

# **The Biology of Australian Plants**

Edited by

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## CHAPTER 9

# The Biology of Australian Seagrasses

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## 9.1 INTRODUCTION

Seagrasses are angiosperms which have ventured into the marine environment, where they produce totally submerged flowers which are pollinated under water. They occur in many regions of the world, but the following account is concerned primarily with studies on the biology of these plants in Australian waters. It also attempts to contrast some of the features displayed by the seagrasses with those of more familiar terrestrial plants.

## 9.2 DISTRIBUTION

Australian seagrasses belong to four families of monocotyledons; there are 11 genera and 25 described species (Table 9.1), three of which have only recently been described (Greenway 1979, Cambridge and Kuo 1979). Many of the collections of seagrasses found in Australian herbaria, and used by den Hartog (1970) to map Australian seagrasses, were collected as drift on the beach. Since 1970 the herbarium collections have been greatly increased by the deposition of specimens taken from their actual habitats; nevertheless many areas are still unexplored, and further taxonomic work is needed.

In contrast to the more familiar terrestrial Australian floras, which are characterised by a high degree of endemism, Australian seagrasses have strong affinities with those of other continents and island groups (den Hartog 1970). As examples, *Posidonia oceanica* (L.) Delile from the Mediterranean is closely related to *P. australis*, and *Thalassia testudinum* Banks ex König in the Caribbean is very similar to *T. hemprichii*, found in tropical areas of Australia and the eastern shores of Africa. Some other species represented throughout the Indo-Pacific region are *Syringodium isoetifolium*, *Halophila ovalis*, *Enhalus acoroides* and *Cymodocea serrulata*.

The seagrasses occur in our waters through all latitudes, but the species may be grouped into those found only in tropical areas, those which are found only in temperate areas, and those which are ubiquitous (Table 9.1, Fig. 9.1). The areas where temperate and tropical species overlap occur at the 23 °C summer isotherm.

Australian seagrasses have not been adequately mapped. A few areas have been studied intensively for various reasons, such as their convenient location, or because of suspected changes which might be due to man's activities, or if deemed representative of much larger, less accessible areas. These study areas are shown on the map (Fig. 9.1), where it is clear that they often occur near centres of population. In contrast, only a very uncertain demarcation of geographical limits for species can be made for most of the Australian coastline. We may especially note the lack of information on seagrasses from Port Hedland in Western Australia to the Gulf of Carpentaria. Nevertheless, enough is known of the ecology and habitat requirements of these plants for one to predict, for the unexplored littoral and sublittoral areas of the continent, those areas in which one would expect certain species to be growing.

Seagrass plants are generally restricted to shallow (<30 m) areas of reduced water activity, but stands are often difficult to map in detail because of inaccessibility, and

Table 9.1

*The Australian Seagrasses*

Genus	Species	Map*	Distribution†
Hydrocharitaceae			
<i>Enhalus</i>	<i>acoroides</i> (L.F.) Royle	26	N
<i>Halophila</i>	<i>decipiens</i> Ostenfeld	4	S
	<i>ovalis</i> (R. Br.) Hook F.	1	C
	<i>ovata</i> Gaud, in Freycin	2	N
	<i>spinulosa</i> (R. Br.) Aschers.	3	N
	<i>tricostata</i> Greenway	5	N
<i>Thalassia</i>	<i>hemprichii</i> (Ehrenb.) Aschers.	6	N
Cymodoceaceae (Zannichelliaceae; Potamogetonaceae)			
<i>Amphibolis</i>	<i>antarctica</i> (Labill.) Sonder et Aschers.	27	S
	<i>griffithii</i> (J. M. Black) den Hartog	28	S
<i>Cymodocea</i>	<i>rotundata</i> Ehrenb. & Hempr. ex Aschers.	10	W
	<i>serrulata</i> (R. Br.) Aschers. & Magnus	9	N
	<i>angustata</i> Ostenfeld	11	N
	<i>pinifolia</i> (Miki) den Hartog	14	N
<i>Halodule</i>	<i>univervis</i> (Forsk.) Aschers. in Boissier	13	N
	<i>isoetifolium</i> (Aschers.) Dandy	12	C
<i>Syringodium</i>	<i>ciliatum</i> (Forsk.) den Hartog	7	N
<i>Thalassodendron</i>	<i>pachyrhizum</i> den Hartog	8	S
	Posidoniaceae (Potamogetonaceae)		
<i>Posidonia</i>	<i>angustifolia</i> Cambridge and Kuo	18	S
	<i>australis</i> Hook F.	15	S
	<i>sinuosa</i> Cambridge and Kuo	16	S
	<i>ostenfeldii</i> den Hartog	17	S
Zosteraceae (Potamogetonaceae)			
<i>Zostera</i>	<i>capricorni</i> Ashers.	22	S
	<i>mucronata</i> den Hartog	23	N
	<i>muelleri</i> Irmisch & Aschers.	21	S
<i>Heterozostera</i>	<i>tasmanica</i> (Martens ex Aschers.) den Hartog	25	S

\* Numbers refer to the locations shown in Fig. 9.1.

† N, occurring only in northern, tropical waters; S, occurring only in southern, temperate waters; C, cosmopolitan, occurring in tropical and temperate waters. See also Fig. 9.1.

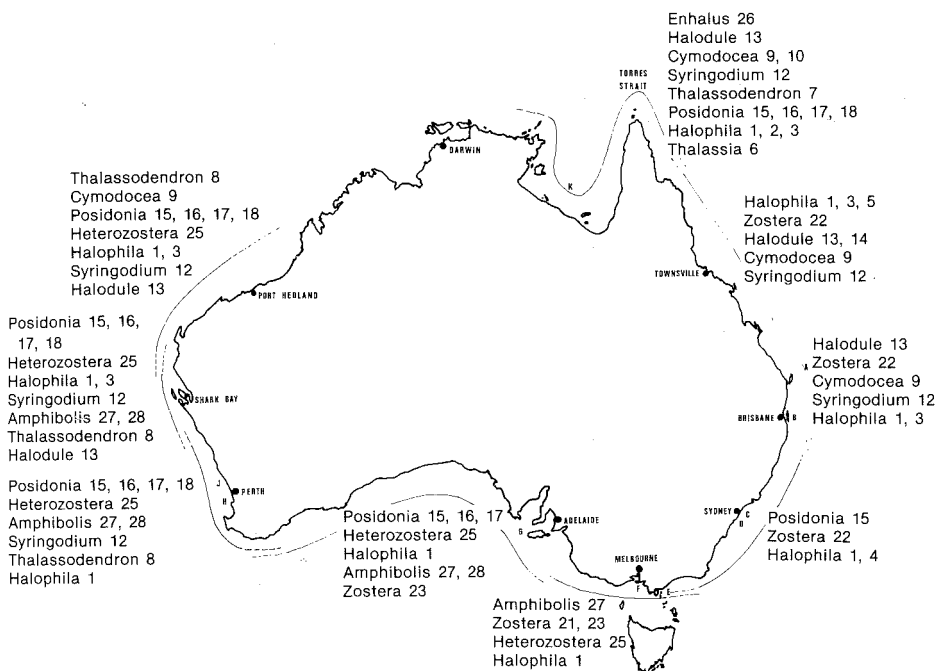


Fig. 9.1 The general distribution of seagrasses along the Australian coast. Sites for which detailed information is available are indicated, and references are given in Table 9.2.

they cannot always be distinguished from reef or deep water in aerial photographs. Seagrasses may form submarine meadows of considerable extent (Fig. 9.2), which have been mapped in a number of areas (Table 9.2). The largest, densest beds are found in Spencer Gulf, the Gulf of St Vincent and along the Western Australian coast to Exmouth including vast areas in Shark Bay; the extent of meadows is illustrated in Fig. 9.3, for Gulf St Vincent. Although these areas are characteristically sheltered, shore habitats, seagrasses such as *Halophila* may extend into estuaries where they may tolerate salinities as low as 2 parts per thousand (ppt) for short periods of time, or up to 46 ppt in estuaries such as the Peel/Harvey system (McComb *et al.* 1979) where there is seasonal freshwater input, high evaporation, and little exchange with the open ocean.

While the total area of Australian seagrasses is unknown, preliminary estimates would suggest that they occupy about  $2.4 \times 10^3 \text{ km}^2$ , equivalent to the area covered by sugar cane in Australia, or a quarter of that taken up by tropical rain forests (Cameron 1978).

### 9.3 PRODUCTIVITY

#### STANDING CROP

While seagrasses may occupy relatively large areas, this does not in itself tell us how productive they are. One approach is to simply determine how much plant

Table 9.2

*Areas of the Australian Coast where Seagrasses have been Mapped*

Map Reference*	Region	Reference
A	Tin Can Bay, Queensland	Dredge, <i>et al.</i> 1977
B	Moreton Bay, Queensland	Young and Kirkman 1975
	Moreton Bay, Queensland	Kirkman 1978(b)
	Moreton Bay, Queensland	Kirkman 1975
C	Botany Bay, New South Wales	Larkum 1976, Anon. 1978
	Tuggerah Lakes, New South Wales	Higginson 1965
D	Port Hacking, New South Wales	Kirkman and Reid 1979
E	Corner Inlet, Victoria	Poore, G. C. B. 1978
F	Westernport Bay, Victoria	Anon. 1974
G	Spencer Gulf, Gulf St Vincent	Shepherd and Sprigg 1976
H	Cockburn Sound, Western Australia	Cambridge 1975
	Warnbro Sound, Western Australia	Cambridge 1979
J	Mullaloo Point, Western Australia	Kirkman (unpubl.)
K	Torres Strait Queensland	(Unpubl. Alpha Helix cruise 1979)

material is carried per unit area, the standing crop, preferably harvested as near as possible to the maximum standing crop of the year and expressed as dry weight per square metre. Data for Australian seagrasses are gathered in Table 9.3, along with other information for comparison. The figures are for apparently healthy, growing stands of plants, not those at the edges of their distributional range. The seagrasses are rhizomatous perennials; and in most cases the above-ground material consists only of leaves. For *Amphibolis*, in which prominent erect stems are present, quite different figures are obtained depending on whether or not the stems are included.

Values for standing crops of seagrasses are in general quite high, and approach those shown by emergent rhizomatous perennials in wetlands. The latter tend to contain larger amounts of fibrous material. The largest standing crop figures for seagrasses come from studies in Alaska (McRoy and McMillan, 1976) but in general Australian data resemble those for other parts of the world.

As with many terrestrial plants it is difficult to obtain information on the biomass of below-ground parts. In mature *Posidonia australis* meadows near Sydney Kirkman and Reid (1979) found that the ratio of leaves to roots plus rhizomes was about 1:4; for 2-year-old plants growing near Perth the ratio was about 1:1.8 (Hocking *et al.* 1979a).



Fig. 9.2 A meadow of *Posidonia australis* near Perth, Western Australia. (Photo: P. Baker.)

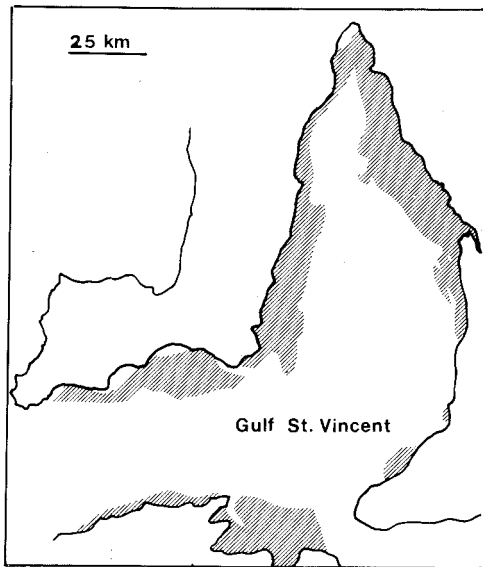


Fig. 9.3 The area occupied by seagrass meadows (mainly *Posidonia australis*) in Gulf St Vincent, South Australia. Scattered seagrasses also occur outside the shaded area. Redrawn from Shepherd and Sprigg (1976).

## LEAF AREA INDEX

Photosynthesis, and hence net productivity, relies mainly on the area of green plant material which receives sunlight. The 'leaf area index'—the leaf area expressed in relation to ground area covered—is thus a useful concept to employ when expressing photosynthetic potential. First suggested by Watson (1947) in relation to crop plants, the concept has received considerable attention in agronomy (e.g. Loomis *et al.* 1971). Table 9.4 gives leaf area indices for some tropical and temperate seagrasses. Caution must be expressed in the use of these figures, because in addition to one leaf shading another, a coating of epiphytes on the leaves may further reduce the light available to each leaf. As with standing crop, the leaf area indices of these seagrasses appear comparable with those of land plants.

## PRODUCTION RATES

Standing crop and leaf area index, interesting though they are when comparing communities, do not provide direct information about production rates, which are even more difficult to obtain for seagrasses than for terrestrial species. Methods of net production measurement using  $^{14}\text{C}$ , or based on oxygen exchange, are fraught with technical and interpretational difficulties, many of which have not been resolved (Vollenweider 1974; Weiner and Kirkman 1979). As examples, seagrass plants store gases in lacunal spaces which ramify through all parts of the plant, and oxygen may be lost into the sediments from rhizome and root systems. However, above-ground productivity can be measured with some accuracy by means of tagging leaves with staples (Zieman 1974) or punching shoots with holes (Kirkman and Reid 1979). The marked plants can be harvested later, and the increment of plant material produced in the intervening time measured. Fig. 9.4 is an example of data collected over a year in Warnbro Sound (near Perth, Western Australia), and it is clear that leaf growth occurs throughout the year, with peak growth in summer. Table 9.5 presents some above-ground productivities determined for Australian seagrasses, with other data for comparison. A well-developed meadow has a very high productivity, comparable in fact with that of a marsh or coniferous forest. The high productivities of seagrasses in other regions have been pointed out on several occasions (e.g. Whittaker 1970).

There is as yet no suitable method for measuring below-ground production, but some indication of this may be given by knowing the morphology and growth patterns of the particular seagrass species concerned (Tomlinson 1974). It is thought that the productivity of below ground parts is at least an order of magnitude lower than leaves.

## LIGHT LIMITATION

While seagrass meadows may be quite large, there are clearly physical boundaries to the area over which a meadow can exist. The minimum water depth which can be tolerated is usually imposed by instability of substrate or exposure at low tide and one must presume that the maximum depth to which a species grows is typically imposed by light availability. Like benthic freshwater angiosperms, the seagrasses are precluded if light intensities are less than about 1-5% of those reaching the water



Table 9.3

## The Standing Crops of Australian Seagrasses and Other Plants

Taxon	Standing crop*	Region	Reference
<i>Halophila ovalis</i>	49	W. Aust.	Carstairs, 1978
<i>Thalassia hemprichii</i> etc.	70	Queensland	Kirkman, unpubl.
<i>Amphibolis griffithii</i>	220†	W. Aust.	Kirkman, unpubl.
	780‡	W. Aust.	Cambridge, 1978
<i>Cymodocea serrulata</i>	60	Queensland	Dredge, et al. 1977
<i>Cymodocea serrulata</i>	44	Queensland	Dredge, et al. 1977
<i>Posidonia australis</i>	440	W. Aust.	Cambridge 1978
<i>Posidonia australis</i>	140	N.S.W.	Kirkman and Reid 1979
<i>Posidonia australis</i>	134	N.S.W.	Larkum 1976
<i>Posidonia australis</i>	90	N.S.W.	Larkum 1976
<i>Posidonia australis</i>	320	S. Aust.	Shepherd and Branden 1974
<i>Posidonia sinuosa</i>	660	W. Aust.	Cambridge 1979
<i>Posidonia sinuosa</i>	360	W. Aust.	Kirkman, unpubl.
<i>Zostera capricorni</i>	26	Queensland	Dredge, et al. 1977
<i>Zostera capricorni</i>	55	N.S.W.	Kirkman and Reid M.S.
<i>Zostera mucronata</i>	10	W. Aust.	Congdon 1977
<i>Thalassia testudinum</i>	104	Cuba	Buesa 1972
<i>Zostera marina</i>	1000	Alaska	McRoy and McMillan 1977
Other Aquatics, Marsh Plants, etc.			
<i>Ruppia</i>	403	Estuary, W. Aust.	Congdon & McComb 1979a
<i>Potamogeton pectinatus</i>	132	Estuary, W. Aust.	Congdon 1977
<i>Baumea juncea</i>	1030§	Fen, W. Aust.	Atkins 1976
<i>Juncus kraussii</i>	1400§	Marsh, W. Aust.	Congdon & McComb 1979b
<i>Spartina alterniflora</i>	1300	Marsh, U.S.A.	Teal 1962
<i>Spartina alterniflora</i>	2600	Marsh, U.S.A.	Kirby and Bosselink 1976
Terrestrial Systems			
Saltbush steppe	91	N.S.W.	Charley and Cowling 1968
Mallee	915	S. Aust.	Specht 1966
Jarrah Forest	38000	W. Aust.	Glossop 1978

\* g dry wt m<sup>-2</sup>. Data for above ground material, which in most seagrasses is mainly or entirely leaves

† Stems removed

‡ Stems included

§ Dead standing material omitted

surface. In clear water, for example off Cape Naturaliste, at the southwest of the Australian continent, *Posidonia angustifolia* survives to a depth of 45 m, while *Halophila decipiens* reaches 40 m at Houtman's Abrolhos, off the Western Australian coast. In shallow estuaries, where waters are much more turbid, the depth limit

Table 9.4

## Leaf Area Indices of Australian Seagrasses

Taxon	Index	Reference
<i>Enhalus acoroides</i>	2.3	Kirkman (unpubl. Alpha Helix cruise 1979)
<i>Thalassia hemprichii</i>	5.1	Kirkman (unpubl. Alpha Helix cruise 1979)
<i>Amphibolis griffithii</i>	3.3	Kirkman (1979, unpubl.)
<i>Amphibolis antarctica</i>	4.3	Kirkman (1979, unpubl.)
<i>Posidonia sinuosa</i>	4.6	Kirkman (1979, unpubl.)
<i>Posidonia sinuosa</i>	6.5	Cambridge (1979)
<i>Posidonia australis</i>	4.9	Cambridge (1979)

Examples for Terrestrial Plants		
'Optimum' for grasses	9-10	Meyers (1972)
Ryegrass	7.1	Brougham (1958)
Wheat	3	Watson (1947)
'Optimum' for clovers	5	Meyers (1972)
White clover	3.5	Brougham (1958)
Trees (broad-leaf)	4-6	Evans (1972)

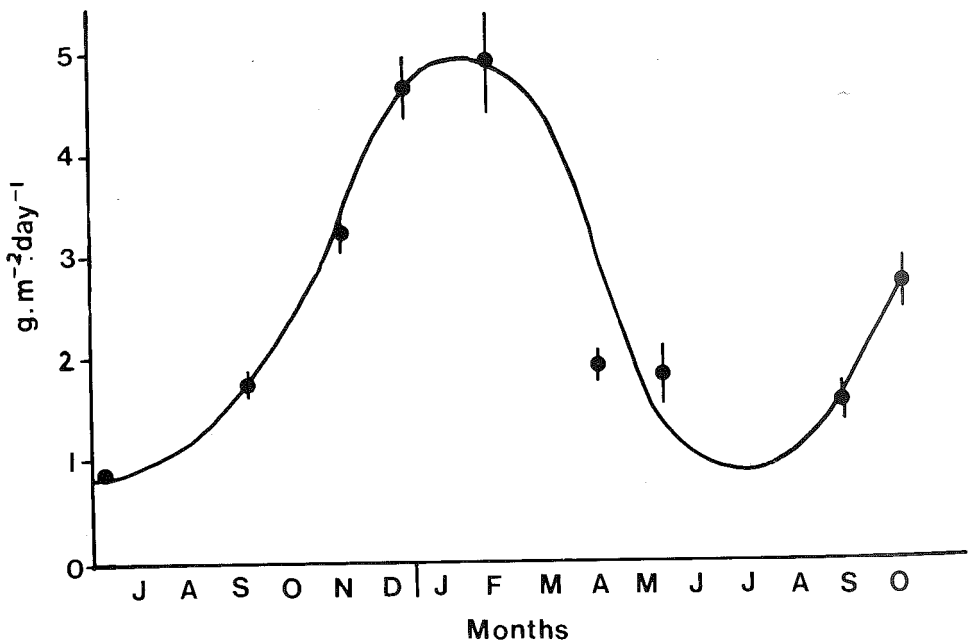


Fig. 9.4 Leaf productivity measurements for *Posidonia australis* from Warnbro Sound, Western Australia. Data from Cambridge (1979.)

may be as little as 2 m for species such as *Halophila ovalis* in the Peel-Harvey estuarine system (Western Australia), and *Zostera capricorni* in Moreton Bay, Queensland. Quite apart from imposing a depth limit, light probably limits the productivity achieved by seagrasses over much of the range in which they occur, as it does with other benthic plants. Nevertheless, one may speculate that in shallow waters where light intensities are relatively high, seagrasses grow particularly well because their root systems are able to withdraw nutrients from the sediments, a source not so readily available to pelagic species or benthic algae. In fact, in shallow waters in the United States the addition of nutrients to the sediments was shown to promote the growth of the seagrasses (Orth 1977). In contrast, attached macroalgae cannot directly tap the sediment nutrient bank. At depth, on the other hand, the attached algae may have a competitive advantage because they have a relatively small amount of non-photosynthesizing tissue to support in comparison with the seagrass.

Table 9.5

*The Productivities of Australian Seagrasses and Other Plants*

Taxon	Productivity*	Reference
<i>Halophila ovalis</i>	0.1	W.A., Carstairs 1978
<i>Posidonia australis</i>	2.4	N.S.W., Kirkman and Reid 1979
<i>Posidonia australis</i>	1.9	W.A., Cambridge 1979
<i>Posidonia sinuosa</i>	1.4	W.A., Cambridge 1979
<i>Zostera capricorni</i>	1.3	N.S.W., Kirkman and Reid, unpubl.
<i>Thalassia testudinum</i>	1.8	Cuba, Buesa 1972
<i>Zostera marina</i>	3.6	Alaska, McRoy and McMillan 1979
<i>Ruppia</i>	0.5	W.A., Congdon and McComb 1979a
<i>Juncus kraussii</i>	0.9	W.A., Congdon and McComb 1979b
<i>Spartina alterniflora</i>	1.6	U.S., Squires and Good 1974
Coniferous forest	2.8	Westlake 1963
Tropical forest	4.9	Westlake 1963

\* g carbon m<sup>-2</sup> day<sup>-1</sup> of above-ground material, averaged over a year. In most cases published figures were for g dry weight, but have been multiplied by the fraction 0.36 to convert to carbon, and if necessary converted to a daily rate.

## 9.4 LIFE HISTORY

Attention is now turned to some aspects of the life history of these plants, using this as a framework to introduce other information about the plant's biology. It is convenient to begin with flowering and then describe seed production, germination and vegetative growth before returning to the community.

## FLOWERING AND FRUIT FILLING

In some species flowering appears to be a rare event. For example, in *Cymodocea serrulata* flowers have been recorded on only one occasion (Kirkman 1975), while in *Halodule uninervis* flowers are extremely rare. Flowering of the tropical *Enhalus acoroides* is periodic and gregarious coinciding with spring tides, a few days after new moon and full moon, if these tides occur in the daytime (den Hartog 1970). But in most species flowering occurs quite regularly. In *Posidonia* on the western coast (Fig. 9.5), flower initiation occurs in April, when day lengths are shortening and temperatures are falling, and the flowers then open in October. In *Heterozostera tasmanica* initiation occurs during the lengthening days and increasing temperatures of August, and flowers open in November. For *Halophila ovalis* in the Peel-Harvey estuary (Western Australia), initiation occurs before September, and flowering in January to April (Carstairs 1978).

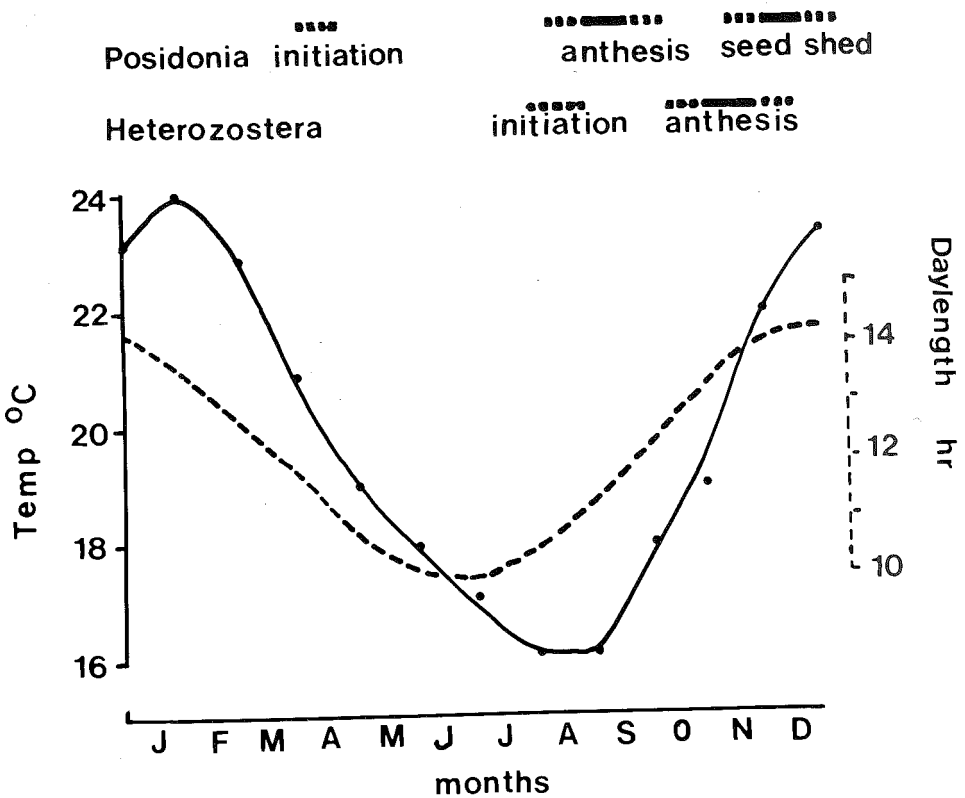


Fig. 9.5 The phenology of two seagrasses near Perth, Western Australia.

Let us look in greater detail at *Posidonia*. The flowers are carried in groups of short spikes, and have no perianths (Fig. 9.6A); details of the structure of these and other Australian seagrasses are given by den Hartog (1970) and Aston (1973). The pollen consists of long, narrow grains, which are released underwater, and drift submerged until perhaps chancing to lodge against a stigma; the pollination of sea-

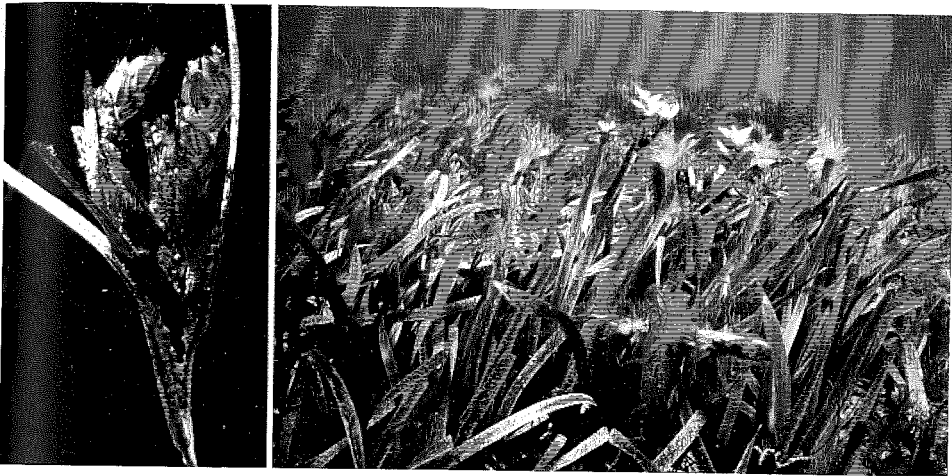


Fig. 9.6 Flowers and fruits of *Posidonia australis*. A. Flowers at the time of anthesis. B. Fruit carried above the leaf canopy of the meadow. (Photo: P. Baker).

grasses has been discussed by Ducker and Knox (1976) and Ducker *et al.* (1978). Open flowers are found in a meadow over a period of some six weeks, but each individual flower undergoes anthesis over a much shorter period.

The fruit is a drupe with a fleshy green pericarp surrounding an ellipsoid seed 1-2 cm long, and *Posidonia* plants may produce up to about 500 of these quite large fruits per square metre of meadow (e.g. Cambridge 1975). Maturation takes 12 weeks from anthesis (Fig. 9.6B). During the first three weeks, growth is largely

Table 9.6

*The Concentrations of Mineral Elements in Posidonia australis Fruit\**

Macronutrients	Pericarp mg.g <sup>-1</sup>	Seed (dry weight)	% in seed
N	8.5	13.0	74
P	1.0	3.2	85
K	48.1	7.3	22
S	6.3	2.9	45
Ca	2.5	0.5	28
Mg	11.1	3.3	35
Na	60.8	2.2	6
Micronutrients	µg.g <sup>-1</sup>	(dry weight)	% in seed
Fe	52.0	22.4	44
Zn	32.9	32.3	64
Mn	4.4	5.9	71
Cu	2.9	2.9	65

\* After Hocking *et al.* (1980)

restricted to the pericarp, seed dry weight increasing exponentially from weeks 7-11. When mature, the fruits have 70-75% of their fresh weight in the pericarp and 25-30% as seeds; but 65-70% of the fruits' dry weight consists of seeds (Fig. 9.7). The dry weight of the pericarp falls slightly during late stages of maturation, and this lost material would, if transferred to the seed, account for the equivalent of 9% of the seed's dry matter.

Much of the accumulated dry matter is starch, but at the same time nitrogen, phosphorus, and other macro- and micronutrients accumulate; the time course of accumulation is shown in Fig. 9.7. Concentrations of mineral elements in mature

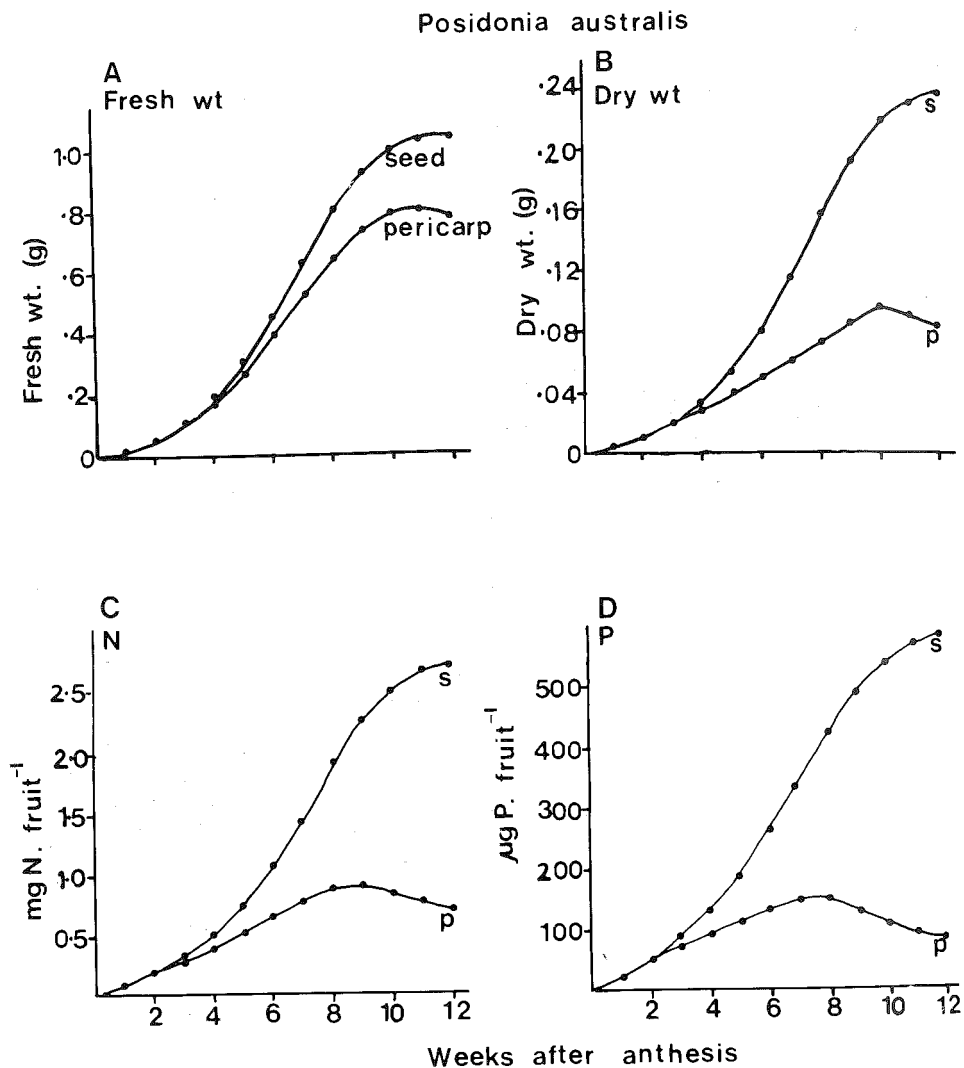


Fig. 9.7 Fruit development in *Posidonia australis*. A. increase in fresh weight; B. increase in dry weight; C. increase in nitrogen; D. increase in phosphorus. Redrawn from Hocking *et al.* (1980).

seeds (Table 9.6) are in general comparable with those of familiar terrestrial plants. Elements are apparently transferred from pericarp to seed with varying degrees of efficiency, the highest efficiencies being recorded for phosphorus and nitrogen, the lowest for calcium and sodium. The seeds are considerably more concentrated for most elements than the surrounding seawater, though calcium and sodium are present at relatively lower concentrations. Elements may also be more concentrated in seeds than in other plant parts; for example, nitrogen and phosphorus are about three times more concentrated in seeds than in leaves.

#### SEED SHED, GERMINATION AND SEEDLING GROWTH

Once shed a fruit floats to the water surface, buoyed up by the pericarp, which is green and probably photosynthetic; after a day or two the pericarp ruptures and the seed sinks to the sediment surface, unless it has already been cast up on the beach (Fig. 9.8A, B). If the seeds lodge in deep water survival is precluded by lack of light, and if they lodge in still water they will not be buried, and remain susceptible to grazing for a long period. Quantitative data are lacking on these points despite their obvious importance to establishment. The seeds lie flat on the sediment surface, and



Fig. 9.8 Seed shed and seedling development in *Posidonia australis*. A. fruit floating above the seagrass meadows, Geographe Bay, December, 1976; B. whole fruit and separate seeds and pericarps lost to the beach, Geographe Bay, December 1976; C. seeds settled among ripple marks on the sediment surface, Warnbro Sound, December 1976; D. seedlings approximately 10 months old being transplanted in pollution studies, Warnbro Sound, November 1978.

so obtain some protection against water movement, but as they are shuffled about they may well come to lie in small depressions such as ripple marks (Fig. 9.8C). With luck they will then be buried by further movements of the sand surface.

Germination of seagrass seed begins even before the seeds fall from the fruit, so that in contrast to most terrestrial plants there is no period of desiccation and/or dormancy. Accordingly young seedlings may be found quite commonly in early December, only a few weeks after fruit shedding (Fig. 9.8D).

The young seedling is initially dependent upon the reserves laid down by the parent plant, and the time course of change in dry weight of the seed remnants attached to the young seedling is shown in Fig. 9.9. During the first month there is a rapid and exponential decline, followed by a gradual decline over the next 6 months; loss of dry weight ceases by 9 months, when the seed coat and spent endosperm have lost 75-80% of their dry weight; they can still be found on seedlings up to two years old.

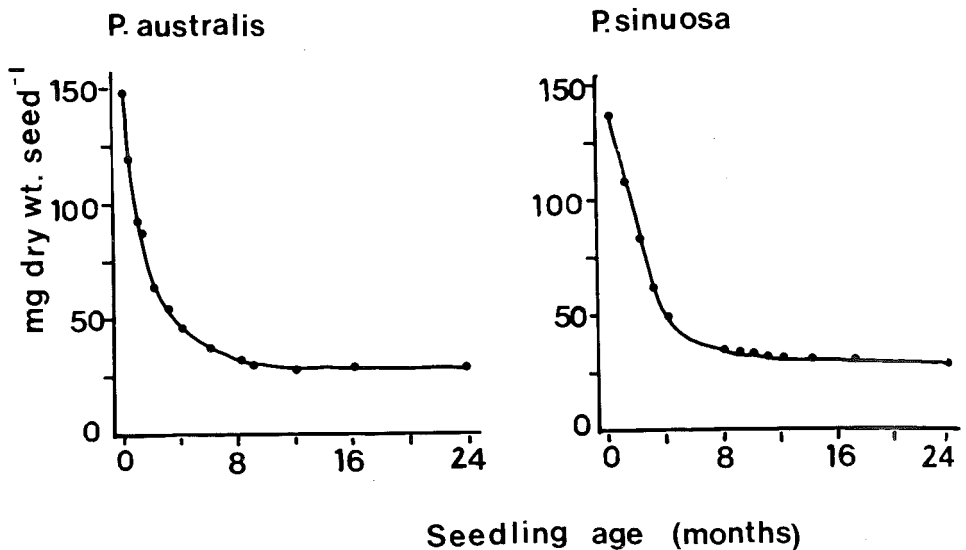


Fig. 9.9 The loss of dry weight from germinating *Posidonia* seeds. Redrawn from Hocking *et al.* (1981).

The nitrogen and phosphorus contents of the seeds are linearly related to dry weight (Fig. 9.10). At 4 months 50% of the nitrogen and phosphorus had been withdrawn, at 9 months 95%; a very efficient retrieval of these elements from the seed, which finds parallels with terrestrial plants (e.g. Collins and Sutcliffe 1977).

Seedlings developing in the field grow slowly at first, so that by 8 months, at the end of winter, they have about one fifth of the dry matter of 2-year-old plants; they then grow more rapidly (Fig. 9.11).

Nitrogen and phosphorus accumulation is similar to that of dry weight (Fig. 9.11), and by 8 months the seedlings have about a quarter of the amounts of these elements found in the 2-year-old seedlings. By 9 months the seedlings would be totally dependent on the environment. The importance of parent and seed reserves to the plants



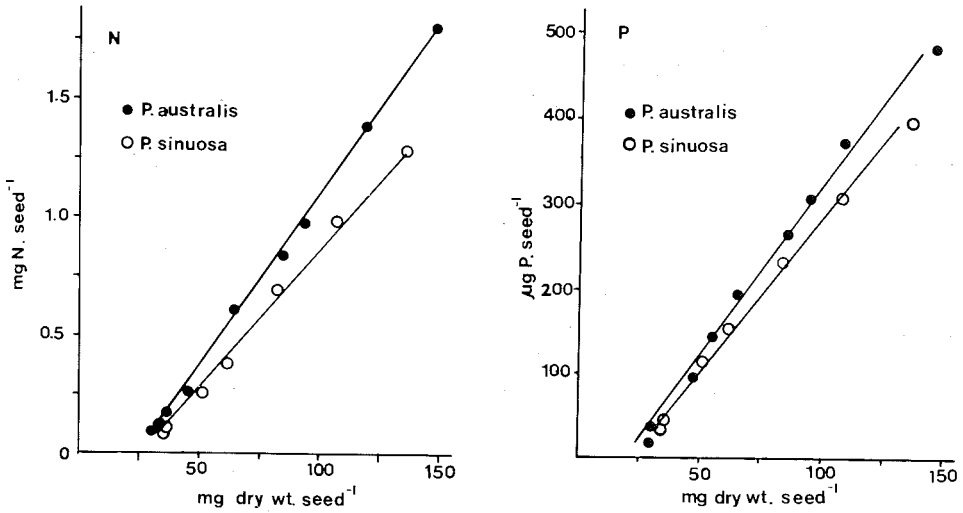


Fig. 9.10 The relation between nitrogen, phosphorus, and dry weight in germinating seeds of *Posidonia australis* and *Posidonia sinuosa*. Mature seeds have the highest dry weight and nutrient contents, and other data represent seeds attached to seedlings up to 2 years after germination. Redrawn from Hocking *et al.* (1981).

diminishes with maturity, of course, but even in a 2-year-old seedling some 20% of the phosphorus and 14% of the nitrogen can be accounted for from that source. It is also possible to work out the amount of nitrogen and phosphorus required to be absorbed per square metre to account for the growth of a stand of seedlings of a particular density (Table 9.7).

Despite the large seed production, and the presence of seedlings in the field, much of the growth of seagrasses is due to vegetative propagation by the growth of rhizomes.

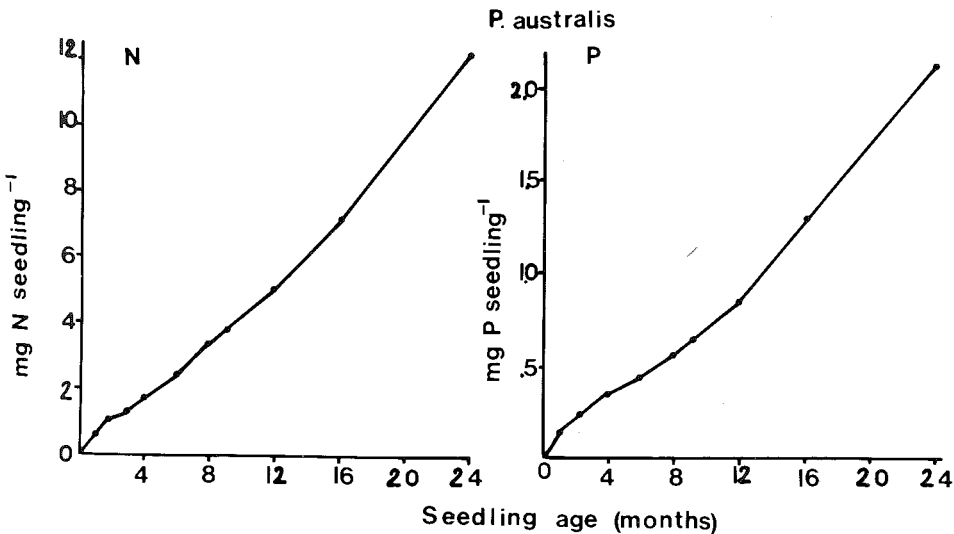


Fig. 9.11 The accumulation of nitrogen and phosphorus by young seedlings of *Posidonia australis*. Redrawn from Hocking *et al.* (1981).

Table 9.7

*The Nitrogen and Phosphorus in Seedlings Three Years Old,  
Expressed per Square Metre\**

	<i>P. australis</i>	<i>P. sinuosa</i>
No. of seedlings	15	13
Nitrogen (mg)	155	99
Phosphorus (mg)	25	17

\* After Hocking *et al.* (1980)

## 9.5 STRUCTURE

### LEAF

#### *Leaf Blade*

The structure of these plants will now be considered, and again particular attention is given to *Posidonia* (Kuo 1978). Fig. 9.12A-C shows transverse sections though the leaf blades of several seagrasses, and we see a number of prominent features. There are many longitudinal vascular bundles embedded among thin-walled parenchyma cells. There is a single layer of epidermal cells, which are densely stained, surrounding the parenchyma (see also Fig. 9.14B,C). Fibre cells lie just beneath epidermal and (if present) hypodermal cells. There are many large gas lacunae and as in other aquatics these are likely to be important as temporary reservoirs in gas exchange.

Some of these points will now be addressed in greater detail. Fig. 9.12D-F are surface views; distinctively, there are no stomata. The shape of the epidermal cells offer a useful taxonomic character (Cambridge and Kuo 1979). There is a definite cuticle in *Posidonia* (Fig. 9.12G), shown by histochemical tests to contain protein and lipid, but it has a markedly porous appearance. In other taxa [*Thalassia hemprichii*, *Cymodocea serrulata*, *C. rotundata* (Doohan and Newcomb 1976) and *Syringodium isoetifolium* (Fig. 9.12G)] the cuticle is a thin, electron-transparent layer, and it has even been reported as absent in the northern hemisphere *Thalassia testudinum* (Benedict and Scott 1976). On the available evidence, then, the cuticle does not appear to provide the barrier between leaf cells and environment that one is familiar with in terrestrial species. The reduction in cuticle of seagrasses, as in other aquatics (e.g. Sculthorpe 1967), must presumably facilitate direct entry of inorganic carbon sources for photosynthesis, thus compensating for the absence of a stomatal system.

The epidermal cells of the leaf have thickened walls which are rich in pectin, and not lignified (Kuo 1978). Ultrastructurally, two distinct layers occur in the outer wall (Fig. 9.12G), and there are small cupshaped depressions at the boundary of cuticle and outer cell wall in *Zostera* and *Heterozostera* (Fig. 9.12I; see also Barnabas *et al.* 1977). Epidermal transfer cells have been observed in *Thalassia*, *Cymodocea* (Doohan and Newcomb 1976), *Zostera* and *Heterozostera* (Barnabas *et al.* 1977;

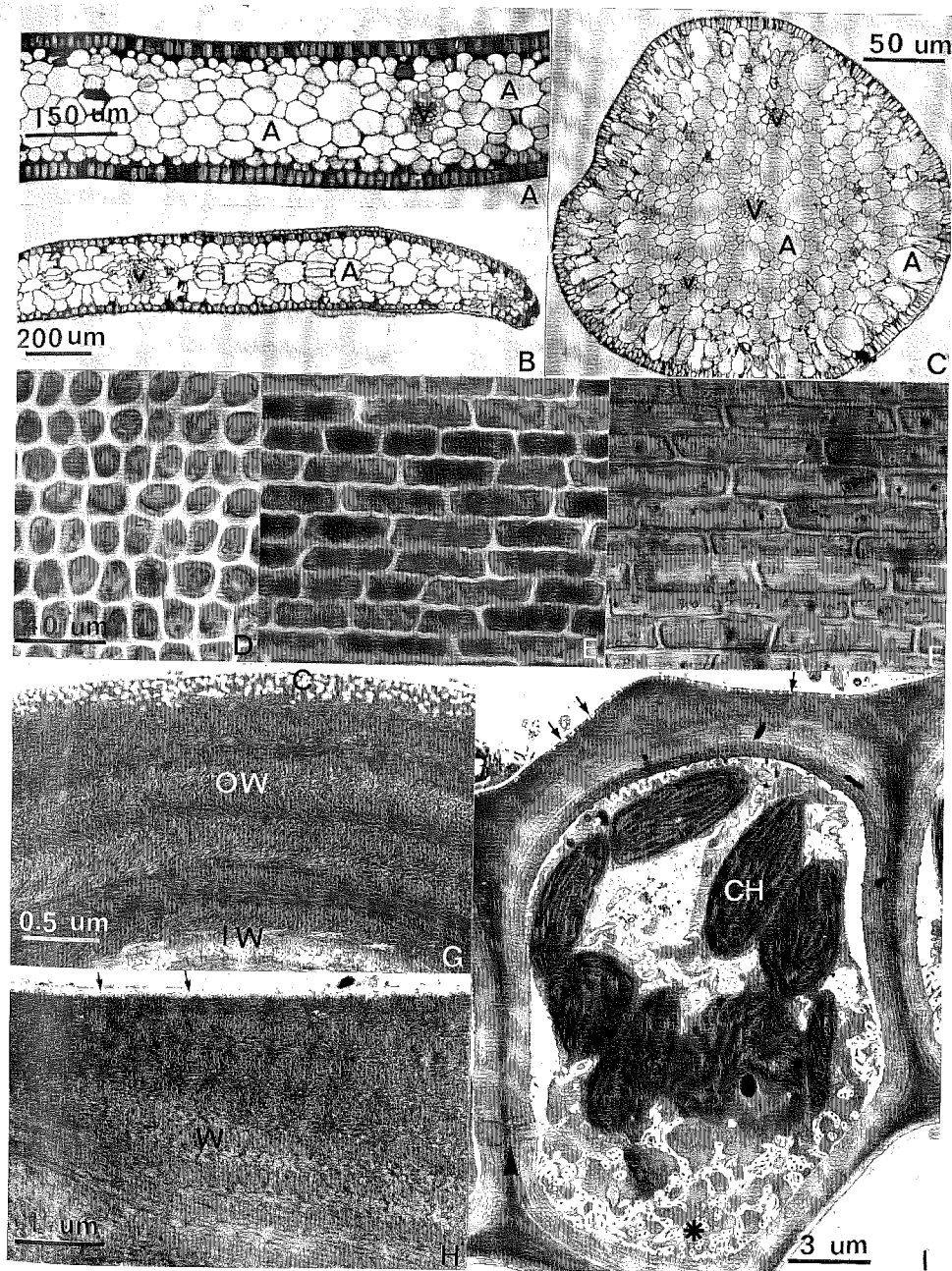


Fig. 9.12 The anatomy of seagrass leaves.

A-C—transverse sections of leaves; A. *Posidonia angustifolia*; B. *Zostera muelleri*.

C. *Syringodium isoetifolium* (V = vascular bundles, A = gas lacunae).

D-F—surface views of the dorsal epidermis of *Posidonia*; D. *P. australis*. E. *P. sinuosa*; F. *P. angustifolia*. (Same magnification).

G, H—outer cell wall of the epidermis; G. *Posidonia ostenfeldii*; (C = cuticle, OW = outer wall, IW = inner wall); H. *Syringodium isoetifolium* (w = wall, arrow = cuticle).

I.—epidermal cell of *Zostera muelleri*. (Note cup-shaped invaginations of outer wall, plasmodesmata through lateral wall, cell wall ingrowths marked with asterisk; CH = chloroplast).

Kuo, unpublished), but are not present in *Posidonia*; *Posidonia* has epidermal plasmodesmata (Kuo 1978). The epidermis is distinctive in that it contains most of the chloroplasts of a leaf (Figs 9.12I, 9.13B, C); among terrestrial plants few species have epidermal chloroplasts, and where they do occur they are best known for shade plants (Esau 1977). It is significant that in seagrasses and other aquatics, the chloroplasts are sited close to the inward-diffusing carbon substrates, which have relatively low rates of diffusion in an aquatic medium. For seagrasses, bicarbonate is the predominant form of carbon used in photosynthesis (Beer *et al.* 1977). The epidermal cells are also rich in mitochondria and golgi bodies, and many microbodies have been reported for *Thalassia* and *Cymodocea* (Doohan and Newcomb 1976).

The number of longitudinal veins varies with species and can be used as a taxonomic character, but inter-vein space is rather constant, and transverse veins connect longitudinal veins at fairly regular intervals. Examples of cross sections of vascular bundles are seen in Fig. 9.13A-E.

Vascular bundle sheath cells could not be distinguished in *Thalassia testudinum* (Benedict and Scott 1976), but can be readily identified in some species. They have lignified walls in *Posidonia* (Kuo 1978; Fig. 9.14D), and suberin lamellae in *Syringodium* (Kuo, unpublished) which resemble those which occur in certain terrestrial grasses (Carolin *et al.* 1973). In *Zostera* and *Heterozostera* they are transfer cells in the case of the phloem bundles; these have reduced chloroplasts, which do not contain starch (Fig. 19.13E). The leaves do not show 'Kranz' anatomy. Despite this, although most seagrasses probably show a Calvin (C<sub>3</sub>) pattern of photosynthesis, some are C<sub>4</sub> plants, or at least have intermediate characteristics (e.g. Andrews and Abel 1979, Beer *et al.* 1980, Doohan and Newcomb 1976).

Seagrasses have rudimentary xylem systems; there is little secondary wall thickness, and the number and size of xylem elements is small (Fig. 9.13D). The reduced xylem system has led some researchers to suggest that there is little xylem transport in seagrasses (e.g. Tomlinson 1972), but experimental work on this point appears to be lacking. On the other hand, the phloem is prominent and that of *Posidonia* (Fig. 9.13D), *Zostera* and *Heterozostera* is very similar in structure to that found in terrestrial plants; the sieve tubes of *Zostera* and *Heterozostera* are nacreous, or thick-walled (Fig. 9.13E).

The prominent fibre cells of the leaves are of particular interest. They have thickened walls, which consists of pectin and cellulose, but do not contain lignin (Fig. 9.13B; Kuo 1978). Thus they provide tensile strength but retain a high degree of flexibility, allowing the leaves to withstand vigorous wave action.

### Leaf Sheath

The leaf sheath, to which the blade is attached, encloses the rhizome and lies beneath the sediment surface. In its anatomy the sheath differs markedly from the blade (Fig. 9.13F, G). The structure and contents of the epidermal cells are quite different. The cuticle is electron-transparent and is not porous, and the cell wall is not layered in appearance. A thin lignified or suberized layer is present on the wall of the abaxial epidermal cells. The cells lack chloroplasts, and are highly vacuolated with a thin peripheral cytoplasm. In contrast to the blade, the fibre groups are widely distributed among the parenchyma tissues of the sheath and are also lignified.

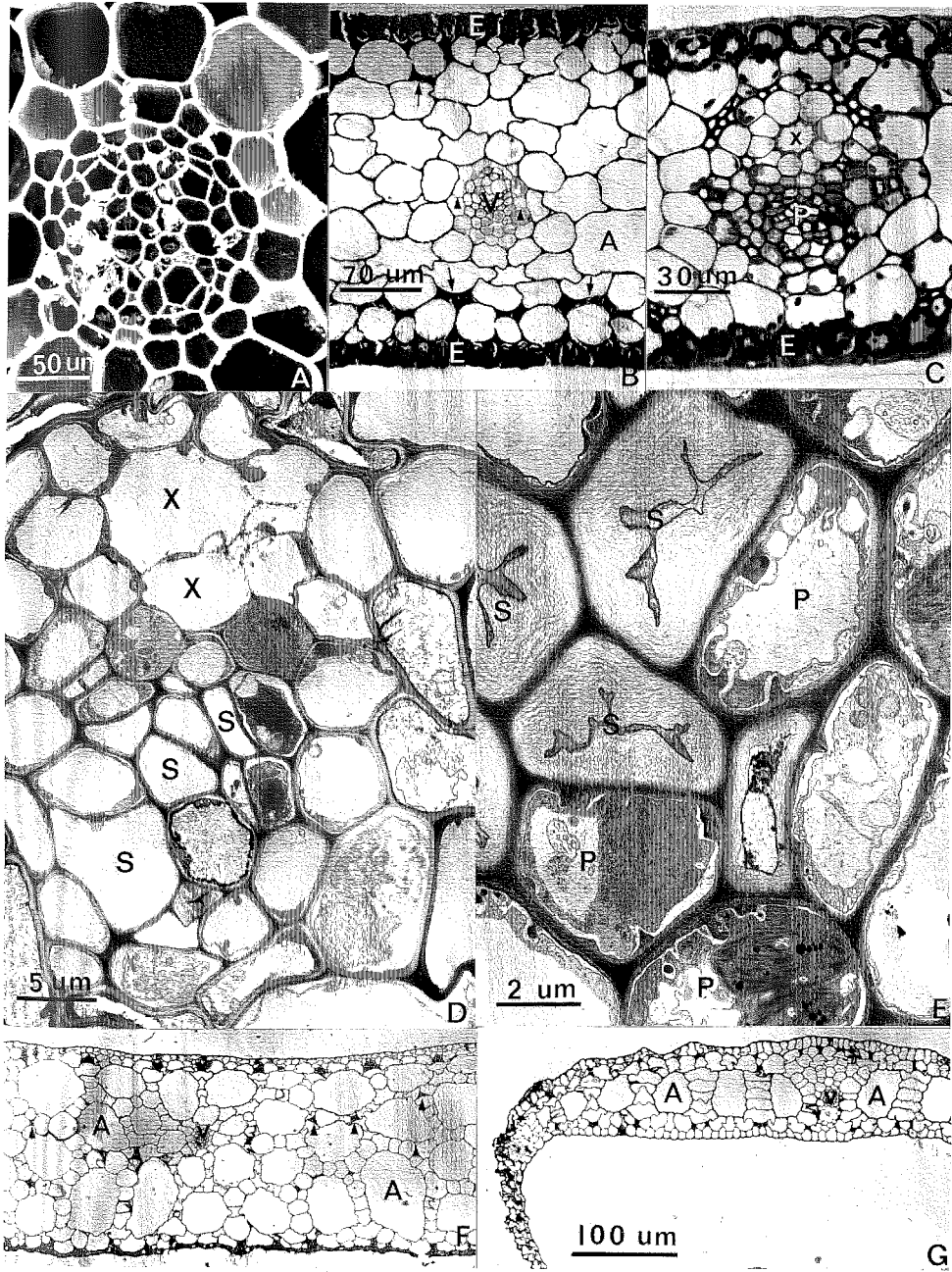


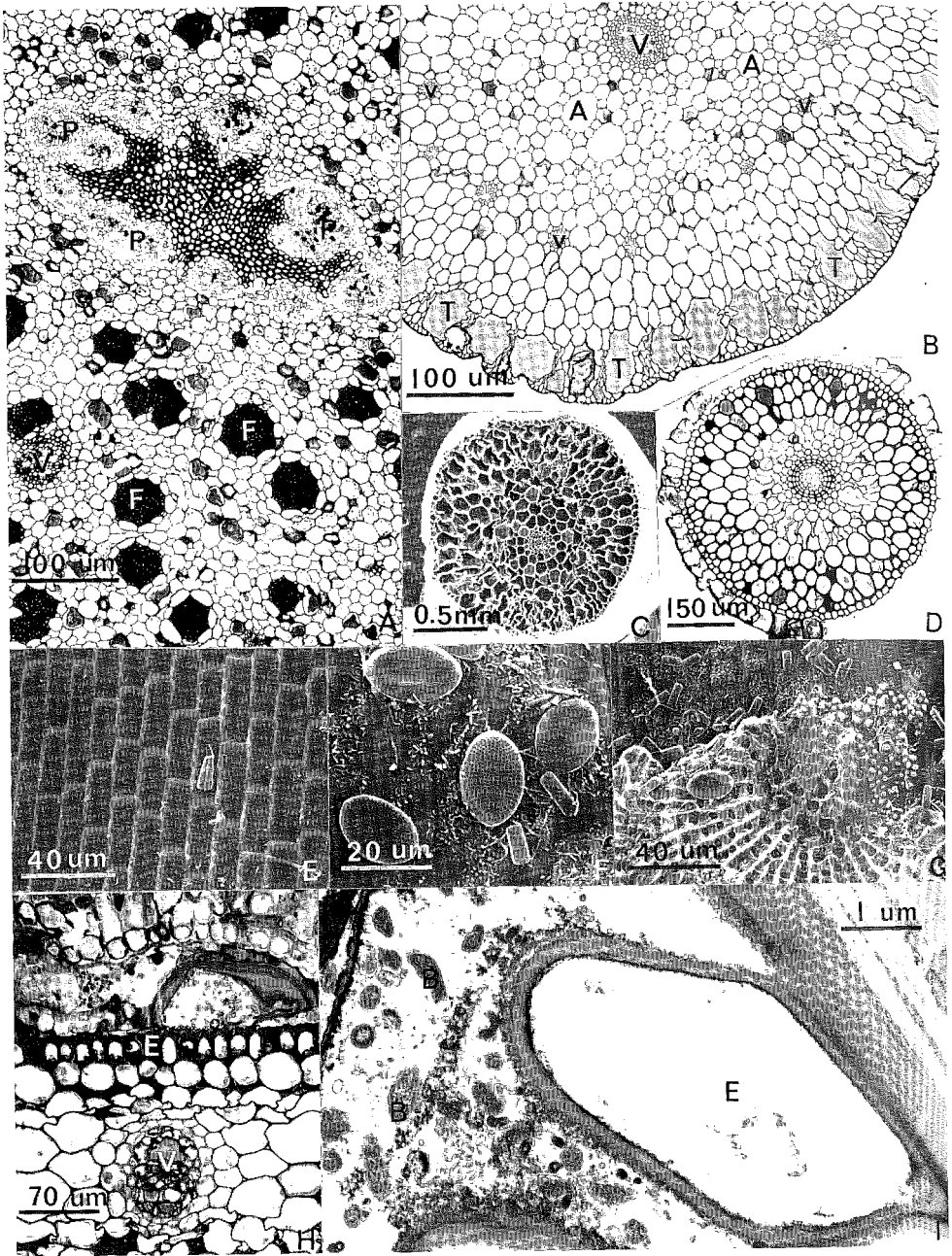
Fig. 9.13 The anatomy of seagrass leaves and leaf sheaths.

A-E—details of leaf blade vascular bundles; A. *Posidonia australis* vascular bundle, scanning electron micrograph; B. *Posidonia sinuosa* leaf blade (A = gas lacuna, E = epidermis, V = vascular bundle; note fibres and bundle sheath cells). C. *Heterozostera tasmanica* (E = epidermis, P = phloem, X = xylem); D. *P. australis* vascular bundle (S = sieve tube, X = xylem); E. *Heterozostera tasmanica* (P = phloem, S = sieve tube transfer cells).

F-G—leaf sheaths. F. *P. australis*; G. *Zostera muelleri* (A = gas lacunae; V = vascular bundles; note fibres).

Because of lignification, these fibres persist on the rhizomes long after the other tissues of the leaf base have rotted away.

Between the blade and the sheath there is a region of transition, where the changes in structure of epidermis, and in the distribution and structure of fibre cells, leave the region mechanically weak. The blades may break off at this 'abscission zone', though in strict anatomical terms no true abscission layer differentiates.



*Epiphytic Plants and Animals.*

The leaf surface of seagrasses differs basically from that of most terrestrial species by its very heavy load of epiphytes. These may be so dense that, in the words of Ducker and Knox (1978), there is 'standing room only'; indeed epiphytes may be equivalent to about half the seagrass standing crop. The epiphytes include bacteria, algae and animals such as hydroids, ascidians, sponges and Foraminifera. Even on the surface of newly-emerged leaf blades there are numerous bacteria and diatoms in the 'phyllosphere' (Fig. 9.14E). Some epiphytes are large, others small and calcareous, and even diatoms may form a crust several layers thick. The attachment between epiphytes and host appears for the most part to be superficial, though Ducker and Knox (1978) have observed that the red alga *Heteroderma cymodoceare* is capable of local erosion of the cuticle of *Amphibolis antarctica*, thus making direct contact with the epidermal cells of the seagrass. Epiphytes reduce the photosynthetic rate of the old leaves of the seagrass by reducing light intensity and, if photosynthetic, depleting dissolved carbon (Sand-Jenson 1977). The transfer of nutrients between host and algal epiphytes and vice versa has been demonstrated for certain species in other countries (Harlin 1973, Goering and Parker 1972, McRoy and Goering 1974). May *et al.* (1978) have reported the use of changes in epiphytes on *Posidonia* as indicators of environmental change in Botany and Jervis Bays, New South Wales, and Cambridge (1979) has pointed out that, as with submerged freshwater aquatics, nutrient enrichment, through the enhancement of epiphyte development, may inhibit the growth of seagrasses by reducing light intensity.

## RHIZOME AND ROOT

Turning briefly to the rhizome and root (Fig. 9.14A-D), the cell walls of the rhizome epidermis and hypodermis are slightly thickened and lignified (Kuo and Cambridge 1978). Starch grains are prominent in the cortical cells of the rhizome (Fig. 9.14A), and groups of lignified fibre cells with lignified lamellae and vascular bundles are arranged among the cortical tissues in a manner which differs distinctively between taxa. The rhizome stele has a central xylem surrounded by phloem bundles in *Posidonia*, and radial walls of the root and rhizome endodermis have a

Fig. 9.14 Anatomy of seagrasses.

A-C—transverse sections of rhizomes. A. *Posidonia australis* (F = fibre bundles, P = phloem bundles, X = xylem, V = vascular bundles. Note small starch granules in parenchyma cells); B. *Syringodium isoetifolium* (A = gas lacunae, T = tannin cells, V = vascular bundles. Note absence of fibre bundles); C. *Posidonia sinuosa*, scanning electron micrograph.

D. transverse section of *Zostera muelleri* root.

E-G—epiphytes on the leaves of *Posidonia ostenfeldii*. Surface views, using the scanning electron micrograph, of leaves of increasing ages; E. shows mainly bacteria; F. bacteria and diatoms; G. bacteria, diatoms, and calcareous red alga).

H.—epiphytes on a leaf of *Posidonia sinuosa*. In transverse section, these lie outside the epidermis; E. (V = vascular bundles).

I.—rhizosphere of *P. australis*. Bacteria, B, and other microorganisms in association with epidermal cells, E.



Casparian strip similar to that of terrestrial plants. The thickened hypodermal walls of the root each have a suberin lamella, and there is a vascular system with a well developed phloem and a weakly lignified xylem. Root hairs are sparse and poorly developed.

### *Rhizosphere*

Like the leaves, the roots of seagrasses provide an environment for micro-organisms. The seagrass rhizosphere has an appearance superficially at least like that of terrestrial plants (Fig. 9.14I), and it would not be surprising if these rhizosphere organisms play a similar role in mediating between the plant and environment, aiding nutrient uptake, affecting pathogen invasion, and fixing nitrogen. Indeed, nitrogen fixation in the seagrass rhizosphere, described overseas (e.g. Capone *et al.* 1979), has been recently confirmed in tropical Australian waters (Chapman 1979, pers. comm.)

## 9.6 NUTRITION IN MATURE PLANTS

### DISTRIBUTION OF DRY MATTER AND NUTRIENTS IN PLANTS

Let us now return to some aspects of nutrition, which were introduced earlier in relation to seed filling and seedling establishment, but will now be considered in the context of the more mature seagrass meadow, which has an essentially stable structure from year to year. Again, we will direct our attention to *Posidonia*. The distribution of dry weight for a plant estimated to be about 5 years old is shown in Table 9.8, and there are several interesting features. Almost 20% of the dry weight is in the leaves, and 28% in the rhizomes; in older plants we would expect an even higher proportion of rhizome. Dead leaf bases, which remain attached to the plant, account for 24% of the total dry weight. As far as phosphorus is concerned, 28% is in the leaves, and no less than 27% in the living leaf bases, which contain a high concentration of this element. Note that the concentration is markedly lower in dead leaf bases; they lose 95% of their phosphorus, 84% of their nitrogen, and 54% of their dry matter during senescence, and this is presumably retrieved by translocation into the remainder of the plant (Hocking *et al.* 1980a).

The distribution of nitrogen differs from that of phosphorus. The leaf base has only 14% of the total nitrogen, while the leaves have no less than 40%, largely because of their relatively high concentration of nitrogen.

### DISTRIBUTION OF DRY MATTER AND NUTRIENTS IN THE MEADOW

#### *The Hypothetical Meadow*

To help us gain some insight into the processes which take place in a seagrass meadow, we have simply converted figures of nutrient content per plant up to a square metre for a hypothetical meadow with a plant density giving an above-ground standing crop chosen at  $500 \text{ g. m}^{-2}$ , which corresponds with a below-ground standing crop of  $1196 \text{ g. m}^{-2}$  (Fig. 9.15A). Our hypothetical square metre has above



Table 9.8

*The Distribution of Dry Matter, Nitrogen and Phosphorus in P. australis Plants\**

Plant part	Dry weight		Nitrogen		Phosphorus	
	g	%	mg.g <sup>-1</sup>	%	mg.g <sup>-1</sup>	%
Leaf blade						
Young	0.85	1	13.8	10	1.24	7
Mature	1.81	10	12.9	18	1.03	13
Old	1.61	8	8.9	12	0.68	8
		19		40		28
Leaf base						
Live	1.44	7.6	11.0	14	2.73	27
Dead	4.47	23.6	3.9	15	0.31	9
Rhizome						
Young	0.95	5	5.3	4	1.58	15
Old	4.34	23	2.6	10	0.49	10
		28		14		25
Root	3.48	18	5.8	17	0.42	10

\* Plants approximately 5 years old; data expressed on a dry weight basis, from Hocking *et al.* (1981).

it 0.5 m (500 l) of water, and includes 10 cm (100 l) of sediment. Let us emphasise that the quantitative details of what we are about to discuss are likely to have to be modified or qualified before applying them to a mature, established meadow, but the general interpretations are still probably correct.

### *Phosphorus Distribution*

Figure 9.15B shows estimates for phosphorus. The values in the boxes are the amounts present at an instant in time—it will be appreciated, for example, that water may be moving past the plants at a high rate, so that the amount shown within the box is of little real interest, since it represents a mere fraction of a much larger moving pool of dissolved substances. One may note the relatively high levels of phosphorus in the sediment, a sandy sediment enriched with organic materials, in which seagrasses had been growing in Cockburn Sound. Another feature of interest is the high level of phosphorus being lost from the sediment. This is based on a measured rate of 'reactive' phosphate loss from a *P. australis* meadow near Sydney (Kirkman *et al.* 1979); the measurements were made over several tidal cycles, and have been multiplied up, for our purpose, to a year. Incidentally, the loss which Kirkman *et al.* recorded occurred only in the seagrass meadow, but was liberated from the sediment, not the plants themselves. (Previous work overseas had shown similar rates, but had attributed the loss to the plants; McRoy *et al.* 1972).

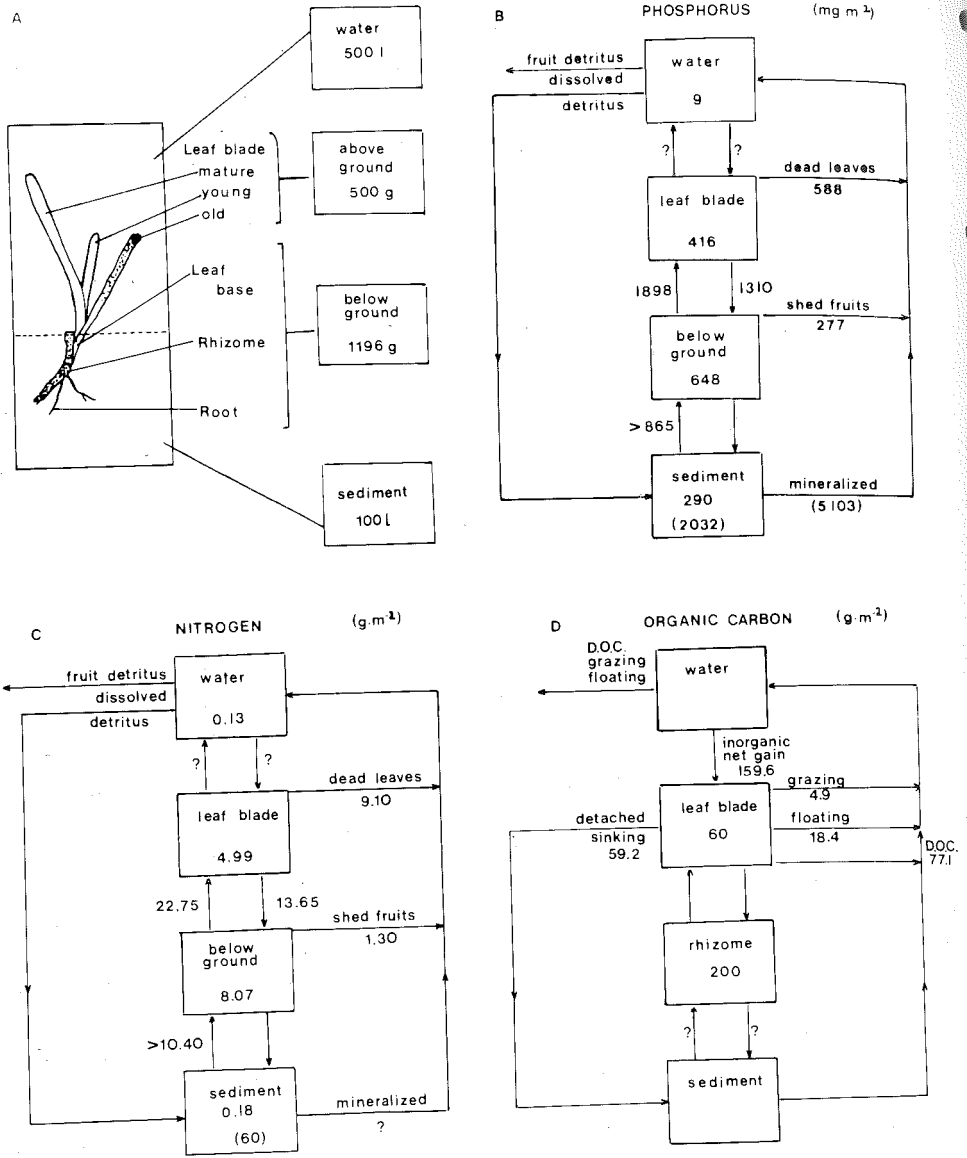


Fig. 9.15 The distribution and estimated yearly net transfer of nitrogen, phosphorus and carbon in a hypothetical square metre of *Posidonia sinuosa* meadow. The data, for A, B and C are for plants 5 years old (Table 9.8), computed for an above-ground standing crop of 500 g dry weight. The level in the water is for total phosphorus or nitrogen in Owen Anchorage (Chiffings pers. comm.), and the sediment is the salt-water extractable or total acid digestible phosphorus or nitrogen in Cockburn Sound (Welch pers. comm.). Input and loss from leaves is based on known turnover rate of canopy, and nutrient content of senescent material. Data calculated from Cambridge (1979) and Hocking *et al.* (1980,81). A. the hypothetical model ecosystem. B. phosphorus distribution and estimated transfer. The mineralized loss from sediments is based on work by Kirkman *et al.* (1979) near Sydney (see text); C. nitrogen distribution and estimated transfer; D. carbon transfer, calculated from data of Kirkman and Reid (1979) for a *P. australis* meadow near Sydney.

### Nitrogen Distribution

Figure 9.15C shows the same flows for nitrogen. Here we might note again the relatively high level in the sediments, and the loss through shed leaves and fruit. We have no information about remineralization of nitrogen, nor quantitative data about nitrogen fixation. As with phosphorus, the impression is one of loss from the system.

### Carbon Distribution

Figure 9.15D is a budget for carbon obtained over a year from an established meadow of *P. australis* at Port Hacking (Kirkman and Reid 1979), and so is not as speculative as the other budgets we have been considering. In fact, the measured losses of carbon differed from measured gains of carbon through growth by only 13%. Of particular note here is the very large loss of dissolved organic carbon, released from leaves and sediments, which accounts for 48% of all losses. Detached, sinking leaves account for an additional 37% of the total losses, and these remain to decompose in the seagrass beds.

### General Considerations

The nutrient studies leave one with the strong impression that the seagrass meadows accumulate nutrients to a much higher level than the bare sandy sediment in which seedlings become established, and in this they show parallels with the increasing nutrient status evident in the successional series of certain terrestrial plant communities. The impression of accumulation is enhanced by the observation of the efficiency with which nitrogen and phosphorus are removed from senescing leaves and germinating seeds.

In contrast, one is also left with the impression that there are likely to be substantial rates of losses of nitrogen, phosphorus and organic carbon from the seagrass meadow and from this it would appear that nutrient depletion from, not accumulation, by the ecosystem should occur.

The question therefore remains, as to how the nutrient budgets of the meadow are to be balanced. Some nutrient uptake may well take place through the leaves, and in the case of nitrogen there is presumably a contribution through fixation. Another important source of nutrients may be the detritus arising from epiphytic plants and animals, the 'infauna', unattached animals which dwell in the leaf canopy, and the burrowing organisms of the sediments. It is possible that, just as the root exudates of terrestrial plants encourage the establishment of a root microflora (Rovira 1969), the apparent 'losses' of nutrients from the seagrass ecosystem represent an investment which encourages the development of organisms other than the seagrass. In this manner an increase in the overall nutrient status of the seagrass meadow would be accomplished, with positive feedback to the system in terms of success of the seagrass component.

## 9.7 ROLE IN FOOD CHAINS

Because of their high standing crops, high productivity located at the base of the water column, and ability to concentrate available nutrients, one would expect sea-

grasses to be important to the general ecology of the regions in which they are prevalent. It is not surprising to find that different fish species may occur among seagrass meadows than outside (Dybdahl 1979), and the same is true of Crustacea (e.g. Young and Carpenter 1977) and gastropods (e.g. S. Slack-Smith, pers. comm). It is consequently of interest to discover by how much, and by what mechanisms, the productivity of the seagrasses may be channeled into animal food chains. This is not easy to answer firmly, and based on the somewhat sketchy information presently available, the conclusion appears to differ to some extent between the tropical and temperate seagrasses.

### Grazing

Surprisingly, in temperate regions direct grazing pressure appears to be low. There is certainly a little grazing. For *P. australis* meadows near Sydney the fan-bellied leatherjacket (*Monocanthus chinensis* (Osbeck)) and other monacanthids take in apparently large accounts of *Posidonia* (Bell *et al.* 1978) but this was estimated by Kirkman and Reid (1979) to be the equivalent of only 3% of the standing crop. Blaber (1974) found large proportions of seagrass in the stomachs of fish he was studying, but showed that it was organisms attached to leaves, rather than the leaves themselves, which were important nutritionally. This appears to be the case with the monacanthids, and there is no record of cellulase in any of these fish. Kirkman (1978a) has recorded amphipods eating large quantities of *Zostera capricorni* in aquarium tanks. Sea urchins (*Temnopleurus michaelsonii*) occasionally occur in large populations which may denude patches of *P. australis* meadow in a brief period off the western coastline. Kirkman and Young (1981) have recorded urchins (*Paracentrotus lividus* (Link.)) eating fresh *Posidonia oceanica* (L.) Delile off the French Mediterranean coastline.

In contrast, in tropical regions large animals—the dugong (*Dugong dugon* (Müller)), the green turtle (*Chelonia mydas* (Linn.)), and the half-beak (*Hemiramphus* sp.) eat large quantities of seagrass, but even there it appears that only a small part of the productivity is grazed.

### Detritus

Instead, it seems that in seagrass ecosystems of both tropical and temperate waters by far the larger fraction of a meadow's production (including nutrients) passes into and interacts with wider food chains of the ocean via the so-called 'detritus' of the meadow; fragments of decaying seagrass with associated microorganisms support small crustacea and filter feeders, which in turn are preyed upon by organisms at higher trophic levels.

As we have seen, in Port Hacking near Sydney, Kirkman and Reid (1979) found that 49% of a meadow's productivity passed into detritus and most of this never left the seagrass bed; indeed, large amounts of dissolved organic carbon, again equivalent to about half the productivity, were being produced by the system, and might be used indirectly by attached animals, zooplankton and infaunal species. Feeding on the detritus, and the epiphytes and infauna of the seagrass meadow, are many fish and crustacea, and it turns out that most of the fish in the meadows depend upon

crustacea for food (e.g. Dybdahl 1979). However, it is worth emphasising again the great importance of the epiphytic plants and animals in the food chains, as they create their own detritus, and in many cases themselves feed on detritus. Gastropods and other animals, including the leatherjackets mentioned above, depend on epiphytic animals for food. More direct evidence for the incorporation of seagrass carbon into food chains is available for overseas systems, using stable carbon isotope ratios (e.g. Thayer *et al.* 1978).

Seagrass detritus may, of course, be lost to the meadows. In Westernport Bay, Spencer Gulf and the Western Australian coastline large wracks or drifts appear on the beaches. The eventual fate of the material in these wracks is unknown, and it is conceivable that a comparable amount is lost to the seaward side of the seagrass bed. Zieman *et al.* (1979) have shown that considerable amounts of seagrass are transported offshore, often to great distances as surface export or bedload. The importance of seagrass detritus to nearshore and even offshore productivity must be considerable, but remains to be quantified.

### 9.8 PATTERN AND PROCESS

In the seagrass plant community, just as with terrestrial plants (Watt 1947), one recognizes zonation of different species, and patterns of community development in essentially pure stands, which inevitably lead to speculation about succession and cyclic processes. Probably the nearest terrestrial analogies to the behaviour of a seagrass community are to be seen among sand dune grasses, for both communities involve an interplay between plant growth and rate and pattern of substrate deposition. Wave energy is also of particular importance to the seagrasses. Let us take two examples. Fig. 9.16A shows rows of plants in a meadow of *P. sinuosa*. The width of

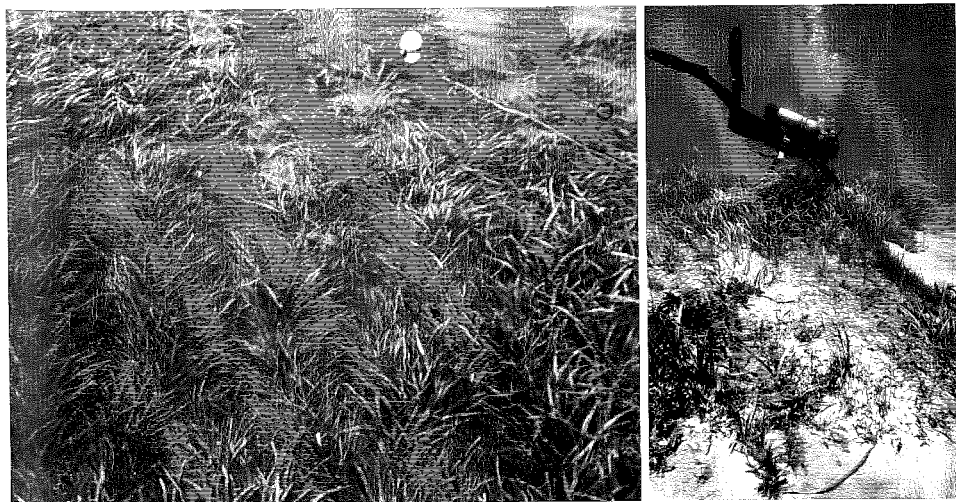


Fig. 9.16 Examples of meadow structure. A. rows of plants in a meadow of *Posidonia sinuosa*. Each is 30-40 cm wide. B. a dune-like structure consolidated by growth of *Posidonia australis*. Both examples are from Warnbro Sound, Western Australia (Photo: P. Baker).

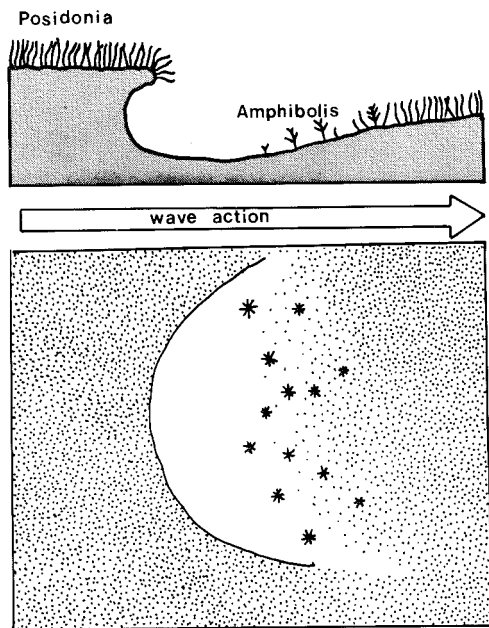


Fig. 9.17 Crescentic scours in a meadow of *Posidonia australis*. Such structures have been recorded in South Australia and Western Australia. Redrawn from Cambridge (1975) and Shepherd and Sprigg (1976).

the rows of grass is 30-40 cm, with bare sand between, and the appearance resembles long sand dunes which anastomose from time to time. The arrangement is one of cyclic succession, of unknown time-scale, for a few centimetres beneath the sand can be found the fibrous remains of seagrass meadow. One can visualise the sand ridges moving laterally with time, creating conditions favourable or unfavourable to *Posidonia* growth. Such furrowing occurs under conditions of high wave energy, but in which little sediment deposition is occurring.

A second example is the occurrence of crescentic scours in seagrass meadows (Fig. 9.17), well documented for Gulf St Vincent in South Australia (Shepherd and Sprigg 1976) and off the Western Australian coast (Cambridge 1975). These structures occur in regions of high turbulence, and have their longest axes at right angles to the waves. Aerial photographs taken near Fremantle show no significant changes in the positions and shapes of the crescents in meadows of *P. australis* over a period of 20 years, but they can apparently be colonized by either *P. australis* or other species, which invade from the floor of the crescent and proceed as far as the scouring action of the waves permits. Some patches become completely colonized, as shown by the occurrence of crescent-shaped areas of *Amphibolis* in *Posidonia* meadows.

Some species, such as *P. australis*, grow particularly well in regions of high sediment input (Fig. 9.16B), in a way somewhat analogous to that observed after the top-dressing of a lawn with soil or sand. Once established, the seagrass bed increases the rate of sediment deposition, first by a reduction in water velocity and so a local encouragement to settling of sediment from the water column; secondly by the accu-

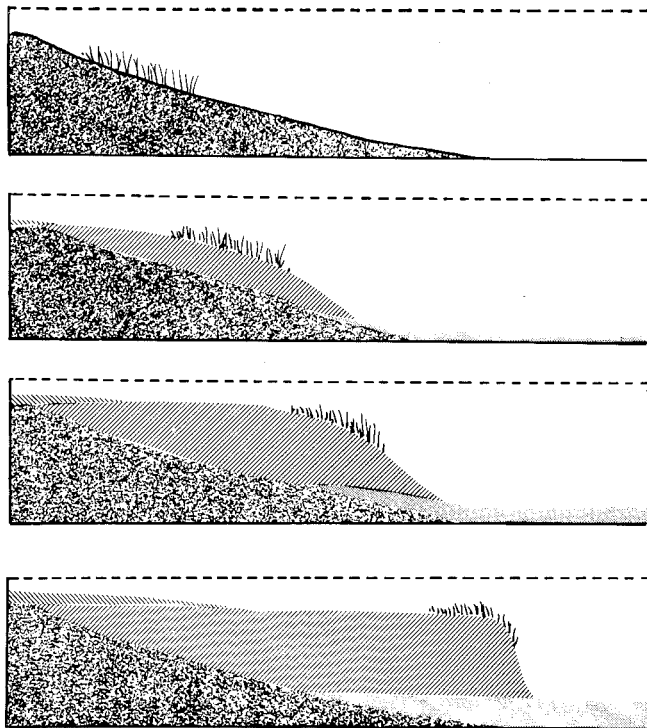


Fig.9.18 Build-up of submarine shore platforms through the consolidation of sediment beneath seagrass meadows. Based on Hagan and Logan (1974).

mulation of fibrous peaty material derived from the below ground parts; and thirdly because of the growth of calcareous epiphytes and molluscs, the skeletal remains of which accumulate in the meadow. This accretion of material has produced dramatic changes in submarine shore morphology, and the main processes are summarised in Fig. 9.18. Such changes have, for example, caused the shoreline to migrate seaward several kilometres in Gulf St Vincent over the past 6,000 years or so (Shepherd and Sprigg 1976), and submerged coastal platforms show the same characteristic morphology in Western Australia, for example in the barrier banks of Cockburn Sound near Perth. A particularly spectacular change in sublittoral bank morphology, which can be attributed to seagrasses, has been documented at Shark Bay, Western Australia, by Hagan and Logan (1974). There the elevation of banks because of the presence of seagrasses has cut off an area of water about twice that of Sydney Harbour; the area has become hypersaline, leading to dramatic changes in biota.

### 9.9 REDUCTION OF SEAGRASS MEADOWS

Some comments about the demise of seagrass communities are necessary. The seagrasses appear well adapted to their environment, and individual seagrass plants

seem able to withstand considerable environmental stress, but the stability of meadows can still be markedly affected by environmental change. It could be argued that the death of patches of seagrass from a few areas is of no great consequence in view of the vast areas of seagrass we have spoken about, but reasons for concern develop because of the local importance of the seagrass. This is because of the ability of the seagrasses to stabilise sediments, to act as a nursery area for juvenile fish and crustacea, to concentrate nutrients and provide detritus, to filter water and to act as a substratum for numerous sessile plants and animals. Estuaries and marine embayments may be individually small, but the Australian coast, and especially the western half, is far from rich in such structures. These bays and estuaries are important in the food chains of fish and birds, in the life cycles of commercial fish and crustacea, and are significant for fisheries and recreation.

Young (1978) suggested that any destruction of littoral areas in Moreton Bay, Queensland will be accompanied by a corresponding decrease in the commercial prawn fishery, and he concluded that this decrease will be magnified greatly where seagrass components are affected. Part of the prawn fishery of Moreton Bay is made up of tiger prawns (*Penaeus esculentus* Haswell), and the recruits of this species are particularly concentrated in seagrass meadows adjacent to river mouths near the ocean in Moreton Bay (Young and Carpenter 1977). *Metapenaeus bennettiae* Racek and Dall, the greasyback prawn, occurs in large numbers only in seagrass areas and would therefore be decimated were the beds destroyed.

*Zostera marina* L. on the eastern coast of America and the coasts of Europe died back dramatically in the early thirties and there was an enormous decrease in associated animals found in these areas (Rasmussen 1977). The dieback of *Z. marina* was associated with an increase in a fungus (*Labyrinthula*) apparently due to a temperature rise of a few degrees in the water of the Gulf Stream. Thus a relatively minor change in the ecosystem had caused elimination of enormous areas of *Z. marina*.

We therefore need to know the causes and be able to recognize the early symptoms of deterioration of seagrasses. Poore (1978) has described an area in Victoria from which *P. australis* has disappeared for an unknown reason, while Kirkman (1978b) has documented a case in which the decline of a seagrass bed was attributed literally to too rapid an accumulation of sand; in the latter case the reason for the rapid accumulation of sand would provide the clue to understanding the loss of seagrass. The decline of seagrass associated with the activities of man has been recorded by Cambridge (1975 and 1979) in Cockburn Sound, Western Australia. She found that, over the period 1954-79, seagrass meadows in the area were reduced from 4,000 ha to 800 (Fig. 9.19). Apart from localised mechanical damage and toxicity by effluents (Brittan 1979), the major cause of the decline has probably been through reduction of light. Larkum (1976) has suggested that reduced light may be the cause of dieback in seagrasses in Botany Bay, N.S.W. (Anon 1978). Light may be reduced for several reasons: first, an increase in nutrients in the water column may cause phytoplankton to increase, so increasing turbidity; secondly, some effluents may remain suspended in the water and so reduce light; thirdly, mechanical disturbance may cause an increased load of suspended sediments, thus cutting down light available to the seagrasses; and finally, as is probably most important in Cockburn Sound, increased nutrients in the water may lead to abnormally large populations of epiphytic algae, thus reducing light availability to the seagrass leaves.



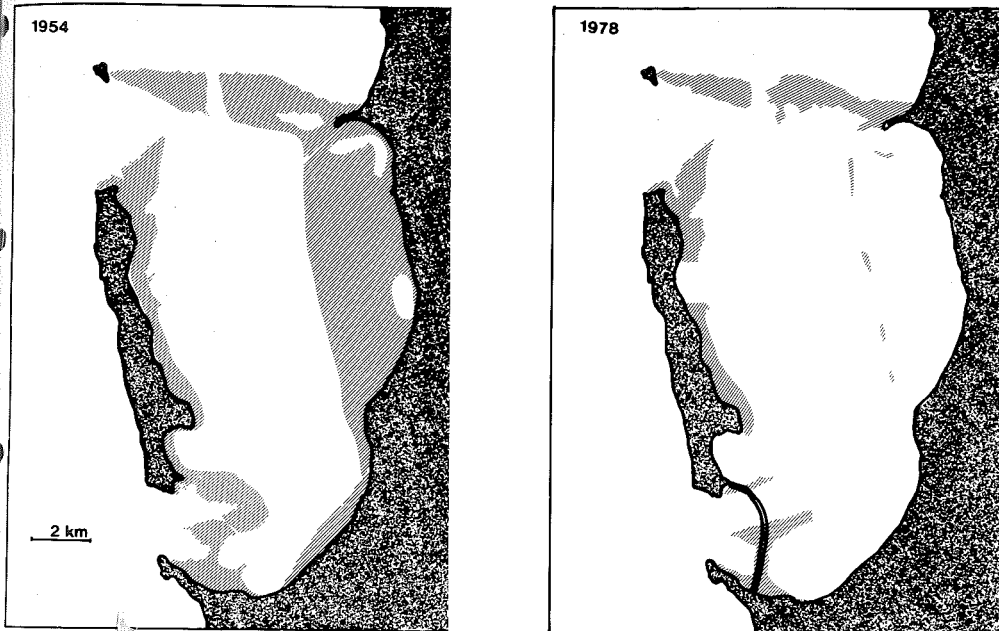


Fig.9.19 The distribution of seagrass in Cockburn Sound in 1954 (left) and 1978 (right). Redrawn from Cambridge (1979).

#### 9.10 CONCLUDING REMARKS

While much is still to be learned about the distribution of seagrasses and the magnitude of their meadows, it is clear that they constitute a major component of our native plant resources, as they occupy large areas and show high productivities.

In many ways the seagrasses resemble terrestrial plants and so many of the concepts developed by botanists for terrestrial communities—for example succession, photosynthetic efficiency, and uptake, transport, storage and retrieval of nutrients—can be profitably transposed to these submarine communities.

It is interesting to compare the seagrasses with those macroalgae which build up to large populations, and which also show high productivities (e.g. Mann, 1973). Perhaps the most striking differences are the absence of roots and the relatively low levels of epiphytes on the algae, as compared with the seagrasses. One cannot help wondering if these differences are related, and whether the inputs made by epiphyte and animal detritus to the substratum of the seagrass bed are not mutually advantageous, contributing an important element to meadow productivity, and culminating in the uptake of remineralized nutrients by the seagrass roots. While a satisfactory synthesis of the role of seagrasses in nutrient and energy cycling cannot yet be made, these processes appear to have considerable importance to the ecology of the nearshore waters of the continent.

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