British Ecological Society

Some Recent Work on Water and Marsh Vegetation

Der Transpirationsstrom der Wasserpflanzen. by K. Snell; Systematisch-anatomische Untersuchungen des Blattes der Hydrocharitaceen. by H. Solereder; Beobachtungen über das Etiolment bei Wasserpflanzen. by H. Beyrer; The Determinative Action of Environic Factors upon *Neobeckia Aquatica* Green by D. T. MacDougal; Beitrage zur Biologie der Gattungen *Potamogeton* und *Scirpus*. by E. Esenbeck; Pildammarnas Vegetation efter Torrla ...

Journal of Ecology, Vol. 2, No. 3 (Sep., 1914), pp. 185-190

Published by: [British Ecological Society](#)

Stable URL: <http://www.jstor.org/stable/2255519>

Accessed: 02/01/2015 11:09

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was also much less than in the second series, a result which was also found, though to a much less degree, in the cultures in weakest concentration of nutrient solution.

In conclusion it would seem necessary to call attention to two criticisms which may be made on the work here dealt with. The first criticism deals with the quantity of solution in which the cultures were growing. In nearly all cases each culture consisted of six plants growing together in one culture jar containing 250 c.c. of solution. This means only 42 c.c. of solution per plant, and although the solutions were changed every three days and although the plants were small, yet it is quite possible that the plants were absorbing salts quite fast enough to alter appreciably the proportion of the various salts in such a small quantity of solution.

In the second place, no account is taken of the great variability of plants growing in water cultures under exactly the same conditions. As only one culture containing six plants was grown in the same solution it is very possible that some of the differences of dry weight on which emphasis is laid, are within the limits of the error due to this. But in the absence of any data in regard to probable error it is not possible to say whether this is so.

But regarded generally it would appear that Mr Tottingham's work has been most carefully carried out, and most of his conclusions are probably justified. It is probably difficult for those who have not conducted work involving the use of water-cultures to realise the great amount of labour involved in carrying to a successful conclusion such a piece of work as that here considered with the care that has evidently been bestowed upon it.

To the ecologist of course the interest of this work lies very largely in the application of the results obtained to questions relating to the soil solution. How far it is permissible to argue from effects produced in water-culture to problems of the soil it is impossible at present to say. That such effects must have some bearing on soil problems is obvious, but we must wait before we can tell definitely to what extent differences in concentration of the soil solution or in the ratio between different substances in the soil solution are really operative in influencing the distribution of vegetation.

WALTER STILES.

SOME RECENT WORK ON WATER AND MARSH VEGETATION

- (I) **Snell, K.** "Der Transpirationsstrom der Wasserpflanzen." *Ber. d. deutsch. bot. Ges.*, **30**, 1912, pp. 361—362.
- (II) **Solereder, H.** "Systematisch-anatomische Untersuchungen des Blattes der Hydrocharitaceen." *Beih. z. Botan. Centralbl.*, **30**, Abt. 1, 1913, pp. 24—104, 53 figures.
- (III) **Beyrer, H.** "Beobachtungen über das Etiolment bei Wasserpflanzen." *Jahresber. Staats.-Gymn. in Tetschen*, **14**, 1913, pp. 3—16, 1 plate.
- (IV) **MacDougall, D. T.** "The determinative action of environic factors upon *Neobeckia aquatica* Green." *Flora*, **106**, pp. 264—280, 14 text-figures.
- (V) **Esenbeck, E.** "Beiträge zur Biologie der Gattungen *Potamogeton* und *Scirpus*." *Flora*, **107**, 1914, pp. 151—202, 59 text-figures.
- (VI) **Gertz, A.** "Pildammarnas vegetation efter torrläggningen." *Bot. Notiser*, 1913, pp. 113—130.

The papers cited above are selected, for notice here, from the very extensive recent literature on the ecology of freshwater aquatic and marsh vegetation, as a supplement to the collective notice of papers on the subject which appeared in an earlier number of this JOURNAL (**1**, 1913, pp. 107—115). This literature is growing so rapidly that we have again omitted notices of those contributions which appear to be of minor general interest to the ecologist, and have as a rule

chosen such as appear likely to lead to further investigation along lines more or less obviously suggested by the papers noticed.

(I) The following note on Snell's work—inadvertently omitted from the collective notice already referred to—should be read in connexion with that on Brown's work (this JOURNAL, **1**, 1913, pp. 110—111). In an earlier paper, Snell (*Flora*, **98**, 1908, pp. 213—249) found that rooted plants of *Elodea* and various other submerged aquatics grew much more vigorously than plants not rooted in soil, hence he concluded that the roots of these plants are not merely organs of attachment but serve for the absorption of salts. He also found that when *Elodea* shoots were cut "bleeding" took place, and with potassium ferrocyanide solution demonstrated the existence of an ascending current of water through the reduced vascular system of the stem. In his recent paper he recalls these observations, in connexion with the interesting results obtained by Hannig (*Ber. d. deutsch. bot. Ges.*, **30**, 1912, pp. 194—204), who found that water plants agreed with both mesophytic and xerophytic land plants in showing greater osmotic pressure in the leaf cells than in the root cells. According to Snell, the free pendent roots of *Pistia stratiotes* serve for absorption, only the young leaves of this floating plant absorbing water by their lower surface; whereas in *Lemna*, with similar habit, the roots serve a purely mechanical function and absorption takes place solely through the leaves—plants with the roots removed grew quite as vigorously as intact plants.

(II) Solereder's thorough investigation of the structure of the leaf in all the genera and most of the species of Hydrocharitaceae forms a useful contribution to the biology of phanerogamic water-plants, by helping to complete our knowledge of the vegetative morphology of this family. The detailed portion of the paper, in which the histology of the leaf is described for each genus, is preceded by a general account in which the author points out that in aquatic plants, to a degree not met with in any other biological or ecological group, there are very few minutiae of structure which cannot be directly correlated with the conditions of life, and that so close is the correlation between the internal structure of the leaf and its external form, and between the latter and the external conditions, and so often do the various types of aquatic leaf recur in different families, that there is not a single anatomical character which can be said to be peculiar to the Hydrocharitaceae as a family and to mark it off from other families of Monocotyledons. On the other hand, despite the close parallelism between internal structure and external form seen in each of the main types of leaf found in the family, there are certain small but constant characters which serve to distinguish the different genera and species, and afford a good means of determining sterile specimens. These characters refer mainly to the peculiar glandular cells which occur chiefly in the partitions of the air-chambers and which secrete either oily or tannin-like substances, and to certain differences in the arrangement and structure of the mechanical tissues which cannot be explained simply by reference to differences in the external conditions under which the plants grow. The author distinguishes in the Hydrocharitaceae (see this JOURNAL, **1**, 1913, p. 109) three main types of leaf form: (1) the simplest—i.e. most reduced—type represented by the submerged sessile single-veined leaves of *Hydrilla*, *Elodea* and *Lagarosiphon*; (2) submerged and usually greatly elongated ribbon-like leaves with several longitudinal veins, as seen in *Vallisneria*, *Blyxa*, *Enallus* and *Thalassia*—to the same general type belong also the partly aerial leaves of *Stratiotes* and the submerged leaves of some species of *Ottelia* and *Boottia*; (3) stalked leaves with broad lamina—to this type belong the submerged leaves of *Halophila*, the submerged and floating leaves of some species of *Ottelia* and *Boottia*, and the floating and aerial leaves of *Hydrocharis*, *Limnobium* and *Hydromystris*. The simplest type of leaf structure is found in *Hydrilla*, *Elodea*, *Lagarosiphon* and *Halophila*, where the leaf consists mainly of two layers of cells (upper and lower epidermis) and, except around the veins, no mesophyll is present, the two epidermal layers being separated by narrow intercellular air-passages. The highest type, approximating to that of land-plants, is seen in the aerial portions of the leaf in *Stratiotes*, and in the aerial and floating leaves of *Ottelia*, *Boottia*, *Hydrocharis*, *Limnobium* and *Hydromystris*, in which palisade tissue and stomata are developed. In the remaining forms the mesophyll consists of uniform elongated cells forming the (usually one-layered) partitions of the air-passages.

(III) In 1895 Möbius showed that certain aquatic plants show somewhat remarkable etiolation phenomena. When *Ceratophyllum demersum* was kept in darkness for a few days, the

stem grew about six times more rapidly in length than did that of a plant exposed to light. A similar acceleration of growth in length of stems is seen in land plants placed in darkness, but whereas in land plants the increased growth is shown by the new internodes formed in darkness, in *Ceratophyllum* there occurred a lengthening of the lower internodes which had previously ceased to grow. Beyrer has investigated the growth in light and in darkness of a number of marsh and aquatic plants, and confirms this observation by Mobius, for in all the plants examined the full-grown internodes were found to start growing again when the plant was placed in darkness. The most striking etiolation effects were observed in *Lysimachia nummularia* and *Hippuris vulgaris*. The author gives details of the minute structure of the stems and leaves of darkened as compared with lighted plants, showing that in the former there is a general lengthening of the cells in all the tissues, non-formation of anthocyan and tannin in cortical and glandular cells, reduction in diameter and in number of both sieve-tubes and vessels, little or no lignification of the walls of vessels, slight development of cuticle, etc. Though the marsh species showed the most marked changes in structure, as might have been expected from their having better developed xylem, etc., in the normal form, and were far more plastic than the submerged aquatics (*Elodea*, *Myriophyllum*), it was only in the latter that the stem internodes showed any marked power of resuming growth in length in darkness.

(IV) The author precedes his account of experiments made with *Neobeckia aquatica* (also known as *Roripa americana* or *Nasturtium lacustre*) by some general considerations. As is well known, the march of development of the metamerer, or "joints," in many seed plants is attended by the formation of a series of foliar organs varying progressively through a wide range of form and structure from the primary or juvenile ("nepionic") leaves to the floral bracts. That the different characters of these leaves are indicative of a complex of morphogenic and physiological characters essentially different in the internodes which bear the leaves is evidenced by the fact that the rejuvenation phenomena and the mature individuals which may follow propagation by metamerer from the earlier or later part of the series may be widely different. One phase of this behaviour is illustrated by the work of Shull (1905) on *Sium cicutaefolium*, in which it was shown definitely that the rejuvenescence of a bud borne on any internode was followed by the formation of foliar organs, the approximation of which to the normal primary leaves corresponded to the nearness of the internode to the senescent or floral end of the series. Another phase is shown by plants in which propagation from juvenile individuals representing the earlier part of the ontogenetic series results only in other juvenile individuals which do not display characters included in adults in which the entire progression to senescence has been followed. It is generally agreed that these facts must rest upon a definite physical basis of formative or specialised material characteristic of stages of development with respect to the various organs. The fact that the structure of the leaves of any part of the series is generally of an obvious suitability for activity under the seasonal conditions in which they are usually formed has led many writers to assign a directly determinative action to the environment. The coincidence of amplitude of range in intensity of environmental conditions and of correlated diversity of structure—as exemplified by *Neobeckia* (*Roripa*), *Bidens*, *Cubomba*, *Ranunculus*, *Proserpinaca*, *Sium*, etc.—might be one of simple survival by fitness, or, on the other hand, fitness might in itself be induced by the agencies encountered. In any case the question arises as to how far the various forms of a polymorphic series are morphologically determinative, following an unmodifiable procedure, and to what extent the morphogeny of the metamerer may be modified by manipulation of the external conditions affecting their development. Shull's results seem to show that the ontogeny of *Sium* is independent and that external conditions may be modified to increase the range of variability or to cause rejuvenescence at any stage, yet their range goes no farther.

Neobeckia is usually found rooted in the mud at the bottom of lakes and pools at a depth of 20 to 30 cm.; when in flower the stem extends above the water surface a few centimetres, the emerged part bearing a few oblong or oblong-ovate leaves or bracts subtending the inflorescences; the submerged part bears finely dissected leaves and a dense cluster of these is usually found about the base of the stem. The plant is not found above the high water level; almost any part of the shoot serves to propagate the plant, and numerous individuals are found on the muddy strand between high and low water levels. The full series of foliar organs ranges from

broadly oblong lanceolate or ovate leaves in the early stages to narrowly ovate or lanceolate floral bracts in the senescent stage; the mature or adult leaf of the highest type in aquatics is cut into fine threadlike divisions, and the mature leaf of terrestrially grown plants is much divided with narrow strap-shaped segments. The spread and size of the early leaves vary with the conditions under which they are formed, and the structure of the mature leaves varies between the limits of the two types according to the environment (submerged without stomata, parenchyma compact and elongated longitudinally; emerged with stomata, parenchyma cells elongated vertically with distinct palisade and spongy tissue). Normal aquatic specimens showed a single main root not more than 2 mm. in diameter and 10 cm. long, with very thin branches. Terrestrially grown specimens of the same age had a clump of thickened roots produced by numerous offsets and branches from the crown; these thickened roots were 10 to 15 cm. long with a diameter as great as 1 cm. at the junction with the crown. As compared with the roots of aquatic plants the central cylinder had become greatly enlarged by secondary thickening, with corresponding increase in the cortex; but besides the greater number and size of the various elements concerned, the roots of the terrestrial plants were crammed with starch which was apparently quite lacking from the aquatic roots, thus showing that the roots have been altered from a form suitable to fixation only to a structure adapted for receiving sugar and converting this into starch which is stored in the parenchymatous tissues.

Juvenile leaves showed a more pronounced development of the lamina on free cuttings than on awakened lateral buds on entire stems, on the upper part of thickened rootstocks than on the lower. Cuttings placed in water invariably produced juvenile forms immediately, but when the water was allowed to evaporate, leaving the plantlets growing as terrestrials, the type of leaf changed gradually from the aquatic to the terrestrial type without the intervention of juvenile forms. Abrupt change from aquatic to terrestrial conditions, however, was followed by the interposition of juvenile types indicative of rejuvenescence. Anchorage of aquatic plantlets when submerged was followed by modification of the aquatic leaves towards the terrestrial type without the interposition of juvenile forms. Anchorage and exposure of the stems to the air would occur together under natural conditions, but either may bring about the modifications ensuing when the two act together. The development of juvenile leaves also occurred in terrestrial cultures with the change from cool to warm seasons or from warm to cool conditions, or with rapid changes in the supply of moisture either way, and might also be induced simply by the increased aëration following stirring of the soil about the roots.

Aquatically grown plants remained alive when placed in strong (10 %) potassium nitrate solution, but the aquatic leaves were killed. Terrestrially grown plants retained the strap-like divisions of the leaves unharmed, the terminal buds remained inactive, but the lateral buds opened and formed the broadly laminate juvenile leaves of the usual type. In this connexion, attention is called to the fact that the aquatic leaves and the main actively growing points would be most easily dehydrated and, to an injurious extent, by the solution; the terrestrial leaves and the resting lateral buds would endure the concentration, and these buds undergo the changes that constitute the basis of rejuvenation. Aquatically grown plants with the characteristic threadlike segments continued to be active when placed in more dilute (0.5 % to 0.05 %) potassium nitrate solutions with a range of osmotic pressure from 2 to about 17 atmospheres, and formed a series of leaves passing gradually toward and into the broadly laminate juvenile type. Continuance in the solution was followed by a gradual return in the series to the finely segmented aquatic type. The reaction was as if the immersion in the solution produced a brief and temporary effect only—leaves already partly formed in the bud were affected but little, others less developed might be altered to a greater extent; later, the unknown accommodations of the plant having taken place, the return or progression from the juvenile to the aquatic or mature type occurred in the usual manner.

According to the author, it seems impossible to ascribe rejuvenation of buds and the formation of leaves to any hydration effect or to any other simple change in colloidal condition which might be described as liquidity or lability. The disturbance resulting in rejuvenescence, like many other striking phases of reaction in plants, may be initiated by a wide range in agencies—changes in temperature or in moisture or in concentration of the medium, separation of a segment of the vegetative body, injury to neighbouring buds, etc. The direct effect of all of these so-called

stimuli would embrace far too wide results to be included in any distinctive colloidal or osmotic reaction, and the only permissible view is that which refers the whole matter back to modifications of the supply of formative nutritive material.

The author concludes by pointing out that the plant dealt with—the experiments upon it including cultures as terrestrial and aquatic in a temperate house of the New York Botanical Garden, cultures in the soil at the same place, cultures in a tropical climate at Cinchona in Jamaica (7345 feet) in the soil in the open, in the montane plantation of the Desert Laboratory in Arizona (8000 feet), in the glass house of this Laboratory (2700 feet) in a subtropical climate with extreme temperatures, and in the garden of the Coastal Laboratory at Carmel (California) in a foggy cool equable oceanic climate—has been shown to endure an extremely wide range of conditions, in which the diversity of its leaf structure may be a factor of importance; that the development of thickened roots, already mentioned as accompanying its cultivation as a terrestrial, is a reaction that probably does not occur in nature; and that the form and structure of the roots and leaves of *Neobeckia* have been shown to be determined by environmental conditions to a much greater extent than in *Sium*, *Proserpinaca*, or probably any other so-called “polymorphic” species, yet the reaction to such external agencies is not a direct or physical adjustment.

(V) In the first part of this paper, dealing with the biology of *Potamogeton*, the author points out that while many observations regarding the external morphology of the European species are recorded in floristic works, little has been done in the direction of experimenting with a view to determining which species are capable of producing land forms and how far these differ anatomically from the normal forms. A land form might appear at first sight easily definable as a form which is able to live with its aerial organs exposed to the air, that is, a plant which on being taken out of the water does not die off, but the author considers such a definition much too wide. Many so-called land forms of normally aquatic species can grow for months under regulated conditions, and yet anatomical investigation shows that they are simply water plants which have been able to eke out existence on land. True land forms are exemplified in *Polygonum amphibium*, *Marsilea*, etc., which show not merely alteration in external form but also extensive modification of internal structure. His objects were therefore to ascertain whether the naturally occurring land forms of *Potamogeton* differ markedly in anatomy from the normal submerged type, and what alterations, internal as well as external, occur when the various species are cultivated as land plants. Cultures showed that “land forms” could be obtained of all the species which normally or occasionally produce floating leaves in addition to submerged leaves (*P. natans*, *P. fluitans*, *P. coloratus*, etc.) when the plants were cultivated in more or less saturated air and were also shaded. In the case of species which have only submerged leaves, or at any rate in which floating leaves have never been observed (though “land forms” have sometimes been described), Esenbeck found it impossible to keep the plants alive for long in cultures in damp air; in *P. lucens* and *P. densus* he could only keep them for 14 days, in *P. perfoliatus* and *P. pectinatus* for about a month. However, his experiments make it probable that all species of *Potamogeton* may, under favourable conditions, produce so-called land forms, that is, are capable of growing in saturated air. But in the aerial leaves produced in normally occurring or artificially induced “land forms,” palisade tissue is found only in those species where it is also found in the normal floating leaves; the lower tissue of the aerial leaves has the same lacunar structure as in floating leaves—true spongy tissue, one of the most characteristic features of the leaves of true land plants, is as completely absent from these land forms of *Potamogeton* as it is from the water forms. Details are given regarding the number and distribution of stomata, but the author lays very little stress upon these, because in homophyllous species the normal submerged leaves as well as the aerial leaves possess stomata, while in heterophyllous species stomata are found on the lower side of both the floating leaves and the aerial leaves—in no case was the lower side of the aerial leaves found to have more stomata than the upper.

The second part of Esenbeck's paper deals with *Scirpus lacustris* and some other “leafless” Cyperaceae. Most of the Cyperaceae have well developed and numerous leaves, others have few and chiefly radical leaves, others have very short-bladed leaves, while in some cases the lamina is almost or quite absent. This transition is seen within certain subfamilies of Cyperaceae, but especially among *Scirpus* and its allies. For instance, *Scirpus sylvaticus* has well developed

grass-like leaves along the whole stem, *S. lacustris* has only occasionally laminae or mere rudiments of these, while *S. prolifer* is quite leafless, as are also various species of *Heleocharis*, *Isolepis gracilis*, etc. It has long been known that *S. lacustris* may produce grass-like laminae in deep or rapidly flowing water; Baumann showed that seedlings began with grass-like leaves, Raunkiaer that the dorsiventral floating leaves differ in structure from the isobilateral submerged leaves, Goebel that when the main stem (haulm) is cut away the lateral branches produced bear the grass-like leaves. That neither depth nor current alone induces this return to the juvenile condition is proved by the author's simple experiment of placing pieces of rhizome with buds in a flat dish containing only a few centimetres of distilled water—the opening buds produce the same grass-like water leaves as in a deep basin or in a trough of running water. Cultures were also made in which pieces of stem with buds, or whole plants with the main stem cut down, were grown on garden soil or sand, in full light and in total or almost darkness, etc. His general conclusions from these experiments with a few members of the Cyperaceae (further work is in progress to be published later) are that the usually leafless *Scirpus lacustris*, *S. prolifer* and *Isolepis gracilis* can produce foliage leaves under unfavourable conditions of life such as are set up experimentally by culture in weak light, by removal of organs containing reserve food or by low nutrition.

(VI) Two lakes near Malmo became dried up, the larger one in the autumn of 1911, the smaller in March 1912, and the author has made observations on the early terrestrial vegetation that colonised the new substratum between the time of drying-up and the end of 1912. The original vegetation was chiefly submerged and consisted mainly of a dense growth of *Myriophyllum spicatum* and *Chara* spp. The author gives a list of 65 species which colonised the mud, and notes as the chief features of the new vegetation that the individual plants though spaced out widely showed luxuriant growth, doubtless attributable to the rich nature of the soil, in which owing to the high lime content of the underlying morainic clay active nitrate formation had taken place after the drying-up. The vegetation was derived in part from the former aquatic flora (*Myriophyllum*, *Ranunculus aquatilis*, *Phragmites*, etc.), but mainly from that of the adjacent cultivated land. The *Myriophyllum* endured the dry summer of 1912 as a land form, which the author describes in detail and compares with the normal aquatic form, but in the larger lake it was killed off by the cold of the first winter. About 30% of the colonists grew from seeds carried by wind; a few (*Salix*, etc.) from twigs and other vegetative organs carried by water.

The author gives the following list showing the number of species in the new flora belonging to each of the types in the "biological spectrum" of Raunkiaer¹: phanerophytes, 5; hemi-cryptophytes, 26; cryptophytes, 7; therophytes, 24. As compared with the new flora of some islands formed by partial drying-up of a lake near Hjälmars, as analysed by Raunkiaer in 1909, the flora of these dried Malmo lakes shows a higher proportion of therophytes and a lower proportion of hemi-cryptophytes. Since the Hjälmars flora was examined at a later stage after the new land surface was formed, it would appear that as colonisation proceeds the therophytes (annuals) dwindle in importance and are more and more outclassed by the phanerophytes and hemi-cryptophytes.

¹ Smith, W. G. "Raunkiaer's 'life-forms' and statistical methods." This JOURNAL, 1, 1913, pp. 16—26.