptions by Scheuchzer, Haller and Allioni. However, there is no doubt that Host, in excluding these synonyms, was referring to *C. juncifolia,* the same plant as Schkuhr, i.e. the one which later on was assigned the name *C. stenophylla.* This is evident partly from his record of the distribution of *C. juncifolia,* and partly from his later description of *C. glomerata.*

According to Host *C. juncifolia* grows "In collibus herbidis, campis, pratis Austriae, Pannoniae", thus in Austria and Hungary. This statement agrees well with the distribution of *C. stenophylla* but not with that of *C. maritima* Gunn. which has a few outpost localities in the westernmost part of the Tyroles, but occurs there mainly in the alpine region.

In the detailed description of *C. glomerata* in his Icones et descr. Gramin. Austriacorum (1801) Host cited "Carex juncifolia. Schkuhr handb. p. 330. Host syn. p. 503" as a synonym. Thus, he there exchanged the invalid name *C. juncifolia,* which he had used earlier for a new one, *C. glomerata,* but this also turned out to be invalid. Thunberg had earlier (1794) described a South African species as *C. glomerata.* Since Host's own specimens of *Carex,* which were in the Naturhistorisches Museum of Vienna, were destroyed during the last war (1945), together with the other collections of *Cyperaceae,* is it no longer possible to verify from herbarium specimens, if his *C. glomerata* was identical with *C. stenophylla.* However, Host's plate of *C. glomerata* (tab. 44) is quite detailed, and there is very little doubt that the plant figured belonged to the form series of *C. stenophylla.* Kükenthal and several other specialists on *Carex* have included it in *C. stenophylla,* and one may presume that at least Kükenthal had studied Host's specimen of *C. glomerata* before he made it a synonym of *C. stenophylla.*

Thus, it appears that the first two real descriptions and illustrations of *Carex stenophylla* were published in 1801 by Host and Schkuhr but their respective names for the plant, *C. glomerata* and *C. juncifolia,* were invalid. It was first given the valid name *C. stenophylla* Wg when it was described for the third time (1803).

Since Wahlenberg cited Schkuhr's figures of *C. juncifolia* when he described *C. stenophylla* one may choose the specimen figured by Schkuhr as type of the species. Among the material of *C. stenophylla* in Schkuhr's herbarium there is a specimen (Fig. 1) corresponding exactly to his tab. 286 G, fig. 32, and in a capsule with a reference to this figure there are also some well preserved, but perhaps not completely mature utricles (Fig. 5A). The above mentioned specimen had at one time been detached from its sheet but judging from the remaining paste-strips it was originally fastened above a label which read as follows "Carex juncifolia. All. pedem. Loc. frequens in pratis aridis des Brigithenau viennae. Hedwig 1798". Thus, Vienna must be considered the type locality of the species. Vienna would also have been the type locality, if the above mentioned specimen in the Naturhistoriska Riksmuseum, which was named *C. stenophylla* by Wahlenberg himself, had been chosen the type of the species.

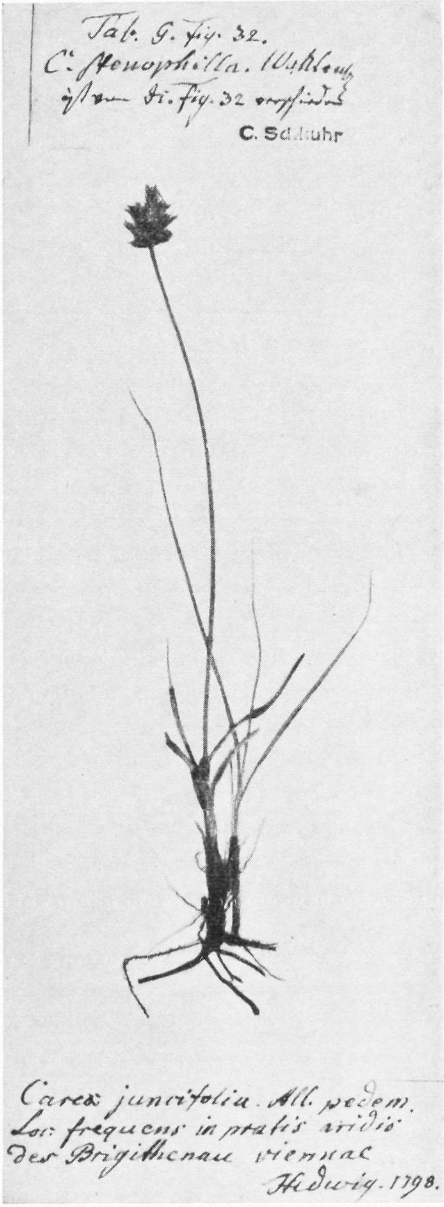


Fig. 1. *Carex stenophylla* Wg (syn. "*C. juncifolia*" Schkuhr, non All.). The lectotype in the Schkuhr herbarium (HAL.). — C:a ×3/4.

Inside the cover of *Carex stenophylla* in Schkuhr's herbarium there are, excepting the specimen I have selected as lectotype, two other plants, viz. one named

C. curvula All. and the other *C. glomerata* Host. Neither of these is correctly named. The former, "*C. curvula*", which was collected by Hedwig in 1795 at Pfüterjock in the Tyrole Alps is *C. maritima* Gunn. (syn. *C. juncifolia* All. 1785 neque Schkuhr). The latter, "*C. glomerata*", which consists of five spiked culms and several leaves, is difficult to determine because the material is incomplete and in a poor condition. No doubt it represents the plant which Schkuhr (1806, p. 6) mentions having cultivated in his garden. As regards the appearance of its culms, inflorescences and leaves, the plant shows greater agreement with *C. divisa* Huds. than with *C. stenophylla.* Unfortunately Schkuhr's herbarium specimens lack a rhizome which in this case would have been necessary for an accurate determination. *C. divisa* is, to be sure, characterized by a thick, lignified rhizome, contrary to *C. stenophylla* which has a long, thin, creeping rhizome. Only one of the inflorescences is fairly well developed, viz. the one whose culm carries the determination label "*Carex glomerata*". This inflorescence is about 1.5 cm long with the lower two spikelets somewhat remote and with the subtending bract of the spikelet next below having a long protruding midrib. Although one inflorescence is considerably damaged and the others incompletely developed, only 0.5—0.8 cm long, I consider the existing characteristics of the inflorescences, culms and leaves to be sufficient to refer the plant to the form series of *C. divisa.* It is *inter alia* very similar to a specimen of *C. divisa* collected by E. Hackel at Türkenschanze in Vienna (LD).

In his "Nachtrag der Riedgräser" (1806, pp. 6, 7) Schkuhr divided *C. juncifolia* as he had earlier delimited it, into two species. Here he accepts the name *C. stenophylla* Wg for the plant, tab. G, fig. 32, illustrated in his previous work (1801). The other plant, figured in the same work as tab. Ii, fig. 32 was now given a new name, *Carex Hostii* (*Hosti*), and as a synonym of it he cited *C. glomerata* Host gram. I, p. 34, tab. 44. Judging from the figures, these two plants belong to the form series of *C. stenophylla,* and then *C. Hostii* should as usually has been the case, be regarded completely as synonym of this species. However, the description of *C. Hostii* agrees only partly with *C. stenophylla* and it is clear, that *C. Hostii* is based mainly on material of some other species than *C. stenophylla.* Schkuhr himself declared that the whole plant (*C. Hostii*) was very unlike the preceding (*C. stenophylla*). The plant which Schkuhr first considered, when he described *C. Hostii,* was received from Vienna in the fresh condition under the name of "*C. glomerata* Host". Obviously it was not the true *C. glo-*

merata Host, but *C. divisa* that he had received for cultivation. As pointed out before, I consider the plant called "*C. glomerata*" in Schkuhr's herbarium to be *C. divisa.*

As not only *C. stenophylla* but also *C. divisa* occur in the Vienna area, e.g. on the Türkenschanze, and as they may be rather similar in habit, it is not surprising that they happened to be confused with each other. According to Schkuhr's description of the cultivated specimens of *C. Hostii,* their inflorescences were 1/2 to 1 inch long or even longer and their mature spikes often bent down to the ground. In Schkuhr's herbarium there is no specimen preserved under the name of *C. Hostii.* However, his specimen of "*Carex glomerata*" Host which is now considered by me to be one of the above mentioned cultivated specimens of *C. divisa* must represent *C. Hostii,* because Schkuhr cited *C. glomerata* as a synonym of it. Thus, I have come to the conclusion that *C. Hostii* is a nomen ambiguum which is based partly on *C. stenophylla* (quoad Schkuhr 1801, tab. Ii, fig. 32 et Host 1801, tab. 44), and partly on *C. divisa* (quoad pl. cult. sub nom. "*C. glomerata*").

At a later date one more name, viz. *Carex uralensis* C. B. Clarke, has been used for a European biotype group of the *C. stenophylla* complex. A detailed account of *C. uralensis* and a discussion of its taxonomic value is given in the third chapter (pp. 11—13) of this paper.

Morphology and variation

In the *C. stenophylla* populations which occur in Austria, Hungary, Czechoslovakia and several other countries west of the Soviet Union, i.e. in the rather confined distribution area which Kreczetowicz reported for this species, I have found a surprisingly large variation.

Normally the plant grows in tufts and in older specimens the primary tuft has as a rule given rise to a whole series of secondary tufts, connected to each other by a ± horizontal rhizome. A new tuft is formed vegetatively from an older one by a plagiotropic shoot growing out, usually first obliquely and then horizontally, after which its young terminal part turns up and by continued growth the apex of the shoot gradually forms a tuft. The length of the string-shaped rhizome, which connects two tufts may vary quite considerably. Judging from the herbarium material the connecting rhizomes are usually only a few (3—7) cm long and provided with some 10 nodes but in extreme cases they can become dm-long. For example, there is a specimen (Fig. 2) with a rhizome string more than 2 dm long and provided with some 20

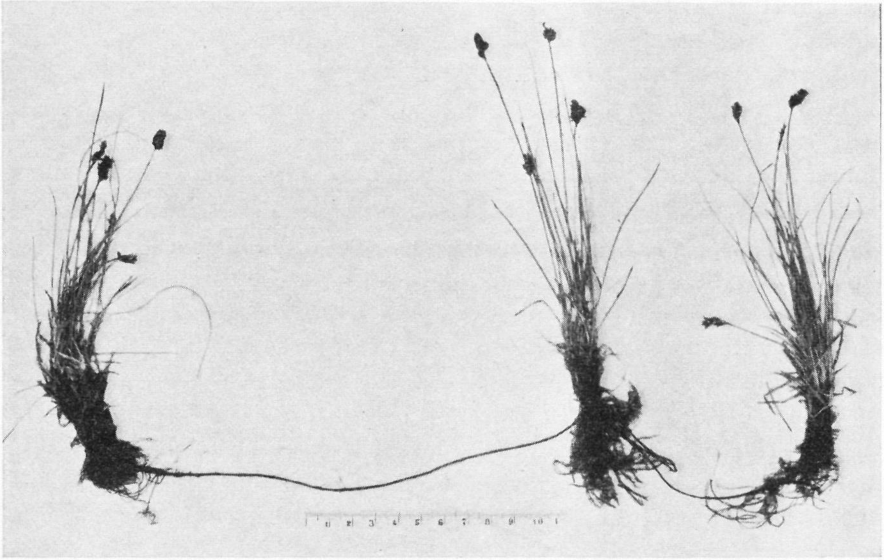


Fig. 2. *Carex stenophylla* Wg. The rhizome string connecting two of the tufts extremely long, about 2 dm, and provided with some 20 nodes. Specimen from a sandy hill at Mutienice in Southern Moravia, leg. R. Sterner, Sept. 1923 (LD). — C:a ×1/3.

nodes, collected by R. Sterner (LD) on a sandy hill to the north of the railway yards of Mutienice (Mutienitz) in Southern Moravia. In the specimens growing in deep, dry sand the rhizome strings are as a rule considerably longer than those in specimens growing in moist soil. From the morphological point of view the tuft in *C. stenophylla* is formed by the sympodially branching, orthotropic part of the rhizome. It is composed of a varying number of fertile and vegetative shoots which are ± densely crowded together. Older tufts often comprise some 10 shoots.

The orthotropic parts of the rhizome have not always developed as real tufts. Whether it has taken the shape of a tuft or not depends upon the stage of development of the orthotropic part. In the young stage often only one or two sterile or fertile shoots are developed.

The culms are most often reported to be slightly rough at the top but according to what I have seen they can be smooth just as often. Sometimes they are provided with very short, sparse glandular hairs. The length of the culms varies considerably depending on the habitat condition or on the genetic constitution. Heinrich Huber's comprehensive collections of *C. stenophylla* from the Lower Austria give a rather good idea of the influence of the environmental factors on the length of the culms, etc. Among his collections one can find extremely tall as well as extremely short specimens. An example of the first mentioned type can be seen in his fruiting specimens from a shady locality at Erlach. This shade-form of the species has a culm about 3 dm tall. An example of the latter type can be seen in his flowering and fruiting specimens from a sandy grass plot at Katzelsdorf having culms only (0.2—)0.3—0.5 dm tall and his fruiting specimens from Burgenland with culms only 0.4—0.7 dm tall. Such a great variation in regard to the length of the culms can be met in a fairly limited area also. I prefer to interpret the tall and short forms of the species from Lower Austria as modifications within the same biotype group. In Hungary there also appears remarkably tall and short specimens of *C. stenophylla.* An excellent example of the latter is Holmström's collection (LD) from Nagyhortobágy, in which fruiting culms in certain cases are only about 0.4 dm tall.

In regard to the length of the culms the mean value for the Austrian biotypes is 10.4 cm (50 culms measured), whereas it is 11.7 cm for the Hungarian biotypes. No doubt the higher value for Hungary depends on the fact that the climatical conditions there are more favourable for the plant than those in Austria.

The leaves in *C. stenophylla* are canaliculate, setiformly involute, complicate or often partly flat but are completely flat only in exceptional cases. In the Danube area the variation amplitude as regards the breadth of the leaves is 1—2(—2.8) mm. An extremely broad- and flat-leaved, and tall form of the species has been collected by Matz on moist meadows at Angern in Lower Austria (LD). In it the broadest leaves are nearly 3 mm and the longest culm 2.5 dm. The proportion between the length of the culm-leaves and the culms varies, not only in different individuals of the species but also in the tufts of one and the same specimen. In most fruiting specimens the culms seem to be longer than the leaves just as in the lectotype. However, in quite a few specimens the culms are about as long as, or shorter than the culm-leaves.

In the inflorescences of *C. stenophylla* the scale (empty glume) which subtends each spikelet and which is homologous to the bract agrees as a rule with the glumes. Thus, this bract which is provided with 0.5—1 mm broad, white-hyaline margins may be called glumaceous. However, it is sometimes quite different from the glumes and more like a normal *Carex*-bract. It seems to be only the lowermost or the two lowest bracts which sometimes show atavistic features and are more or less leaf-like. As examples of extremely long bracts in *C. stenophylla* the following collections may be cited: Wettstein's in 1888 from near Budapest (WU) in which the inflorescence has a green, leaf-like bract 2 cm long; that of an unknown collector in 1900 from Laaerberg in Vienna (WU) with a green bract 1.6 cm long; and Keller's in 1892 from the same locality (LD) with a bract 1.1 cm long. In all these cases the lower, fairly broad scale-like part (2—4 mm long) of the bract has a median green zone running its full length and it has scarious margins. The midrib, the secondary nerves and the adjacent green tissue protrudes from that part as a long, more or less bristle-shaped or linear-subulate extension with serrulate margins.

There are varying statements as regards the relationship between the length of the glumes and the utricles. According to Hegi and others the glumes are longer than the utricles but in most cases this statement is probably due to the fact that both the glumes and utricles have been compared with each other at a stage preceding the maturity of the utricles. When considering only those specimens which have fully ripe utricles, it has been found that as a rule the glumes are either somewhat shorter than or equal in length to the utricles. Only rarely do the glumes exceed the fully developed utricles. The glumes are provided with white-hyaline margins which are 0.3—0.5(—0.8) mm broad in the female glumes. In Bubela's collection (LD) from Bzenec in Moravia they are extremely broad, almost 1 mm.

The utricles which are always plane-convex vary in the Central European biotypes in length from 3 to 4 (4.5) mm (incl. beak and stipe) and in colour from light brown to dark chestnut. When fully ripe, they are as a rule ± chestnut-coloured, at least on the outer surface.

The venation of the utricles varies considerably. When magnified the convex outer side proves to have 7—13, ± distinctly elevated, often somewhat dark veins. Some of them extend from the base to the beak while others only reach about half way up the utricle. The flat inner side is provided with fewer, 3—7(—9) veins, which as a rule are less prominent, and sometimes almost invisible.

The account given here concerning the variation of rhizomes, culms, leaves and utricles of *C. stenophylla* in Austria, Hungary and neighbouring countries, may seem to be unnecessarily detailed. But without a thorough knowledge of the variation in the biotype group in which the lectotype is included, it is difficult to estimate correctly the characteristics which have been used for separating species and other taxa in the *C. stenophylla* complex. Several of these taxa have been based upon quantitative, non-essential characteristics, e.g. the proportion between the length of the culm-leaves and culm, the breadth of the leaf, the venation etc., which have proved to fall within the variation amplitude presented by the *C. stenophylla* populations the Danube area.

The data which I have now obtained from a study of the variation of *C. stenophylla* in Central Europe, will serve in a later paper as the basis for a discussion of those taxa in the *C. stenophylla* complex which have been distinguished in Asia.

However, I wish to treat one of these, *C. uralensis,* in this paper, because the *C. stenophylla* populations which occur in the European Russia, have been included in *C. uralensis* by Kreczetowicz and others. This was described from a locality in Western Siberia near the mouth of the Ural River, thus not far from the European border.

Comparison of the type of Carex uralensis and C. stenophylla

When C. B. Clarke typified *C. uralensis* in 1908 he based his description of the species on a specimen collected by Fischer at Lake Indersk which is situated about 150 km to the north of the Caspian Sea and just east of the Ural River. This specimen (B) and another (A) from the same locality and by the same collector are mounted together on a sheet in the Kew herbarium. According to a note on the sheet the two specimens have earlier been in Boott's herbarium under the name *C. stenophylla.*

Clarke based the name *C. uralensis* on specimen B alone (Fig. 3) and kept the original determination *C. stenophylla* for specimen A. After the name *Carex uralensis* he wrote on the label "sp. nova vel saltem var. mirabilis". This variety name alludes to the styles. Clarke has stated that *C. uralensis* has trifid styles, which is very noteworthy, because all taxa belonging to this group of plants have bifid styles. In studying the type specimen I have not been able to discover that the plant really has trifid styles. In any case, the ovaries or young utricles which now are left in the inflorescence are provided with bifid styles. However, some of them seem to be trifid, because the style branches from the near-by utricles often are curved and intertwined. The statement that this plant has trifid styles probably depends on faulty observation. If a trifid style appears in a rare case this has to be interpreted as an abnormality.

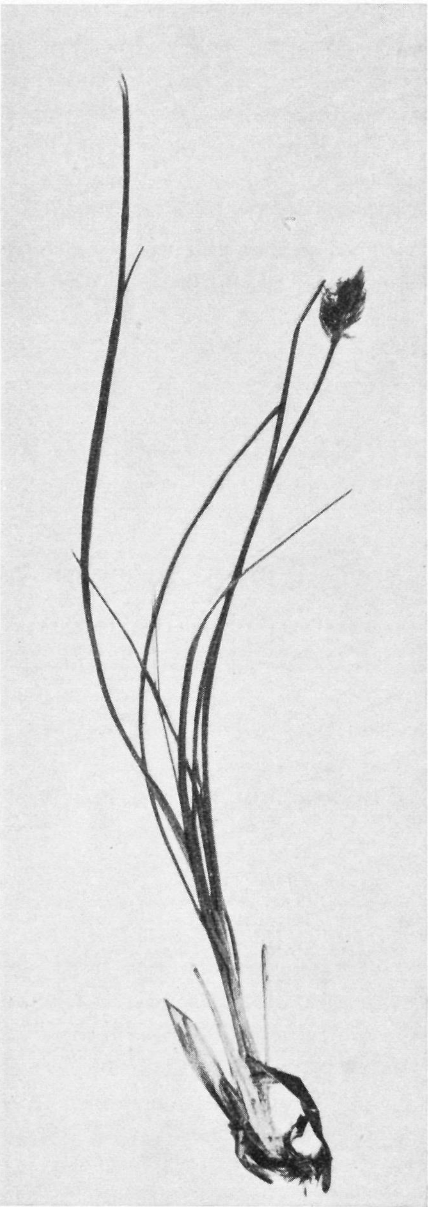


Fig. 3. Type specimen of *Carex uralensis* C. B. Clarke collected by Fischer at Lake Indersk just east of the Ural River and c. 150 km N of the Caspian Sea (K). — Nat. size.

In my opinion the two specimens from Indersk belong to the same species. They represent merely different stages of plants belonging to the same biotype group. The type specimen (B) seems to have grown in a somewhat less arid habitat than the other. The type is in the flowering stage, has a light inflorescence, and leaves up to 1.5 mm broad. Two of the leaves are partly flat but the remainder are more or less strongly complicate. However, in its associated specimen (A) which is in an advanced fruiting stage the inflorescence gives the impression of being rather dark, because of its ± chestnut-coloured utricles. Its leaves are more complicate and somewhat narrower than in the type. Shorter parts of single leaves are ± flat but only up to 1 mm broad.

Although I have made a thorough comparison of the lectotype of *C. stenophylla* from Austria (Vienna) and the type of *C. uralensis* from Indersk near the mouth of the Ural River I have not been able to find any essential characteristics separating them, either concerning the rhizomes, leaves or glumes. Below are given some examples of similarities as well as differences between the above mentioned specimens.

Each of the specimens consists of one fertile and one vegetative shoot. From the base of these shoots both adventitious roots and plagiotropic shoots extend. In *C. stenophylla* there are two fully developed, plagiotropic shoots which have been torn off about 1 cm from the point of attachment and which are provided with fimbriate, brownish vaginate leaflets on the nodes. In the type (B) of *C. uralensis* there are also two plagiotropic shoots, one of which is very young, bud-like, only 3 mm long and provided with entire vaginate leaflets, while the other, which is torn off near the base has fimbriate, yellow-brown vaginate leaflets. However, its associated specimen (A) consists of an older, dense tuft, composed of many fertile and vegetative shoots.

The leaves in the two type specimens agree with each other by being largely complicate or canaliculate and only to a small degree flat, with the flat part about 1—1.5 mm broad. After splitting lengthways the sheath is still a little broader than the leaves, viz. c. 2 mm. In the type of *C. uralensis* at least one of the culm-leaves is considerably longer (c. 4 cm) than the culm itself. One other leaf which was broken off on a level with the inflorescence might have been longer than the culm. On the contrary, the culm is longer than the culm-leaves in the lectotype of *C. stenophylla.* This should be pointed out particularly because the proportion between the length of the culm-leaves and culm has been used as a distinguishing characteristic in keys to species belonging to the *C. stenophylla* complex. When making this comparison the leaves and culms are of course supposed to be fully developed.

Regarding the fruit characteristics it is impossible to compare the types with each other directly. As pointed out above the type (B) of *C. uralensis* lacks ripe utricles. However, its associated specimen (A) from Indersk has fully mature utricles. These two specimens (A and B) undoubtedly belong to the same biotype group and the type of *C. uralensis* would have had utricles of the same shape and size as the specimen (A) if the plant had been mature. Thus, in my opinion it is justified to accept the utricles in specimen A as being representative of *C. uralensis* and also to compare these utricles with those of the lectotype of *C. stenophylla.* The utricles in the former plant are 4.5—5 (—5.5) mm long but only about 3 mm long in the latter. Thus, in regard to their length the utricles of specimen A from Indersk show a fairly large variation amplitude. They are not only considerably longer than those in the lectotype from Vienna, but some of these utricles are even longer than those of all other European specimens which I have examined. On the outer surface of the utricles in the two above mentioned specimens there are several ± elevated and distinct veins, viz. 9—11(—13) in the former and 7—9 in the latter.

Thus there are some differences between the type of *C. uralensis* and its associated specimen on the one hand and the lectotype of *C. stenophylla* on the other hand. It is however mainly a matter of quantitative, and in this case, non-essential characteristics.

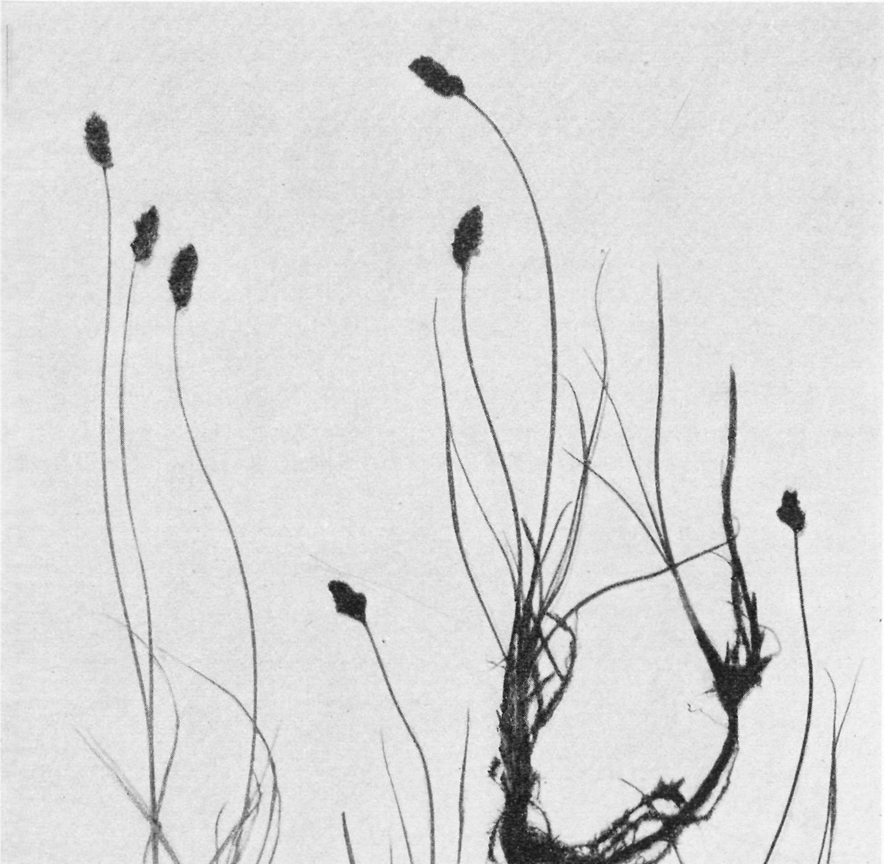
The characteristics of Carex uralensis compared with European C. stenophylla

Carex uralensis seems to have been overlooked since 1908, when Clarke established it as a species, until 1935 when Kreczetowicz (Fl. URSS III) accepted this name for those populations of *C. stenophylla* which occur in the southern part of European Russia, Western Siberia (Upper Tobol, southern Irtysh) and Central Asia (Aralo-Caspia, northern Balkash, Dzungaria and Mongolia). Hitherto I have not found, that Kükenthal has made any statement about *C. uralensis.* Since it was described from Western Siberia it certainly should have been treated by Kükenthal in Fedtschenko, Primitiae Florae Sibiricae, 1911.

According to the map which Kreczetowicz prepared for publishing in Ianiszevski's paper on *Carex* (1937), *C. uralensis* and *C. stenophylla* sensu Krecz. are geographically isolated. According to Kreczetowicz *C. uralensis* extends to the west as far as the floristic regions of the Black Sea and Crimea. Between the westernmost outposts of *C. uralensis* in this area and the easternmost outposts of *C. stenophylla* sensu Krecz. in Transsilvania the map shows a gap of almost 600 km. This gap is very likely due to a lack of observation and it probably will be partially filled in by future investigation.

Regarding the geographical distribution, the difference between these two taxa was clearly expressed by Kreczetowicz. However, this does not seem to be the case regarding the morphological characteristics. Neither in Flora URSS III nor in any other publication after that in which Clarke described *C. uralensis,* have I been able to find a statement concerning characteristics used for separating *C. uralensis* from *C. stenophylla.*

Fig. 4. Representatives of the *Carex stenophylla* complex in southeastern Russia (left) and Hungary (right). As shown by the figure these biotypes agree extremely well with each other in their morphology. — The left specimen (LD) collected by Iljin et Grigoref (n. 47) at Lake Elton in Reg. Astrakhan; the two right specimens (UPS) collected by Dorner at Pest (Budapest). — According to distribution map 1 by Kreczetowicz in Ianiszevski 1937 the former should belong to *C. uralensis* and the latter to *C. stenophylla.* — C:a ×1/2.


1 2 3 4 5 6 7 8 9 10

When comparing the type materials, as mentioned above (pp. 12, 13), I came to the conclusion, that *C. stenophylla* and *C. uralensis* do not differ from each other in regard to any essential features.

In the following I will make a comparison between the populations from Central Europe and those from the southeastern part of Europe, which latter Kreczetowicz and Lavrenko class among *C. uralensis*. Kreczetowicz, in Flora URSS III (1935), p. 141 as well as Lavrenko in Flora RSS UCR II (1940), p. 457 have made exhaustive descriptions of *C. uralensis*. That of Lavrenko probably only refers to the biotypes in Ukraine and differs somewhat from Kreczetowicz's description. The features which have been described for these biotype groups agree fairly well with those characteristics I have found in the populations in the Danube area, viz. the biotype group which includes the lectotype of *C. stenophylla*. The specimens from the latter area and those from Southern Russia show broadly speaking the same variation amplitude. The form which grows in the neighbourhood of Budapest, e.g. on the sand dunes of the island Czepel, agrees extremely well with forms occurring at Lake Elton in the Astrakhan Region (Fig. 4).

In the following account the name *C. stenophylla* refers only to the populations in the Danube area.

The culms of *C. uralensis* are, according to Kreczetowicz, in most cases rough and 1—4 dm tall; according to Lavrenko, often smooth and 1—2.5 dm tall. In *C. stenophylla* they are almost as often smooth as rough, and in the fruiting stage (0.2—)0.3—3 dm tall.

The leaves of *C. uralensis* are, according to Kreczetowicz, 1.5—2.5 mm broad and shorter than the culms; according to Lavrenko, 1.5—2 mm broad and equal to, or shorter than, the culms. But when studying the type of *C. uralensis* at Kew I have found on the contrary that it also has leaves which exceed the culm. In *C. stenophylla* the leaves are (1—)1.5—2.5(—3) mm broad, and equal to, or shorter than, the culms; they seldom exceed the culms. Thus, in delimiting taxa in the *C. stenophylla* complex, the proportion between the length of the culm-leaves and culms is useless as a distinctive characteristic.

The inflorescenses in *C. uralensis* are ebracteate according to Lavrenko, and they are similar in *C. stenophylla* according to Kükenthal, i.e. the subtending scale (sterile glume) of the spikes has the same appearance and is of about the same size as the female glumes. However, as pointed out above, this characteristic is not constant and in some cases inflorescences are provided with ± normal bracts which are green and several times longer than the glumes.

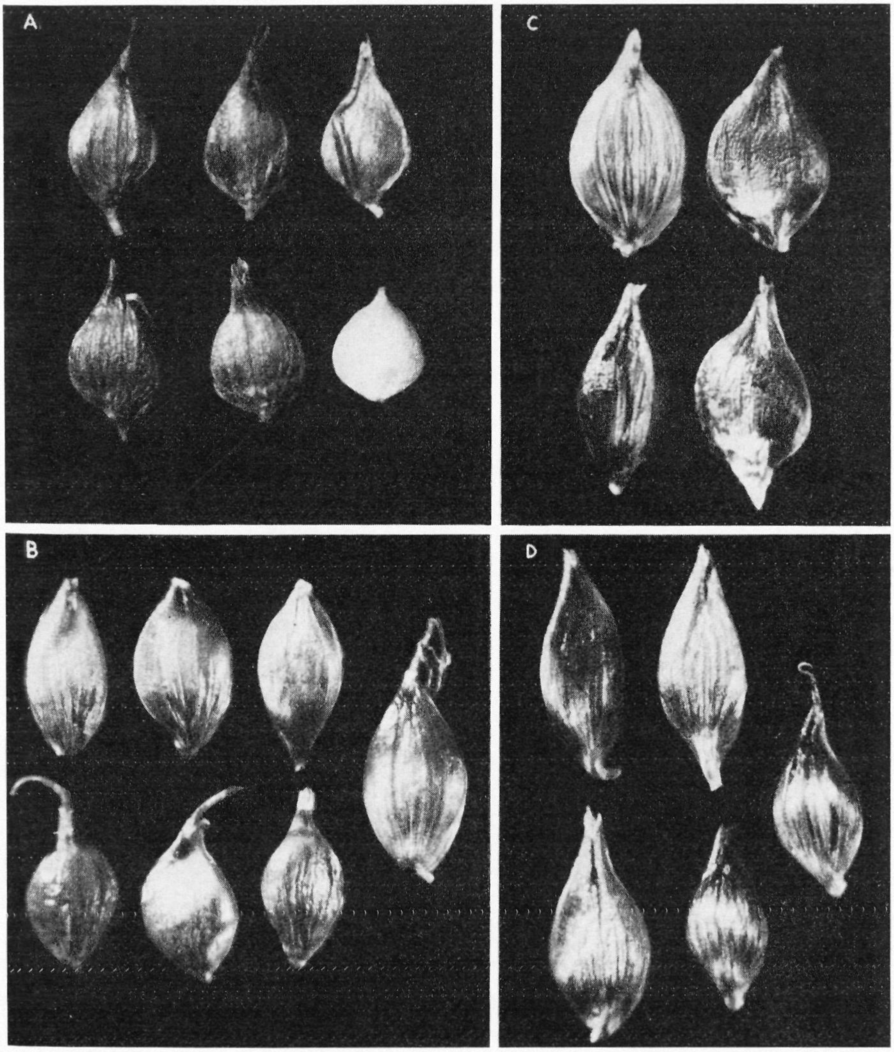


Fig. 5. Fruit forms in *Carex stenophylla* Wg. The shape and venation of the utricles, and the length of their beak and stipe varies more or less, even in the same specimen. — A: 4 utricles seen from the outer surface, 1 utricle (the upper right) from the inner surface, and 1 nut (the lower right). The utricles are only c. 3 mm long and probably not fully mature (Lectotype from Austria, HAL). — B: 7 utricles, outer surface, 3—3.5 mm long (Hungary, "Pestim", Dorner, UPS). — C: 4 utricles, outer surface, 3.5—4 mm long (Southern Russia, Reg. Astrakhan, Lake Elton, Iljin et Grigoref, 1925, n. 47, LD). — D: 5 utricles, outer surface, 3.3—4.5 mm long (Ukraine, Tauria, Perekop N of Crimea, Egerova, 1901, LD). — According to distribution map 1 by Kreczetowicz in Ianiszevski 1937 the former two (A and B) should belong to *C. stenophylla* and the latter two (C and D) to *C. uralensis*. — Enlarged about: A ×8/1; B ×9/1; C ×9/1; D ×8.5/1.

The glumes of *C. uralensis* are shorter than the utricles according to Kreczetowicz; according to Lavrenko they are on the contrary longer than, or equal to them. In *C. stenophylla* the glumes are usually shorter than, or equal to, the fully mature utricles; however the glumes rarely exceed the utricles.

The utricles of *C. uralensis* are, according to Kreczetowicz, (3—)4—4.5 mm long; according to Lavrenko 3.5—4 mm long. However, in Fischer's specimen (A) named *C. stenophylla,* which is from the type locality of *C. uralensis,* at least some of the utricles are still longer, viz. 4.5—5.5 mm (incl. beak and stipe). In Central Europe I have found the variation amplitude in *C. stenophylla* to be 3—4(—4.5) mm.

Finally, the venation of the utricles is found not to be constant. In *C. uralensis* the utricles are, according to Kreczetowicz, provided with up to 10 veins on the outer surface, while the inner surface has 5—7 veins. In *C. stenophylla* I have found that the number of veins varies, on the outer surface from 7 to 13, and on the inner surface from 3 to 7 (9). When studying the venation of the utricles it is necessary to use a fairly high magnification and strong light, because the veins are often not very prominent.

The variation amplitudes just given for the series of characteristics in *C. uralensis* and *C. stenophylla* show quite clearly, that these taxa cannot be kept apart as separate species. Neither is there any justification for distinguishing *C. uralensis* as a subordinate taxonomic unit within the *C. stenophylla* complex.

No doubt *C. stenophylla* in Europe consists of a series of morphological and physiological races which are slightly different from each other and between which a free exchange of genes occurs. During the study of extensive herbarium material one will find continuous form series which connect the extremes with each other. Judging from the herbarium material, there is not a sufficiently distinct geographical zonation of the biotype groups in Europe, to justify division of *C. stenophylla* into subspecies.

Summary

1. A specimen in the Schkuhr herbarium of the University of Halle has been designated the lectotype of *Carex stenophylla* Wg.

2. The type locality of *C. stenophylla* is situated in Austria. According to a label which undoubtedly belongs to the lectotype in the Schkuhr herbarium, which reads as follows "Loc. frequens in pratis aridis des Brigithenau viennae. Hedwig 1798" the exact locality is Vienna.

3. The biotype group of *C. stenophylla* growing in the Danube area, thus that comprising the lectotype of the species, has proved to have a rather wide variation amplitude.

4. From a morphological point of view *C. uralensis* C. B. Clarke is indistinguishable from *C. stenophylla,* because their variation amplitudes overlap greatly.

Literature and nomenclature of Carex stenophylla

(Mainly applied to the European species populations)

G. Wahlenberg in Kongl. Vet. Akad. Nya Handl. XXIV, 1803, p. 142; (*C. stenophylla*) entirely or partly based on "*C. juncifolia*" Schkuhr, Beschreib. u. Abb. d. Riedgr. (1801), p. 26, n. 18, tab. G, fig. 32 (non All. 1785).

Schkuhr, Nachtr. d. Riedgr. (1806), p. 6, n. 11 — Hoppe, Caric. German. (1826), p. 10. — Treviranus in Ledebour, Fl. Rossica IV (1853), p. 270 (excl. var.) — Meinshausen in Acta Hort. Petrop. XVIII (1901), p. 316. — Ascherson et Graebner, Synops. Mitteleurop. Fl. II: 2 (1902), p. 24. — Kükenthal in Engler, Pflanzenr. IV: 20, Heft 38 (1909), p. 120, pro max. parte. — D. I. Litvinow in Fedtschenko, Fl. Ross. Austro-Orient. III in Acta Hort. Petropol. T. XV, fasc. 3 (1929), p. 288. — Hegi, Ill. Fl. v. Mitt.-Europa, ed. 2, II (1939), p. 76. — Meusel, Vergl. Arealkunde, 1943, K. 3 e.

Syn.: "*C. juncifolia*" Host, Synops. pl. Austria (1797), p. 503, pro parte (non All. 1785). — "*C. juncifolia*" Schkuhr, Beschreib. (1801), p. 26, n. 18. — *C. glomerata* Host, Icon. et descr. gramin. Austr. I (1801), p. 34 (non Thunb. 1794). — *C. Hostii* Schkuhr, Nachtr. (1806), p. 7, pro parte, quoad tab. cit. et synon., non plant. hortens. eius. — *C. uralensis* C. B. Clarke in Kew Bull., Addit. Ser. VIII (1908), p. 76. — Kreczetowicz in Komarov, Fl. URSS III (1935), p. 141. — Ianiszevski in Sovietskaia Botanika 1937, nr 4, p. 46. — Lavrenko in Bordzilowskoi, Fl. RSS UCR II (1940), p. 457. — *Vignea stenophylla* Rchb.: H. G. L. Reichenbach, Fl. Germ. Excurs. (1830), p. 56.

Icon.: Schkuhr, Beschreib. (1801), tab. G, fig. 32 et tab. Ii, fig. 32 (sub nom. *C. juncifolia*). — Host, Icon. (1801), tab. 44 (sub nom. *C. glomerata*). — Litvinow, op. cit. (1929), p. 289, fig. 150 (sub nom. *C. stenophylla*). — Kreczetowicz, op. cit. (1935), tab. X a—c (sub nom. *C. uralensis*). — Hegi, Ill. (1939), fig. 333 (sub nom. *C. stenophylla*). — Lavrenko, op. cit. (1940), fig. 33 (sub nom. *C. uralensis*). — Fig. nostrae 1—5.

BOTANISKA NOTISER 1960 · VOL. 113 · FASC. 1 · LUND

Säivis-Bredviken, en märklig bottnisk växtlokal

AV ERIK JULIN
Haparanda

Bredviken, den öppna och grunda havsvik, som lik en rektangel skjuter in mellan Säivisnäs i väster och Staffansnäs i öster i sydöstra hörnet av Nedertorneå socken i Norrbotten (fig. 1), har trots sin relativa närhet till Säivis folkrika by och den norra strandens lockande sandplage hitintills förblivit ett stycke storslagen natur av orörd jungfrulighet. Norr om Bredviken utbreder sig Bredvikshedens vidsträckta sandfält med till största delen av tallhed bundna men på några punkter också levande dyner, vilka längs vikens norra strand genom landhöjningens inverkan erhålla nytt material från den ytterligt långgrunda sandbottnen. En mycket svårframkomlig körväg norrifrån över Bredvikshedens sand har hittills utgjort den enda tillfarten från landsidan. Detta jämte det förhållandet, att Bredviken liksom vänder ryggen åt bygden, har varit dess effektivaste skydd mot mänsklig exploatering.

Under år 1958 blev emellertid den nya landsvägen till Säivisnäs färdig, vilket starkt stegrat besöksfrekvensen. Samtidigt har Säivis-Bredviken börjat tagas i anspråk som fritidsområde. Framför allt för strandens revlar med deras känsliga vegetation, har detta betytt svår skadegörelse.

Bredvikens strandflora är ur flera synpunkter märklig. Berggrunden är karelsk, och dess gynnsamma inverkan på vegetationens floristiska sammansättning gör sig starkt gällande på Säivisnässtranden i väster, där t.ex. *Malaxis monophylla* växer blott få meter från havsstranden, mindre starkt på den öppnare och jämnare östra stranden. Här skall emellertid presenteras floran på vikens innersta, ungefär i öst-västlig riktning löpande låga sandstrand med dess revelkomplex, vars ytvidd är beroende av det växlande vattenståndet.

Bredviken är genom sin belägenhet på ett utskjutande kustparti, sin öppenhet mot havet, vilken förstärkes genom det breda sundet utanför

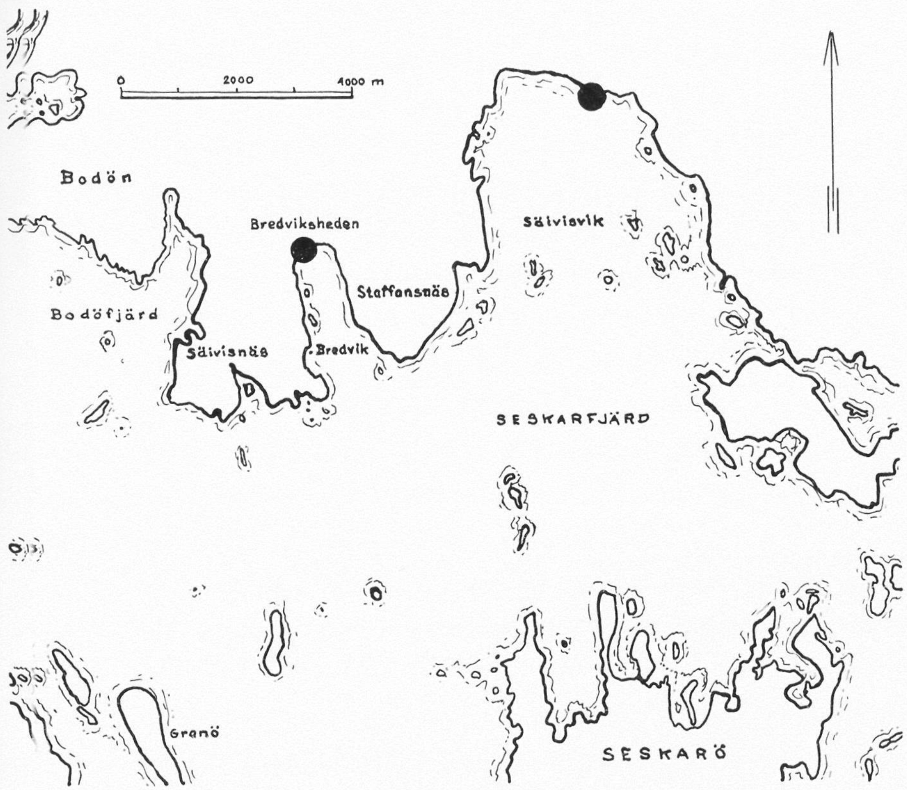


Fig. 1. Bredviken och dess omgivningar med de båda norrländska lokalerna för *Juncus ranarius* — För spridning godkänd i Rikets Allmänna Kartverk den 2 mars 1960.

mellan Seskarö och Granö, samt på grund av sin relativt stora längdutsträckning en effektiv fälla för i vattendriften ingående diasporer. Den är öppen för sydliga vindar, och vid storm från detta väderstreck pressas vatten in och dränker stranden och revlarna i vikens inre del. Grovt timmer slungas långt upp mot dynernas tallskog, tämligen stora stenar med påvuxen *Fontinalis antipyretica,* som anger deras proveniens från vikens yttre delar, återfinnas i norra strandens drift, och revlarna ha efter varje sådan storm ett helt nytt ansikte. En så dynamisk biotop har alltid gott om grobäddar för konkurrenssvaga främlingars diasporer.

Stabil vegetation med sammanhängande bälten av fasta växtsamhällen förekommer icke. Fragment av gråalstrandsnår finnas, och stundom utvecklas utanför dessa antydan till en zonering med *Carex*

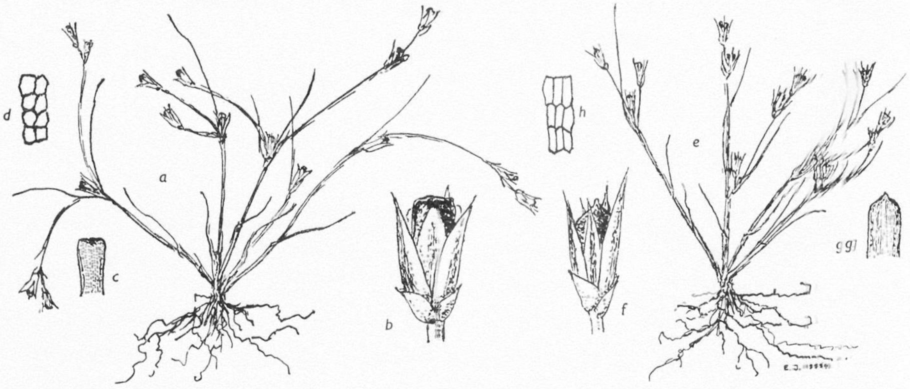


Fig. 2. a—d *Juncus ranarius* (Bredviken 23.8.1957), e—h *J. bufonius* (Bredviken 8.8.1957). b och f kapslar. c och g valvler, övre delen. d och h epidermisceller från do. (a och e 2/3 nat. stor., b, c, f och g 2 ggr. nat. storl., d och h 50 ggr. nat. storl.).

nigra - *C. glareosa* - bälte, på något torrare partier ersatt av en *Festuca rubra* - zon med *Potentilla anserina* ssp. *Egedii*. Utanför dessa vidtar måhända ett bälte av *Juncus Gerardi* och *J. arcticus* ssp. *balticus* med *Carex paleacea*. Därutanför mot vattnet uppträder *Eleocharis uniglumis* var. *fennica* som dominant i områdets enda någotsånär sammanhängande vegetationsbälte och slutligen *Eleocharis acicularis* med *Triglochin palustre* och fåtalig *T. maritimum*. Här antydda zonationskomplex är emellertid på det hela taget en rekonstruktion, som svårligen skulle låta sig göras utan erfarenhet från mindre våldsamt föränderliga kustavsnitt.

Som exempel på vegetationens ringa konstans kan nämnas att mer än halva beståndet av *Juncus ranarius* (se nedan), ett område på ett par tiotal meters längd och 2 à 3 meters bredd den 13.9.1959 befanns täckt av ett 2—3 dm tjockt sandlager. Vid samma tillfälle kunde intet spår av *Tripleurospermum maritimum* (se nedan) återfinnas, medan ett litet, tydligen alldeles nykommet individ av *Lathyrus maritimus* var. *pubescens*, en här ej tidigare observerad art, nu upptäcktes.

Juncus ranarius är den märkligaste av de arter, som funnit fäste på sandstranden i Bredvikens innersta del. Den har nämligen tidigare icke ansetts tillhöra den norrländska floran. I Sverige anmärktes den för första gången av Samuelsson i andra upplagan av Lindmans flora (1926, s. 166). Den där angivna utbredningen, östkusten till Uppland, synes icke senare ha vidgats genom nordligare fynd (se exempelvis Hylander 1953, s. 166). Från Finland däremot föreligga enstaka lokaler ända uppe i mellersta Österbotten. Över huvud taget är artens finska utbredning åtskilligt bättre känd än den svenska. För detta har man främst att tacka Harald Lindbergs uppsats av 1934 med karta och goda fotografier. Häri anges flera karaktärer, med vars hjälp arten lätt kan skiljas från den närstående *J. bufonius*. Sålunda igenkännes den redan habituellt på de i jämförelse med nämnda art mera utspärrade, bågböjda, liksom nedtrampade stammarna och den gulare färgton, som Olsoni (1937, s. 19) tillspetsat kallar orange. När frukten mognar, böja sig dess valvler inåt, så att den i spetsen verkar tvärt avhuggen. *J. bufonius* har spetsig frukt. De inre kalkbladen äro kortare än de yttre och sakna tydlig spets. Hos *J. bufonius* äro alla kalkblad spetsiga och i det närmaste lika långa. Under lupp synes fruktens övre del prickig, medan den hos *J. bufonius* förefaller längsstrimmig. Detta beror på att epidermiscellerna hos *J. ranarius* äro kortare och ej så regelbundna som hos *J. bufonius* (fig. 2). Jag har tillåtit mig detta utförliga referat av *J. ranarius*' karaktäristika, emedan jag anser att arten mångenstädes i vårt land sannolikt är förbisedd och bör eftersökas.

Beståndet av *Juncus ranarius* vid Bredviken upptog, då det 1957 upptäcktes, ett femtiotal kvadratmeter av den låga, vid högvatten helt och hållet överspolade sandstranden i vikens nordvästra hörn. Här och var inblandar sig *J. bufonius,* och då kan man liksom på Lindbergs bild (l.c., s. 246, jämför också s. 248) få se samma tuva innehålla individ av båda arterna. Det är icke möjligt att närmare inpassa Bredvikens *J. ranarius*-bestånd i strandens ovan skisserade zonationskomplex, emedan hållpunkter i form av angränsande någotsånär tydliga samhällsfragment saknas.

Juncus ranarius är en inom vårt floraområde gammal art, tydligen spridd längs Ancylussjöns stränder (Lindberg l.c., s. 248). Reliktuppträdande i inlandet är därför tänkbart, men något sådant är icke känt, om man bortser från en förekomst vid Onega. Att arten vid våra kuster ter sig sällsyntare än *J. bufonius,* torde stå i samband med kräsnare krav på ståndort, även om ett intensifierat sökande här liksom i Finland kommer att resultera i åtskilliga nya fynd.

Ett sådant har redan gjorts. Den 1.8.1959 fann jag arten i ett rikt bestånd vid Säivisviken, den större vik, som skär in närmast öster om Bredviken. Lokalen är belägen på västsidan av den lilla udde som bildas av Harriojaåsen, när denna sjunker ner under vikens vattenyta (fig. 1). Här växer arten i en tät matta utan inblandning av *J. bufonius* på en i övrigt vegetationsfri sandyta ovanför *Eleocharis uniglumis* var. *fennica*-bältet.

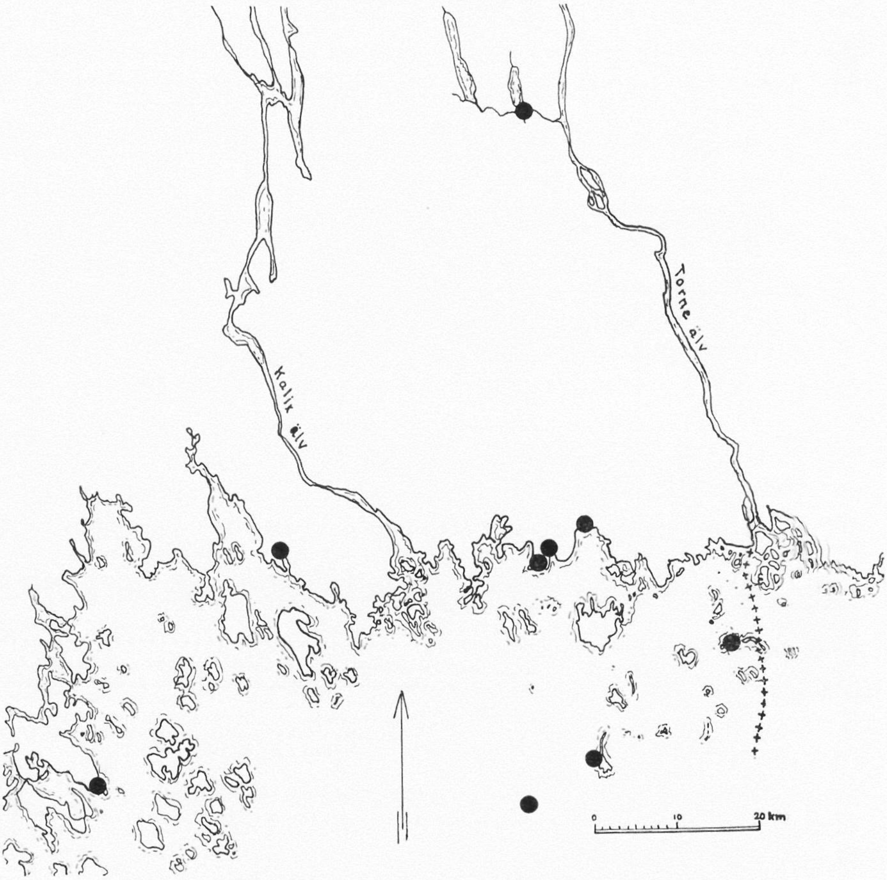


Fig. 3. *Scirpus Tabernaemontani* i Norrbotten. — För spridning godkänd i Rikets Allmänna Kartverk den 2 mars 1960.

Scirpus Tabernaemontani upptäcktes i Norrbotten så sent som 1955 av O. Lönnqvist (1956, s. 18). Detta fynd är ytterst märkligt, emedan det gjordes i myren vid sjön Armasjärvis sydända i Hietaniemi socken drygt 50 km från nuvarande kustlinjen och arten där hade sällskap med en annan havsstrandväxt, *Carex Mackenziei*. Sjön Armasjärvis vattenyta ligger 49 m över havet. Utom dessa båda havsstrandsrelikter, som här förekomma i stor mängd, har myren flera andra egenartade floraelement, vilka sammantagna kvalificera den som ett av Nordsveriges värdefullaste naturdokument.

I Bredviken fanns 1957 endast ett fåtal strån av blåsäv, alla utom två sterila, i kanten av en sandrevel i vikens innersta del. Ungefär lika sparsamt uppträder arten på de övriga Norrbottenslokalerna utom på Sandskär och i Pålänge hamn, där större bestånd finnas. De f.n. kända förekomsterna i Norrbotten äro (karta, fig. 3):

Hietaniemi, myr S om Armasjärvi 28.8.1955 O. Lönnqvist (1956, s. 18),
Nedertorneå, Sandskär, västra stranden 6.8.1957 E. Julin, confirm. H. Luther,
  Bredviken 8.8.1957 E. Julin,
  Säivisnäs, Kilpilahti 8.8.1957 E. Julin,
  Stora Hamnskär 11.8.1957 E. Julin,
  Säivisviken vid Harrioja, några m^2 1.8.1959 E. Julin,
Nederkalix, Malören 15.8.1958 E. Julin,
  Pålänge hamn 27.7.1959 E. Julin,
Nederluleå, Hertsölandet å stranden mitt för Kälkholmen 12.8.1956 samt ett par hundra m längre åt NV 10.9.1956 O. Lönnqvist (1956, s. 18).

De talrika stora sävruggar, som delvis uppfylla Nikkalaviken utanför Keräsjokis mynning liksom ett litet bestånd i Kurkisviken, båda lokalerna i Nedertorneå samt en stor förekomst i havet vid Strömsund i Råneå utgöras däremot av *Scirpus lacustris.*

Tripleurospermum maritimum anträffades 23.8.1957 i några exemplar på den sandrevel i Bredviken invid vilken *Scirpus Tabernaemontani* växte. Denna art är i motsats till sin var. *inodorum* en stor sällsynthet här, och förekomsten i Bredviken är den enda jag känner från Norrbottens östra skärgård. Dr Gunnar Marklund, Helsingfors, har haft vänligheten att kontrollera min bestämning.

Polygonum aviculare uppträder i en stor och grovvuxen nedliggande form på Bredvikens sandstrand. Arten är icke allmän som spontan strandväxt i östra delen av Norrbottens skärgård men väl som adventiv antropokor vid öarnas fiskestugor. Med tanke på *P. Raii* ssp. *norvegicum* som en möjlig invandrare nordost ifrån till Bottnikum har jag gjort till en regel att ta prov, när jag anträffat trampört som havsstrandsväxt. Dessa kollekter har dr Marklund granskat och därvid alltid funnit att det dock endast rört sig om former av den starkt variabla *P. aviculare.* Övriga lokaler äro Sandskär och Seskarfurö i Nedertorneå samt Malören i Nederkalix. En kollekt (dock ej från havsstrand), samlad vid kanten av vägen mellan Haparanda och Sundholmen (Nedertorneå) den 27.8.1956, bestämdes av Marklund till *P. aviculare* var. *calcatum.*

Carex paleacea har i Bredviken en av sina fåtaliga norrbottniska fastlandslokaler. Den uppträder här i en ovanligt kortvuxen form.

Ur den mer eller mindre koloniartade vegetation, som här och där bildar små fragment av växtsamhällen, och av de blott som enstaka

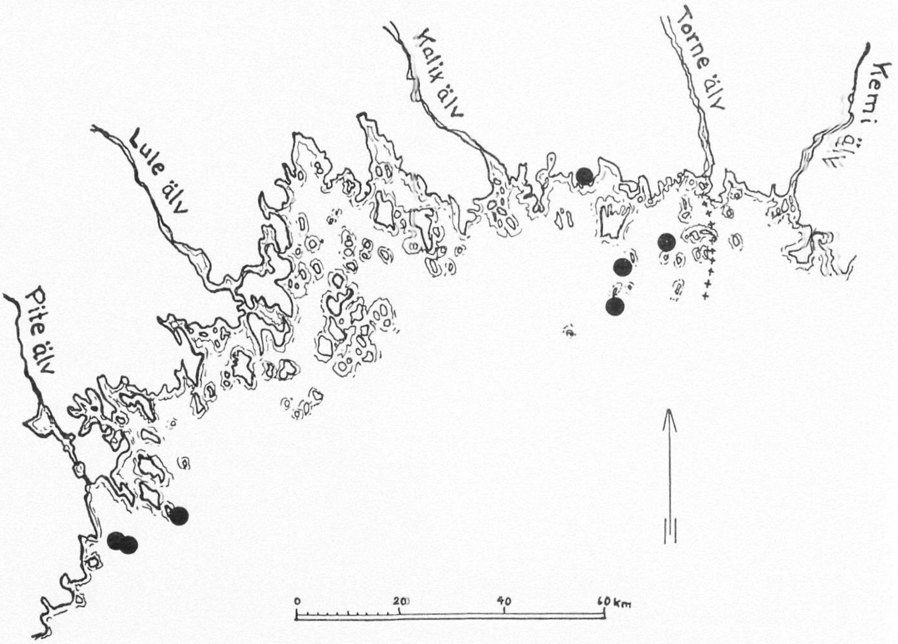


Fig. 4. De nordsvenska förekomsterna av *Scleroderma aurantium.*

individ antecknade kärlväxtarterna från Bredvikens norra sandstrand kunna måhända följande vara värda att uppräknas: *Agrostis gigantea, Artemisia vulgaris* var. *coarctata, Barbarea stricta, Eleocharis palustris, Equisetum palustre, Glaux maritima, Hieracium coniops* (det. S. Nordenstam), *Minuartia peploides, Myrica gale, Nardus stricta, Phalaris arundinacea, Rumex longifolius, Sagina nodosa, Salix repens. Silene maritima, Sonchus arvensis* var. *bottnicus* och *Spergula arvensis.*

Scleroderma aurantium har en sedan gammalt känd utbredning i södra Sverige upp till södra Norrland. 1930 fann Th. Arwidsson denna röksvamp på tre öar i Pite skärgård, och så har jag funnit den på tre öar i Haparanda skärgård och slutligen 1957 i några exemplar på de levande sanddynerna vid Bredvikens norra strand, sålunda på fastlandet.

Den bottniska formen avviker rätt mycket från typisk *Scleroderma aurantium,* och Lundell & Nannfeldt vilja endast med viss tvekan föra den till denna art. Om en kollekt från Sandskär i Nedertorneå, som utgivits i deras exsickat (nr 2258), säga de: »Typical *Scl. aurantium* is subsessile or substipitate but this collection has a prolonged, strong and broad, irregularly corrugated stem-like base. Also the peridium is thicker and firmer than usual.» Stödjande sig på ett sjöstrandsfynd från Femsjö i Småland (nr 2259 i exsickatet), som företer avvikelser från typformen i samma riktning, anse de emellertid att det blott är fråga om en luxurierande ståndortsmodifikation.

Jag vore snarare böjd att uppfatta sanddynformen från Norrbottens skärgård som en genetiskt underbyggd ekotyp av *Scl. aurantium*, möjligen värd att urskiljas som egen art. Härför talar ej blott de stora morfologiska olikheterna formerna emellan utan även dessas från varandra isolerade arealer jämte skillnaden i biotop. Detta hindrar ju inte, att Femsjö-kollekten kan vara en ståndortsmodifikation i samma morfologiska riktning som den nordliga ekotypen. Man kan invända, att arealerna kunna komma att bindas ihop genom framtida fynd längs den föga genomforskade Norrlandskusten, men under alla förhållanden är problemet värt att uppmärksammas.

De nordsvenska lokalerna för *Scl. aurantium* äro följande (karta, fig. 4):

Piteå, Storrebben 3.9.1930, Sandskär och Stenskär 4.9.1930 Th. Arwidsson (1936, s. 537),

Nedertorneå, Seskarfurö 27.8.1947, Suutari 1.10.1950, Sandskär 22.8.1952 (Lundell & Nannfeldt 1954, nr 2258; Julin 1956, s. 265), Säivis-Bredviken 15.9.1957 E. Julin.

Summary

Säivis-Bredviken (parish of Nedertorneå, province of Norrbotten, Northeastern Sweden) is a rectangular inlet which cuts deeply into a projecting part of the coast of the Gulf of Bothnia (Fig. 1). The inner part of the inlet is very shallow. Storms make water rush into the inlet and violently change the inner shore with its shoals of sand. The shoals and the shore thus become a good germinating-bed for diaspores of foreign species which are feeble in competition, and which are caught by the inlet from the sea drift. Vegetation and flora are described. Fig. 2 shows *Juncus ranarius* compared with *J. bufonius*. The former species has been overlooked in Sweden. It is here presented as being new to Norrland (localities: Fig. 1). Fig. 3 shows the distribution of *Scirpus Tabernaemontani* in Norrbotten with 7 new localities. Of the gastromycete *Scleroderma aurantium* there occurs in Norrbotten a form morphologically deviating from the type with an isolated area and another biotope (drift-sand), which is supposed to constitute a special ecotype or own species (distribution: Fig. 4).

Citerad litteratur

ARWIDSSON, TH. 1936: Norrländska gasteromycetlokaler. — Bot. Not. Lund.

HYLANDER, N. 1953: Nordisk kärlväxtflora I. — Uppsala.

JULIN, E. 1956: Sveriges östligaste hörn — i Haparanda bygd och skärgård. — Natur i Västerbotten och Norrbotten under redaktion av F. EBELING och K. CURRY-LINDAHL. Uppsala.

LINDBERG, H. 1934: Juncus ranarius' Song. & Perr. förekomst inom det östfennoskandiska floraområdet. — Mem. Soc. F. Fl. Fenn. 10. Helsingforsiae.

LINDMAN, C. A. M. 1926: Svensk fanerogamflora. Andra uppl. — Stockholm.

LUNDELL, S. & NANNFELDT, J. A. 1954: Fungi exsiccati suecici, praesertim upsalienses. Fasc. XLV—XLVI. — Uppsala.

LÖNNQVIST, O. 1956: Scirpus Tabernaemontani (blåsäv) funnen i Norrbotten. — Norrbottens Natur 1956: 1. Boden.

OLSONI, B. 1937: Botaniskt från Lavansaari, Seiskari o. Penisaari. — Mem. Soc. F. Fl. Fenn. 13. Helsingforsiae.

BOTANISKA NOTISER 1960 · VOL. 113 · FASC. 1 · LUND

Seed Development in Larix

By ARTUR HÅKANSSON

Institute of Genetics, Lund, Sweden

This paper contains a continuation of my embryological investigation of seed development of Conifers in Sweden (Håkansson 1956, 1959). The embryo development of *Larix* has been described very closely by Schopf (1943) and one hardly can hope to find new traits. I have, however, paid attention to the embryological aspect of the seed sterility which is shown by certain *Larix* species. The investigated material was received from the Swedish Forest Tree Breeding Association at Ekebo, Svalöf. I am very indebted to Dr. C.-A. Kiellander who has attended to the fixation of the ovules. The ovules have been collected from cones of the same three grafts. It has been shown that there is no difference between such ovules and ovules from trees (Håkansson 1959). Three species, *Larix decidua, L. leptolepis* and *L. sibirica,* were investigated. Most fixations were made in 1958. The investigation has been economically supported by "Fonden för skogsvetenskaplig forskning".

The embryology of *Larix* species was studied early by Strasburger and then by the Polish morphologist Woycicki. There are several more modern investigations. The studies of Buchholz on early stages of embryo development showed *Larix* to be similar to *Picea, Abies* and *Pseudotsuga,* the primary embryo not forming secondary embryos, in contradistinction to *Pinus* and other genera of the family *Pinaceae.* Smolska (1929), a pupil of Woycicki, has closely studied the forming of the archegonia, fertilization and proembryo in *L. decidua*; fertilization occurred on the 10th of June, two weeks after pollination. Doyle and his co-workers have investigated similar stages in *L. leptolepis* growing in Eire. The trees investigated by Schopf were growing in Illinois, U.S. and belonged to *L. decidua* but also to *L. laricina, L. leptolepis* and *L. eurolepis* (=*decidua*×*leptolepis*). As indicated the investigation of Schopf concerned embryo development and all stages of seed development have thus been investigated. The embryo development is perhaps more closely known than in any other genus of *Pinaceae*.

Schopf discerns several stages in embryo development which he calls pro-stage, meta-stage, ana-stage and telo-stage. These names have, however, found no further use, presumably being too similar to the wellknown cytological terms. The pro-stage begins with fertilization and ends when the proembryo is complete, meta-stage ends when a massive embryo is formed, ana-stage is the period of rapid and extensive growth, telo-stage begins when the cotyledons appear. A chart (l.c. p. 18) with embryological sequences in *L. decidua* shows that pro-stage lasted 2, meta-stage 13, ana-stage 11 and telo-stage 11 days. The development had been very early and rapid, fertilization could occur on May 20—25th and the embryo was fullgrown on June 30th. Schopf had made fixations in two consecutive years and writes: "Unfavorable environmental factors operating in 1932 were probably not only responsible for the preventing of abundant fertilization, but also for the retardation of the development of the embryo". There was no further reference to sterility in the material investigated by Schopf.

In the ovules investigated here following observations were made.

1956. — There were many gaps in the results gained in the year 1956 owing to the fact that the integuments had not been peeled from the nucellus of the ovule before fixation, therefore it was difficult to cut the imbedded material satisfactorily.

June 11th. — *L. decidua.* Unfertilized, no ventre canal cell is formed in the archegonia.

L. leptolepis. The same.

L. sibirica. A ventre canal cell is generally present in the archegonia.

June 25th. — *L. decidua.* Proembryos are formed, mostly with four or eight cells.

L. sibirica. Proembryos are complete with sixteen cells.

July 9th. — *L. leptolepis.* The suspensor of the embryo has attained full length, the embryos have a length of 12—16 cell layers.

L. sibirica. The embryo is larger having for instance a length of 25 cells and a breadth of 7—8 cells, still larger embryos were observed. The embryo cavity may be rather wide and once contained a small inversed embryo with a bent suspensor.

July 23rd. — *L. decidua.* The length of the embryo may be about 40 cells.

L. leptolepis. The embryo was somewhat smaller here. The embryo may be thin with a breadth of 3—4 cells or thicker, about 12 cells.

August 5th. — *L. decidua.* The embryo has grown rapidly and now filled $^3/_4$ of the embryo cavity, it had large cotyledons.

L. leptolepis. The embryo was here less advanced with shorter cotyledons.

L. sibirica. The embryo has full length, the cotyledons are large.

August 20th. — *L. leptolepis.* The embryo was large with large cotyledons.

L. sibirica. The embryo showed the inner anatomical organization.

September 3rd. — *L. decidua.* A second small embryo may still occur at the base of the large embryo. The embryo does not fill the upper, broader part of the cavity.

1958. — July 1st. — *L. decidua.* Ovules are fertilized and a proembryo with four or eight nuclei is often seen. There is still no striking assembling of starch in the prothallium.

L. leptolepis. Most ovules were unfertilized. A few were fertilized, the egg nucleus may be divided two times.

L. sibirica. The suspensor was growing or had attained full length. The proper embryo may have eight cells. The forming of the embryo cavity was under the way and more starch occurred in certain parts of the endosperm.

July 22nd. — During three weeks the seeds had undergone great changes.

L. decidua. There is newly formed storage in the protallium which now changes to an endosperm. The embryo had varying size, for instance a length of 18—20 cells, sometimes smaller, but may also be larger.

L. leptolepis. The embryo is smaller for instance with a length of 10 cells.

L. sibirica. The embryo filled half the cavity and showed small cotyledons, in most seeds it was smaller. Two seeds with a short, very thick undifferentiated embryo were found.

July 29th. — *L. decidua.* A well developed embryo filled $^1/_3$ of the embryo cavity. The cotyledons were rather small.

L. leptolepis. The embryo was somewhat less advanced showing no or only an indication of cotyledons.

L. sibirica. The embryo had rather large cotyledons. In one seed a second smaller embryo with smaller cotyledons was present.

August 5th. — *L. decidua.* The embryo was large, it had root cap with starch. More rarely the embryo had only small cotyledons.

L. leptolepis. The embryo had in most seeds rather small but in some seeds larger cotyledons.

L. sibirica. There is storage in the whole embryo, also in the cotyledons.

August 12th. — *L. decidua.* The embryo seemed fully developed.

L. leptolepis. No large seeds were investigated.

L. sibirica. Once a second small embryo was observed.

August 19th, August 26th, September 2nd, September 9th, September 15th. — The embryos were morphologically and anatomically complete. September 15th certain seeds in *leptolepis* had only small embryo in an endosperm with incomplete storage, *sibirica* seeds could have a second embryo.

1959. — A few fixations of *Larix sibirica* were made in this year. In 1959 spring and summer showed warm weather and development of the seeds had been early and rapid. Flowering was, however, very scanty, most ovules were unfertilized. June 22nd there was much starch in the prothallium, the suspensor of the embryo had full length and the embryo in the embryo cavity had a length of for instance 9 layers and a breadth of 6 cells. July 13th the endosperm was filled of storage and also the embryo had storage grains. The cotyledons were large. July 20th the embryo had attained full size. July 27th the fullgrown embryo does not fill the uppermost part of the embryo cavity.

In 1958 pollination had occurred on May 5—9th, in *sibirica* one or a few days earlier. This means that in *L. decidua* there was about seven weeks between pollination and fertilization, a slightly shorter interval than found by Smolska. The time of pollination naturally depends on the development of vegetation in spring. In 1958 therefore fertilization seemingly occurred more than a week later than in 1956 owing to unfavourable weather. Thus embryo development was delayed in 1958, this was still evident on July 22nd. *L. sibirica* was in 1959 much more advanced than in 1956.

There is also time differences between different species. In *leptolepis* development always was somewhat less advanced than in *decidua*. On the other side the young seeds of *sibirica* were always considerably more developed in all stages than those of the other species. The great difference in *sibirica* can hardly be explained exclusively through the somewhat more early pollination. One may guess that the pollen tubes grow more rapidly in *sibirica* than in *decidua* and *leptolepis*.

The pollen grains of larch are smaller than pine or spruce pollen grains. On the other side the cap of the nucellus is lower in larch. Through this cap the tubes after pollen grain germination on the surface of nucellus grow towards the archegonial chamber, the way of the tubes thus is shorter in *Larix*.

The forming of the archegonia in the prothallium was described by Smolska. Though the ovule is comparatively small it often contains five rather large archegonia. The archegonial neck consists mostly of four cells forming one layer. The prothallium tissue grows higher than the neck and a sort of micropyle is formed (Fig. 1). Shortly before the arrival of the pollen tube the nucleus of the archegonium divides and a ventre canal cell is separated, a very low and broad cell which here is very ephemeral. The pollen tube was observed growing through the "micropyle". Fertilization has been described by Smolska. A high but varying percentage of the archegonia remained unfertilized, sometimes all archegonia of the ovule. The egg nucleus in unfertilized archegonia generally increases in size and also undergoes certain structural changes. Sometimes the nucleus shows changes in form, particularly in *leptolepis*. It may have a peculiar appearance for instance having a long tube-like outgrowth directed towards the bottom of the archegonium. More rare was a second such outgrowth in opposite direction.

The prothallium is differentiated as jacket layer around each archegonium but in *Larix* the latter has no pronounced differentiation (Fig. 1). During the development of the proembryo starch grains appear in the prothallium, first along the axis of the prothallium where later the way of the growing suspensor is, but then also in the parts surrounding the group of archegonia and in the peripheral part of the prothallium. Much of this starch disappears when the embryo grows through the prothallium and the embryo cavity is formed. Later true endosperm storage begins to fill the prothallium cells, fats, starch and proteins.

Only recently a chemical analysis with modern methods of storage contents in ovules of gymnosperms has been made. Konar (1958 a and b) has investigated *Pinus roxburghii.* The year before Barthels had identified a number of amino acids and sugars in germinating seeds of pine and spruce and had cultivated their embryos *in vitro*; Konar made separate analysis of amino acids and sugars in gametophyte and embryo. The young gametophyte contains three sugars, viz. fructose, glucose and sucrose, but gradually the fructose and glucose disappear and only sucrose is left. Later on proteins and fats are synthesized and together with starch form the reserve products. Nearly all amino acids disappear as the more complex proteins are formed.

The forming of the proembryo with 16 cells was not studied here. Clearly it was more than two days between fertilization and the definite proembryo. The four apical cells of the proembryo as usual form the embryo, the rosette cells are ephemeral and as a rule do not divide in *Larix,* thus rosette embryos usually are not formed. The suspensor cells elongate and form the suspensor which pushes the apical cells into the prothallium. The four basal nuclei remain in the archegonium which degenerates. More suspensor cells are formed through the first divisions of the apical cells. The apical cells then begin their embryonal divisions. The embryo first consists of four rows of cells. In *Pinus* and other genera the cell rows separate each forming a secondary embryo, three of them degenerating. In *Larix* they remain together though they are of different length. Schopf tries to show that the bulk of the embryo is formed from only one of the cell rows — a delayed secondary polyembryony. He assumes a competition between derivates from the four united rows until one of them gets predominance. This competition must delay embryo development which he considers to be slower than in pine. He thinks that there is a similar competition and delay in *Picea*. However, Buchholz has shown that the forming of secondary embryos in pine delays embryo development owing to competition between the secondary embryos. In *Pinus silvestris* embryo development was delayed compared with *Picea abies* (Håkansson 1956). This speaks against the views of Schopf. It is true that in the *Larix* embryo consisting of four cell rows two of the rows are longer, that development then becomes slow, but it was here not possible to study the following development in the same close way as Schopf, thus his interpretations could not be confirmed. The embryo becomes thicker as well as it increases in length. It was hardly possible to discern the limit between the cell sectors derived from the different cell rows.

The ana-stage of Schopf ended with the appearance of the cotyledons, meta-stage and ana-stage lasted in Illinois 24 days in *L. decidua*. This is not very different from the time found here, the general delay in embryo development in the *decidua* and *leptolepis* material investigated here seems mainly to be the result of different times of fertilization.

The growth and morphological differentiation of the embryo during "telo-stage" has been described minutely by Schopf. The embryo lies in the embryo cavity which is formed through the disappearance of endosperm. The basal (upper) end of the cavity is more or less funnel-shaped through the early disappearance of the archegonia and surrounding parts of the prothallium; these parts may be rather large. The apical end of the seed has the cotyledons and the plumule which are imbedded in endosperm, in the basal end is the root and the root cap. In *L. sibirica* the embryo is short, it does not reach the funnel part of the cavity (Fig. 2). In *decidua* and *leptolepis* the embryo is longer but it was never observed in contact with the basal end of the seed which frequently is the case in spruce. The embryo becomes more or less filled of storage grains. The last part of the embryo where such grains appear is the cotyledonar periblem.

Polyembryony is more or less frequent in *Pinaceae*. It has two aspects, as one large and one or more supernumary small undifferentiated embryos or as two large differentiated embryos. The former condition is much more frequent, particularly in species where secondary embryos are formed. In *Larix* polyembryony is rare. However, in two seeds of *sibirica* a second differentiated embryo was present, it was smaller and was in higher position in the embryo cavity.

Seed sterility. — The origin of the seed sterility was more closely studied in the material fixed in 1958. The causes of seed sterility are of two kinds, the failure of fertilization and developmental disturbances leading to embryo lethality, that is, the degeneration of the embryo during development. Sometimes all archegonia of the ovule remain unfertilized and no egg nucleus divides. In *decidua* and *leptolepis* such ovules have no starch and no storage in the prothallium. As in normal fertilized ovules the archegonia degenerate rather rapidly, no embryo cavity is formed, but the prothallium increases considerably in volume because the cells widen; the cytoplasm then seems to have disappeared from the cells. In older unfertilized ovules the nuclei of the prothallium shrink and take a chromophilous appearance. The structures in unfertilized ovules may long be distinct. The pollen grains in *Larix* lack air-sacs, which must obstruct pollination in a varying degree.

The embryo lethality had in *Larix sibirica* a somewhat different aspect, but first observations made in 1958 on *L. decidua* and *L. leptolepis* will be described. Some time after the suspensor has been elongated the growth of the embryo may slow down and stop. One does not observe any mitosis in such embryos and the nuclei shrink. Fig. 4 and Fig. 5 are typical cases of such embryos with interrupted growth. The occurrence of such embryos was clear on July 22nd and still more on July 29th. Observed were degenerating embryos with for instance 12, 28, 40 and 60 cells, but still larger embryos were observed in degeneration. An earlier degeneration on the proembryo stage did not occur but was once observed in material fixed in 1956. On the other side no embryo which had attained any stage of morphological differentiation was degenerating. An exception was found in 1956: a fully developed embryo seemed to be dead.

Such seeds which have a degenerated or a subdeveloped embryo have less endosperm storage than seeds with normal embryo. There is on the whole parallelism in development between embryo and endosperm. Thus it does not seem that unsufficient storage in the endosperm causes embryo lethality or *vice versa* that the bad endosperm is a result of embryo death. Surely there are exceptions to this parallelism; certain young seeds lacking embryo showed starch grains in the peripheral and some other part of the prothallium, similar to the first stages is starch formation. A still more rich starch formation presumably indicated that the embryo had disappeared, that fertilization had occurred. On the other side in *L. sibirica* a seed was found having embryo with large cotyledons but lacking storage in the endosperm (Fig. 3). In the embryo, however, there were numerous grains

Fig. 1. *Larix leptolepis,* July 1st. Fertilized ovule. In the middle archegonium the "micropyle" is opened through the pollen tube, the egg nucleus is divided. Fig. 2. *L. sibirica,* August 12th. The embryo has attained full size. Fig. 3. *L. sibirica,* October 9th. Abnormal endosperm lacking solid storage substances. Fig. 4. *L. leptolepis,* July 29th. Seed with degenerating embryo. Fig. 5. *L. decidua,* July 29th. Seed with degenerating embryo. Fig. 6. *L. sibirica,* August 19th. Endosperm with very large fat drops. — Fig. 6 is more highly magnified.

of reserve substances. Probably the endosperm contained sugars and amino acids but certain synthesizing enzymes, which lead to the forming of proteins, fat and starch, were absent. In the embryo, however, such enzymes were clearly present which formed storage grains. The embryo in this seed was though differentiated of an abnormal appearance having cotyledons of different length.

Still on September 15th seeds could be find with a small embryo and an endosperm similar to a normal endosperm in early July. In some seeds with bad endosperm its abnormality did not involve the rapidity of development but certain other changes. Fat appears as drops and as seen in Fig. 6 such drops may be abnormally large. Fig. 7 shows a seed with no embryo but the embryo cavity filled by a loose tissue with starch. This surely belongs to the inner part of the prothallium which has not degenerated here. The endosperm is normal which is surprising in view of the absence of an embryo.

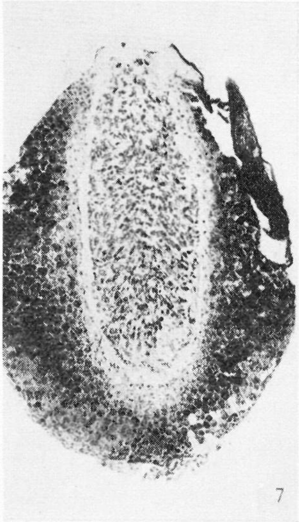
In *Larix sibirica* small underdeveloped, degenerating embryos were not observed in 1958, but abnormal embryos were rather frequent. The embryo abnormality was usually connected with polyembryony. A few such cases are figured here. Fig. 8 shows three broad but very short embryos from the upper part of the embryo cavity. They are orientated in different directions and have cotyledons. The inversed embryo had in reality rather long cotyledons, not visible in the figure. A normal embryo was absent. Several times the seeds contained embryos which had no polarity. They thus were clumsy, and in older seeds they had edges which were abortive cotyledonar outgrowths. They were only in the upper or middle part of the narrow embryo cavity. There may be a second normal but smaller embryo in the lower end (Fig. 9; here, however, the upper embryo was more normal). In Fig. 10 there is a second embryo with stunted growth in the upper part of the seed. It has an inversed position probably owing to the suspensor being bent very early or perhaps it was an exceptional rosette embryo. Once the embryo cavity was divided by endosperm cells; there was a developing embryo in each room of the cavity, the lower one seemed degenerating.

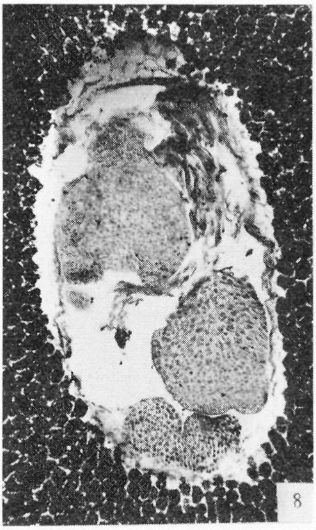
The embryo may have reduced size but be perfectly normal as is seen in Fig. 11. This embryo is mature, the cotyledons are somewhat spreading which is unusual.

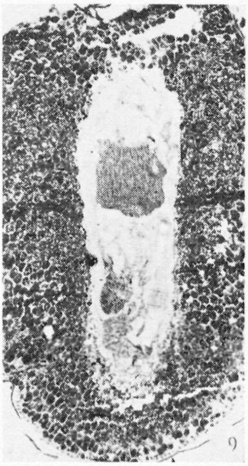
In the ovules of *L. sibirica* fixed in 1959 a large number of seeds had aborted, the cones had only a few seeds. Most young seeds had no embryo but contained a normal embryo cavity and much starch in the prothallium.

In *Pinus silvestris* and *Picea abies* I did only rarely observe any abnormal embryos or the degeneration of the only embryo. They explain the seed sterility observed in *Larix*.

The embryo-less seeds were different in *sibirica* compared with *decidua* and *leptolepis*. Such seeds in the former species had more or less







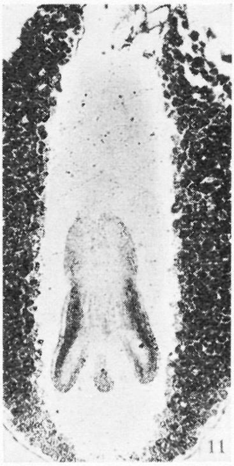


Fig. 7. *L. decidua,* August 19th. There is no embryo, but the endosperm surrounds persisting prothallium tissue with starch. Fig. 8. *L. sibirica,* August 19th. Three abnormal embryos. Fig. 9. *L. decidua,* August 5th. Abnormal and normal embryos. Fig. 10. *L. decidua,* August 5th. The upper (basal) part of the seed contains a second embryo which is abnormal. Fig. 11. *L. sibirica,* September 15th. Small but normal embryo. — Fig. 8 is at a higher magnification.

starch as well as a normal embryo cavity in the prothallium while in unfertilized ovules of the other species starch only exceptionally was observed and embryo cavity is absent. The exceptions were in latter cases interpreted as due to early disappearance of a young embryo. It is less probable that in 1959 pollination had occurred in embryo-less *sibirica* seeds and thus in this species unfertilized seeds have other properties than in *decidua* and *leptolepis.* The large embryo cavity in embryo-less *sibirica* seeds surely does not indicate disappearance of an embryo.

After the first or second week in August the embryo of *decidua* and *leptolepis* had attained full size. About that time the embryos of *Pinus silvestris* and *Picea abies* are fullgrown (see Håkansson 1956). When the stage of growth sets in, development is very rapid. The embryo of *Larix sibirica* was always most advanced. The weather certainly influences development and in the favourable year 1959, fixation made July 20th, *sibirica* seeds had a fullgrown embryo, considerably more early than the year before. Probably the time of pollination is largely responsible of this variation between different years. The general earliness of *sibirica* may be an adaption to the long winters of the arcto-boreal regions where this species is native.

Summary

Embryological investigation of three species of *Larix* showed that the embryo had attained full size at early or middle August, and had complete storage before the end of this month. In *L. sibirica* development was most rapid. The seed usually had only one embryo. Several and sometimes all archegonia of the ovule are not fertilized, and a variable number of ovules lack embryo. A second cause of seed sterility is embryo lethality during certain stages of development and in *L. sibirica* abnormal embryos, which mostly are in connection with polyembryony.

Literature cited

BARTELS, H. 1957. Kultur isolierter Koniferenembryonen II. — Naturwissenschaften 44: 596—597.

BUCHHOLZ, J. T. 1920. Polyembryony among Abietineae. — Bot. Gaz. 69: 153—167.

DOYLE, J. 1918. Observations on the embryology of *Larix leptolepis.* — Sci. Proc. Roy. Dublin Soc. 15: 310—330.

HÅKANSSON, A. 1956. Seed development in *Picea abies* and *Pinus silvestris.* — Medd. Statens Skogsforsk.-inst. Bd 18, Nr 2: 1—23.

— 1959. Seed development of pine grafts. — Botaniska Notiser 112: 67—72.

KONAR, B. N. 1958 a. A qualitative survey of the free amino acids and sugars in the developing female gametophyte and embryo of *Pinus Roxburghii.* — Phytomorphology 8: 168—173.

— 1958 b. A quantitative survey of some nitrogenous substances and fats in the developing embryos and gametophytes of *Pinus Roxburghii.* — Phytomorphology 8: 174—176.

Schopf, J. M. 1943. The embryology of *Larix*. — Illinois Biol. Monogr. 19: 1—97.

Smolska, A. 1929. Die Entwicklung des Archegoniums und der Befruchtung bei *Larix europea* D.C. — Bull. Acad. Polonaise des Sci. et des Lett., Cl. Sci., Math. et Nat., B. 1927: 903—1038.

Strasburger, E. 1879. Die Angiospermen und die Gymnospermen. — Jena.

Woycicki, Z. 1923. Einige Beobachtungen über Prothallien und Archegonien bei Larix dahurica Turcz. und L. europaea DC. — Acta Soc. Bot. Polon. 1: 149—164.

Botaniska Notiser 1960 · Vol. 113 · Fasc. 1 · Lund

Pollen Walls and Angiosperm Phylogeny[1]

By G. Erdtman

Palynological Laboratory, Nybodagatan 5, Stockholm-Solna

With regard to the number of apertures (Gr. tremata, sing. trema) pollen grains are atreme or mono- to polytreme. As to the position of the apertures cormophyte spores (pollen grains or spores according to the context) are either cata-, ana-, zono-, or pantotreme. In catatreme spores there is one aperture in the proximal, in anatreme grains one in the distal face. Zonotreme grains have several apertures zonally arranged, usually at the equator. Pantotreme grains have apertures regularly distributed over the surface. Some apertures are long (colpi), others short (pori). Some are simple, others composite. The latter consist of an outer, colpal or poral, part underlain by another part (Lat. os, gen. oris), differing in size, outline, or both. Grains with composite apertures are thus either colporate (colp-or-ate) or pororate (por-or-ate). The concept aperture is not always easy to define and the knowledge of some types of composite apertures is still poor.

Pollenmorphologically angiosperms can be subdivided into two groups, here referred to as A and B. "A" comprises the monocotyledons and the monocotyledonoid dicotyledons, "B" the typical dicotyledons. Examples of atypical (often more or less "monocotyledonoid") dicotyledons are Austrobaileyaceae, Calycanthaceae, Canellaceae, Chloranthaceae (e.g. *Ascarina*), Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae, Monimiaceae (Atherospermoideae etc.), Myristicaceae, Nymphaeaceae, Piperaceae, Saururaceae, Winteraceae etc. In group A the pollen grains are usually anatreme, or zenotreme with transverse colpi ("sulculi"); the apertures are simple. In group B the grains are either zonotreme (with pori or longitudinal colpi) or pantotreme; the apertures are simple or composite. Transition from A to B occurs in Magnoliales,

---

[1] Abstract of paper read at the IX International Botanical Congress, Montreal 1959.

Ranales (Nymphaeaceae), and Piperales (Chloranthaceae; the grains are anacolpate in *Ascarina* and *Hedyosmum,* acolpate in *Sarcandra,* more or less zonocolpate in *Chloranthus*). Cf. also the occurrence of zonocolpate and acolpate grains in the Aristolochiaceae (Ikuse, Pollen Grains of Japan, 1956). The transitional state, at least in the Piperales, has existed for a very long time if a recent identification of two pollen types — one of Ascarina-Saururaceae-type, the other of Chloranthus-type — from Late Senonian (Maastrichtian) beds is correct (material from Oebisfeld submitted by Dr. W. Krutzsch, Berlin).

In spite of these transitions the pollenmorphological line of demarcation between groups A and B is, is a rule, very distinct. In the first edition of "The Families of Flowering Plants" Hutchinson referred the Canellaceae and Calycanthaceae to group B. Both, however, have pollen of the A-type, anacolpate in the former, zonocolpate with transverse furrows ("clinocolpate") in the latter family. In the second edition (1959) the Canellaceae have been placed in A whereas the Calycanthaceae are retained in B (Rosales). From a pollenmorphological point of view, however, it seems quite impossible to refer the Calycanthaceae to this group.

In the B-group some probably more or less primitive aperture types are met with. Thus in *Cercidiphyllum* the apertures may vary in size as well as in shape; one of the three colpi is, as a rule, shorter than the others, almost poroid or leptomoid. (A leptoma, or tenuitas, is a thin, usually vaguely delimited apertural area which is less differentiated than a typical aperture.) The distance — measured along the equator — between this aperture and the other two is greater than the distance between the latter. Similar apertural conditions characterize the early Jurassic sporomorpha *Eucommiidites troedssonii.* Pollen grains with colpi of unequal length have also been encountered in the Hamamelidaceae, Fagaceae, etc. Also in *Juglans,* e.g. *J. cathayensis,* the apertures (pori) are often slightly varying both in size and shape. Grains of Juglans-type are said to have been found in Jurassic strata. Another noteworthy feature in *Juglans* as well as in *Carya* pollen is a leptomoid area in — according to Wodehouse — the distal face.

There are also aperture types which, from reduction or increase of the aperture number, may be considered pollenmorphologically "advanced". *Solanum* has usually 3-colporate pollen grains. In the subgenus *Lycianthes,* characterized by relatively small grains, there are some species, e.g. *S. andrieuxi, S. ciliolatum,* and *S. somniculentum,* with pollen grains with two apertures only or with one small and two large apertures. Similar apertural conditions also occur in the Tropaeolaceae. *Tropaeolum majus* (unreduced chromosome number 28) and *T. pentaphyllum* have 3-colporate radiosymmetric grains. In *T. kingii* there are also, as a rule, three apertures one or two of which are smaller than the other(s). *T. tuberosum* (unreduced chromosome number 42) and *T. tricolor* belong to a group with 2-colporate, bilateral grains of a very different shape: the polar axis in *T. tricolor* is about 13 μ and the equatorial diameters 33 and 5.5 μ respectively. The colpi are situated at the ends of the longest equatorial diameter (cf. also Ricardi et al., Bol. Soc. Biol. Concepción, vol. 22, 1957; a detailed study of the pollen morphology in *Tropaeolum* is actually being made at the University of Concepción). The pollen morphology can be adduced in favour of the idea of Hutchinson and others of a relationship between the Tropaeolaceae and the Balsaminaceae. Among the latter *Hydrocera triflora* has 3-colpate grains. In some more "advanced" species (*Impatiens* spp.) the number of colpi is, however, usually not reduced as in *Tropaeolum* but increased: (2—3—)4(—6).

The aperture number in the Labiatae is, as a rule, three or six. Pollen grains with six apertures are shed in a 2-nucleate, those with six apertures in a 3-nucleate stage. The Verbenaceae, in contradistinction to the Labiatae, are eurypalynous, not stenopalynous. The large and strange pollen types met with, e.g., in *Bouchea,* should be studied with due consideration of the cytological findings (cf. papers by Schnack). Reduction in aperture number may ultimately leave one equatorial aperture only, as in *Leiphaimos flavescens* (Gentianaceae), or lead to degeneration or disappearance of the aperture system (cf. e.g. *Populus*). In *Rorippa silvestris* there is an intraspecific variation with regard to aperture number: some specimens have normal, small, 3-colpate pollen grains whereas other specimens have large acolpate grains or grains exhibiting transitions between these extremes (Flora 146: 408, 1958).

Angiosperm pollen walls (sporoderms) consist of exine and intine. Outside the exine proper and/or in interstices in its outer part certain substances (oil etc.), not very resistant to chemicals, may be found. As an appendage to the sporoderm they may provisionally be lumped together under the name tryphine (Gr. tryphos, softness, delicacy, luxury). In the last few years refined techniques led to a better knowledge of the details of the sporoderms and their stratification. In attempts to bridge the gap between electron microscopy (fine structure revealed by the electron microscope is outside the scope of the present paper) and ordinary light microscopy sections from about half a micron to about a twentieth of a micron in thickness have been studied i.a. in UV light with and without phase contrast (for technique see e.g. "Pollen and Spore Morphology/Plant Taxonomy", vol. 2, pp. 135—147). In photomicrographs certain superficial details (processes etc.) and LO-patterns come out particularly well if the pollen grains are immersed in water, in a mixture of water and glycerine with an index of refraction of 1.40, or in silicon oil [Berglund, Erdtman, and Praglowski in Svensk Bot. Tidskr., vol. 53, 1959 (1960)].

As a rule the exine can be subdivided into a sculptured part, sexine (cf. Lat. secare, to cut) and a non-sculptured part, nexine (cf. Lat. nectere, to bind, to put together). As first clearly exhibited by Faegri the nexine sometimes consists of two layers. In pollen grains fixed, e.g., in glacial acetic acid the outer and thinner of these ("nexine 1") is, in conformity with the sexine, easily stained by basic alcoholic fuchsine. Contrarily the inner layer ("nexine 2") does not, or but faintly, take the stain. These two layers frequently seem to be underlain by a third, strongly refracting layer, originally described by Erdtman as endonexine, later as mexine (Kouprianova) and mesine (Hall). Also the intine is often stratified.

In her studies of the complicated sporoderm stratification in the Compositae Erika Stix (Grana Palynologica, Vol. II: 2, in print) has been able to trace nexine 1 and 2 throughout the family. She has, i.e., found the index of refraction of acetolyzed exines to be about 1.55, whereas in non-acetolyzed grains the index of the sexine and nexine 1 is less and that of nexine 2 higher than that of methylene iodide (1.754). Nexine 1 and 2 have also been traced in the Acanthaceae (not in *Ruellia* and *Thunbergia* however) by Bhoj Raj (unpublished). In *Abelia, Acicarpha, Cephalaria, Cobaea, Eryngium, Plumbago* (the pollen grains of which, contrary to statements hitherto made, seem to be dimorphic althoug in a less apparent way than, e.g., in the dimorphic *Armeria* species), *Valeriana* etc. no sign of a subdivision of the nexine into two layers has been encountered (Praglowski unpublished). For the occurrence of supposed endonexine in aperture membranes see Ehrlich 1958 [Exptl. Cell Res. 15 (3), 463] and Erdtman 1959 [Bot. Not. 112 (2), 147; aperture membranes in the Proteaceae]. In some haloragidaceous and sapindaceous (cf. e.g. *Pometia*) pollen grains the nexine, particularly in the aperture walls, seems to consist of several lamellae [cf. also Ehrlich's electron micrograph of a portion of the nonapertural region in an Eocene pollen grain showing a series of concentric lamellae varying in electron density (Pl. 1, facing p. 34 in Grana Palynologica

2: 1)]. In other pollen types the nexine, or parts of it, is more or less "baculate" (cf. e.g. Fig. 2 in Erdtman and Praglowski, Bot. Not. 112: 147, 1959). A baculation may also be found within sexinous tegilla (some tegilla actually seem to consist of densely packed, radial, baculoid elements).

These findings and many others tend to show that pollen morphology is more complicated — and at the same time probably more useful in taxonomical and phylogenetic context — than hitherto has been realized.

BOTANISKA NOTISER 1960 · VOL. 113 · FASC. 1 · LUND

On Three New Genera from the Lower Headon Beds, Berkshire

By G. ERDTMAN

Palynological Laboratory, Nybodagatan 5, Stockholm-Solna

Milfordia, Aglaoreidia, and *Lymingtonia* are three organ genera (pollen genera) encountered in the Lower Headon Beds (Oligocene or possibly Late Eocene) at Hordle Cliff not far from Milford-on-Sea and Lymington in Berkshire, England. The three species described below were found in slides made in July 1935 from material collected by the present writer July 10, 1935. *Milfordia* should, according to our present knowledge, be referred to the Restionaceae (or possibly the Centrolepidaceae), *Aglaoreidia* to a monocotyledonous group of unknown affinity (it has some characteristics in common with certain representatives of the Amaryllidaceae, Liliaceae, etc.), and *Lymingtonia* to the Nyctaginaceae (probably near *Phaeoptilon*).

Milfordia

Generic diagnosis (genotype *Milfordia hypolaenoides*): *Pollen grains monocolpate. Colpus with slightly jagged margin. Exine psilate, its outer layer (sexine) provided with small, densely spaced circular pits (scrobiculi).*

Specific diagnosis based on the holotype from the Lower Headon Beds, Hordle Cliff, Pl. I, a (from slide marked "Chara Bed, B" in the collections of the Palynological laboratory, Stockholm-Solna).

Characters besides those mentioned in the generic description: *Pollen grain bilateral (about 45×60×? μ), monocolpate. Colpus about 30×10 μ. Colpus margin slightly jagged, surrounded, as it seems, by easily detachable exine fragments* (the dark, more or less square dots with a diameter of about 1.5 μ in Pl. I, a). *Exine about 1.3 μ thick, consisting of sexine and nexine. Sexine as thick as nexine or slightly thicker, provided with small scrobiculi (diameter about 0.5 μ or less) spaced about 2 μ apart.*

The dark shade of the exine fragments in Pl. I a is a phase contrast effect. Among recent plants similar fragments have been encountered in some restionaceous plants, e.g., *Hypolaena lateriflora* (cf. Fig. 220 A, p. 376, in Erdtman. Pollen Morphology and Plant Taxonomy, Uppsala 1952), *Lepyrodia interrupta* and *L. muelleri.*

Pollen grains (referred to the "incertus-group") of cf. restionaceous plants have been found in Central Europe in Upper Palaeocene to Upper Oligocene deposits (maximum occurrence in Middle and Upper Eocene; cf. p. 521 and Pl. X, Figs. 40—45, in W. Krutzsch, Sporen- und Pollengruppen aus der Oberkreide und dem Tertiär Mitteleuropas und ihre stratigraphische Verteilung. Z. angew. Geol., H. 11/12, 1957).

Megascopical remains of a plant (*Rhizocaulon brongniarti* Sap.) referred to the Restionaceae (or Cyperaceae?) have been found in Oligocene beds in southern France (cf. p. 367 in Gothan and Weyland, Lehrbuch der Paläobotanik, Berlin 1954).

At present the Restionaceae are restricted mainly to the southern hemisphere, particularly South Africa and parts of Australia (cf. map, p. 700, in Hutchinson, The Families of Flowering Plants, Vol. 2, second edition, Oxford 1959).

Aglaoreidia

Generic diagnosis (genotype *Aglaoreidia cyclops*): *Pollen grains monoporate, spheroidal—slightly bilateral. Pore circular with incrassate margin. Exine reticulate. Reticulation coarse in the area surrounding the pore (except in the immediate vicinity of the pore), otherwise finer.*

Specific diagnosis based on the holotype from the Lower Headon Beds, Hordle Cliff, Pl. I, b—c (from slide marked "Chara Bed, B"). Characters besides those mentioned in the generic description: *Pollen grains probably slightly bilateral, about* $40\times55\times?$ *μ. Pore diameter about 7.5 μ. Exine about 2.2 μ in thickness. Sexine generally thicker than nexine, reticulate. Muri in the coarsely reticulate part of the grains about 0.5 μ wide, simplibaculate. Lumina up to 4.5 μ wide* (for sexine pattern in the not coarsely reticulate parts of the grains, see Figs. b and c; these parts also comprise a more or less narrow zone, not exhibited in the photomicrographs, connecting — in the non-poriferous face of the grains — the "lateral", finely reticulate areas shown in the same figures). *Nexine about 1.5 μ thick at the pore margin, otherwise thinner.*

Lymingtonia

Generic diagnosis (genotype *Lymingtonia rhetor*): *Pollen grains spherical, pancolpate (with 12 colpi at least). Colpi about 4—6 times as long as broad, tenuimarginate. Exine thickness about five per cent of pollen diameter.*

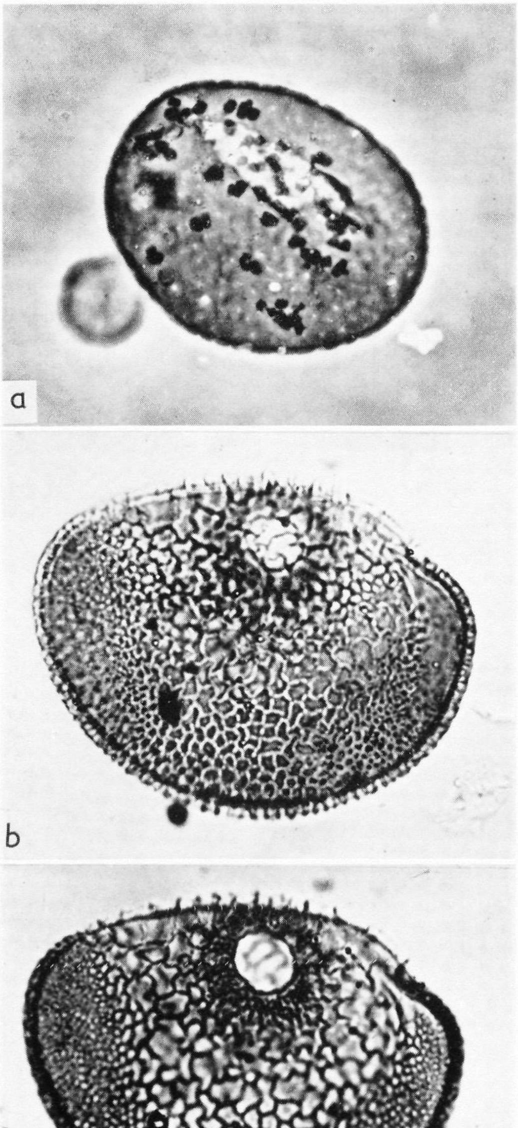
Sexine consisting of tegillum and supporting bacula. Tegillum perforate. Total sexine thickness slightly less than that of nexine.

Specific diagnosis based on the holotype from the Lower Headon Beds, Hordle Cliff, Pl. II b—c (from slide marked "Chara Bed, W"): Characters besides those mentioned in the generic diagnosis: *Total diameter about 50 μ. Colpi membranes granulate. Tegillum about 1 μ thick, provided with punctoid, rounded (or slightly elongate) perforations (about 1 μ wide, spaced 1—2 μ apart). Bacula about 1 μ or less in length, very densely spaced.*

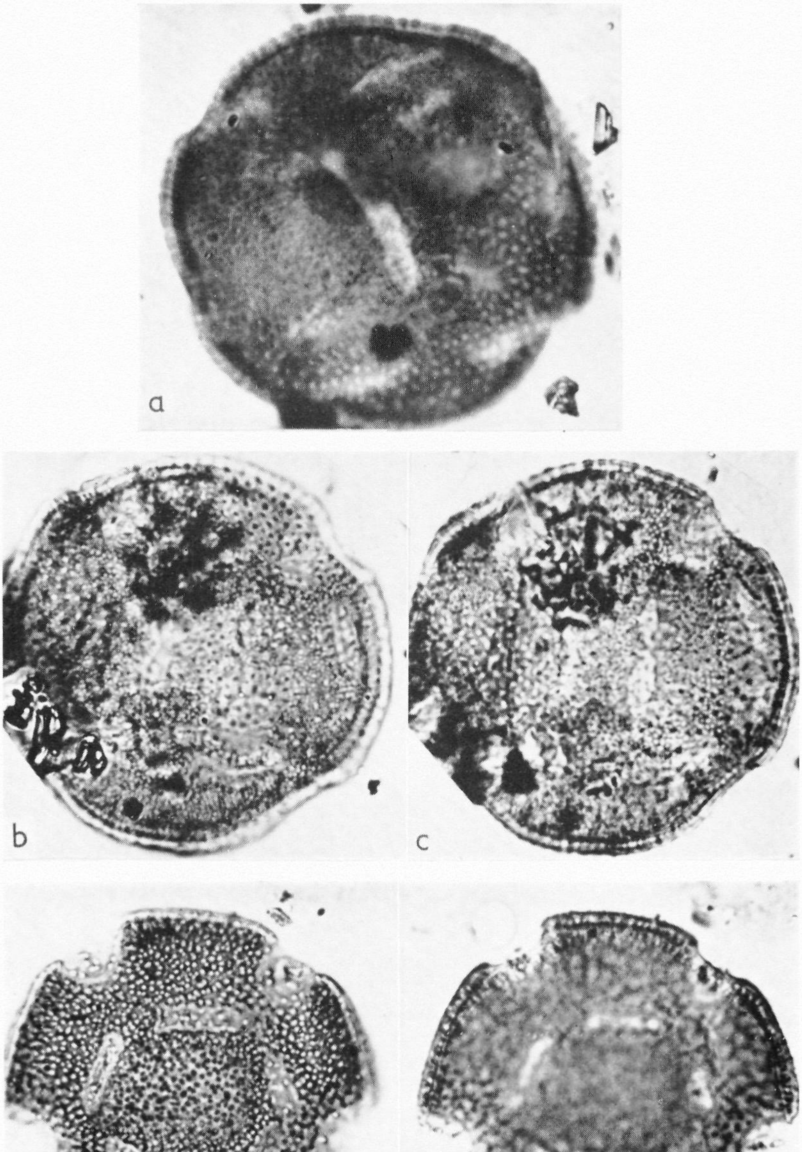
LO-patterns (in grains embedded in glycerine jelly): 1. OL (punctoid holes in the tegillum; O-pattern dots slightly smaller than those of the L-pattern indicating that the lumen of the perforations becomes smaller towards the upper surface of the sexine; O-pattern distinctly shown e.g. in Pl. II, b "between noon and two o'clock"; L-pattern quite apparent, e.g., in the lower part of the deteriorated grain shown in Pl. II, a). — 2. LO (bacula; these patterns are clearly shown in various parts of Pl. II, b and c).

No spinules have been found in *Lymingtonia rhetor* which otherwise shows a marked resemblance — particularly as far as the apertures, their number and place, and the main features of the exine stratification are concerned — to the pollen grains in *Phaeoptilum spinosum* Radlk. A grain of the latter species (South Africa, Hafström n. 1060) is shown in Pl. II, d and e (in d at slightly higher focus than in e). The nexine is relatively thinner than in *Lymingtonia,* the bacula are not so densely spaced, and the perforations (not clearly shown in the photographs) smaller (diameter less than 1 μ).

With regard to the present knowledge of pollen morphology it seems justified to assume that *Lymingtonia* has been produced by a member of the Nyctaginaceae. The eloquent (cf. "rhetor") characters of the sporomorpha speak in fact decidedly in favour of this assumption. Previous fossil finds of Nyctaginaceae are not known to the author.



Pl. I. a. *Milfordia hypolaenoides* n. sp. Phase contrast. ×750. — b, c. *Aglaoreidia cyclops* n. sp. ×1125. E. Samuelsson photo.



Pl. II. a—c. *Lymingtonia rhetor* n. sp. ×1125. — d, e. *Phaeoptilum spinosum* Radlk. Acetolyzed pollen grain. ×1125. E. Samuelsson photo.

BOTANISKA NOTISER 1960 · VOL. 113 · FASC. 1 · LUND

The Accumulation of Sulphate in Isolated Leaves as Affected by Light and Darkness

By ANDERS KYLIN
Institute of Plant Physiology, Lund

Contents

Introduction 49
Materials and methods 51
  1) Plant materials 51
  2) Experimental procedure 56
  3) General characteristics of the uptake, and significance of the measurements 58
Experiments, part I 61
  1) Effects of DNP, cyanide, and selenate 61
  2) Interactions and adaptations of light and dark systems 62
  3) Significance of the chloroplast pigments 65
Experiments, part II 67
  1) Effect of azide 67
  2) Effects of CMB and arsenite 67
  3) Effects of arsenate, gramicidin, and ATP 69
  4) Effect of ammonium ions 70
Discussion 71
Summary 77
References 77

Introduction

In a paper on the uptake and transport of sulphate in wheat, Kylin and Hylmö (1957) postulated that the uptake mechanisms functioning within the shoot are the same as those well-known from roots, that is a passive equilibration through diffusion and related processes between the nutrient solution — in intact leaves presumably the xylem sap — and the apparent free space (AFS) or outer space, followed by an active uptake (accumulation) into the cells. The experimental material presented in the paper mentioned did not, however, touch directly upon these points, and therefore a number of investigations have been undertaken by the present author in order to elucidate the problem further. For practical reasons the results have been subdivided in publication: passive sulphate uptake to the outer space of *Vallisneria* leaves was demonstrated earlier (Kylin 1957), and a forthcoming paper will be concerned with the same phenomenon in some other plants, whereas still other publications will be devoted to osmotic influences on sulphate accumulation, and to sulphur incorporation into organic fractions. *Only the accumulation of sulphate in leaves, especially as affected by light and darkness, is treated here.*

In a review article Burström (1957, p. 226) pointed out that as a consequence of the classical concept of salt respiration one should expect an active delivery of ions to the external solution — and thus an inhibition of uptake — from illuminated leaves, where the internal oxygen concentration is presumably greater than the external one. On the other hand, most investigations directly touching upon the problem of illumination effects on ion accumulation in isolated leaves or algal tissues report an increase in light as compared with darkness (table 1); only for the special mechanisms of ion extrusion do experimental findings support the above theory (table 2). In the present paper evidence will be presented to the effect that sulphate accumulation in green tissues in darkness follows the respiration-dependent pathway known from roots and storage tissues; whereas illuminated leaves receive the energy necessary for salt uptake from a light-dependent process (cf. Scott & Hayward 1955, van Lookeren Campagne 1957) at the same time as the dark mechanism is inhibited. For theoretical interpretations of these phenomena it is possible to apply both the salt respiration theory originally at issue and a picture connected with phosphorylation energy.

As for table 1, no pretensions are made of presenting a complete bibliography of light effects on uptake of phosphate ions, since many observations on this subject have been published cursorily in connection with studies of photosynthesis and phosphorylation. Also, studies on re-distribution between phosphate fractions on illumination without concomitant uptake studies are not included.

Only in a few cases has it been critically demonstrated how the light effects on ion uptake are mediated (van Lookeren Campagne 1957), but judging from the existing investigations and the experience of the present author, it seems reasonable to suppose that the results recorded in table 1 are produced via the chloroplast system. They should be distinguished from the influence of illumination on the active salt uptake by roots and yeasts (Simonis & Ehrenberg 1957), and from the general effect of illumination on plasma permeability, which has been noted for instance by Lepeschkin (1930, 1940). These points will be discussed in connection with some of the experiments.

It should be noted that the influence of light on the salt uptake to roots or leaves of intact plants does not fall within the scope of the present investigations. These phenomena include evidently such things as the effects of carbohydrate supply to the roots and transport by the transpiration stream, which complicate the issue. The reader is referred to Brauner (1956), Robertson (1958), and Withrow (1951) for compilations of the literature on the influence of light in these respects. As for leaf feeding there are recent reviews by for instance Tamm (1958) and Wittwer & Teubner (1959).

The following abbreviations will be used: AFS=apparent free space; ADP=adenosine-diphosphate; ATP=adenosine-triphosphate; CMB=para-chloromercuribenzoate; DNP=2,4-dinitrophenol; GSH=glutathione.

Materials and methods

1) Plant materials

The species to be used were chosen according to the following considerations. From table 1 it is evident that only aquatic plants have earlier been investigated from the present point of view, with the sole exception of nitrate uptake to tomato leaf discs (Mendel & Visser 1951). As the *Vallisneria gigantea* already in use (Kylin 1957) represents a water-inhabiting species, attention was directed towards isolated parts from different land plants. The moss *Thuidium tamariscinum* represented the first attempts, and later floating leaf pieces of the succulent *Crassula argentea* were tried since, anatomically, they are fairly homogeneous. Finally it was shown that the results obtained are valid also for wheat and barley; the last-mentioned species was used since it represented a possibility to obtain a comparison between green and chlorophyll-free leaf tissues. — Within this assortment the basic experiments have been made on all the species, but the most extensive material is available for *Crassula,* which proved to be the plant most easily handled from a technical point of view.

Since the material taken for investigation to a large extent was derived from the greenhouse or from nature, a suitable pretreatment period in laboratory conditions was introduced so as to make it more uniform. These pretreat-

Table 1. Effects of light on ion uptake by isolated leaves and algal cells or tissues as noted in the literature

Ion	Reference	Material	Effects of light +, 0, —	Remarks
K^+	Eppley 1958	*Porphyra perforata*	+	CO_2 inhibits the uptake in dark.
	Ingold 1936	*Elodea canadensis*	+	Same results reported for *Ceratophyllum demersum* and *Myriophyllum* sp., but experimental values given only for *Elodea.*
	Jacques & Osterhout 1934	*Valonia macrophysa*	+	No uptake in darkness.
	— — 1935	*Nitella flexilis*	(—)	
	Mc Robbie & Dainty 1958	*Rhodymenia palmata*	+	Light increases also loss of K^+.
	Scott & Hayward 1953, 1954, 1955	*Ulva lactuca*	+	
		Valonia macrophysa	+	
NH_4^+ $(+NH_3+NH_4OH)$	Jacques 1939	*Valonia macrophysa*	+	Light hastens also the washing out of ammonia. Ammonia interferes somehow with uptake and loss of K^+ and Na^+.
Cs^+	R. Scott 1954	*Rhodymenia palmata*	+	CO_2 needed. — No leakage detected.
Ca^{2+}	Lowenhaupt 1958	*Potamogeton crispus*	±	Dependent upon treatment. — Possibly also indirect effects connected with HCO_3^- uptake during photosynthesis (*cf.* Ruttner 1948, Steemann Nielsen 1951).
Co^{2+}	R. Scott & Ericson 1955	*Rhodymenia palmata*	+	Co lost again in darkness. CO_2 increases the loss in darkness and inhibits the uptake in light. — Light uptake not connected with vitamin B_{12} content.

Cl^-	Arisz 1947 a, b; van Lookeren Campagne 1957; Sol 1958	*Vallisneria spiralis*	+	No direct relation between light effect and CO_2 assimilation. — Light saturation lower than in photosynthesis.
	Ingold 1936	*Elodea canadensis*	+	See K^+.
Cl^-, Br^-, I^-	Hoagland & Davis 1924; Hoagland, Hibbard & Davis 1927	*Nitella clavata*	+	
NO_3^-	Gessner 1943	*Potamogeton perfoliatus*	+	Especially during spring and early summer.
	Hoagland & Davis 1924	*Nitella clavata*	+	
	Mendel & Visser 1951	*Tomato*	+	
$H_2PO_4^-$	Ingold 1936	*Elodea canadensis*	+	See K^+.
	Simonis & Grube 1952; Grube 1953	*Elodea densa*	0	Uptake to inorganic fraction decreased by light.
	Simonis & Kating 1956 a, b	*Ankistrodesmus braunii*	?	Tables and text not in accordance (a). — CO_2 inhibits in light. Uptake to inorganic fraction decreased by light.
	Wintermans 1955	*Chlorella vulgaris*	+	CO_2 inhibits the light effect.
HPO_4^{2-} $(+H_2PO_4^-)$	Aronoff & Calvin 1948	*Chlorella vulgaris*	0	Anaerobiosis. — Oxygen increases uptake in the dark.
	Baslavskaya & Veber 1959	*Scenedesmus quadricauda*	+	
	Gest & Kamen 1948	*Chlorella pyrenoidosa*	+	Same for the photosynthetic bacterium *Rhodospirillum rubrum*.
	Pirson & Kuhl 1958	*Hydrodictyon reticulatum*	+	Strong illumination and CO_2 needed.
	Scott & Hayward 1953	*Ulva lactuca*	(+)	
SO_4^{2-}	Kylin 1957	*Vallisneria gigantea*	—	
	Wedding 1959	*Chlorella pyrenoidosa*	+	

Table 2. Effects of light on ion extrusion from leaves and algal tissues as noted in the literature

Ion	Reference	Material	Effects of light +, 0, —	Remarks
Na^+	Eppley 1958	*Porphyra perforata*	+	
	Mc Robbie & Dainty 1958	*Rhodymenia palmata*	+	Light increases also uptake of Na^+.
	Scott & Hayward 1953, 1954, 1955	*Ulva lactuca*	+	
		Valonia macrophysa	+	
OH^-	Steemann Nielsen 1951	*Myriophyllum spicatum*	+	A special photochemical process is rate-limiting at low light intensities.

ments consisted of suspension of the plant material in at least 100 times its volume of aerated nutrient solution as indicated in table 3. A temperature of 25° ± 1°C was used together with continuous light of approximately 9000 lux from incandescent bulbs with a heat-absorbing layer of streaming water. When for special purposes a different pretreatment was given, this will be indicated in the description of the experiment proper.

The sulphate concentrations were chosen so as to give later an uptake conveniently measurable without involving too much radioactivity (maximum 1 mC/l, usually much less — see table 3).

a) *Thuidium tamariscinum* (Hedw.) B. & S. — The moss was found as pure carpets on the borders of a brooklet near Blistorp, Villands Vånga. Suitable pieces of the mat were collected on different occasions and kept cold overnight in a big polythene bag. The following day the material was brought to the laboratory, the youngest parts of the plants separated and freed from contaminating twigs and needles, and finally cut into lengths of about 3 cm. The moss pieces were pretreated for 3 or 4 days with daily changes of the nutrient solution. In regard to the natural habitats of the species (S. Waldheim, oral communication) a rather low initial pH was chosen, but after the first day of pretreatment it rose about 0.7 unit within four hours of a nutrient change. No harmful effects due to this rise could be observed.

b) *Crassula argentea* Thunb. — Two rather big plants in the greenhouses of the Botanical Garden were used; according to the records, they have been grown from seeds obtained from La Mortola at Ventimiglia, Italy, in 1911. Leaves of the 3rd to the 5th pair as counted from the top of a twig were taken for the samples and cut at right angles to the long axis into pieces of 3 mm thickness by means of a number of razor blades fixed by nuts on two long screws in a holder. The basal and apical pieces were discarded and the rest washed in running tap water for a couple of hours before being treated in nutrient solution for one day (20—24 hours). — In some experi-

Table 3. Data on the conditions of pretreatments and experiments

Pretreatments at 25°C in continuous light of 9000 lux from incandescent bulbs. Daily exchange of nutrient solution. — Experiments at 25°C, either at 9000 lux or in darkness. — Strongest S^{35} dosage applied 1 mC/l. — Analytical grade reagents.

	Condition	*Thuidium*	*Crassula*	*Vallisneria*	Wheat	Barley
Composition of solutions, m*M*	$Ca(NO_3)_2$	1	1	1	1	1
	$CaCl_2$	—	0.5	0.5	—	—
	KCl	1	—	—	1	1
	KH_2PO_4	1	1	1	1	1
	K_2HPO_4	0.05	1	1	0.5	0.5
	$MgSO_4$	0.05	0.5	0.05	0.5	0.5
	$MgCl_2$	0.45	—	0.45	—	—
	Fe-versenate	0.01	0.01	0.01	0.01	0.01
	$MnCl_2$	0.001	0.001	0.001	0.001	0.001
	H_3BO_3	0.001	0.001	0.001	0.001	0.001
Pretreatments	Time in days	3 or 4	1	2 or 3	1	1
	pH, initial	5.5	6.8	6.8	6.5	6.5
	pH, after 1 day	6.2	6.8	6.8	6.5	6.5
Experiments	Amount of S^{35} commonly used, mC/l	0.25	0.125	0.25	0.5	0.5
	Hours on radioactivity	4	4	3 or 4	2 or 4	2
	Hours of washing	1	4	1	0.5 or 2	0.5
	Approximate fresh weight for assay, g	0.3	0.9	1.1	0.4 (roots 0.7)	0.4

ments chiefly concerned with outer space a pretreatment time of three days has also been used without any apparent changes in the absorption characteristics of the pieces. — It should be noted that it has been necessary to move the two plants according to the season: during summer they have been outdoors or in a greenhouse with painted windows, whereas in winter supplementary light has been provided from 5 a.m. to 7 p.m. from blended light lamps of 250 watts (Gelin & Burström 1949); the plants have flowered during the winter.

c) *Vallisneria gigantea* Graebn. — The plants were the same as those used by Kylin (1957), but they were moved from the greenhouse pond to a small concrete basin in another compartment, where the conditions could be better controlled. The basin had a capacity of 300 litres and was filled with rain water kept at a constant temperature of 25°C. Water losses were made up for every two or three days. The plants were grown in pots containing common garden-soil covered by a layer of gravel. Illumination was from daylight reinforced by two incandescent lamps of 500 watts each, hanging about 60 cm over the surface. The specimens and the basin were kept free from algae by a stock of aquaria fishes (*Mollienesia* sp.), and by an aquarium filter driven by compressed air, which at the same time ensured good aeration. — The plants made good growth, and the leaves were harvested about every four weeks, cut to pieces 1.5 cm long, and pretreated for 2 or 3 days. — The above description refers to the winter; during the summer the strong daylight and high temperature of the special compartment made it impossible to use the small basin, since the growth of algal plankton could not be prevented, and the *Vallisneria* plants had to be moved to the big pond used earlier. A few experiments have been made also on material grown there.

d) Wheat, Eroica variety. — The plants were reared on cloth stretched over a shallow disc in a way described before (Kylin & Hylmö 1957, p. 470), although in the present experiments the plants were given continuous illumination at 25°C after the addition of nutrient solution. After 4 days the roots were loosely made into bundles by means of a nylon string and taken for the experiment in the manner described (*l.c.*), whereas the top halves of the shoots were cut to pieces 2—3 mm in length, washed in running tap water and then pretreated for another day (20—24 hours) before being used.

e) Barley, Bonus variety, treatment X_1 —49. — This is a strain produced as an X-ray mutant. Due to coupled lethals the seeds on germinating give rise to 1/4 heterozygous plants turning green in light and 3/4 homozygous albina plants. In the latter only traces of carotenoids and no chlorophyll can be detected in extracts (Virgin 1957), but traces of chlorophyll may none the less be contained in the guard cells of the stomata (G. Holm, personal communication). — In principle the barley seedlings were grown and treated as described for wheat, but the period of growth on nutrient salts had to last for 9 days, during which time the solution was changed every second day. In order to get about the same development of the two different types of plants the temperature was kept at 18°—21°C and light given for 8—10 hours a day at 1500 lux from an incandescent bulb. After this period the leaves were cut, washed, and pretreated for one day (20—24 hours) at 25° and 9000 lux.

2) **Experimental procedure**

The principle of the experiments proper was to transfer a suitable amount of the plant material into beakers containing an aerated solution of the same kind as that used for pretreatment, but labelled with carrier-free radiosulphate from the Radiochemical Centre, Amersham. The amounts of solution have been big enough — at least 50 times the volume of the plant material, more if necessary — to ensure that practically no changes took place in the outside concentrations. The temperature amounted to 25°C, with either the same light conditions as during the pretreatment or complete darkness. After some hours in the radioactive solutions the pieces were again transferred to inactive solutions for a time long enough to wash out the radioactivity of the apparent free space. Their surface was then thoroughly dried and their fresh weight rapidly determined within ±1 per cent. The sulphate taken up was finally analyzed according to one of the two procedures mentioned below. — In table 3 there are given also the approximate amounts of plant material and the experimental times most commonly used. Cases with differing times will be denoted in the proper connection, but where no misunderstanding can arise the reader is referred to table 3. It should be noted that the experimental periods could be determined by purely practical considerations, since leakage of the actively incorporated sulphate is small or negligible under the present conditions (cf. figure 2).

The analytical treatment of the material followed two different lines. In cases where the active uptake of sulphate can be considered to be approximately equal to incorporation into the inorganic fraction, the leaf pieces were directly submitted to a wet combustion, after which the radioactivity was precipitated as $BaSO_4$ under conditions giving samples of standard weight and area (Kylin 1953). If a considerable amount of the sulphate (> 5—10 %) takes part in the synthesis of organic substances, the material was instead put into polythene bags, frozen, and stored at $-25°$C. Within a few days the samples were rapidly thawed and the sap expressed according to a method used earlier (Kylin 1953), at which the inorganic, soluble organic, and protein fractions of sulphur in the leaf pieces were determined. Combustion and precipitation of the $BaSO_4$ followed as above. — Detailed figures justifying these differences of method will be published in connection with investigations on the sulphur incorporation in organic fractions. In the present paper the method used will be indicated in each case.

The experimental points have regularly been determined in duplicate on different sets of leaf or moss pieces. All the main results have been obtained in at least two independent series of experiments of more or less different design. These experiments lead to the same general conclusions, although the absolute amounts of uptake may be rather different, as can be expected from plants collected in different times of the year from a natural habitat or from ordinary greenhouse conditions (*cf.* figures 3 and 4). — The general sources of error were extensively discussed earlier (Kylin 1953). From the point of view of possible radiation damages it should be mentioned that the effects noted by Barber & Neary (1958) on ion uptake were obtained at radiation doses more than 1000 times those at any time applied in the present investigations. A technical change in the analyses has been introduced by the fact that the Philip's automatic sample exchanger now in use in this laboratory does not allow an automatic correction for radioactive decay during the counting procedure (Kylin 1953, page 779). Practice has shown, however, that the half life of S^{35} is long enough to make this of no significance for the actual determinations.

A few words should also be devoted to the use of inhibitors and other extra additions. All the solutions of this kind were freshly made up on the day of an experiment, and no stock solutions were kept. In all the cases where it proved necessary the pH was adjusted to that of the control solution (table 3) by means of additions of HCl or NaOH. In the case of KCN this means a certain danger of losses of hydrocyanic acid (van Lookeren Campagne 1957, Eliasson 1959). By using especially large volumes of solution, the mean concentration of the inhibitor during the experimental period could, however, be kept at a value not more than 10 % lower than the original one, according to the calculations of van Lookeren Campagne (1957, p. 563). — As for possible pH influences on the effects of DNP, see Stenlid (1949). The question is not pertinent to the present investigations, where for a given species the same pH has been used throughout.

3) General characteristics of the uptake and significance of the measurements

Some data from different experiments available are collected in table 4 and figures 1 and 2 in order to give a general characterization of the sulphate uptake to the inorganic fraction of the leaves. Gravimetric determinations of the total sulphate contents show that they are considerably higher than in the nutrient solutions, and measurements of uptake indicate that within a limited time more sulphate is taken up per gram fresh weight of tissue than is contained in 1 ml of the external solution (table 4). *The process must thus be one of active uptake against a concentration gradient.*

Table 4. Sulphate contents of leaves and the accumulation character of sulphate uptake

Pretreatment conditions and solutions according to table 3. In experimental solutions of sulphate contents lower than those of table 3, $MgCl_2$ has been added to make up for the difference; all other salts and washing times according to the description given there. — Gravimetric analyses according to standard methods (Kylin 1953).

	Sulphate contents, gravimetric determinations. μM/g fresh weight	Sulphate uptakes measured by S^{35} method			
		External sulphate μM/ml	Uptake μM/g fresh weight	Experimental conditions	Fraction analyzed
Thuidium	—	0.05	0.15	4 hours; light	Total S
			0.22	4 hours; darkness	
Crassula	1.5	0.5	0.73	12 hours; light; 0.3 *M* mannitol	
			0.62	12 hours; darkness	
		0.005	0.0055	4 hours; light	SO_4^{2-}
			0.0065	4 hours; darkness	
Vallisneria	4.1	0.05	0.072	65.5 hours; light	
Wheat	2.9	0.05	0.070	4 hours; light	
			0.052	4 hours; darkness	

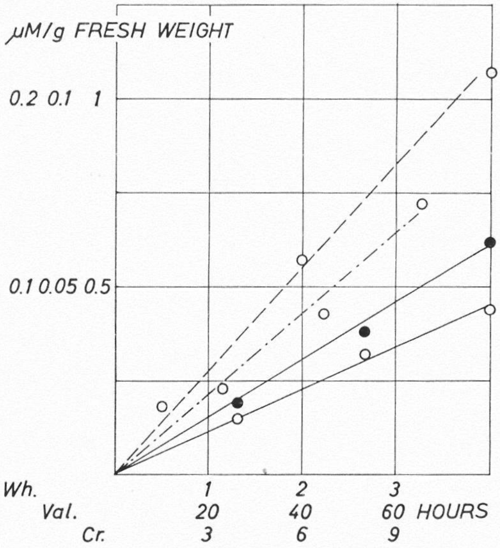


Fig. 1. Dependence of active sulphate uptake upon time. Total S determinations for *Crassula* and wheat, sulphate S for *Vallisneria*. Experimental conditions as indicated in table 3 except time of uptake. ——— *Crassula* —·—·— *Vallisneria* - - - - - *Wheat.* ○ Light ● Darkness.

During the present conditions accumulation is dependent upon time in a rectilinear fashion (figure 1), and leakage of radioactivity from the tissue to the solution is small or negligible (figure 2). This means that the conditions of Kylin & Hylmö (1957, p. 469) for experimental isolation of uptake in tracer studies are fulfilled. — A mathematical treatment of these questions in one-cell systems is given for instance by Mc Robbie & Dainty (1958).

The above facts must not be taken to mean that uptake and time are linearly correlated in all conditions or that no leakage at all occurs. There is no doubt that sulphate loss takes place at the same time as uptake, but as is shown above it is no source of error for the measurements with the present type of tracer application (*cf.* Kylin & Hylmö 1957, Kylin 1957). As for uptake, other experimental conditions can give other correlations with time. Also induction phenomena of the type theoretically predicted by Briggs & Robertson (1957, p. 16) and dependent upon successive filling up of the AFS with radioactivity may be met with (Kylin, preliminary evidence), but during experiments of the present type they will be concealed by the corresponding events with reversed sign during the final washing. — The investigations do not present any evidence as to the final place of accumulation, but from general considerations vacuoles and mitochondria are the structures most likely concerned (*cf.* Butler 1953),

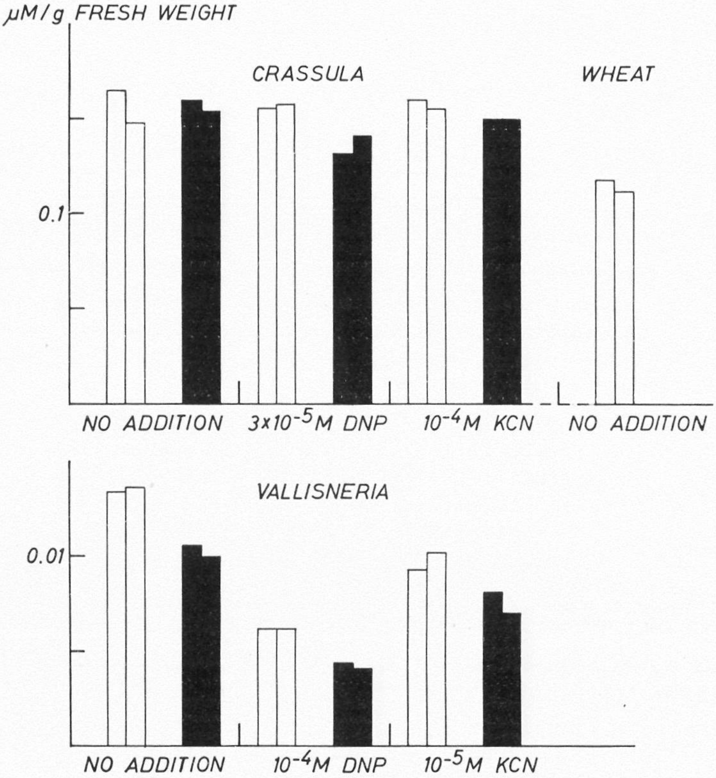


Fig. 2. Effect of prolonged washing upon total radio-sulphur contents of leaf pieces. Total S determinations. Empty columns: light; shadowed columns: darkness. — *Crassula*: Uptake period 4 hours without inhibitors, washing period with addition as indicated. First column of each pair: washing time 4 hours; second column: washing time 20 hours. — *Wheat*: Uptake period 2.2 hours. First column: washing time 0.6 hours; second column: washing time 2.0 hours. — *Vallisneria*: Inhibitors added both during uptake and washing. Uptake period 3.0 hours. First column: washing time 1.25 hours; second column: washing time 3.25 hours. — In all cases extra changes of solution during the long washing period.

although cytological investigations reveal also other possibilities (Whaley *et al.* 1959). The possibilities of the chloroplasts in this connection are unclear (*cf.* Diamond & Solomon 1959, Sager 1958, Weier 1953).

It is realized that the experiments presented above are incomplete or lacking for *Thuidium* and barley. This is due to lack of plant material, in the case of barley because of the limited amount of seeds available and in the case of *Thuidium* dependent upon the adverse conditions of the summer 1959 and the subsequent engagement of the author in other work. The results to be recorded

Table 5. Freezing–point depressions of the cell sap of Crassula leaves treated according to the procedure recorded in table 3

Beckman thermometer and the heat exchange and freezing characteristics of the cryoscopic system controlled by determinations of the freezing points of distilled water and 0.1 *M* KCl. Each experimental value represents the mean of 10 consecutive freezings of the same sap preparation; maximum deviation from the mean noted within such a series was 0°.008 C.

Series	Conditions during the experiment	Freezing-point depression of cell sap, °C
Control of reproducibility of cell sap preparation procedure	Darkness	0.263
	Darkness	0.255
Main experiment	Darkness	0.265
	Light	0.270

for these two species are, however, so well in accordance with those obtained with *Crassula, Vallisneria* and wheat that it seems reasonable to assume the same general significance in all cases. — In figure 2 the results with *Vallisneria* were obtained by analyses of total S^{35}, although a considerable part of it consists of protein sulphur. This is justified by the purpose of the experiment and the results on organic S fractions referred to above (page 57).

Finally, it should be pointed out, that no differences in the concentration of the cell sap could be observed after the light-dark treatments employed here, as revealed by the freezing-point depressions recorded in table 5. This is taken to mean that the differences in sulphate uptake do not depend upon general differences in the contents of soluble substances induced by photosynthesis or respiration during the uptake period. The conclusion is corroborated by the fact that light has no fixed increasing or decreasing effect upon accumulation (*cf.* figures 3 and 4). — The freezing-point depression observed corresponds to an osmotic pressure of about 4.0 atm.

Experiments, part I

1) Effects of DNP, cyanide, and selenate

In the basic experiments the influence of DNP, KCN, and selenate on the light and dark uptakes of sulphate was studied in all the species used, and the results are given in figure 3. Among the inhibitors chosen, selenate competes specifically with sulphate because of their chemical relationship (Shrift 1958). DNP and KCN, on the other hand, are known to interfere with the systems connecting active ion uptake with the energy sources necessary, in which DNP acts as an uncoupler of respiratory phosphorylation and KCN inhibits heavy metal enzymes (James 1953).

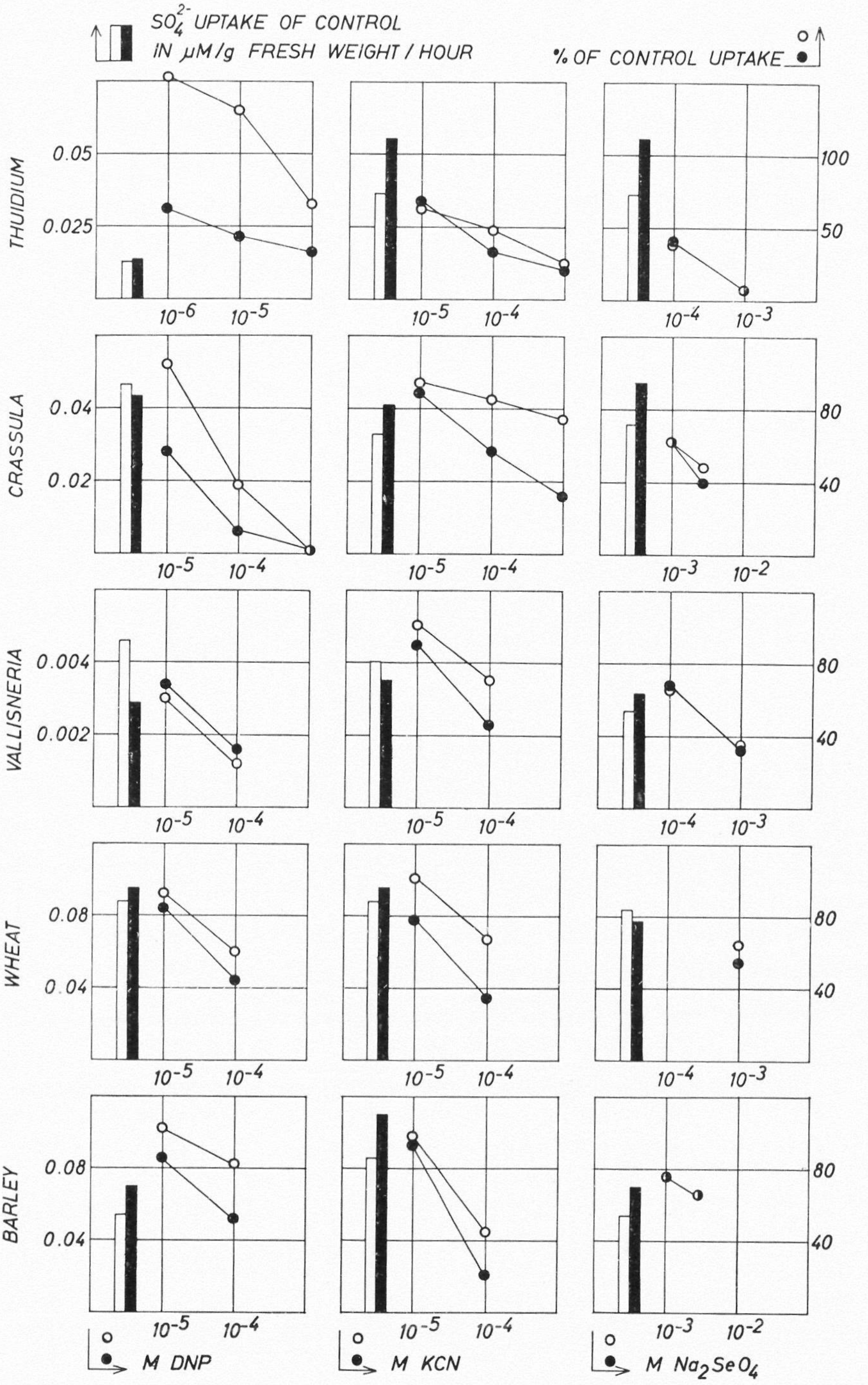
In two of the experiments presented in figure 3 the experimental procedure differed somewhat from the one described earlier (table 3). In the case of *Thuidium* and DNP, the active uptake was determined as the increase in radiosulphate contents between 70 and 265 minutes from the start (*cf.* Kylin & Hylmö 1957, table 2), and to obtain the selenate effect on active sulphate uptake in wheat, a standard correction for the AFS was applied to the total figure for (passive+active) uptake.

From figure 3 it is evident that the inhibition given by selenate is independent of the light conditions, whereas DNP and KCN depress sulphate uptake more in darkness than in light. For *Thuidium*/KCN and wheat/DNP this may be somewhat unclear, but only *Vallisneria*/DNP represents undoubtedly an exception to the rule. In regard of the general properties of the inhibitors, the experiments as a whole must be taken to mean that we have a "light uptake system" and a "dark uptake system", the energy necessary for sulphate accumulation coming from different sources in the two cases. The theoretical significance of these findings will be discussed later. — As for DNP a higher inhibition of sulphate uptake in darkness than in light was reported also by Wedding (1959) for *Chlorella,* and similar findings with this genus were made by Wintermans (1955) for the (primary) phosphate and by Kandler (1955) for the glucose uptake. With cyanide more pronounced effects upon uptake in the dark than on illumination were reported for *Vallisneria spiralis* and chloride (van Lookeren Campagne 1957) and for *Chlorella* and glucose (Kandler 1955).

2) **Interactions and adaptations of light and dark systems**

Figure 3 also shows that the processes of sulphate uptake in light and darkness are not additive to each other:

Fig. 3. The effects of DNP, KCN, and Na_2SeO_4 on the uptake of sulphate to green tissues. Total S values except for *Vallisneria,* which was analyzed for sulphate-S. Empty symbols: light. Filled symbols: darkness. — Left ordinate/columns: sulphate uptake of control in μM/g fresh weight/hour. — Right ordinate/circles: per cent of uptake of control. — Abscissa/circles: concentration of inhibitor in *M*.


SO_4^{2-} UPTAKE OF CONTROL
IN μM/g FRESH WEIGHT / HOUR
% OF CONTROL UPTAKE
THUIDIUM
0.05
0.025
100
50
10^{-6} 10^{-5}
10^{-5} 10^{-4}
10^{-4} 10^{-3}
CRASSULA
0.04
0.02
80
40
10^{-5} 10^{-4}
10^{-5} 10^{-4}
10^{-3} 10^{-2}
VALLISNERIA
0.004
0.002
80
40
10^{-5} 10^{-4}
10^{-5} 10^{-4}
10^{-4} 10^{-3}
WHEAT
0.08
0.04
80
40
10^{-5} 10^{-4}
10^{-5} 10^{-4}
10^{-4} 10^{-3}
BARLEY
0.08
0.04
80
40
10^{-5} 10^{-4}
10^{-5} 10^{-4}
10^{-3} 10^{-2}
M DNP
M KCN
M Na_2SeO_4

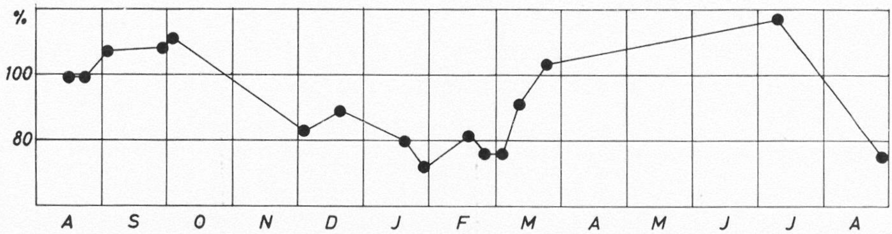


Fig. 4. Uptake of radiosulphate in the light to leaf pieces of *Crassula* during the period August 1958—August 1959 as per cent of the corresponding dark values. Total radiosulphur.

illumination sometimes increases but more often decreases the accumulation. The logical explanation for this seems to be that the dark uptake is inhibited by light just as the light uptake as a matter of course cannot function in darkness, and that the actual effect of illumination depends upon the general adaptation of the two systems to the surroundings of the leaf.

Figure 4 represents an attempt to illustrate the last-mentioned point. The ratios between the uptakes of sulphate in light and darkness by *Crassula* leaves show a long-time periodicity, which seems fairly well correlated with the corresponding light conditions of the two mother plants (*cf.* section on plant materials), so that ample illumination tends to increase the relative light uptake and vice versa. This long-time adaptation is evidently not broken by the pretreatment accounted for in table 3. — It should be noted that the autumn of 1958 was very sunny and that in August 1959 the plants had been kept for some time in a greenhouse with painted windows. During the period March—June 1959 several experiments were made, which corroborate the general trend of the curve, although they are not used here since sulphate accumulation was measured at other external concentrations. It is also pertinent to the question at issue that the *Vallisneria* plants when showing a definite inhibitory effect of light on sulphate uptake (Kylin 1957, figure 2) were grown in the winter without artificial illumination, whereas the improved light conditions of the present material are connected with stimulations or slight inhibitions only (figure 3). — With *Chlorella* a consistent increase of sulphate uptake on illumination has been reported by Wedding (1952). Long-time variations were noted by Gessner (1943) in the influence of light on nitrate uptake to *Potamogeton* leaves.

Table 6. The effect of pretreatment with distilled water on the subsequent uptake of radiosulphate by leaf pieces of Crassula

Total S determinations.

Pretreatment	Uptake, µM/g fresh weight/hour	
	Light	Darkness
Nutrient solution	0.047	0.041
Distilled water	0.066	0.065

It was shown by Sol (1958) that the stimulating effect of light upon chloride accumulation in *Vallisneria* leaves, which has always been noted by the Groningen school (*cf.* table 1), is usually diminished during prolonged periods of uptake or if the material is pretreated with different salt solutions instead of with distilled water. Because of this it was thought that the dissimilar behaviour of our materials might be due to general differences between "high salt" and "low salt" plants (*cf.* Kylin 1957), the former being used in the present investigations and the latter by the Dutch workers; this line of reasoning led to the experiment accounted for in table 6. As can be seen, the sulphate uptake by the Crassula leaf pieces was on this occasion stimulated by light (*cf.* figure 4), but the effect was decreased instead of increased by the pretreatment with distilled water. — A general increase in the accumulation was induced both in light and darkness in the "low salt" as compared with the "high salt" tissues; this is in accordance with the results of Sol (1958) and seems to be a phenomenon commonly met with in studies on active ion uptake.

3) **Significance of the chloroplast pigments**

By measuring the action spectrum, van Lookeren Campagne (1957) was able to connect the light effects on chloride uptake in *Vallisneria* with the chlorophyll system. At the same time Simonis & Ehrenberg (1957) showed, however, that effects of illumination upon phosphate uptake could be found also in such objects as barley roots and yeast. Experiments to define more clearly the system responsible for the light effects demonstrated in the present case were thus indicated, and to this end some chlorophyll-free objects were taken for investiga-

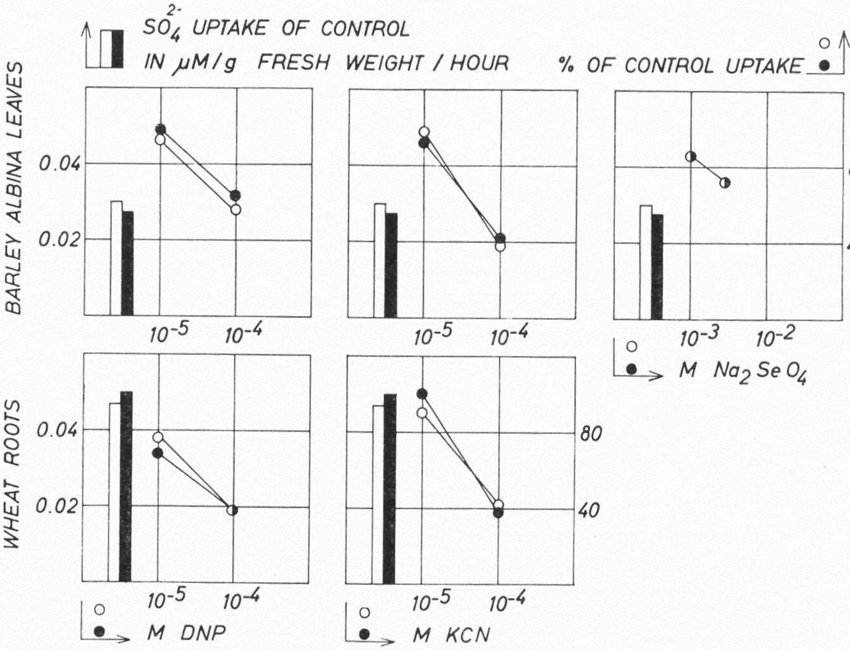


Fig. 5. The effects of DNP, KCN, and Na_2SeO_4 on the uptake of radiosulphate to tissues free from or low in chlorophyll. Total radiosulphur. Symbols and legends as for figure 3.

tion. The results are shown in figure 5, and evidently neither leaves of albina type barley nor wheat roots are affected by light in their sulphate accumulation. It is thus reasonable to consider the influence of light on sulphate accumulation in green tissues as mediated by the pigments of the chloroplasts. — Since Burström & Hejnowicz (1958) have shown that chlorophyll is formed by roots under certain conditions, it should be noted that the present material was free from this substance.

The general increase of permeability, which in many cases has been shown to arise as a consequence of light treatments of chlorophyll-free as well as of green tissues (Lepeschkin 1930, 1940; see also Brauner 1956 for references), need not be discussed here as a possible explanation for the results of figure 3, since the general characteristics of radiosulphate uptake exclude this alternative (*cf.* figures 1 and 2 and the accompanying discussion).

Experiments, part II

As pointed out in the introduction and more fully treated in the general discussion, theoretical considerations seem to indicate two main possibilities of explaining the results accounted for above. The anion respiration according to Lundegårdh (1954 a, 1960) should be inhibited by light in green tissues — i.e. the output of the dark uptake mechanism should diminish — but, on the other hand, this might be compensated for by a mechanism dependent upon cytochrome f, which is oxidized in illuminated chloroplasts (Lundegårdh 1954 b, Sager 1958). On the other hand an ion uptake mechanism dependent upon respiratory high energy phosphates was suggested by Robertson, Wilkins & Weeks (1951), and such a process might conceivably be inhibited by competition over phosphate acceptors in cases where light phosphorylation (Arnon, Allen & Whatley 1956, Whatley, Allen & Arnon 1959) comes into play, in which the latter would also constitute a new possibility for producing the energy necessary for salt accumulation. A number of experiments were performed in order to elucidate these points further. For this work *Crassula* was chosen, since this material shows the most pronounced differences between light and dark uptakes (figure 3) and at the same time is the one most easily handled.

1) Effect of azide

Sodium azide is known to act as an inhibitor of phosphate transfers as well as of heavy metal enzymes (James 1953; *cf.* Kandler 1955 and Stenlid 1949), that is, it combines the characteristics of DNP and KCN. As shown by figure 6 (top row, left), also in the case of azide there is a pronounced difference between the uptakes of sulphate in light and darkness, the former process being considerably less inhibited than the latter. In other experiments even a stimulation by the lowest azide concentration has been obtained in the illuminated tissues. — Kandler (1955) found a similar difference in the action of azide on the uptake of glucose to *Chlorella* in light and darkness.

2) Effects of CMB and arsenite

Two sulfhydryl group inhibitors, p-chloromercuribenzoate (CMB) and arsenite were used, alone as well as in conjunction with glutathione (GSH), which is known to reverse more or less the actions of such

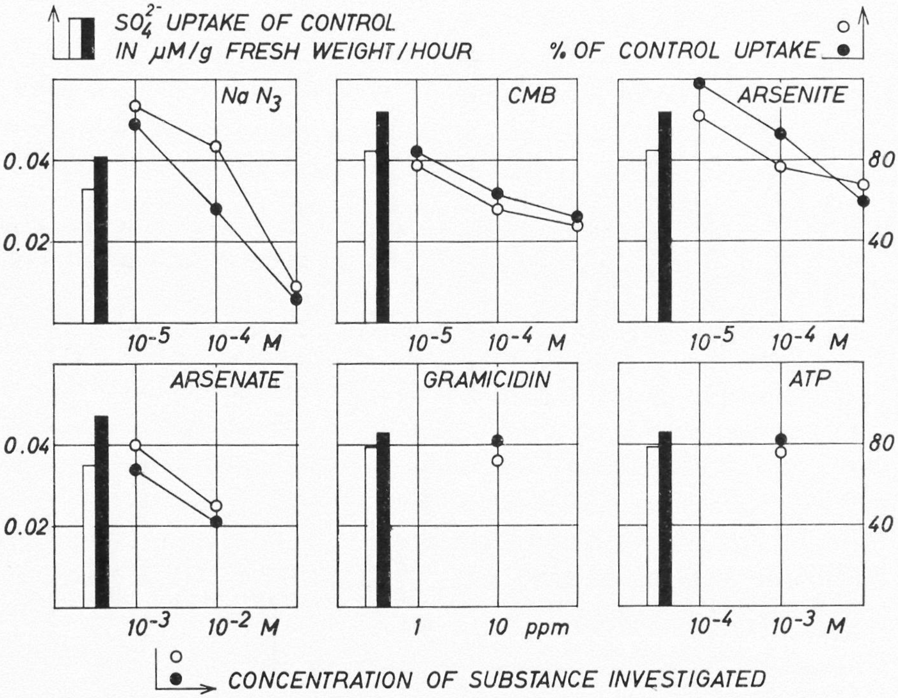


Fig. 6. The effects of different inhibitors and of ATP on the uptake of radiosulphate to leaf pieces of *Crassula*. Total radiosulphur. Symbols and legends as for fig. 3.

poisons. The results are accounted for in figures 6 (top row, middle and right) and 7 (left). As for CMB there is no significant difference between the action in light and in darkness, and in both cases the inhibitor is counteracted by GSH (which in itself is slightly inhibitory both with and without illumination). — The effects of arsenite, on the other hand, are rather different. There may be a difference between light and darkness, but the effects are in such a case reversed at high concentrations of the inhibitor. On the whole fairly high arsenite concentrations seem to be needed in order to obtain depressions of sulphate uptake worth mentioning — *i.e.* the effects may be better regarded as indirect — and these depressions are additive to the inhibitory effect of GSH instead of being reversed by the sulfhydryl compound.

It should be noted that the experiments with CMB had to be performed at a pH of 7.5 due to the solubility characteristics of its sodium salt. In the concentration denoted 10^{-3} *M* an insoluble residue was present in the beakers.

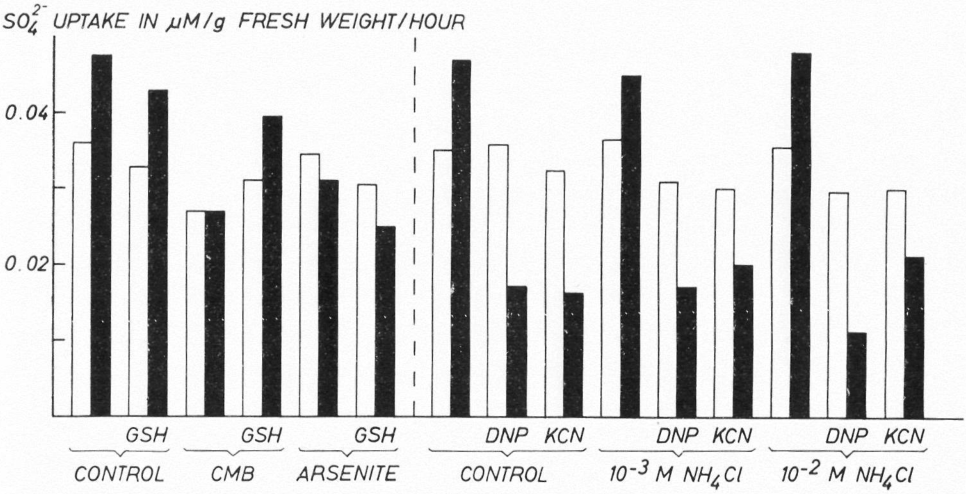


Fig. 7. The effect of GSH on the action of sulfhydryl inhibitors (left) and the effect of NH_4Cl on the action of DNP and KCN (right) in the uptake of radiosulphate to leaf pieces of *Crassula*. Total radiosulphur. — Empty columns: light. Filled columns: darkness. Concentrations used: 10^{-3} *M* GSH, 10^{-4} *M* CMB, 3×10^{-4} *M* $NaAsO_2$, 3×10^{-5} *M* DNP, 10^{-4} *M* KCN.

It is interesting to observe that in the case of CMB a strong inhibition of cyclic photophosphorylation has been reported, whereas arsenite is inactive on this portion of the photosynthetic complex and counteracts only the carbon dioxide fixation of the chloroplasts (Arnon, Allen & Whatley 1956, Whatley, Allen & Arnon 1959). Just as in the present case the action of CMB was completely reversed by GSH also in the investigations by Arnon *et al.*, at the same time as the effect of arsenite on CO_2 fixation could only to a small extent be prevented by added sulfhydryl groups. — Kandler (1955) observed a differential effect of light-darkness in arsenite-inhibited *Chlorella*, uptake of glucose being less affected in illuminated cells; and for CMB Eppley (1958) found no difference between its action on sodium extrusion and potassium accumulation in *Porphyra* fronds with and without light.

3) Effects of arsenate, gramicidin, and ATP

Arsenate was used, because its relation to phosphate makes it an interesting agent in phosphorylation reactions. Since the results accounted for so far must be taken to indicate different systems for sulphate uptake in light and darkness, it was hoped that divergent affinities of different phosphorylating systems possibly concerned might manifest themselves also in the actions of arsenate. The results (figure 6, bottom row, left) do not, however, justify these expectations, since no significant differences could be observed between the inhibitions in light and darkness, but they corroborate in a general way the conclusion that the production of high energy phosphates must, at least partly, be a prerequisite for the uptake of sulphate in illuminated as well as in non-illuminated *Crassula* leaves. — In the paper mentioned before, Kandler (1955) noted that arsenate inhibits the uptake of glucose to *Chlorella* cells to the same extent in light and darkness.

The results with gramicidin and ATP should be mentioned in this connection. It was claimed by Arnon, Allen & Whatley (1956) that gramicidin does not inhibit photosynthetic phosphorylation, although it is active as a poison in the corresponding oxidative mechanism. The substance was, therefore, tried also in the present investigations (figure 6, bottom row, middle), but it gave about the same results as arsenate, *i.e.*, a general inhibition of sulphate uptake with no differential effect of light-darkness. Later it has been reported that gramicidin counteracts also cyclic phosporylation (Whatley, Allen & Arnon 1959). — Since the participation of high energy phosphates in the sulphate uptake seemed to be indicated, ATP was tried (figure 6, bottom row, right). In the concentration used it was, however, slightly inhibitory, and the experiments with the substance were discontinued for the moment, since the conditions for uptake of unchanged ATP are ill-defined.

4) **Effect of ammonium ions**

It has recently been noted that ammonium ions are reversible uncouplers of photophosphorylation *in vitro* (Ohmura 1958, Krogman, Jagendorf & Avron 1959). It was therefore decided to investigate the effect of ammonium chloride on sulphate uptake *in vivo*. Special attention was also given to the effects of DNP and KCN in this connection, since it was thought possible that an inhibition of a "light" mechanism might be concealed by increase of the corresponding "dark" mechanism; this should manifest itself by an increased inhibition brought about by DNP or KCN in the light in the presence of ammonium chloride as compared with the corresponding controls without ammonium ions (*cf.* figure 3 and the accompanying discussion).

The results accounted for in figure 7 (right) show that ammonium chloride did not affect the uptake of sulphate ions significantly either in light or in darkness. There may, however, have been an increased inhibition of DNP in the light under the conditions stated above, although its significance is doubtful. As for cyanide no complications due to the addition of ammonium ions could be noted. — Due to other duties of the author this line of research could not be continued for the time being; the possible interpretation of the results will be discussed later.

Discussion

Already in connection with the experiments two conclusions were indicated which must logically be drawn from the material presented, namely that a) the energy delivering processes leading to sulphate uptake must be different in light and in darkness (figure 3), and that b) the dark mechanism(s) must be inhibited on illumination (figures 3, 4). It is also evident that c) the effects of light are connected with the chloroplast pigments, since illuminated and non-illuminated roots and albina leaves showed no significant differences (figure 5 and commentaries). — It should be noted that the characteristics of the dark mechanism are in accordance with what is known about ion accumulation in roots and storage tissues (Robertson 1958).

A review of the literature (tables 1 and 2) gives at hand that the effects of inhibitors have led to conclusions corresponding to (a) above in the cases of chloride absorption to *Vallisneria spiralis* (van Lookeren Campagne 1957) and of potassium uptake and sodium extrusion in *Ulva* and *Valonia* (Scott & Hayward 1953, 1954, 1955). Since the total light effect almost always has been one of consistent stimulation, it has on the other hand been impossible to reach conclusion (b) earlier. The accumulation mechanisms can, of course, be different for different ion species — Stenlid (1959) for instance, arrived at the conclusion that the conditions for phosphate uptake in roots are different from those regulating chloride and nitrate accumulation, and the present series of papers will partly be concerned with the fact that for sulphate, *i.e.* even for a single ion, more than one incorporation process seems to be active. Since in the present case, however, the different properties of the "light" and "dark" systems can be demonstrated with inhibitors like DNP and KCN but not with selenate (figure 3), which competes directly with sulphate, the reversing effect of light on the dark mechanism should be connected with the delivery of energy for active uptake and thus be of general significance.

Table 1 gives no indication that a consistent increase of total uptake upon illumination should be connected with the ion under investigation, but it may be significant that all investigators recorded there have used aquatic plants (with the sole exception of Mendel & Visser 1951; nitrate uptake). In the present case the ratio between total uptakes in light and darkness seemed to be determined by long-time adaptations connected with the general conditions of illumination (figure 4, and commentaries) and the aquatic *Vallisneria gigantea,* contrary to the other species used, gave the impression of obtaining a high value of this ratio already at fairly moderate light intensities. — The effects of light and darkness on *Crassula* leaf pieces are influenced by the pretreatment (table 6), although not in the same way as described by Sol (1958) for *Vallisneria spiralis,* but such effects can of course also help to explain the different results on the point at issue.

There is no reason to expect the inhibition of the dark uptake of sulphate by illumination to be complete, since respiration is certainly influenced but not abolished by photosynthesis (Brown & Weis, Weis & Brown 1959; Krotkov, Runeckles & Thimann, 1958). It is, of course, impossible to give an exact value of how much of the total uptake in light corresponds to the dark process(es), but in cases where an inhibitor acts differently on accumulation in light and in darkness, and where these inhibitions, especially in the light, are not too big, one might perhaps venture an estimate, making the assumptions that A) the light dependent system(s) for sulphate uptake are not affected at the concentration of inhibitor used, and that B) the action of the inhibitor on the dark system(s) for sulphate uptake is the same in light as in darkness. The following equations can then be developed:

C_L =uptake of control in light
C_D = ,, ,, ,, ,, darkness
I_L = ,, with inhibitor added in light
I_D = ,, ,, ,, ,, ,, darkness
x = ,, due to light uptake mechanism(s) in the control in light
y = ,, ,, ,, dark ,, ,, ,, ,, ,, ,, ,,
r =residual fraction of chemically inhibited dark uptake mechanism

$$x+y=C_L$$
$$x+yr=I_L$$
$$r=\frac{I_D}{C_D}$$

; giving on solution:

$$y=\frac{(C_L-I_L)\ C_D}{(C_D-I_D)}$$

Assumption (B) above is verified by the experiments with chlorophyll-free tissues (figure 5), and the main uncertainty will be connected with assumption (A). The estimate of the activity of the "dark" system(s) in illuminated leaf pieces will be too high if the "light" process(es) are also inhibited, and it will be too low if the latter should happen to be stimulated by the substance added. These two tendencies may well be expected to be working at the same time — that is counteracting each other — notably with the mechanisms to be discussed later from a theoretical point of view.

Some estimates of this kind are recorded in table 7. DNP and KCN have

Table 7. Estimates of the contribution of the dark mechanism(s) to total uptake of sulphate in illuminated leaf pieces

Calculations according to procedure described in text. Radiosulphate determinations for *Vallisneria*, otherwise total S^{35}.

	M inhibitor	Uptake, μM/g fresh weight/hour				Dark component	
		C_L	C_D	I_L	I_D	% of total uptake in light	% inhibition by light
Crassula	KCN 10^{-5}	0.033	0.041	0.031	0.036	50	60
	10^{-4}	,,	,,	0.028	0.024	37	71
	10^{-3}	,,	,,	0.024	0.013	40	68
	KCN 3×10^{-5}	0.034	0.047	0.030	0.025	25	82
	DNP 3×10^{-5}	,,	,,	0.030	0.028	29	79
	KCN 10^{-4}	0.035	0.047	0.032	0.016	13	90
Vallisneria	KCN 10^{-4}	0.0041	0.0035	0.0028	0.0016	58	32
Wheat	KCN 10^{-4}	0.088	0.095	0.058	0.032	51	52
	DNP 10^{-5}	,,	,,	0.080	0.081	62	43
	10^{-4}	,,	,,	0.052	0.042	73	32
	KCN 10^{-4}	0.084	0.077	0.068	0.046	47	48
	DNP 10^{-4}	,,	,,	0.040	0.027	81	12
Barley	KCN 10^{-5}	0.086	0.111	0.084	0.105	43	67
	10^{-4}	,,	,,	0.038	0.023	70	45
	DNP 10^{-5}	,,	,,	0.075	0.090	68	48
	10^{-4}	,,	,,	0.061	0.047	51	61
	KCN 10^{-5}	0.055	0.070	0.051	0.063	73	43
	10^{-4}	,,	,,	0.025	0.020	76	40
	DNP 10^{-4}	,,	,,	0.045	0.036	37	71

been chosen, since they represent the main experiments of the series. Cases showing almost complete inhibitions — *i.e.,* more or less unphysiologic conditions — have been excluded. Cases showing an increased uptake due to the substance added must also be excluded, as no *a priori* assumption, allowing an equation system to be developed, can be made at all. The values indicate that between one and two thirds of the total uptake in light should be due to the dark mechanism(s) — somewhat less in *Crassula argentea* than in the other species — which means that the inhibiting action of light on the latter may have been in the order of 60—90 per cent in *Crassula* and 30—70 per cent in the rest.

The observation that light inhibits the delivery of energy in the dark mechanism(s) for sulphate uptake to green tissues is also of theoretical interest, since there has been a discrepancy between the increasing effects of illumination upon ion uptake observed and the decreasing one predicted by the theory of salt respiration (Burström 1957), according to which the accumulation of ions is dependent upon the direction of the oxygen gradient in relation to the respiratory cytochrome system (Lundegårdh 1954 a, 1960; Robertson 1957, 1958). It is evident that present-day knowledge offers a possibility of explaining the phenomena discussed here in terms of the Lundegårdh theory. The inhibited dark process would then correspond to the action of a reversed oxygen gradient upon the respiratory cytochrome chain, whereas the light uptake would be mediated by chloroplastic cytochrome f, which has been shown to be oxidized in illuminated tissues (Lundegårdh 1954 b, Sager 1958). It is realized that a prerequisite of such a situation is that cytochrome f is not greatly inhibited by cyanide *in vivo,* but no data concerning this point seems to be available at present, and that it is unclear whether the structural relationships will allow such a light uptake to function. — The concept of salt respiration was criticized by Laties (1957), but, on the other hand, Lundegårdh (1960) recently modified his theory.

The possibility that respiratory phosphorylation delivers energy to ion uptake was, moreover, pointed out by Robertson, Wilkins & Weeks (1951) and has both theoretically and experimentally gained support for instance from Laties (1957, 1959 a, b). The results of the present investigation could be explained also in these terms, applying the knowledge of photosynthetic phosphorylation brought forward by Arnon and co-workers (Arnon 1959, Arnon *et. al.* 1956, Whatley *et. al.* 1959) as well as by others. It is now generally accepted that the intensity of respiration is dependent upon the amount of phosphate acceptors available (Laties 1957), and it is thus conceivable that photosynthetic phosphorylation can draw so much ADP and similar substances from a common pool that the respiratory process is inhibited. The energy delivery for sulphate uptake would then shift from the one type of phosphorylation to the other, and the results expected coincide with those presented here. As with the cytochrome mechanism discussed above it is unclear to what extent the structural prerequisites exist — in this case the common pool of ADP for mitochondria and chloroplasts — but the data of figures 3, 6, and 7 (left) are in good accordance with what is known about the action of the inhibitors used on the phosphorylating mechanisms (papers by Arnon *et. al.* cited; *cf.* Kandler 1958, Wessels 1959). — Working with *Vallisneria spiralis,* van Lookeren Campagne (1957) suggested a light phosphorylation mechanism to explain the increase of chloride uptake brought about by illumination. Scott & Hayward (1953, 1954, 1955) worked out an elaborate scheme for the influence of light upon potassium uptake and sodium extrusion in *Ulva* and *Valonia,* in which they discerned one mechanism working through interference with respiratory intermediates and another more direct one; it seems possible to regard their scheme as related to the one presented in this paragraph, although photosynthetic phosphorylation was not known at the time. Also the uptake of cobalt (II)-ions to *Rhodymenia palmata* (R. Scott & Ericson 1954) could easily be interpreted in these terms — especially the inhibition in light brought about by CO_2 should be expected in an uptake dependent upon photosynthetic phosphorylation — although, since they started looking for vitamin B_{12} but did not find it, they discussed the phenomenon as due to formation of an unknown organo-cobalt complex. That the uptake of phosphate itself has been discussed in relation to different types of phosphorylation is a matter of course (table 1).

Turning now to the properties of the sulphate ion, they seem to indicate that both the schemes presented above may theoretically be realized. The salt respiration according to Lundegårdh (1954 a, 1960) must be thought of as a mechanism working on all anions and thus also on sulphate, although the output in different cases is modified by the special characteristics of the ion in question and its carrier; that sulphate can be active in this connection has been shown for instance by Lundegårdh (1960), Miller & Evans (1956), and Sutcliffe (1952), although Handley & Overstreet (1955) did not detect any effects in their material. On the other hand, it has recently become clear that sulphate reacts with ATP to form adenosine-3′-phosphate-5′-phosphosulphate or “active sulphate” (Lipman 1958, Young & Maw 1958). This compound is an important intermediate in the incorporation of sulphur in organic compounds, and it may well be visualized as mediating sulphate accumulation in analogy to the tentative explanation of Stenlid (1959) on the effects of sugars and DNP on phosphate accumulation; it is probable that active sulphate occurs in *Chlorella* during sulphate absorption (Schiff 1959).

It has already been pointed out that the phosphorylating pathway is strongly indicated by the results obtained with inhibitors (DNP, figure 3; CMB and others, figures 6 and 7 left). The results with *Vallisneria* and DNP (figure 3) and with ammonium chloride and *Crassula* (figure 7 right, and commentaries) cannot, however, be explained in these terms without additional hypotheses — for instance that light phosphorylation in Vallisneria is more sensitive to DNP than in other objects and that *in vivo* ammonium ions can only partly reach the photosynthetic phosphorylation sites in *Crassula*. It is then equally possible that the *Vallisneria* results are due to the prevalence of cytochrome-mediated sulphate uptake in this species, where also a high incorporation of sulphate in the organic fractions (Kylin, figures to be published) may tend to leave only minor amounts of adenosine-3′-phosphate-5′-phosphosulphate available for ion accumulation; and that the presence of a cytochrome mechanism side by side with a phosphorylating one is the explanation for the behaviour of *Crassula*. — On the whole, the best working hypothesis for the moment seems to be that within each one of the “light” and “dark” uptakes of sulphate to green tissues at least two different mechanisms of energy delivery are active, which may conceivably be represented by the “cytochrome” and “phosphorylating” systems discussed above, perhaps with possibilities for interactions between them. — Two different mechanisms for the uptake of potassium were noted in yeast (Foulkes 1956), and in barley roots Leggett & Epstein (1956) observed the presence of two different types of carrier sites for sulphate accumulation.

Both the above mechanisms presume some sort of interference between photosynthesis and respiration. Such an interaction has also been observed in several cases (Blinks 1959; Brown & Weis, Weis & Brown 1959; Krotkov, Runeckles & Thimann 1958), but as yet it is not possible to correlate the results with those on sulphate uptake. On the other hand, the interactions demonstrated are so diverse, that in the future it may be possible to explain most of the observations recorded in tables 1 and 2 along the principles outlined above; at present especially those on phosphate uptake to Hydrodictyon (Pirson & Kuhl 1958) and perhaps those on Cs^+ uptake to Rhodymenia (R. Scott 1954) seem to fall outside the general scheme.

Summary

In green tissues from different water and land inhabiting species the uptake in darkness of sulphate to the inorganic fraction resembles what is known about ion accumulation in roots and storage tissues. This uptake type is inhibited by light and at the same time more or less compensated for by another, depending upon the chloroplast pigments. These effects of illumination can theoretically be described either in terms of salt respiration (effects on different cytochrome systems) or of phosphorylation (photosynthetic and respiratory). Many data on the effects of different inhibitors fit well into the latter picture, but effects better correlated with the former also seem to be at hand, and both systems may thus be at work at the same time.

I wish to express my sincere gratitude to Professor H. Burström and Dr. B. Hylmö for their interest and helpful suggestions, to my colleagues of the Botanical Laboratory for friendship and discussions, to Mr. G. Hagman for cultivating the *Vallisneria* and *Crassula* plants, to Mr. G. Holm for the gift of the mutant barley seeds, to Dr. R. Cigén for help with the cryoscopic determinations, to Fil. mag. E. Kylin, and Mrs. A. Ulfstrand for their help in preparing the manuscript, and to Mrs. E. Kylin for making the work possible at all. The work was partly carried out by means of grants from the Fund for Pre-doctoral Research Workers of the Faculty of Mathematics and Science, University of Lund, and from the "Professor Svante Murbeck's Fund" of the Lund Botanical Society, which are gratefully acknowledged.

References

ARISZ, W. H.: Uptake and transport of chlorine by parenchymatic tissue of leaves of Vallisneria spiralis. I, II. — K. Nederl. Akad. Wetenschap. 50: 1019 & 1235. 1947 a, b.

ARNON, D. I.: Conversion of light into chemical energy in photosynthesis. — Nature 184: 10. 1959.

— ALLEN, M. B. & WHATLEY, F. R.: Photosynthesis by isolated chloroplasts. IV. — Biochim. Biophys. Acta 20: 449. 1956.

ARONOFF, S. & CALVIN, M.: Phosphorus turnover and photosynthesis. — Pl. Physiol. 23: 351. 1948.

BARBER, D. A. & NEARY, G. J.: Effect of radiation on salt uptake in plants. — Proc. IInd Int. Conf. of the U.N. on the Peaceful Uses of Atomic Energy 27: 8. 1958 (1959).

BASLAVSKAYA, S. S. & VEBER, G.: The effects of light on phosphate transformations in plants. — Doklady, Bot. Sci. Sect. (Transl.) 124: 19. 1959.

BLINKS, L. R.: Chromatic transients in the photosynthesis of a green alga. — Pl. Physiol. 34: 200. 1959.

Brauner, L.: Die Beeinflussung des Stoffaustausches durch das Licht. — Handb. Pflanzenphysiol. II: 381. 1956.

Briggs, G. E. & Robertson, R. N.: Apparent free space. — Ann. Rev. Pl. Physiol. 8: 11. 1957.

Brown, A. H. & Weis, D.: Relation between respiration and photosynthesis in the green alga Ankistrodesmus Braunii. — Pl. Physiol. 34: 224. 1959.

Butler, G. W.: The connexion between respiration and salt accumulation I. — Physiol. Plantarum 6: 662. 1953.

Burström, H.: Mineralstoffwechsel. — Fortschr. Bot. 19: 221. 1957.

— & Hejnowicz, Z.: The formation of chlorophyll in isolated roots. — Fysiogr. Sällsk. Förh. 28: 65. 1958.

Diamond, J. M. & Solomon, A. K.: Intracellular potassium compartments in Nitella axillaris. — Jour. Gen. Physiol. 42: 1105. 1959.

Eliasson, L.: The effect of glucose and dinitrophenol on the cyanide inhibition of oxygen uptake in wheat root tissue. — Physiol. Plantarum 12: 681. 1959.

Eppley, R. W.: Sodium exclusion and potassium retention by the red marine alga, Porphyra perforata. — Jour. Gen. Physiol. 41: 901. 1958.

Foulkes, E. C.: Cation transport in yeast. — Jour. Gen. Physiol. 39: 687. 1956.

Gelin, O. E. V. & Burström, H.: A study of artificial illumination of greenhouse cultures. — Physiol. Plantarum 2: 70. 1949.

Gessner, F.: Untersuchungen über die Nitrataufnahme der Wasserpflanzen. — Internat. Rev. ges. Hydrobiol. u. Hydrogr. 43: 211. 1943.

Gest, H. & Kamen, M. D.: Studies on the phosphorus metabolism of green algae and purple bacteria in relation to photosynthesis. — Jour. Biol. Chem. 176: 299. 1948.

Grube, K. H.: Über den Zusammenhang von Phosphathaushalt und Photosynthese bei Helodea densa. — Planta 42: 279. 1953.

Handley, R. & Overstreet, R.: Respiration and salt absorption by excised barley roots. — Pl. Physiol. 30: 418. 1955.

Hoagland, D. R. & Davis, A. R.: Further experiments on the absorption of ions by plants, including observations on the effect of light. — Jour. Gen. Physiol. 6: 47. 1924.

— Hibbard, P. L. & Davis, A. R.: The influence of light, temperature and other conditions on the ability of Nitella cells to concentrate halogens in the cell sap. — Jour. Gen. Physiol. 10: 121. 1927.

Ingold, C. T.: The effect of light on the absorption of salts by Elodea canadensis. — New Phytol. 35: 132. 1936.

Jaques, A. G.: The kinetics of penetration. XVI. — Jour. Gen. Physiol. 22: 501. 1939.

— & Osterhout, W. J.: The accumulation of electrolytes. VI. — Jour. Gen. Physiol. 17: 727. 1934.

— — The kinetics of penetration. XI. — Jour. Gen. Physiol. 18: 967. 1935.

James, W. O.: The use of respiratory inhibitors. — Ann. Rev. Pl. Physiol. 4: 59. 1953.

Kandler, O.: Über die Beziehungen zwischen Phosphathaushalt und Photosynthese. III. — Zeitschr. Naturforsch. 10 b: 38. 1955.

— The effect of 2,4-dinitrophenol on respiration, oxydative assimilation, and photosynthesis in Chlorella. — Physiol. Plantarum 11: 675. 1958.

KROGMANN, D. W., JAGENDORF, A. T. & AVRON, M.: Uncouplers of spinach chloroplast photosynthetic phosphorylation. — Pl. Physiol. 34: 272. 1959.

KROTKOV, G., RUNECKLES, V. C. & THIMANN, K. V.: Effect of light on the CO_2 absorption and evolution by Kalanchoë, wheat, and pea leaves. — Pl. Physiol. 33: 289. 1959.

KYLIN, A.: The uptake and metabolism of sulphate by deseeded wheat plants. — Physiol. Plantarum 6: 775. 1953.

— The apparent free space of Vallisneria leaves. — Physiol. Plantarum 10: 732. 1957.

— & HYLMÖ, B.: Uptake and transport of sulphate in wheat. Active and passive components. — Physiol. Plantarum 10: 467. 1957.

LATIES, G. G.: Respiration and cellular work and the regulation of the respiration rate in plants. — Survey Biol. Progress 3: 215. 1957.

— The generation of latent ion-transport capacity. — Proc. Natl. Acad. Sci. U.S. 45: 163. 1959 a.

— Active transport of salt into plant tissue. — Ann. Rev. Pl. Physiol. 10: 87. 1959 b.

LEGGETT, J. E. & EPSTEIN, E.: Kinetics of sulphate absorption by barley roots. — Pl. Physiol. 31: 222. 1956.

LEPESCHKIN, W. W.: Light and the permeability of protoplasm. — Amer. Jour. Bot. 17: 953. 1930.

— Einfluss des Lichtes auf Exosmose und Speicherung von Salzen in Kartoffelknollengewebe. — Protoplasma 34: 55. 1940.

LIPMAN, F.: Biological sulphate activation and transfer. — Science 128: 575. 1958.

LOWENHAUPT, B.: Active cation transport in submerged aquatic plants. I, II. — Jour. Cell. and Comp. Physiol. 51: 199 & 208. 1958.

LUNDEGÅRDH, H.: Anion respiration. — Symposia Soc. Exptl. Biol. 8: 262. 1954 a.

— On the oxidation of cytochrome f by light. — Physiol. Plantarum 7: 375. 1954 b.

— Salts and respiration. — Nature 185: 70. 1960.

MC ROBBIE, E. A. C. & DAINTY, J.: Sodium and potassium distribution and transport in the seaweed Rhodymenia palmata (L.) Grev. — Physiol. Plantarum 11: 782. 1958.

MENDEL, J. L. & VISSER, D. W.: Studies on nitrate reduction in higher plants. I. — Arch. Biochem. and Biophys. 32: 158. 1951.

MILLER, G. W. & EVANS, H. J.: The influence of salts on the activity of particulate cytochrome oxidase from roots of higher plants. — Pl. Physiol. 31: 357. 1956.

OHMURA, T.: Photophosphorylation by chloroplasts. — Jour. Biochem. (Tokyo) 45: 319. 1958.

PIRSON, A. & KUHL, A.: Über den Phosphathaushalt von Hydrodictyon I. — Arch. Mikrobiol. 30: 211. 1958.

ROBERTSON, R. N.: Electrolytes in plant tissue. — Endeavour 16: 193. 1957.

— The uptake of minerals. — Handb. Pflanzenphysiol. IV: 243. 1958.

— WILKINS, M. J. & WEEKS, D. C.: Studies in the metabolism of plant cells. IX. — Australian. Jour. Scient. Res. Ser. B 4: 248. 1951.

RUTTNER, F.: Zur Frage der Karbonatassimilation des Wasserpflanzen. II. — Österreich. Bot. Zeitschr. 95: 208. 1948.

SAGER, R.: The architecture of the chloroplast in relation to its photosynthetic activities. — Brookhaven Symposia in Biol. 11: 101. 1958 (1959).

SCHIFF, J. A.: Studies on sulphate utilization by Chlorella pyrenoidosa using sulphate S^{35}; the occurrence of S-adenosyl methionine. — Pl. Physiol. 34: 73. 1959.

SCOTT, G. T. & HAYWARD, H. R.: Metabolic factors influencing the sodium and potassium distribution in Ulva lactuca. — Jour. Gen. Physiol. 36: 659. 1953.

— — Evidence for the presence of separate mechanisms regulating potassium and sodium distribution in Ulva lactuca. — Jour. Gen. Physiol. 37: 601. 1954.

— — Sodium and potassium regulation in Ulva lactuca and Valonia macrophysa. — SHANES, A. M., ed.: Electrolytes in Biological Systems p. 35. Amer. Physiol. Soc., Washington 1955.

SCOTT, R.: A study of caesium accumulation by marine algae. — JOHNSTON, J. E., ed.: Proc. 2nd Radioisotope Conf. Oxford I: 373. Butterworth's, London 1954.

— & ERICSON, L.-E.: Some aspects of cobalt metabolism by Rhodymenia palmata with particular reference to vitamin B_{12} content. — Jour. Exptl. Bot. 6: 348. 1955.

SHRIFT, A.: Biological activities of selenium compounds. — Bot. Rev. 24: 550. 1958.

SIMONIS, W. & EHRENBERG, M.: Untersuchungen zur lichtabhängigen Phosphorylierung II. — Zeitschr. Naturforsch. 12 b: 156. 1957.

— & GRUBE, K.-H.: Untersuchungen über den Zusammenhang zwischen Phosphathaushalt und Photosynthese. — Zeitschr. Naturforsch. 7 b: 194. 1952.

— & KATING, H.: Untersuchungen zur lichtabhängigen Phosphorylierung I & III. — Zeitschr. Naturforsch. 11 b: 165 & 704. 1956 a, b.

SOL, H. H.: Pretreatment and chloride uptake in Vallisneria leaves. — Acta Bot. Neerlandica 7: 131. 1958.

STEEMANN NIELSEN, E.: Passive and active ion transport during photosynthesis in water plants. — Physiol. Plantarum 4: 189. 1951.

STENLID, G.: Some notes on the effect of sodium azide, 2,4-dinitrophenol, and orthophenanthroline upon oxygen consumption in green leaves. — Physiol. Plantarum 2: 61. 1949.

— Salt losses and redistribution of salts in higher plants. — Handb. Pflanzenphysiol. IV: 615. 1958.

— On the effect of some sugars and of 2,4-dinitrophenol upon the absorption of phosphate ions by excised roots. — Physiol. Plantarum 12: 199. 1959.

SUTCLIFFE, J. F.: The influence of internal ion concentration on potassium accumulation and salt respiration of red beet root tissue. — Jour. Exptl. Bot. 3: 59. 1952.

TAMM, C. O.: The mineral sources of plants. C) The atmosphere. — Handb. Pflanzenphysiol. IV: 233. 1958.

VAN LOOKEREN CAMPAGNE, R. N.: Light-dependent chloride absorption in Vallisneria leaves. — Acta Bot. Neerlandica 6: 543. 1957.

VIRGIN, H. I.: Stomatal transpiration of some variegated plants and of chlorophylldeficient mutants of barley. — Physiol. Plantarum 10: 170. 1957.

WEDDING, R. T.: Sulphate uptake and active sulphate in Chlorella. — Pl. Physiol. 34 suppl.: XX. 1959.

WEIER, T. E.: The cytology of leaf homogenates. — Protoplasma 42: 260. 1953.

WEIS, D. & BROWN, A. H.: Kinetic relationships between photosynthesis and respiration in the algal flagellate Ochromonas Malhamensis. — Pl. Physiol. 34: 235. 1959.

WESSELS, J. S. C.: Dinitrophenol as a catalyst of photosynthetic phosphorylation. — Biochim. Biophys. Acta 36: 264. 1959.

WHALEY, W. G., MOLLENHAUER, H. H. & KEPHART, J. E.: The endoplasmic reticulum and the Golgi structures in maize root cells. — Jour. Biophys. and Biochem. Cytol. 5: 501. 1959.

WHATLEY, F. R., ALLEN, M. B. & ARNON, D. I.: Photosynthesis by isolated chloroplasts. — Biochim. Biophys. Acta 32: 32. 1959.

WINTERMANS, J. F. G. M.: Polyphosphate formation in Chlorella in relation to photosynthesis. — Mededel. Landbouwhoogesch. Wageningen 55: 69. 1955.

WITHROW, R. B.: Light as a modifying influence on the mineral nutrition of plants. — TRUOG, E., ed.: Mineral Nutrition of Plants, p. 389. Univ. of Wisconsin Press. 1951.

WITTWER, S. H. & TEUBNER, F. G.: Foliar absorption of mineral nutrients. — Ann. Rev. Pl. Physiol. 10: 13. 1959.

YOUNG, L. & MAW, G. A.: The metabolism of sulphur compounds. — Methuen's Monographs on Biochem. Subjects, London 1958.

BOTANISKA NOTISER 1960 · VOL. 113 · FASC. 1 · LUND

Experiments with Cereal Rusts on Detached Leaves in Benzimidazole

By INGVAR BJÖRKMAN

Swedish State Plant Protection Institute

When working with obligate parasites, such as rust fungi, one is often faced with intricate problems arising from the interaction between parasite and host as well as from environmental factors and their influence. To ensure fully comparable results from different series of experiments one would need a constant environment or at least a reasonable limit to the changes in environmental conditions. Unfortunately, this is not possible in an ordinary greenhouse. For example, it is impossible to prevent all solar radiation, which, of course, brings about changes in light intensity, temperature, and relative humidity. In addition, it is difficult to prevent spores from being transported from one culture to another, thereby causing contaminations, especially during the hot season when the greenhouse must be aired.

In the spring of 1959, as an attempt to master these problems, a new method was tried in the laboratory of the Swedish State Plant Protection Institute at Svalöv. The fundamental idea of this method is to grow rust fungi on leaves detached from the host in a solution of benzimidazole. It was Dr. J. Mac Key, of Svalöv, who suggested the use of this substance; he had personally studied some of the experiments with stem rust of wheat [*Puccinia graminis* (Pers.) f.sp. *tritici* (Erikss. & Henn.)] and leaf rust of wheat (*P. triticina* Erikss.) made by Samborski, Forsyth, and Person. They have proved (1958) that the protein breakdown that sets in as soon as a wheat leaf is detached is interrupted if the leaf is floated on the surface of benzimidazole or if part of it is submerged in benzimidazole of a suitable concentration. The amino acids formed in connection with the protein breakdown are of vital importance for the rust reactions that ensue. It is therefore important to find the benzimidazole concentration that provides the proportions of protein and amino acids most in accordance with those of the leaf in the natural condition. If the concentration is low, there is an increase in amino acids and, at the same time, a decrease in rust resistance; if the concentration is high, the conditions are the reverse.

In the recently carried out experiments with the method the concentrations of benzimidazole in distilled water employed varied from 0 to 120 p.p.m. The experiments were made in 9-cm petri dishes, partly with the leaves floating on the solution (20 ml) in horizontal dishes, partly with the lower part of the leaves submerged in the solution (10 ml) in tilted dishes. In the latter case the leaves lay on a glass-rod placed in the middle of the dish, and they were pressed down into the liquid by means of a smaller glass-rod placed across the lower portion of the leaves (Figure 1). The dishes were tilted at an angle of about 15°. Artificial light (fluorescent lamps of about 3,000 luxes) was used for about 14 hours a day, the temperature varying from 19° to 25°C. A more constant temperature would have been desirable, but the laboratory conditions did not permit this.

The primary leaf of wheat and oats was used. The waxy coating was removed, and, after they had been put in their respective dishes, the leaves were sprayed with a little water. The spores were scattered over the leaves by means of a hair brush, and then the dishes were immediately closed. Thus, after the inoculation the isolation was complete. After 9 or 10 days it was possible to determine the infection types or to increase the amount of spores.

Successful experiments in which a wetting agent was used to make the removal of the wax coating superfluous had already been made in connection with cultivation of fungi on plants with normal growth (Björkman 1959). But when the method described was applied to those experiments, the results were negative, probably because closed dishes had had to be used.

In the identification of races only one leaf of each differential variety was used as a rule and each determination was made twice or several times. For the sake of control, parallel identification of races was carried out on plants growing normally in greenhouses.

Examinations of stem and leaf rust of wheat, stem rust of oats [*Puccinia graminis avenae* (Pers.) Erikss. & Henn.] and crown rust of oats [*P. coronata avenae* (Corda) Erikss. & Henn.] were made according to the benzimidazole method. Most of the experiments were made with

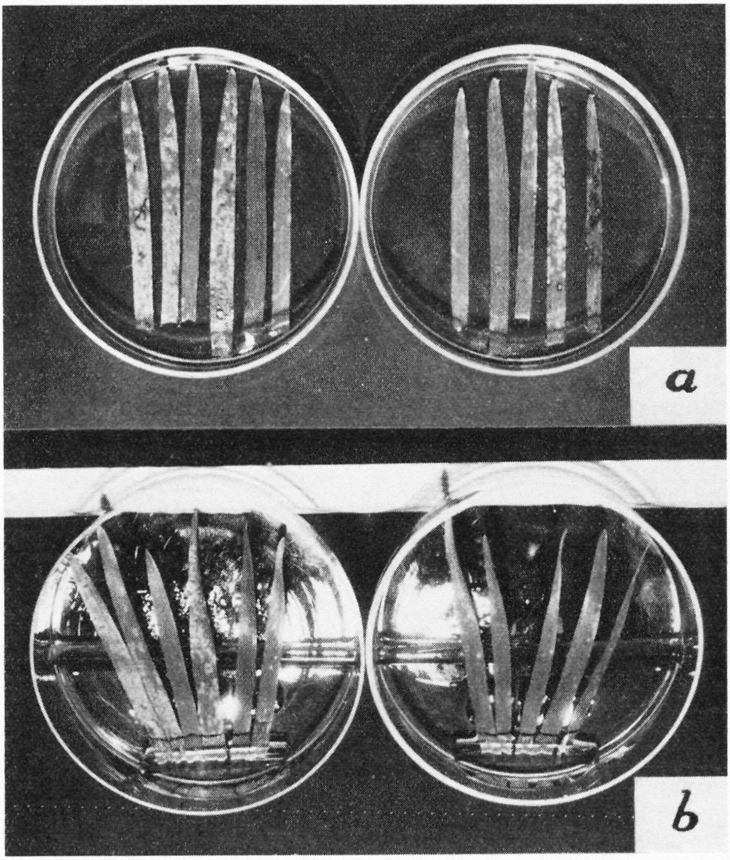


Fig. 1 a and b. Differentials for crown rust races in benzimidazole. Race 237. Varieties (from left to right): Seger I (susceptible control variety), Anthony, Victoria, Appler, Bond, Landhafer, Santa Fe, Ukraine, Trispernia, Bondvic, and Saia. — a. horizontal dishes. b. tilted dishes.

crown rust of oats, and therefore the results and conclusions accounted for below refer without exception to this species.

The concentration of 40 p.p.m. of benzimidazole turned out to be the most suitable in horizontal dishes and 60 p.p.m. in tilted ones. Ten races of crown rust were examined, namely, 212, 226, 228, 229, 230, 235, 237, 239, 240, and 284. At first certain difficulties arose in the differentiation of the infection types. Just as practice is needed to identify types on oat-plants that grow normally, experience itself will, after some time's comparative work, be the decisive factor when this method is

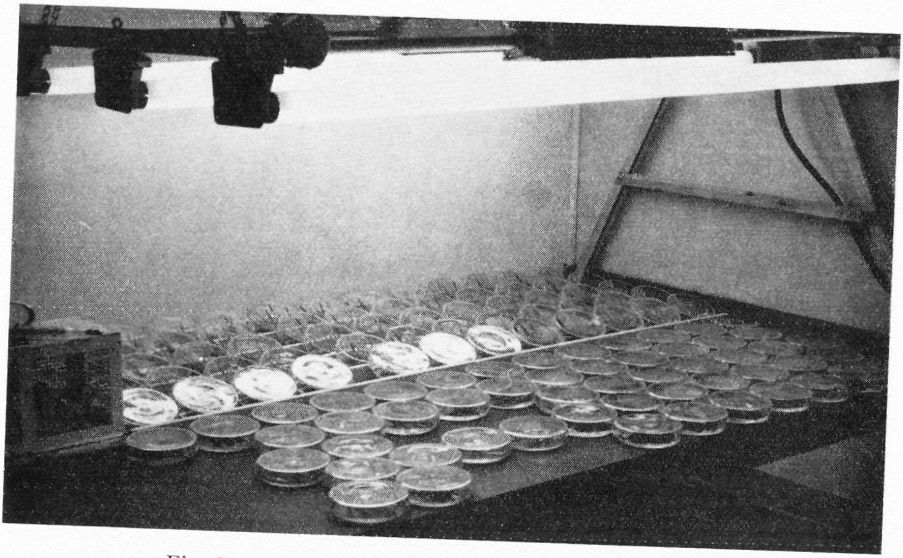


Fig. 2. Arrangements for benzimidazole experiments.

applied. Certain differentials, such as Anthony and Appler, sometimes showed a tendency to chlorosis at an early stage, which rendered the identification more difficult. But the same tendency is also often noticeable in greenhouses. In order to examine the influence of benzimidazole on uninfected leaves, controls were made with such leaves in each of the concentrations. Slight discoloration was sometimes noticeable, but it was never so marked as to cause confusion with rust infection.

On the whole, the infection types appeared rather more clearly on the leaves in the tilted dishes than on the floating leaves, partly because the liquid moistened the new spores on the latter. This is also the reason why, when spores are to be cultured according to this method, tilted dishes should be used to ensure successfull collection of dry spores.

The method involves certain disadvantages. Thus, differential varieties seem to respond somewhat differently from what is usually the case in greenhouses. But those differences are so unimportant that they will be compensated for by practice in identification of infection types and the experience gained by making parallel experiments in greenhouses. The method may also involve a little more work in the inoculation. However, these disadvantages are offset by the fact that there is hardly any need for watering and care in greenhouses.

The benzimidazole method has proved to have several obvious advantages. Environmental conditions can be kept almost constant. Less space is needed than when races are identified in greenhouses. Moreover, 3 or 4 days are saved in each generation of the fungi. One of its chief advantages is, perhaps, that the method facilitates satisfactory isolation. Thus the method is very suitable for cultivation of fungi. This holds good especially for single-spore isolates. Some experiments of the kind have been made with good results.

Literature Cited

BJÖRKMAN, I. 1959. Fysiologiska raser av stråsädesrost i Sverige 1958. — Bot. Not. 112: 433—440.

SAMBORSKI, D. J., FORSYTH, F. R. & PERSON, C. 1958. Metabolic changes in detached wheat leaves floated on benzimidazole and the effect of these changes on rust reaction. — Can. Journ. Botany 36: 591—601.

BOTANISKA NOTISER 1960 · VOL. 113 · FASC. 1 · LUND

Some Ecologic Studies on Lakes and Brooks in the South Swedish Uplands

By NILS MALMER
Laboratory of Plant Ecology, Botanical Museum of the University, Lund

(Meddelande från Lunds Botaniska Museum, Nr 140)

Introduction

The south Swedish oligotrophic area has been studied for a long time by several limnologists. Naumann founded the Limnological Laboratory at Aneboda and worked out several fundamental studies (e.g. 1917, 1921 b, 1922, 1932). Thunmark has among other things treated the regional limnology of this area (e.g. 1937, 1942, 1945 a, 1945 b). Several authors have published monographs of lakes (e.g. Blomgren & Naumann 1925; Thunmark 1931; Lillieroth 1938, 1950) or have dealt with special problems (e.g. Åberg & Rodhe 1942; Thunmark 1945 a; Lillieroth 1950).

During my studies on the mire vegetation of the southwestern part of this area I have made several chemical analyses of mire water including both cations and anions. It has, however, proved impossible to get any comparable values of lakes and rivers within this area from other authors. The results of my analyses also deviate in several respects from the values given by Lohammar (1938) for similar lakes in Dalarna and Norrland. In order to obtain such comparable values for water on mineral soil within this district, I have sampled about 15 localities in the vicinity of the Åkhult mire at Aneboda, where I have made most of my studies on the mire vegetation. Together with some of these samples I have also sampled the bottom substratum and treated it in the same manner as I have done with the mire peat in order to find out the possibilities of such investigations in ecologic studies of the higher vegetation of lakes and rivers. In this paper will mainly be discussed the results of the analyses of the sampling sites in the lakes and the brooks.

Acknowledgements. The work has been carried out in the Laboratory of Plant Ecology in the Botanical Museum of Lund University (head of the institutes Professor H. Weimarck and Laborator S. Waldheim). During the field work space was kindly placed at my disposal in the laboratories of the Södra Sveriges Fiskeriförening in Aneboda by the director fil. lic. Bruno Berzinš. The investigation was financed through grants from Lund University. For valuable assistance in the samplings and at Aneboda I wish to thank Messrs. G. Ahrne, F. Andersson and L. Eurenius. Mrs. Mimmi Varga has given technical assistance in the laboratory work.

Methods

Sampling was made during three periods, viz., 12—13 November 1957, 5—14 August 1958 and 6—13 August 1959. During the first period the water temperature was about +1°—+2°C. In the mornings a thin sheet of ice covered the lakes along the shores and the pools. The water level in the lakes was rather high. Somewhat more rain than normal had fallen during the period just before. Also during the second sampling period the wheather was rainier than normal. The temperature of the water was about 18°C. During the third period the weather was very hot and dry and the water level in the lakes extremely low.

Water. The samples were taken at the surface of the water and kept in plastic bottles, each containing 0.5 l.

pH was determined electrometrically using a glass electrode. The standard deviation calculated according to Hald (1948, p. 244) from measurements on duplicated samples is ±0.03 pH-units ($n=33$). The measuring was always carried out on the same afternoon.

Specific conductivity was measured at the same time as the pH with a Wheatstone bridge using bright platinum electrodes with a cell constant of 0.242. The values given are all calculated at 20°C and the conductivity due to the hydrogen ions is subtracted (cf. Sjörs 1948, 1952). These final reduced values multiplied by 10^6 and designated $\varkappa_{red}$ are given in the text and the tables. The values cited from other authors are treated in the same manner. — The standard deviation in $\varkappa_{red}$ calculated as above is ±0.9.

Sodium and potassium were determined in a part of the samples, which were filtered, evaporated to dryness and then treated with a few drops of HNO_3+HClO_4 (4 : 1) in order to destroy all organic matter. The residue was dissolved in diluted HCl. Then Na and K were determined with a flame photometer from Kipp and Zonen (type H 45 with interference filter and "gasol"-air flame connected with a galvanometer type A 75 Pb with a sensitivity of $3 \cdot 10^{-10}$ A/mm). The standard deviation may be estimated to about ±0.005 mmol/l for Na and to about ±0.001 mmol/l for K.

Magnesium and calcium were determined titrimetrically with versenate in the same part of the samples using methods described by Schwarzenbach (1957). In the determination of Ca calcon (eriochrome blue black R) was used as the indicator instead of murexid.

Iron was determined with orthophenanthroline in the evaporated part of the samples.

Aluminium was determined colorimetrically with eriochrome cyanine R. A. using a method described by Jones & Turman (1957). Addition of sodium thioglycolate and ferrous ammonium sulphate was made in order to compensate for the interference of iron.

Chloride was determined titrimetrically with 0.02- or 0.05-N $AgNO_3$ using potassium chromate as the indicator according to Maucha (1932). A correction corresponding to his "Verbesserungswert" is subtracted. Duplicates were always run. The standard deviation calculated from the differences is ± 0.013 mmol/l.

Alkalinity was determined with 0.01-N HCl using mixed bromcresol green—methyl red as the indicator. After subtraction of 0.060 meq/l (cf. Ruttner 1931, p. 208; Åberg & Rodhe 1942, p. 92) the results are calculated as bicarbonate. These figures are, of course, very uncertain. The correction often amounts to about 50 % or more of the total alkalinity. It is also possible that not only HCO_3^- but also other weak acids, e.g., humic acids, take part in the reaction.

Sulphate was determined gravimetrically as $BaSO_4$. Before the precipitation pH was adjusted to about 4.5 with NH_4Cl. In 1957 the original samples were used, but in the waters most rich in iron Fe-humate was precipitated together with $BaSO_4$ and these analyses were spoilt. For that reason the evaporated part of the samples was used in 1958.

Silicon was determined colorimetrically in the original samples as blue silicomolybdate complex according to Jörgensen (1953). Amino-naphtholsulphonic acid was used as the reduction reagent.

Phosphorus was determined colorimetrically in the evaporated part of the samples with ammonium molybdate using $SnCl_2$ as the reduction reagent. The solution was treated with acids according to Tamm (1953, p. 14). Cf. Malmer & Sjörs, 1955.

Potassium permanganate consumption was determined on an unfiltered part of the original sample in acid solution in the usual way.

Water colour was determined in a Hellige comparator with 30 cm tubes.

In table 1 are calculated the total number of cations and the total number of anions. The former is the sum of equivalents of Na^+, K^+, Mg^{2+} and Ca^{2+} (major cation constituents according to Rodhe 1949) together with H^+. The latter is made up in the same manner by Cl^-, HCO_3^- and SO_4^{2-} (major anion constituents). From the ionic determinations also a value of $\varkappa_{red}$ is calculated (designated "calculated $\varkappa_{red}$"). The following values of the ionic conductivities are then used: Na^+ 45.1, K^+ 66.3, Mg^{2+} 96.2, Ca^{2+} 108, Cl^- 68.5, HCO_3^- 40.4 and SO_4^{2-} 145.

Bottom substratum. The samples (volume 450 cm^3) consisted of the substratum between about 3—15 cm below the surface of the bottom.

Dry matter was determined by drying at 100°—110°C and loss of ignition by ashing in a muffle furmace at 550°C.

Nitrogen. The values refer to the total contents determined by the micro-Kjeldahl procedure.

pH was determined with a glass electrode directly inserted into the samples except in the samples nos. 51—59 from 1957. In these cases the fresh samples were shaken with the same volume of distilled water and the pH determined in the supernatant water. Thus unfortunately the determinations in these samples are not quite comparable with those from 1959.

Redox potential. In the samples from 1959 the redox potential was determined with a Beckmann pH-meter, model N-2, equipped with a bright platinum electrode and a reference electrode. The electrodes were directly inserted into the samples. The readings on the pH-scale converted to mV are designated E_h and give the redox potential at the actual pH. In order to make the E_h-values at different pH comparable, the corresponding rH-values are calculated according to the formula

$$rH = \frac{E_h}{k} + 2\ pH$$

where k is a constant, which is proportional to the temperature at the measuring in degrees Kelvin. At 20°C k has the value 29.1. It seems more suitable to use the rH-values than to reduce the E_h to a certain pH-value, e.g., like Pearsall (1938) to pH=5 or Mortimer (1941) to pH=7. A more thorough discussion of this subject is given by Pearsall (1938) and Flaig, Scharrer & Judel (1955). — This method has been worked out together with fil. lic. Åke Persson.

During the summer of 1959 I made several determinations of the redox potential in peat from different sites together with the determinations discussed here. On every sample three different measurements were made. The standard deviation in E_h calculated from these readings is ± 18 mV (n=244). Together with the standard deviation of the peat-pH (± 0.13) these values give a standard deviation of ± 0.9 in rH.

Exchangeable ions were extracted from the fresh samples with normal acetic acid (abbrev. Ac) and normal ammonium acetate (abbrev. Am) with the same methods as I have used on peat samples (Malmer & Sjörs 1955). Thus the change in pH in the Ac and Am solutions respectively gives the sum of exchangeable metallic cations and exchangeable hydrogen ions. The exchange capacity for cations is calculated from the sum of exchangeable cations. The degree of neutralization gives the exchangeable metallic cations as percentage of exchange capacity.

For the further analyses the solutions were treated in the same manner as the water samples. The methods for the determinations of the separate ions were also the same. Cf. also Malmer & Sjörs, op.c. The standard deviation in the flame photometric determinations of Na and K may be estimated to about ± 0.05 and ± 0.03 mmol/1000 g fresh weight respectively. Contamination of Na through leaching from the glass may sometimes occur in Am-solutions but not in the Ac-solutions. When Fe in the Ac-extractions exceeded 5 mmol/1000 g fresh weight it was determined titrimetrically with versenate according to Schwarzenbach (1957) using thiosalicylic acid as the indicator.

During the determinations of exchangeable ions with these methods that fraction which is dissolved in the water is also measured. It is, however, evident from the results that among the elements studied only Na is dissolved in the water to more than a few percent of the adsorbed amounts (cf. table 4).

The nomenclature of vascular plants follows Hylander 1955. *Sphagna* are named according to Waldheim 1944 and most other mosses according to Jensen 1939. For terminology of lakes, especially the vegetation zones see, e.g., Thunmark (1931, p. 29 ff) or Lillieroth (1950, p. 14 ff) and the literature quoted there. For terminology of the mires and their subdivisions reference is made to Du Rietz (e.g. 1949, 1954) and to Sjörs (1948, 1952).

Sampling area

The sampling area is situated in Kronobergs län, Aneboda and Moheda parishes (fig. 1 and fig. 2). It belongs to the river system of Mörrumsån, but is close to the watershed of the river Lagan. This southernmost part of the South Swedish uplands lies about 210 m above sea-level and far above the highest postglacial marine shore line. The bedrock is of archæan origin and like the glacial deposits derived from it very poor in lime and phosphorus. The mean annual precipitation is about 725 mm with a maximum in July—October (about 80 mm/month) and minimum in the spring (about 40 mm/month). The characterizing vegetation is coniferous forest on podsolic soil with *Vaccinium myrtillus* dominating in the field layer and *Hylocomium splendens*+*Pleurozium schreberi* in the bottom layer. The fen vegetation is mostly of the extremely poor fen type, more seldom of the moderately poor fen type. Rich fen vegetation has not been found. The cultivated part of the area is rather restricted. For further notes see, e.g., Thunmark 1931, p. 1—7.

All unpolluted lakes within this area have a decidedly oligotrophic character. The amount of humus in the water varies considerably between the different lakes depending on their situation, the character of the precipitation area and the shores. The organogenic bottom sediments in the lakes treated here are made up of different types of mud, mostly detritus gyttja. Different kinds of iron deposits occur nearly always, but in varying quantities (Naumann 1921 a, 1922; Thunmark 1937). — The sampling sites represent three lakes, viz., Fiolen, Förhultsjön and Stråken, one brook, viz., Fiolenbäcken, which flows from lake Fiolen to lake Stråken and one well.

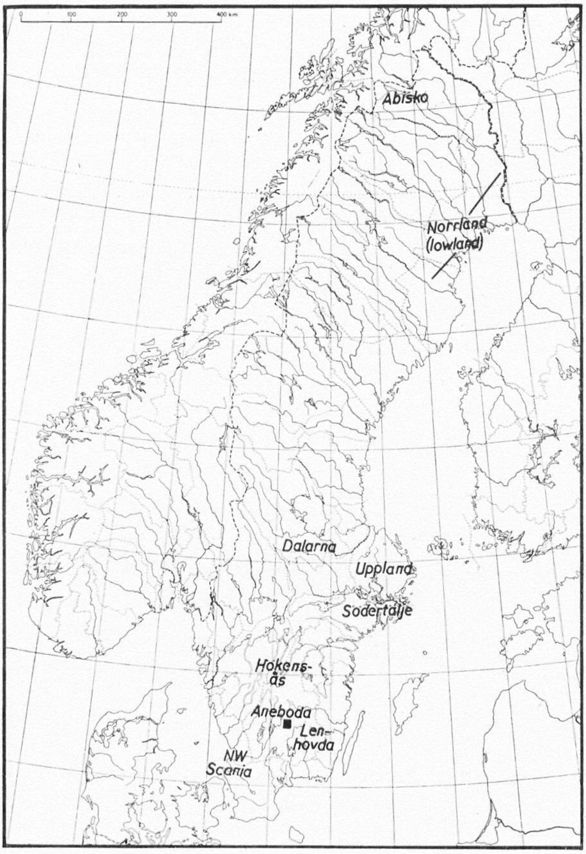


Fig. 1. The situation of the sampling area at Aneboda together with some other regions discussed in table 2.

Lake Fiolen. Thunmark (1931) gives a very comprehensive description of the lake and its vegetation. Åberg & Rodhe (1942, p. 156) give several chemical analyses of water from the lake including most of the analyses made by previous investigators. The area of the lake amounts to 1.6 km^2 and the greatest depth to 10 m. The precipitation area is 7.6 km^2. The low water level is regulated at the outlet and is about 0.5 m below the high water level. The flow of water to the lake from mires and arable land is very restricted. The shores are everywhere composed of moraine or rocks. The summer transparency is usually about 5.0—5.5 m and the lake colour yellow-green (Thunmark 1931, 1937; Åberg & Rodhe, op.c., p. 128; Cronholm 1946) indicating a water poor in humus.

Site 51 is situated in the sublitoral zone of a sheltered bay ("Söregårdsviken") in the southernmost part of the lake (fig. 3). Influence of man is restricted to watering of cattle. One of the few small brooklets to the lake discharges its water into this bay. Sampling depth about 1 m beneath the high water level. The bottom consists of grey-black mud, intermingled with sand

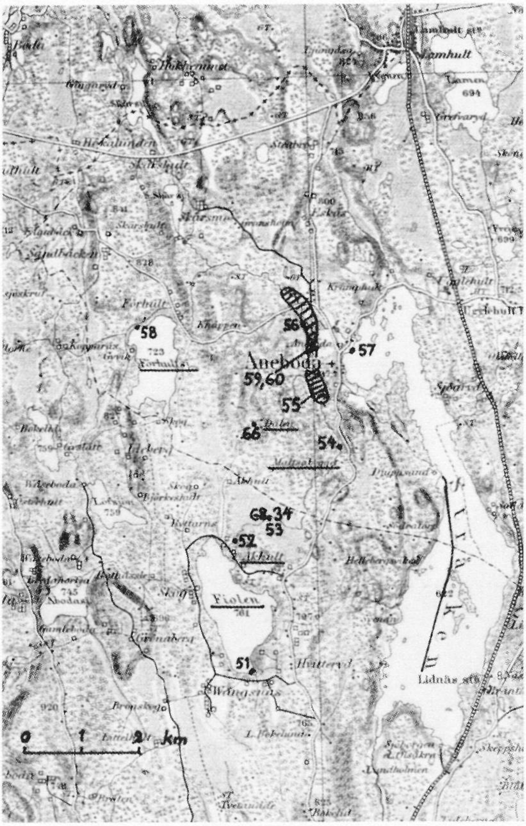


Fig. 2. Part of the topographical map-sheet no. 20 Växjö with the situation of the sampling sites and the fishpond area at Aneboda indicated. — Scale c. 1 : 130 000. (För spridning godkänd i Rikets Allmänna Kartverk den 2 mars 1960.)

and some small stones. The vegetation at the sampling site (plot area 100 m^2) was dominated by *Lobelia dortmanna* which grew together with *Juncus bulbosus*; *Isoëtes lacustris, Littorella uniflora, Subularia aquatica, Drepanocladus fluitans* and *Fontinalis antipyretica*. Around the sampling site there were small reeds of *Equisetum fluviatile* and of *Carex rostrata* with *C. lasiocarpa* intermingled. In the sublitoral zone also the following species were listed: *Alisma plantago-aquatica, Calla palustris, Glyceria fluitans*; *Nuphar luteum, Nymphaea alba, Potamogeton natans, Sparganium friesii*; *Myriophyllum alterniflorum*; *Isoëtes echinospora* and *Ranunculus flammula* v. *reptans*. There is no typical eulitoral zone at this site. For a description of the vegetation of this zone in other parts of the lake the reader is referred to Thunmark 1931, p. 64 f.

Lake Förhultsjön is smaller (area about 1 km^2) and shallower (greatest depth 7.5 m) than lake Fiolen. The precipitation area, which amounts to about 14 km^2, includes several mires and two smaller lakes but little arable land. The water level is regulated, and the differences between high and low water may be about 0.8—1.0 m. The shores are everywhere composed of moraine. Summer transparency may be about 2.5 m and the lake colour brown (Lönnerblad 1931, Gessner 1934) indicating a water rather rich in humus.

Site 58 is situated in the sublitoral zone of a moderately exposed bay in the northwestern part of the lake. A ditch from some small fields discharges its water into this bay. That is the only influence by man on this site worth mentioning. Water depth 1 m beneath the high water level. The bottom is minerogenous, largely composed of brown-coloured gravel. The vegetation at the sampling site (plot area 100 m^2) was dominated by *Lobelia dortmanna*, which grew together with *Scirpus palustris*; *Juncus bulbosus*; *Littorella uniflora, Ranunculus flammula* v. *reptans* and *Subularia aquatica*. Around the sampling site also the following species were listed: *Carex rostrata, Equisetum fluviatile, Glyceria fluitans, Menyanthes trifoliata*; *Nuphar luteum* and *Potamogeton natans*. From the adjacent eulitoral zone the following species may be mentioned: *Circium palustre, Drosera intermedia, Lycopodium inundatum, Lycopus europaeus, Lysimachia thyrsiflora, Potentilla erecta, P. palustris, Ranunculus flammula* v. *reptans, Scutellaria galericulata, Sparganium minimum, Veronica scutellata, Viola palustris, Agrostis canina, Carex echinata, C. oederi, C. panicea, C. rostrata, Eriophorum angustifolium, Juncus filiformis, Rhynchospora alba*; *Bryum* sp., *Sphagnum auriculatum, Marchantia polymorpha* s. lat. and *Riccardia pinguis*. At the mouth of the ditch there were also *Alisma plantago-aquatica, Iris pseudacorus* and *Juncus effusus*.

Lake Stråken. Blomgren & Naumann (1925) give a comprehensive description of this lake, especially the higher vegetation in the northern part (the "Aneboda bay"). Åberg & Rodhe (1942, p. 157) give several chemical analyses of water from the lake including most of the analyses made by earlier investigators. It is the largest one sampled (area 8.1 km^2) with a maximum depth of 12 m. Its precipitation area is also much greater and includes the abovementioned lakes. The variation of the water level, which is regulated at the outlet in the southern part, is somewhat more than 1 m. Most of the shores in the northern part are composed of moraine. The summer transparency seems to be rather variable but is usually about 3.5 m and the lake colour yellow—yellow-brown (Blomgren & Naumann, op.c.; Thunmark 1937; Åberg & Rodhe, op.c., p. 28) indicating a water moderately rich in humus.

The arable land around this lake, especially its northern part, has a much greater extent than around the two other lakes studied. The population is also denser, which has an obvious influence on the lake. However it is far from polluted. The most important influence by man on the lake in this way is through fertilization of the fields. By the drainage water a good deal is brought to the lake. Owing to this the oligotrophic character of the Aneboda bay is not as pronounced as of the other two lakes. It is also evident from the photos in Blomgren & Naumann (op.c.) that especially the reeds cover a larger area and are taller and denser today than in 1924. Since that time also a stand of *Typha latifolia* has grown up in the southern part of the bay.

Site 57 is situated in a rather sheltered locality on the western side of the Aneboda bay some hundred meters south of the outflow of the brook Fiolenbäcken. In the neighbourhood there is a boating place. The water depth is about 1 m beneath the high water level. The bottom consists of sand rather

Fig. 3. From the southern part of lake Fiolen at site 51. — Aug. 1959.

much intermingled with grey-black mud. The vegetation is dominated by dense reeds of *Phragmites communis*. In patches without such reeds (where the samples were taken) scattered individuals of the following species grew (plot area 100 m^2): *Equisetum fluviatile, Glyceria fluitans, Scirpus palustris*; *Nuphar luteum, Nymphaea alba, Potamogeton natans*; *Elodea canadensis, Juncus bulbosus, Utricularia vulgaris*; *Lobelia dortmanna* and *Ranunculus flammula* v. *reptans*. In the adjacent eulitoral zone among others the following species were listed: *Myrica gale, Alisma plantago-aquatica, Bidens tripartita, Filipendula ulmaria, Galium palustre, Iris pseudacorus, Lycopus europaeus, Lysimachia thyrsiflora, L. vulgaris, Lythrum salicaria, Peucedanum palustre, Potentilla erecta, P. palustris, Ranunculus flammula, Carex lasiocarpa, C. oederi, C. rostrata, Glyceria fluitans, Molinia coerulea*; *Calliergonella cuspidata, Campylium stellatum* and *Sphagnum auriculatum*.

Fig. 4. The brook Fiolenbäcken at the farm Åkhult (site 52). Aug. 1959.

The brook Fiolenbäcken takes the water from lake Fiolen to lake Stråken. It is about 6 km long and the difference in level between the two lakes is 41 m. This brook and its higher vegetation has been described by Naumann (1921 a, 1924). Analyses of water are given by Ahlgren (1919), Naumann (1921 a), Lönnerblad (1931), Gessner (1934) and Berzinš (1955). From the northern part of lake Fiolen it flows at the farm Åkhult over mineral soil. The water is here clear and poor in humus. Then the brook passes the large mire Åkhultmyren. Down the mire from Maltsabygget (or Bygget) to Aneboda it runs mainly over morainic deposits again. At Aneboda the fishponds and other establishments of the Södra Sveriges Fiskeriförening (The South Swedish Fishery Society or SSFF) are built up along the brook. The water has here

Fig. 5. The coarse of the brook Fiolenbäcken in the Åkhult mire (site 53). Aug. 1959.

acquired a dark brown colour and it is very rich in humus owing to supplies of water from mires and forests in the surroundings of the brook. The precipitation area above Aneboda (except that of lake Fiolen) may be roughly estimated to 7—8 km². The flow of water through the brook is very variable. According to a personal communication from fil. lic. B. Berzinš the following values (in m³/sec) were measured in Aneboda at the samplings: in 1957 on 1/11 0.30, on 8/11 0.16 and on 15/11 0.13; in 1958 on 1/8 0.06, on 8/8 0.10 and on 5/9 0.03; in 1959 there was no flow of water between 17/7 and 16/10.

Most of the course has been more or less canalized in connection with draining of the surroundings. At the Åkhult mire, e.g., the water level may have been lowered about 0.7 m. Most of the work seems to have been done

Fig. 6. The bog slope with the brooklet at site 68 in the Åkhult mire. — Aug. 1949.

about 1920 or still earlier (cf. pictures in Naumann 1924). Here and there along the course, especially at the edges of the Åkhult mire, there are restricted areas of arable land. They consist mainly of second class grazing land physiognomically characterized by tufts of *Juncus conglomeratus* and *J. effusus* together with *Circium palustre* and *Filipendula ulmaria*. The establishments of SSFF influence very greatly the character and the higher vegetation of the brook at Aneboda. The fishponds are often manured or fertilized in different ways, e.g., with lime or phosphate (cf. e.g. Ahlgren 1919; Nordqvist 1921, 1925; Naumann 1925).

In the following part I will give a description of the four sampling sites, each of which represents a different part of the course. Two sampling sites on the Åkhult mire close to the brook and two in fishponds at Aneboda are also represented.

Fig. 7. Part of the fen soak in the Åkhult mire. — Aug. 1949.

Site 52 is situated at the farm Åkhult (fig. 4). The water is rather fast-running and about 0.4 m deep. The breadth of the brook is 2—3 m. The bottom is minerogenous, made up of grey sand. The vegetation in the brook is dominated by dense stands of *Sparganium simplex*. *Alisma plantago-aquatica*, *Calla palustris* and *Glyceria fluitans* also grow there (plot area 75 m^2). From the shore vegetation the following species may be mentioned: *Rhamnus cathartica*, *Salix aurita*, *Circium palustre*, *Filipendula ulmaria*, *Potentilla erecta*, *Peucedanum palustre*, *Scutellaria galericulata*, *Viola palustris*, *Hylocomium splendens*, *Pleurozium schreberi*, *Polytrichum commune*, *Sphagnum nemoreum* and *S. palustre*.

Site 53 is situated in the brook in the Åkhult mire (fig. 5). The water is rather slow-running and about 0.8 m deep. The breadth of the brook is about 2 m. The bottom is organogenous, made up of black, muddy peat with much iron precipitated. The vegetation in the brook (plot area 50 m^2) consists of *Calla palustris, Sparganium* sp. (ster.), *Nuphar luteum, Potamogeton polygonifolius* and *Callitriche polymorpha.* In the fen vegetation surrounding the brook the following species may be mentioned: *Alnus glutinosa, Betula pubescens, Salix aurita, Epilobium palustre, Filipendula ulmaria, Galium palustre, Lycopus europaeus, Lysimachia thyrsiflora, Lythrum salicaria, Peucedanum palustre, Potentilla erecta, P. palustris, Viola palustris, Agrostis canina, Carex echinata, C. lasiocarpa, C. nigra, C. rostrata, Juncus conglomeratus, J. filiformis, Molinia coerulea, Polytrichum commune, Sphagnum fimbriatum, S. palustre* and *Marchantia polymorpha* s. lat.

Site 68 is situated in a little fast-running brooklet coming from the bog of the Åkhult mire and running to the brook (fig. 6). Most of the water is ombrogenous. From a hydrologic point of view it cannot, however, be excluded that there may be a small addition of mineral soil water. In the brooklet grow only *Sphagnum cuspidatum* and tussocks of *Eriophorum vaginatum* together with filamentous algae, e.g., *Batrachospermum vagum, Mougeotia* sp., *Oedogonium* sp., *Tribonema* cfr *ulitrichoides* Pasch. and *Zygogonium ericetorum.* Around this little brooklet there is a bog vegetation of the *Ledo-Parvifolion* alliance with e.g. *Pinus silvestris, Calluna vulgaris, Empetrum nigrum, Eriophorum vaginatum* and *Cladonia* spp. but without exclusive fen plants like *Carex* spp. or *Eriophorum angustifolium* and without mire expanse plants like *Rhynchospora alba* or *Trichophorum caespitosum.*

Site 34 is also situated in the Åkhult mire, but in a fen soak with slow-running, mineral soil water. The vegetation is very different from that of the foregoing site. In the mud-bottom communities where the samples were taken the following species were found: *Menyanthes trifoliata, Utricularia intermedia, Carex lasiocarpa, C. limosa, C. rostrata, Eriophorum angustifolium, Rhynchospora alba, Scheuchzeria palustris, Sphagnum apiculatum,* and *S. pulchrum.* Also *Narthecium ossifragum, Molinia coerulea, Trichophorum caespitosum, Calliergon stramineum* and *Sphagnum papillosum* may be mentioned from this site. A thick layer of iron ochre is always found. See also Malmer 1951 ("drågkärret").

Site 54 is situated in the brook at Maltsabygget. The water is rather fast-running and about 0.5 m deep. The breadth of the brook is about 3 m. The bottom is made up mostly of brown-coloured gravel. The vegetation of the brook (plot area 100 m^2) consists of the following species: *Calla palustris, Menyanthes trifoliata, Potamogeton polygonifolius, Sparganium minimum* and *Callitriche ~~polymorfa~~.* In the fen vegetation surrounding the brook the following species were listed: *Alnus glutinosa, Betula pubescens, Rhamnus cathartica, Salix aurita, Calla palustris, Caltha palustris, Galium palustre, Lycopus europaeus, Lysimachia thyrsiflora, Peucedanum palustre, Potentilla erecta, P. palustris, Viola palustris, Agrostis canina, Carex canescens, C. echinata, C. nigra, C. rostrata, Hylocomium splendens, Rhytidiadelphus squarrosus, Sphagnum apiculatum* and *S. palustre.*

Site 59 is situated in a dammed up part of the brook (Kvarndammen) at the establishments of SSFF in Aneboda. The bottom is made up by black mud mixed with gravel. The vegetation consists of *Alisma plantago-aquatica, Iris pseudacorus, Carex lasiocarpa, C. rostrata* (small reeds), *Glyceria fluitans,* *Typha latifolia*; *Nuphar luteum, Nymphara alba, Potamogeton natans* and *Sparganium minimum.*

The fishponds were sampled only in November 1957. At that time they were empty. The only water was found in ditches taking water from the surrounding forests to the brook. The bottom consists of black, peaty mud mixed with some gravel. The vegetation is strongly influenced by man (cf. e.g. Haglund 1911; Nordqvist 1921, 1925; Naumann 1924; Lillieroth 1949; Björk 1955). At site 56 in Jämfälledammen there are dense stands of *Typha latifolia* and *Potamogeton natans* together with, e.g., *Alisma plantago-aquatica, Iris pseudacorus, Sparganium simplex, Carex lasiocarpa, C. rostrata, Clyceria fluitans*; *Lemna minor, Ricciocarpus natans* and *Drepanocladus fluitans.* At site 55 in Övre Hållsdammen grow in the ditches (plot are 50 m^2) *Alisma plantago-aquatica, Bidens tripartita, Equisetum fluviatile, Iris pseudacorus, Glyceria fluitans, Scirpus palustris, Typha latifolia*; *Potamogeton natans, P. polygonifolius, Sparganium minimum*; *Lemna minor*; *Callitriche polymorfa, Juncus bulbosus* and *Drepanocladus fluitans.* Around the sampling site were found, e.g., *Epilobium palustre, Gnaphalium uliginosum, Polygonum hydropiper, Rumex longifolius, R. obtusifolius, Alopecurus geniculatus, Brachythecium* cfr *rutabulum* (juv.), *Bryum* sp. (juv.) and *Marchantia polymorpha* s. lat.

The original vegetation in these sites may have been wet forests and fens. Only small areas are occupied by such vegetation today. One such locality may however be mentioned (site 60 at the edge of the pond above "sluss IV"). The following species were noted in this *Carex rostrata - Sphagnum palustre* - soc. (plot area 100 m^2): *Betula pubescens, Picea excelsa, Pinus silvestris, Salix aurita, Vaccinium oxycoccos, V. uliginosum*; *Calla palustris, Drosera rotundifolia, Epilobium palustre, Galium palustre, Menyanthes trifoliata, Potentilla erecta, P. palustris, Agrostis canina, Carex canescens, C. echinata, C. lasiocarpa, C. limosa, C. nigra, C. rostrata, Eriophorum angustifolium*; *Calliergon stramineum, Calliergonella cuspidata, Drepanocladus exannulatus* s.str., *Sphagnum apiculatum, S. inundatum, S. palustre* and *S. papillosum.* pH was 5.4 and $\varkappa_{\mathrm{red}}$ 65 in a sample taken 26/8 1959.

The well. In addition also water samples from an old well, site 66, situated at the deserted cottage Dalen will be discussed in this paper. It is at least 4 m deep. Only during short periods in the summer small amounts of water are taken up from it, e.g., for rinsing milking-jars. It is not used for watering of cattle, even if the old tilled ground around it is used as grazing land. The water level in the well varies appreciably. In early spring and in the autumn it is near the ground surface, but in the summer it is much lower. At the samplings the water level was (in cm beneath the ground surface) on 13/11 1957 3 cm, on 14/8 1958 57 cm and on 12/8 1959 275 cm.

Disregarding the difference between the lakes and the brook it is evident from the description of the sampling localities above that the vegetation is rather uniform with a clear poor and oligotrophic character. There is, however, also a marked difference between localities with none or very little influence by man on the vegetation (sites 51—54 and 58) and localities with stronger influence (sites 55—57 and 59). Most occurrences of species like, e.g., *Alisma plantago-aquatica, Bidens tripartita, Iris pseudacorus, Typha latifolia, Lemna minor, Ricciocarpus natans* and *Elodea canadensis* may in this region depend on influence by man (cf. e.g. Thunmark 1948, 1952). Of great importance in this case is probably also the influence on the production per unit area on the different sites. Compare, e.g., the small reeds of *Carex rostrata* and *Equisetum fluviatile* at site 51 with the dense stands of *Phragmites communis* and *Typha latifolia* at site 57 and 56 respectively.

The natural vegetation surrounding the brook (sites 53, 54 and 60) is a mire vegetation, which may be characterized as a moderately poor fen vegetation of the mire margin type. It differs greatly from the vegetation of the fen soak (site 34), which ought to be characterized as an extremely poor fen vegetation of the mire expanse type, and from the vegetation of the bog locality (site 68). The vegetation in the eulitoral zone of the lake shores described above and by Blomgren & Naumann (1925) or Thunmark (1931) does not build up any peat deposits and may not be treated as a mire vegetation though many species are common, e.g., *Sphagnum auriculatum* (poor fen), *Campylium stellatum* (rich fen), *Rhynchospora alba* (mire expanse vegetation), *Galium palustre, Potentilla erecta, Agrostis canina* and *Carex nigra* (mire margin vegetation). It comes, however, closest to a moderately poor fen vegetation of mire margin type.

Water analyses

Within the analytical errors there are equivalent amounts of cations and anions (table 1). The values calculated for $\varkappa_{\mathrm{red}}$ from the major constituents (Rodhe 1949) are also about the same as those measured except in some samples rich in humus where the measured values are lower. These agreements show that only small amounts of constituents are not analyzed. Fe, Al and P are not taken into account in these calculations as it is questionable whether they are in a true soluble state in these samples. They also belong to minor constituents according to Rodhe (1951). More important minor constituents not analyzed here are probably Sr with about 0.3 μmol/l, Mn with about 0.5 μmol/l and N with about 5 μmol/l (Åberg & Rodhe 1942, Witting 1948).

The differences between the samples from the different periods are rather slight. The autumn samples from 1957 are all richer in Si than

Table 1. Water analyses. Values calculated per litre.

Locality	The lakes			The brook Fiolenbäcken				The fishponds at Aneboda		The Åkhult mire		The well at Dalen
	Förhultsjön	Stråken	Fiolen	Åkhult	The mire	Bygget	Aneboda			Bog	Fen soak	
Site no.	58	57	51	52	53	54	59	55	56	68	34	66
November 1957												
pH	6.1	5.9	6.3	6.4	5.2	4.9	5.2	4.0	4.7	4.0	4.3	5.7
$\varkappa_{red}$	46	49	48	48	39	40	42	21	37	9	15	58
Na .... μmol	166	165	146	157	120	149	146	154	155	60	108	105
K .... ,,	16	24	22	25	16	18	17	13	22	3	4	180
Mg .... ,,	53	46	44	45	40	46	43	41	53	12	20	60
Ca .... ,,	70	82	69	73	53	67	69	38	58	17	23	74
Al .... ,,	<1	2	<1	<1	3	1	2	12	5	4	7	5
Fe .... ,,	2	7	1	1	6	10	11	15	24	2	14	2
Cl .... ,,	190	240	190	210	200	230	230	230	220	200	140	130
HCO_3 ...... ,,	60	70	70	70	<10	<10	30	<10	<10	<10	<10	300
Si .... ,,	54	79	19	12	30	66	68	40	140	7	48	68
SO_4 .... ,,	79	70	71	81	72	64	65	—	—	23	—	59
P .... ,,	0.6	0.5	0.5	0.5	1.5	0.9	0.6	0.8	1.0	0.6	0.8	0.5
Σ cations .... μeq	430	450	400	420	330	410	390	420	420	280	250	560
Σ anions .... ,,	410	450	400	440	340	360	390	—	—	250	—	550
Calc. $\varkappa_{red}$	48	52	46	50	40	45	45	—	—	23	—	60
August 1958												
pH	6.5	6.5	6.5	6.4	5.7	5.6	5.9	—	—	3.8	4.5	5.6
$\varkappa_{red}$	42	54	47	47	44	44	44	—	—	12	30	62
Na .... μmol	149	171	136	161	151	150	149	—	—	94	122	119
K .... ,,	16	28	29	25	23	17	15	—	—	4	5	153
Mg .... ,,	43	63	54	50	60	57	46	—	—	24	45	65
Ca .... ,,	71	99	70	87	78	78	94	—	—	28	45	81
Al .... ,,	2	<1	<1	<1	1	2	4	—	—	3	3	2
Fe .... ,,	1	2	1	1	4	12	15	—	—	12	41	2
Cl .... ,,	200	230	220	220	220	200	180	—	—	140	190	80
HCO_3 ...... ,,	70	120	80	60	60	80	120	—	—	<10	<10	300
Si .... ,,	40	19	5	4	20	55	33	—	—	3	31	39
SO_4 .... ,,	65	78	67	68	79	62	62	—	—	32	23	71
P .... ,,	0.2	0.4	0.9	0.5	1.3	0.4	0.6	—	—	0.9	1.1	0.3
Σ cations .... μeq	390	520	410	460	450	440	440	—	—	360	340	570
Σ anions .... ,,	390	510	430	420	440	410	420	—	—	210	240	530
Calc. $\varkappa_{red}$	45	58	48	50	51	48	48	—	—	24	31	59
August 1959												
pH	6.7	6.5	6.7	6.3	5.9	6.8	6.6	—	—	3.7	4.3	6.1
$\varkappa_{red}$	46	56	51	57	50	53	64	—	—	40	59	68
November 1957												
$KMnO_4$-cons. mg	64	130	63	58	120	230	150	460	220	130	210	35
Colour .... mg Pt	100	180	60	60	120	170	200	310	350	130	310	50
August 1958												
$KMnO_4$-cons. mg	91	53	34	27	105	140	160	—	—	290	270	—
Colour .... mg Pt	60	55	18	20	80	190	230	—	—	270	380	—

the summer samples from 1958. Some of those also contain less amounts of K, Mg and Ca. The determinations of $\varkappa_{red}$ from the dry summer 1959 indicate that there was an increase in the concentration of electrolytes at that time. My values for $\varkappa_{red}$ agree with those given by Åberg & Rodhe (1942) but are higher than those given by Lönnerblad (1931) and Gessner (1934). My figures for P are insignificantly higher than those given by Åberg & Rodhe (op.c.). See also Lohammar 1938, p. 23.

With few characteristic exceptions discussed below the concentration of the major constituents is rather constant in all samples. The equivalent proportions are also the same in most of the samples with Na^+ and Ca^{2+} dominating among the cations and Cl^- among the anions. The well water deviates from all other sites sampled in having a much higher content of potassium. K^+ and HCO_3^- are there the dominating ions. The results agree with analyses of subsoil water from similar sites given by Sjörs (1954, p. 81). Troedsson (1955) states that subsoil water is much richer in K than surface water, which is instead richer in Al. In the samples from the other sites there seems to be a connection between the contents of Fe, Al, Si and humus measured as the $KMnO_4$-consumption. (The water colour cannot be used as it is influenced also by pH and Fe.) In most cases the samples rich in these substances are low in K. This is valid especially for the fen water and the water from the fishponds, which at the sampling time comes from the surrounding forests. As at least most of the water is ombrogenous in the bog brooklet, it is rich in humus but rather low in the other substances. The dominating cation is in this case H^+. The concentration of Ca^{2+} is the lowest one, just about 25 µmol/l, which value Witting (1947, 1948) states as the upper limit for the concentration in ombrogenous bog waters. The concentration in the water of the fen soak usually exceeds this value.

Along the brook Fiolenbäcken from lake Fiolen to the sampling site at Aneboda there is an increase in the contents of Fe, Al, Si and humus and a decrease in the concentration of K and in pH. This shows that along the brook the water from lake Fiolen is mixed with acid surface water from adjacent mires and forests. Addition of subsoil water ought to be of little importance. Among the lakes studied Fiolen is poorest in Al, Fe, Si and humus. It has also the smallest precipitation area. Cf. also Gessner 1934, Ohle 1940 a and Åberg & Rodhe 1942. Their and my values also show that Stråken is richer in electrolytes than Fiolen. Lake Förhultsjön is poorest. The low value for K^+ is especially noticeable in this case. Lake Fiolen has somewhat higher percentage concentration of K^+ than the other localities studied except the well. In Lohammar's analyses from Dalarna Gorham (1955) has shown that seepage lakes, lacking inflow and outflow, are richer in K than drainage lakes. See also Sjörs 1954, p. 81.

Table 2. Analyses of major constituents in fresh waters poor in electrolytes from different parts of Sweden.

Values calculated in µeq/l. The situation of the regions appears from fig. 1.

Region	$\varkappa_{\text{red}}$	Na^+	K^+	Mg^{2+}	Ca^{2+}	Cl^-	HCO_3^-	SO_4^{2-}
North and Central Sweden								
Abisko [1]	28	—	—	34	250	29	230	130
Norrland (lowland) [2]	28	68	14	92	150	32	250	42
Dalarna [2]	67	110	24	140	420	73	490	90
Uppland [2]	38	76	12	78	190	60	240	54
Södertälje [3]	41	—	—	—	—	61	190	—
Rivers [4]	—	—	—	—	—	86	—	42
South Sweden								
Aneboda [5]	47	155	23	101	153	210	80	143
,, [6]	49	—	—	—	—	—	90	—
,, [7]	47	—	—	—	—	260	—	—
Lenhovda [7]	31	—	—	—	—	200	—	—
Hökensås [8]	73	—	—	—	—	320	230	—
NW Scania [9]	77	—	49	—	—	390	210	—
,, [10]	90	—	35	220	500	370	250	180
Rivers [4]	—	—	—	—	—	220	—	130

[1] Ohle 1940 b. Six samples from the lakes Kårsajaure, Katterjaure and Torne träsk together with one sample from the river Abiskojokk. Some lakes in this region may perhaps be characterized as sulphate lakes. The Cl^--concentration is higher in the more westwardly situated lakes (Ekman et al. 1950).

[2] Lohammar 1938. Norrland (lowland) includes the lakes 101—165, Dalarna 26—75 and Uppland 1—3. The values are taken from the diagrams in Rodhe 1949. Gorham (1955) has shown that the Dalarna region is not quite homogenous.

[3] Florin 1957. Nine samples from the five "Upland lakes".

[4] Eriksson 1929. Mean values from localities in rivers which have a Ca-concentration (mean) of less than 180 µmol/l. North Sweden represented by 20 localities north of the rivers Klarälven and Dalälven; South Sweden by nine localities in rivers coming from the South Swedish uplands.

[5] My own samples from the lakes given in this paper.

[6] Åberg & Rodhe 1942. Eleven samples of surface water in the lakes Fiolen, Ryssegöl, Skärshultsjön and Stråken.

[7] Thunmark 1948, p. 680.

[8] Personal communication from fil. lic. Bruno Berzinš, Aneboda. One sample from each of the lakes Alvasjön, Nordvattnet, St. Havsjön and St. Öjasjön Aug. 1958.

[9] Lillieroth 1950. One sample from each of the lakes Bälingesjön, Fedingesjön, Värsjön and Åsljungasjön Sept. 1947.

[10] Almestrand & Lundh 1951. Lake Rösjön and lake Västersjön, together 16 samples. The values of $\varkappa_{\text{red}}$ (mean 64) given by them is too low compared with the ionic determinations. The value in the table is calculated from these.

There are no other total analyses of the major constitutents in the waters of oligotrophic lakes and rivers in this part of Sweden available in the literature. Lohammar (1938) has made extensive investigations on this subject in lakes in some other parts of Sweden. Rodhe (1949, 1951) treats his values by means of statistical methods. He states that there is a correlation between the spec. conductivity and the different major constituents. He also finds that (with very few exceptions) the order of concentration of the major constituents is the same in all lake groups. This is believed to result from ionic exchange between the dissolved ions and the colloidal systems of soils and lake muds. The order between the cations is $Ca^{2+} > Mg^{2+} > Na^{+} > K^{+}$ in these samples. In my samples the order is $Na^{+} \backsimeq Ca^{2+} > Mg^{2+} > K^{+}$. Among the anions Rodhe finds the order $HCO_3^- > SO_4^{2-} > Cl^-$ except in three lakes, where SO_4^{2-} dominates. The order is quite another in my samples from Aneboda, viz., $Cl > SO_4^{2-} > HCO_3^-$. In table 2 are compared some analyses of fresh waters from Sweden with about the same $\varkappa_{red}$ as in the Aneboda region. All values given there show very clearly that among the anions in waters from the south of Sweden the figures for Cl^- and SO_4^{2-} are much higher than those from the northern part of the country. Contrary to that the figures for HCO_3^- are higher in north Sweden. Also the concentration of Na seems to be highest in south Sweden even if the difference is smaller than among the anions. In north Sweden probably Norrland (lowland) is the region most similar to the sampling area. The concentration of K^{+}, Mg^{2+} and Ca^{2+} is about the same as in the Aneboda region. This is valid also for a few lakes in Dalarna, e.g. no. 30 Valbosjön (Lohammar, op.c.). Concerning the spec. conductivity there seems to be a significant difference between the oligotrofic area in south Sweden and similar areas in the northern part of the country. A comparison is made in the following survey where the mean values of the spec. conductivity in a number of lakes are compilated.

Region	Number of lakes	Specific conductivity at 20°C.			
		Mean	Standard deviation	Standard error	Range
South Sweden (oligotrophic part)	117	$51 \cdot 10^{-6}$	$\pm 16 \cdot 10^{-6}$	$\pm 1.48 \cdot 10^{-6}$	$26 \cdot 10^{-6}$—$121 \cdot 10^{-6}$
Norrland (lowland)	65	$26 \cdot 10^{-6}$	$\pm 10 \cdot 10^{-6}$	$\pm 1.20 \cdot 10^{-6}$	$12 \cdot 10^{-6}$— $59 \cdot 10^{-6}$

For south Sweden figures from lakes with pH > 6.0 given by Thunmark (1937, 1948), Lillieroth (1938; 1950, only Värsjön and Fedingesjön) Åberg & Rodhe (1942, not Vättern and Växjösjön) and Cronholm (1946) are used together with own analyses, in all 148 values. For Norrland (lowland) figures from summer samples given by Lohammar (1938, the lakes number 101—165) are used, in all 146 values.

From the analyses carried out up to now it seems probable that this regional difference to the greatest part may be due to the higher values for Na^+, Cl^- and SO_4^{2-} in south Sweden. The lower values for HCO_3^- there only partly counteract that increase. Mire waters including waters from ombrotrophic parts also show these differences. Compare the figures from the Åkhult mire in this paper and in Malmer & Sjörs (1955, p. 67) and from other south Swedish mires in Witting (1947, 1948) with the figures given by Sjörs (1948, p. 100) from Dalarna. It may also be mentioned that about the same amounts and the same proportions as in south Sweden are to be found among the anions in lake waters from the Lake District in England (Pearsall 1920, Mortimer 1942, p. 156) and in similar lakes in northwestern Germany (Ohle 1934).

These regional differences concerning the concentration of Na^+, Cl^- and SO_4^{2-} in waters poor in electrolytes in Sweden may to the greatest part depend on the differences in the amounts brought to the ground by atmospheric transport. It is shown through analyses of precipitation and air that south Sweden is supplied in this way with much more Na, Cl and S than north Sweden. It is thought that most of these elements in fresh waters of this type come from airborn salts (Emanuelsson et al. 1944; Eriksson 1955, 1959 a, 1959 b). Differences in the rate of evaporation and the intensity of weathering ought to be of less importance. Sometimes an increase of the SO_4^{2-}-conc. in water may result from lowering of the water level in a lake (cf. Lohammar 1938, 1949). It ought to be mentioned that Almestrand & Lundh (1951) have found higher Cl^--conc. in the Scanian eutrophic lakes than Lohammar (1938) in corresponding lakes in Uppland. They suggest that it depends on their situation nearer the Swedish west coast. Concerning HCO_3^-, which is the anion of a weak acid, the regional differences probably are secondary, as the concentration in these types of water seems to result from the amounts of anions of strong acids, esp. Cl^- and SO_4^{2-} in the water.

Bottom substratum analyses

From table 3 it appears that as in peat samples equal amounts of Na, K, Mg and Ca are soluble in the two extraction solutions used (cf. Malmer & Sjörs 1955). Large differences, however, are met with concerning Fe. Very probably more iron is extracted with HAc than is in the truely exchangeable state. The amounts of exchangeable metallic cations calculated from the change of pH in the HAc-solution are of the same

Table 3. **Bottom substratum analyses.** Values calculated per dm³ fresh sample.

Locality		The lakes			The brook Fiolenbäcken				The fishponds at Aneboda		The Åkhult mire	
		Förhult-sjön	Stråken	Fiolen	Åkhult	The mire	Bygget	Aneboda			Bog	Fen soak
Site no.		58	57	51	52	53	54	59	55	56	68	34
November 1957												
Weight . . . g		1480	1360	1070	1180	1060	1180	1180	960	1020	1030	990
Dry matter . . . ,,		1020	610	330	560	82	520	340	270	180	155	66
Loss of ignition . . . ,,		35	140	120	46	70	120	66	210	160	150	60
Do. % of dry matter . . .		3 %	23 %	37 %	8 %	85 %	23 %	19 %	79 %	92 %	96 %	91 %
Kjeldahl-N . . . g		1.2	1.2	2.8	1.6	2.3	1.9	2.3	4.8	4.0	2.5	1.0
pH . . .		5.1	5.4	5.1	5.1	4.4	4.9	5.4	4.8	5.4	3.1	4.5
Exch. H⁺ . . . meq		24	30	49	32	74	73	55	106	71	84	17
,, met. cations . . . ,,		26	51	44	42	55	71	79	63	59	11	18
,, capacity . . . ,,		49	82	93	74	129	145	134	169	120	95	34
Degree of neutralization . . .		52 %	63 %	47 %	56 %	43 %	49 %	59 %	37 %	45 %	11 %	51 %
Exch. Na⁺ . . . mmol	Am	0.62	0.91	0.91	0.65	0.71	0.94	0.84	0.92	0.86	0.83	0.66
	Ac	0.44	0.62	0.83	0.54	0.58	0.68	0.65	0.68	0.78	0.75	0.66
,, K⁺ . . . ,,	Am	0.26	0.58	0.52	0.59	0.42	0.80	0.63	0.33	0.25	0.88	0.56
	Ac	0.27	0.58	0.64	0.50	0.49	0.79	0.62	0.37	0.23	0.52	0.50
,, Mg²⁺ . . . ,,	Am	2.2	3.9	4.2	3.1	0.61	1.2	3.2	3.1	4.5	2.4	1.3
	Ac	2.2	3.3	2.3	2.2	—	0.9	3.0	2.2	6.1	2.8	1.8
,, Ca²⁺ . . . ,,	Am	3.5	10.1	13.6	13.0	2.7	10.2	17.3	21.2	20.6	2.3	2.4
	Ac	4.1	11.5	17.6	12.4	2.7	10.6	16.0	21.3	23.8	2.3	3.2
,, Mn . . . ,,	Ac	0.92	0.47	0.31	0.24	0.17	1.16	0.33	0.20	0.37	0.04	0.09
,, Fe . . . ,,	Am	0.06	0.7	2.0	2.5	12.0	3.0	1.5	0.5	1.5	—	—
	Ac	0.9	10.7	10.5	9.8	28.8	32.2	20.0	1.6	6.5	0.7	9.2
Sum of analyzed met. cations in meq.	Am	13	31	41	38	32	30	45	51	54	—	—
	Ac	17	53	63	50	c. 66	91	80	52	74	13	30
Soluble P . . . mmol	Ac	0.09	0.33	0.16	0.39	0.18	0.19	0.22	0.10	0.19	0.37	0.06
August 1959												
pH . . .		5.9	6.2	5.4	5.6	5.8	6.2	6.2	—	—	3.5	5.0
E_h . . . mV		+140	±0	−80	−20	−30	−70	−50	—	—	+490	+20
rH . . .		17	12	8	11	11	10	11	—	—	24	11

magnitude as the sum of the analyzed metallic cations. Fe and Mn are in this case calculated as bivalent. From the determinations of the redox potential this degree of oxidation seems most probable for the exchangeable part in the samples discussed here.

The differences between the sampling sites in the lakes and the brook are rather small. The reaction may be characterized as moderately acid. The degree of neutralization is throughout about 50 %. As long as further confirmations are lacking the somewhat higher figures found in the sample from lake Stråken may be considered as accidental, even if the tendency ought to be noted. The samples with high contents of organic matter show in most cases comparatively high figures for exchangeable H^+, exchangeable metallic cations (both total and the different ions) and exchange capacity. Also Kjeldahl-N varies with the organic matter. High in N are especially the samples from the fishponds. Depending on the fertilization with lime the fishpond sites show higher figures in Ca than the others. The Ca-level seems, however, surprisingly low in these cases as very much lime must have been supplied to them during the years. Nor can any increase in P be found in spite of fertilization with phosphate. Compare also analyses in Haglund 1911. In the brook sample from site 53 in the mire the Ca-content is as low as in the bog. In the first-mentioned site Mg is also very low while Fe is very high and by far the dominating exchangeable constituent. Most of the sites are characterized by comparatively high figures for Fe and Mn. All analyses indicate the great importance of iron in the sediments.

There are no comparable determinations from Swedish lakes and brooks. Misra (1938) and Gorham (1953 b) have studied the bottom substratum of lakes in the Lake District, England. They have found higher pH and degree of neutralization in these lakes. Also Kjeldahl-N and exchangeable Ca and Mg are higher. The vegetation seems to be of a more eutrophic character in the localities studied by them.

The measurements of the redox potential show that with one exception the samples ought to be characterized as reducing according to Pearsall (1938). The values are rather uniform and only the minerogenous sample from Lake Förhultsjön deviates. Only the bog sample is oxidizing. Pearsall & Mortimer (1939) and Mortimer (1941) have found similar values in English lakes.

It is evident from the analyses that compared with the exchangeable amounts in the bottom substratum only small amounts of the elements studied are found in the water. Table 4 gives figures for this relation from some of the sampling sites. It is found that the percentage of the

Table 4. The distribution of the elements between water and bottom substratum.

The figures give the concentration in water in % of the soluble amounts in the bottom substratum in November 1957. For Na and P in the bottom substratum the Ac-values are used; for K, Mg and Ca the mean of Am and Ac. In Fe figures for both are given.

Site	No.	Na	K	Mg	Ca	Fe		P
						Am	Ac	
Lake Förhultsjön	58	37	6.2	2.4	1.8	3.3	0.22	0.65
Lake Stråken	57	26	4.2	1.3	0.8	0.9	0.07	0.11
Lake Fiolen	51	18	4.2	1.5	0.5	0.08	0.02	0.31
Fiolenbäcken at Aneboda	59	22	2.7	1.4	0.4	0.7	0.05	0.27

ions in the water decreases in all samples in the order $Na^+ > K^+ > Mg^{2+} > Ca^{2+}$. That is the same order as I have found in the relation between water and peat in the mires (Malmer & Sjörs 1955; Malmer 1957). The figures are also of the same magnitude. They seem, however, also to depend on the contents of organic matter in the substratum. This equilibrium can be expected from the relation between the volume and charge of the ions. It may be of great importance in establishing the rather constant proportions between the cations of the major constitutents in lake and river waters discussed above (p. 106). Concerning the major constituents among the anions no such definite equilibrium can be expected as Cl^- is probably very slightly adsorbed on the different soil substratums and S to a great extent is involved in the organic turnover. It is shown above that the proportion between the anions in water of this type varies and probably depends on several different factors.

Discussion

The relative importance of the chemical composition of the water and the bottom substratum for the mineral nutrition of the rooted aquatic plants has been discussed several times in the literature. Compare, for example, Lohammar 1938, Lillieroth 1950, Lundh 1951 and Hürlimann 1951 and the literature quoted there. It is shown above that most of the elementary constituents studied are highly concentrated in the bottom substratum. Even if the influence of the mobility of water is taken into account, it is evident that the contents in the bottom substratum ought to be the most important available source for mineral nutrients to the rooted aquatic plants when calculated per unit area. It also seems probable that organic deposits like mud are richer in mineral nutrients than minerogenous bottom. As there is an equilibrium between the concentration in water and in bottom substratum there also ought to be a parallelism between the species of rooted aquatic plants found and the composition of the water even if there should be no causal connection (cf. Lohammar 1938, Iversen & Olsen 1943, Lundh 1951).

The amounts of elementary constituents taken up by plants per unit area may sometimes form a considerable part of the amounts found in the bottom substratum in the same manner as I have earlier demonstrated for some communities in the mire vegetation (Malmer 1958). This may happen, for example, for reeds with fairly high production. Calculated from the values for the standing crop of *Phragmites communis* given by Gorham & Pearsall (1956) and the values for the composition of the ash given by Hürlimann (1951) the amounts of K but not Na and Ca taken up by such stands may form an important part of the amounts found in the bottom substratum. It seems possible that per unit area there is at least about the same amount of K in the standing crop as in the bottom substratum, while concerning Na and Ca only 5—10 % or less is to be found in the standing crop. Also P is probably included in plants in the same degree as K.

In the treating of the Swedish vegetation the contrast between "poor" and "rich" types of plant communities is discussed very often, for example, the division into heath forest—meadow forest or poor fen—rich fen (cf. e.g. Sjörs 1956). The division of the lakes into oligotrophic and eutrophic (or archaean and nonarchaean in Almestrand & Lund 1951 or Lundh 1951) is parallel to this grouping. Several attempts have been made to analyse the habitat conditions underlying the differences within this poor—rich direction of variation in the vegetation. Then the main interest has been drawn to the complex which Sjörs (1954, p. 130, op.c., p. 57) calls the "acid-base status", e.g., the pH and the degree of neutralization or to the contents of Ca and other elementary constituents.

When the poor—rich direction of variation is considered, only small differences between the sampling sites are found in the vegetation of the lakes and the brook. In the chemical analyses, too, only small differences are found between the sampling sites. Nor can more than negligible influences by the action of man be found in the samples. They give, however, a description of the conditions prevailing within the sampling area. Compared with the lake waters in the eutrophic (nonarchaean) areas of Scania (Almestrand & Lundh 1951), Södermanland (Thunmark 1948, 1952) and Uppland (Lohammar 1938) with their very deviating vegetation the waters from the area studied are very poor in electrolytes, especially Ca^{2+} and HCO_3^- but also in nearly all other elements studied, e.g., K and P. See Rodhe 1949. Unfortunately there are no corresponding analyses of the bottom substratum in these eutrophic lakes available. To judge from analyses by Misra (1938) and Gorham (1953 b) the pH may be about 7 or higher and the degree of neutralization 100 % or nearly so. The analyses in Hürlimann 1951, p. 105 seem to come from localities with eutrophic vegetation and show pH 7.4—8.0 and presence of $CaCO_3$ in the substratum. His figures for K are not higher than mine. The methods used for extracting P are unfortunately not comparable.

The methods described in this paper have also been applied to the studies of the substratum for the mire vegetation (Gorham 1953, Malmer & Sjörs 1955, Malmer 1957, 1958 and Persson 1956) in order to elucidate the habitat conditions underlying the differentiation along the bog—poor fen—rich fen series of plant communities. The border between poor and rich fen vegetation seems to coincide with a peat-pH of about 5.0—5.3 and a degree of neutralization of about 50—60 %. These values are about the same or somewhat lower than those found in the lakes and the brook studied. The amounts of exchangeable ions studied are also about the same. In extremely poor fens and in bogs the pH, degree of neutralization and contents of exchangeable Ca are always lower than in the lakes and the brook studied. As it has been shown above the vegetation surrounding the brook and in the eulitoral zone of the lakes is of the moderately poor fen type or transitional to the moderately rich fen type. Sjörs (1954) has studied park-meadows in Dalarna and gives values for pH, degree of neutralization and exchangeable Ca in the soil. In these respects my figures from the lakes and the brook agree most with those from the *Geranium silvaticum - Deschampsia flexuosa* - ass., which has the lowest productivity, but especially the pH seems to be higher in the bottom substratum and falls partly within the range of the other associations. Sjörs infers that this association left to itself would develop to a *Myrtilletum*-forest according to Arnborg (1940). At the same time the pH is probably lowered. Gorham (1953 a) has studied forest soils in Lake District, England. He has found that “mor” samples from what could be designated as heath forests give a pH ranging between 2.5 and 4.8 and a degree of neutralization of 6 to 47 %. “Mull” samples from what could be called meadow forests give figures higher than pH 4.6 and 67 % degree of neutralization.

As far as can be judged from these scanty determinations discussed above and several others, it is evident that the bottom substratum studied does not provide any particular extreme habitat conditions concerning the acid-base status or the contents of elementary constituents as, e.g., Ca or total-N. The reducing conditions prevailing counteract the rise of strong acid conditions. Through leaching from the surrounding mineral soil the lake ecosystem (Du Rietz 1954, Sjörs 1955) ought to be supplied with mineral constituents which are then concentrated in the bottom substratum in the sedimentation of the organic materials and through exchange reactions with the water. Especially the supply of Ca also contributes to increasing the degree of neutralization. In mire pools surrounded by peaty shores more acid and base-deficient conditions may prevail. The character of the vegetation is obviously poorer there.

Summary

Redox potential, pH, degree of neutralization, exchangeable amounts of Na, K, Mg, Ca, Mn, Fe and P are studied in samples from the soils of waterlogged habitats in the oligotrophic Aneboda region, Småland. Samples of water from these 11 localities and one well are also analyzed for these elements (except Mn) together with Al, Cl, HCO_3^-, Si, SO_4^{2-} and humus contents. A short description of the higher vegetation on the sampling sites is also given.

The results show that the waters are poor in electrolytes. There is a connection between low figures for K and high values for Al, Fe, Si and humus. Compared with similar areas in north Sweden the figures for HCO_3^- are low while Na, Cl and S are significantly higher. This is probably due to atmospheric transport of these elements from the ocean. There seems to be a fairly definite equilibrium between the concentration of the different cations in the water and the exchangeable amounts in the bottom substratum. All elements studied show much higher concentration in the soils than in the water. A comparison is made with similar investigations in mire and mineral soil vegetation.

Literature Cited

Ahlgren, G. 1919. Är kalkbrist orsaken till de dåliga resultaten av karpövervintringarna i Aneboda? — Skr. utg. av Södra Sveriges Fiskerifören. 1918. Lund.

Almestrand, A. & Lundh, A. 1951. Studies on the vegetation and hydrochemistry of Scanian lakes I—II. — Bot. not. Suppl. 2:3. Lund.

Arnborg, T. 1940. Der Vallsjö-Wald, ein nordschwedischer Urwald. — Acta phytogeogr. suec. 13. Uppsala.

Berzins, B. 1955. Cykliska förändringar av några miljöfaktorer i Fiolenbäcken. — Skr. utg. av Södra Sveriges Fiskerifören. Årsskr. 1953—1954. Lund.

Björk, S. 1955. Om förekomsten av spirodelider i Södra Sveriges Fiskeriförenings dammar i Aneboda. — Ibid.

Blomgren, N. & Naumann, E. 1925. Untersuchungen über die höhere Vegetation des Sees Stråken bei Aneboda. — K. Fysiogr. Sällsk. handl. N.F. 36: 6. Lund.

Cronholm, M. 1946. Über die Hydracarinen der Aneboda-Seen. — Medd. Lunds Univ. Limn. inst. 6. Lund.

Du Rietz, G. E. 1949. Huvudenheter och huvudgränser i svensk myrvegetation. — Sv. bot. tidskr. 43. Uppsala.

— 1954. Sydväxtberg. — Ibid. 48.

Ekman, S., Lohammar, G., Rodhe, W. & Skuja, H. 1950. Undersökningar av sjöar i Torne lappmark med särskild hänsyn till deras plankton och vattenkemi. — Stat. Naturvetenskapl. Forskningsråds årsbok 1948/49. Stockholm.

Emanuelsson, A., Eriksson, E. & Egnér, H. 1954. Composition of atmospheric precipitation in Sweden. — Tellus 6: 3. Stockholm.

Eriksson, E. 1955. Air borne salts and the chemical composition of river water. — Ibid. 7.

— 1959 a. The yearly circulation of chloride and sulphur in nature; meteorological, geochemical and pedological implications. — Ibid. 11 and 12.

— 1959 b. Tillförseln av näringsämnen i luft till mark och vegetation. — Växtnäringsnytt 15. Stockholm.

Eriksson, J. V. 1929. Den kemiska denudationen i Sverige. — Medd. Stat. Met.-Hydrogr. Anst. 5: 3. Stockholm.

Flaig, W., Scharrer, K. & Judel, G. K. 1955. Zur Methodik der Bestimmung des Redoxpotentials im Boden. — Z. f. Pflanzennähr., Düng., Bodenkunde. 68. Berlin.

Florin, M.-B. 1957. Plankton of fresh and brackish waters in the Södertälje area. — Acta phytogeogr. suec. 37. Uppsala.

Gessner, F. 1934. Nitrat und Phosphat im Dystrophen See. — Arch. f. Hydrobiol. 27. Stuttgart.

Gorham, E. 1953 a. The development of the humus layer in some woodlands of the English Lake District. — J. Ecol. 41. Cambridge.

— 1953 b. Chemical studies on the soils and vegetation of waterlogged habitats in the English Lake District. — Ibid.

— 1955. On some factors affecting the chemical composition of Swedish fresh waters. — Geochim. et Cosmochim. Acta 7. London.

Haglund, E. 1911. Redogörelse för en botanisk-torfgeologisk undersökning af fiskdammar på torfjord vid fiskeriförsöksstationen i Aneboda. — Skr. utg. af Södra Sveriges Fiskerifören. 8, 1911. Lund.

Hald, A. 1948. Statistiske metoder. — Köbenhavn.

Hürlimann, H. 1951, Zur Lebensgeschichte des Schilfs an den Ufern der Schweizer Seen. — Beitr. z. geobot. Landesaufnahme der Schweiz 30. Bern.

Hylander, N. 1955. Förteckning över Nordens växter. 1. Kärlväxter. — Lund.

Iversen, J. & Olsen, S. 1943. Die Verbreitung der Wasserpflanzen in Relation zur Chemie des Wassers. — Bot. Tidskr. 46. Köbenhavn.

Jensen, C. 1939. Skandinaviens bladmossflora. — Köbenhavn.

Jones, L. H. & Thurman, D. A. 1957. The determination of aluminium in soil, ash, and plant materials using eriochrome cyanine R.A. — Plant and Soil 9. The Hague.

Jörgensen, E. G. 1953. Silicate assimilation by diatoms. — Phys. plant. 6. Lund.

Lillieroth, S. 1938. Die höhere Vegetation des Sees Lammen bei Aneboda. — K. Fysiogr. Sällsk. handl. N.F. 49: 14. Lund.

LILLIEROTH, S. 1949. Om syrgasförhållandena i några dammar vid fiskeriförsöksstationen i Aneboda. — Skr. utg. av Södra Sveriges Fiskerifören. 1948: 2. Lund.

— 1950. Über Folgen kulturbedingter Wasserstandsenkungen für Makrophyten- und Planktongemeinschaften in seichten Seen des südschwedischen Oligotrophiegebietes. — Acta limnologica 3. Lund.

LOHAMMAR, G. 1938. Wasserchemie und höhere Vegetation schwedischer Seen. — Symb. bot. ups. 3: 1. Uppsala.

— 1949. Über die Veränderungen der Naturverhältnisse gesenkter Seen. — Verh. int. Ver. theoret. angew. Limnol. 10. Stuttgart.

LUNDH, A. 1951. Studies on the vegetation and hydrochemistry of Scanian lakes. III. — Bot. not. Suppl. 3: 1. Lund.

LÖNNERBLAD, G. 1931. Zur Kenntnis der Chemie einiger Humusseen. — Arch f. Hydrobiol. 22. Stuttgart.

MALMER, N. 1951. En småländsk förekomst av Sphagnum Lindbergii. — Bot. not. 1951. Lund.

— 1957. Myrvegetationsundersökningar i SV Götaland. I. Vegetation och ståndortsförhållanden på Åkhultmyren i Kronobergs län. — Unprinted thesis for the degree of fil. lic.

— 1958. Notes on the relation between the chemical composition of mire plants and peat. — Bot. not. 111 (1958). Lund.

MALMER, N. & SJÖRS, H. 1955. Some Determinations of Elementary Constituents in Mire Plants and Peat. — Ibid. 108 (1955).

MAUCHA, R. 1932. Hydrochemische Methoden in der Limnologie mit besonderer Berücksichtigung der Verfahren von L. W. Winkler. — Die Binnengewässer 12. Stuttgart.

MISRA, R. D. 1938. Edaphic factors in the distribution of aquatic plants in the English lakes. — J. Ecol. 26. Cambridge.

MORTIMER, C. H. 1941. The exchange of dissolved substances between mud and water in lakes. I and II. — Ibid. 29 (1941) and 30 (1942).

NAUMANN, E. 1917. Undersökningar öfver fytoplankton och under den pelagiska regionen försiggående gyttje- och dybildningar inom vissa syd- och mellansvenska urbergsvatten. — K. Sv. Vet.-Akad. handl. 56: 6. Uppsala.

— 1921 a. Untersuchungen über die Eisenorganismen Schwedens. I. — Ibid. 63: 4.

— 1921 b. Einige Grundlinien der regionalen Limnologie. — Lunds Univ. årsskr. N.F. Avd. 2, 17: 8. K. Fysiogr. Sällsk. handl. N.F. 32. Lund.

— 1922. Södra och mellersta Sveriges sjö- och myrmalmer. — Sv. geol. unders. Ser. C 297. Stockholm.

— 1924. Die höhere Wasservegetation des Bach- und Teichgebietes bei Aneboda. — Ark. f. bot. 19: 2. Uppsala.

— 1925. Undersökningar över fytoplankton i dammar vid Aneboda fiskeriförsöksstation åren 1911—1920. Lunds Univ. årsskr. N.F. Avd. II, Bd 21: 8. K. Fysiogr. Sällsk. handl. N.F. Bd 36. Lund.

— 1932. Grundzüge der regionalen Limnologie. — Die Binnengewässer 11. Stuttgart.

NORDQVIST, H. 1921. Studien über das Teichzooplankton. — Lunds Univ. årsskr. N.F. Avd. 2. Bd 17: 5. K. Fysiogr. Sällsk. handl. N.F. Bd 32: 5. Lund.

— 1925. Studien über die Vegetations- und Bodenfauna ablassbarer Teiche. — Ibid. Bd 21: 8 resp. Bd 36: 8.

OHLE, W. 1934. Chemische und physikalische Untersuchungen norddeutscher Seen. — Arch. f. Hydrobiol. 26. Stuttgart.

OHLE, W. 1940 a. Chemische Eigenart der smäländischen Seen. — Verh. int. Ver. theoret. angew. Limn. 9. Stuttgart.

— 1940 b. Chemische Gewässerkundung in Schwedisch-Lappland. — Arch. f. Hydrobiol. 36. Stuttgart.

PEARSALL, W. H. 1920. The aquatic vegetation of the English lakes. — J. Ecol. 8. Cambridge.

— 1938. The soil complex in relation to plant communities. I. Oxidation-reduction potentials in soils. — Ibid. 26.

PEARSALL, W. H. & GORHAM, E. 1956. Production ecology. I. Standing crops of natural vegetation. — Oikos 7. Odense.

PEARSALL, W. H. & MORTIMER, C. H. 1939. Oxidation-reduction potentials in waterlogged soils, natural waters and muds. — J. Ecol. 27. Cambridge.

PERSSON, Å. 1956. Myrvegetation på nordsidan av Torne träsk. — Unprinted thesis for the degree of fil. lic.

RODHE, W. 1949. The ionic composition of lake waters. — Verh. int. Ver. theoret. angew. Limnol. 10. Stuttgart.

— 1951. Minor constituents in lake waters. — Ibid. 11. Stuttgart.

RUTTNER, F. 1931. Hydrographische und hydrochemische Beobachtungen auf Java, Sumatra und Bali. — Arch. f. Hydrobiol. Suppl. 8. Stuttgart.

SCHWARZENBACH, G. 1957. Complexometric titrations. — Bath.

SJÖRS, H. 1948. Myrvegetation i Bergslagen. — Acta phytogeogr. suec. 21. Uppsala.

— 1952. On the relation between vegetation and electrolytes in North Swedish mire waters. — Oikos 2: 2 (1950). Lund.

— 1954. Slåtterängar i Grangärde finnmark. — Acta phytogeogr. succ. 34. Uppsala.

— 1955. Remarks on Ecosystems. — Sv. bot. tidskr. 49. Uppsala.

— 1956. Nordisk växtgeografi. — Stockholm.

TAMM, C. O. 1953. Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendens). — Medd. fr. Stat. Skogsf.-inst. 43: 1. Stockholm.

THUNMARK, S. 1931. Der See Fiolen und seine Vegetation. — Acta phytogeogr. suec. 2. Uppsala.

— 1937. Über die Regionale Limnologie von Südschweden. — Sv. geol. unders. Ser. C 410. Stockholm.

— 1942. Über rezente Eisenocker und ihre Mikroorganismengemeinschaften. — Bull. Geol. inst. Upps. 29. Uppsala.

— 1945 a. Die Abwasserfrage der Växjö-Seen in hydrobiologischer Beleuchtung. — Medd. fr. Lunds Universitets Limn. inst. 4. Lund.

— 1945 b. Zur Soziologie des Süsswasserplanktons. — Fol. limn. scand. 3. Lund.

— 1948. Sjöar och myrar i Lenhovda socken. — Lenhovda. En Värendssocken berättar, p. 665—710. Moheda.

— 1952. Karaktärsdrag i sörmländsk sjövegetation. — Natur i Södermanland. Göteborg.

TROEDSSON, T. 1955. Vattnet i skogsmarken. — K. Skogshögsk. skr. 20. Norrtälje.

WALDHEIM, S. 1944. Die Torfmoosvegetation der Provinz Närke. — Lunds Univ. årsskr. N.F. Avd. 2. 40: 6. Kungl. Fysiogr. Sällsk. handl. N.F. 55: 6. Lund.

WITTING, M. 1947. Katjonbestämningar i myrvatten. — Bot. not. 1947. Lund.

— 1948. Preliminärt meddelande om fortsatta katjonbestämningar i myrvatten sommaren 1947. — Sv. bot. tidskr. 42. Uppsala.

ÅBERG, B. & RODHE, W. 1942. Über die Milieufaktoren in einigen südschwedischen Seen. — Symb. bot. ups. 5: 3. Uppsala.

BOTANISKA NOTISER 1960 · VOL. 113 · FASC. 1 · LUND

Från Lunds Botaniska Förenings förhandlingar 1959

Den 27 februari. Civiljägmästare, greve Hans Wachtmeister talade om »Granens sydgräns i Blekinge». Av allt att döma var granen sällsynt i Blekinge vid slutet av 1600-talet men är i våra dagar allmän i större delen av landskapet. Planterad gran har otvivelaktigt haft betydelse för spridningen de senaste 150 åren. På grundval av omfattande fältstudier hade föredragshållaren utarbetat en karta över sydgränsen i Blekinge för granens nuvarande uppträdande i slutna bestånd. Granskogsbestånd, som kunde påvisas vara planterade, hade icke medräknats. Den av föredragshållaren upprättade grangränsen visade relativt god överensstämmelse med Hesselmans och Schottes år 1907 publicerade gräns.

Fil. lic. Björn Berglund höll föredrag om »Torhamns skärgård ur botanisk synvinkel». Från länsstyrelsen i Karlskrona har föreslagits, att en del öar i Torhamns skärgård skulle avsättas som naturreservat, och det föreslogs även, att de då skulle planteras med skog. Föredragshållaren gav en översikt över detta områdes nuvarande utseende. Öarna är ofta trädlösa med en mer eller mindre tät enbuskvegetation. Gräsmarker med en trivial flora är ett dominerande inslag. Härifrån kan nämnas *Deschampsia flexuosa, Agrostis tenuis, Festuca ovina, Nardus stricta, Achillea millefolium, Campanula rotundifolia, Rhytidiadelphus squarrosus.* I vissa fall kan ett något rikare buskskikt förekomma med bl.a. hagtorn, slån, *Rosa*-arter och *Lonicera periclymenum.* Vegetationens nuvarande utformning är i hög grad beroende av betningen. Betning har pågått åtminstone sedan 1500-talet och av lantmäterikartor från 1700-talet att döma fanns redan då ett beteslandskap av samma utseende, som man idag finner på de platser, där betningen fortgår. Föredragshållaren framhöll som önskvärt, att dessa öars ur kulturhistorisk och ekologisk synpunkt intressanta betesmarker bevaras så vitt möjligt i oförändrat skick.

Professor H. Weimarck demonstrerade material av *Cerastium macilentum* och *C. dolosum,* vilka i regel räknas in under *Cerastium semidecandrum.* Deras systematiska värde är emellertid icke tillräckligt klarlagt. Vidare visades *Scleranthus polycarpos,* som står nära *Scl. annuus,* med vilken den ofta sammanslås, men den skiljer sig i flera karaktärer från denna.

Den 19 mars. Sammanträde hölls tillsammans med Zoologiska föreningen i Lund på Zoologiska institutionen, där professor Paul Errington höll föredrag om naturskydd i Amerika. Bisonoxen höll på att utrotas men räddades, mycket tack vare privatpersoner, som skyddade hjordar på privat mark, innan reservat inrättades. Föredragshållaren framhöll nödvändigheten av ett allsidigt inriktat naturskydd, och nämnde såsom exempel på motsatsen ett område, där större rovdjur praktiskt taget utrotats. Här ökade antalet betande vilda djur så starkt, att betningen ödelade vegetationen. Vissa prärieområden har blivit skyddade. Här har man funnit att brand och bete i viss omfattning är nödvändiga för ett bibehållande av den ursprungliga vegetationen. Föredragshållaren hyste farhågor för att Alaskas vidsträckta vildmarker skulle lida allvarlig skada, när landet inom en snar framtid blev mera lättillgängligt.

Den 21 april. Revisionsberättelse framlades, varvid full ansvarsfrihet beviljades.

Föredrag om det finska myrtypsystemet hölls av professor Risto Tuomikoski. Först lämnades en översikt över Finlands skogstyper, vilka först urskildes av Cajander. Huvudgrupperna i detta system är lundar och hedskogar, och dessa två grupper motsvarar ungefär den indelning som A. Nilsson har i sina vegetationsserier. Huvudgrupperna indelas sedan vidare i ett flertal typer. Dessa typer definieras på basis av vegetationen i den hyggesmogna skogen. Cajander tog hänsyn både till den kvantitativa och den kvalitativa sammansättningen av vegetationen. Troligen kan de finska skogstyperna »översättas» till motsvarande enheter i Braun-Blanquets system.

Från Finland är omkring 150 myrtyper beskrivna, men en del av dessa får betraktas som synonyma, och en del är av låg rang. Teoretiskt skulle det i Finland finnas 400—500 typer av myr. Föredragshållaren ansåg, att växtsociologien ej borde bygga upp sina enheter till ett system av det slag, som man har inom den taxonomiska systematiken, då ett sådant system för vegetationsenheter icke kan bygga på något slag av släktskap utan endast på likheter. Istället borde ett växtsamhälle karakteriseras med en formel, som utvisade dess läge inom var och en av de olika variationsriktningar, som kan fastställas på en lokal.

Den 6—7 juni. Exkursion på Öland med professor H. Weimarck som ledare. Första dagen var färdvägen: Borgholm—Högsrum—Vickleby—S. Möckleby—Stenåsa—Sandby—Gråborg—Borgholm.

I Högsrums socken, Halltorp, studerades en vacker orkidéäng på en sedan flera år övergiven åker. Där antecknades bl.a. *Anthyllis vulneraria, Bellis perennis, Carlina vulgaris, Centaurea scabiosa, Cirsium acaule, Galium verum, Hieracium pilosella, Linum catharticum, Orchis militaris, O. ustulata, Plantago lanceolata, P. media, Polygala amarella, Primula veris, Avena pubescens, Briza media, Carex flacca, Cynosurus cristatus, Festuca ovina* och *Poa pratensis*. Vid Halltorp besöktes även Halltorps hage med de fridlysta jätteekarna, där lundvegetationen bestod av *Carpinus betulus, Corylus avellana, Crataegus* sp., *Fraxinus excelsior, Quercus robur, Tilia cordata*; *Aegopodium podagraria, Anemone hepatica, Cardamine bulbifera, Galium odoratum, Geranium silvaticum, Lathyrus vernus, Mercurialis perennis, Orchis mascula, Pulmonaria officinalis, Ranunculus ficaria, Rumex sanguineus, Sanicula europaea, Stellaria holostea*; *Carex silvatica, Melica uniflora, Poa nemoralis.*

I Vickleby socken nära gränsen till Resmo gjordes ett besök på Stora Alvaret. På grund av den tidiga våren och den påfallande torkan var många av alvarväxterna redan överblommade och förbrända. Bland påträffade arter kan nämnas *Galium pumilum, G. triandrum, Globularia vulgaris, Viscaria alpina, Poa alpina, Cetraria nivalis* och *Tamnolia vermicularis.*

I Albrunna, S. Möckleby, besöktes en lokal med riklig förekomst av *Adonis vernalis.* Våradonisen växte i utkanten av en liten lövskogslund, som med ett stengärde var skild från alvaret. Den del av lunden, där *Adonis* förekom, var av lövängskaraktär med endast enstaka träd och buskar.

Väster om Ekelunda i Sandby socken studerades karstområdet, där *Asplenium ruta-muraria* och *trichomanes* sågs i sprickorna.

Strax intill landsvägen väster om Sandby kyrka demonstrerades en riklig förekomst av *Carex obtusata,* som växte utmed en stengärdesgård.

Andra dagens färdväg var: Borgholm—Persnäs—Lilla Horn—Grankullaviken—Neptuni åkrar—Byxelkrok—Byrum—Sandvik—Borgholm.

På ett litet alvarområde i Persnäs c. 1,5 km söder om stationen tilldrog sig bladrosetter av *Draba incana* särskilt intresset.

Den paradisiska lövängen i Lilla Horn ägnades ett ingående studium vid en rundvandring. På de öppna ytorna sågs bl.a. *Anthyllis vulneraria, Chrysanthemum leucanthemum, Galium boreale, Geum urbanum, Gymnadenia conopsea, Inula salicina, Linum catharticum, Melampyrum cristatum, Orchis militaris, O. ustulata, Parnassia palustris, Pinguicula vulgaris, Polygala amarella, Potentilla erecta, Primula farinosa, P. veris, Ranunculus acris, Rhinanthus serotinus, Rumex acetosa, Saxifraga granulata, Scorzonera humilis, Serratula tinctoria, Trifolium pratense, Anthoxanthum odoratum, Briza media, Carex flacca, C. hostiana, C. panicea, Scirpus pauciflorus,* och i buskagen förekom *Anemone hepatica, Campanula trachelium, Convallaria majalis, Laserpitium latifolium, Lathyrus vernus, Listera ovata, Maianthemum bifolium, Melampyrum pratense, M. silvaticum, Paris quadrifolia, Rubus saxatilis* och *Poa nemoralis.*

I Böda kronopark besöktes de gamla dynområden, som Linné skildrat i sin »Öländska Resa».

I närheten av Grankullaviken fanns rikligt med *Cephalanthera longifolia* i ett blandskogsbestånd, och i ett kärrområde norr om detta växte bl.a. *Cladium mariscus.*

Färden gick sedan söderut längs västra kusten till Neptuni åkrar. Frånvaron av högre vegetation gjorde här ett starkt intryck. Nästan endast där någon enstaka buske slagit sig ned, kunde några kärlväxter uppletas. De arter, som iakttogs, var: *Juniperus communis, Pinus silvestris, Ribes alpinum, Calluna vulgaris, Hieracium pilosella, Hornungia petraea, Lactuca muralis, Sedum acre, Senecio vulgaris, Silene nutans, Taraxacum* sp. och *Festuca ovina.*

Den 20 september. Exkursion till sydvästra Skåne under ledning av professor H. Weimarck och docent Börje Lövkvist.

Färdväg: Lund—Malmö—Bunkeflo—Skanör—Skanörs ljung—Ljunghusens stn—L. Hammars Näs—Bernstorp—Vellinge—Malmö—Lund.

Vid stranden väster om Ängsslätt i Bunkeflo demonstrerade ingenjör P. G. Perby *Iris spuria.* Strandängarna var ovanligt torra och mycket hårt betade, men en del arter kunde trots allt identifieras, exempelvis *Bupleurum tenuissimum, Centaurium pulchellum* och *vulgare, Gentianella uliginosa* och *Trifolium fragiferum.*

I Skanör besöktes lokalen för *Gnaphalium luteo-album*, vilken såg ut att trivas väl och förekom i rik mängd.

Vid vegetationsstudier i sydöstra kanten av Skanörs ljung ägnades uppmärksamheten åt *Deschampsia setacea* i synnerhet. I en fuktig svacka växte den tillsammans med *Drosera intermedia, D. rotundifolia, Erica tetralix, Hydrocotyle vulgaris, Litorella uniflora, Lycopodium inundatum, Pedicularis silvatica* och *Molinia coerulea*.

I en *Phragmites*-vass vid stranden nedanför Ljunghusens stn fick deltagarna tillfälle att studera *Sonchus palustris*.

På L. Hammars Näs demonstrerade docent Lövkvist olika typer av *Agropyron repens* och *Aster tripolium*.

Vid Bernstorp i Vellinge socken kunde på den södra backen 10 exemplar av *Orobanche major* uppletas, och här gavs också möjlighet att stifta bekantskap med den misskända arten *Pimpinella nigra*. På en pilevall ett par hundra meter längre österut visades ytterligare en raritet nämligen *Senecio erucifolius*, som växte tillsammans med bl.a. *Inula salicina* och *Serratula tinctoria*.

Den 2 oktober. Docent Börje Lövkvist demonstrerade material av havsstrandstyper av *Agropyron repens* från sydvästra Skåne. Av allt att döma förekommer här tre olika kromosomtalstyper av *Agropyron repens* nämligen tetraploider, hexaploider och ytterligare en typ, som kan förmodas vara octoploid. Dessa olika kromosomtalstyper av *A. repens* kan bilda hybrider med *A. junceum*. Hybriderna tycks ha viss fertilitet varför introgression är tänkbar mellan arterna.

Dr. E. A. Schelpe, Cape Town, höll föredrag om ormbunkväxternas utbredning i södra Afrika. Elden spelar i Afrika inom många områden en väsentlig roll för vegetationens utformning. Proteacéer och ormbunkar dödas ofta av dessa bränder, medan t.ex. restionacéer i regel kan överleva och skjuta nya skott från sina rotstockar. På skyddade lokaler kan emellertid vissa ormbunkar undgå att förstöras av eld: *Cyathea dregei* kan ses i små raviner men saknas på omgivande plana marker, där elden gått fram.

Som exempel på en till synes paradoxal utbredning nämndes *Marsilea*. Denna vattenormbunke har sin rikligaste förekomst i de torrare delarna av Sydafrika, där den uppträder i tillfälliga gölar, vilka i samband med en regnperiod kan ha en varaktighet av c. 3 månader. Med sina sporokarp, som kan behålla sin grobarhet flera år, överlever ormbunken torrperioderna. Gametofytens bristande förmåga att uthärda extrema förhållanden kan vara den faktor, som begränsar en arts möjligheter till större utbredning. Hos *Acrostichum aureum* förmodas gametofyten ha denna begränsande betydelse. Denna ormbunke förekommer i mangrovevegetation, men har ej påträffats på liknande lokaler vid sötvatten.

Den 25 november. Till styrelse för år 1960 valdes: Professor H. Weimarck, ordförande; docent O. Almborn, vice ordförande; fil. mag. J. Ericson, sekreterare; fil. kand. Hans-Ebbe Lindskog, vice sekreterare; docent B. Hylmö, docent B. Lövkvist, fil. lic. A. Kylin, fil. mag. S.-O. Strandhede, fil. mag. S. O. Falk.

Till revisorer under 1960 utsågs lektor O. Palmgren och fil. dr Asta Almestrand med fil. lic. Pär Fransson och fil. lic. Bo Peterson som suppleanter.

Ett förslag om ändring av stadgarna så, att korresponderande ledamöter skall kunna kallas, bifölls.

Professor Gunnar Erdtman höll föredrag om »Modern palynologi». Inledningsvis berördes den av kvartärgeologer använda terminologien för att beteckna de växter, som uppträder under de olika epokerna mellan två istider. De under en istid förekommande benämnes kryokrater; efter isens avsmältande under den första postglaciala epoken utgöres floran av protokrater; på ett senare stadium med ett gynnsamt värmeklimat behärskar mesokraterna vegetationen; under den nedgångstid, som är en inledning till en ny istid, har telokrater övertagit herraväldet.

Under alla dessa epoker, bortsett från själva istiden, kan man på lämpade växtplatser påträffa arter, som utmärkes av att de koloniserar nyligen blottad mark, d.v.s. de uppsöker lokaler med mycket liten eller ingen konkurrens. För dessa arter föreslog föredragshållaren benämningen apokrater. Som exempel på var apokrater uppträder i nutiden nämndes vissa typer av alvarmark, flodstränder med fortgående erosion, deltaområden, ruderatmarker och åtskilliga andra kulturskapade ståndorter.

Vid studium av pollen av vissa närstående arter, som ur pollenanalytisk synpunkt kan vara av intresse att särskilja, t.ex. *Alnus glutinosa* och *incana*, *Quercus robur* och *petraea*, har det visat sig, att vattenpreparat ger möjlighet att iaktta användbara skiljekaraktärer.

Att uppleta lokaler, där prov kan insamlas, vilka genom pollenanalys kan ge upplysning om ett områdes vegetationshistoria, är i torrare trakter ofta ett otacksamt arbete. I sydvästra Asien hade föredragshållaren gjort insamlingar i grottor, dels i en grotta med fladdermusexkrementavlagringar, dels i en grotta, som ansågs ha varit bebodd av människor i 70.000 år.

I pollenprov från torvlager på Omberg hade pollen av en *Helianthemum*-art, som skulle kunna vara *oelandicum*, påträffats. Fyndet daterades till den tid, då Omberg var en nunatak under avsmältningsskedet efter senaste istid.

Den 11 december. Överläkare Gunnar F. Lundgren höll föredrag om Skandinaviens orchidéer. Med utomordentliga färgbilder illustrerades alla skandinaviska arter av familjen. Här kan blott nämnas ett par av dessa.

Orchis palustris på Gotland har ju alltid varit en raritet, och man kunde kanske frukta, att den skulle försvinna i samband med de utdikningar, som företagits. Den ser emellertid ut att överleva och förekom t.o.m. i kanten av en utdikningskanal.

Även en annan av våra sällsyntaste orchidéer hade föredragshållaren lyckats återfinna i förhållandevis riklig mängd, nämligen *Platanthera oligantha* på Nuolja vid Torne träsk.

Av *Orchis maculata* visades ett flertal olika typer. Bland dem även den märkliga typ med varmt röd, treflikad läpp, som påträffades i Uppland för några år sedan (Hultén SBT 49; Afzelius SBT 52).

JAN ERICSON

Litteratur

J. SCHMITHÜSEN: Allgemeine Vegetationsgeographie. — Lehrbuch der Allgemeinen Geographie, Band IV. Walter de Gruyter & Co. Berlin 1959. XVIII+261 sid. Pris DM 28: —.

Detta arbete utgör en del i en serie läroböcker i geografi, men erbjuder genom sitt ämne även stort botaniskt intresse.

Efter en kort inledning med historik och ämnesdefinition ger förf. en skildring av olika arealtyper och en redogörelse för den botaniskt-floristiska indelningen av jorden. Han ger även en karakteristik av de olika florarikena. Framställningen illustreras av välkända utbredningskartor från Good, Hutchinson m.fl. Större intresse rent geografiskt torde växternas livsformer erbjuda och följdriktigt behandlas detta avsnitt utförligare. Den använda grupperingen bygger på Drudes system, men innebär delvis en omarbetning av detta. En anknytning till Raunkiaers välkända system är lätt genomförbar. Denna första del av boken avslutas med ett avsnitt om orsakerna till de taxonomiska enheternas och livsformernas fördelning på jordytan. De klimatiska, edafiska och antropogena förhållandena står i förgrunden, men även biologiska och historiska orsakskomplex diskuteras.

Eftersom förf. betonar att »nicht die einzelnen Lebewesen, sondern . . . die Pflanzenbestände sind die landschaftlich wirksamen kleinsten Einheiten der Vegetation», ägnar han en ingående framställning åt växtsamhällsläran. Givetvis behandlas den fysionomiska grupperingen av växtsamhällena i olika formationer mycket ingående. Emellertid får även metoderna för den floristiska indelningen en utförlig beskrivning. Han följer därvid helt de principer, som tillämpats av Tüxen m.fl. under senare år. Även de viktigaste ekologiska begreppen behandlas liksom även ekosystembegreppet och andra därmed jämförliga. När sedan vegetationens roll i landskapet behandlas ur mera geografisk synpunkt sker det på grundval av det av Tüxen införda begreppet »potentiell naturlig vegetation». Därvid betonas alldeles särskilt människans betydelse för uppkomsten av de nutida växtsamhällena på jorden inte blott i den tempererade zonen utan också i tropikerna.

I bokens avslutande avsnitt beskrives jordens olika klimatiska vegetationszoner. Det är närmast frågan om en beskrivning av de karakteriserande vegetationszonernas fysiognomiska utseende. Vidare behandlas framförallt de klimatiska förhållandena och jordmånstyperna. Från botanisk synpunkt är det beklagligt, att i alltför ringa utsträckning de arter och släkten, som karakteriserar dessa växtsamhällen floristiskt, omnämnes. I bilder, diagram och tabeller finns många goda ansatser med en del utbredningskartor, typiska bergszoneringar eller översikter över vikarierande arter inom olika områden, men det stannar tyvärr vid ansatser.

Det är alltid med intresse och förväntan man tar del av nyutkomna, moderna läroböcker i allmän växtgeografi. Det finns ju redan nu en lång rad, t.ex. av Cain, Good, Walter eller Wulff för att nu nämna några mera kända författarnamn. Ingen av dessa ger emellertid en fullständig framställning av växtgeografin. De behandlar antingen enbart en del av ämnet eller bara en del av jorden. Förf. av det här behandlade arbetet strävar uppenbarligen efter att ge en fullständig framställning av ämnet från geografisk synpunkt. Tyvärr blir arbetet från botanisk synpunkt oavslutat främst därför att, som ovan framhållits, en floristisk beskrivning av de olika vegetationsregionernas växtsamhällen saknas.

Nils Malmer

Natur i Bohuslän. Under red. av Carl Skottsberg och Kai Curry-Lindahl. Svensk Natur, Stockholm, 1959. 485 s. Pris 65 kr.

Den senaste delen i Svensk Naturs landskapsserie har ägnats Bohuslän. Detta är ju framför allt ett strandens och kustens landskap, vilket i hög grad sätter sin prägel på de botaniska skildringarna i det föreliggande verket. Ett annat drag som också ständigt framträder i beskrivningarna, är de stora lokala motsättningarna i såväl topografi som klimatförhållanden; denna omväxling har gjort att Bohuslän har en förvånande rik flora och i artantal överträffar de flesta andra svenska landskap. Detta framgår tydligt bl.a. av den översikt »Bohusläns högre flora», som skrivits av Carl Skottsberg. Förf. gör en överblick över floran med hänsyn till dess regionala fördelning och växtgeografiska anknytning. Det är åtskilliga utbredningsgrupper som stråla samman inom landskapet: oceaniska, subkontinentala, nordliga och sydliga arter, och grupperna kunna ytterligare uppdelas. Bland de oceaniska elementen lägger man särskilt märke till de euoceaniska arterna, bland vilka t.ex. *Carex punctata* och *Digitalis purpurea* inom Sverige ej förekomma utom Bohusläns område, medan andra i sin utbredning nå ned till Halland eller Skåne, andra än längre in i Sydsverige. (Att *Cerastium tetrandrum* förekommer vid Öresund, torde dock ej numera äga sin giltighet.) En annan intressant grupp, vars historia något diskuteras, är de fjällväxter som finnas bland de nordliga arterna; till dessa höra *Poa alpina, Viscaria alpina, Sedum rosea* och *Alchemilla alpina,* medan *Polystichum lonchitis* försvunnit ur landskapets flora och *Cryptogramma* ej kunnat återfinnas på senare tid.

Några artiklar ge en speciell behandling av vissa vegetationstyper. Därvid har som sig bör havsstrandens vegetation fått en framskjuten plats; den har fått en sakkunnig skildrare i V. Gillner, som skriver om »Havsstranden i Bohuslän och dess växtvärld». Alltefter vegetationen uppdelas stranden i klippstranden, med sparsam växtlighet, blockstranden, där åtskilliga intressanta arter förekomma, som *Limonium humile, Euphorbia palustris, Crambe, Glaucium* och *Mertensia,* sandstranden (med bl.a. *Eryngium*), och strandängarna; de senare indelas i två huvudtyper efter saltvattnets större eller mindre påverkan. En annan, mera speciell vegetationstyp skildras av R. Ivarsson i artikeln »Bohuslänska kustkratt». Det påvisas hur buskvegetationen spelar en stor roll i Bohusläns kusttrakter och omfattar många olika arter, bl.a. även liguster och idgran, den förra endast förekommande i norra Bohuslän, den senare vanligare där. Över havets vegetation ger T. Levring en översikt i ett bidrag »Bohushavets växtvärld», där de viktigaste representanterna för olika alggrupper skildras och deras förekomst och biologi behandlas.

Bland de uppsatser, som behandla särskilda områden av Bohuslän, märks en rad intressanta skildringar av olika öar. I främsta rummet bör här nämnas A. Frisendahls artikel »Kosteröarna». En mängd sällsyntheter, tillhörande olika floraelement, få här passera revy, såsom *Ranunculus cymbalaria, Mertensia* och *Glaucium, Botrychium simplex, Tilia platyphyllos, Sorbus obtusifolia* och ett antal av de eljest i Bohuslän ej så vanliga orkidéerna. Ett par andra öar, som också ha mycket att bjuda på, är Älgön och Brattön, skildrade av T. Lundqvist. En mångfald anspråksfulla lundväxter omtalas från östra delen av Älgö; f.ö. finns *Sedum rosea,* som här har sitt förnämsta tillhåll i Bohuslän, och *Viscaria alpina,* samt, den märkligaste av dem alla, den av förf. anträffade *Lathyrus sphaericus,* som växer på en klipphylla på Brattön, tydligen ganska väl skyddad. Andra öar som skildras äro Orust och Tjörn, som behandlas av E. Manker; här får man liksom i andra fall en tydlig bild av den starka kontrasten mellan lummiga dalar med ädla lövträd och karg klippvegetation.

Bland andra uppsatser bör särskilt nämnas S. Woldmars artikel: »Botaniska strövtåg i Uddevallatrakten», som ger ett gott belägg för omdömet att Bohusläns flora är omväxlande och rik. En mängd olika vegetationstyper skildras, från skalgrusbankar — där *Galeopsis angustifolia* är en speciell karaktärsväxt — och *Cladium*-sjöar till mossrika granskogar och fattiga myrmarker. Från ett annat område är Sture Nilssons skildring »I Kvistrumsdalen och kring Kärnsjön», som behandlar den botaniskt ovanligt rika Kvistrumsdalen, där *Potentilla rupestris* och *Inula salicina* förekomma som karaktärsväxter, och vidare vegetationen kring Kärnsjön, med dess starkt kontrasterande väst- och öststrand. En mer torftig natur möter i N.-G. Karviks bidrag: »Kynnefjäll», där man får ett exempel på en tidigare skogklädd mark, som genom avverkning, svedjning och ljungbränning blivit till kalmark men där skogen nu står i begrepp att återvända.

Om vegetationens — och speciellt skogens — historia från allra äldsta tid ges en sakkunnig utredning av Magnus Fries i »Vegetationslandskapets historia i Bohuslän», stödd såväl på pollenanalysens resultat som på historiska källor. Här skildras skogens första invandring, dess tillbakaträngande i historisk tid och den senaste tidens revansch; denna utveckling är tydligen vanlig i landskapet. Den sista fasen i utvecklingen skildras även i artikeln »Bohuslän — ett skogsland i vardande» av G. Wennmark.

Ett par intressanta artiklar behandla vissa mindre växtgrupper och deras förekomst i Bohuslän. Sålunda skildrar I. Segelberg landskapets *Rosa-* och *Rubus*-arter i »Rosor och björnbär i Bohuslän». Det ges här en översikt över de »stor-arter» av *Rosa,* som förekomma i Bohuslän, ej mindre än 7 av de 8 i Sverige förekommande, samt över *Rubus*-arterna, särskilt de »äkta» björnbären, bland vilka ett par ha sin enda svenska förekomst i Bohuslän. Om lavar och mossor handlar G. Degelius' bidrag: »Oceaniska drag i Bohusläns lav- och mossflora», där förf. tar upp till behandling ett antal arter av intressant utbredning (delvis också ovanligt storvuxna och praktfulla), av vilka ett par euoceaniska arter höra till den bohuslänska florans största sällsyntheter.

Som vanligt, när det gäller denna serie, är framställningen illustrerad med ett stort antal utmärkta fotografier. Särskilt fäster man sig kanske vid N. J. Nilssons och S. Schiölers detaljbilder av olika växter; den förre bidrager också med förstklassiga landskapsbilder. Färgbilderna äro kanske ej alltid helt lyckade.

H. Hjelmqvist

The Lichenologist. Vol. I h. 1—3. Utgiven av British Lichenological Society 1958—1959.

Den engelska lavforskningen har under flera decennier visat en påtaglig stagnation. De av Annie Lorrain Smith utgivna utförliga lavflororna (A Monograph of the British Lichens 1—2, 1918—1926, och A Handbook of the British Lichens, 1921) var visserligen i många stycken kompilatoriska, men man hade ändå väntat sig att de skulle främjat den brittiska lavforskningen i större utsträckning än vad som skedde. Trettio- och fyrtiotalen såg knappast flera aktiva lichenologer än W. Watson († 1960) och I. Mackenzie Lamb. Den sistnämnde, som på trettiotalet var knuten till British Museum, lämnade tidigt England och är nu chef för Farlow Herbarium, Cambridge, U.S.A.

A. L. Smiths floror utgjorde dock trots allt ett ferment, som kom att bli verksamt på längre sikt. I februari 1958 bildade 24 för lavar intresserade botanister British Lichenological Society, som efter två år vuxit till c:a 200 medlemmar. På programmet har stått möten med flera dagars exkursioner i olika delar av England samt en lavkurs för nybörjare. Man har även lagt grunden till ett herbarium och ett bibliotek, som båda lånar ut material till medlemmar.

Sällskapet har även lyckats förverkliga det gamla önskemålet om en särskild lichenologisk tidskrift. Tre häften av The Lichenologist (tillsammans 124 sidor) har hittills utgivits. Redaktör är P. W. James, vilken förestår lavherbariet vid British Museum. Innehållet är mångsidigt och ger en god bild av det nyvaknade intresset för lavar i England. Främst märks en serie koncisa revisioner — mest i form av examinationsschemata — av de brittiska arterna av släktena *Cladonia* (av J. H. Tallis), *Collema* (A. E. Wade), *Usnea* (Tallis) och *Alectoria* (Wade). Den kritiska översikten över *Usnea* är utan tvekan tidskriftens värdefullaste bidrag. Vidare finner man en rad notiser om för öriket nya lavar, varibland må nämnas så märkliga arter som *Parmelia alpicola* och *Cavernularia Hultenii.* Även andra områden än systematik och växtgeografi är representerade, t.ex. kortare uppsatser om faktorer, som orsakar lavarnas försvinnande i städerna, och om sporspridning och groning hos *Peltigera.*

Medlemskap i sällskapet kan erhållas även av utlänningar efter anmälan till sekreteraren Mr. A. E. Wade, Dept. of Botany, National Museum of Wales, Cardiff. För medlemsavgiften (1 £ årligen) erhåller man 2 häften av tidskriften.

Ove Almborn

Ursula Duncan: A Guide to the Study of Lichens. Arbroath (T. Buncle & Co.) 1959. 164 s. 19 planscher. Pris 25/–.

Den nyväckta lichenologiska aktiviteten i England har även manifesterat sig i en ny lavflora. Den framträder närmast som en översiktlig handledning för nybörjare och är snarare avsedd att användas som komplement till A. L. Smiths floror än att ersätta dem. Författarinnan har veterligen ej tidigare skrivit om lavar. Hon har emellertid grundligt gått igenom de sista decenniernas litteratur, vilket lett till åtskilliga ändringar i A. L. Smiths artavgränsning och nomenklatur. Femtiotalets omdaningar inom nomenklaturreglerna har beaktats. Sålunda möter man för första gången i en sammanfattande lavflora namn av typen *Hypogymnia physodes* var. *physodes*. Arterna har ej avgränsats alltför snävt. De kemiska reaktionerna anges, men rent »kemiska» arter har ej accepterats.

Boken inledes med ett högst kortfattat kapitel om »Structure of lichens» (mindre än 3 sidor utan bilder!) och ett ännu kortare om »Ecology». Sedan följer korta nycklar till ordningar, familjer och släkten. En allvarlig brist är emellertid att inga nycklar ges till arterna. I stället har förf. valt den originella metoden att beskriva en art i varje släkte rätt utförligt och sedan ganska summariskt omnämna ett urval av övriga arter. För en nybörjare torde det bli svårt att på så sätt orientera sig i de stora släktena, såsom *Cladonia, Lecanora* och *Lecidea*. Säkerligen är A. L. Smiths överskådliga bestämningsnycklar, som dessutom kompletteras av teckningar över habitus och anatomi, fortfarande mera användbara. Det hade avgjort varit en fördel, om förf. i stället gjort en moderniserad version av A. L. Smiths Handbook.

Miss Duncan följer W. Watsons system och släktavgränsning, vilket ibland konfunderar den som är van vid Zahlbruckners, som trots brister rätt allmänt accepterats inom lichenologien. Hon börjar alltså med *Usnea* och slutar med pyrenokarperna, *Thelocarpaceae* och *Pyrenidiaceae*. Man återser en rad släkten, som numera övergivits av flertalet lichenologer, t.ex. *Aspicilia, Squamaria, Psora, Biatora, Biatorina* och *Platysma*. *Buellia* kommer intill *Rhizocarpon*, vilket får anses som en naturlig gruppering.

Korrekturläsningen avslöjar ofta att förf. ej är någon erfaren lichenolog. Släktet *Ionaspis* stavas genomgående felaktigt *Ionapsis*. Likaså skriver hon konsekvent *Lecania helicopsis* i st.f. *helicopis*. Från A. L. Smith har hon ärvt det helt omotiverade skrivsättet *Lecanora pinastre* i st.f. *pinastri*. En rad kända lavforskares namn har felstavats i litteraturförteckningen, där särskilt tyska boktitlar blivit svårt förvrängda.

Boken är knappast att rekommendera för svenska lichenologer. Det är emellertid nyttigt att erinra sig att vårt land — trots 150 års obruten lichenologisk verksamhet och en rad lavforskare av första rangen — ej kunnat åstadkomma någon motsvarighet till Miss Duncans bok, d.v.s. en översiktlig och någorlunda fullständig svensk lavflora.

Ove Almborn

Naturens värld. Svensk redaktör: Ivar Agrell. Bokförl. Diana, Hälsingborg.

Den nystartade tidskriften »Naturens värld» är en svensk upplaga av den sedan länge i Danmark utgivna tidskriften »Naturens Verden». Det första häftet, för januari 1960, innehåller en rad artiklar som översatts från danskan — ett par av dem författade av T. W. Böcher —, men i fortsättningen är det meningen att även svenska originaluppsatser skall ingå i tidskriften. Att döma av första häftet är illustrationsmaterialet rikt och vackert. Priset är relativt högt, 54 kr. för årgång om 12 häften.

H. H.

BOTANISKA NOTISER 1960 · VOL. 113 · FASC. 1 · LUND

Notiser

Ny professor. Fil. dr Kåre Fröier, Svalöv, har utnämnts till professor och sekreterare i Kungl. Skogs- och Lantbruksakademien från den 1 jan. 1960.

Riksmuseets botaniska avdelning. Till amanuenser vid Naturhistoriska Riksmuseets botaniska avdelning har Vetenskapsakademien utsett Benkt Sparre och Hans Tralau.

Utmärkelser. Till utländsk ledamot i klassen för botanik har Kungl. Vetenskapsakademien den 9 mars valt professor William Owen James. Den Lindbomska belöningen, bestående av 500 kr. eller guldmedalj av samma värde, har av akademien tilldelats docent Gerd Bendz, Uppsala, för hennes arbeten om vissa högre svampars kemi.

Doktorsdisputationer. Vid Stockholms högskola disputerade fil. lic. Måns Ryberg den 12 mars 1960 på avhandlingen »Studies in the morphology and taxonomy of the Fumariaceae». Vid Uppsala universitet försvarade fil. lic., lektor Vilhelm Gillner den 19 mars avhandlingen »Vegetations- und Standortsuntersuchungen in den Strandwiesen der schwedischen Westküste».

Forskningsanslag. K. Skogs- och Lantbruksakademien har i jan. 1960 utdelat bl.a. följande anslag: Till intendent C. L. Behm, Hammarö, doc. S. Bingefors och t.f. prof. E. Åberg, Uppsala, 5.000 kr. för agrobotanisk bearbetning av insamlat kulturväxtmaterial från sydvästra Asien; till doc. S. Bingefors, Uppsala, 2.000 kr. för fortsatt undersökning av resistensförhållanden mot lusernnematod hos i Sverige odlingsbara lusernstammar; till fil. lic. T. Denward, Svalöv, 2.000 kr. för fortsatta undersökningar rörande identifiering av bladmögelraser i södra Sverige; till fil. lic. S. Ellerström, Svalöv, 2.000 kr. för jämförande ekologisk studie av förädlingsmaterial av olika kulturväxter odlat i Sverige och Medelhavsområdet; till prof. G. Erdtman, Solna, 5.000 kr. för undersökning av pollenkornens finstruktur hos svenska träd; till Föreningen för växtförädling av fruktträd, Fjälkestad, 447 kr. för vissa kostnader för två avhandlingar över växternas, speciellt fruktträdens, temperaturreaktioner av P. Tamas; till universitetslektor K. Gundersen, Göteborg, 6.670 kr. för undersökningar rörande fysiologiska förlopp hos rotrötesvampen vid tillförsel av cycloheximid jämte bekämpningsförsök; till agronomerna W. Johansson och B. Svensson, Uppsala, 4.500 kr. för fortsatta studier över utvecklingen hos potatis som funktion av vattentillgången i marken; till agr. dr J. Mac Key, Svalöv, 1.000 kr. för fortsatta studier rörande artdifferentieringen inom släktet *Triticum*; till prof. C. Malmström, Stockholm, 15.000 kr. för undersökningar rörande analyser av torvprov; till fil. kand. Magnhild Umaerus, Svalöv, 3.000 kr. undersökningar av olika dagslängders och ljuskvalitéers inflytande på skilda rödklöverekotypers utvecklingsrytm och övervintringsförmåga.

Statens naturvetenskapliga forskningsråd har den 17 febr. 1960 utdelat följande anslag till botanisk forskning: Till laborator S. Florin, Uppsala, 3.000 kr. för kvartärgeologisk undersökning över nivåförändringar, senkvartär vegetationsutveckling och paleo-pedologiska förhållanden inom vissa fornlämningsområden i Uppland; till prof. N. Fries, Uppsala, 13.800 kr. för växtfysiologiska fältundersökningar; till doc. O. Mårtensson, Uppsala, 4.440 kr. för bryologiska studier i nordvästra Alaska; till laborator F. Ossiannilsson, Uppsala, 12.820 kr. för studier av den biokemiska och fysiologiska bakgrunden till resistensen mot *Heterodera rostochiensis* hos potatis; till doc. H. Runemark, Lund, 16.000 kr. för insamling av botaniskt material i Aegaeis.

K. Fysiografiska Sällskapet i Lund har den 9 mars 1960 utdelat bl.a. ett anslag å 900 kr. till fil. lic. V. Stoy för undersökning av nettoassimilationshastigheten (NAR) hos vårvete samt ett anslag om 2.400 kr. till fil. mag. S.-O. Strandhede för en växttaxonomisk undersökning inom släktet *Eleocharis* i Skandinavien. Ur Nilsson-Ehlefonden utdelades 1.500 kr. till doc. A. Hagberg för fortsatt undersökning av rasdifferentieringen inom *Hordeum bulbosum*, 1.600 kr. till fil. lic. O. Hall för fortsatta undersökningar över den biokemiska naturen hos korsningsbarriären mellan växter, 1.600 kr. till fil. kand. G. Holm för fortsatta undersökningar av alleli- och kopplingsförhållandena hos klorofyllmutationer av korn, 1.600 kr. till fil. kand. G. Ising för en cytologisk undersökning inom släktet *Cyrtanthus*, 2.000 kr. till doc. A. Lundqvist för fortsatta undersökningar över inavels- och korsningseffekt hos råg, 1.750 kr. till fil. kand. S. Malmborn för fortsatta studier av den fenotypiska variationen hos kornsorter samt 2.500 kr. till prof. E. Åkerberg för undersökning av vissa embryologiska problem hos *Poa pratensis*.

K. Vetenskapsakademien har i mars 1960 ur Hierta-Retzius' stipendiefond utdelat bl.a. 1.500 kr. till doc. O. Almborn, Lund, för arbeten i samband med utgivandet av en flora över Sydafrikas lavar; 2.000 kr. till fil. lic. B. Berglund, Lund, för studier av sydöstra Sveriges senkvartära vegetationshistoria; 2.000 kr. till fil. lic. G. Jansson, Stockholm, för studier av groningshämning hos korn vid groning under speciella betingelser; 4.000 kr. till fil. dr Britta Lundblad, Stockholm, till inköp av instrument för paleobotaniska undersökningar; 2.000 kr. till civiljägmästare H. Wachtmeister, Wambåsa, och fil. lic. B. Berglund, Lund, för inventering av Blekinges kärlväxtflora. Ur fonden för reseunderstöd till yngre naturforskare utdelades 425 kr. till fil. mag. P. E. Lindgren, Stockholm, för undersökning av algfloran i skärgårdsområdet utanför Göta älvs mynning och de ekologiska betingelserna där.