

# DREDGED MATERIAL RESEARCH PROGRAM



CONTRACT REPORT D-74-9

## STATE-OF-THE-ART SURVEY AND EVALUATION OF MARSH PLANT ESTABLISHMENT TECHNIQUES: INDUCED AND NATURAL VOLUME I: REPORT OF RESEARCH

by

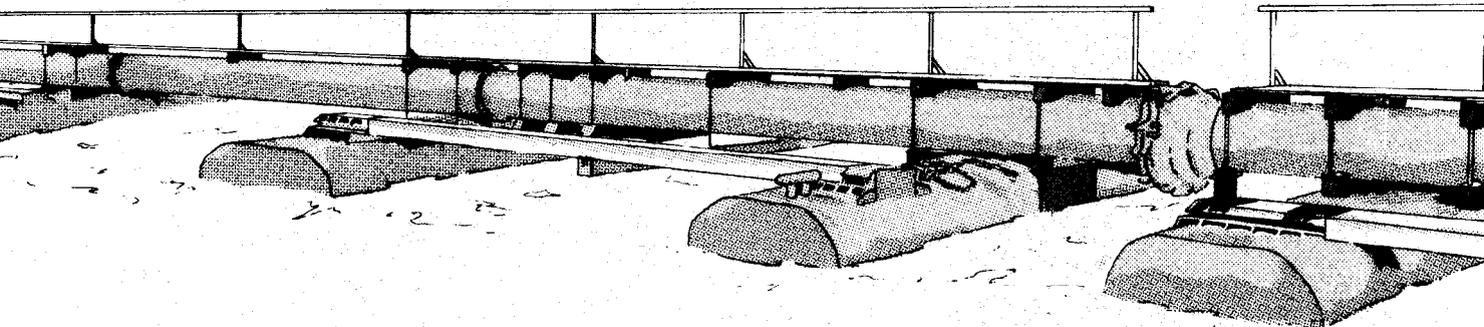
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SUBJECT: Transmittal of Contract Report D-74-9

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1. The contract report transmitted herewith represents the results of one of a series of research efforts (work units) undertaken as part of Task 4A (Artificial Marsh and Island Creation) of the Corps of Engineers' Dredged Material Research Program (DMRP). Task 4A is part of the Habitat Development Research Project, which, among other considerations, includes the development of land disposal alternatives which are not conflicting with the Corps' mandate and environmental interests.
2. The basic concepts of deliberate habitat creation have been used successfully by wildlife and fisheries biologists to provide specialized habitats for a large number of desirable species of waterfowl, fish, and mammals. In terms of current state-of-the-art, island and marsh creation are the most promising concepts of habitat creation using dredged material that are likely to involve a volumetrically significant amount of material. Numerous examples exist, some of which have been studied and documented, in which low mounds of material deposited in shallow bays and sounds have unintentionally become valuable habitat.
3. Significant ongoing research has confirmed that intentional marsh creation using dredged material is technically feasible and can be developed into a viable system; however, considerable additional research, development, and testing are essential. Critical studies are well under way under sponsorship of the DMRP and include conceptual, laboratory, and field investigations into multiple aspects of biological, engineering, and operational considerations.
4. In terms of the biological considerations, specific questions being addressed by research include: Which plant species are most desirable for a given geographical area in terms of productivity? How do various species respond physiologically to environmental stress? To what extent do marsh plants take up heavy metals? and What are the most effective establishment techniques to use for various species on different substrates? Pilot-scale (greenhouse) studies are now in progress to

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investigate different establishment techniques, and full-scale verification of results will be an integral part of the DMRP field studies in marsh creation. However, before any of these studies were initiated, it was necessary to conduct a state-of-the-art survey and evaluation of existing technology to serve as a guide in planning the subsequent efforts. The results of this review are presented in this report prepared under contract by the University of Michigan.

5. Whether it be emergent, floating-leaved, submerged, or free-floating, and whether it be fresh, brackish, or saline vegetation, the authors found few reports dealing with either natural or induced establishment on new land. Contacts with agencies and individuals at the Federal and state level as well as commercial suppliers of aquatic and marsh plant planting materials were similarly unproductive.

6. From the literature, it was discerned that, other factors being equal, local species are more likely to succeed than introduced ones. It is also apparent that some species are sensitive to water-quality degradation, and other species tend to invade or increase in abundance in turbid or polluted waters or on disturbed sites. Site-peculiar characteristics, such as tides, salinity, drainage, climatic factors, and light penetration, are quite important in determining establishment success. As far as propagation procedures are concerned, seeding usually is least expensive, but transplants have the highest rate of success. It can be expected that the basic problems to be encountered in marsh establishment will be physically unsuitable substrates, nutrient deficiencies, contaminated sediments, excessive wind or current action, excessive turbidity, unfavorable patterns of water-level fluctuations, and unfavorable water depths. Some of these problems can be dealt with in the design of the disposal operation and others by marsh management practices; however, physically unsuitable substrates will be a major deterrent.

7. Attention is called to the fact that this report is published in two volumes, the second being an indexed bibliography containing over 700 references. The two volumes together provide a rapid index to much of the literature on the ecology and management of aquatic and marsh plants.



G. H. HILT  
Colonel, Corps of Engineers  
Director

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## 20. ABSTRACT (Continued)

quality, turbidity, and currents and wave action are particularly important to plant establishment. Aquatic and marsh plants propagate naturally by both seeds and vegetative parts. The propagules are dispersed by wind, water, animals, and man. By controlling various environmental factors, it is possible to promote and encourage the natural invasion and growth of aquatic and marsh plants, especially in freshwater systems. In many cases, plantings of aquatic and marsh plants will be necessary to vegetate a new substrate. Seeding appears to be the least expensive procedure, but environmental conditions must be favorable or success will be low. Transplants usually provide faster establishment and are hardier than seedlings. Efforts at establishing Spartina alterniflora in Atlantic coast marshes have shown good results. The basic problems encountered in the establishment of aquatic and marsh plants are physically unsuitable substrates, nutrient deficiencies, polluted sediments, excessive wind or current action, excessive turbidity, unfavorable patterns of water level fluctuations, and unfavorable water depths. Research is needed in aquatic and marsh plant taxonomy, biology, and ecology. Special effort should be devoted to the study of site conditions and propagule collecting and planting methods.

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## EXECUTIVE SUMMARY

This report reviews the available information on the establishment of marsh and aquatic plants on newly available substrates such as deposits of dredged material.

Knowledge of marsh and aquatic plant establishment was assessed by reviewing the literature and by contacting agencies and individuals likely to have relevant information useful for vegetating new sites created by dredging activity. Reports dealing directly with either natural or induced establishment were few. Most of the earlier work was done by waterfowl managers interested in freshwater and brackish areas. Their emphasis has now switched to environmental control. A recent survey of the literature on salt marsh creation (Larimer 1969) found only 13 useful references in a survey of 5,470 publications on estuaries. Recently, there has been considerable work on Spartina spp. for stabilizing deposits of dredged material.

Marsh and aquatic species can be classified into four basic life forms: emergent, floating-leaved, submerged, and free-floating. Each of these forms has different adaptations, reflected in the sources from which they obtain mineral nutrients and carbon for photosynthesis. These differences often result in zonation, where the submerged forms occupy the deepest water, floating-leaved species somewhat shallower, and emergents the shallowest water. Free-floating plants are not restricted by depth but do require calm and protected waters.

In selecting a species for establishment, not only is it necessary to select a suitable life form, but consideration should be given to the fact that native species are more likely to succeed. Some marsh and

aquatic plants are widespread, having ranges that encompass whole continents or hemispheres. Lemna minor, Phragmites australis (P. communis) and Typha latifolia are found in freshwater marshes throughout the world. Many genera have essentially worldwide distributions. At the opposite extreme are species found only in a single valley or region. For convenience, in this study the U. S. and Canada were divided into six geographic regions. Selected marsh and aquatic plants were classified according to their main regions of occurrence. These are broad regions with ill-defined boundaries, but they do provide a guide to plant distribution.

- a. Atlantic and Gulf coasts.
- b. Inland eastern U. S.
- c. Northern U. S. to the northern Great Lakes, plus most of Alaska and Canada.
- d. Dry interior U. S.
- e. Southern California.
- f. Pacific Northwest to the Alaskan peninsula.

Studies of plant distribution also have revealed some species which apparently are sensitive to water quality degradation. Examples are Najas flexilis, many Potamogeton spp., Scirpus americanus (Table 3). Other species seem to invade or increase in abundance in turbid or polluted waters or disturbed sites. These merit special consideration for establishment on dredged material and include species such as Potamogeton pectinatus, Vallisneria americana, Typha latifolia (Table 4).

Each site has a particular set of characteristics that determines which species might be established. A basic distinction exists between

freshwater habitats and saltwater habitats. Inland saline areas differ from saltwater habitats in the absence of tidal fluctuations, but have similar species. The factors affecting plants in salt marshes and shallow seawater include tides, salinity, drainage, aeration, water table, rainfall, soil, evaporation, temperature, biota, water depth, light penetration, and current and wave action.

Length and frequency of tidal submergence is critical for some species, especially during establishment. High ionic concentrations impose a physiological stress on plants which few species can tolerate. A selected list of species were classified (Table 2) by their natural occurrence in salt water (25-35 ppt), brackish water (5-25 ppt), or fresh water (0-5 ppt).

Impeded drainage and high evaporation cause high salinities (over 35 ppt) tolerated by only a few species, such as Salicornia spp., and occasionally they exceed the tolerances of all plants. Poor drainage and a high water table can result in poor aeration, or waterlogging. This results in strongly reducing conditions in the sediments which may be detrimental to the growth of some plants. Other salt marsh plants, such as Spartina alterniflora, are adapted to grow even in such areas.

Animals such as muskrats, nutria, and waterfowl sometimes consume great quantities of marsh and aquatic plants, but usually do no permanent damage to established stands. They can, however, be serious problems when new plantings are attempted.

The physical stress of current and wave action makes it difficult to establish plants in exposed situations. In brackish and fresh water, Scirpus spp. are most tolerant of wave action. Currents and waves also suspend materials to cause turbidity, as do the activities of man and some animals. Turbidity reduces light penetration, precluding growth of all but the hardiest submersed plants, such as Potamogeton pectinatus.

Many of the factors important in saline areas are also important in fresh water. In the absence of the strong influences of tides and salinity, a wider variety of factors seem to influence the plants. Particularly important are water levels or depths, substrate, water quality, turbidity, and current and wave action.

Freshwater plants often sort by small variations in water depth, in spite of relatively large depth tolerances (Table 2). Water-level fluctuations are particularly important, both in restricting species composition and in maintaining marsh fertility. An important group of waterfowl food plants is adapted to receding summer water levels.

The local distribution of freshwater plants is also determined by substrate composition. Freshwater substrates are always waterlogged, and are strongly reducing if they contain more than 5 to 10 percent organic matter. Highly organic, coarse inorganic, and marl substrates often support little plant growth. Water quality is particularly important to submersed freshwater plants (Table 2). Hard or calcareous waters are most productive.

Within a geographic region and habitat type, local populations of

a particular marsh or aquatic species are sometimes genetically distinct, and thus, are classified as ecotypes. Ecotypic variation is known in Spartina alterniflora, Typha spp. and Sagittaria graminea, three common and valuable marsh species. With these species, and probably many others, establishment is more likely to be successful if local sources of planting stock are used.

As a group, marsh and aquatic plants rely more heavily on vegetative propagation than on seeding. Plants are established naturally from movement of whole plants (freely-floating species) and plant fragments (submersed, free-floating, and floating-leaved species). Many species form special structures called hibernacula during adverse seasons. Vegetative spread by stolons and runners is common. Many emergents, as well as other forms, have rhizomes, rootstocks, or tubers which will generate new plants even though they are primarily food storage organs.

Seed production is unpredictable and unreliable, but information on approximate quantities produced by some species is summarized in Table 6. Dormancy due to required afterripening, impermeable or mechanically constraining seed coats, presence of chemical inhibitors, or environmental reasons is a common cause of problems in attempts to establish new stands by direct seeding. Nevertheless, many species of marsh and aquatic plants have seeds that remain viable for many years if buried in sediments.

Seeds and vegetative propagules are dispersed naturally by wind, water, and animals including man. Light seeds carried by wind disperse

far and wide, so that species such as Typha spp., Salix spp., Populus spp., and Phragmites australis appear quickly on newly exposed wet substrates. Seeds of many species and most vegetative propagules must stay wet or moist to remain viable. These are dispersed chiefly by water movements and usually remain within contiguous waters. Floods occasionally carry seeds across land barriers. Animals, particularly waterfowl and shorebirds, may carry small propagules externally on feet, feathers, or fur. Tough coated seeds may be transported within the digestive tract. The importance of such dispersal is not clear. Man inadvertantly spreads aquatic and marsh plants by his activities in and around marshes--fishing, hunting, boating, rice-farming, dredging, etc.

Regardless of the type of plants to be established, it will be necessary to obtain propagation materials, such as transplanting stock, entire plants, cuttings, vegetative structures, or seeds. For small quantities, nearby natural marshes are probably the best source. For more extensive plantings, commercial outlets may be used, but at present only a few such sources exist (Table 7). Caution is urged in making purchases from these companies for distant plantings because the stock may not be adapted to local conditions. The cost of developing local sources of supply may well be offset by greater success of the planted material.

Seeding is usually the least expensive procedure in terms of collection, storage, and planting, but unless environmental conditions are

favorable, success in establishment may be low. Seeding may be best on large areas, particularly if it is possible to improve conditions for germination by water-level control. On sites exposed to wave or current action, seeds or seedlings may be washed away before they become established. When economically feasible, barriers or structures which reduce the impact of waves and currents may be warranted. Seeds may be collected locally where substrate and water-level conditions permit, with modified farm machinery such as combines.

Transplants usually provide faster establishment, which may be particularly important when rapid substrate stabilization is a major concern. Transplants are usually hardier than seedlings and can be used in harsher situations. They are usually dug by hand from natural or nursery beds, kept moist, and planted immediately. Transplanting during the dormant season may improve success. If nursery beds are the source of material, provision for mechanical digging may increase harvesting efficiency. In one case, hand digging produced 180 to 200 transplants of Spartina alterniflora per man-hour, and when a plow was used, 300 to 400 were lifted per man-hour.

Entire floating plants may be skimmed from the surface of existing beds, kept moist, and dispersed in a new site. Entire submerged plants can be raked or harvested with barge-mounted cutters used in lake "weed control." The plants must be kept in water until dispersed in the desired location. Perennial submersed species can be moved at any time; annuals should be moved only when seed is present.

Mangroves are of considerable importance for shoreline stabilization and protection in Florida. Avicennia seedlings develop good root systems rapidly and are relatively easy to transplant. Nurseries to provide such seedlings could be developed.

The establishment of Spartina alterniflora in salt marshes has been studied intensively by Garbisch et al. (1973) and Woodhouse et al. (1972, 1974). Detailed planting instructions for the mid-Atlantic coast are now available.

The basic problems encountered in the establishment of marsh and aquatic plants on dredged material are physically unsuitable substrates, nutrient deficiencies, polluted sediments, excessive wind or current action, excessive turbidity, unfavorable patterns of water-level fluctuations, and unfavorable water depths. Some of these problems are best dealt with in the design of the sediment disposal operation. Protection from wind, waves, and currents, and proper water depths are best provided in the beginning, for they are difficult to deal with later. Water-level control should also be planned as part of the disposal operation if it is to be part of marsh management operations. If waves and currents are held to a minimum and water-level fluctuations are not excessive, turbidity problems are likely to be controllable by manipulating biotic factors such as carp populations.

Little can be done about physically unsuitable substrates. If all other conditions are favorable, any kind of plant growth which can be encouraged will help ameliorate the habitat. Water-level control which allows agricultural soil conditioning practices is obviously helpful.

Knowledge of substrate-plant nutrient relationships is too scanty to provide a good basis for recommendations on fertilization. Nitrogen and phosphorous fertilizers do improve the growth of emergent plants in some situations.

Very little is known about the effects of pollutants in the sediments on marsh and aquatic plants.

The selection of marsh and aquatic plants for establishment in a specific area should be based on a knowledge of the species native to the area, the specific characteristics of the site, the possible restrictions of local ecotypes, the potential for site preparation and control, the ease of establishment, and the objectives in creating the marsh. Various plant species have excellent, good, fair, or poor potentials as waterfowl food and cover (Table 8). These plants are rated in a very general way, for local circumstances have a great influence on the local value of a species. Most aquatic and marsh plants have value for a variety of birds, mammals, reptiles, amphibians, and fish. Coastal marshes have a well established value in terms of salt-water fisheries.

When substrate stabilization is an important objective, plants should have an extensive underground system of roots and rhizomes and should be easy to establish. Species suggested for this purpose by various authors are listed in Table 8.

Some species of marsh and aquatic plants tend to dominate an area and exclude other plants for a long period of time. This may be a desirable characteristic for substrate stabilization, but detrimental

to other objectives. A list of plants which may cause problems is given in Table 8.

Research is needed on aquatic and marsh plant taxonomy, biology, and ecology. Special effort should be devoted to the study of site conditions, including both physical and chemical characteristics, and propagule collecting and planting methods.

Many species of aquatic and marsh plants have value for use on dredged material disposal sites. On some sites, appropriately adapted plants will readily volunteer and planting will not be necessary. On other sites, planting will greatly accelerate plant community development, stabilize substrates, and enhance wildlife values.

## PREFACE

This is a report of research initiated by the Coastal Engineering Research Center (CERC) for the U. S. Army Engineer Waterways Experiment Station (WES) through Contract DACW72-74-C-0010. This study is part of the Dredged Material Research Program (DMRP), Habitat Development Research Project (HDRP). The DMRP is sponsored by the Office, Chief of Engineers (DAEN-CWO-M), and is assigned to the WES under the Environmental Effects Laboratory (EEL).

The report is contained in two volumes: Volume I, Report of Research, prepared by John A. Kadlec and W. Alan Wentz; and Volume II, A Selected Annotated Bibliography on Aquatic and Marsh Plants and their Management, prepared by W. Alan Wentz, Rachel L. Smith, and John A. Kadlec. Throughout the text of this report, aquatic and marsh plants are referred to by their scientific names. Widely used common names are included in the index and cross-referenced to the appropriate scientific name.

The research, State-of-the-Art Survey and Evaluation of Marsh Plant Establishment Techniques: Induced and Natural, was conducted by John A. Kadlec and W. Alan Wentz for the School of Natural Resources, University of Michigan. Rachel Smith, Steve Dawson, Mark Bergland, Stephen Anderson, and Greg Koerper served as research assistants during the study. Don Woodard (CERC) served as contract manager. At the time of publication, COL James L. Trayers was Director of CERC.

Dr. Conrad J. Kirby was project manager of the HDRP at the time this study was initiated. The contract was monitored by Ms. Jean Hunt under the general supervision of Dr. John Harrison, Chief, EEL, and Dr. R. T. Saucier, Assistant Chief, EEL.

The Directors of WES during the period of this contract were BG E. D. Peixotto, CE, and COL G. H. Hilt, CE. Technical Director was Mr. F. R. Brown.

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STATE-OF-THE-ART SURVEY AND EVALUATION OF  
MARSH PLANT ESTABLISHMENT TECHNIQUES:  
INDUCED AND NATURAL

PART I: INTRODUCTION

New aquatic and marsh substrates may be created by natural means, such as flooding, and through man's activities, such as dredging. If environmental conditions are satisfactory these new substrates may support plant growth. The objective of this report is to review available information on the establishment of vegetation on such sites with special emphasis on dredged material disposal sites.

Several kinds of information are available to help assess the probabilities and potentials for marsh plant establishment on dredged material. These include information on (a) the physical, chemical, and ecological requirements of the major marsh and aquatic plants; (b) the rates of colonization and species replacement on new substrates; (c) the success of plantings of marsh plants, largely by people interested in waterfowl; and (d) the effects of site treatment and other cultural practices on the success of marsh plant establishment. A survey and evaluation of these sources of information were undertaken to provide guidelines for selection of plant species and site requirements for establishment and maintenance techniques.

Perspectives

The major interest in the planting and control of aquatic and

marsh vegetation in the United States has been among those concerned with the waterfowl resource. Prominently involved have been the U. S. Fish and Wildlife Service and its predecessors, the state wildlife agencies, university wildlife programs, and private waterfowl hunting clubs and similar organizations. Certain plants have also been of concern to agricultural interests, either because of their crop potential (e. g. Zizania aquatica) or because of their status as weeds (e. g. Cyperus spp., Polygonum spp.) in fields of cultivated crops. More recently, interest in wetland ecosystems and marsh and aquatic plants has become much broader. Because new values and uses of these areas and plants are being recognized and developed, new kinds and levels of information are required.

Although their work is poorly documented, the members of private duck hunting clubs were probably among the first to be interested in planting specific aquatic and marsh plants, primarily to attract ducks and geese. As the continental waterfowl population declined, probably primarily through overshooting, the federal government became involved via the Bureau of Biological Survey of the U. S. Dept. of Agriculture in 1901 (Martin and Uhler 1939). Early studies were concerned with waterfowl food habits (e.g. McAtee 1911) and programs for planting and encouraging duck food plants (McAtee 1915). The drought of the 1930's further reduced waterfowl populations and lent additional impetus to these programs. The federal wildlife refuge program progressed apace in the 1930's, partly by acquisition of tax-

reverted lands during the Depression. A substantial effort during the period of 1930 to 1950 was devoted to the propagation of wild duck foods (Griffith 1948). The publication, in 1939, of Martin and Uhler's "Food of Game Ducks in the United States and Canada" summarized an enormous volume of information on marsh and aquatic plants and their value to waterfowl. Their bulletin was reprinted in 1951 and remains a major source of information even today. In an introduction to a revised set of "Planting Instructions for Refuge Personnel" issued April 15, 1949, J. Clark Salyer II, Chief, Branch of Wildlife Refuges, U. S. Fish and Wildlife Service said: "The development of marsh and aquatic habitat by use of seeds, tubers, and rootstocks is one of the most important and exacting duties required of a refuge manager."

Planting programs continued through the 1950's, but the record of accomplishment showed failures outnumbered successes (e. g. Wright 1958, Smith 1960).

Gradually, the emphasis shifted from planting to environmental control. Managers came to recognize that if they could manipulate the conditions required for growth, the plants would respond, in most cases without necessity for the expense and effort of plantings (R. Meeks, Winous Point Shooting Club, Sandusky, Ohio, pers. comm.). Efforts therefore shifted to control of water depths and turbidities, to control of competing plant species, to regulation of biotic influences such as carp (Cyprinus carpio) or muskrat (Ondatra zibethicus), and to other ways of affecting the environment. As we will detail later,

marsh and aquatic plants invade most new environments within a few growing seasons; their means of dispersal are remarkably efficient.

Planting is still an important part of waterfowl management, but rarely is it concerned with the establishment of native species. A major program is concerned with essentially agricultural programs of grain production on wet or drained soils with subsequent flooding to make the seed available to ducks (Givens and Atkinson 1957, Linde 1969). Planting of marsh and aquatic plants still occurs, but in general planting now receives little attention. For example, the "Techniques Handbook of Waterfowl Habitat Development and Management" (Atlantic Waterfowl Council 1972) devotes only two short, general paragraphs to planting submerged aquatics and mentions planting in only a few other places. Specific mention is, however, made of the use of emergents to reduce wave action for control of erosion and turbidity. Linde (1969) does not discuss planting of marsh or aquatic species in "Techniques for Wetland Management."

Current thinking by many wetland ecologists is that the environmental conditions determine plant species composition and that the appropriate species will appear quickly, even in newly created habitats. For example, newly dug experimental ponds on a long dry floodplain in North Dakota developed vegetation appropriate to the water quality and pattern of water-level fluctuation, within one to three growing seasons (G. Swanson, pers. comm.). Studies of aquatic and marsh plant response to environmental factors in experimental ponds

in Wisconsin (Linde 1966, 1967) and New York (Lathwell et al. 1969) were hampered by difficulties in establishing particular species. In both cases, a set of species "appeared" which did well under the conditions in the ponds!

Wetlands and their plants and animals are becoming more and more widely recognized as a resource valuable to many more interests than just those of duck hunters. The work of Teal (1962) and others on salt marshes has illustrated their value to estuaries and hence to a large fraction of the saltwater fisheries. The potential importance of marshes as filters of at least some kinds of pollution is being investigated (Odum 1972, Kadlec and Kadlec 1974). Their importance to local hydrology is also being recognized (Larson 1973). Marshes also may function to trap sediments, thus reducing sheet erosion and turbidity. The culture of wild rice is attracting attention (Stoddard 1960, Rogalsky et al. 1971). And, of course, the appeal of a varied and visible fauna within the marsh environment is gaining as the populace becomes more environmentally aware.

The possibility of using dredged material to create new marshes has only recently been considered. The process involves transporting sediment from the dredging site to an unproductive shoreline or shallow water area. The material, deposited and graded to a suitable elevation, is then available for colonization by plants and animals. Left unaltered such a substrate may prove to be a very harsh environment, perhaps too harsh to allow plants to colonize. In these instances it

is important that plants be introduced by man.

Before plants can be established it is necessary to decide which species are best suited for growth on the area and at the same time valuable for the overall marsh system. In order to make this decision it is necessary to know: substrate type and fertility, water quality, water depth and degree of fluctuation, species available and their value, etc. With such questions in mind, the current work was undertaken to summarize information which would be helpful to those interested in establishing marsh and aquatic plants.

The published literature on planting efforts is limited. Much of the work on planting was done on a very random basis with no thought of experimental design or dissemination of the results. Not surprisingly, failures were rarely reported! Larimer (1969) reported that the U. S. Bureau of Sport Fisheries and Wildlife had completed a survey of the literature on the creation of salt marsh along the Atlantic and Gulf coasts. In their survey of 5,470 publications on estuaries only 13 useful references on salt marsh creation were found. He also noted that "Interviews were comparatively less productive."

#### Categories of Marsh and Aquatic Plants

Selecting potentially useful plants from among the many hundreds of species which grow in wet or aquatic situations may be simplified by classifying them into categories. Several criteria for classifying marsh and aquatic plants are possible. The three main criteria we will

use are: (a) geographic range, usually determined by temperature or day length considerations; (b) salinity tolerance, representing a continuum of variation in plant tolerance of salt concentrations; and (c) the life form of the species, determined principally by whether the leaves are submersed (submerged), floating, or emersed (emergent). The first two criteria, which are basic and readily understandable, will be treated in detail in appropriate later sections. The third criterion is outlined below to simplify subsequent discussions.

Sculthorpe (1967) classified hydrophytes (literally, water plants) as follows:

a. Hydrophytes attached to the substrate

(1) Emergent hydrophytes. Occur on exposed or submerged soils, from where the water table is 50 cm or more below the soil surface to where the soil is covered with 150 cm or more of water. Leaves and flowers of mature plants erect in the air.

(2) Floating-leaved hydrophytes. Occur on submerged soils in water depths of about 25 to 350 cm. Leaves floating horizontally on the water, although some species regularly also have submerged leaves; some also produce aerial leaves in certain circumstances.

(3) Submerged hydrophytes. Occur on submerged soils at all water depths to about 10 to 11 m. Foliage entirely underwater.

b. Free-floating hydrophytes. Occur mainly in sheltered sites on standing or slow-flowing waters. Some species with extensive root systems may become anchored in shallow water; some will grow on wet

soils. Very variable leaves.

In freshwater ponds and lakes, these forms are often observed in zones: the submerged species in the deeper water nearest the center of the lake, followed shoreward by a band of floating-leaved forms, and emergents in the zone of shallow water and wet soil at the shore (Sculthorpe 1967, Spence 1967, Belonger 1969). Many variations from this pattern exist where factors other than water depths determine distribution. Wave action, especially, may prevent the development of the floating-leaved zone and sometimes also the emergent zone.

Tidal areas often have submerged plants below the low tide level. Between the tide lines, the periodic absence of surface water limits the vegetation mainly to emergent forms.

According to Sculthorpe (1967), all vascular hydrophytes have been derived, through natural selection, from terrestrial plants. The emergent forms are least modified from the terrestrial. For them, the substrate is the primary source of water and mineral nutrients required for their growth. The atmosphere provides the carbon dioxide ( $\text{CO}_2$ ) needed for photosynthesis. Nutrient availability in the soil and soil solution is therefore important to the growth of these plants.

Floating-leaved plants also have roots in the substrate and use atmospheric  $\text{CO}_2$  for photosynthesis. Thus, they are similar to emersed species in terms of the sources of nutrients needed for growth. The floating-leaves are subject to considerable mechanical stress and hence these plants occupy relatively sheltered water. Such areas may

have accumulations of organic sediments which are highly anaerobic. Many floating-leaved plants possess special structures and physiology that permit them to grow in such circumstances.

For both emergent and floating-leaf plant forms, the spring growth of new leaves to the water surface takes place without access to atmospheric oxygen ( $O_2$ ). This growth may generate a severe physiological stress and thus account for the depth limitations observed in the two kinds of plants.

Submerged species obtain  $O_2$  and  $CO_2$  wholly or partly from gasses dissolved in the water. Their thin and limp leaves facilitate the exchange of dissolved substances directly through the leaves and reduce the need for nutrient uptake via roots. Both routes of uptake are used by many, and perhaps all, species (McRoy and Barsdate 1970, Bristow and Whitcombe 1971). For these plants, water chemistry is extremely important. Some even use dissolved bicarbonates as a source of carbon for photosynthesis. The substrate has some influence on these plants through its physical capacity to anchor the plants, indirectly by its influence on water chemistry, and to varying degrees, depending on species, as a source of mineral nutrients.

Floating plants are completely dependent on dissolved materials for mineral nutrients but use atmospheric  $CO_2$  for photosynthesis. Water chemistry and shelter from waves and currents are of great importance to these species.

The varying requirements and adaptations of these four ecological

groups of plants determine within broad limits which will grow where. Some aquatic habitats do not support the growth of any vascular hydrophytes. Many times this is for physical reasons--impossibly hard or soft substrates, excessive wave or current action, or inadequate light. Occasionally there may be mineral nutrient deficiency or imbalance, as in marl or bog lakes. In most environments, however, there exists some plant which can grow and thrive--the problem is to be sure the right plant reaches the site by either natural or artificial means.

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## PART II: METHODS

Our major approach to the survey was a systematic search of the published literature. A list of the serial publications searched is included as Appendix A. The tables of contents of each of these series were scanned in their entirety. When a likely title was encountered, the paper itself was scanned. The paper was abstracted if it contained relevant information. All abstracts contained a list of subject headings for cross-referencing.

A second major source of information was through letter contact to all state game agencies and many individuals who were or are presently involved in some aspect of wetlands research and/or management. Response from these sources was outstanding. A list of the individuals who responded to our request for information is given as Appendix B.

Much of the research on the topics of interest has been conducted by the U. S. Fish and Wildlife Service or the state wildlife agencies under the cooperatively state-federal funded Pittman-Robertson program. Unpublished reports from both of these sources are on file at the Conservation Library Reference Service (LRS) of the Denver Public Library. The LRS supplied computer generated lists of references with key word descriptors. Copies of the reports which seemed likely to be of value were obtained from the LRS.

Letters were also sent to many commercial suppliers of aquatic and marsh plant materials in the United States requesting information on species available, source of materials, present costs, and season of availability. These suppliers responded by sending current catalogs and brochures.

Key individuals, agencies, and research facilities were visited or contacted by telephone to verify that our information was up to date. Surprisingly little directly applicable work on marsh plant establishment is currently in progress; even less is producing data available for use in this report. Most of the current work is concerned with saltwater areas.

To organize and manage the information from these multiple sources, we developed a scheme for handling documents. Figure 1 is a flow chart of our procedure.

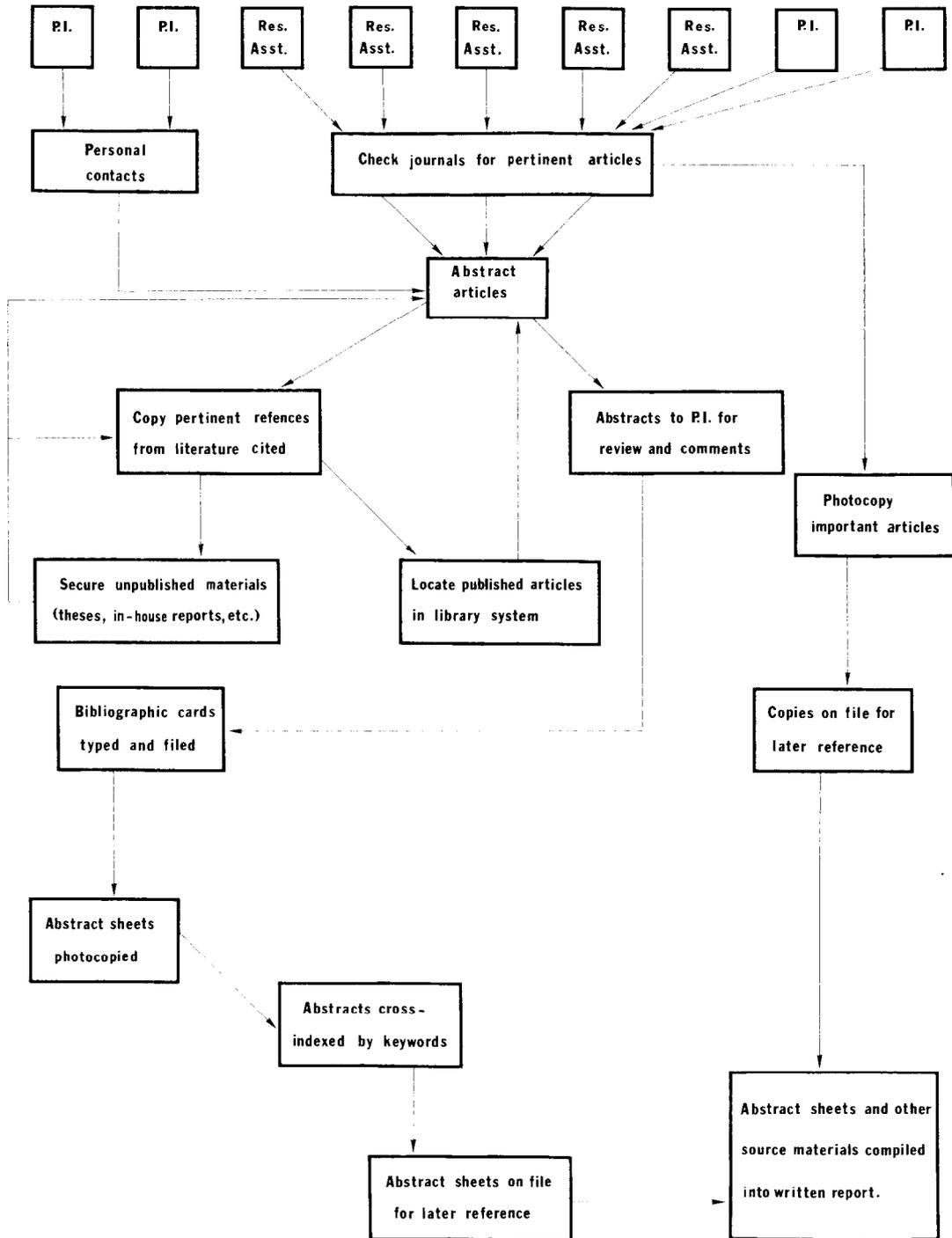


Figure 1. Data Acquisition and Handling Scheme.

### PART III: GEOGRAPHIC REGIONS AND SPECIES DISTRIBUTIONS

A prime consideration in any plant establishment program is an understanding of the geographic distributions of the species involved. There are two levels on which this must be considered: (a) the broad level of the total range of the species, and (b) the much more narrow range of individual populations (ecotypes or races) within the species. The following discussion is concerned with the broad geographic ranges of species. Ecotypic variation within species will be discussed in Part V.

The distributions of aquatic and marsh plants are of two main types: widespread and regional or local.

a. Widespread. Plants whose ranges encompass whole continents or hemispheres are considered widespread. Classic examples of widespread species familiar to persons in many parts of North America and other continents are Lemna minor, Phragmites australis (P. communis), and Typha latifolia. These plants are found in freshwater marshes throughout the world. Zostera marina is probably the most widely known marine angiosperm due to its extensive distribution along the Pacific and Atlantic Ocean coasts. When considered at the generic level the number of widespread aquatic and marsh plants is greatly expanded. The genera Bidens, Calamagrostis, Carex, Elodea, Juncus, Lycopus, Myriophyllum, Najas, Panicum, Polygonum, Potamogeton, Ranunculus, Scirpus, Spartina, and Utricularia are only a few of those which have nearly worldwide distributions. Among these widespread groups, however, individual species may be restricted in distribution by many factors. The existence of a

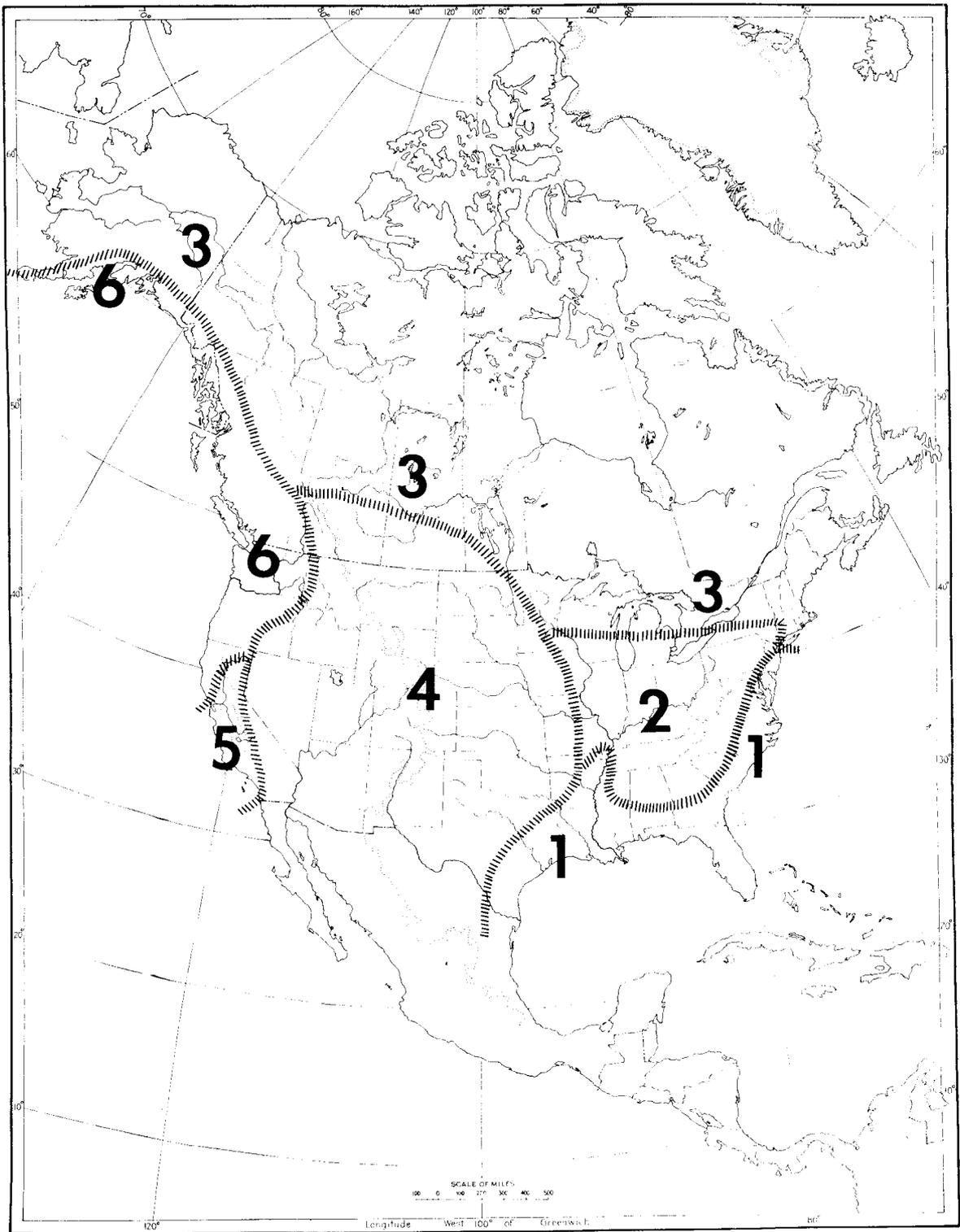
species on a continent does not imply its presence in all wetlands. Most species have at least some fairly distinct habitat requirements and some species, although found on more than one continent, are actually rather rare.

b. Regional or local. Other genera and species of aquatic and marsh plants are more restricted in geographic range and are here termed regional or local. Examples of this group are: Sagittaria sanfordii, which is restricted to the Central Valley of California (Mason 1957); Najas ancistrocarpa, found only in the southeastern U. S. and Japan (Haynes and Wentz 1974a); and Cladium jamaicense, found primarily along the U. S. Atlantic and Gulf coasts (Martin and Uhler 1939).

### Geographic Regions

Any discussion of the ranges of plants to be used in marsh creation is facilitated by some sort of geographic breakdown. We selected the six broad geographic regions indicated in Figure 2. While these regions are arbitrary, they were delineated on the basis of vegetational characteristics.

Region 1 includes those low-lying lands which border the Atlantic and Gulf coasts of North America north to New Jersey. This area has extensive coastal and inland wetlands. The wetland habitats vary from salt marshes to freshwater oxbow lakes to the Okefenokee Swamps to the Florida Everglades. Many of the wetland plants in the area are common and widespread. Large amounts of commercial shipping and pleasure boating take place in this region and more dredging is done here than



**Figure 2. Geographic regions of North America.**

in any other region of North America (Boyd et al. 1972, Woodhouse et al. 1972).

Region 2 is broadly defined as the eastern hardwood forest area. It includes many of the states east of the Mississippi River, all of Lake Erie, and the southern part of Lake Michigan. On the north this region is bordered by the transition zone of the northern or boreal forest and on the west by the Great Plains grasslands. This region is heavily populated and almost every lake and waterway is subject to some degree of dredging and filling by private, commercial, or governmental interests.

Region 3 is an extensive area that consists of New England, the Great Lakes States, and most of Alaska and Canada. Our primary area of interest in this region is the Great Lakes--New England section including the North Atlantic coast. This section can be characterized as transition forest since it is generally a mixture of the northern species and the more southern species that reach their northernmost stations here. The area to the north of this section in Canada and Alaska is dominated by the boreal forest and tundra. Most of region 3 is as yet sparsely populated and relatively unaffected by dredging. In the Great Lakes and New England, dredging is prominent along shipping routes, such as the St. Lawrence Seaway and some of the more southern harbors. It is highly probable that dredging will become more widespread throughout region 3.

Region 4 is a diverse area that includes the Great Plains, the southwestern deserts, and various mountain ranges east of the Cascades.

This area is characterized as semi-arid to arid and water is often a limiting factor. Many of the water bodies in this region are alkaline or saline and the development of artificial marshes is restricted primarily to areas with reliable water supplies. Extensive dredging is almost nonexistent in this region (Boyd et al. 1972).

Region 5 includes southern California and its coast north to San Francisco and inland to Sacramento. Inland water bodies in southern California tend to be intermittent and seasonally fluctuating, while the coastal marshes, estuaries, and bays are permanent but physiologically demanding for plants (Mason 1957). Dredging is prominent here, especially in the Los Angeles and San Francisco areas (Boyd et al. 1972).

Region 6 includes the Pacific Northwest from northern California to the Alaska peninsula. Except for the "rain shadow" areas and high mountains, this region is characterized by mild temperatures and high rainfall. There is an extensive amount of coast line in this region and dredging is prevalent in the Columbia River Basin and Puget Sound.

#### Species Distributions

The six regions discussed above are purposely indistinctly defined and are only artificial vehicles to assist in discussions of species distributions. Many plant species which are primarily confined to one or two of the regions may actually occur in small numbers in the other regions and most of the widespread species that are found in all of the regions will be of varying abundance.

While it is relatively simple to identify most aquatic and marsh plants to the generic level, there is still a great deal of taxonomic confusion over the delineation of species within a genus. Most hydrophytes show a great deal of vegetative variability. This variability has led to a proliferation of the numbers of species and subspecies that are recognized by some taxonomists. Recent ecological and taxonomic investigations in Halodule (Phillips 1960, Haynes and Wentz 1974b), Najas (Wentz and Haynes 1973, Haynes and Wentz 1974a), Nymphaea (Williams 1970), Polygonum (Mitchell 1971), and Potamogeton (Haynes 1973), have shown that many of the described species and subspecies do not warrant separate recognition since the variability is primarily a result of environmental conditions. However, in some other genera (e. g. Sagittaria, Wooten 1970) genetic variability among infraspecific taxa has been shown.

The many names that have been used in the literature make it difficult to determine species distributions without extensive field and herbarium work. It is readily apparent that much ecological and taxonomic research is needed on aquatic and marsh plants (Mason 1957). It would be especially valuable if some of the older identification manuals could be updated to include recently published works.

With the above limitations in mind, it is possible to identify aquatic and marsh plants with the many guides that are available. Although hydrophytes are almost always included in any flora or manual of the plants for a specific area, it may prove easier to use a

specialized identification manual for such plants. A list of useful publications and the areas to which they apply is presented in the following tabulation:

Region(s)*	References
1 - 6	Hotchkiss 1967, Muenscher 1944
1 - 2	Eyles et al. 1963, Fairbrothers and Moul 1965
2 - 3	Fassett 1957, Gleason and Cronquist 1963
4 - 5	Correll and Correll 1972
5	Mason 1957
6	Steward et al. 1963

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\*See Fig. 2

The user is cautioned that many of these manuals are incomplete or out of date and specimens that prove difficult to identify should be sent to an expert on the group (see Shetler and Read 1973 for an index to taxonomists and their specialities).

According to Sculthorpe (1967) about 60% of all aquatic plants have distributions that encompass more than one continent and many range over wide latitudinal areas. He attributes this broad distribution to the "less violent variations of temperature and edaphic factors in the aquatic environment" (as opposed to upland environments). Conversely, 25 to 30 percent of hydrophytes are restricted endemics, most of which occur in the tropics.

Table 1 is a partial list of aquatic and marsh plants that are

Table 1

Widespread Aquatic and Marsh Plants (compiled from many sources).

Submersed or Floating Species	Emersed Species
<u>Bacopa monnieri</u>	<u>Alisma plantago-aquatica</u>
<u>Ceratophyllum demersum</u>	<u>Carex lasiocarpa</u>
<u>Elodea canadensis</u>	<u>Carex rostrata</u>
<u>Lemna minor</u>	<u>Cyperus esculentus</u>
<u>Lemna trisulca</u>	<u>Echinochloa crusgalli</u>
<u>Menyanthes trifoliata</u>	<u>Eleocharis acicularis</u>
<u>Myriophyllum exalbescens</u>	<u>Eleocharis palustris</u>
<u>Myriophyllum verticillatum</u>	<u>Limosella aquatica</u>
<u>Najas flexilis</u>	<u>Phalaris arundinacea</u>
<u>Najas guadalupensis</u>	<u>Phragmites australis</u>
<u>Najas marina</u>	<u>Sparganium angustifolium</u>
<u>Najas minor</u>	<u>Typha angustifolia</u>
<u>Pistia stratiotes</u>	<u>Typha latifolia</u>
<u>Potamogeton alpinus</u>	
<u>Potamogeton crispus</u>	
<u>Potamogeton gramineus</u>	
<u>Potamogeton natans</u>	
<u>Potamogeton pectinatus</u>	
<u>Potamogeton perfoliatus</u>	
<u>Potamogeton praelongus</u>	
<u>Potamogeton pusillus</u>	
<u>Ruppia maritima</u>	
<u>Sparganium minimum</u>	
<u>Spirodela polyrhiza</u>	
<u>Utricularia gibba</u>	
<u>Utricularia intermedia</u>	
<u>Utricularia vulgaris</u>	
<u>Vallisneria americana</u>	
<u>Zannichellia palustris</u>	

widespread throughout the world and are found in North America. This list is presented because these species are found in a wide variation of habitats probably through the mechanism of locally adapted populations. Few of these species have been investigated for possible use on dredged material disposal sites. It is likely that many would prove useful in at least some situations.

Many additional aquatic and marsh species are well distributed across the North American continent, but others are restricted to specific regions. Information on the distribution and habitats of these species is given in Table 2. This table does not list all known hydrophytes in North America. It does, however, list most of the common species and those potentially useful for marsh creation.

### Changes in Species Distributions

There is a growing body of literature about changes in aquatic vascular plant communities. These papers are primarily concerned with conspicuous species composition changes over long time periods. These studies have been done in lakes and river systems on which there exists some sort of long-term record of the presence of aquatic plant species.

Although most of these studies have relied heavily on qualitative observations, they are important because, together, they give a very good indication of the ecological range over which a species exists. This information is important to marsh creation since species that are tolerant of harsh conditions may be easily established in a variety of habitats.

Table 2

Physical-Chemical Conditions Under Which Certain Aquatic and Marsh Plants are Found

<u>Species</u>	<u>Regions</u> <sup>1</sup>	<u>Depth</u> <u>range (cm)</u> <sup>2</sup>	<u>Salinity</u> <sup>3</sup>	<u>Alkalinity</u> <sup>4</sup>	<u>Bottom</u> <u>type</u> <sup>5</sup>	<u>pH</u>	<u>References</u> <sup>6</sup>
<u>Acorus calamus</u>	1-3	-	F	20.0-202.5	-	5.9-8.8	33,57
<u>Alisma plantago-aquatica</u>	1-6	<15	F	31.8-297.5	-	7.0-8.8	33,56
<u>Alternanthera philoxeroides</u>	1	-	F	-	-	7.4-8.0	52,78
<u>Aster tenuifolius</u>	-	mean 80 above MSL	B	-	Si-C, Sa	-	1,38
<u>Atriplex patula</u>	-	80 above MSL	B-S	65	-	7.5	53,57,61
<u>Avicennia nitida</u>	1	-15 to +2.5	B	-	-	5.7-7.7	38,52
<u>Baccharis halimifolia</u>	-	80-100 above MSL	F-S	-	-	4.0-7.5	38,52,53,61
<u>Bidens</u> spp.	1-6	-	-	-	O, Sa, Si	-	59
<u>Borrchia frutescens</u>	-	mean-90 above MSL	B-S	93.3-161.1	-	6.1-8.0	1,38,52,78
<u>Brasenia schreberi</u>	1-3,6	<180	F	32.5-144.0	00,0,L	4.9-8.8	33,56,57,60 68,78
<u>Carex rostrata</u>	2-6	0 - 90	F	45 - 160	-	5.1-7.8	43,57

1 see Figure 2

2 M/LW = Mean Low Water, LW = Low Water, MSL = Mean Sea Level, MHW = Mean High Water

3 F = Fresh, 0-5ppt; B = Brackish, 6-25 ppt; S = saline, 25+ ppt.

4 ppm as CaCO<sub>3</sub>5 C = clay, Si = silt, Sa = sand, BO = brown mud, P = peat, PO = peaty mud, O = organic, Bl O = black mud  
OO = ooze, Ma = marl, L = loam, G = gravel

6 numbers refer to list of references at end of table.

Table 2 (continued)

Species	Regions	Depth range (cm)	Salinity	Alkalinity	Bottom		pH	References
					type	type		
<u>Carex</u> spp.	1-6	<15	F	45 - 160	P,0,B0		4.5-7.8	29,37,52,56,57
<u>Cephalanthus occidentalis</u>	1-6	-	F	4.2 -127.2	-		4.9-8.9	38,52,78
<u>Ceratophyllum demersum</u>	1-6	30 - 150	F-B	8.5-376.0	0		5.4-9.1	33,51,56,57,78
<u>Chara</u> spp.	1-6	30 - 800	F-B	70-256.6	0, Ma,Sa		5.9-9.5	7,23,33,51,52,54
<u>Cladium jamaicense</u>	1	-15 to +100	F-B	-	L,Si-L,00		4.5-7.5	55,56,57,59,78
<u>Cyperus</u> spp.	1-6	<30	F	-	Sa,C,Si-L		-	56,68,74
<u>Decodon verticillatus</u>	1-3	-	F	-	-		4.5-5.3	52
<u>Distichlis spicata</u>	1-6	30 below MSL	B-S	170-8600	Si-C,Sa,C		4.1-9.5	1,3,19,20,35,36,
<u>Echinochloa</u> spp.	1-6	to 150 above MSL	F	17.0-127.2	0		6.2-8.7	38,39,52,53,58,78
<u>Eichornia crassipes</u>	1,4,5	-	F	4.2-182.3	Sa		4.5-9.1	56,60,78
<u>Elodea canadensis</u>	1-6	30 - 300	F	35.3-297.5	00,B0,C		5.4-8.8	15,52,78
<u>Eleocharis acicularis</u>	1-6	<120	F	18.7-376.0	P,0,Sa,Si		7.0-8.0	29,33,43,51,56,
<u>Eleocharis equisetoides</u>	1-3	-	F	4.2-46.6	0		4.4-7.6	57,71
<u>Eleocharis palustris</u>	1-6	<50	F	0.5-220.0	Sa,Si		5.9-9.0	33,56,59
<u>Eleocharis parvula</u>	1-6	wet soil	F-B	-	-		3.7-6.7	33,56,57,59,73
<u>Eleocharis robbinsii</u>	1-3	-	-	-	0		-	35,52
<u>Equisetum fluviatile</u>	2-4,6	-	-	7.5-297.5	-		6.8-8.8	13
<u>Eriocaulon septangulare</u>	1-3	-	F	10.0-44.3	P		6.7-7.8	33
<u>Fimbristylis castanea</u>	1-4	mean 90 above MSL	B	-	-		5.4-7.8	33,59

Table 2 (continued)

Species	Regions	Depth range (cm)	Salinity	Alkalinity	Bottom type	pH	References
<u>Frankenia grandifolia</u>	5	60 above MSL to MHW	-	-	C	-	19
<u>Glyceria borealis</u>	2-4,6	-	F	8.0-187.5	-	5.9-8.8	33,57
<u>Glyceria grandis</u>	2-4,6	-	F	8.0-245.0	-	5.9-8.8	33,57
<u>Halodule wrightii</u>	1	40-60 below MLW	B-S	34.0-195.0	Sa, Si-Sa	7.3-9.2	25,66,77,78
<u>Heteranthera dubia</u>	1-6	-	-	22.5-245.0	0	7.6-9.0	33,60
<u>Hibiscus palustris</u>	1-3	-	B	-	P-Sa	-	27
<u>Hippuris vulgaris</u>	3,4,6	-	-	30.0-297.0	-	6.8-8.8	33
<u>Isoetes braunii</u>	2-4,6	-	F	8.0-45.0	Sa, Si, P, 0	7.0-8.0	33,59
<u>Isoetes lacustris</u>	-	-	-	-	C, Sa, Si	6.0-7.9	29,37
<u>Juncus roemerianus</u>	1	mean 70 cm above MSL	F-B-S	8.5-243.8	Si-C, Sa, I	4.3-9.5	1,38,39,52,55,78
<u>Jaumea carnosa</u>	5-6	50-9 above MSL	-	-	C	-	19
<u>Leersia oryzoides</u>	1-6	wet soil	F	30.4-277.0	-	7.2-9.0	33,60
<u>Lemna minor</u>	1-6	-	F	41.2-262.5	-	5.9-9.0	33,56,57
<u>Lemna trisulca</u>	1-6	-	F	41.2-297.5	-	4.9-8.8	33,57,60
<u>Limnium carolinianum</u>	-	mean 70 above MSL	B	-	Si-C, Sa	-	1,53
<u>Littorella wrightora</u>	3	20-60	F	-	Sa, Si	5.5-8.0	29,43
<u>Lobelia dortmanna</u>	2-4,6	10-240	F	12.5-42.0	Si, B0, Sa, P	5.5-8.0	29,33,43,59,75

Table 2 (continued)

<u>Species</u>	<u>Regions</u>	<u>Depth range (cm)</u>	<u>Salinity</u>	<u>Alkalinity</u>	<u>Bottom type</u>	<u>pH</u>	<u>References</u>
<u>Megalodonta beckii</u>	2-4	-	F	31.8-190.0	-	7.0-8.8	33
<u>Menyanthes trifoliata</u>	-	-	F	80-90	C	4.5-7.3	29,57
<u>Myriophyllum alterniflorum</u>	3	-	-	"soft"	all	-	22,43,59
<u>Myriophyllum exalbescens</u>	1-6	-	F-B	22.5-376.0	0,Sa	7.2-8.9	33,51,57,60
<u>Myriophyllum heterophyllum</u>	1-4	-	F	4.2-46.6	0	5.2-7.2	45,78
<u>Myriophyllum pinnatum</u>	-	-	-	-	0,Sa	-	13,60
<u>Myriophyllum spicatum</u>	-	30-270	F-B	-	C,all	5.8-9.5	4,24,29,43,56
<u>Najas flexilis</u>	1-4,6	30-800	F-B	18.7-307.7	B1 0,00,Sa Si	6.9-9.0	29,33,37,56,57, 59,60
<u>Najas guadalupensis</u>	1-6	-	F	27.6-237.4	-	6.2-9.1	33,54,78
<u>Najas marina</u>	1-6	-	F-B	146.8-376.0	00	8.2-9.0	14,23,33
<u>Nelumbo lutea</u>	-	30-150	F	-	Si,C-0	5.3-6.2	29,37,43
<u>Nitella opaca</u>	-	90-300	F	-	B1 0, Si, Sa	5.5-7.2	29,37,43
<u>Nuphar advena</u>	1-4	< 300	F	2.1-139.9	00	3.7-8.9	56,60,78
<u>Nuphar microphyllum</u>	2-3	< 300	F	7.5-41.1	0	6.8-7.3	33,56
<u>Nuphar rubrodiscum</u>	2-3	-	-	0.5-31.8	0	6.8-7.3	33
<u>Nuphar variegatum</u>	2-4	100-300	F	7.5-220.0	0,Sa, Si	5.8-8.6	33,57,59
<u>Nymphaea alba</u>	-	90-160	-	-	Si,C, B0	5.3-6.2	29,37,43
<u>Nymphaea odorata</u>	1-3	< 300	F	2.1-297.0	00,0,P,Sa, Si	4.4-9.1	56,60,78
<u>Nymphoides aquaticum</u>	1	-	F	4.2-50.9	0	4.9-8.2	13,78

Table 2 (continued)

<u>Species</u>	<u>Regions</u>	<u>Depth range (cm)</u>	<u>Salinity</u>	<u>Alkalinity</u>	<u>Bottom type</u>	<u>pH</u>	<u>Reference</u>
<u>Phalaris arundinacea</u>	1-6	-	F	22.5-160	-	6.9-8.8	33,57
<u>Phragmites australis</u>	1-6	-100 to +200	F-B	0.5-297.5	BO,Sa,Sl, C,P-Sa	3.7-9.0	17,18,29,33,38,43, 51,52,53,57,65,78
<u>Potamogeton alpinus</u>	2-6	-	F	12.5-113.7	BO,0,Sl,00	5.4-8.6	29,33,35,37,43,60
<u>Potamogeton amplifolius</u>	1-3,5,6	100-800	F	12.5-208.7	0,Sa,Sl	7.1-8.8	33,57,59
<u>Potamogeton angustifolius</u>	1-6	-	F	12.5-307.5	-	7.0-9.0	33
<u>Potamogeton crispus</u>	1-6	-	F	113.2-262.5	-	7.6-8.4	33
<u>Potamogeton epihydrus</u>	2-6	100-300	F	10.0-113.7	Sa,Sl,0,00	6.7-8.6	33,59,60
<u>Potamogeton foliosus</u>	1-6	60-180	F-B	37.5-228.7	-	5.9-8.8	8,33,56,57,60
<u>Potamogeton friesii</u>	2-4	-	F	71.6-376.1	-	7.7-8.8	33
<u>Potamogeton gramineus</u>	3,4,6	0-800	F	0.5-226	Sa,Sl,0,G	5.9-8.8	33,57,59,60
<u>Potamogeton illinoensis</u>	1-6	-	F	8.5-164.0	-	5.5-9.1	33,57,78
<u>Potamogeton natans</u>	2-6	90-200	F	18.7-307.7	B1 0,P,Sa, Sl,00,C	5.9-9.0	29,33,37,43,57,59, 60,76
<u>Potamogeton nodosus</u>	1-6	-	F	41.2-312.0	-	7.3-8.5	33,57
<u>Potamogeton obtusifolius</u>	3-6	-	-	30.4-70.0	-	7.0-7.9	33
<u>Potamogeton pectinatus</u>	1-6	5 - 300	F-B	31.8-376.0	Sl,Sa,0	5.9-9.0	33,34,35,43,48,50
<u>Potamogeton perfoliatus</u>	1-6	60-240	F-B	-	C,Sl,B1 0, BO,Sa	5.5-7.2	51,52,54,55,56,78
<u>Potamogeton pusillus</u>	1-6	60-800	F-B	31.5-187.8	Sa,Sl,0	7.0-8.8	29,35,37,55,56
<u>Potamogeton praelongus</u>	1-4,6	160-280	F	12.5-307.7	Sl,Sa,0	7.1-9.0	33,37,51,56,57,59 60
<u>Potamogeton richardsonii</u>	1-4,6	0-250 below MLW	F-B	31.8-376.0	Sl-0	7.0-9.1	29,33,35,37,43,59 33,51,69

Table 2 (continued)

Species	Regions	Depth range (cm)	Salinity	Alkalinity	Bottom type	pH	References
<u>Potamogeton robbinsii</u>	2-4,6	100-800	F	32.5-173	Sa,Si,0	7.2-8.6	33,57,59
<u>Potamogeton spirillus</u>	1-6	0-300	F	18.7-46.0	Sa,Si,0	7.2-8.6	33,57,59
<u>Potamogeton strictifolius</u>	2-4	-	-	31.8-262.5	-	7.4-9.0	33
<u>Potamogeton vaginatus</u>	3,6	-	-	107.5-307.7	-	8.0-9.0	33
<u>Potamogeton zosteriformis</u>	3,4,6	800	F	18.0-245.0	0	6.9-9.0	33,51,57,60
<u>Paspalum lividum</u>	-	-	B-S	-	-	-	3
<u>Pontederia cordata</u>	1-3	<120	F	4.2-144.2	0	4.9-8.9	33,38,56,78
<u>Polygonum amphibium</u>	2-6	<300	F	30.0-260.0	Sa,Si,0	5.4-8.8	29,33,56,57,59
<u>Polygonum coccineum</u>	2-6	-	-	73.0-208.7	-	7.7-8.8	33
<u>Polygonum spp.</u>	1-6	wet soil	F	45-160	Si,Sa	5.1-7.8	3,35,57,60
<u>Ranunculus lengirostris</u>	2-4	-	-	113.2-144.0	-	7.9-8.4	33
<u>Ranunculus trichophyllus</u>	2-6	-	-	12.5-297.5	-	7.1-8.8	33
<u>Rhizophora mangle</u>	1	-	F-S	106.0-233.2	-	7.7-9.1	78
<u>Ruppia maritima</u>	1-6	30-300 below MLW	F-B-S	33.9-284.0	Si,Sa,0	3.7-9.5	7,9,35,46,49,51,52, 54,55,56,58,60,68, 78
<u>Sagittaria cristata</u>	2-4	-	F	18.7-183.0	-	7.2-8.8	33
<u>Sagittaria cuneata</u>	2-4	-	F	20.0-376.0	00	7.3-9.0	33,60
<u>Sagittaria lancifolia</u>	1-2	-	F-P	2.1-136.0	-	4.8-8.9	3,38,39
<u>Sagittaria latifolia</u>	1-6	<30	F	0.5-297.5	0	5.9-8.8	33,56,57,71

Table 2 (continued)

<u>Species</u>	<u>Regions</u>	<u>Depth range (cm)</u>	<u>Salinity</u>	<u>Alkalinity</u>	<u>Bottom type</u>	<u>pH</u>	<u>References</u>
<u>Sagittaria platyphylla</u>	1	<30	F-B	-	-	-	3,56
<u>Sagittaria rigida</u>	1-4	-	F	32.5-297.5	-	7.4-8.8	33
<u>Salicornia ambigua</u>	-	30 above MSL to MHW	S	-	C	-	19
<u>Salicornia bigelovii</u>	5	-	B-S	-	-	6.6-8.5	3,52
<u>Salicornia europea</u>	-	mean 70 above MSL	B-S	-	Si-C,Sa,P	-	1,10,20,27,56
<u>Salicornia perennis</u>	-	mean 80 above MSL	S	-	Si-C,Sa	-	1,53
<u>Salicornia virginica</u>	-	mean 60 above MSL	S	-	P	-	27
<u>Salix spp.</u>	1-6	-	F	4.2-237.4	-	4.5-8.3	57,78
<u>Scirpus acutus</u>	2-6	<150	F-B	17.1-220.0	Sa,all even hard	6.7-9.1	33,51,56,57,63,60
<u>Scirpus americanus</u>	1-6	<60	F-B	12.7-277.0	Sa,C	6.7-8.9	33,53,56,71,78
<u>Scirpus californicus</u>	1,4,5	<180	F-B	6.4-144.2	Si,Sa	4.1-6.2	3,38,52,60,68,78
<u>Scirpus fluviatilis</u>	1-6	<50	F-B	30.4-220.0	-	7.0-9.1	33,51,68
<u>Scirpus heterochaetus</u>	2-4,6	-	-	41.2-198.7	-	7.3-8.6	33
<u>Scirpus olneyi</u>	1,4,5	-7 to +120	B-S	175-630	O,C	3.7-8.0	3,38,52,56,58,71
<u>Scirpus paludosus</u>	4-6	-	(F)-B	146.8-197.5	-	8.4-9.0	33,51
<u>Scirpus robustus</u>	1-6	-15 to +120	F-B	140-890	O,C	4.0-6.9	3,35,38,52,56,58,71
<u>Scirpus subterminalis</u>	2-4,6	-	F	8.0-42.5	00	6.8-7.5	30,33
<u>Scirpus validus</u>	1-6	<120	F	115	Sa,C,Ma	5.3-7.8	51,52,56,57,63,68,71,76

Table 2 (continued)

<u>Species</u>	<u>Regions</u>	<u>Depth range (cm)</u>	<u>Salinity</u>	<u>Alkalinity</u>	<u>Bottom type</u>	<u>pH</u>	<u>References</u>
<u>Sparganium americanum</u>	1-4	<30	-	-	-	-	56
<u>Sparganium chlorocarpum</u>	2-4	-	F	16.5-160	-	7.0-8.4	33,57
<u>Sparganium eurycarpum</u>	1-6	<120	F	35.3-376.0	-	6.7-8.8	33,56,57
<u>Sparganium fluctuans</u>	2-3	<180	F	20.0-45.0	00	7.0-7.3	33,60
<u>Sparganium minimum</u>	2-4,6	-	F	86-115	BO,P,BI 0,	5.4-7.8	29,57
<u>Spartina alterniflora</u>	1	slightly below MSL to more than	B-S	33.9-555.4	Si-C,Sa,P	4.5-8.5	1,3,19,20,35,36,38,39,52,53,58,78
<u>Spartina cynosuroides</u>	-	high marsh	B(S)	-	-	4.3-6.9	3,38,52
<u>Spartina foliosa</u>	5	0-100 over MSL	-	-	C	-	19
<u>Spartina patens</u>	-	30 below MSL to +40 over MHW	B-S	170-8600	Si-C,Sa,P, Sa-P, 0	3.7-7.9	1,3,6,20,27,35,36,38,52,53,58
<u>Spartina spartinae</u>	-	-10 to +5	F-S	4.2-131.4	-	4.9-8.5	3,36,52,78
<u>Spirodela polyrhiza</u>	1-6	-	F	49.0-297.5	-	5.9-8.8	33,56,57
<u>Syringodium filiforme</u>	1	45-60 below LW	S	-	Sa,Si-Sa	-	25,66,77
<u>Thalassia testudinum</u>	1	below LW to 800 above	B-S	-	P,Sa,Si-Sa	4.9-7.2	31,47,66,77
<u>Typha angustifolia</u>	1-6	60 to 90 above MSL, 100	F-B	86-115	0,BI 0	3.7-8.5	29,51,52,57,61
<u>Typha domingensis</u>	1,4,5	-	F-B	12,7-148.1	-	6.0-8.5	3,35,78
<u>Typha glauca</u>	-	<60	F-B	45-160	0	4.5-7.8	51,57,70
<u>Typha latifolia</u>	1-6	<30	F-B	10.0-376.0	P,0	4.5-9.0	27,28,30,33,37,38,51,57
<u>Utricularia intermedia</u>	2-4,6	-	F	8.0-245.0	-	5.1-8.6	33,57
<u>Utricularia vulgaris</u>	1-6	-	F-B	16.5-287.5	-	6.7-8.9	33,39,51,57

Table 2 (continued)

<u>Species</u>	<u>Regions</u>	<u>Depth range (cm)</u>	<u>Salinity</u>	<u>Alkalinity</u>	<u>Bottom type</u>	<u>pH</u>	<u>References</u>
<u>Vallisneria americana</u>	1-3	30-300	F-B	18.7-277.0	Sa-O, Si, Sa, O	5.9-9.1	33, 34, 54, 55, 56, 59, 60, 78 33, 57, 60
<u>Wolffia columbiana</u>	1-2	-	F	85.0-220.0	-	6.4-8.4	
<u>Zannichellia palustris</u>	1-6	30-150	F-B	75.0-337.5	Si	7.6-9.0	33, 51, 56, 60
<u>Zizania aquatica</u>	1-3	5-180	F	8.0-297.5	O, C	6.2-8.8	32, 33, 35, 42, 56, 57, 60, 71, 78 3, 38, 78
<u>Zizaniopsis miliacea</u>	-	-	F-B	6.4-63.6	-	6.0-7.4	
<u>Zostera marina</u>	1, 3, 5, 6	<LW 30-180	B-S	-	Sandy mud, Sa, G	-	2, 56, 67, 72

Table 2 (concluded)

References for Table 2

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Papers on this general topic have been published in North America (Volker and Smith 1965, Lind and Cottam 1969, Stuckey 1971, Wentz and Stuckey 1971), Finland (Suominen 1968, Uotila 1971) and Australia (Higginson 1965, 1971). In general these papers indicate that water temperature increase, oxygen decrease, turbidity increase, pollution, dredging, and other physical disturbances are primary causes for the species composition changes. Many species have shown a low level of tolerance to these changes and have either greatly decreased in abundance or disappeared altogether (Table 3). It is possible that these species would be difficult to establish in the rigorous environments often associated with dredging. While these species should not be abandoned as useless for marsh creation purposes, they are probably not amenable to establishment in dredged areas.

Most of these papers also list species that invaded or increased in abundance in the respective study areas (Table 4). These species are apparently tolerant of disturbance, turbidity, and some forms of pollution. In general these species are of widespread occurrence throughout North America, and are found in a wide variety of habitat types (primarily fresh water). These species merit special consideration in establishment efforts.

The information presented in these studies was obtained primarily from observations. Even though there is some experimental evidence to support the conclusions of these authors (Meyer and Heritage 1941,

Table 3

Aquatic and Marsh Plant Species Apparently Intolerant  
of Turbidity, Pollution, and Related Factors.\*

<u>Submersed and Floating Species</u>	<u>Emersed Species</u>
<u>Megalodonta beckii</u>	<u>Carex aquatilis</u>
<u>Myriophyllum alterniflorum</u>	<u>Equisetum fluviatile</u>
<u>Najas flexilis</u>	<u>Hibiscus militaris</u>
<u>Najas gracillima</u>	<u>Justicia americana</u>
<u>Najas guadalupensis</u>	<u>Lippia lanceolata</u>
<u>Potamogeton amplifolius</u>	<u>Rumex verticillatus</u>
<u>Potamogeton filiformis</u>	<u>Sagittaria rigida</u>
<u>Potamogeton friesii</u>	<u>Saururus cernuus</u>
<u>Potamogeton gramineus</u>	<u>Scirpus americanus</u>
<u>Potamogeton praelongus</u>	<u>Scirpus expansus</u>
<u>Potamogeton richardsonii</u>	
<u>Potamogeton zonsteriformis</u>	

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\*Compiled from information in Lind and Cottam 1969, Stuckey 1971, Stuckey and Wentz 1969, Suominen 1968, Uotila 1971, Wentz and Stuckey 1971.

Table 4

Aquatic and Marsh Plant Species Apparently Tolerant of  
Turbidity, Moderate Pollution, and Related Factors.\*

<u>Submersed and Floating Species</u>	<u>Emerald Species</u>
<u>Alisma plantago-aquatica</u>	<u>Butomus umbellatus</u>
<u>Ceratophyllum demersum</u>	<u>Polygonum hydropiper</u>
<u>Elodea spp.</u>	<u>Polygonum lapathifolium</u>
<u>Heteranthera dubia</u>	<u>Polygonum pennsylvanicum</u>
<u>Lemna minor</u>	<u>Polygonum punctatum</u>
<u>Myriophyllum exalbescens</u>	<u>Sagittaria latifolia</u>
<u>Myriophyllum verticillatum</u>	<u>Sagittaria sagittifolia</u>
<u>Najas minor</u>	<u>Sparganium eurycarpum</u>
<u>Nuphar lutea</u>	<u>Typha angustifolia</u>
<u>Potamogeton crispus</u>	<u>Typha latifolia</u>
<u>Potamogeton pectinatus</u>	
<u>Riccia fluitans</u>	
<u>Ricciocarpus natans</u>	
<u>Spirodela polyrhiza</u>	
<u>Utricularia vulgaris</u>	
<u>Vallisneria americana</u>	
<u>Zannichellia palustris</u>	

\*Compiled from information in: Lind and Cottam 1969, Stuckey 1971, Stuckey and Wentz 1969, Suominen 1968, Uotila 1971, Wentz and Stuckey 1971.

Meyer et al. 1943), more is necessary. The real causes for the increase or decrease in the abundance of these species should be sought through controlled experiments.

## PART IV: SITE REQUIREMENTS

A knowledge of site characteristics and species requirements permits prudent use of time and money to encourage the establishment of marsh and aquatic plants in new habitats. Newly created wetland or marsh environments vary greatly in their physical and chemical characteristics, and it is essential to consider them when assessing the need for, and the design of, a management program. Perhaps the most basic dichotomy is the distinction between saline and freshwater habitats.

### Saltwater Habitats

Saline marshes occur in two distinct regions of North America: the coasts, where the salinity is due to seawater and is largely represented by chlorides; and the interior, mostly in the West, where the salinity is due to evaporative concentration and is often largely represented by sulfates.

Interior wetland salinities sometimes exceed the salinity of seawater (Martin and Uhler 1939). In addition, saline interior wetlands differ in not being subjected to regular tidal fluctuations in water level. Nevertheless, many of the plants found in interior saline areas are closely related to those found in coastal saltwater habitats; often they belong to the same genera. Consequently, much of the discussion of coastal plants and habitats applies to inland saline areas as well. We concentrated our attention on coastal areas, since most dredging and new habitat creation is likely to occur there.

Chapman (1938) listed ten factors affecting plants in salt marshes: tides, salinity, drainage, aeration, water table, rainfall, substrate, evaporation, temperature, and biota. These factors are neither mutually exclusive nor independent; rather they interact in various ways to produce environmental conditions that exert a strong influence on the kinds of plants which will be successful in a given area. Chapman's concern was primarily with emersed marsh vegetation, while our survey also includes the submersed plants. To his list of factors we therefore add water depth, light penetration, and current and wave action.

### Tides

Chapman (1938) pointed out that the vertical elevation of a substrate with respect to tidal fluctuations determines the number of times per year the substrate and plants will be flooded with salt water (Fig. 3). At very high elevations, for example, only when spring and storm tides coincide will high tides bring salt water to the plants. This may happen only a few times per year. At this height in the marsh, the replenishment of plant nutrients via seawater addition occurs rarely and this has a marked effect on the vegetation. As an example of the direct influence of tides, Wiehe (1935) found that Salicornia europea seedlings required two or three days undisturbed by tides immediately after germination to survive. In contrast, Hinde (1954) found that Spartina foliosa could tolerate 21 hours of continuous flooding.

The average number of hours submerged per month and the average

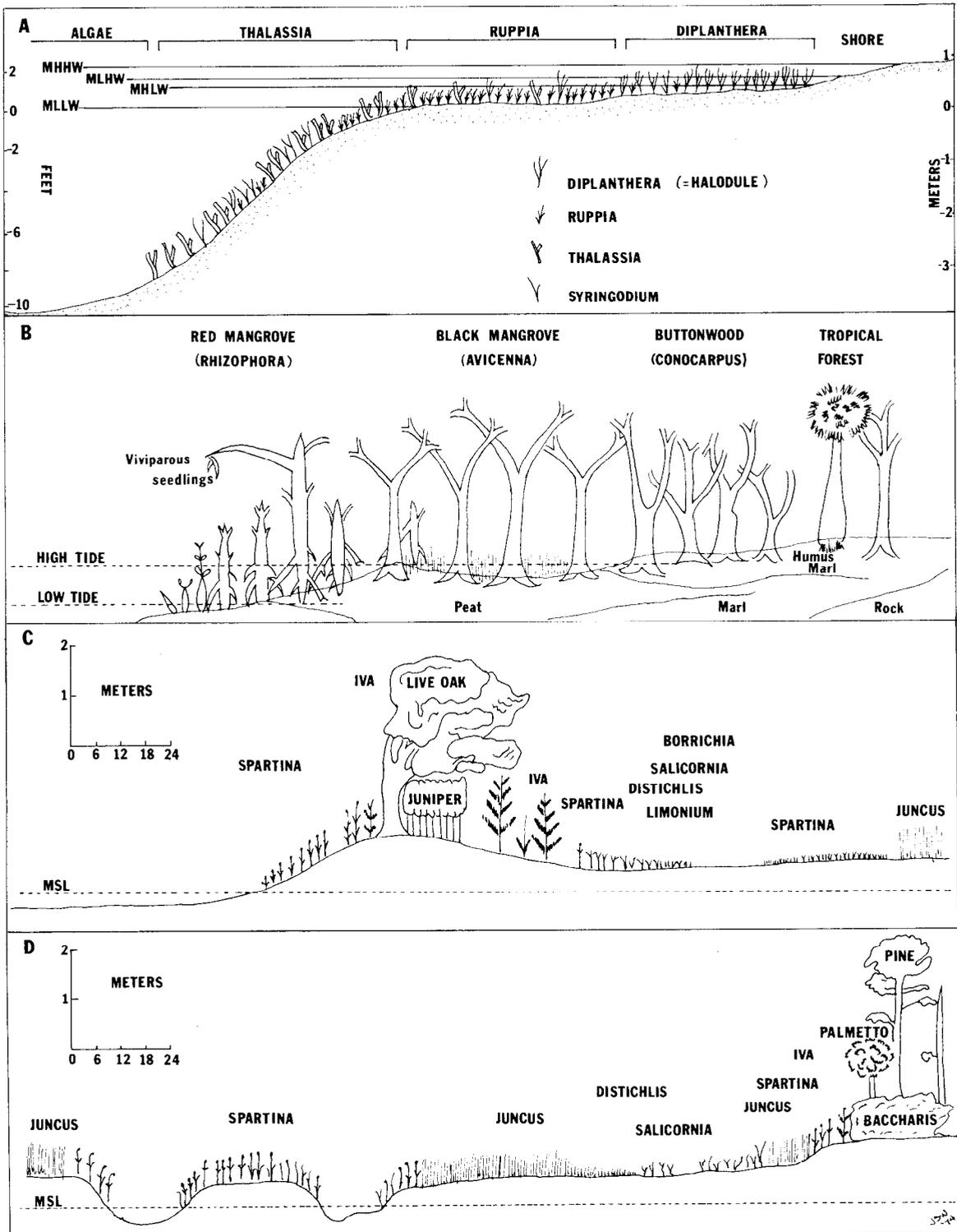


Figure 3. Diagrammatic representation of A) seagrass zonation, B) a mangrove swamp, C) a barrier island of the Gulf Coast, and D) a transect from tidal channels to flatwoods on the Gulf Coast. MHHW= mean higher high water; MLHW=mean lower high water; MHLW=mean higher low water; MLLW=mean lower low water; MSL=mean sea level (Redrawn from McNulty et al. 1972).

number of hours submerged during daylight are important in determining plant distribution according to Chapman (1938). In his study of a British salt marsh, he found that the separation of "upper" from "lower" marsh plants occurred at about 360 submergences per year and about 1.2 hours of submergence per day during daylight.

In estuaries, sounds, and bays, tides are critical in determining the degree of mixing of seawater and fresh water (Thompson 1972). Tidal effects in such areas are related to salinity, water level, and light penetration variables which are discussed below.

### Salinity

Variation in salinity is commonly considered one of the critical factors in plant establishment and growth. High ion concentrations, either from seawater or from evaporative concentration, impose a physiological stress on plants. Relatively few species can tolerate seawater salt concentrations for very long. Since salt concentration is easily measured, there exists a great volume of general data on salinity in relation to marsh and aquatic plants (see Table 2 for a listing of ranges).

Salinity of the water in salt marshes varies depending on the amount of mixing of seawater with fresh water, as occurs in estuaries. In general, this produces a gradient of decreasing salinity from open ocean toward the land (Thompson 1972). Under some circumstances, however, the reverse is true. Salt water from very high tides may be

trapped in depressions in upper marshes and, concentrated by evaporation, may reach very high salinities (Hannon and Bradshaw 1968), unless diluted by rainfall, freshwater runoff, or another high tide. In upper marshes, then, there is often highly variable salinity and a few species, such as Salicornia spp. (Purer 1942) are tolerant of this range. Interestingly, Salicornia is less tolerant of submergence than other salt-tolerant species, so it is clearly well adapted to upper marsh conditions.

Although the salinity of the water is of importance and widely used as an indicator of environmental suitability for salt marsh plants, soil water salinity may be the factor acting directly on the plants (Penfound and Hathaway 1938). Emerged plants in general take up water and nutrients through their roots, as discussed earlier, so the salinity in the root zone is likely to be more critical. Soil water salinity is usually somewhat higher than that of the water over the surface and is highest where the average water level is closest to the soil surface (Penfound and Hathaway 1938). Purer (1942) listed the following factors as affecting soil salinity: (a) height of the tide, (b) elevation of the marshland, (c) proximity to ocean, creeks, or ditches, (d) inputs of fresh water, (e) depth in the soil, and (f) evaporation. Regular flushing with either salt or fresh water prevents excessive increase in salinity. Salinities of soil water near small bodies of water cut off from the ocean may reach 234.23 ppt (parts per thousand) in late summer, much too high to support plant growth (Purer 1942).

Most salt marsh plants will not tolerate a salinity greater than twice that of seawater, or about 70 ppt (Adams 1963).

Another aspect of the influence of salinity is that many salt-tolerant plants grow better in fresh water or very low water salinities (Adams 1963, Barbour and Davis 1970, Gosselink 1970, and Phleger 1971). Boorman (1968) found that seawater reduced the germination percentage and the seedling growth of two species of Limonium. Many "salt marsh" plants apparently would do better in less saline habitats, indicating other factors also influence their distribution. The important point here is that the salinities observed where these plants occur naturally are not necessarily the best criteria for determining where the plants might best be encouraged on new sites. For many species, however, we lack other information.

#### Drainage

The degree of drainage of a site influences a variety of other factors which impinge directly on the plants. According to Purer (1942) a slight rise of land, which clearly improved drainage, greatly improved aeration and allowed different species to invade. Further, the degree of drainage determines whether high marsh depressions will hold pools of salt water between tides. If drainage is poor the soil water level will be near the surface, yielding higher salinities (Penfound and Hathaway 1938). The phenomenon of waterlogging may also result, as discussed below.

## Aeration

Tidal marsh soils, in contrast to fresh marsh soils, are in many cases drained free of excess water between tides. This permits air to invade the pores and maintains a supply of oxygen for soil organisms and possibly also plant roots. According to Chapman (1938):

"...at flooding tides, even when the tide was covering the marsh, the soil water-table rarely rose into the surface mud layer. In other words, there was always an aerated soil layer between the water-table and the flooding tide." "...true of all the marshes (except bare sand or mud flats) irrespective of height or position!"

Such aeration may be absent where the soil is poorly drained for topographic reasons or where the sediments are very fine textured (Goodman 1960). Conditions in deeper sediments are probably continuously anaerobic.

The roots of many if not all marsh plants are supplied to some degree with oxygen by way of air passages from the leaves (Sculthorpe 1967, Purer 1942) so the lack of soil oxygen is not necessarily detrimental. In fact, Adams (1963) suggested that Spartina alterniflora has a high iron (Fe) requirement that is best met when reduced Fe is made available by anaerobic bacteria. Adams (op cit.) suggested that the lack of Fe led to chlorosis in S. alterniflora. More recently, Broome et al. (1973) showed the chlorosis was due to a deficiency of nitrogen (N) rather than Fe. Goodman (1960) suggested Spartina townsendii was adversely affected by some toxic reduced ion associated with poor soil aeration. Poor aeration, or waterlogging, was associated with reduction of sulfates to sulfides, and with the production of

strongly odoriferous hydrogen sulfide ( $H_2S$ ). A negative redox potential also indicated strong reducing conditions.

The complex interactions of Fe, phosphate ( $PO_4$ ), pH, and oxidation state in a salt marsh are illustrated in Figure 4. These cycles are undoubtedly linked to marsh plant growth and coastal productivity, but only the broad outlines are currently understood.

#### Water table

The level of the water table is important in determining aeration as discussed above. The relation of the anaerobic zone in the substrate to the rooting habits of the various plants may influence plant distribution. In the uppermost zones of the marsh, the water table level may also determine the water supply for plant growth during long intertidal intervals. Coarse sands could become too dry to support marsh plants.

#### Rainfall

Rainfall is important as a diluting agent which reduces salinities. In regions of heavy rainfall and little tidal action, salinities may be substantially lower than in regions where the opposite conditions prevail.

#### Substrate

Marsh, estuarine, and shallow saltwater substrates vary widely in physical and chemical composition. Sands, silts, clays, and organic materials of various kinds are common. Physical composition seems to be

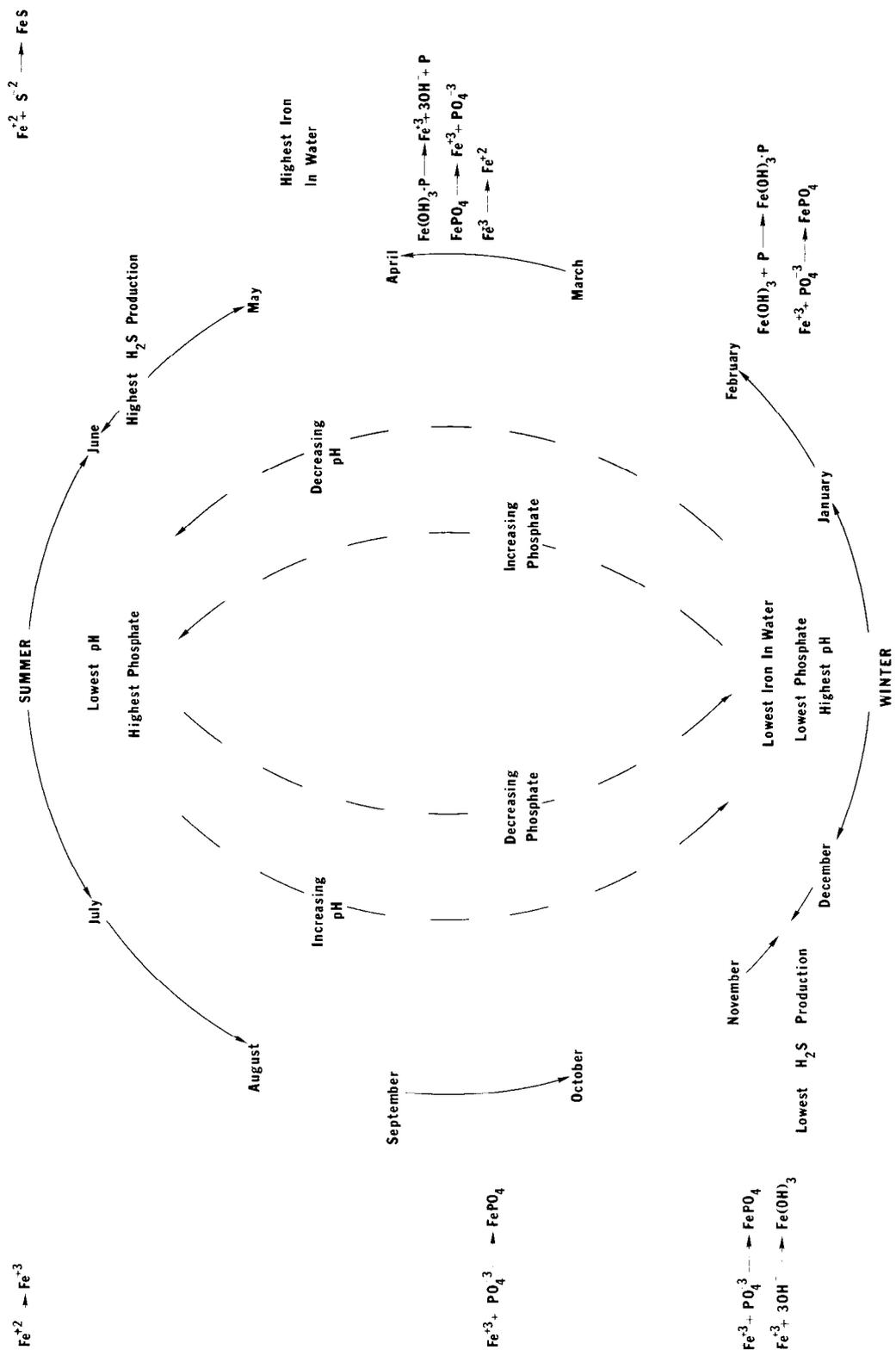


Figure 4. Chemical processes which cause the release of inorganic phosphorus (redrawn from Reimold and Daiber 1970).

important primarily with respect to water relations and to erodibility. Salt marshes may **accumulate** peat or other organic material. Alternately, waterborne materials, primarily silt but also sands and clays, may be deposited. Most plants will do quite well on any substrate unless it is too unstable or waterlogging occurs. Some plants, such as Thalassia testudinum, accomodate to erosion or silting by rapid growth either upward or downward (Tomlinson and Vargo 1966). Redfield (1972) estimated sedimentation rates in a Massachusetts salt marsh as about 15 cm in six years, ranging from a low of about 3 cm to a high of about 30 cm. Siltation may be an important source of nutrients for plant growth. Ranwell (1964) estimated that this source supplied 800 kg/ha/yr of potassium (K). He found slight decreases in the amount of K, P, N and organic carbon (C) from the outer edge of the marsh in toward dry land. In contrast, calcium (Ca) content increased over the same transect.

The physical structure of the substrate between diurnal tide lines is very important in determining the degree of drainage. Clays and fine silts may retain substantial quantities of water between tidal inundations. In the extreme, this retention reduces aeration to a very low level and the substrate is considered waterlogged. Anaerobic conditions then develop, with increases in  $H_2S$  and the reduced form of Fe in the soil solution. Some plants may be killed by these conditions; for example Spartina townsendii (Goodman 1960) as discussed earlier.

Salt marsh substrates are usually rich in nutrients and hence form valuable potential agricultural land (Chapman 1960). Severe nutrient limitation is therefore relatively rare among salt marsh species. Nevertheless, growth responses do result from fertilizer addition (see Garbisch et al. 1973, Jeffries 1972, Woodhouse et al. 1974).

Alteration of the natural water regime of coastal soils may create a serious problem called "cat clay". In silty clay substrates continuously or nearly continuously submerged, S from decaying organic matter combines with Fe in the clay to form complex iron polysulfides (Neely 1962). As long as the soil remains wet, this material has little or no influence on plant growth. If the soil is drained or dried, or, more generally, becomes aerobic, these iron complexes are broken down and the sulfides are oxidized to sulfates. Sulfuric acid is formed on rewetting, and the soil becomes very acid (Neely 1962, Adams 1963). The pH may drop from 7 or 8 to as low as 2.5. This is too acid for plant growth and the substrate is sterile. The condition can be corrected only with the application of enormous quantities of lime (ca. 50 tons/acre) to neutralize the acidity. Reflooding provides little relief as the pH remains around 2-3 (Neely op cit.). Repeated draining and flushing seems to correct the problem. Neely reports 9 to 12 flushings were required to raise the pH to 5.5-6.0. He also said that pH 4.5-5.0 was the approximate lower limit for most duck food plants.

### Evaporation

Evaporation and transpiration contribute to variations in salinity.

Evaporation is reduced under dense emergent vegetation; conversely, transpiration is increased and may compensate for the reduced evaporation in such areas. Usually, however, salinity is lower in areas of emergent vegetation, implying less evaporative concentration (Morss 1927).

### Temperature

Temperature obviously affects evaporation and the many biological processes in the salt marsh ecosystem. In northern areas, ice action physically lifts and transplants clumps of Spartina alterniflora (Redfield 1972).

### Biota

The plants of salt marshes and shallow salt water are eaten by a variety of animals. The plants also compete with one another, so the resulting zones and assemblages of plants are the result of interactions among the physical environment and other plants and animals. Some indication of the relationships among plants may be derived from the transplant experiments of Stalter and Batson (1969). They found that Spartina alterniflora and Limonium carolinianum did not transplant well even within their natural zones of occurrence. Salicornia virginica, Limonium carolinianum, Spartina alterniflora, Borrichia frutescens and to lesser degree Spartina patens were found to survive and even thrive when moved to other zones. Evidently they were not absent from those zones because of physical-chemical factors. Stalter and Batson suggest-

ed that Spartina patens was limited by chlorinity (salinity), excessive duration and depth of flooding, and competition. Salicornia and Limonium did best when there were high soil solute concentrations. (Recall, however, that Boorman (1968) found that Limonium germination and seedling growth were inhibited by sea water).

Waterfowl--ducks, geese, and swans--consume many marsh and aquatic plants as food items. Occasionally, their feeding activities remove substantial quantities of plant material (Lynch et al. 1947). Such feeding usually does not harm established stands. Seedlings and newly invading shoots may be destroyed, however (E. P. Garbisch, Envir. Conc. St. Michaels, Md., pers. comm.). Muskrats can literally "eat out" established stands of favored species (Krummes 1940) and in the south the introduced nutria (Myocastor coypus) may be equally destructive (Swank and Petrides 1954).

### Water depth

For submersed saltwater plants; water depth determines the amount of light reaching plants on the bottom. It may also influence the amount of wave and current action. Both of these factors are discussed in more detail below. General water depth ranges for a selected list of marsh and aquatic plants are given in Table 2.

### Light penetration

Light is essential for plant photosynthesis. Even the clearest water reduces light transmission, both in total amount and selectively

by wavelengths (Hutchinson 1957). At some depth, light is adequate to support only enough photosynthetic activity to balance respiratory use of carbohydrates and no growth is possible, although the plant will survive (Meyer et al. 1943).

Transmission of light through water is reduced by turbidity. Turbidity in turn is related to substrate texture, waves and currents, material washed in from surrounding uplands, and biotic influences (Chamberlain 1948). Clays are notorious for contributing to turbidity. In general, fine soil particles sink more slowly than coarser particles and are more easily stirred into the water column. Currents and waves create the turbulence necessary to lift particles off the bottom into the water.

Man is probably the biotic agent most often responsible for increasing turbidity. Dredging is an example of an activity creating substantial turbidity (Baker 1965). Such turbidity may be highly transient, and its effects similarly short-lived. Baker found that turbidity usually subsided within seven days except in very exposed areas which consistently had high waves. Such wave action caused the turbidity to persist up to a month.

#### Current and wave action

While many aspects of the effects of currents and waves have already been discussed, their effects on the sorting of bottom sediments and their direct mechanical action on plants must still be considered. Strong waves or currents wash away fine materials, leaving coarse-

grained sediments. Even these are frequently shifting and unstable, providing poor anchorage for plants in a situation where stability is crucial if the plant is to withstand the physical stresses imposed. In extreme cases, no plants grow.

The combination of current or wind and ice can be very destructive, as the moving ice grinds, plows through, or overruns any vegetation in its path.

### Freshwater Habitats

Many of the considerations discussed in relation to saltwater habitats also apply to freshwater habitats. In the absence of the dominant factors of tides and salinity, however, plant zonation and distribution is less clearcut. A wider variety of factors seem to influence plant establishment, so that it is more difficult to predict which plant will occur in a specific habitat. Further, the array of species is larger--relatively fewer have adapted to saline environments. The following factors will be discussed: (a) water levels or depths, (b) substrate, (c) water quality, (d) turbidity, and (e) currents and waves.

#### Water levels or depths

In fresh water, two aspects of water level are important: the degree of fluctuation and the water depth. The sorting of species into submersed, floating-leaved, and emersed categories is usually closely associated with water depth. Even within categories, however, there is a close association of species with water depth in a given habitat

(Kadlec 1960, Spence 1967). Several factors may lead to this relationship: (a) variations in light penetration, (b) variations in competitive ability with depth, and (c) variations in the conditions under which seedlings become established. Table 2 summarizes considerable information on species depth preferences.

Water-level fluctuations are detrimental to many submersed freshwater plants (Anderson 1940). The perennials will survive even complete dewatering (removal of surface water) for short periods of time unless the sediments become too dry (Kadlec 1962). Annuals may be encouraged if competition is reduced and fertility improved (Kadlec, op cit.). Floating-leaved plants are quite tolerant of water-level reduction, but may be seriously damaged or killed by water levels high enough to submerge the leaves for substantial periods of time. Emersed species tolerate or are encouraged by water-level fluctuations. Many of them germinate and begin growth better on wet soils than under water, even though established plants grow well in standing water. However even these species may be damaged or killed by prolonged high water (McDonald 1955). Typha latifolia, for example, is susceptible to winter flooding, apparently because the rhizomes and roots cannot obtain atmospheric oxygen via the stubble of last year's stems and leaves (Mathiak 1971).

Although water level fluctuations may be detrimental in some circumstances they may also have beneficial effects. Productive marshes occupy river backwaters or deltas where periodic flooding contributes

nutrient-rich silt to maintain their fertility. The productive Lake Erie marshes may be similarly benefited by both long-term variations in lake level and short-term wind-generated changes (which may be several decimeters in magnitude). The upper region of an estuary is often completely fresh, but still subject to tidal fluctuations. These fresh tidal marshes may be very productive marshes, but Philipp and Brown (1965) found them less productive than tidal brackish marshes.

A substantial number of plants of high value for wildlife occur at the edges of lakes, marshes, rivers, and creeks. These are largely annual grasses (Leersia and Echinochloa, for example) and smartweeds (Polygonum sp.). They require wet, bare soils for germination and early growth, and later tolerate deeper water. These plants are found where fluctuating water levels (and perhaps wave or ice action) inhibit the establishment of other plants, thus reducing competition. The water level fluctuations must also provide the proper soil moisture.

Martin and Uhler (1939) list the following species as being tolerant of fluctuating water levels where the substrate is alternately submerged and drained free of surface water.

Soil always quite moist

Potamogeton americanus  
P. gramineus  
Sparganium spp.  
Triglochin maritima  
Sagittaria spp.  
Glyceria striata  
Distichlis spp.  
Leersia oryzoides

Soil sometimes dry

Panicum dichotomiflorum  
Echinochloa spp.  
Cyperus esculentus  
Polygonum spp.

Soil always quite moist (con't)

Leptochloa fascicularis  
Eleocharis quadrangulata  
E. parvula  
E. acicularis  
Scirpus americanus  
S. acutus  
S. robustus  
S. paludosus  
Rynchospora spp.  
Cladium jamaicense  
Pontederia spp.  
Salicornia spp.  
Acnida cannabinus  
Proserpinaca spp.  
Cephalanthus occidentalis

### Substrate

Misra (1938) made a strong case for the dominant role of the substrate in the distribution of aquatic and marsh plants. Studies of the relation of aquatic plants to the substrate include the works of Pond (1905), Pearsall (1920), Cook and Powers (1958), Spence (1967) and Hannan and Dorris (1970). Not all investigators have found that the substrate is important in the distribution of hydrophytes (Segadas-Vianna 1951, Walker and Coupland 1968).

In contrast to salt marsh soils, most freshwater substrates are always water-logged. Misra (1938) found that sulphides are abundant in all submerged muds containing more than 5-10 percent organic matter. Pearsall and Mortimer (1939), Mortimer (1941, 1942) and Gorham (1953) have investigated the oxidation state of submerged and marsh soils in great detail. Oxygen levels are never high, but oxygen dissolved in the water may provide an oxidizing environment under some circumstances,

particularly if there is some water movement. Normally, however, bacterial decomposition of organic matter produces a high oxygen demand and the substrate is strongly reducing. A sharp transition from oxidizing to reducing conditions frequently occurs at the mudwater interface (Mortimer 1941, 1942). The reducing conditions seem to be important in maintaining Fe and P in solution (Mortimer, op cit.). Under these circumstances Fe and manganese (Mn) sometimes accumulate to very high levels, perhaps to the point of toxicity to plants (Cook and Powers 1958). There is, in fact, a close relation between the forms and solubility of Fe and P and a whole complex of bacterial and chemical factors as outlined in Figure 5.

Substrate fertility is related in part to sediment type. Highly organic material, if poorly decomposed, can be quite infertile. This is partly because the nutrients are tied up in organic form and partly because the peats restrict water movement, effectively sealing basins from nutrient rich groundwater entering from below (Bay 1967). Misra (1938) found Potamogeton alpinus and Sparganium minimum grew on highly organic soils by virtue of a high tolerance of Fe and a low N requirement. In some regions, bottom deposits may be of marl, a deposit of  $\text{CaCO}_3$  found under waters high in bicarbonate or "alkalinity". Marl lakes have notoriously low quantities of aquatic and marsh plants (e. g., Rich et al. 1971). Marl deposits normally have very low organic matter contents, but Oosting (1933) studied a marl lake where there was some organic matter (less than 15 percent) in the marl which supported

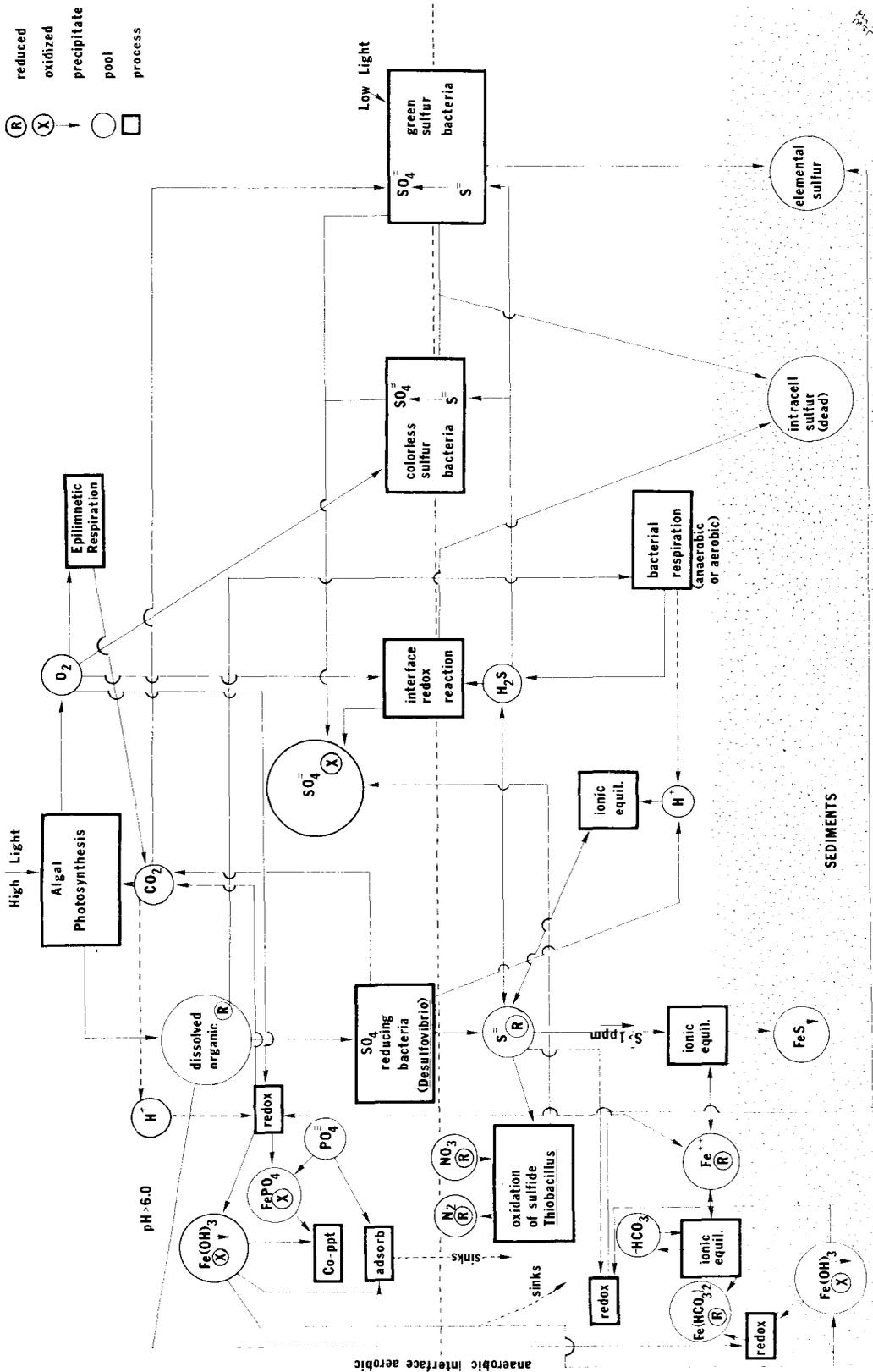


Figure 5. Ionic interactions in a freshwater system.

a stand of wild rice, Zizania aquatica.

Between the extremes of very organic peats and low organic marls is a series of bottom types including sands, silts, and clays with various admixtures of organic material. Sites exposed to considerable wave and current action may have low levels of organic material, and these typically do not support dense marsh or aquatic vegetation. Silts and mixed organic-inorganic substrates seem to be most favorable for plant growth. Pearsall (1920) found that pondweeds (Potamogeton spp.) preferred substrates with 5 to 40 percent organic matter, Myriophyllum sp. and associated species 20 to 65 percent organic, and Juncus fluitans and associated species including Sparganium minimum 60 to 96 percent organic matter in the substrate. Modin (1970) found muck (firm, fine organic material) bottoms most favorable, and marl, sand, gravel or suspended ooze (loose, organic material) poor. Smith (1960) considered excessively hard substrates to be one of the chief causes of failure of planted marsh and aquatic vegetation. Hannan and Dorris (1970) related aquatic plant standing crops to substrate type in a dredged river. They found that "mud" bottoms produced 355 gm/m<sup>2</sup>, silt-pebble bottoms 354 gm/m<sup>2</sup>, mud-gravel 174 gm/m<sup>2</sup>, and gravel 43 gm/m<sup>2</sup>.

Floating plants such as Eichornia crassipes clearly derive needed mineral nutrients from the water, but the quantity of dissolved nutrients is related to substrate conditions (Fig. 5). Gossett and Norris (1971) showed that there were specific responses of E. crassipes to increases of N and P in the water. Floating-leaved and emersed plants derive most of their mineral nutrients from the substrate, but again

water chemistry is closely related. Boyd and Hess (1970) demonstrated significant correlations of Typha latifolia standing crop with soil P, and also with P and Ca in the water. Boyd and Walley (1972) found the growth of Saururus cernuus to be correlated with P, pH and "general soil fertility". In general, the interrelations between substrate and water chemistry are so close (Fig. 5) that it should not be surprising to find correlations with both.

In an experimental study of marsh and aquatic plant production in new habitats, Lathwell et al. (1969) found significant associations with many substrate and water factors. In the first year after the marshes were created, production was found to be a function of total alkalinity (hardness) and water temperature, and substrate Fe, P, K, magnesium (Mg), and organic matter. In the second year, total alkalinity, temperature, pH, and dissolved oxygen in the water and N, Mg, P, Mn, organic matter, and pH in the substrate were significant. With some year to year variation, similar parameters were important in later years. Notably, substrate Ca and aluminum (Al) were added to the list of significant variables. The plant species in the study were all important marsh and aquatic forms: Sparganium americanum, Zizania aquatica, Polygonum amphibium, Scirpus acutus, Najas flexilis, Chara spp., Potamogeton pectinatus, and Vallisneria americana.

A substantial body of data on aquatic substrate chemical analyses is beginning to accumulate; for example Misra (1938), Cook and Powers (1958), Sincock (1960), and Chabreck (1972). The relationship between

such analyses and marsh and aquatic plant performance is not well understood. In agriculture, long experience provides the background for empirical interpretation of standard chemical soil tests. A similar backlog of experience is not yet available for marsh and aquatic plants.

### Water quality

In a comprehensive study of aquatic plant distribution in Minnesota, Moyle (1945) found three groups based on water quality: (a) soft water, where total alkalinity is usually less than 40 ppm, sulfate ion is less than 5 ppm, and pH is less than 7.4; (b) hard water, where total alkalinity is 90-250 ppm, sulfate ion is less than 50 ppm, and the pH is 8.0 to 8.8; and (c) alkali or sulfate waters where the total alkalinity is greater than 150 ppm, sulfate ion is greater than 125 ppm, and the pH is 8.4-9.2. Characteristic softwater species include Lobelia dortmanna, Isoetes braunii, Scirpus subterminalis, and Sarganium minimum. Examples of hardwater species are Chara spp., Potamogeton spp., Najas flexilis, Elodea canadensis, and Ceratophyllum demersum. The alkali-water group included Ruppia occidentalis, Najas marina, and Scirpus paludosus. Moyle states that these are broad groups and that local distribution is greatly influenced by the type of bottom soil. Moyle's extensive data on the ranges of total alkalinity and pH within which various species are found are incorporated in Table 2.

Spence (1967) categorized the lochs of Scotland as calcareous-rich; noncalcareous; slightly saline-moderately rich; and peaty-poor.

The criteria on which these were based were pH, Ca, electrical conductivity, alkalinity, and Cl. The peaty-poor lochs were near neutral in pH, and had very little Ca, low alkalinity and Cl, and a conductivity of only about 44 umhos. Rainwater in Michigan has a conductivity of 30-40 umhos, so the poor lochs were indeed low in nutrients.

Other work on the relationship between water quality and marsh and aquatic plants includes Ellis (1955), who also studied alkalinity, and Stewart and Kantrud (1972), who proposed a series of salinity categories for Great Plains potholes.

Water quality parameters are attractive indices of habitat suitability for various marsh and aquatic plants in that they are relatively easy to measure. However they often vary considerably with season (Cook and Powers, 1958, Kadlec 1962), time of day (Bamforth 1962, Lathwell et al. 1973) and, in new habitats, they change with time (Lathwell et al. 1973, Windom 1972). Sampling must therefore be planned carefully if meaningful relationships are to be indicated.

Quantities of O<sub>2</sub>, CO<sub>2</sub>, mineral nutrients, and such measures as total alkalinity, redox potential, and pH are the results, largely, of known and measurable processes such as inflow, outflow, evapo-transpiration, exchange with the substrate, plant uptake and release (CO<sub>2</sub> for example), and microbial activity. By taking these all into account, detailed interpretations with respect to potential plant growth are in principle possible. In practice, however, one rarely has all the relevant information, so interpretations are not nearly so precise

as might be desired. In such a circumstance, indices such as total alkalinity, pH, and conductivity (a measure of total ion content) may provide a general guide to habitat conditions.

As pointed out earlier, substrate fertility and substrate-water interaction are probably the more relevant features relating to plant growth. More work is badly needed to relate water-quality indices to the parameters that actually affect plant growth.

In some new habitats, toxic materials such as mercury (Windom 1972) may be a problem, but little is known about the behavior of these materials in marsh systems. In Europe, however, Scirpus lacustris is being used in a scheme of sewage treatment (Seidel and Kickuth 1967). One interesting facet of this work is that S. lacustris apparently takes up and metabolizes phenols.

### Turbidity

In freshwater habitats, relatively constant water levels result in submersed plants playing a more important role in the ecosystem. They provide food directly for many forms of wildlife, harbor large numbers of invertebrates (Krull 1970), and shelter small fish from predators. Turbidity is therefore very important in freshwater habitats, for it strongly influences submersed plant distribution and abundance. For example, Meyer and Heritage (1941) found that high turbidity in Lake Erie reduced the compensation point for Ceratophyllum demersum from 8-10 m to 1-2 m. In fresh water, turbidities are often the re-

sult of waves or currents resuspending fine particles from the sediments. Some rivers and some large shallow lakes are continuously turbid for this reason. Aquatic plants, particularly emersed species, may reduce wind-generated waves and even currents to some extent, thus reducing turbidity.

Violent storms sometimes produce turbidity even in normally clear water. Kadlec (1960) observed one storm in a four year study that stirred organic matter into suspension, resulting in anaerobic conditions throughout the water column. Iron and manganese precipitates were observed as the water became re-oxygenated, suggesting that the soluble reduced forms had been released from the bottom mud during anaerobiosis. Such turbidities and consequent effects are fortunately rare and short-lived, and usually do no lasting damage.

A common biotic cause of turbidity is the introduced common carp (Cyprinus carpio) (Chamberlain 1948). The carp thrives in shallow, warm, rich waters where its bottom feeding activities may stir substantial amounts of fine sediments into suspension thereby creating turbidity and limiting plant growth. Reducing carp populations improved submersed plant growth in a number of well documented cases (Cahoon 1953, Threinen and Helm 1954, Tryon 1954, and King and Hunt 1967).

Suspended clay particles causing turbidity may be precipitated by the addition of organic matter. Decomposition of organic material produces CO<sub>2</sub> and forms carbonic acid. The hydrogen ions combine with the negatively charged clay micelles, which results in their precipitation

(Uhler 1955, Cook and Powers 1958).

### Currents and Waves

As in saltwater habitats, the physical action of waves and currents on aquatic and marsh plants significantly affects their distribution. Most species require relatively calm and sheltered water. In clear water, submersed species may grow deep enough to be protected from waves. Floating-leaved species are particularly vulnerable. Obviously, floating plants will be carried by currents and wind until they lodge in sheltered water. Among the emersed species, the bulrushes (Scirpus spp.) do best in exposed situations. In areas with moderate wave action and coarse substrates, water willow (Justicia americana) persists (Penfound 1940). If emersed plants become established, their presence will further reduce wave and current action, permitting a greater variety of plants to become established. Reduced water movement increases silting and the accumulation of organic material, thus increasing the fertility of the site.

### Habitat Tolerances of Selected Species

Table 2 serves as a guide to the general habitat conditions tolerated by various marsh and aquatic species. It also indicates geographic distribution over the zones discussed earlier. The data were compiled from many references, as listed in the table, and this information should be interpreted cautiously. Different studies are not strictly comparable for many reasons, so an amalgamation as in Table 2 unavoidable.

ably introduces some error. For example, depth data for salt marsh species were frequently given with respect to MSL (mean sea level), but, as Chapman (1938) has pointed out, duration of flooding and hence position with respect to tidal range may be the important parameters.

Salinity data vary with season, tidal stage, and local topography, so a single value, or even a range, is only broadly indicative. For that reason, salinity data were listed in the general categories of fresh (0 to 5 ppt), brackish (6 to 25 ppt) or saline (25+ ppt).

Alkalinities also are not consistently reported, but most of the data is from Moyle's (1945) excellent paper and are comparable. Even then only a few samples were available in many cases, so that seasonal and diurnal fluctuations may have caused bias. Moyle (op cit.) also presented sulfate ion data, but almost no one else has done comparable work. On that basis and because sulfate ion, or alkali, is at least roughly comparable to salinity, his sulfate data are not presented.

Aquatic substrate data are notoriously difficult--it is nearly impossible to tell what someone means by "mud"! Some physical categories now have good definitions in soil science, such as sand, silt, and clay; but unfortunately, it is often difficult to tell if these definitions are being used. In the older literature, they were not. Categories of organic soils are even more vague, and all too often the descriptions are not backed up with any measurements. Certainly the area of aquatic substrates could stand rigorous research.

The data on pH are widespread, but their importance is question-

able. Possibly pH is an index of chemical state and thus broadly related to the environmental requirements of plants. However, as can be seen from the table, most plants tolerate a wide range, so that pH is often of little help in narrowing the list of potential species for establishment. Small ranges may be more indicative of scanty data than true restriction. Even though pH has long been measured, there are variations in sampling and measurement techniques which militate against rigorous interpretation.

In the final analysis, Table 2 should be considered only as a general guide. Even if the data were completely accurate, tolerances for local populations are often much more restrictive than for the whole geographic range of a species. Put another way, the local distribution of a species is frequently much more restricted than its entire range would indicate. In any given situation, then, it is important to consider the plants as they occur nearby--the local ecotypes as discussed in the next section.

## PART V: ECOTYPIC VARIATION

The successful establishment of a plant species may depend upon the geographic location of the sources of planting material (propagules). Adaptation to local conditions frequently results in the formation of genotypic and phenotypic populations, especially in species with wide geographic ranges. Unfortunately "the possibility of genetic fixation in local strains has often been overlooked in applied ecology" (Odum 1971). Krebs (1972) has reviewed many studies of intraspecific variation in terrestrial plants that demonstrated that genetic strains often develop in different populations of the same species. Throughout Part V, genotypic and phenotypic forms of the same species will be referred to as ecotypes and ecophenes, respectively (see Mooring et al. 1971).

The problem of ecotypic variation in revegetation attempts was cited as needing further research by the International Seagrass Workshop (McRoy 1973). They noted that development of local physiological races may make it impossible to transplant stock successfully over a great geographic distance. They therefore recommend that "determination of the presence and/or extent of physiological race distinction" be a critical part of any transplanting program.

The following section reviews ecotypic and ecophenic variation studies of marsh and aquatic plants. It demonstrates that the problem of local genetic adaptation is at least as important in aquatic systems as it is in forestry and agriculture.

## Specific Examples

### Spartina alterniflora

Several investigators have recently studied ecotypic variation in S. alterniflora.

Seneca (1974) found germination rates above 50 percent in twelve Atlantic and Gulf coast populations of S. alterniflora. He concluded that there were no inherent differences in germination potential among the populations tested. Stalter (1973a) had earlier suggested that there may have been some genetic reason for an observed difference in germination rate for two Atlantic coast populations. Because his germination rates were so low (8 and 12 percent), it is possible that experimental error accounted for the difference.

Stalter and Batson (1969) and Stalter (1973b) suggested, on the basis of transplant data, that tall and dwarf forms of S. alterniflora were genetic ecotypes. Mooring et al. (1971), however, concluded that the three recognized height forms of S. alterniflora (Adams 1963) could best be described as ecophenes since there was no apparent genetic difference in the forms. Seneca and Broome (1972) found that differences in seedling height and biomass could be produced by different photoperiod and temperature treatments. This information logically leads to the speculation that the variations in adult form may be a result of environmental influences. Woodhouse et al. (1974) concluded that there are naturally occurring populations of S. alterniflora distinctly different in adaptation to specific sites, vigor, morphology, and flowering dates.

Thus, there are serious risks in obtaining planting material from distant geographic sources. Woodhouse et al. (op cit.) believe it is possible to move transplants within a restricted area such as the North Carolina coast, and they commented that "Propagation of such populations could have real practical application in nursery production of material that might be used for stabilization purposes on a variety of sites. This is one area of study that warrants additional attention."

Typha latifolia, T. angustifolia, T. domingensis

Ecotypic variation is thoroughly documented in Typha spp. McNaughton (1966a) demonstrated that coastal populations of T. latifolia were more tolerant of saline conditions than were inland populations. Coastal populations continued to grow for a longer period, achieved a greater growth rate, and recovered faster than inland populations when both were subjected to a salt solution of 2.6 percent.

Seeds collected from southern areas with milder climates germinated at lower temperatures for the three cattail species (McNaughton 1966a). For T. latifolia, North Dakota, South Dakota-Oklahoma, and Texas populations failed to germinate below 24, 18, and 13 C, respectively. Similar results were obtained for T. angustifolia and T. domingensis.

Individual T. latifolia plants from northern areas were smaller than those from lower latitudes, but in T. angustifolia and T. domingensis this pattern was reversed (McNaughton 1966a). Additional experiments suggested that height "is under rather stringent environmental

control" rather than genetic control (McNaughton 1966a).

Only slight correlations between latitude of origin and the beginning of growth were found for all three species (McNaughton 1966a). No evidence of ecotypic flowering patterns was found in T. angustifolia, but T. domingensis and T. latifolia showed variation in flowering from north to south among transplanted populations. The heaviest fruits were produced by southern populations and the lightest by northern populations (McNaughton 1966a).

Standing crops of roots and the ratio of root weight to shoot weight decreased from north to south (McNaughton 1966a). Northern populations were considerably more responsive to environmental influences than were southern populations. Southern populations, on the other hand, were more resilient and were able to maintain similar levels of production regardless of environmental fluctuations. The most widespread species, T. latifolia, was less affected by environmental influence than T. angustifolia and T. domingensis, which have more restricted ranges.

A number of biochemical differences between different ecotypes of T. latifolia were detected also. McNaughton (1966b) has demonstrated that enzymatically distinct populations of T. latifolia are characteristic of climatically distinct sites.

McNaughton (1973) has also demonstrated differential photosynthetic requirements between Quebec and California ecotypes of T. latifolia. The Quebec ecotype had a narrower temperature tolerance than the California ecotype and California plants performed better over a broader

range of warm temperatures. Clearly, distinct differences between different ecotypes of the three Typha species have been documented. Even greater differences have been recorded for ecotypes of terrestrial species, however, and McNaughton (1973) concluded that cattail ecotypes are more similar than those of most other species.

#### Festuca rubra and Agrostis stolonifera

Populations of F. rubra and A. stolonifera in Wales are subdivided into genetic ecotypes based on differential salinity tolerance (Hannon and Bradshaw 1968). F. rubra is found both in upper and lower salt marshes and in adjacent uplands, while A. stolonifera coexists with F. rubra in the uplands. Upper salt marsh populations were the most salt tolerant, while upland populations were the least tolerant. The upper salt marsh populations are exposed to higher salt concentrations than lower salt marsh or upland populations, and this has apparently resulted in greater salinity tolerance in the upper populations.

#### Sagittaria graminea

Sagittaria spp. has in the past been regarded as a good example of phenotypic variability resulting from changing environmental conditions (Wooten 1970). Wooten (1970) demonstrated that these phenotypic differences are, in fact, the result of genetic differences and are not caused by changes in water level. Rhizomes of S. graminea var. graminea, S. graminea var. chapmanii, and S. graminea var. weatherbiana divided into parts and grown in differing water levels produced plants similar

to the parent plant; genetic similarity of seedlings from the same populations was also demonstrated. Reciprocal transplant studies demonstrated that lake populations can survive only where water is present throughout the year (Wooten 1970). It appears that the degree of water level fluctuation and substrate are the critical factors causing genetic differentiation of the ecotypes. Plants from one habitat were often unable to survive in different habitats, but could be successfully transplanted within the same habitats.

#### Zostera marina

Addy and Aylward (1944) successfully transplanted eelgrass from Newburyport Harbor, Massachusetts, to nearby creeks and tidal areas. They note, however, that plantings of the Pacific variety of eelgrass (Z. marina var. latifolia) on the Atlantic coast survived for only a year or two. It is not clear from their article whether these attempts failed because of different requirements between varieties or because of pathogens which had earlier affected the Atlantic variety. It is possible that ecotypic variability was responsible for the failure.

#### Nuphar luteum

Nine subspecies of N. luteum have been recognized, the most divergent being N. luteum ssp. macrophyllum and N. luteum ssp. sagittifolium (DePoe and Beal 1969). Apparent close associations between habitat and leaf shape could be due to: "1) plasticity within a limited gene pool, i. e., ecophenic response, or 2) the selection of particular

non-plastic genotypes from a large gene pool, i. e., ecotypic response."

DePoe and Beal (1969) found that (a) within-clone variability was significantly less than between-clone variability in the same habitat; (b) seedlings grown under uniform conditions were true to parental type; and (c) rhizome transplants also produced leaves true to parental type regardless of habitat. Based on the above, DePoe and Beal concluded that leaf shapes are genetically controlled and are not the result of phenotypic plasticity.

#### Summary

The preceding case studies have demonstrated that local genetic adaptation in aquatic and coastal plant species may critically influence the degree of success achieved in revegetation attempts. Although ecotypic variation occurs in Spartina alterniflora and Typha latifolia, it appears to be less prominent than in some terrestrial species. Nevertheless, it is important to obtain propagules from sources as close to revegetation sites as is possible, regardless of the species in question. This practice has the added benefit of reducing transportation costs (McRoy 1973). When possible, pilot studies should be undertaken to verify that propagules from a given location will be viable in a new habitat before massive transplantation and/or extensive seedings are attempted.

## PART VI: NATURAL ESTABLISHMENT

### Propagule Types

Aquatic and marsh plants have developed a large variety of reproductive modes (Table 5). In addition to sexual reproduction through the development and dispersal of seeds, aquatic and marsh plants often reproduce by vegetative structures. Most hydrophytes are capable of both sexual and vegetative reproduction. In fact, many species seem to rely quite heavily on vegetative reproduction. According to Sculthorpe (1967), vegetative reproduction is probably advantageous since flowering is often unsuccessful in aquatic environments. It is also possible that vegetative propagules have allowed some plants to extend their ranges to areas where seed development is impossible (due to short growing seasons or sporadic dry seasons).

Many authors feel that the formation of specialized vegetative propagules is partly a response to unfavorable environmental conditions, such as low temperatures or insufficient nutrients (Arber 1920, Sculthorpe 1967). It is also clear that an inability to flower, perhaps due to increasing water depth, sometimes initiates vegetative propagation. This is true in Littorella uniflora, which normally flowers when emersed on sand or mud flats, but spreads by runners when submerged (West 1905). Other species, however, typically flower and produce vegetative propagules all in the same growing season (Arber 1920).

Table 5

## Common North American Aquatic and Marsh Plants and Their Methods of Propagation\*

Species	Perennial	Annual	Transplants	Whole plants and fragments	Rootstocks and rhizomes	Cuttings	Tubers	Winter buds (Hibernacula)	Seeds
<u>Acnida cannabina</u>		x							x
<u>Bacopa</u> spp.	x		x			x			x
<u>Bidens</u> spp.		x							x
<u>Brasenia schreberi</u>	x		x		x			x	x
<u>Butomus umbellatus</u>	x		x		x				x
<u>Carex</u> spp.	x		x		x				x
<u>Cephalanthus occidentalis</u>	x		x						x
<u>Ceratophyllum demersum</u>	x			x					
<u>Chara</u> spp.			x	x					
<u>Cladium jamaicense</u>	x		x		x				x
<u>Cyperus</u> spp.	x		x	x	x		x		x
<u>Dama sonia californicum</u>			x						x
<u>Distichlis</u> spp.	x		x		x				x

\* Primary sources: Martin and Uhler 1939, Pirnie 1935, Salyer 1949, Sculthorpe 1967, and Singleton 1965.

Table 5 (continued)

Species	Perennial	Annual	Transplants	Whole plants and fragments	Rootstocks and rhizomes	Cuttings	Tubers	Winter buds (Hibernacula)	Seeds
<u>Echinochloa</u> spp.		x							x
<u>Eleocharis</u> spp.	x	x	x		x		x		x
<u>Elodea canadensis</u>	x		x	x		x			
<u>Glyceria</u> spp.	x		x		x				x
<u>Halodule wrightii</u>	x		x						
<u>Heteranthera dubia</u>	x		x						x
<u>Hippuris vulgaris</u>	x		x						x
<u>Hydrocotyle</u> spp.	x		x		x	x			x
<u>Juncus roemerianus</u>	x		x						
<u>Leersia oryzoides</u>	x		x		x				x
<u>Lemna minor</u>	x			x					
<u>Lemna trisulca</u>	x			x					
<u>Limnium spongia</u>	x		x		x	x			x
<u>Lophotocarpus calycinus</u>	x		x				x		x
<u>Marsilea</u> spp.	x		x		x				
<u>Myrica</u> spp.	x		x		x				
<u>Myriophyllum</u> spp.	x		x	x		x			x

Table 5 (continued)

Species	Perennial	Annual	Transplants	Whole plants and fragments	Rootstocks and rhizomes	Cuttings	Tubers	Winter buds (Hibernacula)	Seeds
<u>Najas</u> spp.		x	x	x					x
<u>Nuphar</u> spp.			x		x				x
<u>Nymphaea</u> spp.	x		x		x				x
<u>Panicum</u> spp.	x	x	x		x				x
<u>Panicum virgatum</u>	x		x						x
<u>Paspalum</u> spp.	x		x		x				x
<u>Peltandra virginica</u>	x								x
<u>Phalaris arundinacea</u>	x		x		x				x
<u>Phragmites australis</u>	x		x		x				x
<u>Planera aquatica</u>	x		x						x
<u>Polygonum amphibium</u>	x		x		x				x
<u>Polygonum hydropiperoides</u>	x		x						x
<u>Polygonum lapathifolium</u>		x							x
<u>Polygonum pensylvanicum</u>		x							x
<u>Polygonum portoricense</u>	x		x			x			x
<u>Polygonum punctatum</u>	x		x						x
<u>Pontederia cordata</u>	x		x		x				x

Table 5 (continued)

Species	Perennial	Annual	Transplants	Whole plants and fragments	Rootstocks and rhizomes	Cuttings	Tubers	Winter buds (Hibernacula)	Seeds
<u>Potamogeton amplifolius</u>	x		x		x	x			x
<u>Potamogeton foliosus</u>	x		x					x	x
<u>Potamogeton gramineus</u>	x		x		x	x			x
<u>Potamogeton natans</u>	x		x		x				x
<u>Potamogeton nodosus</u>	x		x		x	x			x
<u>Potamogeton pectinatus</u>	x		x		x	x	x		x
<u>Potamogeton perfoliatus</u>	x		x		x	x			x
<u>Potamogeton pusillus</u>	x		x					x	x
<u>Potamogeton spirillus</u>			x	x					x
<u>Potamogeton zosteriformis</u>	x		x		x			x	x
<u>Proserpinaca</u> spp.	x		x						x
<u>Ranunculus</u> (Batrachium)	x		x	x					x
<u>Ruppia maritima</u>	x		x		x	x			x
<u>Rynchospora</u> spp.	x		x		x				x
<u>Sagittaria latifolia</u>	x		x				x		x
<u>Sagittaria platyphylla</u>	x		x				x		x
<u>Salicornia</u> spp.	x	x	x		x				x

Table 5 (continued)

Species	Perennial	Annual	Transplants	Whole plants and fragments	Rootstocks and rhizomes	Cuttings	Tubers	Winter buds (Hibernacula)	Seeds
<u>Scirpus acutus</u>	x		x		x				x
<u>Scirpus americanus</u>	x		x		x		x		x
<u>Scirpus californicus</u>	x		x		x				x
<u>Scirpus fluviatilis</u>	x		x		x		x		x
<u>Scirpus olneyi</u>	x		x		x				x
<u>Scirpus paludosus</u>	x		x		x		x		x
<u>Scirpus robustus</u>	x		x		x				x
<u>Scirpus validus</u>	x		x		x				x
<u>Setaria spp.</u>	x	x	x		x				x
<u>Solanum dulcamara</u>	x		x		x				x
<u>Sparganium spp.</u>	x		x		x				x
<u>Spartina alterniflora</u>	x		x						x
<u>Spartina cynosuroides</u>	x		x						x
<u>Spartina foliosa</u>	x		x		x				x
<u>Spirodela polyrhiza</u>	x			x				x	
<u>Thalassia testudinum</u>	x		x						

Table 5 (concluded)

Species	Perennial	Annual	Transplants	Whole plants and fragments	Rootstocks and rhizomes	Cuttings	Tubers	Winter buds (Hibernacula)	Seeds
<u>Triglochin maritima</u>	x		x						x
<u>Typha spp.</u>	x		x		x				x
<u>Vallisneria americana</u>	x		x				x		x
<u>Wolffia spp.</u>	x			x					
<u>Zannichellia palustris</u>		x							x
<u>Zizania aquatica</u>		x							x
<u>Zostera marina</u>	x		x		x				x

## Vegetative Propagules

There are many vegetative structures that serve as reproductive organs. In some cases whole plants or fragments of plants can multiply and/or segment into new plants. Hibernacula are vegetative organs that serve as reproductive units in many species of aquatic plants. Other species have above ground stolons and runners which may produce new plants or overwintering organs. A variety of underground structures including rhizomes, rootstocks, and tubers also serve as perennial and reproductive organs.

### Above ground structures

Whole plants and fragments. Many free-floating and unattached hydrophytes are capable of forming new populations by a variety of means. Such free-floating plants as Azolla spp., Lemna spp., Salvinia spp., Wolffia spp., Spirodela spp., Eichhornia spp., Pistia spp., and others are easily dispersed and will form new plants by gemmiparous growth (development of new plants from vegetative buds on the parent plant) and other means. Once individuals of these plants occupy new and suitable environments, their growth and spread is notoriously rapid. Examples of the speed with which these plants occupy new habitats are legion (Sculthorpe 1967) and for this reason, they are usually considered undesirable weeds.

In most aquatic species, almost any detached stem fragment that includes a bud has the capacity to develop into a new individual. Many

of the most common aquatic species, such as Ceratophyllum, Elodea, and Myriophyllum, can begin new growth from a dormant bud. Even many marsh species are capable of regenerating from fragments. Most marsh grasses have the capacity to sprout from culm nodes. Lynch et al. (1947) found that Spartina and Panicum culm nodes can remain dormant for up to 20 months and still be viable. The sprouting of these fragments led to the rapid colonization of storm-created openings in Gulf coast marshes.

Almost all submersed hydrophytes have stages in their life cycle when they are brittle and easily fragmented. This is especially true in the latter part of the growing season, and fragmentation may be a result of senescence in the individual plant. In culture it has been found that concentrations of 10 ppm of indole-3-acetic acid (IAA) increased fragmentation of Azolla mexicana while gibberellic acid inhibited it by depressing the rate of senescence (Dusek and Bonde 1965). Wentz and Stuckey (1971) observed that several species of Najas become brittle only near the end of the growing season when the plants appear to be dying.

Some species characterized by slender, elongated stems are easily broken at any time. Most species of Ceratophyllum, Elodea, and Myriophyllum are quite susceptible to any disturbance by currents, winds, boats, or animals. These species easily fracture and since almost any part of the stem or leaves has viable buds, the fragments are effective dispersal agents. Indeed, in almost any water body which has these plants present, the shores will be conspicuously littered with broken plant parts.

The fragments of such plants are very effective colonizers as evidenced by the common classification of these species as weeds. Myriophyllum plants fragment after flowering and adventitious roots form rapidly (Patten 1956, Stanley et al. 1966). Cabomba caroliniana is quite common in some areas because of the high reproductive potential of its fragments (DeWit 1961, Riemer and Ilnicki 1968). In most species of Utricularia new shoots will develop from almost any fragment (Goebel 1904, Gluck 1906). In Elodea spp. and Brasenia schreberi, fragmented stem apices and small branches are usually capable of regeneration (Yeo 1966). Several of the perennial species of Potamogeton also are known to fragment into viable segments (Moore 1913).

Although it is a widespread form of vegetative reproduction, the process of gemmipary in aquatic plants is not well understood (Sinnott 1960). In some cases this vegetative process occurs naturally on individual leaves, but it also may result from injury to leaves. In some species, such as Cicuta bulbifera, each leaf may have several buds that are capable of developing into a plantlet or bulbil. These plantlets or bulbils may readily detach from the leaf and become independent or remain attached until after the leaf decays. Many members of the family Cruciferae (Cardamine, Dentaria, Rorippa, and Armoracia aquatica) have gemmipary. It is also not unusual in other families, such as Alismataceae.

Many fragment-type reproductive units develop almost immediately into new plants. However the majority of these propagules are capable

of overwintering and forming new plants in the spring.

Hibernacula. Many aquatic plants, especially in north temperate regions, produce specialized vegetative structures that are capable of remaining dormant during adverse conditions, such as winter or drought. These reproductive units take on a variety of forms, but most consist of dense layers of modified leaves, stem tissue, or bud scales that surround and protect meristematic tissue. A variety of names have been applied, sometimes interchangeably, to these structures including turions, winterbuds, dormant apices, offsets, and hibernacula. Hibernacula is probably the most inclusive term since the others seem to refer to particular locations on the plant or have other connotations.

Very little is known about why various hibernacula form. However, it has been long suspected that hibernacula formation is a response to one or more unfavorable environmental factors such as nutrient deficiency, low temperature, and possibly low light intensity (Sculthorpe 1967). Jacobs (1947) has demonstrated a direct relationship between nitrogen deficiency and turion formation in Spirodela polyrhiza. He further stated that the nitrogen deficiency occurs during peak photosynthetic periods (midsummer) when carbohydrate production is well above that required for growth and respiration. Jacobs concluded that nitrogen deficiencies in combination with high carbohydrate content are necessary for turion formation. This is in general agreement with Goebel (1893) and Gluck (1906), who concluded that nutrient deficiencies initiated turion formation in Myriophyllum verticillatum. However,

Bristow and Whitcombe (1971) have shown that a rooted aquatic plant can take up nutrients from the substrate and this makes it less likely that nutrients will become limiting for rooted species. Perry (1968) has concluded that turion formation can be induced in Spirodela polyrhiza by short day length. In work on Potamogeton nodosus, Frank (1966) postulated that a lack of indole-3-acetic acid (IAA) may be the cause of hibernacula formation after he discovered that IAA would break the dormancy of such organs.

The control of dormancy of hibernacula is not well understood. While hibernacula typically have only low levels of growth hormones present (Frank 1966), it is possible that growth inhibitors are also present (Jacobs 1947, Sculthorpe 1967). Most authors seem to feel that these chemical controls are somehow a result of environmental factors, especially increasing temperature and day lengths (Terras 1900, Arber 1920, Muenscher 1936a, 1936b, Jacobs 1947, Frank 1966, Sculthorpe 1967, Adams 1969, and Weber 1972). Additional research to ascertain controlling factors in hibernacula formation is needed.

The forms that hibernacula take are quite variable. No two species have identical hibernacula. Even within a single genus, such as Potamogeton, the forms are so diverse that species may be distinguished by them (Moore 1913). In Potamogeton, hibernacula vary from tight, few-leaved clusters (P. pusillus) to ornate, winged-leaved forms (P. frieseii) to hard, open, cone-like structures (P. crispus). In Ceratophyllum demersum and Elodea canadensis, hibernacula are little more

than tight leaf clusters, while those of Myriophyllum and Utricularia are compact, club-shaped organs (Sculthorpe 1967, Weber 1972). Many other genera typically form some type of hibernacula: e. g. Zostera (Keller 1963), Hydrilla (Steward 1969), Hydrocharis (Terras 1900), and Brasenia (Adams 1969).

The formation of hibernacula is undoubtedly crucial to the survival of many aquatic plants during adverse conditions. In some habitats individual species may be almost exclusively maintained by overwintering hibernacula (Weber 1972). At the same time these organs serve as effective dispersal agents, particularly within a single water body. The factors which control hibernacula formation, dormancy, and germination are little known. Research into this subject would be desirable for a better understanding of natural aquatic plant establishment and for manipulative techniques for propagation of desirable species.

Stolons and runners. Many perennial plants develop runners that grow at or just above the surface of the substrate and stolons that occur in the surface of the soil. These organs are developed as reproductive structures and rarely overwinter. Typically they grow away from the parent plant and form a new plant which is usually anchored by adventitious roots. Occasionally long chains of such plants may develop (Arber 1920). When the runner or stolon breaks or decomposes, the new plants become independent. In some cases physical breaking of the connecting runner will set young plants adrift in lakes and rivers. Many of these plants are colonizers of new and often coarse substrates

and shores (Sculthorpe 1967). Stuckey (1969, 1970), and Stuckey and Phillips (1970) have found plants with this habit (especially Lycopus asper, L. europaeus, Epilobium hirsutum, and Sagittaria spp.) to be primary invaders of sandy beaches and sand and mud flats in the western Lake Erie region.

Additional species which commonly spread by stolons and runners are: Littorella uniflora, Lobelia dortmanna, Vallisneria americana (Masters 1966); Eichornia crassipes (Penfound and Earle 1948); Pistia stratiotes, Nelumbo, Limosella, Sagittaria, Justicia (Penfound 1940); Polygonum (Mitchell 1971); Spartina townsendii (Oliver 1925); Hydrilla verticillata (Steward 1969); and Hydrocharis morsus-ranae (Terras 1900). Once these plants reach a suitable habitat they are very vigorous invaders.

With the exception of a few descriptive studies, little work has been done on the processes by which these plants grow. It is obvious that such species have great potential for the stabilization of suitable new habitats and hence additional work on them is in order.

Some stolons and runners produce tubers, these will be discussed in the following sections.

#### Underground structures

Rhizomes and rootstocks. Numerous species of aquatic and marsh plants perennate by rhizomes and rootstocks. These structures take on a variety of habits and may be herbaceous or woody, long or short, swollen or slender, and of varying densities. Rhizomes and rootstocks

function primarily as food storage organs but many also promote spreading of the species.

Many papers have discussed the spreading of Phragmites australis (P. communis) by its rhizomes (Bolen 1964, Haslam 1968, 1969a, 1969b, 1970, 1971, 1972). Additional species known to perennate or spread by rhizomes and rootstocks include: Acorus, Eleocharis, Marsilea, Peltandra, Pontederia, Scirpus, Typha, Nuphar, Nymphaea, Potamogeton natans (Sculthorpe 1967); Brasenia schreberi (Adams 1969); Vallisneria americana (Choudhuri 1966); Spartina foliosa (Hinde 1954, Mason 1973); Zostera marina (Keller 1963, Tutin 1942); Scirpus olneyi and Distichlis (Lynch et al. 1947); Hippuris vulgaris (McCully and Dale 1961); Spartina alterniflora (Marchant and Goodman 1969a, 1969b, 1969c); Polygonum (Mitchell 1971); Potamogeton (Muenscher 1936a, 1936b); Justicia americana (Sterling 1949); and Eleocharis palustris (Walters 1949a). This list is by no means exhaustive, but it does give some idea of the wide variety of aquatic and marsh plants that survive in this manner.

Tubers. Tubers are formed by both roots and stems (stolons and runners). They are normally at least partly buried in the substrate. Tubers are formed from nodal and internodal tissue and they are swollen with stored starch. Each one usually has a bud protected by a compressed stipule (Yeo 1966). A single plant may develop a large number of tubers that will survive adverse conditions and eventually grow into new plants.

Several genera and species are noted for their tuber production.

Cyperus esculentus is especially known for extensive tuber production on sandy flats that become dry in the late summer (Tumbleson and Kommedahl 1962, Willis 1971). Vallisneria americana regularly forms tubers (Pirnie 1935, Martin and Uhler 1939). Most of the widely distributed species of Sagittaria (S. sagittifolia, S. subulata, S. graminea, S. cuneata, and S. latifolia) produce tubers in the northern part of their range (Yeo 1966, Sculthorpe 1967). Most perennial species of Potamogeton (e. g. P. pectinatus, P. richardsonii, and P. nodosus) produce large numbers of tubers (Moore 1913, Yeo 1966).

While tubers function primarily as overwintering organs, they also serve as effective agents for local dispersal since many animals uproot them while feeding. Williams (1970) discusses both natural and artificial propagation of Nymphaea by tubers.

There seems to be very little information available on tuber formation and its controlling factors. Willis (1971) discusses some of the environmental factors that influence tuber production in Cyperus esculentus. Yeo (1966) and various other workers (Moore 1913, Muenscher 1936b) have made some observations on Potamogeton tubers. It would seem that further investigation into the ecology of these underground organs would be profitable.

### Seeds

Although much research has been devoted to the study of the seeds of aquatic and marsh plants, understanding of the factors that affect production, dormancy, and germination is still weak.

Seed production. The production of seeds by aquatic and marsh plants varies not only among species, but also within a species and even among individuals of a single population. Without the use of crossbreeding and hybridization, little can be done to alter the innate seed production capacity of a species. However, within that innate capacity, environmental factors can cause large variations.

Some species, such as Cabomba caroliniana (Riemer and Ilnicki 1968) and Spartina foliosa (Phleger 1971, Mason 1973), apparently rarely produce large seed crops. In some cases the seeds produced are sterile and will not germinate (Riemer and Ilnicki 1968). Woodhouse et al. (1974) have noted that maximum seed production in Spartina alterniflora is obtained from young, open stands while old stands tend to produce few seeds.

Arundinaria spp. has been found to have an erratic pattern of flowering which results in unreliable seed production (Hughes 1951). Winterringer (1952) noted that freezing of Arundinaria upright culms during the winter seemed to be one factor which instigated flowering. Many other species apparently produce seeds only when environmental conditions are favorable. Potamogeton crispus rarely bears seed unless water levels drop 7 to 30 cm soon after the last killing frost (Hunt and Lutz 1959).

Grainger (1964) has postulated that two conditions are necessary before a plant will initiate flowering: a sufficient number of young leaves and a sufficiently high level of carbohydrate in the shoot. Thus,

many species of totally submersed plants flower in midsummer when the loss of carbohydrate to the surrounding water is minimal. A minimum requirement of young leaves may impose a restriction on flowering in species which achieve great densities and may therefore be subject to reduced nutrient availability. Broome et al. (1973) found that those Spartina alterniflora plants which had recently colonized an area produced the most vigorous plants and the most seed. Hubbard (1970) noted earlier flowering in Spartina anglica when mowed repeatedly during the previous season.

With these examples of the variability in seed production, Table 6 is presented. This table is a compilation of several measurements of seed production. There are surprisingly few references on this subject and additional research might be profitable.

Seed dormancy and germination. Natural dormancy of seeds can result from several conditions. These include required afterripening periods, mechanical imprisonment of the embryo within the seed coat, the presence of inhibiting substances, and environmental conditions that affect seed metabolism (Sculthorpe 1967). For most species the cause of dormancy has not been investigated satisfactorily.

Absence of dormancy has been most often noted in tropical and southern species (Brunner 1959). Seed dormancy is apparently a principal means by which the more northern species overwinter. This is reflected by some species, such as Lobelia dortmanna (Woodhead 1951a) and Zizania aquatica (LaRue and Avery 1938), whose seeds germinate readily

Table 6

## Seed Production, Germination, and Storage in Aquatic and Marsh Plants

Species	Seed Production (in kg/ha)**	Dormancy or After- ripening	Ripening Dates	Storage	Sources*
<u>Alisma plantago-aquatica</u>	144,000/plant	yes	***		3, 35
<u>Cephalanthus occidentalis</u>	1200				14
<u>Cladium jamaicense</u>	592				14
<u>Cyperus erythrorhizos</u>	674				14
<u>Cyperus esculentus</u>	125	yes			13, 14
<u>Cyperus strigosus</u>	370				14
<u>Distichlis spicata</u>		yes	Early Sept.-Oct.	dry, room temp.	2
<u>Echinochloa crusgalli</u>	1681-2925				14, 16
<u>Echinochloa frumentaceae</u>	3276				14

\* 1) Addy 1947, 2) Amen, et al. 1970, 3) Barton 1961, 4) Boorman 1968, 5) Chapman 1947, 6) Choudhuri 1966, 7) Dill and Greenwell 1948, 8) Garbisch pers. comm. 1974, 9) Haslam 1972, 10) Holm et al. 1969, 11) Hunt and Lutz 1959, 12) Jemison 1961, 13) Justice 1946, 14) Low and Bellrose 1944, 15) Mason 1973, 16) Miller and Arend 1960, 17) Moyle 1967, 18) Muenschler 1936a, 1936b, 19) Palmisano and Newsom 1968, 20) Patten 1956, 21) Pearl 1906, 22a) Richards 1943a, 22b) Richards 1943b, 23) Salyer 1949, 24) Sifton 1959, 25) Simmonds 1945a, 26) Singelton 1951, 27) Smith 1973, 28) Taylor 1957a, 1957b, 29) Timson 1966, 30) Tomlinson 1969, 31) Walters 1949a, b, 32) Woodhead 1951a, 33) Woodhouse et al. 1974, 34) Yeo 1964, 35) Yeo 1966

\*\* unless otherwise noted

\*\*\* omission indicates information not available

Table 6 (continued)

Species	Seed Production (in kg/ha)	Dormancy or After- ripening	Ripening Dates	Storage	Sources
<u>Echinochloa walteri</u>	912-1500				14
<u>Echinodorus cordifoliosus</u>	26,900/plant				35
<u>Eichornia crassipes</u>	up to 500/plant				10
<u>Eleocharis palustris</u>	15-40/spike	yes			31
<u>Eleocharis quadrangulata</u>	9				26
<u>Eragrostis hypnoides</u>	396				14
<u>Eragrostis pectinacea</u>	155				14
<u>Juncus filiformis</u>	75-150/capsule		July - Sept.		22b
<u>Juncus macer</u>	100-300/capsule				22a
<u>Leersia oryzoides</u>	154				26
<u>Limonium vulgare</u>	5/spike		Late Sept.	dry, room temp	4
<u>Lobelia dortmanna</u>	ave. 118/capsule	no	July - Oct.	wet, 1-3° C.	18,32
<u>Lophotocarpus calycinus</u>	401		Sept.		14,18
<u>Myriophyllum spicatum</u>		yes	Nov.		20
<u>Najas guadalupensis</u>	78,500/plant				35
<u>Nelumbo lutea</u>	ave. 26/pod				21
<u>Phragmites australis</u>	up to 1,000/panicle		Nov.	dry, room temp	9
<u>Polygonum hydropiper</u>	300-900/plant	yes	Aug.		29
<u>Polygonum lapathifolium</u>	772	yes	late summer		14,25
<u>Polygonum muhlenbergii</u>	49	yes			14
<u>Polygonum pensylvanicum</u>	1000	yes	Sept.		7,14,23
<u>Polygonum persicaria</u>	200-800/plant	yes	June		25
<u>Polygonum punctatum</u>	150	yes			14
<u>Pontederia cordata</u>	388-722		Sept.	wet, 1-3° C.	14,18

Table 6 (continued)

Species	Seed Production (in kg/ha)	Dormancy or Alter- ripening	Ripening Dates	Storage	Sources
<u>Potamogeton crispus</u>	960/plant				11,35
<u>Potamogeton foliosus</u>	up to 124,950/plant				35
<u>Potamogeton nodosus</u>	959	yes	Sept.	wet, 1-3° C.	14,18
<u>Potamogeton pectinatus</u>	63,000/plant	yes	Aug.	wet, 1-3° C.	18,23
<u>Potamogeton richardsonii</u>	114-29,200/plant				35
<u>Potamogeton vaginatus</u>	90/plant				35
<u>Ranunculus aquatilis</u>	150/plant				35
<u>Ruppia maritima</u>	15				12
<u>Rhynchospora corniculata</u>	1021				26
<u>Sagittaria latifolia</u>	313	yes	Sept.	wet. 1-3° C.	3,14
<u>Scirpus americana</u>	240	yes	Sept.	dry, room temp.	14,18,23
<u>Scirpus californicus</u>	49	yes		dry, room temp.	23,26
<u>Scirpus olneyi</u>	27	yes		dry, cool or room temp.	19,23,26
<u>Scirpus robustus</u>	335	yes		dry, room temp.	26
<u>Scolochloa festucaeae</u>		yes	July		27
<u>Sparganium eurycarpum</u>	930		Oct.		14,18
<u>Spartina alterniflora</u>	40-210	yes	Sept.	wet, 1-3° C.	33
<u>Spartina foliosa</u>		yes			15
<u>Suaeda maritima</u>	up to 1,000/plant	yes	Oct.		5
<u>Subularia aquatica</u>	8-25/plant	no			32
<u>Thalassia testudinum</u>		no	June (Fla.)		30
<u>Typha latifolia</u>	222,000/ 7" spike	yes	Late Aug.	dry, room temp.	8,24,34
<u>Vallisneria americana</u>	several hundred/pod		Sept.	cool, wet	6,18,23

Table 6 (concluded)

Species	Seed Production (in kg/ha)	Dormancy or After- ripening	Ripening Dates	Storage	Sources
<u>Zannichellia palustris</u> <u>Zizania aquatica</u> <u>Zostera marina</u>	2,080,000/plant 28-45	yes no	Sept. Aug.	wet, 1-3° C.	35 17,18 1,28

before they are completely ripe, tend to be difficult to germinate during the afterripening period, and then germinate readily after they become fully ripe. In these species the afterripening period coincides with winter and therefore functions as a dormancy stage. It is thought that this phenomenon is due to the presence of a germination-inhibiting substance in the fully mature seed which is slowly destroyed during the afterripening period.

Vose (1962) found that dormancy in Phalaris arundinacea is caused by a water soluble inhibitor in the caryopsis. Aeration of the tissues, by removing or puncturing the palea, destroys the inhibitor. In Myriophyllum spicatum simple storage may effect afterripening (Patten 1955). For species such as Zizania aquatica (Simpson 1966), Distichlis spicata (Amen et al. 1970), Polygonum hydropiper (Timson 1966), and Spartina alterniflora (Broome et al. 1973), cold water (2-3 C) appears to be suitable for afterripening, but freezing may impair afterripening and even cause death (Broome et al. 1973).

A great number of seeds are inhibited only by the presence of the intact testa. Mechanical or chemical alterations in the seed coat, without injury to the embryo, which permit the entry of air and water have been found to promote germination in Distichlis spicata (Amen et al. 1970), Myrica spp. (Bond 1971), Nelumbo lutea (Jones 1928), Phalaris spp. (Sifton 1959), Typha latifolia (Sifton op. cit.), and Vallisneria spiralis (Choudhuri 1966) among others. Yeo (1964, 1965) obtained 100 percent germination after rupturing the seed coats of Typha latifolia and Potamogeton pectinatus. Perhaps the most pronounced case of seed

dormancy due to an impervious testa is exhibited by Nelumbo lutea whose seeds have been found to remain dormant and viable for several hundred years (Ohga 1926a, 1926b).

Environmental influences on dormancy and subsequent germination are varied. Concentration of salts and gases, depth of burial, light, temperature, and moisture are all known to influence germination by either promoting or terminating dormancy.

Lesko and Walker (1969) have found that germination of most halophytic seeds is inhibited by a 1.0 to 1.5 percent salt solution, a concentration less than half that of sea water. Joanen (1964) attributed this inhibition by salts to the increased osmotic pressure of the ambient solution so that the seed has difficulty absorbing water. Phragmites australis (Ranwell et al. 1964) seeds germinated at 1 percent chlorinity, but did not become established. Even mature plants were limited to areas of less than 1.2 percent chlorinity at 10 cm water depths. Palmisano (1972) showed that Distichlis spicata, Scirpus olneyi, S. americanus, S. robustus, Setaria magna, Echinochloa walteri, Oryza sativa, Polygonum pensylvanicum, and Sacciolepis striata all exhibited a reduction of germination as salinities increased. Similar results were obtained by Christiansen and Low (1970) for Typha spp., Scirpus spp., and Potamogeton spp.

In some cases an initial treatment of seeds with salt water and subsequent submergence in fresh water actually enhances germination (Christiansen and Low 1970). Limonium spp. seed showed highest germination rates after 25 days of soaking in a 5.25 percent salt solution

followed by 25 days in fresh water (Boorman 1968). Contact with sea water appears to induce osmotic shock thus weakening the seed coat.

Apparently seeds of local varieties are sometimes adapted to germinate at higher salinities than usual (Mooring et al. 1971). Seeds of Zostera marina germinated best in water of low salinities, but subsequent growth of the seedling was inhibited (Taylor 1957b). This probably reflects adaptation to the natural fluctuations where salinities progressively increase after spring rains cease. Mayer and Low (1970) found that although seeds of Ruppia maritima germinated best in low salinities (below 12,000 ppm) and six-week-old plants could tolerate salinities up to 27,000 ppm, eight to twelve-week-old plants could not withstand salinities higher than 21,000 ppm. Similar findings were recorded for Uniola paniculata (Seneca 1972).

The influences of partial pressure of gases are known for several species (Morinaga 1926a). Both Typha latifolia and Zizania aquatica germinated best in reduced oxygen pressures, but shoot and chlorophyll development required higher oxygen concentrations (Moyle 1967). Boorman (1968) found that a 50 percent reduction in oxygen produced the highest germination rate in Limonium vulgare and L. humile. No germination of Typha latifolia occurred in the complete absence of oxygen (Morinaga 1926c). Similarly, no germination of Limonium spp. seed was obtained by Boorman (1968) in the absence of oxygen. It appears, therefore, that although the complete absence of oxygen may be harmful for seeds, low oxygen pressures probably aid in the breaking of dormancy.

The response of seeds to light is also poorly understood, but is closely linked to other chemical reactions which determine whether and to what extent there will be a response to illumination (Mayer and Poljakoff-Mayber 1963). Several studies implicate the phytochrome system as a participating and perhaps even controlling mechanism in seed germination (Taylorson 1970). Basically, the theory implies the presence of a pigment which, when stimulated by certain wavelengths of light, becomes excited and begins an energy transfer chain reaction to initiate germination (Mayer and Poljakoff-Mayber 1963). Studies have shown that light in the range below 2900 Å inhibited germination in most seeds; between 2900 Å and 4000 Å, no clear-cut effects on germination were observed; and in the 6500 Å to 7000 Å range, germination was promoted by red light and inhibited by blue light (Mayer and Poljakoff-Mayber 1963). Far red light has also been shown to inhibit germination even after initial treatment with red light (Taylorson 1970). This process, known as photoreversibility, has been documented for several species of seeds (Mayer and Poljakoff-Mayber 1963). Though much of the research on seed response to light was done with upland weed species, the limited data available for wetland species shows comparable reactions. Juncus maritimus, J. tenuis, Alisma plantago-aquatica, Suaeda maritima, and Iris pseudoacorus are a few of the marsh species in which germination is stimulated by light (Mayer and Poljakoff-Mayber 1963).

Salisbury (1970) stated that seeds from different individuals of the same species can differ greatly in their response to light but that

this variation is one of degree rather than kind. Thus, only rarely did 100 percent of the seeds of a species being tested all germinate in either dark or light. The most likely explanation of the widely varying results of seed germination tests is that the seeds contain an inhibitor that varies in amount in the individual seeds and is inactivated by light (Salisbury 1970). Seeds which germinate in the dark may contain little or no inhibitor. Mimulus ringens is one marsh plant which demonstrates 100 percent germination after several days in bright light (Hutchings 1932).

Sauer and Struick (1964) have observed that, for some species of plants such as Carex, only a flash of light is necessary to initiate germination. Richards and Clapham (1941) have shown that many species of Juncus require light for germination. Scirpus olneyi and S. robustus were found to germinate only under alternating conditions of 35 C with light for 14 hours and 20 C without light for 10 hours (Palmisano and Newsom 1968). Submergence apparently inhibits germination in these species. Since S. robustus is often associated with disturbed sites and is a primary invader on exposed soil in brackish marshes, it is likely that the exclusion of light by water prevents the destruction of an inhibitor and precludes germination. Similar dormancy under water has been noted for seeds of Spartina spp., Typha spp., Distichlis sp., and Scirpus spp. These seeds have been reported to germinate only on exposure to air (Lynch et al. 1947), but it is likely that the response is to light, especially since Typha has been shown to germinate best under low oxygen pressures (Morinaga 1926a). Although Thompson (1970)

noticed the response of Lycopus europaeus to light, he felt that alternation of temperatures was a more important influence. Wesson and Wareing (1969a, 1969b) have demonstrated induction of sensitivity to light in terrestrial weed species. In their experiments, seeds which appeared to be unaffected by light prior to burial germinated only in light after a period of 50 weeks burial in soil.

The role of temperature on dormancy and germination is undoubtedly of primary importance. Harrington (1923) stated that the alternation of temperatures can take the place of exposure to light, though none of the species he tested were aquatic. Different lots of seeds of the same species, in similar tests, showed varying sensitivities to alternating as opposed to constant temperatures--a finding which may indicate differences in degree of afterripening or simply variation among individuals of the same species. The temperature changes which gave the best germination rates for weed seeds corresponded closely with those soil temperatures which induce the most prompt and vigorous seedling growth (Harrington 1923).

Many species of northern plants undergo afterripening during the cold months, while more southern species can often germinate soon after dehiscence (Hughes 1951). Recently harvested or wet seeds of many species germinate more rapidly at higher temperatures, probably due to increased respiration of the tissues. Within the range of temperatures over which a certain seed germinates there is usually an optimum temperature below and above which germination is delayed, and eventually

prevented (Mayer and Poljakoff-Mayber 1963). The higher limit is more often known since it is easier to determine. Thus, seeds of Nyssa sylvatica var. biflora were stimulated to germinate rapidly at 21 C but were inhibited when the temperature reached 33 C. Simpson (1966) found that the optimum rate of germination of Zizania aquatica occurred at a constant 20 C after it had been afterripened 6 to 8 months at 1 to 3 C. Potamogeton pectinatus was reported by Crocker (1907) to germinate readily when gathered green and kept at 23 C. However, afterripening of some sort appears to be desirable since Yeo (1965) reported enhanced germination if P. pectinatus seeds are dry stored at 2 C for 3 to 5 months. The percent of germination decreased when seeds were stored wet or dry at 21 C. The discrepancy in results may be explainable in terms of ripeness of the seed. Ungar (1967) and Mason (1973) have noted that higher temperatures always favored Salicornia germination.

Alternating temperatures which approximate natural environmental conditions often produce the highest rate of germination in aquatic species. Although Morinaga (1926b) stated that Typha spp. requires alternating temperatures, Yeo (1964) placed somewhat less emphasis on this factor.

Water levels can greatly affect the breaking of dormancy and subsequent germination. For most aquatic emergents, the most favorable conditions for germination occur when the water level has been severely reduced (drawdown) or the water completely removed from an area (Lynch et al. 1947). Linde (1963) found that Typha spp., Acorus calamus,

Sparganium, Scirpus spp., Echinochloa walteri, Polygonum spp., Salix spp., and Cyperus spp. germinated best when mud flats were exposed by drawdown; the optimum time for germination appeared to be immediately after draining and before crusting occurred. Swamp tupelo (Nyssa aquatica) seed was also found to germinate best when the soil was moist-drained, but it could also germinate under water with no soil present (Debell and Maylow 1972). Typha spp. under greenhouse conditions required flooding of 3 to 18 cm for germination; the fastest rate of seedling growth occurred in about 3 cm of water although seedlings did nearly as well on saturated soil and in 18 cm of water. Zostera marina will germinate in either moist sand or water (Addy 1947). Phragmites australis germinates best on saturated soil (Haslam 1972) as does Echinochloa walteri (Miller and Arend 1960) and Taxodium sp. (Demaree 1932).

The failure of some aquatic plant seeds to germinate under even a small amount of water may be due to the exclusion of light or improper temperatures. Miller and Arend (1960) report that Echinochloa crusgalli will not germinate even when planted 0.5 cm in areas with any standing water. Salisbury (1970) has suggested that the seed coat of some species needs to dry and crack open before germination can occur.

Other aquatic species seeds are destroyed by drying (Tutin 1942, Miller and Arend 1960). Seeds of Alisma plantago-aquatica need to be submerged in about 25 cm of water to germinate, and seeds of Zizania aquatica (Moyle 1967), Spartina alterniflora (Woodhouse et al. 1972, 1974), and Potamogeton spp. (Muenscher 1936a, 1936b) should never be

dried. Depth of burial of seeds in the soil influences the duration of seed viability. In general, deeper burial results in longer viability than does shallow burial (Taylorson 1970). This condition has been documented primarily for terrestrial weed species (Shenstone 1923), but probably applies to marsh plants as well. Shull (1914) has shown that many seeds, from both terrestrial and aquatic species, remain viable under water for as much as 12 years. Stuckey (pers. comm.) has noted that dredged material from the western end of Lake Erie frequently supports luxuriant growth of Polygonum lapathifolium soon after deposition, and concluded that the seeds for this species must have been present in the substrate for several years. Simmonds (1945a, 1945b, 1945c) also mentions indirect evidence of retention of viability when P. lapathifolium seeds are buried in anaerobic pond mud. Stoller and Wax (1974) found that Polygonum pensylvanicum seeds decayed faster when buried under only 2.5 cm soil than when buried 10.2 cm below the surface. The development and/or maintenance of hard seed coats was considered the principal mechanism for seed survival in the species tested (Stoller and Wax 1974). Crocker's (1938) experiment demonstrated that Phalaris arundinacea gave 11.5 percent germination following twenty years burial at depths of 12, 55, and 105 cm in sterile soil in clay flower pots. Under these same conditions two species of Polygonum gave 55 percent and Hibiscus spp. produced 57.7 percent germination.

Several studies have been carried out on the rate of deterioration of waterfowl food seeds. Neely (1956) and Shearer et al. (1969) sub-

merged various seeds for periods of 30, 60, and 90 days in bottom muck. Species which normally dehisce seed in marshy areas showed the least deterioration as determined by weight loss. Arber (1920) noted that a large proportion of aquatic plants have fruits that are indehiscent and one-seeded or have other methods of dehiscence that allow the seeds to be protected by both the pericarp and the testa. Such protection probably enables them to resist the decaying effect of prolonged submergence.

### Dispersal

Many water plants apparently possess very efficient dispersal mechanisms for it is a rare stream, river, pond, lake, swamp, or marsh that is unoccupied by one or more species. Indeed, many aquatic and marsh plants are widely distributed throughout the world.

Godwin (1923), in his study of pond plant dispersal, proposed that when aquatic plants are not growing in a certain area it is mainly because they cannot survive, not because their propagules were unable to reach the area. While in some situations this idea may have merit, it probably underestimates the barriers to the dispersal of aquatic plants. It also does not account for those many instances when some very widely distributed species are totally lacking from an individual water body even though the conditions for growth are proper.

Some short range dispersal within a single water body or river system can be accounted for by currents, winds, and animal movement.

Long range dispersal and the occupation of new, isolated habitats is poorly comprehended.

There are apparently four primary agents of dispersal for aquatic and marsh plants: wind, water, animals, and man. Seeds of wetland plants have obvious characteristics that make them amenable to the various types of dispersal. Many species of plants have seeds which do not all ripen at the same time (Dill and Greenwell 1948) or which have differing requirements for germination (Salisbury 1970). These traits give the plant an advantage in dispersal by permitting seeds to be exposed to a greater variety of environmental conditions and dispersal agents (Datta and Biswas 1970).

#### Wind

Dispersal via wind is undoubtedly important for many aquatic and marsh plants. Such common and widely distributed species as Typha latifolia, T. angustifolia, Phragmites australis, Salix spp., Populus spp., Epilobium spp., and Scirpus cyperinus are wind transported. These species produce seeds that are well adapted to wind dispersal. Many of the common invader species that rapidly occupy any barren mud or sand flat are carried by the wind (Salisbury 1970). Seeds that are wind transported are usually able to withstand drying (Muenscher 1936b). Other seeds and vegetative propagules of aquatic plants are killed by drying and must be kept moist during transport.

#### Water

Water movement serves as an effective dispersal mechanism for

many aquatic and marsh plants. Ridley (1930) wrote of millions of seeds being carried by rivers around the world. This is undoubtedly not an exaggeration, for streams and rivers have been shown to carry enormous numbers of seeds and other propagules (Hanson 1918, Hall 1940).

Many water-transported seeds can be buoyant for a few days to several months and are easily spread by water currents. Some seeds are buoyant because of corky winglike structures, corky seed coats (Spence et al. 1971), or air trapped in bracts around the seed (Lambert 1947). When the seeds become waterlogged, they usually sink and, if conditions are favorable, germinate. Ridley (1930) presented information on the buoyancy of seeds of different species.

Several authors have commented on the apparent results of new habitat colonization by floating seeds. Hall (1940) reports that Saururus cernuus seeds are transported by river currents. Hanson (1918) recorded the deposition of seeds of many marsh plant species on flood plains behind barriers such as logs and trash piles. Stuckey (1968a, 1968b, 1969, 1970) and Stuckey and Phillips (1970) feel that many introduced marsh species (Epilobium hirsutum, Butomus umbellatus, Lycopus spp.) are water transported.

Many aquatic plants may be widely distributed by floods. The strong forces exerted by floodwaters easily transport seeds, hibernacula, and fragments over both long and short distances. Emerson (1961) cites examples of the appearance of members of the Ceratophyllaceae, Hydrocharitaceae, Lemnaceae, Najadaceae, Potamogetonaceae, and Sparganiaceae in isolated ponds after flooding. Floods also result in many

underground parts being uprooted and moved over long distances.

A number of aquatic plants have seedlings that float (Ridley 1930). These seedlings are widely dispersed by all forms of water movement. Seedling survival may vary greatly because the small plant may have environmental requirements different from those of the germinating seed. Boorman (1968) found that Limonium spp. seeds germinated best in a sandy substrate, but that mud was better for seedling growth. Salinity requirements between germination and seedling growth or between seedling growth and adult plants may also differ (Boorman 1968). Seedlings that begin growth at low elevations may be destroyed by the scouring action of waves before they have a chance to become well established (Broome et al. 1973). Wiehe (1935) noted that Salicornia europea seedling survival in the neap tide zone where there was daily submergence was only 25 percent, while in the spring tide zone survival was 65 percent and total germination was greater.

Although many freshwater plants are well adapted to water transport, most estuarine plants are not (Sculthorpe 1967). Seedlings of few estuarine plants do well in salt water. Indeed, many need to establish in freshwater and most grow better in freshwater. The successful dispersal distance of estuarine plants is probably less than that of freshwater plants (Sculthorpe 1967). The plants that are successful in brackish habitats have rapid germination and attachment of the seedling to the substrate.

Sculthorpe (1967) disagreed with Love's (1963) generalization that

marine plants are well adapted to dispersal in seawater. Many of the seeds of seawater angiosperms (Halophila, Thalassia, and Syringodium) sink immediately or float for only a short time. Some even remain attached to the parent plant. Those that do have floating seedlings will soon die if they do not rapidly find suitable anchorage. Most such seedlings are very vulnerable to wave action and currents. Sculthorpe (1967) stated that "...long-range dispersal of the seeds, seedlings, or vegetative fragments by sea-currents is not likely to be significant in the dispersal of marine angiosperms."

None the less, there are many examples of sea transported plant propagules and sea drift is probably important for some species (Tansley and Fritsch 1905). Taylor (1957a) reported that wave action moved seeds of Zostera marina along the ocean bottom. The Gulf Stream currents are known to transport many seeds and plant fragments, including Avicennia, Laguncularia, Rhizophora, and Thalassia testudinum (Blomquist and Pyron 1943; Savage 1972a, 1972b, Gunn and Dennis 1973). In several cases such seeds (especially mangroves) have been found to be viable. Seeds of Spartina townsendii are often carried by tides and deposited in drift lines on the strand where they germinate (Oliver 1925). Spartina alterniflora is apparently also dispersed in this manner (Woodhouse et al. 1974). In both cases the surviving seedlings occur primarily in a narrow band near the drift line. On a more limited scale, the seeds of many marsh annuals and perennials are known to be distributed by tides (Harshberger 1916, Oliver 1925, Lynch et al. 1947).

## Animals

A variety of animals are involved in the transport of aquatic plant propagules. Jacobs (1947) found that muskrats effectively transported Spirodela, Lemna, and Wolffia between small, isolated ponds and marshes. The feeding of many animals uproots and fragments plants which are then dispersed by currents. Domestic animals such as dogs and cattle transport propagules over short distances. Some seeds excrete a sticky substance which allows them to adhere to animals (Matheny 1931).

Birds have long been suspected as primary dispersal agents. Unfortunately, much of the available literature on dispersal of aquatic species is based largely on casual observations and assumptions with no experimental basis.

It is possible that water birds transport aquatic plant seeds in two ways: (a) internally--seeds are consumed and transported to a new location where they are voided either by regurgitation or defecation; and (b) externally--seeds or other viable parts are transported by adherence to the bird's body.

There is ample evidence that many seeds of dry-land plants are effectively transported by birds, but studies on aquatic seeds and water birds are few. Guppy (1906) found that seeds of Potamogeton natans survived the digestive system of a domestic duck and had a higher percent germination than noneaten seeds. Low (1937) obtained a high percentage of germination of Scirpus paludosus seeds fed to a mallard. Ridley (1930) listed Alisma plantago-aquatica, Potamogeton foliosus,

P. friesii, P. lucens, P. natans, P. pectinatus, P. praelongus, P. pusillus, Sagittaria spp., Sparganium androcladum, and S. eurycarpum as capable of surviving the digestive systems of birds.

Although there are many additional reports in the literature of seeds in the gullets of waterfowl, few authors have discussed the viability of those seeds. Moreover, removal of seeds from the gizzard does not necessarily mean that those seeds would have passed through the bird and been viable. Retention in the gut is important to viability and excessive retention times probably reduce viability.

DeVlaming and Proctor (1968) have conducted the most detailed study to date on the transport of seeds by water birds. Their results indicate that the viability of seeds after ingestion by water birds is dependent on the nature of the seed coat and the species of the bird. Their evidence supports the contention that long distance dispersal by shorebirds and waterfowl is possible for at least some species (e. g. Potamogeton pectinatus, Scirpus paludosus, Eleocharis macrostachya). Other species are apparently not well adapted to avian transport (e. g. Samolus parviflorus, Nasturtium officinale, Phalaris arundinacea, Echinochloa pungens).

The composition of the bird's diet affects the proportion of seed that can escape the gizzard unharmed. If a large amount of soft vegetation is consumed along with the seeds, the chances for seed to be passed undamaged are much greater than if the diet were entirely seed. DeVlaming and Proctor (1968) believe that additional research is war-

ranted to determine the actual role of shorebirds and waterfowl in seed transport.

According to Ridley (1930), vegetative propagules of many aquatic species are externally transported by birds. He cited examples of Elo-dea canadensis, Potamogeton crispus, P. perfoliatus, and P. praelongus as having been dispersed in this manner. It is, of course, possible that seeds could also adhere to bird's feathers or feet (Matheny 1931). Gleason and Cronquist (1964) have suggested that transport of seeds attached to the feathers or bill or contained in mud carried on the feet is the primary avenue of dispersal. Extended transport in this manner is not possible for many species due to desiccation and death of the propagule. It may, however, be important and is deserving of additional research.

### Man

Man is almost surely the most significant dispersal agent. Ridley (1930) and van der Pijl (1969) devoted extensive discussions to man's influence on plant distributions. Many common activities result in the unintentional dispersal of aquatic angiosperms (Stuckey 1970). Rice (Oryza sativa) seed transported for planting is usually contaminated with weed species, many of which are aquatic plants such as Najas graminea (Mason 1957). Many activities such as fishing, hunting, and boating result in dispersal of seeds on boots, clothing, and equipment.

Construction and farming activities surely result in the transport

of seed on agricultural machinery, dredges, and other heavy equipment. Escape from cultivation and intentional introduction (especially aquarium plants) has also been important. The introduction by man and subsequent spread of aquatic and marsh plants in North America is well documented for several species (see Appendix C, Selected References on Naturalized and Introduced Aquatic and Marsh Angiosperms in North America).

## PART VII: ARTIFICIAL OR INDUCED ESTABLISHMENT

Artificial or induced establishment depends on the introduction of propagation material to the new substrate. The steps in this process include: collection and storage of plant propagules, shipping propagules, planting, site selection and preparation, and water management and control.

### Collection and Storage of Plant Propagules

Regardless of the type of plants to be established, it will be necessary to obtain propagation materials. Planting stock (from natural sites or nurseries) may consist of entire plants, cuttings, vegetative structures, or seeds. At least initially these materials probably will be obtained from either natural marshes or commercial outlets. Later, it may be feasible and economically desirable to cultivate the species in nurseries for use on other local or nearby sites.

It is difficult, if not impossible, to formulate hard and fast rules on when to collect propagation materials. Numerous authors (Kubichek 1940, George 1963, Woodhouse et al. 1974, and others) commented on the variability in seed maturation dates for wetland plants. Other types of propagules, such as tubers and hibernacula, generally are available at the end of the growing season, but this varies according to geographic location and environmental conditions (Sculthorpe 1967).

### Propagule selection

The physical characteristics of the planting site may restrict the

type of propagule used. If the planting site is subject to high physical stresses such as erosion, siltation, or current and wave action, seeding will probably not be as successful as transplanting (Woodhouse et al. 1974). On the other hand, if the site is stable and sheltered and the substrate is favorable, seeds or combinations of seeds and transplants may be desirable and more economical.

The size of the planting site also will influence the choice of propagule type. If the planting site is very large, obtaining and planting transplant materials may be prohibitively expensive (Garbisch et al. 1973). In addition, unless nursery stock is available, it may be difficult to acquire enough planting stock. Other propagules, such as seed and vegetative parts can be harvested in large amounts and are more easily distributed over extensive areas.

While some propagules are adapted to the fluctuating water levels that are often prevalent on marsh sites, others are not. If water level control capabilities (such as dikes and pumping facilities) are available, a wider range of propagule types may be used. The lack of these capabilities will restrict the range of propagule types and species that can be used.

The time of year when planting can be undertaken may limit the possible selection of materials. While transplant material is essentially available at all times of the year, seeds and certain vegetative structures are available only during certain seasons. If a site must be planted immediately and seeds or vegetative propagules are not avail-

able from storage, then it will be necessary to rely on transplants. In an on-going program, a variety of propagule types should be available on a year-round basis from storage, greenhouse production, and nurseries.

When propagation materials are being collected from natural areas, the collecting site may limit what parts may be used. If the collecting site is small or subject to physical stresses, the removal of large numbers of transplants may result in serious degradation of the collection site. The collection of small numbers of transplants or even large numbers from extensive and stable marshes probably does no harm (Woodhouse et al. 1974) and may actually benefit wildlife by creating openings. As a rule, the collection of seeds from perennials will probably not harm the plant population.

The manpower available for collecting materials will be a primary consideration. In some cases the manpower must come from a permanent or seasonally employed staff. In others, the work force will be from outside contractors. The size of the work force will be critical if a large planting program is begun. If few workers are available, efforts may be concentrated on seed collection since more individual propagules may be collected per man-hour (Woodhouse et al. 1974). If large numbers of workers are employed, then collection of transplant materials may be more feasible. The substitution of machine power for man power may be prudent. In most cases, however, machine use will not be practical unless large numbers of propagules are needed or long-term projects are

planned, since initial costs for specialized machinery will be high.

### Collection methods

Both manual and mechanical methods have been used to collect propagules of aquatic and marsh plants. Primary considerations in determining which techniques and equipment will be used are accessibility of the collection site and numbers of propagules needed. If the materials are to be gathered on sites with very unstable substrates, it may be impractical to use heavy machinery. In addition, unless water-level control is possible, there may be no way of getting a site dry enough to use equipment.

Manual collection methods are straightforward and require a minimum of equipment. Modified garden tools can be used. Other equipment will consist of temporary storage containers, such as plastic or burlap bags, buckets, or wicker baskets. Boats and canoes are used in deep water areas.

Machinery used for collecting marsh and aquatic plant propagules is often modified farm harvesting equipment. Combines, tractors, rototillers, and backhoes have been used. Although some specialized equipment has been developed, very little effort has been devoted to this area. It would seem that additional equipment could easily be developed. Much of the equipment that has been developed for mechanical aquatic plant control (Burkhalter et al. 1974) might easily be adapted for harvesting useful plants.

Transplant materials. The primary method of obtaining transplant materials has been hand-digging. Woodhouse et al. (1972, 1974) found that Spartina alterniflora is most easily dug from young stands on sandy substrates. Plants from older marshes were harder to dig because of denser root systems and the plants were usually smaller and lacked the growth vigor of plants from younger stands. Woodhouse et al. (1974) used a tractor-drawn plow to lift and loosen S. alterniflora for transplanting. This speeded up the job of gathering planting stock and doubled the production of hand digging (300-400 plants/man/hr as opposed to 180-200 plants/man/hr for hand-digging). They found that transplant materials can be transported in any manner as long as they are kept wet and cool. If long storage periods are necessary, S. alterniflora can be heeled-in for several month in trenches in the intertidal zone (Woodhouse et al. 1974).

The works of Woodhouse et al. (1972, 1974) are the only well-documented materials on techniques used to gather transplant material. Fuss and Kelly (1969), Kelly et al. (1971), Emerson (1961), and others have described the use of transplants for revegetation purposes, but few have discussed their techniques for gathering the plants. In most cases the plants were hand-dug and quickly transported to the planting site. Apparently there have been no attempts at large-scale transplanting, and, therefore, machinery has not been developed for uprooting whole plants (other than that used by Woodhouse et al. 1972, 1974). If large numbers of transplants are to be gathered from natural sites or

even from field nurseries, it would seem that the development of such equipment is necessary.

Although rarely mentioned, it is always necessary to keep emergent plants moist and aquatic plants totally immersed during field collection and transport (Martin and Uhler 1939). Avoiding excessive heat or cooling during field operations is only prudent.

It is difficult to recommend the best time for collecting whole plants for transplanting. Collection of transplants during their dormant periods may reduce physiological shock.

Fragments and floating plants. The collection of entire plants usually involves free-floating and nonrooted or sparsely rooted aquatics such as members of the Ceratophyllaceae, Hydrocharitaceae, and Lemnaceae. The free-floating plants are easily skimmed from the water's surface either while wading or from a boat. Large mechanical harvesters (modified dredges and barges with cutting equipment) have been used to remove excessive growths of floating and submersed aquatic plants (such as Eichornia crassipes and Najas guadalupensis) from canals, rivers, and lakes (Burkhalter et al. 1974). These harvesters could probably be used to collect aquatic plants such as Lemna spp., Spirodela polyrhiza, Elodea spp., and Ceratophyllum spp. for transfer to new sites. Whole plants of almost any submersed aquatic species can be collected with long-handled rakes or draghooks on handlines. Many of these plants are perennials and have the capacity for regenerating from any part which has a bud (see Part VI on natural establishment). Perennial

plants are viable throughout the growing season and may be collected whenever convenient. Others, such as Najas spp. and Ranunculus spp., are annuals and should be collected only when viable seed is present. Submersed plants should be kept moist at all times during collecting and transport (Martin and Uhler 1939). Any extended exposure to the air will result in death of the plant due to desiccation. Excessive heat or freezing will easily damage these plants. Submersed plants can be maintained in temporary storage in well-aerated tanks.

Vegetative structures. Many aquatic and marsh plants produce hibernacula and underground organs that can be easily collected. The hibernacula produced by submersed aquatic plants can be collected by scooping them from the bottom of lakes or by collecting whole plants before the overwintering organs have separated from the plant.

Underground organs, such as rhizomes, rootstocks, and tubers, are usually hand-dug (Martin and Uhler 1939, Salyer 1949). A weighted rake or long-handled fork may be used for uprooting the tubers of various submersed aquatics. Once uprooted, the tubers of many aquatic plants (e. g. Potamogeton pectinatus and Vallisneria americana) will readily float to the surface (Fellows 1951). Emerged and mud-flat species that have tubers (e. g. Cyperus spp. and Sagittaria spp.) can be hand-dug. Many tubers are crisp and fragile and easily damaged when fully mature (Fellows 1951), so care must be exercised during collecting.

Although some vegetative structures are adapted to resist

desiccation, most should be kept moist and cool whenever possible (Martin and Uhler 1939, Salyer 1949, Fellows 1951).

Seeds. Many methods have been developed for the collection of seed to be used in marsh planting. Both manual and mechanical methods have been used extensively.

The ripening of seeds, even in a single locality, is a very gradual process; because of this, specific times for harvesting must be determined locally. In order to harvest seeds when most are mature, they should be collected just before the majority of the seeds begin to shatter (fall from the inflorescence) or when easily removable from the spike (Martin and Uhler 1939). Generally, harvesting later in the ripening season increases the chances of obtaining viable seed. It also increases the chance that storms will cause the seed to shatter, so most of the crop will be lost.

Sometimes seeds can be collected before they are ripe. Garbisch (pers. comm.) collects Spartina spp. inflorescences and stores them in plastic bags in the shade for two weeks to allow them to ripen and shatter. After ripening, the inflorescences are thrashed by rolling on fencing wire.

Many seeds produced by aquatic plants detach at maturity and float for a few days to several months (Ridley 1930). Such seeds can often be collected from windrows along the edges of lakes (Martin and Uhler 1939, Salyer 1949). Erickson (1964) pointed out that it is very

difficult to gather pure collections of seeds from windrows. If windrowed seeds have suffered severe drying, they may be dead (Muenscher 1936a, 1936b) and should be tested for viability before investing much effort in collection, storage, or planting. If these windrows contain large quantities of seeds, sifting them through screens of various mesh sizes may separate some species or species groups.

Manual harvest methods are primarily hand-picking or clipping with shears, but several other methods have been used. The methods used to hand harvest wild rice (Zizania aquatica) have possible applications for other species. One method, which involves bending stalks over a canoe and beating them with a stick until the seeds fall, may also be useful for Scirpus spp. and other emergents. A similar method in very shallow marshes involves a cradle-like canvas bag that is worn over the shoulders and positioned so that the wearer can shake ripe seeds into it (Martin and Uhler 1939). Harvests by these techniques may be repeated more than once in the same area, since the seeds tend to ripen over several days or weeks.

A few specialized collecting devices have been developed. For example, Sypulski (1943) described a rake-like device that can be used to harvest the seeds of Scirpus spp.

In drier marshes, those where water levels can be lowered or in some tidal marshes, machinery can be used to harvest seeds. The seeds of Echinochloa spp., Polygonum spp., and Scirpus spp. have been harvested with modified combines (Kubichek 1940, Miller and Arend 1960,

George 1963).

Special harvesting equipment is used to collect wild rice. One type of commercially built harvester is elevated about five feet above the ground and mounted on tracks in order to maneuver about in marshlands. The following description is from Rogalsky et al. (1971):

"The swather-like harvester is equipped with pointed metal pans projecting from the front of the machine, instead of the conventional guards and knife. The kernels are knocked from the head by the reel, which is driven just fast enough to dislodge the ripe seeds."

This harvester could surely be used to collect the seeds of Echinochloa spp., Polygonum spp., Scirpus spp., Spartina spp., and most grasses and sedges. A similar harvester has been mounted on a small boat and used for collecting wild rice (Dore 1969). This machine could probably be used for emerged plants in areas where the water cannot be drawn down.

Storage requirements for seeds vary greatly. Most aquatic species must be stored in water and at cool temperatures if seeds are to retain maximum viability (Muenscher 1936a, 1936b). Mooring et al. (1971) found that while Spartina alterniflora seed cannot withstand drying at moderate temperatures (22 C), seed will remain viable for 40 days when stored dry at 6 C and for at least 8 months when stored in sea water at 6 C. Subsequent work has emphasized the importance of storing S. alterniflora seed in seawater at 2 or 3 C to delay germination and allow afterripening (Broome 1972, Woodhouse et al. 1972, 1974). Some other emergents (e. g. Zizania aquatica) must also be stored wet. Fellows (1951) and Kubichek (1940) each described flow-through storage

cellars that can be used for storing large quantities of aquatic seeds. Other authors (Addy 1947, Dore 1969, and others) recommended storing seeds in bags in animalproof cages on the bottom of ponds, rivers, and estuaries. Sharp (1939) recommended storing Sagittaria seeds on open platforms in marshes.

Many seeds, such as those of Echinochloa spp., Polygonum spp., and Scirpus spp., should be stored dry. After air-drying these seeds need only be stored in a cool dry place away from rodents and other pests. Although seeds can be simply bagged and kept in storage, it may be practical to store large volumes of seeds in grain bins that are equipped with gas driers.

Costs of harvest and storage. There are few cost analyses of harvesting and storing the propagules of aquatic and marsh plants. Due to changing costs for labor and machinery most of the published cost analyses are out-of-date.

Woodhouse et al. (1974) have, however, estimated the time required for harvesting Spartina alterniflora transplants as:

By hand digging	180-200 plants/man/hour
By backhoe (from natural stands)	300 plants/man/hour
Lifted by plow (from nursery plantings)	400 plants/man/hour

On a hectare basis, harvesting and replanting (spacing of 0.91m x 0.91m or 12,000 plants per hectare) would require:

Hand digging and planting	134 man-hours/hectare
Machine digging (from a nursery) and planting	63 man-hours/hectare

These time estimates do not allow for travel time, machinery movement, weather effects, fixed costs for equipment, and management and over-

head. Woodhouse et al. (op cit.) believe that large scale operations would have a somewhat lower productivity, but this might be offset "...with experience in handling larger volumes, and by further development of harvesting equipment".

Due to large variations in seed production on different sites and at different times, it is difficult to estimate the cost of harvesting seed. After three trials, Woodhouse et al. (1974) estimated that approximately five man-hours were required to harvest enough seed of Spartina alterniflora to plant one hectare. Threshing of the seed required about one-half as many man-hours as harvesting.

No cost estimates for storing aquatic and marsh plant propagules have been found. Dry storage of such seed should be comparable to the costs of storing agricultural seed. Costs of specialized types of storage (such as wet storage and refrigeration) will be higher.

In any extensive marsh creation program, the economies of scale will quickly become apparent. Creating small marsh areas is expensive simply because of proportionately greater fixed costs. As more marsh area is created, costs per acre will surely decrease. But, just as surely, overall costs will increase.

Purchase of Propagules. Several companies specialize in the sale of aquatic and marsh plant propagules. Some of these companies are listed in Table 7. Additional sources for seed and other propagules probably exist. George (1963) mentioned that seed of Scirpus robustus can be purchased from "rice dryers" in the South Dos Palos area of

Table 7

Some Suppliers of Aquatic and Marsh Plants.

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Diamond Rice Company  
Kelliher, Minnesota 56650  
ph. 218-647-4349

Everglades Aquatic Nurseries, Inc.  
P. O. Box 587  
Tampa, Florida 33601

Game Food Nurseries  
P. O. Box 2371  
Oshkosh, Wisconsin 54901

R. A. Gasser  
Route 2  
Box 75  
Stuart, Florida 33494

Slocum Water Gardens  
1101 Cypress Gardens Rd.  
Winter Haven, Florida 33880  
ph. 813-293-7151

Three Springs Fisheries  
124 Hougar Road  
Lilypons, Maryland 21717

William Tricker Inc.  
74 Allendale Avenue  
Saddle River, New Jersey 10758  
ph. 201-327-0721

William Tricker Inc.  
7125 Tanglewood Drive  
Independence, Ohio 44131  
ph. 216-524-2430

Van Ness Water Gardens  
2460 North Euclid Avenue  
Upland, California 91786  
ph. 714-982-2425

Wildlife Nurseries  
P. O. Box 399  
Oshkosh, Wisconsin 54901

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Merced County, California. Many submersed plants that are used as aquarium ornamentals can be obtained in quantity from wholesale growers. In Florida, these growers and wholesalers are licensed and a list of current licenses can be obtained from the Florida Department of Natural Resources. Caution should be exercised in purchasing seeds and other propagules from unknown sources. In most cases plantings of propagules obtained from similar and nearby habitats will have a greater probability of success than those from distant sources (see Part V). Consequently, it may be more economical in the long run to pay a slightly higher cost by contracting to have the propagules collected from a local source than by purchasing them from distant suppliers.

#### Shipping propagules

If propagules are obtained near the planting site, long distance shipping will not be necessary. However, if shipping does become necessary, several precautions should be exercised.

The shipment of dry seeds presents no unusual problems. The transport of agricultural seed is a routine occurrence in the United States and many wetland plant seeds can be handled in the same manner.

While most seeds can be shipped without any extraordinary precautions, those that are injured by desiccation must be kept wet during shipping. Muenscher (1936a, 1936b) shipped several small lots of seeds in tightly stoppered jars of tap water from Ithaca, New York, to several parts of the United States and Europe via parcel post. He found that seeds of Alisma plantago-aquatica, Butomus umbellatus, Calla palustris,

Eriocaulon septangulare, Heteranthera dubia, Juncus articulatus, Nasturium aquaticum, Nymphaea tuberosa, Peltandra virginica, Pontederia cordata, and Vallisneria americana survived shipping periods of 2 to 13 days with no harm. Only one species, Sagittaria latifolia, did not survive well. Muenscher recommended that small commercial shipments of seeds should be placed in waterproof packets or small cotton bags packed in wet sphagnum moss and large quantities should be packed in water or moist sphagnum and shipped under refrigeration. Refrigeration will probably be necessary during warm periods if fermentation is to be avoided.

Martin and Uhler (1939) recommended that vegetative propagules, such as leafy cuttings, young plants, and rootstalks, be packed as follows:

"Spread a layer of wet peat moss about 1 inch thick on a long sheet of heavy waxed paper and scatter the plants thinly over it. Then roll the paper and its accompanying layer of plants loosely and ship in a closed container to prevent evaporation."

They also suggest that the quickest possible type of transportation should be used.

### Planting

Transplants, vegetative organs (above and below ground), and seeds have all been used in planting programs for aquatic and marsh plants. Few of the sophisticated agricultural planting techniques have been applied to wetlands revegetation attempts. Table 5 is a guide to the various types of propagules that can be used for different aquatic and marsh plants. In general, annuals must be propagated by seed and

perennials may be propagated by seed or any of several vegetative parts.

### Freshwater planting

Whole plants, cuttings, hibernacula. Most perennials can be easily propagated from pieces of stems and leaves. For some species, such as Elodea spp., Ceratophyllum, and Lemna spp., propagation is simply a matter of putting a few of the plants into the water at the planting site. It may be desirable to anchor these plants by pushing the ends of stems into the soil (Addy and MacNamara 1948) or by attaching small clay balls (to serve as weights) to the base of the plant (Martin and Uhler 1939, McAtee 1939). In most cases the weight itself is not important so long as it keeps the plant in place. Addy and MacNamara (1948) recommended laying long (1 m) stems on the bottom and covering them at intervals with mud so that roots develop on the underground portions and shoots on the aboveground parts. These vegetative parts should be planted as soon as possible as drying will kill them (Addy and MacNamara 1948).

Tubers and rootstocks. Most tubers and rootstocks are hand-planted by simply pushing the material into the bottom. Martin and Uhler (1939) recommended embedding small tubers in clay balls to be planted. They described a planter that consists of a probe used for making a hole into which a tuber is placed. Tubers that can survive on semidry sites (Cyperus spp.) can be broadcast on land that has been disked, dragged, or raked (Martin and Uhler 1939).

Autumn is normally the recommended time for planting tubers and rootstocks (Addy and MacNamara 1948). The planting depth varies a good deal with species but these structures should never be planted more than a few centimeters deep.

Williams (1970) planted tubers of Nymphaea in soil in clay tiles with good success. George (1963) found that hand-planting of Scirpus rootstocks was effective, but more expensive than seeding. Moyle and Hotchkiss (1945) transplanted sprouting ends of Typha rootstocks.

Seeds. Several methods have been developed for inducing germination. Seeds have been induced to germinate by chemical or mechanical destruction of the seed coat. Weakening of the seed coat by chemical decomposition may be similar to the processes of microbial activity or passage through an animal's digestive tract (Mayer and Poljakoff-Mayber 1963). Choudhuri (1966) obtained 83 percent germination of Vallisneria seed by soaking for three minutes in concentrated sulfuric acid ( $H_2SO_4$ ). Others (George 1963, O'Neill 1972) recommended soaking the seeds of Scirpus in a 0.05 percent sodium hypochlorite solution to promote germination.

Mechanical scarification is also an effective method of inducing germination (Addy and MacNamara 1948). Vose (1956, 1962) used a variety of mechanical techniques to accelerate the germination of Phalaris seeds. Rupture of the seed coats of Typha spp. and Potamogeton pectinatus produced 100 percent germination (Yeo 1964, 1965). Further treatment of

the scarified seed with chemicals increases germination of seeds of some species. Jones (1928) used both abrasion and soaking in  $H_2SO_4$  to promote germination in Nelumbo lutea. Ipomoea aquatica seeds were induced to germinate by abrasion with sandpaper and soaking in  $H_2SO_4$  (Datta and Biswas 1970).

Many seeds of aquatic plants require stratification. Sharp (1939) found that Potamogeton seeds germinated better after stratification under water. Freezing increased germination in Suaeda maritima (Chapman 1947). Arber (1920) suggested that freezing may induce germination by mechanical action on the seed coat.

Simply soaking in water improves the germination of many of the seeds of marsh plants. Scirpus spp. will germinate after long periods of soaking (Harris and Marshall 1960a). Echinochloa crusgalli responds to soaking with rapid germination (Miller and Arend 1960).

If seeds are germinated under some sort of controlled conditions, they must be rapidly planted or they will die (Miller and Arend 1960, O'Neill 1972). Martin and Uhler (1939) recommend that water-saturated seeds be broadcast directly on the water. If large areas are to be planted, seed should be scattered from an airplane (Harris and Marshall 1960a, Miller and Arend 1960, George 1963, O'Neill 1972). Small areas can be easily seeded by scattering seed on the water surface or at its edge (Sharp 1939, Uhler 1962). Whenever possible the planting area should be roughed up with a disc, plow, or rake before or after seeding (Martin and Uhler 1939).

If the seeding of emergents is to be successful, the ability to control water levels is almost mandatory. O'Neill (1972) recommended gentle drawdowns and refloodings to promote the growth of Scirpus paludosus and S. robustus. George (1963) felt water control is critical for establishing S. robustus. Harris and Marshall (1960a) recommended the draining of S. acutus and S. validus flats during the winter. Miller and Arend (1960) recommended manipulating water levels for germinating, promoting growth, and promoting seeding of Echinochloa crusgalli.

Many authors have reported the rapid growth of marsh plants on areas that were for some reason drained (Crail 1951, Salisbury 1970, Dirschl 1972). Apparently the seeds of aquatic and marsh plants can be buried and remain viable in the substrate of wetland systems for up to several decades (Crocker and Davis 1914, Shull 1914, Shenstone 1923, Goss 1925, Crocker 1938, Milton 1939, Simmonds 1945a, Lynch et al. 1947, Ermacoff 1968, and Salisbury 1970). Drawdowns and the resultant wetting and drying seem to be a very effective method of initiating germination (Crocker 1907, Crail 1951). Ermacoff (1968) notes that former marshlands rarely need seeding with aquatic plants because large numbers of seeds are present in the bottom soils. Lynch et al. (1947) state that exposure to the air (by low tides or drawdowns) will stimulate germination.

In freshwater areas, aquatic and marsh plant seeds are present in the bottoms of lakes, ponds, and marshes. These seeds have considerable potential for revegetating dredged areas. On a dredged material disposal site on the western end of Lake Erie, material from a marsh was used to create a large sand-mud flat in 1968. The flat was rapidly colonized

by a diverse assemblage of species (Scirpus spp., Echinochloa spp., Polygonum spp., Zizania aquatica, etc.) (Moore 1973). There is little doubt that the seeds of these plants were present in the bottom muds because species appeared on the flat that had not been seen in the western Lake Erie region in several decades! In freshwater areas it seems likely that revegetating dredged fill may be primarily a matter of providing the proper conditions for germination.

#### Brackish-saltwater planting

Brackish water plants. Several plants are very characteristic of brackish water lakes, ponds, and estuaries. Ruppia maritima and Potamogeton pectinatus are the most common of these plants. Several additional species, including Vallisneria americanus, Myriophyllum spp., Phragmites australis, Eleocharis spp., and Scirpus spp., are also commonly found in brackish waters. Propagation techniques for most of these species have been discussed in the foregoing section on freshwater plants. The following discussion concerns primarily Ruppia maritima and Potamogeton pectinatus and the special problems that are presented by brackish waters.

Almost any coastal impoundment that has stable water levels will be invaded by Ruppia maritima (Carl 1940, Carpelan 1957, Neely 1962, Chabreck and Palmisano 1973, J. Monte, pers. comm.); in fact, Ruppia maritima cannot tolerate fluctuating water levels (Joanen 1964, Joanen and Glasgow 1965, Levin no date).

It seems to be a relatively easy matter to establish Ruppia maritima and Potamogeton pectinatus in brackish waters. Bourn (1935), Neely (1962), and Yocum (1951) have grown R. maritima from cuttings and Neely (1962) recommended simply scattering a few bushels of the plant about in a lake at any time of the year. Donnelly (1968) successfully transplanted both R. maritima and P. pectinatus by moving 15 cm square plugs (substrate with attached plants) to the desired location. Yocum (1951) recommends growing R. maritima from cuttings, winter buds, rootstocks, and seeds.

Both R. maritima and P. pectinatus have been successfully grown from seed in brackish waters. The seeds of both species germinate better in freshwater than in brackish water (Bourn 1935, Joanen 1964, Joanen and Glasgow 1965, Teeter 1965, Yeo 1965, and Donnelly 1968), but once started the plants can tolerate increased salinities (Teeter 1965). Whenever possible seeds should be planted when salinities are lowest to promote germination. Joanen and Glasgow (1965) recommend planting the seeds of R. maritima 5 cm into the substrate to avoid excessive salts and thus increase germination.

Salt marsh plants. Although several species of plants have been used for marsh creation, grasses, primarily Spartina, are the principal type of plant used. Spartina alterniflora has been used more than any other species and much of the following discussion comes from work on this species.

There were very few attempts at planting salt marsh grasses in the

United States before 1970. However, in Great Britain some work has been done with various species of Spartina (primarily S. townsendii) (Chapman 1960, Chater and Jones 1957, Oliver 1925, Marchant and Goodman 1969a, 1969b, 1969c). Much of the work in planting salt marsh grasses in the U. S. has been for experimental purposes. Only recently have there been large scale attempts at using salt marsh grasses for substrate stabilization and marsh creation (Garbisch et al. 1973, Mason 1973, Woodhouse et al. 1972, 1974).

In these planting programs, transplants, seedlings, seed, and vegetative parts have been used. Most plantings have been done by hand and consist of simply making holes in the substrate and inserting the plant. Some recent attempts at using modified agricultural or tree planting machines for planting nursery stock do show promise.

Plantings are normally spaced at about one meter intervals and are put in parallel rows. Woodhouse et al. (1974) commented that this spacing is probably an adequate compromise between cost and speed of stabilization. It is possible that plantings should be closer on areas subject to high levels of physical stress.

Although Woodhouse et al. (1974) have shown that the timing of planting is critical for best survival, they believe that the development of rules would be unreasonable since conditions vary with sites. They do comment that early in the growing season may be the best time since this gives the plants a maximum period of time for establishment before the dormant season.

As yet there seem to be few guidelines as to where salt marsh grasses should be planted in relation to tides. Woodhouse et al. (1974) planted Spartina alterniflora throughout the intertidal zone and found optimum growth slightly below mean high water. Garbisch (pers. comm.) recommends that the lower the planting elevation relative to mean high water, the greater the amount of foliage that should be left above the substrate surface. Other authors give only vague reference to their specific planting site (i. e., "the intertidal") and few comment on where they attained the greatest success. Additional information on the planting zone and factors controlling its limits would be very useful.

Hand-planting of S. alterniflora is efficient on small, irregularly shaped areas where equipment access is difficult or where the substrate is too soft for equipment (Garbisch et al. 1973, Woodhouse et al. 1974). Two people working together can plant fairly rapidly; Woodhouse et al. (1974) averaged 180 hills/man/hour. The first person makes the hole and the second positions the plant (roots about 5-10 cm deep) and firms the substrate around it. Planting depth is important only in that the roots must be buried enough to anchor the plant until growth begins (Woodhouse et al. 1972).

Machine planting of transplant materials is feasible for mud/sand flats and intertidal areas where the substrate can be exposed (either by water-level control or between tides). If standing water is present, the plants tend to float away before the soil can be packed around them.

Woodhouse et al. (1974) recommend the use of a tractor with dual wheels and flotation tires to pull any of several commercial transplanters designed for cultivated truck crops. Most commercial tree and vegetable planters could probably be adapted for use with marsh vegetation. Woodhouse et al. (1974) were able to machine plant S. alterniflora at twice the rate of hand-planting; 360 hills/man/hour as opposed to 180.

The production of planting stock in greenhouses or outdoor nurseries shows promise. Garbisch (pers. comm.) grows seedlings of S. alterniflora in a greenhouse. Seed is germinated at high temperatures on wet sand and plants are raised in individual peat pots. Most are ready for planting after two months but seedlings for high physical stress areas are kept for up to five months.

In December, January, and February, Garbisch (pers. comm.) prepares the plants for transplanting by subjecting them to cold and causing them to become dormant. Before transplanting, the dormant culms are shortened by clipping to facilitate handling. Garbisch has obtained good survival of seedlings and he has found that plants planted in peat pots survive better than bare root seedlings of similar size and age (Garbisch et al. 1973).

Woodhouse et al. (1974) established a nursery for S. alterniflora in the intertidal zone where a tractor and plow could be used to lift young plants out of the sand. Plants were established in the nursery by seeding or transplanting plants from other sites. After one year the plants were removed from the nursery and planted in natural areas.

The plants tended to be very uniform in size and of better quality than natural stock. Upland, floodable nurseries also worked, but invasion by "weeds" was a problem. Upland nurseries were not as economical as intertidal nurseries.

Direct seeding on intertidal areas is also being used for establishing S. alterniflora. Garbisch et al. (1973) state that the optimum time for sowing seed is winter and spring. Broome et al. (1973) recommend the broadcasting of seeds rather than planting in rows. Germination methods and a viability testing technique for S. alterniflora seeds have been described (Mooring et al. 1971, Stalter 1972, 1973b).

Garbisch (pers. comm.) uses an all terrain vehicle (ATV) with a rear mounted seed broadcaster for distributing seeds on dredged material flats. He also uses a rubber mat drag to incorporate the seed into the substrate (ca. 2.5 cm deep). Garbisch believes that seed of S. alterniflora should never be planted deeper than 10 cm and Broome et al. (1973) recommend 1 to 4 cm. Woodhouse et al. (1974) worked seeds into the substrate by discing, raking, and harrowing. Seed must normally be buried to keep it from washing away.

Woodhouse et al. (1972, 1974) found that broadcast seeding was better than drill seeding since a more even distribution of plants was obtained. They recommend that for areas too small for machinery, seed should be broadcast by hand and incorporated with a roto-tiller. They also recommend sowing the seed as early in the spring as possible at a rate of approximately 100 seeds per square meter.

Fertilization with N and P has been beneficial on some areas (Broome et al. 1973, Garbisch et al. 1973, Woodhouse et al. 1974). If fertilizer is used, the whole site must be treated. Otherwise local areas of more vigorous growth will trap drifting sand, creating higher areas or "jetties" that will erode during the winter and expose the roots of the plants to freezing and desiccation.

In areas of high physical stress, seed will be difficult to keep in place. Garbisch et al. (1973) attempted to use breakwater-like devices to protect seeds on exposed sites, but then concluded that it is cheaper to transplant mature plants. Woodhouse et al. (1974) have suggested the use of sandbags to help break the force of waves and currents.

Woodhouse et al. (1974) concluded that seed supply is a limiting factor in many natural areas and natural invasion could be encouraged by establishing small seed patches. Since even small transplanted plants usually produce seed the first year, this may represent an economical method of establishing vegetation.

The cost of propagating S. alterniflora is reasonable and not unlike that of agricultural crops except for gathering seed and access of equipment to planting sites (Woodhouse et al. 1974).

Although Spartina alterniflora has been the primary grass used for revegetating salt marsh, several other species, such as Distichlis spicata, Juncus roemerianus, Panicum amarulum, P. virgatum, Phragmites australis, Salicornia spp., Scirpus olneyi, S. robustus, Spartina cynosuroides, S. foliosa, S. patens, and Typha spp., have been used.

These species have mostly been used on a small, experimental scale and Garbisch et al. (1973), Mason (1973), and Woodhouse et al. (1972) have been successful in establishing them.

Mangroves. Mangroves constitute the main shrub and tree species in many saltwater areas of Florida (See Fig. 3, B). Recently, effort has been devoted to using the three species of mangrove (Avicennia germinans, Laguncularia racemosa, and Rhizophora mangle) to colonize unstable shorelines and new habitats.

Work on mangroves has been especially active in Florida, where Savage (1972a, 1972b) studied the biology of the species and methods for establishing new populations. Savage investigated planting methods using nursery-raised seedlings, transplanted seedlings from natural stands, and seeds. Much of the following discussion is condensed from his work.

Although Rhizophora has long been considered the principal mangrove for planting, Savage's study suggests that Avicennia may be a better choice for future shoreline and stabilization programs. Of the three species, only A. germinans has an extensive geographic range and tolerates wide variation in temperature, substrate conditions, salinities, and burying in sand. Because of these tolerance Avicennia should grow well on disposal sites.

Avicennia rapidly develops an extensive root system that helps to stabilize shifting substrates. In contrast, Rhizophora requires several years to develop an equivalent root system and thus, it is not so

effective a stabilizer as Avicennia during the first few years of establishment. Laguncularia apparently does not develop a large root system (Savage 1972a, 1972b) even though it may be a primary invader of dredge fill sites (Snedaker, pers. comm.).

In some areas, large numbers of naturally established mangrove seedlings may be found. Savage developed a polyethylene coring instrument that removes a seedling and its associated substrate. The same tool is later used to make holes for transplanting seedlings at a new site.

Several transplants have been made on disposal areas and disturbed sites. Transplanted seedlings did as well as natural seedlings. For all species the transplant did better when planted nearer shore or in the higher portions of the intertidal area.

Although natural transplant materials are available in many areas, Savage believes that nurseries should be developed and maintained according to the best silvicultural practices. A single nursery would apparently be able to supply well-developed seedlings to all available planting sites in Florida.

Savage has been successful in germinating the seeds of all three species of mangrove. Rhizophora seeds are easily germinated on almost any substrate that can be kept wet. Avicennia and Laguncularia seeds apparently germinate well only when buried and kept wet. Both germinate faster in tapwater than in bay water.

Savage (1972a, 1972b) concluded that Avicennia is best suited for use in stabilization programs. His present research is directed toward

determining the optimum plant age for successful transplanting. In order to make most effective use of mangroves, additional research is needed into: the basic biology of the species, the effects of salinity, nursery culture methods, and planting methods.

Seagrasses. Seagrasses are marine angiosperms adapted to live primarily in estuaries, bays, lagoons, and shallow coastal areas at or below mean low tide (Fig. 3, A). However, some seagrasses, such as Halophila spp., are restricted to much deeper water (Humm 1956). While most seagrasses will die of desiccation if exposed to the air for any length of time (Strawn 1961, Moore 1963, McNulty et al. 1972), Zostera marina does grow in areas that are briefly exposed to the air at mean low tide (see Taylor 1933, Cottam 1935, Tutin 1942, Cottam and Munro 1954, Keller 1963, Keller and Harris 1966, McRoy 1970, McRoy et al. 1970, 1972, and Thayer et al. 1973 for discussions of the life history and ecology of Zostera marina). Taylor (1954) noted that seagrasses tend to dominate in saltwater areas that are fairly large, have good circulation of seawater, and have water 3 to 12 cm deep at low tide. Zieman (1972) observed that Thalassia testudinum attains its maximum development when growing on mangrove peat deposits. Humm (1956) and Thorne (1954) have discussed the general ecology and geographic distribution of several seagrasses (Halodule wrightii, Halophila engelmannii, H. baillonis, Ruppia maritima, Syringodium filiforme, and Thalassia testudinum). den Hartog (1970) reviews the taxonomy and

distribution of the seagrasses of the world.

Although seeds may be useful for the propagation of seagrasses, there has been very little work in this area. Primarily because it has long been recognized as an important species, the seeds of Zostera marina have received attention from a few authors. Taylor (1957a, 1957b) has worked on the development of Zostera seeds and seedlings. Addy (1947) found that seed of Zostera marina collected in August could be planted and established by September of the same year. Seeds of Zostera should be planted on irregular bottoms (among mussel beds, etc.) so that they will not wash away before germination (Addy and Aylward 1944). Thalassia testudinum seeds are known to germinate and anchor within three days after settling to the bottom (Orput and Boral 1964). Apparently Ruppia maritima can be easily propagated by burying seeds at least 5 cm deep in the substrate (to avoid high salt concentrations which delay germination) and maintaining water levels at about 60 cm deep (Joanen 1964, Joanen and Glasgow 1965). More research is needed on all aspects of the propagation of seagrasses by seed.

Transplant techniques seem to have great potential for establishing seagrasses on suitable substrates (McRoy 1973) primarily because transplants are likely to survive better on areas of shifting sands than are seeds. However, very little is known about the general effectiveness of transplanting techniques. Zostera marina and Thalassia testudinum are the only seagrasses that have been successfully transplanted. Even with these species no large scale plantings have been accomplished.

Further, there have been no long term evaluations of plantings. This would seem to be a critical need, as plantings of Zostera marina have been done all along the north Atlantic coast, but have yielded few good results (Cottam and Munro 1954). The one recorded attempt at transplanting Pacific coast Zostera marina to the U. S. Atlantic coast was a complete failure (Addy and Aylward 1944). It would seem that an understanding of the existence of physiological races (ecotypic variation) would eliminate many future transplant failures.

McRoy (1973) lists four successful transplant methods for seagrasses and a fifth that may eventually prove useful:

- a. Transplanting with an anchoring device.
- b. Seeds planted with anchors.
- c. Turions planted with anchors.
- d. Use of turf with their associated plants.
- e. Planting of seedlings from culture or hibernacula in biodegradable containers.

According to Addy and Aylward (1944), Kelly et al. (1971) transplants are usually moved in the spring and planted on soft to moderately firm sandy bottoms that are not exposed at low tide. A single transplant may consist of 12 to 15 individual plants with their attached soil.

The observations of Fuss and Kelly (1969) led them to believe that field transplanting of Thalassia testudinum is feasible. T. testudinum spreads vegetatively by rhizomes. Growth is dependent on the activity of the meristematic tissue at the apex of the rhizome (Tomlinson and Vargo 1966). This actively growing tissue must be present on any plant or plant part that is to be used for a transplant.

Kelly et al. (1971) have outlined several transplanting procedures that seem to work well. Transplants of Thalassia testudinum consist of either plugs (whole plants with attached substrate) or sprigs (plants without substrate). Plugs were planted in burlap bags, polyethylene bags, and tin cans. Only the plants in tin cans were successful. Sprigs were attached to pieces of cast iron, 2-inch (5.1 cm) pipe, bricks, and construction rods. The construction rods were easiest to handle and yielded the best survival. Planting consisted of wiring the sprig to the rod with plastic-coated wire and placing it in a hand-dug hole. NAPH (Naphthalene Acetic Acid) applied to the sprigs promoted rapid and heavy root growth and was necessary for best establishment. Taylor et al. (1973) have shown that the leaves of Thalassia can be clipped without harming the transplant. Doing this would help to hold the plants in place as they have a tendency to float away (Kelly et al. 1971).

No large-scale planting programs have yet been attempted and more work is needed on all aspects of the biology and propagation of sea-grasses. McRoy (1973) recognized the following three areas of research as being essential before transplanting can be fully effective:

- a. Determine the presence and extent of physiological races.
- b. Determine the effects of various forms of pollution.
- c. Develop resistant and hybrid stocks.

### Site Selection and Preparation

#### General site characteristics

The following basic problems may be encountered in the establish-

ment of marsh and aquatic plants on dredged material:

- a. Physically unsuitable substrates.
- b. Nutrient deficiencies, both soil and water.
- c. Sediment pollution.
- d. Excessive wind or current action.
- e. Excessive turbidity.
- f. Unfavorable patterns of water-level fluctuations.
- g. Unfavorable water depths.

If the dredged material is to be used in the creation of new marshes, the first step is the proper planning of the disposal operation. It is usually easier to avoid a problem by design of the sediment discharge than to remedy the same problem later. Two general methods of shallow water disposal are in use: diked disposal areas, to prevent sediment and effluent run-off; and uncontained, allowing the material to spread as dictated by local circumstance. Diking has the advantage of control (Windom 1972). If the interior of the diked area is not filled and if it is possible to maintain desired water levels over the fill material, then the area probably can be converted to a productive marsh. An undiked deposition site is likely to develop into a productive area, depending on thickness of the deposit, elevation changes of the disposal area, and the criteria described in the following paragraphs.

#### Substrate characteristics

Physically unsuitable substrates. Physically unsuitable substrates

are basically those which are too soft or too hard. For example, a report of the Skidaway Institute of Oceanography (1974) discusses muddy dredged material deposited along the Georgia coast in July of 1971 that was too soft to work on that summer. In 1972 the mud dried to a hard crust that seedlings could not penetrate. Spartina alterniflora was, however, established by transplanting in March and April of 1973.

Excessively soft substrates can sometimes be consolidated if they can be dried (Kadlec 1962, Linde 1969). This, of course, implies that control of water level is possible. Soft substrates are also subject to erosion by waves and currents, perhaps contributing substantially to turbidity problems. Time may be required for such substrates to "settle down" to the point where planting is practical. If sufficiently protected, soft bottoms are suitable for planting some species (see Table 5) but hand methods must generally be used.

Excessively hard substrates are likely to be either gravel or clay. Very few plants will grow on gravel, so if addition of finer material is not possible, little can be done. Clay substrates are difficult, both because of the hardness and because of their contribution to turbidity. Organic matter additions do help control such turbidity (Uhler 1955, Cook and Powers 1958).

Occasionally sand bottoms are also excessively firm (Martin and Uhler 1939), especially if subjected to wave action. Protection and cultivation to permit plant establishment may be helpful. Plants should be selected that are adapted to sand bottoms. Mechanical site treatment

is relatively easy on firm sands if the water can be removed or if the site drains well between tides.

For all bottom types, mechanical tillage by conventional agricultural techniques, when possible, often improves the substrate as a bed for direct seeding of plants.

#### Nutrient deficiencies.

Windom (1972) analyzed sediment cores taken before, during, and after dredging for oxidation-reduction potential, sulfide ion concentrations, pH, and concentration of certain plant mineral nutrients. He demonstrated changed chemical characteristics in the sediments, which endured for some time where dredged material was relatively thickly deposited. Where the depth of the new deposit was relatively thin, the original chemical characteristics of the sediment were reestablished in a fairly short period of time. Windom concluded that depth of deposited material dictates which portions of an area can become productive.

In addition, the mechanism for transport of mineral nutrients to plant roots (migration of soluble ions upwards in a reduced medium) was disturbed by the deposition of dredged material. The boundary between the oxidized and reduced layers was deeper, so that the supply of ions from the reduced layer was farther from the plant roots (Windom 1972). Odum (1963), however, has noted that the addition of dredged material may increase the nutrient supply of an existing substrate. This increase would probably be temporary, and might not last until the oxidation-reduction boundary has a chance to reestablish itself near the surface

of the substrate. Indirect evidence of the nutrient content of dredged material has been provided by Garbisch et al. (1973) and Woodhouse et al. (1972, 1974). These workers fertilized various disposal sites in attempts to increase the productivity of transplanted areas. Although fertilizer application on some sandy sites led to increased production, fertilization on compacted, fine-grained material did not increase production and in some cases led to plant fatalities due to already high nutrient content and poor permeability.

These studies indicate that thickness, particle size composition, time since deposition, and nutrient composition of dredged material are crucial factors in site selection for plant establishment. In those situations where nutrient deficiencies do occur, it would appear simple to correct them through appropriate fertilization. Although the response of some marsh plants to fertilization is known (e. g. for Spartina alterniflora, Broome et al. 1973, Woodhouse et al. 1974), in general, the mineral nutrient requirements of marsh and aquatic plants have not been studied. It is, therefore, difficult to know whether the amount of nitrate, phosphate, or other nutrients indicated by soil analysis does or does not represent a deficiency. Enough fertilizer trials have not yet been conducted to yield useful generalities. Further, the interactions of substrate and overlying water, particularly with respect to oxidation state, may be such that all added nutrients are rapidly immobilized (Garbisch et al. 1973).

Currents, tides, or fluctuating water levels may actually flush added fertilizers out of wetlands. McRoy and Barsdate (1970) and

Reimold (1972) suggested that Zostera and Spartina alterniflora act as "pumps", receiving phosphorus from the root zone deep in sediments and releasing them during tidal flushing. In general, these processes do not seem detrimental to plants, suggesting that there is an abundance of phosphorus in the bottom soils. Greater response to N than P fertilization (Broome et al. 1973, Woodhouse et al. 1974) reinforces that suggestion. In fresh water, however, the likelihood of effectiveness of nitrogen fertilization is less clear. Considerable experience in fertilizing domestic rice (Oryza sativa) suggests that nitrate is rapidly lost, some to the atmosphere as gaseous nitrogen. Fertilization with ammonia is more promising, but so far there has not been sufficient work to draw conclusions for freshwater marshes.

Acidity is a special form of nutrient problem. Lime is often recommended, based on agricultural experience, as a remedy for highly acid substrates. As pointed out earlier, this is not always successful, and in some cases the amount needed is beyond practical limits. The addition of lime to experimental ponds in New York was found not to have a significant effect on marsh and aquatic plant growth (Lathwell et al. 1969, 1973). In the case of acidity due to cat clay, repeated flushing has been shown to be effective (Neely 1967). In freshwater marshes, flushing may be effective if the acidity is due to conditions within the impoundment, such as accumulations of organic acids. However, the water supply for such marshes often lacks the carbonates needed to overcome acidity.

Cook and Powers (1958) concluded that the flushing of freshwater marshes by spring floodwaters could result in a serious loss of nutrients. During the winter, anaerobic conditions often extend through the entire water column in north temperate marshes. This brings large amounts of iron and manganese into solution in their reduced forms. Concomitantly, dissolved phosphates also increase and may be lost in heavy outflow. If outflow can be minimized until the water column is re-oxygenated, the phosphorus, iron, and manganese will again be immobilized in the bottom muds and retained within the basin.

Sediment pollution. Reimold and Durant (1973) analyzed the concentration of toxaphene in selected estuarine fauna, flora, sediment, and dredged material prior to, during, and after the dredging of Terry Creek, Brunswick, Georgia. A toxaphene plant uses this creek for the disposal of effluent. Concentrations of toxaphene were the highest in dredged material, approaching 1000 ppm, compared to the other components analyzed. Dredging definitely increased the concentration of toxaphene in all biotic and abiotic components analyzed, but there was no decrease in productivity due to toxaphene contamination. Spartina alterniflora appeared to be most affected by toxaphene pollution. Windom (1972) demonstrated that the dredging of polluted sediments produces very complex interactions which are not easily understood. It is therefore difficult to predict influences of polluted sediments. Little is known of the effects of many potential pollutants on marsh ecosystems; consequently, more information is urgently needed.

## Water characteristics

Excessive wind or current action. The establishment of vegetation is one of the major measures to reduce wave and current action. In severe cases, however, it will be impossible to establish even such hardy species as Scirpus acutus by transplanting. Under such circumstances, temporary physical means may be required to reduce waves, currents, or wind transported soil for a growing season or two while the plants gain a firm foothold. A first possibility is to deposit dredged material in such a way that the potential marsh area is protected. If necessary, additional protective devices, such as wing dams (Martin and Uhler 1939), dikes, and sand fences (Woodhouse et al. 1974), may be installed. Many of the techniques devised for sand dune stabilization have counterparts in marsh protection.

If characteristics of the dredged sediments permit, the construction of dikes capable of protecting the proposed new marsh may be decidedly beneficial, particularly if it is then possible to regulate water levels (Smith 1942; also see following paragraphs on water management). The cost may be high, however, and additional benefits may be necessary to justify the cost. Confined disposal on salt marshes is not necessarily the best procedure (Windom 1972) unless accompanied by the proper hydrologic conditions for controlling salinity and water depths.

Less severe cases of wind, wave, or current action may be counteracted with less expensive measures which offer temporary protection.

A log boom may break up waves and large mesh wire fence laid flat on the substrate may hold planting stock in place until it becomes established. Woodhouse et al. (1974) have suggested sandbags be used for control of waves and currents. In most cases, the necessary measures will be highly specific and they will depend on the local situation, species, and available materials.

Excessive turbidity. The successful establishment of vegetation on dredged material may depend upon turbidity control as well as upon stabilization (Larimer 1969).

"It is futile to attempt propagation of submerged aquatics in waters, even though shallow, where quality and quantity of light transmitted to the levels of expected active growth will be insufficient to meet the photosynthetic requirements of the species under consideration" (Salyer 1949).

Floating-leaved species probably require less light than completely submerged plants such as Potamogeton sp., which require high light intensities.

Turbidity adversely affects plant diversity as well as abundance. In a survey of Wisconsin lakes, Modin (1970) found that the greatest abundance and diversity of plant life occurred in the most transparent lakes. If only temporary turbidity is induced by dredging operations, plantings may not be adversely affected because of the short developmental period of most submerged aquatics.

Maximum depths at which plants can be established are dependent upon the interaction of water depth and turbidity. For example, the maximum depth of plant distribution on Lakes Butte des Morts, Poygon,

and Winneconne in Wisconsin was about 120 cm. Aquatic plants "are apparently unable to store sufficient food reserves in their perennating organs to sustain growth of photosynthetic organs up to the light in the spring in turbid waters more than four feet deep" (Harriman 1970). Thus, levels of turbid water must be held as shallow as possible if plants are to become established.

The degree of turbidity resulting from a dredging operation depends upon the nature of the substrate, the frequency and duration of disturbance, and the amount of water movement through the disposal area. If substantial quantities of fine-grained substances such as clay are contained in the deposit from the dredging operation, a long term problem could result. Reduction of wave and current action, as discussed earlier, will help alleviate the problem. Any procedure that adds organic material to the system will be beneficial (Uhler 1955, Cook and Powers 1958). Water-level reductions will permit submerged growth in shallow water and emergent growth on the wet edges, both of which will help to stabilize the clay.

Sometimes turbidity is the result of animal activity, perhaps most often by carp. Carp removal by commercial netting or a fish poison such as rotenone has had markedly beneficial results in some systems (Anderson 1950, Cahoon 1953).

Unfavorable patterns of water-level fluctuation. Generally, some plant can be found adaptable to any but the most excessive water-level fluctuations. In some large reservoirs, however, power or flood-control

requirements result in impossibly large water-level fluctuations. In some of these, small bays or arms of the impoundment have been diked off to provide manageable subimpoundments.

In general, water-level control is one of the best means for encouraging or discouraging specific marsh or aquatic plants. The knowledge needed to create specific kinds of wetlands and marshes by this means is steadily accumulating. Water management is discussed in more detail in the next section.

Unfavorable water depths. Much of the preceding discussion on water-level fluctuations also applies to water depths. Water depths, however, are also controllable by the dispersal of the dredged material. In general, shallow water is most productive and leveling the dredged material deposit to a gentle slope will help maximize the productive area. For specific depth ranges, consult Table 2. Bear in mind that the greatest depths recorded are usually from clear and sheltered waters.

#### Water Management and Control

The relative importance of water depths and their fluctuations, both tidal and nontidal, in determining the distribution of marsh and aquatic vegetation has already been discussed. Broad general depth ranges for many of the common species are given in Table 2. Here we wish to discuss some of the advantages derived from purposeful water-level management. Even if such control is not possible, the discussion will point out the natural circumstances under which some of the same

benefits may accrue.

Water-level control has become the manager's chief tool in aquatic vegetation management. Early efforts were aimed at stabilizing water levels, based on observations that stable level ponds had good aquatic plant growth, particularly pondweeds (Potamogeton spp.) (Anderson 1940). More recently, natural and planned water-level fluctuations have been recognized as valuable in maintaining the productivity of wetlands (Uhler 1956, Harris and Marshall 1963, Kadlec 1962, Meeks 1969, G. Swanson, pers. comm.).

#### Favoring wetland plants

One of the basic reasons for planning water-level fluctuations is to favor a very large number of shallow water plants, including some of the most valuable for wildlife. Penfound et al. (1945) observed: "De-watering was usually necessary for the sprouting of underwater perennating parts, germination of seeds, or flowering and fruiting." De-watering is one of the terms used to indicate the seasonal removal of water from a marsh, the other common term is drawdown. Among the plants favored by drawdowns are Decodon verticillatus, Phragmites australis, Polygonum spp., Rumex spp., Sagittaria spp., Sparganium spp., Typha latifolia (Belonger 1969); Alisma spp. (Bue 1956), Bidens spp. (Hanson 1918), Echinochloa spp. (Burgess 1969), Rhynchospora spp. (Stieglitz 1972), Leersia spp. (Kadlec 1962), Scirpus spp. (Linde 1963), Cyperus (Hanson 1918), and many other members of the sedge family (Cyperaceae).

For many of these plants, either a wet soil or very shallow water provides the optimum conditions for germination and establishment. Haslam (1971) found that Phragmites australis required a wet soil or no more than one cm of water over the soil for establishment. Lazenby (1955) found it was essential that the water table be at the surface of the soil for establishment of Juncus effusus. The moisture is needed for germination, and also for reducing the competition from non-marsh plants. Bedish (1967) found that Typha glauca germinated equally well in depths of 2.5-15 cm in the greenhouse, but he could not obtain germination in the field. Shallow flooding apparently stimulates bud development in Phragmites australis provided the rhizomes are aerated through upright stems (Haslam 1970). Recall that rhizome aeration is also apparently important for overwinter survival in Typha, implying that this may be an important mechanism in many emergent species.

Many of these wetland plants volunteer rapidly on moist exposed soils (especially in freshwater areas), but to ensure rapid establishment or dense growth, seeding is sometimes undertaken. Better results are obtained if the site can be cleared of other plants and a seedbed prepared. Ability to control water level also permits drying to allow equipment access. If annual species, such as Polygonum spp. or Echinochloa app., are seeded, this becomes essentially a farming operation. Detailed directions for this procedure are given in Linde (1969), Atlantic Waterfowl Council (1972), and Givens and Atkinson (1957). If perennials are planted, the operation need be repeated only infrequently. There is, in fact, reason to believe that many marsh plants are

adapted to natural fluctuations of a similar nature. Sustained high water decreases and eventually eliminates Rhynchospora traceyi, Polygonum spp. (Stieglitz 1972), and Typha spp. (Mathiak 1971, Harris and Marshall 1963, McDonald 1955). Periodic low water, through natural causes, seems necessary to regenerate these stands. A similar cycle seems to help maintain the productivity of the northern prairie pot-holes (R. Stewart, G. Swanson, pers. comm.) and riverine marshes. In any event, draining and seeding, or seeding during natural low water levels, is an excellent procedure for establishing such desirable plants as Scirpus spp., Polygonum spp., Echinochloa spp., and Leersia spp. in fresh water.

If the water level is lowered every summer or for more than one year, invasion by terrestrial weeds and willow (Salix spp.) often occurs (Harris and Marshall 1963, Meeks 1969). One year of reflooding during the growing season eliminated most terrestrial weeds (Harris and Marshall 1963). Meeks (1969) found that removing the water in May, rather than March, April, or June, produced the best results in terms of wetland and seed-producing plants for wildlife.

#### Favoring submerged aquatics

Another group of plants requires reasonably stable water levels. Wild rice (Zizania aquatica) is a notable example in fresh water, as are some pondweeds (Potamogeton spp.). Impoundments containing brackish water are probably best managed with stable water levels 30 to 100 cm

deep to promote Ruppia maritima and Najas marina (Stieglitz 1972). J. Monte (pers. comm.) noted that, in Louisiana, R. maritima quickly invades brackish ponds that are created by dredge banks. Diked salt marsh sometimes converts to fresh marsh, so water-level control in such situations needs to be approached cautiously (Kosinski and Ferrigno 1971). Salinity considerations in this situation may outweigh the benefits of water-level control.

#### Promoting growth

The range of water depths over which best growth is made is often quite narrow, even though a species may tolerate a fairly wide range of depths. Robel (1962) found that the combined production of Potamogeton pectinatus, Zannichellia palustris, Ruppia maritima, and Chara spp. increased as water depth increased from 7.5 to 45 cm and then the production decreased with further depth increases.

According to Ward (1942), Phragmites will not grow in permanent water or tolerate even temporary water depths over 15 cm. He claims Phragmites tolerates late summer drought but requires spring flooding. Haslam (1970) said that Phragmites will dominate in drier sites when the fertility is low and competition is reduced.

Chater and Jones (1957) pointed out that Spartina townsendii stands (and by inference other Spartina spp.) will be invaded by other species if water depth is not optimum or if the substrate is relatively poor--for example, coarse sand. Bedish (1967) found that Typha X glauca made

its best growth with only 2.5 cm of water over the substrate, but growth was almost as good on saturated soil or in 15 cm of water. Harris and Marshall (1963) found that Potamogeton pectinatus made its best growth and fruited heavily the year after a drawdown. Water-level control permits the encouragement or discouragement of these species by regulating depth.

### Controlling zonation

Natural zonation of plants is often related to very small differences in water depth or, in tidal areas, differences in elevation with respect to sea level. In a Delaware salt marsh, Bourn and Cottam (1950) observed the following ranges of elevation over mean sea level (msl):

	<u>Elevation above msl, cm</u>
<u>Iva frutescens</u>	72.5- 98.5
<u>Baccharis halimifolia</u>	77.5-100.5
<u>Spartina alterniflora</u>	56.5- 88.0
<u>Distichlis spicata</u>	70.5- 87.0
<u>Spartina patens</u>	77.5- 99.5

When the marsh was ditched for mosquito control, there was a decided shift toward Iva and Baccharis, even though their natural elevations of occurrence are normally very close to those of the other species. In fact there is surprisingly little difference among the species elevations, even though they normally sort into well defined zones. The obvious exception is S. alterniflora, which has the lowest lower limit and occupies the outermost zone. Perhaps the internal water table may be more important than elevation above msl.

That the relation of plant zonation to water level is not simple

is illustrated by the observations of Eleuterius (1972) in Mississippi. Consistent with Bourn and Cottam's (1950) data, he found that the muddy perimeters of disposal islands were rapidly colonized completely by S. alterniflora, but that the drier (and higher) centers rapidly converted to Baccharis halimifolia. In contrast, a Juncus roemerianus salt marsh covered with about 120 cm of dredged material converted to Spartina patens. Also, a Juncus marsh covered with varying amounts of material up to just below mean high water (mhw) was colonized variously with Spartina alterniflora, S. patens, S. cynosuroides, Salicornia bigelovii, and Fimbristylis spadicea. In this latter case a shallow high-water channel was present, allowing more or less typical zonation.

Soil moisture content during seedling establishment is clearly important in determining species composition in freshwater marshes. For example, Kadlec (1960) found that sedges, particularly Carex spp., and some kinds of Scirpus dominate over Typha latifolia on drier substrates.

#### Controlling invasion of competitors

Certain patterns of water-level fluctuations may serve to reduce or eliminate competition, particularly from species characteristic of drier habitats. In fresh water, newly exposed wet soils are often colonized rapidly by willows (Salix spp.) (Nielson and Moyle 1941, Skau and Day 1959, Lindsey et al. 1961, Harris and Marshall 1963). Uplift of the Copper River delta in Alaska during an earthquake led to quick colonization by forbs and grasses (Gramineae) along with willow and alder (Alnus sp.) (Shepard et al. 1968). Penfound et al. (1945) observed

that increasing water levels would eliminate such invaders. Godwin and Bharucha (1932) believed that a high water level for a few weeks in winter was important in keeping shrubs out of Phragmites and Cladium stands.

Prolonged high water is needed to eliminate some plants. Harris and Marshall (1963) found that Eleocharis spp. and Scirpus validus were destroyed by flooding with about 40 cm of water for three years; Typha latifolia and Carex spp. were gone in four years. Two-year-old Salix died in two to four years in all depths; but four or five year willow was killed only by flooding with 60 cm for three to four years.

#### Control of wave action

The establishment of new stands of marsh and aquatic vegetation is often inhibited by excessive waves or currents, either by direct mechanical action on the plants or by eroding and shifting substrate material. Lowering the water level can permit establishment of perennial plants such as Scirpus or Spartina which, after they develop extensive anchorage, can tolerate waves and currents. The presence of these plants, by reducing the impact of waves and currents, will then permit other plants to become established.

In northern areas, ice action can be significant, as expansion and contraction scrapes shores or moving floes plow shallows clear of vegetation. If freezing extends into the bottom deposits in shallow water, water-level increases prior to thawing can literally lift out and transport whole sections of marsh. If water levels can be controlled, each of

these processes could be used to benefit establishment of desirable plants in certain circumstances.

#### Improvement of soil-water fertility

Water-level fluctuations are often the key to soil and water fertility. Kadlec (1962) showed that soil fertility and physical structure were improved by drawdown in a freshwater marsh. On the other hand, Cook and Powers (1958) believed that drainage, particularly in spring, might remove valuable nutrients if anerobiasis had resulted in large movement of soil nutrients into the water. In very poor sites, such losses could be significant (Kadlec 1960).

In general, the relationships between soil fertility, nutrients dissolved in the water, and plant growth are understood only in broad outline. More work is needed in this area.

#### Methods of water-level control

Water-level control is usually achieved by dikes or dams in conjunction with control structures or pumping facilities. The several wetland or waterfowl management handbooks (Atlantic Waterfowl Council 1972, Linde 1963) outline methods for small installations.

#### Evaluation of Plant Species to be Established

The primary goals of marsh creation and revegetation are substrate stabilization and/or provision of wildlife habitat. For either purpose, any vegetation that can be grown on a bare soil is better than none.

Often, however, several choices of species to favor exist and one or more values of the area can be selectively enhanced by encouragement of the proper plants. With marsh plants, especially, the original invader often has an advantage over species arriving later. This will be discussed in more detail later, but the point here is that a good first choice may minimize future problems.

The value of a marsh may be more dependent on basic fertility and water depth than plant species composition, since fertile shallow marshes provide an environment favorable to the majority of plants and animals usually considered desirable. Such sites require little management effort, as desirable plants will probably invade as rapidly by natural means as by planting.

However, many sites are less than optimal and will require some work to encourage plant colonization. Selection of species to establish will need to be based on those native to the geographic area, the specific characterization of the site, the possible restrictions of local ecotypes, the potential for site preparation, the ease of establishment, and the objectives in creating the marsh.

#### Wildlife values

Martin et al. (1951) summarized much of the information on the values of plants to wildlife. The older studies should be interpreted with caution, for confounding factors, such as seasonal biases and short-term studies, are often present; nevertheless, this is often the only information available. Marsh and aquatic plants have been con-

sidered in terms of their value for waterfowl by McAtee (1939), Martin and Uhler (1939), Pirnie (1935), and others. From these publications we have derived a list (Table 8) of the plants considered useful for waterfowl food and cover (shelter from weather, predators, or man). Table 8 should be considered a general guide as local circumstances may often completely reverse these evaluations. For example, Potamogeton crispus is considered a poor food source because it rarely produces seed, yet when or where it does set seed, it might be a high value species (Hunt and Lutz 1959). In general, the value of a stand of a particular marsh or aquatic plant depends on its density, water depth, seed production, accessibility of edible parts, and the associated production of invertebrates. Stands that are too dense may be impenetrable by waterfowl, while those that are too sparse will be unattractive. Not only must the plant parts consumed be abundant, but they must be available at the right times and in the right places to be accessible. Water depth is important, since many species of ducks are reluctant to feed out of water and seeds or tubers in deep water may be out of reach. Sagittaria spp. produce tubers which may be valuable food if they are near the surface of a soft substrate and hence easily obtained by ducks or geese. Such tubers are useless for feeding when buried deep in the substrate. Wet soil plants such as Echinochloa spp. and Polygonum spp. are usually annuals and prolific seed producers. To make the seed available as food for waterfowl, it is necessary to flood the stands, which usually requires some form of water-level control. If seeds deteriorate rapidly

Table 8

Evaluation of Marsh and Aquatic Plants for Wildlife, Substrate Stabilization, and Potential Nuisances\*

Species	Waterfowl foods		Water-fowl cover	Birds other than waterfowl		Muskrat food	Substrate stabilization	Potential nuisance
	Part consumed	Value rating		food cover	food cover			
	a**	g***	x#	##	##			
<u>Acnida cannabina</u>								x
<u>Acorus calamus</u>								x
<u>Alisma plantago-aquatica</u>	a	f						x
<u>Alternanthera philoxeroides</u>	a	e						
<u>Aneilema keisak</u>								
<u>Aster spp.##</u>			x					
<u>Atriplex patula</u>	a,c	g						
<u>Avicennia sp.</u>							x	

\*Compiled from: Burkhalter, et al. 1974, Chabreck and Palmisano 1973, Cook 1958, Davison 1947, Garbisch 1974 - pers. comm., Joanen and Glasgow 1965, Mall 1969, Martin et al. 1951, Martin and Uhler 1939, McAtee 1939, McGilvrey 1964, More Game Birds in America 1933, Moyle and Hotchkiss 1945, Myers 1955, Neely 1967, Neely 1962, Neely 1956, Palmisano and Newsom 1968, Pirnie 1935, Rock 1969, Salyer 1949, Savage 1972a+b, Sculthorpe 1967, Stanton and Smith 1957, Steenis 1939, Steenis and Warren 1959, Stewart 1974 - pers. comm., Taylor et al. 1973, Terrill and Greenwell 1948, Tomlinson and Vargo 1966, Uhler 1962, Wass and Wright 1969, Westlake 1968, Yocum 1951.

\*\* a=seeds or comparable structures, b= tubers and roots, c= foliage and stems

\*\*\* e=excellent, g=good, f=fair, p=poor

# "x" indicates plant is functional in specified category

## a blank space indicates plant is not functional in specified category or information is lacking

### "spp." indicates that species was not specified by author

Table 8 (continued)

Species	Waterfowl foods		Water-fowl cover	Birds other than waterfowl		Muskrat food	Substrate stabilization	Potential nuisance
	Part consumed	Value rating		food	cover			
<u>Azolla caroliniana</u>								x
<u>Baccharis halimifolia</u>								x
<u>Bacopa</u> spp.	a,c	p						
<u>Beckmannia</u> spp.	a	f						
<u>Bidens</u> spp.	a	p	x					
<u>Boltonia asteroides</u>			x					
<u>Brasenia schreberi</u>	a	g						x
<u>Butomus umbellatus</u>	a	f						x
<u>Cabomba caroliniana</u>								
<u>Calamagrostis canadensis</u>			x					
<u>Carex</u> spp.	a	f	x					
<u>Cephalanthus occidentalis</u>	a	g	x					
<u>Ceratophyllum demersum</u>	a,c	f			x			x
<u>Chara</u> spp.	c	g		a				
<u>Cladium jamaicense</u>	a	f	x					x
<u>Cyperus esculentus</u>	a,b	e						
<u>Cyperus odoratus</u>	c	f						
<u>Cyperus</u> spp.	a	f		a				
<u>Damasodium californicum</u>	a	f						
<u>Decodon verticillatus</u>	a	p						
<u>Deschampsia</u> spp.	a	f						
<u>Distichlis spicata</u>	a	f		a			x	
<u>Echinochloa</u> spp.	a	e	x	a				
<u>Eichornia crassipes</u>	a			a				x

Table 8 (continued)

Species	Waterfowl foods		Water-fowl cover	Birds other than waterfowl		Muskrat food	Substrate stabilization	Potential nuisance
	Part consumed	Value rating		food	cover			
<u>Eleocharis acicularis</u>			x					x
<u>Eleocharis palustris</u>	b	g		a	x	x		
<u>Eleocharis spp.</u>	c	f						x
<u>Elodea canadensis</u>	c	p				x		
<u>Equisetum spp.</u>	a	p						
<u>Eragrostis spp.</u>								
<u>Glyceria maxima</u>	a	f					x	x
<u>Glyceria striata</u>	a	p	x					
<u>Heliotropium spp.</u>	a	p						
<u>Heteranthera dubia</u>	a	p						x
<u>Hippuris vulgaris</u>	a	p						
<u>Hydrilla verticillata</u>								x
<u>Hydrochloa carolinensis</u>	a,c	f						x
<u>Hydrocotyl spp.</u>	a	p						x
<u>Iris versicolor</u>			x					
<u>Iva frutescens</u>								x
<u>Juncus roemerianus</u>				a	x			x
<u>Jussiaea spp.</u>	a	g						
<u>Leersia oryzoides</u>	a,b	g	x	a	x			
<u>Lemnaceae</u>	c	g						
<u>Leptochloa fascicularis</u>	a	g						x
<u>Limnium spongia</u>	a	f						x
<u>Lophotocarpus calycinus</u>	a	g						
<u>Ludwigia peruviana</u>	a	f						x

Table 8 (continued)

Species	Waterfowl foods		Water-fowl cover	Birds other than waterfowl		Muskkrat food	Substrate stabilization	Potential nuisance
	Part consumed	Value rating		food	cover			
<u>Marsilea vestita</u>	a	f						
<u>Menyanthes trifoliata</u>	a	f						
<u>Myrica</u> spp.	a	p						x
<u>Myriophyllum brasiliense</u>	a,c	p						x
<u>Myriophyllum spicatum</u>	a,c	p		a				
<u>Myriophyllum</u> spp.	a,c	e						x
<u>Najas flexilis</u>	a,c	e						x
<u>Najas guadalupensis</u>	a,c	e						x
<u>Najas marina</u>	a,c	f						
<u>Najas</u> spp.				a				
<u>Nasturtium officinale</u>	c	f						x
<u>Nelumbo lutea</u>								x
<u>Nuphar luteum</u>								x
<u>Nuphar mexicana</u>				a				x
<u>Nuphar microphyllum</u>				a				x
<u>Nuphar variegatum</u>				a				
<u>Nymphaea odorata</u>	a	f						x
<u>Nymphaea</u> spp.	a	p						x
<u>Nymphaea tuberosa</u>	a	f						
<u>Panicum dichotomiflorum</u>	a	g						
<u>Panicum hemitomum</u>								x
<u>Panicum purpurascens</u>	a	f						x
<u>Panicum repens</u>	a	p						x
<u>Paspalum boschianum</u>	a	g						
<u>Paspalum distichum</u>	a	f						

Table 8 (continued)

Species	Waterfowl foods		Water-fowl cover	Birds other than waterfowl		Muskrat food	Substrate stabilization	Potential nuisance
	Part consumed	Value rating		waterfowl	food cover			
<u>Paspalum fruitans</u>	a	p						x
<u>Paspalum vaginatum</u>	a	f						
<u>Peltandra virginica</u>	a	p	x	a				
<u>Phragmites australis</u>			x		x		x	x
<u>Pistia stratiotes</u>								
<u>Planera aquatica</u>	a	f						
<u>Polygonum amphibium</u>	a	e						
<u>Polygonum aviculare</u>	a	g						
<u>Polygonum coccineum</u>	a	g						
<u>Polygonum densiflorum</u>	a	g						
<u>Polygonum hydropiper</u>	a	g						
<u>Polygonum hydropiperoides</u>	a	g						
<u>Polygonum lapathifolium</u>	a	e						
<u>Polygonum muhlenbergii</u>	a	e						
<u>Polygonum natans</u>	a	g						
<u>Polygonum pensylvanicum</u>	a	e						
<u>Polygonum persicaria</u>	a	e						
<u>Polygonum portoricense</u>	a	e						
<u>Polygonum punctatum</u>	a	e						
<u>Polygonum ramoisissimum</u>	a	g						
<u>Polygonum sagittatum</u>	a	f						
<u>Polygonum spp.</u>			x	a	x	x		
<u>Pontederia cordata</u>	a	p	x					x
<u>Porterpinaca palustris</u>	a	p				x		

Table 8 (continued)

Species	Waterfowl foods		Water-fowl cover	Birds other than waterfowl		Musk rat food	Substrate stabilization	Potential nuisance
	Part consumed	Value rating		food	cover			
<u>Potamogeton amplifolius</u>	a	f						
<u>Potamogeton capillaceus</u>	a	f						
<u>Potamogeton compressus</u>	a,b,c	g						x
<u>Potamogeton crispus</u>	a,b	p						
<u>Potamogeton diversifolius</u>	a	f						
<u>Potamogeton epihydrus</u>	a,b,c	g						
<u>Potamogeton foliosus</u>	a,b,c	g						
<u>Potamogeton friesii</u>	a,c	g						
<u>Potamogeton gramineus</u>	a,b	g						
<u>Potamogeton heterophyllus</u>	a,b,c	g						
<u>Potamogeton illinoensis</u>	a	f						x
<u>Potamogeton natans</u>	a,b	g					x	
<u>Potamogeton nodosus</u>	a	g						
<u>Potamogeton perfoliatus</u>	a,b,c	g						
<u>Potamogeton praelongus</u>	a,b,c	f						
<u>Potamogeton pusillus</u>	a,b,c	g						
<u>Potamogeton richardsonii</u>	a,b,c	g						
<u>Potamogeton robinsii</u>								x
<u>Potamogeton spirillus</u>	a	f						
<u>Potamogeton strictifolius</u>	a	g						
<u>Potamogeton zosteriformes</u>	a	f						
<u>Ranunculus spp.</u>	a,c	p						
<u>Raphanus sativus</u>	a	p						
<u>Rhizophora mangle</u>								x

Table 8 (continued)

Species	Waterfowl foods		Water-fowl cover	Birds other than waterfowl		Muskrat foods	Substrate stabilization	Potential nuisance
	Part consumed	Value rating		food	cover			
<u>Rhynchospora spp.</u>	a	f						
<u>Rumex spp.</u>	a	p						
<u>Ruppia maritima</u>	a,b,c	e		a				
<u>Sagittaria cuneata</u>	a,b	f						
<u>Sagittaria heterophylla</u>	a,b	f						
<u>Sagittaria platyphylla</u>	a,b	e						
<u>Sagittaria spp.</u>			x	a	x	x		
<u>Salicornia virginica</u>	a,c	f						x
<u>Salix interior</u>							x	
<u>Salix spp.</u>								x
<u>Salvinia rotundifolia</u>								x
<u>Saururus cernuus</u>	a	p						
<u>Schoenoplectus spp.</u>								x
<u>Scirpus acutus</u>	a	e					x	
<u>Scirpus americanus</u>	a	g					x	
<u>Scirpus californicus</u>	a	f						
<u>Scirpus campestris</u>	a	g						
<u>Scirpus cyperinus</u>	a	p						x
<u>Scirpus fluviatilis</u>	a	g						
<u>Scirpus heterochaetus</u>	a	e						
<u>Scirpus olneyi</u>	a	e						
<u>Scirpus paludosus</u>	a	e					x	
<u>Scirpus robustus</u>	a	e					x	
<u>Scirpus spp.</u>			x	a,b	x			x

Table 8 (continued)

Species	Waterfowl foods		Water-fowl cover	Birds other than waterfowl		Muskrat foods	Substrate stabilization	Potential nuisances
	Part consumed	Value rating		food	cover			
<u>Scirpus validus</u>							x	
<u>Scolochloa festucacea</u>	a	g						
<u>Sesuvium portulacastrum</u>	a	g						
<u>Setaria lutescens</u>	a	g						
<u>Setaria magna</u>	a	f						
<u>Sparganium americanum</u>	a	f						
<u>Sparganium eurycarpum</u>	a	f						
<u>Sparganium spp.</u>								
<u>Spartina alterniflora</u>	a,b	f	x				x	
<u>Spartina bakeri</u>	a	f						
<u>Spartina cynosuroides</u>	a	f	x				x	
<u>Spartina foliosa</u>	a	f						
<u>Spartina gracillius</u>	a	f						
<u>Spartina patens</u>	a	f					x	
<u>Spartina pectinata</u>								x
<u>Spartina spp.</u>				a	x	x		
<u>Thalassia testudinum</u>	c	f					x	
<u>Thalia divaricata</u>	a	f						
<u>Toretria acuminata</u>	a	f						x
<u>Trapa natans</u>								
<u>Triglochin maritima</u>	a	g						
<u>Typha spp.</u>	b,c	p	x	a	x	x		x
<u>Utricularia spp.</u>	c	p						x

Table 8 (concluded)

Species	Waterfowl foods		Water- fowl cover	Birds other than waterfowl		Muskrat food	Substrate stabilization	Potential nuisance
	Part consumed	Value rating		waterfowl	food cover			
<u>Zanichellia palustris</u>	a, c	g		a				
<u>Zizania aquatica</u>	a	e	x	a	x			
<u>Zizaniopsis miliacea</u>								x
<u>Zostera marina</u>	a, b, c	e		a			x	

underwater, such as those of Fagopyrum esculentum and Echinochloa spp., they are of less value than those which do not (Scirpus spp., Panicum spp., Polygonum spp.) (Neely 1956).

In some cases, the food produced directly by the plant is less important than that produced by the invertebrate animals associated with the plants. Lush beds of marsh and aquatic plants harbor myriads of invertebrates (Krull 1970) which are an attractive food supply for both birds and fish. Even plants that are considered poor food may be very valuable in this indirect way.

Many species of birds other than waterfowl are abundant in most marshes. Although these are frequently attracted by the insects, invertebrates, and other animal foods, some plants have been noted as being used as food or cover (Table 8). A variety of small birds use emerged marsh plants as nesting sites. Many aquatic and marsh plants are used as food by muskrats (Table 8). Given good stands of emergents and adequate water depth, muskrats (and in some areas, nutria) may become so abundant that they destroy established stands by their feeding. When these mammals become overly abundant, control may be necessary.

Marshes and shallow waters are also noted for their reptiles and amphibians. Sea grasses are vital to the endangered and highly valued herbivorous green sea turtles. Most reptiles and amphibians, however, are attracted by the abundant animal material which is their main food supply, and thus are only indirectly affected by the kinds of plants present.

Marshes, beds of submersed vegetation, and estuaries are very important in the life cycle of many fresh and saltwater fish. Salt and estuarine marshes are very important to the productivity of estuaries and associated saltwater fishes (Odum 1971). Basically, it is the high level of organic production which is valuable, rather than any particular species of plant, but Spartina spp., Typha spp., and Phragmites australis are among the most productive plants known (Sculthorpe 1967, Boyd 1971). Some of the subtropical and tropical floating plants such as Eichornia crassipes may be even more productive, but the importance of that productivity in their native habitats is poorly understood.

Aquatic and marsh plants in freshwater habitats are important to fish for spawning areas, protection from predation, and the invertebrate foods associated with the plants (Sculthorpe 1967). Again the plant species per se are not critical; it is their presence and the productivity that is important.

#### Substrate stabilization

To be useful in substrate stabilization, a plant should have an extensive underground system of roots and rhizomes and should be easy to establish. A list of species recommended for stabilization by various authors is given in Table 8. We believe this list is much too restrictive; many other species not mentioned by published studies are likely to be useful in specific circumstances. Even annuals, which

usually do not have large root systems but are often easily established, may be useful as a temporary measure.

Generally, the perennial members of the Gramineae, Cyperaceae, and Typhaceae have dense and spreading root systems that are valuable in stabilizing substrates. Many of the species in Table 8 are from those families, but there are numerous other unlisted, and apparently unstudied, species in those families which might be useful in particular circumstances. We believe that work on these other species might yield valuable results for substrate stabilization.

A variety of other plants, often considered weeds or undesirable, have characteristics which might be exploited when substrate stabilization is of primary importance (Table 8). Basically, these species create problems because of their aggressiveness and tendency to crowd out other plants. That, however, is the quality desired in a plant for substrate stabilization. Not all have the desired root system characteristics; for example, Baccharis halimifolia and Iva frutescens (Garbisch, pers. comm.) may supplant Spartina alterniflora, which has a more extensive root system. However, even species such as these may prove useful on some sites.

#### Problem species, competition, and succession

Some species of marsh and aquatic plants tend to take over an area and exclude other plants for long periods of time. Some marshes have been essentially solid stands of Typha or Spartina for as long as local residents can remember. In relatively undisturbed situations,

beds of submersed and emersed vegetation often remain remarkably similar over long periods of observation (40-50 years) (Sculthorpe 1967). Such monospecific areas are not necessarily static; indeed they are often very dynamic in the sense of turnover or local shifting of channels and elevations. Such relative permanence seems to be based on an environment which through a variety of external influences, such as tides, fluctuating water levels, or temperatures, remains more or less continuously optimal for the particular plant species. In some sense, these outside influences could be considered stresses to which these persistent species are adapted. Moreover, such species are usually perennial and long lived.

Stands of these species have a permanence which might lead to the belief that they form a dominant and stable vegetation. This is true only to the extent that the environmental influences on which they depend are stable. If a ditch is dug through a Spartina alterniflora stand, Baccharis or Iva will probably invade (Bourn and Cottam 1950). If Baccharis is removed the Spartina will return, but only briefly. Baccharis will re-invade. The ditch changed the site from a Spartina habitat to a Baccharis habitat. Similar illustrations are possible for Typha, Carex, and other plants that tend to form persistent stands.

Basically, then, long term species composition of marshes and shallow waters is mainly determined by the habitat or physical-chemical environment.

What of the classic view of succession from submergent to floating-

leaved to emergent vegetation? Quite clearly, each group of plants exist in zones associated with water depth. In sheltered ponds with essentially constant water levels, organic deposits will accumulate, gradually reducing the water level and allowing species associated with shallower water to invade. This sequence is by no means universal or inevitable, nor does it necessarily lead to a terrestrial type of vegetation. Along coastal areas, including the Great Lakes shores, geologic subsidence or uplift may occur more rapidly than organic deposits accumulate (Redfield 1972). Wave or current action may remove organic deposits or smother them in silt. Drought may expose the organic material to the air, permitting rapid decomposition. In sum, when viewed from reasonable management time horizons, classical aquatic succession is very slow, and is only one of the many causes of vegetation change in marsh and shallow water habitats.

As Table 2 illustrates, many marsh and aquatic plants have wide ranges of tolerance and are adapted to a fairly broad spectrum of habitats. On any specific site, the species that colonize will depend on proximity of seed source, relative rates of dispersal, and the growth habit and growth rate of the invader in relation to the growth habit of species already present. On bare sites such as sand bars, willows (Salix spp.) and aspens or cottonwoods (Populus spp.) frequently appear very rapidly (Skau and Day 1959, Nielson and Moyle 1941, Lindsey et al. 1961, etc.) because their wind-disseminated seeds reach new sites quickly. Many species adapted for widespread seed dispersal are annuals

and do not persist unless perennials are prevented from becoming established. Perennials usually can exclude annuals from a site and competition among perennials will eliminate some species.

Problem plants are often perennials adapted for rapid dispersal and competitive ability. Such species tend to take over an area, even though other species might grow there. Some floating species such as Eichornia crassipes and Trapa natans fulfill most of those criteria. Emergents, such as Phragmites australis, Typha spp., Hibiscus spp. and other species, can also become problems.

Once again, it is important to emphasize that the very characteristics that make these species potential problems are those which facilitate their establishment on new substrates. Whether the advantages in establishment outweigh their disadvantages in terms of wildlife or navigational problems is a matter for careful consideration. Once introduced, however, they may be difficult to manage.

Mosquitoes are often associated with marshes and shallow ponds. Whether or not this is a problem depends on the specific habitat, the kinds of mosquitoes, and the proximity to man. In our opinion, if marshes are considered desirable, it is simply necessary to have the inconvenience of mosquitoes. Sometimes a water-level management scheme can reduce the mosquito population; but this is highly dependent on local circumstances.

### Control

Removal of marsh and aquatic vegetation is sometimes desired to

clear navigation channels, to facilitate boating or swimming, or to replace one species with another considered more beneficial or useful. Such efforts are often costly and difficult, for a dense, well established stand of vegetation obviously indicates the species suited to that site. Any control procedure which does not alter the site in some way will probably have to be repeated regularly.

Among the control methods commonly used are herbicides (Myers 1955, Stennis and Warren 1959, Sculthorpe 1967, and Burkhalter et al. 1974), mowing (Chapman 1937, McAtee 1939, and Haslam 1968), plowing (Goss 1925), discing (Neely 1967), and water-level control (Ward 1942). Various organisms such as muskrats, crayfish, insects, and carp, have been used for biological control (Sculthorpe 1967, Dean 1969, and Burkhalter et al. 1974). Special barge mounted machines have been built for mowing submerged aquatics and modified agricultural machines and methods also have been used. Sculthorpe (1967), Linde (1969), Burkhalter et al. (1974), Newsom (1968), and the Atlantic Waterfowl Council (1972) provide recent reviews of techniques and results.

## PART VIII: RESEARCH NEEDED

Throughout this report subjects and problems that need additional research have been indicated. Overall, the biology of aquatic and marsh plants is poorly understood. While any additional knowledge about these plants would be beneficial, there is a definite need for experimental investigation into the basic biological and ecological relationships of most of the species mentioned in this report.

The following listing describes several important areas where information is needed. More detail and additional research needs are included in the appropriate sections of this report.

### Basic Taxonomic Investigation

Aquatic and marsh plants are floristically and taxonomically not well known. Most of the major genera of wetland plants (for example, Potamogeton, Myriophyllum, Scirpus, Carex, Cyperus, Eleocharis, Spartina, Calamagrostis, Panicum, Juncus, Najas, Utricularia, Polygonum, Glyceria, Sparganium, Sagittaria) are in need of critical taxonomic revision. There is no single up-to-date manual of the aquatic and marsh plants of North America. Even most of the regional manuals are in need of revision, while some regions (e. g., southeastern United States) have never had a complete manual. Because a sound understanding of the taxonomic relationships and species distributions is necessary to all ecological work, it would seem logical that these older regional manuals be completely revised and/or a new manual for North America be prepared.

## Ecotypic Variation

Investigations into the existence and extent of physiological races and their adaptations would help to prevent planting failures. Currently there is a great deal of speculation about the importance of ecotypes and the degree of genetic and phenotypic variation that is expressed within a single species. The identification of ecotypes (races) of the important species would contribute to better survival of plantings and consequently lower costs. Work with ecotypic variation must be closely coordinated with taxonomic work.

## Biology of Species

The following areas seem worthy of investigation:

- a. Modes of dispersal and establishment (including methods for influencing natural establishment).
- b. Effects of turbidity, nutrient addition, and pollution on the growth and physiology of aquatic and marsh plants (primarily dredging-related effects).
- c. Relation of aquatic and marsh plants to the chemical and physical conditions of the substrate (including dredging-related conditions).
- d. Developmental biology of important aquatic and marsh plants (emphasis on modes of reproduction).
- e. Dormancy and germination of seeds of aquatic and marsh plants (including environmental effects and methods of manipulating

- dormancy and germination).
- f. Rates of spread and competitive relationships among aquatic and marsh plants.
  - g. Productivity and nutrient cycling (as related to dredging).
  - h. Relations of aquatic and marsh plants to animals (including values of plants to animals and the effects of animals on plantings).

### Collecting and Planting Methods

If planting is to be done on a large scale more efficient and economical methods of collecting and planting propagules must be developed. This may include developing machinery that can operate on dredged material disposal areas.

Additional information is needed on selecting species to plant, planting time, planting site(s), and planting methods. This includes overall establishment methods, economics of spacing, and techniques for placement of dredged material.

Essentially, a well documented backlog of information on both experimental and operational planting efforts is needed. Analysis of the records thus accumulated will provide the necessary guidelines on planting methods, costs, success, etc., necessary to improve future planting success.

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APPENDIX A: SERIAL PUBLICATIONS REVIEWED

Journal Title

American Journal of Botany  
American Midland Naturalist  
Annals of Botany  
Aquarist and Pondkeeper  
Aquarium  
Aquarium Journal  
Botanical Gazette  
Bulletin of the Torrey Botanical Club & Torreya  
Bulletin of Marine Science of the Gulf & Caribbean  
California Fish & Game Journal  
Canadian Journal of Botany  
Castanea  
Chesapeake Science  
Coastal Studies Institute Report (LSU)  
Dissertation Abstracts  
Ecology  
Ecological Monographs  
Fisheries Bulletin (USFW)  
Freshwater Biology  
Hydrobiologia

Japanese Journal of Botany  
Journal of Applied Ecology  
Journal of Botany  
Journal of Ecology  
Journal of Experimental Botany  
Journal of Wildlife Management  
Limnology and Oceanography  
Michigan Botanist  
Nature  
New Phytologist  
New York Conservationist  
New York Fish & Game Journal  
Oecologia  
Ohio Journal of Science  
Oikos  
Trans. of the North Am. Wildlife & Natural Resources Conf.  
Proc. of the Southeastern Association of Game & Fish Comm.  
Publications of the Marine Science Institute of Texas  
Quarterly Journal of the Florida Academy of Science  
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Special Scientific Reports-Wildlife (USFW)

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APPENDIX C: SELECTED REFERENCES ON NATURALIZED AND INTRODUCED  
AQUATIC AND MARSH ANGIOSPERMS IN NORTH AMERICA

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