COMPETITION AND GENERAL RELATIONSHIPS AMONG THE SUBTERRANEAN ORGANS OF MARSH PLANTS.

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The statements and conclusions in the present paper are based mainly upon my work at Skokie Marsh, in the years 1910 and 1911.[1] The marsh itself is closely associated with Skokie Stream, a small, intermittent, meandering stream that begins west of Waukegan, Illinois, and ends west of Glencoe, Illinois. Its vegetation may be described briefly as consisting of reed-swamp, swamp-meadow and true meadow.

Darwin, in his Origin of Species, pointed out that because two species of the same genus usually resemble each other, the struggle between them, if they come into competition, will generally be more severe than between two species of different genera. Clements has since emphasized the fact that similarity in growth form rather than in systematic position determines the intensity with which different species compete. One of the main objects in my investigation at Skokie Marsh was to ascertain how far similarity in growth form among different species (particularly in regard to depth of subterranean organs) results in competition; or, conversely, how far dissimilarity in growth form results in ability to live together harmoniously in a complementary relationship.

We have here [illustrated on screen] a view of the rhizome interrelationships of the bur-reed (*Sparganium eurycarpum*), the arrow-leaf (*Sagittaria latifolia*) and one of the water knot-weeds (*Polygonum Muhlenbergii*), where the three species occur together in the less hydrophytic parts of the reed-swamp. . . . As shown on the screen, the knot-weed rhizomes and roots lie rather deep. . . . It will be seen that the roots of the arrow-

[1] A general and also more elaborate account than here possible will be found in the Botanical Gazette, 53: 415-435, 1912.

leaf pass downward several inches below the surface and consequently compete with the roots of both the bur-reed and the knotweed for water, oxygen, etc. The soil being rich usually in at least water and nitrogenous materials, the root competition is probably not serious. But before passing on we should note the complementary relationship between the rhizomes of the arrow-leaf and those of the bur-reed. At first it might seem that since the rhizomes of both species start growth at the same level—near the surface—they would come to be more or less in each other's way. But usually at the very outset the arrow-leaf rhizomes grow downward for several inches, then take a horizontal direction for some distance, and finally point upward again. At the distal end is produced a stem-tuber and from this arises a new plant the following season. Thus the arrow-leaf may establish new plants at advantageous distances from the parent plant and yet, in doing so, avoid mechanical obstructions to a great extent. To determine exactly how far this freedom from mechanical obstruction promotes the vegetative increase of arrow-leaf plants would demand, of course, accurate experimental investigation in a quantitative way. Some able botanists, notably Clements, are inclined against the consideration of mechanical obstruction as a factor in competition; they insist upon the importance of "physical" (i. e., physiological) factors. And while in the main their contentions are well founded, it cannot be denied that pronounced exceptions do exist. For example, at Skokie Marsh, a study of the water-lily association in the reed-swamp showed that where the arrow-leaf was present its rhizomes had been intercepted in great numbers by the large, semi-decayed rhizomes of the water-lily (*Nymphaea advena*). And, in the majority of such cases, the propagative stem-tubers of the arrow-leaf had decayed. Even in the encasing soil, many instances were found where the stem-tubers had been mechanically impeded and had mostly decayed. And here, while the decay must have been due to some one or more physiological causes, yet these causes could not have operated had not mechanical impediments first retarded the stem-tubers for a sufficient length of time.

As our knowledge of the interrelationships of subterranean organs progresses in the future, we shall probably find that often, in the case of certain species with large subterranean parts, there is offered or received mechanical resistance which is immediately decisive in competition because of the physiological processes that it promotes.

Our last picture is that of a community containing chiefly the blue flag (*Iris versicolor*) and the blue violet (*Viola cucullata*). Their rhizomes are short and thick, lie just below or at the soil surface, and form a dense mat. Nevertheless, when one or more square feet of this mat were carefully removed and the soil in the interstices among the rhizomes was taken away, it was estimated that the interstices, as viewed from above, constituted from 35 to 60 per cent of the total. Evidently, then, so far as mere room was concerned, several other species could have grown —in fact, did grow—in these interstices. But they were plants which rooted higher or lower; or, if at the same level, they were species not largely dependent upon rhizomes or stolons for multiplication. Thus, where the blue flag had reached a maximum of frequency, the water knot-weed, with a low root system, and the bedstraw (*Galium Claytoni*), with a high root system, might live; but the sweet flag (*Acorus calamus*), with rhizomes similar to those of the blue-flag and lying at a similar depth, and dependent largely on rhizomes for multiplication, was absent.

A detailed presentation of the conclusions growing out of my work is impossible here. But in closing I would point out the importance of exhaustive study, in the future, of the interrelationships among subterranean organs, especially since these have much to do with the compactness of vegetative growth in an association. For, induced directly or indirectly by the conditions following such compactness, have doubtless arisen many of the most important adaptations in the growth forms of various species.