PHYSIOLOGY OF PHOTOSYNTHESIS IN TWO MANGROVE SPECIES: RESPONSES TO SALINITY AND OTHER ENVIRONMENTAL FACTORS

by

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A thesis submitted for the degree
of Doctor of Philosophy in the
Australian National University

October 1981

DECLARATION

The work presented in this thesis is my own with the following exceptions.

Photosynthetic responses to light intensity (Chapter 4) were studied in collaboration with Dr Christa Critchley who collected and analysed the fluorescence data shown in Figs. 4.5, 4.6 and 4.7.

Photosynthetic responses to humidity were studied in collaboration with Dr Tom Sharkey who made the measurements on *Gossypium* and *Xanthium* shown in Fig. 7.13 and Table 7.2.

Dr Ian Cowan designed the gas exchange system and wrote the equations for determination of gas exchange rates given in the appendix.

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ACKNOWLEDGEMENTS

I wish to express my gratitude for the opportunity to study in the Department of Environmental Biology and for generous support of the thesis research by the Australian National University.

The members of my thesis committee deserve special thanks. I wish to thank Dr Ian Cowan for his assistance in developing the equipment and theory without which this project would have been impossible. I am grateful to Dr Graham Farquhar for his advise, encouragement and thoughtful criticism throughout my course of study and for patiently explaining gas exchange principles in a comprehensible manner. Dr Farquhar has provided considerable academic guidance and an invaluable insight into the physiology of photosynthesis. I am especially thankful to Professor Barry Osmond for advice and constructive criticism on this thesis and other endeavours. I have benefitted greatly from his comprehensive knowledge of plant physiology and his willingness to take the time to share it. It is a pleasure to thank Professor Bruce Thom for an introduction to the mangroves of Australia, for the opportunity to gain teaching experience in his courses and for enthusiastically supporting this research project. I also wish to thank Drs Malcolm Gill and Alison McCusker for their advice.

I am thankful for all the stimulating discussion, support and encouragement of my good friend Dr Christa Critchley, who has been an inspiration to me.

Special thanks are due to Dr Tom Sharkey who has contributed much to my understanding of gas exchange theory and practice. Dr Sharkey has helped me to develop confidence in scientific research and has

stimulated the development of many ideas. His cheerful encouragement has been much appreciated.

It is a pleasure to thank Mr Win Coupland and Dr Chin Wong for expert technical assistance and for patient instruction in gas exchange technology.

I am especially grateful to the members of the Department of Environmental Biology who provided field and technical assistance as well as made my stay in Australia a memorable and enriching experience. Special thanks are due to my friends, Dixie Nott, Bruce Wellington, Mark Stafford-Smith, Stuart Boag, Susanne von Caemmerer, Joe Holtum and Pam Hayward for much fun, cheerful support and encouragement.

I thank Mr Gary Brown for preparation of illustrations and Ms Norma Chin and Jill Hardy for typing the thesis at all hours without a complaint.

Most of all, I would like to thank my husband, Eldon, for his patience, understanding and encouragement.

To Eldon

ABSTRACT

The physiology of photosynthesis was studied in two sympatric mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, in response to variations in humidity, salinity, temperature and light. Relative contributions of photosynthetic metabolism and stomatal conductance to variation in the assimilation rates were assessed by measurement of the assimilation rate on a function of the intercellular CO_2 concentration. These measurements showed that the variation in assimilation rates in response to environmental conditions was largely due to changes in photosynthetic metabolism despite associated changes in stomatal conductance.

Photosynthetic metabolism of *Aegiceras* is more sensitive to salinity than that of *Avicennia*, and the greater sensitivity of the former is correlated with a higher Na^+/K^+ ratio in leaves. The photosynthetic characteristics are typical of C_3 plants and there is no evidence of a switch in photosynthetic pathway in response to salinity. Variation in assimilation rate and carbon allocation are the major factors determining the decline in relative growth rates with increasing salinity. The possible significance of differences in the photosynthetic characteristics of *Aegiceras* and *Avicennia* to their distribution in a temperate mangrove swamp is discussed.

Avicennia shows a broad temperature optimum which does not change with season. Gas exchange characteristics did not differ between leaves grown in understory shade or exposed environments. The possible significance of these characteristics to growth and survival of seedlings is discussed.

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CHAPTER 1

INTRODUCTION

"... and these trees are all watered up to their middle by the sea and are held up by their roots like a polyp. For whenever there is an ebb tide these can be seen ... it is clear as some think, that they are nourished by it and not by fresh water unless some is drawn by the roots from the earth, and that salt water is beneficial for them, for the roots go to no great depth."

Theophrastus, 305 BC
(translated by Bowman, 1917)

1.1 INTRODUCTION

Mangroves have fascinated botanists for more than 2,000 years. The lucid and accurate descriptions of the species and their habitats by the ancient Greeks, followed later by Moorish botanists and the New World explorers, are as appropriate today as when they were written [Bowman, 1917]. Most modern research has also been descriptive, with attention focused on the recognition of ecological relationships from pattern analysis. This work has shown mangroves to be more than botanical curiosities and to be of considerable ecological importance, as shown for example by the role of mangrove primary productivity in marine and estuarine food chains [Odum and Heald, 1972; Snedaker and Lugo, 1973]. Nevertheless, almost nothing is known of the functional interrelationships which underlie the maintenance of these swamp communities.

According to classical ecological theory, an available site is occupied progressively by groups of species, each assemblage modifying

the environment in such a manner as to be unsuitable for its own regeneration but facilitating the occupation of the site by the next group of species, and culminating in a stable, climax community [Clements, 1916, 1926]. While elements of this theory undoubtedly are true, as a whole it is not a satisfactory explanation of community development and persistence. Egler [1954] felt that successional patterns of higher plants could be explained by the initial floristic composition of the species immediately following a disturbance and the way in which relative differences in their life forms and life history characteristics interact to produce a progression of communities as well as affect the success of later colonists. Recent studies on mechanisms of succession also have stressed the importance of life history characteristics of the component species in determining the trends in dominance over time [Drury and Nisbet, 1973; Horn, 1974; Connell and Slatyer, 1977; Noble and Slatyer, 1980].

However, life history characteristics alone are not a sufficient basis on which to understand responses to variations in the physical environment. The physiological characteristics of the component species form the framework for species interactions and responses to environmental conditions which together result in recognisable ecological patterns. Thus the distribution of a species is not usually determined solely by its physiological attributes, but also by its competitive ability among other species sharing at least part of the same range of physiological capabilities [Walter, 1975]. An understanding of physiological processes in an environmental context is therefore fundamental to understanding the mechanisms underlying community dynamics.

Mangroves typically are distributed in a banded zonation pattern, although the structure and composition may vary considerably with local

physical conditions. Using the arguments of Clements [1917, 1926], the zonation pattern has been interpreted as seral stages in succession to the climatic climax, a tropical forest [Davis, 1940; Chapman, 1944 and 1970; Macnae, 1968]. According to this view, the pioneer stage is represented by the coastal zone, with more landward zones being progressively later stages in succession, thereby implying seaward motion of the system [Davis, 1940; Chapman, 1944 and 1970; Macnae, 1968]. However, this classical view is inconsistent with geological data; the predicted patterns of sediment accumulation are not always realised in successive zones [Egler, 1952] and the zonation patterns of some swamps have existed *in situ* for millenia [Thom *et al.*, 1975].

The most likely mechanism determining distribution and one consistent with current ecological theory, has been presented by Thom [1975]. He argued that mangrove distribution can be explained by the responses of the plants to externally imposed changes in habitat due primarily to past and present trends in geomorphological processes and the effects of local disruptions on these trends. These processes in land-form evolution coupled with hydrological characteristics influence several factors such as the salinity of surface and soil water and the degree of soil saturation, which form a collective gradient normal to shore [Thom, 1967]. The mangroves from an available species pool will become distributed differentially along the physical gradient as a result of individual tolerance limits and species interactions [Thom, 1967 and 1975; Thom *et al.*, 1975; Ball, 1980].

An appropriate place to begin to understand physiological processes in relation to ecological functioning is at the seedling level, because

this phase of the life history is an important determinant of ecological pattern. Obviously, it is also appropriate to begin with a simple system, and so the grey mangrove, *Avicennia marina* (Forstk.) Vierh. var. *australasica* (Walp.) Moldenke, was selected for study. *Avicennia marina* is the most widely distributed species in Australia. It occupies all habitats in swamps at higher latitudes. However, in the tropics where 35 mangrove species have been identified [Bunt and Williams, 1980], *Avicennia marina* typically occurs along the seaward fringe of swamps and in the most landward zones, where edaphic conditions may be extreme [Saenger *et al.*, 1977]. Presumably, *A. marina* would occur more widely in tropical habitats if it were not for competition from other species.

In this chapter, the population structure of a temperate mangrove community is examined in relation to environmental factors. This community contains two mangrove species, *Avicennia marina*, which is dominant, and *Aegiceras corniculatum* (L.) Blanco which occurs as scattered individuals except along tidal streams. Thus responses of *Avicennia* to environmental factors can be examined in the absence of substantial competition from other species. The purpose of this exercise is to establish a framework for placing physiological experiments regarding seedling establishment in the context of the natural environment.

1.2 CHARACTERISATION OF A TEMPERATE MANGROVE SWAMP

1.2.1 Study Site

The mangrove swamp covers most of the tidally influenced portion of the Cullendulla Creek drainage basin (Fig. 1.1) which discharges into Bateman's Bay in New South Wales (35°42'S, 150°12'E). The spring

Fig. 1.1: Map and aerial photograph of the Cullendulla Creek study site. The photograph was taken in April, 1972. Scale 1cm = 100 m. Overlay shows the position of the transect (solid line) extending from the creek to the inland edge of the swamp. Letters denote the location of seedling planting sites in the tree (A), coppice (B), shrub (C) and bare zones (D).

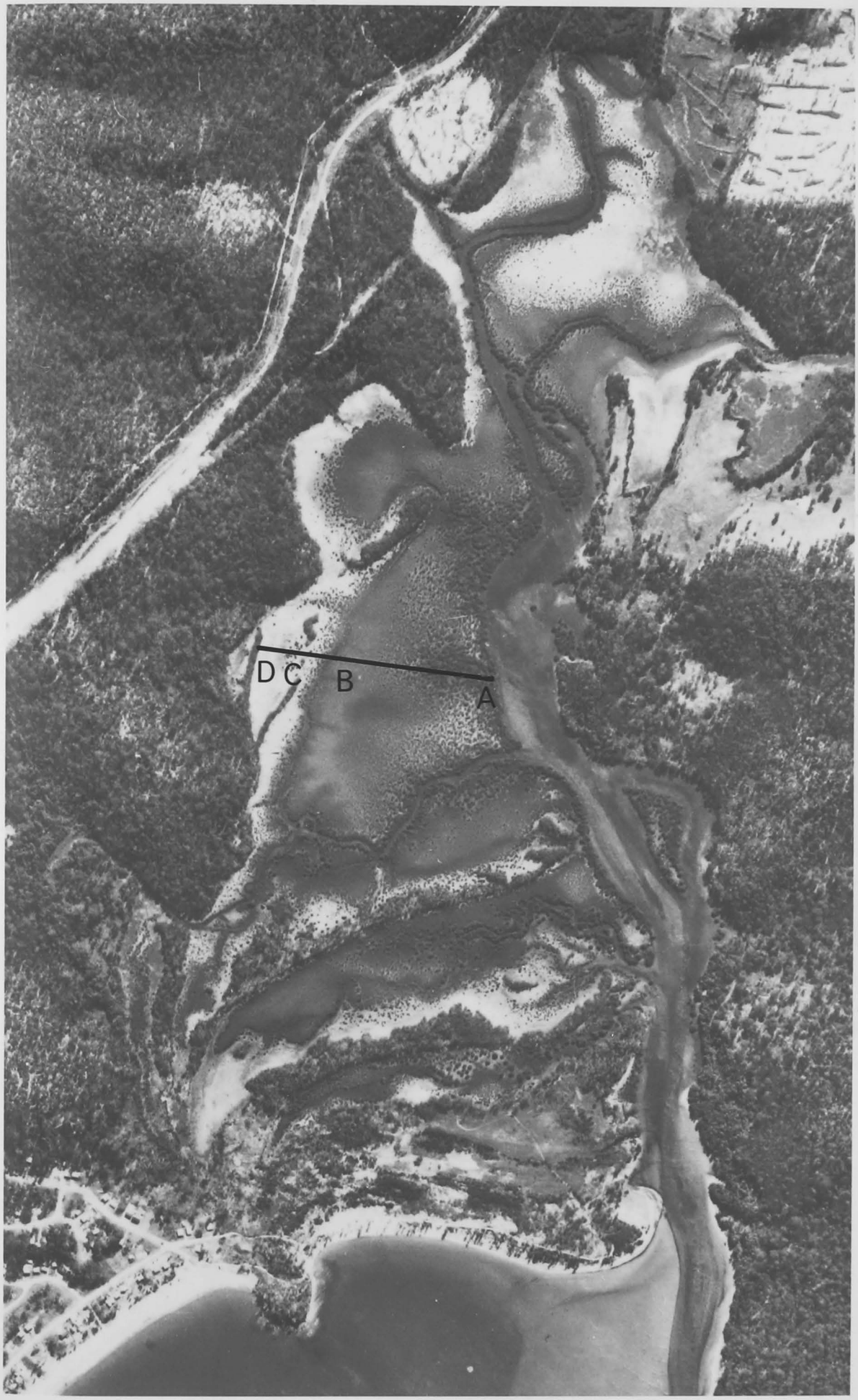
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Table 1.1

Summary of climatic data from Moruya Heads weather station. The station is located on the coast at 11 m above MSL at 35°55'S 150°09'E. All data are from Kalma and McAlpine [1978].

Parameter	Month												Annual
	J	F	M	A	M	J	J	A	S	O	N	D	
Rainfall (mm) from 1911-1970													
Mean	103	84	104	83	99	88	57	51	57	72	78	84	960
Highest	456	434	348	353	867	346	259	216	238	364	260	254	1823
Lowest	1	5	3	4	0	1	0	3	3	6	1	6	544
Temperature (C)													
Highest	43.9	41.7	40.0	32.8	29.4	23.9	25.6	30.0	34.4	37.2	38.9	42.2	43.9
Mean max.	23.0	23.6	22.7	20.8	18.4	16.3	15.6	16.5	18.2	19.6	20.7	22.1	19.8
Mean	19.6	20.2	19.1	16.8	14.1	11.9	11.1	11.7	13.5	15.4	16.9	18.6	15.7
Mean min.	16.2	16.7	15.4	12.8	9.8	7.5	6.5	6.9	8.8	11.2	13.1	15.0	11.7
Lowest	8.3	7.2	6.1	3.3	2.2	0.6	-0.5	1.1	0.6	3.3	4.4	3.9	-0.5
Av. index													
RH(%)*	73	74	73	70	67	65	64	64	68	70	73	75	70
Evaporation													
(mm)	135	108	101	81	60	64	68	79	90	108	117	132	1143

* Average index relative humidity is the ratio of the average 9 am vapour pressure to the saturation vapour pressure at the average mean temperature.

tidal range is approximately 2m. Both the catchment area and the annual rainfall (~960 mm) are small, the latter being fairly evenly distributed throughout the year (Table 1.1). Hence, the creek system is largely maritime, with the creek salinities near the upper reaches of the study site typically ranging from 28 to 30‰ (ie. 428 to 460 mM Cl^-)[Kalma and McAlpine, 1978].

Selection of study sites was based on preliminary reconnaissance of the hydrologic and floristic characteristics in the general area. Study sites were then selected in what were considered to be representative areas of the forest (Fig. 1.1).

Vegetation was analysed by standard field techniques. All living and dead vegetation, except seedlings, was recorded and the heights and basal diameters were measured in 10 x 10 m quadrats along a 500 m transect extending the width of the swamp as shown in Fig. 1.1. Seedlings were counted in ten quadrats, 1 x 1 m, within the larger quadrat, with the former being chosen at random from a grid. In areas that supported very dense vegetation, the quadrat size was reduced to 5 x 5 m with a subset of five 0.7 x 0.7 m quadrats for counting seedlings. Individuals were considered to be mature if they bore flowers. Immature vegetation which showed secondary growth such as stem elongation, thickening, branching and leaf development beyond that growth initially produced by seedlings was classified as sapling.

Samples of surface and ground water were collected at 10 m intervals along the transect at low tide and the Cl^- content was measured by silver titration with a Buchler-Cotlove chloridometer.

1.2.2 General Description of the Vegetation

The forest is composed almost entirely of the grey mangrove, *Avicennia marina*, with a few scattered shrubs of the river mangrove, *Aegiceras corniculatum* (L.) Blanco, occurring mainly along creek margins. The morphology of *Avicennia* varies enormously at different locations in the swamp and these structural differences may be used to distinguish habitats. On this basis, the vegetation may be classified into five zones which are oriented roughly parallel to the shore: mudflat, tree, coppice, shrub and a bare zone (Fig. 1.2).

1.2.2.1 Mudflat Zone

Mudflats largely are bare except for scattered patches of seagrasses in depressions which remain covered with water even at the lowest tides (Fig. 1.2A). Saplings are encountered occasionally on the flats along Cullendulla Creek, even though the plants are submerged completely during high tides, but there are no saplings in the mudflat area along the transect (Fig. 1.3). Seedlings are scattered widely over the mudflat, mostly in seagrass patches, but some occur in shallow portions of the creek in which they would not be exposed even at the lowest tides. These and most other mudflat seedlings developed to the four to six stage and usually persisted for approximately six to twelve months.

1.2.2.2 Tree Zone

The margins of Cullendulla Creek and lesser drainage are bordered by a zone of well developed trees of *Avicennia* with scattered shrubs of *Aegiceras* (Figs. 1.1, 1.2B). Numerous *Avicennia* seedlings at the four to six leaf stage of development are scattered over the forest floor, but saplings are rare, occurring only beneath breaks in the

Fig. 1.2: Vegetation along the transect. A. Mudflats exposed at low tide along Cullendulla Creek. Note scattered seedlings of *Avicennia* (light colour) and abundant pneumatophores in foreground. B. Mature, well developed trees of *Avicennia* along creek margin. C. Vigour of trees diminishes with increasing distance from creek system. D. Die-back and coppicing reduce the canopy level, making the trees become more like shrubs. E. Dense covering of extremely stunted *Avicennia*. F. Large shrubs of *Avicennia* with dense layer of seedlings beneath the parent plant and scattered seedlings in exposed areas. G. Widely spaced shrubs of *Avicennia* with seedlings and saplings of *Avicennia* near transition with bare zone visible in foreground. H. Bare zone separating mangrove swamp from upland Eucalypt forest. Sparse seedlings and saplings of *Avicennia* and occasional clumps of *Salicornia* are visible in foreground.

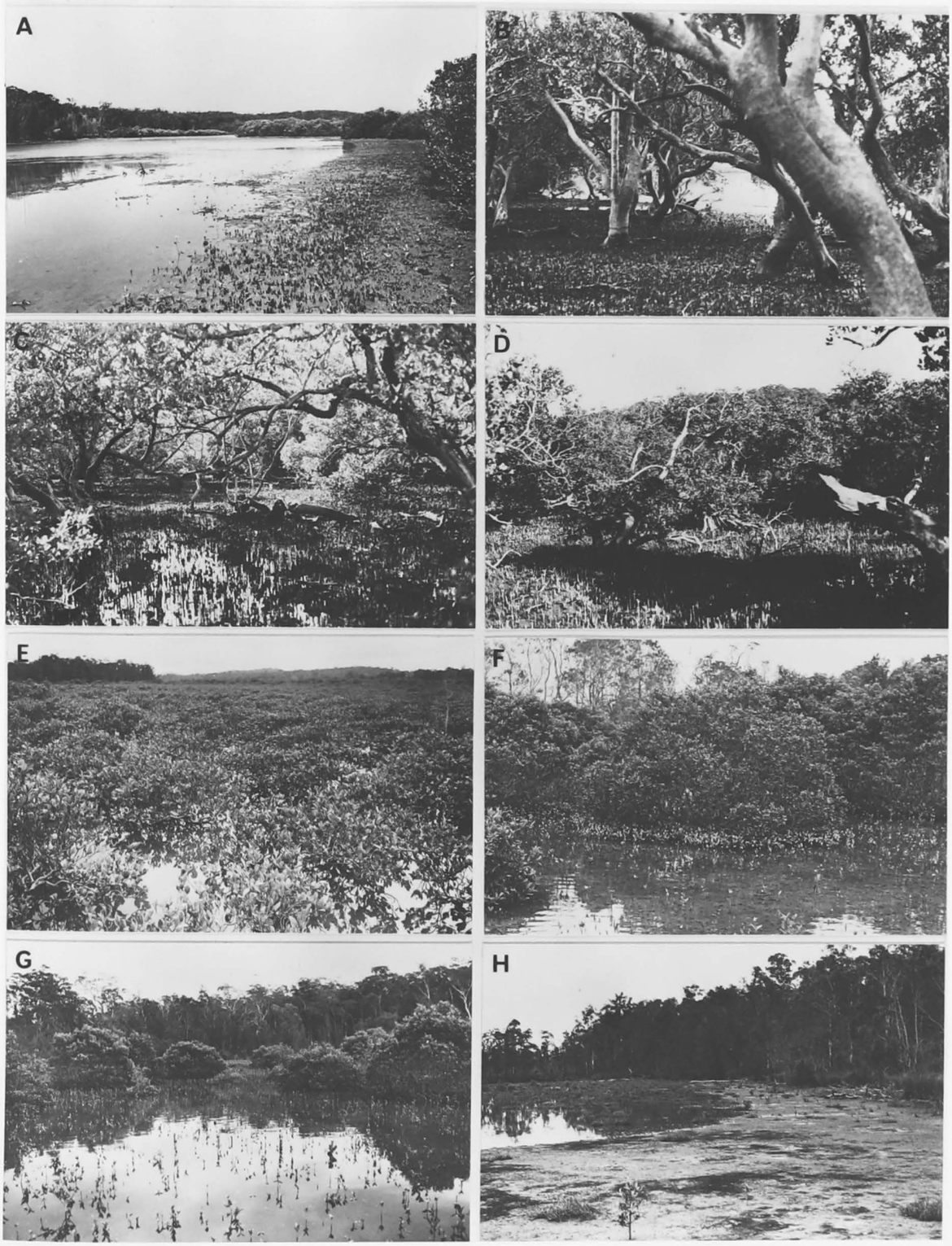
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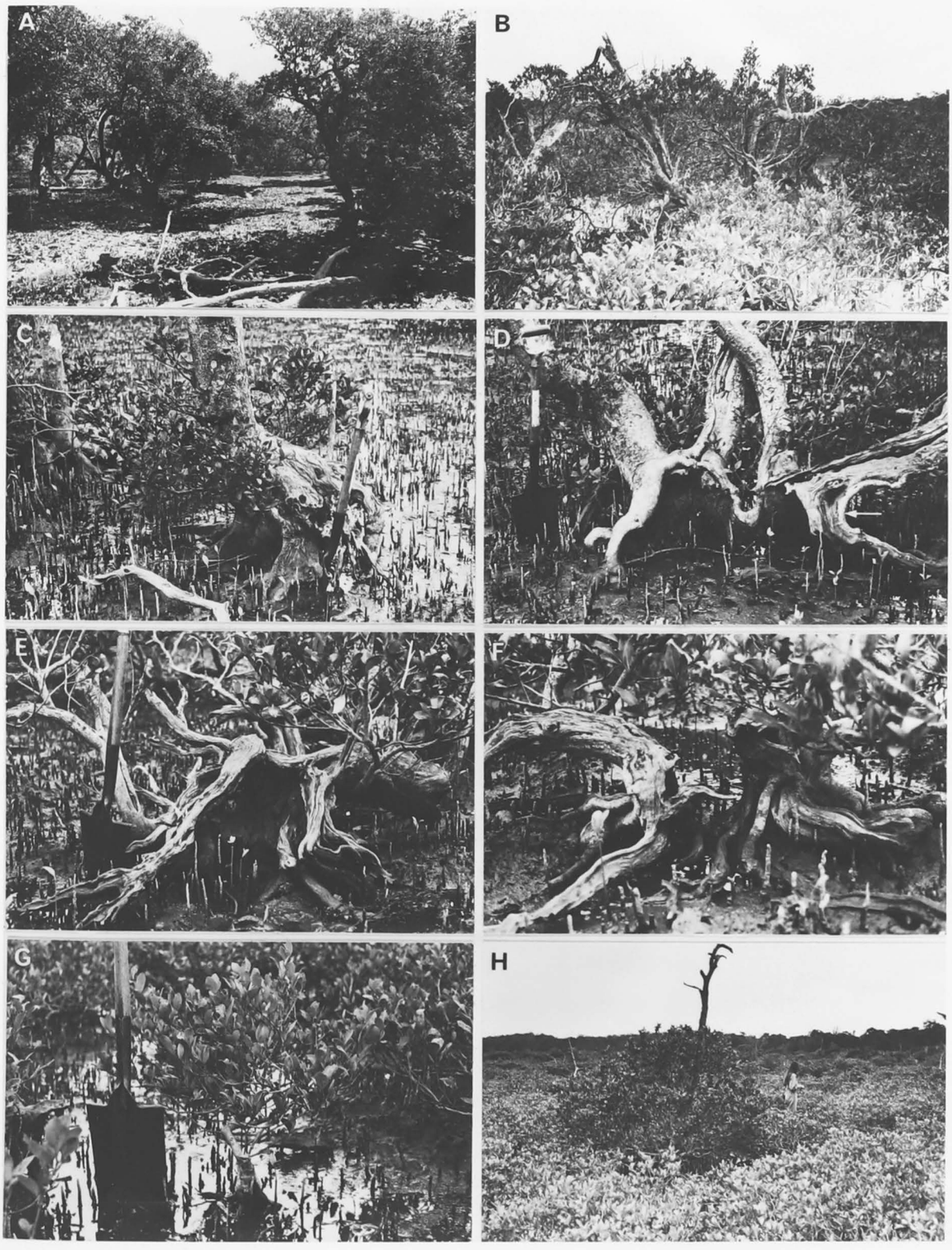
Fig. 1.3: Progression of morphological changes in *Avicennia* along transect. A. Trees bordering tributary of Cullendulla Creek. B. Die-back of crown and coppicing at lower levels on the trunk. C. Coppicing at base of trunk. D. Trunk split and coppicing at base. Living connections are maintained with the root system and are visible in the photograph as lighter coloured areas along the margins of decaying wood (arrow). E. Die-back and coppicing gives rise to an extremely stunted and gnarled form of vegetation, resembling living drift wood. F. Trunks split giving rise to several individuals. G. A remnant of what was once a tree. H. Remaining evidence that trees previously occupied the site which now supports stunted vegetation, apparently coppice in origin. The bleached trunks of other dead trees are visible in background and these are in the transition from trees to coppice. For reference, height of person is 178 cm.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canopy. In another area supporting vegetation similar to that described above, a dense population of saplings, primarily *Avicennia*, was found where several mature trees had died leaving a large gap in the canopy. Chloride concentration in the vicinity of the creek system ranged from 400 to 535 mM (ie. 14.4 to 19.3‰ or 75 to 100% of the Cl^- in seawater, respectively).

The tributary along which the transect runs gradually decreases in depth until only a slight depression in the soil surface is recognisable at 150 m. This marks the beginning of transition in the growth of *Avicennia* from a well developed tree to an extreme form of stunted growth. There is an increase in the density of seedlings and saplings of *Avicennia* (Fig. 1.4, 150-270 m), but there is a marked loss of vigour in the mature vegetation with increasing distance from the creek system. *Aegiceras* disappears (Fig. 1.4, 150-270 m) while *Avicennia* exhibits drastic changes in morphology. The upper branches of most trees are dead with new branches developing at a lower height (Fig. 1.2C and D), thereby lowering the canopy level (Fig. 1.5A). The canopy is also more discontinuous and uneven, fully exposing much of the forest floor to the sun (Fig. 1.2C and D).

The deterioration of the tree form increases with distance from the creek. Coppicing occurs at progressively lower heights (Fig. 1.5, 150-270 m). Trunks which were of substantial circumference are hollow and often split into several sections, each maintaining a living connection to the roots which can be distinguished easily from the dead wood (Fig. 1.3D-F). Coppice growth develops from each section. This pattern continues progressively along the transect culminating in a form of extremely stunted vegetation which largely appears to be

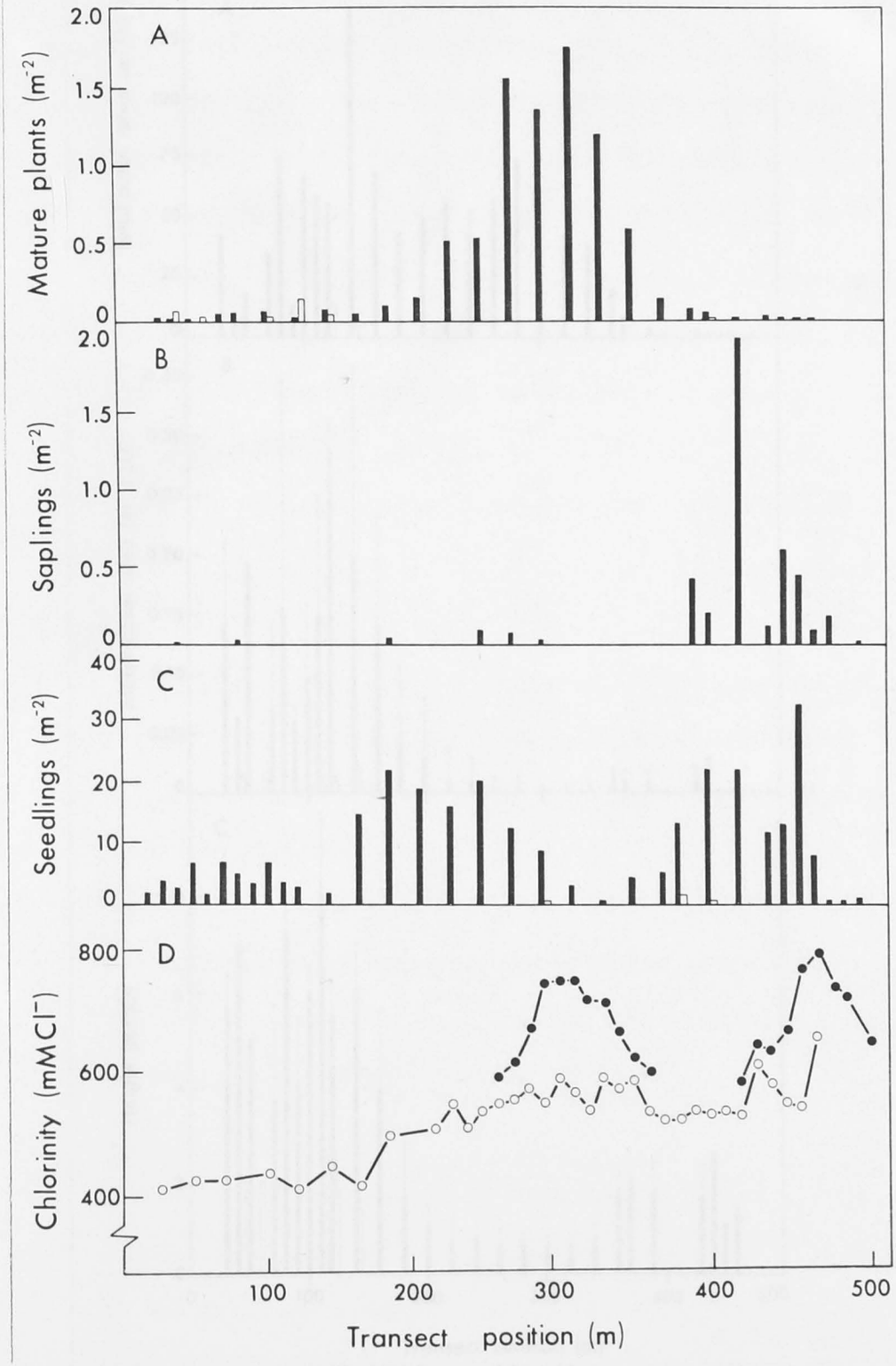


Fig. 1.4: Population structure along the transect in relation to the chlorinity of surface (o) and ground (●) water. *Avicennia*, solid bars, *Aegiceras*, open bars.

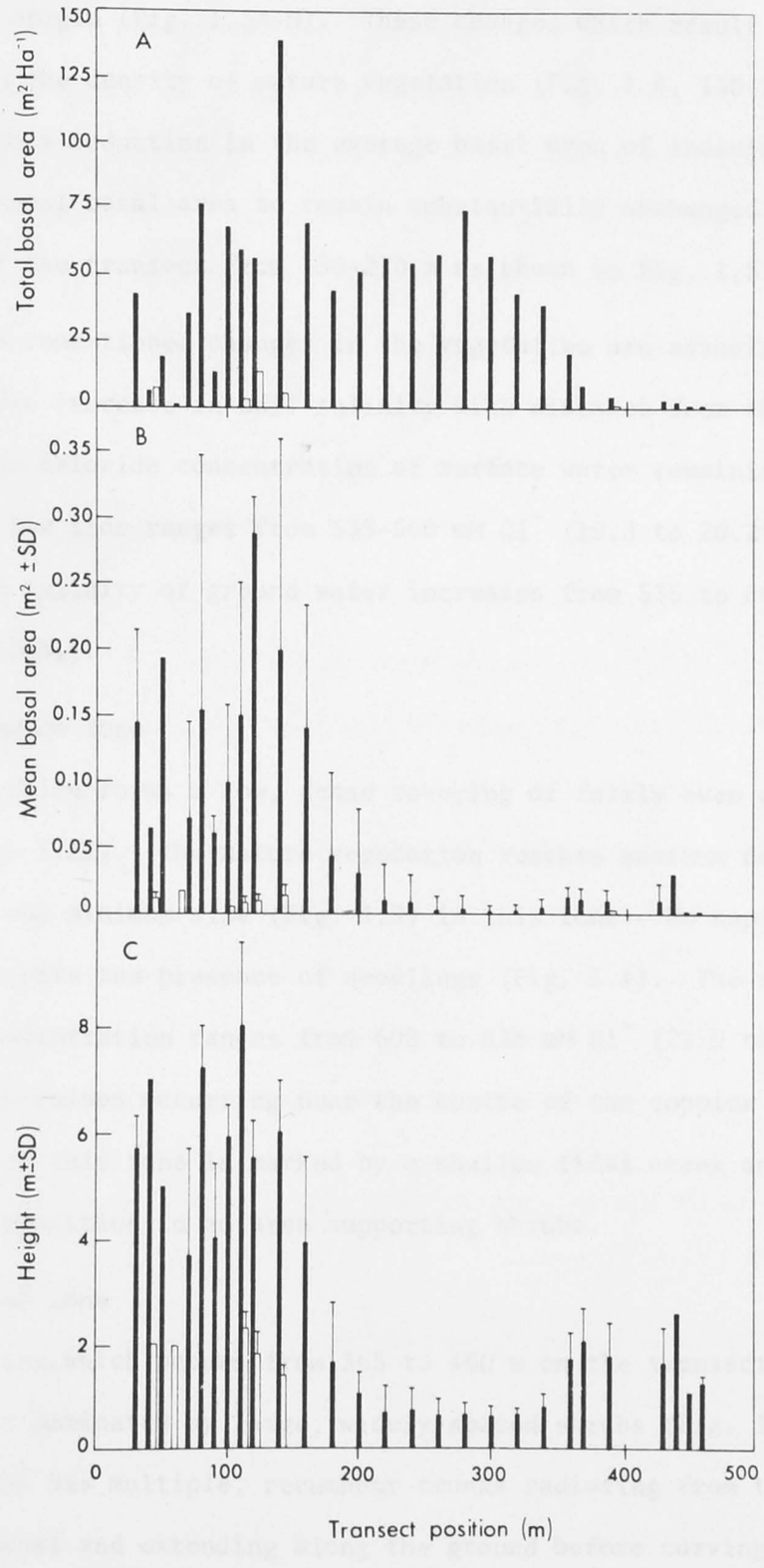


Fig. 1.5: Vegetation properties along the transect. *Avicennia*, solid bars; *Aegiceras*, open bars. Line denotes SD.

coppice in origin (Fig. 1.3A-H). These changes which result in an increase in the density of mature vegetation (Fig. 1.4, 150-270 m) coupled with a reduction in the average basal area of individuals cause the total basal area to remain substantially unchanged over the area of the transect from 150-270 m as shown in Fig. 1.5.

The aforementioned changes in the vegetation are associated with a progressive increase in soil salinity with distance from the creek system. The chloride concentration of surface water remaining in puddles at low tide ranges from 535-560 mM Cl^- (19.3 to 20.2‰) whereas the salinity of ground water increases from 535 to 600 mM Cl^- (19.3 to 21.6‰).

1.2.2.3 Coppice Zone

The coppice forms a low, dense covering of fairly even canopy height (Fig. 1.2E). The mature vegetation reaches maximum density (Fig. 1.4) and minimum size (Fig. 1.5) in this zone. No saplings were observed despite the presence of seedlings (Fig. 1.4). The soil chloride concentration ranges from 608 to 836 mM Cl^- (21.9 to 30.1‰), with maximum values occurring near the centre of the coppice zone. The border of this zone is marked by a shallow tidal creek and there is abrupt transition to an area supporting shrubs.

1.2.2.4 Shrub Zone

This area, which occurs from 365 to 460 m on the transect (Figs. 1.4 and 1.5), is dominated by large, widely spaced shrubs (Fig. 1.2F and G), each of which has multiple, recumbent trunks radiating from the centre at ground level and extending along the ground before curving upwards. These support a dense canopy which covers the shrub completely to ground level. Seedlings are distributed densely (ie. as many as 235 m^{-2})

beneath the shrub canopy and are scattered much less densely over exposed areas. Saplings are numerous in exposed areas, but are not found in the shade of shrubs. Shrubs and seedlings of *Aegiceras corniculatum* are distributed sparsely throughout the area (Fig. 1.4). The density of seedlings and saplings of *Avicennia* increases near the abrupt transition to a bare zone (Fig. 1.4). The concentration of chloride in soil water increases with distance from the creek to a maximum of 690 mM Cl^- (24.8‰) near the transition to the bare zone.

1.2.2.5 Bare Zone

The bare zone (Fig. 1.2H) borders an upland Eucalypt forest and consists largely of a hard mud pavement with intermittent covering by a blue-green algal mat. A few isolated seedlings and saplings of *Avicennia*, as well as occasional individuals of *Salicornia*, are found in this area (Figs. 1.4 and 1.5). The chloride concentration in soil water was maximum (ie. 800 mM Cl^- or 28.8‰) near the transition with the shrub zone and declined to 650 mM Cl^- (23.4‰) near the landward edge of the swamp. Soil chlorinities as high as 1700 mM Cl^- (61.2‰) were recorded in other sampling periods.

1.3 Ecological and Physiological Interactions in the Mangrove Swamp

1.3.1 Dispersal

The floating behaviour of propagules gives some insight into the potential for tidal distribution. Propagules of *Aegiceras* and *Avicennia* were collected from mature individuals along Cullendulla Creek and transported in darkness to the laboratory. The propagules were sorted and placed in tanks containing 5ℓ of either 10, 50 or 100% filtered seawater at 25C. Records were kept of the time required for the propagules to sink and the results are shown in Table 1.2.

Table 1.2

Floating of *Avicennia* propagules in 10, 50 and 100% seawater. Pericarps were either removed (-) or left attached (+) to the propagule at the start of the experiment. Numbers are those remaining afloat from a total of 10. All *Aegiceras* propagules sank at the start of the experiment.

Time (hrs)	Solution (% seawater)					
	10%		50%		100%	
	+	-	+	-	+	-
0	10	1	10	0	10	3
1	6	0	9	0	9	3
2	1	0	5	0	9	3
3	0	0	2	0	9	1
4	0	0	1	0	7	1
6	0	0	1	0	4	0
8	0	0	1*	0	0	0

* continued to float for 24 hrs.

Avicennia appears to have a much greater capability for dispersal by tides than *Aegiceras*. Propagules of the former species float for several hours following their release into seawater whereas those of *Aegiceras* are not buoyant (Table 1.2). Propagules of *A. marina* in the present study lost their buoyancy much more rapidly than those of a South African population, which were reported to float for as long as six days in seawater [Steinke, 1975]. The relatively brief floating period may contribute to the uneven distribution of *Avicennia* seedlings (Fig. 1.4), with seedlings tending to be clustered beneath parent plants (Fig. 1.2F and G).

1.3.2 Establishment

Development of *Avicennia* is retarded until the propagule is stranded and then proceeds rapidly [McMillan, 1971]. *Avicennia* propagules can become established in all areas of the swamp whereas those of *Aegiceras* become established only in limited areas of the swamp as shown by the distribution of seedlings along the transect (Fig. 1.4). To supplement these observations, propagules of both species were positioned in representative habitats to see whether propagules naturally reaching those locations could become established.

Propagules of *Aegiceras* and *Avicennia* from well developed shrubs and trees, respectively, growing along Cullendulla Creek were collected and sorted to give 600 propagules of similar size for each species. Propagules of *Avicennia* were soaked in creek water until they lost buoyancy. The propagules were laid out in plots in six habitats: under exposed (1) and shaded (2) conditions in an area supporting trees, under exposed conditions in an area of coppice growth (3), under exposed (4) and shaded (5) conditions in an area

dominated by shrubs and under exposed conditions in a largely barren area (6). One hundred propagules of each species were planted in five 1 x 1 m plots in each habitat and the site locations are shown in Fig. 1. Records were kept of survival and development. Results are shown in Table 1.3.

More *Avicennia* than *Aegiceras* were established by the end of the first month (Table 1.3). The former were well rooted with the first leaf pair nearly fully expanded whereas the latter had only initiated root growth with the hypocotyl just beginning to lift from the ground. By the end of the second month, *Avicennia* seedlings had reached the four to six leaf stage of development and thereafter showed no further shoot growth. In contrast, *Aegiceras* propagules failed to develop beyond the stage of initial hypocotyl extension and primary root development. Although some of the propagules survived for as long as six months (Table 1.3), none of them ever became established seedlings.

No precautions were taken in this experiment to exclude predators and they definitely influenced the results. The effects were most obvious in the bare zone where none of the propagules showed signs of development. Many may have been eaten by crabs as parts of *Avicennia* cotyledons were found in the entrances to crab holes and *Aegiceras* propagules bore marks of having been grazed. Despite these negative results, establishment of *Avicennia* seedlings in the bare zone is not impossible as shown by the presence of a few seedlings and saplings (Fig. 1.4).

The widespread distribution of *Avicennia* seedlings at the four to six stage of development throughout the swamp (Fig. 1.4), even in areas as obviously unsuitable for further growth as permanent

Table 1.3

Seedling survival under different conditions of the Cullendulla swamp system. Values are mean percent of individuals remaining in five plots.

Genus	Habitat		Months				
	Zone	Light	1	2	4	6	12
Aegiceras	tree	shaded	2 ± 2	0	0	0	0
	tree	exposed	42 ± 8	12 ± 9	1 ± >.5	0	0
	coppice	exposed	26 ± 18	10 ± 6	1 ± >.5	0	0
	shrub	shaded	58 ± 13	33 ± 19	4 ± >.5	3 ± 7	0
	shrub	exposed	28 ± 22	19 ± 13	9 ± 2	4 ± 7	0
	bare	exposed	2 ± 2*	0	0	0	0
Avicennia	tree	shaded	82 ± 12	79 ± 14	75 ± 6	73 ± 14	73 ± 14
	tree	exposed	92 ± 5	70 ± 13	64 ± 14	61 ± 18	59 ± 22
	coppice	exposed	87 ± 9	81 ± 11	64 ± 10	57 ± 14	56 ± 13
	shrub	shaded	78 ± 4	77 ± 15	77 ± 15	75 ± 13	70 ± 12
	shrub	exposed	75 ± 15	67 ± 19	48 ± 17	47 ± 18	46 ± 12
	bare	exposed	28 ± 19*	0	0	0	0

* propagules present, but no sign of development

submergence, suggests that establishment and early growth depends upon cotyledonary reserves. This may minimize the effects of competition during establishment, perhaps contributing to the occurrence of dense aggregations of nearly even sized seedlings beneath parent plants or along strand lines. The role of cotyledonary reserves in seedling establishment is investigated in Chapter 2.

In contrast, establishment by *Aegiceras* is rare as shown by its failure to develop in experimental plots (Table 1.3) as well as the general scarcity of seedlings in the swamp (Fig. 1.4). Of course, these observations are complicated by the extent to which other factors, such as predation, might have influenced seedling establishment. Nevertheless, *Aegiceras* generally is associated with less saline environments than those along Cullendulla Creek and is less tolerant of salinity than *Avicennia*, at least at the seedling stage [Clarke and Hannon, 1970]. A preference for lower salinities would be consistent with the occurrence of *Aegiceras* in the immediate vicinity of the creek system and along the landward edge of the swamp where salinities might periodically be lowered by runoff from upland forests. Differences in salinity tolerance at the propagule stage may be a major factor affecting the relative abundance of seedlings of *Avicennia* and *Aegiceras* in a primarily maritime swamp system and this is the subject of Chapter 2.

1.3.3 Persistence

Competition for resources becomes critical as cotyledonary reserves are exhausted and the seedlings become fully autotrophic. *Avicennia* seedlings failed to develop beyond the initial four to six leaf stage of development in most cases, suggesting that resources required for further growth were not available. However, *Avicennia* seedlings are

able to persist with no obvious growth for lengthy periods, with persistence being greater under shaded then exposed conditions (Table 1.1), although saplings were not observed in shaded environments. These shade suppressed seedlings are, however, viable as it was observed during later physiological experiments that even seedlings which had shown no shoot growth for as long as 18 months, initiated new growth following transplantation to buckets in which competition was eliminated.

Some minimum level of resources must be required for persistence; thus it might seem anomalous that seedlings should persist longer under shaded than exposed conditions. However, these differences in persistence may be due to an interaction between temperature and light intensity. The Cullendulla swamp is near the southern limit of distribution for *Avicennia* [Saenger *et al.*, 1977] and temperature has been found to be a factor limiting photosynthesis by *A. marina* in Westernport Bay [Attiwill and Clough, 1980]. It may be that exposure to extremes of temperature and light is more detrimental under conditions in which other factors, such as competition, limit growth. The combined effects of leaf temperature and light intensity on the gas exchange characteristics of field grown *A. marina* seedlings are investigated in relation to the microclimate experienced at Cullendulla Creek in Chapter 3.

1.3.4 Growth

The successful development of an established seedling into a reproductive member of the community, provided that resources are available to support new members, will depend largely on the effects

of environmental factors on growth processes as well as competition and predation. In the region supporting a well developed swamp forest (30 to 150 m on the transect, Fig. 1.4), seedlings of *Avicennia* were abundant but saplings were rare, occurring only beneath discontinuities in the canopy which allowed ample sunlight to penetrate to the forest floor. A dense population of saplings, primarily *Avicennia*, was found in another area in which several mature trees had died leaving a large gap in the canopy. Of course, interpretation of these observations is complicated by the degree to which factors such as competition for resources other than light, or predation, may affect survival and growth in exposed and shaded habitats. Nevertheless, these observations suggest that light may be a factor limiting growth, and photosynthetic responses to different light levels are investigated in Chapter 4.

Salinity is another factor which may affect the growth of seedlings. Of course, salinities experienced under field conditions are not constant but may vary in different time scales. At one extreme, there are long-term exposures to the average salinities prevailing in a zone, while at the other extreme, salinities may fluctuate during tidal cycles or periods of rainfall.

The soil salinity appears to have increased in certain areas of the Cullendulla Creek swamp system. The vegetation in these hypersaline areas has undergone drastic changes in morphology. The change in growth form from trees to shrubs may be primarily in response to increasing salinity, but other factors are likely to be involved. Humidity may play an important role in the response to salinity because it influences the rate at which water is lost

relative to carbon gain. The interaction of long-term conditions of salinity and humidity on growth is examined in Chapter 5. This work is extended in Chapter 6 to determine the relative contribution of responses of stomata and photosynthetic metabolism to the changes in gas exchange characteristics with long-term variation in salinity and humidity. A similar analysis is then applied to the changes in gas exchange characteristics in response to short-term variation in salinity and humidity in Chapter 7.

Conditions experienced by *Avicennia* at Cullendulla Creek have been surveyed in the present chapter. In subsequent chapters, the physical factors are examined individually to see how they might influence propagule establishment and later growth of seedlings. In the final Chapter (8) the interaction of these individual responses is considered with a view to better understanding the relation of mangrove seedlings to physical aspects of their environment. The possible limitations on community structure imposed by these functional characteristics is then discussed.

CHAPTER 2

DEVELOPMENT AND ION RELATIONS OF PROPAGULES

"Seldom, in nature, is man permitted to make observations that reflect a more intricate and beautiful relationship to the environment than those which pertain to the mangrove. Here is a plant growing in the most unfavorable of environments, in the salty water of the ocean, exposed to the buffeting of waves and storms, and the burning of sun and wind. It is entirely logical that to succeed on such a site, evolution would have endowed the species with cunning and curiously contrived adaptations. Let us examine one phase of the life history of this plant - the seedling."

Frank Egler, 1948

2.1 INTRODUCTION

The distribution of *Aegiceras* and *Avicennia* in the Cullendulla Creek swamp system suggests that salinity may limit the establishment of seedlings of the former but not the latter, except in areas of extreme hypersalinity (Chapter 1). This is consistent with observations of the effects of salinity on the growth of *Aegiceras* and *Avicennia* propagules [Connor, 1969; Clarke and Hannon, 1970]. The present investigation is an extension of these earlier growth studies and seeks a better understanding of the anatomical and physiological attributes of the propagules of *Aegiceras* and *Avicennia* in relation to their differences in growth and development into seedlings under different salinity regimes.

2.2 MATERIALS AND METHODS

2.2.1 Plant Material

Mature propagules of *Aegiceras corniculatum* and *Avicennia marina* were collected from parent plants growing along the Cullendulla Creek study site (Chapter 1). Only propagules of average weight (ie. *Aegiceras* 0.46 to 0.54g; *Avicennia* 5.6 to 6.4g) were used in the present study. These weights are averages for the population of propagules produced by vigorous parent trees; propagules of stunted plants are smaller.

2.2.2 Growth Studies

The propagules were cultivated on sand beds sub-irrigated with 10, 50 and 100% filtered seawater, which in its undiluted state contained 535 mM Cl^-, 457 mM Na^+ and 10 mM K^+. Water levels were maintained by daily addition of fresh water and solutions were changed weekly. The beds were kept in a growth cabinet adjusted to give day/night leaf temperatures of 25/20C, 12 hr photoperiods with average quantum flux density at leaf height of 400 $\mu E\ m^{-2}\ s^{-1}$ and a leaf to air vapour pressure difference of 12 mbar. One hundred propagules of each species were grown under each salinity treatment. A group of five seedlings (which were selected at random using random number tables) was harvested at the start of the experiment and thereafter at weekly intervals from each salinity treatment. The total study period was eight weeks for *Aegiceras* and six weeks for *Avicennia*. The seedlings were divided into four parts, ie. storage tissue (cotyledon or hypocotyl), roots, stems and leaves. There were washed in distilled water for one minute, blotted dry and weighed. The

parts were then oven dried at 35C and analysed for total Cl^-, Na^+ and K^+ as described in the appendix.

Measurements of water use and salt secretion were made during development of a separate set of propagules of *Aegiceras* and *Avicennia* grown in parallel with the aforementioned growth experiment. Five propagules of each species were grown in each salinity treatment. The propagules were placed in plastic containers (volume 200 ml for *Aegiceras* and 500 ml for *Avicennia*) covered with aluminised mylar and fitted with soft plastic lids for hydroponic culture in 10, 50 or 100% filtered seawater. The solution level was maintained by the addition of fresh water every other day and solutions were changed weekly. Records were kept of the total water loss. Measurements of total secretion of Cl^-, Na^+ and K^+ ions from leaves and cotyledons over the 12 hr photoperiod were made at three day intervals by the method described in the appendix.

2.2.3 Cotyledon Removal

Propagules of *Avicennia* were grown on sand beds sub-irrigated with 10, 50 and 100% filtered seawater in a growth cabinet as previously described. One hundred propagules were used in each salinity treatment. The cotyledons were removed from groups of five seedlings selected at random from each salinity treatment at the start of the experiment and at weekly intervals for four weeks. These seedlings together with a group of five untreated seedlings were harvested after six weeks, separated into parts, dried at 35C and weighed.

2.2.4 Anatomical Observations

Hand sections of fresh propagules were prepared and photographed on a Zeiss photomicroscope.

2.2.5 Gas Exchange Measurements

Gas exchange measurements were made on intact, attached leaves with a conventional open gas exchange system as described in the appendix. Measurements were made on one leaf of the first leaf pair of the hydroponically grown seedlings. The assimilation rate was measured as a function of the intercellular CO_2 concentration (c_i) by varying the external CO_2 concentration according to the sequence 330, 200, 100 and 50 µl l^{-1}. Other conditions were similar to those experienced in the growth chamber, ie. leaf temperature 25C, quantum flux density 500 µE m^{-2} s^{-1} and leaf to air vapour pressure difference of 12 mbar.

2.3 RESULTS

2.3.1 Anatomical Characteristics

The propagule of *Aegiceras* is less anatomically complex than that of *Avicennia* (Fig. 2.1A). The surface of the hypocotyl in *Aegiceras* is covered with a heavily cutinised epidermis which lacks both stomata and salt secretion glands (Fig. 2.2A). A narrow hypodermal layer lies directly beneath the epidermis (Fig. 2.2C) with the remainder of the hypocotyl consisting of thick walled cells densely packed with chloroplasts (Fig. 2.2E).

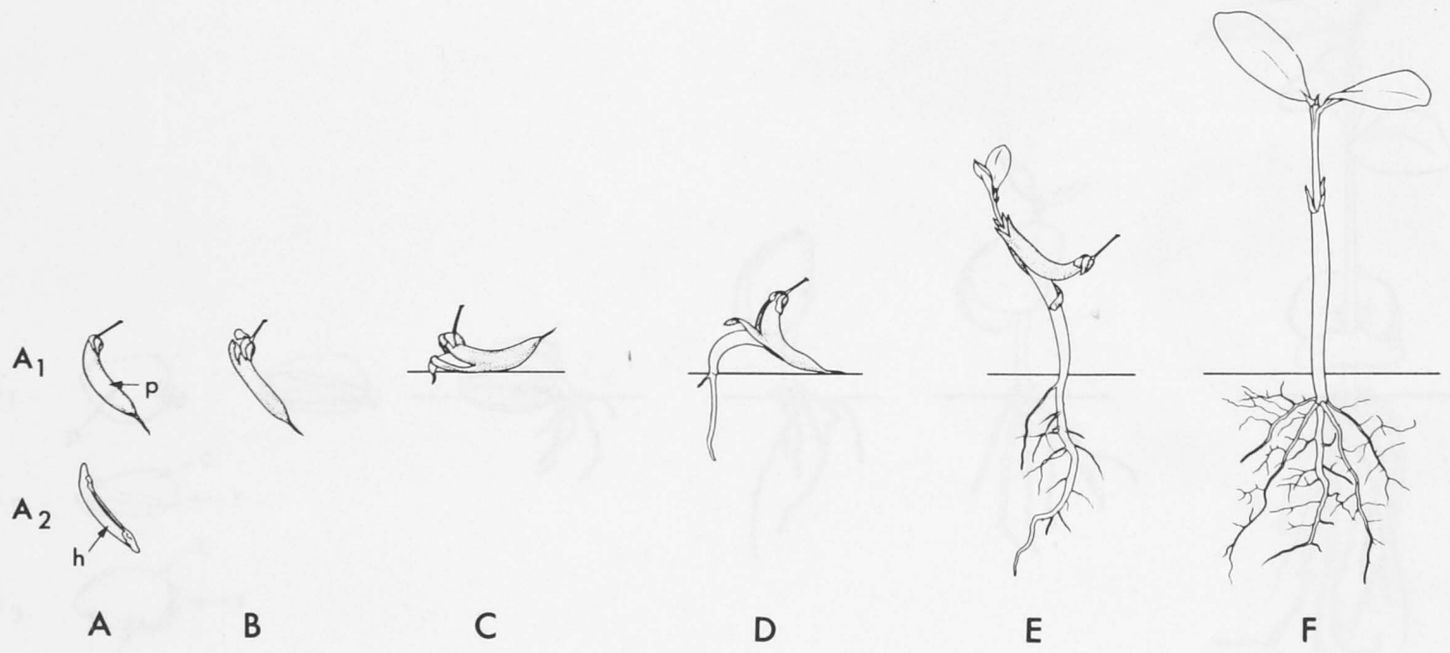


Fig. 2.1A Stages in development of *Aegiceras* propagules into seedlings. The propagule is anatomically simple (A) with a pericarp (P) enclosing the embryo or hypocotyl (h). The cotyledons are concealed by the integument and endosperm which remain like a sheath over the tip of the hypocotyl. Soon after release from the parent tree, the hypocotyl emerges (B) and primary roots begin to develop (C). The propagule arches (D) and leaves emerge when the seedling becomes upright (E). A mature seedling (F). Scale x 1/2.

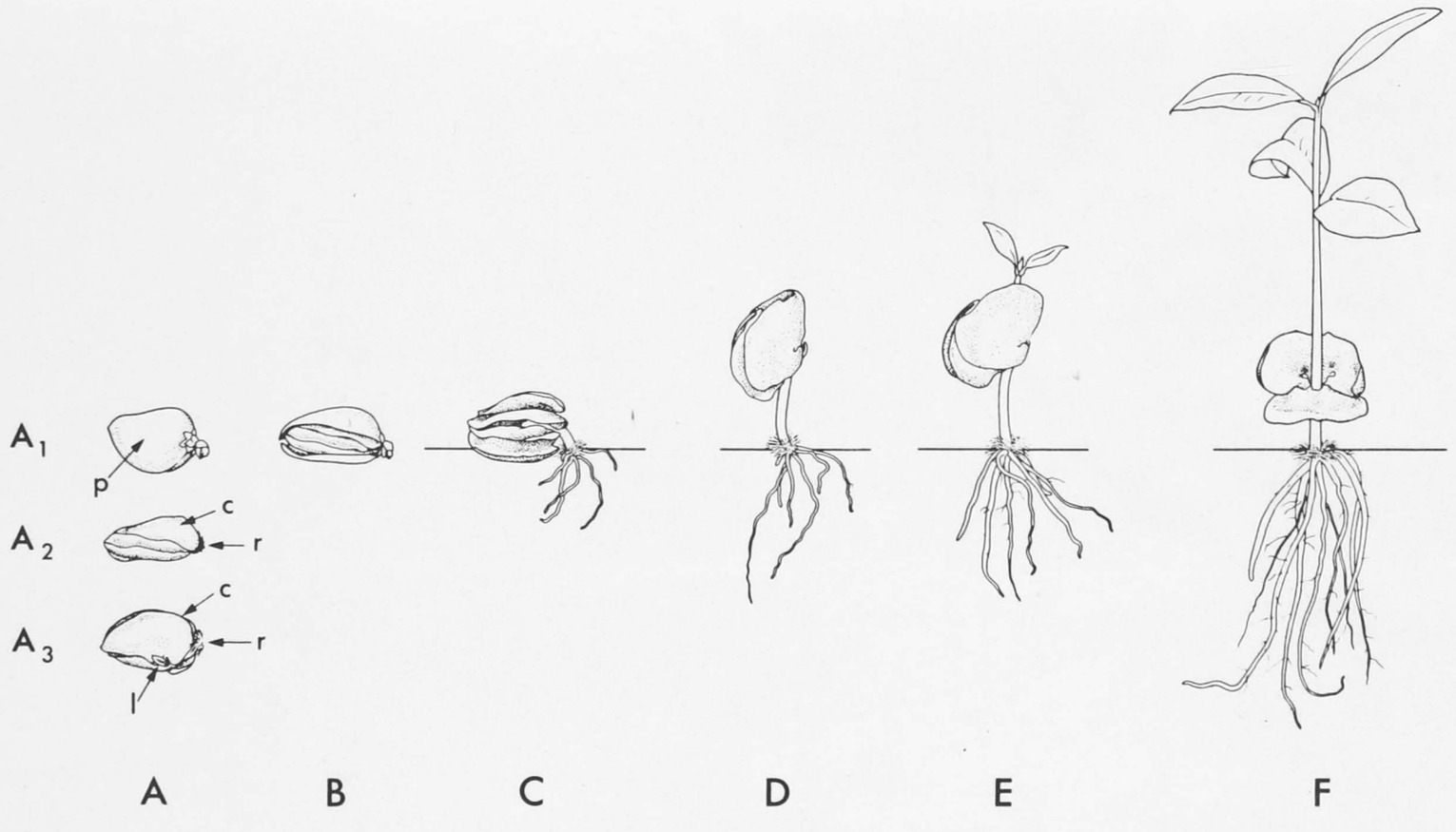
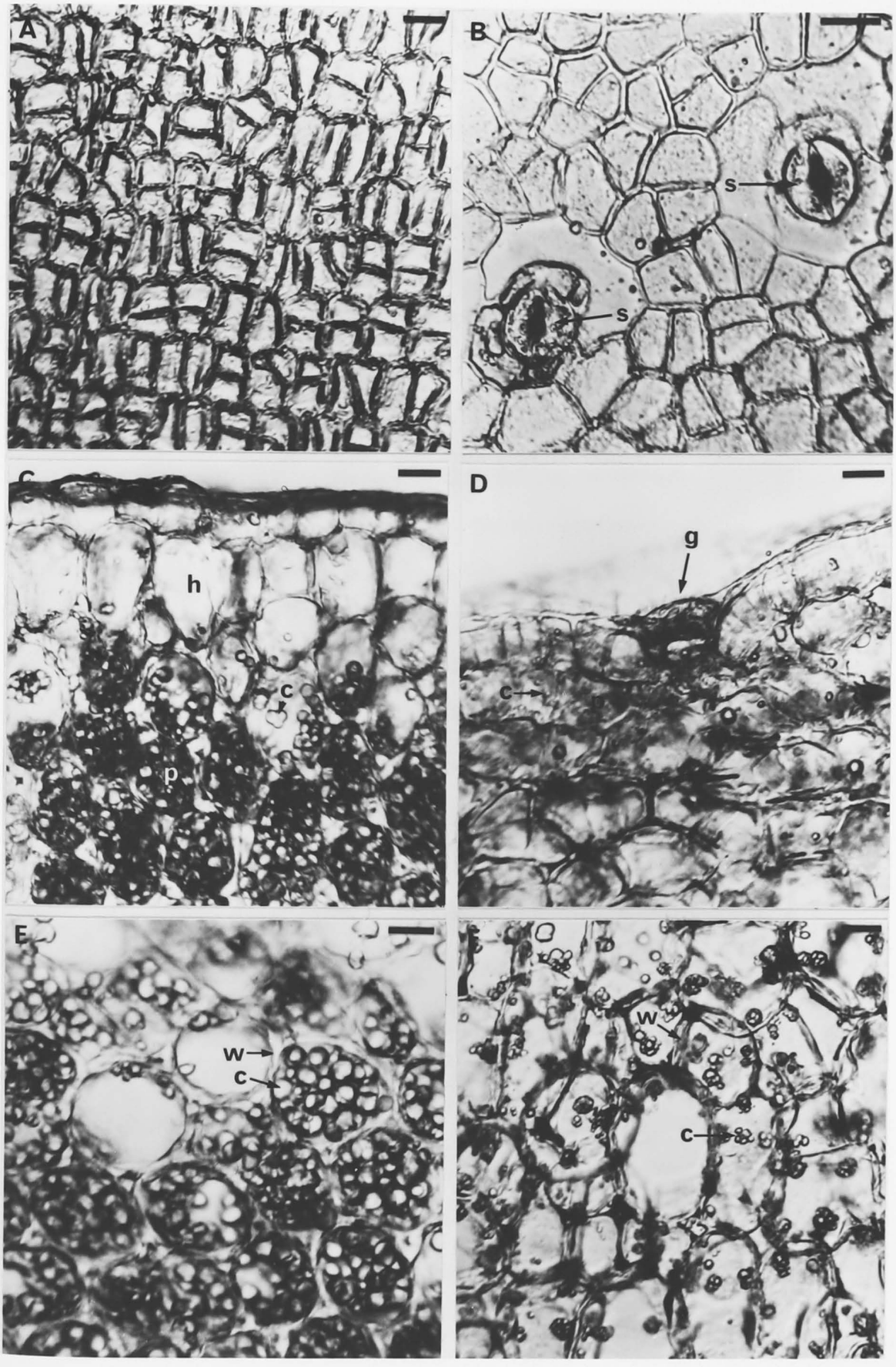


Fig. 2.1B Stages in development of an *Avicennia* propagule into a seedling. The propagule is anatomically complex (A). A pericarp (p) encloses two large epigeal cotyledons (c) folded around a tiny plant with a primary root system (r) and two embryonic leaves (1). The propagule is shown as it appears upon release from the parent tree (A_1), with the pericarp removed (A_2) and with one cotyledon removed (A_3). Within a few hours of its release, the propagule sheds the pericarp (B). Roots rapidly develop, anchoring the propagule (C) and the cotyledons are lifted from the ground (D). The cotyledons open and spread and leaves emerge and develop (E). A mature seedling (F). Scale x 1/3.

Fig. 2.2 Anatomical features of propagules of *Aegiceras* and *Avicennia*. A. Epidermal peel from hypocotyl of *Aegiceras* which lacks stomata. B. Eperidermal peel from cotyledon of *Avicennia* showing stomata (s). C. Transverse section through hypocotyl of *Aegiceras* showing epidermis overlying hypodermis (h) and photosynthetic tissue (p) with dense population of chloroplasts (c). D. Transverse section through cotyledon of *Avicennia* showing salt secretion gland (g) and photosynthetic tissue with scattered chloroplasts (c). E. Photosynthetic tissue from C showing thick cell walls (w). F. Photosynthetic tissue from D.


A
B
s
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The propagule of *Avicennia* consists mainly two large cotyledons folded around a seedling with a pair of embryonic leaves and a primary root system (Fig. 2.1B, Table 2.1). The cotyledons have a thin epidermis with both stomata (Fig. 2.2B) and salt secretion glands (Fig. 2.2D). The epidermis overlies a narrow layer of photosynthetic cells, with the bulk of the cotyledon consisting of storage tissue (Fig. 2.2D). The photosynthetic cells have relatively thin walls and contain few chloroplasts (Fig. 2.2F).

Average ion concentrations in propagules of *Aegiceras* and *Avicennia* are given in Table 2.2 Only the measurements made on cotyledons are shown for *Avicennia* because the other seedling parts were too small for accurate calculation of ion concentrations based on tissue water. However, the distribution of ions among the various parts of *Avicennia* propagules is shown in Table 2.1. The *Aegiceras* hypocotyl contains greater concentrations of Cl^-, Na^+ and K^+ and has a lower Na^+/K^+ ratio than cotyledons of *Avicennia*.

2.3.2 Physiological Characteristics

2.3.2.1 Propagule establishment and development of seedlings

The stages in propagule establishment and development into mature seedlings of the two species are illustrated in Fig. 2.1. The term "propagule" applies to the dispersal unit, ie. that which is released from the parent tree while "seedlings" refers to a juvenile but primarily autotrophic plant with well developed roots, stems and leaves.

The rates of development of various plant parts in *Aegiceras* and *Avicennia* grown in 10, 50 and 100% seawater are shown in Fig. 2.3.

Table 2.1

Distribution of dry weight and ions (Cl^-, Na^+ and K^+) in different parts of propagules of *Avicennia* collected directly from the parent tree. Values are mean ± SE, n = 5.

Part	Total dry weight (g)	Total ion content (μmol)		
		Cl^-	Na^+	K^+
Cotyledon	2.41 ± 0.07	70 ± 22	137 ± 35	399 ± 155
Roots	0.03 ± 0.01	11 ± 1	4 ± 1	15 ± 3
Stem	0.05 ± 0.01	12 ± 2	14 ± 3	21 ± 3
Leaves	0.01 ±<0.005	3 ± 1	1 ±	1 ± <0.5
Total	2.50 ± 0.08	92 ± 22	156 ± 38	436 ± 157

Table 2.2

Concentrations of Cl^-, Na^+ and K^+ in the major storage tissues of propagules of *Aegiceras* and *Avicennia* collected directly from the parent tree. Values are mean ± SE n = 5.

Parameter	*Aegiceras* (hypocotyl)	*Avicennia* (cotyledon)
Weight relationships		
Fresh weight	0.49 ± 0.02	6.93 ± 0.19
Dry weight	0.27 ± 0.01	2.41 ± 0.07
Fresh/Dry weight	1.83 ± 0.01	2.88 ± 0.05
% water	45.3 ± 0.4	65.3 ± 0.5
% Cl^-, Na^+, K^+ (of dry weight)	1.0 ± 0.05	0.9 ± 0.3
Ion concentrations		
(mmol ion l^{-1} tissue water)		
Cl^-	56 ± 3	16 ± 6
Na^+	55 ± 8	31 ± 9
K^+	218 ± 11	91 ± 37
(μmol ion g^{-1} dry weight)		
Cl^-	47 ± 0.5	29 ± 10
Na^+	45 ± 1	57 ± 15
K^+	180 ± 1	166 ± 66
$\frac{Na^+ + K^+}{Cl^-}$	4.91 ± 0.40	8.17 ± 2.56
$\frac{Na^+}{Cl^-}$	0.99 ± 0.17	2.16 ± 0.42
$\frac{Na^+}{K^+}$	0.25 ± 0.04	0.61 ± 0.19

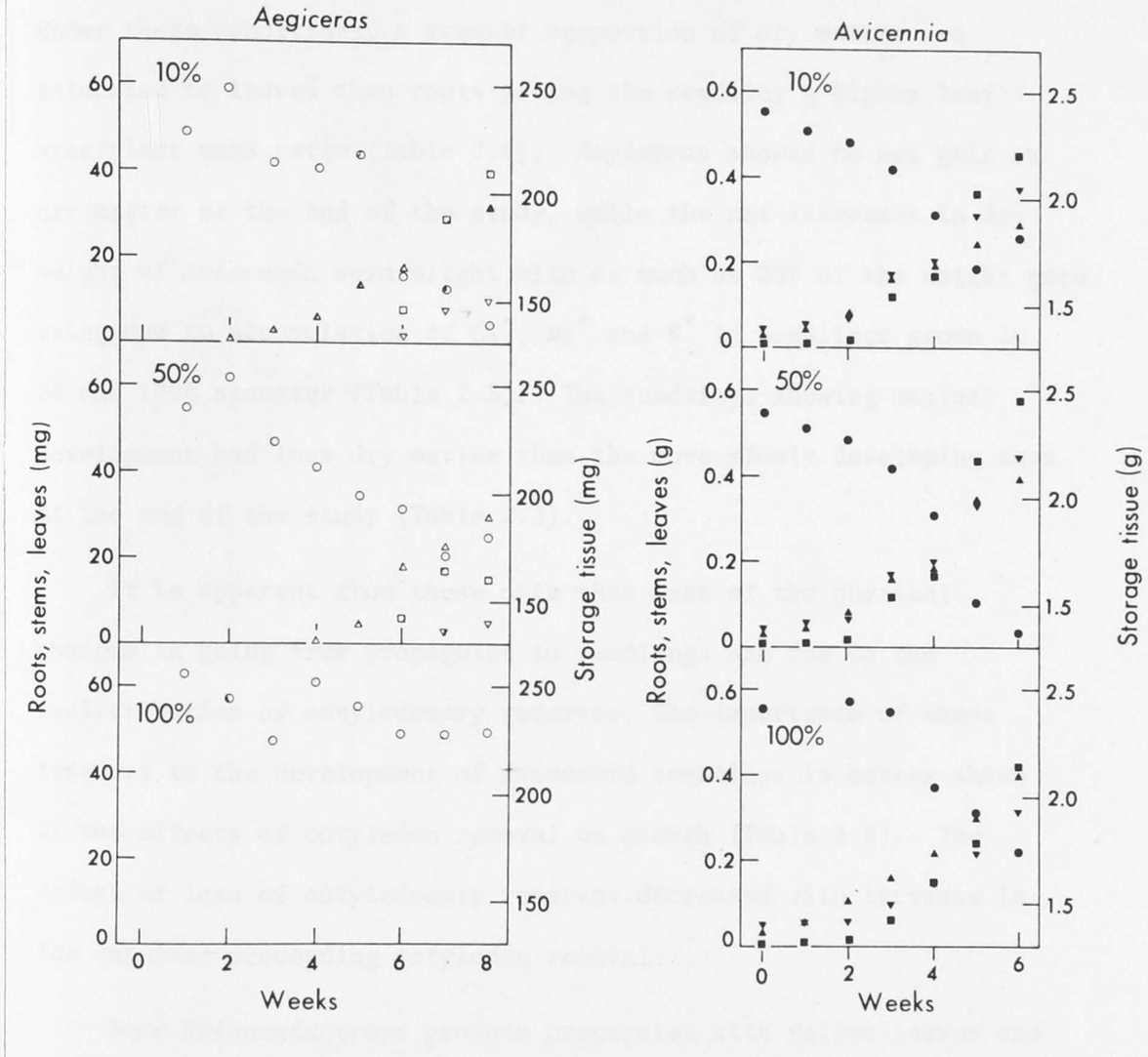


Fig. 2.3: Weight distribution among plant parts during development of propagules into seedlings in *Aegiceras* (hollow symbols) and *Avicennia* (solid symbols). Symbols indicate mean dry weight, n = 5 of storage tissue (o,●), roots (△,▲), stems (▽,▼) and leaves (□,■).

Development was more sensitive to salinity in *Aegiceras* than in *Avicennia*, the appearance of plant parts in the former being substantially delayed with increase in salinity from 10 to 50% seawater and failing to emerge in 100% seawater (Fig. 2.3).

Development of *Aegiceras* and *Avicennia* seedlings was maximal in 10 and 50% seawater, respectively, as shown more clearly in Table 2.3. Under these conditions, a greater proportion of dry matter was allocated to leaves than roots giving the seedling a higher leaf area/plant mass ratio (Table 2.4). *Aegiceras* showed no net gain in dry matter at the end of the study, while the net increases in dry weight of *Avicennia* were slight with as much as 50% of the weight gain being due to accumulation of Cl^-, Na^+ and K^+ in seedlings grown in 50 and 100% seawater (Table 2.3). The seedlings showing maximal development had less dry matter than the more slowly developing ones at the end of the study (Table 2.3).

It is apparent from these data that most of the physical changes in going from propagules to seedlings are due to the redistribution of cotyledonary reserves. The importance of these reserves to the development of *Avicennia* seedlings is better shown by the effects of cotyledon removal on growth (Table 2.5). The effect of loss of cotyledonary reserves decreased with increase in the interval preceeding cotyledon removal.

Some *Avicennia* trees produce propagules with yellow leaves and cotyledons which are deficient in chlorophylls a and b and lack photosynthetic activity (Table 2.6). Such propagules were cultured in 10, 50 and 100% seawater for six weeks. All propagules showed normal development (Fig. 2.4) although the seedlings produced were smaller than those of normal seedlings of the same age (Table 2.7). These results show that *Avicennia* propagules can become established and reach at least the 2-4 leaf stage of development from redistribution of cotyledonary reserves.

Table 2.3

Dry matter accumulation in seedlings of *Aegiceras* and *Avicennia* grown in 10, 50 and 100% seawater. Growth periods were eight and six weeks, respectively. Values are mean dry matter ± SE, n = 5. NO = no data; propagules failed to develop.

Parameter	*Aegiceras*			*Avicennia*		
	10%	50%	100%	10%	50%	100%
Storage tissue (g)	0.14± 0.01	0.18± 0.01	0.23± 0.03	1.82± 0.07	1.37 ± 0.09	1.75±0.12
Roots (g)	0.03±<0.005	0.03±<0.005	ND	0.30± 0.02	0.39 ± 0.04	0.40±0.03
Stems (g)	0.01±<0.005	0.01±<0.005	ND	0.37± 0.02	0.45 ± 0.03	0.31±0.03
Leaves (g)	0.04± 0.01	0.01±<0.005	ND	0.45± 0.03	0.58 ± 0.04	0.42±0.03
Total weight (g)	0.22± 0.01	0.23± 0.01	0.23± 0.03	2.95± 0.14	2.79 ± 0.15	2.89±0.14
Total net gain (g)	-0.05± 0.01	-0.04± 0.01	-0.04± 0.03	0.45± 0.06	0.33 ± 0.16	0.39±0.14
Net gain due to $Cl^-+Na^++K^+$	0.01±<0.005	0.01±<0.005	0.01± 0.01	0.07±<0.005	0.15 ± 0.02	0.18±0.03
Relative growth rate ($g\ g^{-1}\ week^{-1}$)	-0.03± 0.01	-0.02± 0.01	-0.02± 0.02	0.03±<0.005	0.02 ± 0.01	0.02±0.02

Table 2.4

Dry matter partitioning in seedlings of *Aegiceras* and *Avicennia* grown in 10, 50 and 100% seawater. Growth periods were eight and six weeks, respectively. Values are mean dry matter ± SE, n = S. ND = no data; propagules failed to develop.

Parameter	*Aegiceras*			*Avicennia*		
	10%	50%	100%	10%	50%	100%
Root/shoot ($g\ g^{-1}$)	0.17± 0.02	0.15± 0.01	ND	0.11± 0.01	0.16± 0.01	0.16± 0.01
Root/shoot ($g\ g^{-1}$)	0.89± 0.18	2.64± 0.75	ND	0.66± 0.04	0.68± 0.03	0.95± 0.03
Root/leaf area ($g\ m^{-2}$)	32 ±17	393 ±116	ND	90 ± 5	78 ± 5	133 ± 4
Leaf area/plant mass ($m^2\ kg^{-1}$)	2.46± 0.22	0.52± 0.18	ND	1.13± 0.07	1.78± 0.08	1.04± 0.06
Leaf area (cm^2)	5.5 ± 0.6	1.2 ± 0.4	ND	33.5 ± 2.3	49.9 ± 1.7	29.9 ± 1.8

Table 2.5

Influence of the loss of cotyledon on the development of *Avicennia* seedlings grown for six weeks in 10, 50 and 100% seawater. Values are mean per cent dry weight of control ± SE, n = 5 except *, n = 3. ND - no data; all plants died after the cotyledons were removed.

Treatment		Development			
Salinity (% seawater)	Cotyledon removed (weeks)	Roots	Stem	Leaves	Total
10%	0	6.1±0.0	11.8±0.1	3.4± 0.1	6.8± 0.5
	1	12.7±1.5	16.1±2.0	5.6± 1.0	11.1± 1.1
	2	18.2±2.7	21.3±0.8	10.8± 1.7	16.3± 1.7
	3	36.3±2.4	30.3±3.0	21.0± 3.6	28.7± 2.8
	4	53.3±7.7	51.6±8.3	48.2±16.2	50.9±11.0
50%	0	ND	ND	ND	ND
	1	17.7±1.7	12.9±1.8	4.7± 1.0	10.9± 0.8
	2	22.9±3.3	18.1±1.6	8.6± 2.4	15.6± 2.2
	3	50.3±5.0	37.6±3.1	38.4± 5.7	41.4± 4.4
	4	56.0±8.0	39.5±4.7	42.0± 7.3	45.0± 6.5
100%	0	ND	ND	ND	ND
	1*	13.3±1.3	24.6±1.8	7.1± 0.0	15.5± 1.7
	2	16.0±1.8	24.2±2.7	8.6± 1.4	16.9± 1.8
	3	26.4±5.5	39.0±5.7	14.3± 3.2	27.6± 4.7
	4	52.8±5.3	52.6±6.7	42.9±20.3	50.4± 8.6

Table 2.6

Gas exchange characteristics of "albino" seedlings of *Avicennia* grown in 10, 50 and 100% seawater. Measurements were made under normal atmospheric conditions with a leaf temperature of 25C, leaf to air vapour pressure difference of 12 mbar and quantum flux density of 500 $\mu Em^{-2}s^{-1}$. Values are mean ± SE, n = 3.

Parameter	10%	50%	100%
Assimilation rate ($\mu mol\ m^{-2}\ s^{-1}$)	-1.59±0.01	-1.28±0.24	-1.84±0.01
Stomatal conductance ($mmol\ m^{-2}\ s^{-1}$)	11 ±1	10 ±1	10 ±2
Evaporation rate ($mmol\ m^{-2}\ s^{-1}$)	0.15±0.02	0.14±0.01	0.14±0.02

Table 2.7

Dry matter distribution in "albino" seedlings of *Avicennia*. Values are mean dry weight (g), n = 3, after culture for six weeks in 10, 50 or 100% seawater.

Parameter	10%	50%	100%
Total	1.5± 0.4	1.5 ± 0.2	1.6 ± 0.2
Cotyledons	1.0± 0.4	1.0 ± 0.1	1.0 ± 0.1
Roots	0.2± 0.0	0.2 ±<0.05	0.2 ± 0.0
Stems	0.1± 0.0	0.1 ±<0.05	0.1 ±<0.05
Leaves	0.2± 0.0	0.2 ± 0.1	0.3 ± 0.1
Net gain	0.1± 0.05	0.05±<0.05	0.10±<0.05
Leaf area (cm^2)	17.3± 1.0	14.7 ± 3.0	13.0 ± 0.4

Fig. 2.4: Comparison of *Avicennia* seedling deficient in chlorophyll and lacking photosynthetic CO_2 assimilation (left) with a normal seedling (right).

2.3.2.2 Gas Exchange Characteristics

The gas exchange characteristics of the first fully developed leaf pair of *Aegiceras* and *Avicennia* grown under different salinity regimes are summarised in Table 2.8. The measurements made on leaves of *Aegiceras* grown in 100% seawater are included for comparison, but these plants were not grown as part of the present study because the seedlings required almost six months for development under seawater conditions. Salinity had little affect on the gas exchange characteristics of *Avicennia* leaves (Table 2.8, Fig. 2.5), but the assimilation rates of *Aegiceras* decreased with increasing salinity

Table 2.8

Gas exchange characteristics of the first leaf pair of *Aegiceras corniculatum* and *Avicennia marina* grown in 10, 50 and 100% seawater. Measurements were made under conditions similar to those experienced in the growth chamber, ie. leaf temperature 25C, leaf to air vapour pressure difference 12 mbar, quantum flux density 500 or 0 (dark respiration) $\mu Em^{-2}\ s^{-1}$, and normal atmospheric conditions (330 $\mu l\ l^{-1}$ CO_2, 210 $ml\ l^{-1}$ O_2), except those parameters labelled ††. These were calculated by linear regression of pooled data obtained from measurements of assimilation rate as a function of the intercellular CO_2 concentration in which the latter was varied by changing the ambient CO_2 concentration. Values are mean ± SD, n = 4, except *, n = 2. † Data included for comparison as described in text.

Parameter	*Aegiceras*			*Avicennia*		
	10% *	50% *	100% †	10%	50%	100%
Assimilation rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	11.0±0.7	6.9±1.9	4.6±1.0	11.6±1.2	12.0±2.3	11.3±1.3
Stomatal conductance ($mmol\ m^{-2}\ s^{-1}$)	250±64	125±33	68±16	192±51	239±53	159±33
Intercellular CO_2 concentration ($\mu l\ l^{-1}$)	207±11	213± 8	176±10	168±13	196± 9	166±19
Evaporation rate ($mmol\ m^{-2}\ s^{-1}$)	1.78±0.21	1.22±0.21	0.75±0.16	1.54±0.29	1.84±0.21	1.42±0.22
Water use efficiency ($mmol\ CO_2\ mol\ H_2O^{-1}$)	6.19±0.34	5.62±0.57	8.90±2.27	7.61±0.73	6.50±0.67	7.98±0.85
Mesophyll conductance †† ($mol\ CO_2\ m^{-2}\ s^{-1}$)	0.08 (r^2=1.00)	0.05 (r^2=0.91)	0.04 (r^2=0.96)	0.09 (r^2=0.99)	0.09 (r^2=0.99)	0.09 (r^2=0.92)
CO_2 compensation ~~concentration~~ point†† ($\mu l\ l^{-1}$)	43±1	50±1	49±1	46±2	44±1	46±1
Dark respiration ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	0.6±0.1	0.4±<0.05	0.6±0.1	1.0±0.2	1.2±0.3	1.5±0.3

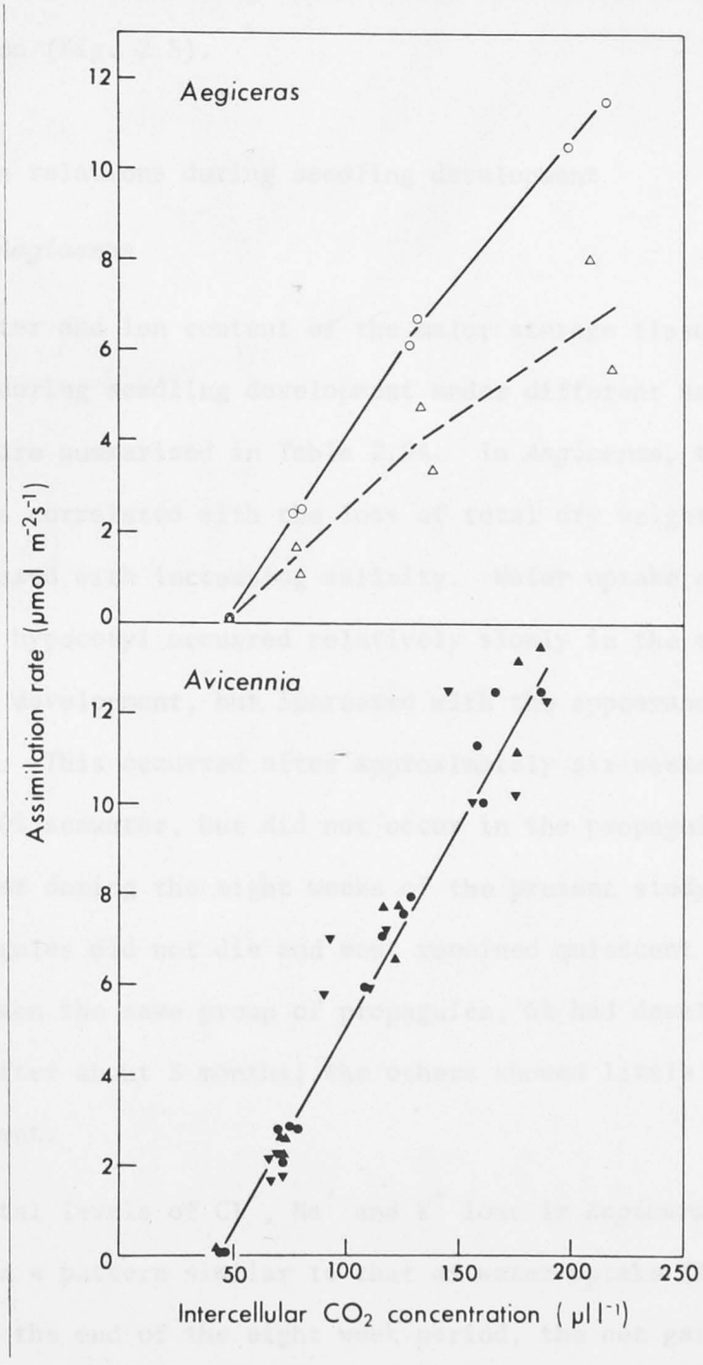


Fig. 2.5: Assimilation rate as a function of the intercellular CO_2 concentration in the first leaf pair of *Aegiceras* (open symbols) and *Avicennia* (closed symbols) grown in 10 (o,●), 50 (△,▲) and 100% seawater (▽,▼). Conditions of measurement were leaf temperature of 25C, quantum flux density of 500 µE m^{-2} s^{-1}, and leaf to air vapour pressure difference of 12 mbar.

(Table 2.8). This decrease was due largely to a decline in mesophyll conductance, here calculated as the slope of the initial, linear region of the curve relating assimilation rate and intercellular CO_2 concentration (Fig. 2.5).

2.3.2.3 Ion relations during seedling development

2.3.2.3.1 *Aegiceras*

The water and ion content of the major storage tissue, ie. the hypocotyl, during seedling development under different salinity conditions are summarised in Table 2.9A. In *Aegiceras*, the absorption of water was correlated with the loss of total dry weight, both of which decreased with increasing salinity. Water uptake and dry weight loss by the hypocotyl occurred relatively slowly in the early phases of seedling development, but increased with the appearance of other plant parts. This occurred after approximately six weeks incubation in 10 and 50% seawater, but did not occur in the propagules kept in 100% seawater during the eight weeks of the present study (Fig. 2.3). These propagules did not die and most remained quiescent. In subsequent observations on the same group of propagules, 6% had developed the first leaf pair after about 3 months; the others showed little of no sign of development.

The total levels of Cl^-, Na^+ and K^+ ions in *Aegiceras* hypocotyls increased in a pattern similar to that of water uptake (Table 2.9A). However, at the end of the eight week period, the net gain of Cl^-, Na^+ and K^+ in the hypocotyl was greatest in propagules grown in 50% seawater and least in those grown in 100% seawater. The net changes in ion levels were greater than could be accounted for solely from the

Table 2.9A

Changes in weight and ion concentration in the major storage tissues of propagules during development into seedlings. The net change is the difference between values measured at the start (harvest 0) and end of the experiment. Values are mean ± SE, n = 5. Changes in the hypocotyl of *Aegiceras* *propagules grown in 10, 50 and 100% seawater for eight weeks.*

Salinity (% seawater)	Harvest (weeks)	Fresh wt. (g)	Dry weight (g)	Fresh/Dry wts.	% water	Cl^- (Total µmol)	Na^+ (Total µmol)	K^+ (Total µmol)	% Cl^- + Na^+ + K^+ (of dry weight)
Direct from tree	0	0.49±0.02	0.27± 0.01	1.83±0.01	45.3±0.4	13	12	48	1.0±<0.05
10%	1	0.46±0.02	0.23± 0.01	2.02±0.03	50.3±0.8	36	29	61	1.9± 0.2
	2	0.53±0.01	0.25± 0.01	2.18±0.09	53.7±1.8	37	4	6	1.8± 0.1
	3	0.56±0.01	0.21± 0.01	2.64±0.08	61.9±1.1	46	41	72	2.3± 0.1
	4	0.57±0.02	0.21± 0.01	2.72±0.10	63.0±1.4	43	39	69	2.1± 0.1
	5	0.73±0.03	0.22± 0.01	3.34±0.10	70.0±0.8	72	71	89	3.3± 0.3
	6	0.67±0.01	0.16± 0.01	4.26±0.33	76.0±1.7	113	69	82	3.9± 0.9
	7	0.72±0.05	0.16± 0.01	4.66±0.04	78.5±0.2	188	98	107	5.1± 0.3
	8	0.69±0.04	0.14± 0.01	4.93±0.06	79.7±0.3	156	132	120	4.5± 0.5
Net change		+.20	-.14	+3.10	+34.4	+143	+120	+78	+2.6
50%	1	0.46±0.03	0.24± 0.02	1.93±0.02	48.1±0.6	4	9	55	1.6± 0.1
	2	0.51±0.02	0.25± 0.01	2.01±0.03	50.3±0.8	42	43	61	1.9± 0.1
	3	0.51±0.03	0.22± 0.01	2.29±0.04	56.3±0.7	47	51	68	2.4± 0.2
	4	0.50±0.03	0.21± 0.01	2.39±0.04	58.1±0.8	58	79	64	2.9± 0.3
	5	0.49±0.06	0.20± 0.03	2.51±0.13	59.6±2.2	76	80	76	3.2± 0.4
	6	0.64±0.04	0.19± 0.01	3.35±0.22	69.6±1.9	245	134	97	6.0± 1.2

continued/

Table 2.9A continued

Salinity (% seawater)	Harvest (weeks)	Fresh wt. (g)	Dry weight (g)	Fresh/Dry wts.	% water	Cl^- (Total µmol)	Na^+ (Total µmol)	K^+ (Total µmol)	% Cl^- + Na^+ + K^+ (of dry weight)
	7	0.59±0.04	0.17± 0.02	3.62±0.32	71.6±2.2	249	199	108	7.7± 1.2
	8	0.68±0.03	0.18± 0.01	3.79±0.09	73.5±0.7	212	191	115	5.7± 0.3
Net change		+0.19	-0.09	+1.96	+28.2	+199	+179	+67	+3.8
100%	1	0.47±0.02	0.26± 0.01	1.85±0.03	45.9±0.9	35	23	56	1.5± 0.1
	2	0.46±0.03	0.24± 0.01	1.88±0.01	46.8±0.2	52	44	54	2.0± 0.1
	3	0.44±0.02	0.23± 0.01	1.93±0.01	48.3±0.2	70	53	71	3.7± 0.8
	4	0.50±0.01	0.25± 0.01	1.98±0.03	49.4±0.7	54	48	71	2.3± 0.1
	5	0.47±0.01	0.24± 0.005	1.96±0.02	48.9±0.6	51	61	70	2.5± 0.6
	6	0.50±0.03	0.23± 0.01	2.21±0.10	54.4±2.0	92	51	79	3.4± 0.5
	7	0.50±0.03	0.23± 0.01	2.18±0.01	53.8±1.6	66	68	83	3.7± 0.6
	8	0.54±0.04	0.23± 0.03	2.43±0.20	57.8±3.3	102	68	79	3.6± 0.8
Net change		+0.05	-0.04	+0.60	+12.5	+89	+56	+31	+1.7

influx of water required to effect the observed changes in fresh weight and the ion concentration of the external water supply. Further the internal ion levels differed from those in the external environment.

Ions accumulated in various plant parts during development of *Aegiceras* seedlings and the levels present at the end of the eight week study are shown in Tables 2.10A and B. The concentrations of Cl^- and Na^+ increased with increasing salinity, whereas those of K^+ increased in the hypocotyls and roots but decreased in the stems and leaves. The Na^+/K^+ ratio increased in all tissues with increasing salinity, with the change being least in the roots. The roots were the major site of K^+ accumulation.

2.3.2.3.2 *Avicennia*

In *Avicennia* the loss of dry weight by cotyledons during seedling development was greatest in plants maintained in 50% seawater (Table 2.9B). This was not correlated with the water content of the cotyledons which decreased with increasing salinity (Table 2.9B). The weight loss corresponded to the more rapid rates of development of other plant parts in propagules incubated in 50% seawater than in those kept in other salinities (Table 2.3).

The Cl^-, Na^+ and K^+ levels in *Avicennia* cotyledons were affected by the external salinity (Table 2.9B). The cotyledons accumulated Cl^- and Na^+ such that the levels of Na^+ exceeded those of Cl^- except in cotyledons from propagules grown in 10% seawater. There was a greater accumulation of Cl^- than Na^+ by these cotyledons, whereas cotyledons from propagules grown in 50% seawater accumulated roughly equivalent amounts of Cl^- and Na^+ and those from seedlings grown in

Table 2.9B

Changes in weight and ion concentration in the major storage tissues of propagules during development into seedlings. The net change is the difference between values measured at the start (harvest 0) and end of the experiment. Values are mean ± SE, n = 5. Changes in the cotyledons of *Avicennia* propagules grown in 10, 50 and 100% seawater for eight weeks.

Salinity (% seawater)	Harvest (weeks)	Fresh wt. (g)	Dry weight (g)	Fresh/Dry wts.	% water	Cl^- (Total µmol)	Na^+ (Total µmol)	K^+ (Total µmol)	% Cl^- + Na^+ + K^+ (of dry weight)
Direct from tree	0	6.93±0.19	2.40±0.07	2.89±0.05	65.3±0.5	70	137	399	0.9±0.3
10%	1	7.89±0.28	2.32±0.10	3.41±0.05	70.6±0.4	190	315	957	2.2±0.2
	2	8.37±0.21	2.27±0.05	3.69±0.03	72.9±0.2	309	277	783	2.1±0.1
	3	8.43±0.32	2.14±0.09	3.93±0.03	74.6±0.2	326	349	455	1.7±0.1
	4	8.21±0.25	1.93±0.11	4.34±0.34	76.3±2.0	366	484	461	2.2±0.2
	5	7.99±0.23	1.67±0.10	4.79±0.24	9.0±0.9	304	241	234	1.5±0.3
	6	8.45±0.16	1.82±0.07	4.67±0.23	78.4±1.1	310	226	244	1.4±0.2
Net change		+1.52	-0.58	+1.78	+13.1	+240	+89	-155	+0.5
50%	1	7.84±0.30	2.51±0.12	3.13±0.06	68.0±0.6	78	281	452	1.1±0.3
	2	7.71±0.20	2.36±0.05	3.26±0.03	69.3±0.3	229	340	631	1.7±0.7
	3	7.60±0.21	2.05±0.04	3.70±0.05	73.0±0.3	291	642	302	1.8±0.3
	4	7.43±0.13	1.68±0.05	4.45±0.16	77.4±0.8	352	1443	441	3.8±0.5
	5	7.16±0.15	1.51±0.04	4.74±0.13	78.8±0.6	391	762	348	3.0±0.3
	6	5.60±0.18	1.37±0.09	4.12±0.18	75.5±1.0	682	801	335	4.1±0.4
Net change		-1.33	-1.03	+1.23	+10.2	+612	+664	-64	+3.2

continued/

Table 2.9B continued

Salinity (% seawater)	Harvest (weeks)	Fresh wt. (g)	Dry weight (g)	Fresh/Dry wts.	% water	Cl^- (Total µmol)	Na^+ (Total µmol)	K^+ (Total µmol)	% Cl^- + Na^+ + K^+ (of dry weight)
100%	1	7.70±0.27	2.62±0.08	2.94±0.06	65.9±0.7	110	215	459	1.0±0.4
	2	7.25±0.32	2.45±0.11	2.97±0.05	66.3±0.5	457	1013	790	2.9±0.2
	3	7.78±0.32	2.40±0.14	3.25± 0.08	69.2±0.8	524	1872	759	3.5±0.3
	4	7.81±0.19	2.05±0.14	3.92±0.41	73.5±2.4	412	1646	652	3.8±0.3
	5	7.40±0.21	1.91±0.10	3.89±0.12	74.2±0.8	495	1788	417	3.9±0.8
	6	5.96±0.33	1.75±0.12	3.42±0.11	70.6±1.0	491	1167	398	3.4±0.5
Net change		-0.97	-0.65	+0.53	+5.3	+421	+1030	-1	+2.5

Table 2.10A

Concentrations of Cl^-, Na^+ and K^+ in different plant parts of 8 week old seedlings of *Aegiceras corniculatum* grown in 10, 50 and 100% seawater. Values are mean ± SE, n = 5.

Salinity (% seawater)	Part	Fresh/Dry weight ($g\ g^{-1}$)	% water	Cl^-	Na^+ (mmol ion l^{-1} water)	K^+ tissue
10%	Hypocotyl	4.93±0.06	79.7±0.3	149.6±26.9	127.0± 7.1	81.2± 5.2
	Roots	8.71±0.45	88.4±0.7	151.5±24.0	116.9±12.6	165.0± 4.0
	Stems	6.70±0.28	85.0±0.7	215.1±23.8	40.3± 5.9	186.1±19.5
	Leaves	6.08±0.16	83.5±0.4	116.4±19.1	163.1±22.2	116.9± 6.4
50%	Hypocotyl	3.79±0.09	73.5±0.6	264.7± 8.4	272.3± 5.8	125.2± 3.3
	Roots	7.56±0.18	86.7±0.3	340.8±36.3	202.7±17.7	228.9± 9.2
	Stems	6.50±1.08	82.8±2.9	212.6±48.0	142.5±35.9	95.3±23.2
	Leaves	4.65±0.21	78.3±1.1	124.8±28.6	187.6±37.2	90.7±15.2
100%	Hypocotyl	2.43±0.20	57.8±3.3	285.5±64.5	208.1±14.1	249.4±18.0

Table 2.10B

Concentrations of Cl, Na^+ and K^+ in different plant parts of 8 week old seedlings of *Aegiceras corniculatum* grown in 10, 50 and 100% seawater. Values are mean ± SE, n = 5.

Salinity (% seawater)	Part	Ion content (% of dry weight)	Cl^-	Na^+	K^+	$\frac{Na^+ + K^+}{Cl^-}$	$\frac{Na^+}{Cl^-}$	$\frac{Na^+}{K^+}$
			(µmol ion g dry weight^{-1})					
10%	Hypocotyl	4.5±0.5	591±113	498± 28	320± 24	1.53±0.20	0.95±0.15	1.60±0.15
	Roots	15.2±4.9	1198±244	860± 66	1277± 97	2.22±0.35	0.95±0.19	0.73±0.08
	Stems	9.0±1.0	1236±155	225± 28	1057±120	1.09±0.15	0.20±0.05	0.22±0.03
	Leaves	6.3±0.4	594±101	825±107	598± 50	2.74±0.51	1.65±0.40	1.44±0.25
50%	Hypocotyl	5.7±0.3	740± 43	761± 36	349± 15	1.50±0.03	1.03±0.01	2.18±0.07
	Roots	16.8±0.9	2238±242	1322±101	1499± 58	1.36±0.25	0.65±0.14	0.88±0.05
	Stems	7.1±0.9	1050±196	675±135	475±115	1.21±0.21	0.65±0.05	1.89±0.61
	Leaves	4.6±0.9	460±113	715±161	338± 66	2.57±0.68	1.80±0.60	2.14±0.50
100%	Hypocotyl	3.6±0.8	444±159	299± 49	334± 26	1.92±0.38	0.87±0.18	0.85±0.08

100% seawater showed a greater accumulation of Na^+ than Cl^-. The levels of K^+ followed a different pattern, increasing in all salinities at the start of the study and later declining. By the end of the six week period, there was a net loss of K^+ which was greatest at the lowest salinity. Loss of K^+ through secretion from the cotyledons was trivial, averaging 0.1 µmol K^+ per day and hence translocation to other plant parts probably accounted for most of the decline in K^+.

The average concentration of Cl^-, Na^+ and K^+ in different tissues of *Avicennia* at the end of the six week period are summarised in Tables 2.11A and B. In contrast to the situation in *Aegiceras*, the concentration of K^+ increased in all plant parts with increasing salinity. The Na^+/K^+ ratio also increased with increasing salinity, except in the roots where the ratio remained constant with increase from 10 to 50% seawater and sharply decreased with further increase in salinity to 100% seawater. In contrast to *Aegiceras*, the leaves of *Avicennia* were the major site of K^+ accumulation except in seedlings grown in 100% seawater where most of the K^+ content was in the roots.

2.3.2.4 Estimates of ion uptake and transport

In contrast to *Avicennia* propagules, those of *Aegiceras* lack salt secretion glands (Fig. 2.2). However, the leaves of both species possess salt secretion glands and those of *Aegiceras* are shown in Fig. 2.6. Thus, ions could be excluded, accumulated or secreted during seedling development.

The net uptake of Cl^-, Na^+ and K^+ was considered to be the sum of net accumulation and total secretion during the growth period (Table 2.12). The net accumulation was calculated on the difference

Table 2.11A

Concentrations of Cl^-, Na^+ and K^+ in different plant parts of 6 week old seedlings of *Avicennia marina* grown in 10, 50 and 100% seawater. Values are mean ± SE, n = 5 except *, n = 4.

Salinity (% seawater	Part	Fresh/Dry weight ($g\ g^{-1}$)	% water	Cl^-	Na^+ (mmol ion l^{-1} water)	K^+ tissue
10%	Cotyledon	4.67±0.23	78.4±1.1	45.6± 6.1	32.8± 5.3	36.2± 2.9
	Roots	6.06±0.10	83.5±0.3	330.7±33.6	184.3±32.3	47.4± 4.0
	Stems	4.07±0.04	75.4±0.2	185.4±17.6	81.2± 8.5	106.5±13.5
	Leaves	3.98±0.08	74.9±0.5	220.6±16.0	124.3±14.1	150.1±16.6
50%	Cotyledon	4.12±0.18	75.5±1.0	154.5±23.5	192.8±43.7	79.3± 5.0
	Roots	6.37±0.12	84.3±0.3	228.4±68.9	194.1±38.6	47.9± 7.5
	Stems	4.16±0.06	76.0±0.4	284.4±39.6	189.2±22.0	125.4±13.5
	Leaves	4.77±0.13	79.0±0.6	420.8±11.6	360.9±66.8	174.6± 8.7
100%	Cotyledon*	3.42±0.11	70.6±1.0	111.0± 7.3	263.1±52.5	90.1±12.9
	Roots	5.02±0.19	80.0±0.8	820.2±42.7	369.3±20.8	305.4±15.0
	Stems	3.92±0.07	74.5±0.5	447.7±99.1	301.8±59.8	151.3±16.2
	Leaves	4.17±0.06	76.0±0.3	521.4±52 8	406.3±26.7	174.3±17.8

Table 2.11B

Concentrations of Cl^-, Na^+ and K^+ in different plant parts of 6 week old seedlings of *Avicennia marina* grown in 10, 50 and 100% seawater. Values are mean ± SE, n = 5 except *, n = 4.

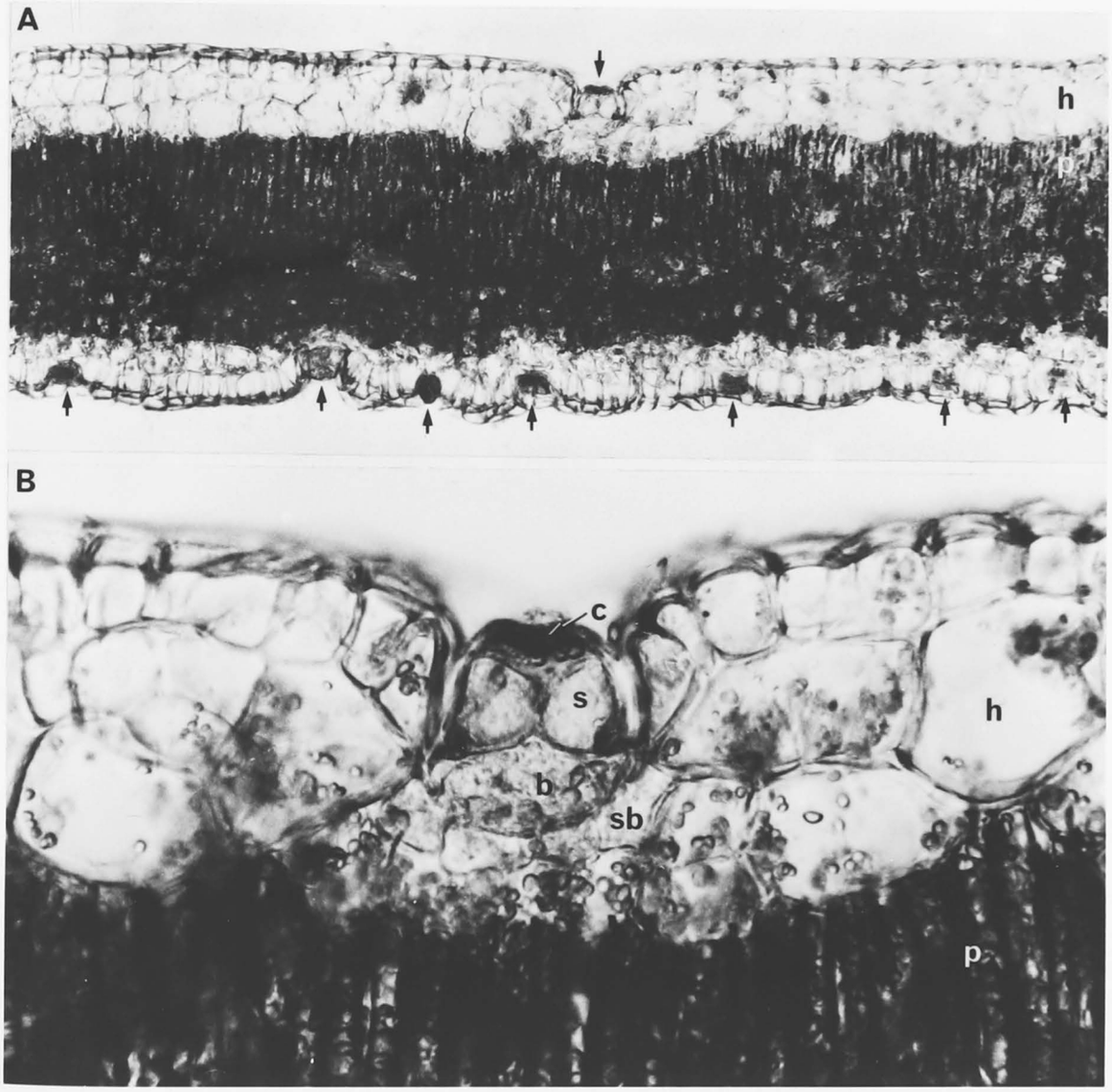
Salinity (% seawater)	Part	Ion content (% of dry weight)	Cl^- (µmol ion g dry weight^{-1})	Na^+	K^+	$\frac{Na^+ + K^+}{Cl^-}$	$\frac{Na^+}{Cl^-}$	$\frac{Na^+}{K^+}$
10%	Cotyledon	1.4±0.2	170± 28	124± 27	134±16	1.54±0.07	0.72±0.04	0.89±0.10
	Roots	9.1±1.2	1685±204	945±185	240±21	0.70±0.04	0.55±0.04	4.05±0.82
	Stems	3.9±0.3	566± 49	248± 24	325±39	1.02±0.06	0.44±0.04	0.80±0.10
	Leaves	4.9±0.3	654± 39	368± 40	443±39	1.24±0.08	0.56±0.05	0.84±0.09
50%	Cotyledon	4.1±0.4	496±104	583±105	244±10	2.03±0.55	1.45±0.45	2.36±0.39
	Roots	7.8±2.0	1232±380	1045±214	257±41	1.16±0.09	0.92±0.07	4.00±0.27
	Stems	6.1±0.7	896±121	600± 75	397±45	1.15±0.14	0.69±0.10	1.53±0.15
	Leaves	11.3±0.4	1583± 50	1341±215	657±36	1.28±0.16	0.86±0.17	2.11±0.43
100%	Cotyledon*	3.4±0.5	280± 45	666±140	227±32	3.12±0.44	2.31±0.37	2.88±0.90
	Roots	20.0±1.3	3324±293	1492±120	1218±23	0.83±0.05	0.45±0.02	1.23±0.11
	Stems	8.3±1.5	1285±268	869±159	439±40	1.09±0.13	0.71±0.08	1.91±0.22
	Leaves	10.9±0.9	1643±149	1284± 78	549±50	1.13±0.06	0.80±0.05	2.38±0.13

Table 2.12

Net absorption of Cl^-, Na^+ and K^+ during development of seedlings of *Aegiceras corniculatum* and *Avicennia marina* grown in 10, 50 and 100% seawater. ND = no data; leaves did not develop during the study period. Calculations are as explained in the text.

Ions (µmol)	*Aegiceras*			*Avicennia*		
	10%	50%	100%	10%	50%	100%
Total net accumulation						
Cl^-	143	199	106	1221	2389	2808
Na^+	120	179	59	607	2101	2413
K^+	72	67	37	201	558	814
Total secretion						
Cl^-	100	171	ND	660	1259	708
Na^+	85	169	ND	552	1010	689
K^+	1	3	ND	60	104	45
Total net uptake						
Cl^-	243	370	106	1881	3648	3516
Na^+	205	348	59	1159	3111	3102
K^+	73	70	37	261	662	859

Fig.2.6A : Transverse section through mature *Aegiceras* leaf showing photosynthetic tissue (p) bordered by a hypodermal layer (h) on both surfaces in which numerous salt secreting glands are located (↓). B. Hand section through salt secretion gland showing sub-basal (sb) and basal cells (b), secretary cells (s) and the collecting compartment (c).


A
h
p
B
c
s
h
b
sb
p

between the average ion contents measured in propagules and seedlings at the start (Tables 2.1 and 2.2) and end (Tables 2.10 and 2.11) of the experiment, respectively and these data are shown in Table 2.13.

These data were used to calculate the relative proportion of ions accumulated or secreted during development of *Aegiceras* and *Avicennia* seedlings and the results are shown in Table 2.14. *Aegiceras* secreted 40 to 50% of the total net uptake of Cl^- and Na^+ but retained almost all of the K^+. *Avicennia*, however, secreted a smaller proportion of the net uptake of Cl^- and Na^+, but a much larger proportion of the net K^+ uptake and the portion of all ions secreted declined with increasing salinity. More than half of the total K^+ uptake was retained in the roots in *Aegiceras* and in the shoots in *Avicennia* except at the highest salinity.

Net ion uptake was related to total water use to obtain an estimate of the average concentrations of ions in absorbed water relative to those in the water supply and the results are shown in Table 2.15. A similar estimation of the average ion concentrations in the transpiration stream was made on the assumption that mass flow of water through the xylem is the major means of ion transport to the shoot [Sutcliffe, 1976].

These calculations suggest that both *Aegiceras* and *Avicennia* exclude roughly 90 to 95% of the external Cl^- and Na^+ but admit most of the K^+ during water absorption. Differences between *Aegiceras* and *Avicennia* in K^+ uptake and retention in the roots cause the calculated concentrations of K^+ in the transpiration stream to remain nearly constant in *Aegiceras* but increase in *Avicennia* with increasing salinity. An important consequence of root activity is to cause the

Table 2.13

Distribution of Cl^-, Na^+ and K^+ ions in seedlings of *Aegiceras* and *Avicennia* at the start of the experiment and after growth in 10, 50 and 100% seawater. Values are mean total µmol ion, n = 5. The growth periods were 8 weeks for *Aegiceras* and 6 weeks for *Avicennia*.

	Plant			Storage Tissue			Roots			Stems			Leaves		
	Cl^-	Na^+	K^+	Cl^-	Na^+	K^+	Cl^-	Na^+	K^+	Cl^-	Na^+	K^+	Cl^-	Na^+	K^+
Aegiceras															
Start	13	12	48	13	12	48	-	-	-	-	-	-	-	-	-
10%	143	120	72	82	69	44	38	28	41	12	2	11	24	33	24
50%	212	191	115	133	137	63	67	40	45	5	3	2	7	11	5
100%	119	71	85	119	71	85	-	-	-	-	-	-	-	-	-
Avicennia															
Start	96	158	436	70	137	399	11	4	15	12	14	21	3	3	1
10%	1317	765	637	310	226	244	499	280	71	212	93	122	296	166	200
50%	2485	2259	994	682	801	385	485	412	101	400	268	177	918	778	381
100%	2808	2413	814	491	1167	398	1323	594	485	403	273	138	687	537	229

Table 2.14

Accumulation and secretion of Cl^-, Na^+ and K^+ ions in developing seedlings of *Aegiceras* and *Avicennia* grown in 10, 50 and 100% seawater. Values are mean percent of the total ion uptake calculated from the data given in Table 2.12. * = no development; all ions contained in propagule.

Distribution	*Aegiceras corniculatum*			*Avicennia marina*		
	10%	50%	100%	10%	50%	100%
Accumulation in roots						
Cl^-	16	18	0	27	13	38
Na^+	14	11	0	24	14	19
K^+	56	65	0	27	15	57
Accumulation in shoots						
Cl^-	43	36	100*	38	52	42
Na^+	45	40	100*	28	54	59
K^+	43	31	100*	50	69	38
Secretion from shoots						
Cl^-	41	46	0	35	35	20
Na^+	41	49	0	48	32	22
K^+	1	4	0	23	16	5

Table 2.15

Calculated average ion concentrations in absorbed water and in the transpiration stream of *Aegiceras* and *Avicennia* seedlings grown in 10, 50 and 100% seawater.

Parameter	*Aegiceras*			*Avicennia*		
	10%	50%	100%	10%	50%	100%
Absorbed water						
Average ion concentration (mM) (ion uptake/water uptake)						
Cl^-	4.3	10.5	ND	6.9	15.0	42.3
Na^+	3.6	9.8	ND	4.2	12.8	37.3
K^+	1.3	2.0	ND	1.0	2.7	10.3
Ion uptake (%) (absorbed/external concentration)						
Cl^-	8.0	8.2	ND	12.9	5.6	7.9
Na^+	7.8	4.3	ND	9.3	5.6	8.2
K^+	127.0	40.0	ND	100.0	54.3	103.2
Transpiration stream						
Average ion concentration (mM) $\left(\frac{\text{Accumulation in shoot + secretion}}{\text{water loss + shoot fresh wt}}\right)$						
Cl^-	3.6	8.6	ND	5.1	13.0	26.4
Na^+	3.1	8.7	ND	3.2	11.1	30.1
K^+	0.6	0.7	ND	0.7	2.3	4.5
Ion uptake (%) (transpiration/external concentration)						
Cl^-	6.7	3.2	ND	9.5	4.9	4.9
Na^+	6.8	3.8	ND	7.0	4.9	6.6
K^+	60.0	14.0		70.0	46.0	45.0

continued/

Table 2.15 continued

Parameter	*Aegiceras*			*Avicennia*		
	10%	50%	100%	10%	50%	100%
Estimated change in Na^+/K^+						
External	45.6	45.7	45.7	45.7	45.7	45.7
Absorbed water	2.8	4.9	ND	4.2	4.7	3.6
Transpiration stream	5.2	12.4	ND	4.6	4.8	6.7
Leaves	1.4	2.1	ND	0.8	2.1	2.4

(Data from Tables 2.10 and 2.11)

Na^+/K^+ ratio in absorbed water to be considerably less than that in the external environment.

2.4 DISCUSSION

Although a few mangrove species produce true seeds, most mangroves, including *Aegiceras* and *Avicennia*, are viviparous and regularly release large numbers of propagules [Jones, 1971]. The viviparity of mangroves is a classic example of convergent evolution among unrelated species sharing a common habitat. Various authors have speculated on the adaptive value of viviparity and it has been suggested to be a means of allowing the progeny to germinate and develop to a phase which can cope with a saline environment [Walsh, 1974].

2.4.1 Responses to Salinity

Propagules of *Aegiceras* and *Avicennia* differ in their responses to salinity, with development into established seedlings occurring at maximum rates in 10 and 50% seawater, respectively (Table 2.3). These results are consistent with other studies [Connor, 1969; Clarke and Hannon, 1970]. However, these authors failed to recognise that the early phases of development are dependent largely on redistribution of propagule reserves. Mobilisation of these reserves appears to be affected by salinity because of its influence on both water absorption, which probably plays a role similar to that of inbibition in seed germination, and ion uptake.

The propagules of *Aegiceras* and *Avicennia* differ in several anatomical attributes which may influence their respones to salinity. First, the *Avicennia* propagule is in an advanced stage of development,

possessing a primary root system and embryonic leaves, which may contribute to its relatively rapid rate of development into an established seedling. In contrast, development of *Aegiceras* to a comparable stage requires more time even under optimum conditions (Fig. 2.3). Second, the cotyledons of *Avicennia* are epigeal and photosynthesis by these modified leaves although not required for seedling development (Fig. 2.4), may contribute substantially to the carbon economy of the seedlings as found in other species [Marshall and Kozlowski, 1974a and b, 1976]. In contrast, the cotyledons of *Aegiceras* are vestigial (Fig. 2.1); photosynthesis might be possible in the hypocotyl, but this structure is heavily cutinised and lacks stomata (Fig. 2.2). Substantial carbon gain is therefore probably delayed until development of the first leaf pair. Third, possession of salt secretion glands by the cotyledons of *Avicennia* may assist regulation of internal ion levels during imbibition whereas *Aegiceras* propagules lack these structures (Fig. 2.2). Salt secretion glands are present on the leaves of both species.

The propagules of *Aegiceras* and *Avicennia* also differ in several physiological attributes which influence the responses to salinity. First, it may be necessary for the water content of the propagule to reach a threshold level before development can proceed. Water absorption by propagules of both species decreases with increasing salinity (Table 2.9). In *Aegiceras*, development appears to be limited by water uptake as the propagules remained quiescent until the water content reached approximately 70%, and this was followed by an increase in the loss of dry matter and the development of other plants parts. Development in *Avicennia*, however, was maximal in 50% seawater, suggesting the involvement of another factor (s) besides water absorption.

Second, the two mangroves differ in the effect of salinity on carbon partitioning. In *Aegiceras*, the proportion allocated to leaves decreases with increasing salinity, whereas it is maximum in *Avicennia* grown in 50% seawater (Table 2.3). These allocation patterns are correlated with the development rates; seedlings showing the most rapid development (Table 2.3) have the highest ratio of leaf area to plant mass (Table 2.4). Monsi [1968], has shown that small differences in carbon partitioning may have large effects on relative growth rates. Variation in carbon partitioning with increasing salinity is likely to have played a major role in the enhancement of *Avicennia* development in 50% seawater.

Third, the effects of salinity on gas exchange characteristics differ in *Aegiceras* and *Avicennia*. Rates of dark respiration in leaves were not substantially influenced by salinity in either species (Table 2.16). Photosynthetic metabolism in the first leaf pair also was not affected by salinity in *Avicennia*, but the assimilation rates declined with increasing salinity in *Aegiceras*, apparently due to a decline in mesophyll conductance (Table 2.16). This response in *Aegiceras* is similar to those observed in several species [Gale and Poljakoff-Mayber, 1970; Longstreth and Strain, 1977; De Jong, 1978a; Longstreth and Nobel, 1979]. The relative constancy of the assimilation rates in *Avicennia*, further emphasises the importance of variation in carbon partitioning on changes in the growth rates in response to salinity. In contrast, the decline in assimilation rates with increasing salinity would accentuate the effects of a concomitant decline in the ratio of leaf area to plant mass on the growth rates. The reasons for these differences in photosynthetic responses are not clear, but may be related to the influence of ions on metabolism.

Fourth, *Aegiceras* and *Avicennia* differ in ion relations. Halophytes typically absorb large quantities of ions which apparently are stored in the vacuole for osmoregulation [Flowers *et al.*, 1977]. *Aegiceras* and *Avicennia* propagules use Cl^-, Na^+ and K^+ as osmotica as shown by the high concentrations of these ions in all plant tissues (Tables 2.10 and 2.11) and thus it is not surprising that substantial ion uptake should accompany growth. The requirements for osmotica can be met by the uptake of only a fraction of the external Na^+ and Cl^- ions. Both *Aegiceras* and *Avicennia* appear to exclude approximately 90 to 95% of the external Na^+ and Cl^- from the transpiration stream (Table 2.15). These results are consistent with other estimates based on the analysis of extruded sap from mature *Aegiceras* and *Avicennia* growing in seawater [Scholander *et al.*, 1962; Scholander *et al.*, 1966; Scholander, 1968].

The capacity to selectively absorb K^+ in the presence of high concentrations of a chemically similar ion, Na^+, is an important adaptation of halophyte, [Rains, 1972]. The calculations of K^+ uptake in relation to water use (Table 2.15) suggest that *Aegiceras* may absorb K^+ more effectively than *Avicennia* at low salinity, but the latter may be more effective than the former at high salinity. *Aegiceras* maintains greater concentration of K^+ in the roots at low salinities than *Avicennia* (Tables 2.10 and 2.11, respectively) with retention of K^+ in the roots of *Aegiceras* accounting for more than half the estimated net K^+ uptake (Table 2.14). The K^+ concentration in *Avicennia* roots increased markedly with increase in salinity from 50 to 100% seawater (Table 2.11). These data are consistent with observations on other halophytes [Jefferies, 1973; Storey and

Wyn Jones, 1979] and it has been suggested that the ability to maintain or increase the concentrations of K^+ in roots in the presence of increasing NaCl may be an important aspect of salt tolerance [Storey and Wyn Jones, 1979].

Similarly, the ability to maintain low Na^+/K^+ ratios and some minimum level of K^+ in the shoot during growth in saline environments is also associated with salt tolerance [Flowers *et al.*, 1977]. The Na^+/K^+ ratios in leaves of *Aegiceras* and *Avicennia* were similar and increased with increasing salinity (Tables 2.10 and 2.11), consistent with measurements made on several other halophytes [Black, 1960; Mozafar *et al.*, 1970a and b; Jefferies, 1973; Storey and Wyn Jones, 1979]. *Avicennia* exhibits a high selectivity for K^+ absorption, as Rains and Epstein [1967] have shown that K^+ uptake by leaf slices of *Avicennia marina* from a solution containing 10 mM K^+ was unaffected by Na^+ concentrations as great as 500 mM, the same ratio as exists in seawater. Indeed, the K^+ concentration in *Avicennia* leaves increased with increasing salinity from 10 to 50% seawater and the level was maintained with further increases to 100% seawater (Table 2.11). In contrast, the K^+ concentration in *Aegiceras* leaves declined with increasing salinity. It is possible that differences between *Aegiceras* and *Avicennia* in requirements for K^+ and in the capacity to satisfy those needs may contribute to the greater sensitivity of the former species to salinity.

The greater sensitivity of *Aegiceras* to salinity may at least partially explain the low density of seedling of this species in the Cullendulla Creek swamp. Once the seedlings are established, the

potential for subsequent growth will depend largely on competition and on the physical factors affecting carbon gain which are the subjects of succeeding chapters.

CHAPTER 3

PHOTOSYNTHETIC RESPONSES TO LEAF TEMPERATURE

3.1 INTRODUCTION

Mangroves are mainly a tropical and sub-tropical association, diminishing in diversity and vigour with increasing latitude [Chapman, 1970]. *Avicennia marina* is one of the most cosmopolitan species with a range extending from 27° North in the Ryuku Islands [Vu Van Cuong, 1964] and 27° 40' North in the Red Sea [Zahran, 1975] to 38° 45' South at Westernport Bay and Corner Inlet, Australia [Saenger *et al.*, 1977]. The distribution of *A. marina* in Australia ranges from tropical areas such as Darwin, where the average January and July air temperatures are 29 and 25 C, respectively, to temperate locations such as Westernport Bay, where the mean January and July air temperatures are 18 and 10 C, respectively [Saenger *et al.*, 1977]. *A. marina* is sympatric in northeastern Australia with *Avicennia eucalyptifolia* Zipp. ex Moldenke [Saenger *et al.*, 1977], a species found in the tropical Indo-Pacific [Chapman, 1970].

The distribution of *A. marina* suggests that it is tolerant of wide variation in temperature. McMillan [1975] has shown that populations of *A. marina* from temperate and tropical regions of New Zealand and Australia differ in their ability to survive low night temperature. However, leaf temperature has been found to be a major factor limiting photosynthesis in *A. marina* under field conditions in

a temperate swamp [Attiwill and Clough, 1980] and in other mangrove species in sub-tropical [Miller, 1972; Moore *et al.*, 1972 and 1973] and tropical environments [Andrews and Clough, 1980]. Therefore, leaf temperature may be an important factor influencing seedling growth. For this reason, the effects of leaf temperature on the gas exchange characteristics of *A. marina* were examined and assessed in relation to the micro-climate experienced by seedlings during their growth in a temperate swamp.

3.2 MATERIALS AND METHODS

3.2.1 Plant Material

Seedlings of *Avicennia marina* were selected for field and laboratory studies from a shaded and an exposed environment along Cullendulla Creek at Batemans Bay, New South Wales, Australia. These environments supported good tree growth as described in Chapter 1 and were separated by about 10 m.

The first set of measurements was made in summer, 1979, a year in which *Avicennia* failed to produce propagules [Chandrashekar and Ball, 1980]. These measurements were made on existing seedlings which were approximately 12 months old. Seedlings of about one and six months of age were obtained in the following year, when propagule production was prolific. All measurements were made on the second or third leaf pairs which are formed during the first four to six weeks of growth (Chapters 1 and 2) and on seedlings which had completed the cotyledonary phase of development (Chapter 2). In most cases, the seedlings did not initiate further shoot growth (Chapter 1) and therefore the observations are influenced by the effects of age and season over the two years of the study.

3.2.2 Microclimate

Measurements of leaf microclimate were made hourly for ten shaded seedlings and ten exposed seedlings on the day preceding laboratory gas exchange measurements, except in summer, 1979, when only two seedlings in each site were examined. Leaf and air temperatures were sensed by means of copper/constantan thermocouples (42 swg) referenced against a mercury and glass thermometer maintained in a water bath, the temperature of which was allowed to fluctuate naturally during the day. The voltage output was measured with a Keithley microvoltmeter. Air temperature was measured at seedling height (i.e. ~ 25 cm), the thermocouple being shielded from direct sunlight. Soil and water temperatures were measured with a mercury and glass thermometer. Ambient vapour pressure was calculated from wet and dry bulb measurements taken with an Assman psychrometer. A Lambda quantum sensor model LI-185 was used to measure the quantum flux density incident on the adaxial surfaces of leaves and that of vertical insolation, the sensor being held horizontally in an open area. Measurements were made at hourly intervals.

3.2.3 Gas Exchange Measurements

After sunset, a total of four seedlings, two from the shaded and two from the exposed habitats, were selected for gas exchange studies on the basis of having received the least and the most irradiance, respectively. Each seedling was transplanted to a bucket, the soil containing the root system being maintained intact and flooded with saline creek water, and then was transported in darkness to the laboratory.

Gas exchange measurements were made on intact, attached leaves as

described in the appendix. All measurements were made during normal photoperiods. On the first day, assimilation rate was measured as a function of the intercellular CO_2 concentration by varying the ambient CO_2 concentration according to the sequence 330, 200, 100, 50 and 330 $\mu l\ l^{-1}$ allowing 30 minutes at each concentration to permit variables relating to gas exchange to attain steady state. Leaf temperature was maintained at 25 C, quantum flux density was 1000 $\mu E\ m^{-2}\ s^{-1}$, and leaf to air vapour pressure difference was approximately 12 mbar. The set of conditions with ambient CO_2 concentration equal to 330 $\mu l\ l^{-1}$ will be called the standard condition.

Measurements of the effects of leaf temperature and irradiance on gas exchange characteristics were begun on the second day using the same leaves. During the summer, leaf temperature was varied by step changes of 5 C from 25 to 40 C followed by 25 to 5 C. In winter the sequence from 25 to 5 C was performed before that from 25 to 40 C. The quantum flux density was varied at each temperature in the sequence 1000, 2000, 500, 250 and 1000 $\mu E\ m^{-2}\ s^{-1}$, the last point only to check that photosynthetic characteristics had not varied during the measurements before proceeding to the next leaf temperature. It was not possible to maintain a constant leaf to air vapour pressure difference (vpd) as leaf temperature was changed due to limitations on the extent to which ambient vapour pressure could be varied. The vpd experienced with increase in leaf temperature averaged 4 mbar at 5 C, 6 mbar at 10 C, 9 mbar at 15 C, 10 mbar at 20 C, 12 mbar at 25 C, 19 mbar at 30 C, 35 mbar at 35 C and 53 mbar at 40 C.

Measurements were made frequently under standard conditions to monitor possible changes in photosynthetic metabolism. The experiment was concluded with measurement of dark respiration as a function of

leaf temperature. The entire set of temperature and light responses typically required five to six days for completion.

Details of other experiments are given in the text. Only field grown seedlings were used in these experiments, the seedlings being collected on the day preceding the experiment.

3.3 RESULTS

3.3.1 The Natural Environment

Characteristics of the microclimate of leaves of seedlings grown in the exposed and shaded environments are shown in Figs. 3.1 and 3.2, respectively. These measurements were made on clear sunny days, except for the onset of an overcast period at 1500 in summer, 1979. The maximum air temperatures were 23 and 26 C in summer and 17 and 16 in winter in 1980 and 1979, respectively. It was unusually cold on the winter study day in 1979, when frost was observed before dawn on exposed sand and mud. Absolute humidity changed little during the day.

There was considerable variability in the quantum flux density incident on the upper surfaces of leaves from exposed areas, depending on the azimuth and inclination of the leaves. However, the light intensity received by exposed leaves was greater than that of shaded leaves throughout the day. Leaves typically were 2 to 6 C warmer than the air, and as much as 10 C warmer during periods of high insolation on still days. These large differences between leaf and air temperatures correspond to large leaf to air vapour pressure differences (vpd). Thus the microclimate experienced by exposed leaves is effectively more arid than might be expected in a swamp environment. During overcast periods, as occurred at 1500 in the

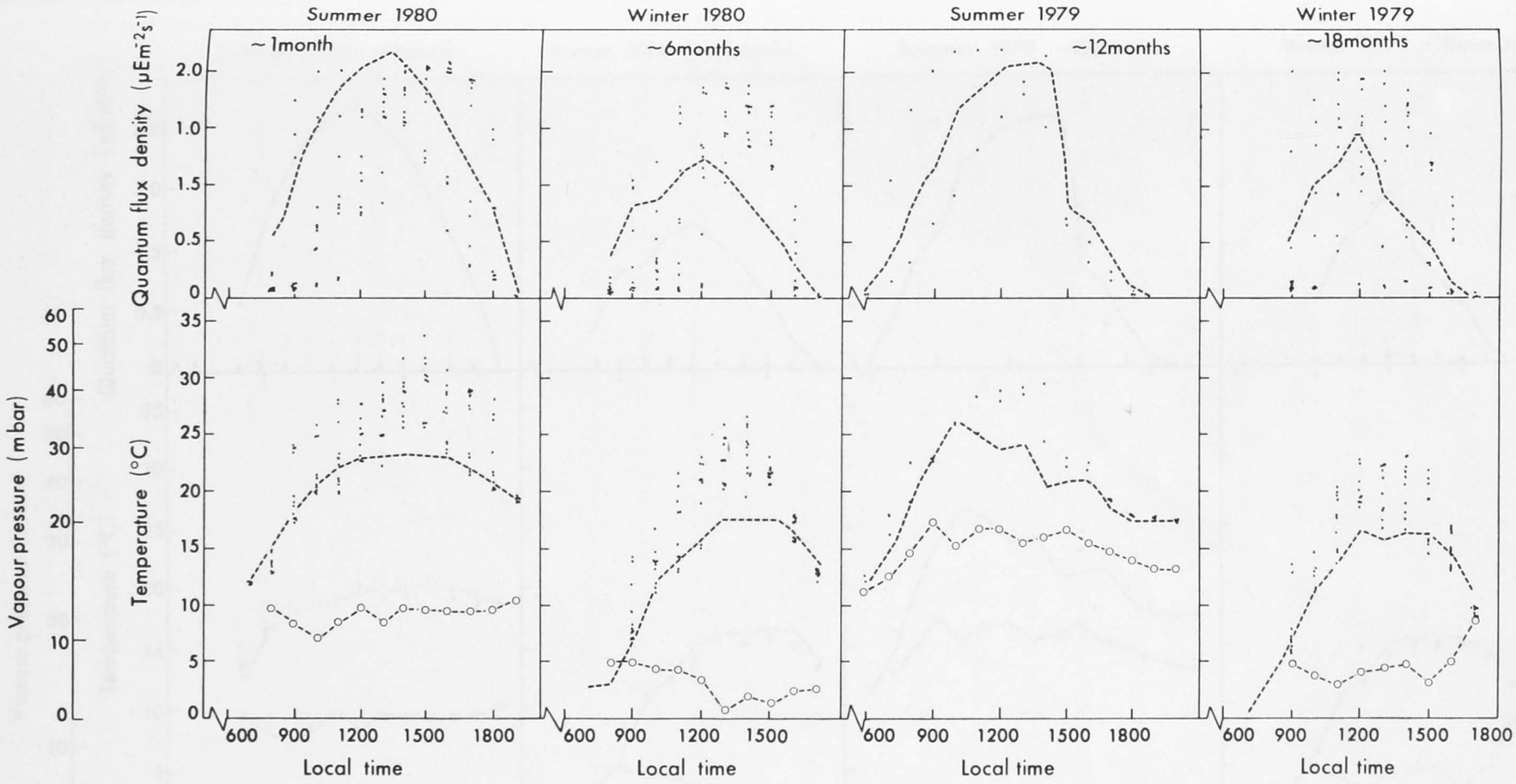


Fig. 3.1: Microclimate of exposed leaves during two summer and winter days. The quantum flux densities of vertical insolation and of light incident on the adaxial leaf surface are shown by (– – –) and (●), respectively. Leaf and air temperatures are indicated by (●) and (– – –), respectively. These same symbols also correspond to the saturation vapour pressures at leaf and air temperature. Ambient vapour pressure is indicated by (○).

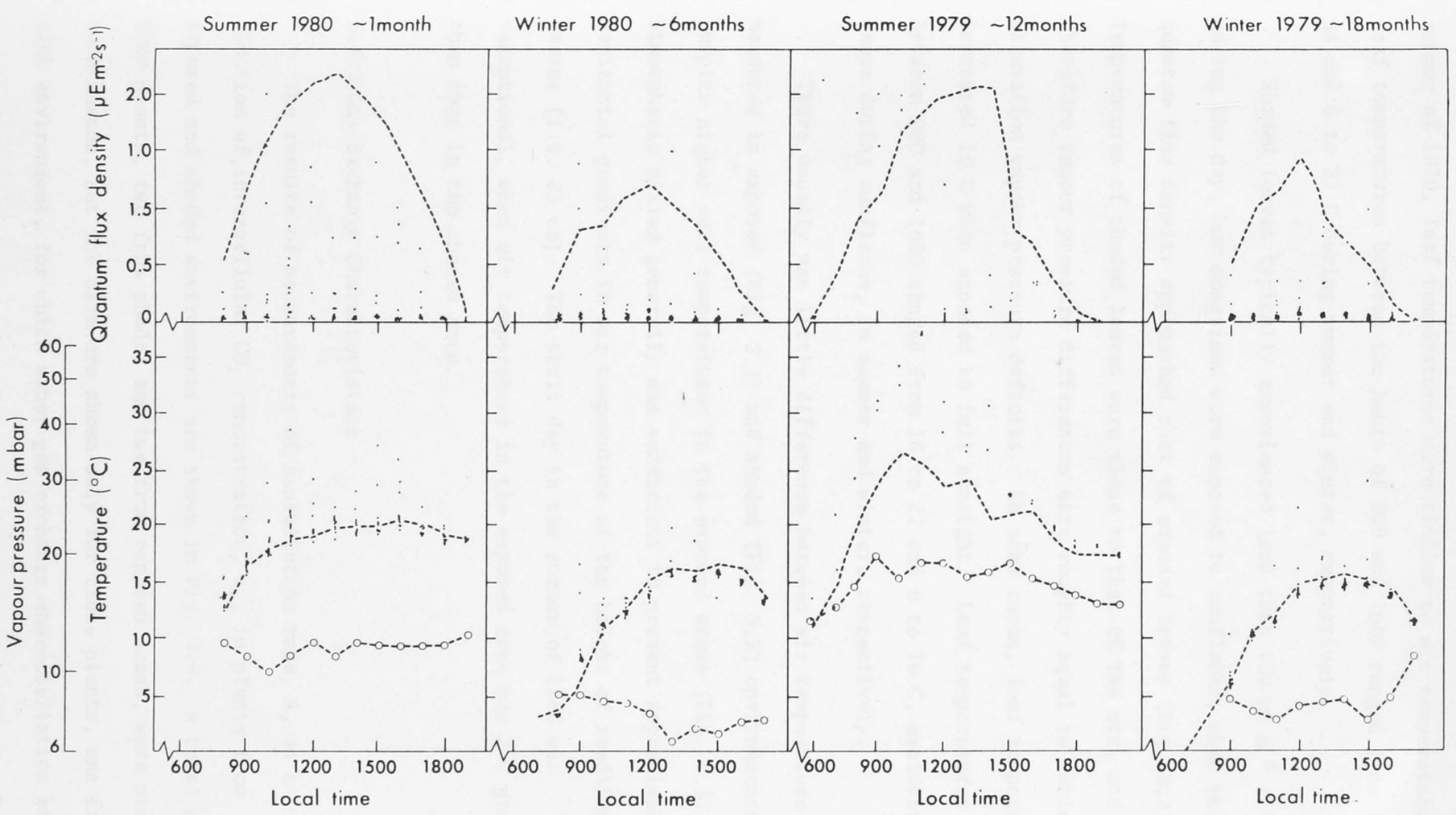


Fig. 3.2: Microclimate of shaded leaves during two summer and winter days. The symbols are the same as in Fig. 3.1.

summer of 1979, leaf temperatures were similar to air temperature. Leaf temperatures between the hours of 900 and 1600 ranged from 18 to 34 and 6 to 27 C during summer and winter, respectively.

Shaded leaves typically experienced less than 100 $\mu E\ m^{-2}\ s^{-1}$ during the day, but sometimes were exposed to sunflecks, when the quantum flux density approached that of exposed leaves (Fig. 3.2). Temperatures of shaded leaves were close to that of the air, and therefore vapour pressure differences were roughly equal to ambient saturation vapour pressure deficits. In some cases, leaf temperature increased 10 C when exposed to full sunlight. Leaf temperatures between 900 and 1600 ranged from 16 to 22 and 6 to 16 C, exclusive of those during sunflecks, in summer and winter, respectively.

There usually was little difference between air temperature measured in exposed (Fig. 3.1) and shaded (Fig. 3.2) environments. Despite higher soil temperatures in the exposed areas (Fig. 3.3), atmospheric mixing generally was sufficient to prevent appreciable horizontal gradients in air temperature at the height of seedling leaves (i.e. 25 cm). The still day in the summer of 1980 was exceptional, when air temperature in the exposed area was 3 C greater than that in the shaded area.

3.3.2 Gas Exchange Characteristics

The results of measurements of assimilation rate, A, as a function of intercellular CO_2 concentration, c_i, in plants from exposed and shaded environments are shown in Fig. 3.4. A total of four plants, two from shaded and two from exposed areas, were studied each season, but the data are shown only for those plants, one from each environment, for which other gas exchange characteristics are

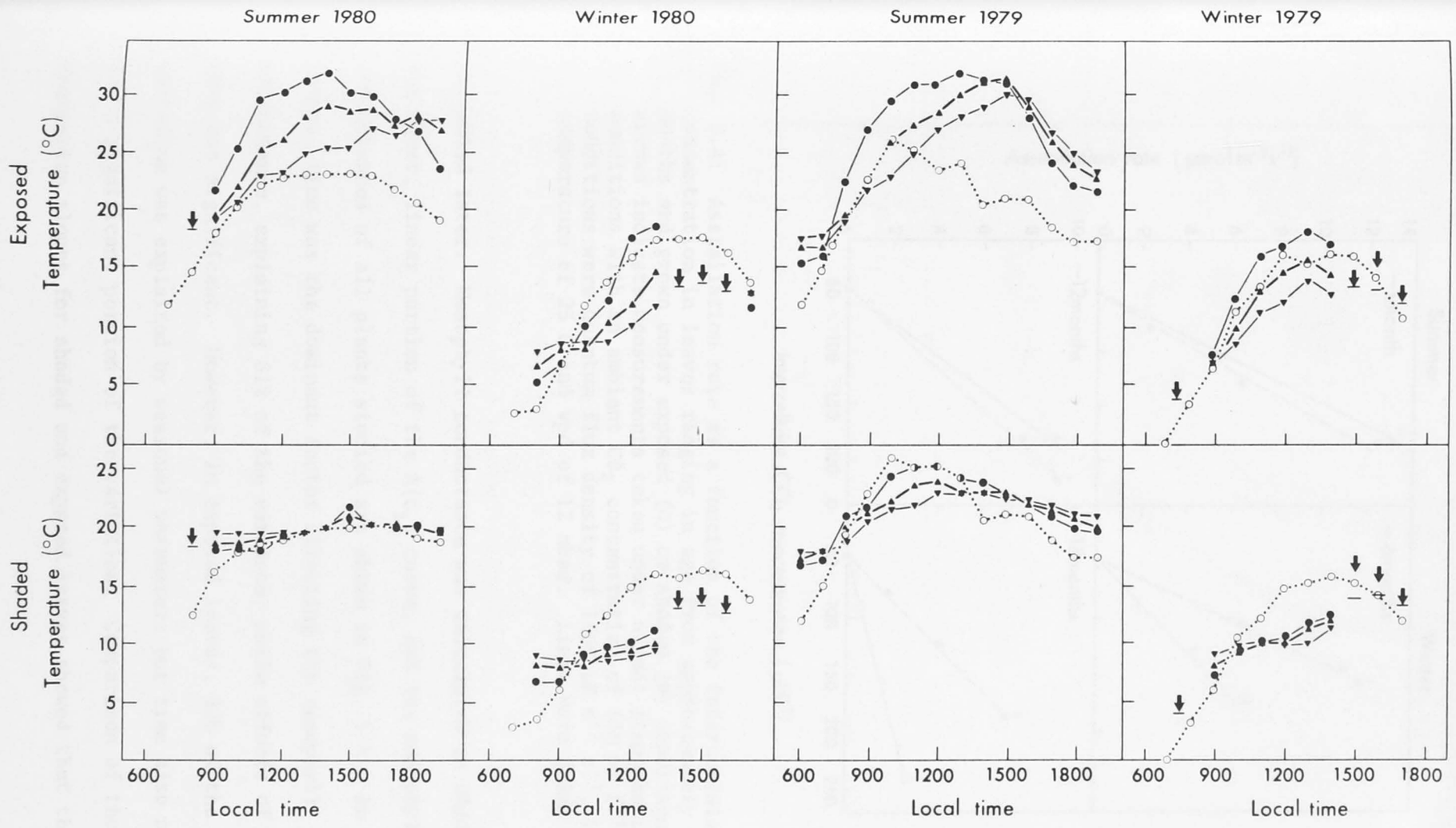


Fig. 3.3: Soil temperature at depths of 1 (●), 5 (▲) and 10 cm (▼) in exposed and shaded areas during summer and winter. Air temperature is indicated by (○) and the temperature of flooding tidal water is shown by ⊻.

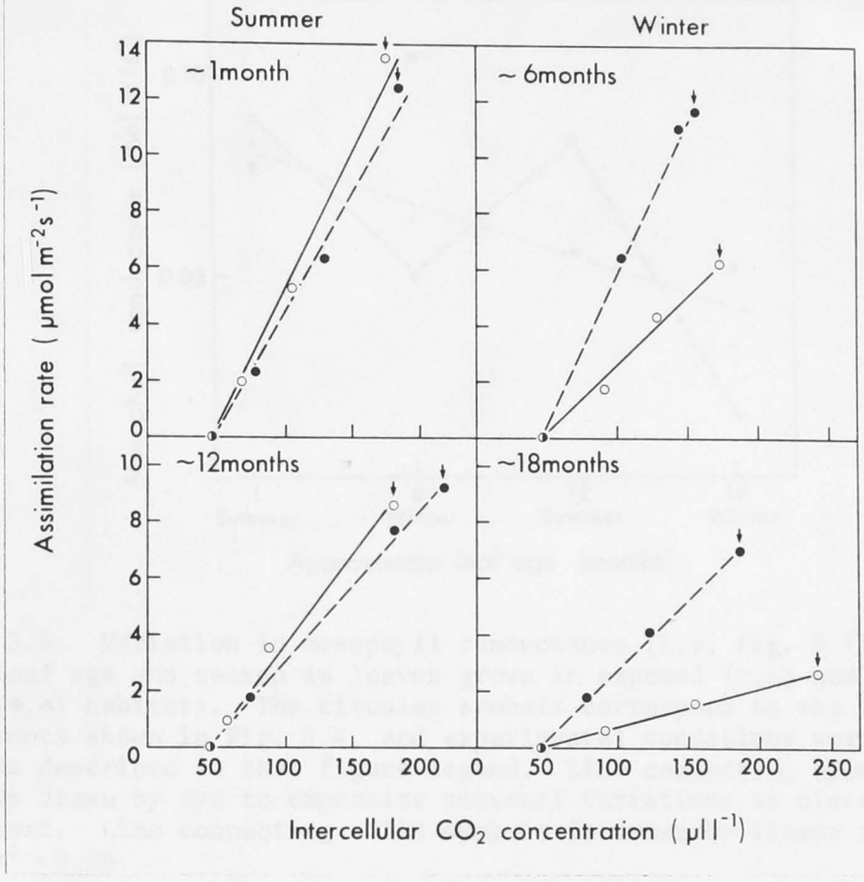


Fig. 3.4: Assimilation rate as a function of the intercellular CO_2 concentration in leaves ranging in age from approximately 1 to 18 months and grown under exposed (○) or shaded (●) conditions. The arrows indicate measurements taken under normal atmospheric conditions with an ambient CO_2 concentration of 330 $\mu l\ l^{-1}$. Other conditions were quantum flux density of 1000 $\mu E\ m^{-2}\ s^{-1}$, leaf temperature of 25 C and vpd of 12 mbar. Lines were drawn by eye.

presented later. Mesophyll conductance was calculated as dA/dc_i for the lower, linear portion of the $A(c_i)$ curve, and the mesophyll conductances of all plants studied are shown in Fig. 3.5. In shaded leaves, time was the dominant factor affecting the mesophyll conductance, explaining 81% of the variance, while effects of season were not significant. However, in exposed leaves, 82% of the variation was explained by seasonal parameters but time also accounted for a significant portion of the variation. Comparison of the regression slopes for shaded and exposed leaves showed that the

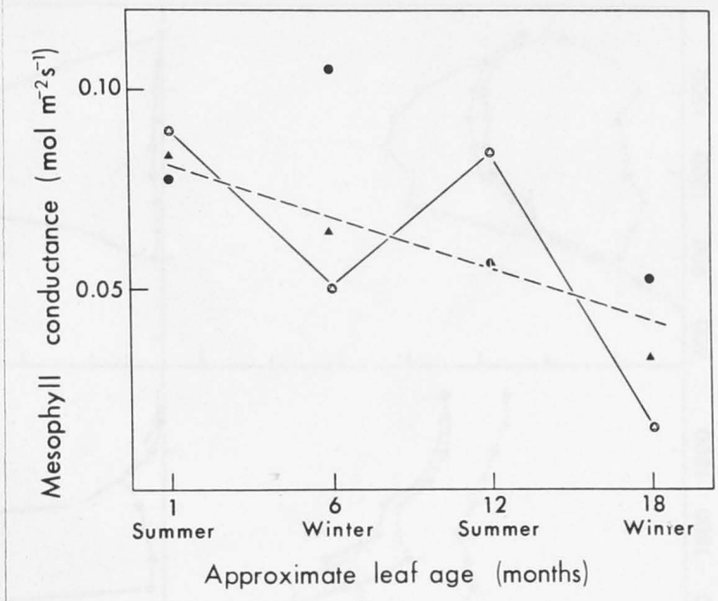


Fig. 3.5: Variation in mesophyll conductance (i.e. Fig. 3.4) with leaf age and season in leaves grown in exposed (○,△) and shaded (●,▲) habitats. The circular symbols correspond to the measurements shown in Fig. 3.4, and experimental conditions were the same as described in that figure legend. Line connecting open symbols is drawn by eye to emphasize seasonal variations as discussed in text. Line connecting solid symbols is drawn by linear regression, $r^2 = 0.59$.

overall decline in mesophyll conductance with time was the same for both groups of leaves.

The effects of leaf temperature and light intensity on the gas exchange characteristics of leaves from exposed and shaded habitats (Fig. 3.6) are shown in Figs. 3.7 and 3.8, respectively. Aside from differences in the magnitude of the responses due to the decreased photosynthetic capacity of exposed leaves during the winter, there were no obvious differences between the responses of shaded or exposed leaves to either temperature or light intensity. There was some variability in the temperature optima between plants but there were no consistent trends indicative of seasonal acclimatization of the temperature optimum for photosynthesis, which typically occurred at

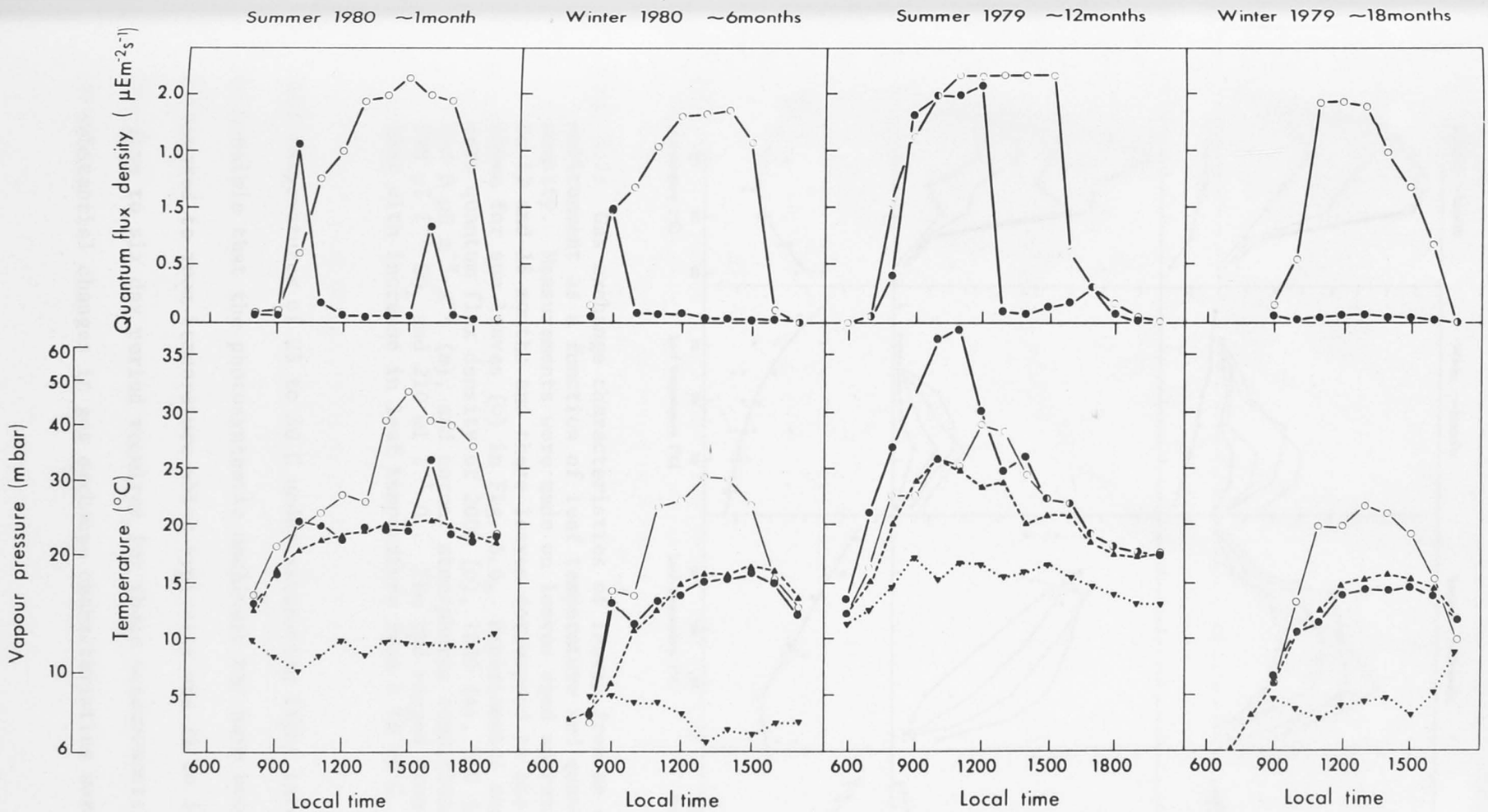


Fig. 3.6: Microclimate of the sun (○) and shade leaves (●) on the day before gas exchange measurements. Parameters shown are quantum flux density incident on the adaxial leaf surface, leaf temperature (with the same point also indicating saturation vapour pressure at leaf temperature), air temperature and saturation vapour pressure at air temperature (▲) and ambient vapour pressure (▼).

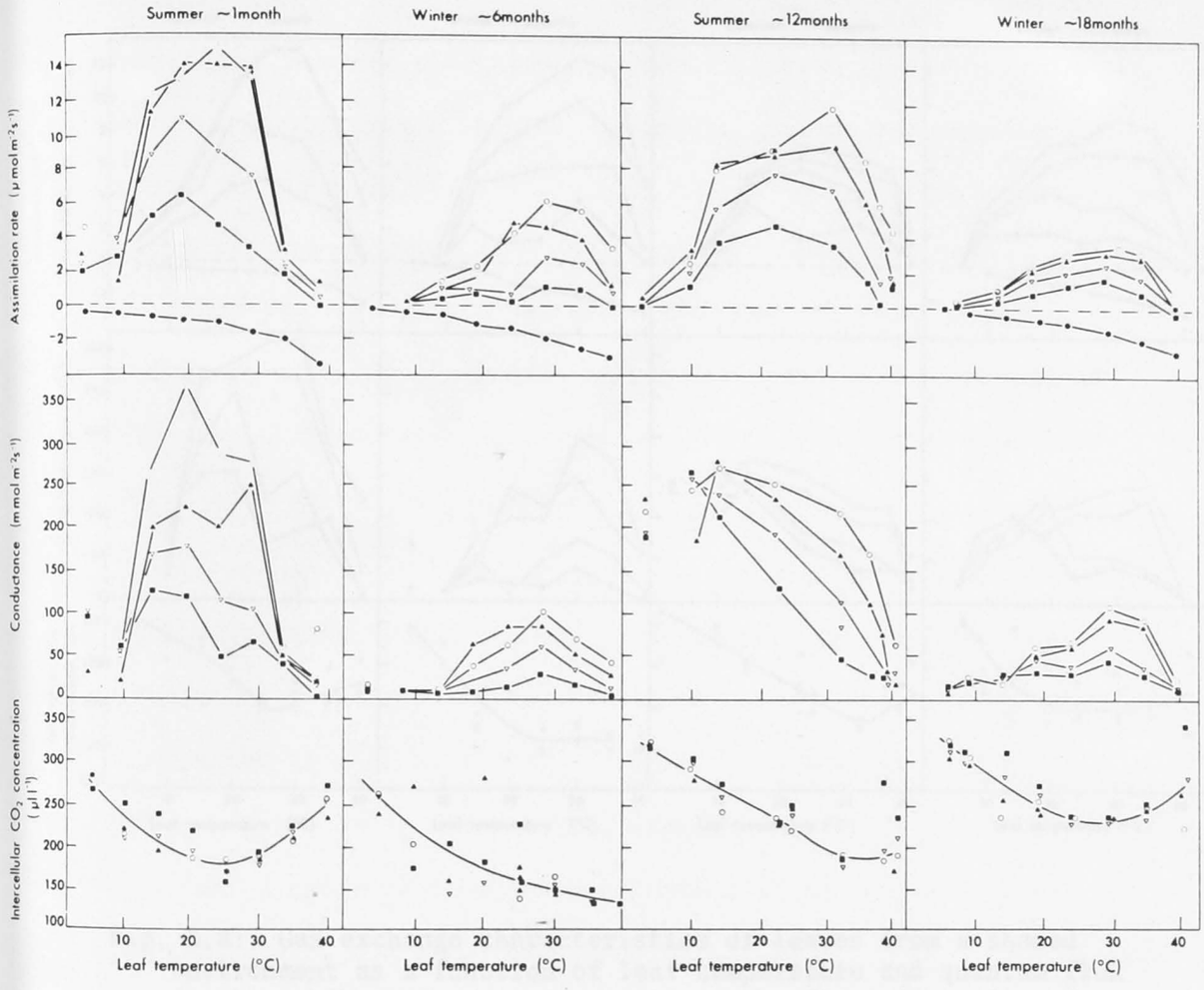


Fig. 3.7: Gas exchange characteristics of leaves from an exposed environment as a function of leaf temperature and quantum flux density. Measurements were made on leaves aged approximately 1, 6, 12 and 18 months and these leaves correspond to the field data shown for sun leaves (○) in Fig. 3.6. Experimental conditions were quantum flux density of 2000 (○), 1000 (▲), 500 (▽), 250 (■) and 0 μE m^{-2} s^{-1} (●), and normal atmospheric conditions of 300 μl l^{-1} CO_2 and 210 ml l^{-1} O_2. The vpd ranged from 4 to 53 mbar with increase in leaf temperature from 5 to 40 C.

leaf temperatures of 25 to 30 C under saturating light intensity. It is possible that the photosynthetic machinery may have become acclimated to room temperature which typically was 28 to 30 C during the five to six day period required for these measurements. However, no substantial changes in gas exchange characteristics were found in

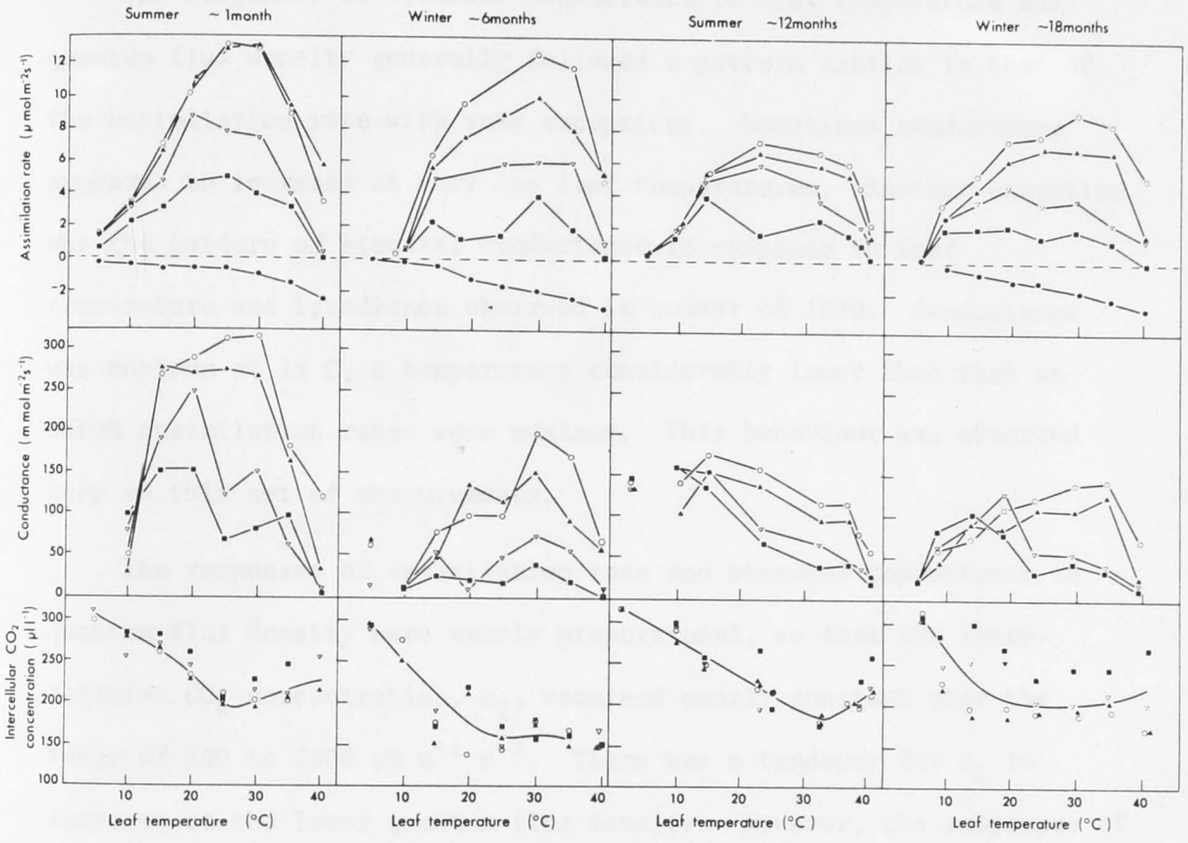


Fig. 3.8: Gas exchange characteristics of leaves from a shaded environment as a function of leaf temperature and quantum flux density. These leaves correspond to the field data shown for shaded leaves (●) in Fig. 3.6. Symbols mean the same as in Fig. 3.7.

measurements made periodically at a standard condition during the course of measuring the responses to leaf temperature and light intensity as shown in Figs. 3.7 and 3.8. Thus, the responses were reversible and photosynthetic metabolism suffered no obvious damage after experiencing conditions as extreme as leaf temperatures of 5 or 40 C with a quantum flux density of 2000 μE m^{-2} s^{-1} for at least 30 minutes. The data presented in Figs. 3.7 and 3.8 were selected for presentation on the basis of having shown the least changes in gas exchange characteristics under the standard condition.

The responses of stomatal conductance to leaf temperature and quantum flux density generally followed a pattern similar to that of the assimilation rate with some exceptions. Sometimes conductance appeared to increase at very low leaf temperatures. Another exception was the pattern of stomatal conductance in response to leaf temperature and irradiance observed in summer of 1979. Conductance was maximum at 15 C, a temperature considerably lower than that at which assimilation rates were maximum. This behaviour was observed only in this set of measurements.

The responses of assimilation rate and stomatal conductance to quantum flux density were nearly proportional, so that the intercellular CO_2 concentration, c_i, remained nearly constant over the range of 500 to 2000 $\mu E\ m^{-2}\ s^{-1}$. There was a tendency for c_i to increase at the lower quantum flux density. However, the responses of assimilation rate and stomatal conductance to variation in leaf temperature were not proportional, with the effect that c_i was minimum near the temperature optimum for assimilation.

The stomata of leaves from exposed and shaded habitats were sensitive to humidity as shown in Fig. 3.9. These measurements were made on the plants collected in summer of 1980 (see Fig. 3.4). Stomatal conductance and assimilation rate declined approximately 60 and 40%, respectively, with increase in the vpd from 5 to 25 mbar, values typically encountered in the field environment (Figs. 3.1 and 3.2).

To place the temperature responses of *A. marina* in the perspective of the temperate climate experienced by this population, comparative measurements were made on a closely related species,

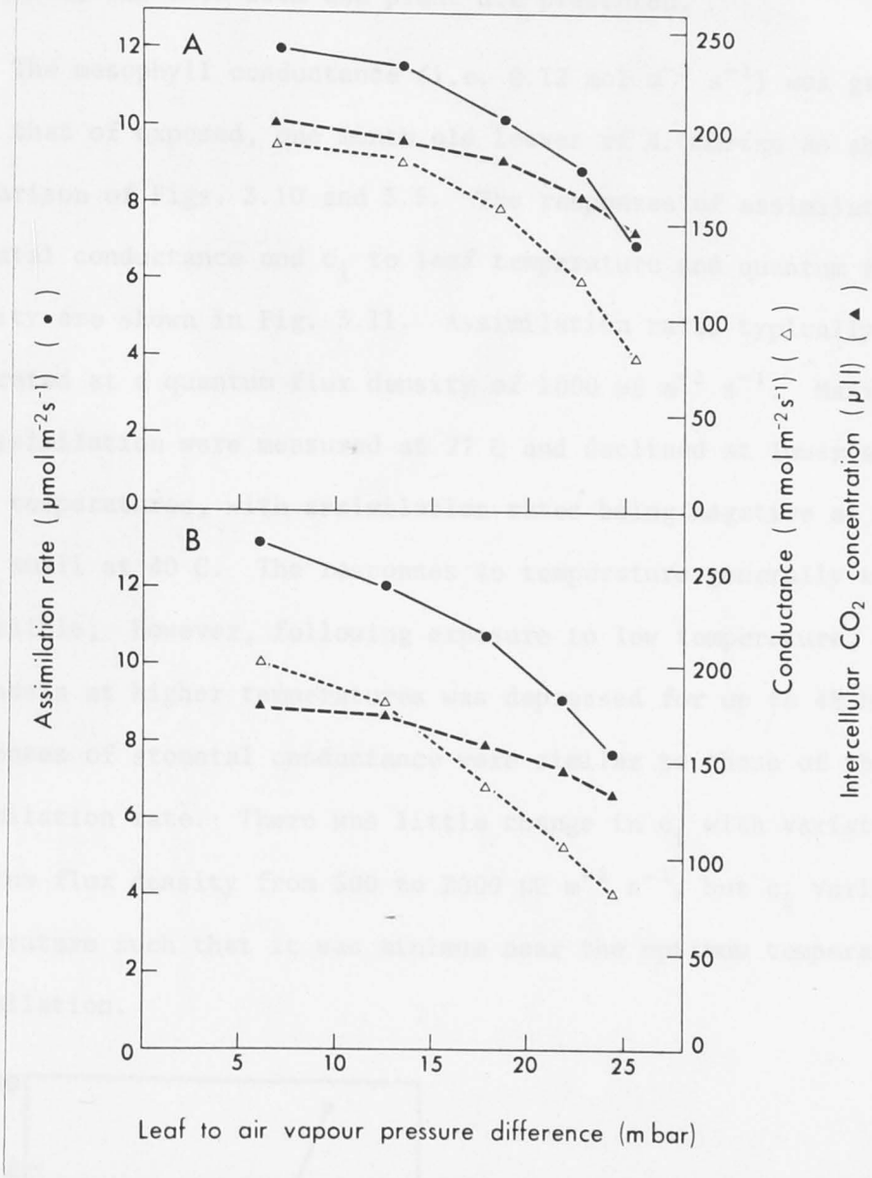


Fig. 3.9: Gas exchange characteristics of leaves from exposed (A) and shaded (B) field conditions as a function of vpd. Measurements were made at a leaf temperature of 25 C, quantum flux density of 1000 μE m^{-2} s^{-1} and under normal atmospheric conditions, i.e. 330 μl l^{-1} CO_2 and 210 ml l^{-1} O_2.

Avicennia eucalyptifolia, collected from a tropical environment. The seedlings were from an exposed area on Hinchinbrook Island, North Queensland, and the leaves studied were approximately one month old. Measurements were made on four seedlings, all of which gave similar

responses, and data from one plant are presented.

The mesophyll conductance (i.e. 0.12 mol m^{-2} s^{-1}) was greater than that of exposed, one month old leaves of *A. marina* as shown by comparison of Figs. 3.10 and 3.5. The responses of assimilation rate, stomatal conductance and c_i to leaf temperature and quantum flux density are shown in Fig. 3.11. Assimilation rates typically were saturated at a quantum flux density of 1000 µE m^{-2} s^{-1}. Maximum rates of assimilation were measured at 27 C and declined at lower and higher leaf temperatures, with assimilation rates being negative at 15 C and very small at 40 C. The responses to temperature generally were reversible; however, following exposure to low temperature, photosynthesis at higher temperatures was depressed for up to 48 hours. Responses of stomatal conductance were similar to those of the assimilation rate. There was little change in c_i with variation in quantum flux density from 500 to 2000 µE m^{-2} s^{-1}, but c_i varied with temperature such that it was minimum near the optimum temperature for assimilation.

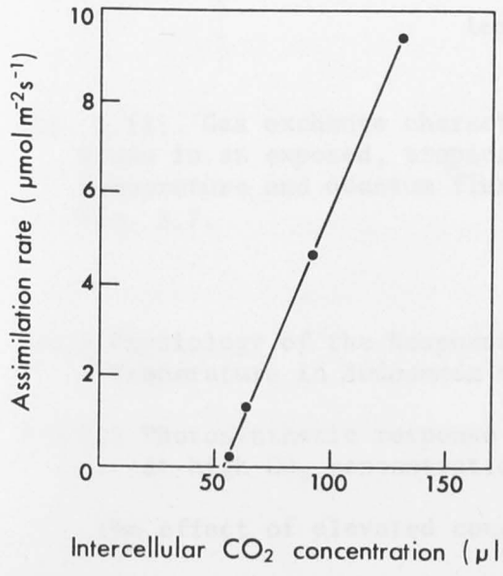


Fig. 3.10: Assimilation rate as a function of the intercellular CO_2 concentration in *Avicennia eucalyptifolia*. Measurements were made under the standard conditions, i.e. leaf temperature of 25 C, quantum flux density of 1000 µE m^{-2} s^{-1} and vpd of 12 mbar.

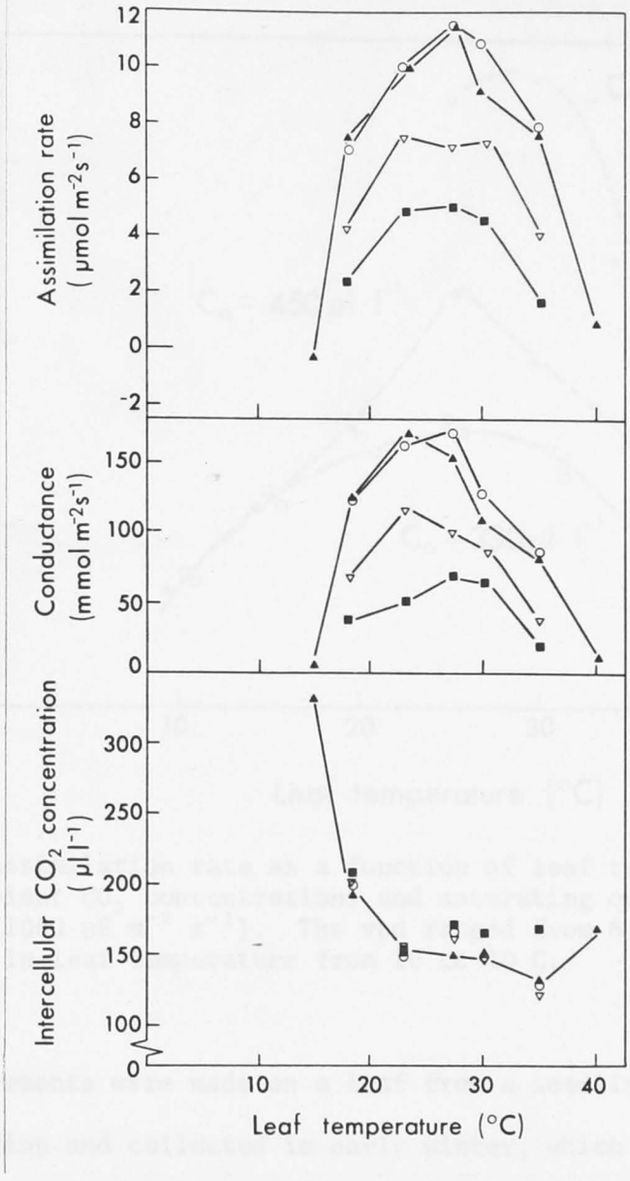


Fig. 3.11: Gas exchange characteristics of *Avicennia eucalyptifolia* grown in an exposed, tropical environment as a function of leaf temperature and quantum flux density. Symbols mean the same as in Fig. 3.7.

3.3.3 Physiology of the Response to Temperature in *Avicennia marina*

3.3.3.1 Photosynthetic response to temperature at high CO_2 concentration

The effect of elevated concentrations of ambient CO_2, c_a, on assimilation rate as a function of leaf temperature is shown in Fig.

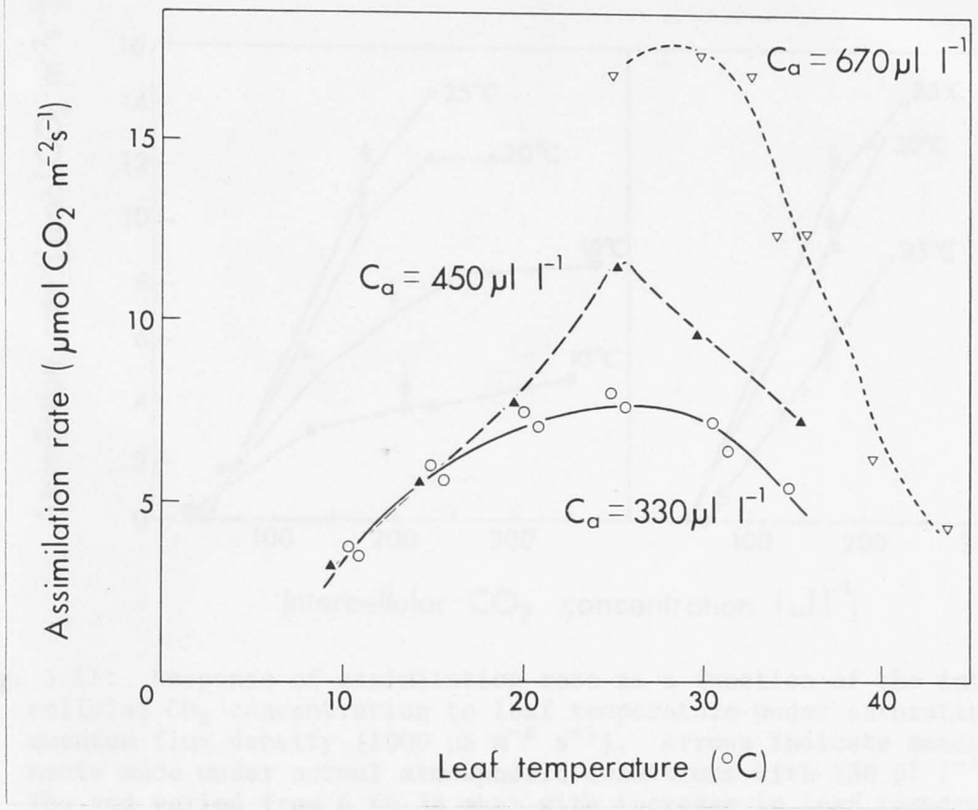


Fig. 3.12: Assimilation rate as a function of leaf temperature under three ambient CO_2 concentrations and saturating quantum flux density (1000 μE m^{-2} s^{-1}). The vpd ranged from 6 to 53 mbar with increase in leaf temperature from 10 to 40 C.

3.12. Measurements were made on a leaf from a seedling grown in an exposed location and collected in early winter, which partially explains its relatively low photosynthetic capacity (see Fig. 3.4). Increase in c_a from 330 to 450 μl l^{-1} had no effect on assimilation rate when leaf temperature was less than 20 C, but enhanced it considerably at higher leaf temperatures. Rate of assimilation was increased further by increase in c_a to 670 μl l^{-1}, and the temperature optimum was shifted slightly upwards. An appreciable assimilation rate occurred at leaf temperatures of 40 C and greater under this high CO_2 concentration.

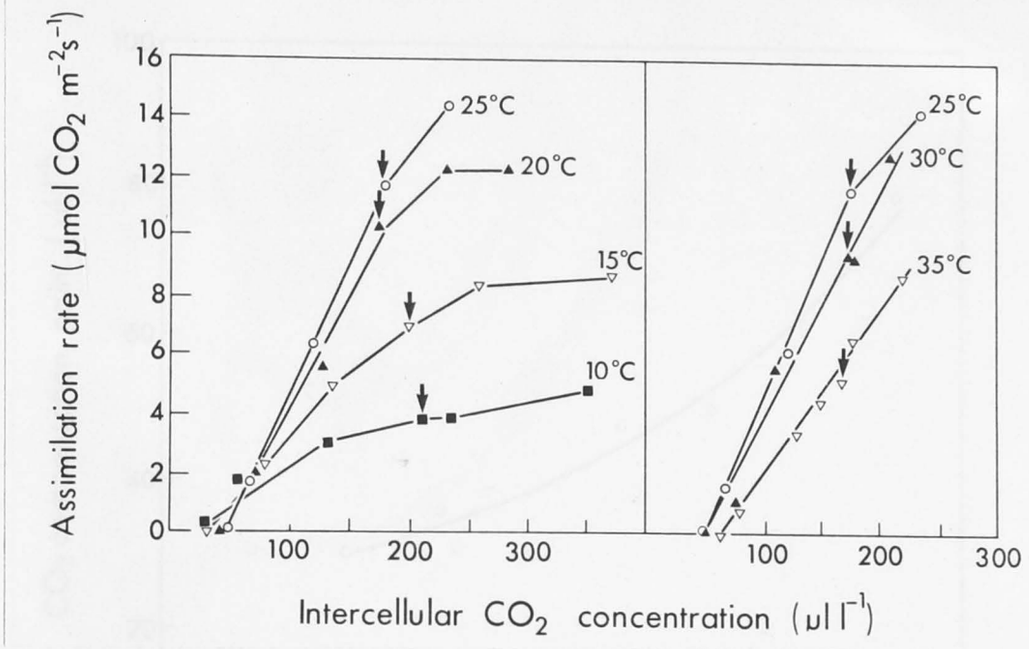


Fig. 3.13: Response of assimilation rate as a function of the intercellular CO_2 concentration to leaf temperature under saturating quantum flux density (1000 μE m^{-2} s^{-1}). Arrows indicate measurements made under normal atmospheric conditions with 330 μl l^{-1} CO_2. The vpd varied from 6 to 38 mbar with increase in leaf temperature from 10 to 35 C.

3.3.3.2 Effect of leaf temperature on the $A(c_i)$ relationship

The effect of leaf temperature on the $A(c_i)$ curve is shown in Fig. 3.13. Measurements were made on three plants, all of which showed the same trends but differed in photosynthetic capacity. The data shown were obtained from one leaf. Variation in c_i was obtained by changing c_a in the sequence 330, 400, 500, 200, 100 μl l^{-1} and finally homing in on the CO_2 compensation point, i.e. that c_i at which the net assimilation rate is zero.

Variation in leaf temperature affected all aspects of the $A(c_i)$ curve (Fig. 3.13). The CO_2 compensation point, Γ, increased with temperature and the data are replotted for clarity in Fig. 3.14.

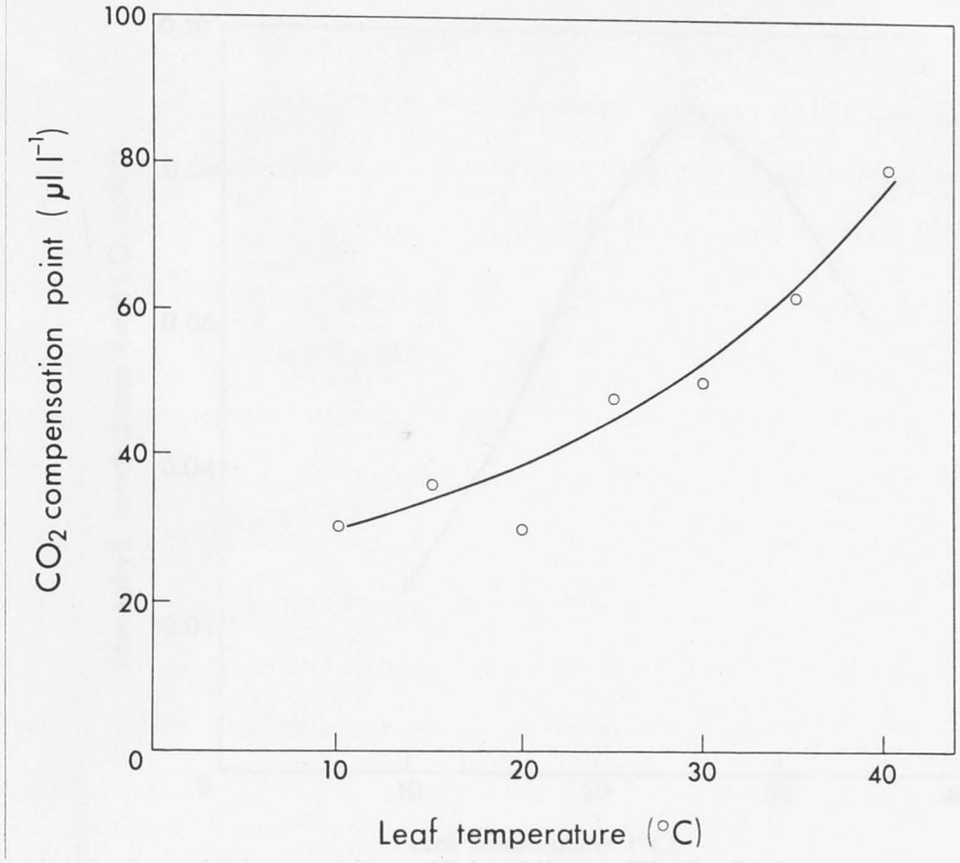


Fig. 3.14: The CO_2 compensation point as a function of leaf temperature at saturating quantum flux density (1000 $\mu E\ m^{-2}\ s^{-1}$). Data are replotted from Fig. 3.13. Line is drawn by eye.

Mesophyll conductance varied with temperature, being maximum at 25 C, as indicated by variation in the initial slopes of the curves in Fig. 3.13, and demonstrated more clearly in Fig. 3.15. The magnitude of c_i at which the lower portion of the $A(c_i)$ curve departed from linearity changed with temperature (Fig. 3.13). Unfortunately, stomata closed so much with increase in c_a from 330 to 500 $\mu l\ l^{-1}$ at temperatures above 25 C that the c_i remained in the initial linear region and changes in curvature of the upper portion of the curve could not be assessed. The changes in the $A(c_i)$ relationship with temperature caused the photosynthetic capacity, here arbitrarily taken to be the

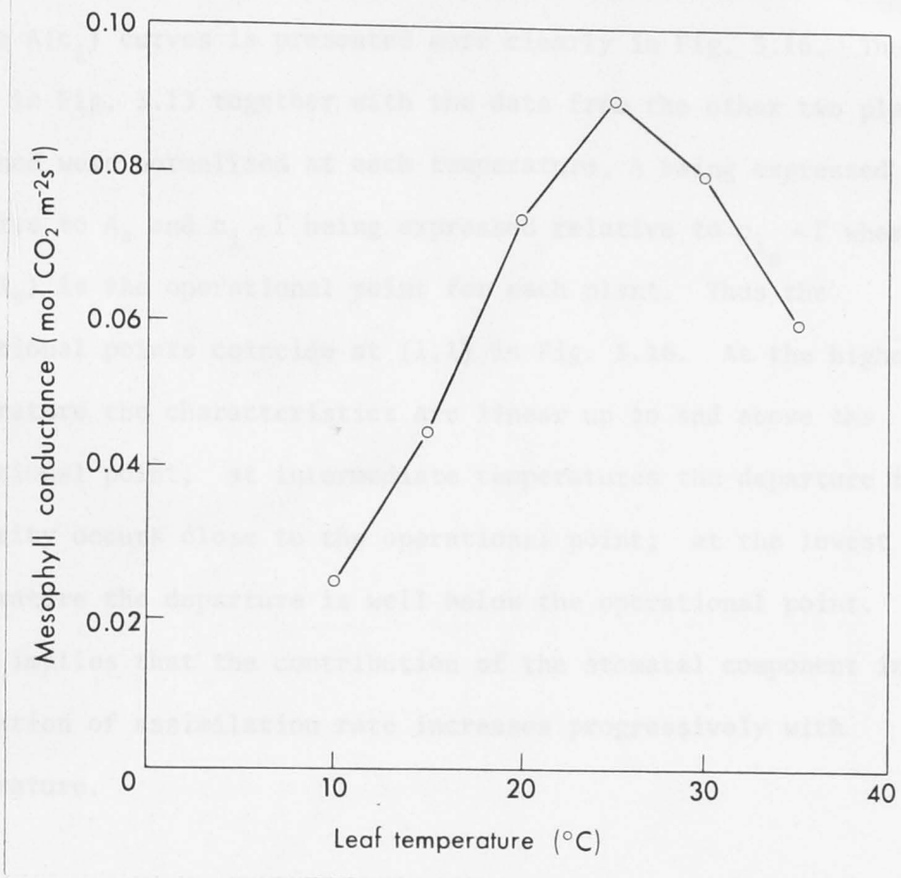


Fig. 3.15: Mesophyll conductance as a function of leaf temperature under saturating quantum flux density (1000 µE m^{-2} s^{-1}). Data are replotted from Fig. 3.13.

assimilation rate at a constant c_i of 200 µl l^{-1}, to be maximal at 25 C.

3.3.3.3 Influence of stomata on the effect of temperature on the assimilation rate

The influence of stomata on the assimilation rates obtained under normal atmospheric conditions is shown by examining the shape of the $A(c_i)$ curve for a particular set of conditions with reference to the point at which the leaf normally functions, i.e. those corresponding to a c_a of 330 µl l^{-1}. These operational points are shown in Fig.

3.13, but the significance of these points in relation to the shapes of the $A(c_i)$ curves is presented more clearly in Fig. 3.16. The data shown in Fig. 3.13 together with the data from the other two plants examined were normalized at each temperature, A being expressed relative to A_0 and $c_i - \Gamma$ being expressed relative to $c_{i_0} - \Gamma$ where (c_{i_0}, A_0) is the operational point for each plant. Thus the operational points coincide at (1,1) in Fig. 3.16. At the highest temperature the characteristics are linear up to and above the operational point; at intermediate temperatures the departure from linearity occurs close to the operational point; at the lowest temperature the departure is well below the operational point. This trend implies that the contribution of the stomatal component in the limitation of assimilation rate increases progressively with temperature.

3.3.3.4 Effect of leaf temperature on stomatal behaviour

The effect of leaf temperature on stomatal conductance as a function of c_i is shown in Fig. 3.17. These data were obtained from three plants during the measurement of $A(c_i)$ curves at different temperatures (see Fig. 3.13). The data are erratic, but some trends are apparent. Stomatal conductance generally declined with increase in c_i from the compensation point up to the operational point. This decline continued at higher c_i at temperatures from 20 to 35 C, but stomatal conductance tended to increase with c_i above the operational point at 10 and 15 C.

Stomatal conductance varied with leaf temperature in the same sense as the photosynthetic capacity. This is shown in Fig. 3.18, in which conductance at a constant c_i of 200 $\mu l\ l^{-1}$ was interpolated from

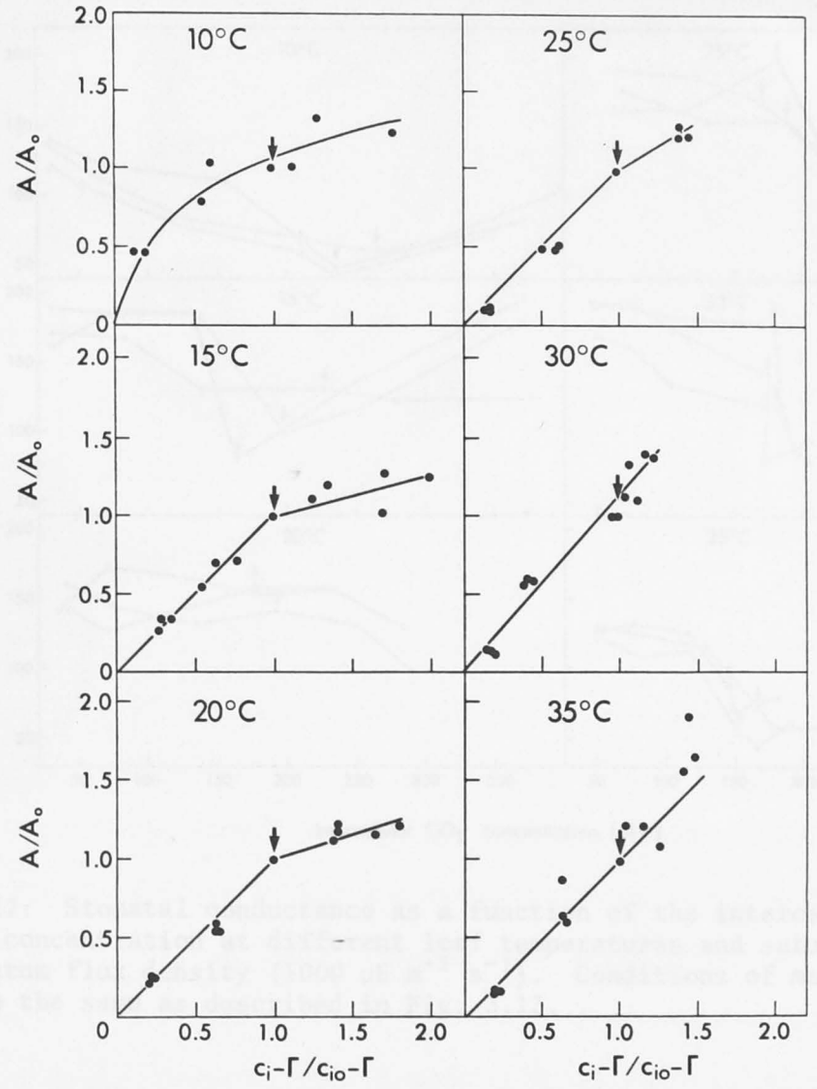


Fig. 3.16: Normalization of $A(c_i)$ curves measured at different leaf temperatures to emphasize the position of operational values relative to the shape of the curve. A_0 and c_{i_0} are values measured under normal atmospheric conditions with a CO_2 concentration of 330 $\mu l\ l^{-1}$ and these are indicated by the arrow. A and c_i are values measured at all other concentrations of ambient CO_2. Conditions during measurements were the same as described in Fig. 3.13. Lines are drawn by eye.

the data as shown in Fig. 3.17, and plotted as a function of leaf temperature. Conductance increased with leaf temperature to a maximum at 25 C, and declined sharply at higher temperatures.

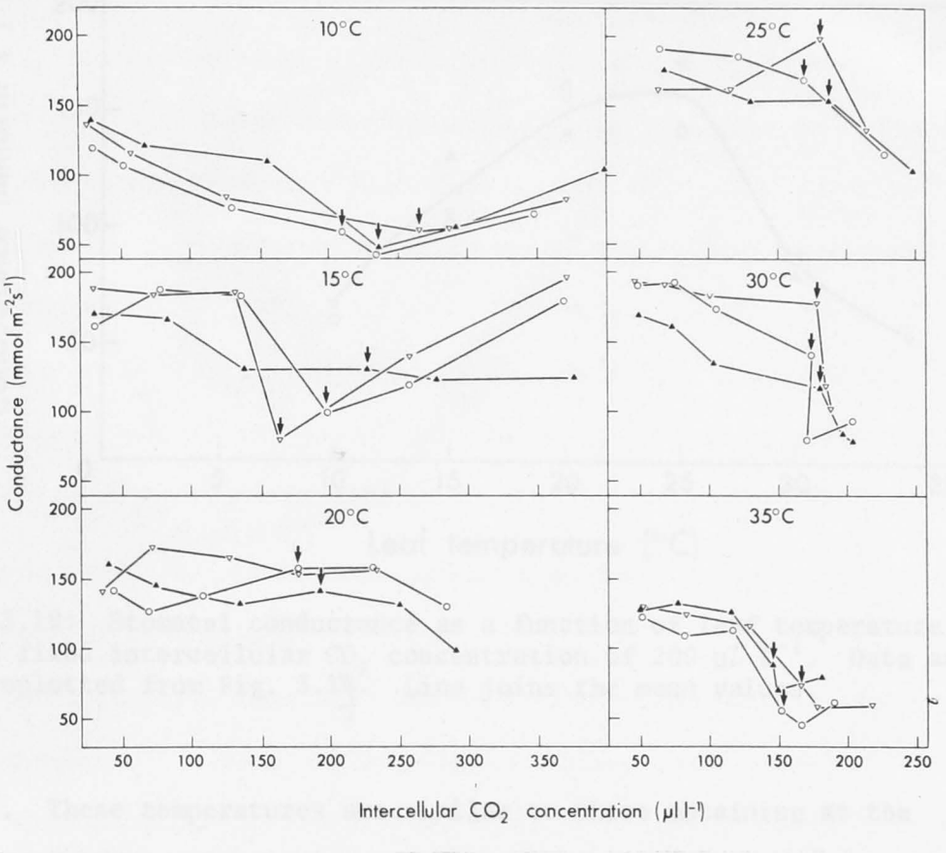


Fig. 3.17: Stomatal conductance as a function of the intercellular CO_2 concentration at different leaf temperatures and saturating quantum flux density (1000 µE m^{-2} s^{-1}). Conditions of measurement were the same as described in Fig. 3.13.

3.4 DISCUSSION

The photosynthetic responses of naturally occurring plants to leaf temperature include effects of temperature at different levels, i.e. adaptation to regional climatic conditions, acclimatization to seasonal and microclimatic variation, and direct response to leaf temperature experienced during a day. The study site at Cullendulla Creek occurs in a cool, coastal climate as described in Chapter 1. The mean January and July air temperatures differ by almost 10 C, with measurements taken from 1911 to 1970 at Moruya Heads near Cullendulla Creek averaging 19.6 and 11.1 C, respectively [Kalma and McAlpine,

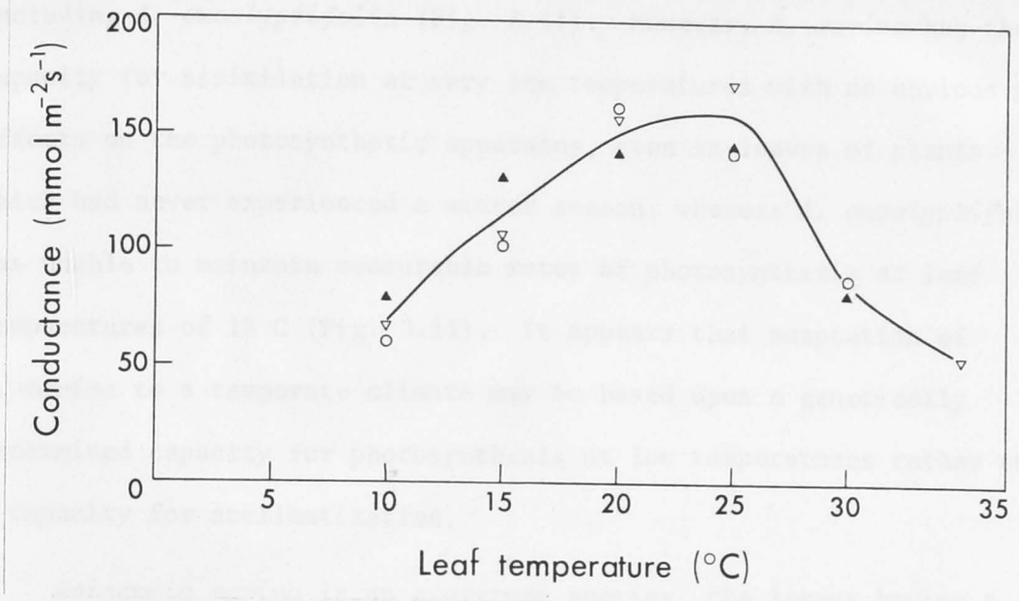


Fig. 3.18: Stomatal conductance as a function of leaf temperature at a fixed intercellular CO_2 concentration of 200 $\mu l\ l^{-1}$. Data are replotted from Fig. 3.17. Line joins the mean values.

1978]. These temperatures are similar to those obtaining at the southern limit of distribution for *A. marina* in Australia [Saenger *et al.*, 1977]. The days on which microclimatic measurements were made (Figs. 3.1 and 3.2) were typical of summer and winter days in the area (see Table 1.1). However, the climate is relatively unpredictable, frequently having unseasonable cold or hot periods [Kalma and McAlpine, 1978].

The temperature optimum for assimilation was not focused sharply. The light saturated assimilation rates did not vary greatly over the range from 20 to 30 C, and in some plants from 15 to 30 C (Figs. 3.7 and 3.8). These responses are similar to those reported from another temperate population of *A. marina* [Attiwill and Clough, 1980]. The responses at high temperature do not differ substantially from those of other mangrove species from sub-tropical [Moore *et al.*, 1972 and 1973] and tropical habitats [Andrews and Clough, 1980], the latter

including *A. eucalyptifolia* (Fig. 3.11). However, *A. marina* has the capacity for assimilation at very low temperatures with no obvious ill effects on the photosynthetic apparatus, even in leaves of plants which had never experienced a winter season, whereas *A. eucalyptifolia* was unable to maintain measurable rates of photosynthesis at leaf temperatures of 15 C (Fig. 3.11). It appears that adaptation of *A. marina* to a temperate climate may be based upon a genetically determined capacity for photosynthesis at low temperatures rather than a capacity for acclimatization.

Avicennia marina is an evergreen species, the leaves having a life span of approximately two years (Fig. 3.5) and hence it might be expected to undergo seasonal changes in the photosynthetic responses to temperature. However, there was no evidence of seasonal acclimatization of the temperature optimum for assimilation rate in either exposed or shaded leaves (Figs. 3.7 and 3.8). In summer, leaf temperatures typically were within the range at which assimilation rates were maximum. This also occurred in winter provided that the leaves received a high quantum flux density (Figs. 3.1 and 3.2). Leaves from exposed and shaded habitats did not differ in the temperatures at which assimilation rates were maximum, although the shaded leaves typically were about 5 C cooler than exposed leaves except during sunflecks. In contrast, the temperature optimum of shaded leaves of a sub-alpine species was found to be 5 C lower than that of exposed leaves, corresponding to an average 5 C difference in leaf temperatures under field conditions [Young and Smith, 1980]. Leaves from sunny and shaded environments also showed no substantial differences in their photosynthetic responses to light intensity and this is pursued further in Chapter 4.

However, the photosynthetic capacity of exposed leaves of *A. marina* fluctuated seasonally with minimum values occurring during winter superimposed over a decline with age similar to that of shaded leaves (Fig. 3.5). This reaction in exposed leaves may result from an interaction between temperature and light intensity. It may also be that exposed leaves experience lower night temperatures. Nevertheless, a significant aspect of these changes in photosynthetic capacity is that stomatal conductance changed in the same sense (Figs. 3.7 and 3.8) thereby minimizing variation in water use efficiency. Similarly, proportional adjustment of photosynthetic capacity and stomatal conductance resulting in nearly constant c_i and hence also constant water use efficiency has been observed during long term exposure of *Eucalyptus pauciflora* to variation in light and nitrogen regimes [Wong, 1979]. The mechanism of this behaviour is unknown, but it seems probable that such long term responses might involve hormonal control.

Effects of leaf temperature on assimilation rates under field conditions are complicated by concomitant effects of vpd on stomatal conductance. It was not unusual for the vpd to increase 10 mbar or more above the ambient saturation vapour pressure deficit because of the increases in leaf temperature associated with receipt of high irradiance (Figs. 3.1 and 3.2). This has the effect of making the leaf microclimate effectively more arid than might be anticipated in a coastal swamp. Typically, the vpd experienced by exposed leaves was 20 to 25 mbar at a leaf temperature of 25 C (Fig. 3.1), conditions which would depress the assimilation rates shown in Fig. 3.7 by approximately 30% (Fig. 3.9). Therefore, the assimilation rates under field conditions would be expected to be lower than those measured in

the laboratory under more moderate vpd conditions.

In a recent review, Berry and Björkman [1980] noted that the variation in assimilation rates with leaf temperature could be attributed largely to effects of temperature on photosynthetic metabolism. However, stomatal conductance, through its influence on the intercellular CO_2 concentration (c_i) may affect the expression of such changes in metabolism on the assimilation rate [Berry and Björkman, 1980]. Measurement of the effect of leaf temperature on the assimilation rate as a function of c_i when the latter is varied by changing the ambient CO_2 concentration, c_a allows assessment of the relative contribution of the metabolic and stomatal components to the response of assimilation rate to variation in leaf temperature under normal atmospheric conditions.

Increases in leaf temperature affected all aspects of the $A(c_i)$ curve, as shown in Fig. 3.13. The CO_2 compensation point increased with leaf temperature, but increase in the initial slope (or mesophyll conductance) together with changes in the c_i at which curvature began caused the photosynthetic capacity to increase to a maximum at 25 C. The decline in the photosynthetic capacity at higher temperatures, at least that obtained at a physiologically significant c_i such as 200 $\mu l\ l^{-1}$, was due mainly to the decrease in mesophyll conductance.

The CO_2 compensation point is considered to be a balance between the carboxylase and oxygenase activities of RuBP carboxylase-oxygenase [Badger and Andrews, 1974] although the contribution of dark respiration in the light is unknown [Graham, 1980]. Oxygen is a competitive inhibitor of CO_2 in the carboxylase reaction [Ogren and Bowes, 1971] while CO_2 is a competitive inhibitor of O_2 in the

oxygenase reaction [Badger and Andrews, 1974; Laing *et al.*, 1974]. Temperature increases apparently favour oxygenase activity because the $K_m(CO_2)$ increases at a greater rate with temperature than the $K_m(O_2)$ [Laing *et al.*, 1974; Badger and Collatz, 1977]. Thus, the CO_2 compensation point would be expected to increase with leaf temperature. The values shown in Fig. 3.14 are lower than those reported for three other species of mangroves in Florida [Moore *et al.*, 1972] but equivalent to those reported in another mangrove species [Andrews and Clough, 1980] and several C_3 plants [Forrester *et al.*, 1966; Jolliffe and Tregunna, 1968 and 1973; Laing *et al.*, 1974; Smith *et al.*, 1976].

Mesophyll conductance is believed to reflect *in vivo* carboxylation activity [Ogren and Bowes, 1971; Laing *et al.*, 1974; Farquhar *et al.*, 1980]. In general, *in vitro* studies of the effects of temperature on RuBP carboxylase have found that the enzyme is stable over a wide range of temperature, with irreversible damage occurring at temperatures greatly in excess of those normally experienced by the plant [Berry and Björkman, 1980]. In the present study, the effects of leaf temperature on the initial slope were fully reversible, with the decline over the optimum occurring at leaf temperatures encountered under summer field conditions (Fig. 3.1). Similar effects of leaf temperature on the initial slope have been observed in other mangrove species [Moore *et al.*, 1972; Andrews and Clough, 1980] and in wheat [Jolliffe and Tregunna, 1973], *Sesamum indicum* [Hall and Kaufmann, 1975], *Citrus sinensis* and *Citrus paradisi* [Khairi and Hall, 1976] and two desert species, a fern, *Notholaena parryi*, and a shrub, *Encelia farinosa* [Nobel *et al.*, 1978]. Jolliffe and Tregunna [1973] also have shown similar effects of temperature on

the overall shape of the $A(c_i)$ curves in wheat to those shown in Fig. 3.13.

There are several possible explanations for the reversible decrease in the initial slope at leaf temperatures above the optimum based on the assumption that the initial slope does reflect *in vivo* carboxylation activity. First, *in vitro* studies on the differential effects of temperature on the kinetics of this enzyme predict that the oxygenase function would dominate at high temperatures [Laing *et al.*, 1974; Badger and Collatz, 1977]. Second, oxygenase activity might be enhanced by changes in the O_2/CO_2 solubility ratio with increasing temperature [Ku and Edwards, 1977]. Third, there is a possibility of reversible heat inactivation of the Calvin cycle at physiological temperatures [Baldry *et al.*, 1966; Selwyn, 1966; Weis, 1980] and Weis [1980] has presented *in vivo* evidence suggesting that RuBP carboxylase may be the site of inactivation.

It is apparent from Figs. 3.13 and 3.16 that changes in the photosynthetic metabolism of the mesophyll were the major factors limiting the assimilation rate under normal atmospheric conditions except at the highest temperatures at which stomatal conductance was co-limiting. At a leaf temperature of 10 C, the operational c_i, i.e. that c_i obtained under normal atmospheric conditions, was well within the upper curved region of the $A(c_i)$ curve (Fig. 3.13). Further opening of the stomata and subsequent increase in c_i would not substantially increase the assimilation rate as shown in Fig. 3.16. The magnitudes of the operational c_i in the temperature range from 15 to 25 C are in the region of transition between the initial slope and the upper curved portion of the $A(c_i)$ curve, but tend to be progressively more toward the former with increasing temperature (Fig.

3.16). Thus a progressively greater increase in the assimilation rate would be expected if stomata were to open further and increase c_i as shown in Fig. 3.16. At higher temperature, the operational c_i was well within the region of the initial slope (Fig. 3.16) and an increase in stomatal conductance would greatly increase the assimilation rate as shown in Fig. 3.12. The results shown in Fig. 3.12 also suggest that the range of high temperatures at which assimilation is appreciable under ordinary atmospheric conditions might be extended if stomatal conductance were to increase and thereby increase c_i. Nevertheless, a substantial portion of the reduction in assimilation rate at these supra-optimal temperatures is due to the decline in photosynthetic metabolism (Fig. 3.15). This is particularly true in those cases in which c_i increased at high temperature despite a marked decline in conductance.

Responses of stomata to leaf temperature are not understood and often complicated by interactions with leaf water relations [Hall *et al.*, 1976; Berry and Björkman, 1980]. It has been found in *Prunus armeniaca* [Schulze *et al.*, 1974 and 1975], *Sesamum indicum* [Hall and Kaufmann, 1975], *Citrus sinensus* [Hall *et al.*, 1976], and *Larrea divaricata* [Mooney *et al.*, 1979] that stomatal closure at high leaf temperature was due largely to a response to increased vpd. Although the sensitivity to vpd may vary with temperature [Hall and Kaufmann, 1975], the response of *A. marina* to vpd at 25 C (Fig. 3.9) shows that this may be a major contributing factor to stomatal closure at high leaf temperatures.

If there had been no response of stomata to leaf temperature, then c_i would have varied as shown in Fig. 3.19, such that c_i would be minimum near the temperature optimum for assimilation. Similar

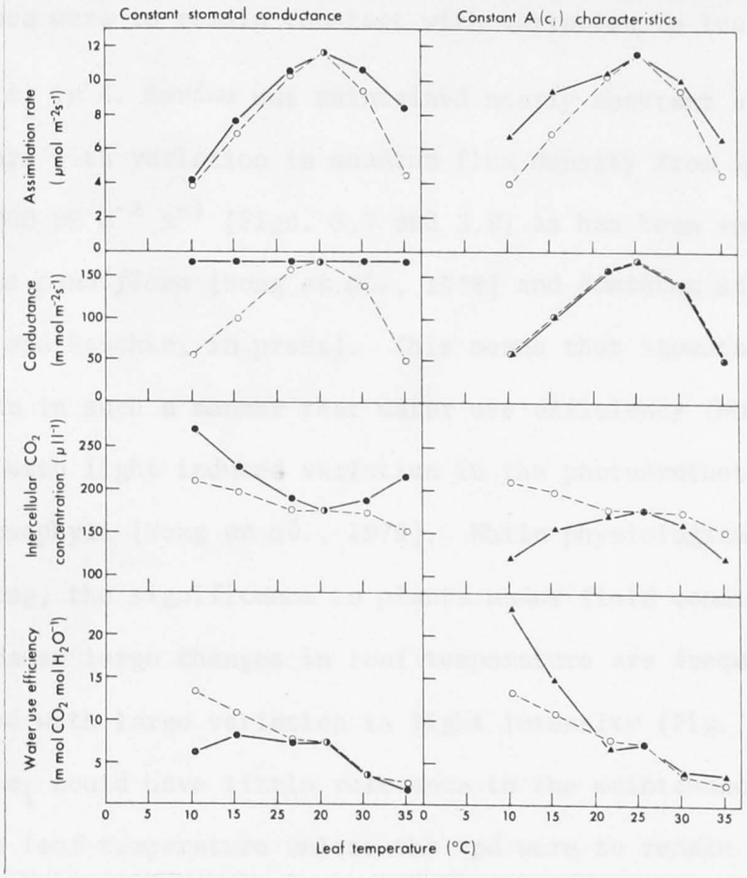


Fig. 3.19: Comparison of calculated gas exchange characteristics (●,▲) to those measured (○) as a function of leaf temperature. All calculations are based on data from Fig. 3.13-3.17 In one simulation, (●) stomatal conductance was held constant at the value obtained at 25 C, the temperature optimum. In the other simulation (▲), the $A(c_i)$ curve obtained at 25 C was held constant while stomatal conductance varied with temperature.

responses have been observed in *A. marina* when excessive increase in vpd was prevented at high temperature (Figs. 3.7 and 3.8) and in experiments with *Larrea divaricata* [Mooney *et al.*, 1979] and *Helianthus annuus* [Farquhar, 1980]. No such precautions were taken during the measurement of the $A(c_i)$ curves shown in Fig. 3.13. Hence the decline in c_i at 35 C is probably a consequence of stomatal response to high vpd. Nevertheless, it is apparent from Fig. 3.19, that changes in c_i were less than they would have been if stomatal

conductance were to remain constant with variation in leaf temperature.

The c_i in *A. marina* was maintained nearly constant at a given temperature with variation in quantum flux density from approximately 500 to 2000 μE m^{-2} s^{-1} (Figs. 3.7 and 3.8) as has been reported in *Eucalyptus pauciflora* [Wong *et al.*, 1978] and *Xanthium strumarium* [Sharkey and Raschke, in press]. This means that stomata responded to irradiance in such a manner that water use efficiency (WUE) remained constant with light induced variation in the photosynthetic capacity of the mesophyll [Wong *et al.*, 1979]. While physiologically interesting, the significance to plants under field conditions is not clear because large changes in leaf temperature are frequently associated with large variation in light intensity (Fig. 3.1) and constant c_i would have little relevance to the maintenance of WUE with change in leaf temperature unless the vpd were to remain constant.

Stomatal sensitivity to c_i changed with leaf temperature in a pattern consistent with the change in photosynthetic capacity, i.e. stomatal closure increased with increasing c_i at high and low leaf temperatures (Fig. 3.17) as also reported for *Helianthus annuus* [Farquhar, 1980]. Wong *et al.* [1978] and Sharkey and Raschke [in press] have shown that stomatal responses to c_i are insufficient to account for the observed responses of conductance to change in light intensity. This is because the gain of the feedback loop involving c_i and conductance [Cowan, 1977; Farquhar *et al.*, 1978] was small [Dubbe *et al.*, 1978]. It is unfortunate that the data in the present study are not sufficiently smooth to calculate the gain of this feedback loop with variation in temperature, but the data shown in Fig. 3.17 suggest that this is not likely to account fully for the stomatal responses to temperature, either. Changes in stomatal conductance

with leaf temperature probably include direct responses to temperature and indirect responses to factors affected by temperature such as c_i, vpd and other aspects of plant water relations [Berry and Björkman, 1980].

On the assumption that laboratory measurements can be extrapolated to the field, leaf temperature is a major factor limiting the assimilation rate of exposed leaves of *A. marina*. As shown in Fig. 3.19, changes in photosynthetic metabolism with temperature are the dominant cause of variation in the assimilation rates. However, stomatal closure at high leaf temperatures or in response to the increase in vpd with increasing temperature can further limit the rates of assimilation by reducing the c_i. Assimilation rates by shaded leaves were most likely to be limited by the low quantum flux densities of less than 100 $\mu E\ m^{-2}\ s^{-1}$ typically encountered in this habitat. However, the photosynthetic characteristics of shade leaves did not differ substantially from those of exposed leaves and hence the former may be able to use effectively intermittent high intensity irradiance.

CHAPTER 4

PHOTOSYNTHETIC RESPONSES TO LIGHT INTENSITY

"At the scale of the size of a seed the physical environment is exceedingly heterogeneous — not only in the biblical sense that some seeds fall on stony ground, but in which to a mustard seed a worm cast is a mountain, a fallen leaf a shade from light (or from the eye of a possible predator), a raindrop is a cataclysm."

John Harper
in: Stebbins, 1974

4.1 INTRODUCTION

There is some circumstantial evidence that competition for light may be a major factor determining the distribution of *A. marina*. Seedlings have been reported to die in shade, as did grown trees when overtopped by dense canopied species of *Rhizophora* or *Bruguiera* [Macnae, 1963 and 1968]. In New South Wales, Australia, *Avicennia* seedlings were observed to persist with no noticeable growth for periods of at least two years in the shade of parent trees, whereas no saplings have been found in this same light environment (Chapter 1). One difficulty in the interpretation of these observations is in the assessment of the degree to which factors such as predation or competition for resources other than light may affect survival in exposed or shaded habitats.

It is generally accepted that the capacity of a species to inhabit a shaded environment is dependent on its ability to adapt its photosynthetic response to a low light environment [Boardman, 1977].

However, the light received by a leaf in an understory is not low intensity white light. The intensity and duration of the component coming directly from the sun through gaps in the canopy varies erratically with time, while another component, that received after reflection and transmission through overlying foliage, differs from sunlight in its spectral composition [Björkman and Ludlow, 1972; Morgan and Smith, 1978]. The relative importance of these components depends largely on the density and structure of the canopy [Morgan and Smith, 1978]. Some species are adapted specifically to the micro-habitat of extreme shade [Anderson *et al.*, 1973; Boardman *et al.*, 1974; Boardman, 1977] whereas others may exploit or persist under certain shaded conditions because they can use intermittent high intensity irradiance.

Understory light conditions change constantly and therefore are very difficult to produce in the laboratory. For this reason, the photosynthetic properties of *A. marina* were examined in response to high and low intensity white light imposed during leaf growth to obtain reproducible conditions in the laboratory. The relevance of measurements on these plants to plants in the natural environment was checked by comparison with the photosynthetic properties of plants brought directly from the field.

4.2 MATERIALS AND METHODS

4.2.1 Plant Material

Seedlings of *Avicennia marina*, approximately three months old and at the four-leaf post-cotyledonary stage of development, were collected from exposed and shaded environments along Cullendulla Creek

at Batemans Bay, New South Wales, Australia. The two light environments were less than 10 m apart in an area supporting good tree growth (Chapter 1). Six plants were taken from each location. The light environment of the leaves was characterized on the day of plant collection by taking hourly measurements with a Lambda quantum sensor of the quantum flux density incident on the adaxial leaf surfaces from sunrise to sunset. Also, the light environment was characterized with hourly measurements made in an open area of direct insolation, with the sensor held normal to the sun, of vertical insolation, with the sensor held horizontally, of diffuse insolation, with the sensor held horizontally and shielded from direct sunlight, and of reflected light, with the sensor held facing the soil surface at the height of the seedling leaves (25 cm). After sunset, each seedling was transplanted to a bucket, the soil containing the root system being maintained intact and barely flooded with saline creek water. The seedlings were then divided into three groups of four, each group with two plants from exposed and two from shaded environments, and were transported in darkness to the laboratory. The leaf characteristics of one group were studied immediately upon return to the laboratory; the remaining two groups were placed outdoors, one in full daylight (high light) and the other beneath shade cloth allowing passage of 6% of the incident sunlight (low light). These seedlings were watered daily with fresh water to avoid increase of salinity, and received Hoaglands solution once a week. Measurements were made on the third leaf pair, which developed entirely under these light conditions.

4.2.2 Gas Exchange

Details of the gas exchange apparatus, method of CO_2 and water

vapour measurements, preparation of gas mixtures and calculation of gas exchange rates across a leaf surface are described in the appendix. Experiments were carried out during normal photoperiods on intact, attached leaves. Seedlings were brought into the laboratory on the night before measurements which were made during the normal photoperiod. Leaf temperature was maintained at 25 C, corresponding to 32 mbar internal leaf water vapour pressure [Farquhar and Raschke, 1978]. Leaf to air vapour pressure difference was approximately 12 mbar. Ambient concentration of CO_2 was 300 $\mu l\ l^{-1}$ unless otherwise stated. Gas exchange responses to light intensity were made successively at quantum flux densities of 250, 100, 50, 25, 500, 1000 and 2000 $\mu E\ m^{-2}\ s^{-1}$. The responses of assimilation rate to c_i were measured by changing the ambient CO_2 concentration in the sequence 330, 200, 100 and 50 $\mu l\ l^{-1}$ under saturating quantum flux density (i.e. 1000 $\mu E\ m^{-2}\ s^{-1}$) with other variables as described above. The minimum interval between measurements was 30 min to permit variables relating to leaf gas exchange to reach steady state.

4.2.3 Fluorescence Measurements

Chlorophyll fluorescence induction kinetics of the intact, attached leaves were measured with a Plant Productivity Fluorometer, Model SF10 (Richard Brancker Research Ltd., Canada). Quantum flux density was 30 $\mu E\ m^{-2}\ s^{-1}$, centering around 670 nm, which was sufficient to induce electron transport. The fluorescence transients were recorded on a Tektronix 564 storage oscilloscope and photographed. All experiments were carried out at room temperature ($\sim$ 25 C). The measurements were taken from plants immediately before dawn (dark adaptation overnight). Chlorophyll was determined using the method of Arnon [1949].

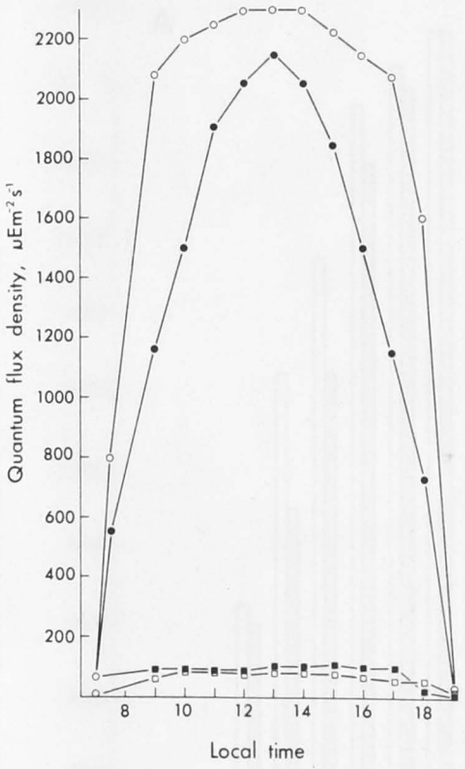


Fig. 4.1: Summary of the light environment at Cullendulla Creek, New South Wales, on February 25, 1980. Symbols are measurements of the quantum flux density of direct (○), vertical (●), diffuse (■), and reflected (□) light. Measurements were made in an open area.

4.3 RESULTS

4.3.1 The Natural Light Environment

Characteristics of the light environment on February 25, 1980, at Cullendulla Creek are shown in Fig. 4.1. It was a clear sunny day with maximum insolation occurring from 1100 to 1500 hours. The quantum flux densities incident on the adaxial surfaces of two leaves in exposed and two leaves in understory shade environments are shown in Figs. 4.2 A and B, respectively. The exposed leaves received uninterrupted sunlight throughout the day (Fig. 4.2A), whereas shade leaves generally experienced low quantum flux density (i.e. 30 to 120 $\mu E\ m^{-2}\ s^{-1}$) interspersed in the morning and afternoon by sunflecks ranging from 800 to 1550 $\mu E\ m^{-2}\ s^{-1}$ (Fig. 4.2B). The durations of these sunflecks were not recorded. These same leaves were used for study of the photosynthetic properties of field grown leaves (see below).

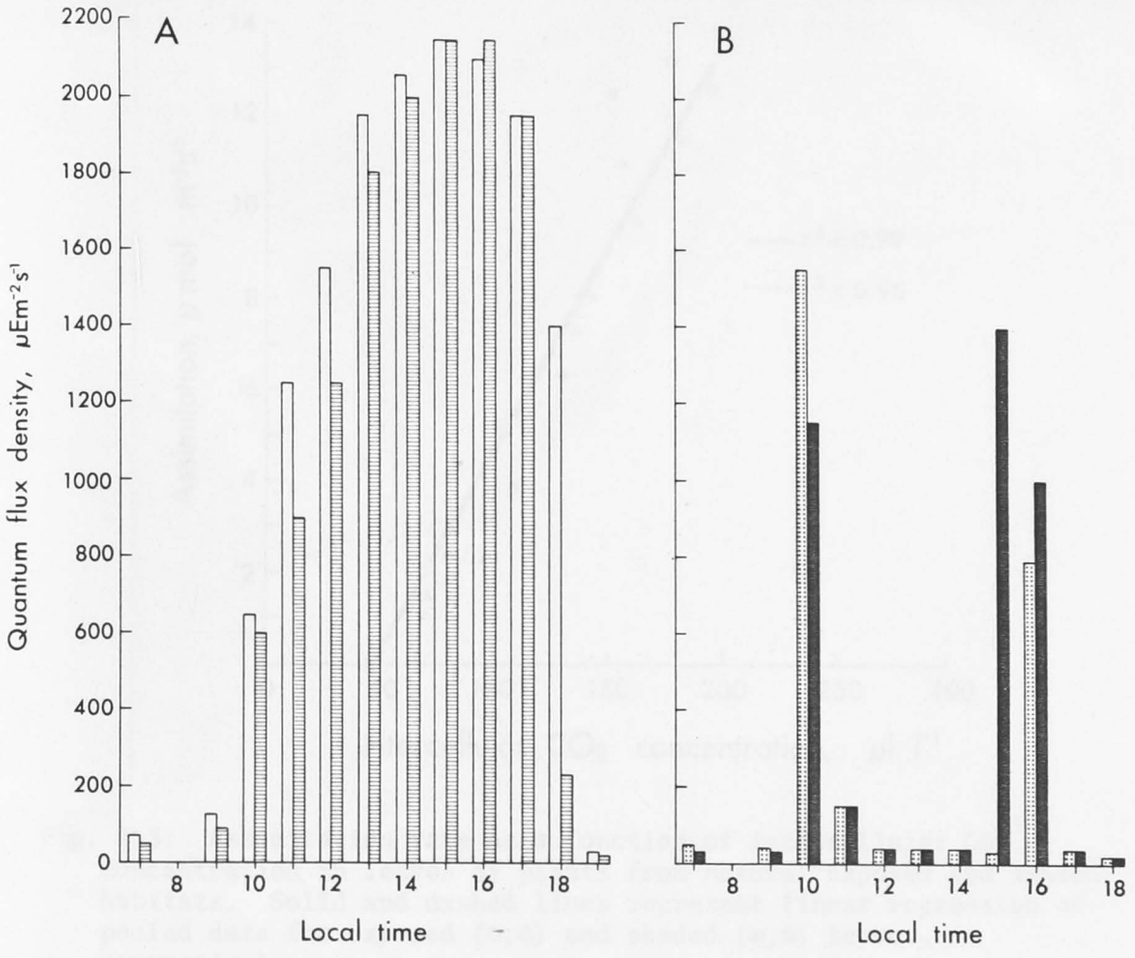


Fig. 4.2: Quantum flux density incident on the adaxial surface of experimental leaves in an exposed (A) and shaded (B) environment along Cullendulla Creek on February 25, 1980. The shading indicates exposed leaves 1 ( ) and 2 ( ) and shaded leaves 1 ( ) and 2 ( ). These correspond to the symbols for exposed leaves 1 (○) and 2 (△) and shaded leaves 1 (●) and 2 (▲) shown in the results of gas exchange studies on field grown leaves.

4.3.2 Gas Exchange Characteristics

The responses of assimilation rate to c_i in field grown leaves from exposed and shaded environments are shown in Fig. 4.3. The mesophyll conductance (i.e. the initial linear slope of the $A(c_i)$ curve) averaged 0.08 ± 0.01 mol CO_2 m^{-2} s^{-1} and the CO_2 compensation point was approximately 50 μl l^{-1} in leaves from both environments.

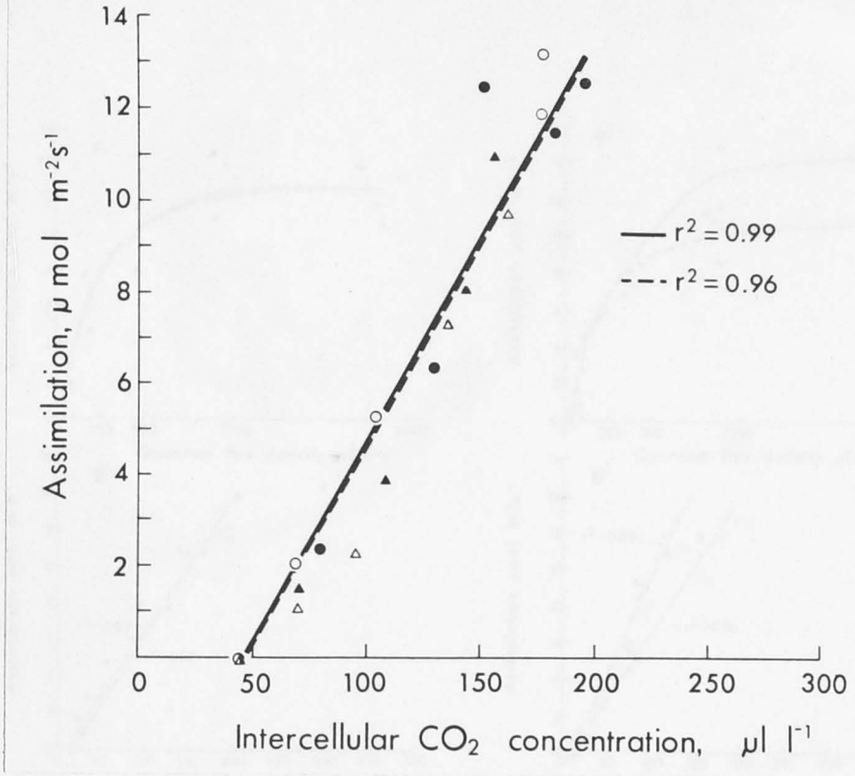


Fig. 4.3: Assimilation rate as a function of intercellular CO_2 concentration in leaves of plants from natural exposed and shaded habitats. Solid and dashed lines represent linear regression of pooled data for exposed (○,△) and shaded (●,▲) leaves, respectively.

The effects of light intensity on other gas exchange characteristics both of leaves developed under natural conditions and those grown in the laboratory under high and low light regimes (i.e. 100% and 6% sunlight), are summarized in Fig. 4.4. Leaf properties are given in Table 4.1. The data presented for the laboratory grown leaves are grouped according to the light regime experienced during development of these leaves because there were no obvious differences between those originating from exposed or shaded field locations. There are no results for the plants which were collected from an exposed site and transferred to the high light environment in the laboratory, because they were lost in an accident before gas exchange

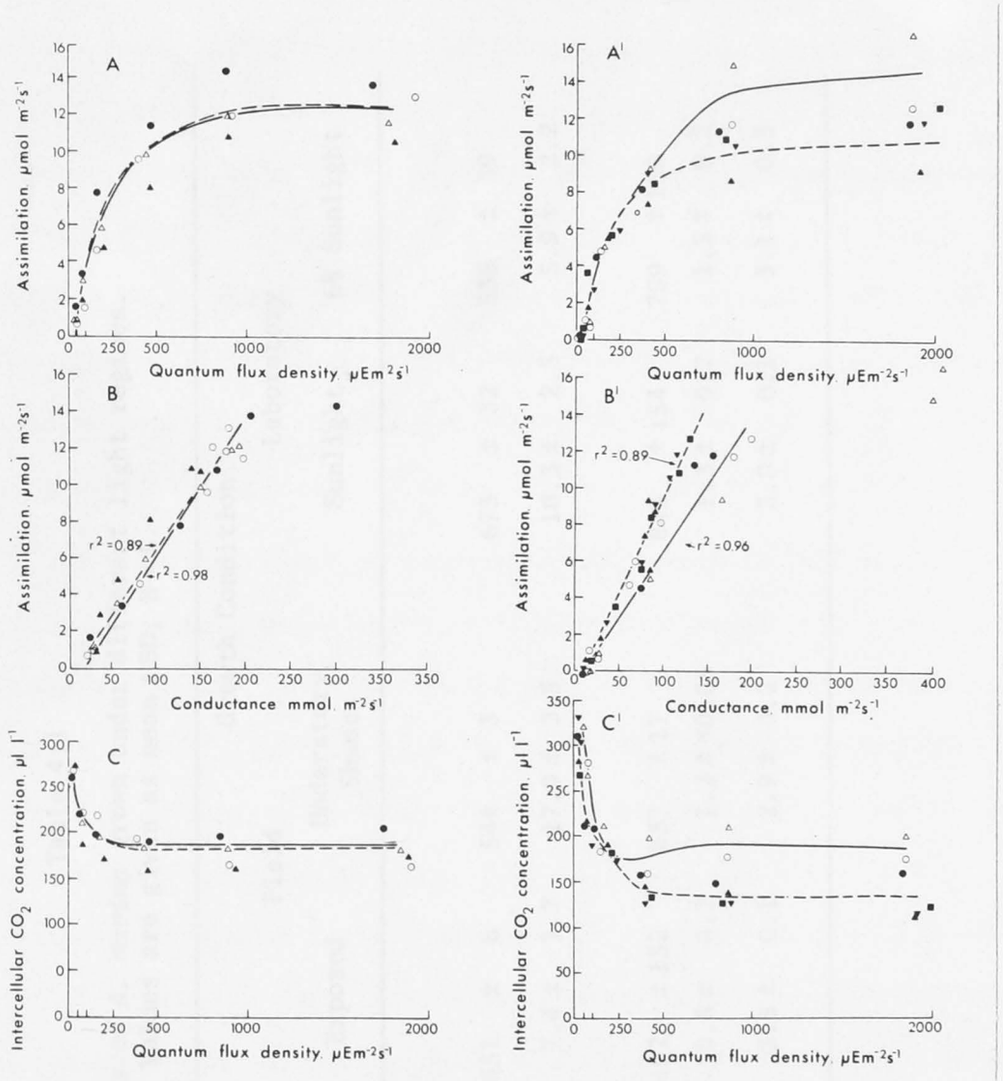


Fig. 4.4: Gas exchange characteristics of leaves grown under different light regimes. Results shown in A, B, C are from leaves grown under natural understory shade (●,▲) and exposed conditions (○,△). Results shown in A', B', C' are from leaves grown under laboratory high (○,△) and low light conditions (●,▲,▼,■). All points are from the same set of measurements.

A,A': Rate of assimilation as a function of quantum flux density. Lines are drawn through mean values.

B,B': Assimilation rate as a function of stomatal conductance. Lines are drawn from linear regression excluding the saturating conductance values.

C,C': Intercellular CO_2 concentration as a function of quantum flux density. Lines are drawn through mean values.

Table 4.1

Leaf properties of *A. marina* grown under different light regimes.
Values are given as mean ± SD, N = 5.

Property	Growth Condition			
	Field		Laboratory	
	Exposed	Understory Shade	Sunlight	6% Sunlight
Specific leaf weight (g fresh wt.m^{-2})	631 ± 6	544 ± 3	673 ± 32	535 ± 39
Leaf area (cm^2)	7.4 ± 1.7	17.0 ± 2.3	10.3 ± 2.3	5.9 ± 2.2
Chl content				
($mg.m^{-2}$)	492 ± 132	637 ± 17	843 ± 154	799 ± 169
($mg.g^{-1}$ fresh wt)	0.8 ± 0.2	1.2 ± <0.05	1.3 ± 0.2	1.5 ± 0.2
Chl a/b ratio	3.8 ± 0.1	2.9 ± 0.2	3.0 ± 0.1	3.1 ± 0.3

measurements could be made. There were no significant differences ($p < .01$) in three major photosynthetic characteristics of field and laboratory grown leaves despite their different light histories (Fig. 4.4 A,A'). The assimilation rates became light saturated at approximately 1000 $\mu E\ m^{-2}\ s^{-1}$, apparent light compensation points were 25 to 30 $\mu E\ m^{-2}\ s^{-1}$, and apparent quantum yields, determined in the region from 50 to 150 $\mu E\ m^{-2}\ s^{-1}$ incident light, averaged $.041 \pm .007$ $\mu mol\ CO_2 . \mu E^{-1}$. These values are termed "apparent" because they have not been adjusted for either light absorption or the effect of changing c_i [Ehleringer and Björkman, 1977; Farquhar *et al.*, 1980].

Light saturated rates of assimilation appeared to be affected by the light conditions under which the leaves were grown (Fig. 4.4 A,A'). There was a tendency ($p < .01$) for the average light saturated rate of assimilation (i.e. 10.9 ± 1.2 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) in leaves grown under the low light regime to be lower than those of leaves grown under either the high light regime (i.e. 14.0 ± 2.2 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) or under exposed or shaded field conditions (12.3 ± 0.6 and 12.5 ± 1.9 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$, respectively. The maximum rates of assimilation in these latter three groups were not significantly different from each other.

Stomatal conductance declined with light intensity in much the same manner as the assimilation rate (Fig. 4.4 B,B'). The stomatal conductances of leaves grown under low light (Fig. 4.4 B', closed symbols) were significantly lower ($p < .01$) than those of leaves grown under either the high light (Fig. 4.4 B', open symbols) or exposed and shaded conditions (Fig. 4.4B), whereas the responses of the latter three groups were not significantly different from each other. As quantum flux density was decreased from 2000 to 500 $\mu E\ m^{-2}\ s^{-1}$,

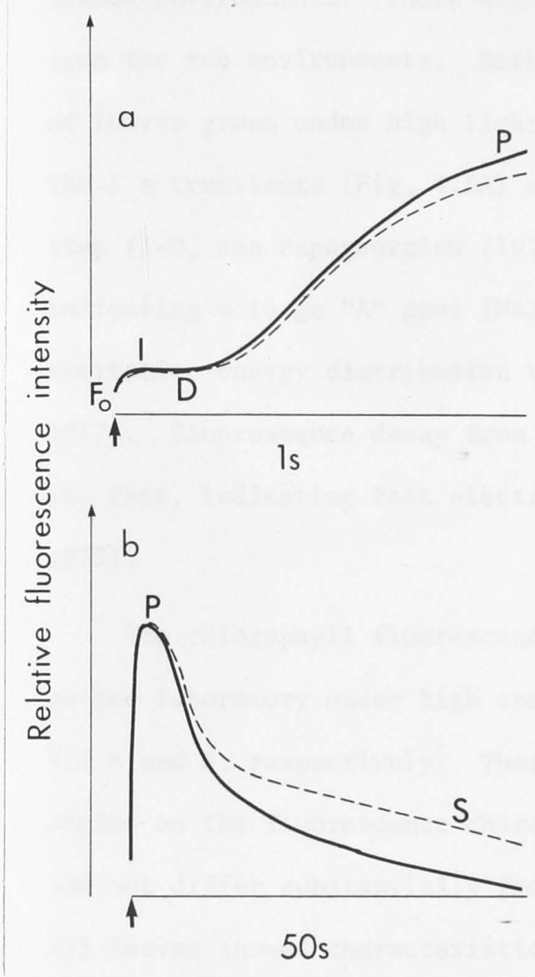


Fig. 4.5: Chlorophyll fluorescence induction kinetics of intact attached leaves of *A. marina* from exposed ——— and shaded — — — habitats, measured just before the onset of the light period (dark adaptation overnight). a: fast 1 s transients; b: slow 50 s transients. ↑ light on.

assimilation and conductance declined proportionally such that c_i was maintained nearly constant, at approximately 130 $\mu l\ l^{-1}$ in the low light grown leaves (Fig. 4.4 C') and at 180 $\mu l\ l^{-1}$ in leaves from all other light treatments (Fig. 4.4 C,C'). The c_i increased with further reductions in light intensity, reaching the level of the ambient CO_2 concentration as quantum flux density approached the compensation point.

4.3.3 Fluorescence Properties

In Fig. 4.5, typical chlorophyll fluorescence induction curves are shown for intact, attached leaves of *A. marina* from natural exposed and

shaded environments. There were no major differences between plants from the two environments. Both groups showed characteristics typical of leaves grown under high light conditions [Schreiber *et al.*, 1977]: the 1 s transients (Fig. 4.5A) were very slow with a long intermediate step (I-D, see Papageorgiou [1975]) and a slow rise to the peak (D-P), indicating a large "A" pool [Malkin and Kok, 1966] or preferred excitation energy distribution to photosystem I [Schreiber *et al.*, 1977]. Fluorescence decay from the peak (P-S) in the 50 s transients was fast, indicating fast electron transport activity [Papageorgiou, 1975].

The chlorophyll fluorescence induction kinetics of leaves grown in the laboratory under high and low light regimes are shown in Figs. 4.6 A and B, respectively. There was no obvious effect of the light regime on the fluorescence characteristics of these leaves, and they did not differ substantially from those of field grown leaves, i.e. all leaves showed characteristics typical of leaves grown in a high light environment [Schreiber *et al.*, 1977].

In other species, the chlorophyll fluorescence induction characteristics of the undersides of high light leaves are similar to those of the upper and lower sides of low light leaves, while the upper sides of high light leaves are unique in showing high light characteristics [Schreiber *et al.*, 1977]. However, in *A. marina*, the upper sides of leaves grown under both high and low light conditions showed high light characteristics (Fig. 4.7). The under sides of leaves grown under both high and low light conditions gave responses typical of low light leaves (Fig. 4.7) with a significantly increased rate in the D-P rise and much shorter intermediate step I-D [Schreiber *et al.*, 1977].

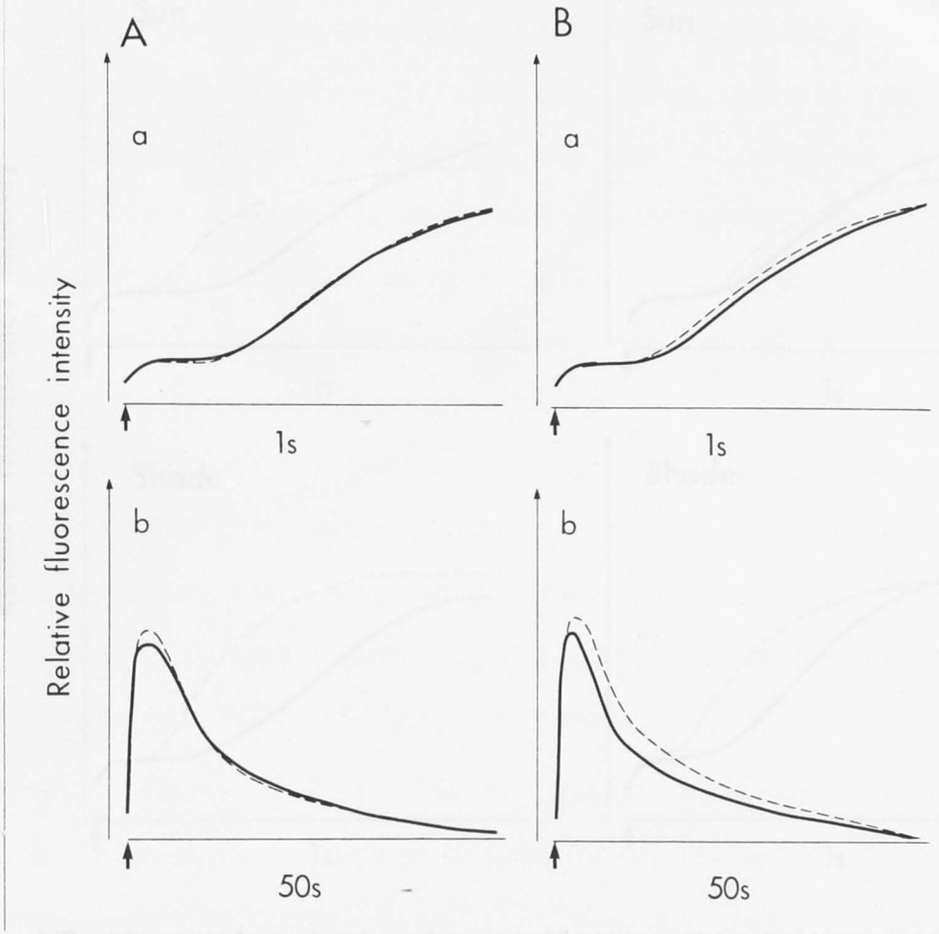


Fig. 4.6: Chlorophyll fluorescence induction kinetics of intact attached leaves of *A. marina* from originally exposed ——— and shaded — — — habitats which developed A: under 100% sunlight, and B: under 6% of full sunlight.

4.4 DISCUSSION

The capacity of a species to inhabit a shaded environment is believed to depend upon its ability to adapt its photosynthetic metabolism to low light levels [Boardman, 1977]. However, understory shade is a complex, heterogeneous light environment which varies spatially and temporally depending upon the structure of the overlying canopy [Morgan and Smith, 1978]. Leaves grown in understory shade typically are enriched in chlorophyll b relative to a (see Table 4.1),

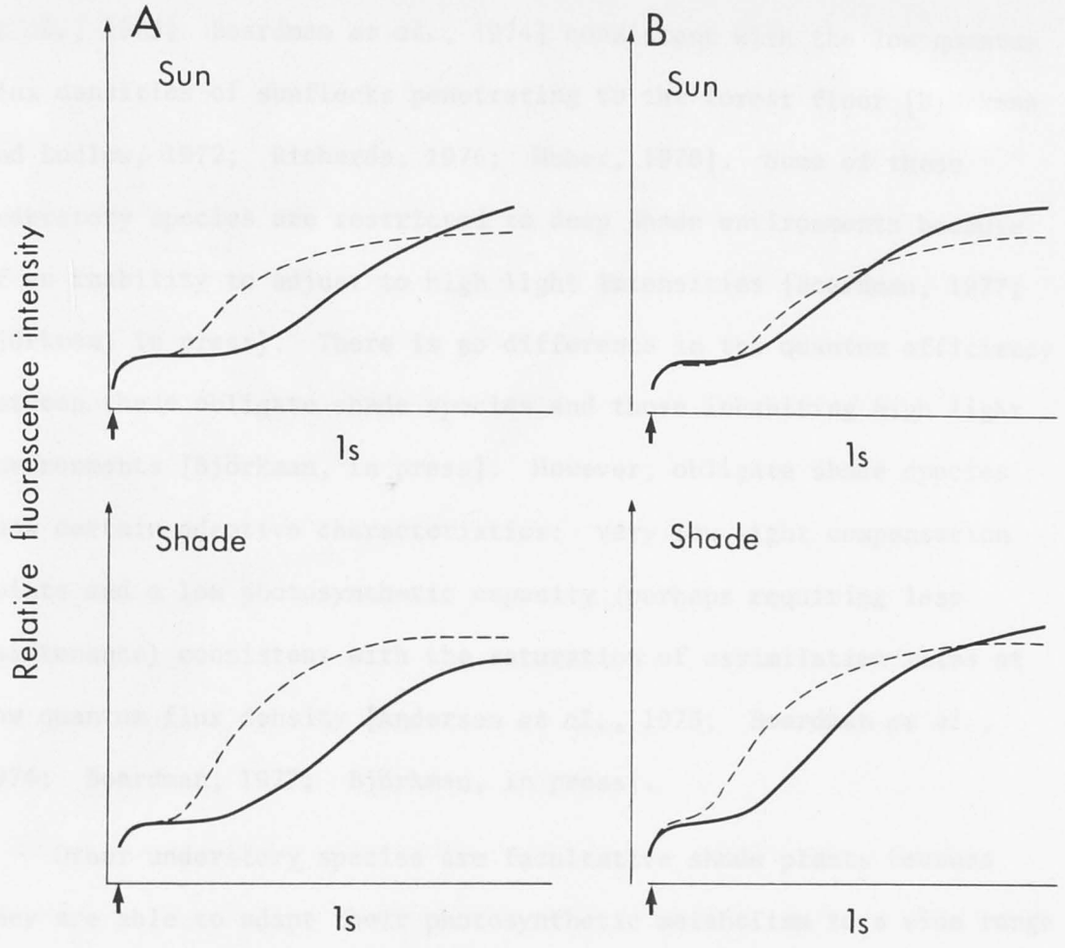


Fig. 4.7: Fast chlorophyll induction kinetics measured immediately before onset of the light period on upper ——— and lower — — — leaf surfaces of *A. marina* grown after transfer to A: 100% sunlight, and B: 6% of full sunlight. "Sun" and "Shade" indicate the original habitat of the field seedlings.

presumably reflecting spectral differences between understory shade and sunlight, and enhancing the capacity to absorb photosynthetically active light under shaded conditions [Anderson *et al.*, 1974]. However, most of the photosynthetically active radiation reaching a forest floor is contributed by sunflecks [Björkman and Ludlow, 1972; Björkman *et al.*, 1972; Morgan and Smith, 1978].

The photosynthetic systems of species inhabiting the floor of dense tropical rainforests are adapted to low light levels [Anderson

et al., 1973; Boardman *et al.*, 1974] consistent with the low quantum flux densities of sunflecks penetrating to the forest floor [Björkman and Ludlow, 1972; Richards, 1976; Huber, 1978]. Some of these understory species are restricted to deep shade environments because of an inability to adjust to high light intensities [Boardman, 1977; Björkman, in press]. There is no difference in the quantum efficiency between these obligate shade species and those inhabiting high light environments [Björkman, in press]. However, obligate shade species show certain adaptive characteristics: very low light compensation points and a low photosynthetic capacity (perhaps requiring less maintenance) consistent with the saturation of assimilation rates at low quantum flux density [Anderson *et al.*, 1973; Boardman *et al.*, 1974; Boardman, 1977; Björkman, in press].

Other understory species are facultative shade plants because they are able to adapt their photosynthetic metabolism to a wide range of light levels [Björkman, in press]. These species show a decrease in photosynthetic capacity with decrease in the light level experienced during growth as shown by decline in mesophyll conductance [Holmgren, 1968; Ludlow and Wilson, 1971; Hall and Kaufmann, 1975; Nobel *et al.*, 1975; Young and Smith, 1980], RuBP carboxylase activity [Björkman, 1968; Björkman *et al.*, 1972; Bowes *et al.*, 1972; Powles and Critchley, 1980] and electron transport capacity [Boardman *et al.*, 1974; Powles and Critchley, 1980]. Hence, there is a decline in the maximum assimilation rates and in the light intensity at which assimilation rates become saturated with decrease in the light level under which the leaves are grown [Burnside and Böhning, 1957; Björkman *et al.*, 1972; Boardman *et al.*, 1974; Nobel *et al.*, 1975; Powles and Critchley, 1980). Leaves grown under low light regimes

typically had lower light compensation points than those grown under high light conditions with a few exceptions [Burnside and Böhning, 1957; Björkman *et al.*, 1972; Boardman *et al.*, 1974]. However, the quantum efficiency at limiting light intensities was the same whether the leaves were grown under high or low light regimes [Björkman *et al.*, 1972; Boardman *et al.*, 1974]. Thus when species normally found in high light environments are grown under low light conditions, the photosynthetic characteristics typically undergo changes tending toward those of shade plants [Björkman, in press].

In contrast to the dense rainforests, sunflecks of full light intensity occur in more open forests [Morgan and Smith, 1978; Young and Smith, 1980] such as the mangrove swamps of the present study (Fig. 4.2). The photosynthetic metabolism of facultative shade plants grown under the understory conditions becomes adapted to a light intensity proportional to the total daily exposure to sunlight [Nobel, 1976; Smith and Nobel, 1978; Young and Smith, 1980] and similar results were obtained under laboratory conditions [Chabot *et al.*, 1979]. For example, the assimilation rates of shaded leaves of *Arnica cordifolia* were maximal under 300 $\mu E\ m^{-2}\ s^{-1}$, although these leaves typically experienced 100 $\mu E\ m^{-2}\ s^{-1}$ during shaded periods but 800 to 1000 $\mu E\ m^{-2}\ s^{-1}$ during sunflecks of 10 to 15 minutes duration [Young and Smith, 1980]. Similar results were obtained with another shrub, *Hyptis emoryi* [Nobel, 1976]. The data given in both these studies suggest that neither the quantum yield nor the light compensation point were affected by growth under exposed or shaded conditions. These shaded leaves would not, therefore, be able to make full use of sunfleck irradiance. Further, Powles and Critchley [1980] have shown that leaves grown under constant low light conditions become photo-

inhibited when exposed to high irradiance in a manner dependent both on the length of exposure and the level of light to which the leaf is adapted. It is not known whether leaves grown in understory shade are also vulnerable to photoinhibition during sunflecks. Thus, the adaptive significance of decreasing the photosynthetic capacity with decrease in total irradiance without increasing the effectiveness (i.e. without lower light compensation points) under limiting light intensities which are experienced most of the day is not clear. Presumably, the benefits of adaptation to low light intensity in understory conditions exceed the "costs" of photoinhibition and of maintaining the photosynthetic machinery needed for efficiency under high light intensities. These results also suggest the possible involvement of a phytochrome system in determining the photosynthetic capacity.

Avicennia marina, in contrast, is an obligate high light plant, in which the photosynthetic characteristics are indicative of leaves grown under exposed or high light conditions regardless of the environment in which they are grown. The photosynthetic metabolism of *A. marina* was not affected by growth under natural exposed or understory shade conditions, as shown by the similarity in chlorophyll fluorescence kinetics (Fig. 4.5) and gas exchange characteristics (Figs. 4.3 and 4.4) of leaves from either habitat. However, similar differences in the fluorescence transients between upper and lower leaf surfaces, independent of the light regime under which the leaves were grown (Fig. 4.7), suggest that differences in light quality may also be involved in the development of the electron transport system. Further, most photosynthetic characteristics of leaves grown under high and low light regimes, the latter having a similar quantum flux

density to understory shade but lacking sunflecks, were similar to those of the field grown leaves. However, the maximum assimilation rates in leaves from the low light treatment were 20% less than those of high light grown leaves, consistent with the c_i being lower in the former (Fig. 4.4). Under field conditions, exposure to high intensity sunflecks may enable shaded leaves to develop a photosynthetic capacity equivalent to that of exposed leaves.

In the present study, leaves in understory shade experienced quantum flux densities near their light compensation points much of the day, interrupted periodically by high intensity sunflecks (Fig. 4.2). These leaves might be able to sustain very low rates of assimilation during shaded periods, but it is doubtful that such rates would be sufficient for prolonged survival. The photosynthetic metabolism of *A. marina* is adapted to high light intensities and it is just such intensities that occur in sunflecks in this environment. This adaptation would enable understory shade leaves to absorb and transduce energy from intense light without damage to their photosystems [Powles and Critchley, 1980], and, given appropriate leaf temperatures and stomatal conductances, would allow full utilization of sunflecks. Such an adaptation could be of particular significance in assisting a species in securing resources of light and space made available by the death of a canopy member. Further, this potential to utilize sunflecks maximally may explain the apparent anomaly that a species with little physiological capacity for adaptation to low light levels can survive in understory shade for at least two years. In summary, *A. marina* is an obligate high light plant which apparently cannot persist in deep shade, but which can survive under shaded conditions provided that there is some minimum degree of canopy openness allowing penetration of sunflecks.

CHAPTER 5

PHYSIOLOGICAL RESPONSES TO STEADY STATE CONDITIONS OF SALINITY AND HUMIDITY

"The response to salinity is very much a response of the whole plant."

John Passioura, 1981
(Seminar)

5.1 INTRODUCTION

Salinity is well known to influence the growth of halophytes [Flower *et al.*, 1977; Winter, 1979]. There have been few analyses of the mechanism, but suppression of growth at sub- or supra-optimal salinities has been associated with the influence of salinity on rates of photosynthesis and rates of leaf area development in beach halophytes [De Jong, 1978b]. Kleinkopf and Wallace [1974], however, suggested that depression of growth by salinity in *Tamarix ramosissima* was due to the energetic demands of salt excretion.

Little is known of the effects of salinity on mangrove growth [Walsh, 1974]. Mangrove propagules have been used in previous studies [Stern and Voight, 1959; Connor, 1969; Clarke and Hannon, 1970], and, as shown in Chapter 2, many of the growth responses to salinity at the propagule stage can be attributed to effects on the redistribution of cotyledonary reserves. Therefore it is doubtful whether the results of these studies can be extrapolated to explain the responses of mature seedlings or other, developmental stages of mangroves to salinity.

Interaction between salinity and humidity has been reported in work with both glycophytes and halophytes. Decreases in the leaf to air vapour pressure difference (vpd) have been found to reduce the adverse effects of salinity on growth of *Gossypium* [Hoffman *et al.*, 1971]. However, *Atriplex* showed maximum growth at a salinity of -5 atm NaCl (approximately 100 mM NaCl) under arid conditions, but growth was suppressed with increasing salinity under humid conditions [Gale *et al.*, 1970].

In the present study, growth of seedlings of *Aegiceras corniculatum* and *Avicennia marina* was studied in a multi-factorial experiment, using three salinities and three humidities, in order to evaluate the relative effects on growth of substrate salinity and rates of salt loading into leaves (the latter by varying vpd). Gas exchange characteristics are considered in this chapter only as they relate to growth. They are analysed in detail in Chapter 6.

5.2 MATERIALS AND METHODS

5.2.1 Plant Material

Propagules of *Aegiceras corniculatum* and *Avicennia marina* were collected from mature shrubs and trees growing along Cullendulla Creek at Bateman's Bay, New South Wales, Australia. Propagules were considered to be mature if they were released by gentle shaking of a branch. The average fresh weights of mature propagules of *Aegiceras* and *Avicennia* were 0.5 and 6.0 g, respectively, and only propagules weighing from 0.46 to 0.54 g and 5.6 to 6.4 g, respectively, were used in this study. Propagules of *Aegiceras* and *Avicennia* were cultivated in sand beds sub-irrigated with 10 and 50% sea water, respectively, at which salinities growth of the respective species is optimum [Connor,

1969; Clarke and Hannon, 1970; Chapter 2]. The beds were kept in a growth cabinet adjusted to provide day/night leaf temperatures of 25/20 C, relative humidity of 70% to give a leaf to air vapour pressure difference (vpd) of approximately 12 mbar, and a 12 hr light period with quantum flux density incident on the bed of 400 $\mu E\ m^{-2}\ s^{-1}$. The propagules were kept in this way until they reached a post-cotyledonary phase of development (see Chapter 2).

5.2.2 Plant Culture

Fifty seedlings of similar dimensions and fresh weights were then selected from the populations of each species and divided into ten groups of five. One group of each species was harvested immediately and its characteristics are given in Table 5.1. The fresh weights and leaf areas of the seedlings in the other groups were measured and these seedlings were placed in plastic containers (volume 200 ml for *Aegiceras* and 500 ml for *Avicennia*) for hydroponic culture. The containers were covered with aluminized mylar and fitted with soft plastic lids. The sea water solutions initially used to cultivate the propagules (10% for *Aegiceras* and 50% for *Avicennia*) were replaced at a rate of 25% per day with Johnson's nutrient solution (see Appendix) amended with the appropriate concentration of NaCl to maintain the salinity. The salinities were then adjusted at a rate of 50 mM NaCl per day (roughly equivalent to 10% sea water) to give the three final concentrations of 50, 250 and 500 mM NaCl. Water levels were maintained by the addition of demineralized water every other day and solutions were changed weekly.

Seedlings receiving these three NaCl treatments were then distributed among three growth cabinets adjusted for high, medium and

Table 5.1

Seedling characteristics at the beginning of the study. Values are mean ± SE, n = 5. A persistent embryo is included in the measurement of the stem weight (*) of *Aegiceras*. All weights are of total dried material.

Parameter	*Aegiceras corniculatum*	*Avicennia marina*
Total dry wt (g)	0.21 ± .01	2.1 ± .22
Roots (g)	0.04 ± <.01	0.6 ± .07
Stems (g)	0.11 ± .02*	0.7 ± .07
Leaves (g)	0.05 ± <.01	0.8 ± .09
Root/Shoot ($g\ g^{-1}$)	.23 ± .01	.40 ± .02
Root/Leaf ($g\ g^{-1}$)	.88 ± .04	.76 ± .05
Root/Leaf area ($g\ m^{-2}$)	51.5 ±3.2	110.3 ±10.5
Leaf area (cm^2)	7.7 ±0.3	55.2 ± 5.6
Leaf area/Plant mass ($m^2\ kg^{-1}$)	3.8 ±0.3	2.7 ± 0.6

low humidity regimes to give a total of nine growth conditions. The light period was 12 hr and the average quantum flux density close to the leaves was 400 $\mu E\ m^{-2}\ s^{-1}$, as measured with a Lambda quantum sensor. Day/night air temperatures were such that average leaf temperatures were 25/20 C. Relative humidities of approximately 90, 70 and 30% were used to give leaf to air vapour pressure differences of 6, 12 and 24 mbar, respectively. Leaf and air temperatures, and the wet bulb depression of the air were sensed with copper-constantan thermocouples (.0081 sq mm) referenced against a platinum resistance thermometer. Five thermocouples were used in each growth cabinet to measure leaf temperature. They were attached with transparent tape to the upper surfaces of the leaves and were connected in parallel to give an estimate of average leaf temperature. The outputs of all sensors were registered continuously for 15 min at 3 hr intervals with a Leeds and Northrop 12 channel strip chart recorder. The vapour

pressure difference was calculated assuming that the partial pressure of water vapour in intercellular leaf spaces is equal to the saturation vapour pressure of water at leaf temperature [Farquhar and Raschke, 1978].

The seedlings were cultivated under these conditions for 12 weeks during which records were kept of water loss, and plant fresh weight was measured at seven day intervals. The seedlings were then harvested and their various parts weighed both before and after being dried at 80 C. Leaf areas were measured with a Lambda leaf area meter. The fresh weights of seedlings at the start of the experiments were converted to dry weights by assuming that the fresh weight/dry weight ratios were the same then as at the end of the growth period. Relative growth rates (RGR) were calculated as

$$RGR = \frac{ln\, W_2 - ln\, W_1}{t_2 - t_1},$$

where W_1 and W_2 are the dry weights at the beginning and end of the 12 week experimental period, $t_2 - t_1$. The relative rate of increase in leaf area was calculated in a similar way.

The net assimilation rate (NAR) in g dry weight m^{-2} leaf area $week^{-1}$ was estimated as $\frac{\Delta W}{t} \Big/ \bar{L}$ [Slatyer, 1970], where ΔW is the average change in dry weight $W_2 - W_1$ over the 12 week experimental period t. The average leaf area $\bar{L}$ is estimated by $\frac{L_2 - L_1}{ln\, L_2 - ln\, L_1}$, where L_1 and L_2 are the leaf areas at the beginning and end of the study period.

5.2.3 Gas Exchange

Details of the gas exchange apparatus, measurement of CO_2 and water vapour, preparation of gas mixtures and calculations of gas

exchange rates across the leaf surface are given in the appendix.

Measurements were made on intact, attached leaves which had developed entirely under the growth conditions. Measurements were made under conditions similar to those in the growth cabinets, i.e. leaf temperature of 25 C, quantum flux density of 500 $\mu E\ m^{-2}\ s^{-1}$, ambient CO_2 concentration of 330 $\mu l\ l^{-1}$ and vpd of 6, 12 or 24 mbar. All measurements were made during normal photoperiods, with measurements of dark respiration made prior to illumination.

5.2.4 Salt Secretion

The rates of salt secretion were measured over the 12 hr photoperiod under growth cabinet conditions on the day before the same leaf was to be used for measurement of gas exchange characteristics. Details are given in the appendix.

5.3 RESULTS

5.3.1 Growth and Dry Matter Allocation

The effects of NaCl and humidity on plant relative growth rates are shown in Table 5.2. Relative growth rates decreased with increase in NaCl concentration from 50 to 500 mM, *Aegiceras* being much more sensitive to changes in NaCl concentration than *Avicennia*. Differences in growth rate associated with differences in vpd generally were small relative to the effect of NaCl.

The relative growth rates of roots, shoots and leaves are shown in Table 5.3. Calculations of the relative growth rates of leaves were made from measurements on the same plants at the beginning and

Table 5.2

Relative growth rates of *Aegiceras corniculatum* and *Avicennia marina* at different salinities and vapour pressure differences. Values are mean $g\ g^{-1}\ week^{-1} \pm SE$, n = 5, calculated from a total growth period of 12 weeks.

Species	mbar vpd	50 mM NaCl	250 mM NaCl	500 mM NaCl	Average (n = 15)
Aegiceras	6	.171 ± .002	.095 ± .010	.046 ± .008	.103 ± .015
	12	.153 ± <.001	.108 ± <.001	.056 ± .007	.109 ± .011
	24	.130 ± .010	.077 ± .010	.051 ± .010	.086 ± .010
	average (n = 15)	.150 ± .005	.093 ± .006	.051 ± .004	
Avicennia	6	.129 ± .008*	.091 ± .008*	.076 ± .011*	.099 ± .008*
	12	.080 ± .008	.078 ± .009	.072 ± .003	.077 ± .004
	24	.082 ± .008	.081 ± .006	.055 ± .006	.073 ± .005
	average (n = 15)	.097 ± .007	.078 ± .006	.068 ± .005	

* Plants were lost in an accident prior to the harvest and these results were calculated from data obtained one week before the accident. The growth period of these plants was 6 weeks.

Table 5.3

Relative growth rates of roots, shoots and leaves of *Aegiceras* and *Avicennia* at different salinities and vapour pressure differences. Values are mean ± SE, n = 5.

Parameter	vpd (mbar)	*Aegiceras*			*Avicennia*		
		mM NaCl			mM NaCl		
		50	250	500	50	250	500
Roots ($g\ g^{-1}\ week^{-1}$)	6	.18 ± .01	.14 ± .01	.10 ± .01	ND	ND	ND
	12	.18 ± .01	.14 ± .01	.12 ± .01	.08 ± .01	.09 ± .01	.09 ± .01
	24	.16 ± .01	.12 ± .01	.12 ± <.01	.10 ± .01	.10 ± .01	.08 ± .01
Shoots ($g\ g^{-1}\ week^{-1}$)	6	.27 ± <.01	.17 ± .01	.14 ± .01	ND	ND	ND
	12	.25 ± <.01	.17 ± .02	.13 ± .01	.07 ± .01	.06 ± .01	.06 ± .01
	24	.22 ± .01	.16 ± .01	.11 ± .01	.07 ± .01	.06 ± .01	.04 ± <.01
Leaf area ($cm^2\ cm^{-2}\ week^{-1}$)	6	.18 ± <.01	.11 ± .02	.05 ± .01	.10 ± .01*	.05 ± .02*	.03 ± .01*
	12	.17 ± <.01	.12 ± .02	.06 ± .01	.05 ± .01	.04 ± .01	.03 ± <.01
	24	.14 ± <.01	.11 ± .01	.03 ± .01	.06 ± .01	.06 ± .01	.02 ± .01

ND: *Avicennia* grown under 6 mbar vpd were lost in an accident prior to harvest and no root or shoot data were available. However, the relative rates of leaf area expansion could be calculated from measurements made in the week preceding the accident. Growth period for these measurements (*) was 6 weeks; all other data are from a 12 week growth period.

end of the experimental period, but those of roots and shoots are based on comparison of the measured root and shoot mass of the seedlings harvested at the beginning of the study (Table 5.1) with those of the seedlings which had grown under the different treatments. The growth rates of roots, shoots and leaves all declined with increasing salinity in *Aegiceras*. Humidity did not have a noticeable effect except that there was a tendency for leaf growth to decrease with increasing vpd. The growth of shoots generally was greater than that of roots, but the differences diminished with increasing salinity because growth of shoots was more affected than that of roots. In contrast, the relative growth rates of roots of *Avicennia* were slightly greater than those of shoots. Growth of roots and shoots in *Avicennia* was not as sensitive to differences in salinity as in *Aegiceras*, and was not obviously affected by vpd.

The cumulative effects of differences in relative growth rates on morphology are shown in Table 5.4. Root mass increased relative to that of shoots, leaves and leaf area with increasing salinity and vpd in both species. However, *Aegiceras* maintained a lower mass of roots relative to aerial parts than *Avicennia* in all treatments.

5.3.2 Gas Exchange Characteristics

The gas exchange characteristics are summarized in Table 5.5. In neither species did salinity or humidity have a substantial effect on rates of dark respiration in leaves, the only exception being the comparatively low rates in *Avicennia* grown at 50 mM NaCl. Dark respiration rates in *Aegiceras* were lower than those in *Avicennia* under all treatments.

Table 5.4

Dry matter allocation in *Aegiceras corniculatum* and *Avicennia marina* grown under different salinity and humidity regimes. Values are mean ± SE, n = 5.

Parameter	vpd (mbar)	*Aegiceras*			*Avicennia*		
		mM NaCl			mM NaCl		
		50	250	500	50	250	500
Root/shoot ($g\ g^{-1}$)	6	0.17 ± 0.03	0.26 ± 0.01	0.31 ± 0.04	ND	ND	ND
	12	0.20 ± 0.02	0.32 ± 0.05	0.34 ± 0.07	0.48 ± 0.03	0.54 ± 0.12	0.59 ± 0.04
	24	0.22 ± 0.03	0.36 ± 0.06	0.39 ± 0.06	0.55 ± 0.04	0.60 ± 0.04	0.62 ± 0.06
Root/leaf ($g\ g^{-1}$)	6	0.27 ± 0.05	0.40 ± 0.02	0.59 ± 0.05	ND	ND	ND
	12	0.30 ± 0.03	0.54 ± 0.12	0.71 ± 0.12	0.73 ± 0.04	0.77 ± 0.17	0.95 ± 0.08
	24	0.35 ± 0.04	0.58 ± 0.13	1.08 ± 0.26	0.90 ± 0.08	0.90 ± 0.07	1.08 ± 0.13
Root/leaf area ($g\ m^{-1}$)	6	36.1 ± 4.5	46.7 ± 3.1	70.9 ± 6.9	ND	ND	ND
	12	39.0 ± 4.7	57.0 ± 9.7	93.1 ± 13.4	130.1 ± 7.8	165.6 ± 13.8	174.9 ± 14.6
	24	43.7 ± 4.2	70.6 ± 23.3	113.4 ± 17.1	144.5 ± 10.4	150.1 ± 6.8	213.8 ± 29.9
Leaf area/ plant mass ($m^2\ kg^{-1}$)	6	3.93 ± 0.18	4.52 ± 0.67	3.16 ± 0.20	2.69 ± 0.14*	2.92 ± 0.24*	2.55 ± 0.15*
	12	4.31 ± 0.28	4.34 ± 0.31	2.93 ± 0.30	2.49 ± 0.07	2.32 ± 0.12	2.14 ± 0.09
	24	4.11 ± 0.15	4.44 ± 0.29	2.38 ± 0.22	2.46 0.10	2.51 ± 0.09	1.85 ± 0.15

ND = no data, plants were lost in an accident prior to harvest. * = data calculated from measurements made after 6 weeks growth; all other measurements were made at the conclusion of a 12 week growth period.

Table 5.5

Gas exchange characteristics of *Aegiceras corniculatum* and *Avicennia marina* grown under different salinity and vapour pressure differences. All measurements were made on fully mature leaves under conditions similar to those experienced during growth, i.e. leaf temperature 25 C, quantum flux density 500 μE m^{-2} s^{-1}, 300 μl l^{-1} CO_2, 210 ml l^{-1} O_2 and leaf to air vpd of 6, 12 and 24 mbar. Values are mean ± SD, (n); ND = no data.

Parameter	vpd (mbar)	*Aegiceras*			*Avicennia*		
		50 mM NaCl	250 mM NaCl	500 mM NaCl	50 mM NaCl	250 mM NaCl	500 mM NaCl
Dark respiration (μmol m^{-2} s^{-1}) (Leaf only)	6	0.6 ± 0.2(5)	0.6 ± 0.2(4)	0.5 ± 0.4(2)	1.3 ± 0.6(6)	1.7 ± 0.2(4)	1.7 ± 0.6(4)
	12	0.7 ± 0.3(7)	0.6 ± 0.1(6)	0.8 ± 0.3(2)	0.8 ± 0.6(7)	1.9 ± 0.6(7)	1.8 ± 0.5(7)
	24	0.5 ± 0.1(5)	0.7 ± 0.2(3)	ND	1.1 ± 0.4(8)	1.8 ± 0.7(7)	1.7 ± 0.7(8)
Assimilation rate (μmol m^{-2} s^{-1})	6	13.0 ± 1.5(5)	8.9 ± 2.1(4)	4.3 ± 2.4(2)	14.4 ± 3.8(6)	12.6 ± 2.6(4)	11.3 ± 1.5(4)
	12	11.5 ± 3.1(7)	9.0 ± 1.7(6)	3.7 ± 1.6(2)	11.8 ± 1.8(7)	9.3 ± 1.5(7)	6.7 ± 1.4(7)
	24	8.8 ± 2.1(5)	7.7 ± 2.9(3)	ND	8.0 ± 2.0(8)	7.7 ± 1.9(7)	5.1 ± 2.7(8)
Conductance (mmol m^{-2} s^{-1})	6	210 ± 80(5)	179 ± 87(4)	150 ± 50(2)	229 ± 125(6)	157 ± 33(4)	136 ± 25(4)
	12	160 ± 60(7)	160 ± 50(6)	160 ± 10(2)	133 ± 40(7)	103 ± 26(7)	67 ± 12(7)
	24	110 ± 50(5)	90 ± 50(3)	ND	72 ± 24(8)	81 ± 41(7)	56 ± 40(8)
Intercellular CO_2 concentration (μl l^{-1})	6	180 ± 23(5)	203 ± 44(4)	227 ± 141(2)	162 ± 32(6)	164 ± 9(4)	161 ± 13(4)
	12	168 ± 14(7)	202 ± 20(6)	270 ± 19(2)	137 ± 25(7)	150 ± 13(7)	150 ± 31(7)
	24	150 ± 26(5)	159 ± 20(3)	ND	109 ± 12(8)	136 ± 31(7)	149 ± 31(8)
Evaporation rate (mmol m^{-2} s^{-1})	6	0.82 ± 0.17(5)	0.69 ± 0.26(4)	0.63 ± 0.14(2)	1.08 ± 0.32(6)	0.93 ± 0.09(4)	0.91 ± 0.13(4)
	12	1.56 ± 0.44(7)	1.51 ± 0.26(6)	1.42 ± 0.06(2)	1.24 ± 0.32(7)	1.10 ± 0.19(7)	0.79 ± 0.13(7)
	24	2.07 ± 0.72(5)	1.79 ± 0.74(3)	ND	1.47 ± 0.44(8)	1.65 ± 0.57(7)	1.18 ± 0.70(8)

Assimilation rates and stomatal conductance declined with increasing salinity in both species, with *Aegiceras* again being the most sensitive to variation in salinity. Differences between the two species in the proportionality between assimilation rate and stomatal conductance are reflected in the intercellular CO_2 concentrations, c_i. It remained nearly constant in *Avicennia*, but increased in *Aegiceras* with increase in salinity. The c_i in the latter species typically was greater than that in the former species. Hence, water use efficiency was nearly constant with variation in salinity in *Avicennia*, but decreased with increasing salinity in *Aegiceras* and was lower overall in *Aegiceras* than in *Avicennia* (Table 5.6).

Assimilation rates and stomatal conductance declined with increasing vpd in both species, and these responses were accompanied by a decrease in c_i (Table 5.5). However, the decrease in stomatal conductance was not sufficient to lower the evaporation rate, and water use efficiency decreased with increasing vpd (Table 5.6). These changes in water use efficiency in response to variation in either salinity or humidity showed the same trends as those estimated from cumulative growth and water use data (Table 5.6).

5.3.3 Salt Secretion

Rates of salt secretion during the photoperiod are shown in Table 5.7. The rates increased with increasing salinity, but varied erratically with vpd. Salt secretion rates per unit of water transpired are shown in Table 5.8. These rates also increased with salinity, but there were no obvious effects of vpd. The average rates of Cl^- secretion increased roughly proportionally with increase in

Table 5.6

Water use efficiency of *Aegiceras* and *Avicennia* grown under different salinity and vapour pressure differences. Calculations are based (a) on water loss and dry matter gain measured during the experimental period and (b) on gas exchange measurements made on fully expanded, mature leaves. The experimental period was 6 weeks in the groups indicated * and 12 weeks in all other treatments. Gas exchange data are from Table 5.5. Values are mean ± SE; n = 5 in (a) and n in (b) is variable as noted in Table 5.5.

Parameter	vpd (mbar)	*Aegiceras*			*Avicennia*		
		mM NaCl			mM NaCl		
		50	250	500	50	250	500
(a)	6	5.7 ± 0.1	3.3 ± 0.4	2.9 ± 0.4	6.6 ± 0.2*	6.4 ± 0.2*	5.8 ± 0.5*
$\frac{\text{mg dw gain}}{\text{g } H_2O \text{ lost}}$	12	4.1 ± 0.2	2.5 ± 0.3	2.3 ± 0.3	4.5 ± 0.2	4.4 ± 0.3	5.1 ± 0.2
	24	2.3 ± 0.2	1.5 ± 0.2	1.7 ± 0.2	3.0 ± 0.1	3.2 ± 0.1	3.2 ± 0.2
(b)	6	16.0 ± 0.7	14.0 ± 2.0	5.1 ± 0.2	13.6 ± 1.0	13.5 ± 0.7	12.5 ± 0.6
$\frac{\text{mmol } CO_2}{\text{mol } H_2O}$	12	7.4 ± 0.2	6.0 ± 0.9	2.6 ± 0.7	9.2 ± 0.2	8.4 ± 0.2	8.5 ± 0.6
	24	5.0 ± 0.9	4.4 ± 0.5	ND	5.5 ± 0.1	4.8 ± 0.2	4.4 ± 0.6

Table 5.7

Rates of salt secretion in fully expanded, mature leaves of *Aegiceras* and *Avicennia* grown at various salinities and vapour pressure differences. Values are mean nEq m^{-2} s^{-1} ± SE, n = 5, calculated from total secretion over a 12 hr photoperiod. ND: No data; plants were lost in an accident before measurements could be made.

Salinity	vpd (mbar)	*Aegiceras*			*Avicennia*		
		Cl^-	Na^+	K^+	Cl^-	Na^+	K^+
50 mM NaCl	6	24 ± 6	28 ± 5	2 ± 1	ND	ND	ND
	12	31 ± 14	37 ± 12	2 ± 1	22 ± 4	20 ± 4	1 ± <1
	24	23 ± 10	29 ± 8	2 ± <1	25 ± 9	29 ± 10	1 ± <1
250 mM NaCl	6	158 ± 24	152 ± 25	2 ± <1	131 ± 32	140 ± 32	4 ± 1
	12	113 ± 17	131 ± 4	4 ± <1	120 ± 20	133 ± 21	7 ± 1
	24	334 ± 98	328 ± 92	4 ± <1	150 ± 20	219 ± 30	9 ± 2
500 mM NaCl	6	343 ± 64	330 ± 63	4 ± 1	180 ± 38	200 ± 41	6 ± 1
	12	211 ± 34	210 ± 18	3 ± <1	128 ± 48	150 ± 50	8 ± 4
	24	177 ± 45	181 ± 38	4 ± 1	264 ± 19	298 ± 20	8 ± 2

Table 5.8

Secretion of Cl^- as a function of evaporation rate by leaves of *Aegiceras* and *Avicennia* grown under different humidity/salinity regimes, i.e. vpd of 6, 12 and 24 mbar and nutrient solution salinized by the addition of 50, 250 and 500 mM NaCl. Values are mean µmol Cl^- mol H_2O^{-1} ± SE, n = 4, except where noted. Evaporation rates (mmol H_2O m^{-2} s^{-1}) were measured with a gas exchange system on the same leaves under the same conditions as those experienced in the growth chamber on the day following salt secretion measurements. * = No data; plants were lost in an accident before measurements could be made; † = No data; unable to measure evaporation rates.

Species	Humidity treatment vpd (mbar)	µmol Cl^- excreted per mol H_2O transpired			
		mM NaCl			
		50	250	500	
Aegiceras	6	34 ± 12	186 ± 9	424 ± 79	(n = 2)
	12	29 ± 12	107 ± 6	155 ± 18	(n = 2)
	24	14 ± 5	233 ± 40	†	
	average	26 ± 6	189 ± 22	289 ± 63	
Avicennia	6	*	116 ± 28	169 ± 36	
	12	13 ± 2	67 ± 13	100 ± 40	
	24	13 ± 4	91 ± 10	263 ± 70	
	average	13 ± 2	91 ± 13	171 ± 31	

NaCl concentration. The rates in *Avicennia* typically were half those in *Aegiceras*.

5.4 DISCUSSION

Only seedlings have been used in previous studies of the effects of salinity on mangrove growth. Comparison of the results of these studies is complicated by variation in the response with developmental status of the seedling. It might well be expected that when seeds, propagules or seedlings are exposed to different salt concentrations,

the effects on growth may be the integration of the effects of salinity on several processes, some of which are peculiar to different phases of the life cycle. These processes include germination, development of propagules during the heterotropic stage when redistribution of reserves takes place, and autotropic growth of mature seedlings.

Both *Aegiceras* and *Avicennia* are viviparous species, i.e. germination occurs on the mother tree [Jones, 1971]. Following propagule release, both the onset of further development and dry matter gain are affected by salinity. Rate of growth is maximum in *Aegiceras* in 10% sea water [Clarke and Hannon, 1970; Chapter 2], and in *Avicennia* in 50% sea water [Connor, 1969; Clarke and Hannon, 1970; Chapter 2]. In the study reported in Chapter 2, there was little change in dry weight of *Avicennia* during development to a 4-leaf seedling. Most of the differences in plant sizes and morphology between treatments apparently were due to effects of salinity on the allocation of cotyledonary reserves. Clarke and Hannon [1970] found that the optimum NaCl concentration for growth decreased with development of *Avicennia* seedlings from the 2- to the 4-leaf stage. This was probably associated with a gradual change from primarily heterotrophic to autotrophic growth (Chapter 2). Once the seedlings are fully mature and no longer dependent upon cotyledonary reserves, growth of both *Avicennia* and *Aegiceras* diminishes with increasing NaCl concentration from 50 to 500 mM, with growth of the latter species being reduced at a greater rate (Table 5.2).

5.4.1 Salt Respiration

Depression of growth in response to salinity is often attributed to increased respiration which is presumed to be due to increased energy requirements for maintenance [Gale, 1975]. Recently, Gale and Schwartz [1980] have demonstrated increased respiration, but it is not clear that this respiration generated energy which was useful for maintenance. Turner and Turner [1980] have suggested that respiration may increase in response to increasing salinity because of effects of ions on the activities of key regulatory enzymes of respiratory pathways, a response which is pathological (metabolic imbalance) rather than adaptive. At present there is no clear consensus on how salinity affects respiration. In glycophytes, dark respiration rates have been found to increase [Nieman, 1962; Livne and Levins, 1967] and to decrease [Flowers, 1972] with increasing salinity of the growth medium. In halophytes, increasing salinity has been found to decrease [Flowers, 1972] and to have no measurable effect on rates of dark respiration [Kuramoto and Brent, 1972; Blacquiére and Lambers, 1981]. This latter result is in agreement with the findings in the present study (Table 5.5).

Salinity might be thought to affect the respiratory losses of a plant because of the potential energetic costs of ion exclusion, transport and secretion. Mangroves partially exclude salt at the roots, apparently by non-metabolic ultrafiltration [Scholander, 1968]. Hence the major "costs" of exclusion are those of construction and maintenance of the root system. The effectiveness of salt exclusion varies, the least effective species being those possessing salt secretion glands in the leaves such as *Aegiceras corniculatum* and

Avicennia marina [Scholander *et al.*, 1962 and 1966].

The rates of salt secretion shown in Table 5.7 agree with values reported for *Aegiceras* and *Avicennia* [Scholander *et al.*, 1962], but generally are at the low end of the range. There is too much scatter in the salt secretion rates with variation in vpd as shown in Figs. 5.7 and 5.8 to determine whether the effectiveness of salt exclusion at the roots changed with humidity (i.e. with evaporation rates). However, if the average quantities of Cl^- secreted per mol water transpired by plants grown under a given salinity, over a range of humidities, are considered, then it appears that the increase in salt secretion rates are roughly proportional to the increase in salt concentration at the roots (Table 5.8). These data suggest that *Aegiceras* is less effective at salt exclusion than *Avicennia*. Hence, *Aegiceras* must secrete a greater quantity of salt per unit carbon gained than *Avicennia*.

Salt secretion has been shown to be an active process in mangroves [Scholander *et al.*, 1962; Atkinson *et al.*, 1967] and other halophytes [Thomson, 1975], although the sources of energy to drive the process in mangroves have not been determined. The main salt gland cells in *Aegiceras* and *Avicennia* contain mitochondria, but do not possess chloroplasts [Atkinson *et al.*, 1967; Cardale and Field, 1971]. Chloroplasts are present in the underlying collecting cells which are ultrastructurally very similar to mesophyll cells [Thomson, 1975; see also Chapter 2]. Rates of salt secretion are enhanced in the light in the mangroves *Aegialitis* [Scholander *et al.*, 1962; Atkinson *et al.*, 1967], *Aegiceras* and *Avicennia*, but to a lesser degree in the latter two species [Scholander *et al.*, 1962]. Light

enhancement may reflect increased rates of salt influx to the leaf in association with increased rates of transpiration in the light. It may also result from the involvement of photosynthetic processes in ion uptake and excretion as has been found in *Atriplex spongiosa* [Osmond *et al.*, 1969; Lüttge and Osmond, 1970; Lüttge *et al.*, 1970]. However, mesophyll cells in *Atriplex* apparently are able to use energy generated by either photophosphorylation or oxidative phosphorylation in ion transport, and hence the salt secretion process probably utilizes whatever energy sources are available [Johansen and Lüttge, 1974].

Some speculations on the quantity of photosynthates required to sustain salt secretion are possible, assuming that all salt secretion in the salt glands of *Aegiceras* and *Avicennia* depends on dark respiration and that one mol ATP is required for the excretion of one mol ion. The secretion consists principally of Na^+ and Cl^-, which occurs in nearly equimolar proportions (Tables 5.7 and 5.8), plus a mixture of other ions [Leshem and Levison, 1972] as has been observed for halophytes in general [Thomson, 1975]. In principle it is only necessary to have active secretion of either the cation or anion, the other can follow passively [Hill and Hill, 1973]. Complete respiration of one mol glucose theoretically yields 40 mol ATP. Therefore, 0.15 mol CO_2 would be released per mol ion secreted. A tenfold increase in Cl^- secretion rates from 25 to 250 nmol m^{-2} s^{-1}, as observed when the salinity of the nutrient solution was increased from 50 to 500 mM NaCl, would then be accompanied by an increase in CO_2 evolution of 34 nmol m^{-2} s^{-1} if only one step requiring active processes were involved.

As shown by comparison of Tables 5.5 and 5.8 large increases in salt secretion rates were not accompanied by measurable increases in the rates of dark respiration. Also, the rates of dark respiration by leaves of *Aegiceras* were approximately 2 to 2.6 times lower than those of *Avicennia*, although the rates of salt secretion and apparently also the rates of salt influx, consistently were greater in leaves of the former species. According to the above calculations, the proportion of assimilates required to sustain the rates of salt secretion shown in Table 5.7 should be less than 1% of the assimilation rate of either species, even under the most strenuous conditions, i.e. high salinity and low humidity. The "cost" of ion transport would also be small if photochemically generated sources of energy were used because rates of ATP formation by photosynthetic electron transport may exceed rates of salt uptake by a factor of 1000 [Osmond, 1979]. The principal source of uncertainty in the above calculations is that the number of membranes which have to be crossed, and the number of times an ion crosses each membrane during secretion events, is unknown. Nevertheless, secretion appears to be a small "cost" to the plant, and the major effects of salinity on growth must lie elsewhere.

5.4.2 Carbon Allocation

Aegiceras and *Avicennia* showed different patterns of carbon allocation, the former species consistently investing a greater proportion of assimilates in shoots than in roots (Table 5.4). However, there was a proportionally greater reduction in the relative growth rates of shoots than roots with increasing salinity and vpd in both species (Table 5.3). This produced an increase in the root/shoot ratios as has been reported in response to increasing salinity in

several species including *Gossypium* [Hoffman *et al.*, 1971] and salt marsh plants [Webb, 1976; Parrondo *et al.*, 1978]. Root/shoot ratios also increase when plants are grown under arid conditions [Mooney, 1972].

The ratio of root mass to leaf area (Table 5.4) is perhaps a better parameter to consider than the root/shoot ratio, because it is a better description of the ability of the plant to supply water, relative to the water demand of a specific environment. One can visualize various mechanisms to explain the increase in this ratio with salinity. In mangroves, salt exclusion by ultrafiltration [Scholander, 1968] might be accompanied by a substantial hydraulic resistance in the roots as has been found when beans [O'Leary, 1969] and the halophyte *Atriplex halimus* [Kaplan and Gale, 1962] were grown in the presence of NaCl. If this resistance were to increase with salinity or with the effectiveness of the ultrafiltration process, then a greater root mass might be needed to supply a given quantity of water at a given tolerable salt concentration. Another possibility is that a higher root/leaf area ratio may help to alleviate the potential accumulation of ions around the roots [Passioura and Frere, 1967].

A similar explanation may apply to the increase in the root mass/leaf area ratio with increase in vpd at a given level of salinity (Table 5.4). The decline in stomatal conductance with increasing vpd was insufficient to reduce the evaporation rate (Table 5.5). Therefore, a greater root mass may be needed relative to leaf area in order to satisfy the greater demand for water as well as to maintain the effectiveness of the ultrafiltration process at a given salinity. Overall, *Aegiceras* has less absorptive biomass per unit of evaporative

surface than *Avicennia* (Table 5.4), which may be related to the apparent lower capacity of the former species to exclude salt at the roots (Table 5.8).

The leaf area/plant mass ratio is perhaps the best parameter to consider in the analysis of growth because it relates the capacity of the plant to supply reduced carbon with the demand for it. Although morphology did change with growth condition, the differences, as for example in the root/shoot ratio, were not reflected substantially in the leaf area/plant mass ratio (Table 5.4), which remained nearly constant except for a decline at the highest salinity. However, the leaf area/plant mass ratio consistently was greater in *Aegiceras* than in *Avicennia* (Table 5.4) and, as shown by Monsi [1968], such differences in carbon allocation may be a major source of differences in growth rates between *Aegiceras* and *Avicennia*.

5.4.3 Net Assimilation Rates

The relative constancy of the leaf area/plant mass ratio for either species suggests that differences in the gas exchange characteristics in response to salinity and humidity treatments should be a dominant influence on the net assimilation rates of plants grown under those treatments. The responses of assimilation rates measured on single, mature leaves and those of net assimilation rates calculated from growth data follow similar patterns with variation in salinity and humidity (Fig. 5.1). Further, there is a close similarity between the trends in water use efficiency determined from plant growth and water loss measurements and those obtained from single leaf gas exchange measurements (Table 5.6).

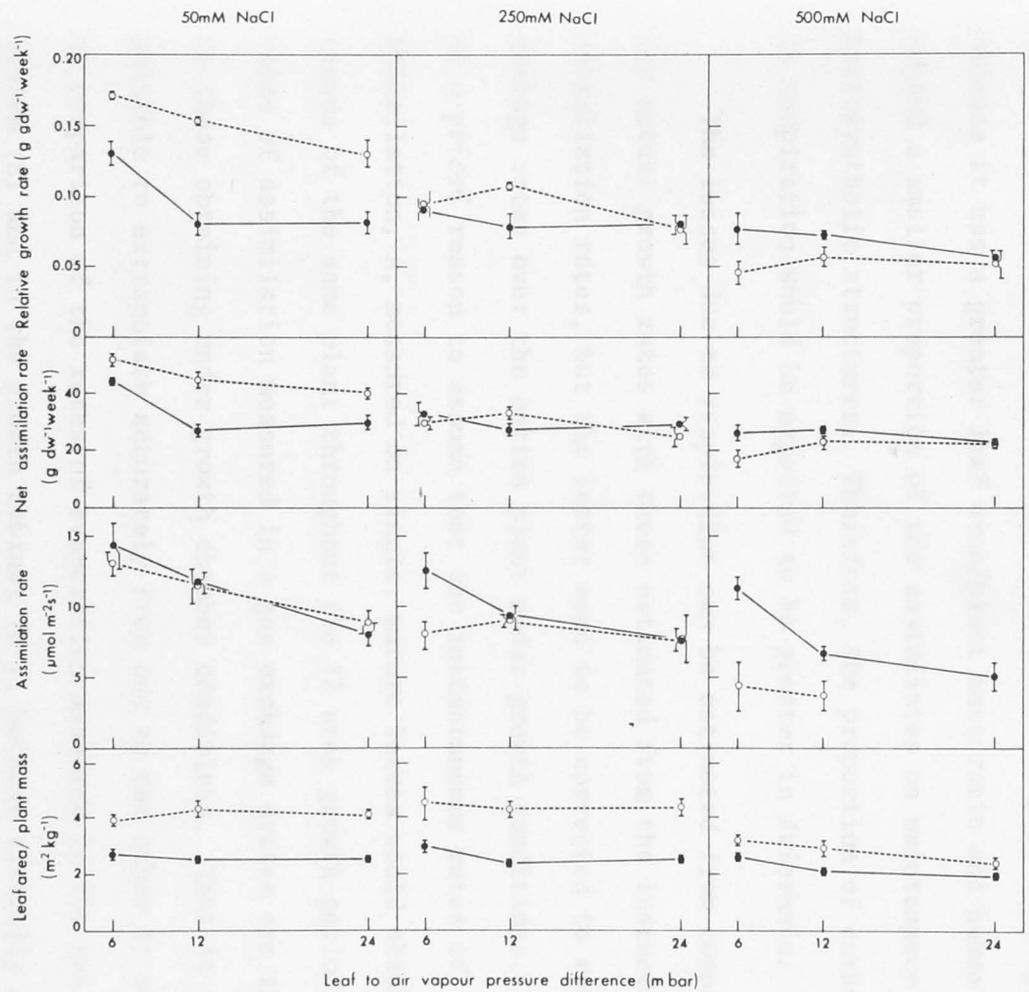


Fig. 5.1: Summary of growth responses of *Aegiceras* (○) and *Avicennia* (●) to different salinity and humidity regimes. Lines connect mean values ± SE; n = 5 except for assimilation rates and the the values of n for these measurements are given in Table 5.5.

It follows then that the net assimilation rates of a species with a constant leaf area/plant mass ratio should decline as the assimilation rates decrease with increasing salinity and vpd as shown in Fig. 5.1. Also, if both *Aegiceras* and *Avicennia* were to have the same assimilation rate, as occurred in response to 50 mM NaCl, then the net assimilation rate of *Aegiceras* should be greater (Fig. 5.1) because it has a greater leaf area/plant mass ratio and hence should expend a smaller proportion of the assimilates on maintenance of non-photosynthetic structures. Therefore, the proportion of carbon lost in respiration would be expected to be greater in *Avicennia*.

The losses due to respiration can be estimated from comparison of the actual growth rates with those estimated from the instantaneous assimilation rates, but the latter need to be corrected to reflect the average rates over the entire plant under growth conditions. There is no *a priori* reason to assume that the instantaneous rates of assimilation, A, measured on single, mature leaves would obtain in all leaves of the same plant throughout the 12 week growth period or that rates of assimilation measured in a gas exchange system are the same as those obtaining under growth chamber conditions. That it is not possible to extrapolate accurately from one to the other is suggested by comparison of the rates of evaporation measured in the gas exchange system (E) and in the growth cabinet (E*), because virtually all water lost by the plant is in association with carbon gain (Fig. 5.2). The correlation between the two sets of measurements is particularly poor in *Aegiceras* because, in contrast with *Avicennia*, developing leaves of *Aegiceras* show little appreciable gas exchange for up to several weeks following full expansion (see Chapter 2). Therefore, inclusion of the total leaf area in the calculations causes an under-estimate of the

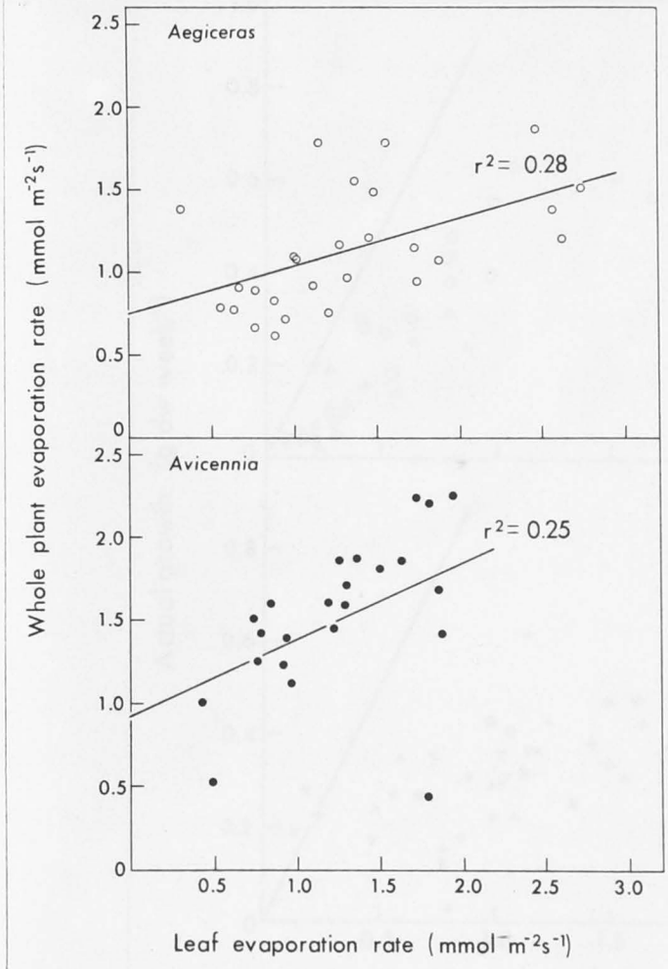


Fig. 5.2: Comparison of instantaneous evaporation rates measured on single leaves with the evaporation rates measured on intact plants of *Aegiceras* (○) and *Avicennia* (●).

evaporation rate in active leaves. If it is assumed that the ratio of assimilation rate to evaporation rate (A/E) measured in the gas exchange system is applicable to the foliage of an entire plant, then the average assimilation rate under growth cabinet conditions, A* in μmol CO_2 m^{-2} s^{-1} is given by (A/E)E*. These calculations give an A* which typically is similar to A in *Aegiceras* and greater than A in *Avicennia*. The trends in response to salinity and vpd are the same for both A* and A.

The actual growth of the plants over a one week period was compared with the calculated total assimilation for that period or potential growth as shown in Fig. 5.3. The potential growth was

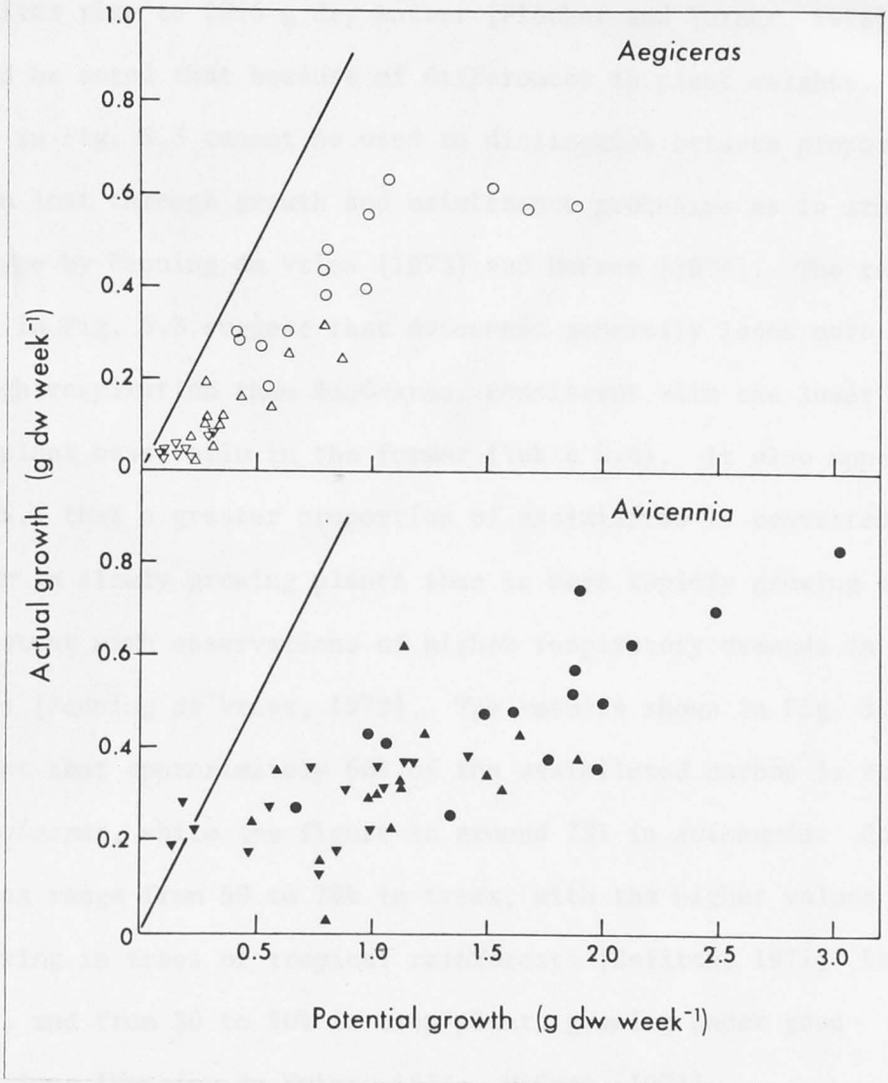


Fig. 5.3: Comparison between measured growth rates and calculated potential growth rates of *Aegiceras* (open symbols) and *Avicennia* (closed symbols) grown in nutrient solution containing 50 (○,●), 250 (△,▲) and 500 mM NaCl (▽,▼). Potential growth was estimated as described in the text. The line represents perfect conversion of assimilates to plant mass (i.e. the case of no respiration).

estimated from A* L t, where A* (μmol CO_2 m^{-2} s^{-1}) is the average assimilation rate for an intact plant as previously discussed, L is the total leaf area (m^2) of a plant and t is 302400, the number of seconds during which photosynthesis take place during a week when each day has a 12 hour photoperiod. The resulting value in mol CO_2 $week^{-1}$ was converted to dry matter on the assumption that one mol assimilated

CO_2 gives rise to 28.6 g dry matter [Fischer and Turner, 1978]. It should be noted that because of differences in plant weights, the data shown in Fig. 5.3 cannot be used to distinguish between proportions of carbon lost through growth and maintenance processes as in studies of the type by Penning de Vries [1973] and McCree [1974]. The results shown in Fig. 5.3 suggest that *Avicennia* generally loses more carbon through respiration than *Aegiceras*, consistent with the lower leaf area/plant mass ratio in the former (Table 5.4). It also appears from Fig. 5.3 that a greater proportion of assimilates is converted to dry matter in slowly growing plants than in more rapidly growing ones, consistent with observations of higher respiratory demands in vigorous plants [Penning de Vries, 1973]. The results shown in Fig. 5.3 suggest that approximately 60% of the assimilated carbon is respired in *Aegiceras*, while the figure is around 75% in *Avicennia*. Comparable figures range from 50 to 78% in trees, with the higher values occurring in trees of tropical rainforests [Zelitch, 1971; Larcher, 1975], and from 30 to 50% in crop plants growing under good conditions [Penning de Vries, 1973; McCree, 1974].

5.4.4 Integration

Trends in the relative growth rates and in the net assimilation rates with increasing salinity and vpd were well correlated in both species as shown in Fig. 5.1, but demonstrated more clearly in Fig. 5.4. The plant mass values used in these calculations need qualification because these are of total dry weight and may include as much as 4 to 10% NaCl depending upon salinity, as well as other inorganic substances (Chapters 2 and 6). This is not likely to affect the relative growth rates, as the proportion of dry weight which is

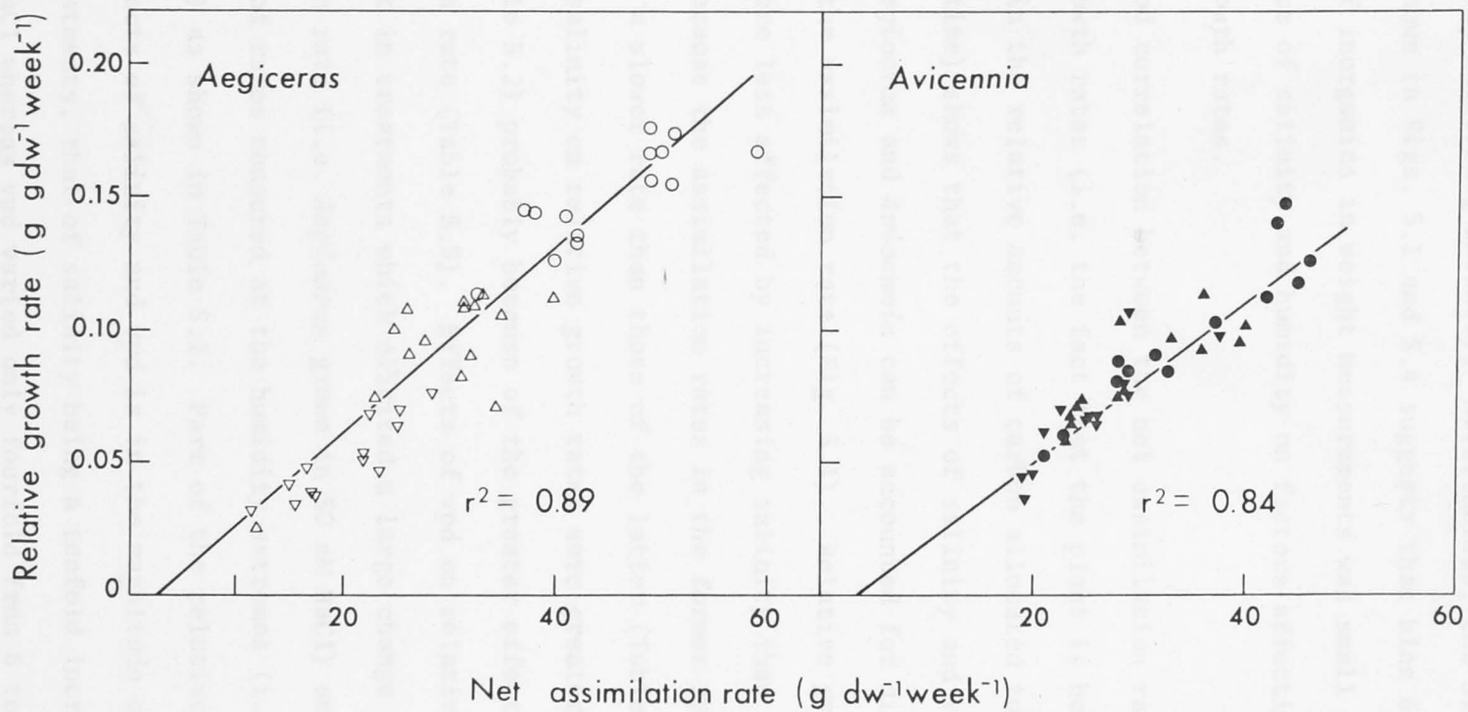


Fig. 5.4: Relationship between the net assimilation rate and the relative growth rate in *Aegiceras* (open symbols) and *Avicennia* (closed symbols) grown in nutrient solution containing 50 (○,●), 250 (△,▲) and 500 mM NaCl (▽,▼). Line drawn by linear regression.

salt is likely to be constant, but it would affect the net assimilation rate, causing the rates to be progressively more over-estimated with increasing salinity. Nevertheless, the similarity in trends as shown in Figs. 5.1 and 5.4 suggests that bias due to inclusion of inorganics in weight measurements was small relative to the influence of salinity and humidity on factors affecting the relative growth rates.

The good correlation between the net assimilation rates and relative growth rates (i.e. the fact that the plant is being consistent in the relative amounts of carbon allocated to different parts over time) shows that the effects of salinity and vpd on the growth of *Aegiceras* and *Avicennia* can be accounted for directly by changes in the assimilation rate (Fig. 5.1). Relative growth rates of *Avicennia* were less affected by increasing salinity than those of *Aegiceras* because the assimilation rates in the former species declined at a slower rate than those of the latter (Table 5.5). Effects of salinity on relative growth rates were greater than those of vpd (Table 5.2) probably because of the greater effects on assimilation rate (Table 5.5). Effects of vpd on relative growth rate are apparent in treatments which elicited a large change in assimilation rate (i.e. *Aegiceras* grown in 50 mM NaCl) and in comparison of rates measured at the humidity extremes (i.e. vpd of 6 and 24 mbar) as shown in Table 5.2. Part of the relative difference between effects of salinity and vpd is in the magnitude of differences between treatments, that of salinity being a tenfold increase from 50 to 500 mM NaCl whereas vpd varied only fourfold from 6 to 24 mbar.

CHAPTER 6

PHOTOSYNTHETIC RESPONSES TO STEADY STATE CONDITIONS OF SALINITY AND HUMIDITY

"What is the reason that seawater nourishes not trees? Is it not for the same reason that it nourishes not earthly animals? ... Nor, though seawater be aliment to marine plants as to its fishes, will it therefore nourish earthly plants, since it can neither penetrate the roots, because of its grossness, nor ascend, by reason of its weight ... Or is it because drought is a great enemy to trees?"

Plutarch, 70 AD
(translated by Bowman, 1917)

6.1 INTRODUCTION

In the previous study (Chapter 5), the decline in growth rates in both *Aegiceras corniculatum* and *Avicennia marina* with increasing salinity could be attributed largely to the decrease in assimilation rate. In other halophytes, the decline in assimilation rate with variation in salinity from optimal levels was largely caused by increase in mesophyll resistance [Gale and Poljakoff-Mayber, 1970; Longstreth and Strain, 1977; De Jong, 1978; Longstreth and Nobel, 1979]. This might also explain the effect of salinity on the assimilation rates in *Aegiceras* and *Avicennia*, because the intercellular CO_2 concentration, c_i, increased in the former species and remained nearly constant in the latter species while both the assimilation rate and stomatal conductance declined with increasing salinity.

However, there are no reports of direct effects of humidity on photosynthetic metabolism [Hall *et al.*, 1976; Cowan, 1977; Raschke, 1979]. The general consensus of opinion expressed in these reviews is that the decline in assimilation rate in some species with increase in the leaf to air vapour pressure difference (vpd) was due to an associated decline in stomatal conductance which caused a decrease in c_i [Hall *et al.*, 1976; Cowan, 1977; Raschke, 1979]. However, this conclusion must be considered tentative in the absence of studies investigating the effect of vpd on photosynthetic capacity.

The purpose of this chapter is to examine the relative contributions of variations in photosynthetic capacity and stomatal conductance to the responses of assimilation rate to long-term salinity and humidity treatments.

6.2 MATERIALS AND METHODS

6.2.1 Plant Material

Seedlings of *Aegiceras corniculatum* and *Avicennia marina* were grown as described in Chapter 5. Gas exchange measurements were made on the same fully mature leaves which were used to study long-term effects of salinity and humidity on growth in Chapter 5.

6.2.2 Salt

The concentrations of Na^+, K^+ and Cl^- in the leaves were measured as described in the appendix.

6.2.3 Gas Exchange Characteristics

The gas exchange apparatus, preparation of gas mixtures and

method of calculations are described in the appendix. Assimilation rate was measured as a function of the intercellular CO_2 concentration by varying the ambient CO_2 concentration in the sequence 330, 400, 500, 200, 100 and 50 $\mu l\ l^{-1}$. A period of at least 30 minutes was allowed between each change in CO_2 concentration to let gas exchange come to a steady state. Measurements were made under conditions similar to those experienced by the leaves during growth. These were a leaf temperature of 25 C, quantum flux density of 500 $\mu E\ m^{-2}\ s^{-1}$, and leaf to air vapour pressure difference of either 6, 12 or 24 mbar depending on the humidity treatment. Atmospheric pressure usually was 950 mbar.

The data presented are pooled from two sets of measurements. In the first set, measurements were made under a range of c_a from 50 to 330 $\mu l\ l^{-1}$, but an accident caused the loss of plants growing under high humidity (6 mbar vpd) before measurements could be made on these plants. A second set of plants was therefore grown under all salinity and humidity treatments. Gas exchange measurements on these plants included additional measurements made under ambient CO_2 concentrations of 400 and 500 $\mu l\ l^{-1}$. There were no obvious differences between the responses of the first and second sets of plants. A second accident again caused the loss of plants growing under high humidity before the leaf properties could be evaluated. Unless otherwise stated, all data presented herein will be a composite of both groups of plants.

6.3 RESULTS

6.3.1 Ion Concentrations in Leaves

The concentrations of Cl^-, Na^+ and K^+ in leaves of *Aegiceras* and

Avicennia grown under different salinity and humidity conditions are summarized in Tables 6.1 and 6.2. Leaves of both species contained high concentrations of these ions which accounted for as much as 4 to 10% of the total leaf dry weight (Table 6.1). There was considerable variability in the data within humidity treatments, but it appears that the foliar ion concentrations may be largely a function of the external salinity (Table 6.2).

The patterns of ion accumulation differed between species (Tables 6.1 and 6.2). The concentrations (Table 6.2) of Cl^- and Na^+ were maximum in leaves of *Aegiceras* grown in solution containing 250 mM NaCl whereas those of *Avicennia* increased with increasing salinity of the growth media. The concentrations of Cl^- and Na^+ in leaves exceeded those of the nutrient solutions except for Cl in *Aegiceras* grown in 500 mM NaCl. The difference between foliar and substrate concentration of Cl^- and Na^+ declined with increasing salinity, the differences being greater in *Aegiceras* grown in 50 and 250 mM NaCl than in *Avicennia* grown under the same conditions. These differences in ion concentration in leaves as shown in Table 6.2 resulted primarily from changes in the absolute quantity of ions per unit leaf weight as shown in Table 6.1.

The concentration of K^+ decreased with increasing salinity in both species, with *Avicennia* maintaining higher foliar levels of K^+ than *Aegiceras* (Table 6.2). These concentrations are considerably greater than the 6 mM K^+ in the nutrient solution (see appendix). The Na^+ concentrations were more than adequate to counterbalance those of Cl^- in *Aegiceras*. However, Cl^- concentrations in *Avicennia* were offset by the combined concentrations of Na^+ and K^+, with the

Table 6.1

Contents of Cl^-, Na^+ and K^+ in leaves of *Aegiceras corniculatum* and *Avicennia marina* grown under different salinity and humidity regimes. Values are mean ± SD, n = 5 except * in which n = 2. ND indicates no data; all plants were lost in an accident prior to measurements.

Genus	Salinity (mM NaCl)	Humidity (mbar vpd)	Ion content (% of dry weight)	Cl^-	Na^+	K^+	$\frac{Na^+ + K^+}{Cl^-}$	$\frac{Na^+}{Cl^-}$	$\frac{Na^+}{K^+}$
				(μmol ion.g^{-1} dry weight)					
Aegiceras	50	6	4.1 ± 0.5	618 ± 91	722 ± 155	52 ± 11	1.26 ± 0.26	1.18 ± 0.27	14.87 ± 6.68
		12	4.6 ± 0.5	616 ± 58	825 ± 220	129 ± 60	1.54 ± 0.12	1.33 ± 0.22	8.82 ± 7.82
		24	4.6 ± 0.5	729 ± 65	671 ± 174	119 ± 38	1.08 ± 0.05	0.91 ± 0.07	6.65 ± 1.97
		Average	4.4 ± 0.5	668 ± 87	727 ± 177	103 ± 50	1.25 ± 0.25	1.10 ± 0.26	9.49 ± 6.48
	250	6	8.6 ± 0.9	1244 ± 168	1700 ± 141	69 ± 9	1.43 ± 0.08	1.37 ± 0.07	25.07 ± 5.28
		12	7.5 ± 0.1	986 ± 97	1663 ± 77	53 ± 21	1.76 ± 0.28	1.70 ± 0.24	33.78 ± 11.35
		24*	9.3 ± 3.7	1060 ± 280	2230 ± 1090	120 ± 50	2.00 ± 0.52	2.05 ± 0.49	19.13 ± 1.24
		Average	8.5 ± 1.9	1095 ± 193	1864 ± 568	79 ± 38	1.78 ± 0.42	1.71 ± 0.39	25.99 ± 8.67
	500	6	5.6 ± 3.2	809 ± 507	1094 ± 598	50 ± 0	1.47 ± 0.18	1.40 ± 0.13	21.90 ± 12.00
		12	7.8 ± 1.0	1075 ± 185	1550 ± 215	98 ± 49	1.55 ± 0.17	1.45 ± 0.13	21.00 ± 13.70
		24	5.6 ± 1.5	702 ± 196	1231 ± 354	66 ± 27	1.85 ± 0.17	1.75 ± 0.18	19.90 ± 7.15
		Average	6.5 ± 1.9	873 ± 291	1331 368	76 ± 38	1.65 ± 0.23	1.56 ± 0.21	20.75 ± 9.79

Table 6.1 (cont'd)

Genus	Salinity (mM NaCl)	Humidity (mbar vpd)	Ion content (% of dry weight)	Cl^-	Na^+	K^+	$\frac{Na^+ + K^+}{Cl^-}$	$\frac{Na^+}{Cl^-}$	$\frac{Na^+}{K^+}$
				(μmol ion.g^{-1} dry weight)					
Avicennia	50	6	ND	ND	ND	ND	ND	ND	ND
		12	6.4 ± 1.5	941 ± 273	622 ± 215	423 ± 105	1.15 ± 0.21	0.67 ± 0.14	1.59 ± 0.80
		24	6.0 ± 1.1	946 ± 188	536 ± 236	401 ± 116	0.96 ± 0.34	0.51 ± 0.25	1.31 ± 0.76
		Average	6.3 ± 1.3	943 ± 230	584 ± 222	412 ± 108	1.08 ± 0.27	0.62 ± 0.18	1.53 ± 0.73
	250	6	9.0 ± 1.1	1511 ± 184	1234 ± 168	207 ± 170	0.96 ± 0.17	0.82 ± 0.09	6.87 ± 3.40
		12	7.4 ± 0.9	1093 ± 149	946 ± 176	332 ± 106	1.17 ± 0.10	0.86 ± 0.09	3.09 ± 1.06
		24	7.8 ± 1.5	1239 ± 245	1065 ± 358	247 ± 107	1.07 ± 0.20	0.86 ± 0.23	4.46 ± 2.38
		Average	8.0 ± 1.3	1255 ± 251	1066 ± 280	266 ± 128	1.08 ± 0.18	0.85 ± 0.16	4.50 ± 2.60
	500	6	ND	ND	ND	ND	ND	ND	ND
		12	7.9 ± 1.7	1320 ± 247	1014 ± 282	225 ± 113	0.93 ± 0.16	0.76 ± 0.11	5.11 ± 1.76
		24	10.8 ± 2.0	1774 ± 321	1513 ± 416	268 ± 83	1.00 ± 0.13	0.85 ± 0.14	6.18 ± 2.42
		Average	9.5 ± 2.4	1562 ± 364	1280 ± 432	248 ± 97	0.97 ± 0.15	0.81 ± 0.13	5.68 ± 2.14

Table 6.2

Concentrations of Cl^-, Na^+ and K^+ in leaves of *Aegiceras corniculatum* and *Avicennia marina* grown under different salinity and humidity regimes. Values are mean ± SD, n = 5 except * in which n = 2. ND indicates no data; all plants were lost in an accident prior to the measurements.

Genus	Salinity (mM NaCl)	Humidity (mbar vpd)	Fresh/Dry Weight ($g\ g^{-1}$)	% Water	Cl^-	Na^+	K^+
					(mmol ion l^{-1} leaf water)		
Aegiceras	50	6	2.71 ± 0.13	63.1 ± 1.8	359.8 ± 35.8	419.3 ± 67.0	30.4 ± 7.5
		12	2.84 ± 0.33	64.5 ± 3.9	343.3 ± 77.5	464.8 ± 169.9	70.1 ± 32.6
		24	2.77 ± 0.25	63.6 ± 3.4	416.1 ± 32.4	378.9 ± 70.6	68.0 ± 21.5
		Average	2.77 ± 0.23	63.7 ± 2.9	380.9 ± 55.2	413.3 ± 100.3	58.3 ± 27.0
	250	6	3.69 ± 0.27	72.8 ± 2.0	462.0 ± 16.9	633.1 ± 9.8	25.9 ± 5.9
		12	3.38 ± 0.42	70.1 ± 3.7	425.6 ± 115.7	709.0 ± 92.1	21.8 ± 4.6
		24*	3.15 ± 0.49	67.9 ± 5.1	488.9 ± 15.7	1005.6 ± 275.0	52.2 ± 11.0
		Average	3.41 ± 0.40	70.3 ± 3.7	458.8 ± 59.9	782.5 ± 218.7	33.3 ± 15.9
	500	6	3.15 ± 1.21	65.6 ± 13.3	369.5 ± 27.5	513.9 ± 11.7	27.8 ± 15.7
		12	3.72 ± 0.13	73.0 ± 0.9	397.1 ± 71.1	570.9 ± 72.7	35.8 ± 18.3
		24	3.26 ± 0.52	68.6 ± 5.8	308.3 ± 37.5	540.3 ± 75.0	28.8 ± 6.9
		Average	3.42 ± 0.57	69.8 ± 6.4	356.0 ± 63.5	547.3 ± 64.6	31.4 ± 13.0

Table 6.2 (cont'd)

Genus	Salinity (mM NaCl)	Humidity (mbar vpd)	Fresh/Dry Weight ($g\ g^{-1}$)	% Water	Cl^-	Na^+	K^+
					(mmol ion l^{-1} leaf water)		
Avicennia	50	6	ND	ND	ND	ND	ND
		12	4.00 ± 1.50	73.1 ± 5.9	336.6 ± 85.7	219.1 ± 59.8	158.7 ± 54.9
		24	3.59 ± 0.34	71.3 ± 2.6	368.3 ± 77.2	203.5 ± 93.6	156.5 ± 48.1
		Average	3.80 ± 1.11	72.5 ± 4.5	351.7 ± 81.2	212.2 ± 74.6	157.4 ± 50.3
	250	6	4.18 ± 0.59	75.7 ± 3.6	482.4 ± 57.8	397.8 ± 82.5	66.6 ± 51.7
		12	3.39 ± 0.21	70.4 ± 1.9	466.7 ± 37.7	403.0 ± 50.7	143.5 ± 49.7
		24	3.66 ± 0.82	71.5 ± 5.0	490.1 ± 141.4	411.2 ± 121.0	97.3 ± 46.0
		Average	3.67 ± 0.67	72.1 ± 4.3	480.5 ± 95.9	405.3 ± 89.5	105.4 ± 55.1
	500	6	ND	ND	ND	ND	ND
		12	3.47 ± 0.20	71.1 ± 1.7	533.6 ± 82.3	409.3 ± 106.5	91.2 ± 47.5
		24	3.53 ± 0.25	71.6 ± 2.1	710.1 ± 169.6	610.7 ± 210.6	104.6 ± 25.3
		Average	3.50 ± 0.22	71.3 ± 1.8	627.7 ± 160.0	516.7 ± 194.6	98.4 ± 36.5

proportion due to Na^+ increasing with the salinity of the nutrient solution (Table 6.2).

6.3.2 Gas Exchange Characteristics

The gas exchange characteristics of *Aegiceras* and *Avicennia* grown under different salinity and humidity treatments and measured under normal atmospheric conditions (ambient $c_a = 330\ \mu l\ l^{-1}$) are shown in Fig. 6.1. The assimilation rates and stomatal conductance of both species declined with increase in salinity and vpd. The associated changes in c_i were such that c_i increased in *Aegiceras* and remained nearly constant in *Avicennia* with increase in salinity, but declined with increase in vpd.

Certain photosynthetic characteristics of the mesophyll can be assayed independently of stomatal influence by measurement of the assimilation rate as a function of c_i ($A(c_i)$ curve) when the latter is varied by changing the ambient CO_2 concentration, c_a. The shapes of the $A(c_i)$ curves were affected by both salinity and humidity, as exemplified in Figs. 6.2 and 6.3, respectively. These figures show $A(c_i)$ curves of individual plants which are representative of those receiving a given treatment. Selection was based on having characteristics which were the most like the averages for the treatment.

Comparison of Figs. 6.2 and 6.3 shows that the lower, linear portion of the $A(c_i)$ curve was affected only by salinity. However, the upper, curved region was sensitive to changes in both salinity and humidity. Neither treatment substantially affected the CO_2 compensation point which was approximately 50 $\mu l\ l^{-1}$ in both species, as shown more clearly in Table 6.3.

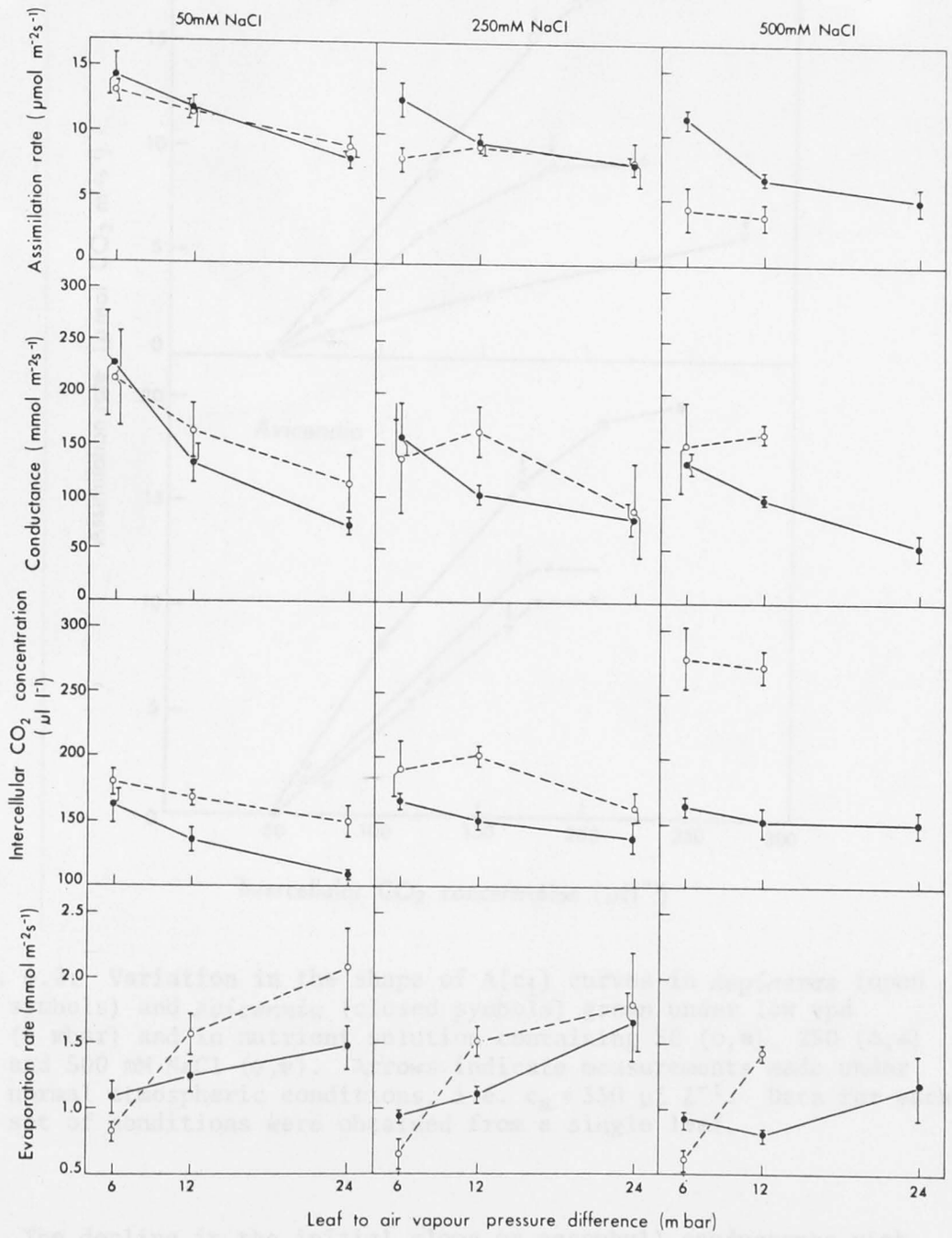


Fig. 6.1: Gas exchange characteristics of *Aegiceras* (○) and *Avicennia* (●) under normal atmospheric conditions, i.e. $c_a = 330\ \mu l\ l^{-1}$. Values are mean ± sE. The values for n are variable and are listed in Table 6.3.

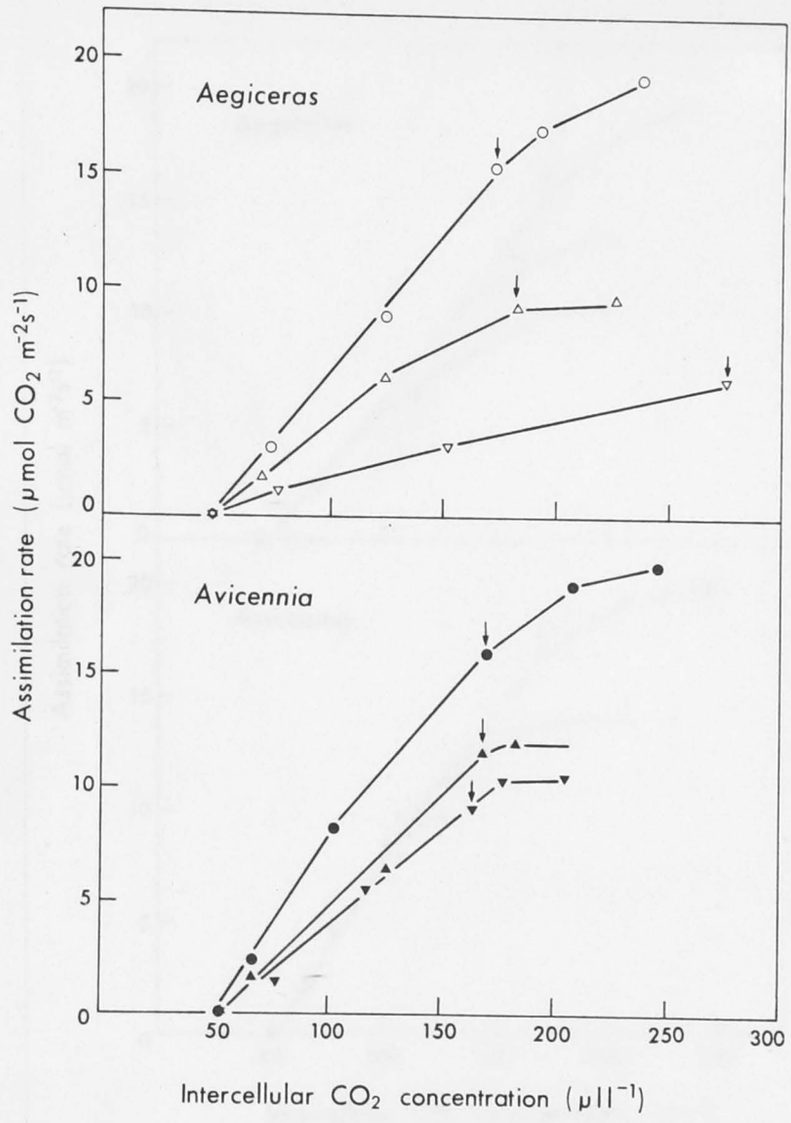


Fig. 6.2: Variation in the shape of $A(c_i)$ curves in *Aegiceras* (open symbols) and *Avicennia* (closed symbols) grown under low vpd (6 mbar) and in nutrient solution containing 50 (○,●), 250 (△,▲) and 500 mM NaCl (▽,▼). Arrows indicate measurements made under normal atmospheric conditions, i.e. $c_a = 330$ μl l^{-1}. Data for each set of conditions were obtained from a single leaf.

The decline in the initial slope or mesophyll conductance with increase in salinity was consistent among the plants receiving a given salinity treatment as shown in Table 6.3. Mesophyll conductance was calculated by linear regression using measurements made under a c_a of 50, 100 and 200 μl l^{-1} at which the relationship of assimilation rate

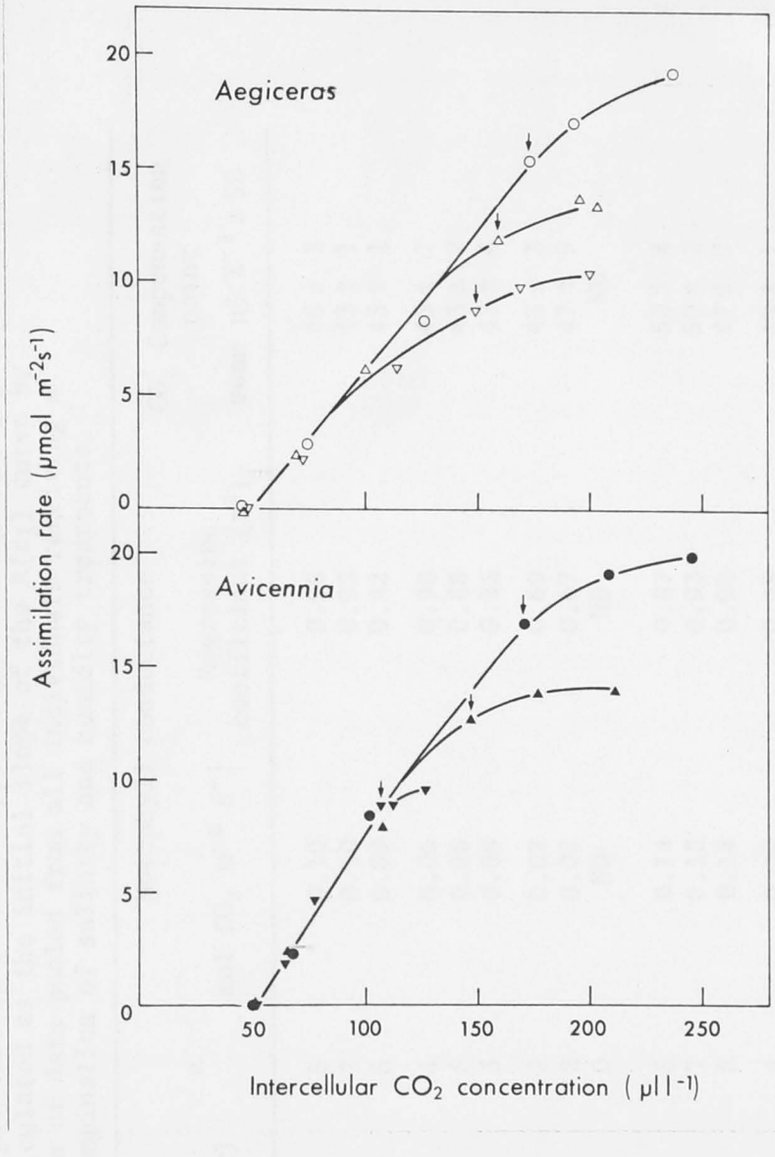


Fig. 6.3: Variation in the shapes of $A(c_i)$ curves in *Aegiceras* (open symbols) and *Avicennia* (closed symbols) grown in nutrient solution containing 50 mM NaCl and under a vpd of 6 (○,●), 12 (△,▲) and 24 mbar (▽,▼). Arrows indicate measurements made under normal atmospheric conditions, i.e. $c_a = 330\ \mu l\ l^{-1}$. Data for each set of conditions were obtained from a single leaf.

vs. c_i was linear. The values for mesophyll conductance shown in Table 6.3 were calculated from the pool of data gathered by measurements on n individuals from each combination of salinity and humidity. The regression coefficients for these calculations using pooled data were less than those for calculations using the data for individual

Table 6.3

Variation in mesophyll conductance and in the CO_2 compensation point in *Aegiceras* and *Avicennia* grown under different conditions of salinity and leaf to air vapour pressure difference (vpd). ND = no data. Mesophyll conductance is calculated as the initial slope of the $A(c_i)$ curve by linear regression of data pooled from all individuals receiving a particular combination of salinity and humidity treatments.

Genus	Salinity (mM NaCl)	vpd (mbar)	n	Mesophyll conductance		CO_2 Compensation point
				mol CO_2 m^{-2} s^{-1}	Regression coefficient (r^2)	mean μl l^{-1} ± SD
Aegiceras	50	6	5	0.10	0.96	46 ± 3
		12	7	0.10	0.93	43 ± 1
		24	5	0.09	0.92	43 ± 1
	250	6	4	0.06	0.90	45 ± 7
		12	6	0.06	0.88	43 ± 2
		24	3	0.08	0.83	47 ± 4
	500	6	2	0.02	0.69	43 ± 3
		12	2	0.02	0.67	47 ± 9
		24	0	ND	ND	ND
Avicennia	50	6	6	0.14	0.87	50 ± 4
		12	7	0.13	0.93	50 ± 2
		24	8	0.14	0.90	47 ± 7
	250	6	4	0.09	0.98	45 ± 1
		12	6	0.10	0.94	50 ± 4
		24	7	0.10	0.92	50 ± 10
	500	6	4	0.08	0.95	55 ± 1
		12	7	0.07	0.85	49 ± 6
		24	8	0.08	0.74	56 ± 5

plants, the latter often being unity. The mesophyll conductance typically was greater in *Avicennia* than in *Aegiceras*, and was less sensitive to increasing salinity in the former genus (Table 6.3).

There was considerable variability in the magnitude of c_i at which the curve departed from linearity in plants of a given salinity and humidity treatment, i.e. the photosynthetic capacity was not consistent among individuals receiving the same treatment. This gave rise to the variability in gas exchange characteristics measured under normal atmospheric conditions (Fig. 6.1). Nevertheless, the overall trends appeared as illustrated in Figs. 6.2 and 6.3 in which the level of the upper, curved portion of the $A(c_i)$ curve declined with increasing salinity and vpd. The net effect of these changes in mesophyll conductance and in the upper level of the $A(c_i)$ curve was a decrease in photosynthetic capacity with increase in salinity and vpd, with *Aegiceras* being the more sensitive species.

The influence of stomatal conductance on the assimilation rates obtained under normal atmospheric conditions is shown by examining the shape of the $A(c_i)$ curve for a particular set of conditions with reference to the point at which the leaf normally functions, i.e. the point corresponding to a c_a of 330 $\mu l\ l^{-1}$. These operational points are summarized in Fig. 6.1, but the significance in relation to the shape of the $A(c_i)$ curves is presented more clearly in Fig. 6.4. It is apparent that the variation in stomatal conductance was such that the operational c_i (Fig. 6.1) occurred in the region of transition between the lower, linear and upper, curved portions of the $A(c_i)$ curves in all treatments. Thus, stomatal conductance and photosynthetic capacity changed in the same sense with variation in

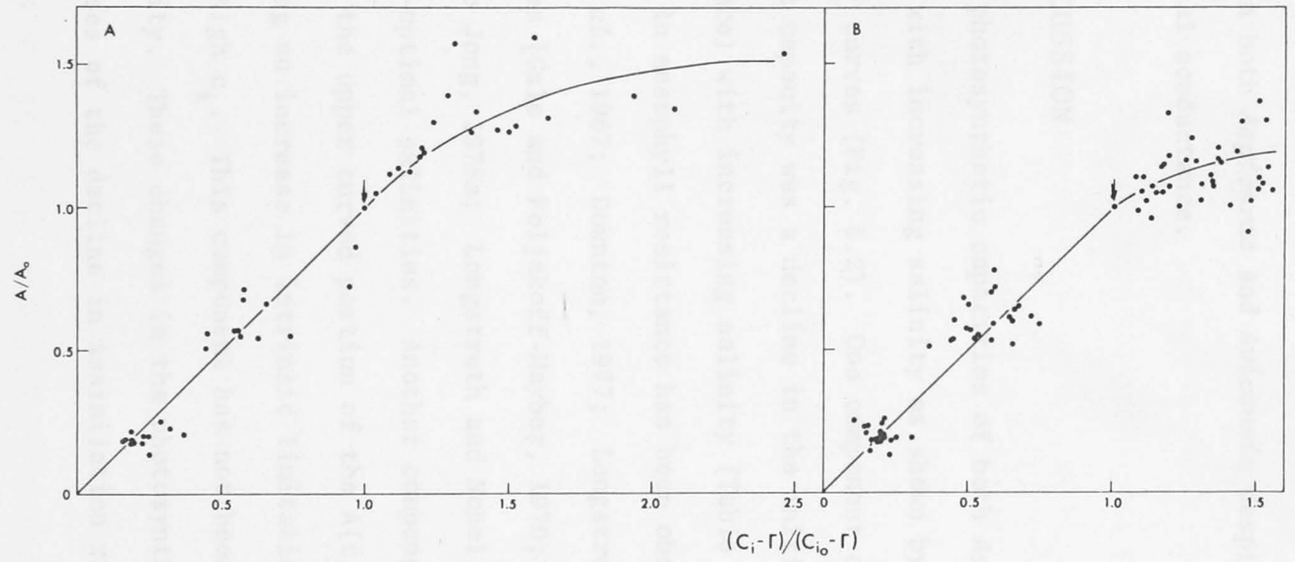


Fig. 6.4: Normalization of $A(c_i)$ curves measured in *Aegiceras* (A) and *Avicennia* (B) grown under all salinity and humidity treatments to emphasize the position of the operational c_i (↓) relative to the shape of the $A(c_i)$ curve. The assimilation rate, A, is expressed relative to A_0 and $c_i - \Gamma$ is expressed relative to $c_{i_o} - \Gamma$ where (c_{i_o}, A_0) is the operational point, i.e. the characteristics obtaining under normal atmospheric conditions of $c_a = 330\ \mu l\ l^{-1}$, for each plant. The operational points thus coincide at (1,1) and are indicated by the arrows. Lines are drawn by eye.

salinity and vpd, the changes in stomatal conductance being such that the operational c_i was coincident roughly with the photosynthetic capacity. These data show that the decline in assimilation rates with increasing salinity or vpd was primarily the result of non-stomatal factors in both *Aegiceras* and *Avicennia* despite the associated decline in stomatal conductance.

6.4 DISCUSSION

The photosynthetic capacities of both *Aegiceras* and *Avicennia* declined with increasing salinity as shown by changes in the shapes of the $A(c_i)$ curves (Fig. 6.2). One component of the decrease in photosynthetic capacity was a decline in the initial slope (mesophyll conductance) with increasing salinity (Table 6.3). Similarly, an increase in mesophyll resistance has been observed in glycophytes [Gale *et al.*, 1967; Downton, 1977; Longstreth and Nobel, 1979] and halophytes [Gale and Poljakoff-Mayber, 1970; Longstreth and Strain, 1977; De Jong, 1978a; Longstreth and Nobel, 1979] when grown in sub- or supra-optimal salinities. Another component was the decline in the level of the upper curved portion of the $A(c_i)$ curve (Fig. 6.2), indicating an increase in intrinsic limitation to the assimilation rate at high c_i. This component has not been studied in previous work on salinity. These changes in the photosynthetic capacity were the main causes of the decline in assimilation rates with increasing salinity.

One of the main differences between the two species of the present study is that the photosynthetic metabolism of *Aegiceras* is far more sensitive to salinity than that of *Avicennia*. This

sensitivity may be related to differences in internal ion concentrations, particularly the Na^+/K^+ ratio. Maintenance of low Na^+/K^+ ratios is generally associated with salt tolerance, although a mechanistic basis is unknown [Flowers *et al.*, 1977]. Rains and Epstein [1967] have shown that *Avicennia marina* has the ability to absorb K^+ selectively in the presence of high Na^+ concentrations and suggested that this was an important aspect of the high degree of salt tolerance exhibited by this species. In the present study, *Avicennia* maintained a much lower ratio of Na^+/K^+ than *Aegiceras* with increase in salinity (Table 6.1). These data suggest that the lower K^+ selectivity of *Aegiceras* is associated with the greater loss of mesophyll conductance and perhaps some metabolic disfunction with increasing salinity.

The photosynthetic capacities of both *Aegiceras* and *Avicennia* also declined with increase in vpd. This decline in photosynthetic capacity was due to changes in the upper, curved portion of the $A(c_i)$ curve. As shown in Fig. 6.3, with increasing vpd, departure from the initial linear slope began at lower c_i, thereby causing a decline in the assimilation rate of high c_i. In other respects, the response to humidity was as previously described, i.e. mesophyll conductance (initial slope) was insensitive to humidity [Ludlow and Wilson, 1971; Hall and Kaufmann, 1975; Khairi and Hall, 1976]. These changes in photosynthetic capacity were the main cause of the decline in assimilation rates with increasing vpd. It is tempting to suggest that the effects of vpd on photosynthetic metabolism are due to effects of increased rates of salt loading into leaves in association with increased evaporation rates and this will be discussed in greater detail in Chapter 7.

The relationships between gas exchange characteristics and photosynthetic biochemistry has been modelled recently by Farquhar *et al.* [1980] and von Caemmerer and Farquhar [in press]. According to their interpretation of the $A(c_i)$ curve, the characteristic occurrence in the present study of the operational c_i in the transition between the lower, linear and upper, curved portions of the $A(c_i)$ curves (Figs. 6.2, 6.3, 6.4) suggests that the assimilation rate under normal atmospheric conditions is co-limited by factors relating to the activity of RuBP carboxylase-oxygenase (represented by the lower portion of the curve) and by other inherent limitations to carboxylation, presumably the RuBP regeneration rate (indicated by the upper portion of the curve).

There are several possible explanations for the decline in mesophyll conductance (i.e. the initial slope) with increasing salinity based on the above interpretations of the $A(c_i)$ curve. First, Berry and Downton [in press] have suggested that it may be due to the effect of internal ions on the solubility ratio of CO_2 and O_2 which would be expected to favour oxygenase activity. This notion is supported by the increase in the CO_2 compensation point with increasing salinity in the glycophyte *Vitis vinifera*, with concomitant increase in c_i (as mesophyll resistance increased) and increase in the proportion of ^{14}C labelled intermediates of the photorespiratory pathway [Downton, 1977]. However, this explanation would not be applicable to the results of the present study because mesophyll conductance declined while the CO_2 compensation point remained constant with increasing salinity (Table 6.3). There are other difficulties in the application of this hypothesis as the intracellular locations of ions are not well known [Flowers *et al.*, 1977],

and mesophyll resistances of some halophytes are minimal when the plants are grown under saline conditions [Gale and Poljakoff-Mayber, 1970; Longstreth and Strain, 1977; De Jong, 1978a].

Two other possible explanations would be consistent with the results of the present study. RuBP carboxylase activity may be inhibited directly by ions as has been reported in *in vitro* studies [Osmond and Greenway, 1972]. Equal inhibition of both the carboxylase and oxygenase functions of RuBP carboxylase-oxygenase would be required to explain the decline of mesophyll conductance with a constant CO_2 compensation point. Last, there may be a decline in the total quantity of enzyme with increasing salinity as mesophyll conductance (or mesophyll resistance) has been found to be correlated with extractable enzyme activity in several species [Ogren and Bowes, 1971; Plaut, 1971; Jones, 1973; Johnson *et al.*, 1974; Laing *et al.*, 1974; Hall and Kaufmann, 1975; O'Toole *et al.*, 1977; von Caemmerer and Farquhar, in press].

While the photosynthetic capacities and stomatal conductances declined with increasing salinity and vpd in both *Aegiceras* and *Avicennia*, differences in the proportionalities between these two processes caused the water use efficiencies (WUE) of the two species to differ. It decreased in *Aegiceras*, but remained nearly constant in *Avicennia* with increase in salinity, and WUE decreased in both species with increase in vpd (Table 5.6). There is no consensus in the literature and the WUE of some species has been reported to remain constant [Winter, 1979] whereas that of other species increased in response to increasing salinity [De Jong, 1978b; Gale and Poljakoff-Mayber, 1979; Nobel, 1980].

However, von Caemmerer and Farquhar [in press] have noted that operation is the transition zone between the lower, linear and upper, curved portions of the $A(c_i)$ curve allows maximization of both nitrogen and water economies, i.e. it is optimal behaviour. In the present study, the influence of stomatal conductance on c_i was such that it consistently occurred in the transition region of the $A(c_i)$ curve (Fig. 6.4). Thus, despite differences between *Aegiceras* and *Avicennia* in WUE (Table 5.6), stomatal behaviour in both species maximized carbon gain relative to water loss for the metabolic conditions obtained in response to salinity and humidity.

There have been several reports of changes in photosynthetic pathways in response to salinity. However, the only substantiated report is that of salinity induced CAM in the C_3 halophyte, *Mesembryanthemum crystallinum* [Winter and von Willert, 1972; Winter and Lüttge, 1976]. Other studies have claimed switches between C_3 and C_4 photosynthetic pathways in response to salinity on the basis of ^{14}C labelling patterns in mangroves [Joshi *et al.*, 1974; Joshi, 1976] and in another halophyte [Shomer-Ilan and Waisel, 1973]. However, the conclusions reached in the aforementioned studies with mangroves are doubtful because of serious experimental deficiencies [Clough *et al.*, 1980] while the claim of the latter report could not be substantiated in subsequent work on Na^+ deficiency in C_4 plants [Downton and Törökfalvy, 1975].

Similar claims of shifts between C_3 and C_4 pathways in response to salinity have been based on changes in $\delta^{13}C$ values [Guy *et al.*, 1980]. However, these results can be explained by theory relating c_i and carbon isotope discrimination [Farquhar, 1980; Farquhar *et al.*,

in press b]. This theory has been confirmed recently with the demonstration that $\delta^{13}C$ decreases (i.e. becomes more negative) with increase in c_i in several species grown under different conditions, including the mangroves of the present study [Farquhar *et al.*, in press a]. In both *Aegiceras* and *Avicennia* the $\delta^{13}C$ values approximated those expected from the changes in c_i in response to variations in salinity and humidity [Farquhar *et al.*, in press a]. These changes are substantial as shown for example by the decrease in $\delta^{13}C$ in *Aegiceras* from -23.42 to -26.37 $^{0}/_{00}$ with increase in c_i from 132 to 185 $\mu l\ l^{-1}$. The results of the present study further show that the photosynthetic characteristics of *Aegiceras* and *Avicennia* are typical of C_3 plants under all combinations of salinity and humidity and there was no suggestion of a change in photosynthetic pathway.

CHAPTER 7

PHOTOSYNTHETIC RESPONSES TO TRANSIENT CONDITIONS OF SALINITY AND HUMIDITY

"Thus we sailed up the straits, groaning in terror, for on the one side we had Scylla, while on the other the mysterious Charybdis sucked down the salt sea water in her dreadful way."

The Odyssey,
Homer

7.1 INTRODUCTION

The problems of coping with environments of different salinities pose a Homeric dilemma: the plant must regulate ion uptake so as to maintain turgor, but at the same time protect sensitive metabolic processes from ion stress, the latter presumably involving maintenance of favourable Na^+/K^+ ratios [Flowers *et al.*, 1977]. Under steady-state conditions, *Aegiceras* and *Avicennia* may maximize carbon gain for a specific set of environmental factors by a complex array of interactions involving plant architecture (Chapter 5), photosynthetic metabolism and stomatal behaviour (Chapter 6). However, mangroves in the natural environment must cope with transient changes in soil salinity and in rates of salt influx to the leaves, the latter due to variation in both salinity and evaporative demand. The purpose of the present study is to determine changes in gas exchange characteristics with short-term variation in salinity and vpd and the extent to which these are due to responses of stomata and photosynthetic metabolism.

7.2 MATERIALS AND METHODS

7.2.1 Plant Material

7.2.1.1 Salinity studies

Propagules of *Aegiceras corniculatum* and *Avicennia marina* were collected from trees growing along Cullendulla Creek, New South Wales, Australia. Propagules were cultivated in sand, sub-irrigated with 10% seawater in a growth cabinet adjusted to give day/night leaf temperatures of 25/20 C, a relative humidity of ~ 70% to give a leaf to air vapour pressure difference of 12 mbar, and a 12 hr photoperiod with an average of 400 μE m^{-2} s^{-1} incident at leaf height. Upon reaching a post-cotyledonary phase of development, seedlings of *Aegiceras* and *Avicennia* were transferred to 200 and 500 ml containers, respectively, for hydroponic culture in Johnson's nutrient solution (see appendix) which was made roughly equivalent to 10% sea water by addition of 50 mM NaCl. Four seedlings of each species (three experimental seedlings plus a control) were then hydroponically grown until the next flush of leaves was fully developed before beginning the experiment. Solutions were changed weekly. The time required for leaf development under these conditions is approximately six weeks for *Avicennia* and twelve weeks for *Aegiceras*.

7.2.1.2 Humidity studies

The humidity responses of *Avicennia marina* (grown as described above) were compared with those of two glycophytes, *Xanthium strumarium* (L.) and *Gossypium hirsutum* L. var. Deltapine. These were grown in a glasshouse with peak quantum flux density of about 2000 μE m^{-2} s^{-1}. Daylength was extended to 20 hrs to prevent flowering. The

plants were watered three times per day and given nutrients three times per week. The temperature inside the glasshouse was kept below 34 C.

7.2.2 Gas Exchange

7.2.2.1 Salinity studies

Gas exchange characteristics and rates of salt secretion were determined on the same leaf of each plant over a period during which the NaCl concentration of the nutrient solution was increased from 50 to 500 mM NaCl and then returned to the original salinity by step changes of 50 mM NaCl. Solutions were changed at the beginning of the dark period with an interval of 24 and 48 hours, respectively, between changes. The difference in intervals was due to the time required for measuring salt secretion rates and gas exchange characteristics which were determined in consecutive photoperiods. These measurements were made at concentrations of 50, 150, 250, 350, 500 and 50 mM NaCl. The nutrient solution of the control plant also was changed daily, with the salinity maintained at 50 mM NaCl.

Details of the gas exchange apparatus, preparation of gas mixtures and calculations of gas exchange rates across a leaf surface are given in the appendix. Measurements of dark respiration rates were made before illumination and followed by measurement of the assimilation rate as a function of the intercellular CO_2 concentration, c_i, with variation in the latter obtained by changing the ambient CO_2 concentration, c_a, in the sequence 330, 400, 500, 200, 100 and 50 $\mu l\ l^{-1}$. Other conditions were similar to those experienced in the growth chamber, i.e. leaf temperature of 25 C, quantum flux density of 500 $\mu E\ m^{-2}\ s^{-1}$ and a leaf to air vapour pressure of 12 mbar. Atmospheric

pressure usually was 950 mbar. Leaf area was measured with a Lambda leaf area meter.

7.2.2.2 Humidity studies

Measurements of assimilation rate as a function of c_i were made as described above on intact, attached leaves following humidity pre-treatments as described in the text.

7.2.3 Salt Secretion

Total salt secretion was measured over a 12 hr photoperiod under growth cabinet conditions on the day preceding gas exchange measurements as described in the appendix.

7.3 RESULTS

7.3.1 Effects of Transient Changes in Salinity

7.3.1.1 Gas exchange characteristics under ambient conditions

The effects of short-term changes in salinity on the gas exchange characteristics of *Avicennia marina* under normal atmospheric conditions are shown in Fig. 7.1. The assimilation rates at the start of the experiment (i.e. when the salinity was 50 mM NaCl) averaged 14.9 ± 1.3 μmol m^{-2} s^{-1} at a mean intercellular CO_2 concentration (c_i) of 177 ± 6 μl l^{-1}. The assimilation rates decreased with increase in salinity above 250 mM NaCl to average rates of 9.1 ± 1.7 μmol m^{-2} s^{-1} at 500 mM NaCl, a decrease of approximately 37% from the original rates at 50 mM NaCl. The decline in assimilation rates was accompanied by comparable decreases in both stomatal conductance and c_i. The evaporation rate was related directly to stomatal conductance because vpd remained constant and so decreased from approximately

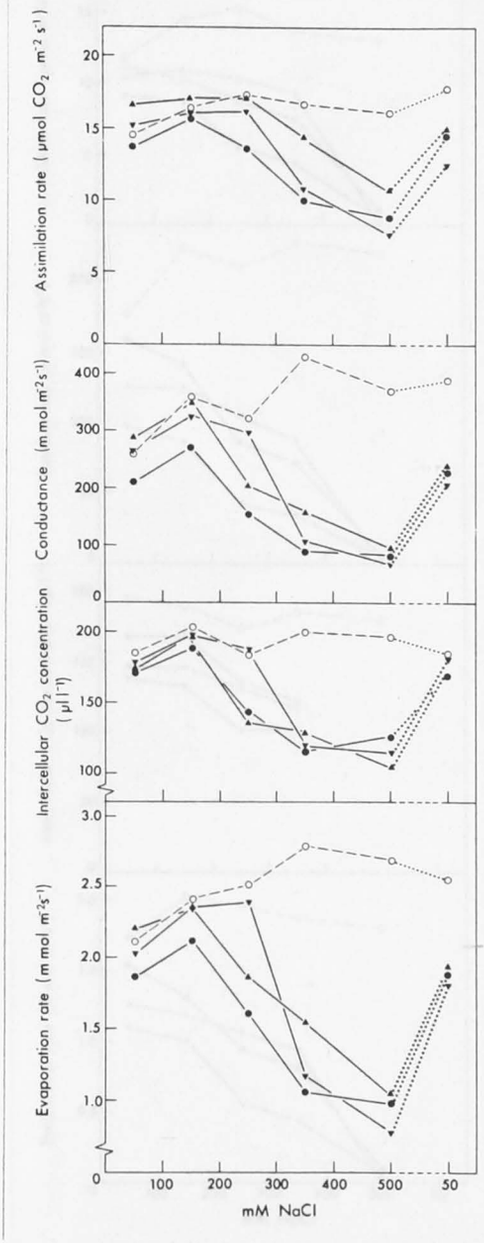


Fig. 7.1: Gas exchange characteristics of mature leaves of *Avicennia marina* in response to transient changes in salinity. Symbols identify the control plant (○) and three plants receiving salinity treatments (●,▲,▼). Measurements were made during increase of salinity from 50 to 500 mM NaCl (points joined by solid lines) and at the conclusion of decrease in salinity from 500 to 50 mM NaCl (points joined by dotted lines). The conditions during measurements were leaf temperature 25 C, quantum flux density 500 μE m^{-2} s^{-1}, leaf to air vapour pressure difference 12 mbar and normal atmospheric conditions of CO_2 300 μl l^{-1}, O_2 210 ml l^{-1}.

2.05 ± 0.14 to 0.94 ± 0.14 mmol m^{-2} s^{-1} with tenfold increase in salinity from 50 to 500 mM NaCl, respectively. These responses were reversible upon return to the original salinity.

The gas exchange characteristics of mature leaves of *Aegiceras* (Fig. 7.2) were more sensitive to short-term changes in salinity, particularly at the highest level, than those of *Avicennia*.

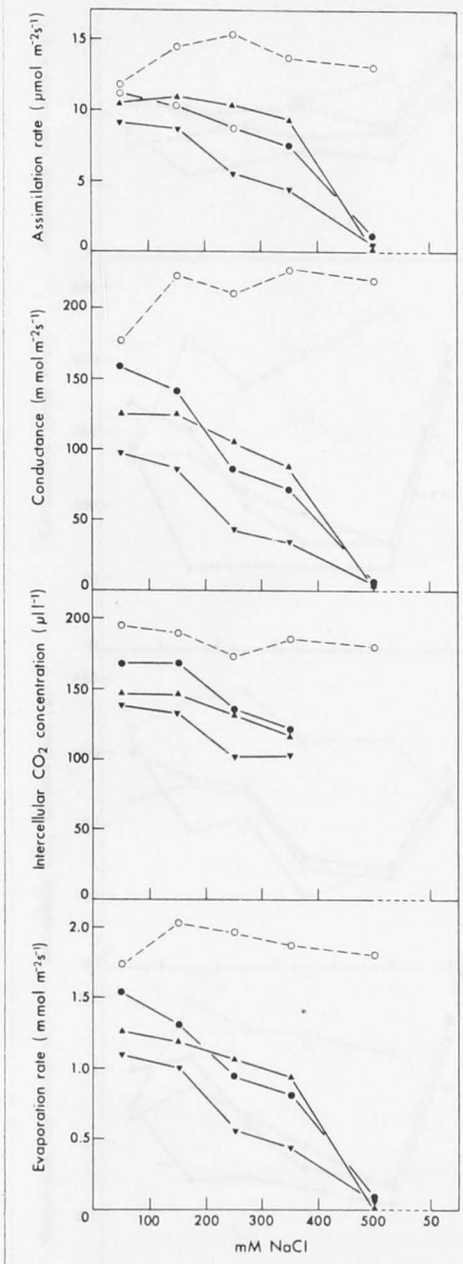


Fig. 7.2: Gas exchange characteristics of mature leaves of *Aegiceras corniculatum* in response to transient changes in salinity. Symbols as in Fig. 7.1.

Assimilation rates, stomatal conductance and c_i decreased proportionally with increasing salinity with nearly complete stomatal closure occurring at 500 mM NaCl. Unfortunately, all the plants were lost in a growth cabinet failure before the salinity could be returned to 50 mM NaCl.

The pattern of gas exchange characteristics in response to transient salinity conditions was slightly different in young leaves

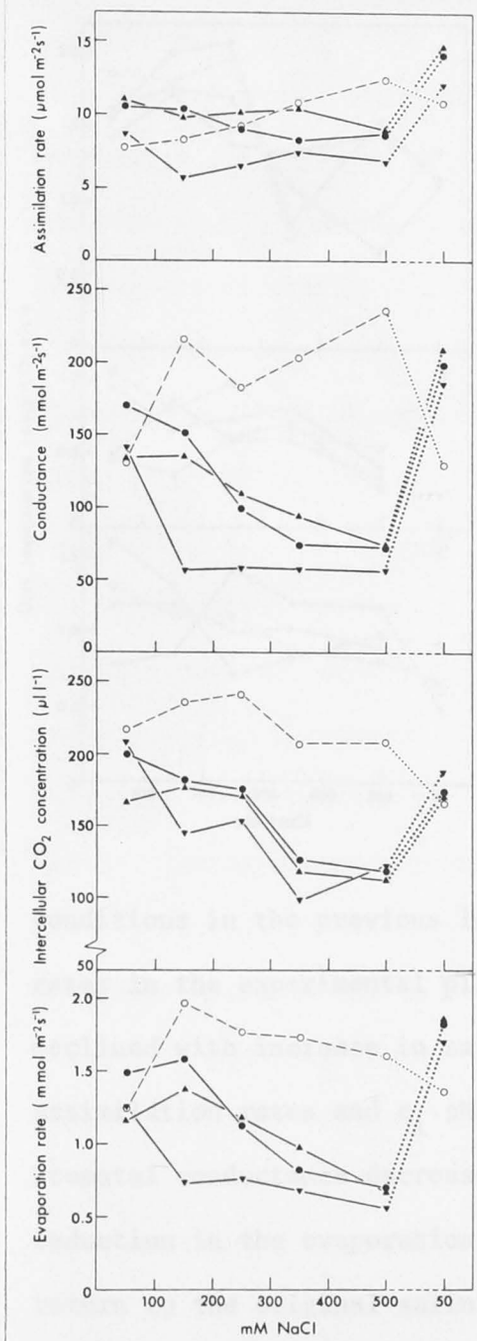


Fig. 7.3: Gas exchange characteristics of young leaves of *Aegiceras corniculatum* in response to transient changes in salinity. Symbols as in Fig. 7.1.

of *Aegiceras* (Fig. 7.3) than in mature leaves. The series of measurements shown in Fig. 7.3 was made on newly expanded leaves which apparently had not yet reached full photosynthetic capacity. In the control plant, the assimilation rates gradually increased with concomitant decrease in c_i, finally reaching characteristics similar to those of other plants grown under 50 mM NaCl and 12 mbar vpd

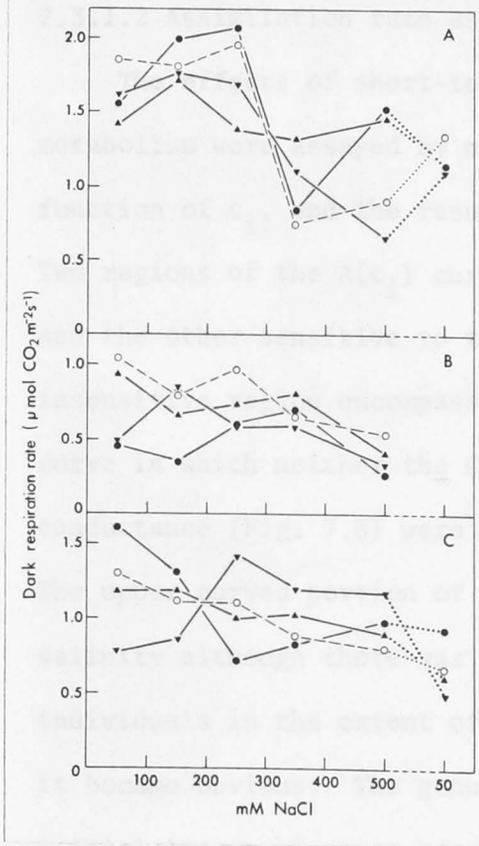


Fig. 7.4: Rates of dark respiration with transient changes in salinity in mature leaves of *Avicennia* (A) and *Aegiceras* (B) and in young leaves of *Aegiceras* (C). Symbols as in Fig. 7.1.

conditions in the previous long-term study (Chapter 6). Assimilation rates in the experimental plants changed very little, although c_i declined with increase in salinity from 50 to 500 mM NaCl, but both assimilation rates and c_i sharply increased upon return to 50 mM NaCl. Stomatal conductance decreased with increasing salinity, causing a reduction in the evaporation rate, and substantially recovered upon return to the original salinity.

The rates of dark respiration varied erratically (Fig. 7.4), showing no discernible effect of changing salinity in either *Avicennia* or *Aegiceras*. The rates in leaves of the former species typically were from 2 to 2.7 times greater than those measured in mature leaves of the latter species.

7.3.1.2 Assimilation rate as a function of c_i

The effects of short-term changes in salinity on photosynthetic metabolism were assayed by measuring the assimilation rate as a function of c_i, and the results are shown in Figs. 7.5, 7.6 and 7.7. Two regions of the $A(c_i)$ curves can be distinguished, one insensitive and the other sensitive to temporary changes in salinity. The insensitive region encompasses the lower, linear portion of the $A(c_i)$ curve in which neither the CO_2 compensation point nor the mesophyll conductance (Fig. 7.8) were affected appreciably by changing salinity. The upper curved portion of the curve was sensitive to changing salinity although there was considerable variability between individuals in the extent of the effect and in the salinity at which it became obvious. The general trend was for curvature from the initial linear slope to commence at progressively lower values of c_i with increments in salinity beyond some threshold level which ranged from approximately 150 to 250 mM NaCl. The net effect of these changes in the $A(c_i)$ curves was a lowering of the photosynthetic capacity with increasing salinity, and the effects were reversible.

7.3.1.3 Stomatal behaviour

Stomata, through their influence on c_i, may affect the expression of the aforementioned changes in photosynthetic metabolism on the assimilation rates observed under normal atmospheric conditions. The influence of stomata is shown by examining the gas exchange measurements made under a c_a of 330 $\mu l\ l^{-1}$ (Figs. 7.1 and 7.3) with respect to the shapes of the $A(c_i)$ curves (Figs. 7.5 and 7.7). Stomatal conductance was such that the operational c_i, i.e. that c_i obtained under normal atmospheric conditions, was in the region of transition

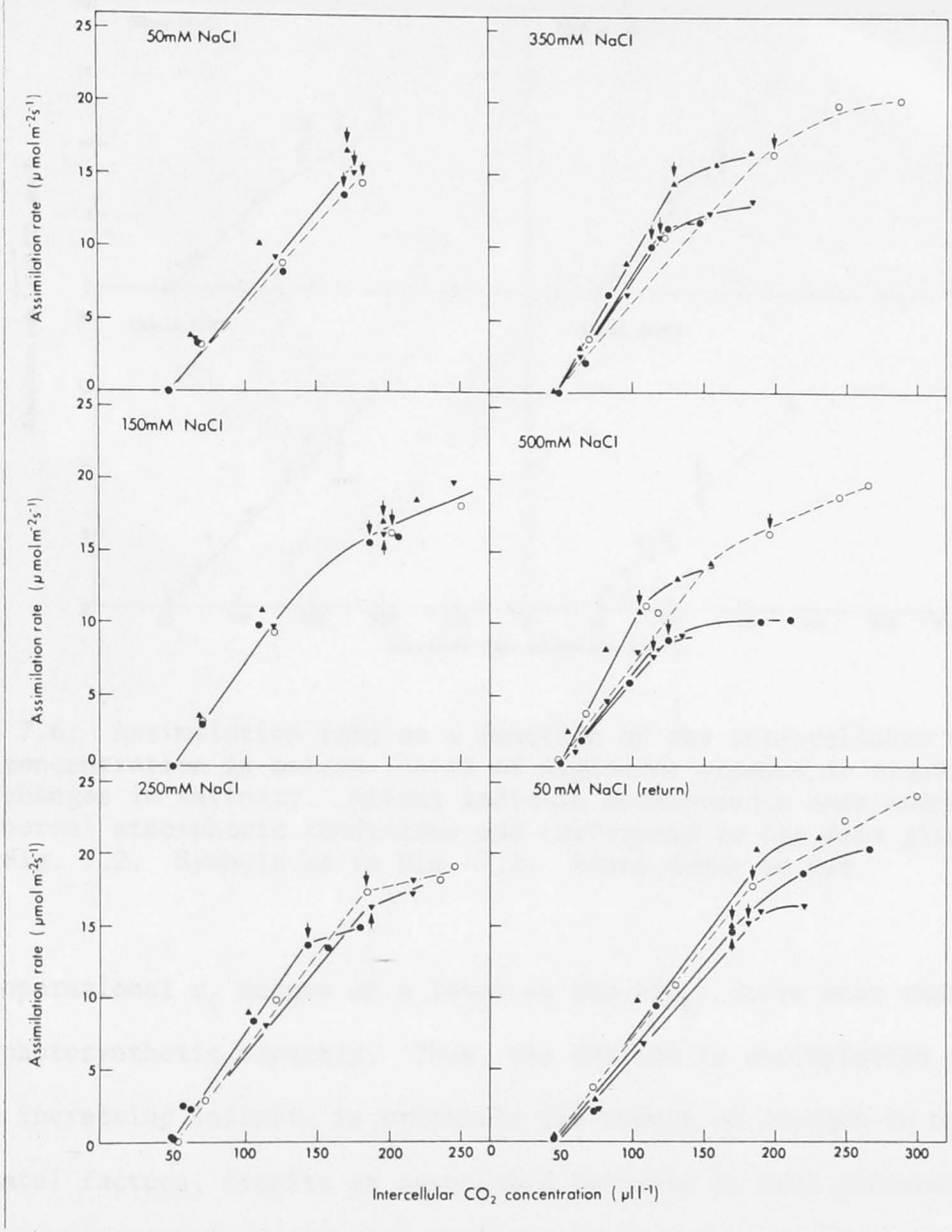


Fig. 7.5: Assimilation rate as a function of the intercellular CO_2 concentration in mature leaves of *Avicennia* in response to transient salinity conditions. Arrows indicate measurements made under normal atmospheric conditions and are the same measurements used in Fig. 7.1. Symbols as in Fig. 7.1. Lines drawn by eye.

between the lower, linear and upper, curved portion of the $A(c_i)$ curves. These points are indicated by arrows in Figs. 7.5 and 7.7, but the relationship of the operational points to the shape of the $A(c_i)$ curves is shown more clearly in Fig. 7.9. These plots show that

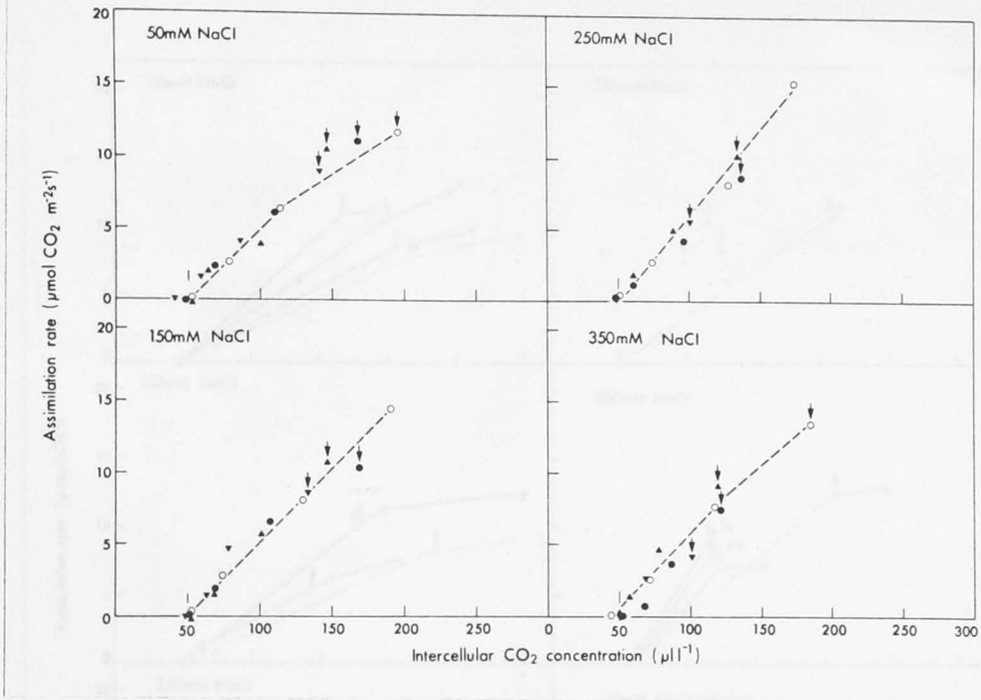


Fig. 7.6: Assimilation rate as a function of the intercellular CO_2 concentration in mature leaves of *Aegiceras* exposed to transient changes in salinity. Arrows indicate measurements made under normal atmospheric conditions and correspond to the data given in Fig. 7.2. Symbols as in Fig. 7.2. Lines drawn by eye.

the operational c_i occurs at a level on the $A(c_i)$ curve near that of the photosynthetic capacity. Thus, the decline in assimilation rates with increasing salinity is primarily the result of changes in non-stomatal factors, despite an associated decrease in both stomatal conductance and c_i.

7.3.1.4 Salt secretion

Rates of salt secretion varied during the experiment as shown in Fig. 7.10. The rates increased with time in the control plants. However, increase in the NaCl concentration of the nutrient solution initially had no substantial effects on the salt secretion rates, but they later changed at higher salinities and increased upon return to the original salinity.

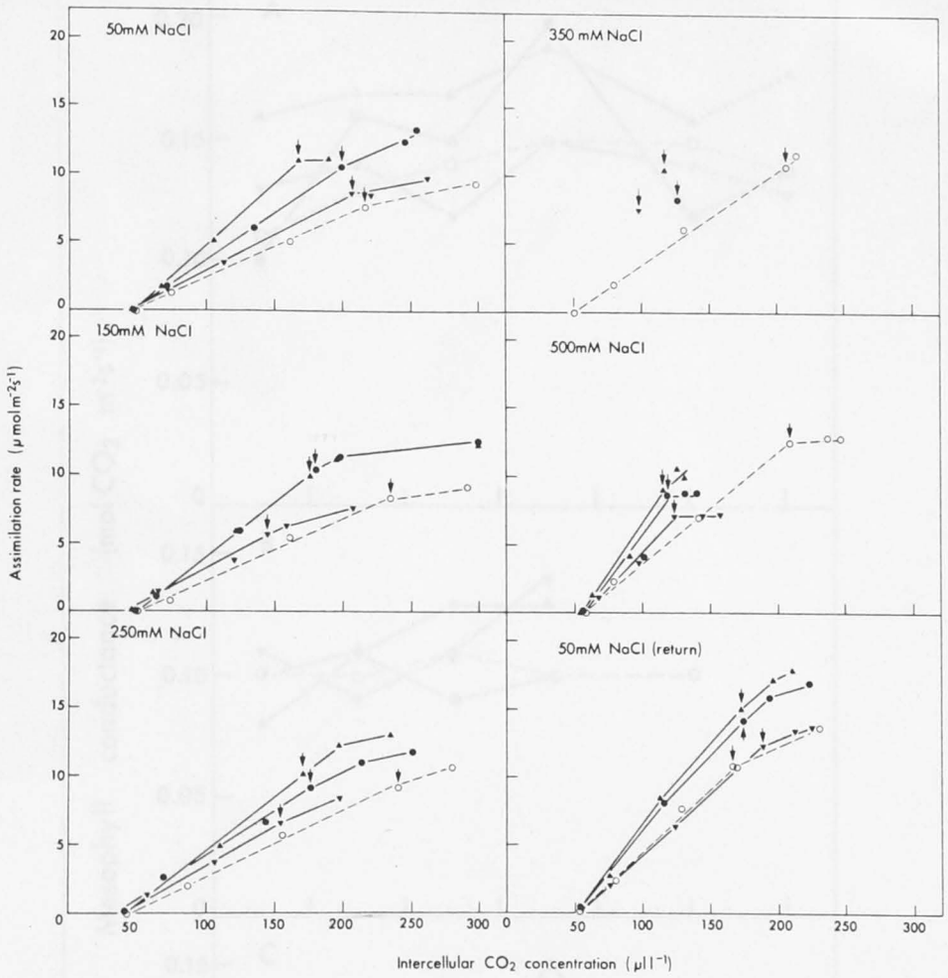


Fig. 7.7: Assimilation rate as a function of the intercellular CO_2 concentration in young leaves of *Aegiceras* exposed to transient levels of salinity. Arrows indicate measurements made under normal atmospheric conditions and correspond to the data shown in Fig. 7.3. Symbols as in Fig. 7.3. Lines drawn by eye.

7.3.2 Effect of Transient Changes in vpd

7.3.2.1 Assimilation rate as a function of c_i in *Avicennia*

Rapid and reversible changes in the relationship between assimilation rate and c_i were observed in individuals of *Avicennia* with variation in vpd. These responses are exemplified by those shown in Fig. 7.11 for two plants, one exposed for two hours to each vpd before measurement of the $A(c_i)$ characteristics under the same

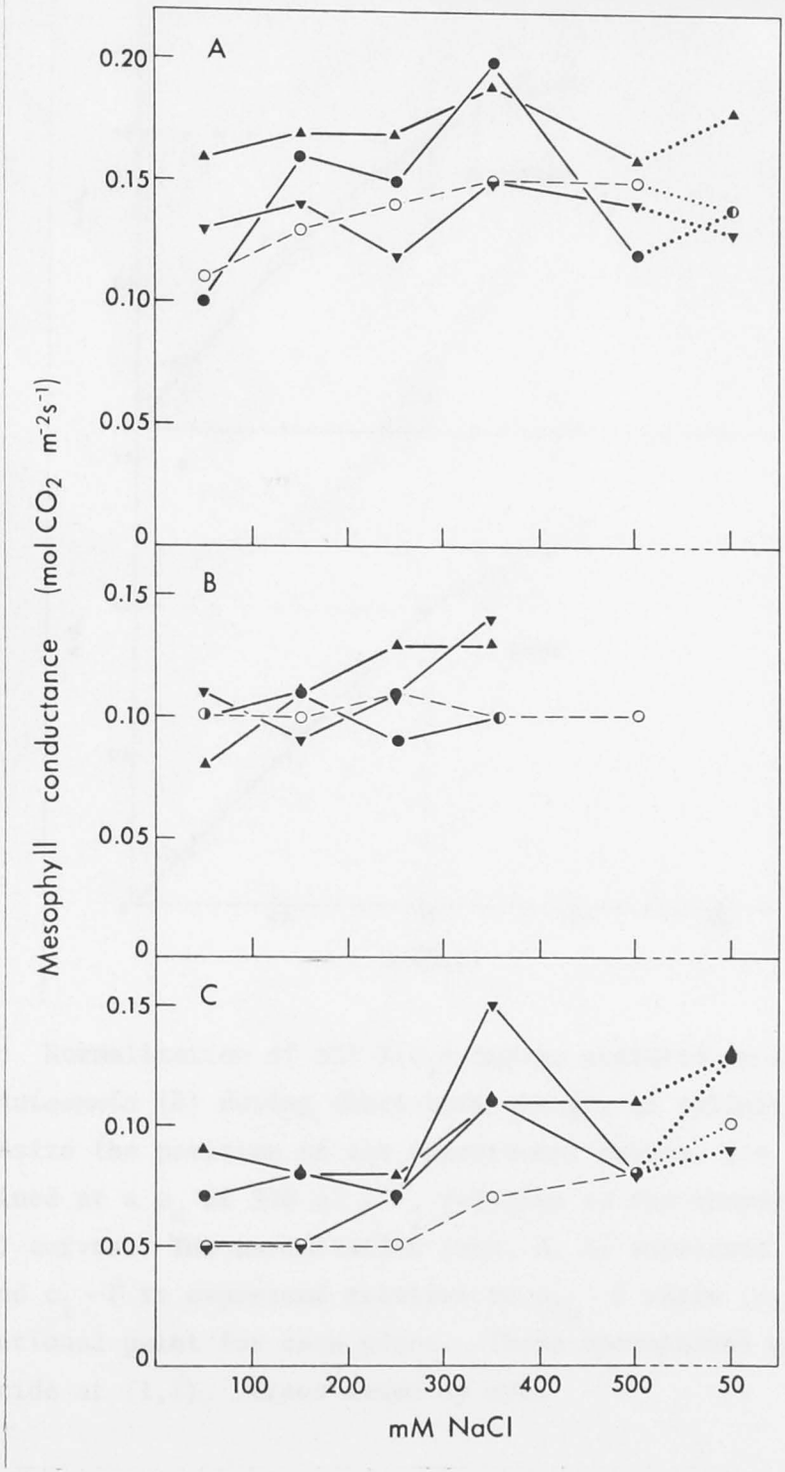


Fig. 7.8: Response of mesophyll conductance (i.e. the initial, linear slope of the $A(c_i)$ curve) to transient levels of salinity in mature leaves of *Avicennia* (A) and *Aegiceras* (B) and in young leaves of *Aegiceras* (C). These data were calculated from the results shown in Figs. 7.5, 7.6 and 7.7, respectively, and the symbols mean the same as in those graphs.

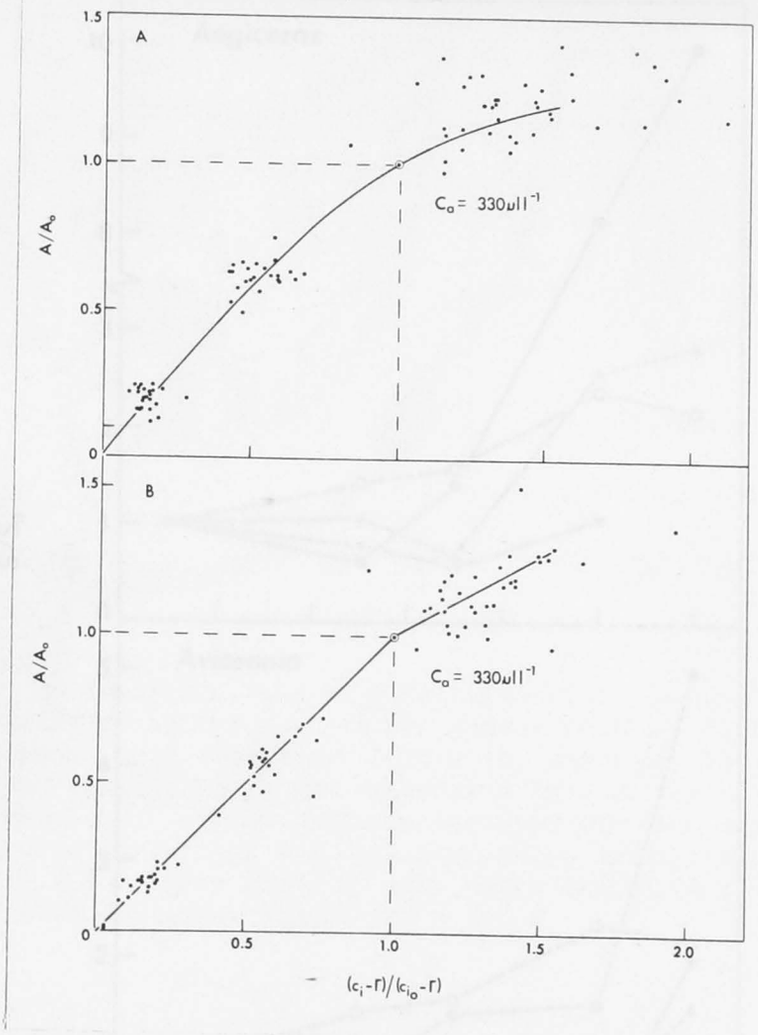


Fig. 7.9: Normalization of all $A(c_i)$ curves measured in *Aegiceras* (A) and *Avicennia* (B) during short-term changes in salinity to emphasize the position of the operational points, i.e. those obtained at a c_a of 330 $\mu l\ l^{-1}$, relative to the shapes of the $A(c_i)$ curves. The assimilation rate, A, is expressed relative to A_0 and $c_i - \Gamma$ is expressed relative to $c_{i_o} - \Gamma$ where (c_{i_o}, A_0) is the operational point for each plant. These operational points coincide at (1,1). Lines drawn by eye.

conditions, while the other received humidity pre-treatment of two days. These data show that *Avicennia* has the capability to respond to changes in vpd both above and below that experienced during growth, i.e. 12 mbar. Also the responses are enhanced by lengthening the exposure period.

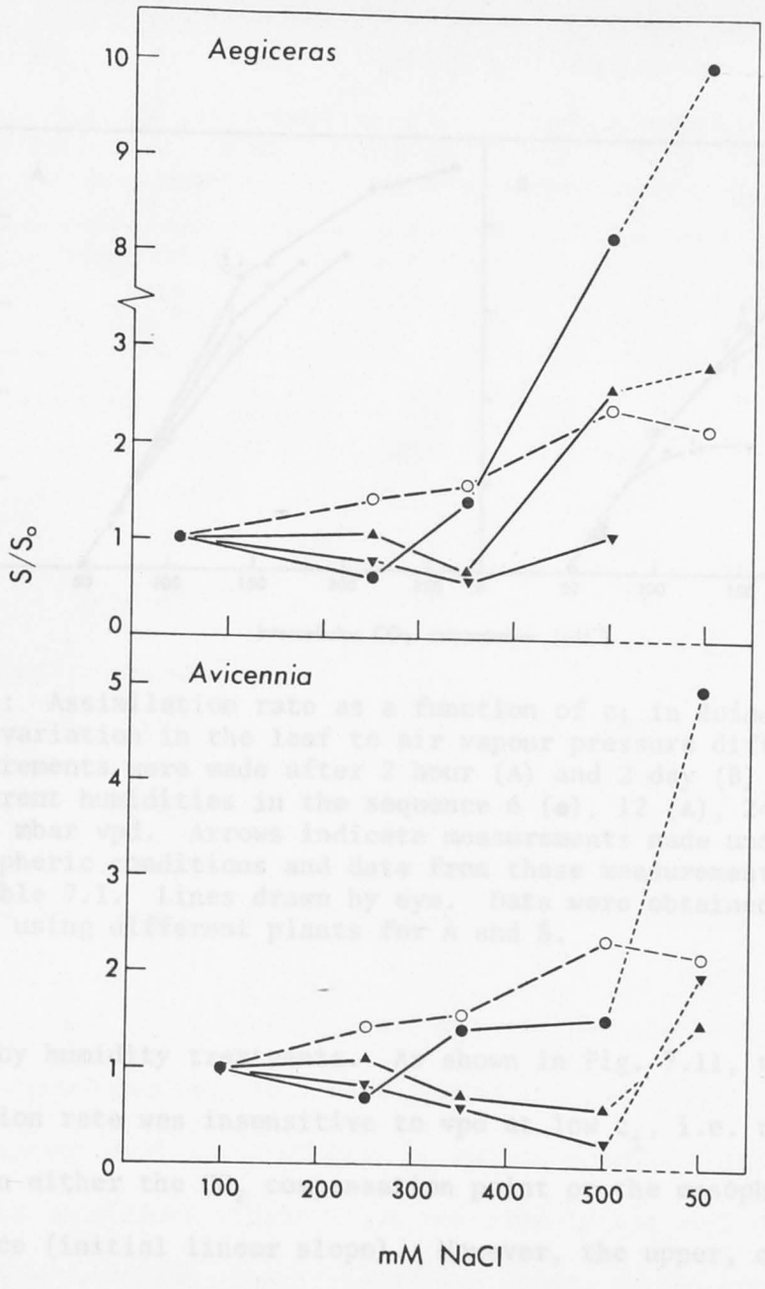


Fig. 7.10: Variation in salt secretion rates in *Aegiceras* and *Avicennia* with short-term changes in salinity. Salt secretion rates, S, are expressed relative to those measured at the start of the study, S_0. Data and symbols correspond to those of gas exchange measurements shown in Figs. 7.1 and 7.2.

Although there was considerable variability in the extent of the changes in the $A(c_i)$ curves between individuals, there were no differences in the way in which the gas exchange characteristics were

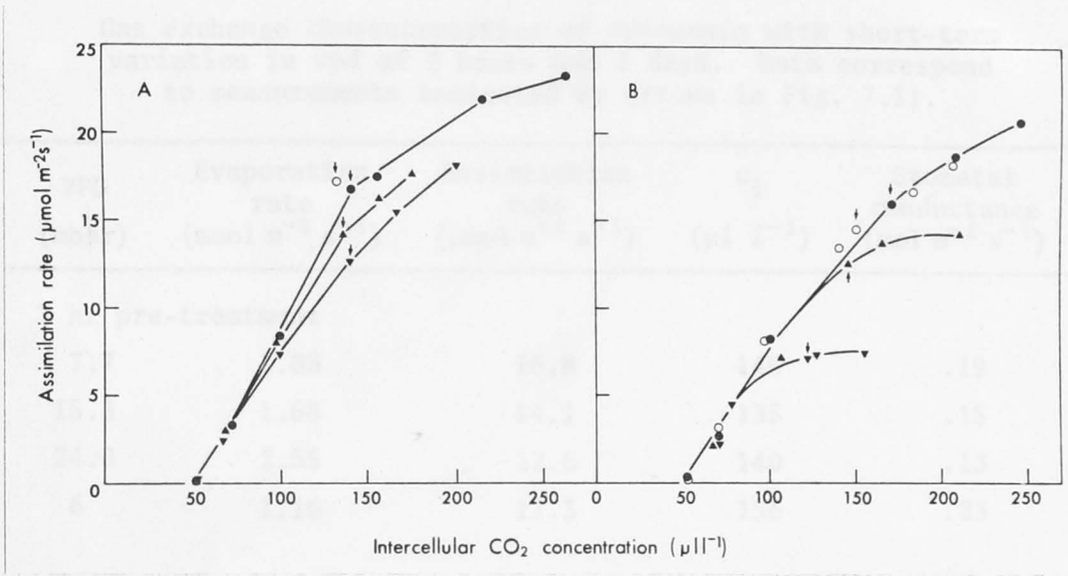


Fig. 7.11: Assimilation rate as a function of c_i in *Avicennia marina* with variation in the leaf to air vapour pressure difference (vpd). Measurements were made after 2 hour (A) and 2 day (B) exposures to different humidities in the sequence 6 (●), 12 (▲), 24 (▼) and 6 (○) mbar vpd. Arrows indicate measurements made under normal atmospheric conditions and data from these measurements are given in Table 7.1. Lines drawn by eye. Data were obtained from one leaf, using different plants for A and B.

affected by humidity treatments. As shown in Fig. 7.11, the assimilation rate was insensitive to vpd at low c_i, i.e. there were no affects on either the CO_2 compensation point or the mesophyll conductance (initial linear slope). However, the upper, curved portion of the $A(c_i)$ curve was sensitive to changes in vpd. Curvature from the initial, linear slope began at lower c_i with increasing vpd, thereby causing the assimilation rate to decline at high c_i. Thus, the photosynthetic capacity of *Avicennia* decreased with increase in vpd.

The gas exchange characteristics measured under normal atmospheric conditions ($c_a = 330\ \mu l\ l^{-1}$) with variation in humidity are summarized in Table 7.1. These data are a sub-set of the data shown

Table 7.1

Gas exchange characteristics of *Avicennia* with short-term variation in vpd of 2 hours and 2 days. Data correspond to measurements indicated by arrows in Fig. 7.11.

VPD (mbar)	Evaporation rate (mmol m^{-2} s^{-1})	Assimilation rate (μmol m^{-2} s^{-1})	c_i (μl l^{-1})	Stomatal conductance (mol m^{-2} s^{-1})
2 hr pre-treatment				
7.7	1.03	16.8	140	.19
15.3	1.68	14.1	135	.15
24.8	2.55	12.6	140	.13
6	1.16	17.3	156	.23
2 day pre-treatment				
6.5	1.03	16.0	170	.25
13.5	1.50	12.6	146	.15
26.0	2.02	7.1	122	.10
6	.67	14.7	149	.11

in Fig. 7.11 and it is in this context that they are best understood. Stomatal conductance declined with increasing vpd (Table 7.1) such that the operational c_i, i.e. that c_i obtained under normal atmospheric conditions (Table 7.1), occurred in the region of transition between the lower, linear and upper, curved portions of the $A(c_i)$ curves (Fig. 7.11). The operational c_i thereby coincided approximately with the photosynthetic capacity as shown in Fig. 7.11 but demonstrated more clearly, along with the data from all other similar measurements, in Fig. 7.12. Thus, stomatal conductance declined in the same sense as the photosynthetic capacity with increase in vpd, but the accompanying decrease in assimilation rate was due mainly to non-stomatal factors.

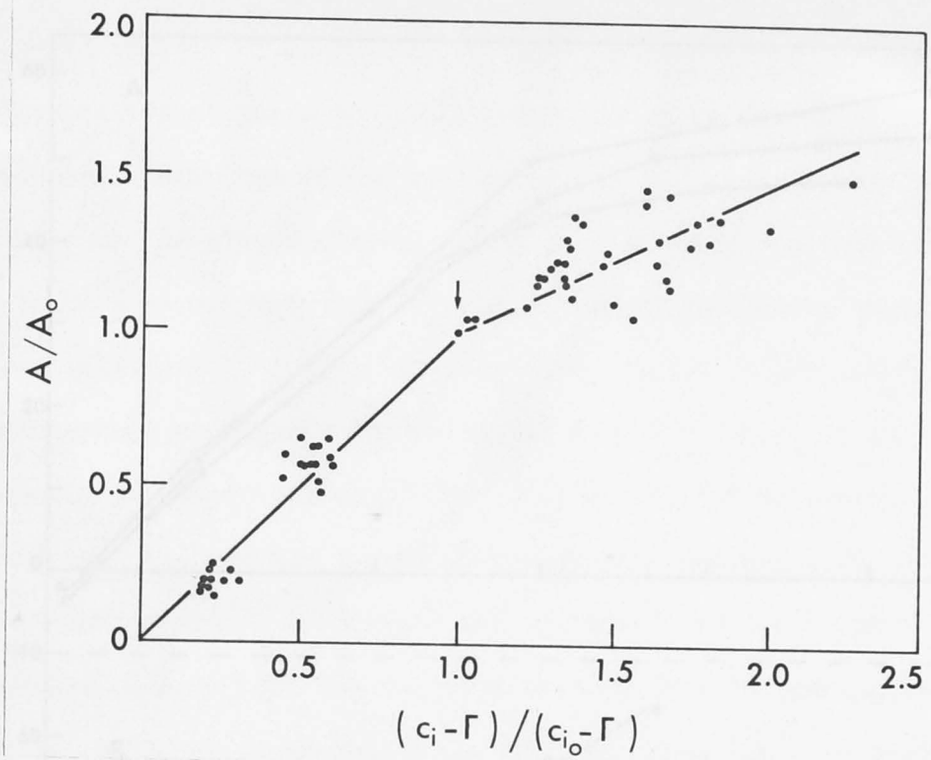


Fig. 7.12: Position of the operational point with respect to the shape of $A(c_i)$ curves in *Avicennia* exposed to short-term variations in vpd. Data from nine plants were normalized as described in Fig. 7.9. The operational point (1,1) is indicated by ↓.

7.3.2.2 Assimilation rate as a function of c_i in two glycophytes

It is tempting to attribute the decrease in photosynthetic capacity with increasing vpd in leaves of mangroves to increased inflow of salt to the leaves as a result of increased evaporation rates. To separate this possibility from the other factors associated with evaporation rates, similar measurements of $A(c_i)$ curves were made under varying vpd conditions in two glycophytes, *Xanthium strumarium* and *Gossypium hirsutum* in collaboration with Dr. Tom Sharkey. These species differ in their stomatal responses to humidity, the degree of stomatal closure in response to increasing vpd being such that the evaporation rate increases in *Xanthium* but decreases in *Gossypium*.

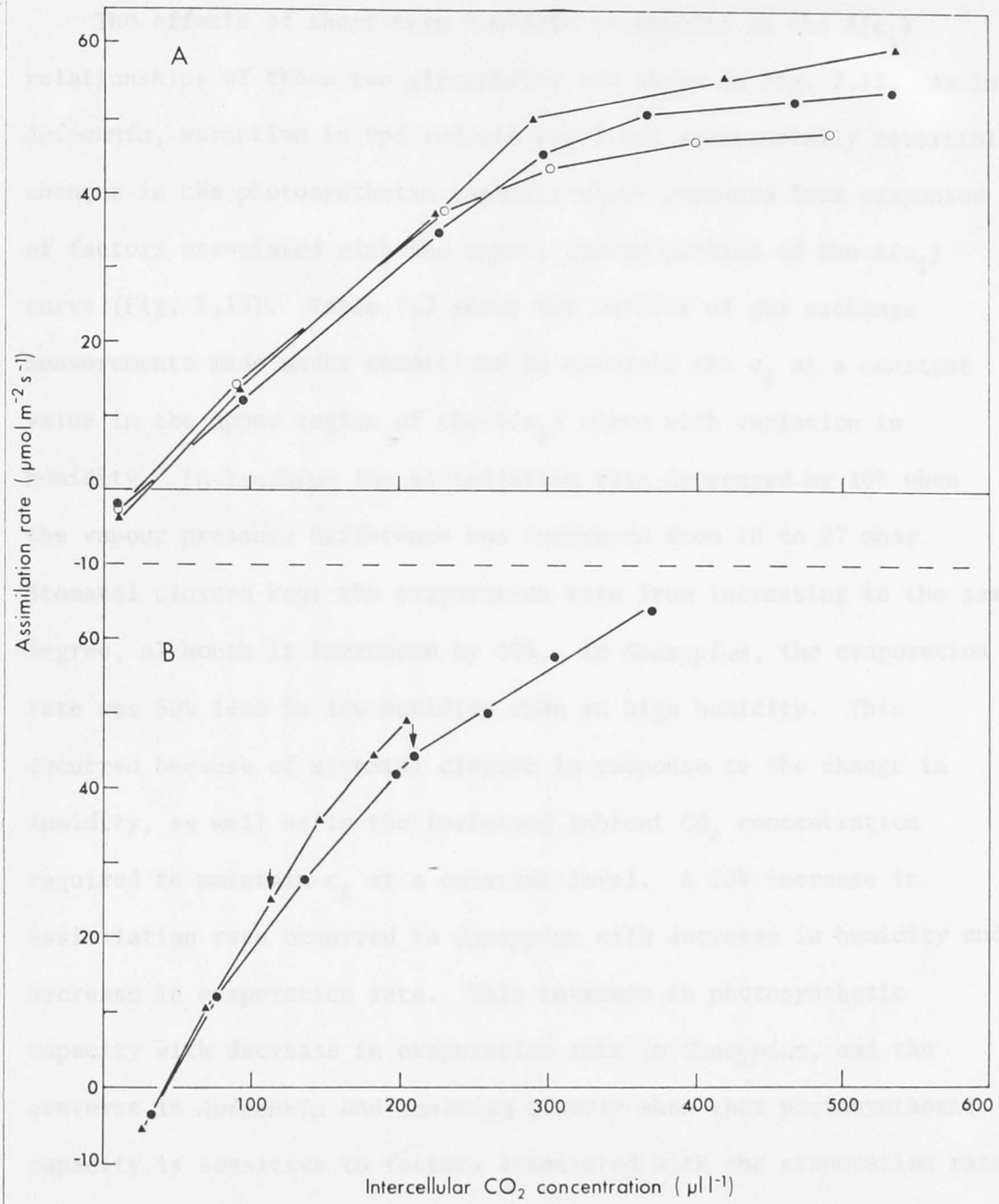


Fig. 7.13: Assimilation rate as a function of c_i with short-term variation in vpd in two glycophytes, *Xanthium strumarium* (A) and *Gossypium hirsutum* (B). Arrows indicate measurements made at a c_a of 330 $\mu l\ l^{-1}$. Humidity treatments were imposed according to the sequence 17 (●), 6.5 (▲) and 17 mbar vpd (○) in *Xanthium* (A) and 15 (●) followed by 30 mbar vpd (▲) in *Gossypium* (B). Quantum flux density was 1500 $\mu E\ m^{-2}\ s^{-1}$. Leaf temperature varied from 22-24 C in *Xanthium* and from 27-28 C in *Gossypium*.

The effects of short-term humidity treatments on the $A(c_i)$ relationships of these two glycophytes are shown in Fig. 7.13. As in *Avicennia*, variation in vpd induced rapid and substantially reversible changes in the photosynthetic capacity which resulted from responses of factors associated with the upper, curved portion of the $A(c_i)$ curve (Fig. 7.13). Table 7.2 shows the results of gas exchange measurements made under conditions to maintain the c_i at a constant value in the upper region of the $A(c_i)$ curve with variation in humidity. In *Xanthium* the assimilation rate decreased by 10% when the vapour pressure difference was increased from 10 to 27 mbar. Stomatal closure kept the evaporation rate from increasing to the same degree, although it increased by 60%. In *Gossypium*, the evaporation rate was 50% less in low humidity than in high humidity. This occurred because of stomatal closure in response to the change in humidity, as well as to the increased ambient CO_2 concentration required to maintain c_i at a constant level. A 10% increase in assimilation rate occurred in *Gossypium* with decrease in humidity and decrease in evaporation rate. This increase in photosynthetic capacity with decrease in evaporation rate in *Gossypium*, and the converse in *Avicennia* and *Xanthium* clearly show that photosynthetic capacity is sensitive to factors associated with the evaporation rate and that it is not a response peculiar to halophytes.

As in *Avicennia*, stomatal conductance and photosynthetic capacity in *Xanthium* changed in the same sense in response to changes in the evaporation rate. These responses were such that the operational c_i occurred in the transition between the lower, linear and upper curved portions of the $A(c_i)$ curve and hence the assimilation rate was

Table 7.2

Gas exchange characteristics of *Xanthium* and *Gossypium* with short-term variation in vpd. Measurements were made under conditions to maintain the c_i at a constant level. Other conditions were a quantum flux density of 1500 $\mu E\ m^{-2}\ s^{-1}$ and leaf temperatures of 23 C for *Xanthium* and 27 C for *Gossypium*.

Genus	VPD (mbar)	Evaporation rate ($mmol\ m^{-2}\ s^{-1}$)	Assimilation rate ($\mu mol\ m^{-2}\ s^{-1}$)	c_i ($\mu l\ l^{-1}$)	Stomatal conductance ($mol\ m^{-2}\ s^{-1}$)
Xanthium	(45 min between first and second point)				
	10	10.0	69.5	402	.97
	27	16.0	63.6	398	.57
	12	7.2	66.0	381	.60
*Gossypium**	(4 hr between measurements)				
	15	9.0	44.0	208	.56
	28	4.5	48.0	206	.16

* Data from Fig. 7.13B.

limited largely by the photosynthetic capacity (Fig. 7.13A). However, in *Gossypium*, the photosynthetic capacity increased with decrease in the evaporation rate, due to stomatal closure at low humidity. This increase in photosynthetic capacity was not manifest in the assimilation rate under normal atmospheric conditions because stomatal closure restricted the diffusion of CO_2, thereby causing the operational c_i to occur well down in the lower, linear region of the $A(c_i)$ curve (Fig. 7.13B). Thus the decline in the assimilation rate in *Gossypium* with increase in vpd could be attributed to stomatal limitation to gaseous CO_2 diffusion.

7.4 DISCUSSION

Rapid and reversible changes in the photosynthetic capacities of both *Avicennia* and *Aegiceras* were induced by short-term variations in salinity. The photosynthetic capacities declined with increasing salinity as shown by changes in the shapes of the $A(c_i)$ curves (Figs. 7.5, 7.6 and 7.7). This decline in photosynthetic capacity was due only to a decrease in the level of the upper portion of the $A(c_i)$ curve such that the assimilation rates declined at high c_i, but were unaffected at low c_i (Figs. 7.5, 7.6 and 7.7). These results contrast with those obtained from plants receiving long-term salinity treatments in which mesophyll conductance of *Aegiceras*, *Avicennia* (Chapter 6) and other halophytes [Gale and Poljakoff-Mayber, 1970; Downton, 1977; Longstreth and Strain, 1977; De Jong, 1978b; Longstreth and Nobel, 1979] decreased with increasing salinity.

These temporary changes in photosynthetic metabolism may be the product of several interacting processes. Under steady-state

conditions, the rates of NaCl secretion in both *Aegiceras* and *Avicennia* were proportional roughly to the NaCl concentration experienced at the roots (Table 5.8). However, in the present study, rates of salt secretion were not changed substantially by transient increases in the NaCl concentration at the roots except at the highest salinity, although they then increased upon return to the original NaCl concentration (Fig. 7.10). Since exclusion at the roots is believed to be a passive filtration process [Scholander, 1968], and since secretion rates are proportional to salinities of the root environment in the long-term, but not in the short-term, it appears likely that transient salinity changes produces a disruption in internal ion levels which interferes, directly or indirectly, with photosynthetic metabolism.

Mature leaves of *Aegiceras* were more sensitive to transient changes in salinity than those of *Avicennia* and this may be related to some of the physiological differences found in previous studies. *Aegiceras* may suffer greater ion stress during short-term increases in salinity because it has a lower apparent capacity for ion exclusion at the roots (Table 5.8) and for K^+ uptake (Table 6.1) than *Avicennia*. Osmotic adjustment may also take place more slowly in *Aegiceras* because the differences between Na^+, K^+ and Cl^- concentration between mature leaves and the root environment diminish with increasing salinity at a greater rate than in *Avicennia* (Table 6.2), so that additional osmotica when needed by *Aegiceras* must come from other sources.

The sensitivity of photosynthetic metabolism to salinity in *Aegiceras* appears to vary with the developmental status of the leaves

with mature leaves being more sensitive than young leaves as suggested by comparison of Figs. 7.2 and 7.3. As an aside, gas exchange characteristics were measured on leaves that had reached maturity at 50 mM NaCl three months after the plants had been transferred gradually to 500 mM NaCl and the results are shown in Table 7.3. The gas exchange characteristics in these leaves were intermediate between those of leaves which had only experienced salinities of 50 and 500 mM NaCl (Tables 5.5 and 6.3). These data suggest that leaves of *Aegiceras* grown at low salinity can adjust to high salinity with some loss of photosynthetic capacity, but that growth at high salinity causes a greater impairment of photosynthetic capacity.

The photosynthetic capacity of *Avicennia* and two glycophytes declined with increase in evaporation rates due to short-term changes in vpd. The decline in photosynthetic capacity was due to decrease in the level of the upper, curved portion of the $A(c_i)$ curve, indicating an increase in intrinsic limitations to the assimilation rate at high c_i. These results are similar to those obtained in *Aegiceras* and *Avicennia* grown under long-term humidity treatments (Chapter 6). The occurrence of evaporation-dependent effects on the photosynthetic capacities of the glycophytes, *Xanthium* and *Gossypium* shows that this response is neither peculiar to mangroves nor halophytes, but that it is probably a widespread phenomenon related by a common factor, possibly leaf water potential. The decline in photosynthetic capacity could be the result of solute accumulation or local depression of the leaf water potential in the vicinity of evaporation sites within the leaf [Oertli, 1968]. Conversely, the increase in photosynthetic capacity accompanying a reduction in evaporation rate could result from an increase in leaf water content.

Table 7.3

Gas exchange characteristics of leaves of *Aegiceras* following gradual increase in the salinity of the nutrient solution from 50 to 500 mM NaCl. The leaves had developed fully during growth in the original salinity before transfer to the final salinity. Measurements were made under conditions similar to those experienced during growth, i.e. leaf temperature 25 C, quantum flux density 500 μE m^{-2} s^{-1}, vpd 12 mbar.

Parameter	mean ± SD, n = 6
Assimilation rate, μmol m^{-2} s^{-1}	8.9 ± 1.1
Stomatal conductance, mmol m^{-2} s^{-1}	113 ± 26
Intercellular CO_2 concentration, μl l^{-1}	163 ± 26
Evaporation rate, mmol m^{-2} s^{-1}	1.27 ± 0.19
CO_2 compensation point, μl l^{-1}	52 ± 4
Mesophyll conductance, mol CO_2 m^{-2} s^{-1} (linear regression of pooled data)	0.07, regression coefficient (r^2) = 0.86

A recent model relating gas exchange characteristics and photosynthetic biochemistry provides a useful conceptual framework for the interpretation of $A(c_i)$ curves [Farquhar *et al.*, 1980; Farquhar and von Caemmerer, in press; von Caemmerer and Farquhar, in press]. According to their interpretation, the insensitivity of the lower, linear portion of the $A(c_i)$ curve to short-term changes in salinity and evaporation rates suggests that these treatments did not affect the activity of RuBP carboxylase. However, the decline in the upper level of the $A(c_i)$ curve with increasing salinity and evaporation rates shows that these treatments caused an increase in intrinsic limitations to the carboxylation rate, possibly via effects on the rate of RuBP regeneration. It follows then that these insensitive and sensitive processes, respectively, co-limit the assimilation rate when the operational c_i occurs in the transition between the lower, linear

and upper curved portions of the $A(c_i)$ curve as occurred with short-term increases in salinity in *Aegiceras* and *Avicennia* and with short-term increase in evaporation rate in *Avicennia* and *Xanthium*.

However, the operational c_i also decreased with short-term increase in salinity in both *Aegiceras* and *Avicennia*. Thus a greater proportion of the assimilate would be expected to flow through the photorespiratory pathway with increasing stress because of changes in the ratio between internal O_2 and CO_2 concentrations which are, respectively, competitive inhibitors of the carboxylase and oxygenase function of RuBP carboxylase-oxygenase [Badger and Collatz, 1977; Laing *et al.*, 1974]. This interpretation of the $A(c_i)$ curve from the model of Farquhar *et al.* [1980], Farquhar and von Caemmerer [in press] and von Caemmerer and Farquhar [in press] agrees with observations of a greater proportion of ^{14}C label occurring in the photorespiratory intermediates of leaves exposed to rapid water stress [Lawlor and Fock, 1975; Lawlor, 1976; Lawlor and Fock, 1977], a treatment in which c_i is commonly observed to decline because of decrease in stomatal conductance [Hall *et al.*, 1976; Cowan, 1977; Ludlow, 1980]. Thus, changes in c_i can effect temporary changes in metabolic balances which are distinct from pathological disorders.

Stomatal conductance generally is considered to be the major factor limiting the assimilation rate when changes in stomatal conductance can account fully for the changes in c_i and the relationship between the assimilation rate and c_i remains unchanged. According to these criteria, the decline in assimilation rates in *Aegiceras* and *Avicennia* in response to increasing salinity and vpd could be attributed entirely to decrease in stomatal conductance as

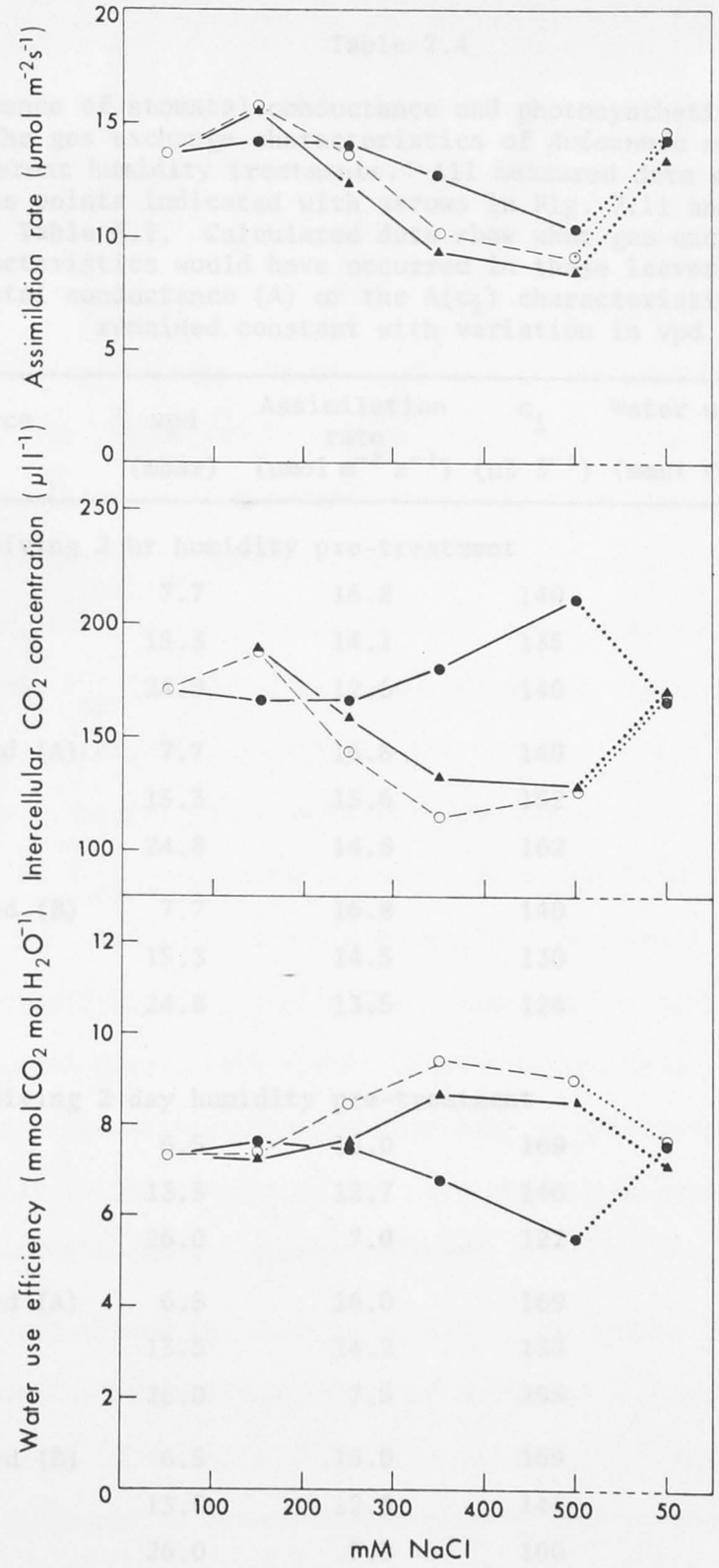


Fig. 7.14: Influence of stomatal conductance and photosynthetic capacity on the gas exchange characteristics of *Avicennia* in response to short-term changes in salinity. All calculations are from the $A(c_i)$ data of the leaf denoted (●) in Figs. 7.1 and 7.5. Symbols are actual measured data (○) and the gas exchange characteristics which would have occurred in the leaf if stomatal conductance (▲) or the $A(c_i)$ characteristics (●) were to remain unchanged with variation in salinity.

Table 7.4

Influence of stomatal conductance and photosynthetic capacity on the gas exchange characteristics of *Avicennia* exposed to different humidity treatments. All measured data correspond to the points indicated with arrows in Fig. 7.11 and given in Table 7.1. Calculated data show what gas exchange characteristics would have occurred in these leaves if either stomatal conductance (A) or the $A(c_i)$ characteristics (B) had remained constant with variation in vpd.

Data source	vpd (mbar)	Assimilation rate (μmol m^{-2} s^{-1})	c_i (μl l^{-1})	Water use efficiency (mmol CO_2 mol H_2O^{-1})
Leaf receiving 2 hr humidity pre-treatment				
Measured	7.7	16.8	140	16.3
	15.3	14.1	135	8.4
	24.8	12.6	140	4.9
Calculated (A)	7.7	16.8	140	16.3
	15.3	15.6	152	7.5
	24.8	14.8	162	4.4
Calculated (B)	7.7	16.8	140	16.3
	15.3	14.5	130	8.6
	24.8	13.5	124	5.3
Leaf receiving 2 day humidity pre-treatment				
Measured	6.5	16.0	169	15.5
	13.5	12.7	146	8.5
	26.0	7.0	122	4.8
Calculated (A)	6.5	16.0	169	15.5
	13.5	14.2	188	6.6
	26.0	7.5	255	1.8
Calculated (B)	6.5	16.0	169	15.5
	13.5	12.8	144	8.5
	26.0	7.8	100	5.4

shown in calculations for *Avicennia* in Fig. 7.14 and Table 7.4. However, these calculations also show that the assimilation rates of *Avicennia* would have declined in response to increasing salinity and vpd in the absence of any change in stomatal conductance (Fig. 7.14 and Table 7.4).

A method to estimate the relative contribution of stomatal and biochemical limitations to the assimilation rate using $A(c_i)$ curves has been suggested by Sharkey and co-workers [unpublished] and is discussed in detail in Farquhar and Sharkey [in press]. According to this method, the photosynthetic capacity is the maximum rate of assimilation, A_{max}, achieved under conditions at which stomatal conductance is infinite, i.e. c_i is limited only by the boundary layer conductance. The change in photosynthetic capacity is shown by comparison of A_{max} of a control leaf or of a leaf before treatment with that of a leaf receiving a treatment. The stomatal limitation is shown by comparison of A_{max} with the assimilation rate occurring at the operational point, both values being obtained from the same $A(c_i)$ curve because stomatal limitations can only be considered realistically in the context of how they affect the expression of a specific set of metabolic characteristics.

The above method was used to calculate the extent of stomatal influence on the assimilation rates of *Avicennia* subjected to short-term variations in salinity (Fig. 7.5) and humidity (Fig. 7.11B). It was often difficult to obtain a sufficiently high c_i to measure A_{max} because of stomatal closure in response to high CO_2 levels. Thus, only those $A(c_i)$ curves in which the upper level could be measured to obtain A_{max} adequately by extrapolation were considered in these

calculations. The results showed that the limitations to the assimilation rates due to decrease in stomatal conductance decreased from 50 to 21% of the total limitation with increase in salinity from 250 to 500 mM NaCl and decreased from 19 to 4% of the total limitation with increase in vpd from 12 to 24 mbar (2 day pre-treatments). Similar values would be expected from other measurements as shown by the general relationship between the operational points and the photosynthetic capacity with short-term stress in both *Aegiceras* and *Avicennia* (Figs. 7.9 and 7.12). Thus, the assimilation rates in these species were limited largely by non-stomatal factors, and the degree of limitation due to stomatal restriction of gaseous CO_2 diffusion decreased with increasing stress.

The main role of stomata was to minimize adverse effects of short-term stress on the water use efficiency (WUE) as shown in Fig. 7.14 and Table 7.4. The decline in stomatal conductance had the effect of increasing WUE which otherwise would have decreased with increase in salinity (Fig. 7.14) and the effect of reducing the decrease in WUE with increasing vpd (Table 7.4). In both cases, the stomatal behaviour was optimal as shown by the consistent occurrence of the operational c_i in the transition zone between the lower linear and upper curved portions of the $A(c_i)$ curves (Figs. 7.9 and 7.12). Under these circumstances, carbon gain is maximum relative to water loss for a particular set of metabolic characteristics [von Caemmerer and Farquhar, in press].

The results of the present study show that rapid and reversible variation in photosynthetic capacity can be a dominant influence on the change in assimilation rate in response to short-term variation in salinity and humidity.

CHAPTER 8

INTEGRATION AND SPECULATION

Mangrove swamps of temperate Australia are floristically simple [Saenger *et al.*, 1977] and only two mangove species, *Aegiceras corniculatum* and *Avicennia marina*, occur in the Cullendulla Creek swamp of the present study (Chapter 1). Here, *Aegiceras* occurs mainly along creek margins where the salinities may fluctuate from about 75 to 100% seawater. *Avicennia*, which is the dominant species, occupies all areas of the swamp. Its morphology varies enormously at different locations in the swamp, ranging from well formed trees along creek margins to stunted shrubs in hypersaline areas. Differences in the physiological attributes of these species are important in determining their location and relative success in different areas of the swamp. In the following discussion, some of these attributes are examined to see how they might relate to the mechanisms underlying community dynamics in the Cullendulla Creek swamp system.

Propagules of *Aegiceras* and *Avicennia* differ in several physiological characteristics which may influence recruitment of seedlings along a salinity gradient (Chapter 2). First, the *Avicennia* propagule is more anatomically complex than *Aegiceras* which may contribute to the more rapid development of the former into an autotrophic seedling. Second, *Avicennia* absorbs water more rapidly and appears to have a lower threshold water content needed to initiate the redistribution

of reserves. Third, the photosynthetic properties of the first leaf pair of *Avicennia* were not substantially influenced by salinity over the range from 10 to 100% seawater, whereas the photosynthetic capacity of the first leaf pair in *Aegiceras* declined with increasing salinity. Fourth, differences between *Aegiceras* and *Avicennia* in requirements for K^+ and in the capacity to satisfy those needs may contribute to the greater sensitivity of the former to salinity.

Effects of high salinity on growth and development of propagules may be a major factor limiting the distribution of *Aegiceras* in saline wetlands. Propagules develop maximally under low salinity conditions whereas development was rare in undiluted seawater (ie. an average of six fully developed seedlings per 100 propagules). The delay in the onset of development during exposure to high salinities causes the propagule to remain quiescent, enhancing the probability that it may become stranded in areas of more favourable salinity. These results may at least partially explain the low density of *Aegiceras* seedlings in the primarily maritime swamp along Cullendulla Creek.

On the other hand, *Avicennia* is well adapted for rapid establishment and development over a wide range of salinities. The development of the seedling to at least the 2-4 leaf stage occurs largely through the redistribution of cotyledonary reserves. While this process is enhanced in 50% seawater, the effects of 10 and 100% seawater are not sufficient to limit seedling establishment. These results probably explain the widespread occurrence of *Avicennia* seedlings of at least the 2-4 leaf stage of development throughout the Cullendulla Creek swamp system, even in areas which are obviously unsuitable for further growth (ie. permanently submerged in the creek) and showing no preferences for exposed or shaded conditions.

Once the reserves are depleted, the potential for growth will depend largely on competition and on the physical factors affecting carbon gain. The Cullendulla Creek swamp is located near the southern limit of distribution for *Avicennia* [Saenger *et al.*, 1977]. Leaf temperature might be expected to be a major factor limiting photosynthesis under field conditions as was found by Attiwill and Clough [1980] in a study of *Avicennia* in another temperate swamp.

Avicennia marina is an evergreen species, the leaves having a life span of approximately two years, and hence it might be expected to undergo seasonal changes in the photosynthetic responses to temperature (Chapter 3). However, there was no evidence of seasonal acclimitisation of the temperature optimum for assimilation rates in either exposed or shaded leaves. The temperature optimum was not focused sharply, with little variation in the maximum light saturated rates of assimilation over the range from 20 to 30C, and in some plants from 5ϕ to 30C. However, the photosynthetic capacity of exposed leaves fluctuated seasonally with minimum values occurring during winter. This fluctuation was superimposed on a general decline in photosynthetic capacity with age similar to that of shaded leaves. This seasonal fluctuation in exposed leaves may result from an interaction between temperature and light intensity, and may contribute to the greater longevity of suppressed seedlings under shaded conditions.

Changes in the assimilation rates with variation in leaf temperature were due mainly to responses of the photosynthetic metabolism except at the highest temperatures at which stomatal conductance was co-limiting. Photosynthetic capacity, at least that obtained at a physiologically significant c_i such as 200 $\mu l\ l^{-1}$, was

maximal at 25C, with the decline at higher temperatures resulting mainly from the decline in mesophyll conductance. At high temperature, stomatal closure, whether in direct response to leaf temperature or to the increase in vpd accompanying increase in leaf temperature, may further limit the assimilation rate by reducing the c_i.

On the assumption that laboratory measurements can be extrapolated to the field, leaf temperature is a major factor limiting the assimilation rates of exposed leaves of *Avicennia*. In the summer, the leaf temperatures usually are within the range at which assimilation rates are maximum. This also occurred in winter if the leaves received high quantum flux density. However, the leaf temperatures during periods of high insolation average from two to six degrees warmer than air temperature, and can become as much as ten degrees warmer on still days. This has the effect of making the leaf microclimate considerably more arid than might be expected in a coastal swamp and, because the stomata are sensitive to vpd, this may cause the assimilation rates to be much less than those measured in the laboratory.

In contrast to exposed leaves, assimilation rates of shaded leaves were more likely to be limited by the low quantum flux densities characteristic of this habitat (Chapter 4). The gas exchange characteristics of leaves from understory shade did not differ substantially from those of exposed leaves. Thus leaves in understory shade might be able to sustain very low rates of assimilation during shaded periods when quantum flux densities typically were 100 $\mu E\ m^{-2}\ s^{-1}$ or less. Adaptation to high light conditions may enable shaded leaves to utilise periodic high intensity sunflecks without damage to the

photosystems [Powles and Critchley, 1980]. Although this may contribute to survival under shaded conditions, it is doubtful that carbon gains in an understory environment would be sufficient to support growth because these shaded leaves failed to develop lower light compensation points or rates of dark respiration than exposed leaves. These results suggest that light may be a factor limiting growth under shaded conditions, possibly explaining the general absence of saplings in shaded environments in Cullendulla Creek. The remaining discussion will therefore be concerned with autotrophic performance in exposed habitats.

Salinity is a major factor influencing seedling establishment and development from propagules, as previously discussed, and might be expected to also influence autotrophic growth. Under field conditions, seedlings may experience variations in salinity over different time scales. There are long-term ranges of salinity which may characterise a habitat or zone and there are short-term changes, such as those which might occur during tidal cycles or periods of rainfall.

Under steady state conditions of salinity and humidity, the relative growth rates of both *Aegiceras* and *Avicennia* declined with increasing salinity but were not noticeably affected by humidity (Chapter 5). *Aegiceras* had a higher relative growth rate at low salinity than *Avicennia*, but the former was more sensitive to increasing salinity than the latter. Differences in relative growth rates were due primarily to differences in carbon allocation and gas exchange characteristics.

In contrast to *Avicennia*, *Aegiceras* consistently invested a greater proportion of assimilation in shoots than in roots. This caused

the leaf area/plant mass ratio to be greater in *Aegiceras* than in *Avicennia*. This ratio remained relatively constant in both species with increasing salinity and vpd. Therefore, decline in net assimilation rates in response to these treatments was due mainly to changes in the gas exchange characteristics. The relative growth rates were well correlated with the net assimilation rates, indicating that the effects of salinity and vpd on the growth of *Aegiceras* and *Avicennia* could be accounted for directly by changes in the assimilation rates.

At low salinities, both *Aegiceras* and *Avicennia* had the same assimilation rates. However, the relative growth rate of *Aegiceras* was greater than that of *Avicennia* because the former species has a greater leaf area/plant mass ratio, and hence expends a smaller proportion of the carbon gain on respiration. The relative growth rate of *Aegiceras* was more affected by salinity than that of *Avicennia*, because the assimilation rate of the former declined a greater rate with increasing salinity than the latter.

These results suggest a way in which different strategies of carbon allocation associated with different degrees of salt tolerance could influence the relative competitive abilities of two sympatric mangrove species. Maintenance of a higher root mass/leaf area ratio in *Avicennia* than in *Aegiceras* appears to be related to a greater capacity for salt exclusion at the roots in the former species. This is probably not advantageous in a brackish environment because the "cost" of maintaining an extensive root system is large relative to that of maintaining favourable internal salt levels by secretion. Hence, a strategy which maximised photosynthetic capacity would be favoured over one which maximised salt exclusion under brackish conditions. This may partially explain the characteristic dominance of *Aegiceras* in brackish environments [Clarke and Hannon, 1970].

The maintenance of a higher capacity for salt exclusion may enable *Avicennia* to retain a relatively stable, albeit slow growth rate over a wide range of salinities. This may allow *Avicennia* to exploit highly saline environments or habitats subject to transient periods of hypersalinity in which competition from other species would be minimal. Thus despite showing maximum growth under slightly brackish conditions, the adaptations which enable *Avicennia* to tolerate highly saline conditions appear to exclude it from being an effective competitor at low salinities. This may partially explain the characteristic dominance of *Avicennia* in highly saline environments [Clarke and Hannon, 1970] such as the maritime swamps of Cullendulla Creek (Chapter 1). Under these conditions, the occurrence of *Aegiceras* is limited largely to the waterlogged margins of creeks and other watercourses [Clarke and Hannon, 1970], where the salinities are not likely to exceed that of sea water.

The decline in assimilation rates in both *Aegiceras* and *Avicennia* in response to long term conditions of salinity and humidity was due primarily to decrease in photosynthetic capacity as shown by changes in the shapes of $A(c_i)$ curves (Chapter 6). One component of the decline in photosynthetic capacity was a decrease in the initial slope (ie. the mesophyll conductance) of the $A(c_i)$ curve and this response was uniquely related to increasing salinity. Another component was a decline in the level of the upper portion of the $A(c_i)$ curve which occurred in response to both increasing salinity and vpd.

Similarly, rapid and reversible changes in photosynthetic capacity were the primary causes of decline in assimilation rates with short-term increase in salinity or vpd (Chapter 7). The lower, linear portion

of the $A(c_i)$ curves was insensitive whereas the upper, curved portion was sensitive to these treatments. Transient increase in either salinity or evaporation rate (the latter by increasing the vpd) caused a decline in the upper level of the $A(c_i)$ curve thereby causing a decrease in photosynthetic capacity.

According to a recent model relating gas exchange characteristics with the biochemistry of CO_2 fixation, the lower, linear and upper, curved portions of the $A(c_i)$ curve reflect *in vivo* RuBP carboxylation activity and rates of RuBP regeneration, respectively [Farquhar *et al.*, 1980; Farquhar and von Caemmerer, in press; von Caemmerer and Farquhar, in press]. Interpretation of changes in the shapes of the $A(c_i)$ curves suggests that the capacity for RuBP regeneration is reduced with short or long term increases in either salinity or vpd whereas the carboxylation activity is decreased only with long term exposure to increasing salinity. The latter effect is also suggested by the decrease in the $\delta^{13}C$ values of leaves of *Aegiceras* and *Avicennia* with increasing salinity of the culture solution [Farquhar *et al.*, in press a). This decrease in $\delta^{13}C$ could be totally accounted for in physical terms, the $\delta^{13}C$ becoming less negative with increasing c_i [Farquhar *et al.*, in press a], further indicating that carboxylation metabolism was adversely affected by increasing salinity. The photosynthetic characteristics are typical of C_3 plants and there was no evidence of a change in photosynthetic pathway. The main difference between the response of *Aegiceras* and *Avicennia* is that the photosynthetic metabolism of the former species is much more sensitive to salinity than that of the latter speices. This sensitivity is correlated with a higher Na^+/K^+ ratio in the leaves of *Aegiceras*.

These results do not distinguish between the effects of ions and of low water potentials associated with salinity on photosynthetic metabolism. The responses to increasing salinity in the long term are similar to those observed in glycophytes in response to long term water stress, ie. that obtained by exposing plants to fixed osmotic potentials during growth or by allowing plants to gradually deplete the soil water content of a pot. For example, similar changes in the slopes of $A(c_i)$ curves were observed in *Eucalyptus socialis* [Collatz *et al.*, 1976], *Simmondsia chinensis* [Collatz, 1977] and *Larrea divaricata* [Mooney *et al.*, 1977] with gradual imposition of water stress. Few other workers have reported measurements of $A(c_i)$ curves, but similar effects to the decrease in mesophyll conductance are evident from calculated increases in mesophyll resistance with increasing water stress in several species [Bunce, 1977; O'Toole *et al.*, 1977; Nobel *et al.*, 1978].

The changes in gas exchange characteristics of *Aegiceras* and *Avicennia* in response to transient changes in salinity or vpd are similar to those observed in glycophytes in response to short term water stress, ie. that obtained by sudden changing of the water potential of a culture solution, by rapid dessication of detached leaves, or by allowing the plant to rapidly deplete the soil water content of a pot. Sharkey *et al.* (in preparation) found that only the upper curved portion of the $A(c_i)$ curve was sensitive to rapid imposition of water stress and that these changes in photosynthetic capacity were largely responsible for the observed decline in assimilation rate just as in the present study. These results are consistent with reports that mesophyll resistance was unaffected by rapid decrease of

the leaf water potential in several species [Moldau, 1973; Mederski *et al.*, 1975]. These authors concluded that the decline in assimilation rate was due solely to decrease in stomatal conductance, but their conclusions must be considered tentative because they did not measure the $A(c_i)$ curves and hence it is not known to what extent the photosynthetic capacity might have changed.

Changes in the gas exchange characteristics of *Aegiceras* and *Avicennia* grown under long-term salinity conditions suggested that the decrease in photosynthetic capacity with increasing salinity was due to effects of salinity on both carboxylation metabolism and metabolism associated with RuBP regeneration. Carboxylation enzymes are sensitive to ions [Osmond and Greenway, 1972] and therefore the effects of salinity on photosynthetic capacity might be explained by effects of ions on the activity and K_m RuBP of RuBP carboxylase. Some preliminary measurements were made according to the methods of Lorimer *et al.* [1977] with crude extracts prepared from *Avicennia* leaves for which gas exchange characteristics had been determined as described in Chapter 6. The results of these measurements showed that the decline in mesophyll conductance with increasing salinity was not due to a decrease in the quantity of RuBP carboxylase. Addition of NaCl to the assay media decreased the activity of RuBP carboxylase in a manner consistent with the theoretical relationship between the *in vivo* activity of this enzyme and mesophyll conductance described in the model of Farquhar *et al.* [1980]. Preliminary measurements also showed that the K_m RuBP increased with increasing NaCl. Further preliminary measurements made with Dr Christa Critchley showed that NaCl had little effect on *in vitro* electron transport activity in preparations from *Avicennia* leaves. These results together with the gas exchange

data given in the present study suggest that effects of salinity on carboxylase itself may be a major cause of the decline in photosynthetic capacity with increasing salinity in the long term and this should be a rewarding area of future research.

Other observations suggest that the decline in photosynthetic capacity due to decrease in mesophyll conductance with increasing salinity in the long term may be associated with K^+ deficiency. This is suggested by the correlation between greater sensitivity of photosynthetic metabolism to salinity in leaves with higher Na^+/K^+ ratios. The photosynthetic capacity declined with increasing salinity in leaves in which the K^+ concentration decreased with increasing salinity (Chapter 6). However, the photosynthetic capacity was unaffected by the same range of salinities (10 to 100% seawater) in leaves of *Avicennia* in which the K^+ concentration either increased or remained constant (Chapter 2).

Although K^+ is required in large quantities, its role in plant metabolism is not well known. However, chloroplasts appear to be a major site of K^+ accumulation as shown by measurements of K^+ concentration in non-aqueously extracted chloroplasts of a halophyte, *Limonium vulgare* [Larkum and Hill, 1970] and a glycophyte, *Pisum sativum* [Nobel, 1969]. The photosynthetic rates of *Beta vulgaris* [Terry and Ulrich, 1973a and b] and *Medicago sativa* [Peoples and Koch, 1979] decreased when grown under K^+ deficient conditions, apparently due to an increase in mesophyll resistance. This response to K^+ deficiency in *Medicago* was correlated with decreased activity of RuBP carboxylase whereas K^+ deficiency did not affect the capacity of the electron transport system [Peoples and Koch, 1979].

Thus, the results of the present study would be consistent with symptoms of K^+ deficiency. The high levels of Na^+ present in saline environments can interfere with K^+ absorption [Mozafar *et al.*, 1970b; Jefferies, 1973; Storey and Wyn Jones, 1979]. Mozafar *et al.* [1970a] found that growth and tolerance to low external water potentials were enhanced in *Atriplex halimus* grown on saline media containing equal proportions of KCl and NaCl. It is possible that the plants in the present study experienced some metabolic disfunction due to K^+ deficiency with increasing salinity, when other, potentially harmful ions such as Na^+, may have substituted for K^+. The influence of Na^+/K^+ ratios on the sensitivity of photosynthetic metabolism to salinity seems to be a promising area for future research.

APPENDIX

Gas Exchange Measurements

Gas exchange apparatus Rates of CO_2 and water vapour exchange in intact, attached leaves were determined with an open system gas analysis apparatus fitted with four leaf chambers, each consisting of a water-jacketed aluminium cuvette enclosing 195 mm^2 of the abaxial leaf surface and a transparent water jacket pressing tightly against the opposite, adaxial leaf surface. Water was supplied to the jackets from a temperature controlled bath. This chamber arrangement did not interfere with normal photosynthetic activity of hypostomatous leaves. Air flow through the chamber was 0.4 ℓ min^{-1}, monitored with a Brooks mass flow meter. Illumination was provided by a water-cooled, high pressure xenon arc lamp (Osram XBF 2500W). Irradiance was varied by interposing copper screens of different mesh widths and by changing the distance between the lamp and the leaf. Temperature was sensed by means of a copper-constantan thermocouple fixed to the adaxial leaf surface. All temperature measurements were referenced against a platinum-resistance thermometer kept in a constant temperature bath of 35C. Irradiance was measured with a Lambda quantum sensor near the leaf surface. The outputs of all sensors were registered continuously on a Rikadenki six-pen potentiometric recorder.

Measurement of CO_2 and water vapour CO_2 was measured with a Beckman 865 infra-red gas analyzer (IRGA) calibrated with a series of 3 Wösthoff precision mixing pumps (models SA 18/3, SA 27/3 and 627/3F). These pumps mix by volume to produce a known mole fraction of CO_2. However an IRGA senses density of CO_2. Therefore, an apparent concentration,

derived from use of the calibration characteristic, is corrected by multiplication by P_o/P where P_o and P are the total pressures during calibration and measurement, respectively.

Water vapour was measured with a Vaisala humidity sensor maintained at 35C in a constant temperature bath. The instrument senses relative humidity, r, and the mole fraction of water vapour is found as

$$w = \frac{re'_s}{P}$$

where e'_s is the saturation vapour pressure of water at the temperature of the humidity sensor.

Preparation of inlet gas mixture In this system, dry CO_2-free air was first humidified by bubbling through a 35C water bath and then brought into equilibrium with liquid water at a known temperature during passage through a double coil condenser. Dry air containing 0.5% CO_2 was then introduced into the mixture with a Whitney precision micro metering valve. A constant pressure difference was maintained between the two gas streams by means of a differential manometer and an electronic sensing device. The mole fraction of water vapour in the final mixture, w_o, is given by

$$w_o = \frac{e'_0 \ (1 - c_o/c)}{P}$$

in which e'_o is the saturation vapour pressure at the temperature of the condenser, P is total gas pressure within the condenser, c is the mole fraction of CO_2 in the dry air and c_o is the mole fraction of CO_2 in the final mixture.

Determination of gas exchange rates across a leaf surface Calculations and units follow those recommended by Cowan [1977] and are for one side of the leaf. The rate of transpiration per unit area of leaf E, expressed in mmol H_2O m^{-2} s^{-1}, is found from the difference between the mole fraction of water vapour in the influent w_o and effluent w_1 air streams, as determined from humidity sensor measurements. The assimilation of CO_2 by the leaf is balanced by a release of O_2 of the same magnitude; however, the efflux of vapour from the leaf causes the flow of gas out of the chamber to be increased by the amount ES, where S is the leaf area enclosed by the chamber. Therefore

$$E = \frac{U(w_1 - w_o)}{S(1 - w_o)}$$

where U is the flow rate (mol s^{-1}) out of the chamber.

The assimilation rate, A, expressed as μmol CO_2 m^{-2} s^{-1}, was

$$A = \frac{U(c_o - c_1)}{S} - E\, c_o$$

where c_o and c_1 are the fractions of CO_2 in the ingoing and outgoing air streams, respectively.

The total conductance to vapour diffusion, g_t, expressed as mol m^{-2} s^{-1}, was calculated from the flux equation

$$E = g_t\,(w_i - w_a) + \frac{E(w_i + w_a)}{2}$$

where w_i is given by the saturation vapour pressure of water at leaf temperature [Farquhar and Raschke, 1978] divided by the total pressure within the chamber, and w_a is the ambient vapour concentration in the

chamber, here taken to be 0.5 ($w_o + w_i$). The second term on the right accounts for the effect of mass flow through the stomatal pores [Jarman, 1974]. The leaf conductance to vapour diffusion g, expressed as mol m^{-2} s^{-1}, was calculated from

$$g = g_t/(1 - \frac{g_t}{0.4})$$

where the value 0.4 mol m^{-2} is the measured boundary layer resistance to vapour transfer in the leaf chamber. The intercellular concentration of CO_2 in μl l^{-1} (c_i) was found from the equation

$$A = g_t^{\dagger} (c_a - c_i) - E \frac{(c_i + c_a)}{2}$$

where c_a is the ambient CO_2 concentration in the chamber, here taken to be $\frac{c_o + c_1}{2}$ and $g_t^{\dagger}$ is the total conductance to CO_2 diffusion determined from

$$g_t^{\dagger} = g/(1.6 + 1.37\ g/0.4)$$

in which 1.6 is the ratio of the diffusivities of water vapour and CO_2 in air, and 1.37 is the ratio of the boundary layer conductances for water vapour and CO_2 [Cowan, 1972].

Prediction of gas exchange characteristics Calculations were made of how gas exchange characteristics would change with given changes in conductance or photosynthetic characteristics according to the method described in a recent review [Farquhar and Sharkey, in press]. A sample calculation is shown in Fig. A.1 which shows how the results in Fig. 7.14 were obtained from the data given in Figs. 7.1 and 7.5.

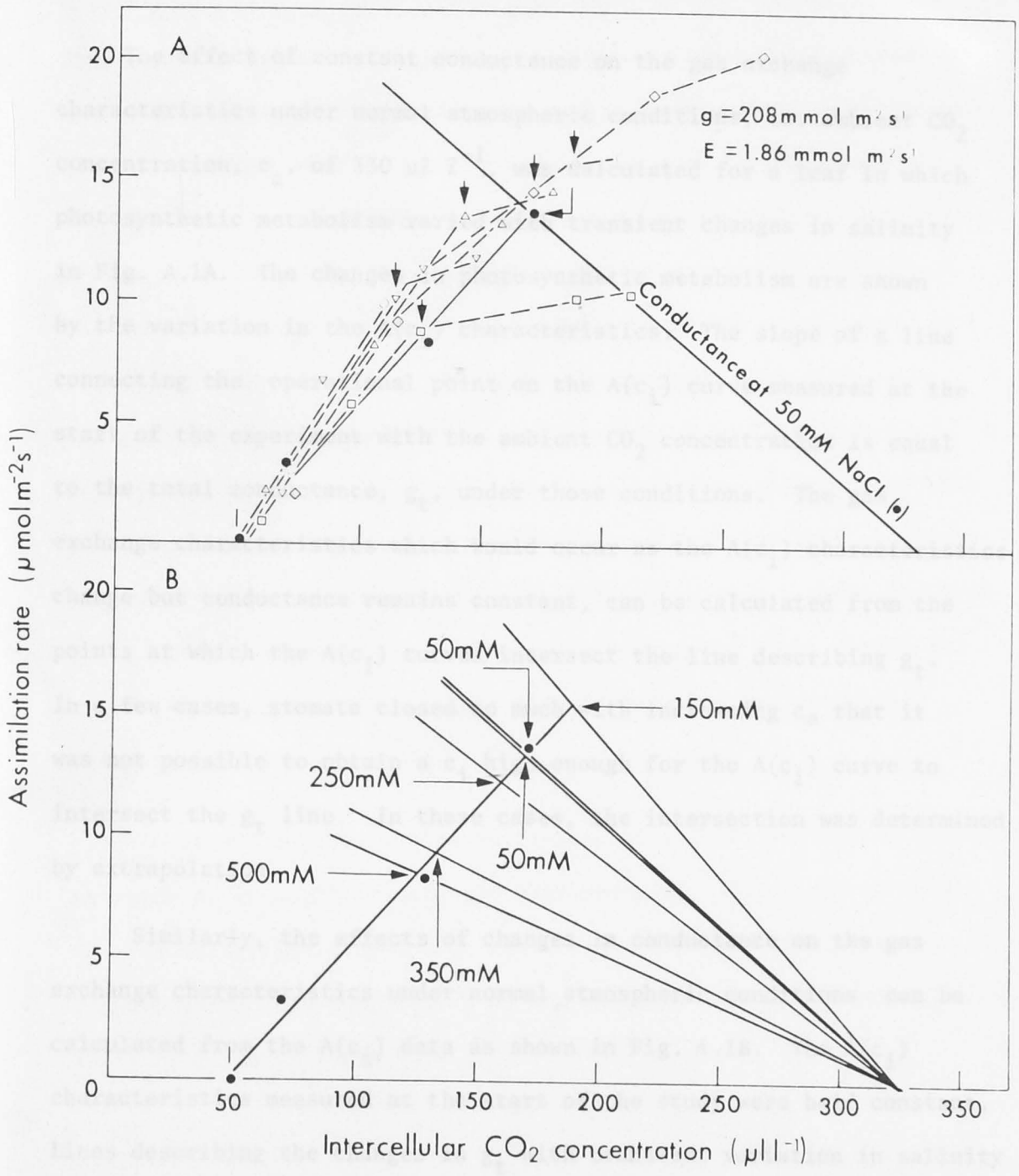


Fig. A.1 Calculation of the changes in gas exchange characteristics which would occur if (A) conductance were to remain constant or (B) $A(c_i)$ characteristics were to remain constant. Further explanation is given in the text.

The effect of constant conductance on the gas exchange characteristics under normal atmospheric conditions, ie. ambient CO_2 concentration, c_a, of 330 $\mu l\ l^{-1}$, was calculated for a leaf in which photosynthetic metabolism varied with transient changes in salinity in Fig. A.1A. The changes in photosynthetic metabolism are shown by the variation in the $A(c_i)$ characteristics. The slope of a line connecting the operational point on the $A(c_i)$ curve measured at the start of the experiment with the ambient CO_2 concentration is equal to the total conductance, g_t, under those conditions. The gas exchange characteristics which would occur as the $A(c_i)$ characteristics change but conductance remains constant, can be calculated from the points at which the $A(c_i)$ curves intersect the line describing g_t. In a few cases, stomata closed so much with increasing c_a that it was not possible to obtain a c_i high enough for the $A(c_i)$ curve to intersect the g_t line. In these cases, the intersection was determined by extrapolation.

Similarly, the effects of changes in conductance on the gas exchange characteristics under normal atmospheric conditions can be calculated from the $A(c_i)$ data as shown in Fig. A.1B. The $A(c_i)$ characteristics measured at the start of the study were held constant. Lines describing the changes in g_t with transient variation in salinity were drawn by connecting the respective operational points of each $A(c_i)$ curve (as shown in Fig. A.1A) with c_a. The changes in gas exchange characteristics due to variation in conductance could then be calculated from the intersection of these lines describing g_t with the $A(c_i)$ curve.

Measurements of salt secretion rates Rates of salt secretion were determined on intact, attached leaves during normal photoperiods in the growth cabinet. The conditions during measurements were average leaf temperature of 25C, quantum flux density of approximately 400 $\mu E\ m^{-2}\ s^{-1}$, and an average leaf to air vapour pressure difference of either 6, 12 or 24 mbar, depending on the experiment. The leaf was rinsed thoroughly with distilled water prior to illumination and rinsed again at the end of the 12 hr photoperiod. The wash water was analysed for Cl^- by silver titration with a Buchler-Cotlove chloridometer and for Na^+ and K^+ by flame emission spectroscopy with a Varian Techtron Series AA.6 spectrophotometer. The leaf was either harvested or traced and its area was measured with a Lambda leaf area meter. The average salt secretion rate during the light period was expressed in units to facilitate comparisons with gas exchange measurements, ie. $mol\ m^{-2}\ s^{-1}$.

Plant culture Seedlings were cultivated in either dilutions of filtered seawater or in nutrient solution containing 50, 250 or 500 mM NaCl to give salinities roughly equivalent to 10, 50 and 100% seawater, respectively. The composition of the nutrient solution [Johnson *et al.*, 1957] is given in Table A.1.

Table A.1

Composition of nutrient solution [Johnson *et al.*, 1957]

Ingredient	Concentration
KNO_3	6 mM
$Ca(NO_3)_2$	4 mM
$(NH_4)_2\ HPO_4$	2 mM
$Mg\ SO_4$	1 mM
FeH_2 - EDTA	20 μM
$H_3\ BO_3$	25 μM
$Mn\ SO_4$	2 μM
$Zn\ SO_4$	2 μM
$Cu\ SO_4$	0.5 μM
$H_2\ MoO_4$	0.5 μM
NaCl	50, 250 or 500 mM

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