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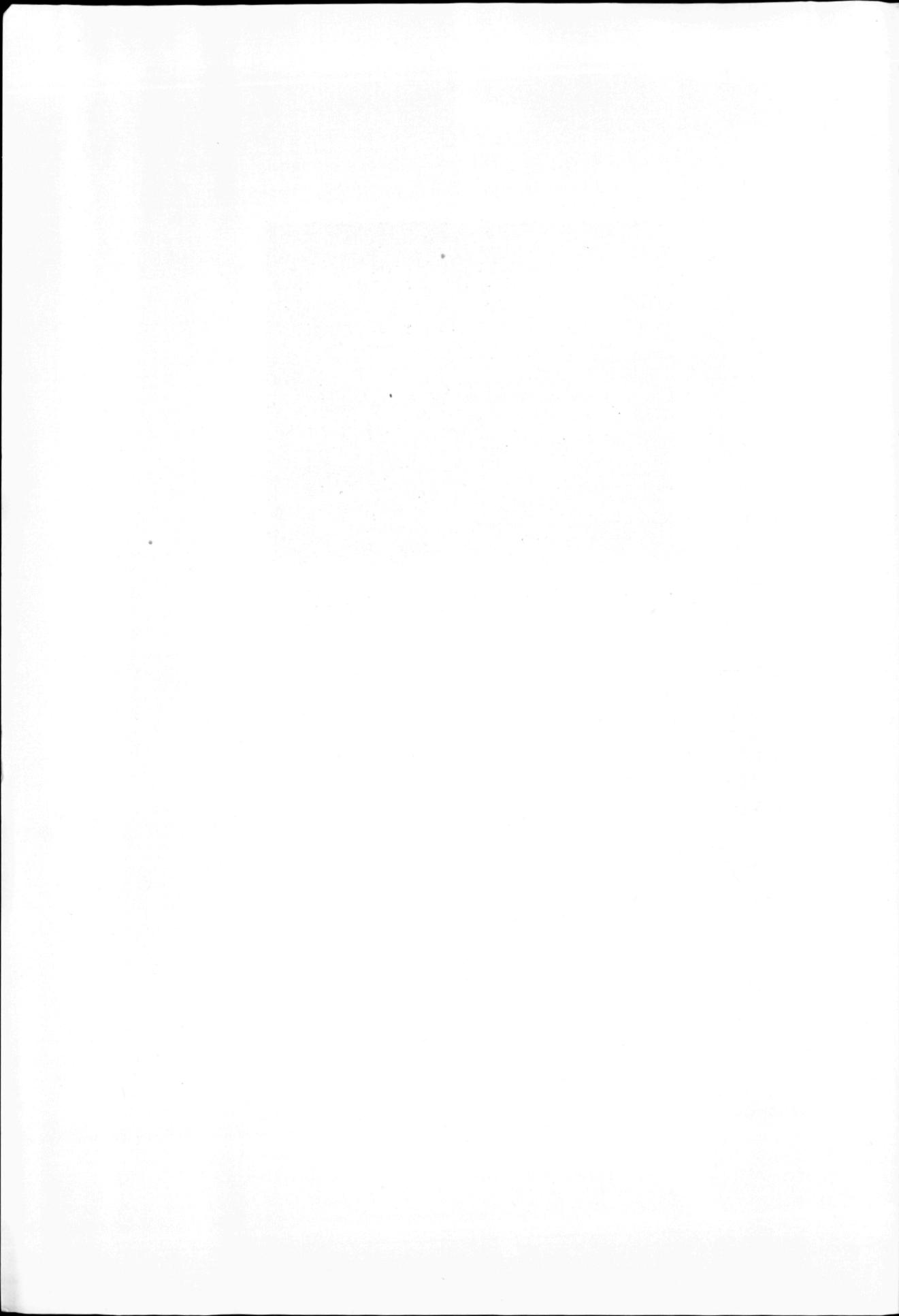
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The Use of Permanent Sample Plots in Studying the Quantitative Ecology of Algae in Salt Marshes

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Temporal changes in the benthic algal vegetation and in the environment of salt marshes can be studied quantitatively by means of permanent sample plots. The author worked with permanent quadrats of salt marshes in the Netherlands (W. Europe). The methods, including the sampling procedure, are described and some results given. The following aspects were studied over a period of years: periodicity, fluctuations, and succession in the algal vegetation; ecological relations between algae and algae and between algae and higher plants; taxonomic problems, viz., changes in reproduction and morphology of algae.

INTRODUCTION

Quantitative plant ecology studies two aspects of the vegetation and the environment, viz., the variation in space (pattern, structure) and the variation in time (process, dynamics). A fairly high number of investigations are devoted to the structural aspects of the benthic marine algal vegetation on rocky shores (6). Algal vegetation on soft substrates of salt marshes and sand and mud flats is less frequently studied owing to taxonomic difficulties. Chapman, in particular, has associated his name with this branch of phycology (1-4).

Temporal changes occurring in the algal vegetation in salt marshes have seldom been investigated quantitatively. The only exact way to study these phenomena is with the aid of permanent sample plots or permanent quadrats (P.Q.'s). These quadrats have to be marked out in the field and analyzed over a number of years.

The author is working in the estuaries of the rivers Rhine, Meuse and Scheldt and in the southern coastal area of the Netherlands. The extensive salt marshes found there are covered with halophytes and algae. The algae live on and in the topsoil among the phanerogams or as epiphytes on the halophytes. The tidal differences are 3 to 4 meters and the salt marshes, intersected by deep creeks, are situated around and above

the mean high water line. Descriptions of the algal communities are given by Nienhuis (8).

The salt marshes along the North Sea coasts are constantly being reduced by the embanking of the wetlands for urban or industrial expansion, as well as by the closure of the mouths of estuaries for the sake of security, recreation and fresh water supply. They are also continually threatened with pollution by crude oil and indestructible waste. Long-term investigations of the present situation are therefore urgently needed.

METHODS

The permanent sample plots, measuring 2×2 m each, are pegged out on the salt marshes in areas of homogeneous algal vegetation. In the center of a plot a 0.5×0.5 m area is considered to be the permanent quadrat proper (P.Q.); it will be left undisturbed during the investigations. The remaining fringe functions as the place where algae and soil can be sampled. Once a month the permanent sample plots are examined. In the central part of the plot (the P.Q.) the combined abundance and cover of all algal species or species-groups and phanerogams is estimated. For every species or species group observed in the P.Q. a sample is taken in the fringe surrounding the P.Q. At the same time a sample is

taken from the uppermost centimeter of the soil, the layer upon which and in which the algae live. The moisture content of these soil samples and the salinity of the soil moisture are determined and expressed as g H₂O/100 g oven-dried soil (105°C), and g NaCl/liter soil moisture (% Cl⁻), respectively. Less regularly, pH, temperature, nitrogen and lime compounds in the soil are determined.

The algal samples are analyzed in the laboratory, a species list is made and the quantity of every species in the sample is estimated. Then the data gathered in the field and the data deduced from the samples are converted into the combined abundance and cover data on all algal species found in the P.Q. and are expressed in the following arbitrary scale: O=plant occurrence is rare or occasional; F=frequent (in both cases cover is less than 5%); C=common (5–30%); A=abundant (30–60%); D=dominant (cover is more than 60%).

A very important supposition in this procedure is that the proportions in the algal samples taken in the fringe are representative of the proportions in the P.Q. Questions of sample size have often centered around the concept of minimal area. The minimal area is pragmatically defined as the area one must investigate minimally in order to get a representative picture of the vegetation. A sample has to be considered as adequately representative if, between that sample and a survey of the total homogeneous vegetation, a floristic affinity exists of more than 80% (7). A thoroughly investigated sample from an algal mat of microscopically small plants (threadlike green algae, blue-green algae, Haptophyceae and *Vaucheria* spp.*), with an area larger than 2 to 3 cm² proves to give a representative picture of the vegetation. Naturally, in the case of larger algae (e.g. coarse *Enteromorpha* spp., *Fucus vesiculosus* f. *volubilis*) the minimal area is larger too.

A difficulty inherent in this method is that almost no information is obtained about the thickness of the algal mat on the soil.

Without these data the total quantity of the algae cannot be determined. Estimating the dry weight of the algae gives no solution because the algae are interwoven with the sediments and organic particles. It is hardly possible to separate the living algae from the sediment and the detritus in a mechanical way.

RESULTS

Periodicity, fluctuations and succession.

1. Seasonal periodicity determined by climatic influences is clearly shown by the annual cycles of, e.g., *Ulothrix* spp., some *Enteromorpha*, *Vaucheria* and blue-green algal species. An example of this is the genus *Ulothrix* (*U. flacca*, *U. pseudoflacca*, *U. subflaccida*) which occurs in the salt marsh in quantity only during late winter and early spring and seldom appears during the rest of the year (Fig. 1A).

2. Fluctuations in the algal vegetation, viz. irregular changes in abundance and cover connected with local variations in weather conditions, can be studied in P.Q.'s.

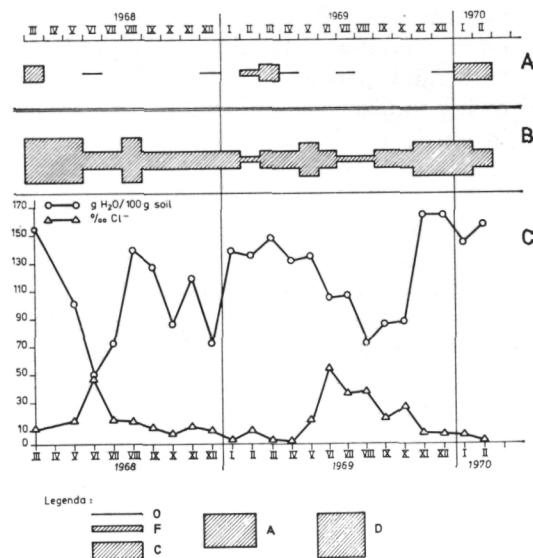


FIG. 1. A: Seasonal periodicity of *Ulothrix* spp. on permanent quadrat I of a Dutch salt marsh.

B: Fluctuations in the *Vaucheria* vegetation on permanent quadrat II of a Dutch salt marsh.

C: Moisture content and salinity of the soil moisture in permanent quadrat II of a Dutch salt marsh.

* Nomenclature according to Parke and Dixon (10).

The semiterrestrial, often perennial salt-marsh algae, such as *Rhizoclonium riparium*, *Percursaria percursa*, *Bostrychia scorpioides* and some *Enteromorpha* and *Vaucheria* species, are negatively influenced by extreme conditions. The local fluctuations in *Vaucheria* spp. vegetation (*V. coronata*, *V. intermedia*, *V. thuretii* and *V. arcassonensis*) are superimposed on the seasonal periodicity acting in the same population (Figs. 1B and 1C). In March 1968 *Vaucheria* spp. dominated a certain permanent quadrat in a marsh. The rather dry spring weather brought about a gradual desiccation of the soil. In June the highest salinity value of 1968 was measured, caused by the strong desiccation of the soil. This combination proved to be fatal for the *Vaucheria* mat. The vegetation dried up and lost its color and the cover decreased. The late summer months' wetness, combined with low salinity, brought a temporary revival of the *Vaucheria* spp., followed again by a decrease influenced by lowered moisture conditions.

February 1969 was characterized by some weeks of frosty weather (-2.5°C soil temperature). The algal vegetation suffered from these extreme temperatures; a marked decrease in the algal cover occurred. A revival followed in the rather wet spring period, with maximal development in May. Afterwards a dry summer and autumn with desiccation and consequent high salinity caused a continually decreasing algal cover. In late autumn the moisture content of the topsoil rose quickly and the *Vaucheria* vegetation recovered.

This example shows a clear-cut correlation of algal abundance and cover with local weather influences. The limiting factors in this case are the moisture content of the soil and, incidentally, lethal temperatures of the soil water. More information about these phenomena is given by Nienhuis and Simons (9).

3. Succession (the cumulative changes in the structure of the vegetation) can be recorded quantitatively by using P.Q.'s. The salt marsh is an unstable environment and thus it is understandable that most salt marsh algae belong to rapidly growing vegetation

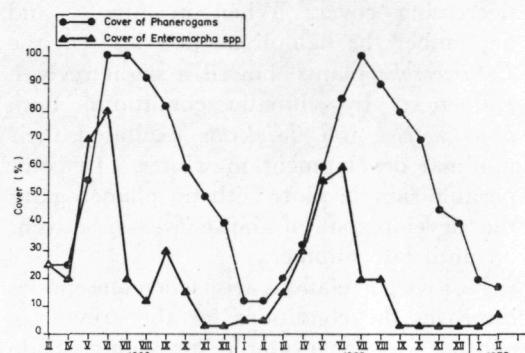


FIG. 2. Changes in the cover of phanerogams and *Enteromorpha* spp. on a permanent quadrat of a Dutch salt marsh.

types composed of only a few species. On the bare, silty soil of a marsh, an algal vegetation consisting of green and blue-green algae develops among the initial phanerogams within two years. This kind of succession was observed in P.Q.'s, which had been stripped of their algae for this purpose.

The succession of more complex, stratified vegetation takes much more time. First the halophytes must grow up; then the algae can settle among the stems of the higher plants (e.g., *Bostrychia scorpioides* association among *Halimione portulacoides*).

Ecological relations between algae and algae and between algae and phanerogams.

The most common cause of interspecific correlation is mutual response to the same or to different environmental factors. Negative correlations can arise from competition for the various resources (space, light) as can be seen by the following example (Fig. 2): *Enteromorpha* spp. (e.g. *E. prolifera*, *E. torta*, *E. flexuosa*, *E. intestinalis*) live on the moist soil of the marsh under the phanerogams. In the early spring of 1968, when air temperatures rose, the *Enteromorpha* spp. and the halophytes (*Triglochin maritima*) developed explosively. In summer the *Triglochin* vegetation became so dense (100% cover) that the light could hardly penetrate to the underlying soil on which the algae live. Light probably became the limiting factor and the *Enteromorpha* vegetation began to die, as was clearly shown by the sharply

decreasing cover. When in August and September the halophytes deteriorated, the *Enteromorpha* plants showed a slight revival. Influenced by climatic conditions, both *Enteromorpha* and *Triglochin* exhibited their minimal development in winter. In comparable sample plots with no phanerogams the development of the *Enteromorpha* went on until late summer.

Positive correlations arise when one species improves the conditions for the growth of another by, for example, providing shade and an actual substrate. This was observed in the more stable, stratified plantcommunities such as those in which *Halimione portulacoides* and *Limonium vulgare* are found with *Bostrychia scorpioides* and *Catenella repens*.

Taxonomic problems

From monthly P.Q. samples it appeared that in a number of green algae living in salt marshes (*Rhizoclonium riparium*, *Percursaria percursa*, *Blidingia minima*, *B. marginata*, *Enteromorpha prolifera*, *E. flexuosa*, *E. intestinalis*, *E. torta*, *Cladophora* spec.) reproduction by means of vulnerable spores rarely occurs. This suggests an adaptation to the extreme semiterrestrial salt marsh conditions.

Under these desiccating conditions the thalli of the green algae *Enteromorpha prolifera* and *E. torta* showed a tendency to change their morphological character in the course of the summer. The square and rectangular cells, originally arranged in longitudinal rows, grew out irregularly in an unordered pattern. The cell walls became thicker and the chloroplasts shifted to one side of the cells. The thalli became broader and inflated, intestine-like. Much of this algal material might be considered *E. intestinalis*.

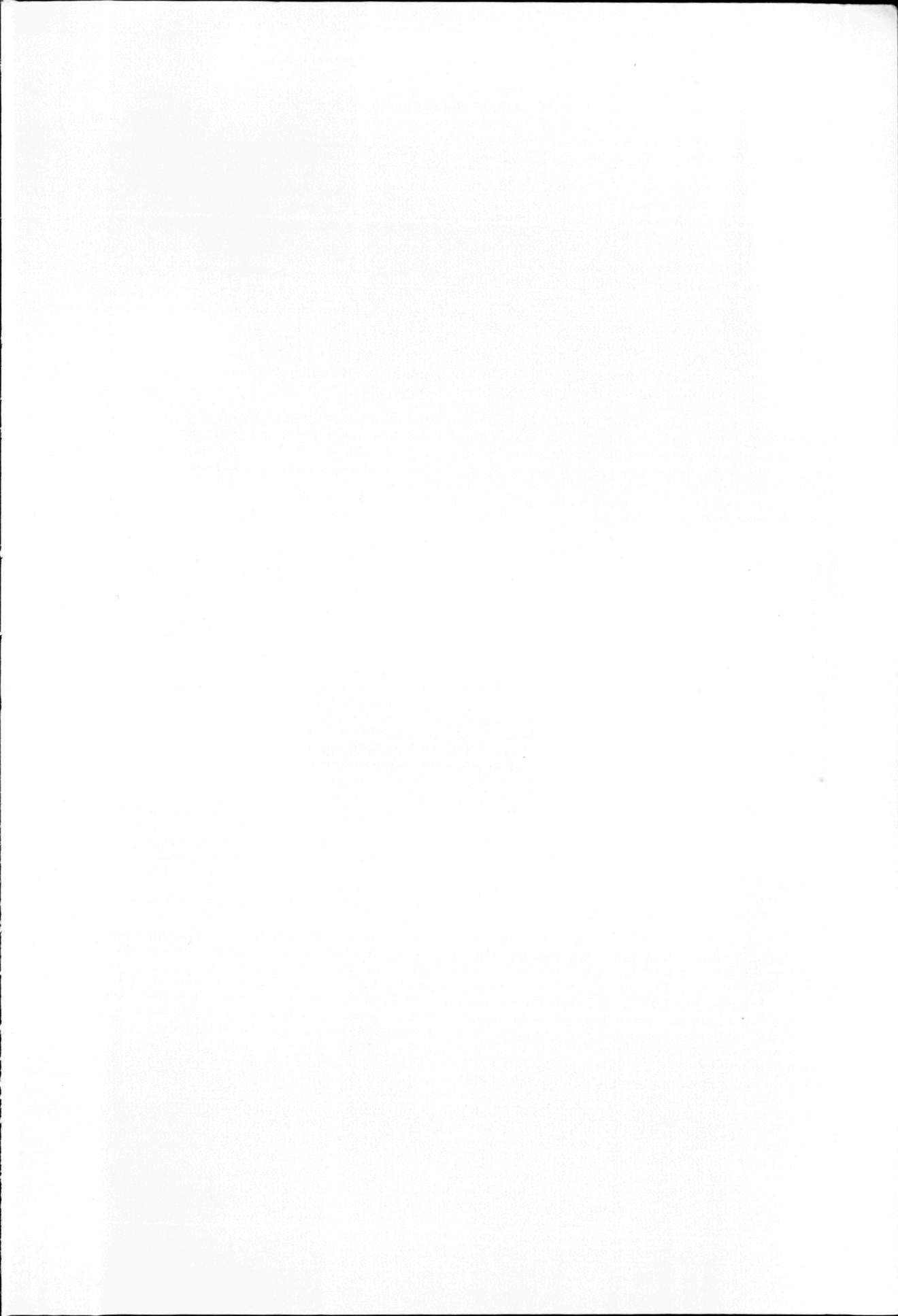
Since the beginning of this century the use of permanent quadrats and transects has become customary procedure in quantitative studies of vegetations of higher plants (5). As far as the author knows this method has been seldom used in ecological studies

of small, benthic algae, probably owing to taxonomic difficulties and to the fact that microscopically small algae are not recognizable in the field.

The present author worked with permanent sample plots for over three years. It is impossible in this paper to give a survey of all of the results of the more than thirty P.Q.'s that have been studied; they will be published elsewhere. It is hoped that this paper makes clear that permanent quadrats are indispensable to a quantitative approach to the study of the dynamics of benthic algal vegetations.

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