

VEGETATIVE MORPHOLOGY AND MERISTEM DEPENDENCE — THE FOUNDATION OF PRODUCTIVITY IN SEAGRASSES

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ABSTRACT

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Shoot organization in seagrasses varies from the unspecialized condition of *Enhalus* and *Posidonia* to the highly differentiated shoot systems of plants like *Halophila*, *Thalassodendron* and *Thalassia*. In the former type proliferation of vegetative meristems seems to be an unordered process, whereas in the latter type proliferation can be very ordered. In some examples, e.g. *Syringodium*, proliferation of rhizomes is not regularized in shoot organization but is largely a consequence of perturbation by the environment. Since production of new organs and proliferation of indeterminate shoot systems is dependent entirely on continually active meristems, with either a limited tendency to form resting meristems or often no such ability at all, seagrasses show a high degree of meristem dependency.

INTRODUCTION

Seagrasses in natural habitats persist to a large extent by vegetative growth. In some species flowering, the production of seeds and their subsequent dispersal and establishment may be common, but even under these circumstances seagrass meadows are built largely by extension and branching of rhizomes. The need for investigation of general morphology as the foundation for productivity studies is clear. Familiarity with the growth habit of seagrasses will demonstrate a condition which may be described as “meristem dependence” i.e. the need for continually active shoot apical meristems to maintain populations. Dormant or otherwise inactive but persistent vegetative meristems are absent from many seagrasses so that “meristem dependence” is for them complete. Some species do seem to develop winter-dormant terminal shoot meristems in seasonal climates (e.g. *Zostera* spp.) from which renewal growth begins each spring. Most seagrasses, however, show no evident dormancy although growth may be slowed in winter. Of more significance is the extent to which rhizomes can proliferate i.e. multiply from

existing meristems, dormant or otherwise.

Meristems are the original source of biomass. Productivity studies should logically begin with them and particularly should be concerned with how they proliferate.

Despite this, knowledge of branching habit of seagrasses is very incomplete. In part this is because descriptive morphology is neglected (even spurned) by botanists but also because material in sufficiently large quantities to permit the necessary investigations can be obtained only by wading or swimming. Herbarium specimens are always too fragmentary and are too poorly preserved in the dried state to permit detailed study. They often represent flotsam. The recent tendency is to rely on older descriptions without re-investigation by modern methods. For example, the excellent description of *Cymodocea nodosa* by Bornet (1864) has in itself almost become a "type specimen" and his illustrations have been reproduced and copied many times even though this seagrass is relatively accessible to European botanists.

My interest in seagrass morphology arose largely from an appreciation that in an area where turtle grass (*Thalassia testudinum*) was receiving increased and detailed attention there initially existed no accurate description of the morphology of the species, or its method of branching. Currently *Thalassia*, *Syringodium* and *Zostera* have been investigated in reasonable microscopic detail, but information for other genera is still quite limited or even completely absent. This article, therefore, simply summarizes existing knowledge and is based on a relatively superficial examination of most genera by dissection, together with a survey of the literature. The approach is preliminary but is useful in drawing attention to areas where detailed investigations are needed. The incompleteness of our understanding must at all times be emphasized.

CRITERIA USED

Certain parameters of growth and morphology which are used in categorizing seagrasses should be emphasized. A distinction is made between *monomorphic* species (i.e. species with shoots bearing only one kind of leaf, foliage leaves) and *dimorphic* species (i.e. species with two types of shoot which bear either scale leaves or foliage leaves, respectively). In the more highly organized species the morphological difference between these two types of shoot is absolute. In addition to this distinction based on leaf type alone there can be a distinction based on the direction of growth such that axes may be *horizontal* or *erect*. Furthermore, branching may be either *sympodial* or *monopodial*. The sequence of branching may be *continuous* (i.e. a branch at every node), *diffuse* (i.e. branches produced at irregular intervals), or *periodic* (i.e. branches produced at regular intervals). It is important to emphasize that production of lateral *meristems* may be sequentially different from their development as branches, meristems produced continuously may lead to diffuse branching. Axes may have consistently either long or short internodes (often leading to

a distinction between *long shoots* and *short shoots*) or there may be an alternation between series of long and short internodes along a single axis which in some instances seems to be seasonal. Shoot systems may be highly organized (e.g. *Thalassia* and *Halophila*) with the growth habit well programmed, with clear-cut differentiation between types of axis and a precise branching pattern; otherwise the habit may be little organized, branch differentiation obscure and branching imprecise (e.g. *Halodule*, *Posidonia* and *Enhalus*). Other less significant criteria are the position of flowers and roots, and whether roots are branched or not. Leaf arrangement is typically distichous in all species and right-handed and left-handed symmetries may be pronounced. Leaf arrangement in *Halophila* is a modified distichy.

OUTLINE

The following dichotomous key conveniently summarizes the types of sea-grass habit; it is intended for purposes of comparison, not identification.

1. Shoots monomorphic; axes all alike, bearing essentially only foliage leaves. (The first leaves on a shoot are typically scale-like under any circumstances.)
 2. Axes all approximately horizontal and equivalent, without specialized erect leafy shoots; vegetative branching diffuse; inflorescences on specialized lateral shoots.
 3. Inflorescences in every alternate leaf axis; roots unbranched. *Enhalus* p.108.
 3. Inflorescences irregularly produced; roots branched. *Posidonia* p.109.
2. Axes not all equivalent, differentiated into major (perennial) horizontal and minor (annual) erect shoots; both bearing foliage leaves; vegetative branching usually diffuse.
 4. Erect axes produced by diffuse branching, commonly annual, elongated and usually well differentiated from horizontal axes. Ultimate flower clusters conspicuous, spike-like, forming sympodia terminating erect shoots. Roots unbranched.
 5. Horizontal axes elongated, monopodial (?) *Zostera* p.109.
 5. Horizontal axes elongated, sympodial *Heterozostera* p.110.
 5. Horizontal axes congested, monopodial *Phyllospadix* p.110.
4. Erect axes either produced by continuous branching, or often not well differentiated from horizontal axes; not evidently annual. Flowers in terminal pairs, inconspicuous.
 6. Differentiation between long and short shoots, or contrasted regions with either long or short internodes usually clear-cut; roots branched. *Cymodocea* p.112.
 6. Differentiation between long and short shoots, or regions of long and short internodes not clear-cut; roots unbranched. *Halodule* p.114.
1. Shoots dimorphic; some axes scale-bearing (horizontal); other axes actually

- or apparently (*Halophila* section *Halophila*) foliage bearing (approximately erect).
7. Scale-bearing rhizome sympodial, erect shoots long (to 20 cm or more) morphologically distinct from horizontal shoots.
 8. Branching of scale-bearing rhizome diffuse, with 2–7 or more intervening branch-free nodes. *Amphibolis* p.114.
 8. Branching of scale-bearing rhizome periodic from every fourth node. *Thalassodendron* p.116
 7. Scale-bearing rhizome monopodial, erect shoots long or short.
 9. Branching continuous:
 10. Internodes on rhizomes uniformly long, erect shoots variable, often determinate; flowers in terminal cymose inflorescences. *Syringodium* p.118.
 10. Internodes on rhizomes alternately long and short (scale leaves in subopposite pairs); erect shoots either actually determinate, or apparently determinate (section *Halophila*) by suppression; flowers solitary. *Halophila* p.120.
 9. Branching periodic always to produce indeterminate axes (short shoots) at regular intervals separated by 9–13 nodes, flowers in lateral groups. *Thalassia* p.122.

This layout presents information which shows a progressive increase in organization and specialization of the vegetative system but this should not be construed as an evolutionary sequence. What is perhaps more significant is that the sequence represents an apparent decrease in the plasticity of the organism, which may be of ecological significance. The key to a large extent groups genera of close taxonomic affinity but in part does not (e.g. *Enhalus* is separated from the two other hydrocharitaceous genera reflecting the morphological diversity within its family). The close juxtaposition of *Enhalus* and *Posidonia*, which are quite unrelated, suggests parallel evolution.

In the following account only selected references are cited. The monograph by Den Hartog (1970) has been referred to continuously and is not cited except for details. Genera are described in the same order as they appear in the key.

Enhalus (not investigated in detail, but see Cunnington, 1912; Svedelius, 1904; Troll, 1931)

Vegetative axes monomorphic, branching monopodially, represented by a horizontal rhizome bearing erect foliage leaves; older parts clothed with persistent fibrous remains of foliage leaves. Rhizome dorsiventral with lateral meristems produced in axil of every other leaf on upper side and developing into determinate inflorescences (Troll, 1931). Vegetative branching diffuse and irregular to produce indeterminate leafy shoots with short internodes which repeat the construction of the parent rhizome. Roots unbranched (Fig.10a).

There is no detailed information about vegetative branching in *Enhalus* which seems irregular and infrequent, nor is there any indication of the site of origin of vegetative lateral meristems. Roots apparently originate close to active shoot meristems. There is no indication of the existence of dormant vegetative meristems.

The description of Troll (1931) is the most complete account but refers largely to the biology of flowering.

Posidonia (not investigated in detail, but see Grenier, 1869; Ostenfeld, 1916; Weber, 1956; the following account refers to *P. oceanica*)

Vegetative axes monomorphic, monopodial, represented by a horizontal rhizome bearing erect foliage leaves; older parts densely clothed by persistent fibrous remains of foliage leaves. Rhizome flattened; branching diffuse, from meristems produced in axils of leaf at irregular intervals, usually with long series of empty leaves alternating with a series of branch-bearing leaves. Meristem either growing out precociously, to produce a branch which repeats the construction of the parent axis, or commonly aborted (or inhibited) and persisting as a potentially dormant meristem. Precocious branch usually equal in size to parent axis and often simulating a dichotomy. Inflorescence apparently axillary but produced infrequently. Roots developed irregularly, not obviously associated with nodes; branched (Fig.1 and 10a).

Posidonia oceanica, despite its abundance, has not been investigated very thoroughly. Vegetative branches are produced at irregular intervals from axillary meristems, the intervening nodes being without axillary meristems. Commonly meristems, though initiated, remain suppressed. It is not known if such meristems can function as "reserve buds" i.e. can regenerate a new branch belatedly. Examination of rhizome systems does not suggest this function.

Posidonia ostenfeldii, from its description by Den Hartog (1970), is distinctive in having rhizomes with alternating series of long and short internodes. *Posidonia australis* can also have long internodes, as illustrated by Den Hartog (1970). Ostenfeld (1916) describes this species as having short erect shoots with densely arranged leaves in the axil of each leaf on the rhizome, suggesting a dimorphic condition. There seems to be no information about vegetative branching in these two Australian species and existing accounts of their vegetative morphology seem to be very incomplete.

Zostera (Setchell, 1929; Setchell, 1933; most descriptions refer mainly to *Z. marina*, as does the following)

Vegetative axes essentially monomorphic i.e. all bearing foliage leaves, but with differentiation between (a) horizontal, indeterminate rhizomes and (b) erect, short-lived (usually annual) axes with determinate growth. Erect axes either unbranched or branched sympodially when flowering. Rhizome branching monopodially, with a meristem associated with each leaf; branches

producing new rhizomes developing diffusely. Roots in two clusters at each node, unbranched (Fig.2a–d; Fig.10b).

Horizontal axes in *Zostera marina* branch monopodially*, with each leaf subtending an axillary meristem which is initiated within the third or fourth plastochrone. The meristem becomes separated from the node at which it is initiated by intercalary growth and so comes to occupy a leaf-opposed position immediately below the node above (Fig.2c). Further development of the meristems varies. Some abort, others may be inhibited and possibly function as reserve meristems (Fig.2d), although this function remains undocumented. Meristems otherwise develop either as erect leafy shoots which may be annual and on which the flowers are borne (Fig.2a), or as rhizomes which repeat the construction of the parent axis and so bring about proliferation of the perennial system (Fig.2b). The mechanism for this selective differentiation is not known and its frequency seems not to have been reported in detail.

Other species of *Zostera* so far examined are similar in their morphology. Den Hartog (1970) records *Z. caespitosa* as having a “sub-erect” rhizome with short internodes.

Heterozostera (not investigated in detail, see Setchell, 1933)

Vegetative axes essentially monomorphic i.e. all bearing foliage leaves but with a marked differentiation between horizontal (rhizomatous) and erect shoots. Rhizomes with elongated internodes, branching sympodially and apparently diffusely to produce erect leafy shoots at irregular intervals; many rhizome nodes not supporting erect shoots. Erect shoots unbranched when vegetative, branching sympodially when reproductive; ephemeral and shed in winter. Roots in pairs at each node, unbranched.

I have seen no material of this species; the above account is taken largely from the description by Den Hartog (1970). *Heterozostera* is unusual in the family Zosteraceae in having a sympodial and not a monopodial rhizome. From available literature there is no indication of how new rhizomes are originated; detailed anatomical information would be helpful.

Phyllospadix (not investigated in detail, but see Dudley, 1893)

Vegetative axes monomorphic and all bearing foliage leaves but with a sharp differentiation between horizontal and erect shoots. Branching continuous and monopodial to produce either (a) erect flower-bearing shoots, leafy below and branched sympodially above or (b) new leafy rhizomes. Roots either in pairs or in clusters forming two rows on each internode of the rhizome. Roots apparently unbranched, short and usually adpressed to the rocky substrate.

I have seen insufficient material to describe this genus adequately. The above account refers to *Phyllospadix torreyi*, and is based on an examination of fluid-preserved material and from the description by Dudley, 1893. It is evident that the creeping axes branch monopodially, each foliage leaf sub-

*A sympodium is suggested where the rhizome apex is determinate by flowering.

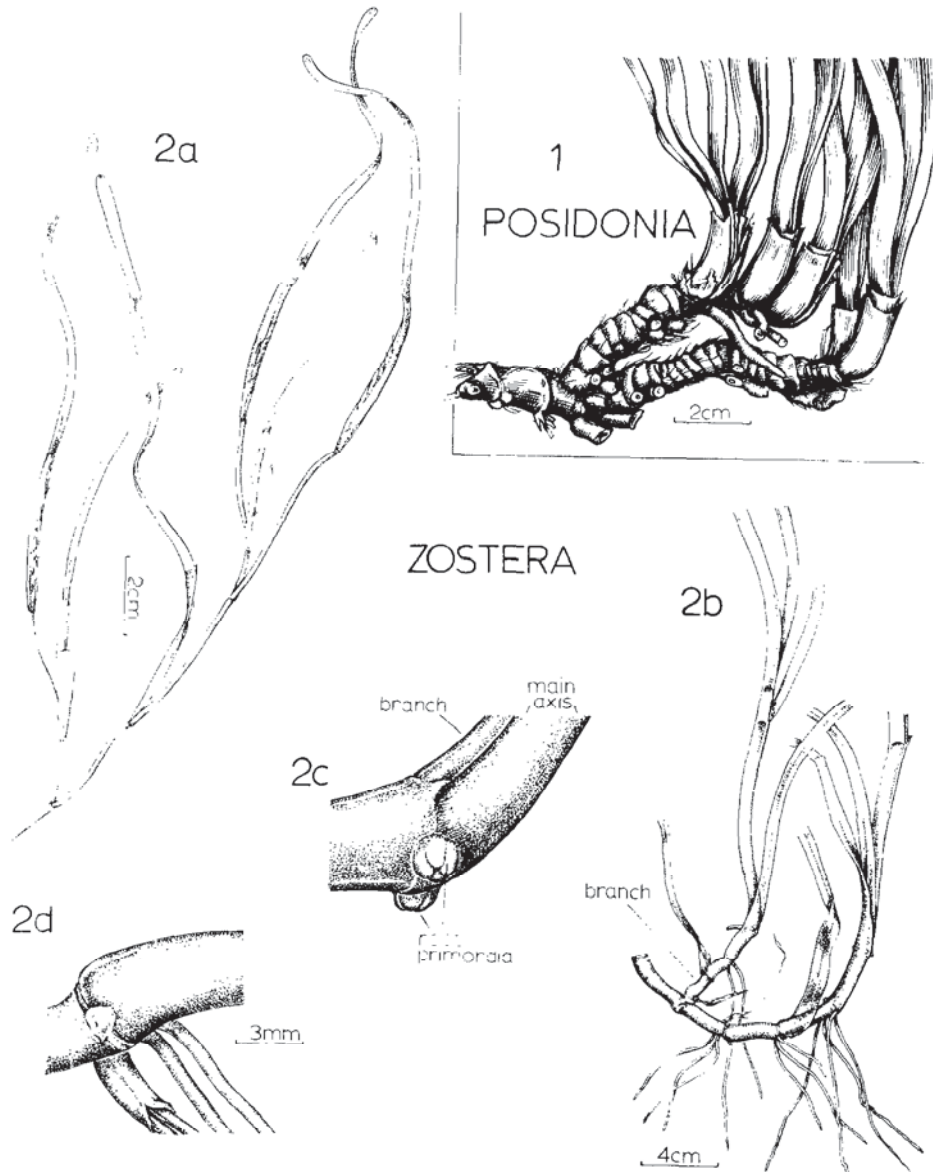


Fig.1. *Posidonia oceanica*. Habit of a small portion of plant with branched rhizome (complete leaf blades not shown).

Fig.2. *Zostera marina*. (a) Distal part of erect shoot (sympodially branched) with inflorescences. (b) Basal, rhizomatous part of rhizome with foliage leaves (drawn incompletely) and a branch. (c) Detail of attachment of adnate branch. (d) Node with aborted or inhibited bud.

tending an axillary bud. By subsequent intercalary growth this bud becomes separated from its subtending leaf in such a way that it appears to be inserted immediately below and opposed to the next most distal leaf. Branches are initially leafy; many have a determinate development and extend into a sympodially branched flower-bearing axis of limited life span. Other branches are indeterminate and initiate new long-lived rhizomes. The circumstances which determine these alternative modes of development are not certain. It is possible that lateral meristems may remain in an inhibited state and function as resting buds.

In its essential construction *Phyllospadix torreyi* is identical with *Zostera marina*, but distinguished by its congested rhizomes. No detailed information is available for the Alaskan and Japanese species of *Phyllospadix*.

Cymodocea (the following description refers entirely to *C. nodosa*; see also Bornet, 1864; Sauvageau, 1891)

Vegetative axes monomorphic i.e. all bearing foliage leaves, but with some differentiation between horizontal long shoots (rhizomes) and erect short shoots. Seasonal periodicity of growth largely conditioning shoot morphology. Rhizomes in early, vigorous period of growth each season developing long internodes, branching monopodially and more or less continuously with each foliage leaf subtending a lateral meristem; rhizomes in late season less vigorous, producing short internodes and remaining unbranched. Branch meristems of rhizome developing in three possible ways, either (a) becoming new units of the rhizome (long shoots) or (b) becoming short shoots of indeterminate growth or (c) becoming short shoots of determinate growth ending in a terminal flower but further development via lateral meristems possible by sympodial branching below the terminal flower. Roots usually solitary at each node (in pairs in seedling axis) and normally only developed on axes with long internodes; where roots develop on short shoots they are slender. Roots branched (Fig.3a and b; Fig.10c).

Cymodocea nodosa, according to the careful and beautifully illustrated account by Bornet (1864) shows a clear morphological differentiation of its axes which relates directly to the seasonality of its growth. Essentially the axis is a leafy rhizome (long shoot) which branches monopodially (Fig.3a), each lateral meristem becoming an erect short shoot which may terminate in flowers. This basic construction is modified because the terminal meristem grows seasonally, being more or less dormant in winter, at which time most of the older leaves are lost. In the transition to the dormant state (Fig.3b), the rhizome directly develops as a short shoot, producing short internodes, few or no roots and no branches. Re-growth the following year re-instates the long-shoot condition. Annual increments of growth can thus be determined by this alternation of long-shoot and short-shoot cycles. Since horizontal axes do not maintain a constant morphology a marked segregation between horizontal and erect shoots is not maintained. Organization is further lost because of the evident tendency of lateral shoots, which are initiated as short shoots,

to revert to the long-shoot (rhizome) condition. This, together with direct development of lateral meristems into rhizomes accounts for the proliferation of rhizomes.

The remaining species of *Cymodocea* (*C. angustata*, *C. rotundata* and *C. serrulata*) have not been investigated in detail and I have had no material for detailed study. Existing descriptions (e.g. Den Hartog, 1970) suggest that they have the essential construction of *C. nodosa*. In view of their more tropical distribution, however, their morphology may be less conditioned by a seasonal pattern of growth. Detailed investigation of these species is much to be desired.

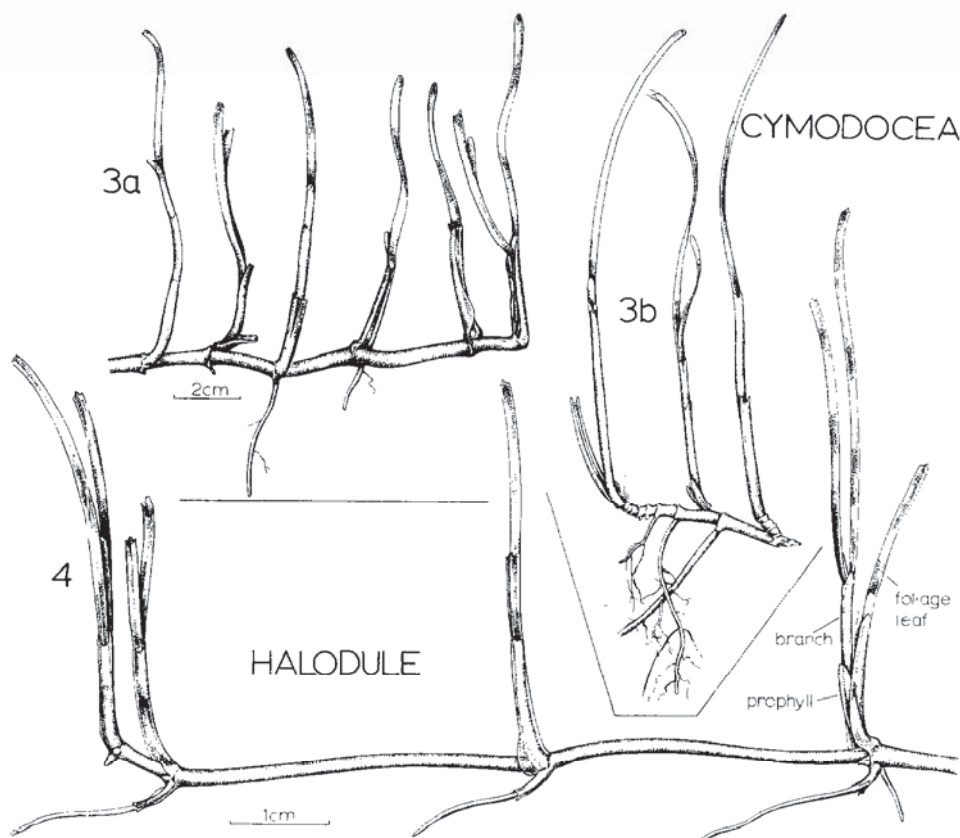


Fig. 3. *Cymodocea nodosa*. (a) Terminal part of rhizome with long internodes, each foliage leaf subtending a branch. (b) Part of rhizome with segments including series of short internodes.

Fig. 4. *Halodule beaudettei*. Terminal part of rhizome with long internodes, each foliage leaf subtending a branch.

Halodule (see Den Hartog, 1970)

Vegetative axes monomorphic, all bearing foliage leaves but with some differentiation between (a) long shoots (rhizomes) (internodes up to 5 cm long) with roots, continuous vegetative branching, flowers uncommon and (b) short shoots (internodes usually c. 1 mm) with or without roots, branching uncommon, flowers common. Short shoots sometimes held erect but this positional difference never very pronounced. Long shoots branching continuously, each leaf subtending a meristem which may grow out as a short-shoot branch, less commonly as a long-shoot branch. Flowers terminal on lateral branches, which continue to develop by sympodial growth. Roots one to five at each node on long shoots, often absent from short shoots; roots unbranched (Fig.4 and 10c).

Halodule varies widely in its growth habit, even within a single population. The above account provides a generic description without any attempt to distinguish between the seven closely related species. I have examined fluid-preserved collections from two widely separated geographical localities which probably represent *H. beaudettei*, *H. wrightii* (South Florida) and *H. pinifolia* (Fiji). Despite its considerable quantitative variation *Halodule* has a very constant architecture. All shoots bear foliage leaves and on the main axes each leaf subtends an axillary meristem (Fig.4). Where there is clear differentiation between long and short shoots, the laterals become short shoots which remain more or less unbranched, presumably by abortion of lateral meristems. Frequently this differentiation is obscured so that either a lateral meristem will become a long shoot directly, or a branch, after some period of growth as a short shoot, will develop into a long shoot. Both these methods proliferate the rhizome system.

Under certain circumstances short shoots branch, their laterals being either long or short shoots. Under the latter circumstances a cluster of more or less erect short shoots can develop. This habit may, in part, be pathological in relation to infection by *Plasmodiophora diplantherae* (Den Hartog, 1970). Terminal flowers usually occur on short shoots, but are not uncommon on long shoots. They induce sympodial branching of the axis from a meristem in the axil of the second leaf below the flower.

In its general habit *Halodule* resembles *Cymodocea nodosa* (Fig.10c) but differs in that the periodicity of long versus short shoots is either not present or is expressed irregularly. This in part reflects the non-seasonal environment in which the pantropical *Halodule* grows. *Halodule* apparently lacks any resting or reserve buds.

Amphibolis (see Sauvageau, 1891; Ostenfeld, 1916)

Vegetative axes dimorphic with sharp segregation between (a) horizontal creeping rhizomes, bearing scale leaves and roots and (b) erect shoots bearing foliage leaves (Fig.5c) and lacking roots except in their basal parts. Rhizomes branching diffusely and sympodially by eviction of a terminal bud which

becomes a leafy shoot, a lateral branch functioning as a renewal shoot. Erect shoots branching monopodially and also diffusely, the branches becoming either further leafy shoots or flowers. Proliferation of rhizome by development of a second-order renewal shoot from the base of a first-order erect shoot. Roots singly (less commonly in pairs) at each rhizome node, always towards the dorsal side of a scale leaf; roots branched (Fig.5a and b; Fig.10d).

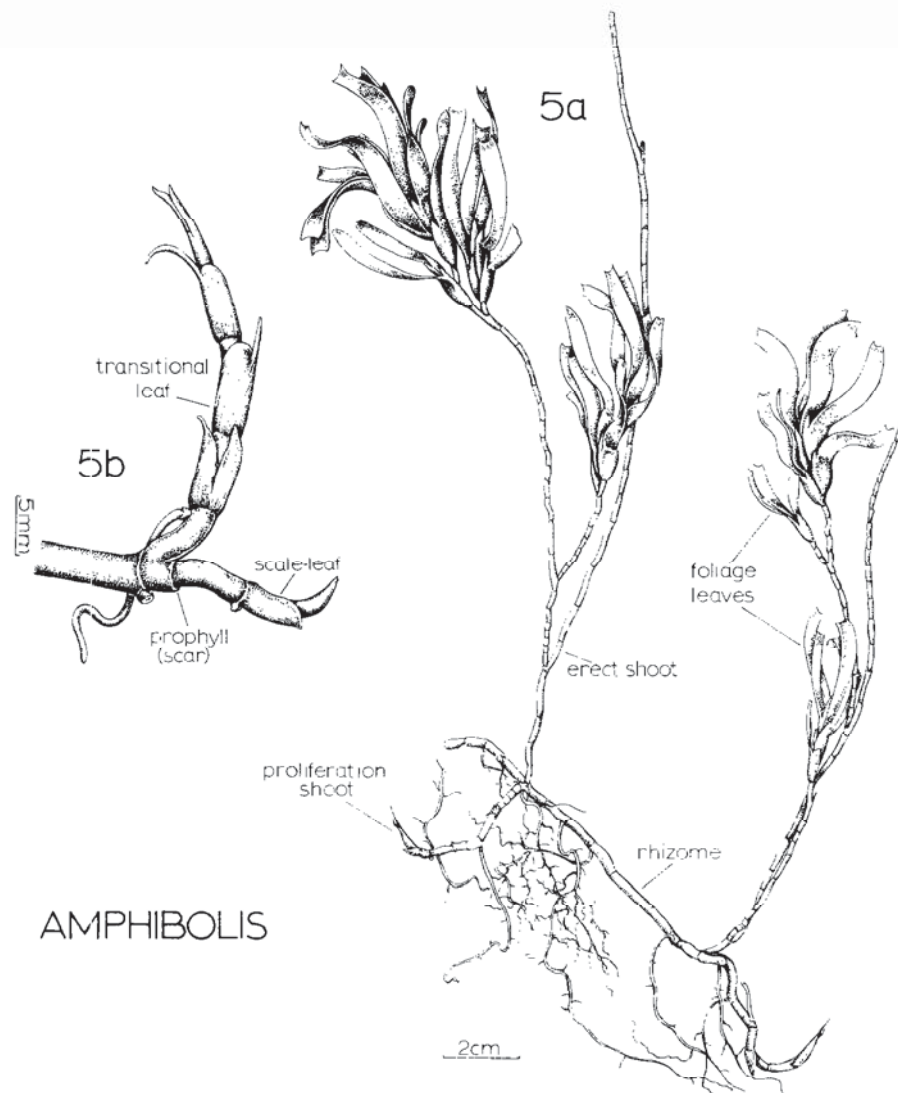


Fig.5. *Amphibolis antarctica*. (a) Habit showing shoot dimorphism, branch rhizome (proliferation shoot) at base of erect shoot to left. (b) Details of sympodial rhizome branch, lateral branch to right; terminal shoot erected, bearing leaves transitional to foliage leaves.

This account is based largely on the investigation of limited material of *Amphibolis antarctica*, in part examined microscopically. Both erect (leafy) and horizontal (rhizome) shoots have the same basic organization. Microscopic examination suggests that each leaf subtends a single lateral meristem but most of these abort and there may be very little vestige of them at the mature node. Branching of the rhizome is diffuse with a series (usually three to seven) of branch-free nodes between each successive branch (Fig. 5a). The terminal bud grows erect, to become a leafy shoot and its displacement is associated with the development of a single lateral meristem, which becomes the renewal bud for the next segment of the scale-bearing rhizome. This sympodial growth is readily recognized because the lateral bud has a basal prophyll inserted a short distance (c. 1 mm) along the renewal shoot (Fig. 5b). The lateral branch can thus always be identified by the scar of this prophyll. Prophylls themselves do not subtend buds. The arrangement of leafy scars at levels of branching is clearly evident in the illustrations included in Den Hartog (1970).

The evicted erect leafy shoot normally branches one or more times near its base, at levels where it still produces either scale or transitional leaves. Commonly there is a branch at its first node which is immediately sympodial, such that a further renewal bud is formed, developing as a second rhizome segment. Ostenfeld suggests that a second renewal bud may be developed directly on the parent rhizome, but I have not seen this. Proliferation of the rhizome system is thus accountable. Further diffuse branches are developed along the erect shoot at irregular and usually distant intervals; this branching is always monopodial and the branch may be somewhat adnate to the parent main axis.

The overall result is a sympodial rhizome system producing erect branched leafy shoots at intervals, with proliferation of the rhizome commonly occurring as a second-order branch on a first-order erect shoot. Sympodial branching both maintains and increases the number of rhizomes. Resting buds apparently are not formed. *Amphibolis* is comparable to *Thalassodendron* but lacks the precise organization of the latter genus. It tends to have the same vertical distichy, but less precisely so and without the same adaptive significance.

Amphibolis griffithii has not been described in detail, but the illustrations by Den Hartog (1970) suggest the same construction.

Thalassodendron (see Sauvageau, 1891)

Vegetative axes dimorphic, with a sharp segregation between (a) creeping rhizomes bearing scale leaves and roots and (b) erect, sparsely branched axes bearing foliage leaves and no roots. Branching of rhizome periodic and sympodial, producing an erect axis at each fourth internode and commonly a resting bud at the first node of the erect shoot, from which rhizome proliferation may occur. Erect axes branching monopodially, diffusely and infrequently to produce further leafy shoots, more commonly to produce flowers. Roots restricted to regions of rhizome branch, usually two to five on the lower surface; roots branched (Fig. 6 a and b; Fig. 10c).

The above account is largely based on examination of limited material of *Thalassodendron ciliatum* of which no rhizome apices have been available for microscopic study; it largely confirms earlier descriptions. *Thalassodendron* shows a high degree of vegetative organization with a precise and fixed system of rhizome branching. This is related to the unusual scale-leaf insertion, with the plane of distichy vertical and not horizontal as in most other seagrasses (but cf. *Amphibolis*). Consequently leaves on the rhizome are inserted alternately on upper and lower surfaces. In older rhizomes the ventral side of the leaf scar is usually recognizable by means of the discontinuity marking where the leaf margins did not quite meet and this is useful in establishing planes of symmetry. Every fourth leaf subtends a bud which develops precociously to become a further unit of the rhizome sympodium, displacing the terminal bud of the previous unit which becomes an erect, leafy shoot (Fig. 6a). The displacement is carried out in such a way that each leafy shoot appears to be inserted at the middle of each fourth rhizome internode (Fig. 6b). By virtue of the regularity of branching from the axil of a leaf morphologically inserted on the lower surface of the rhizome, eviction always displaces the erect axis into the desired vertical position. The leaf at the base

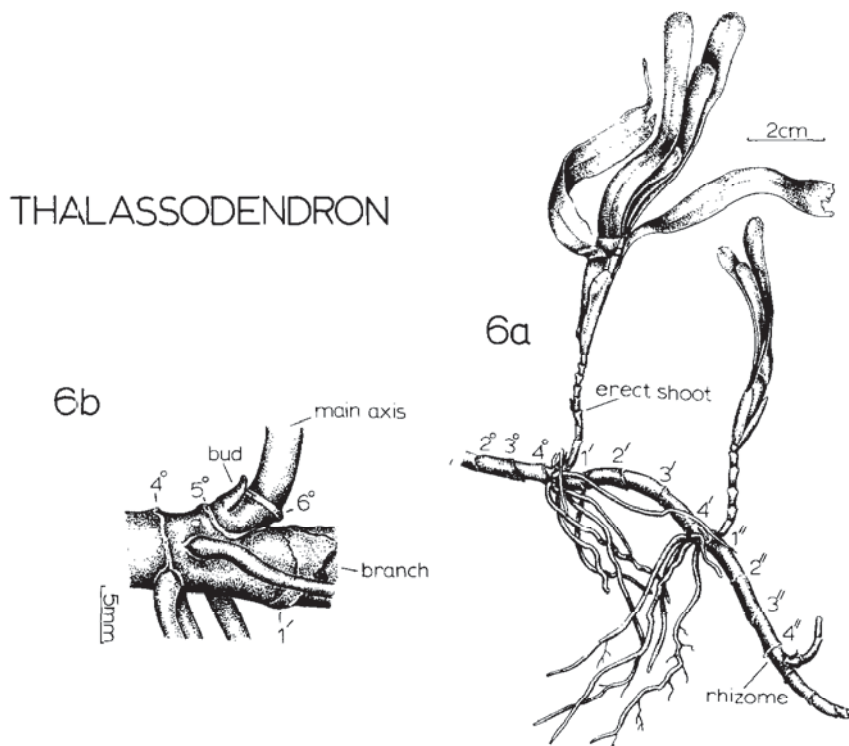


Fig. 6. *Thalassodendron ciliatum*. (a) Habit showing shoot dimorphism, scale leaves 1—4 numbered on each unit of the sympodium. (b) Details of sympodial rhizome branching, lateral branch to the right, main axis erected; undeveloped bud in axil of leaf 5.

of the erect axis often subtends a meristem which may grow out as a further erect leafy shoot; otherwise it remains partially suppressed, presumably as a "reserve bud" (Fig.6b). No examples of branched (i.e. proliferated) rhizomes have been seen or described, but it is reasonable to assume that it is from such a reserve bud that a new branch rhizome is initiated, but under what circumstances remains to be investigated. The supposition is further made reasonable because it is from a meristem in the equivalent position that the much less well organized rhizome of *Amphibolis* proliferates.

From limited microscopic examination of erect shoots it seems that each foliage leaf subtends an axillary meristem. Most of these abort but they are capable of developing into either further leafy shoots, or flowers.

No material of *T. pachyrhizum* has been examined, but the description and illustration by Den Hartog (1970) suggest that it has a precise organization identical with *T. ciliatum*.

Syringodium (see Sauvageau, 1891; Ostenfeld, 1916)

Vegetative axes dimorphic. Symmetry of shoots in terms of leaf arrangement quite precise, but not described further. Shoots differentiated as (a) horizontal rhizome, bearing exclusively scale leaves separated by long internodes; scale leaves ephemeral (but shrivelling rather than abscising); branching monopodially (Fig.7c) at each node to produce (b) a more or less erect foliage-bearing shoot, usually with short internodes; foliage leaves eventually deciduous and abscising cleanly. Roots restricted to rhizome nodes, usually three and always initiated within terminal meristem; roots infrequent on short shoots. Short shoots essentially indeterminate but commonly determinate by conversion of the terminal meristem into a cymose inflorescence, similar inflorescences also developed as lateral shoots on the short shoots. Dormant meristems not produced. Proliferation of rhizomes by irregular modification of lateral short shoots, as described below (Fig.7a—c; Fig.10f).

This account is based on the incomplete unpublished investigation of *S. filiforme*; *S. isoetifolium* seems similar, but has not been described in detail.

In the above outline description of the vegetative morphology of *Syringodium*, there is no indication of an ordered mechanism whereby the rhizome proliferates, in its monopodial branching it normally produces only leafy lateral shoots (Fig.7a and b). Examination of a population of this plant shows that branching does occur in a number of ways, some of which produces new rhizomes. This propagation is not regular and indeed it is clear that in many cases branching is stimulated by destruction of an existing rhizome apex. In such instances there is replacement of a dead by a living rhizome, with renewal rather than proliferation of rhizome apices.

A short shoot directly may become converted into a long shoot. This process can occur early or late in the development of the short shoot, normally it is late such that there is a succession of close leaf scars, typical of those on a short shoot before the conversion occurs. Examples have been seen where the short shoot may revert to the scale leaf bearing characteristics

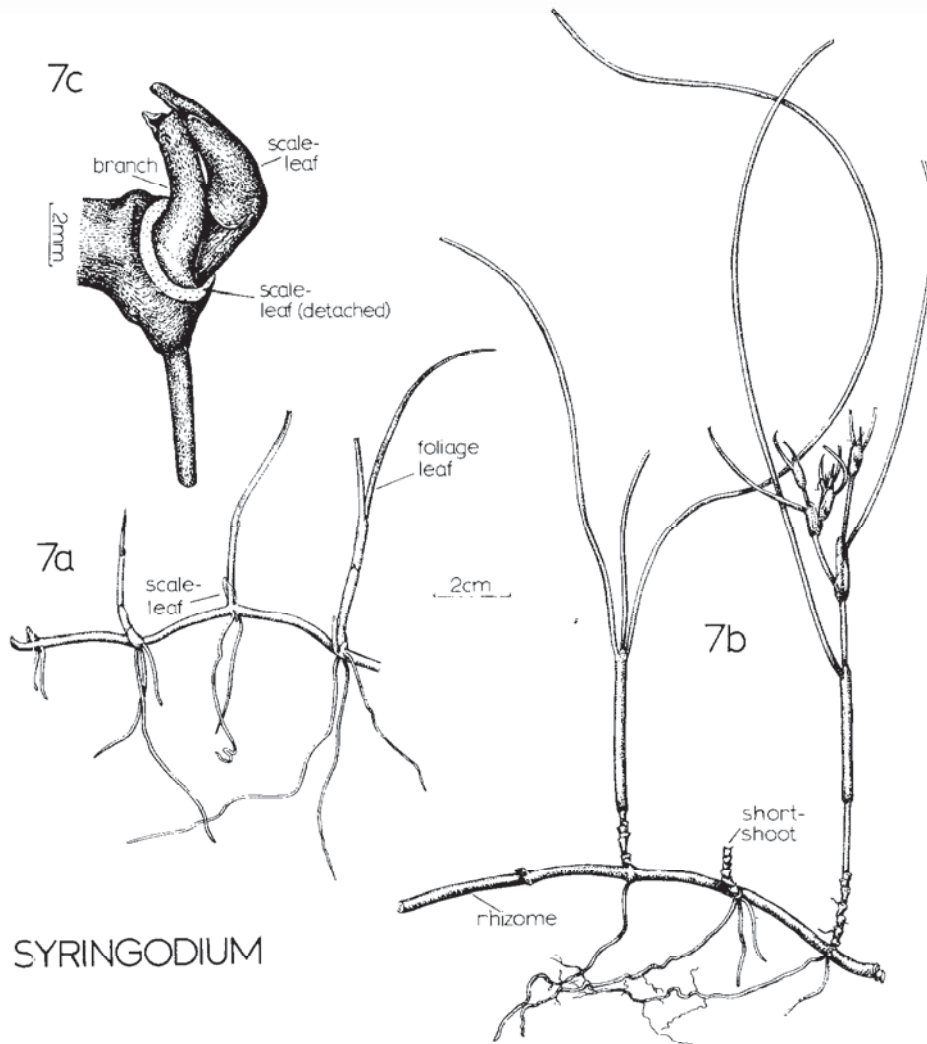


Fig.7. *Syringodium filiforme*. (a) Terminal part of rhizome with scale leaves each subtending a lateral, erect shoot. (b) Proximal, older part of rhizome to show shoot dimorphism. (c) Details of rhizome apex; branch (largely represented by its prophyll) in axil of a scale leaf which has been detached, next younger scale leaf enveloping apex is shown.

of a long shoot after producing only one foliage leaf. Such an example gives the appearance of a rhizome branching to produce a rhizome directly. It seems, however, that this is not possible, all lateral meristems of the rhizome are programmed to become short shoots, but they can make the switch to a rhizome meristem quite early. This switch, in natural populations seems always the result of damage to the parent rhizome apex. Proliferation (as

distinct from substitution) of rhizome apices may well be a function of age at which the short shoot overcomes this apparent control of its morphology by the parent rhizome i.e. a short shoot would show an increasing tendency to revert to a rhizome the more distant it was from the parent rhizome, other things being equal.

The short shoot itself, however, has a considerable plasticity in its further development as follows. As a determinate shoot, it can be terminated by an inflorescence (Fig.7b). Otherwise, it may branch monopodially to produce either foliage-bearing shoots (further short shoots) or lateral inflorescences. The morphology and development of the short shoot is not very constant; internode length itself is very variable and one can sometimes find leafy shoots with successive series of long and short internodes. This hardly can be a consequence of a seasonal periodicity of growth, as in *Cymodocea nodosa*.

In conclusion, although knowledge of the developmental morphology of *Syringodium* is limited, it is clear that there is no ordered mechanism for producing new rhizomes from existing ones, lateral meristems produced by rhizomes are normally all specialized leafy shoots, their conversion into rhizomes occurs when they substitute a damaged rhizome apex or possibly when they reach a certain age.

Halophila (see Balfour, 1879; Den Hartog, 1957, Isaac, 1968)

Vegetative axes essentially dimorphic, but not always strictly so. All species with creeping rhizomes bearing subopposite pairs of scale leaves, successive pairs separated by a long internode. First scale of each pair on the lower surface of the rhizome associated with a single unbranched root but otherwise empty, second scale of each pair on the upper surface always subtending a lateral meristem which arises by more or less equal division of the shoot apex. Lateral meristem developing into a determinate or an indeterminate shoot. In section *Americanae* shoot determinate, producing a sub-basal pair of scale leaves not associated with a root and terminating in two to four pairs of foliage leaves but proliferating sympodially by a meristem, which can become a new rhizome, arising in association with one of the sub-basal scales. In section *Halophila* lateral meristems essentially indeterminate, with a basal pair of foliage leaves and subsequently capable of continuing growth as a scale-bearing rhizome; in other sections lateral meristems developing a determinate short shoot, branched only at the base. Flowers solitary in the axil of a basal foliage or scale leaf of a lateral shoot (Fig.8a-c; Fig.10g).

The above account is based on examination of fluid-preserved material of *Halophila engelmanni*, *H. decipiens* and *H. ovalis* (including subspecies *H. bullata*), together with published descriptions of which that by Balfour (1879) is much the most complete. *Halophila* is one of the most complex, diverse and yet highly organized seagrasses in its vegetative morphology so that the above brief account is necessarily very incomplete. In particular, no reference has been made to the very elegant symmetry of leaf arrangement, as described by Balfour such that a strict distichy is not maintained; instead

the symmetry of the shoot is repeated only at every second leaf cluster.

For gross morphological purposes, I have regarded the shoot as dimorphic although this is strictly true only for section *Americanae* of the genus (Fig.8c). (Section *Microhalophila* and *Spinulosae* seem to be similar but details are lacking.) Here there is a clear distinction between creeping, scale-bearing rhizomes and more or less erect leafy shoots of determinate growth. Proliferation of such rhizomes is, however, regular with a new shoot (rhizome) arising at the base of each leafy shoot. In section *Halophila* (Fig.8a and b) shoots are strictly monomorphic since each essentially has the same construction. Although in its gross morphology the plant appears to consist of a scale-bearing rhizome with lateral leafy shoots, in fact the lateral shoots are potentially all further rhizomes. Each consists of a basal pair of foliage leaves (an unusual condition for monocotyledons) with subsequent scale leaves

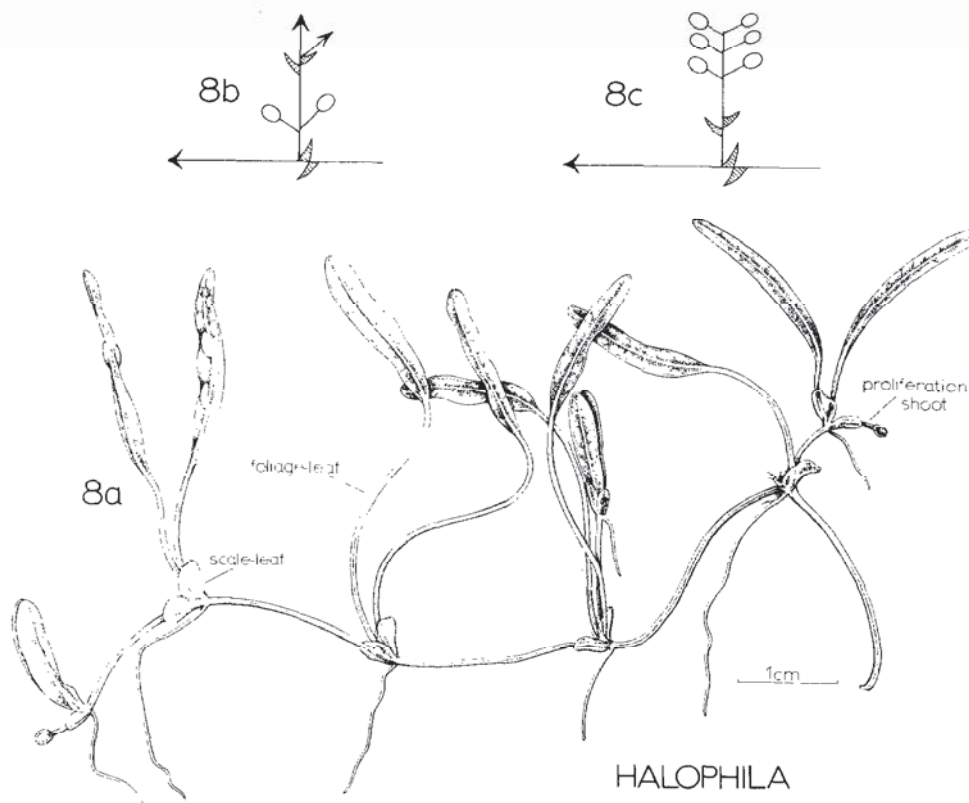


Fig.8. *Halophila*. (a) *H. decipiens*, habit with lateral shoots (oldest one developing as a proliferation shoot) in axil of each scale leaf. (b) Diagram of same species to show arrangement of parts at each node and origin of a proliferation shoot. (c) Diagram of e.g. *H. engelmanni* to show lateral branch developed as a determinate shoot.

(Fig.8b). Despite this indeterminate nature most lateral meristems either abort or remain suppressed after the production of the first leaf pair so that their true potential is not revealed and shoot dimorphism is simulated. Branching in all *Halophila* species is continuous in terms of meristem production, but the conditions under which the actual diffuse manner of proliferation is brought about is not obvious. It is clear that *Halophila* has the ability to produce dormant or at least resting meristems, but the part they play in regulation of rhizome populations is not known.

Thalassia (Tomlinson and Vargo, 1966; Tomlinson and Bailey, 1972)

The description refers to *Thalassia testudinum*; from the description by Pascasio and Santos (1930) *Th. hemprichii* seems to be identical.

Plant highly organized, vegetative axes dimorphic with an absolute distinction between (a) scale-bearing horizontal rhizomes or long shoots with large internodes and (b) foliage-bearing erect short shoots with short internodes. Branching monopodial, wholly within terminal meristems, without the production of dormant meristems. Branching of rhizome apices periodic, alternately left and right, with usually 9, 11 or 13 (always an odd number) of scale leaves separating successive branches. Lateral meristem on rhizome always becoming short shoot. Vegetative branching of short shoots at irregular intervals (diffuse) to produce always a rhizome. Flowers restricted to short shoots, sessile, one to eight in leaf axil (more male flowers than female per leaf axil). Roots developed only close to shoot meristems, unbranched. Growth continuous i.e. without evident dormancy but rate of growth fluctuating seasonally in climates with an appreciably cold winter (e.g. South Florida; Zieman, 1973) (Fig.9a and b; Fig.10h).

Thalassia is distinctive in its meristem proliferation; in the rhizome, meristems are initiated precociously, within one plastochrone of the apical meristem and they are leaf opposed. Terminal and lateral meristems develop equally so that for a period they are morphologically identical and the shoot appears to have dichotomized. This precocious branching, however, is characteristic of some other Hydrocharitaceae where a true dichotomy may exist (e.g. *Limnobium*; Wilder, 1974). In *Thalassia* differentiation of main and lateral axis occurs after about five plastochrones such that the branch meristem is displaced into a lateral position and becomes a short shoot (Fig.9a). The process is repeated at intervals of about 11 plastochrones so that the successive branches fall on opposite sides of the rhizome. Under these circumstances there is no branching of the rhizome directly. Proliferation to produce a new rhizome apex only occurs indirectly by branching of a short-shoot apex (Fig.9b). This branching is morphologically of the same kind as in the rhizome apex, but is infrequent and seemingly irregular, but as a function of the age of the short shoot.

This overall precise organization of the shoot system in *Thalassia* is invariable, with a complete and complex symmetry, as described by Tomlinson and

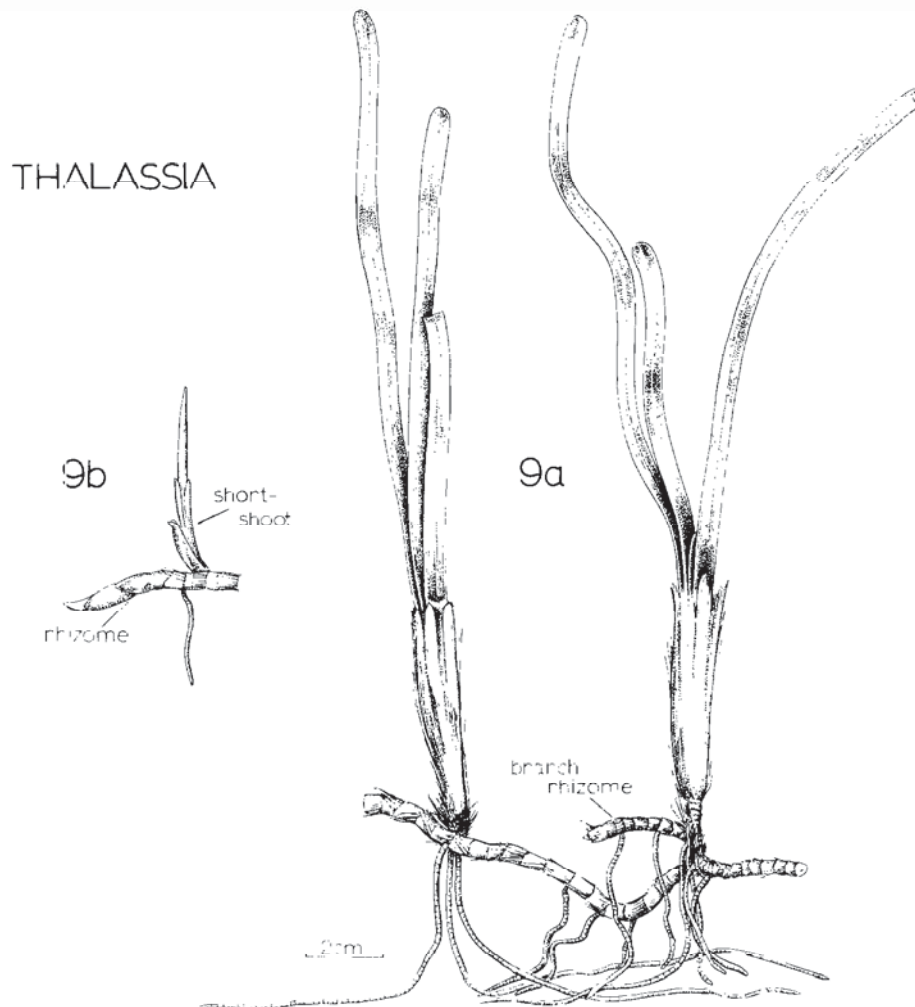
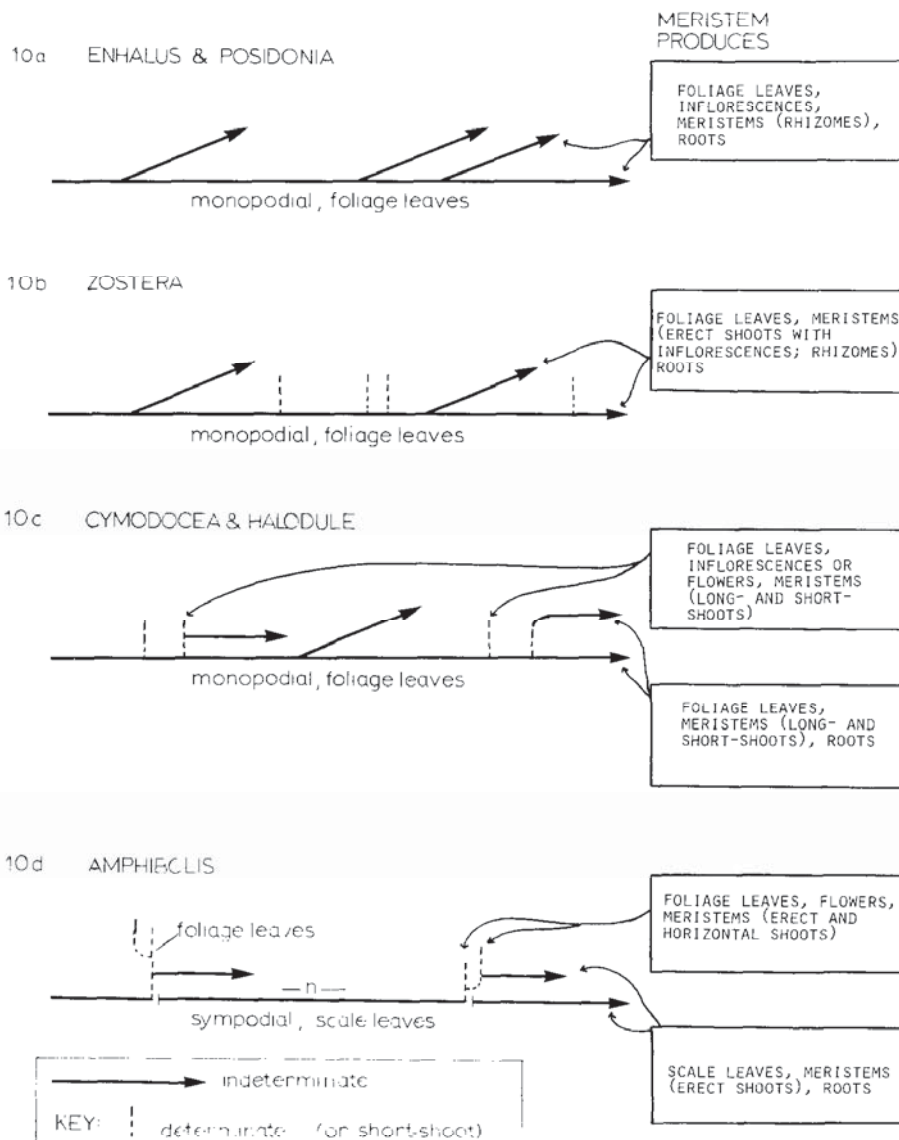


Fig.9. *Thalassia testudinum*. (a) Habit of older part of plant to show origin of a branch rhizome (proliferation shoot) from a short shoot. (b) Terminal part of rhizome to show origin of a short shoot as a lateral branch of a rhizome (see text).

Vargo (1966). *Thalassia* is efficient in exploiting its habitat because rhizome apices maintain a fixed depth within the substrate, re-adjusting this level as either sedimentation or erosion occurs. Branch rhizomes always arise at a higher level than the parent rhizome because of their position on an erect short shoot, re-adjustment of these branches to the appropriate substrate level is rapid.

Thalassia is completely meristem dependent since all organs, including roots and branch meristems are initiated within terminal meristems. Isolated fragments without meristems cannot be propagated because there is no mechanism for regeneration in such circumstances. No dormant meristems are produced and there are no specialized responses to wounding or damage. Multiplication of rhizomes is indirect and seemingly the least organized aspect of the morphology of the plant.



DISCUSSION

Branching of vegetative axes in seagrasses may be described as “regenerative” when it maintains the general form of the plant without leading to vegetative propagation, or “proliferative” when it increases the number of

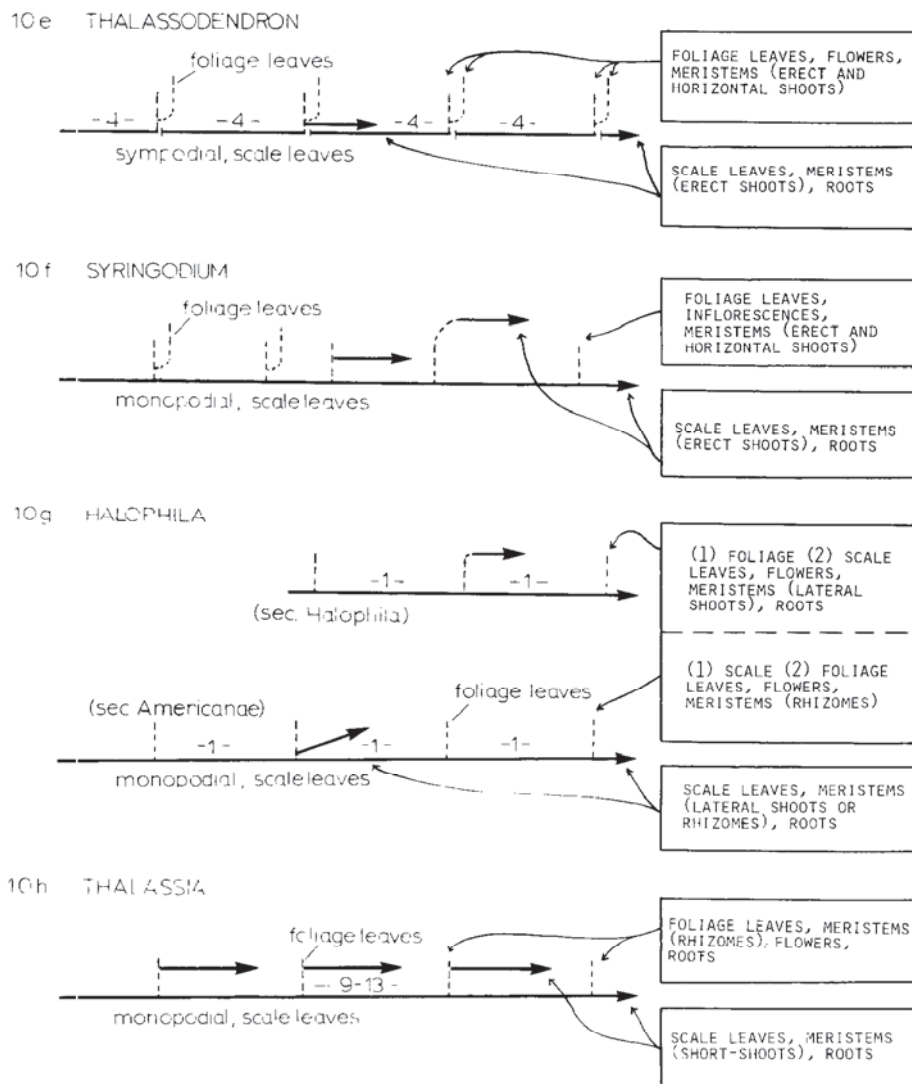


Fig.10. Seagrass habit and proliferation represented diagrammatically. Only essential features of morphology in relation to activity and branching meristems are indicated on a qualitative basis. No attempt is made to indicate the complete range of variation for each type. Further explanation in the text. (Note: the term “meristem” is meant to indicate a lateral shoot meristem whose potential for development is variable.)

indeterminate meristems and so leads to vegetative propagation. Most branching in seagrasses is of the regenerative kind. It is exemplified in the production of meristems which become branches of limited growth. Specialized lateral shoots may be relatively short-lived (e.g. in *Zostera*, *Cymodocea*, *Halodule* and *Syringodium*) or if they are long-lived, as in the highly organized short shoots of *Thalassia*, do not directly add new rhizome meristems. Sympodial branching of the rhizome of *Amphibolis* and *Thalassodendron* is of this regenerative type. Proliferative branching varies widely in seagrasses and may or may not be ordered.

If one looks at shoot organization of seagrasses in the simplest comparative terms, as is done in Fig.10, it is evident that progressive increase in organized growth actually leads to a decrease in the ability of the rhizome system to proliferate. In the simpler conditions, represented by *Enhalus* and *Posidonia* (Fig.10a), lateral axes repeat the construction of the parent axis, but their production is a seemingly irregular and ill-ordered process which is not at all predictable. In more organized systems like *Zostera*, *Cymodocea* and *Halodule* (Fig.10b and c) there is a clearer distinction between main and lateral axes in regenerative branching, but the production of proliferative shoots still remains irregular and without an immediately obvious pattern.

In the remaining genera of seagrasses, with the development of a more precise shoot dimorphism indicated by a clear-cut distinction between scale-bearing and foliage-bearing axes, proliferative branching becomes a more restricted, regular and usually predictable process. In *Amphibolis* and *Thalassodendron* (Fig.10d and e) new rhizomes seemingly can only originate at the base of the erect shoots, in *Thalassia* (Fig.10h) they develop exclusively from short shoots. *Halophila* is variable (Fig.10g) but it is safe to say that an axis never proliferates directly; new indeterminate meristems arise from lateral shoots or their branches. *Syringodium* is distinctive in that in its normal pattern of growth, branching is so ordered that all lateral meristems develop as short shoots, seemingly of limited growth. Proliferation does occur, however, (Fig.10f) by modification of or branching in these lateral meristems. The stimulus for this is some disturbance of the growth pattern. This suggests a high degree of economy in branch production.

The production of lateral meristems essentially involves three steps: initiation, determination and development. In the more highly organized seagrasses the three steps are more or less continuous and invariant. In *Thalassia*, for example, lateral meristems are produced only at regular intervals on rhizomes, they are always determined as short shoots and they develop precociously. There is no provision in this type of shoot system for meristems which are either delayed in their development or uncommitted in their determination. This is not so in the less precisely organized seagrasses where, as in *Zostera* and *Posidonia*, development of a lateral meristem is sometimes delayed. Here, there is at least the possibility for reserve or resting meristems to develop. Such a property is, however, restricted neither to unorganized

shoot systems nor to sea grasses of temperate oceans. For example *Thalassodendron* seems regularly to develop a bud at the base of an erect shoot which is potentially a reserve meristem, capable of delayed development.

In general, however, seagrasses seem to approach the *Thalassia* type, in which the overall organization of the shoot depends on terminal meristems which remain permanently active. Simply, one cannot propagate *Thalassia* unless one has an active rhizome apex.

This property is particularly significant when one considers the sites of initiation for new roots. These are, by definition, adventitious roots in all seagrasses since they arise from stems. However, sites of initiation for roots are always within active shoot apical meristems; microscopic examination of most seagrasses is likely to show that roots are formed in precise positions and in precise numbers within apical meristems. Roots are initiated in no other position. This further restricts the regenerative capacity of seagrasses. Indeed, in many seagrasses the roots themselves never branch (all genera except *Posidonia*, *Cymodocea*, *Amphibolis*, *Syringodium* and *Thalassodendron*)

From this overall view of shoot organization in seagrass there emerges a picture of "meristem dependence", a precise and organized restriction of growth such that branching is dependent on active meristems, with dormancy of meristems commonly lacking. It is important to grasp this morphological point where ecological, physiological or productivity studies are contemplated. The present account is only a preliminary one and many statements are based on quite insubstantial observations. Most information has to be verified by extensive studies, of populations in the field as well as of growing parts dissected in the laboratory. It is hoped that a point of view has been established which will guide these future studies.

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