

https://dspace.org/

studies on the brown alga dictyopteris longifolia (Dictyotales), with special reference to the effects of wave action

Blackmore, Natalie Lynn

2016-08-05
http://hdl.handle.net/10539/20835

Downloaded from a DSpace repository. https://dspace.org/

STUDIES ON THE BROWN ALGA *DICTYOPTERIS LONGIFOLIA* (DICTYOTALES), WITH SPECIAL REFERENCE TO THE EFFECTS OF WAVE ACTION

NATALIE LYNN BLACKMORE

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in the fulfillment of the requirements of the Degree of Magister Scientae.

June 1992

ABSTRACT

Aspects of the brown alga Dictyopteris longifolia at Palm Beach, Natal, were investigated with special reference to the effect of wave exposure.

A description of the species is given and the nomenclature discussed. Distribution of D. longifolia was determined from literature and herbarium specimens.

Various methods of measuring wave exposure were assessed and reviewed. Attempts were made to quantify sand abrasion and deposition in the study sites.

Morphological and structural aspects of the thallus were found to vary considerably with season and wave exposure.

Light and scanning electron microscopy studies indicated the relatively complex cell organisation of this brown alga.

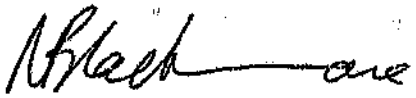
The prolific regeneration from various thallus sections of D. longifolia indicate that regeneration is an important survival strategy following damage.

Sexual reproduction and tetrasporogenesis were investigated. Sexual reproduction was not prolific in the field, however, tetraspores were abundant and are believed to be particularly important in high wave exposure areas.

D. longifolia experiences a range of environmental conditions and responds to these with morphological, structural and reproductive adaptations.

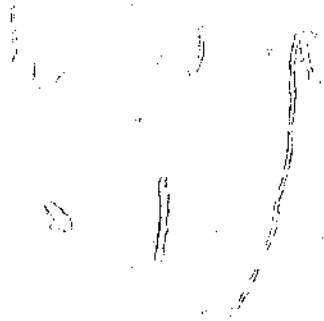
DECLARATION

I declare that this thesis in my own, unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



NATALIE LYNN BLACKMORE

1st Day of June, 1992



He saw that the water continually flowed and flowed and yet it was always there; it was always the same and yet every moment it was new.

(Siddharta, by H. Hesse)

ACKNOWLEDGEMENTS

The author wishes to express deep gratitude and appreciation to everybody who has assisted with this study. In particular to:

the Foundation for Research and Development, for financial assistance in the form of a bursary granted for the first two years of the study.

the University of Witwatersrand for financial assistance and the use of facilities.

the Department of Botany, University of Witwatersrand and, in particular, the Phycology Unit for use of facilities; and all members of staff who gave advice and expressed interest in this study.

the Natal Parks Board, Roads and Reclamation Department and staff for the use of facilities and the understanding and patience shown during the write-up stage.

my parents for their love and continual support in all my endeavors. In particular, to my Dad for financial and computer assistance without which this thesis would never have been completed, and to Mom for the long, hard hours of work assisting with the plates and other tedious aspects of the write-up.

To Cheryl Savage, my friend and co-worker without whose assistance this study would have been difficult and without whose company it would have never have been as enjoyable.

and

To my husband, Andrew, for his continual love, support and understanding. With special thanks for the inspiring discussions and for the hours spent assisting with numerous computer and other technical problems.

My greatest thanks must go to my supervisor, Dr Alan T. Critchley whose support and encouragement for this study never wavered. His enthusiasm made the study enjoyable from beginning to end, and has inspired me to continue pursuing this field.

CONTENTS

ABSTRACT ii

DECLARATION iii

ACKNOWLEDGMENTS v

TABLE OF CONTENTS vi

LIST OF FIGURES xv

LIST OF TABLES xxi

1 INTRODUCTION 1

1.1 PHAEOPHYTA 1

1.1.1 General Characteristics of the Division 1
1.1.1.1 Cell Wall 2
1.1.1.2 Flagella Apparatus 3
1.1.1.3 Chloroplast 4
1.1.1.4 Pigments 5
1.1.1.5 Pyrenoids 5
1.1.1.6 Storage Products 6
1.1.1.7 Physodes and Fucosan 6
1.1.1.8 Growth Forms 7
1.1.1.9 Growth Patterns 9
1.1.2 Life Histories 10
1.1.3 Evolution 14
1.1.4 Classification 20

1.2 ORDER DICTYOTALES 24

1.3 GENUS DICTYOPTERIS 26

1.4 THE SPECIES DICTYPTERIS LONGIFOLIA 29

1.5 PHYSICAL ENVIRONMENT OF THE INTERTIDAL REGION 30

1.5.1 Causes and Types of Water Motion 31
1.5.1.1 The Formation and Arrival of Waves 31
1.5.1.2 Water Flow Over Organisms 34
1.5.1.3 Beach Formation and Structure 35
1.5.2 Desiccation 36
1.5.3 Light Quality and Quantity 39
1.5.4 Nutrient Uptake and the Effects of Salinity 41
1.5.5 Sand Deposition 43
1.5.6 Herbivory 45

1.6 ALGAL RESPONSE TO WAVE EXPOSURE 47

1.6.1 Effects of Wave Exposure on Morphology 47
1.6.1.1 Effects on Attachment 48
1.6.1.2 Effects on Shape 49
1.6.2 Effects of Wave Exposure on Population Dynamics 53
1.6.3 Effects of Wave Exposure on Reproduction 54

1.7 REGENERATION 56

1.7.1 Causes of Regeneration 57
1.7.2 Process of Wound Healing 58
1.7.3 Process of Regeneration 59
1.7.4 Regeneration Potential of Different Regions 60
1.7.4.1 Regeneration from Laminae 60
1.7.4.2 Regeneration from the Stipe 62
1.7.4.3 Regeneration from the Holdfast 62
1.7.4.4 Regeneration from Rhizoids 64
1.7.4.5 Other Regions of the Thallus with Regenerative Potential 66
1.7.5 Polarity 67
1.7.6 Regeneration as a Method of Asexual Reproduction 69

1.8 SEXUAL REPRODUCTION 69

1.9 TETRASPOROGENESIS 71

1.9.1 Tetrasporogenesis in Members of the Dictyotales 71
1.9.2 Studies on Tetrasporogenesis in the Dictyotalean Genus, Dictyopteris ... 72

2 MATERIALS AND METHODS 76

2.1 EXPERIMENTAL ORGANISM 76

2.2 STUDY AREA 76

2.3 DISTRIBUTION 83

2.4 FIELD METHODS 83

2.4.1 Wave Action 84
2.4.1.1 Wave Strength 84
2.4.1.2 Wave Number 87
2.4.2 Water Motion 87
2.4.2.1 Lifesaver Sweet Dissolution Method 87
2.4.2.2 Plaster Block Dissolution Method 88
2.4.3 Sand Content of the Water 89
2.4.4 Sand Deposition 90
2.4.5 Mean Maximum Lamina Length of Population 91
2.4.6 Morphometry 91
2.4.7 Structural Properties 95
2.4.7.1 Tensile Strength 97
2.4.7.2 Attachment Strength 98
2.4.7.3 Sclerophylly and Succulence 100
2.4.7.4 Desiccation Rate and Percentage Rehydration 101

2.5 ANATOMICAL AND DEVELOPMENTAL STUDIES 102

2.5.1 Light Microscope Studies 103
2.5.2 Scanning Electron Microscope Studies 103
2.5.3 Transmission Electron Microscope Studies 105
2.5.4 Regeneration Studies 105
2.5.4.1 Sections of the Lamina 107
2.5.4.2 Whole Laminae and Large Sections of Lamina 107
2.5.4.3 Whole Plant Regeneration 108
2.5.4.4 Sections of the Holdfast 108
2.5.4.5 Regeneration from Rhizoid Sections 108
2.5.5 Sexual Reproduction Studies 109
2.5.6 Tetrasporogenesis Studies 110

2.6 LABORATORY PROCEDURE 111

2.6.1 Culture Medium 111
2.6.2 Isolation of Sections of D. longifolia Laminae 112
2.6.3 Growth Conditions 112
2.6.4 Microscopy 113
2.6.4.1 Light Microscopy Preparation 113
2.6.4.2 Scanning Electron Microscopy Preparation 114
2.6.4.3 Transmission Electron Microscopy Preparation 114

2.7 STATISTICAL ANALYSES 116

2.7.1 Means 116
2.7.2 Tests of Significance 116
2.7.3 Principle Component Analysis 117

3 RESULTS 118

3.1 EXPERIMENTAL ORGANISM 118

3.1.1 External Morphology of Dictyopteris longifolia From Palm Beach 118

3.2 DISTRIBUTION 119

3.3 WATER MOVEMENT 121

3.3.1 Wave Action 122
3.3.1.1 Wave Strength 122
3.3.1.2 Wave Number 122
3.3.2 Water Motion 125
3.3.2.1 Lifesaver Sweet Dissolution Method 125
3.3.2.2 Plaster Block Dissolution Method 127

3.4 SAND CONTENT OF WATER 131

3.5 SAND DEPOSITION 133

3.6 MEAN MAXIMUM LAMINAL LENGTH OF THE POPULATION 135

3.7 MORPHOMETRY 137

3.7.1 Features of the Holdfast 137
3.7.1.1 Diameter 137
3.7.1.2 Holdfast Area 139
3.7.1.3 Holdfast Mass 141
3.7.2 Features of the Lamina 145
3.7.2.1 Laminal Length 145
3.7.2.2 Laminal Width 145
3.7.2.3 Surface Area of the Thallus 148
3.7.2.4 Mass of the Laminae 151
3.7.2.5 Number of Dichotomies per Lamina 151
3.7.2.6 Number of Laminae per Individual 159

3.8 MECHANICAL PROPERTIES 162

3.8.1 Tensile Strength of the Laminae 162
3.8.2 Attachment Strength of the Holdfast 165
3.8.3 Sclerophylly and Succulence 166
3.8.4 Desiccation and Rehydration 175

3.9 ANATOMICAL STUDIES OF D. LONGIFOLIA 179

3.9.1 Apical Tip 179
3.9.2 Wing Structure 180
3.9.3 Midrib Structure 183
3.9.4 Epidermis Structure 184
3.9.5 Surface Cell Structure 185
3.9.6 Holdfast Structure 185
3.9.7 Surface Hairs 186
3.9.8 Other Structural Observations and Associations of D. longifolia. 187
3.9.8.1 Other Hair-Like Structures 187
3.9.8.2 Wounds or Injured Areas 187
3.9.8.3 Algal Epiphytes 188
3.9.8.4 Epidermal Sloughing 188
3.9.8.5 Animal Associates and Herbivores 188

3.10 REGENERATION 188

3.10.1 Regeneration from Small Sections of Lamina 190
3.10.2 Regeneration from Large Sections or Whole Laminae 192
3.10.3 Process of Regeneration from Injured Laminae 196
3.10.4 Regeneration from the Uncut Surface of a Lamina 196
3.10.5 Regeneration from the Holdfast 198
3.10.6 Regeneration from Rhizoid Sections 198

3.11 SEXUAL REPRODUCTION 200

3.11.1 Antheridia 200
3.11.2 Oogonia 202

3.12 TETRASPOROGENESIS AND MORPHOGENESIS 202

3.12.1 Development of the Tetraspores 203
3.12.2 Morphogenesis 204
3.12.3 Growth Rates under Different Temperatures. 209

4 DISCUSSION 211

4.1 EXPERIMENTAL ORGANISM 211

4.1.1 External Morphology 211
4.1.2 Nomenclature 213

4.2 DISTRIBUTION 216

4.3 WATER MOVEMENT 216
4.3.1 Wave Action 219
4.3.2 Water Motion 219

4.4 SAND CONTENT 231

4.5 SAND DEPOSITION 233

4.6 MEAN MAXIMUM LAMINAL LENGTH OF THE POPULATION 236

4.7 MORPHOMETRY 240

4.7.1 Features of the Holdfast 241
4.7.1.1 Diameter of Holdfast 241
4.7.1.2 Holdfast Area 243
4.7.1.3 Holdfast Mass 244
4.7.2 Features of the Lamina 245
4.7.2.1 Laminal Length 245
4.7.2.2 Laminal Width 247
4.7.2.3 Laminal Surface Area 249
4.7.2.4 Mass of Laminae 250
4.7.2.5 Number of Dichotomies per Lamina 251
4.7.2.6 Number of Laminae per Individual 252

4.8 STRUCTURAL PROPERTIES 254
4.8.1 Tensile Strength 254
4.8.2 Attachment Strength 257

4.8.3 Sclerophylly and Succulence 261
4.8.3.1 Lamina Sclerophylly 261
4.8.3.2 Holdfast Sclerophylly 262
4.8.3.3 Lamina Succulence 262
4.8.3.4 Holdfast Succulence 263
4.8.4 Desiccation and Rehydration 264

4.9 ANATOMICAL STUDIES 268

4.9.1 Apical Tip 269
4.9.2 Wing Structure 270
4.9.3 Midrib 271
4.9.4 Structure of the Epidermal Cells 278
4.9.5 Surface Appearance of Epidermal Cells 280
4.9.6 Holdfast 280
4.9.7 Surface Hairs 281
4.9.8 Other Surface Structures 283
4.9.8.1 Hair-like Structures 283
4.9.8.2 Wound-Like Cavities 284
4.9.8.3 Algal Epiphytes 284
4.9.8.4 Sloughing Epidermis 285
4.9.8.5 Herbivores 285

4.10 REGENERATION 288

4.10.1 Regeneration from Small Sections of Lamina 291
4.10.2 Regeneration from Large Sections or Whole Laminae 295
4.10.3 Process of Regeneration from Injured Laminae 298
4.10.4 Regeneration from the Uncut Surfaces of Laminae 300
4.10.5 Regeneration from the Holdfast 301
4.10.6 Regeneration from Rhizoid Sections 303

4.11 SEXUAL REPRODUCTION 307

4.11.1 Antheridia 309
4.11.2 Oogonia 311

4.8.3 Sclerophylly and Succulence 261
4.8.3.1 Lamina Sclerophylly 261
4.8.3.2 Holdfast Sclerophylly 262
4.8.3.3 Lamina Succulence 262
4.8.3.4 Holdfast Succulence 263
4.8.4 Desiccation and Rehydration 264

4.9 ANATOMICAL STUDIES 268

4.9.1 Apical Tip 269
4.9.2 Wing Structure 270
4.9.3 Midrib 271
4.9.4 Structure of the Epidermal Cells 278
4.9.5 Surface Appearance of Epidermal Cells 280
4.9.6 Holdfast 280
4.9.7 Surface Hairs 281
4.9.8 Other Surface Structures 283
4.9.8.1 Hair-like Structures 283
4.9.8.2 Wound-Like Cavities 284
4.9.8.3 Algal Epiphytes 284
4.9.8.4 Sloughing Epidermis 285
4.9.8.5 Herbivores 285

4.10 REGENERATION 288

4.10.1 Regeneration from Small Sections of Lamina 291
4.10.2 Regeneration from Large Sections or Whole Laminae 295
4.10.3 Process of Regeneration from Injured Laminae 298
4.10.4 Regeneration from the Uncut Surfaces of Laminae 300
4.10.5 Regeneration from the Holdfast 301
4.10.6 Regeneration from Rhizoid Sections 303

4.11 SEXUAL REPRODUCTION 307

4.11.1 Antheridia 309
4.11.2 Oogonia 311

4.12 TETRASPOROGENESIS 311

4.12.1 Development of Tetraspores 313
4.12.2 Morphogenesis 316
4.12.3 Growth Rates of Sporelings at Different Temperatures 321

4.13 MORPHOMETRIC AND STRUCTURAL SUMMARY 322

4.13.1 Morphometric Summary 322
4.13.2 Structural Summary 323
4.13.3 Seasonal Variation 324

5 CONCLUSIONS 328

APPENDIX 334

REFERENCES 347

PLATES 382

LIST OF FIGURES

Figure 1: Diagram indicating the different parts of a Dictyopteris longifolia plant 77

Figure 2: Map of South Africa indicating the position of Palm Beach 78

Figure 3: Maps showing the extremely high wave exposure site and the high wave exposure site 80

Figure 3: Maps showing the high, intermediate wave exposure site, and the low, intermediate wave exposure site 81

Figure 3: Maps showing the high, low wave exposure site, and the two low wave exposure sites respectively 82

Figure 4: Diagrams indicating the movement of the dynamometer before, during and after a wave 86

Figure 5: Maps showing positions of measured individuals in the extremely high wave exposure site, and the high wave exposure site 92

Figure 5: Maps showing positions of measured individuals in the high, intermediate wave exposure site, and the low, intermediate wave exposure site 93

Figure 5: Maps showing positions of measured individuals in the (E) high, low wave exposure site, and the two low wave exposure sites respectively 94

Figure 6: Diagram indicating the different measurements taken for the morphometry study of D. longifolia 96

Figure 7: Diagram indicating the different regions of a Dictyopteris longifolia plant where sections were taken for the anatomical study 104

Figure 8: Diagram indicating the different regions of a Dictyopteris longifolia plant, and the shapes of the sections used for the regeneration study 106

Figure 9: Map of South Africa indicating the distribution of Dictyopteris longifolia as compiled from herbarium specimens, personal observation, personal communication and literature 120

Figure 10: Mean wave strength for the two highest wave exposure sites, ie the extremely high wave exposure site and the high wave exposure, from measurements using the modified dynamometer 123

Figure 11: Mean wave number per two minute periods for the extremely high wave exposure site, the high wave exposure site and the high intermediate wave exposure site 124

Figure 12: Mean number of grams of "Lifesaver" sweet lost per minute for all the sites 126

Figure 13: Mean percentage of weight lost from plaster of paris blocks for all the sites .. 129

Figure 14: PCA showing correlation between the measurements of sand content and wave exposure 130

Figure 15: Mean sand content of water from all the sites 132

Figure 16: Mean mass of sand deposited for those sites in which the sites were retrieved 134

Figure 17: Mean monthly population size 136

Figure 18: Mean holdfast diameter from measurements taken over the entire observation period 138

Figure 19: Scatter graph of the laminal length versus holdfast diameter of all individuals studied in the sites, over the entire study period 140

Figure 20: Mean holdfast area from measurements taken over the entire study period 142

Figure 21: Mean holdfast wet mass from measurements taken over the entire study period 143

Figure 22: Mean holdfast dry mass from measurements taken over the entire study period 144

Figure 23: Mean laminal length from measurements taken over the entire study period 146

Figure 24: Mean laminal width from measurements taken over the entire study period 147

Figure 25: Scatter graph of the laminal length versus the laminal width for individuals from the lowest and highest wave action sites for an entire study period 149

Figure 26: Scatter graph of the laminal length versus the laminal width for individuals from the lowest and highest wave action sites for March 150

Figur 27: Scatter graph of the laminal length versus the laminal width for individuals from the lowest and highest wave action sites for October 150

Figure 28: Mean surface area of all the laminae on a single plant from measurements taken over the entire study period 152

Figure 29: Mean wet and dry mass of all the laminae on a single plant, from measurements taken over the entire study period 153

Figure 30: Mean dichotomy number per lamina for the measurements taken over the entire study period 155

Figure 31: Mean dichotomy number per lamina for the measurements taken for the month of March 156

Figure 32: Mean dichotomy number per lamina for the measurements taken for the month of October 156

Figure 33: Scatter graph of lamina length versus the number of dichotomies per lamina 157

Figure 34: Percentage laminae without dichotomies 158

Figure 35: Mean lamina number less than 5mm in length 160

Figure 36: Mean lamina number greater than 5mm in length 161

Figure 37: Mean tensile strength measurements for those sites measured over the entire study period 163

Figure 38: Mean tensile strength measurements for those sites measured in March 164

Figure 39: Mean tensile strength measurements for those sites measured in October 164

Figure 40: Mean attachment strength measurements for all the sites 167

Figure 41: Mean attachment strength measurements for those sites measured in September 168

Figure 42: Mean attachment strength measurements for those sites measured in October 168

Figure 43: PCA of various morphological and structural features of lamina and holdfast structure and strength 169

Figure : Graph of mean laminal sclerophylly .. 171

Figure 45: Graph of mean holdfast sclerophylly . 172

Figure 46: Graph of laminal mean succulence for all the sites 173

Figure 47: Graph of holdfast mean succulence for all the sites 174

Figure 48: Desiccation curves of percentage desiccation versus time 177

Figure 49: Mean percentage rehydration after desiccation for all the sites 178

Figure 50: Detail of the structure of the meristematic, apical tip of Dictyopteris longifolia 179

Figure 51: Complete specimen of Dictyopteris longifolia with diagrams to show the cross-sectional appearance of different regions of the plant 181

Figure 52: Cell detail from the cross-sections of different portions of the Dictyopteris longifolia thallus 182

Figure 53: Cell detail of a surface hair showing the different cells from the small basal cells to the larger cells at the apical tip 187

Figure 54: Composite of silhouetted specimens from the field showing different stages of laminal degeneration in Dictyopteris longifolia 189

Figure 55: Graph indicating the increase in length of five excised apical tips 193

Figure 56: Silhouette of a specimen of Dictyopteris longifolia from the field showing peculiar regeneration of the tip region 194

Figure 57: Drawing of Dictyopteris longifolia showing regeneration of new laminae from the damaged laminal tips of the parent plant 195

Figure 58: Cross-sections through stages of regeneration of Dictyopteris longifolia 197

Figure 59: Regeneration of new laminae from sections of rhizoid from Dictyopteris longifolia 199

Figure 60: Antheridia and oogonia : Stages of developments and comparisons 201

Figure 61: Early stages of spore development and germination in Dictyopteris longifolia . 204

Figure 62: Detail of sections through different stages of tetraspore development in Dictyopteris longifolia 205

Figure 63: Detail of germinating spores in Dictyopteris longifolia 206

Figure 64: Detail of advanced stages of spore germination and sporeling development in Dictyopteris longifolia 208

Figure 65: Sporeling thallus elongation rates with respect to temperature 210

Figure 66: Sporeling rhizoid elongation rates with respect to temperature 210

Figure 67: Diagram to show the regeneration patterns developing from the various lamina sections of D. longifolia used in the regeneration study 306

Figure 68: Diagram showing the suggested life history for Dictyopteris longifolia 310

Figure 69: Diagram to show comparisons between spore formation of Dictyopteris divaricata 315

Figure 70: Diagram showing the "jigsaw puzzle" terminal rhizoid proliferations as reported in Dictyota dichotoma 320

Figure 71: Polygonal graph to represent an inter-site comparison of some of the morphological features of D. longifolia measured in this study 325

Figure 72: Polygonal graph to represent an inter-site comparison of some of the structural features of D. longifolia measured in this study 326

Figure 73: Polygonal graph to represent seasonal variation in some of the morphological and structural features measured in D. longifolia 327

LIST OF TABLES

Table 1: Table showing various classification schemes of the brown algae up to the class level. 20

Table 2: Table showing various classifications of the brown algae up to the order level. 22

Table 3: Comparison of D. Ligulata (Suhr), this alga described by Chihara (1963) and the alga used in this study. 215

1 INTRODUCTION

This chapter will begin with a discussion of the characteristics of Dictyopteris longifolia Papenfuss (in ed.), starting with distinguishing features of the Phaeophyta and continuing with characters of the order Dictyotales, the genus Dictyopteris and finally, the species Dictyopteris longifolia. The discussion will include aspects of anatomy, reproduction, life history and evolution in the brown algae.

The study of D. longifolia outlined in this thesis involved investigations of the effect of various environmental factors, in particular wave action, on aspects of the plants' morphology and population characteristics. The methods of assessing wave action and the physical effects of waves on intertidal organisms and their growth, are discussed. In addition, the regenerative ability, anatomy, sexual reproduction and tetrasporogenesis of D. longifolia are mentioned. Emphasis is placed on areas where adaptation to harsh wave-swept environments may have occurred.

1.1 PHAEOPHYTA

1.1.1 General Characteristics of the Division

The brown algae or Phaeophyta are a large group of plants exhibiting a wide range of morphological and anatomical variation. They are found predominantly in marine environments, with a few genera existing in brackish water and very few in fresh water (only four genera including Heribaudiella, Pleurocladia and Bodrinella). Members of the division are found in both hemispheres, in tropical to Arctic waters. They form a significant part

of the intertidal flora. Members are reported to extend from the Upper Littoral Zone to a depth of 270m (in tropical waters). The greatest diversity of both species and morphological types are, however, reported to occur in the colder water regions (Bold & Wynne, 1978), although members of some orders, eg Dictyotales are most common in warmer tropical or subtropical waters (Dawes, 1981).

1.1.1.1 Cell Wall

The cell wall of members of the Phaeophyta is a two layered structure consisting of an inner, microfibrillar cellulose layer and an amorphous layer consisting of a polysaccharide known as alginic acid, accompanied by fucoidan. The cellulose present in the inner layer differs from that found in higher plants, in that it consists of glucose and xylose, while higher plants have only glucose. The xylose is, however, also present in other groups of algae (Morris, 1967). The ratio of alginic acid to fucoidan varies between different species of brown alga, parts of an individual and environmental conditions (Lee, 1980).

It has been suggested by Evans *et al.* (1973; in Fletcher, 1987) that the amount of fucoidan present in the wall increases with an increase in exposure to the air. Fucoidan is a sulphated polysaccharide and its hygroscopic nature is believed to reduce the effects of desiccation when the seaweed is exposed to air. Alginic acid is composed of primarily mannuronic acid with variable amounts of guluronic acid. Both of these polysaccharides have been found in all species of brown alga, but only the larger kelps are harvested for their alginic acid and fucoidan content. The latter compounds are used as stabilizers in commercial products (Scagel *et al.*, 1982).

The thallus may also have an external "cuticle" or a mucilagenous layer composed of primarily alginic acid and fucoidan (Morris, 1967). Some plants have copious amounts of mucilage and feel very slimy to the touch. Mucilage is found both intercellularly, where it is believed to play a role in adhesion of cells and filaments and extracellularly, where it is thought to play a role in adhesion of the rhizoids to the substratum, in herbivore defence and prevention of epiphyte settlement (Fletcher, 1987). Some members of the Phaeophyta, eg Laminaria and Nereocystis have a system of mucilage ducts and canals for the transport of the mucilage to the surface (Walker & Bisulputra, 1977; Kasahara, 1985; Fletcher, 1987). There are only two calcified members of the Phaeophyta, both members of the Dictyotales (Padina and Zonaria).

The cell walls of brown algae are penetrated by pores which may be scattered or collected into primary pit fields. The latter state is particularly prevalent in members of the more advanced orders such as the Laminariales (Lee, 1980). The cytoplasm is continuous between adjacent cells. These plasmodesmata are thus a means of transport between the cells of the thallus. The larger members of the more advanced orders such as the Laminariales, Fucales and, in a simpler form, the Dictyotales, have transport systems composed of specialised tissue, eg the "sieve elements" of Laminaria (Fritsch, 1965; Sideman & Scheirer, 1977) which may be compared to the transport systems of higher plants.

1.1.1.2 Flagella Apparatus

There are no known unicellular or flagellated members of the Phaeophyta (Trainor, 1978). However, the sexual cells of all orders and asexual spores of all except the Dictyotales, are biflagellate. The cells are characteristically pyriform and have two laterally

inserted flagella. The anterior flagellum is the longer of the two and is covered with two rows of tripartite hairs or mastigonemes. The shorter posterior flagellum lacks hairs and is known as the "whiplash" flagellum. In members of the Fucales, the posterior flagellum of the sperm is longer than the anterior one (Lee, 1980) and there is a proboscis on the cell. These latter two features are what Scagel et al. (1982) use as a basis for their division of the brown algae, into two groups, ie the Fucalean line has this type of flagella structure and the Ectocarpalean line does not. The sperm of Dictyota, a member of the Order Dictyotales has only one flagellum although there are residual basal bodies where the base of the second flagellum would be found (Morris, 1967). The motile reproductive bodies are able to select suitable sites for settlement and attachment, whilst non-motile structures such as the tetraspores of the Dictyotales, are unable to select the site and thus rely on current movement and gravity to determine their attachment point (Fletcher, 1987).

1.1.1.3 Chloroplast

The characteristic Phaeophycean chloroplast consists of lamellae composed of three closely associated, but unattached thylakoids. There is a girdle lamella and the chloroplast is surrounded by a chloroplast envelope and two membranes of the chloroplast endoplasmic reticulum (Bold & Wynne, 1978). The outer of these membranes is continuous with the outer membrane of the nucleus in the less advanced orders such as the Ectocarpales, but discontinuous in more advanced members such as the Dictyotales, Laminariales and the Fucales (Lee, 1980). This feature may differ in the reproductive cells of the higher orders, making it an unreliable taxonomic feature. There is DNA found attached to the membranes in the plastid.

There are various types of chloroplast found in the brown algae, eg discoidal, plate-like, ramified or stellate (Bold & Wynne, 1978), with the most common being the discoidal type (Fletcher, 1987). Members of the Phaeophyta may also vary in the number of plastids that are present in the cells, ie a single, few or many. This, together with shape, is considered to be a dependable taxonomic character (Bold & Wynne, 1978; Wynne, 1981). All members of the brown algae, including parasites, have chloroplasts and photosynthesize to some degree (Scagel et al., 1982).

1.1.1.4 Pigments

The thylakoids in plastids of members of the Phaeophyta contain chlorophyll a, c_1 and c_2, alpha and beta carotene, and xanthophylls such as fucoxanthin, flavoxanthin, lutein, diatoxanthin, diadinoxanthin and violaxanthin. The characteristic brownish colour of the members of the Phaeophyta is mostly dependant on the amount of fucoxanthin (an accessory photosynthetic pigment absorbing light in the range 500-540nm) and violaxanthin present (Bold & Wynne, 1978). These xanthophylls mask the effects of the chlorophyll (Chapman & Chapman, 1973). During senescence, cells lose their xanthophyll pigment and become greenish in colour (Trainor, 1978).

1.1.1.5 Pyrenoids

Pyrenoids are present in at least some members of all the orders. They are considered to be taxonomically important, especially in the lower orders, eg Ectocarpales, although they may vary within species and with the stage of development of the plant (Lee, 1980). In the higher orders, eg Dictyotales (Hori, 1972) and Laminariales, pyrenoids may be absent or rudimentary,

except in the reproductive cells (Fletcher, 1987). However, when a pyrenoid is present, it is stalked, protrudes from and is continuous with the plastid. The chloroplast endoplasmic reticulum surrounds the structure which is not penetrated by any plastidial thylakoids. The pyrenoid contains a granular substance which is believed to be composed of storage products (Lee, 1980), and is surrounded by a layer or sheath of polysaccharide (Bold & Wynne, 1978).

1.1.1.6 Storage Products

The main storage product found in members of the brown algae is a polysaccharide known as laminarin. Another product, an alcohol known as mannitol, is also stored and in some cases so is fat. Laminarin is found as granules in the cytoplasm (Scagel et al., 1982; Fletcher, 1987). Other products which are stored and may be used in classification, at the division level, are sterols. Most members of the brown algae contain a sterol known as fucosterol, while some members are reported to contain sargasterol (Morris, 1967). Iodine is also reported to be stored by the brown algae. Tilden (1935) suggests that the storage of iodine may indicate that the Phaeophyta evolved in conditions where the seawater had a different chemical condition to what it has today.

1.1.1.7 Physodes and Fucosan

Fucosan is the phaeophycean, tannin-like, phenolic substance (Gaillard, 1962) which is stored in structures known as physodes or fucosan vesicles found in the cytoplasm of cells (particularly metabolically active or dividing cells; Zavodnik, 1981). The substance is colourless, highly refractive and slightly reduced (Lee, 1980) and has been identified as a mixture of different phenols (Baardseth, unknown) or as polyphloroglucinols

with possible taxonomic importance (Ragan & Craigie, 1978). Fucosan is oxidised in air, which gives dried seaweed its black or dark brown colour. The physodes are believed to originate in the plastids where the tannins are produced. They then migrate to the cytoplasm where they may fuse into larger vesicles. Tannins and phenols are believed to act as antibiotics, to control the growth of both epiphytes and endophytes, eg the reported reduction of unicellular algal growth by Fucus tannins (Lee, 1980), as well as to act as herbivore deterrents. These compounds are also reported to protect the chloroplasts by excluding excess ultra violet light intensity (Clayton, 1981), and to act in the formation of a wound-plug following injury (Dawes, 1981). The concentration of phenols is believed to increase with a decrease in water salinity, and to vary with season and region of the plant (Zavodnik, 1981). Tannins are reported in most orders, but are more common in the more advanced orders such as the Dictyotales (Fletcher, 1987).

Iridescent bodies are found in some Phaeophyta such as members of the Dictyotales. The bodies contain what is thought to be an electron dense, proteinaceous substance of golgi origin, which gives submerged laminae an iridescent blue or green colouring instead of the characteristic brown, eg Dictyota (Fletcher, 1987).

1.1.1.8 Growth Forms

Members of the Phaeophyta exhibit a number of different growth forms and a great range in size (from a few millimetres to 70m). Brown algae are reported to have the most advanced tissue development of all algae (Trainor, 1978). There are no unicellular members, although the reproductive structures are unicellular. Unbranched filaments, colonies and siphonaceous forms (all Phaeophyta are uninucleate except for reports of

with possible taxonomic importance (Ragan & Craigie, 1978). Fucosan is oxidised in air, which gives dried seaweed its black or dark brown colour. The physodes are believed to originate in the plastids where the tannins are produced. They then migrate to the cytoplasm where they may fuse into larger vesicles. Tannins and phenols are believed to act as antibiotics, to control the growth of both epiphytes and endophytes, eg the reported reduction of unicellular algal growth by Fucus tannins (Lee, 1980), as well as to act as herbivore deterrents. These compounds are also reported to protect the chloroplasts by excluding excess ultra violet light intensity (Clayton, 1981), and to act [illegible] formation of a wound-plug following injury (Dawes [illegible]. The concentration of phenols is believed [illegible] increase with a decrease in water salinity and to vary with season and region of the plant (Zavodnik, 1981). Tannins [illegible]e reported in most orders, but are more common in the more advanced orders such as the Dictyotales (Fletcher, 1987).

Iridescent bodies are found in some Phaeophyta such as members of the Dictyotales. The bodies contain what is thought to be an electron dense, proteinaceous substance of golgi origin, which gives submerged laminae an iridescent blue or green colouring instead of the characteristic brown, eg Dictyota (Fletcher, 1987).

1.1.1.8 Growth Forms

Members of the Phaeophyta exhibit a number of different growth forms and a great range in size (from a few millimetres to 70m). Brown algae are reported to have the most advanced tissue development of all algae (Trainor, 1978). There are no unicellular members, although the reproductive structures are unicellular. Unbranched filaments, colonies and siphonaceous forms (all Phaeophyta are uninucleate except for reports of

multinucleate holdfast cells in some kelps; Scagel et al., 1982) are also absent from the Phaeophyta. There are, however, members which exhibit branched filamentous, pseudoparenchymatous (aggregations of branched or unbranched filaments) and parenchymatous growth forms.

In members of the brown algae which are parenchymatous, there may be considerable complexity. In these forms, eg members of the Laminariales, Fucales and Dictyotales, there is a photosynthetic frond in which most of the chloroplast-containing cells are found. The frond is also the region giving rise to the reproductive structures. The region joining the frond to the attaching organ is known as the stipe or stalk. This is the structure which gives the frond its upright support. It is flexible and resilient to withstand wave forces and participates in the translocation of substances from the photosynthesizing frond to the attachment organ. The holdfast not only attaches the plant in a suitable environment and holds the fronds close enough to the water surface for sufficient light to be received, but must also be able to withstand the drag of the waves on the frond (Trainor, 1978). The attachment organ is usually composed of secondary rhizoids produced from the erect thallus and may come in a number of forms, such as the fibrous mass found in Halothrix, a compact pseudoparenchyma such as that in Sargassum, the parenchymal haptera of Laminaria or the horizontally spreading, stoloniferous attachment found in members of the Dictyotales. All these types are, however, composed of similar filaments with adhesive properties (Fletcher, 1987). The attachment region, together with the presence of thickened walls and a strengthened thallus, are all adaptations to the frequently wave-swept environment of the larger brown seaweeds (Chapman & Chapman, 1973).

On a cellular level, the more complex, parenchymatous forms show some cell differentiation. Even in members consisting of three cell layers there is some differentiation into an inner medulla and a outer cortex. More complex members exhibit advanced differentiation (although not vascular differentiation like that of the higher plants) such as the presence of the transporting sieve elements in members of the Laminariales (Trainor, 1978; Sideman & Scheirer, 1977; Fletcher, 1987).

1.1.1.9 Growth Patterns

Members of the Phaeophyta vary considerably in the type of growth which they undergo. The various patterns exhibited by members of the group are as follows (Fritsch, 1945; Trainor, 1978; Bold & Wynne, 1978; Lee, 1980):

1) Diffuse growth which occurs where most of the cells of the plant are capable of division and the plant can thus increase its size from any cell. This is found in most Ectocarpales and some Chordariales.
2) Apical growth which is found in cases where there is a single apical cell, group of apical cells or marginal cells which divide to give rise to the cells below. The plant will thus only grow through apical division. This method of growth has been reported in members of the Dictyotales, Sphacelariales and Fucales.
3) Trichothallic growth which occurs when a meristematic cell divides into a hair on the surface and a thallus cell below. Members of the Desmarestiales, Cutleriales and some Chordariales as well as the hairs and rhizoids of some orders such as the Dictyotales, exhibit this type of growth .
4) Promeristematic growth which occurs when a non-dividing apical cell controls the growth and division

of a large number of small, dividing cells beneath it.

5) The intercalary zone which is a region composed of dividing or meristematic cells which divide to form new tissue both above and below the zone. An example of this is found in the area between the blade and the stipe of Laminaria. The intercalary meristem adds length to the stipe and the blade.
6) A meristoderm which is a layer of dividing cells found in a peripheral position. The cells divide parallel to the surface to produce tissue below the meristoderm (cortex), and perpendicularly to the surface to increase the cell number of the meristoderm. The meristoderm of Laminaria is found around the stipe and divides to increase the girth of this organ. This type of growth is characteristic of members of the Fucales and Laminariales.

1.1.2 Life Histories

The life history of an individual is a combination of the reproductive and morphological stages of the organism (Fletcher, 1987). In the brown algae, the site of meiosis is considered to be the unilocular sporangium which gives rise to many, haploid, motile zoospores (members of the Dictyotales have 4-8, non-motile zoospores produced in this process). These, in turn give rise to gametophytes which may be dioecious or hermaphrodite (Clayton, 1981) and which produce the haploid gametes from plurilocular organs. These fuse in the water (usually) and the zygote develops into a diploid sporophyte plant. There are, however, variations of this. There may be a "direct" life history which lacks meiosis or fusion and which is known as a plethysmothallus. The latter is a filamentous stage which multiplies itself through the production of spores from a plurilocular sporangium. Dawes (1981) reports two types of sporangium in brown algae. The first is the

plurilocular type which is thought to be taxonomically important (Clayton, 1981; Wynne, 1981). This type may be found on the gametophyte or the sporophyte plant. On the former, it may either produce gametes by meiosis, or reproduce parthenogenetically by mitosis to give rise to gametophyte plants. On the sporophyte plant, the plurilocular sporangium produces diploid zoospores by mitosis. Unilocular sporangia are reported to occur only on the sporophyte, where the haploid zoospores are produced by meiosis (Dawes, 1981). The lack of fusion of haploid gametes is considered to be an indication that vegetative reproduction is primitive and that fusion occurred secondarily (Scagel et al., 1982). The simpler forms are considered to exhibit the more complex life history, whilst the more complex forms undergo a simple cycle (Fletcher, 1987), however, Chapman and Chapman (1973) suggest that none of the life histories are truly simple because all the generations are capable of proliferating asexually.

There are, however, some exceptions to the generalisations concerning the simplicity of the life cycle. The brown algae are a group in which a number of the members produce a chemical, sexual attractant (Clayton, 1981). The Ectocarpales produce a single chemical known as ectocarpene, members of the Fucales produce a single, different chemical called fucoserraten. The other orders, which are believed to be related to the Ectocarpales, all retained the ectocarpene but developed a second or third attractant, such as dictyotene in Dictyota and multifidene in Zonaria (Phillips et al., 1990a). This seems to support the theory of separate evolution of the Fucales from the other brown algae. More research into the sexual attractants of the various different algae, will determine the taxonomic importance of this feature.

There are considered to be three major types of life history in plants (Fletcher, 1987) namely:

Haplontic: The plants are haploid and they produce gametes through mitosis. These fuse and the resulting zygote divides meiotically during the germination, to produce the haploid spores which give rise to the haploid plant.

Diplontic: The plant is diploid and produces haploid gametes through meiosis. Fusion of these give rise to a zygote which germinates mitotically into a diploid plant.

Diplohaplontic: There are two phases in this life history. The first is the gametophyte phase which is haploid. This gives rise to haploid gametes (mitosis) which fuse to give the second phase, ie the sporophyte, which is diploid and gives rise to haploid spores through meiosis within a sporangium. The spores so produced develop into the haploid generation (gametophyte).

All the members of the brown algae belong to the latter life history type, ie diplohaplontic, except the Fucales which exhibit a diplontic life history style. The diplohaplontic life history type was divided into two sections by Kylin (1933; in Clayton, 1981). These were:

1) the isomorphic type in which the haploid and diploid phases exhibit identical morphologies, and
2) the heteromorphic type which has morphologically different phases.

The isomorphic type is reported to be present in the Ectocarpales, Sphacelariales, Cutleriales, Tilopteridales and Dictyotales; whilst the Chordariales, Sporochnales, Desmarestiales, Dictyosiphonales and Laminariales all exhibit the heteromorphic type (Morris, 1967). Kylin

(1933; in Clayton, 1981) classified the brown algae according to these groups which he called the Isogeneratae and Heterogeneratae respectively. Kylin's third group, known as the Cyclosporeae, consisted of the Fucales which lack a free-living second phase (haploid gametophyte), ie lack alteration of generations.

The method of classification employed by Kylin (1933; in Clayton, 1981) was considered to be too artificial and thus, Drew (1955; in Fletcher, 1987) composed a life history classification which consisted of monomorphic life history (a single thallus form which could be haplontic, diplontic or diplohaplontic) and a dimorphic type (two thallus forms which could be haplontic, diplontic or diplohaplontic). This scheme was later simplified to the *Fucus*-type or the *Ectocarpus*-type (Fletcher, 1987).

Vegetative reproduction does occur in members of the Phaeophyta and is thought to be important in colonisation, especially in regions at the limits of geographical distribution, ie where there are too few plants for sexual interaction (Fletcher, 1987). This type of reproduction occurs via sections of the thallus or special propagules, eg *Sphacelaria*. Some brown algae are only capable of reproducing vegetatively, eg *Sargassum* in the Sargasso Sea (Scagel *et al.*, 1982). There may also be perennation exhibited. This is the growth from a prostrate, perennial attachment organ (Chapman & Chapman, 1973), eg in the Fucales and Dictyotales. In members of the Laminariales, which have very localised meristematic tissue, the old holdfasts (which lack vegetative tissue) are capable of proliferating to form normal, new plants (Scagel *et al.*, 1982).

According to Chapman and Chapman (1973), the evolutionary features of life history exhibited by the Phaeophyta

include the elimination of accessory reproduction, ie the plurilocular sporangium in the sporophyte, the tendency towards the collection of sporangia into sori, eg Dictyotales and Laminariales, the tendency from isogamy to anisogamy and then to oogamy, and the tendency to an increase in the haploid number of eight chromosomes, eg Fucales which has 32.

1.1.3 Evolution

There are numerous theories on the evolution of the Phaeophyta and the various orders which comprise this division. The brown algae are poorly represented in the fossil record, due to their lack of calcification or silicification of the thallus (Chapman & Chapman, 1973) and the similarity in morphology between the Phaeophyceae and members of other groups (Clayton, 1981). The earliest fossil record which can be identified as a member of the Phaeophyta, is from the Late Precambium Period (±900 million years; Bold & Wynne, 1978). A fan-shaped brown alga which is similar to extant members of the genus Dictyota was found and dated to the Upper Devonian period (±350 million years). A few fossils have been identified from the Silurian and Devonian periods (400-500 million years; Clayton, 1981). Church (1920) suggests that the Phaeophyta are the modern representatives of the most archaic of all marine plants. Evolution of the division to which the Phaeophyceae belong is suggested to have originated, with the rest of the Chromophyta (Christensen, 1962; in Trainor, 1978), through the invasion of a eukaryotic cell by a prokaryotic cell containing the pigments found in the chloroplasts of the relevant division. According to the scheme suggested by Chapman and Chapman (1973), the original organism was a photosynthetic anaerobe. This gave rise to the primitive eukaryote. The Cryptophytes and the Rhodophytes are considered to be evolutionary dead ends. Two main lines

of evolution are thought to have developed. The first involved the evolution of chlorophyll b and starch-like storage products, ie the Chlorophyta and later the land plants. The second line involved chlorophyll c and Laminarin-like storage products, ie the Chromophyta, which includes the Phaeophyta. A similar theory was suggested by Scagel et al. (1982), who use the evolution of the three different chlorophylls, ie a, b and c, as the basis of the evolution of the three main algal groups, ie the red, green and the brown algae respectively. It is suggested by Tilden (1935) that the initial illumination conditions on earth allowed only those pigments in the oldest group, ie the blue-green unicells, to evolve. It was not until what she called, the "Third Algal Period", occurred, that the illumination available was suitable for brown algal pigments to evolve. The xanthophyll known as Fucoxanthin and certain chlorophylls, still found in the brown algae today, were thought to be the pigments which evolved to cope with the new illumination conditions.

Pederson (1984) suggests that the class Fucophyceae (Phaeophyceae) evolved from a parenchymatous form of the Chrysophyceae. The two groups are biochemically similar and Chapman and Chapman (1973), suggest a similar ancestral stock for the two groups as an alternative to the theory that the Chrysophyceae were the ancestors of the Phaeophyceae.

The evolutionary sequence of the brown algal orders, suggested by Trainor (1978), uses information on reproduction and some vegetative features. There are five lines which he suggests occurred.

1) The ancestral form from which other forms evolved. This was filamentous, isogamous and isomorphic. Clayton (1981) suggests that this ancestral form,

which is believed to be isomorphic, had a dominant gametophyte and a short-lived sporophyte.

2) The life history remained isomorphic but the plants became parenchymatous and in the larger forms, sexual reproduction became oogamous.
3) The life history became heteromorphic with the larger gametophyte being pseudoparenchymatous and the sporophyte being a small, encrusting form.
4) The life history was no longer isomorphic because the sporophyte became a larger, pseudoparenchymatous or parenchymatous form, with the gametophyte being a small, filamentous form. Oogamy occurred.
5) The life histories were heteromorphic with the occasional loss of the free-living gametophyte phase (haploid), as is observed in the extant members of the Fucales. The sporophyte was parenchymatous with differentiation of the cells of the medulla occurring in some cases. Oogamous sexual reproduction occurred.

Chapman and Chapman (1973) suggest two possible alternatives for the evolution of the various orders. Both these schemes begin with the evolution of a branched filament exhibiting only a haploid generation or isomorphic alternation of generations. The latter type of life-history is considered more likely, as the ancestral form was considered to be a primitive "Ectocarpalean-type organism". The major difference between the two schemes is the evolution of the Fucales and the Laminariales. In both cases the Dictyotales are connected evolutionarily to the Cutleriales, the Sphacelariales and the Tilopteridales. This association is also suggested by Johnson (1889), who connects them because, besides other similarities such as apical growth and a parenchymatous form, the spores of the Tilopteridales are quadrinucleate and thus could be linked to the tetraspores of the Dictyotales. However, other authors (Clayton, 1981) separate the Dictyotales from all the other orders due to

the presence of the unique sperm type (1 flagellum) and non-motile meiospores. Recent studies, however, report biflagellated sperm in the Dictyotalean alga Zonaria angustata (Kützing) Papenfuss (Phillips & Clayton, 1991). The presence of uniflagellated sperm and non-motile spores have been used in the past to connect the Dictyotales with members of the red algae which also have non-motile meiospores (Johnson, 1889). Clayton (1981) suggests an early separation of the Dictyotales, supported by the lack of any intermediate taxa.

Church (1920) also considers the Ectocarpalean-type organisation to be the most evolutionarily primitive form. The brown algae display all the organisational types from this primitive type, to the complex parenchymatous form which exhibits tissue differentiation. The ancestral cell type was believed to be a eukaryote which attached to a substratum by its flagella. It then became more firmly attached by the development of a polysaccharide attachment agent. This attachment satisfied some basic features necessary for the existence of the organism, ie having the maximum surface area of the cell exposed to the medium and each cell having its own light supply. Attachment in a moving medium meant an increase in nutrient and gas supply (when compared to moving within the medium). An uniseriate filament would also retain the light, nutrient and gas supply and thus the unicells developed into filaments. The attached cells were believed to be capable of regressing to the planktonic state if the nutrient, gas or light supply changed, eg if the water stopped moving. Different parts of the uniseriate filament would, however, be exposed to different degrees of water movement and light. This could have led to differential development and the production of branches. Development of the holdfast is suggested to have been a response to mechanical tension produced by the drag of the filament.

The body of the plant developed mechanical support in a number of ways, eg an increase in wall thickness, the development of polysaccharides in the walls, formation of a "cable" from the rolling together of the filaments (pseudoparenchyma), the covering of the main axis by special branches or descending filaments, or the septation of the cells in planes other than that of the main axis, ie the formation of a three dimensional, parenchymatous structure. The cells in the centre of the plant in this latter type of structure were not exposed directly to the medium, and thus deteriorated or differentiated causing the plant to develop into a more complex form. Together with this, came the development of the bilateral laminae which allowed maximum exposure to the medium and light (Church, 1920).

Kylin (1933; in Clayton, 1981) used the life history type (ie isomorphic or heteromorphic diplohaplontic, and diplontic) to divide the brown algae into three groups, ie the Isogeneratae, Heterogeneratae and Cyclosporeae (Fucales), respectively. This organisation has been used as the basis for many of the evolutionary systems suggested by other authors (Clayton, 1981). Scagel et al. (1982) report that there is increasing evidence for two evolutionary lines, ie the Ectocarpalean line labelled by them as the subclass Phaeophycidae (11 orders), and the Fucalean line called the Cyclosporidae (1 order). The latter group includes the order Fucales and is separated from the other orders due to differences in life history, flagella structure and biochemistry. It is suggested that these two groups originally had a common ancestor, prior to the evolution of the Ectocarpalean-type ancestor. Delf (1939) agrees with this separation of the Fucales but suggests an early branching rather than a totally independent derivation. The Ectocarpalean group can be divided into several lines of development based primarily on life history, construction and reproduction but all

are believed to have evolved from a simple filamentous Ectocarpalean form (Clayton, 1981). From this form the anisogamous, isomorphic forms; and the oogamous, isomorphic forms could easily have developed. The main division is based on the vegetative construction which forms two groups, ie the filamentous to complex pseudoparenchymatous form composed of an aggregation of filaments (Haplostichinae (Chapman & Chapman, 1973; Clayton, 1981)) and the parenchymatous form which is the result of longitudinal divisions of the primary filament (Polystichinae (Chapman & Chapman, 1973; Clayton, 1981)) and which displays tissue differentiation. The members of the Ectocarpalean line show variation in reproduction from the primitive state of isogamy to the advanced state of oogamy, through the intermediate anisogamy. The Fucalean-line have a similar parenchymatous and differentiated structure to the latter group of the Ectocarpalean-line, ie the parenchymatous forms. There are some problems with grouping the Phaeophyta according to their external morphology, eg the highly compacted filaments of the pseudoparenchyma may be identified as parenchymatous (Wynne, 1981). The Dictyotales are, once again, evolutionarily related to the Sphacelariales and the Cutleriales according to this system.

Contrary to what has been suggested by other authors, Tilden (1935) suggests that the simple filamentous Ectocarpales are the most recently evolved group in the Phaeophyta. It is suggested that the members of the Heterogeneratae and the Cyclosporeae, both of which have very advanced members, are the pioneers of the terrestrial plants although they themselves are not found beyond the spray zone. This theory has not been used by other authors.

1.1.4 Classification

There are numerous suggestions on the classification of the Phaeophyta. The majority of these rely on features of the external morphology, anatomy, pigmentation, storage products, cell wall structure, flagella structure and reproduction to classify the groups. By 1852 (Bold & Wynne, 1978) four groups of algae had been distinguished. These were the red, green and brown algae and the diatoms. This classification was based mainly on colour, which is still an important feature today, although it is now accompanied by many other features of the plants' structure and anatomy. By 1855 (Tilden, 1935) the class Phaeophyceae in the division Phaeophyta had developed and, based on this, many different classification systems have been suggested (see Table 1).

Table 1: Table showing various classifications of the brown algae up to the class level.

Authority	Date	Division	Class
Kylin (Clayton, 1981)	1933	Phaeophyta	Isogeneratae Heterogeneratae Cyclosporeae
Papenfuss (Bold & Wynne, 1978)	1946	Phaeophycophyta	Phaeophyceae
Chadefaud (Wynne, 1981)	1960	Phaeophyta	Phaeosporeae Cyclosporeae
Chapman (Trainor, 1978)	1962	Eucophyta	Phaeophyceae
Christensen (Trainor, 1978)	1962	Chromophyta	Phaeophyceae
Perestenko (Wynne, 1981)	1972	Phaeophyta	Phaecsporophycidae Cyclosporophycidae
Dodge (Bold & Wynne, 1978)	1974	Chrysophyta	Phaeophyceae
* Wynne & Kraft	1981	Phaeophyta	Phaeophyceae

* This classification system was used in this study.

The above classifications is based on different features. Kylin's (1933; in Clayton, 1981) arrangement is based on the life history strategies of the members and Chadefaud (1960) uses a similar strategy with the additional use of specialisation. Papenfuss (1946) changed the suffix of the division because "Chlorophyta" includes all green plants and the change to Chlorophycophyta indicates only green algae, whilst Chapman (1962) groups the red and brown algae into the same division based mainly on the fact that neither have unicellular members. Christensen (1962) grouped all the algae lacking chlorophyll b into the same division. None of these suggestions are widely used, however, the most common system and that used in this study, is that suggested by Wynne and Kraft (* 1981).

There are reports of 32 families, 96 genera and 197 species of brown algae (Fletcher, 1987), whilst Bold and Wynne (1978) report that there are 250 genera and over 1500 species, and Scagel et al. (1982) report 260 genera and 2000 species. The number of orders into which these are grouped range between 11 and 14 and these, in turn, may be placed into different subclasses and one or three classes (see Table 1). These figures vary considerably between researchers and as new species and genera are identified. The state of the orders is also constantly changing (Wynne, 1981), with some researchers adding new orders and others combining old ones (see Table 2).

The classes are divided into orders and, in some cases, subclasses. This division is determined by various features. Chadefaud (1960) groups the orders into subclasses due to the degree of specialisation, ie Proto- being least specialised, Eu- being specialised in the sporophyte generation only and the Para-phaeosporeae being specialised in both generations. Nakamura (1972) uses the mode of construction as the basis for the

formation of subclasses, ie Haplostichidae (non-parenchymatous), Haplopolystichidae (parenchymatous) and Polystichidae (both); with the life history type being used at the ordinal level. Perestenko (1972) uses a totally different feature for the classification of the brown algae into subclasses, ie differences in the germination patterns and early development. Most of the more recent classification changes are, however, differences in the subclass and order level.

Table 2: Table showing various classifications of the brown algae up to the order level.

Authority	Date	Class	Subclass	Order
Tilden	1935	Phaeophyceae	Isogeneratae	Dictyotales Tilopteridales Cutleriales Sphacelariales Ectocarpales
			Heterogeneratae	Chordariales Sporochnales Desmarestiales Punctariales
Dictyosiphonales				
		Cyclosporeae		Laminariales Fucales
Chadefaud (Wynne, 1981)	1960	Phaeosporeae	Protophaeosporeae Euphaeosporeae	Ectocarpales Chordariales Sporochnales Desmarestiales Scytosiphonales
Dictyosiphonales				
			Paraphaeosporeae	Laminariales Dictyotales Tilopteridales Cutleriales Sphacelariales
		Cyclosporeae		Fucales
Norris	1967	Phaeophyceae		Ectocarpales Desmarestiales Cutleriales Laminariales Sphacelariales Dictyotales Fucales Tilopteridales

Dictyosiphonales				
				Chordariales
				Sporochnales
Nakamura (Wynne, 1981)	1972	Phaeosporeae	Haplostichidae	Ectocarpales
				Chordariales
				Sporochnales
			Haplopolystichidae	Desmarestiales
				Ralfsiales
				Scytosiphonales
Dictyosiphonales				
				Laminariales
			Polystichidae	Dictyotales
				Tilopteridales
				Cutleriales
				Sphacelariales
		Cyclosporeae		Fucales
Perestenko (Wynne, 1981)	1972	Phaeosporophycidae	Ectocarpophycidae	Ectocarpales
				Chordariales
				Scytosiphonales
Dictyosiphonales				
			Laminariophycidae	Sporochnales
				Desmarestiales
				Laminariales
				Cutleriales
		Cyclosporophycidae		Dictyotales
				Tilopteridales
				Sphacelariales
				Ascoseirales
				Durvillaeales
				Fucales
Bold & Wynne	1978	Phaeophyceae		Ectocarpales
				Desmarestiales
				Cutleriales
				Laminariales
				Sphacelariales
				Dictyotales
				Fucales
				Tilopteridales
Dictyosiphonales				
				Chordariales
				Sporochnales
				Ralfsiales
				Scytosiphonales
Lee	1980	Phaeophyceae		Ectocarpales
				Desmarestiales
				Cutleriales
				Laminariales
				Sphacelariales

				Dictyotales Fucales
* Wynne & Kraft	1981	Phaeophyceae		Ectocarpales Chordariales Sporochnales Desmarestiales
Dictyosiphonales				
				Scytosiphonales Tilopteridales Cutleriales Sphacelariales Dictyotales Laminariales Fucales Ascoseirales Durvillaeales
Scagel et al.	1982	Phaeophyceae	Phaeophycidae	Dictyotales Tilopteridales Cutleriales Sphacelariales Ectocarpales Chordariales Sporochnales Desmarestiales Scytosiphonales
Dictyosiphonales				
			Cyclosporidae	Laminariales Fucales

1.2 ORDER DICTYOTALES (Kjellman, 1893).

The Dictyotales is a large order and members are common in the warmer waters of the temperate to tropical regions. Members of the order are found in both hemispheres and Clayton (1981) suggests that this indicates that the Dictyotales are an ancient order that, together with the Ectocarpales, Chordariales, Dictyosiphonales and Sphacelariales, were present all over the globe before the splitting of the continents occurred. The Fucales, Laminariales, Desmarestiales and

---

* This classification system was used in this study.

Sporochnales, however, arose after the splitting of the continents since they are only present in one of the hemispheres (Clayton, 1981). There is reported to be either a single family, the Dictyotaceae (Tilden, 1935), with 20 genera having been identified so far (Bold & Wynne, 1978); or two families, the Dictyotaceae and the Dictyotopsidaceae with the latter containing only a single genus, Dictyotopsis (Wynne & Kraft, 1981).

The systematic position of the Dictyotales has been fairly stable in recent years (Table 1 & 2), however, in the past the group (called the Dictyotaceae) was thought to belong to the Florideae (Rhodophyta) due to the presence of the non-motile tetraspores (Johnson, 1889). The other members of the brown algae were reported to belong to the Subclass Melanophyceae in the Class Algae. This author's report placed the Dictyotaceae into the Florideae based on work which was performed on Dictyopteris polypodioides (De Candolle) Lamouroux (Johnson, 1889). Members of the Dictyotales are characterised by the meristematic region which consists of a single apical cell or a marginal row of dividing cells (apically situated) which divide both longitudinally and transversely to produce the thin, parenchymatous thallus (Wynne, 1981). The life history is isomorphic, diplontic and sexual reproduction is oogamous. The oogonia and antheridia are often situated in superficial sori on separate plants. They develop from surface cells which enlarge and protrude above the surface (Chapman & Chapman, 1973). The antheridia give rise to uniflagellate sperm (although Zonaria angustata has been reported to be biflagellated; Phillips & Clayton, 1991) which lack the smooth, anterior flagellum found in the members of the other orders. The adult plant consists of an erect thallus which is parenchymatous in growth form and flattened (Fritsch, 1965; Morris, 1967; Lee, 1980). The laminae are attached to a stolon

(horizontal) type of attachment organ by a cylindrical stalk (Fritsch, 1965). The thalli consist of at least one or more layers of large, colourless medullary cells and a layer of small, cortical cells (Chapman & Chapman, 1973). The cortical cells are reported to contain numerous small, discoid plastids (Bold & Wynne, 1978). A distinctive character of the Dictyotales is that the unilocular sporangium produces 4-8 non-motile zoospores, as opposed to the greater number of motile spores produced by members of other orders of brown algae. Some of the genera placed into this order include Dictyota, Dictyopteris, Padina and Zonaria.

1.3 GENUS DICTYOPTERIS Lamouroux

The lectotype of the genus was identified by Lamouroux as Dictyopteris polypodioides (D. membranacea (Stackhouse) Batters)) in 1809 (in Papenfuss, 1977). The genus had previously been named Halyseris Ag. (Johnson, 1889; Fritsch, 1965) and Neurocarpus (Fritsch, 1965). There are reported to be twenty species in this genus, distributed over the tropical and temperate regions of the world. Simons (1976) lists four species from South African waters (D. delicatula Lamouroux, D. longifolia, D. macrocarpa (Areschoug) Schmidt and D. serrata (Areschoug) Hoyt, while Seagrief (1984) added three more (D. dichotoma (Suhr) Levring, D. ligulata (Suhr) Schmidt and D. polypodioides).

According to Allender and Kraft (1983), the members of the genus Dictyopteris are distinguished from other members of the Dictyotales by the meristem which is marginally situated and composed of a cluster of meristematic cells which divide transversely and longitudinally to produce the thin, thallus and the thicker, prominent midrib region (Johnson, 1889). The

possession of a midrib is also a characteristic feature of the genus which, according to Johnson (1889), has regularly arranged cells. There are reported to be four or five median meristematic cells found in a depression at the tip of the frond (Fritsch, 1965). These cells are larger than the other cells, contain dense cytoplasm and are thought to be the origin of the midrib; they undergo prolific division. The meristematic cells decrease in activity towards the margin. During formation of a dichotomy, the apical cells form two groups, one for the tip of each new branch. Katsaros and Galatis (1988) report that there are three types of meristematic cells in D. membranacea. These are the central, apical initials which give rise to the other meristems and the initials of the midrib, as well as the marginal, apical initials which form the wing and the superficial meristem which is a true meristoderm and forms the midrib. There may be the production of adventitious branches from individual cells along the surface of the midrib region and rhizoids are produced at the base of the lamina. There are reported to be two layers of cells in the wings and four to six in the midrib where differentiation occurs. In some species, the cells of the midrib become elongated and thickened and develop oblique end walls and pit canals (Fritsch, 1965). There are reported to be three cell types in the midrib of D. membranacea, ie the photosynthesizing, epidermal cells; thick cortical cells and slender medullary cells which have thick, end walls perforated by plasmodesmata (Katsaros & Galatis, 1988). There is reported to be a continuity of protoplasm through the cells of the midrib and stalk. This was shown by staining (Johnson, 1889).

Unilocular sporangia are found in sori on the blade surface, although it has been reported that there are some species which have the sporangia scattered on the surface and not in sori (Womersley, 1987). The sporangia

are found on both surfaces of the thallus, amongst scattered hair tufts and are produced from cells of the cortex. They may be positioned under or protruding from the lamina surface, and may or may not have stalk cells (single or more) which are embedded in the peripheral layer and are reported to act in spore discharge (Fritsch, 1965). Numerous studies have been performed on aspects of tetrasporogenesis and germination in this genus (Ohmori & Hashida, 1982), and comparisons with other genera in the Dictyotales (Ishii et al., 1959; Nishibayashi & Inoh, 1959; Gaillard, 1973; 19[illegible]5). Other studies include the effects of various external features such as light wave length (Ohmori & Suemura, 1978) and unilateral light (Ohmori & Ueki, 1979) on the growth of tetraspores; the effect of the addition of cytochalasin B (Ohmori & Ueki, 1980) and colchicine (Ohmori & Hashida, 1982) and deficiencies of calcium, potassium and magnesium (Ohmori & Hashida, 1983), on tetrasporogenesis and germination of the spores in members of the genus.

There are four tetraspores produced in a tetrahedral or cruciate arrangement. Following release of the spores, germination begins with the production of a primary rhizoid which undergoes cell division and elongation prior to thallus development (Inoh, 1936; Nishibayashi & Inoh, 1959). Members of the genus Dictyopteris exhibit a diplohaplontic, isomorphic life history, although sexual plants of some species are rarely observed (Womersley, 1987). The antheridia and archegonia are similar to those described for other members of the Dictyotales.

The dichotomously branched thallus of Dictyopteris is attached to a perennial holdfast or attachment organ by a stalk or "stipe", which consists of the remaining midrib once the wing of the lamina has abraded away at the base of the lamina. This stalk changes from being flattened to cylindrical at the base where the lamina is absent. The

stalk thickening is reported to be due to the activity of the epidermal meristematic region which gives rise to rows of cells on the inner side (Johnson, 1889; Katsaros & Galatis, 1988). Reinke (1878; in Johnson, 1889) is reported to be the first researcher to discover secondary thickening in members of Dictyopteris. The thickening is interrupted at points where the lamina wings protrude, ie the thallus scars. Fritsch (1965) reports the thickening at the base of the lamina to be due to the presence of a thick carpet of rhizoids which covers the base of the lamina. These extend into a "mat" of rhizoids which comprise the attachment region and from which numerous thalli may arise. The thallus and rhizoids at the base of the plant are thought to be active in vegetative reproduction (Fritsch, 1965).

1.4 THE SPECIES DICTYOPTERIS LONGIFOLIA

Material corresponding to this species was identified as Haliseris dichotoma Suhr by Kützing and as Dictyopteris dichotoma by Papenfuss, but was later renamed Dictyopteris longifolia by Papenfuss (in ed., Isaac, 1956). The species has not, as yet, been officially described although Papenfuss did have it in preparation. The plant has been referred to as D. longifolia by many authors (Simons, 1976; Branch & Branch, 1981; Seagrief, 1984) despite the lack of an official description (Bolton, pers. comm.). This study considers the species to be D. longifolia as the material used is similar to D. longifolia as illustrated in other references (Simons, 1976; Branch & Branch, 1981), as well as being similar to specimens identified as D. longifolia from various herbaria in South Africa.

The species consists of a flattened, strap-like thallus which has a prominent midrib and is reported to

dichotomise almost regularly at 50mm intervals (although plants from this study were observed to dichotomise at about 15-20cm intervals; Simons, 1976). It has an entire margin and may reach a length of up to 70cm. Simons (1976) identifies it as having the thallus wings missing on the lower one or two dichotomies, resulting in a stipe which enters the leafy part of the thallus as a midrib and may become covered in rhizoids ("bearded") at the base. The species is reported to occur along the entire east coast of South Africa (Branch & Branch, 1981) and has been observed as far north as Inhaca Island off the Mozambique coast (Isaac, 1956, Macnae & Kalk, 1958). It grows in areas of shallow water and on low intertidal areas in rock pools, in areas of varying wave action. It is reported to be common in the Lower Balanoid zone which is fairly high up on the intertidal slope and is exposed during every low tide (Simons, 1976).

1.5 PHYSICAL ENVIRONMENT OF THE INTERTIDAL REGION

The intertidal zone is one of the most stressful environments in which organisms live, and yet there is a high diversity of species present (Denny, 1988). The zone is defined as being the area between the high and low water marks. It is thus the region which is covered and uncovered by the tide. Due to the periodic submergence and emergence, the organisms in this region are exposed to the stresses of constantly changing conditions, and have to be able to exist in both an aquatic and basically a terrestrial environment (Delf, 1932; Branch & Branch, 1981; Dring, 1982). The changing conditions include variation in exposure to wave action and thus to drag, as well as to sand abrasion. There are also changes in exposure to the atmosphere (desiccation), variation in the light and temperature, as well as changes in the chemical environment. Biological factors in the

intertidal environment, such as herbivory and competition, also place stresses on the inhabitants of the zone.

1.5.1 Causes and Types of Water Motion

The movement of water along the shore is due to the effects of tides, currents (both oceanic and local), oceanic upwellings, and waves. The former three types of water motion are not discussed in this study, although their importance in exposure, salinity, spore dispersal, temperature and light determination, as well as nutrient availability must be realised (McEachreon & Thomas, 1987). Various aspects of waves, including their formation, characteristics and effects on the shore and its inhabitants, will be discussed.

1.5.1.1 The Formation and Arrival of Waves

Waves are initially formed due to storms or winds which cause pressure differences as they blow over the water and wave profiles, thus giving the waves energy and height (Smith, 1976; Dawes, 1981; Lobban et al., 1985). Waves may travel thousands of kilometres before breaking onto a beach. The waves and swells reaching the South African coast come mainly from the south west where storms occur in the "Roaring Forties" (about 40° S; Day, 1974). The direction and height of the waves are affected by the winds that they encounter on the way to the shore, depth of the water predominant currents that they cross, the shape of the coast line, as well as the "fetch" (which is determined by the uninterrupted distance that the wave has travelled; Lobban et al., 1985). The wave action (height and activity) and the topography of the shore (steepness and ruggedness) determine the degree of wave exposure (Lewis, 1964; Dawes, 1981).

As the swell advances onto the shore and the water depth reduces, the velocity and wavelength of the wave decreases due to friction with the bottom substrata. The bottom water of the wave is retarded and the surface water moves forward faster. The velocity of the wave is determined by the water depth and the wave height (Denny, 1988). The wave gets higher (due to energy being transferred from velocity to wave height), until the top water overtakes the bottom water and the wave breaks (Branch & Branch, 1981). Seymour et al. (1989) reported that waves break when the water depth is 1.4 times the height of the wave. Each wave has a gentle back slope and a steep, turbulent front slope (Denny, 1988). There are different types of waves which have different effects on the shore. These include spilling waves which have a small amount of water spilling down the crest and causing turbulence at the top of the water, plunging waves in which the crest arches over and may form a tube, and surging and collapsing waves which have a turbulent crest or collapsing front and cause deep turbulence which may reach the bottom (Denny, 1988).

In very deep water, the water at the lower levels is not in motion, while that at the surface undergoes vertical, circular motion. There is a vertical row of orbits decreasing in diameter and becoming elliptical as the depth increases, with the circular motion being negligible at half a wave depth (Denny, 1988). After a single wave has passed a certain point, the water returns to its original position with no net movement in the direction of the wave (Day, 1974; Denny, 1988). In shallow water (less than half a wave depth), the bottom water only moves back and forth causing a shearing stress on any organisms attached in this region (Vogel, 1981; Lobban et al., 1985). Thus, as the water gets shallower, the orbit flatter and the horizontal movement becomes

greater than the vertical movement, the wave breaks (Seymour et al., 1989).

If the sea is deep right up to the shore, the wave breaks right onto the beach, whilst if the sea is shallow, the wave may break far out (Day, 1974; Denny, 1988). A flat, sandy beach, dissipates the energy of the wave as it washes up the beach, while on a rough rocky beach, the wave does not run up as far and is more turbulent. The height of the run-up is important for the growth of interstitial organisms (ie those living between the sand particles) in the swash zone (Denny, 1988). The offshore region is that which is found outside the surf zone (region from the breakers to the waters edge) and the swash zone is the region which is alternatively covered and uncovered by the waves. The height of the latter region (and that of the surf zone) changes with the tide and this also affects the organisms existing in this area (Denny, 1988).

Waves nearly always break close to parallel, or parallel to the shore because if one moves in at an angle, the shore edge is retarded first and swings the rest of the wave around so that it is forced to come in parallel to the shore (Lewis, 1964; Day, 1974; Lobban et al., 1985). The non-parallel arrival of waves on the shore causes a "longshore current" that transports sediments along the coast (Denny, 1988). This longshore scouring causes long straight beaches such as those in Natal, unless there are areas of harder rock which cause headlands. These deflect the waves and lead to the formation of bays such as those in the southern Cape. Waves breaking parallel to the shore cause greater exposure than those which break at an angle (Dawes, 1981). The water of these waves, as well as that of short waves, rushes up the beach and washes back to meet the oncoming wave, increasing the turbulence (long waves can wash back without causing interference of

the next wave). This backwash may lead to rip currents which are jets of water washing out and then dissipating behind the breakers. The rips turn the longshore currents into offshore currents and may be dangerous to bathers as they often move at great speeds (Branch & Branch, 1981). In rocky environments, the rips are dissipated by the bottom topography.

1.5.1.2 Water Flow Over organisms

Local water flow over organisms and the substrata, may either be laminar, where there is a smooth flow of parallel layers with small scale movements; or turbulent flow, which is the irregular movement of the water even if the flow is in one direction, causing small scale water movements in a direction different to the direction of the main water flow (Vogel, 1981).

No matter what type of flow is experienced by an organism, there is a layer where the velocity of the water is zero due to the friction of the water passing over a surface. This layer is known as the boundary layer. It is defined as " the region from the po where the water velocity begins to slow down to the point immediately adjacent to the object where the water motion is zero" (Neushul, 1972). Boundary layers of macroalgae are reported to be approximately 150μm thick (Lobban et al., 1985). There are gradients of nutrients and dissolved gases across the boundary layer, determined by the diffusion rates of the nutrients. The boundary layer is said to be a function of the size and area of the blade and the velocity of the flow. Little is known about how the lamina deflects or affects water flow passing it or closely adjacent laminae. The thickness of the boundary layer is dependant on the velocity of movement of the surrounding water. A thin layer results in a reduction in resistance to nutrient diffusion thus

increasing nutrient flow to the thallus surface (Neushul, 1972; Dring, 1982; Lobban et al., 1985). The velocity of the flow and thus the nutrient supply, is increased by an increase in turbulence. Turbulence may be increased by the presence of wrinkles or spines on the plant surface, or by the plant remaining rigid and upright or moving in the direction of water movement (Neushul, 1972; Lobban et al., 1985; Koehl & Alberte, 1988). Norton et al. (1982) have reported different degrees of surface proliferations, spines and hairs on seaweeds inhabiting different regions. The theory that seaweeds produce their own turbulence by having an irregular surface is contradicted by reports that some kelps are smoother in sheltered areas than they are in turbulent areas (Norton et al., 1981). In Macrocystis integrifolia Bory the degree of rugosity increases with the increase in wave exposure, contrary to what one would expect in an area of high turbulence. This may be an adaptation of M. integrifolia to reduce drag or to strengthen the laminae, rather than to increase the velocity of flow and decrease the boundary layer (Norton et al., 1982; Lobban et al., 1985). Gerard (1987) reports that, in sheltered areas, the water velocity is lower and thus there is a decrease in the boundary transport of nutrients and a subsequent reduction in growth and production.

1.5.1.3 Beach Formation and Structure

Beaches experiencing rough surfs are composed of coarse sand and protected areas or estuaries, have fine, more stable sediments. The finer sand is found at the bottom of the shore because it is taken down the shore in suspension in the backwash. The coarser sand is, however, found higher up on the shore where it settles out of the water in the incoming waves. The finer sand is also blown out of this upper shore region when it dries, leaving the only coarse sand behind (Gray, 1981). The coarse sand

drains and dries quickly allowing buried organisms to become desiccated, while those living in fine sand are not desiccated because of the slower drainage. However, the finer sand may become stagnant and lacks a constant supply of oxygen (Branch & Branch, 1981; Gray, 1981). Temperature and salinity of the top layers of sand may also change due to solar warming and evaporation (Johnson, 1967). This affects any organisms living in the top few centimetres of the sand.

The main sediment distributor, on a large scale, are the currents (Gray, 1981). However, there is a high degree of water and sediment circulation in the surf zone. On sandy beaches where the waves surge far up the shore, wave action plays a big role (Lobban et al., 1985). In areas of high wave activity, waves may result in a shore with a small beach, a steep face and coarse sand, while the opposite is true in areas of less wave action (Dawes, 1981). The breaking or washing of waves onto a rock face or beach causes the rock to break up, and the sand and rock to be abraded and smoothed. The effect of the waves is concentrated midway between the high and low tide marks, and a rock platform may be eroded at this point on a rocky shore. A stretch of shore may also exhibit different topographies, and thus different exposures, at low and high tide, eg a steep slope which tapers off to a flat platform lower on the shore, would exhibit a high degree of exposure at high tide when the waves break on the steep slope; and low exposure at low tide when the waves break on the platform (Lewis, 1964).

1.5.2 Desiccation

Exposure to wave motion is the major force which affects the organisms in the intertidal zone, however, other wave exposure related factors are also important. Organisms living in the intertidal zone are regularly exposed to

the air for periods of time. This may lead to water loss and desiccation. The form of the plant is determined by the need to be efficient in metabolic functions, and at the same time be able to resist stresses such as desiccation and wave action (Norton et al., 1982). Algal thalli which are exposed to desiccation must either be able to recover from desiccation; or overcome it by avoidance, reduction or physiological tolerance (Dromgoole, 1980). Avoidance includes living in depressions which retain water, or resorting to microscopic or boring phases in summer (Branch & Branch, 1981). There are reports of the resistance to desiccation being a seasonal feature of the intertidal organisms, ie maximal in summer when the temperatures are at their highest (Schonbeck & Norton, 1979).

Tolerance to water loss is thought, by some, to be the main determining feature of the zonation of the shores, especially in the upper regions of the shore (the lower regions are thought to be controlled more by biotic factors such as competition and herbivory; Brown, 1987). Norton et al. (1982) reported that algae found on the upper shore regions were better suited to rapid water loss and recovery which causes biochemical damage, than to slow water loss, ie water conservation which causes physical damage. Within a zone inhabited by the same species, there may be differences in growth-phase (ie gametophyte or sporophyte) and morphology due to different responses to degrees of emersion (Allender, 1977). In some species, the small gametophyte generation is capable of withstanding the long daytime emersion while the macroscopic sporophyte is not (Druehl, 1981a).

Body shape and size are important in determining the rate and degree of water loss, as water is only lost from the surface of the organism (Norton et al., 1982; Brown, 1987). Thus larger organisms have a smaller surface area

to volume ratio and lose relatively less of their body mass (in water), than smaller organisms. Some algae contain a large amount of mucus which loses water, leaving the cell water intact, eg Splachnidium. Water content is thus also important, although to a lesser degree (Dromgoole, 1980). Other organisms store sea water in vesicles, eg Colpomenia, and thus retain water and nutrients to reduce desiccation and allow photosynthesis to continue (Oates, 1988). Some organisms have surface irregularities which trap water or a "false cuticle" which is caused by high concentrations of fatty acids in the epidermal cells, eg Fucus (Quadir et al., 1979). Seaweeds also give other organisms protection from heat and desiccation (Lewis, 1964). Beds or tufts of a single algal species, not only protect the members of the bed, but also offer protection for other organisms, by retaining water (Isaac, 1933). The type of structure which the organism displays is also important in the determination of the degree of desiccation, ie flexible plants collapse on themselves when emergence occurs and thus decrease desiccation more than if the plants were rigid and thus completely exposed to the atmosphere (Dromgoole, 1981).

The surrounding surface of the substratum also affects the degree of water loss, ie a smooth surface drains fast while a rugged surface or sand, retains water and keeps the overlying seaweed damp (Isaac, 1933; Lewis, 1964). In more wave exposed areas, the lower regions of the shore are continually washed by waves and the areas further up are wetted by wave spray, however, organisms are exposed to the air between wetting. The degree of wave action that the area experiences, affects the amount of exposure to the atmosphere that the inhabitants are subjected to (ie high wave activity causes increased spray). Schonbeck and Norton (1979) reported that plants transplanted from a wave exposed area to a sheltered area, demonstrated a

decrease in desiccation resistance and a correlated decrease in the percentage dry matter present. The role that the dry matter plays in the resistance to desiccation is not known, however, the percentage also changes with seasonal change in desiccation resistance (Schonbeck & Norton, 1979).

Emergence causes intertidal organisms to be exposed to extreme temperatures at low tide. On a hot, sunny day the rock on which an emerged seaweed is lying, may increase in temperature to a point higher than that of the air and a great deal higher than that of the water. At night the same rock might drop to a temperature lower than both the air and the water. A plant found in a shaded area would undergo the same temperature changes but to a smaller degree. The temperature of the water in small pools also differs considerably between the day and night. Some of the tips of plants in pools may emerge and become desiccated in calm periods when there is little spray (Norton et al., 1981). The higher up the shore an organism is positioned, the longer it will be exposed to these extreme temperatures and the less likely the chance of it being washed by a wave, ie having the temperature returned to that of the water. Organisms may be adapted to lose heat to the atmosphere or substratum by their shape, colour or texture. The temperature of the plant not only affects the rate of desiccation, but also the metabolism (Dring, 1982). A sudden increase in temperature may lead to a change in blade morphology or an increase in blade abscission (Norton et al., 1981).

1.5.3 Light Quality and Quantity

For the photosynthesizing organisms on the shore, light is an important feature. Under submerged conditions, the organisms that grow lower on the shore may receive little light due to the depth, turbidity of the water (Lewis,

1964), and reflection of the light off turbulence (Cousens, 1982). Increased wave exposure can affect the light reaching organisms by affecting turbulence and silt deposition. Light penetrates water 2000 times less than air (Dring, 1982). Thus light limits the depth of growth and is in turn limited by water turbidity, turbulence and depth (Denny, 1988).

Flatter laminae ensure a larger area exposed to the light and the possibility that the pigments are near the surface of the plant. Norton et al. (1982) reported that most seaweeds maximise their ability to trap light by having the chloroplasts on the outside surfaces of the surface cells and by holding the laminae perpendicular to the sun, eg when flat laminae are spread out by the flow of water (Norton et al., 1982). An increase in the surface area for nutrient uptake, eg branching or hair production as well as lamina overlap, may decrease the area able to absorb light due to self-shading (Koehl & Alberte, 1988). Similarly, shading may occur in dense clumps or kelp beds in which the adult plants are reported to shade younger plantlets and the lower branches of adult plants (Xiugeng & Neushul, 1984). There are reports of higher concentrations of photosynthetic pigments in plants which are found in deeper water or are continually shaded, eg Dictyota dichotoma (Hudson) Lamouroux (Perez-Bermudez et al., 1981).

The algae in small pools compete for light and this may result in elongation of the laminae. Many seaweeds are, however, damaged by too much light and, in these species, the maximum photosynthesis occurs while the plants are submerged. If there is a particularly low spring tide (especially in summer), these plants become damaged and sun bleached (Branch & Branch, 1981; Santelices et al., 1981; Duggins & Dethier, 1985). The time of day at which the low spring tide occurs is of particular importance to

species which become damaged by high light intensities, as low tides occurring at midday would increase the chance of desiccation or excessive light (Lewis, 1964; Dring, 1982). Some algae have adapted to withstand high irradiance by having migrating chloroplasts, eg Codium, or masking pigments, eg the brown algae. Algae may also grow in cracks, crevices, or on shady overhangs, all of which reduce the amount of sun that the plant receives (Denny, 1988). Light is also a limiting factor when young sporelings settle. If there are many adults, the sporelings will not receive sufficient light.

The amount of light which the plant receives is not only dependant on the depth, turbidity and turbulence of the water; but also by the amount of time that it is exposed to the atmosphere between waves. The rate of photosynthesis that the plants are able to achieve, is determined not only by the light received, but also the nutrient availability and uptake.

1.5.4 Nutrient Uptake and the Effects of Salinity

Algae in small pools must be tolerant to salinity changes, and nutrient and gas depletion. Salinity may increase due to evaporation, or decrease due to rainfall or runoff, and the carbon dioxide content may decrease due to algal metabolism (Branch & Branch, 1981; Dring, 1982). Small pools and sheltered areas which lack wave activity for a large part of the tidal cycle also lack the mixing which occurs in open seas (Dawes, 1981). This mixing distributes the salinity, nutrients and temperature of the water (Druehl, 1981a). The organisms deplete the oxygen and nutrient supply in their immediate vicinity and this is not replaced due to the lack of mixing. Depletion is increased by the high degree of epiphytism in these areas (Norton et al., 1982). The salinity is reported to change in the top few metres of

the water thus subjecting an attached alga to salinity variations with waves and change of tide (Druehl, 1981a). The top layers of water may also suffer nutrient depletion due to metabolism of phytoplankton (Smith, 1976; Valiela, 1984). Variation of salinity and nutrient concentration is reported to affect the morphology of algae, eg Fucus vesiculosus Linnaeus (Jordan & Vadas, 1972; Norton et al., 1981). Some of the algae which grow in areas experiencing salinity variation are reported to be able to withstand the decreases in salinity although the plants may exhibit a decreased growth rate. Some are even reported to photosynthesize well under conditions of varying salinity and nutrient conditions experienced in pools or sheltered sites, eg Phaeostrophion irregulare Setchell et Gardner (Mathieson, 1982b). The cell walls of algae (especially members of the Phaeophyceae) contain alginates and fucoidar which are reported to play a role (amongst other functions) in cation exchange and thus in resistance to salinity changes and possibly also to desiccation (Zavodnik, 1981; Mariani et al., 1985).

Wave movement is important for the provision of nutrients due to increased movement around the submerged plant (Kain, 1977; Day, 1974; Gerard & Mann, 1979). In submerged plants, the entire organism is involved in nutrient uptake, thus the surface to volume ratio of the plants is important for nutrient supply. In sheltered areas, there may be a smaller surface area to volume ratio (smaller plants) which decreases the amount of nutrients that are relatively available to the plant. These plants may develop hairs, branches, secondary stipes, spines, surface protrusion or more laminae to increase the uptake ability (Norton et al., 1982). The branches of some species remain rigid and perpendicular to the main axis to increase flow over the thallus and thus increase nutrient availability (Norton et al., 1982). A problem experienced by some marine plants is

that the carbon dioxide necessary for photosynthesis must be dissolved in water and thus some desiccated seaweeds are unable to photosynthesize. Algae in the highest regions of the intertidal zone must be capable of recovering from desiccation, starting to metabolise and absorbing nutrients rapidly when submerged (Dring, 1982; Norton et al., 1982). Brown (1987) reported that all the tested seaweeds (from different parts of the shore), recovered photosynthetic capability following desiccation, after three hours of submergence. The degree of recovery of photosynthesis after drying, shows the best correlation with the position of the individual seaweeds on the shore (Brown, 1987).

1.5.5 Sand Deposition

Sand movement is a further problem experienced by intertidal organisms (McQuaid & Branch, 1984). Intertidal algae may suffer abrasion from sand in suspension or become totally covered by sand for considerable lengths of time (Day, 1974; Dring, 1982). Littler et al. (1983), report that even rocky shores (not normally expected to be greatly affected by sand deposition) have sand mixed in with the benthic biota and sand movement and inundation does occur (especially in pools and depressions). Some species of seaweed cannot survive sand cover, while others thrive when covered, ie are sand-loving or psammophytic (Branch & Branch, 1981) possibly due to the protection provided by the sand, against epiphytes and herbivores (large herbivores are excluded and small attached forms which colonise the plant may be smothered; D'Antonio, 1986). Spores of some algae tolerate sand cover whilst others suffer from smothering, scouring, or becoming attached to sand grains which may be washed away (Mathieson, 1982a).

Sand burial not only affects organisms by physical scouring, but also due to smothering (reduction in light, dissolved oxygen and nutrients) and detrimental chemical changes in the microenvironment (Littler et al., 1983). Sand deposition and abrasion thus selects seaweeds with tolerant or strong basal systems, the potential to regenerate rapidly when abraded, the ability to withstand nutrient depletion and anaerobic conditions (Lobban et al., 1985), the prostrate rather than the erect morph of heteromorphic forms (Fletcher, 1987), those with rapid life histories which reproduce rapidly when the plants are uncovered (Dawes, 1981; D'Antonio, 1986), or incomplete life histories which ensure the continued genetic stability of the resistant plants (Daly & Mathieson, 1977). Sand deposition may affect the branching of the laminae, eg Norton et al. (1981) report very short, bushy plants due to the removal and subsequent regeneration of the apices from scoured plants. The abundance and distribution of both subtidal and intertidal organisms is reported to be reduced where there is regular sand deposition (Daly & Mathieson, 1977; Dawes, 1981). There are reports of periodic sand covering being advantageous to the population by making "free-space" available and allowing an increase in diversity by encouraging the growth of opportunists which appear soon after the initial burial (Littler et al., 1983).

Sand deposition may be seasonal (Lobban et al., 1985); Daly and Mathieson (1977) suggest diurnal, neap-spring, storm and summer sand inundations which may be affected by local topography, wave steepness, angle of wave impact, sand particle size, wind, tidal amplitude and beach slope. There are reports of sand inundation being highest in wave exposed areas (Mathieson, 1982a), although, high wave action may inhibit the settlement of sediment onto the laminae of the plants (reducing the possible shading effect). However, sediments kept

suspended also decrease the light reaching the organisms (Neushul, 1972; Koehl & Wainwright, 1985). It appears, however, (pers. obs.) that there may be a rapid alternation between sand inundation and removal in wave exposed areas on a tidal scale, while in sheltered areas there is a slow filling up which remains for long periods (until a storm or spring tide is experienced).

1.5.6 Herbivory

Lewis (1964) suggests that the effect of wave exposure on algae is indirect and only due to the effect of the exposure on the herbivores. Duggins and Dethier (1985) however, reported that the removal of chitons from experimental sites allowed the extension of the zone of subtidal kelps further up the shore to regions where they were unable to withstand the stresses of summer exposure, and thus died back. Kitching (1987) reports a variable reaction of both faunal and floral epiphytes and herbivores to differences in wave action. In sheltered areas where small herbivores such as snails are common (they cannot survive high wave exposure), grazing herbivores may even be an advantage to the alga in that they remove the surface epiphytes from the laminae (Lubchenco, 1983).

Littler et al. (1983) suggest that the degree of wave exposure may influence the algal population by affecting higher order predators, herbivores and algal competitors. There is reported to be an increase in the abundance and diversity of algae and a change in the predominant morph of the species, following the removal of the herbivores (Duggins & Dethier, 1985), eg upright when there are few herbivores and crustose when the herbivores are more active (Norton et al., 1981). Features of the algal morphology such as size, shape, toughness, calcification, presence of a "cuticle" and any surface irregularities

may affect the preference of herbivores for that individual (van Alstyne, 1988).

Seaweeds are the primary producers of the intertidal zone (phytoplankton play a small role in this region). The tiny algal spores and germlings are more readily grazed by herbivores and filter feeders, than the adult plants. A surviving sporeling must settle and grow fast and large to escape the herbivores. Herbivores assist the late succession species by consuming the often fragile, early succession plants. Thus spores of late succession plants have to land in protected areas in order for the sporelings to escape predation and abrasion (Lubchenco, 1983). There is also believed to be a different preference between the gametophytes and sporophytes of a species (Hannach & Santelices, 1985). Large plants are believed to be less palatable than their sporelings and immature thalli, for both mechanical and chemical reasons, eg less anti-herbivore substance is produced in small plants presumably due to the energy required for quick growth (Lubchenco, 1983). Many algae secrete an anti-herbivorous, secondary metabolite, eg Dictyopteris delicatula (Hay et al., 1988), which stops herbivores such as fish and starfish (smaller herbivores such as amphipods are not affected to such a degree) from eating the plants. Other species of algae have a shield of slime which may have antibiotic properties, while still others are reported to shed their outer surface thus discouraging herbivory, epiphytism and parasitism (Kitching, 1987). In more wave exposed regions, the areas damaged by herbivores are more extensively removed than in less wave exposed areas, and this decreases the chance of recovery or regeneration of these damaged areas (Norton et al., 1981). Aspects of the plant structure such as the toughness and the shape of the lamina, may also affect the herbivory potential, eg a narrow, buoyant

frond is more difficult to grip and manipulate than a flat, broad lamina (Watson & Norton, 1985).

1.6 ALGAL RESPONSE TO WAVE EXPOSURE

It has been reported that if water motion measurements were converted into wind speed, intertidal organisms would be experiencing forces of up to 400 m\s or at least 60 m\s, which is considerable if considering wind acting on terrestrial organisms (Charters et al., 1969). Some algae thrive in areas of high wave action where there is a high degree of water movement and thus high nutrient turnover. Others are unable to remain attached or entire in these stressful conditions (Simons, 1976). Adaptations for survival occur to the detriment of the growth and productivity (Gerard & Mann, 1979). There are reports (Dawes, 1981) of an increase in diversity but a lower productivity and biomass in some populations found in areas of higher exposure, and reports to the contrary in other populations (Gibbons, 1988). Kelp beds or large patches of seaweed, reduce wave action on the shore and thus provide protection for other organisms (Palmisano & Sheng, 1977). Plants growing in the wave-swept intertidal region are exposed to different degrees of wave action, resulting in varying degrees of abrasion, drag, gas and nutrient supply as well as the related environmental conditions discussed in the preceding sections. The plants react to these stresses in a variety of manners involving their morphology, population characteristics, reproduction, physiology and growth.

1.6.1 Effects of Wave Exposure on Morphology

Morphological changes in response to environmental stresses are the most immediately obvious responses displayed by organisms. Organisms adapt to different

conditions by developing the optimal phenotype for those conditions experienced.

1.6.1.1 Effects on Attachment

Intertidal organisms are exposed to intermittent pulls and jerks in different directions, due to the back and forth movement of the waves. Unlike terrestrial plants which have their root systems anchored under the ground, the attachment organs of the seaweeds are also exposed to the movement of the water (Norton et al., 1982). Wave strength determines the type of thallus able to exist in an area, since very flimsy or loosely attached plants are removed by the waves (Lewis, 1964; Day, 1974). Large plants have an advantage in that herbivory and desiccation is reduced, however, the plant may be removed by the waves before it has become reproductive. For this reason, large holdfasts are necessary on large plants. Holdfasts may be weakened by grazing or death of the central rhizoids due to sediment settlement, and this may result in the removal of plants during times of exceptionally high wave activity (Seymour et al., 1989). Areas of calm water often support loosely attached plants (Moss, 1950), and the attachment strength may differ on the sides of a boulder which experiences different degrees of wave exposure (Moss, 1950; Lobban et al., 1985). Individuals inhabiting the most wave exposed parts of the coast require specific adaptations in order to cope with the stresses of drag imposed by the waves, and abrasion due to both sand and being thrashed against the rocks (Lobban et al., 1985). Species in these wave exposed environments have particularly well developed attachment mechanisms which are thought to be stimulated by high wave activity, eg the haptera of Laminaria and Ascophyllum or the mucus adhesive of limpets (Lobban et al., 1985; McEachreon & Thomas, 1987). The majority of the current movement is in the top layers of the water,

thus the force on the holdfast is determined by the speed of the water, ie the drag on the laminae, and the height of the plant (Vogel, 1981). It is not only the size of the holdfast that determines the attachment strength, but also the area in contact with the substratum and the type of substrata (ie sand shifts and is thus not as stable a substratum for attachment as rock; Norton et al., 1982). There is a close association between the rhizoids which constitute the holdfast, and the substratum.

1.6.1.2 Effects on Shape

Cheshire and Hallam (1988) suggest that in any population of seaweed there are different forms and that these range in variation around an average which is correlated to the level of wave exposure experienced by the population. Similarly, it has been suggested that different wave exposure causes different morphologies and life-histories in the same species (Fletcher, 1987). It has also been reported that certain brown algae reduce in size and undergo both anatomical and morphological changes (Fletcher, 1987) in different wave activity areas. Organisms which exist in similar environments often have similar forms, although they are unrelated (Norton et al., 1982).

Plants cannot be easily transplanted from areas of low, to areas of high wave activity. The plant adapts to the environmental conditions early in its development and is thus not able to change rapidly (Lobban et al., 1985). The transfer experiments which have been performed have, however, been successful when juvenile plants were used (Cheshire & Hallam, 1988). It is thought that the main reason for the lack of success in transplant experiments, is that the attachment organs of the plants from calm areas are unable to keep the plant attached in more wave exposed areas due to their reduced size (Armstrong,

1987). Alternatively, the algae show a decrease in growth due to their exposure to light and air during the transfer (Gerard & Mann, 1979). Another possible reason is that fragile laminae are ripped apart in the more stressful environment. The reverse transfer, ie plants from an area of high wave exposure to a calmer area, has had some success and the plants are reported to survive and grow into a form similar to that of the surrounding plants (Gerard & Mann, 1979).

The shape and texture of the plant determines the effect that the waves have. Adaptations to high wave exposure may include rounded, branched thalli to reduce resistance, flexibility to be able to bend in the direction of water movement or rigidity to be able to withstand it (Armstrong, 1987), elasticity or coiling of the stipe to be able to extend with the water motion, splitting of fans, or the production of surface protrusions or mucilage to reduce drag (Norton et al., 1981; Lobban et al., 1985; Gerard, 1987). There are reports that the ripples or frills found on the edges of some algal laminae (previously thought to reduce the drag of the water by reducing the turbulence around the individual; Branch & Branch, 1981), are not to reduce the drag but rather to decrease the chance of the laminae tearing (Vogel, 1981). Some species become flat and encrusting, ie occur within the boundary layer to reduce resistance (Sheath & Hambrook, 1988), others form a cushion, to withstand the wave force. The individuals of a species in wave exposed sites are generally shorter, eg Laurencia papillosa (Forssk.) Grev (Kilar & McLachlan, 1986), thicker, eg Laminaria hyperborea (Gunn.) Fosl. (Kain, 1977), more robust due to an increase in strengthening tissue (Norton et al., 1981) and bushier, with narrower laminae, eg Laminaria longicruris de la Pylaie (Gerard & Mann, 1979) or have more branches and a larger attachment organ, eg Sargassum cymosum C. Agardh,

than those in sheltered sites (Norton et al., 1981; Payri, 1984; de Paula & de Oliveira, 1982; Lobban et al., 1985; de Ruyter van Steveninck & Breeman, 1987). Narrower laminae found in some species of algae from quieter waters are reported to be a result of nutrient depletion caused by lack of water movement (Norton et al., 1982).

Some algae are soft and floppy offering the least amount of resistance to the action of the waves (Norton et al., 1981). Plants consisting of a few flexible laminae will clump together thus reducing the area exposed to the current (Koehl & Alberte, 1988). They bend in the direction of the surge in order to maximise their length in the direction of the wave movement, and to form a single unit for the water to flow around. This acts to reduce the drag around the plant (Charters et al., 1969; Vogel, 1981; Lobban et al., 1985). Streamlining of sessile organisms in turbulent flow is problematic in that the direction of waves is unpredictable, and thus the individual cannot align itself to the direction of the wave, prior to the wave's arrival (Branch & Branch, 1981). In times of turbulent flow, the laminae are moved in different directions and there is no unidirectional drag placed on the plant, such as there would be if there was a single surge or current (Cheshire & Hallam, 1988). Large plants, however, may flap in a current (increase in drag on the fronds; Vogel, 1981) and become abraded or torn. When there is little water movement, the blades spread out and increase the area of the canopy thus increasing the photosynthetic area of the plant (Vogel, 1981; Neushul, 1972). The drag on the fronds can cause tensile or breaking stress in the stipe only when it is parallel to the direction of the waves or currents.

Water keeps submerged bodies buoyant and allows the organisms to expend less energy on support tissue, and they are thus often soft and floppy. Macroalgae are

capable of producing more photosynthetic tissue than terrestrial plants because they do not need to produce supportive tissue. Algae may be very soft but, due to the increased photosynthetic rate, they are capable of growing faster than land plants (Branch & Branch, 1981). However, algae growing in more wave exposed sites need more strengthening and structural tissue, to withstand the wave forces, than those growing in sheltered areas. An increase in support tissue results in an decrease in amount of photosynthetic tissue which is counteracted by an increase in the photosynthesis due to the increase in the uptake of nutrients and gases (Norton et al., 1981). There are reports of thicker cell walls and an increase in the cortical layer of algae in areas of higher exposure (Cheshire & Hallam, 1988). There is also an increase in the alginic acid of cells from the base to the tip of Durvillaea potatorum (La Billardière) Areschoug individuals from high wave exposure. This results in a firm holdfast and base, an elastic, flexible stipe and laminae which are able to withstand wave activity (Cheshire & Hallam, 1985). Gerard (1987) reports that continual, longitudinal tension, such as that placed intermittently on laminae of seaweeds by wave action, causes elongation and narrowing of the laminae of Laminaria saccharina (L.) Lamour due to changes in the orientation of the cell divisions (rather than cell size or division rate).

It is thus apparent that the reaction of plant morphology to different levels of exposure varies with different species. Thus, there is no single reaction which can be used as an index to predict what exposure an individual has experienced, or how a species will react to new conditions.

1.6.2 Effects of Wave Exposure on Population Dynamics

Numerous researchers suggest that waves are one of the most important features in the determination and distribution of a population (Lewis, 1964; Palumbi, 1984; McQuaid & Branch, 1985). The degree of wave exposure is seasonal and thus influences the temporal distribution of species, eg more fragile or rigid individuals are more common in times when the average wave exposure is lower, ie seasons with fewer storms (Santelices, 1977). Some species which are weaker may extend their habitats from sheltered areas to more wave exposed areas in the calmer seasons (Santelices, 1977). Even within one general environment type, eg wave exposed or sheltered, there may be local changes in dominance and distribution of a species (Lewis, 1964). Waves also extend the inhabitable region of the shore, ie the water goes further up the shore in a wave exposed site than in a sheltered area (Day, 1974). This, together with the spray, elevates the zones in high wave activity areas. Some intertidal algae, eg Ascophyllum nodosum (L.) Le Jolis are reported to grow faster under spray conditions than under submerged conditions (Rheault & Ryther, 1983). The zones in sheltered areas are both lower on the shore and compressed, compared to those on wave exposed shores (Powell, 1957; Lewis, 1964; Dawes, 1981). The degree of exposure is also thought to determine the pattern of succession and the climax species (Lubchenco, 1983). Wave activity reduces morphological variability of members of a population by removing some morphological forms. There are also reports that wave exposure affects the age structure of a population. An example of this occurs in populations of Laminaria setchellii Silva which are composed of mainly young plants in wave exposed areas, with a more even spread of age classes in less wave exposed areas (Klinger & DeWreede, 1988).

It is reported that populations of Sargassum cymosum from areas of differing degrees of wave exposure, become ecotypes and thus variation in morphology becomes a genotypic rather than phenotypic response to the environment. This is demonstrated by the lack of change when the plants are transplanted between areas of different wave exposures (de Paula & de Oliveira, 1982). Thus wave exposure affects the physiology, phenotypic expression and genotypic variation of the population (Cheshire & Hallam, 1985).

1.6.3 Effects of Wave Exposure on Reproduction

Payri (1984) reports more rapid development of the thalli and reproductive structures of individuals found in highly wave exposed sites. Spores of some species are unable to germinate unless they are exposed to high wave activity (Dawes, 1981), although most spores, zygotes and germlings are more sensitive. Wave activity is important in the dispersal of the spores of organisms. However, high wave activity may mean that some spores will land in unsuitable areas (eg on areas with unsuitable surface texture or toxic areas) and will thus not survive, eg spores of some algae can withstand only slight degrees of desiccation (Fletcher, 1987). Sexual reproduction is much more difficult in wave exposed areas where the partners and the gametes can be washed away, therefore many plants in these regions reproduce asexually by spores, or by vegetative propagation (Denny, 1988). Plants in wave exposed areas may have their spores swept out to sea and this may result in the sporophytes only growing close to the substratum, eg Alaria or in protected grooves and crevices, eg Postelsia, to decrease the chance of the spore loss (Norton et al., 1982). In some species, spores are not dispersed from the adult before germination. This ensures a suitable habitat for attachment, eg Fucus sporelings (Branch & Branch, 1981). Similarly, the zygote

may be retained on the parent for a short while after fertilisation, eg Sargassum muticum (Yendo) Fensholt. In wave exposed sites, germlings of individuals of S. cymosum may be found growing amongst the branches of the adult plants. This also occurs in sheltered areas but not in the intermediate wave exposure areas (de Paula & de Oliveira, 1982). The released spore has to pass through two boundary layers before settling, ie the layer around the plant and that above the substratum. A special mechanism which aids the spore in passing through the boundary layers may thus be needed (Vogel, 1981). Motile spores or gametes are able to increase the speed at which they can reach the surface, although they are moving at speeds far less than the surrounding water (Lobban et al., 1985). A settled spore must remain in a boundary layer of still or slight flow, to become attached. The chances of attachment are increased after the production of the attaching organ (eg rhizoid/s).

Wave exposure also affects vegetative propagation by increasing plant breakage (ie a source of material for propagation) and spreading plant segments to uncolonised areas. Vegetative propagation is of particular importance at the end of a alga's distribution range (where sexual reproduction potential is reduced), and in the colonisation of new areas.

Spore dispersal is also affected by aspects of the spore itself such as the sinking rate, ie how far the spore is washed before reaching the substratum. The sinking rate is determined by the size of the spore, distribution of the organelles, and the nature of the spore, ie clumped or attached to a slime-like substance which increases the mass (Neushul, 1972). Lewis (1964) reports that, in some cases, more spores are washed onto an area of high wave activity, while in others the spores are washed past the wave exposed area and into a sheltered bay where they may

settle and become attached, but not survive due to the turbidity and low light. There is, however a higher degree of dispersal and wastage in the wave exposed areas (Lewis, 1964). On rocky, wave-swept shores, however, spores are more likely to be washed over a suitable area, and to find a irregularity in the rock to which they can attach (Norton & Fetter, 1981; Lobban et al., 1985). The longer the spore remains in one spot, the more attached it becomes (Lobban et al., 1985), however, particularly violent wave action may dislodge even the most well attached spores (Norton, 1983).

Water movement affects reproduction by affecting spore and gamete dispersal and attachment (by silt deposition and water movement) and dispersal of pieces of plant which act as units of vegetative reproduction (Druehl, 1981a).

1.7 REGENERATION

Intertidal organisms which are exposed to waves and the atmosphere, eaten by herbivores, or abraded by sand may experience damage to various parts of their structure. In seaweeds this may include damage to the attachment organ, the stipe or the laminae. Damaged individuals must be able to repair wounds and regenerate the plant tissue which has been damaged or removed, to enable them to retain their perennial nature.

Regeneration of plants may also be a method of asexual reproduction when removed sections become reattached and grow new thalli. Vegetative propagation occurs in a number of algal species and is important for the dispersal of these species. It is also important when dealing with commercially harvested species which are required to have rapid regeneration rates to be

commercially viable (Moss, 1961). The rate of regeneration differs with plant morphology and age. It must be remembered, during viability studies, that there are reports of differences in the morphology and regeneration of plants in culture and in the field (probably due to the difference in environmental conditions, Fagerberg & Dawes, 1976). Regeneration of algal tissue after wounding is a complicated process which may occur from a variety of plant parts.

1.7.1 Causes of Regeneration

High wave exposure may cause severe damage to intertidal algae due to the sheering force of the waves, increased sand abrasion or lamina removal during storms. Frequently damaged plants need to have the potential to regenerate rapidly. Despite this, the regeneration and recovery of commercially harvested Ascophyllum nodosum is reported to be greater in sheltered areas than in wave exposed areas (Keser et al., 1981). Regeneration allows individuals to remain perennial despite seasonal increases in wave exposure, abrasion and herbivory.

Van Alstyne (1989) reports a positive correlation between the number of Littorina snails and the degree of regenerative branching. The damage caused by herbivores, as with other types of damage, needs to be repaired and the tissue replaced rapidly. In areas of intense grazing, rapid regeneration is important for the continued survival of the individuals. There are reports, however, that damaged laminae of Fucus increase their phenol production thus reducing the attraction to herbivores and allowing the damaged laminae to heal and begin regeneration (van Alstyne, 1988).

Besides the removal of tissue due to herbivory, abrasion and waves, there is also natural senescence of laminae.

This is reported to be seasonal in a number of marine algae (de Paula & de Oliveira, 1982). It is common for the perennial holdfasts of seaweeds to regenerate laminae annually, after all the laminae have been removed. This type of alga is known as a pseudoperennial.

1.7.2 Process of Wound Healing

Recovery after damage involves two processes. Firstly the wound heals, and then the tissue regenerates. Wound healing involves changes in the cells which underlie a wounded area. This may occur through the formation of plugs, layers or plates of a substance which is thought to be sulphated polysaccharide in the brown algae (Fulcher & McCully, 1971; Fagerberg & Dawes, 1976). After wounding, the cells just below the irreparably wounded cells in Fucus, round up and become pigmented (Moss, 1961). There is an accumulation of vesicles, thought to be involved in plug formation and found predominantly at the wound surface (Lobban et al., 1985). Mitochondria and dictyosomes also increase in number, while the number of chloroplasts may decrease. This indicates an increase in secretory and respiratory functions and a decrease in photosynthesis within cells that are devoting their energy to the healing of the wound (Fagerberg & Dawes, 1977). Formation of a plug or plate is followed by the accumulation of polysaccharides at the surface of the wound. The majority of the unwounded cells positioned adjacent to the wounded area, appear not to lose their contents. There is, however, a report of a few layers of medullary cells adjacent to the wound, losing cytoplasm in Sargassum filipendula C. Agardh (Fagerberg & Dawes, 1976). The intact medullary filaments and cells adjacent to the wound in some Phaeophyta, are reported to contain an antibiotic substance (probably a phenol) which is released and may provide the exposed cells with some

chemical protection (S. filipendula, Fagerberg & Dawes, 1976).

Following the initial plug or plate formation, the medullary cells may give rise to filaments which grow through the wound and form a protective layer or new epidermis in Fucus (McLachlan & Chen, 1972). The inner cortical and medullary cells experience longitudinal divisions and the outer layer of cells redifferentiate into epidermal cells, both actively and physiologically (Fritsch, 1945). In Sargassum, there are reports that, following damage, the new epidermal cells have a different shape, ie are irregular rather than the original regular, cuboidal cells (Fagerberg & Dawes, 1976). The cells around the wound not only change in shape, but also in their ultrastructure. The wound repair and regeneration processes are thus unusual in that there is the redifferentiation of previously differentiated tissue.

1.7.3 Process of Regeneration

Once the wound has healed, regeneration may begin. Regeneration can be induced in culture but is more prominent in plants which are prone to damage in the field (McLachlan & Chen, 1972). The type of tissue which is regenerated (rhizoid-like filaments or blade tissue), depends on the position of the wound relative to the base and the tip of the plant (ie polarity; Lobban & Wynne, 1981).

The new epidermal cells of Fucus, in certain regions of the wound, divide to produce branch initials which develop into adventitious branches (or adventive embryos; Fulcher & McCully, 1969; McLachlan & Chen, 1972). The production of a protrusion and its development into a flattened lamina with an apical meristem and rhizoids in

Fucus, is similar to what was observed in Dictyopteris longifolia (this study) and what has been reported for various other species of brown algae. The adventive embryos of Fucus may reach a size equivalent to the parent frond, and differentiate into a midrib, wing region and fertile tips (Moss, 1961). The newly regenerated tissues of Fucus and other species go through a similar developmental sequence to that which has been observed in the developing zygote of that particular species of alga (McLachlan & Chen, 1972; Lobban & Wynne, 1981). If the embryos continue to grow, the plant develops a very bushy growth form.

1.7.4 Regeneration Potential of Different Regions

It has been reported that regeneration occurs more prolifically from the cells in the midrib region than from those in the wing region, eg Fucus (Fulcher & McCully, 1969; van Alstyne, 1989). According to Fulcher and McCully (1969), this is due to the higher concentration of filaments in the midrib region. These filaments, together with the cortical cells, form the new epidermis from which the regeneration takes place in Fucus. Regeneration is reported to occur from different portions of the plant and the regenerative tissue is usually similar to the original damaged tissue (Lobban & Wynne, 1981).

1.7.4.1 Regeneration from Laminae

Regeneration of new laminae may occur on the remains (when the latter are not completely abraded away) or injured areas of old laminae. Fronds of Sargassum species have been shown to be regenerative both in the field and in the laboratory. Whole branches of individuals of this genus were broken off and still remained fertile while free-floating (Paula & Eston, 1987). There are reports

that continual damage and subsequent regeneration from new apical meristems results in an algal growth form which consists of many proliferations from a short, central axis (Norton et al., 1981; Lobban & Wynne, 1981). Damage to the growing apical tips may occur when these are abraded, eaten, or become reproductive and decay after gamete release, eg Enteromorpha (Lobban & Wynne, 1981). Removal of the lamina tip may result in varying regeneration patterns as various parts of the laminae differ in regenerative potential. It has been discovered that the process is greatest in the primary laterals of members of the genus Sargassum (Fritsch, 1945; Lobban & Wynne, 1981; Tsukidate, 1984). However, removal of the apex has been observed to result in greater regeneration of the side laterals due to the removal of the apical dominance (Tsukidate, 1984). The apical region of some algae lack regenerative ability all together; this is thought to be due to an apical dominance effect (Moss, 1961). Older plants and older parts of newly produced thallus have the greatest regeneration potential.

There are reports that regeneration occurs from the wings as well as the midrib, although the former occurs more slowly. This is thought to be due to the smaller number of medullary cells in the wings. The layer of filaments involved in the wound healing and regeneration processes of Fucus, originate from the medullary cells (Moss, 1961). In Fucus vesiculosus there is reported to be regeneration of vegetative branches from both sides of a strip of lamina (Moss, 1961). If sections of this plant are kept on agar, only filaments develop. These do not develop into branches. The ability of pieces of Laminaria lamina to continue to metabolise, grow and possibly regenerate, has been used to study physiological processes such as photosynthesis, when use of the whole plant is impossible (Drew, 1983).

1.7.4.2 Regeneration from the Stipe

The "stipe" or part of the plant attaching the lamina to the holdfast may also exhibit regeneration of new laminae. Stipes of Sargassum filipendula were observed to produce embryos in a similar manner to that reported for the regeneration from other sections of the plant. There is the formation of a new epidermis, the production of meristematically active cells and the development of buds. This is followed by a change from a tubular structure to a flattened thallus, which may exhibit differentiation of tissue and develop an apical pit (Fagerberg & Dawes, 1976). The same authors report that in the initial stages of development when the embryo is merely a tubular structure, the mitotically dividing cells exert a similar effect to the apical cells in the later development, ie control over cell differentiation. Lee (1985) reports that the inner stipe tissue of Laminaria saccharina may produce protrusions that develop into male-like gametophytes. These were observed to produce antheridia in some cases, and female-like branches in others. Furthermore, the regenerating stipe tissue is morphologically and anatomically similar to the tissue of the lamina and not like that of the original stipe (Fagerberg & Dawes, 1977).

1.7.4.3 Regeneration from the Holdfast

Plants which seasonally lose their fronds and regenerate from the holdfast are known as pseudoperennials (Lobban & Wynne, 1981), eg the perennial nature of S. filipendula, is due to continuous regeneration from attached holdfasts (Fagerberg & Dawes, 1976). New fronds were reported to be produced from the holdfast but whether this was regeneration from individual rhizoids or from the base of the original stipe, is not clear. McLachlan and Chen (1972) report that removed or damaged laminae may be

replaced by the development of new embryos from the superficial cells of the holdfast disc in species of Fucus. In Sargassum muticum, the basal and holdfast regions of, in particular, older plants more actively undergo wound healing and the production of new laminae, than the rest of the frond (Fletcher & Fletcher, 1975). Mooney and van Staden (1985) report a large number of lamina initials (protrusions of tissue), developing on the holdfast of S. heterophyllum (Turn.) J. Agardh. In immature holdfasts of S. heterophyllum, however, only the individual protrusion which grew from the remains of the original main axis, developed into a shoot. This indicates that there is apical dominance of the main axis region over other protrusions from the holdfast. Mature holdfasts, however, were reported to develop a plantlet from each of the protrusions that were present on the experimentally cut surface. This suggests some change in the effect of dominance of the main axis (Fletcher & Fletcher, 1975), with an increase in plant age. There does seem to be a minimum holdfast size for the regeneration of new laminae (Lobban & Wynne, 1981; Norton et al., 1981). Individuals which regenerate from the holdfast are reported to frequently be short and bushy.

The ability of holdfasts to regenerate laminae is important for the planned clearing of invasive species from an area, as well as regeneration of a population harvested commercially (Keser et al., 1981; Roland, 1985). For example, it was found that if the holdfast and a small section of the stipe of Ascophyllum nodosum is left during harvesting, recovery of the plants is faster than if the plants are removed totally, thus increasing the profitability of the population (Dring, 1982).

Although the production of new laminae from holdfasts is common, reverse regeneration does not seem to occur in culture. Moss (1961) reports that even when a substratum

is provided, an attached lamina strip of Fucus vesiculosus does not produce a new holdfast but rather develops branches from both sides or individual rhizoids from the basal side.

1.7.4.4 Regeneration from Rhizoids

The holdfasts of many macroalgae are composed of a mat of filaments or rhizoids. There are reports of the production of adventive embryos or new thalli from the rhizoidal filaments in sporelings of the brown alga, Fucus. These embryos were observed to appear spontaneously and not following wounding (McLachlan & Chen, 1972). Development was reported to occur under a variety of environmental conditions, although the conditions did affect growth rate. McLachlan and Chen (1972) also report that the removal of rhizoidal filaments from a holdfast, results in the stimulation of the production of embryos on the removed rhizoids. Both excised filaments which had the initial stages of an embryo at the time of excision, and those that lacked the initial stages, became attached and the embryos developed in a similar manner to those on the holdfast. Excised rhizoidal filaments lack any pigment and thus have to produce photosynthesizing thalli before they can grow further. Even the rhizoids of adventive embryos may develop new adventive embryos in culture (McLachlan & Chen, 1972). The process of rhizoidal adventive embryo formation is similar to that reported for regeneration of new laminae from other regions of the thallus. The only difference between the rhizoidal adventive embryos and those produced by the epidermal cells, is that the former are superficial to the parent plant, at the beginning of the development, and only become closely associated later in the development (McLachlan & Chen, 1972).

In the initial stages of embryo formation on the rhizoids of Fucus sporelings, the normally empty rhizoidal cells were observed to experience an increase in cellular material. The first division of the cell was parallel to the axis of the rhizoid, and this was followed by rapid division and the production of a flattened embryo which had rhizoids and an apical depression (McLachlan & Chen, 1972). From this stage, the development was similar to the development of a normal zygote, although in some species of Fucus, further development was not experienced unless the parent suffered damage. This suggests an apical dominance effect exerted by the parent plant. There may be many adventive embryos associated with a single sporeling, with the majority developing near the proximal end of the rhizoid.

A similar process of regeneration from pieces of sporeling rhizoid, has been reported for Pelvetia (Saga, 1978), in which the colourless sections of rhizoids from germlings grown from eggs, were used. This author does, however, suggest that the regeneration of the embryo was stimulated by injury followed by isolation. Another important point that was mentioned by this author, is that the irreversible polarity which is expressed by the germinating egg, is changed during the production of another lamina apex out of the side of a holdfast rhizoidal cell. A similar process has also been reported for the rhizoids of Sargassum vulgare C. Agardh (Paula & Eston, 1987) and Dictyopteris divaricata (Okam.) Okamura (Tokida et al., 1953). The latter is a genus in which plants grow repeatedly in similar areas, with little seasonal fluctuation in plant number. The propagation of new plants from rhizoids is reported to be the principle means of reproduction in some species of Dictyopteris (Tokida et al., 1953).

1.7.4.5 Other Regions of the Thallus with Regenerative Potential

Various other sections of algal thalli have been reported to be able to regenerate new thalli. Laminaria sporophytes and Alaria gametophytes have been grown from single sporophyte cells (Saga et al., 1978); and Lobban and Wynne (1981) report that isolated rhizoid cells of Pelvetia have been induced to produce new thalli. The ability to regenerate from small numbers of cells could be important in mariculture.

The conceptacles of Sargassum have been found to produce regenerative tissue (Paula & Eston, 1987). Fletcher and Fletcher (1975) report the production of small, adventitious branches with receptacles on the tips, from the damaged terminal regions of S. muticum receptacles. It is thought that the conceptacles are not affected by the influence of apical dominance and are controlled by a different hormone system which directs regeneration of new conceptacles after the originals are damaged. This is not, however the case in all species of Sargassum. Mooney and van Staden (1985) report a lack of regeneration from the cut end of the apical receptacle of the primary lateral in S. heterophyllum. Sections of the receptacles of Fucus vesiculosus are also reported to lack the ability to regenerate (Moss, 1961; Lobban & Wynne, 1981). In individuals in which the gametes have already been released from the receptacle, fertile proliferations may be produced by the branch below the receptacle. This is thought to be due to some reproduction related substance which diffuses from the receptacle into the cells below (Moss, 1961).

Another section of the brown algal thallus reported to have regenerative abilities, are the hairs which are sometimes produced by the thallus. Trichothallic hairs in Fucus have a meristematic base, while the rest of the

hair is composed of empty cells (Fries, 1985). When these hairs are detached, they float and may develop into branched, filamentous plants. It has been shown that the hairs need indole-acetic-acid (IAA) and other hormones to develop further (Fries, 1985).

1.7.5 Polarity

The effect of the apical cells on the rest of the thallus and its growth and regeneration, is obviously very important. Lateral branches may be inhibited by the apical cells or the meristem which determines whether any regenerative proliferations are produced and whether they develop into blades or rhizoids. In Sargassum muticum, the sections which included the apical cells were observed to lack regeneration of new laminae and continue to elongate. The subapical regions exhibited the development of lateral branches when there was no apical dominance (Moss, 1965; Fletcher & Fletcher, 1975; Chamberlain et al., 1979). Apical dominance in S. muticum is exhibited by the inhibition of secondary laterals by the primary apices. The secondary apices inhibit, in turn, the tertiary laterals. When the primary apex is removed, the secondary apex may take over the role of the apical section (Chamberlain et al., 1979). In this species, the effect of the apex decreases with an increase in distance away from the apex (Chamberlain et al., 1979). There are also reports that there is no regeneration of sections of the stipe while the apical tip is still attached. This indicates another example of the effect of the inhibition due to the apical cells (Fagerberg & Dawes, 1976).

Inhibition by the apical region of the lamina is believed to be caused by the production of some substance by the apical cells. Kingman and Moore (1982) and Lobban and Wynne (1981) extracted indole-acetic-acid (IAA),

abscissic acid (ABA), cytokinins, as well as some other unknown growth regulators, from Ascophyllun nodosum. In Sargassum muticum, the application of IAA inhibited the apical segments of the primary laterals (Chamberlain et al., 1979). Growth inhibitors were also reported in S. heterophyllum by Mooney and van Staden (1985). The latter inhibitors were said to be produced in the apex and then transported down the axis. There are conflicting reports about the decreasing effect of apical dominance towards the base of the plant (due to a decrease in concentration of the growth inhibitor), eg a decrease (Lobban & Wynne, 1981) or no decrease in the effect of apical dominance (Fletcher & Fletcher, 1975). For example, the number of rhizoids that are produced from damaged tissue may increase with an increase in the distance away from the apical region in Fucus (Lobban et al., 1985).

There are many reports of the basal end of a lamina segment regenerating rhizoids and the apex producing laminae (Lobban & Wynne, 1981). An example of this was observed in Dictyota dichotoma (Russell, 1970), where rhizoids were produced by the basal side of the lamina section, and laminae from the opposite side. However, an exception is observed in Sargassum muticum, in which only the basal regions are reported to produce adventive embryos or regenerative shoots. Furthermore, the number of rhizoids produced by S. muticum may also increase towards the basal region, ie a basipetal increase (Lobban & Wynne, 1981). McLachlan and Chen (1972) report that thin sections of Fucus thallus do not exhibit the regeneration of rhizoids on the opposite side of the section to the adventive embryos. Instead, the embryos may be observed on both surfaces which is contrary to the strict polarity observed in the zygotes of the same species. However, Fulcher and McCully (1969) report that Fucus only regenerates adventive embryos on one side of sections.

Towards the apex of the frond of S. muticum, the rhizoids produced grow from the cut edge, while lower down, they are produced from the surface of the lamina. There are reports of lower counts of rhizoids observed when the apical cell is left intact, which seems to indicate that there is an apical control over rhizoid production, ie some kind of rhizoid inhibitor (Russell, 1970).

1.7.6 Regeneration as a Method of Asexual Reproduction

Regeneration of new plant tissue from pieces of the adult plant, is also a method of asexual reproduction or vegetative propagation, which increases the colonisation of an area by a species (Fritsch, 1945). This type of reproduction is of particular importance at the end of the range of a species, where sexual reproduction is unlikely to occur due to the low number of individuals. A section of the parent plant must be removed and become attached in a suitable environment before new tissue is generated and the section develops into a new individual. Regeneration potential is also important when dealing with invasive species such as Sargassum muticum (Paula & Eston, 1987; which has spread from Japan to North America and South West Europe). In the latter case removal programs must ensure complete removal of the entire plant to prohibit regeneration of tissue.

1.8 SEXUAL REPRODUCTION

The wave exposed, intertidal environment is not optimal for sexual forms of reproduction, as wave action reduces the chance of the individual gametes meeting for fertilization (either internally where sperm has to reach the internally retained egg, or externally where the motile sperm and egg cells are released and have to meet

to fuse). In some species, the gametes are released synchronously to increase the chance of fertilisation. Examples of this occur in members of the Dictyotales, in which gametes are released with varying periodicity in different species, eg Dictyopteris muelleri (Sonder) Reinbold which has a periodicity of seven days and is stimulated to release gametes by light (Phillips, 1988). Another member of the Dictyotales, Dictyota dichotoma, is reported to exhibit a periodicity related to the tide experienced by the plant, ie the periodicity changes with locality (Hoyt, 1927; Vielhaben, 1963); or to the phase of the moon (Phillips et al., 1990a). In these cases, as well as in the species which have some form of sperm attractant produced by the egg (eg the pheromone multifidene which is reported in a member of the Dictyotales known as Zonaria angustata) (Phillips et al., 1990a; Kajiwara et al., 1985), there are large numbers of gametes produced and released but very few fertilised. There are various reports that members of the Dictyotales exhibit a sporophytic majority amongst the plants of a population (Tokida et al., 1953; Fritsch, 1945; Phillips, 1988). Phillips (1988) reports that the gametophytes of the Dictyotales studied in her research, went through periods of being more common, indicating that there may be a temporal or spatial variation in the distribution of gametophytes. The antheridial sori of Dictyopteris species are irregularly shaped patches found in fertile zones. The antheridia are dense with cytoplasm and swell above the surface of the lamina. The female gametophyte of members of this genus, may be confused with the sporophyte as the immature oogonia are scattered and swollen above the surface, and resemble the sporangia (Phillips, 1988).

1.9 TETRASPOROGENESIS

As has already been discussed, vegetative propagation (see 1.7.6) is a method of reproduction without gamete fusion which is highly successful in a great number of species inhabiting areas of high wave exposure. Another method of asexual reproduction common in these organisms, is the production of spores. These may be haploid or diploid, and are normally produced by the diploid sporophyte through meiosis (Dring, 1982). It is thought that the production of spores rather than gametes, is under the control of environmental factors, eg temperature (Dring, 1982). Reproduction in the form of the production of spores, is reported to be particularly prevalent in the members of the brown algae (Dawes, 1981), and is even reported to be the most common form of reproduction in primitive forms of Phaeophyta (Lobban & Wynne, 1981). In members of this group, the haploid gametophytes give rise to the diploid sporophytes through the fusion of gametes. These gametes may also act as asexual reproductive bodies and give rise to gametophytes, parthogenetically. Similarly, the diploid sporophytes can produce haploid spores through meiotic division, or can reproduce sporophytes parthogenetically through cells lacking the meiotic division (Dawes, 1981; Fletcher, 1987). Spores can be formed from normal vegetative cells or in specialised sporangia (Lee, 1980). The production and germination of the spores is characteristic for a particular species (Lobban & Wynne, 1981). The spores are produced, settle and develop into new thalli without any fusion occurring (Fletcher, 1987).

1.9.1 Tetrasporogenesis in Members of the Dictyotales

Members of the Dictyotales are characterised by the production of four to eight, nonmotile zoospores from a superficial sporangium (Fritsch, 1945; Chapman & Chapman,

1973; Fletcher, 1987). There are various reports that members of the Dictyotales exhibit a sporophytic majority amongst the plants of a population (Fritsch, 1945; Phillips, 1988). There are various possible reasons for this, including apospory, increased ability for vegetative reproduction of the sporophytic plants, and the possibility of spatial and temporal separation (ie the gametophytes only grow in certain regions or at certain times of the year; Phillips, 1988). The sporophyte and gametophyte plants of members of the Dictyotales, are isomorphic and can only be distinguished when the reproductive structures are mature (Phillips, 1988; Clayton, pers. comm.). Although antheridia are easily distinguished (lightly coloured irregular patches), the female gametophyte members of this order, may be confused with the sporophyte as the immature oogonia are scattered and superficially resemble the sporangia (Phillips, 1988). The sporangia are also assembled in fertile zones, usually flanking the midrib (Phillips, 1988), particularly in the older parts of the frond.

1.9.2 Studies on Tetrasporogenesis in the Dictyotalean genus, Dictyopteris

There have been a large number of studies performed on tetrasporogenesis and morphogenesis in Dictyopteris. Inoh (1936) described the early stages of nuclear and organelle organisation during the development of four tetraspores in Dictyopteris divaricata. Ishii et al. (1959) compared the tetraspore formation in some Dictyotalean species. The differences that were observed include the elevation of a "cuticle" by the sporangia in the sori of Padina japonica Yamada and Padina crassa Yamada (lacking in the other two species studied). Members of this genus are also reported to lack a stalk cell, while individuals of Dictyota dichotoma have two or three, and D. divaricata have two to four stalk cells

(tetrasporangium divides into tetraspore mother cell and small stalk cell; Inoh, 1936). D. dichotoma has a cruciate arrangement of the spores, D. divaricata has a cruciate or tripartite arrangement, and the Padina species have only the tripartite arrangement (Ishii et al., 1959).

The tetrasporophytes of D. divaricata were found to be diploid when the nuclei were Feulgen stained and the quantity of DNA measured. The same method was used to determine that both the germlings and the liberated spore mother cells, were haploid (Ohmori & Hashida, 1985). Nishibayashi and Inoh (1959) performed a comparison of the formation and germination of the spores of these genera of Dictyotales. D. divaricata exhibits a protrusion of one side of the spore, before the first division divides the spore into the rhizoid and thallus cells. The rhizoidal cell undergoes elongation and division, while the thallus cell divides, becomes multicellular, and develops other protrusions (Inoh, 1936; Nishibayashi & Inoh, 1959). P. japonica and D. dichotoma exhibit similar processes. However, in D. dichotoma, the upper segment of the first division becomes the apical cell. In the other species, there is first the production of a multicellular oval body, before the production of a protrusion which becomes the apical cell of the new plant. D. dichotoma is also reported to occasionally develop strange "sucker-like" growths on the rhizoid terminal, the cause of which is unknown (Nishibayashi & Inoh, 1959; Gaillard et al., 1986). The entire sporangial contents of P. japonica may germinate if liberated together. The germination of the tetraspore mother spore of D. divaricata is discussed further by Ohmori and Hashida (1984). These authors report two types of germination in this species. The first involves the irregular segmentation of the body following the production of the primary rhizoid. In the second type of

germination, the spore divides into a few cells first, and then some of the peripheral cells develop into the rhizoids. Erect shoots are reported after 4 days.

There are many studies determining the effect of various environmental factors on the germination patterns of spores of Dictyopteris. Ohmori and Hashida (1984) report that under continuous, unilateral light, rhizoids of D. divaricata developed away from the light source; and under dark conditions, the rhizoids develop in all directions (Ohmori & Ueki, 1979). In plants where two rhizoids developed, they either developed away from, or at right angles to, the light source. The effects of light wavelength on rhizoid production was studied by Ohmori and Suemura (1978). It was observed that rhizoids formed away from the light source at wavelengths of 350nm-530nm and developed randomly at 580nm-750nm and in darkness.

Aspects of the effect of the chemical environment on tetraspore development, have also been observed by a number of authors for D. divaricata tetraspores. Ohmori and Hashida (1983) report that spores died in calcium chloride ($CaCl^2$)-free seawater, became apolar at low concentrations of $CaCl^2$, and developed a ramified rhizoid at higher concentrations of $CaCl^2$. A similar reaction was observed in low concentrations of potassium chloride. Decreasing concentrations of magnesium sulphate inhibited erect shoot formation, and it was discovered that the magnesium ion is vital for the formation of the erect shoot. The addition of cytochalasin B was also reported to affect the development of the tetraspores (Ohmori & Ueki, 1980), with spores placed into solutions containing 100mg/l cytochalasin B, developing into multicellular germlings and only developing rhizoids at the 2-4 cell stage. In solutions of this concentration, the first division of the spore (into rhizoid and thallus cells)

was formed randomly and the rhizoid developed away from the light. The addition of colchicine markedly affected the germination of the spores (Ohmori & Hashida, 1982); low concentrations inhibited the formation of segmentation walls, higher concentrations caused the development of thick rhizoids, while at concentrations of 0.2% the spores died.

It is obvious that the intertidal region is a highly stressful environment that exposes organisms to varying conditions. A variety of adaptations for survival are required for organisms inhabiting the zone. The brown algae, a diverse group of seaweeds, exhibit a number of structural, physiological and reproductive adaptations to the environmental conditions.

2 MATERIALS AND METHODS

2.1 EXPERIMENTAL ORGANISM

The brown alga Dictyopteris longifolia Papenfuss (in ed.) was used in this study. This alga has a (Fig. 1) holdfast (H) composed of intertwined, branching rhizoids. There are numerous young (YL) and mature (ML) laminae growing from each holdfast and attached to the holdfast by a narrow stalk or "stipe" (S) consisting of midrib tissue. The stipe region is the remains of the lamina once the wings have degenerated, and is not (for the purpose of this study) considered to be a true stipe as described for other members of the Phaeophyceae. The laminae are flattened and dichotomously (D) branched, and have been observed to reach a length of 70cm and a width of between 1 and 2cm. There is a thickened midrib (MR) surrounded by wing tissue (W), and an apical meristem which is composed of a few cells (2-8) in a sunken, apical pit (AP). The plants used for the culture experiments were collected from shallow pools and wave exposed intertidal habitats at Palm Beach, Natal and were transported to the laboratory in 2l plastic bottles in insulated boxes cooled by ice blocks.

2.2 STUDY AREA

All field measurements and collections were performed at Palm Beach (30 30, CD (Port Shepstone)) on the Natal South coast (Fig. 2).

Seven sites (Fig. 3, A-G) were chosen according to the abundance and density of Dictyopteris longifolia, as well as relative wave exposure. These sites were subjectively ranked, as observed at low tide (from high to low wave

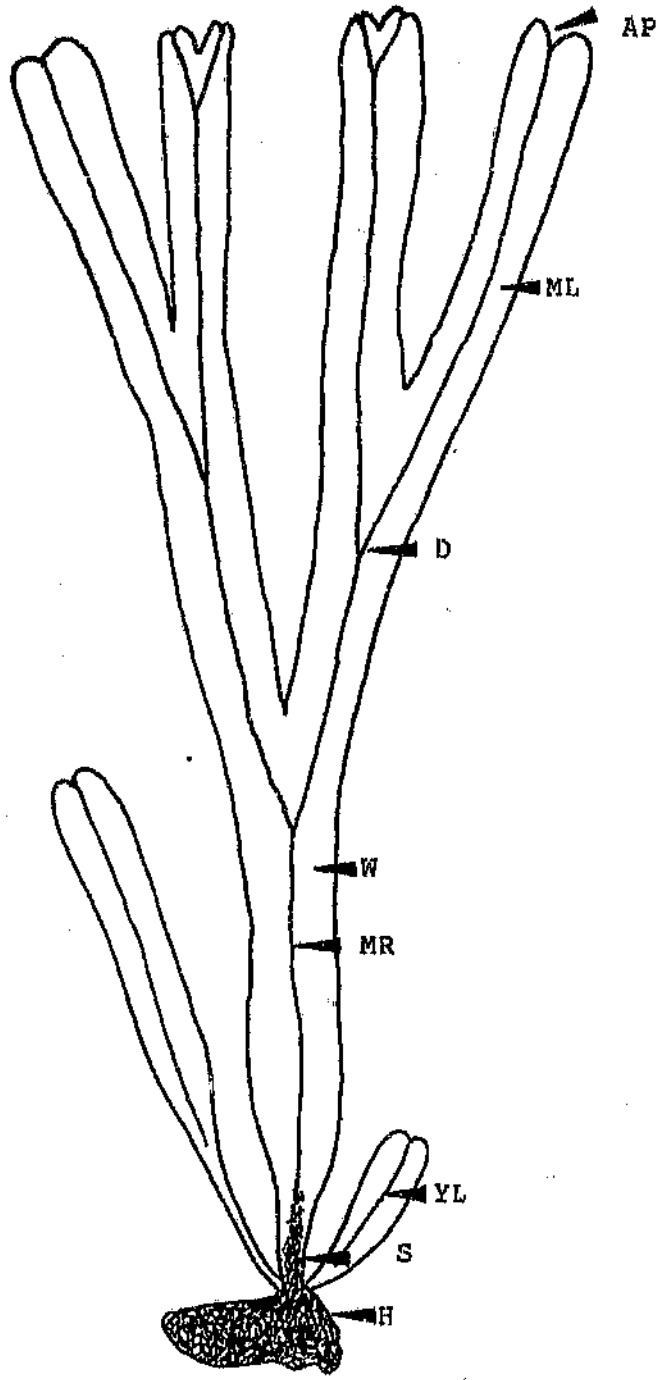


Figure 1: Diagram indicating the different parts of a Dictyopteris longifolia plant. (AP - apical pit, D - dichotomy, H - holdfast, ML - mature lamina, MR - midrib, S - stalk, or "stipe", YL - young lamina, W - wing)

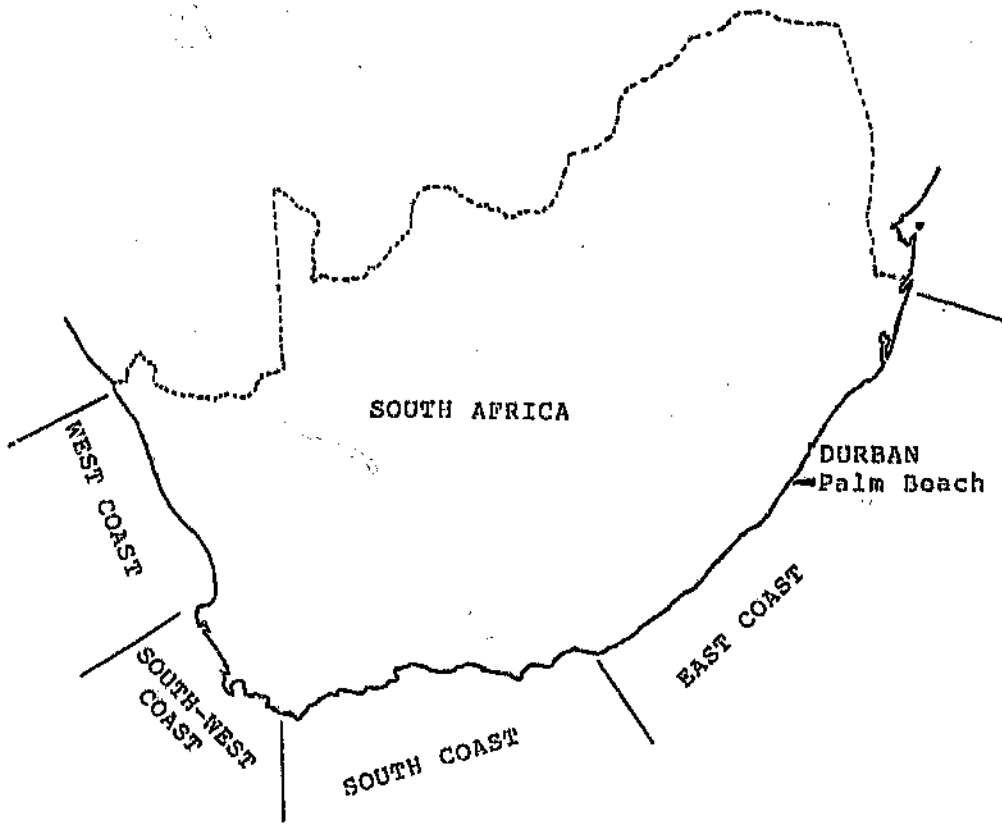


Figure 2: Map of South Africa indicating the position of Palm Beach.

exposure). Sketch maps were made of each site. The approximate width of the sites in the sketch maps are A (30m), B (4m), C (10m), D (2m), E (2m), F (5m) and G (10m). Each site was also was photographed using a Ricoh instamatic camera and 100 ASA, 35mm colour film

A) An extremely high wave activity site (H+), which was composed of a wave exposed, rocky reef subject to severe wave action. This site consisted of a long, flat platform of rock exposed to the breakers on the seaward side and flanked by a deep, sand-bottomed gully on the beach side (Pl. 1, D; Fig. 3, A). Even at low tide this site was subject to the direct breaking of waves.

B) A high wave activity site (H) which was exposed to wave action even at low tide, however, this site was partially protected by a large rock (Pl. 1, E; Fig. 3, B) which prohibited the direct breaking of waves onto the circular, rocky protrusion inhabited by D. longifolia.

C) A high, intermediate wave exposure site (I+) which consisted of a raised pool, flanked on the far side by open sea and exposed to the occasional wave breaking over the seaward side at low neap tide and from midway between low and high spring tides (Pl. 1, F; Fig. 3, C). This occasional washing of waves into the pool caused strong water movement throughout the water body of the pool.

D) A low, intermediate wave exposure gully (I) which consisted of a sandy gully running perpendicular to the oncoming waves, but only exposed to wave activity from when the tide reached the level midway between high and low tide, at low neap tide or when the coast experienced a particularly large wave at low tide (Pl. 1, G; Fig. 3, D).

E) A high, low wave exposure pool (L+) which was connected to numerous other pools and experienced water movement from water flowing out of these pools. This only occurred from [illegible]y tide and low neap tide, when waves were break[illegible]nto the other pools. This site was behind the main rocky area and was close to the beach (Pl. 1, H; Fig. 3, E).

F&G) Two calm pools (L2 and L1) which were situated on raised rock platforms. These platforms were fairly far back on the beach and were surrounded by sandy areas (Pl. 1, I & J; Fig. 3, F & G). The pools only experienced wave activity at high tide.

B) A high wave activity site (H) which was exposed to wave action even at low tide, however, this site was partially protected by a large rock (Pl. 1, E; Fig. 3, B) which prohibited the direct breaking of waves onto the circular, rocky protrusion inhabited by D. longifolia.

C) A high, intermediate wave exposure site (I+) which consisted of a raised pool, flanked on the far side by open sea and exposed to the occasional wave breaking over the seaward side at low neap tide and from midway between low and high spring tides (Pl. 1, F; Fig. 3, C). This occasional washing of waves into the pool caused strong water movement throughout the water body of the pool.

D) A low, intermediate wave exposure gully (I) which consisted of a sandy gully running perpendicular to the oncoming waves, but only exposed to wave activity from when the tide reached the level midway between high and low tide, at low neap tide or when the coast experienced a particularly large wave at low tide (Pl. 1, G; Fig. 3, D).

E) A high, low wave exposure pool (L+) which was connected to numerous other pools and experienced water movement from water flowing out of these pools. This only occurred from midway tide and low neap tide, when waves were breaking into the other pools. This site was behind the main rocky area and was close to the beach (Pl. 1, H; Fig. 3, E).

F&G) Two calm pools (L2 and L1) which were situated on raised rock platforms. These platforms were fairly far back on the beach and were surrounded by sandy areas (Pl. 1, I & J; Fig. 3, F & G). The pools only experienced wave activity at high tide.

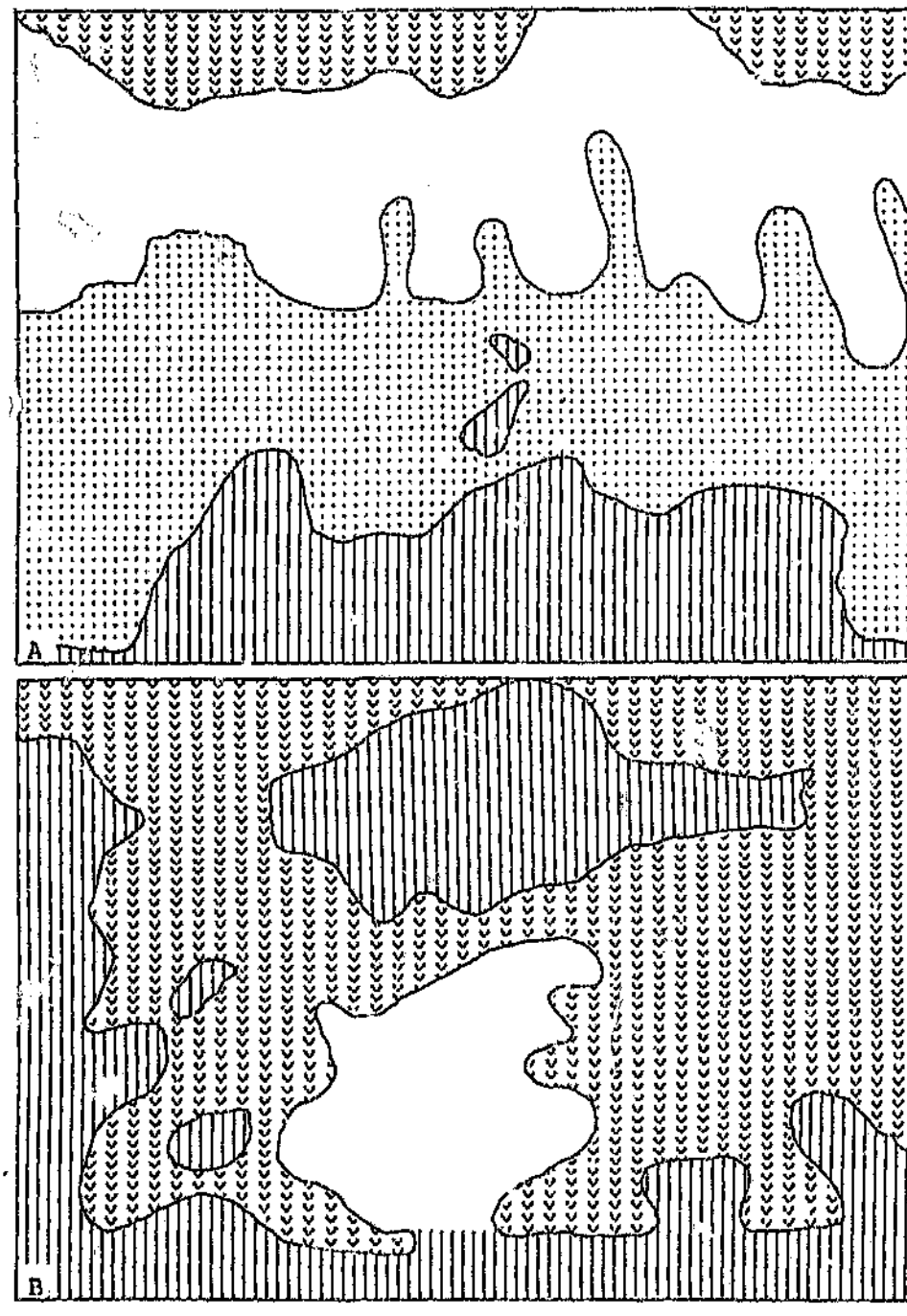


Figure 3: Maps showing the (A) extremely high wave exposure site (H+), and the (B) high wave exposure site (H).

SITE ROCK SAND

DIRECTION OF WATER MOVEMENT

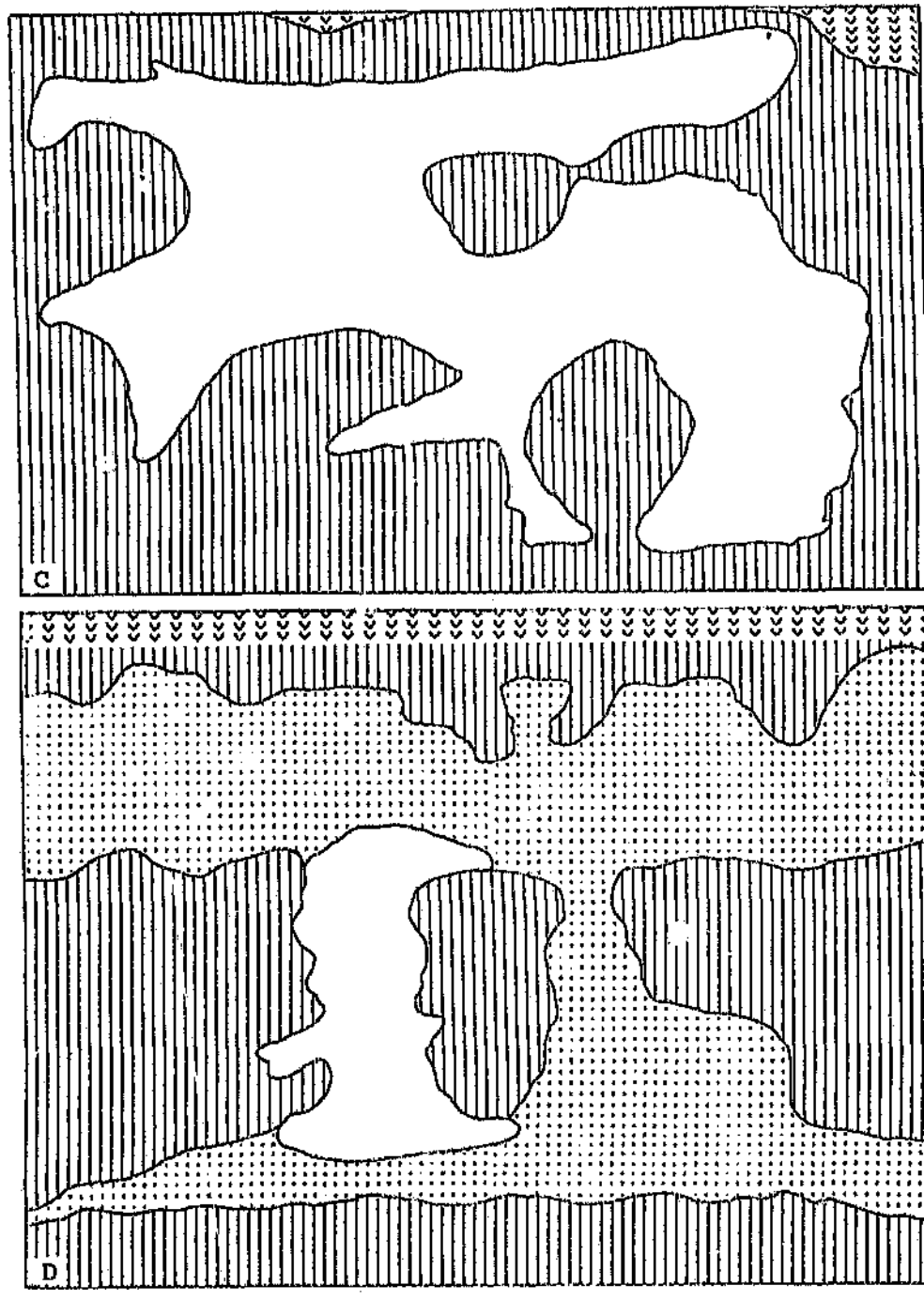


Figure 3: Maps showing the (C) high, intermediate wave exposure site (I+), and the (D) low, intermediate wave exposure site (I).

SITE ROCK SAND

DIRECTION OF WATER MOVEMENT

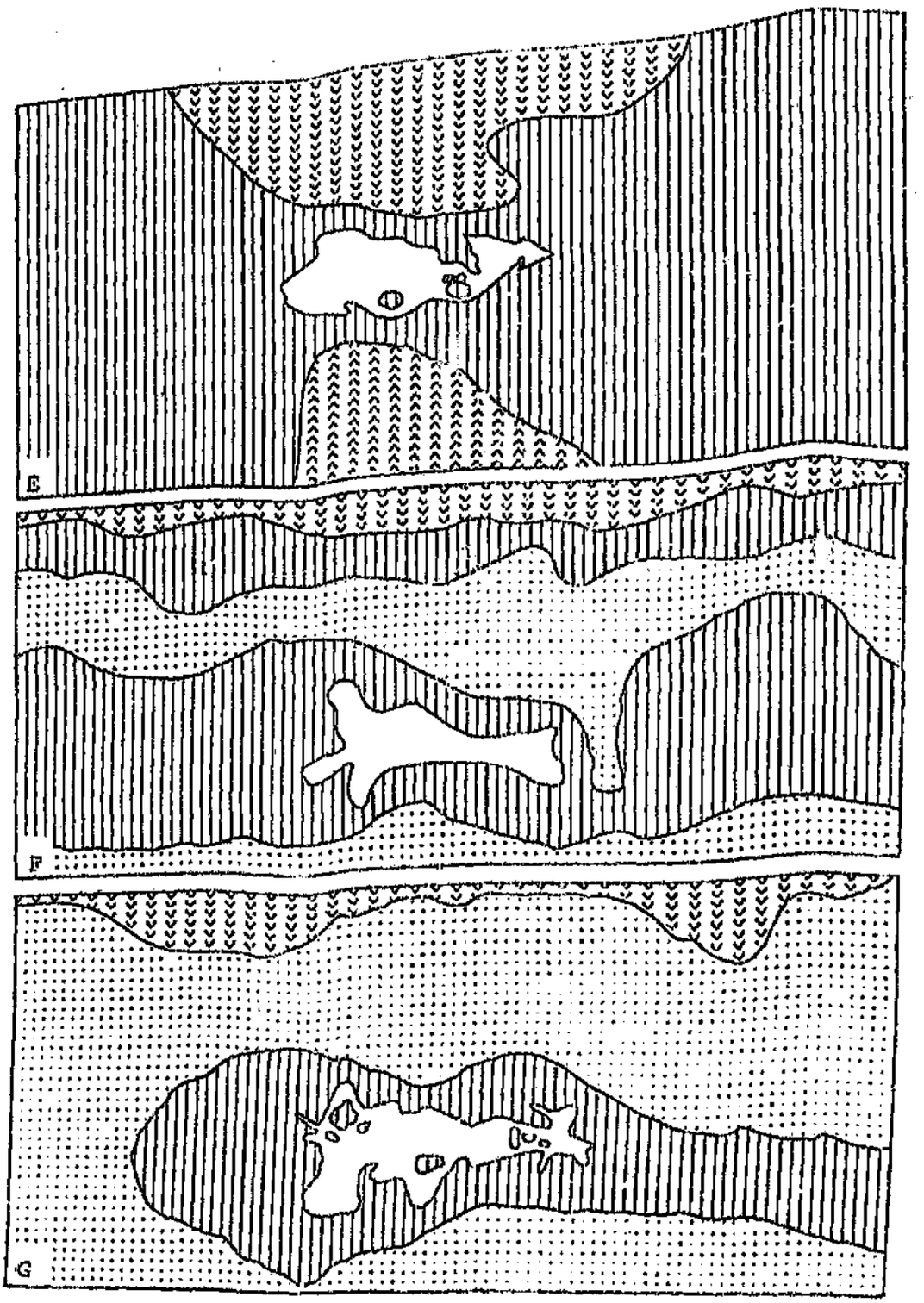


Figure 3: Maps showing the (E) high, low wave exposure site (L+), and the two (F and G) low wave exposure sites (L2 and L1, respectively).

SITE ROCK SAND

DIRECTION OF WATER MOVEMENT

2.3 DISTRIBUTION

The distribution of D. longifolia was determined by obtaining herbarium sheets from the herbaria at the University of Natal; Pietermaritzburg (NU), the Albany museum; Grahamstown (GRA), the Bolus Herbarium (BOL), Kirstenbosch (NBG), and the University of the Witwatersrand (J); as well as from personal observation, Seaweeds of Inhaca (Isaac, 1956; Macnae & Kalk, 1958) and the species list of the De Hoop Nature Reserve, Cape Agulhas (Bolton & Stegenga, 1990). From the herbarium sheets the site, condition of the plants and date of collection were recorded. The information was used to compile a distribution map of D. longifolia, as well as to attempt to determine any possible seasonality in the reproductive or morphological condition of the thallus.

2.4 FIELD METHODS

The intertidal zone is a highly stressful environment for the organisms inhabiting the region. Most of the major forces acting on the intertidal region can be connected to the action of the waves, whether it be the force of the moving water itself, exposure to the atmosphere between consecutive waves or at low tide in the absence of waves, or the abrasive action caused by the sand and particulate matter transported in the moving water. A number of environmental attributes such as aspects of water movement, and sand content and deposition were measured in the various sites studied. Features of the morphology and structural properties of D. longifolia were measured and compared between the sites, to determine any possible response of the species to differing degrees of wave exposure.

2.4.1 Wave Action

The quantification of wave exposure and its related effects is a problem which numerous researchers have addressed. One of the difficulties related to this quantification is the distinction between what the methods are actually measuring (Dring, 1982). Some methods measure the action of waves by determining the strength of individual waves using structures such as the dynamometer (Palumbi, 1984). Other methods are concerned rather with water movement, and may be measured in the absence of actual waves, eg the dissolution of plaster blocks (Doty, 1971). Alternatives use wave height, number or direction, the effects on the shore, or the species composition of the shore as an indication of wave exposure.

Four methods of measuring wave exposure were used in this study in an attempt to determine if the subjective ranking of the study sites was valid. These included methods involving both wave action and water movement:

2.4.1.1 Wave Strength

The first method to be used was the dynamometer, modified from a description by Palumbi (1984). This device reads the maximum force exerted by waves and strongly moving currents in the allotted time period. The apparatus (Pl. 2, A & B; Fig. 4, A-C) consisted of half a hollow, plastic toilet float (10.5cm in diameter) which acted as the drogue. The size of the drogue was much larger than that suggested by Palumbi (1984), however, a small fishing float was used in the pilot study and it was discovered that the waves were too gentle for a drogue with a small cross-sectional area. The drogue was attached to the head of a cable tie (a flat plastic ribbon used to hold electrical wires together) via a

length of string (50cm), with the cut surface of the float away from the cable tie. A cable tie consists of a head which moves along a ribbon which has teeth on one side. A small tongue on the head locks into the teeth, prohibiting the head from moving backwards. The head was cut off and then threaded on to the end of the tie. The head was also attached to the end of the tie with two or three 4cm elastic bands (number depended on the strength of the waves as too few elastic bands allowed the head to be pulled off). The dynamometer was secured in the surf by attachment of the end of the cable tie to a piece of string which was, in turn, tied to the observer's ankle. Palumbi (1984) suggests that the device be attached to the substratum, however, attempts to secure masonry nails to the rock in the study sites (for attachment of the dynamometers), failed. Extremely rough surfs were thus not measured due to danger to the observer. As many measurements as possible (never less than three) were taken within half an hour on either side of low spring tide. The structure remained in the water for one minute intervals. During this time the float was dragged by the waves which, in turn, exerted a force on the drogue and pulled the head along the cable tie, stretching the elastic bands as it did so (Fig. 4, A-B). The head stopped when the force exerted by the elastic bands equaled the force exerted on the drogue by the waves. The head of the cable tie could not slide back along the tie because of the teeth and small tongue which locked it in the furthermost position. The amount of force exerted by the water on the cross-sectional area of the float was determined by measuring the amount of tension in the elastic bands. These elastics bent the cable tie over (Fig. 4, C). Thus, the force exerted by the waves was calculated by measuring the amount of force necessary to stretch these elastic bands until the cable tie was straightened and the head almost moving. This was performed using a 2kg spring balance (Pl. 2, A). The

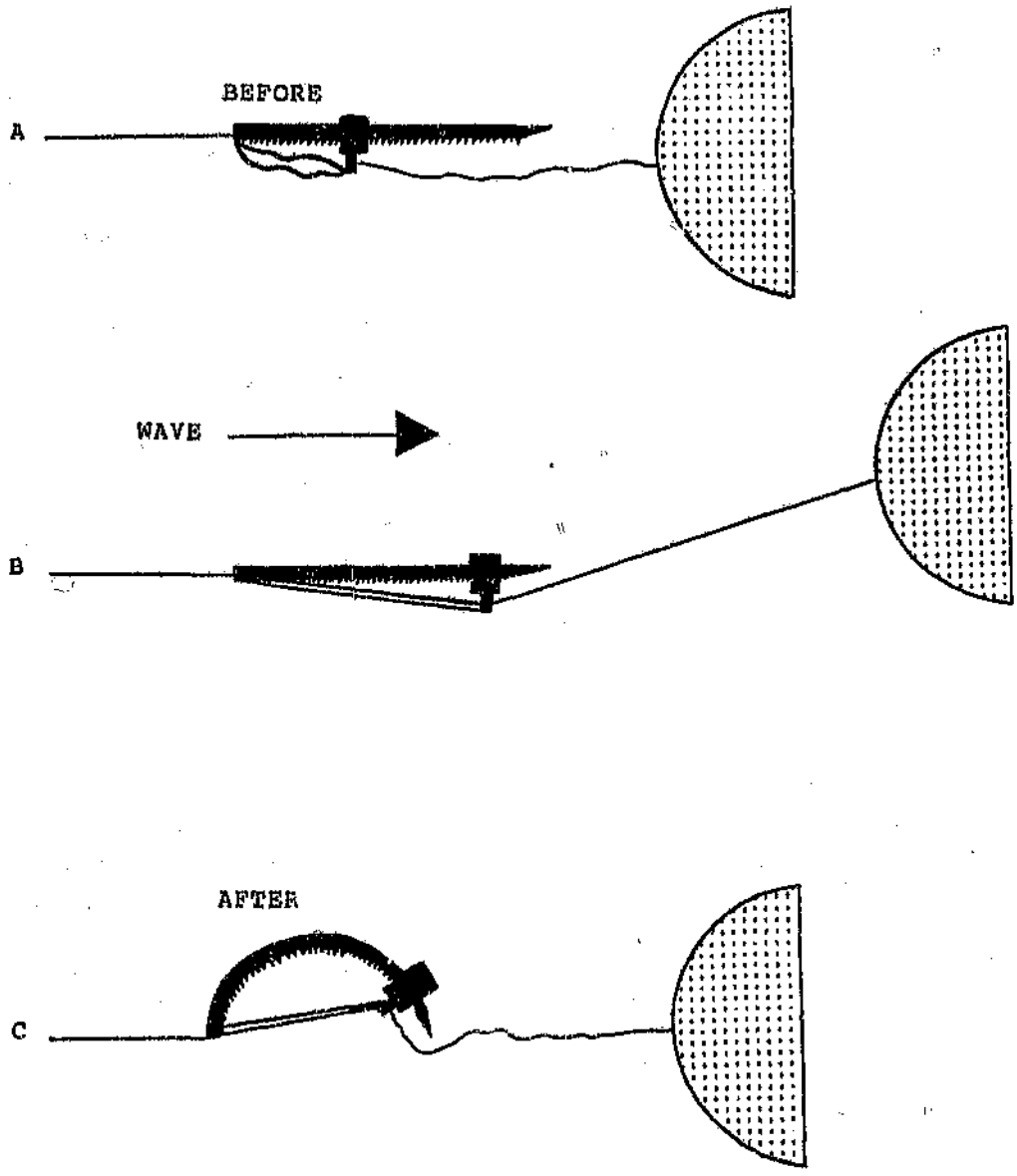


Figure 4: Diagram indicating the position of the dynamometer (Palumbi, 1984) before (A), during (B) and after (C) a wave.

dynamometer was returned to its original position by inserting a sharp object under the tongue and sliding the head back. Each cable tie was used a maximum of 10 times to account for the wearing of the teeth. This technique was only possible in areas which experienced wave action at low tide, ie H+ and H. The strength of the waves acting on the drogue was calculated using the formula:

$$\text{Force/Cross-sectional area of the drogue} = N/m^2$$

2.4.1.2 Wave Number

The second method involved counting the number of waves breaking over the site in a set time interval, within 30 minutes on either side of low tide. The waves were counted for 2 minute intervals, and 6 replicates were performed in each of the sites, on three of the trips. This technique, as with the previous one, was limited because it could only be used where waves were breaking over the site at low tide, ie in this case H+, H and I+.

To overcome this problem, various other techniques were attempted. These involved dissolution rates, and were thus measuring water movement rather than wave action.

2.4.2 Water Motion

2.4.2.1 Lifesaver Sweet Dissolution Method

"Lifesaver" sweets (boiled sweets with holes in the centre) were used for the third method (Martell, pers. comm.). This method works on the principle that dissolution rate increases with an increase in water movement. Lifesaver sweets of different flavours were numbered and pre-weighed in the laboratory. In the field,

5 Lifesavers of randomly distributed flavours were used in each site. It was impossible to obtain sufficient sweets of a similar flavour and, as Martell (pers. comm.) reported that there were differences in the dissolution rates of different flavours, the flavours were randomly distributed amongst the sites (Pl. 2, D & E). The 5 sweets were attached to a wire coat hanger at the end of a long bamboo pole, and then held stationary in the water (Pl. 2, C). Three replicates of different time periods, ie 2, 3 and 5 minutes, were performed in each of the sites within half an hour on either side of low tide. After emersion, the Lifesavers were placed into pre-weighed glass vials, returned to the laboratory, oven dried and re-weighed. The decrease in mass per time unit was used to calculate the dissolution rate of the sweets from each site. The optimum emersion period for Lifesavers was found to be 3 minutes. This method exhibited a similar problem to the previous techniques in that areas which experienced motionless water at low tide could not be quantified, and measurements could not be safely made at high tide.

2.4.2.2 Plaster Block Dissolution Method

Plaster of paris blocks or "Clod cards" (Doty, 1971; Munnik, 1987) were used in the last method attempted in this study. This method uses the same principle as that described in 2.4.2.1, ie the greater the water movement, the higher the dissolution rate. In this case, plaster of paris blocks were made in ice trays (4cm X 3cm X 3cm; Pl. 2, G). Each block had a piece of thin wire inserted into it. Initial attempts to hammer masonry nails into the rocks for attachment of the blocks, proved to be impossible. Eventually, pre-weighed and numbered blocks were wired onto cable ties (Pl. 2, H) and then fastened onto large tufts of firmly attached algae such as Gelidium abbottorium Okam. (Pl. 2, F). Five blocks were

attached in each site and left for a complete tide (ie 12 hours, low tide to low tide). The blocks were then removed, oven dried and re-weighed. The mean percentage mass loss was compared for each site.

Although the latter method (2.4.2.2) did not determine the strength of waves, it was the only method which measured the differences in water motion for the duration of the tidal cycle, during which all the sites were exposed to some degree of water movement. To determine differences in the degree of wave action of a site, a method should be able to be used to safely measure the wave action of all sites at high tide when there is some wave action in all the areas.

The mean values for each site, using each method, were calculated and compared according to the methods described in 2.7.

2.4.3 Sand Content of the Water

Sand and particulate matter content of the water was observed to vary considerably in all the sites, and was thus considered an important feature of intertidal ecology. The degree of turbidity affects various features of the intertidal environment such as light and abrasion potential. The sand content and abrasion was considered to be an important feature in the determination of the morphological state of Dictyopteris, and thus some method of assessment was thought to be necessary. The sand content of the water column is affected by the turbulence or movement of the water, as well as the availability of sand and particulate matter at the site concerned.

The sand and particulate matter content of the water was measured by collecting 100ml water samples from the top of the water column in each site. Five replicates were

taken in each of the sites on each visit to the shore. The samples were filtered through pre-weighed Whatman's Number 1 filter paper. The filter papers were flushed with distilled water to remove the salt from the paper (which would affect the dry mass), and were then oven dried (70°C) and re-weighed. Any increase in mass was a record of the amount of sand and particulate matter present in suspension in the water at the time of collection, at each of the study sites at Palm Beach. The particulate matter in the water was available to cause abrasion and thus change the morphological condition of the plants. The mass of particulate matter was expressed as grams per litre (g/l), and the mean values for each site were calculated and compared according to the methods described in 2.7.

2.4.4 Sand Deposition

Sand deposition is considered to be important in influencing growth and development of intertidal organisms. Complete cover of plants, as observed regularly in D. longifolia, reduces light penetration and changes the temperature and chemical environment. It also reduces the degree of water motion, herbivory and sand abrasion that the organism is exposed to.

Sand deposition was observed to be considerable in some of the sites at Palm Beach (Pl. 6, A-L). On some occasions Dictyopteris individuals were buried under 30cm of sand. This was especially noticeable in the sandy, intermediate wave activity gully (I; Pl. 6, F-I). An attempt was made to quantify the degree of sand deposition in each site. A 20kg air brick (b) consisting of a concrete block with three holes was positioned in each site (Pl. 3, D). A 15cm piece of PVC piping (p), 5cm in diameter was placed into each of the holes. The pipes were held in place by a piece of wire (w) which was

threaded through holes in the top of each pipe and then fastened under the brick (Pl. 3, E & F). The bottom of each pipe (p) was covered by a piece of stretch cotton material (c) which was held in place by two elastic bands and which stopped sand from passing through the pipe. A block with three pipes was placed into each site and left for 24 hours. The sand deposited into the pipes was collected, oven dried and weighed. The mass measurements were expressed in grams. The mean values for each site were calculated and compared according to the methods described in 2.7.

2.4.5 Mean Maximum Lamina Length of the Population

The mean maximum lamina length was determined by measuring the length of the longest lamina of mapped individuals of the populations in each site, on each excursion. The increase in length of the individuals was determined over the study period. The mean values for each site were plotted on a graph. The positions of the individuals were recorded on sketch maps of the sites (Fig. 5, A-G; scale of maps on page 78) to allow for the measurement of the same individuals on return visits.

2.4.6 Morphometry

Various aspects of D. longifolia morphology were measured on randomly chosen, destructively sampled individuals, and the results from the different sites compared. These aspects included (Fig. 6):

a) the mean of 2 holdfast diameter measurements
b) the area of the holdfast
c) the wet and dry holdfast mass measurements
d) the mean of the length of the three longest laminae
e) the mean width of the three longest laminae

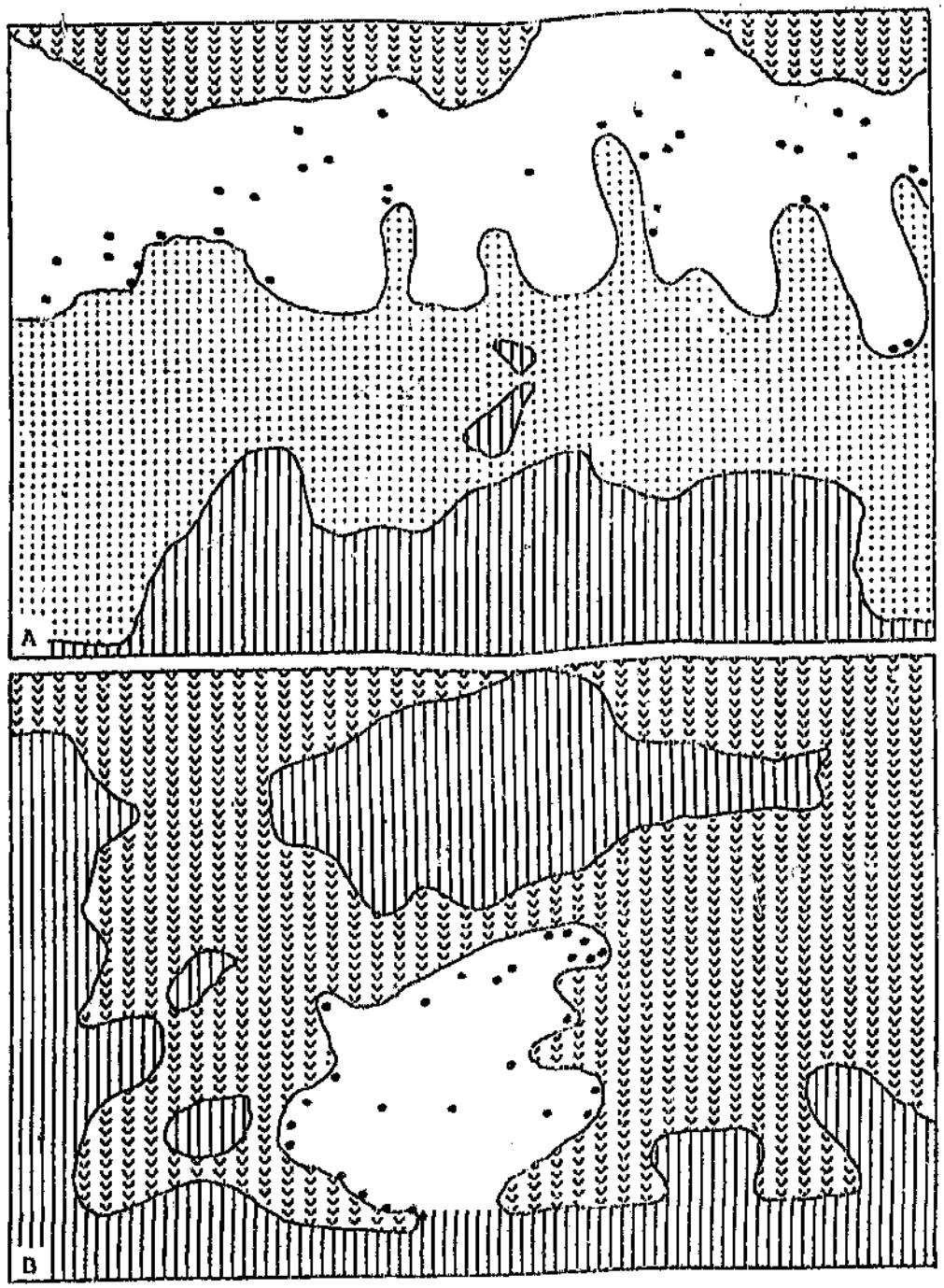


Figure 5: Maps showing positions of measured individuals in the (A) extremely high wave exposure site (H+), and the (B) high wave exposure site (H).

SITE ROCK SAND

DIRECTION OF WATER MOVEMENT INDIVIDUAL •

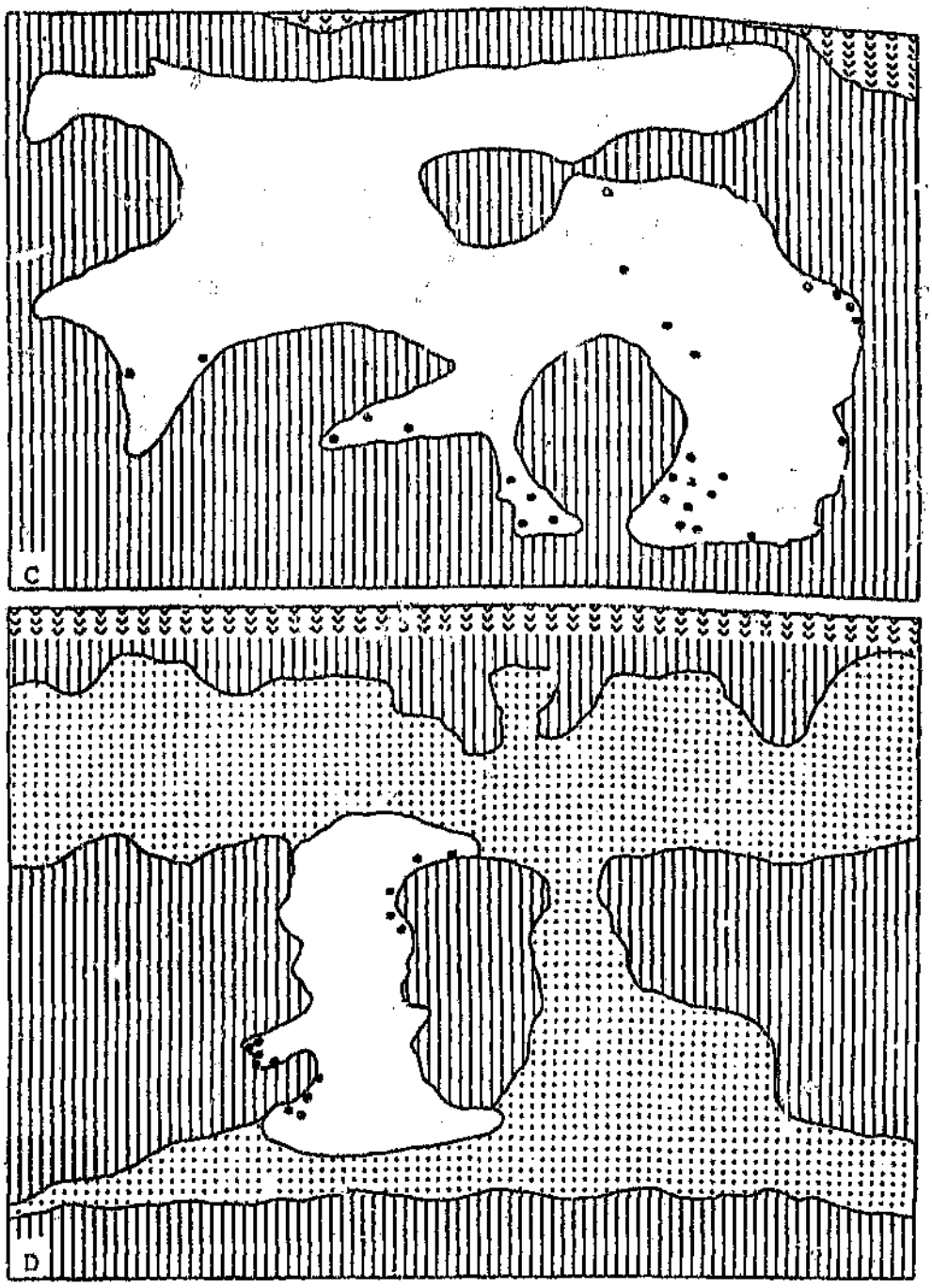


Figure 5: Maps showing positions of measured individuals in the (C) high, intermediate wave exposure site (I+), and the (D) low, intermediate wave exposure site (I).

SITE ROCK SAND

DIRECTION OF WATER MOVEMENT INDIVIDUAL •

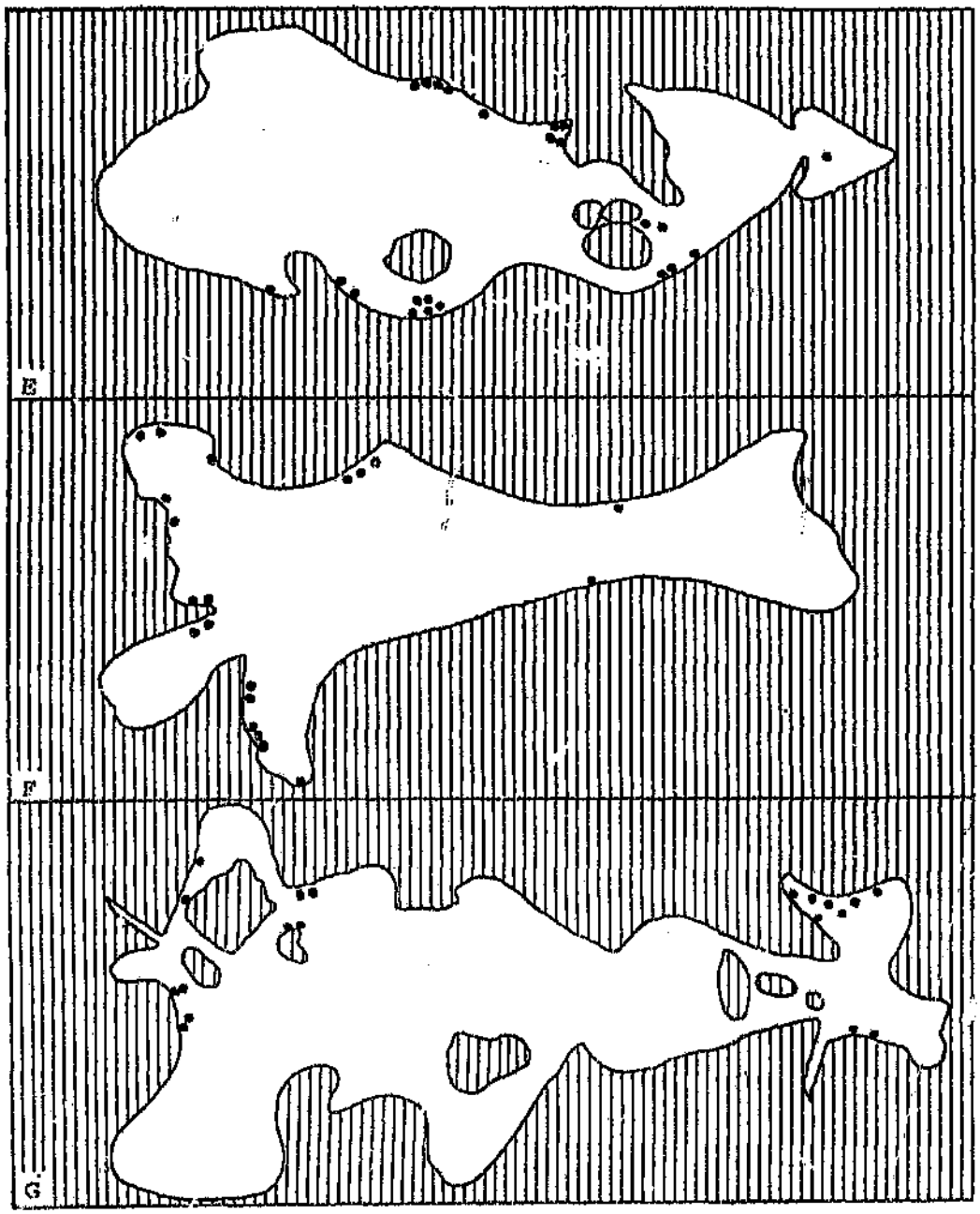


Figure 5: Maps showing positions of measured individuals in the (E) high, low wave exposure site (L+), and the (F and G, two low wave exposure sites (L2 and L1, respectively).

SITE ROCK SAND

DIRECTION OF WATER MOVEMENT INDIVIDUAL •

f) the total area of all the laminae on the plant
g) the wet and dry masses of all the laminae on the plant
h) the maximum number of dichotomies on each lamina
i) the number of laminae arising from each holdfast (less than 5mm and greater than 5mm)

These measurements were taken for as many individuals as possible in each of the sites. On some occasions the plants were too sparse and destructive sampling for the morphometric measurements would have meant the lack of material for other aspects of the study. The mean values for the measurements of each parameter were calculated, and the means of the different sites, compared statistically. The methods used for these comparisons will be discussed in Section 2.7.

The results were summarised, together with the structural features, using polygonal graphs as described by Berquist (1959).

2.4.7 Structural Properties

Intertidal organisms not only develop anatomical and morphological, but also structural adaptations in order to survive the physical stresses experienced in the intertidal environment. Various aspects of structural adaptation have been reported in the literature, including the extensibility or elasticity of algae experiencing wave action and tidal currents. These plants withstand the drag of the water movement by being flexible rather than rigid (Koehl & Wainwright, 1977). The force needed to break the blade or lamina (tensile strength) is another feature which is important when considering algae subjected to high wave forces (Armstrong, 1987). In individuals which are elastic and

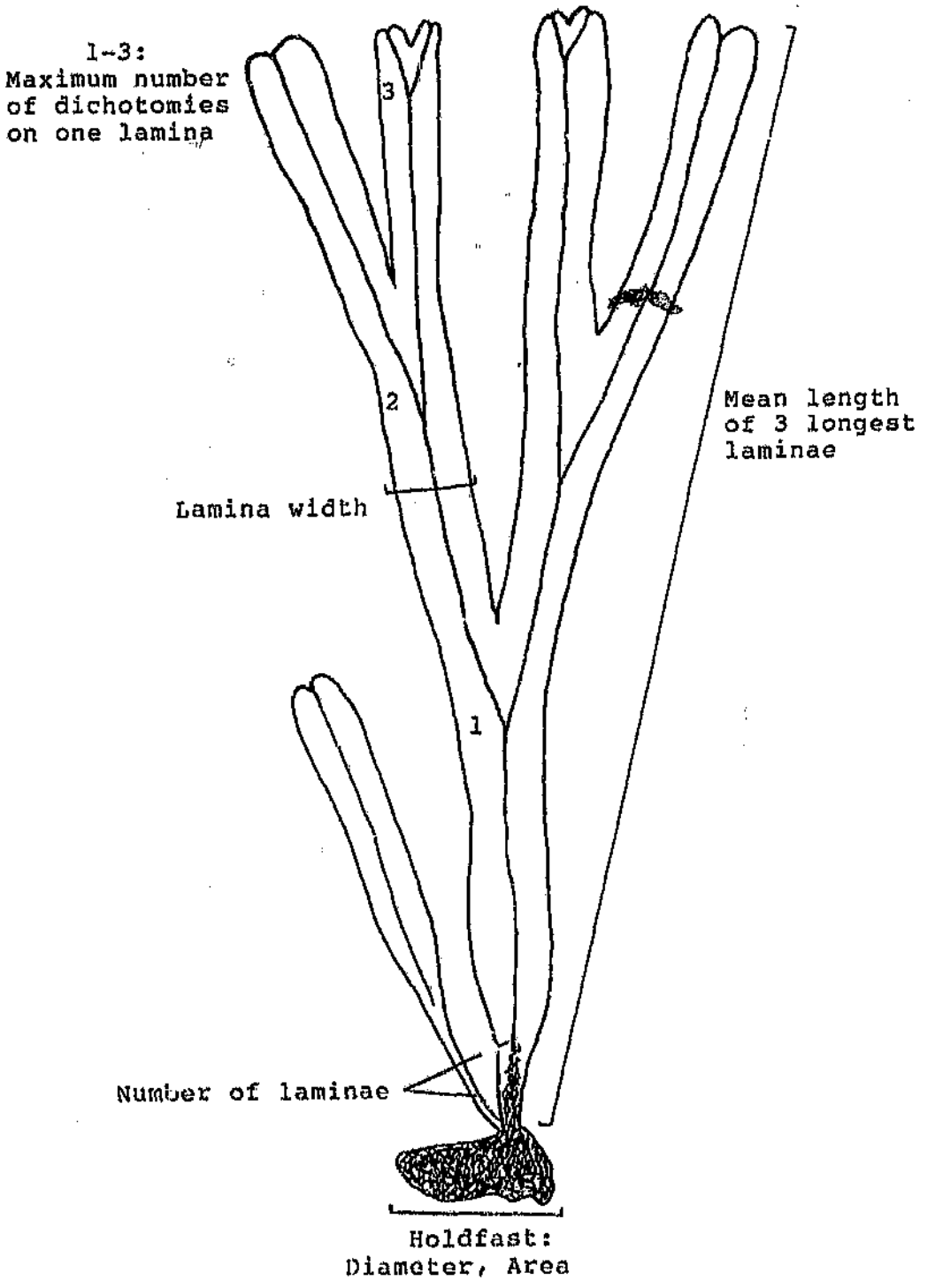


Figure 6: Diagram indicating the different measurements taken for the morphometry study of *D. longifolia*.

have a tensile strength high enough to withstand the force of strong wave action, the remaining structural adaptation needed to survive the wave action is the ability to remain attached. The attachment strength is thus another feature which has been studied in intertidal seaweeds (McEacheron & Thomas, 1987). The "toughness" or sclerophylly, and water content or succulence of intertidal seaweeds were also considered to be potentially important features relating to the ability of the plant to withstand wave forces and abrasion, as well as to recover after exposure to the atmosphere, ie desiccation. Water loss or desiccation is commonly experienced by intertidal algae (Dromgoole, 1980). The ability to withstand desiccation during exposure to the air, and to rehydrate following the return of the water, is thus also vital to the survival of intertidal algae.

A number of structural aspects of D. longifolia were investigated with view to survival in the wave-swept intertidal zone.

2.4.7.1 Tensile Strength

The breaking strain or tensile strength of D. longifolia was measured using a method described (and defined as the force in ounces required to break a single leaf per unit width of leaf at the broken edge) by Martens and de V. Boeysen (1968) for grass studies. This method involved a "tensilimeter" (Pl. 2, I) which consisted of two clamps (c), the lower of which was fixed. The upper clamp (Pl. 2, J) was attached to a 2kg spring balance (b) which, in turn, was attached to an arm which could be screwed up or down. A section of 5cm (or the nearest available length) of fresh, undamaged lamina was fixed between the clamps (Pl. 2, J) and the upper clamp screwed up until the lamina broke. The force required to break the lamina, was measured on the spring balance and was taken as the

reading on the balance just prior to breakage (Pl. 2, K). The width at the point of the tear was also measured. The force (from the balance) required to break the thallus, and the width at the point of the tear were used to determine the tensile strength in the formula:

$$\frac{\text{breaking force in dynes (g X gravity)}}{\text{unit length (mm) at broken edge}} = \text{dynes/mm}$$

At least 20 replicates of tensile strength measurements of D. longifolia, from each site were taken on each trip. The number of replicates was determined by whether the individuals were of sufficient length (greater than 5cm) and not abraded to a large degree. When possible, tensile strength measurements were taken for the three longest laminae of each individual. The mean values were calculated, and the sites were compared according to the methods given in Section 2.7.

2.4.7.2 Attachment Strength

The attachment strength of D. longifolia at Palm Beach was measured using a method described by Carter (1986) who used the technique to establish the attachment strength of Gelidium pristoides (Turner) Kützing (a commercially important agarophyte). The technique is illustrated in Plate 3, A and involved a structure which was used to exert a force on the holdfast of the plant, to determine the force necessary to tear or remove the plant from the substratum. It consisted of a "bull-dog" clamp (c), through which elastic bands (e) of the same length were threaded (Pl. 3, C). The number of elastic bands used was determined by the size and strength of the holdfast. The end of a 30cm ruler (r) was placed onto the substratum and held vertically. The clamp was attached to

the holdfast of the plant as close to the rock as possible. The elastic bands were then pulled up the length of the ruler and the extension at which the plant became detached or broke, was recorded (Pl. 3, B & C). The lengths were converted into force by attaching the clamp to a stationery object and pulling the elastic bands to the length measured in the field, using a 2kg spring balance. The force needed to pull the elastic bands to the previously measured length, was recorded. This measurement was then converted into Newton units using the formula:

Mass recorded (g) X gravity = Force needed to remove plant (N)

The mean values for individuals at each site were calculated and compared according to the methods described in 2.7.

This method of measuring attachment strength worked well on D. longifolia individuals which were growing on a less stable substrata or had small holdfasts. However, when the plants were more firmly attached to rock, the clamp opened slightly and slipped off the laminae. In the latter cases, a cable tie was tightened around the laminae and through the elastic bands and used in a similar way to the clamp method (Pl. 3, A). This modification proved more efficient than the previous method because the cable tie could not slip off the laminae. Unfortunately, however, the tie appeared to damage the laminae more and, in some cases, to cause the tearing of the thallus. Neither method was thus entirely satisfactory. An improvement would be to somehow clamp the holdfast securely and in a manner that would not cause any damage.

2.4.7.3 Sclerophylly and Succulence

Sclerophylly and succulence are parameters which have been studied extensively in terrestrial plant (mainly grass) studies, including studies comparing similar species growing under different conditions (Blackmore, 1992). D. longifolia was studied in sites differing in both the degree of wave exposure and degree of desiccation experienced. It was thus considered as a good opportunity to determine whether sclerophylly and succulence were parameters which could be used in studies performed on intertidal seaweeds, and whether there was any difference in these parameters in material collected from areas differing in wave exposure.

Sclerophylly can be defined as the amount of dry matter per leaf bifacial area and is related to "toughness" . It is calculated using the formula:

$$\text{dry mass (g)/unit area } (m^2) = \text{sclerophylly}$$

Succulence is defined as the maximal water content by leaf bifacial area and is calculated using the formula:

$$\text{wet mass(g)/unit area } (m^2) = \text{succulence}$$

(Cowling & Campbell, 1983).

The material used to measure these two parameters was collected from each site and fixed in 4% formaldehyde in seawater. The area of each thallus was measured using a planimeter which reads area using a light beam. The laminae were fed through the planimeter and the holdfast

area was traced onto paper, cut out and then the paper was fed through the machine. The mass of the laminae and holdfast for each plant, was measured separately after having been blotted dry (wet weight), and then again after being oven dried overnight (dry weight), at 60°C for 12 hours. The number of individuals used, which was dependant on the size and abundance of the plants in the field, was never less than three plants from each site.

2.4.7.4 Desiccation Rate and Percentage Rehydration

Thalli of intertidal algae are exposed to the air for periods of time either between waves or at low tide. In this time period, water is lost from the thallus and desiccation is experienced. The degree of desiccation may affect the metabolism and morphological condition of algae (due to loss of badly desiccated laminae). Wave activity is reported to effect the degree of desiccation due to splash which keeps plants moist between waves at low tide.

The rate of desiccation (Dromgoole, 1980) or water loss was measured by determining the mass of drying D. longifolia at different time intervals. An individual plant, preserved in 4% formaldehyde was used from each study site. The thalli were blotted dry and weighed before being placed in front of an oscillating fan. Each plant was hung from a pre-weighed stand consisting of three disposable glass pipettes strapped onto a plastic petridish with masking tape (Pl. 3, G & I). Individuals that were too large for the stand, were suspended from a shelf above the experimental setup (Pl. 3, H). Each plant was weighed every 5 minutes for the first hour, every 10 minutes for the second hour, every 30 minutes for the subsequent three hours, every hour for the following three hours, and finally weighed again after being oven dried at 60°C overnight. The relative humidity of the air

was measured using a whirling hygrometer at the time of each desiccation period. Three replicate studies were performed. The percentage desiccation was calculated after each observation period, using the formula suggested by (Dromgoole, 1980; Oates & Murray, 1983).

$$\frac{\text{wet weight-desiccated weight}}{\text{wet weight-oven dried weight}} = \% \text{ desiccation}$$

The mean desiccation curves (of the three replicates) were drawn for each of the sites.

After being oven dried and weighed, the Dictyopteris plants were returned to seawater and left overnight. They were then blotted dry and re-weighed to determine the percentage of the original weight that had been regained, ie % rehydration. This was measured for each plant, the mean values were calculated and compared using the methods described in Section 2.7.

2.5 ANATOMICAL AND DEVELOPMENTAL STUDIES

Morphological changes in intertidal organisms are commonly reported, however, there are also considered to be anatomical, reproductive and structural adaptations to allow the organisms to survive under certain environmental conditions. Various aspects of the anatomy and reproduction of D. longifolia were studied with a view to obtaining a better understanding of the mechanisms employed by this species to survive harsh environmental conditions.

2.5.1 Light Microscope Anatomical Studies

Sections for the light microscopic investigation of anatomical features of D. longifolia were made from the various parts of the thallus, including (Fig. 7):

a) the apical pit
b) the wing and midrib of the apical region
c) the wing and midrib of the middle region of the lamina
d) the dichotomising region
e) the wing and midrib near the base of the lamina where the initial stages of rhizoid formation could be observed
f) the midrib at the base of the lamina where the wings had been abraded
g) the holdfast (longitudinal and cross-sectional)
h) the tetraspore, oogonia and antheridia producing laminae
i) the regions of regeneration

Special attention was paid to the midrib region in order to determine the possible presence and nature of any conducting tissue (as reported for Dictyopteris membranacea; Katsaros & Galatis, 1988). The material used for the light microscope sectioning was prepared as described in 2.6.4.1.

2.5.2 Scanning Electron Microscope Anatomical Studies

The thallus structure of D. longifolia was also investigated using the Scanning Electron Microscope (SEM). Sections across various areas of the lamina were prepared using the methods described in 2.6.4.2.

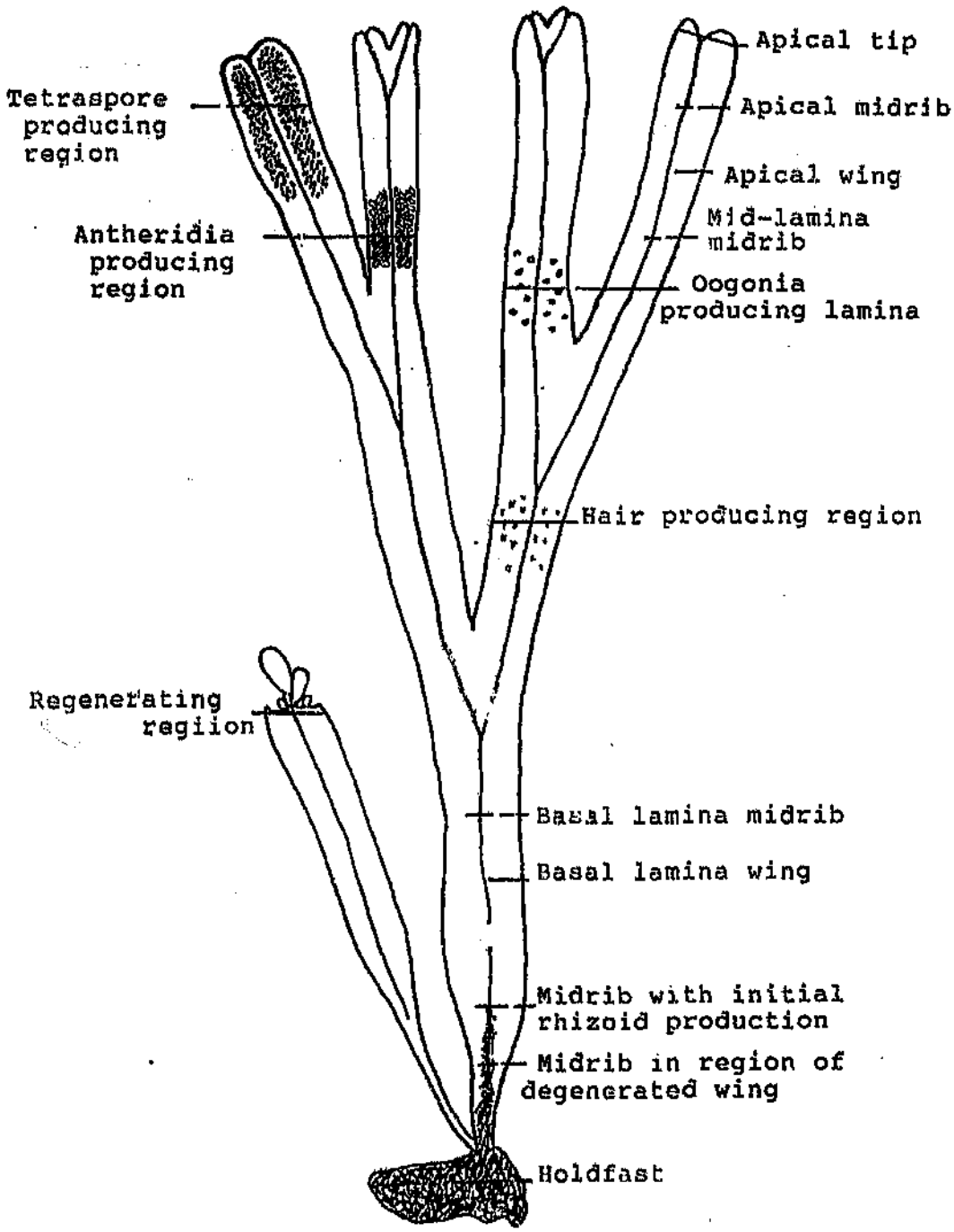


Figure 7: Diagram indicating the different regions of a *Dictyopteris longifolia* plant where sections were taken for the anatomical study.

2.5.3 Transmission Electron Microscope Anatomical Studies

Transmission Electron Microscopy (TEM) was performed on the cells of the different areas of fresh material. In this case, attention was paid to the detail of the cell walls, and especially the presence of any connections between the cells of the midrib. The material was prepared using the method described in 2.6.4.3.

2.5.4 Regeneration Studies

D. longifolia was observed to regenerate new laminae prolifically in the field. Regeneration of thalli from sections of a parent plant not only allows damaged individuals to recover, but also allows for propagation of new individuals (ie vegetative propagation) when sections are removed from the parent plant and then become reattached. Regeneration potential is obviously an important feature in the survival of D. longifolia living in highly wave exposed shores.

The regeneration potential of D. longifolia was studied by placing selected sections of the thallus into culture, to investigate the ease and process with which regeneration occurred. The material used for regeneration studies was collected in March, April and September 1989. A minimum of three, and maximum of six replicates of each type of section were put into culture (ie 3-6 replidishes with 6 compartments per dish; Pl. 3, K) under the conditions described in 2.6.3. The selected sections of the thallus of D. longfolia used for this study are shown in Figure 8.

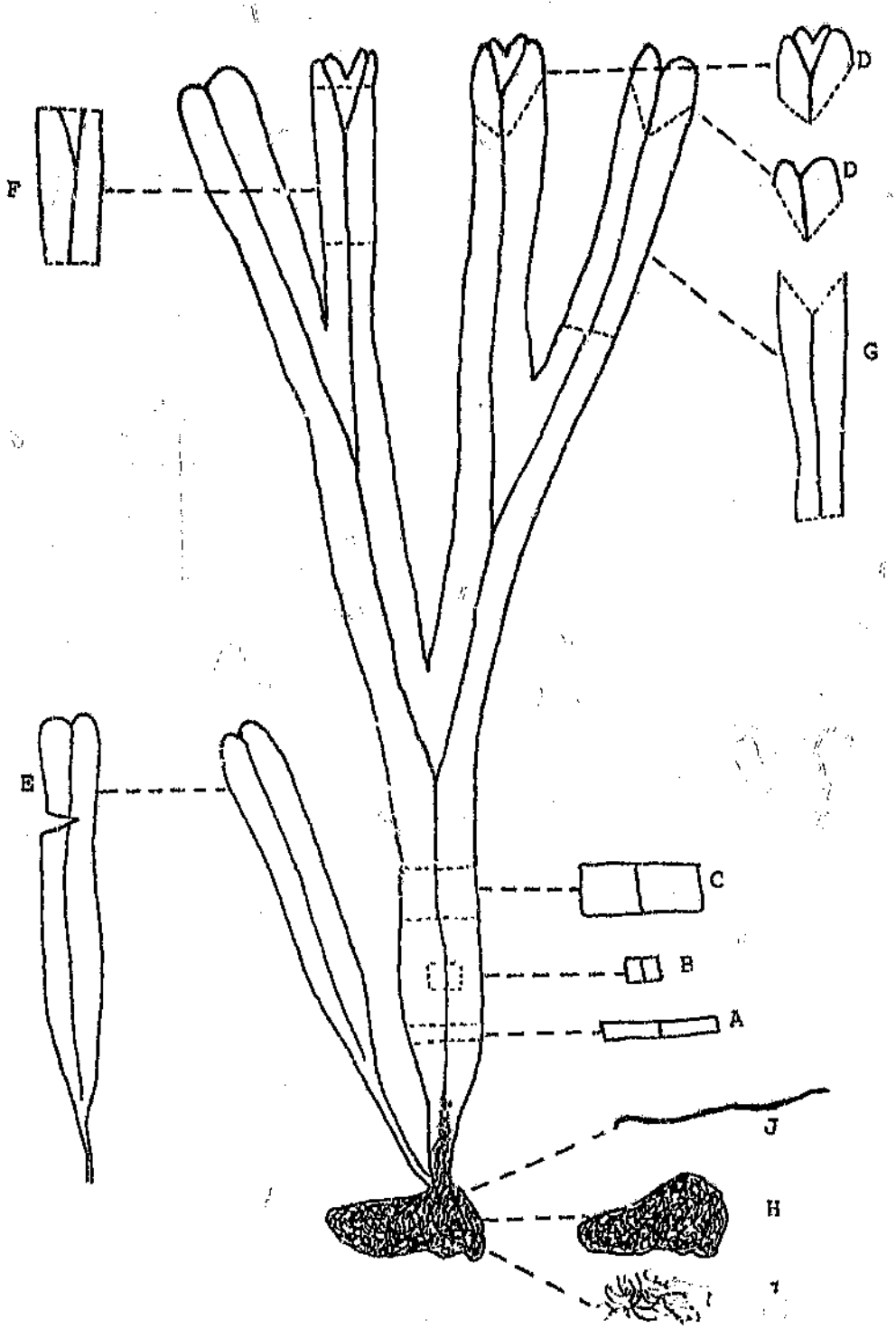


Figure 8: Diagram indicating the different sections of a Dictyopteris longifolia plant used for the regeneration study.

2.5.4.1 Sections of the Lamina

Different sections of the lamina of D. longifolia were studied. These included (Fig. 8, A-D):

A) strips across the lamina, 4mm in length and the width of the lamina
B) sections excluding the margin but including about 3mm on either side of the midrib and up to 1cm in length
C) a section across the lamina, 1cm in length and as wide as the lamina (1-2cm) in width
D) the apical tip, the length of which was measured at weekly intervals (the dichotomised tip was viewed as well).

The weekly increase in length of some of the apical sections (D) were plotted (total length in mm against the time the section had been in culture) as a growth curve.

2.5.4.2 Whole Laminae and Large Sections of Lamina

Individual laminae and large sections (between 5 and 10cm in length) were cultured in pre-sterilised, 250ml Erlemeyer flasks (Pl. 3, L) containing fresh sea water and sealed with tin foil caps. Three replicate sections (of each type of cut) from laminae of D. longifolia were placed into each flask and kept in the walk-in growth chamber under the conditions described in 2.6.3. Several different types of sections were cut from the laminae including sections having (Fig. 8, E-G):

E) a v-shaped cut across the midrib from the side
F) the tips cut off
G) a v-shaped cut which removed the apical cells

2.5.4.3 Whole Plant Regeneration

Whole plants were kept in small glass tanks (t) and 2l plastic bottles in the walk-in growth chamber (Pl. 3, L & J). Each lamina of the three individuals used in this test, had a v-shaped cut removing the apical cells (as in Fig. 8, G). After a month the regenerated laminae were recut with v-shaped cuts and put back into culture. This was repeated once again after the regenerated laminae (second regeneration) had established.

2.5.4.4 Sections of the Holdfast

In the field, D. longifolia grows in clumps. One of the possible reasons for this was considered to be the ability of the bases of old laminae (which remain in the holdfast), as well as individual rhizoids of the holdfast, to vegetatively regenerate the thallus of the plant. Initial attempts to get the holdfast and its component rhizoids to regenerate in different concentrations of Provasoli's Enriched Seawater failed, due to excessive contamination. Eventually these studies were successful in natural seawater. The regeneration of sections of the holdfast were studied (Fig. 8, H).

H) The entire holdfast with the laminae and any remaining midrib sections removed. Six replicate holdfast were placed into 250ml beakers of natural seawater and were kept in the Labex growth chamber under the light conditions specified in 2.6.3.

2.5.4.5 Regeneration from Rhizoid Sections

Regeneration from rhizoids and sections of the holdfast has been reported in Dictyopteris divaricata (Tokida et al., 1953) and other brown algal species. Regeneration

from various sections of rhizoid from D. longifolia were studied (Fig. 8, I-J).

I) Small tufts of rhizoids (12 replicates, ie two dishes) were excised from the holdfast and placed into 5ml of natural seawater in 4cm replidishes and kept in a Labex growth chamber under the conditions described in 2.6.3.

J) Individual sections of rhizoid (about 1cm in length) and excluding branches were dissected out of the holdfast and placed into 4cm replidishes (2 dishes, ie 12 replicates) in natural seawater. These sections were kept in a Labex growth chamber under the conditions described in 2.6.3.

All the regeneration was photographically monitored using an Olympus Photo Automat camera attached to a Wild Dissecting Microscope and the camera attachment of the Zeiss Photomicroscope. Black and white Pan F, 50 ASA, 35mm film was used.

2.5.5 Sexual Reproduction Studies

Sexual reproduction is not believed to be as successful in areas of high wave exposure, as tetrasporogenesis and vegetative propagation. This is due to the necessity for fusion of the two gametes, which may not occur in areas of high wave exposure. Sexual reproduction in D. longifolia was, however, observed infrequently in the field.

Material displaying sexual reproduction was collected in the field at different times throughout the year, prepared, sectioned and viewed on the light microscope using the methods described in 2.6.4.1.

2.5.6 Tetrasporogenesis Studies

The formation of tetraspores is considered to be an important form of reproduction for D. longifolia living in highly wave exposed shores. No meeting of motile cells is necessary (as is needed in sexual reproduction), and as this may not occur easily under conditions of high wave exposure, tetraspores are considered to be more successful in these areas. Material bearing tetraspores was frequently observed in the field and was induced in culture.

Sections across the lamina and 1cm in length were put into culture in individual compartments of replidishes. The material was collected in the middle of May 1989. The dishes were kept in a Labex growth chamber under the conditions described in 2.6.3. Three dishes of sections (6 compartments per dish) were used. After 28 days, tetraspores were observed on the surface of the lamina sections.

The spores were collected with a Pasteur pipette and placed into culture in natural seawater, in 50ml Erlemeyer flasks. The flasks were kept in the walk-in growth chamber under the conditions described in 2.6.3. A flask of spores was kept in each of six thermostatically controlled water baths at 10, 15, 20, 25, 30 and 35°C (±2°C). Tetraspore growth was measured using a Wild Inverted Microscope with a calibrated, graduated eyepiece. The mean of 30 measurements of the thallus and longest rhizoid were calculated on every second day for 20 days. The mean growth rates were graphed for each temperature, over the 20 days of growth and were statistically investigated using the methods described in 2.7.1.

The process of elongation of the spores was also observed using florescence. Germinating spores were placed into 0.1% calcofluor for 20 minutes. Calcofluor has been used as a fluorescent marker in a number of studies (Hughes & McCully, 1975; Waaland & Waaland, 1975). It stains cell walls by binding with cellulose, polysaccharides and callose and has been used in studies of higher plants, fungi and algae. Most of the cytoplasmic contents remain unstained. It is an important stain because it can be added to living cells allowing the processes of elongation and the insertion of new wall material to be observed. Only those walls present at the time of staining, show florescence when exposed to light (ultraviolet and visible light; Hughes & McCully, 1975; Waaland & Waaland, 1975)).

2.6 LABORATORY PROCEDURE

2.6.1 Culture Medium

Various concentrations of Provasoli's Enriched Seawater Medium (0.25, 0.5, 1.0, PES; Provasoli, 1968; Appendix 1) were attempted for the growth studies performed to investigate tetrasporogenesis and regeneration of D. longifolia. It was discovered that all the concentrations of PES that were tested, caused a high degree of associated algal, fungal and bacterial contamination which inhibited the growth of the Dictyopteris sections. However, contamination was kept at a minimum and growth occurred readily in natural seawater (unfiltered and unsterilised). All the cultures had the seawater changed at weekly intervals.

2.6.2 Isolation of Sections of D. longifolia Laminae

Externally visible epiphytes were removed with forceps from the surface of Dictyopteris thallus sections being prepared for regeneration and tetrasporogenesis studies. All sections of lamina were wiped down with 100% alcohol to reduce the possibility of surface epiphytes recovering. The application of alcohol did not appear to adversely affect the growth of the material. The sections were then dipped into germanium dioxide (GeO_2; Appendix 2) which inhibits the growth of diatoms (Lewin, 1966). The material was not cultured in GeO_2 because it has been reported that GeO_2 detrimentally affects the growth of members of the Phaeophyceae (Fletcher & Fletcher, 1975). Bacterial contamination of cultures were treated with the addition of a few grains of Penicillin G (Guillard, 1973) to each well of the culture containers.

2.6.3 Growth Conditions

The majority of sections used in the regeneration and tetrasporogenesis studies were placed into "sterilin" replidishes, 4 cm in diameter, in 5ml of natural seawater (Pl. 3, K). The dishes were sealed with masking tape to stop evaporation of water and the resulting changes in salinity in the wells. The cultures were kept at 21°C (± 2°C) in a Labex (model L.T.G.C.) growth chamber with a light intensity of 22μE $m^{-2}s^{-1}$ and a light:dark cycle of 14:10.

Material cultured in the walk-in growth chamber was kept at 21°C (± 2°C) at an irradiance of 70μE $m^{-2}s^{-1}$ supplied by "cool" white fluorescent tubes under a light:dark cycle of 14:10.

2.6.4 Microscopy

Light microscopic, and Scanning and Transmission Electron microscopic techniques were used to view the external features and growth, as well as to observe the anatomy of sections of the thallus. Whilst the methods used for the preparation of material for light and Scanning Electron microscopic studies were standard and similar to those used for the preparation of other algae and higher plants (described in 2.6.4.1 and 2.6.4.2), the preparation for Transmission Electron microscopy was more difficult. Brown algae are reported to be exceptionally difficult to prepare due to the presence of mucopolysaccharide and alginate extracellular mucilage, as well as polyphenolic physodes (Hallum & Duff, 1988). Physodes have been reported to leak tanrins and distrupt the organisation of the organelles in the cell. The cells also have thick walls and small vacuoles which increase the difficulty of good fixation and infiltration. This means that alternative methods would have to be attempted for the preparation of sections of D. longifolia for Transmission Electron microscopy, if further studies were to be carried out.

2.6.4.1 Light Microscopy Preparation

Living and fixed whole mounts of pieces of the plant were viewed with a Wild Dissecting Microscope and a Zeiss Photomicroscope, to observe external features. Photographic records were made using the cameras attached to these microscopes and black and white Pan F, 35mm, 50 ASA film.

Spore material stained with calcofluor was photographed every seven days, using the fluorescent attachment of the Zeiss Photomicroscope and black and white Pan F, 35mm, 50 ASA film with exposures lasting up to 5 minutes.

Sections of different parts of the lamina and holdfast of D. longifolia were made on a freezing microtome in a supporting medium of Tissue-Tek (Miles Laboratory, USA). Sections of material were also fixed in glutaraldehyde and osmium tetroxide, and embedded in Spurr's resin as described for Transmission Electron microscopy (2.6.4.3). Thick sections were cut on a L.K.B. ultramicrotome with a glass knife. All these sections were stained with Toluidine Blue and mounted on glass slides in glycerol. Sketches were made and photographic records were kept, using a Wild Dissecting Microscope and a Zeiss Photomicroscope.

2.6.4.2 Scanning Electron Microscopy (SEM) Preparation

Sections showing features of general anatomy and material exhibiting regeneration and tetrasporogenesis were prepared for examination by SEM. Small sections were cut by hand, fixed in 2.5% glutaraldehyde and then dehydrated in 10, 20, 50, 70, 80 and 90% ethanol for 10 minutes each and then twice, for half an hour each, in 100% ethanol. The segments were then critical point dried in a Hitachi Critical Point Drier for 1-2 hours. The sections were mounted on 1cm diameter aluminium stubs with an adhesive of colloidal graphite. They were then coated with gold in a Polaron Sputter Coating Unit and viewed on Cambridge S4 and JSM 840 Scanning Electron microscopes. Photographic records were taken of all the observations.

2.6.4.3 Transmission Electron Microscopy (TEM) Preparation

The preparation of material for Transmission Electron microscopy is very difficult in brown algae (Hallam & Luff, 1988). The extracellular mucilage prevents infiltration of the fixatives and resin. The physodes leak tannins into the cytoplasm and disrupt the fixation. The recommended method is a slow fixation and

infiltration (Hallam & Luff, 1988). The method used in this study was a slightly modified version of the method used by Galatis *et al*. (1977) for the brown alga *Sphacelaria*, however, it was not very successful and alternative methods need to be attempted for further studies of this species.

1) The material was cut into small sections and placed into glass vials in 2.5% glutaraldehyde in 0.1M Na cacodylate buffer (Appendix 3). The solution contained 0.25M sucrose at pH 7.2 and the material was kept at room temperature for 5 hours.
2) After fixation, the material was rinsed in solutions of cold 0.1M Na cacodylate buffer with decreasing sucrose concentrations (0.25, 0.2, 0.15, 0.1, 0.05 and 0.0M) for 20 minutes at each concentration.
3) The material was then post-fixed in 1% osmium tetroxide (OsO_4) in 0.1M Na cacodylate buffer and kept in the fridge for 12 hours (pH 7.2).
4) After post-fixation the material was rinsed twice in 0.1M Na cacodylate buffer (20 minutes each rinse).
5) Dehydration was carried out by soaking the material in increasing concentrations of ethanol in 0.1M Na cacodylate buffer (10, 20, 30, 40, 50, 70, 90 and 100%) for 20 minutes at each concentration. This was followed by two 20 minute rinses in 100% ethanol.
6) The material was embedded in increasing concentrations of Spurr's resin (Harper, 1983; Appendix 4) in ethanol (1, 2, 4, 8, 15, 25, 40, 60, 80, and 100% resin) for 6 hours at all concentrations except 60, 80 and 100%, in which the material was kept for 12 hours. Due to the long infiltration periods, the Spurr's with the longer pot-life was used. This was followed by two changes of fresh 100% resin.
7) The material was then polymerised in an oven at 70°C for 12 hours.

8) The material was sectioned on a L.K.B. ultramicrotome using a glass knife. Thick sections were used for light microscopy and ultrathin gold and silver sections (40-70nm) were picked up on 200 hexagonal mesh, copper grids for TEM.
9) The sections were stained with uranyl acetate and lead citrate to enhance the contrast (Reynolds, 1963; Appendix 5).

2.7 STATISTICAL ANALYSES

2.7.1 Means

The mean values of the measurements for each attribute (from measurements taken throughout the year) were calculated for each site. These were plotted as bar, line and scatter graphs. The standard deviation values are included in brackets after the mean values in the text. The mean, standard deviation values and the sample sizes for all the measurements are given in Appendix 6.

2.7.2 Tests of Significance

Significance of differences between the mean values for different sites for selected parameters, was tested using the Student T-test and tables from Garvin (1986).

$$\sqrt{\frac{SD(A)^2}{n(A)} + \frac{SD(B)^2}{n(B)}} = t$$

SD is the standard deviation
n is the number of samples

2.7.3 Principle Component Analysis (PCA)

Principle Component Analyses have been used in various terrestrial and marine ecological studies (Rice & Chapman, 1985) and were used in this study to enable any correlations between

a) some of the environmental measurements and
b) aspects of the algal morphology and physical characters,

to be detected. An abridged interpretation of the PCA ordination biplot is as follows (consult Jongman et al., 1987; Ter Braak, 1988 for detailed explanations):

The intersection of the axes represents the sample mean or nodal point. The lines represent the approximate direction of maximum variation of the variable, whereas, the length of the line equals the rate of change in that direction. The angle between respective lines provides an estimate of correlation. Lines that point in the same direction indicate positively correlated variables, perpendicular lines indicate lack of correlation and lines pointing in opposite directions indicate negatively correlated variables. The principle components (axes) may be quantified by dropping a perpendicular from each variable to the respective axes. The proportional contribution of the variables to each principle component is the length of the segment from the nodal point to the intersection of the variables' perpendicular axis.

3 RESULTS

3.1 EXPERIMENTAL ORGANISM

3.1.1 External Morphology of Dictyopteris longifolia from Palm Beach.

Dictyopteris longifolia is a brown alga composed of numerous flat, strap-like laminae attached to a basal rhizoidal clump (Pl. 4, A; Fig. 1). The rhizoidal clump or holdfast can grow to a few centimetres in diameter and is perennial (while the laminae die back every year). The holdfast gives rise to many (see Section 3.7.2.6) new laminae after the old laminae die back due to natural senescence, abrasion or herbivory (Pl. 4, B-D). The holdfast is comprised of entangled, multicellular, branched rhizoids (Pl. 4, E-G) which appear to be trichothallic (i.e divide from the base). The terminal ends of the rhizoids are rounded and have a high concentration of cell contents in the tips (Pl. 4, H). Rhizoids were also observed to grow from the midrib at the base of the lamina, predominantly where the lamina wing had been removed (Pl. 4, I-K). Occasionally rhizoids were observed growing from the midrib in damaged areas closer to the laminal apex (Pl. 4, L).

The strap-like laminae of D. longifolia are dark, golden brown in colour, flat and dichotomously branched. The apical tips are bluntly to acutely rounded and there is an apical pit containing the meristematic cells (Pl. 5, A & B, I & J; Fig. 50). The laminae are 0.5-1.5cm wide (see Section 3.7.2.2) with the number of dichotomies per lamina varying considerably, however, the maximum number observed was 8 (see Section 3.7.2.5). Immature laminae do not have dichotomies. The mean maximum length of the laminae varied spatially and seasonally and this

variation is described in Section 3.6. For the purpose of this study, a lamina is defined as a single outgrowth from the holdfast. It includes everything from the point of attachment at the holdfast to the tip of the longest branch (Fig. 6).

There is a prominent, centrally arranged midrib which is flat in the apical regions of the lamina (Pl. 5, C), but thicker (approximately 1mm thick) and often giving rise to rhizoids in the more mature regions nearer the base of the lamina (Pl. 5, D). At the base of the lamina, the wings may be removed leaving the midrib which is known as the stipe in some species and which may be covered in fairly long rhizoids (Pl. 5, E & F; Fig. 51, E; Fig. 52, G). The undamaged margins of the wings of the laminae are swollen in the mature regions (Pl. 5, G & H; Fig. 51, B; Fig. 52, F), but not in the immature regions (Fig. 51, A). The laminal wings were observed to give rise to the scattered tetrasporangia (Pl. 5, K), antheridia (Pl. 5, L) and oogonia, both in the field and under the laboratory conditions described in Section 2.6. In some individuals of D. longifolia observed in the field, and on sections in culture (Section 2.6), the laminae were also observed to give rise to multicellular surface hairs (Pl. 5, M-O; Fig. 53).

3.2 DISTRIBUTION

Specimens from the herbaria listed in Section 2.3, included individuals of D. longifolia from as far north as Kosi Bay (26 32, CD), and as far south as Arniston (34 20, CA). D. longifolia is, however also mentioned in Isaac (1956), indicating a distribution which extends along the Mozambique coast northwards to at least Inhaca Island (26 32, AD). The species is also listed in "Seaweeds of the de Hoop Nature Reserve" (34 20, CC;

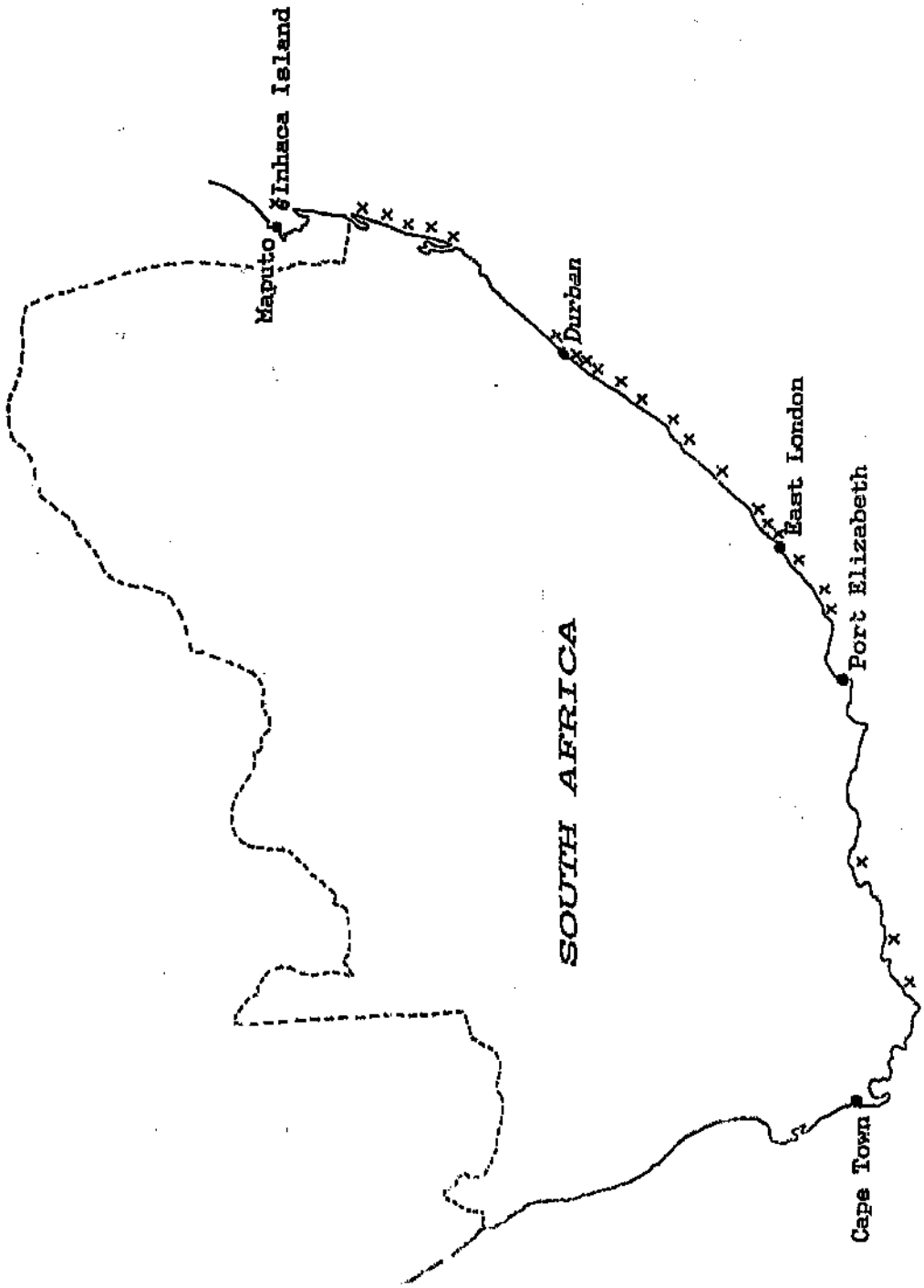


Figure 9: Map of South Africa indicating the distribution of Dictyopteris longifolia as compiled from herbarium specimens, personal observation, personal communication and literature.

Bolton & Stegenga, 1990). Personal communication with researchers on the west coast of southern Africa (J. Bolton & F. Molloy), indicates that D. longifolia is a warm water species and is limited to regions east of Cape Agulhas (Fig. 9).

Specimens of D. longifolia preserved in the herbaria of South Africa have been collected over many years, in different seasons, and at different points along the South and East coasts of southern Africa (Fig. 9). There is great variation in the size as well as the reproductive and morphological condition of the specimens. Unfortunately, due to the lack of sufficient examples from a single area or season, no conclusions about trends in the seasonality of morphological variation can be drawn from these specimens. To determine any seasonal changes in morphology, a continuous measurement of individuals throughout at least one whole season would have to be completed.

3.3 WATER MOVEMENT

D. longifolia was observed growing in areas of different degrees of wave exposure at Palm Beach, Natal. These areas ranged from very calm pools high up the shore (Pl. 1, A; Fig. 3, F & G) to highly wave swept rocky reefs (Pl. 1, B; Fig. 3, A). In some areas the plants were even exposed to the sun and air for long periods of time during low tides (one to two hours during calm, low spring tides; Pl. 1, C).

It must be noted that the values in all graphs mentioned in the rest of this study are arranged in the order of subjective ranking of the sites, ie the two low wave exposure sites (L1 and L2), the higher, low wave exposure site (L+), the intermediate wave exposure site (I), the

higher, intermediate wave exposure site (I+), the high wave exposure site (H) and the extremely high wave exposure site (H+) (see Section 2.2; Fig. 3, A-G).

3.3.1 Wave Action

3.3.1.1 Wave Strength

The method of measuring wave strength (in Newtons/m^2) using a modified dynamometer (Palumbi, 1984; see Section 2.4.1.1; Fig. 4), has a serious drawback in that it is impractical and unsafe to use this method at any time other than extreme low tide. Although the sites higher up the shore can be measured later in the cycle, for comparable results, all sites must be measured at the same time. This means that only those sites experiencing wave activity throughout the tidal cycle (eg H and H+), could be measured using the dynamometer. The usefulness of this method to test a large range of sites experiencing different degrees of wave activity, is limited. However, comparing the two sites which were measured (H and H+), it appears that the extremely high wave exposed site (H^+) experiences a significantly higher ($p<0.001$) degree of wave exposure, with a mean value of 539.49 (±281.04) N/m^2, than the wave exposed site protected by a large rock (H; see Fig. 3, B) which has a mean value of 355.66 (±209.58) N/m^2 (Fig. 10).

3.3.1.2 Wave Number

A similar problem was experienced with counting the number of waves passing over the site per time period (see Section 2.4.1.2). Measurements could only be taken when waves were breaking over the area at low tide. This only occurred in the two sites mentioned above (H and H+) and the higher, intermediate wave exposure pool (I+), which occasionally had small waves breaking into it.

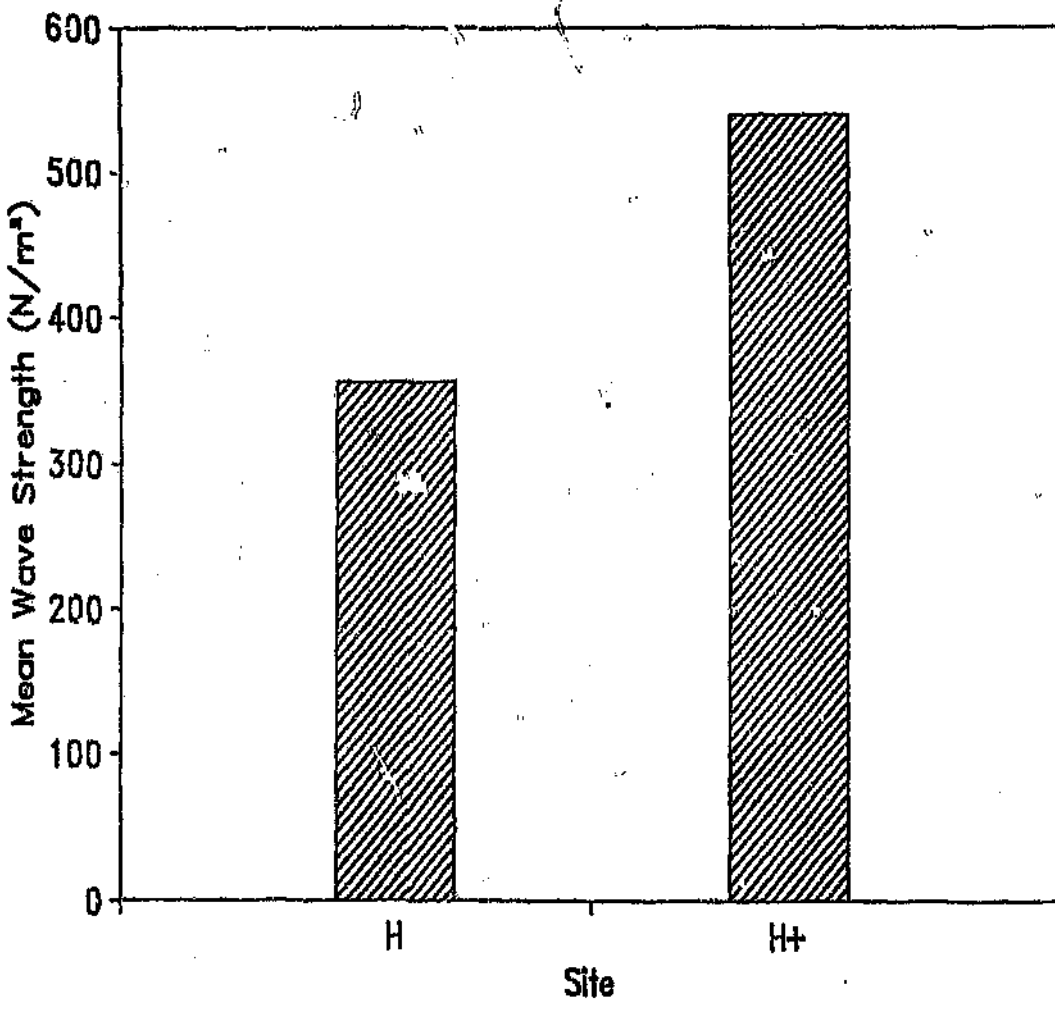


Figure 10: Mean wave strength (N/m^2) for the two highest wave exposure sites, ie the extremely high wave exposure site (H+, n=57) and the high wave exposure (H, n=30), from measurements using the modified dynamometer.

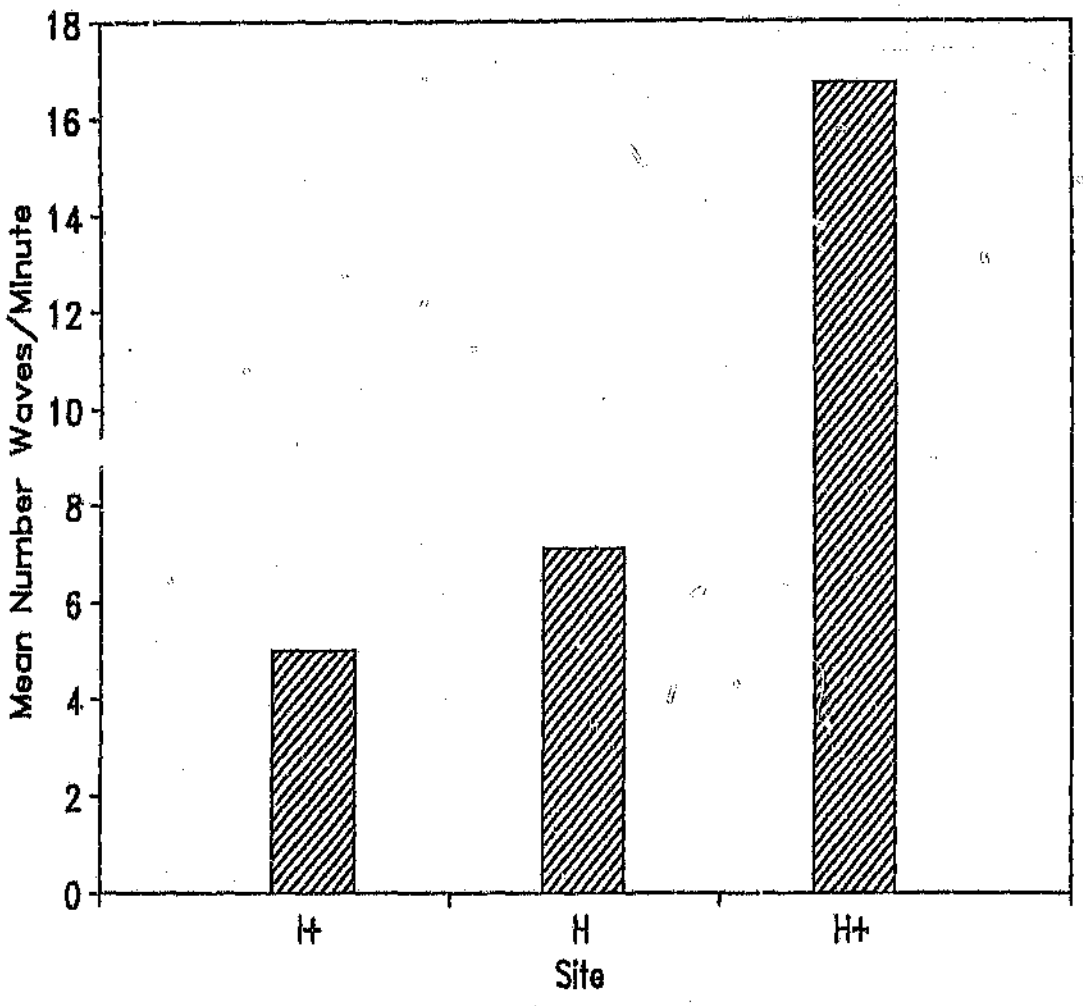


Figure 11: Mean wave number per two minute periods for the extremely high wave exposure site (H+, n=11), the high wave exposure site (H, n=12) and the high, intermediate wave exposure site (I+, n=3).

This method did not distinguish any differences in wave force in the other sites (ie L1, L2, L+ and I). It was found that the most convenient counting period was two minutes. From the graph of the mean number of waves in two minute periods, it appears that there may be a trend in the number of waves experienced by the sites. The trend in wave number of the sites measured, matches the subjective ranking of the sites (ie H+ has a mean of 16.7 (±0.989) waves/2 minutes, followed by H with 7.08 (±1.296) waves/2 minutes and then I+ with 5 (±0.817) waves/2 minutes). The highest wave exposure site (H+) has a significantly larger ($p<0.001$) number of waves than the other two sites (H, I+) with H being higher ($p<0.05$) than I+. This method does indicate that not only do the strengths of the waves differ between sites, but so do the wave numbers (due to the position on the shore and the shore topography).

3.3.2 Water Motion

3.3.2.1 Lifesaver Sweet Dissolution Method

The third method of measuring water movement involves the use of "Lifesaver" sweets (see Section 2.4.2.1). This method differs from the previous two methods in that water motion, not wave force or number, is measured. The method involves the use of dissolution rates, which are assumed to increase with water motion (Martell, pers. comm.). There were various drawbacks to the use of this method. Firstly, it was not determined to what degree the flavour of the sweet affected the dissolution rate and, although the flavours were randomly distributed amongst the sites, this may have affected the mean weight loss values significantly (due to the small replicate number which was used). A second problem was that the continued

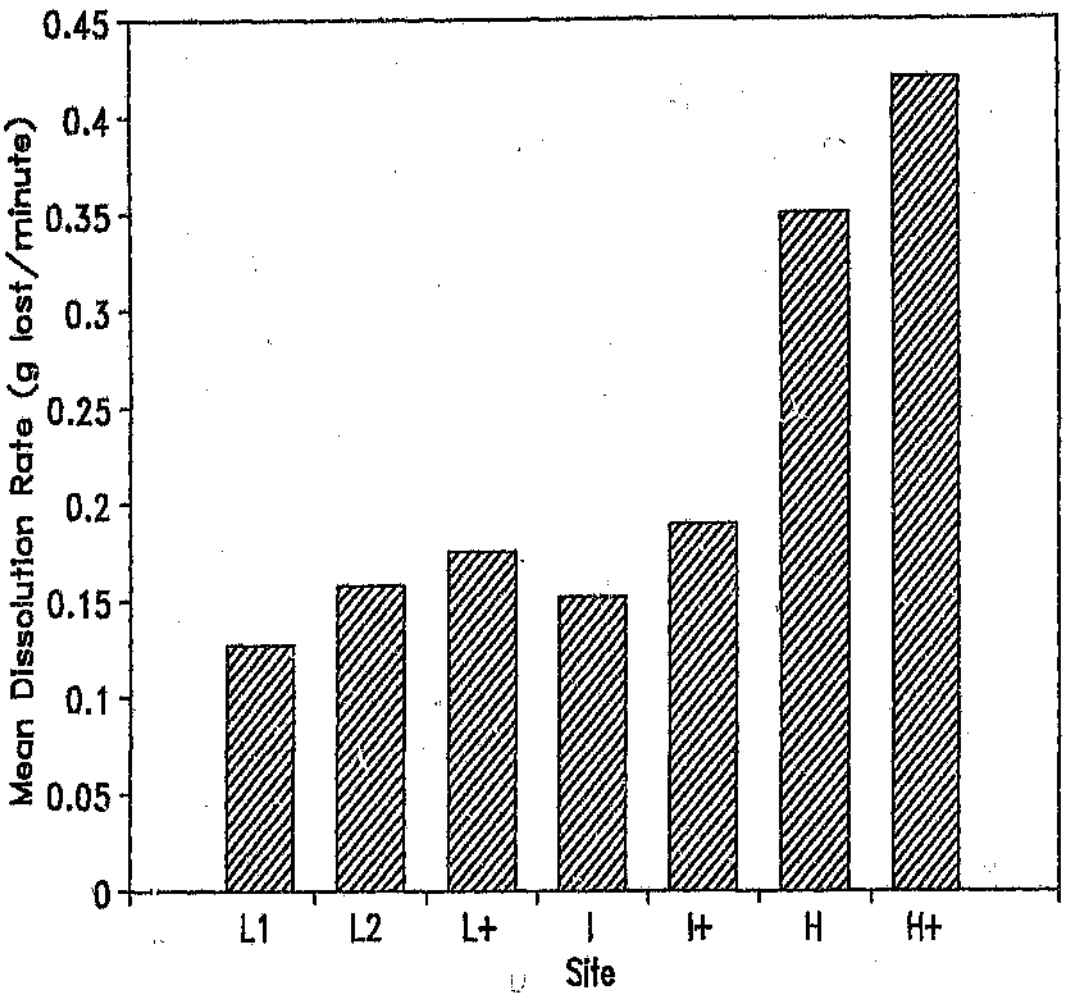


Figure 12: Mean number of grams of "Lifesaver" sweet lost per minute for all the sites (L1, n=9; L2, n=9; L+, n=10; I, n=9; I+, n=10; H, n=10; H+, n=9).

dissolution of the wet sweets after removal from the water, was not initially accounted for. In later experiments, individual sweets were immediately packed into pre-weighed bottles. However, in the latter case, the amount of water included in the weight was not considered. This would vary considerably depending on the size of the remaining piece of sweet. Another problem that was experienced, is similar to that discussed for the previous two methods, ie to get to the more wave exposed sites, the study had to be performed at low tide and at this time the calmer sites (ie L1, L2, L+, I, I+) were not experiencing water movement. From a graph of mean dissolution rates (Fig. 12), it is apparent that there is no significant difference ($p>0.05$) between the water movement of sites experiencing no water movement at low tide, ie L1, L2, L+, I, and I+ had mean dissolution values of 0.1271 (± 0.043) g/min, 0.1572 (± 0.033) g/min, 0.175 (± 0.075) g/min, 0.1514 (± 0.022) g/min and 0.1890 (± 0.093) g/min, respectively. The two sites experiencing water motion at low tide (H and H+) showed a significantly higher dissolution rates ($p<0.001$), with H+ having a mean dissolution rate of 0.4189 (± 0.088) g/min which is significantly higher ($p<0.05$) than H (0.3494 (± 0.027) g/min).

3.3.2.2 Plaster Block Dissolution Method

The final method used to measure water movement in this study, was similar to the previous method in that dissolution rates were measured. In this case, the dissolution rates of pre-weighed plaster of paris blocks. The blocks were fastened to clumps of firmly attached plants such as Gelidium, by means of cable-ties (see Section 2.4.2.2). The blocks were set out at one low tide and removed, to be weighed, at the next low tide. The advantage of this method was that the blocks remained in

the water over a full tidal cycle, thus experiencing water movement at high tide. This was not possible with the other methods. It must be taken into consideration that those sites high up on the shore experience only one short period of high water movement (ie at high tide), whilst those sites nearer the bottom of the intertidal region experience longer periods of water motion. The results may have been different, had it been possible to put the blocks in at low tide and remove them at high tide (either after one tidal cycle, or after two). Unfortunately, this experiment was only performed once, and for some of the sites (I and H+), only a single block was retrieved. No significance can thus be attached to the results received, however, the trends can be observed. Looking at Figure 13 it is apparent that, once again, the two sites with the highest wave exposure (H and H+) show the greatest degree of weight loss (mean percentage weight lost are 61.87 (±11.04)% and 68.94 (±0)%, respectively). However, the difference between these two and the low wave activity site (L1), which has a mean weight loss of 58.09 (±6.20)%, does not seem to be remarkable. The other sites all have a similar degree of weight loss (L2, L+, and I+ have mean values of 42.44 (±3.82)%, 46.14 (±11.66)% and 46.47 (±14.41)%, respectively), except for the sandy, intermediate wave activity gully (I) which experienced a mean weight loss of 22.49 (±0)%. Blocks placed at the latter site recorded a much lower weight loss, however, this was probably due to the fact that the blocks became inundated with sand and had to be dug out after one tide, thus preventing the block from being washed by the waves.

The PCA diagram (see Section 2.7.3), Figure 14, incorporates two of the environmental conditions experienced by the plants. These are the amount of sand present (in suspension in the water and deposited) and the degree of water movement. The former aspect (ie sand)

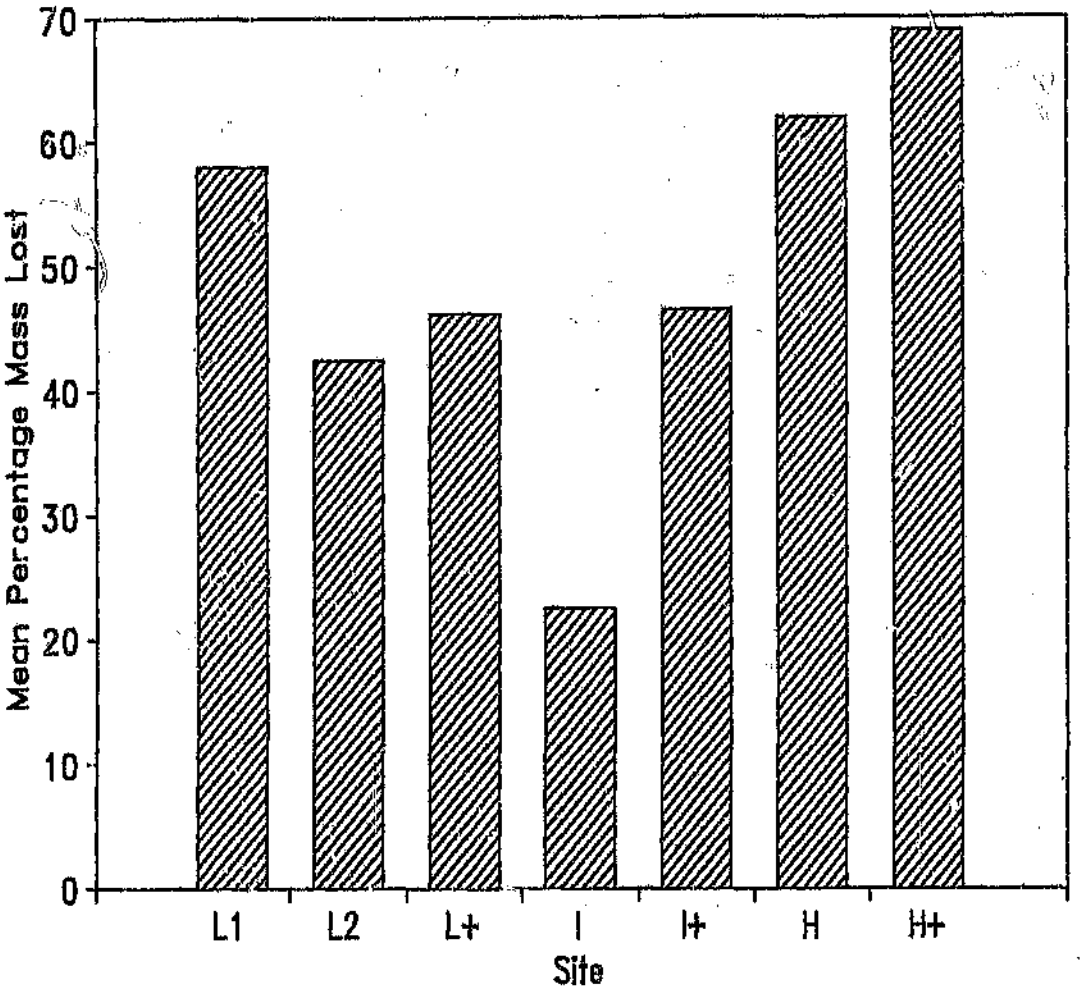


Figure 13: Mean percentage of weight lost from plaster of paris blocks for all the sites (L1, n=2; L2, n=5; L+, n=5; I, n=1; I+, n=5; H, n=4 and H+, n=1).

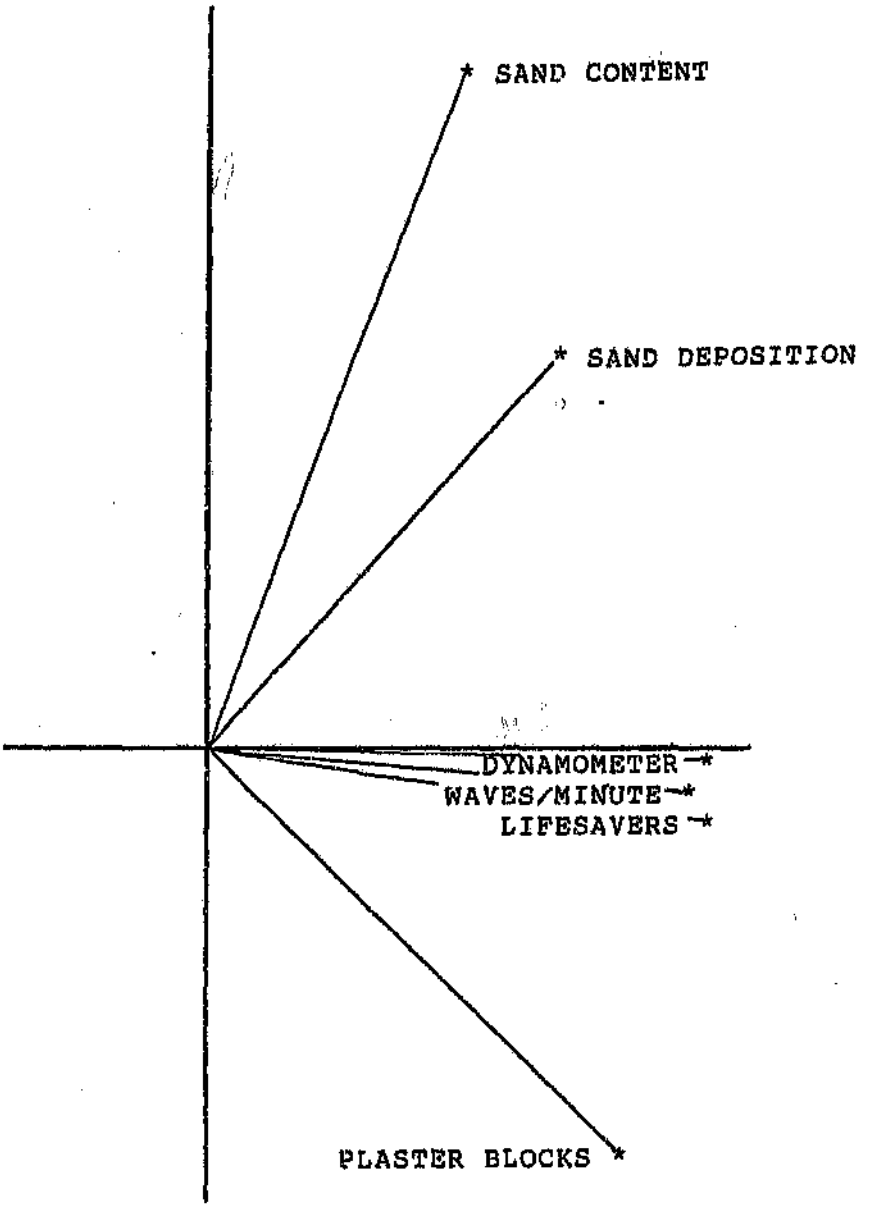


Figure 14: PCA showing correlation between the measurements of sand and wave exposure.

will be discussed under Sections 3.4 and 3.5. Water movement is represented on the PCA, by the four methods of measurement used in this study. The three methods which were only used at low tide, (ie the dynamometer, wave counts and the "Lifesaver" technique) are all very closely correlated on the PCA (PCA angles between the dynamometer and number of waves = 4^{o}, dynamometer and lifesavers = 3^{o}, number of waves and lifesavers = 7^{o}), while the plaster block method which covered the full tidal cycle, is fairly closely correlated to the other three, but not as closely correlated as they are to each other. (PCA angle between plaster blocks and dynamometer = 35^{o}).

3.4 SAND CONTENT OF WATER

The mean sand content of the water samples, taken throughout the year from each site (see Section 2.4.3), is given in Figure 15. The water of the highest wave exposure site (H+) and the intermediate site (I) have significantly higher ($p<0.001$) sand content values than the other sites (0.101 (±0.044) g/100ml and 0.088 (±0.033) g/100ml), respectively), but are not significantly different from each other ($p>0.05$). The water of the second highest (H) and high, intermediate wave exposure (I+) sites both have the lowest ($p<0.001$) sand content values (0.047 (±0.029) g/100ml and 0.044 (±0.004) g/100ml, respectively) but are not significantly different from each other ($p>0.05$). The other sites (L1, L2 and L+; 0.057 (±0.022) g/100ml, 0.062 (±0.002) g/100ml) and 0.072 (±0.006) g/100ml, respectively) all have similar ($p>0.05$) and intermediate sand content measurements. It was initially suspected that the sand content of the water would be found to be correlated with the degree of water motion.

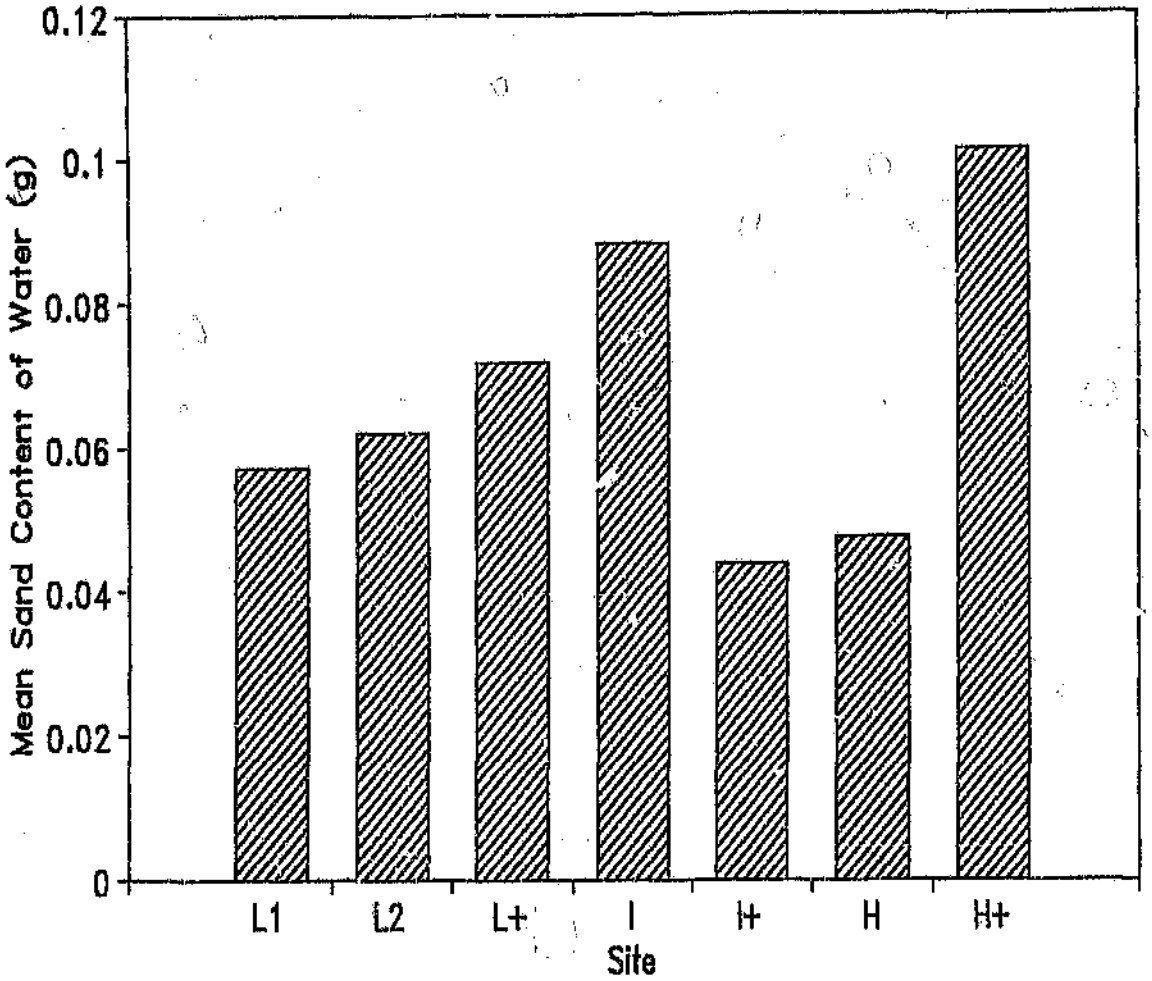


Figure 15: Mean sand content of water from all the sites (L1, n=46; L2, n=12; L+, n=19; I, n=38; I+, n=19; H, n=34; H+, n=39).

Looking at a PCA (Fig. 14) which indicates the relationship between the results from the four different methods of water movement measurement, sand content and sand deposition; the correlation between sand content and deposition, and the degree of water movement (with the methods that were used in this study), is slight (PCA angle between the dynamometer and sand movement = 50^{o}). There does, however, seem to be some correlation between the sand content of the water and the amount of sand deposited (PCA angle = 20.5^{o}), and between the various methods of measuring water motion (see Section 3.3).

3.5 SAND DEPOSITION

Photographic records of the degree of sand inundation experienced by a single plant (Pl. 6, A-E), as well as inundation in the intermediate (I; Pl. 6, F-I) and highest (H+; Pl. 6, J-L) wave exposure sites, indicate that sand deposition may occur extensively. All the sites were observed to continuously differ in depth and shape due to different degrees of sand inundation, which varied considerably over the observation period. The photographic sequences are not the stages of a single inundation, but rather the degree of sand cover at different times or the year, arranged in a sequence of increasing cover. The degree of sand inundation was also observed to change considerably over a 24 hour period.

Unfortunately, the measurement of sand deposition using the sand trap was not successful in many of the sites. It was impractical to repeat the experiment due to the weight of the concrete blocks, the distance of some of the sites and the number of blocks lost or buried. The data presented in Figure 16 can thus not be statistically analyzed. However, it appears as if the low wave exposure site (L1) site has the smallest amount of sand deposition

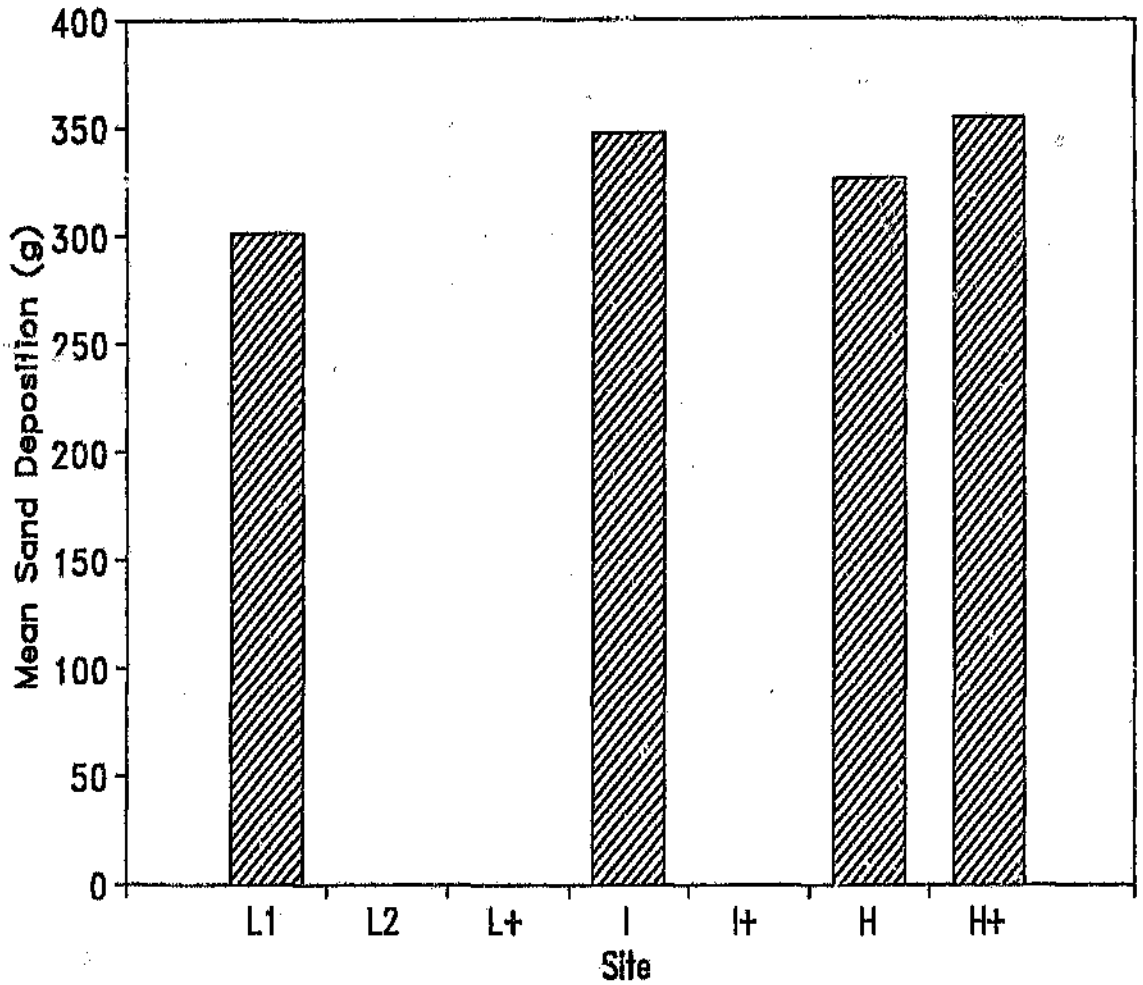


Figure 16: Mean mass of sand deposited for those sites in which the blocks were retrieved (L1, n=3; I, n=3; H, n=3; H+, n=6).

(300.88 (±10.86) g) and the highest wave exposure site (H+), the largest amount (354.66 (±22.84) g. The sand inundated, intermediate wave exposure site (I) showed a similar and high volume of sand to H+ (347.03 (±8.87) g), while the second highest wave exposure site (H), has a slightly lower volume of sand trapped (326.22 (±49.92) g). These observations serve merely to suggest a trend in the pattern of the volume of sand movement in the different sites.

The PCA (Fig. 14) indicates some correlation between the sand captured and the sand content of the water (PCA angle = 20.5°), but this does not appear to be correlated with water movement (as measured in this study).

3.6 MEAN MAXIMUM LAMINAL LENGTH OF THE POPULATION

The mean population size or maximum laminal length of D. longifolia at Palm Beach was determined by measuring the length of the longest lamina of mapped individuals from each site, on each trip (see Section 2.4.5). For this section the individuals remained in situ and were repeatedly measured. Only the populations in the sites experiencing the highest wave exposure (H+ and H), as well as the lowest wave exposure site (L1), were measured throughout the study period. All three of these showed a sharp decrease in the mean laminal length towards the middle of the study period (when abrasion was observed to increase), followed by a slight increase towards the end of the study period (when lamina regeneration was prevalent; Fig. 17, L1, H & H+). Those sites only measured towards the end of the study (L+ and I+) showed a gradual increase in mean population size (Fig. 17, L+ & I+). The intermediate wave exposure site (I), which was inundated by sand for long periods of time during the study period, showed an increase in the mean size of the

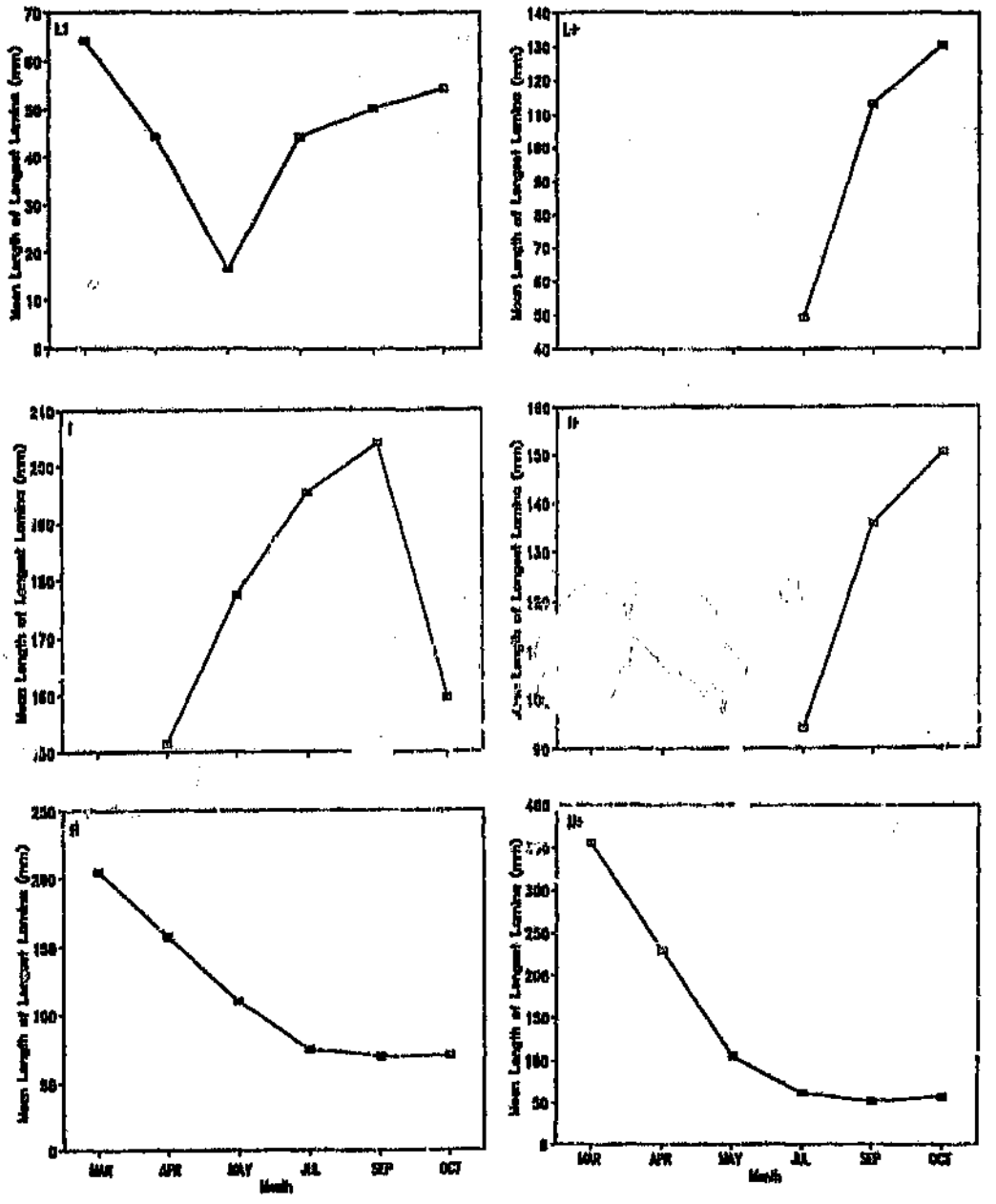


Figure 17: Mean monthly population size (taken as the maximum length of the longest lamina) for L1, L+, I, I+, H, and H+. The other low wave activity site (L2) was not included because only the last two month's measurements were taken.

population when the individuals of the other populations were decreasing in size. The plants in this site began to decrease in size towards the end of the study period when the individuals of the other sites were increasing in size (Fig. 17, I). The one low wave exposure site (L2) was only measured on the last two trips and was thus not included in these graphs. There was, however, little difference between the September and October measurements in this site.

3.7 MORPHOMETRY

Various aspects of the structure of Dictyopteris longifolia were measured, statistically analyzed and represented in bar and scatter graphs. For the purpose of this study, the holdfast is the entire matted, rhizoidal region and the lamina is the region from the point of attachment to the holdfast, to the tip of the longest lamina (Fig. 1).

3.7.1 Features of the Holdfast

3.7.1.1 Diameter

The diameter of the holdfast is one of the morphometric measurements taken on the plant. The mean of this measurement, from data collected throughout the study period, is displayed in Figure 16. The one low wave exposure site (L+) has a significantly lower ($p<0.001$) mean holdfast diameter (12.95 (±2.75)mm) than the other sites. The other two low wave exposure sites (L1 and L2) are similar to each other ($p>0.05$) but significantly higher ($p<0.001$) than the L+ site with mean diameter values of 15.8 (±4.42)mm and 15.7 (±2.8)mm. The other sites (I, I+, H and H+) have higher mean holdfast diameters (18.75 (±0.75)mm, 22.23 (±1.00)mm, 23.23 (±5.28)mm and 21.85 (±7.77)mm, respectively. They are

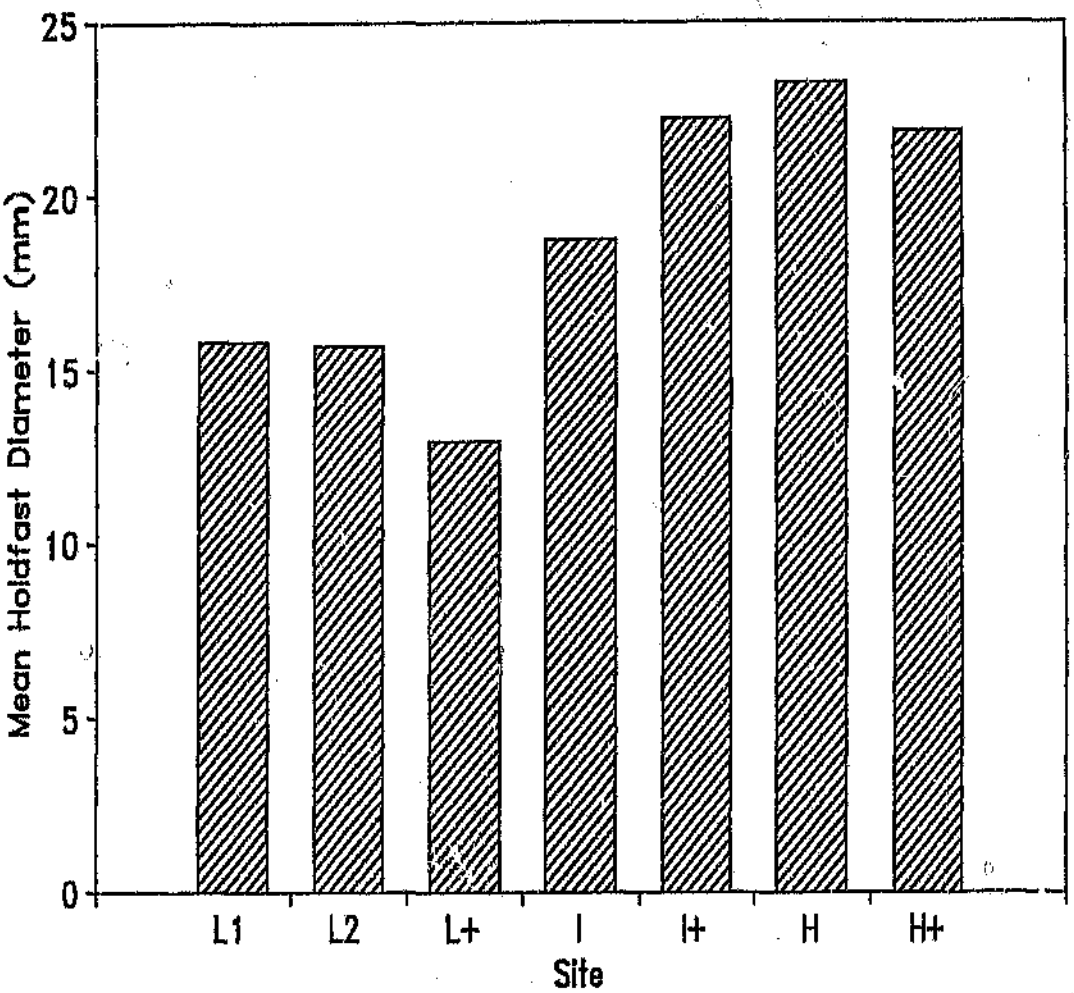


Figure 18: Mean holdfast diameter (mm) from measurements taken over the entire observation period (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41 and H+, n=53).

significantly different ($p<0.001$) from each other (except I+ and H+).

Figure 19 is a scatter diagram of the holdfast diameter of D. longifolia plotted against the maximum laminal length of the individuals, of samples (throughout the study period) from the low wave exposure site (L1) and the highest wave exposure site (H+). From this graph, it appears that there may be five groups of plants present, ie small plants which remain small or may grow and retain small holdfasts (L1 and H+; holdfast diameter 5-38.5mm, lamina length 4-132mm), larger plants which have small holdfasts (H+ only; holdfast diameter 6-19mm, lamina length 170-230mm), short plants with large holdfasts (H+ only; holdfast diameter 28.5-32.5mm, lamina length 39-102mm), medium plants with medium holdfasts (H+ only; holdfast diameter 19-36mm, lamina length 305-375mm) and large plants which have large holdfasts (H+ only; holdfast diameter 52.5-65.5mm, lamina length 477-535mm). Whether these groups are due to different stages of development or to reactions to the different degrees of wave exposure, was not investigated. The third group (large holdfast and short laminae) consists of plants which are considered to be regenerated laminae from the perennial holdfasts. It must be noted that, as this comparison is taken over the whole study period, plants at all stages of development (through the season) are included.

3.7.1.2 Holdfast Area

The mean holdfast area values, from measurements taken throughout the study period, are displayed in Figure 20 which shows the three low wave exposure sites (L1, L2 and L+) as having the lowest mean holdfast area ($0.000219 (\pm 9 \times 10^{-5}) m^2$, $0.000223 (\pm 3.78 \times 10^{-5}) m^2$ and $0.00013 (\pm 4.78 \times 10^{-5}) m^2$, respectively), with L+ having the lowest

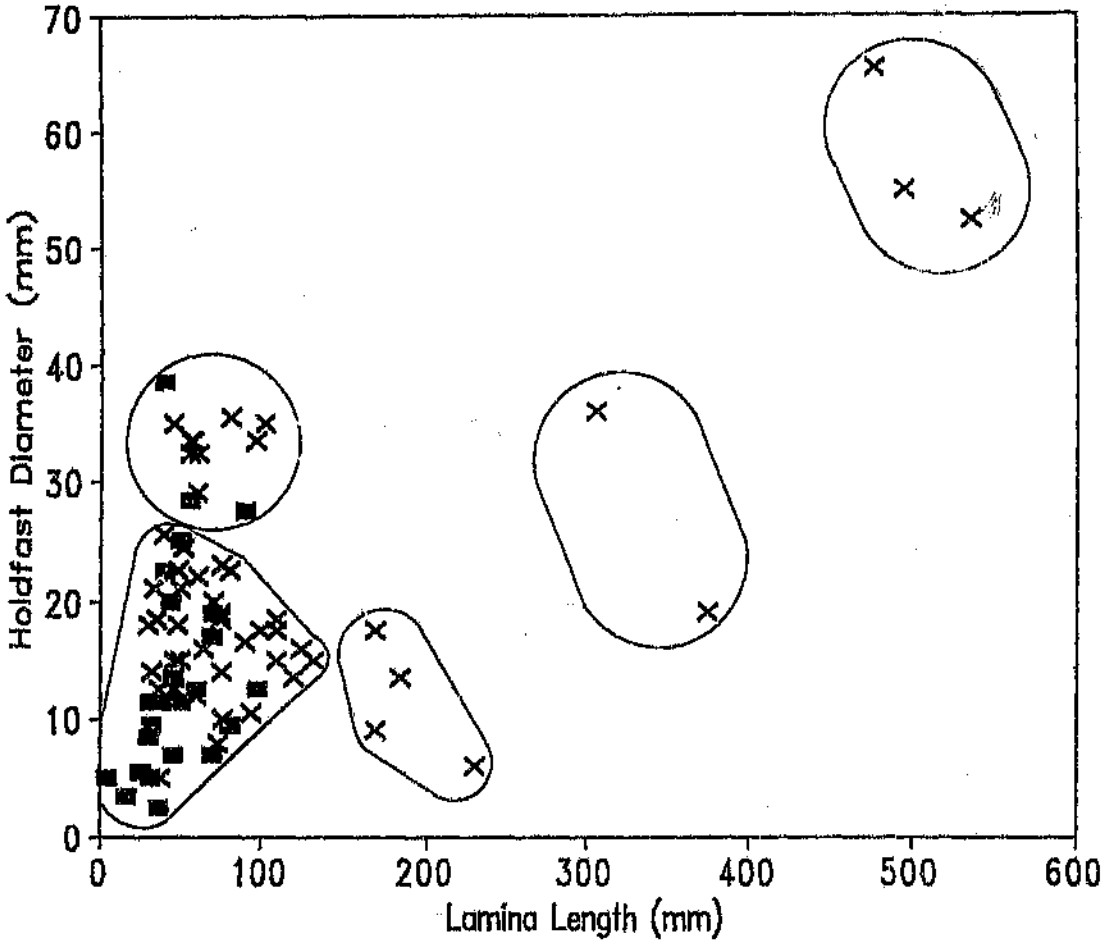


Figure 19: Scatter graph of the laminal length versus holdfast diameter of all individuals studied in the L1 (■) and the H+ (x) sites, over the entire study period.

of the three ($p<0.001$). The other two low wave exposure sites (L1 and L2) are not significantly different from each other ($p>0.05$). The three highest wave exposure sites do not show significantly different holdfast areas ($p>0.05$) but are higher (I+ has a value of 0.000442 ($\pm 6.9 \times 10^{-5}$)m^2, H a value of 0.000418 ($\pm 4.5 \times 10^{-5}$)m^2 and H+ a value of 0.000516 ($\pm 3.6 \times 10^{-4}$)m^2) than the intermediate site (I) which has a mean value of 0.000302 ($\pm 4.5 \times 10^{-5}$)m^2 ($p<0.001$).

3.7.1.3 Holdfast Mass

The mean mass values of the wet and dry holdfasts, from measurements taken throughout the study period, are displayed in Figures 21 and 22, respectively. In both graphs, the results show a similar trend. The low wave exposure site (L+) has the lowest mean holdfast mass (0.372 (± 0.206)g wet and 0.209 (± 0.120)g dry; $p<0.001$), with the other two low wave exposure sites (L1 and L2) being higher ($p<0.001$) but not significantly different from each other ($p>0.05$). The mean holdfast mass values for L1 and L2 are 0.848 (± 0.47)g wet and 0.447 (± 0.29)g dry for L1, and 0.866 (± 0.292)g wet and 0.473 (± 0.161)g dry for L2. The two highest wave exposure sites (H and H+) have the highest mean holdfast mass (3.843 (± 1.68)g wet and 2.553 (± 0.97)g dry, and 5.547 (± 6.29)g wet and 3.675g (± 4.27)g dry, respectively; $p<0.001$) but are not different from each other ($p>0.05$). The two intermediate sites (I and I+) are significantly different ($p<0.001$) from each other and increase with an increase in wave exposure. The mean holdfast mass for these two sites are 1.192 (± 0.05)g wet and 0.793 (± 0.11)g dry, and 2.726 (± 0.71)g wet and 1.738 (± 0.52)g dry, respectively.

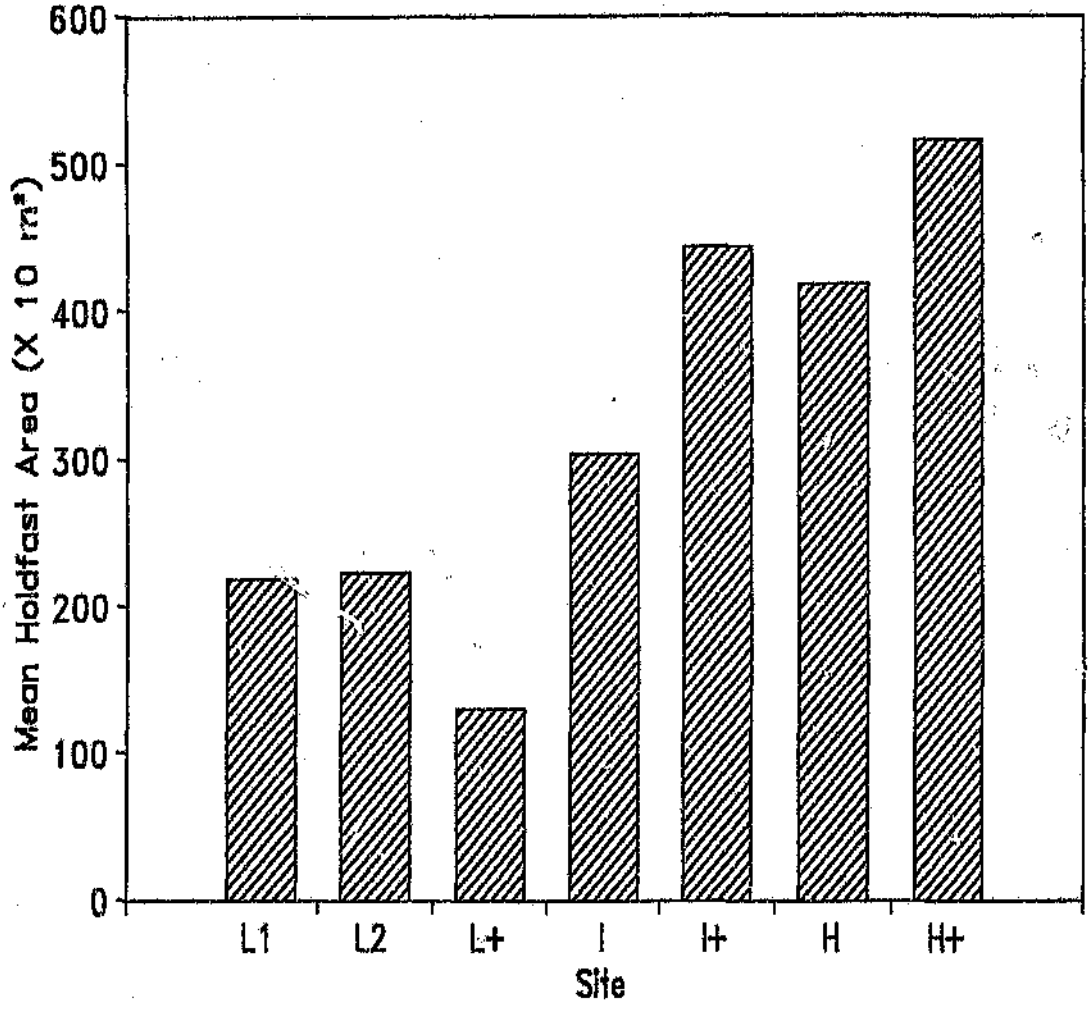


Figure 20: Mean holdfast area (m^2) from measurements taken over the entire study period (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41 and H+, n=53).

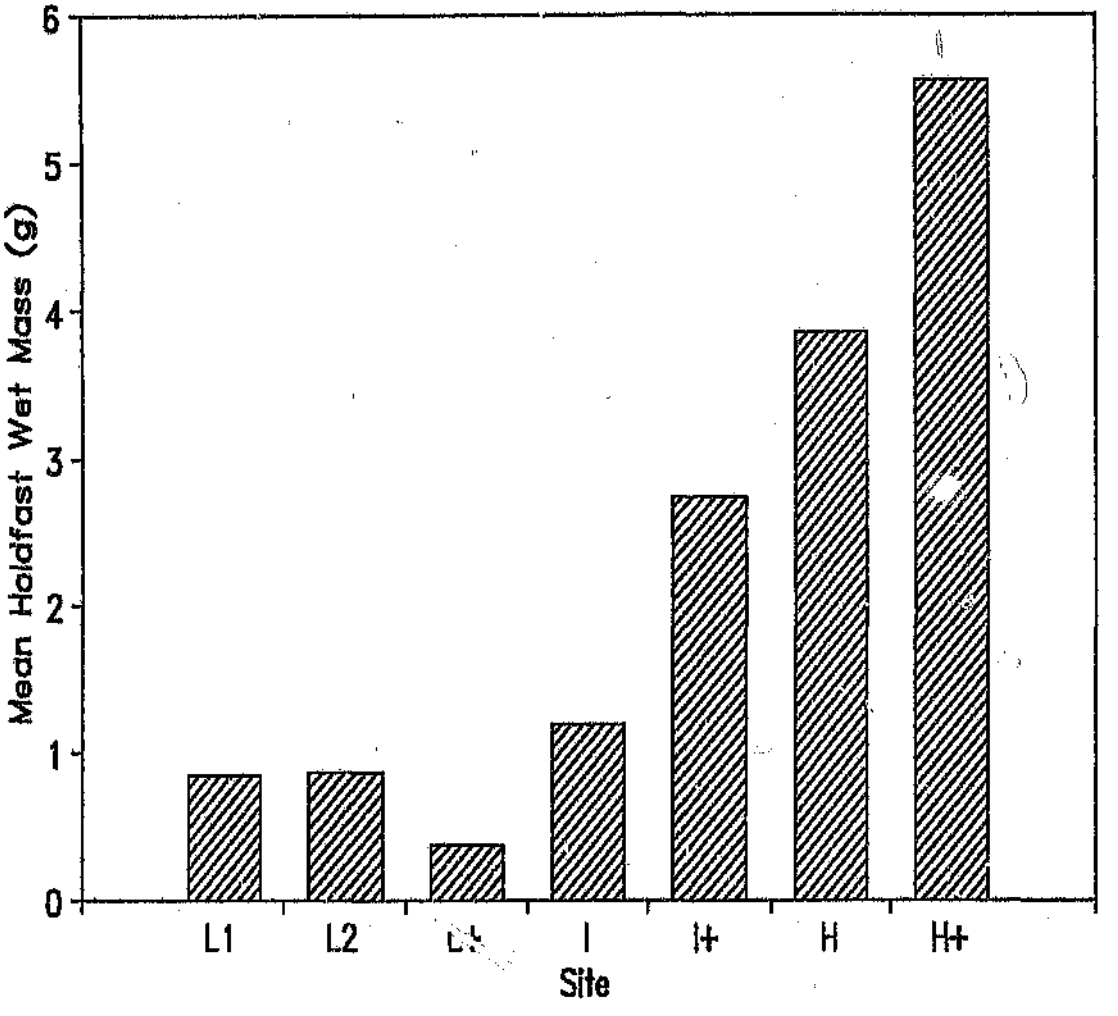


Figure 21: Mean holdfast wet mass (in g) from measurements taken over the entire study period (L1, n=25; L2, n=31; L+, n=27; I, n=26; I+, n=36; H, n=42 and H+, n=56).

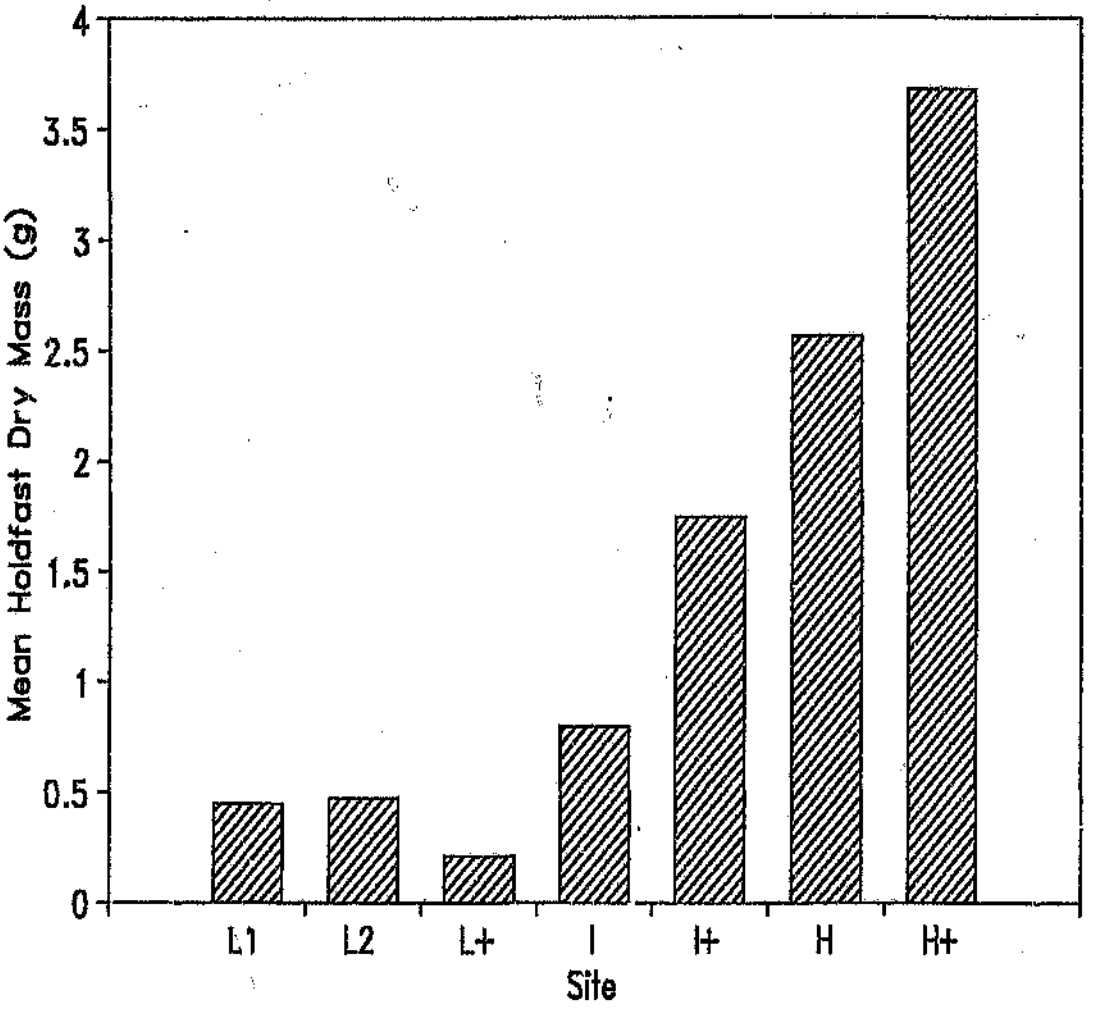


Figure 23: Mean holdfast dry mass (in g) from measurements taken over the entire study period (L1, n=25; L2, n=31; L+, n=27; I, n=26; I+, n=36; H, n=42 and H+, n=56).

3.7.2 Features of the Lamina

3.7.2.1 Laminal Length

The mean laminal length (taken from the mean length of the three longest laminae), from measurements taken throughout the study period, is displayed in Figure 23. The three lowest wave exposure sites (L1, L2 and L+) have the lowest mean laminal lengths (46.19 (±9.49)mm, 86.83 (±21.68)mm and 83.75 (±6.10)mm respectively) with L1 having the lowest of the three ($p<0.001$). The other two low wave exposure sites are higher than L1 ($p<0.001$) but not significantly different from each other ($p>0.05$). The other four sites (I, I+, H and H+) have higher mean lamina length values ($p<0.001$) but, although H+ appears to be slightly higher, the latter four sites do not have significantly different mean laminal lengths ($p>0.05$). The mean laminal length values for the latter four sites are 112.68 (±0.56)mm, 113.96 (±15.44)mm, 113.68 (±58.57)mm and 118.29 (±79.22)mm, respectively.

3.7.2.2 Laminal Width

The mean laminal width measurements are displayed in Figur 24. The laminal width value for the lowest wave exposure site (L1) is significantly lower (8.21 (±1.25)mm; $p<0.001$) than that of the other sites (L2, L+, I, I+, H and H+; 12.75 (±1.05)mm, 12.5 (±0.7)mm, 13.15 (±0.05)mm, 13.7 (±2.18)mm, 12.03 (±0.81)mm and 12.53 (±1.64)mm respectively). The latter sites all have similar mean laminal width values ($p>0.05$).

Figure 25 is a scatter diagram of the individual laminal lengths versus the corresponding laminal widths for the lowest wave exposure site (L1) and the highest wave exposure site (H+), taken throughout the study period.

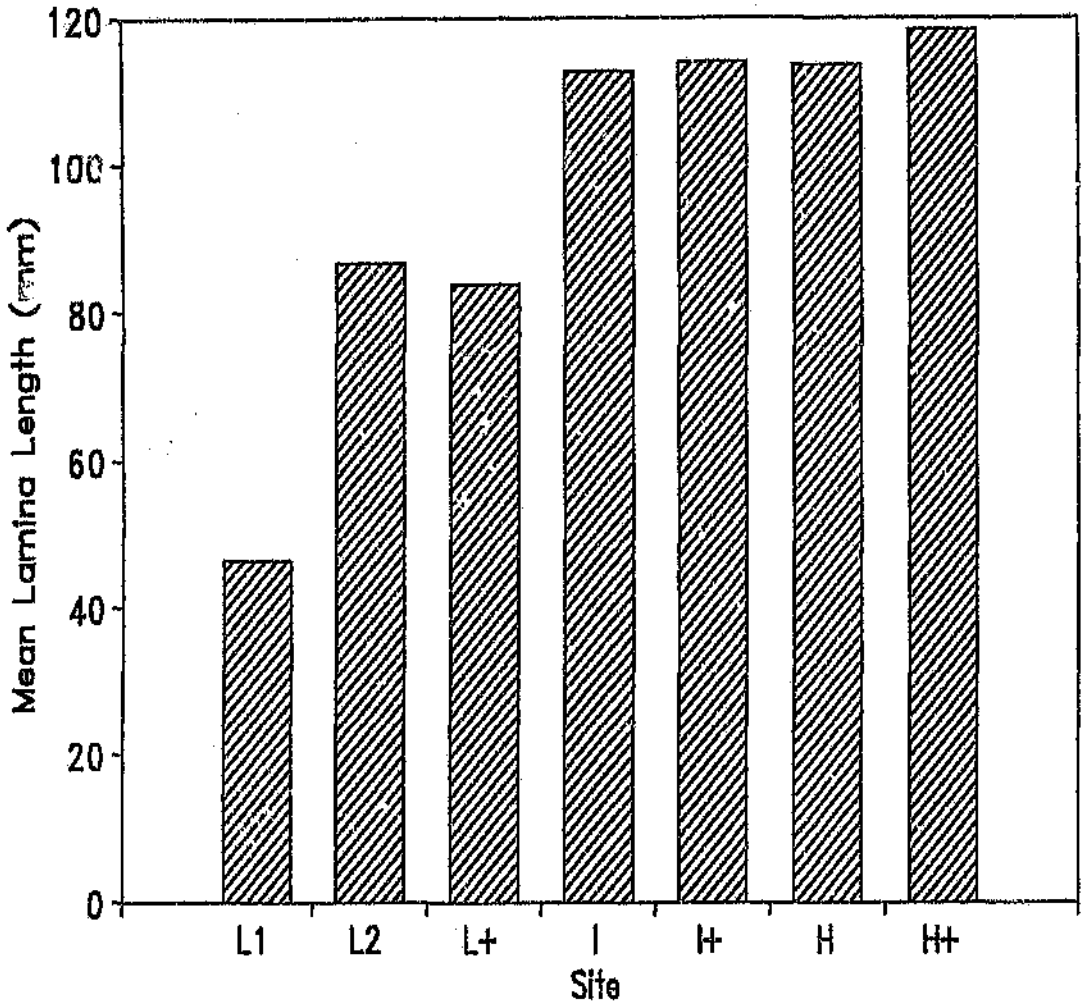


Figure 23: Mean laminal length (mm) from measurements taken over the entire study period (L1, n=79; L2, n=93; L+, n=87; I, n=87; I+, n=112; H, n=131 and H+, n=158).

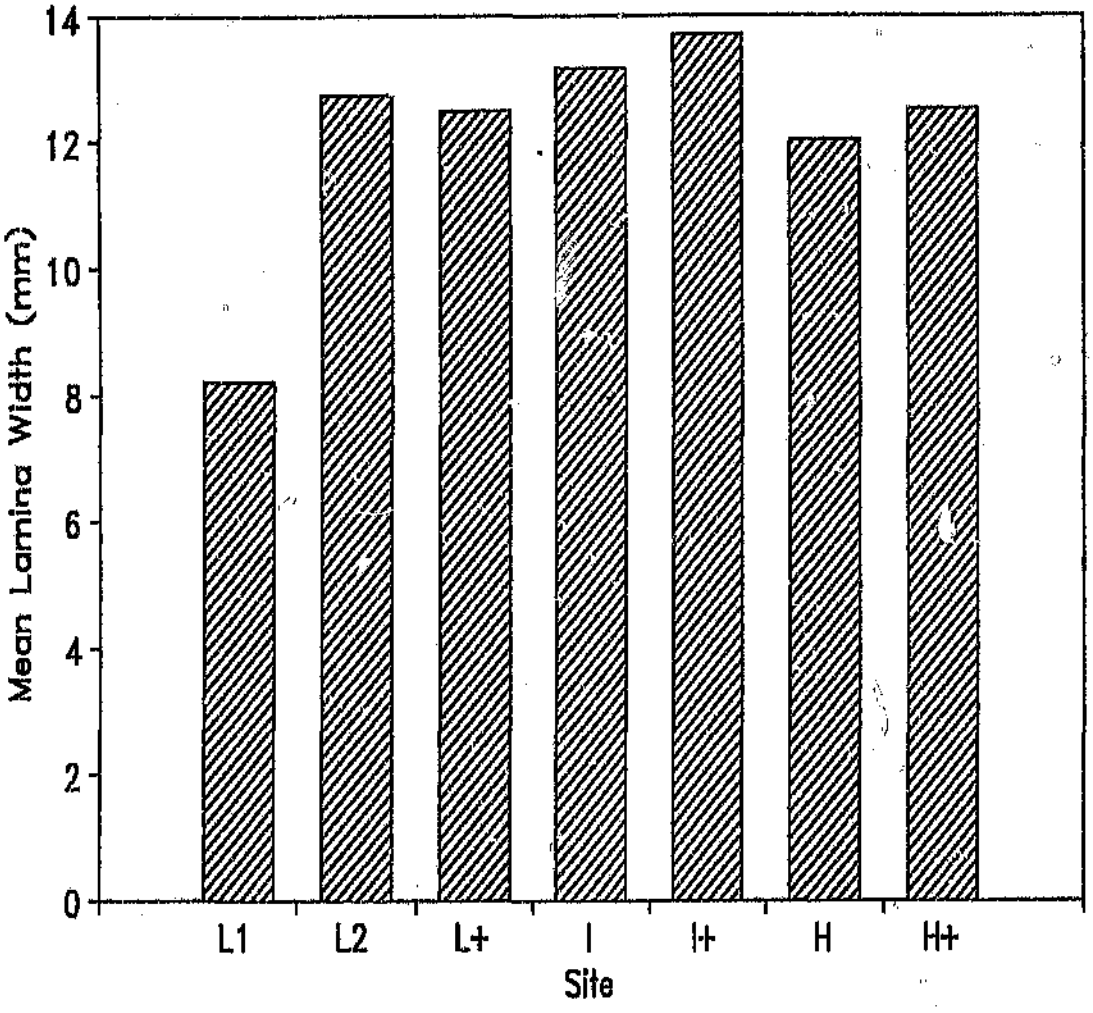


Figure 24: Mean laminal width (mm) from measurements taken over the entire study period (L1, n=79; L2, n=93; L+, n=87; I, n=87; I+, n=112; H, n=131 and H+, n=158).

There appear to be three groups on this graph. The first is comprised of short, narrow individuals from both sites, and is assumed to be the entire population of the L1 site and the juvenile plants of the H+ site (lamina width 2-14mm, lamina length 4-170mm). There are then two groups comprised of H+ plants only. The first of these is intermediate plants (lamina width 14-21.33mm, lamina length 38-235mm) and the second long, wide plants (lamina width 15.6-19.6mm, lamina length 351-535mm). The latter two groups are thought to be composed of the older juveniles and the adult plants, respectively. It must be noted that these groups probably denote different times of the study period and stages of development, as the measurements were taken over the entire study period. If the same two sites (L1 and H+) are compared with only the March readings (Fig. 26), it can be seen that at this point of the growing season there are also three groups. These include a group of narrow, short plants (L1; lamina width 3.3-12.3mm, lamina length 29-132mm), a group of narrow, long plants (H+; lamina width 14-19.66mm, lamina length 52-351mm) and a group of longer, wide plants (H+; lamina width 16.6-19.6mm, lamina length 425-535mm), ie fairly similar to the grouping representing the entire study period. A similar graph (Fig. 27) of the October measurements, shows that there is a single group of plants (plants from L1 and H+) which are shorter than later in the growing season (lamina width 2-17mm, lamina length 4-102mm).

3.7.2.3 Surface Area of the Thallus

Figure 28 shows the mean total area of all the laminae from individual plants, ie a sum total of the area of the laminae of a plant, from measurements taken throughout the study period. The higher, intermediate (I+) and high (H) wave exposure sites are similar ($p>0.05$) with mean values of 0.007341 ($\pm$0.002)m^2 and 0.007301 ($\pm$0.005)m^2

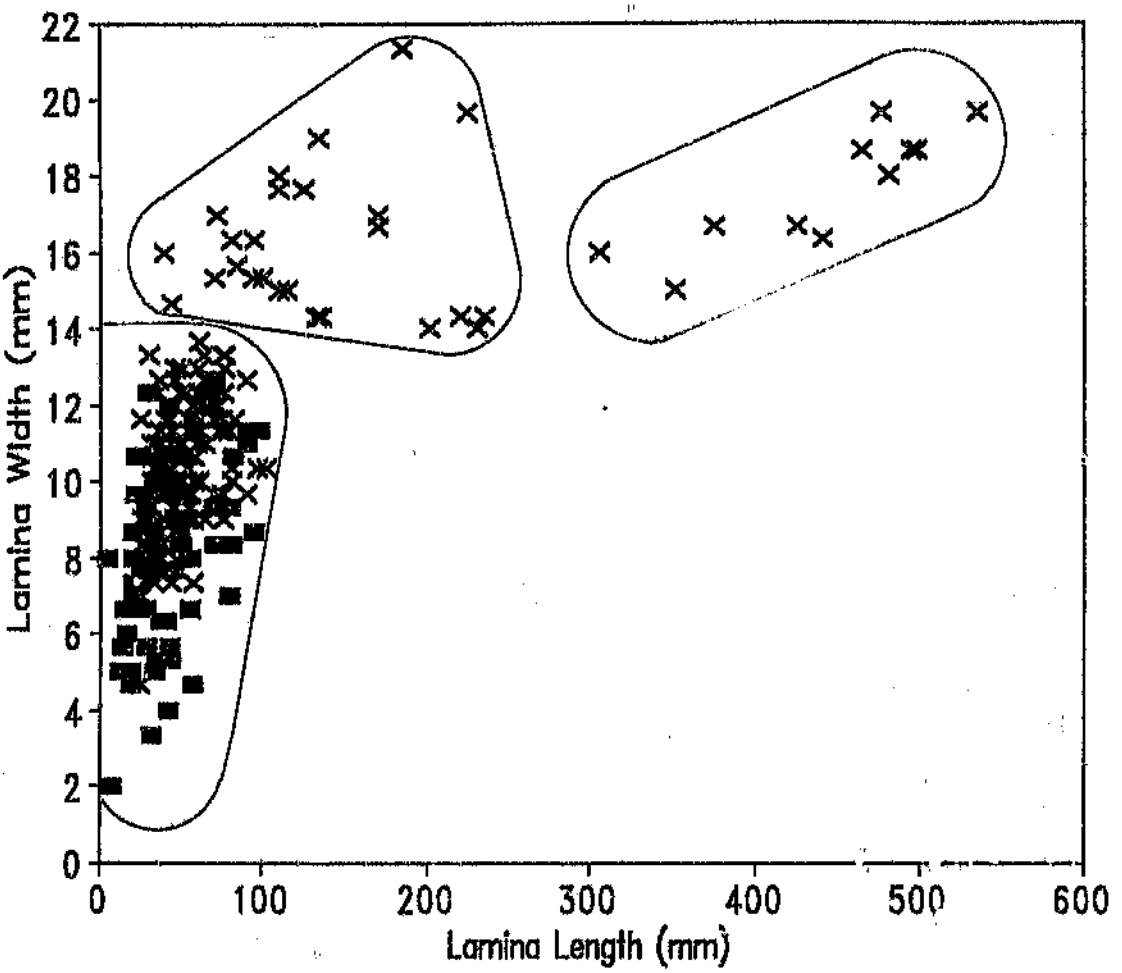


Figure 25: Scatter graph of the laminal length versus the laminal width for individuals from the L1 (■) and H+ (x) sites, from measurements taken over the entire study period.

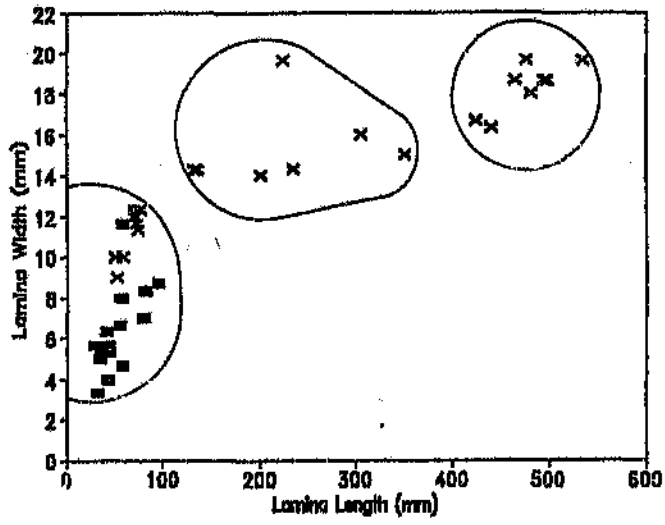


Figure 26: Scatter graph of the laminal length (mm) versus the laminal width (mm) for individuals from the L1 (■) and H+ (x) sites for March.

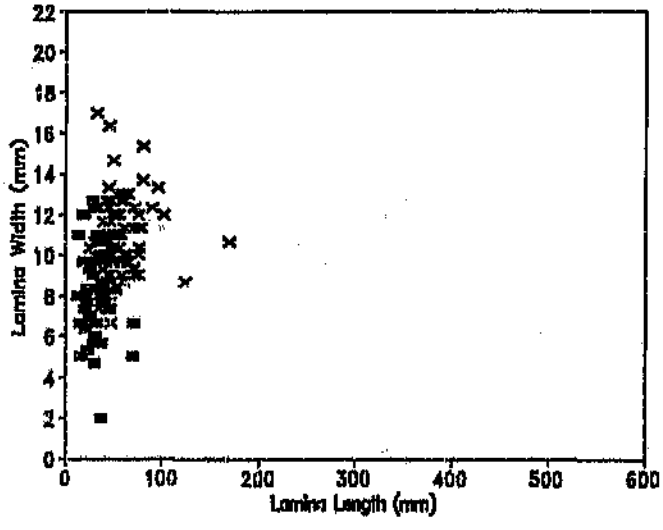


Figure 27: Scatter graph of the laminal length (mm) versus the laminal width (mm) for individuals from the L1 (■) and H+ (x) sites for October.

respectively, whilst all the rest are significantly different from each other ($p<0.001$). Two of the low wave exposure sites (L1 and L+; 0.002345 (±0.001)m^2 and 0.003653 (±0.0007)m^2) have the lowest mean total laminal surface area, whilst the highest wave exposure site (H+) has the by far the highest ($P<0.001$) mean area which was measured as 0.020989 (±0.029)m^2.

3.7.2.4 Mass of the Laminae

The mean total wet and dry mass values of all the laminae from single plants, are combined in Figure 29. In the graph, the plants of the L1 and the L+ sites have the lowest laminal mass (0.583 (±0.285)g wet and 0.0864 (±0.04)g dry; and 1.457 (±0.182)g wet and 0.191 (±0.033)g dry, respectively). These mass values are significantly different from each other and the rest of the sites ($p<0.001$). The values for L2 and I are higher (with wet mass values of 1.890 (±0.85)g and 2.034 (±0.545)g and dry values of 0.277 (±0.154)g and 0.29 (±0.083)g, respectively; $p<0.001$) but not different from each other ($p>0.05$). The mean masses then get progressively higher ($p<0.001$) with an increase in wave exposure ($p<0.001$) except I+ and H which where similar ($p>0.05$). For both wet and dry masses, the highest wave exposure site (H+) has the highest laminal mass ($p<0.001$). The wet mass values for I+, H and H+ are 2.590 (±0.85)g, 2.947 (±1.785)g and 9.133 (±12.81)g, and the dry mass values are 0.355 (±0.117)g, 0.508 (±0.337)g and 1.639 (±2.401)g respectively.

3.7.2.5 Number of Dichotomies per Lamina

The mean total number of dichotomies per lamina length were calculated. Figure 30 indicates the mean dichotomy number per lamina over the whole study period. The low wave exposure site (L1) has a significantly lower

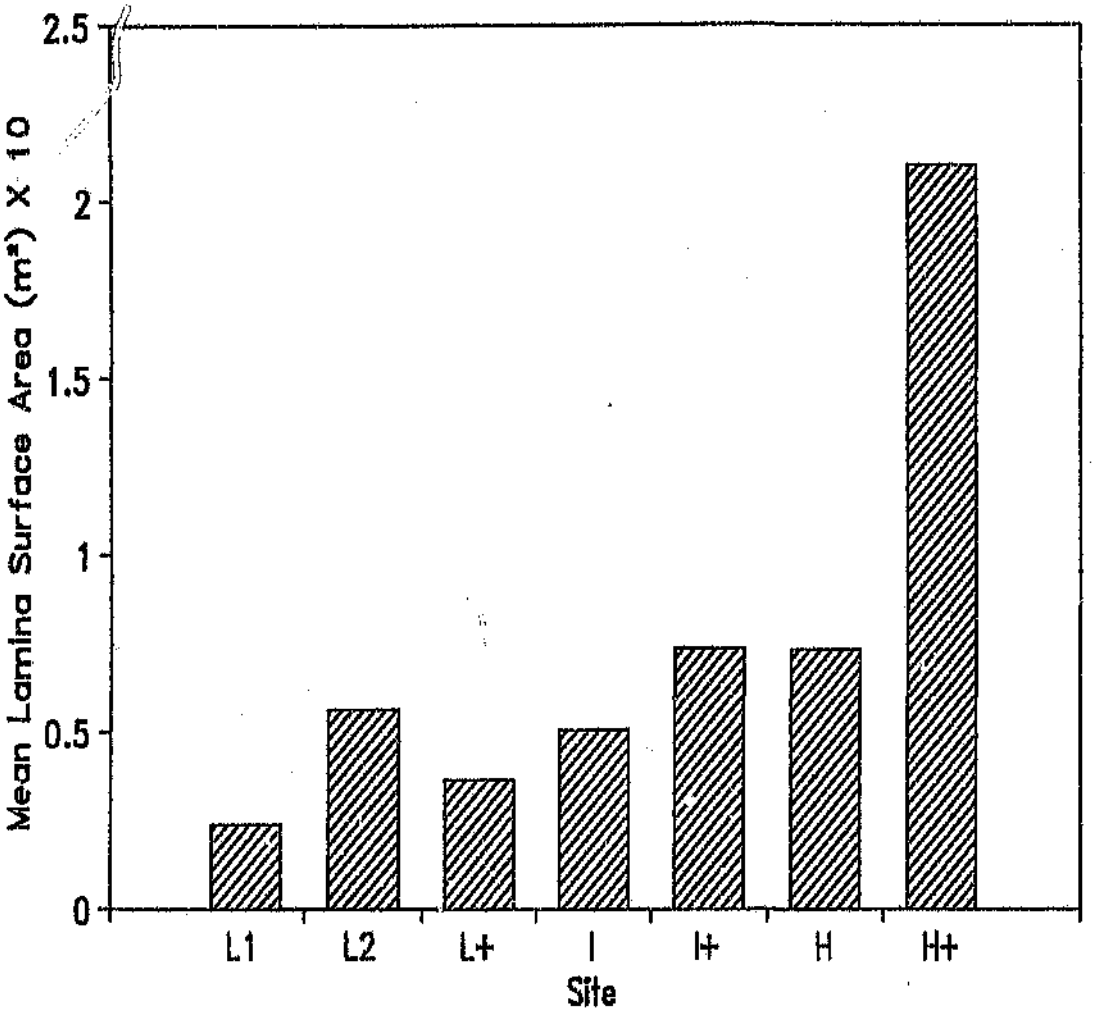


Figure 28: Mean surface area of all the laminae on a single plant (m^2) from measurements taken over the entire study period (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41 and H+, n=53).

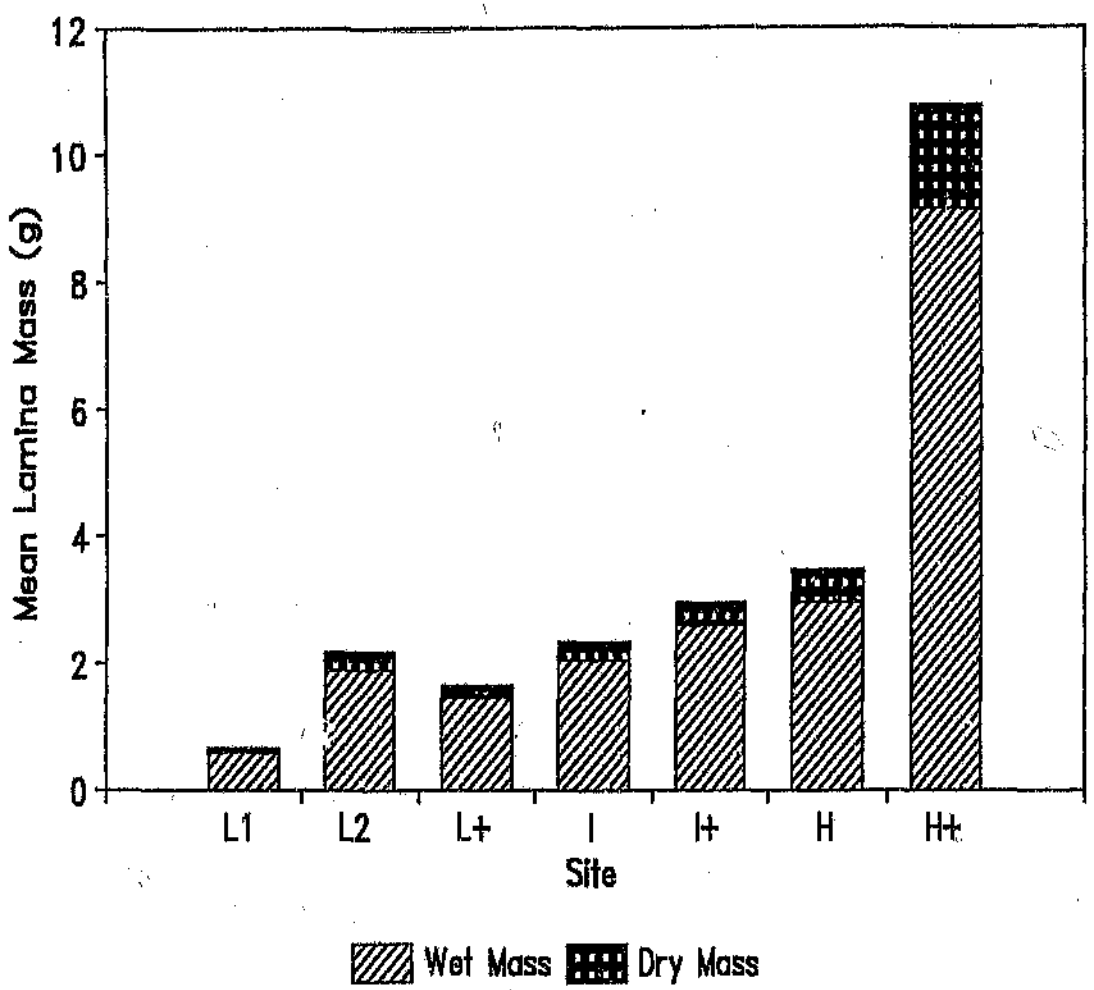


Figure 29: Mean wet and dry mass of all the laminae on a single plant, from measurements taken over the entire study period (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41 and H+, n=53).

($p<0.001$) dichotomy number (0.267 (±0.12) dichotomies) than the other sites. The remaining sites have different dichotomy numbers ($p<0.001$) except L2 and I which are similar ($p>0.05$). L2 has a mean number of dichotomies per lamina of 1.292 (±0.352), L+ has 0.956 (±0.073), I has 1.329 (±0.233) and I+ has a mean of 1.094 (±0.495). The two highest wave exposure sites (H and H+) have the highest ($p<0.001$) dichotomy number per lamina length (1.738 (±1.22) and 1.672 (±1.24) respectively) but are similar to each other ($p>0.05$). A similar plot of the dichotomy numbers of those plants measured in March (Fig. 31) indicates that I has by far the lowest number of dichotomies (0.176 (±0.512); $p<0.001$), followed by H and then H+ with mean dichotomy numbers of 3.461 (±2.134) and 3.652 (±1.15), respectively ($p<0.001$). In Figure 32 the mean number of dichotomies from the October measurements are displayed. The lowest wave exposure site (L1) once again has the lowest number of dichotomies (0.186 (±0.389); $p<0.001$). The highest wave exposure site (H+) has the next highest dichotomy number (0.535 (±0.677)) at this time of the year ($p<0.001$). Sites L+ and H are higher and similar to each other ($p>0.05$) but different from the other sites ($p<0.001$). The mean dichotomy numbers of L+ and H are 1.029 (±1.14) and 0.8068 (±0.12), respectively. The remaining three sites (L2, I and I+) are all higher ($p<0.001$; with values of 1.644 (±0.99), 1.56 (±1.12) and 1.6 (±1.13) respectively) than the other sites but similar to each other ($p>0.05$).

Figure 33 shows a plot of the length of the longest lamina versus the number of dichotomies in that lamina, for individuals from the two extremes in wave activity, ie H+ and L1. From this graph it can be observed that the individuals from L1 have both a low laminal length and a low number of dichotomies. There are individuals from the

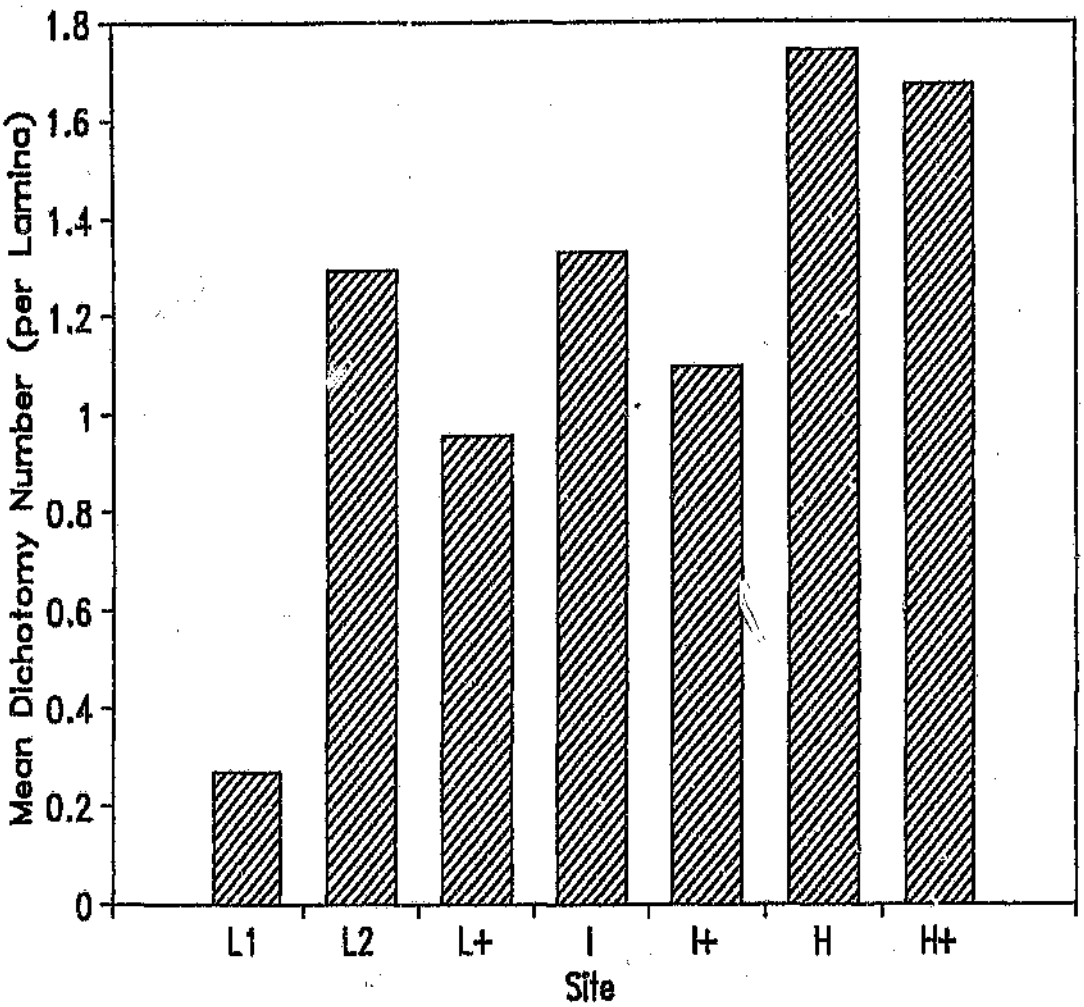


Figure 30: Mean dichotomy number per lamina for the measurements taken over the entire study period (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41 and H+, n=53).

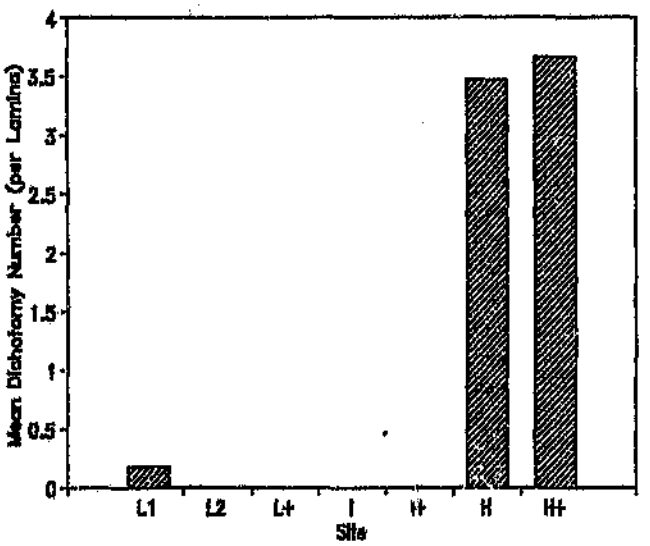


Figure 31: Mean dichotomy number per lamina for the measurements taken for the month of March (L1, n=17; H, n=13 and H+, n=23).

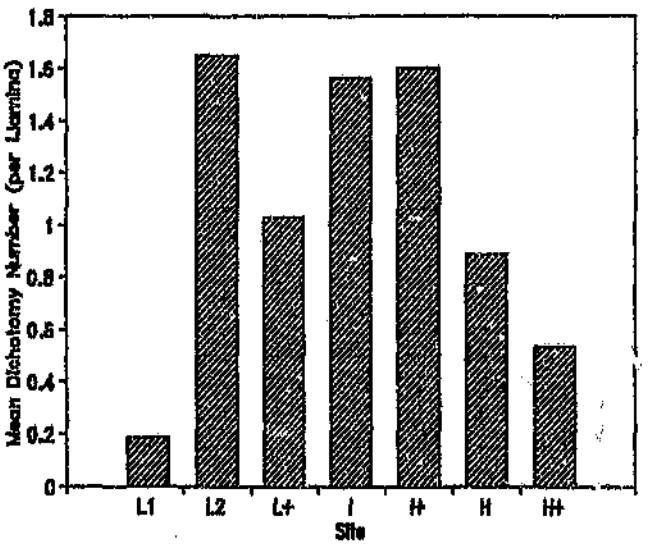


Figure 32: Mean dichotomy number per lamina for the measurements taken for the month of October (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41 and H+, n=53).

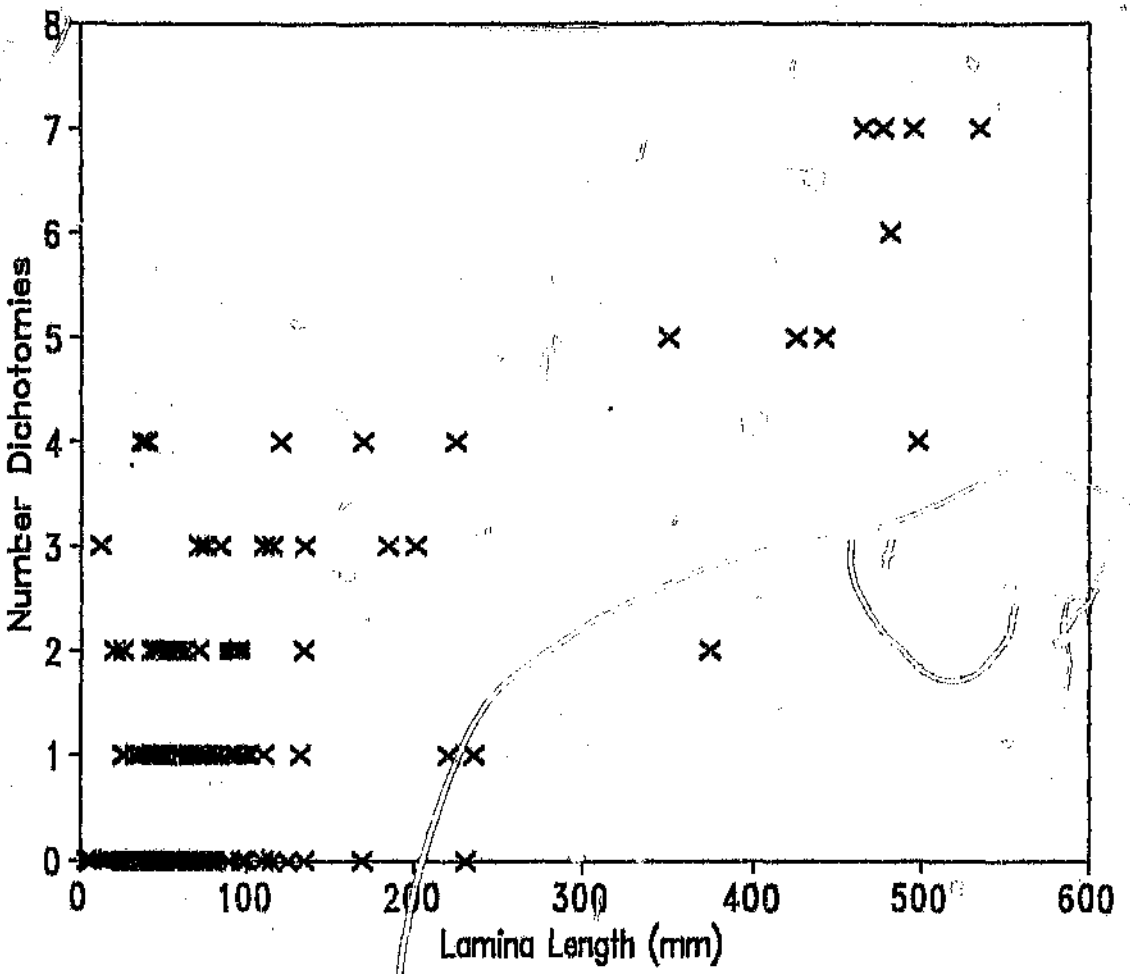


Figure 33: Scatter graph of lamina length versus the number of dichotomies per lamina for individuals from the L1 (■) and H+ (x) sites, from measurements taken over the entire study period.

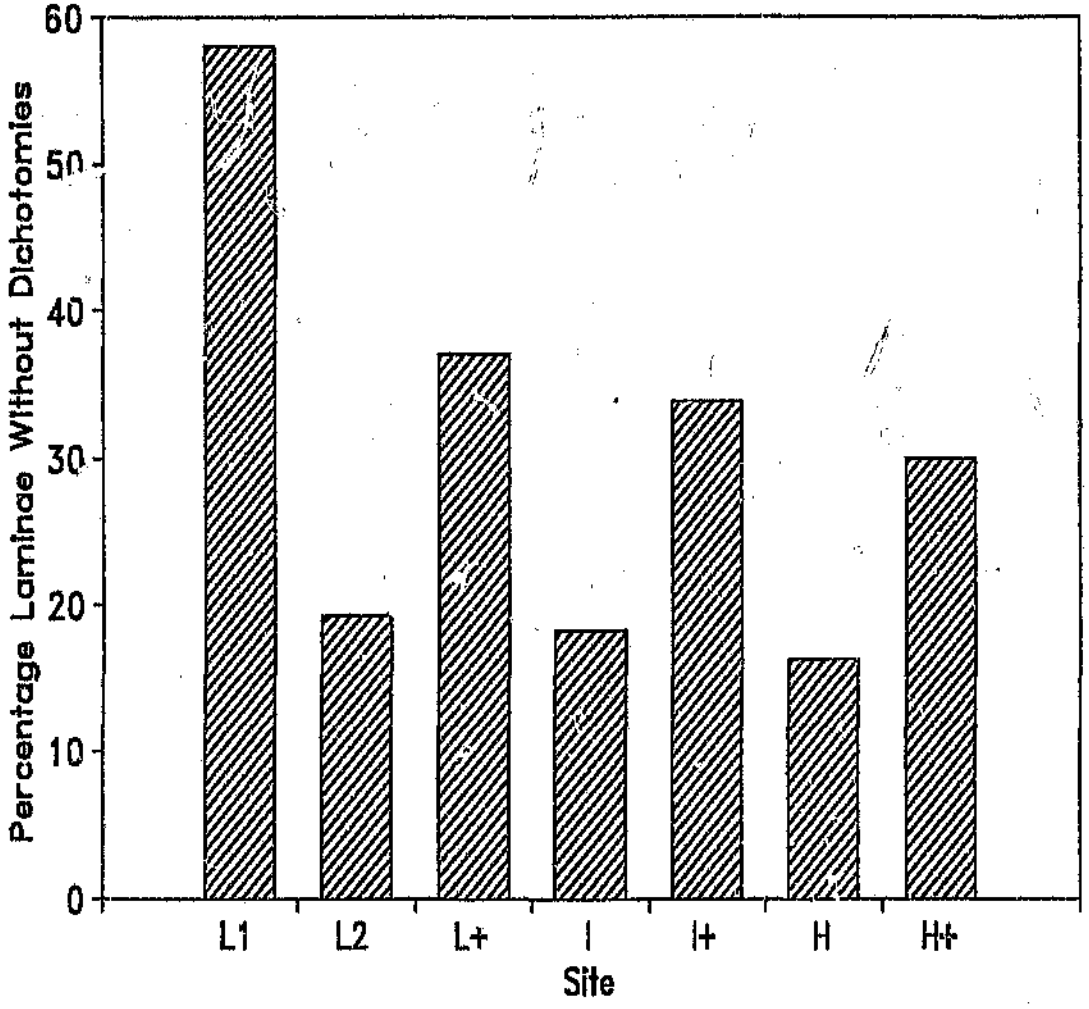


Figure 34: Percentage laminae without dichotomies, from measurements taken throughout the study period (L1, n=79; L2, n=93; L+, n=87; I, n=87; I+, n=112; H, n=131 and H+, n=158).

higher wave exposure site (H+) which have low dichotomy numbers and low laminal lengths, as well as individuals with higher laminal lengths and dichotomy numbers. There seems to be a gradual increase in the number of dichotomies with an increase in the laminal length in individuals of the latter site (H+).

Figure 34 indicates the percentage of laminae totally lacking dichotomies. There does not seem to be any particular trend in these results, other than the lowest wave exposure site (L1) having by far the greatest percentage of laminae lacking dichotomies (57.97 (±30.61)%; $p<0.001$). The L2, I and H sites have similar, low percentages of laminae lacking dichotomies (19.17 (±7.30)%, 18.23 (±15.1)% and 16.20 (±10.72)%, respectively; $p>0.05$) whilst all the other sites have different percentages ($p<0.001$). The percentage laminae lacking dichotomies in L+, I+, and H+ are 37.09 (±1.8)%, 33.76 (±19.81)% and 29.87 (±21.25)%, respectively.

3.7.2.6 Number of Laminae per Individual

The number of laminae per plant were divided into 2 groups, ie the number of laminae less than 5mm in length, and the number greater than 5mm in length. The results are shown in Figures 35 and 36, respectively. In Figure 35, the two low wave exposure sites (L2 and L+) have different ($p<0.001$)) and significantly lower ($p<0.001$) number of small laminae (3.88 (±0.07) and 5.005 (±0.805)) than the other sites which all have higher and similar numbers of laminae less than 5mm in length ($p>0.05$). The mean number of laminae smaller than 5mm (per plant) for L1, I, I+, H and H+ are 6.4 (±2.86), 6.28 (±1.12), 7.04 (±2.28), 5.04 (±2.02) and 5.4 (±1.78), respectively. In the graph of the number of laminae bigger than 5mm (Fig. 36), the intermediate site (I+) has the highest number of longer laminae (23.23 (±4.97); $p<0.001$). The low wave

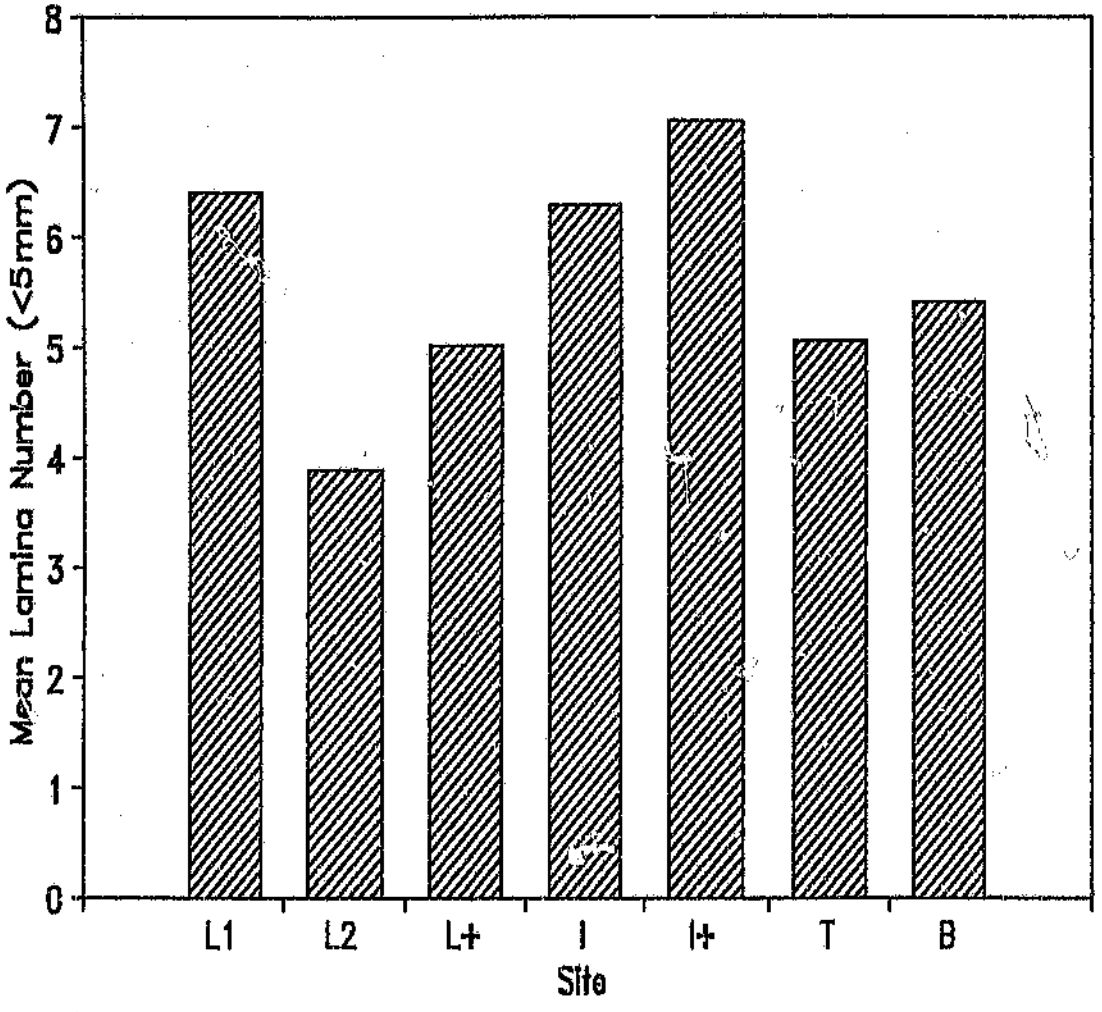


Figure 35: Mean lamina number (per plant) less than 5mm in length, from measurements taken throughout the study period (L1, n=25; L2, n=31; L+, n=27; I, n=26; I+, n=36; H, n=42 and H+, n=56).

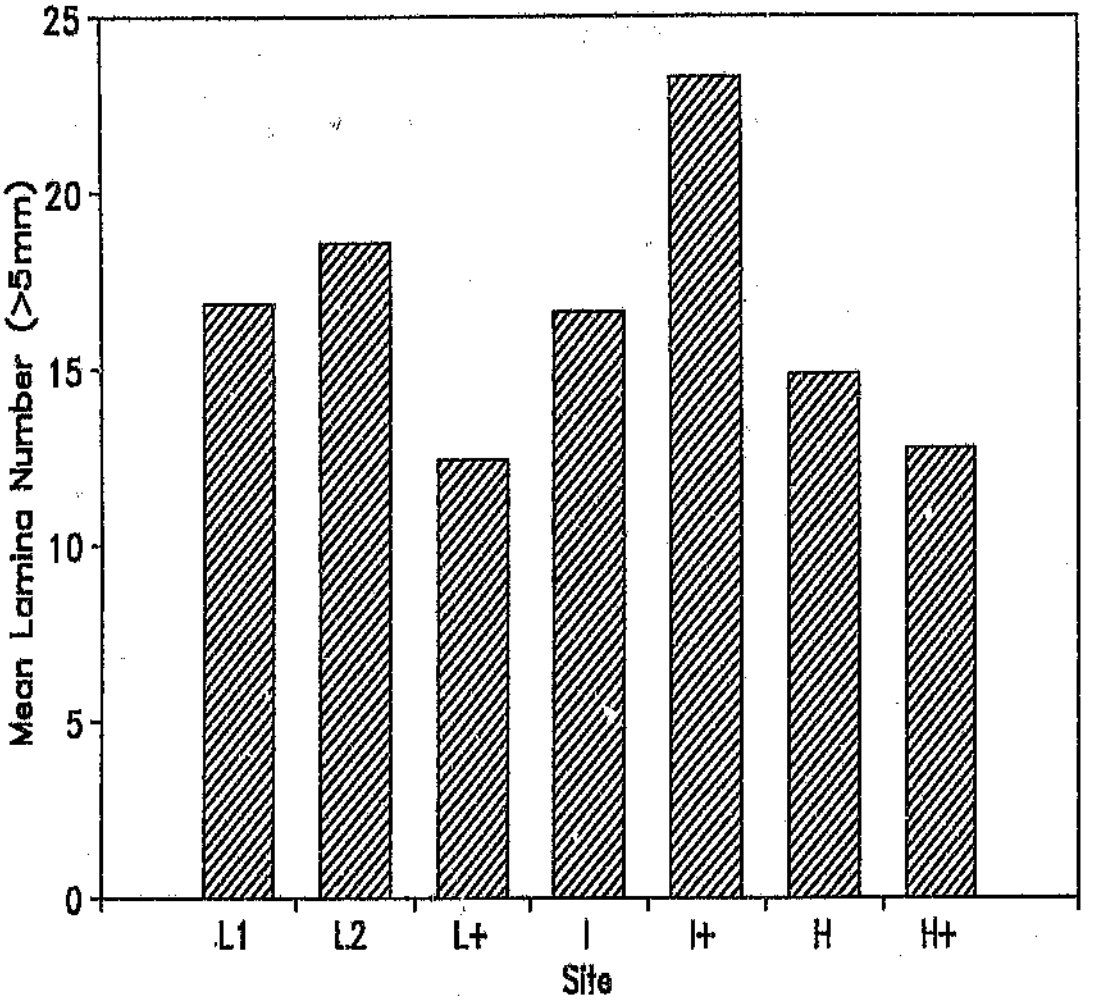


Figure 36: Mean lamina number (per plant) greater than 5mm in length, from measurements taken throughout the study period (L1, n=25; L2, n=31; L+, n=27; I, n=26; I+, n=36; H, n=42 and H+, n=56).

exposure site L+ and the highest wave exposure site (H+), have similar ($p>0.005$) and the lowest number of large laminae (12.4 (±2.8) and 12.68 (±8.59), respectively; $p<0.001$). The other sites (L1, L2, I and H) all have an intermediate and similar ($p>0.05$) number of larger laminae (16.84 (±9.23), 18.55 (±4.75), 16.6 (±3.4) and 14.83 (±5.07), respectively).

3.8 MECHANICAL PROPERTIES

3.8.1 Tensile Strength of the Laminae

Various problems were experienced with the method used to measure tensile strength (see Section 2.4.7.1). Figure 37 shows the mean tensile strength over the entire study period, for as many individuals as possible from each site. There is no obvious trend in the tensile strength measurements on this graph. The highest wave exposure site (H+) does, however, have a slightly higher ($p>0.05$) measurement than the rest of the sites (524.87 (±86.13) dynes/mm), and the lowest wave exposure site (L1) has a significantly ($p<0.001$) lower mean (349.95 (±14.22) dynes/mm) than all the other sites, except H which has a mean tensile strength of 372.21 (±47.34) dynes/mm ($p<0.001$). The four sites L2, L+, I and I+ (477.83 (±92.43) dynes/mm, 500.62 (±13.86) dynes/mm, 497.85 (±44.22) dynes/mm and 413.89 (±27.61) dynes/mm, respectively) are significantly higher ($p<0.001$) than the other sites but not significantly different from each other ($p>0.05$). The mean tensile strength of the sites measured in March are shown in Figure 38. Once again the highest wave exposure site (H+) had the highest mean tensile strength (509.78 (±234.47) dynes/mm). The low wave exposure site (L1) and the high wave exposure site (H) had lower tensile strength (334.80

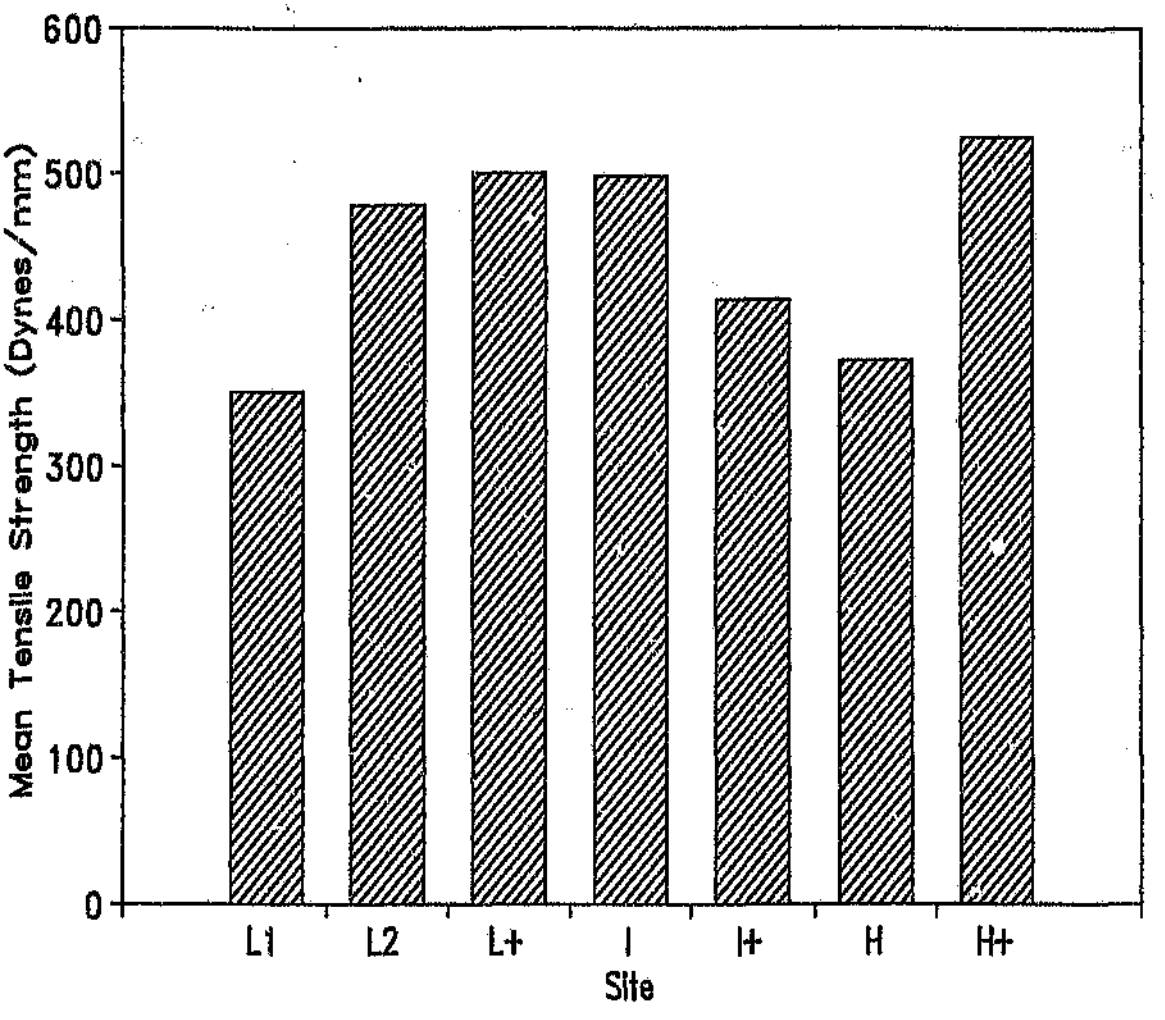


Figure 37: Mean tensile strength measurements (dynes/mm) for those sites measured over the entire study period (L1, n=23; L2, n=45; L+, n=39; I, n=64; I+, n=39; H, n=39; H+, n=48).

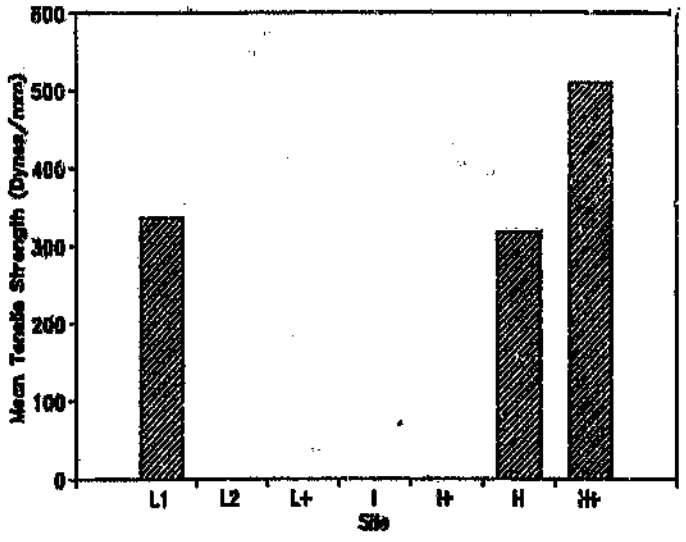


Figure 38: Mean tensile strength measurements (dynes/mm) for those sites measured in March (L1, n=13; H, n=12; H+, n=23).

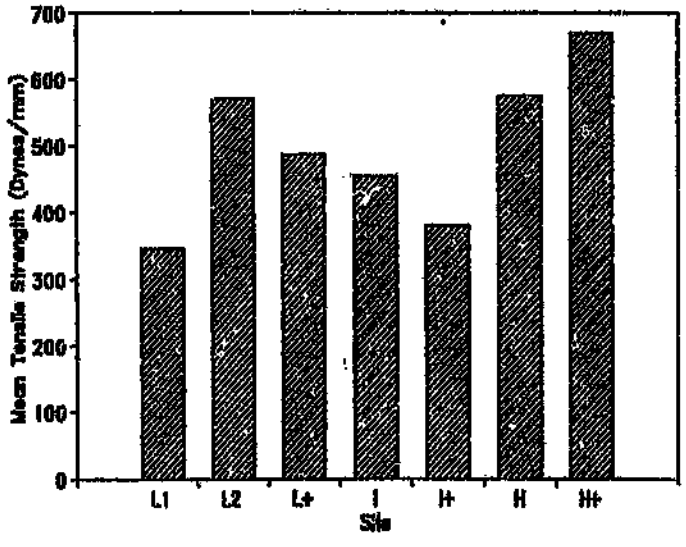


Figure 39: Mean tensile strength measurements (dynes/mm) for those sites measured in October (L1, n=6; L2, n=27; L+, n=31; I, n=48; I+, n=25; H, n=21; H+, n=18).

(±99.32) dynes/mm and 317.02 (±188.15) dynes/mm, respectively). Similarly, means of tensile strength for October (Fig. 39) show a lack of any particular trend, but with H+ having the highest (669.69 (±234.26) dynes/mm) and L1 the lowest (346.06 (±72.77) dynes/mm) mean tensile strength.

The correlation between the tensile strength measurements and other aspects of the lamina measured in this study, was confirmed by a PCA ordination (see Section 3.8.2; Fig. 43).

3.8.2 Attachment Strength of the Holdfast

The mean attachment strength for populations of D. longifolia from the various sites at Palm Beach, was determined and presented in Figure 40. It appears from this graph that the more intermediate wave exposure sites (ie L2, L+, I and I+) all have similar and higher attachment strengths (13.58 (±2.14) Newtons, 12.87 (±2.31) Newtons, 14.50 (±7.97) Newtons and 14.61 (±1.28) Newtons, respectively) than the extreme sites, ie the low wave exposure site (L1; 7.072 (±2.14) Newtons) and the high wave exposure sites (H+ and H; 10.63 (±1.95) Newtons and 9.82 (±4.14) Newtons, respectively). The lowest wave exposure site (L1) is significantly lower ($p<0.001$) than the other sites. In all but the calmer pools (L1 and L+), the October (when the plants were older) attachment strength measurements (Fig. 42) appear to be greater than the September measurements (Fig. 41) when there are many young plants.

The PCA (see Section 2.7.3) of various structural and morphological features of the plant (Fig. 43), indicates any correlation existing between the features measured. It must be noted that, by definition, the attachment

strength (using this method of measurement; Carter, 1986; Carter & Simons, 1987) is the force needed to remove the plant from the substratum or to break the lamina to which the force is being applied (whichever occurs first). This means that the attachment strength measurements were frequently those of laminal tensile strength. From the angles on the PCA (Fig. 43) it appears that the holdfast features, ie holdfast diameter, sclerophylly and succulence are very closely correlated (all within 4^{o} of each other). The laminal features are not highly correlated with the holdfast features (PCA angle between holdfast sclerophylly and laminal length = 63^{o}), however, the laminal features are within 65^{o} of each other. Laminal width, succulence, tensile strength and attachment strength are closely correlated (within 27^{o} of each other). Surprisingly, attachment strength is very slightly correlated with holdfast diameter (114^{o} between them) but closely correlated with aspects of the lamina.

3.8.3 Sclerophylly and Succulence

Mean lamina and holdfast sclerophylly and succulence were measured for individuals of D. longifolia from all the sites (Section 2.4.7.3). Figure 44 shows the mean values of the laminal sclerophylly. It appears that no trend exists in sclerophylly, with respect to the degree of wave exposure. The lowest wave exposure site (L1) has significantly lower ($p<0.001$) sclerophylly measurements (33.81 (±4.34) g/m^2), with the second highest (H) and one of the lower (L+) wave exposure sites having similar ($p>0.05$) but significantly higher ($p<0.001$) sclerophylly measurements (74.72 (±10.99) g/m^2 and 67.99 (±5.40) g/m^2, respectively). The other sites have intermediate but different ($P<0.001$) sclerophylly measurements with only the measurements of I+ and L2 being similar ($p>0.05$). L2, I, I+ and H+ have mean measurements of 43.72 (±4.35) g/m2, 55.84

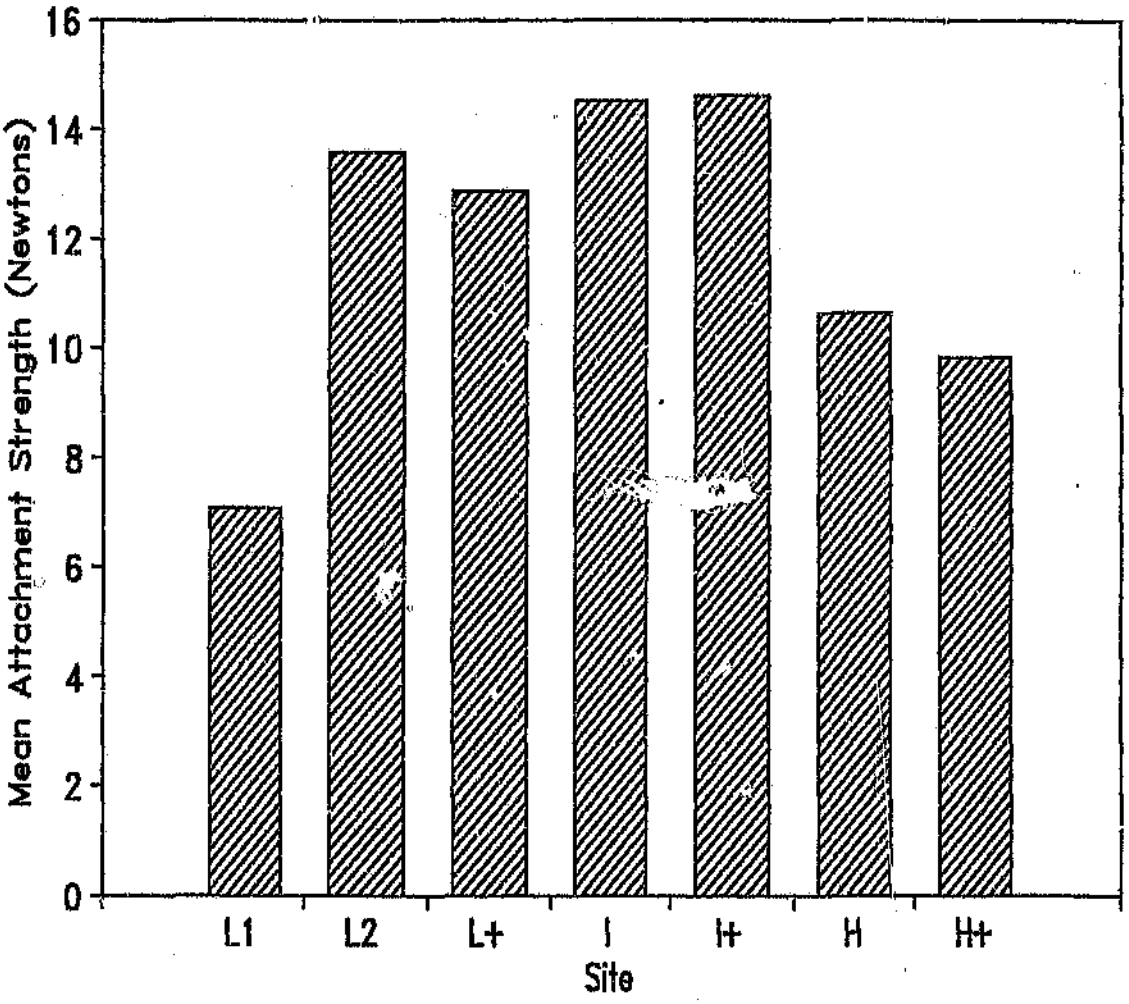


Figure 40: Mean attachment strength measurements (Newtons) for all the sites (L1, n=18; L2, n=31; L+, n=27; I, n=20; I+, n=26; H, n=32; H+, n=30).

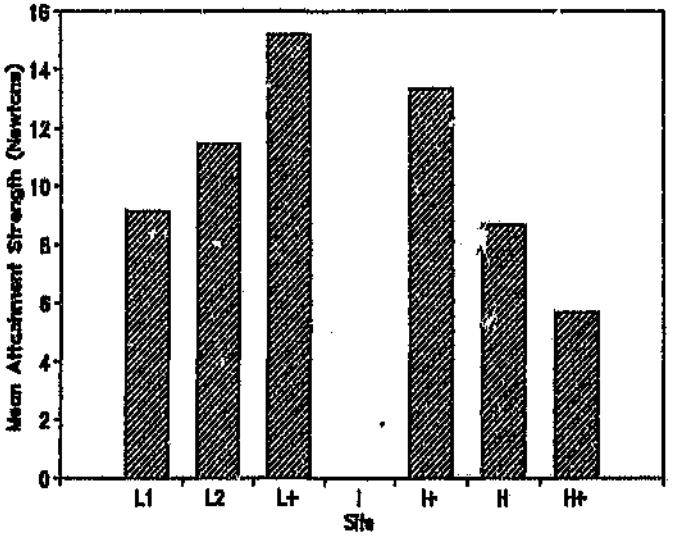


Figure 41: Mean attachment strength measurements (Newtons) for those sites measured in September (L1, n=3; L2, n=11; L+, n=5; I+, n=5; H, n=11; H+, n=10).

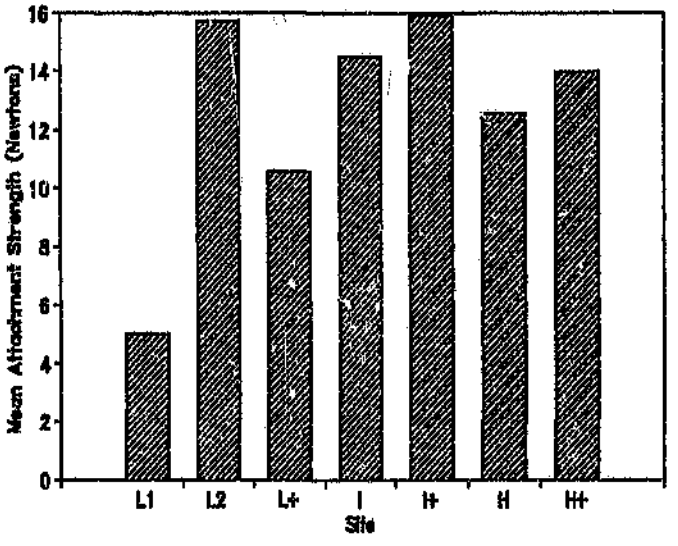


Figure 42: Mean attachment strength measurements (Newtons) for those sites measured in October (L1, n=15; L2, n=20; L+, n=22; I, n=20; I+, n=21; H, n=21; H+, n=20).

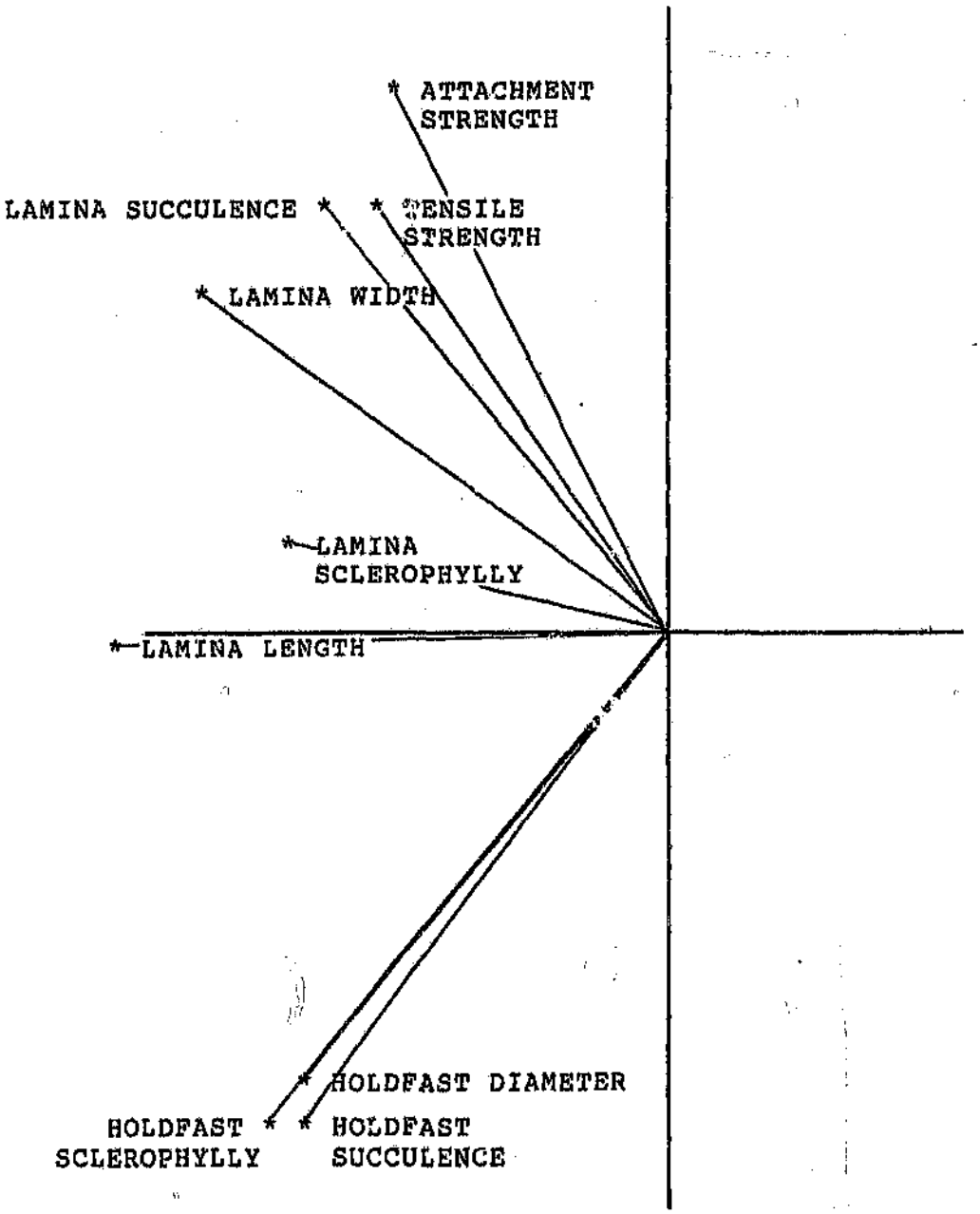


Figure 43: PCA of various morphological and structural features of the lamina and holdfast of *D. longifolia*.

(±11.10) g/m^2, 46.14 (±9.64) g/m^2 and 58.88 (±11.29) g/m^2, respectively.

Figure 45 shows the mean holdfast sclerophylly from measurements taken over the study period. This graph indicates an increase in the holdfast sclerophylly with an increase in wave activity. The two low wave exposure sites (L1 and L+) are similar ($p>0.05$) but significantly lower ($p<0.001$) than the rest of the sites (1344.99 (±432.35) g/m^2 and 1230.21 (±377.47) g/m^2, respectively) which are all different ($P<0.001$) except sites L2 and I ($p>0.05$). L2, I, I+, H and H+ have mean holdfast sclerophylly measurements of 1858.92 (±432.35) g/m^2, 2004.78 (±334.20) g/m^2, 3046.87 (±846.84) g/m^2, 3919.78 (±349.72) g/m^2 and 5085.762 (±3291.85) g/m^2, respectively.

The mean laminal succulence values do not to show a trend with relation to the degree of wave movement experienced (Fig. 46). Figure 46 displays L+ and I as having significantly higher laminal succulence values ($p<0.001$) than the other sites (520.83 (±77.8) g/m^2 and 570.69 (±100.67) g/m^2, respectively) but not different from each other ($p>0.05$). L1 has a significantly lower ($P<0.001$) mean succulence measurement than the other sites (231.82 (±15.26) g/m^2). The remaining sites are all intermediate (H and H+ (423.14 (±37.32) g/m^2 and 422.28 (±98.83) g/m^2); and L2 and I+ (316.98 (±15.26) g/m^2 and 343.86 (±77.17) g/m^2) and similar to each other ($p>0.05$).

Figure 47 is a graph of the mean holdfast succulence from measurements taken over the entire study period. The trends of this graph are similar to those in Figure 45 in that there is an increase in holdfast succulence with an increase in wave activity. All the sites have significantly different measurements of holdfast

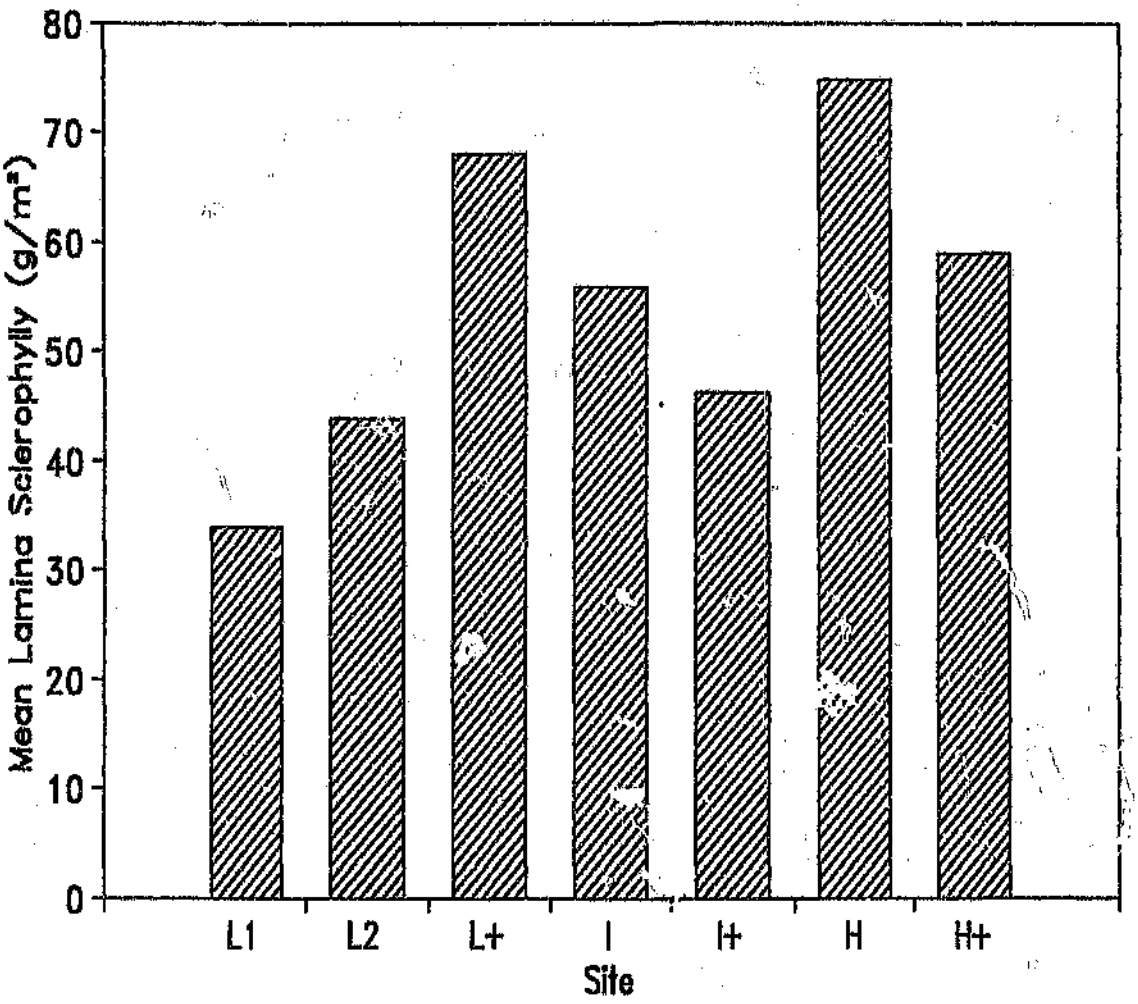


Figure 44: Graph of mean laminal sclerophylly (dry mass (g)/unit area (m^2)) for all the sites (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41; H+, n=53).

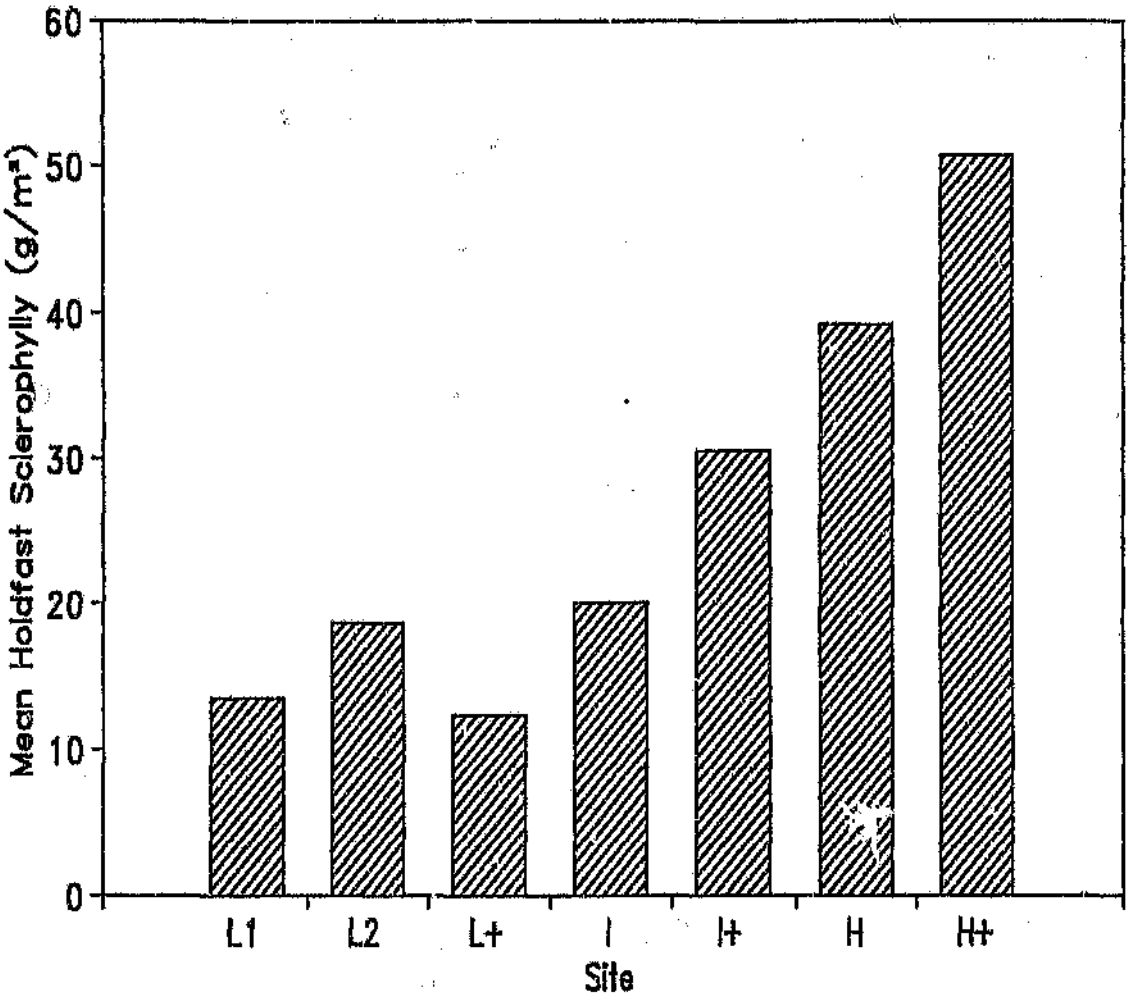


Figure 45: Graph of mean holdfast sclerophylly (dry mass (g)/unit area (m^2)) for all the sites (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41; H+, n=53).

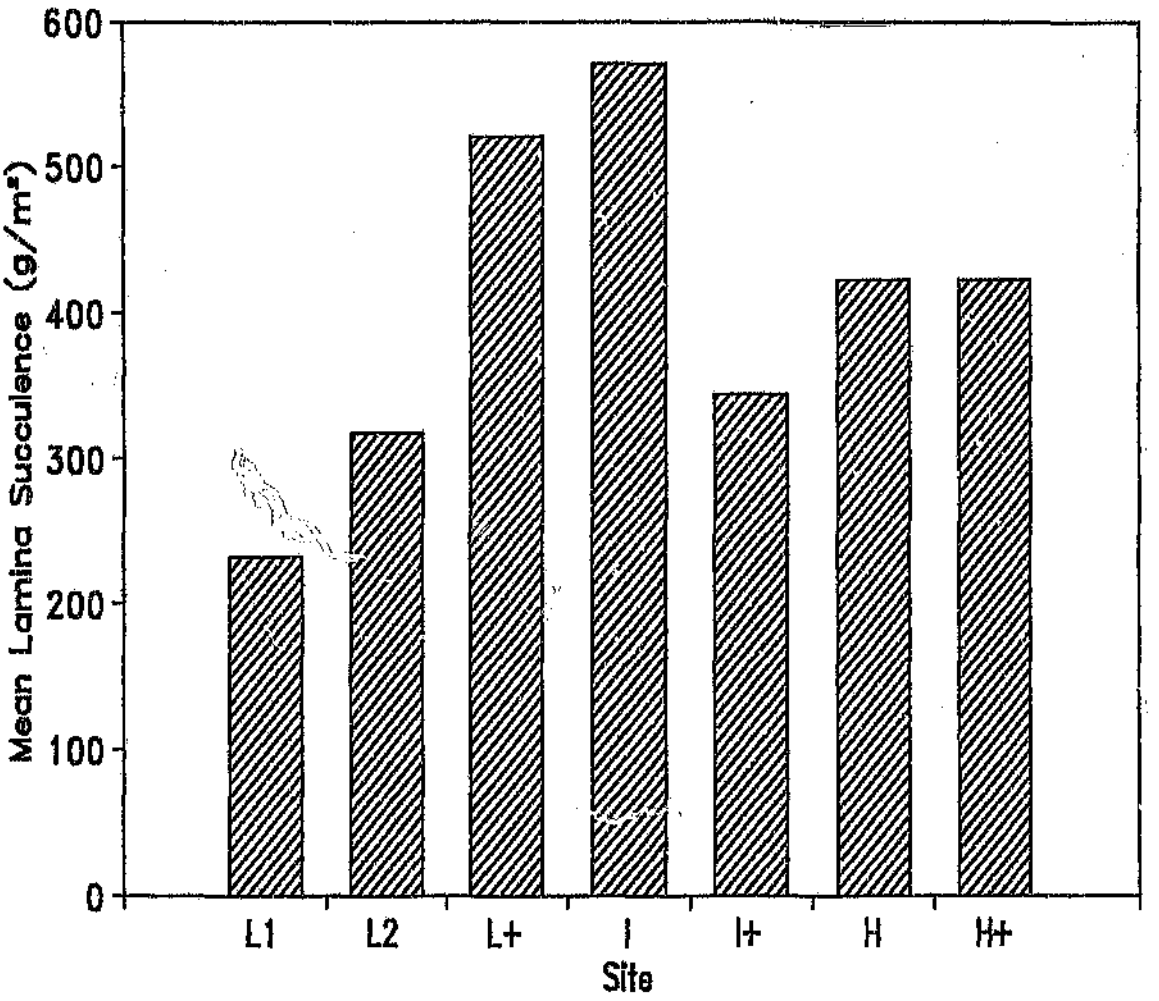


Figure 46: Graph of laminal mean succulence (wet mass (g)/unit area (m^2)) for all the sites (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41; H+, n=53).

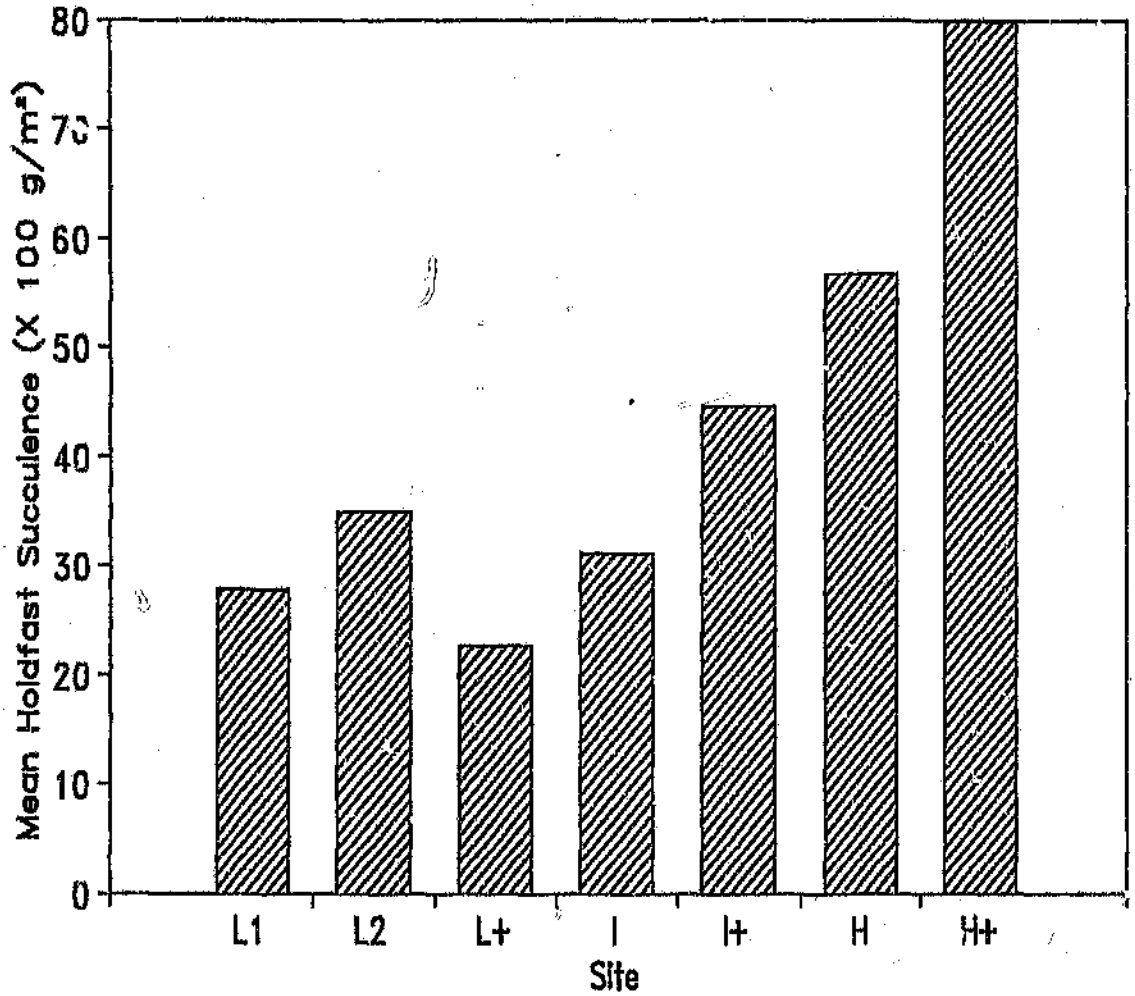


Figure 47: Graph of holdfast mean succulence (wet mass (g)/unit area (m^2)) for all the sites (L1, n=25; L2, n=30; L+, n=28; I, n=24; I+, n=36; H, n=41; H+, n=53).

succulence ($p<0.001$). L1, L2, L+, I, I+, H, and H+ have mean holdfast succulence values of 2779.84 (±583.30) g/m^2, 3488.63 (±583.30) g/m^2, 2253.64 (±538.50) g/m^2, 3109.02 (±20.38) g/m^2, 4459.07 (±456.95) g/m^2, 5674.93 (±456.99) g/m^2 and 7974.56 (±4693.25) g/m^2, respectively.

For both sclerophylly and succulence of the holdfast, it must be noted that the rhizoidal mat of the holdfast retains a large amount of sand, the grains of which were attached to the rhizoids and which were thus not removed before the measurements were taken.

From the PCA (Fig. 43) of various morphological and structural features of the holdfast and lamina, it appears that the factors relating to laminal strength and size are all fairly closely correlated; while the holdfast measurements are not correlated with the lamina factors, but are very closely correlated with each other. The only factor which was expected to show some correlation with the holdfast measurements, and did not, is the measurement of attachment strength (see Section 3.8.2).

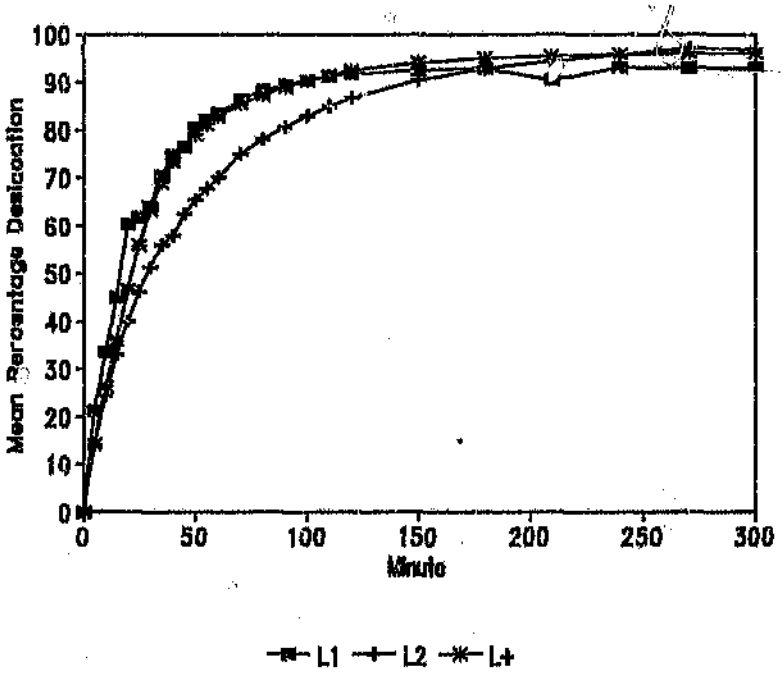
3.8.4 Desiccation and Rehydration

The plants in the field were regularly observed to be exposed to the elements for long periods of time (a few hours over low spring tide) and to thus undergo desiccation, and the subsequent rehydration with the incoming tide. Particularly noticeable was the amount of time that the plants in the more wave exposed sites (such as H and H+) spent exposed to the air, especially at the very low spring tides. Those individuals in the pools (eg L1, L2 and L+) remained submerged for the entire tidal cycle. The plants which did become heavily desiccated appeared to be alive and to recover when the tide turned,

although the heavily desiccated laminae may have been lost. Unfortunately, the lethal desiccation could not be calculated because preserved specimens were used (Section 2.4.7.4).

The mean rate of desiccation was similar in plants from all the sites. Figures 48, A and B, indicate the desiccation curves (as percentage desiccation over time) for all the sites. It appears that the more regularly exposed sites (ie I, I+, H and H+) have a greater percentage desiccation after the allotted time period of 300 minutes (98.08 (±0.271)%, 90.69 (±0.785)%, 97.12 (±1.733)% and 99.94 (±4.173)%, respectively), than the less exposed sites in which the plants are continually submerged (L1, L2 and L+ have mean percentage desiccation values of 93.11 (±8.974)%, 96.76 (±0.524)% and 96.02 (±1.52)%, respectively). It appears that the desiccation curves of all the sites are similar (Fig. 48, A & B) except for the low (L2) and highest (H+) wave exposure sites, both of which have lower desiccation rates than the other sites.

The mean percentage rehydration or percentage of the original mass that was regained after resubmerging the plants (see Section 2.4.7.4) for all the sites, is shown in Figure 49. The lowest wave activity site L1 has the lowest percentage rehydration and only recovered 49.92 (±8.8)% of the original mass. The highest percentage rehydration value was that of the intermediate site I (77.82 (±4.88)%) and the other sites were all similar and between these two values (L2, L+, I+, H and H+ have mean percentage rehydration values of 64.58 (±4.63)%, 67.48 (±1.92)%, 64.09 (±4.2)%, 68.58 (±2.68)% and 63.94 (±5.15)%, respectively). These differences are not, however, significant ($p>0.05$).



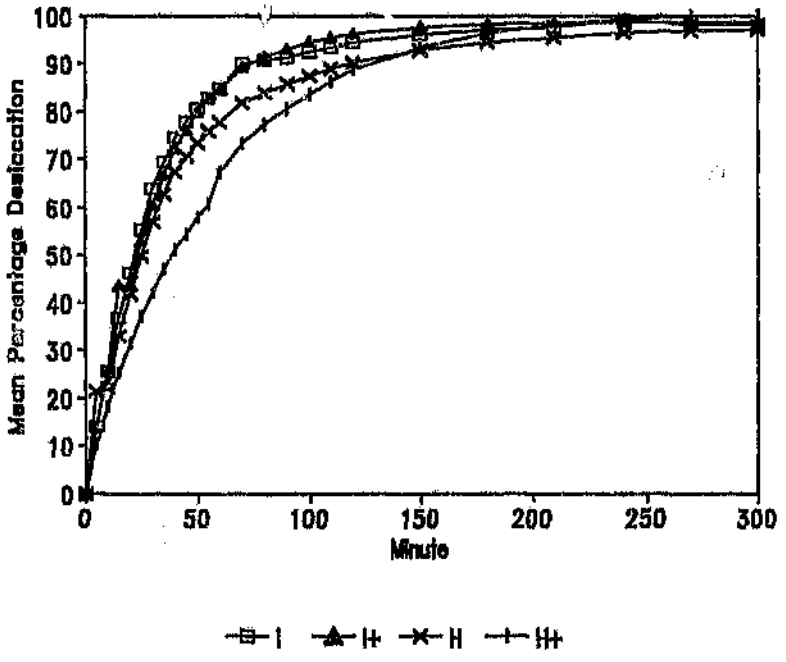


Figure 48: Desiccation curves of percentage desiccation versus time in L1, L2 and L+ (A) and I, I+, H and H+ (B).

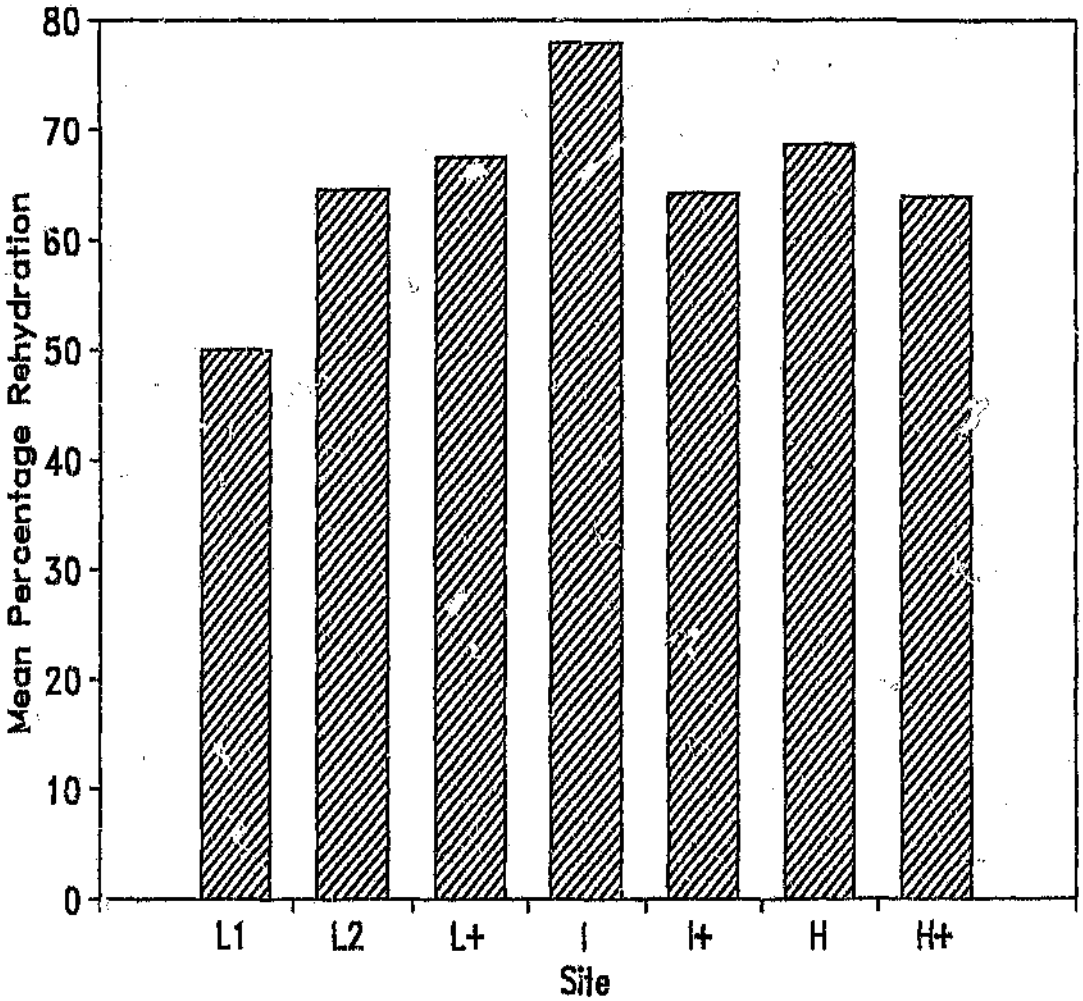


Figure 49: Mean percentage rehydration after desiccation for all the sites (n=3).

3.9 ANATOMICAL STUDIES OF D. LONGIFOLIA

3.9.1 Apical Tip

The apical tip of each lamina consists of a sunken pit (Pl. 7, A & B; Fig. 50). In young laminae (Pl. 7, C) or newly dichotomised branch tips, the pit may not be evident but meristematic cells in the apical region are present (Pl. 7, D & E). These cells become elongated and "sausage shaped" and begin characteristic, longitudinal division (Pl. 7, F & G) which initiates the formation of the apical pit, containing the longitudinally dividing meristematic cells (Pl. 7, H-K). During dichotomising of

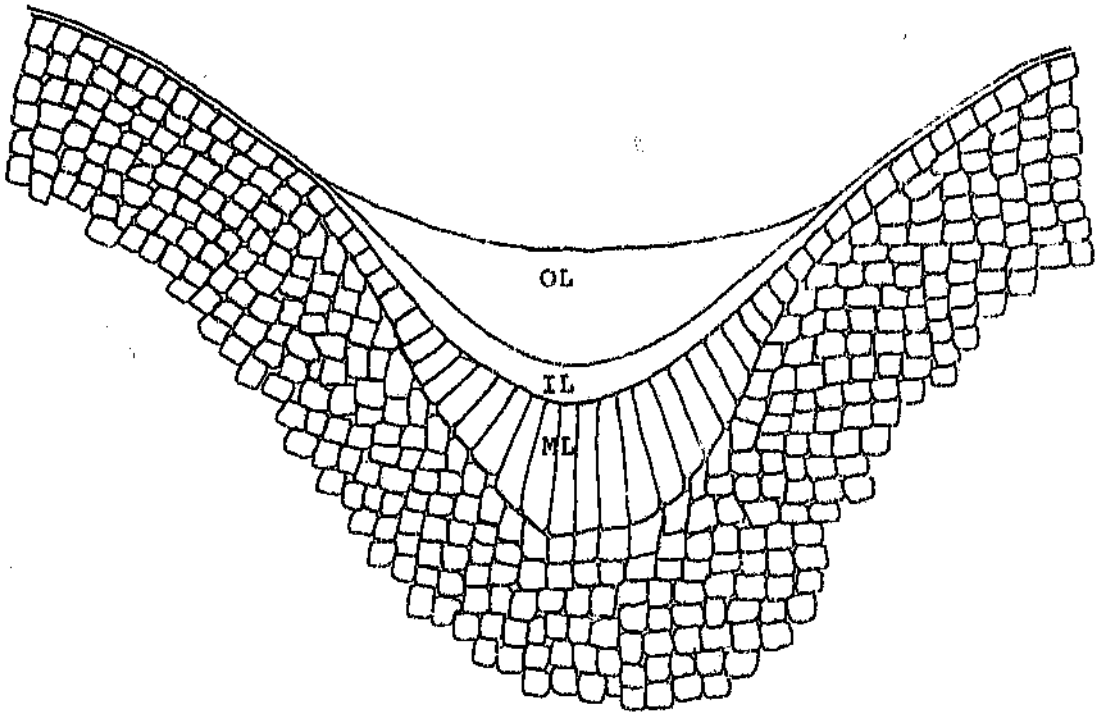


Figure 50: Detail of the structure of the meristematic, apical tip of Dictyopteris longifolia where MC are the meristematic cells, IL is the inner layer of material and OL is the outer layer (Redrawn from Pl. 7, I & J; Pl. 8, D; Scale 1cm = 85μm).

the lamina, two apical meristematic cells appear to initiate the division (Pl. 7, L). Once two apical pits have formed (Pl. 7, M), the growth of the two branches continues.

The apical pit is lined by two layers. The inner layer appears to be fibrous and is narrower (30μm at the widest point) than the outer layer. The former layer is thickest in the centre of the pit and tapers towards the outer edge. The outer layer is wider (up to 100μm in width) and appears to be mucilaginous in nature (Pl. 8, A-D; Fig. 50).

3.9.2 Wing Structure

The wing section of the lamina of D. longifolia terminates in a characteristic marginal bulge (Pl. 9, A-F; Fig. 51, B; Fig. 52, A). In young laminae, the thickened "bulge" region is not as prominent and is composed of only a few cells (Pl. 9, D; Fig. 51, A). In more mature laminae, however, the thickened region is composed of many layers of cells (Pl. 9, E & F; Fig. 52, A). The exterior layer of the wing region is composed of a single layer of epidermal cells. There is a layer of small cells beneath the epidermis in the most marginal region of the bulge (Pl. 9, F). The rest of the thickened area is composed of the normal wing cells. The remainder of the laminal wing is composed of two parallel layers of epidermal cells with a number of layers of wing cells between them. In the very young laminae or newly developed regions of old laminae, the wing is composed of only two layers of wing cells between the two epidermal layers (Pl. 9, G; Fig. 52, B). In the older laminae there may be many layers of wing cells (Pl. 9, H-J & K; Fig. 52, C).

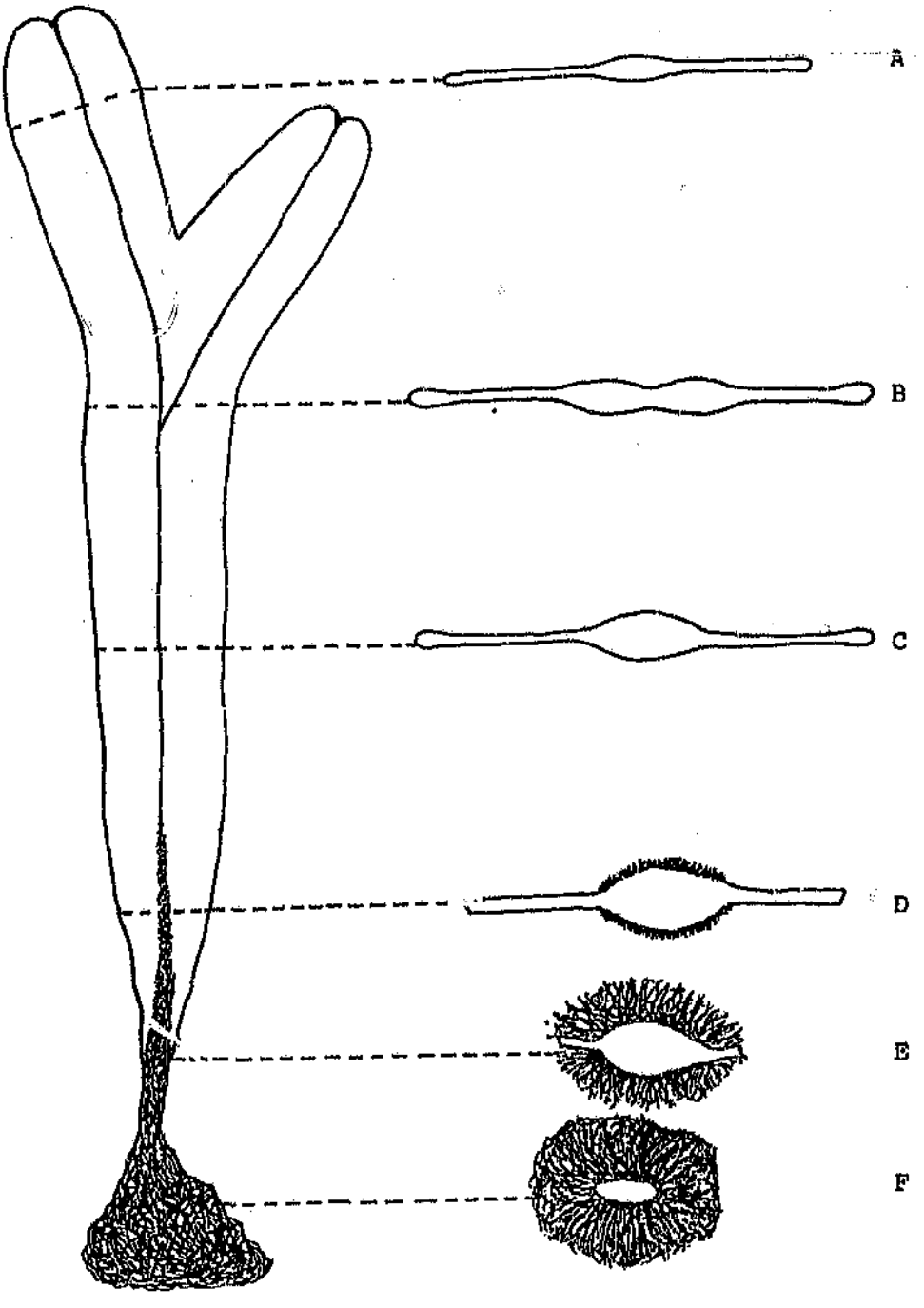


Figure 51: Complete specimen of Dictyopteris longifolia with diagrams to show the cross-sectional appearance of different regions of the plant.

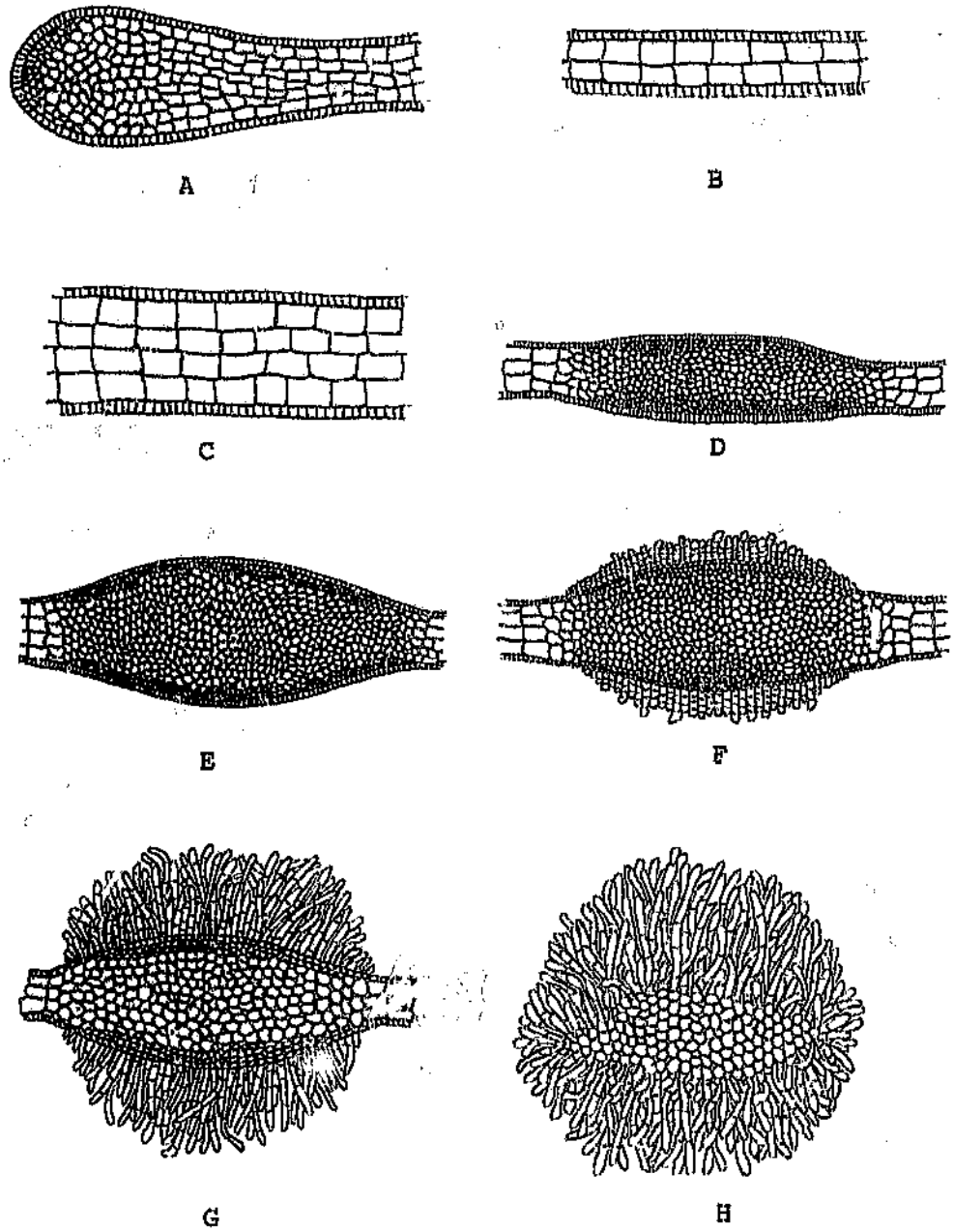


Figure 52: Cell detail from the cross-sections of different portions of the Dictyopteris longifolia thallus (Redrawn from Pl. 9, B, G & H; Pl. 10, B, E, G, K & N; Scale 1cm = 150μm).

The wing cells are large (approximately 75μm), irregularly shaped and divide in all directions (Pl. 9, L & M). The walls of the cells are extremely thin (approximately 1.5μm thick; Pl. 9, N-P).

3.9.3 Midrib Structure

The midrib is the prominent, thickened region which runs down the centre of the lamina. It is initiated by the meristematic cells in the apical pit. At the immature tip of a lamina, or in a newly formed lamina, the midrib is less prominent (Fig. 51, A; Fig. 52, D) and not as thick (approximately 400μm thick) as in more mature regions (Pl. 10, A-C; Fig. 51, B; Fig. 52, E). In these immature regions, the cells of the midrib are smaller with thinner walls. The cells of the epidermis in the immature midrib region are much smaller than those in mature areas. In a fully developed lamina, the more mature regions are found nearer the base of the lamina as growth occurs from the meristematic tip. In the basal regions, prior to the rhizoid producing regions, the midrib is thicker (approximately 1mm thick) with larger, thick-walled cells and a more prominent epidermal layer (Pl. 10, D & E). The midrib cells are similar throughout the mature region (holdfast, laminal base and lamina). In the regions closer to the base of the lamina, but prior to the regions where there is degeneration of the lamina, there may be some production of multicellular rhizoids from the meristoderm (rhizoids develop from the epidermis; Fig 51, C; Fig. 52, F). The midrib has a similar thickness in this region to that in the region lacking rhizoids (1mm; Pl. 10, F-J; Fig. 51, C & D; Fig. 52, E & F). At the base of mature laminae, in the region which may be known as the stipe, the wing of the lamina degenerates, presumably due to abrasion and herbivory. The midrib may be left without any surrounding tissue. The rhizoids in this region may reach considerable length in mature laminae,

and the central core of midrib cells appears to decrease in thickness (200μm). The remains of the wing tissue may be observed surrounding the midrib (Pl. 10, K-M; Fig. 51, D; Fig. 52; G). The base of the lamina becomes incorporated into the holdfast. The latter attaches the plant to the substratum and is composed of a mass of long, intertwined rhizoids and a central core of midrib tissue (200μm; Pl. 10, N & O; Fig. 51, F; Fig. 52, H).

The cells of the midrib have a distinctive shape. In cross-section they are squarish or brick shaped and smaller than those of the wing (approximately 30μm wide; Pl. 11, A-J). The walls of the midrib cells are very thick (approximately 4μm thick) and appear to be composed of different layers of material (Pl. 11, K & L). In longitudinal section, the cells of the midrib are elongated and approximately 65μm long (Pl. 12, A-E). Interestingly, these cells have pores in the longitudinal walls (Pl. 12, F & G), which may be compared to the pores in the longitudinal walls of conducting cells in higher plants.

3.9.4 Epidermis

The epidermis is composed of a single layer of cells on either side of the lamina, in both the midrib and wing regions. The cells appear to be similar in the midrib (Pl. 12, H-K & M) and wing regions (Pl. 12, L). They are rectangular in shape and smaller than the cells of the rest of the lamina (approximately 18μm wide and 30μm long). In the lower regions of the lamina, the epidermis may develop into a meristoderm which gives rise to the rhizoids. The rhizoids protrude from the epidermal cells (Pl. 13, A; Fig. 52, F-H) and then the cells at the base of the rhizoid undergo repeated divisions to give rise to the multicellular rhizoids, ie trichothallic growth (Pl. 13, B-C). The exterior walls of the epidermal cells

appear to be covered by a thick layer of material (Pl. 13, H). This layer was observed to extend over the cells in the initial stages of rhizoid development (Pl. 13, I). In many of the sections a densely stained region was observed between the region of dividing meristoderm cells and the developing rhizoids (Pl. 13, J-L). The layer appeared to be composed of small cells or large grains.

3.9.5 Surface Appearance of Epidermal Cells

The surface appearance of the epidermal cells of the midrib and those of the wing are markedly different. Even in the young laminae (Pl. 14, A), which lack the well developed midrib characteristic of older laminae, there is some difference in the cells (Pl. 14, B & C). In the older lamina where there is a distinctive midrib region, the difference between the epidermal cells can clearly be seen (Pl. 14, D & E). In the surface view, the epidermal cells of the midrib appear to be much longer and narrower than those of the wing. The characteristic longitudinal division of these cells can be observed on the surface (Pl. 14, F-H). The cells of the wing are much more irregularly shaped and may have different concentrations of cell contents in different regions of the lamina (Pl. 14, I-L). For example, the contents were dispersed (Pl. 14, J), aggregated around the nucleus (Pl. 14, K) or peripherally adpressed to the wall (Pl. 14, L) in the various regions of the lamina that were observed.

3.9.6 Holdfast Structure

The holdfast or attachment organ of D. longifolia is a structure which may develop to a few centimetres in diameter. The structure is composed of a mat of entangled rhizoids giving rise to numerous laminae (Pl. 15, A & B). There is a central core of cells similar to those of the midrib (Pl. 15, C; Fig. 51, F; Fig. 52, H). The

development of rhizoids similar to those of the holdfast, was observed to occur on the midrib nearer to the base of the laminae (Pl. 15, D). The length of rhizoids produced from the midrib was observed to increase closer to the laminal base (Pl. 15, E-G). Rhizoids are produced from the epidermal meristoderm (Pl. 15, H-J), may be branched and are multicellular (Pl. 15, K & L). The majority of the rhizoid tips are pointed, with a high concentration of cell contents in the terminal regions (Pl. 15, M & N). Occasionally rhizoids with spherical structures at the terminal tips were observed (Pl. 15, O & P). It is believed that these rhizoids were attached to the substratum prior to being removed from culture for microscopy.

3.9.7 Surface Hairs

Tufts of hairs were observed to grow on the dorsal and ventral surfaces of the lamina, both in the field and in culture, on sections kept under the conditions discussed in 2.6.3 (Pl. 16, A & B). The multicellular hairs appeared to developed in sunken pits on the surface of the lamina (Pl. 16, C & D). Old or deformed tufts of hairs were also occasionally observed (Pl. 16, E & F). In the initial stages of development, numerous hairs were observed to emerge from the pit on the laminal surface (Pl. 16, G). It appeared as if the epidermis around the pit was pushed aside to enable the hairs to grow through (Pl. 16, H & I), and these then enlarged until a fully developed clump was present (Pl. 16, K). The hairs are multicellular with various cell contents visible in the cells (Fig. 53). An interesting observation was the presence of dark brown structures in the cells which appeared to make indentations on the cell walls (Pl. 16, L-N). Tips of the hairs are blunt (Pl. 16, J & O; Fig. 53). The cells at the base (B) of the hair and attaching it to the lamina are small and densely packed with cell

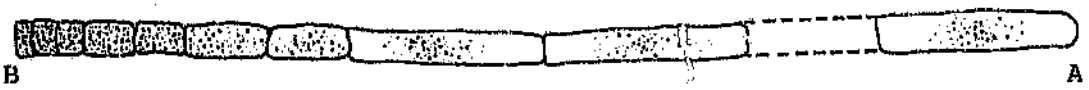


Figure 53: Cell detail of a surface hair showing the different cells from the small basal cells (B) to the larger cells at the apical tip (A) (redrawn from Pl. 16, O & P; Scale 1cm = 33μm).

contents, whilst towards the apex (A) of the hair the cells are larger and more sparsely packed, indicating trichothallic growth of the hairs (Pl. 16, P; Fig. 53).

3.9.8 Other Structural Observations and Associations of D. longifolia.

3.9.8.1 Other Hair-Like Structures

Fairly regularly spaced clumps of hair-like structures were observed on the laminal surface of certain plants. The hairs were unlike those mentioned previously in both distribution and structure. They were far shorter and interspersed with finer hairs (Pl. 17, A-D).

3.9.8.2 Wounds or Injured Areas

On some laminae "wounds" or apparently damaged areas were observed. These went through a few layers of cells and are believed, due to the hazy areas observed in the injuries and often associated with fungal infections, to be caused by a fungus (Pl. 17, E-G).

3.9.8.3 Algal Epiphytes

The plants of D. longifolia were often observed to be contaminated by epiphytes. These included filamentous red algae found growing on the holdfast (Pl. 17, H), tufts of filamentous brown algae (Pl. 17, I & J), red crustose and other types of red algal epiphytes on the laminae (Pl. 17, K-M). The immature apical regions of the laminae appeared to be relatively clear of epiphytes.

3.9.8.4 Epidermal Sloughing

The epidermis of the laminae was observed to slough off occasionally in culture, and this is believed to be a mechanism to rid the plant of damaging epiphytes (Pl. 17, N-P).

3.9.8.5 Animal Associates and Herbivores

Although few animals were observed to graze on plants of D. longifolia in the field, a polychaete worm Pseudonereis variegata was observed to cause some damage to the plant by rolling the laminae up to form a nest (Pl. 17, Q-R). There was also some damage caused to the laminae by what is believed to be, due to the patterns of removed areas, grazing fish (Pl. 17, S Fig. 54, D).

3.10 REGENERATION

Regeneration was observed to occur frequently in the field. Figure 54 is a composite of silhouettes of specimens collected towards the middle of the study period. They show various patterns of degradation. Plate 18 also shows various aspects of degeneration and

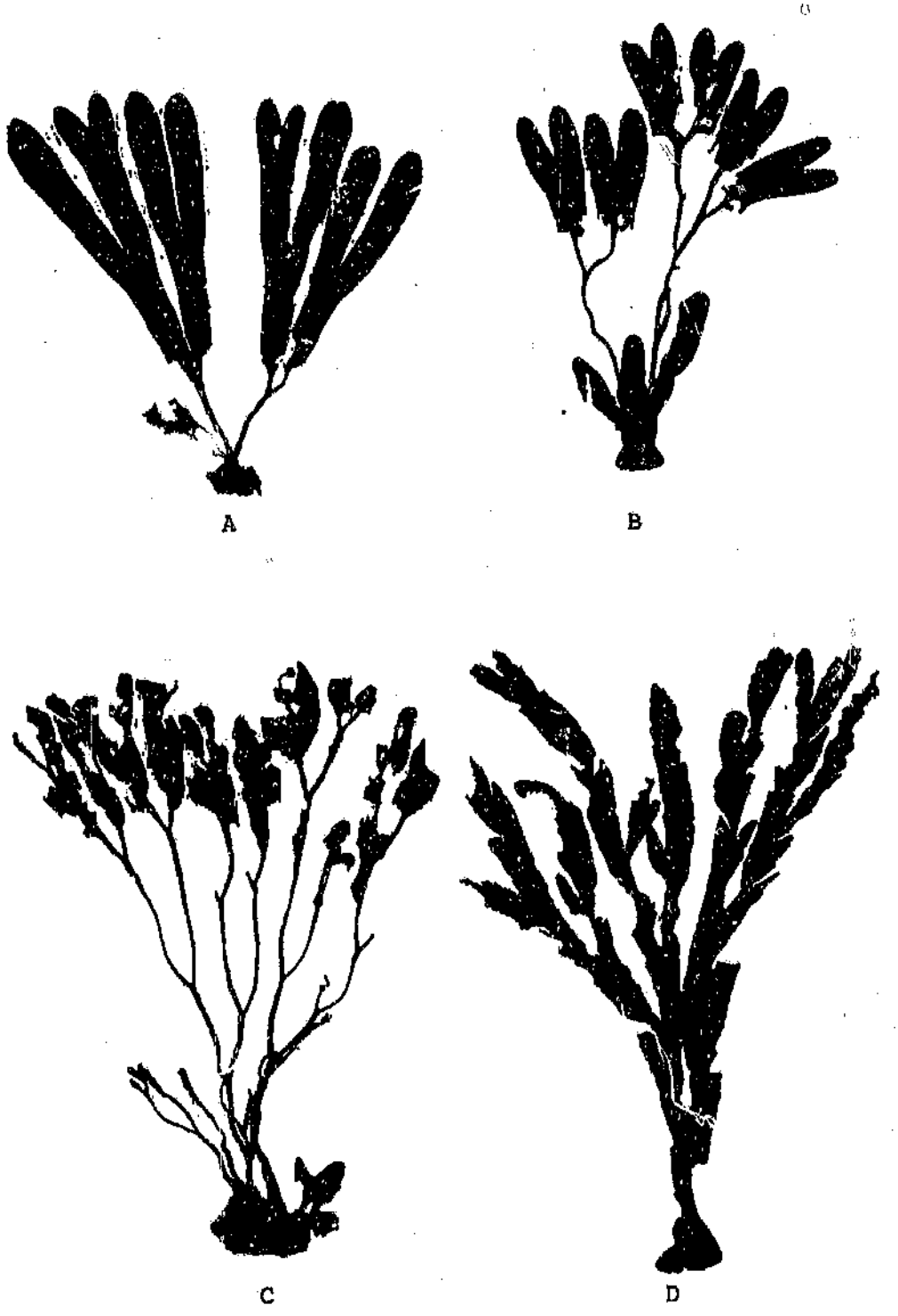


Figure 54: Composite of silhouetted specimens from the field showing different stages of laminal degeneration in Dictyopteris longifolia (Scale 1cm = 0.5cm).

regeneration of plants collected in the field. There is natural seasonal degeneration of the wing tissue at the base of the lamina (Pl. 18, A; Fig. 54, A-C), as well as laminal degeneration due to sand abrasion and grazing by fish and invertebrates (Pl. 18, B; Fig. 54, D). At the end of the winter, just prior to the increased growth and regeneration (although some degree of regeneration occurs throughout the study period), the laminae are reduced to a small amount of terminal material and midrib remains (Pl. 18, C-F). Regeneration of new laminae may occur from the damaged regions of the previous year's laminae (Pl. 18, G-J), from the holdfast whilst the previous year's laminae remains are still attached (Pl. 18, K), or from the holdfas which is perennial) without there being any remaining laminae (Pl. 18, L).

As regeneration is obviously an important part of the survival strategy of D. longifolia, especially in the heavily wave exposed areas, a study of various aspects of and the processes involved in laminal regeneration, was performed.

3.10.1 Regeneration from Small Sections of Lamina

Various small sections of the laminae were used for the regeneration studies under the conditions described in Section 2.6 (see Section 2.5.4, Fig. 8).

A) Strips 4mm in length and the width of the lamina including the wing margins (Pl. 19, A; Fig. 8, A), did not exhibit any regeneration at all.

B) Sections 1cm in length, excluding the margins but including 3mm on either side of the midrib (Pl. 19, B & C; Fig. 8, B) did exhibit some regeneration. Those kept in enriched seawater became overgrown with epiphytic brown and red algal species and did not

regenerate (Pl. 19, B), whilst those cultured in natural seawater developed rhizoid-like outgrowths (Pl. 19, D-F) with some multicellular, thallus-like structures developing (Pl. 19, E). This regeneration occurred mainly from the midrib region but no proper laminae developed.

C) Sections 1cm in length and the width of the lamina including both margins (Pl. 21, A; Fig. 8, C), showed the highest degree of regeneration with laminae developing along the cut edge (Pl. 19, G-K). Regeneration did not only occur along the midrib but on the wing as well. Regenerated laminae developed to an advanced stage with a meristematic apical region, midrib and rhizoids (Pl. 19, K). In some cases small, tubular outgrowths developed instead of laminae and these developed no further (Pl. 19, L).

D) Apical sections of the lamina (approximately 1cm in length), removed with a V-shaped cut (Fig. 8, D) and cultured in natural seawater, were also cultured in the regeneration study. Different responses were observed to occur in the culture of these sections.

In some cases the sections continued to elongate as if they were still attached to the parent plant (Pl. 20, A-C). These sections remained healthy and did not show any signs of regenerating new laminae from the cut edge. Surface hairs developed on the sections. These hairs were observed in a number of the cultures, as well as in the field on specimens collected from (in particular) small pools. The increase in length of these sections was measured and graphed in Figure 55, which shows the gradual increase in length of a number of apical sections kept in culture for 41 days (see Section 2.5.4).

Some sections, cut in a similar way (apical sections removed by a v-shaped cut), did exhibit regeneration of new laminae (Pl. 20, D-H). In some of these sections, there was regeneration of new laminae from the cut edge only, ie in the opposite direction to the original growth direction (Pl. 20, D). Other sections showed a similar regeneration from the cut surface, as well as some development of the apical region (Pl. 20, E), while some regenerated new laminae from both the cut surface and the apical region (Pl. 20, F). Dichotomising tips showed similar regeneration from the cut surface and some growth of the apical regions (Fig. 8, D).

3.10.2 Regeneration from Large Sections or Whole Laminae

Various large sections and similar sized whole laminae (approximately 5cm in length) were also damaged and cultured to observe regeneration patterns (Fig. 8). These segments are shown in Plate 21. The different types of experimental injury used in this study were chosen to try and imitate the damage patterns observed in the field, from which different regeneration patterns were observed to develop. An example of a peculiar regeneration pattern observed in the field is shown in Figure 56 which is a silhouette of a specimen collected in the field. The tips have obviously been damaged but the midrib has remained intact and grown to give rise to a new terminal region (not a new lamina). This was not, however observed in any of the similarly damaged laminae in culture.

E) Complete laminae with horizontal, V-shaped cuts severing the midribs (Fig. 8, E) were cultured and continued to grow from the tips. No regeneration occurred from the cut surfaces (Pl. 21, E & F).

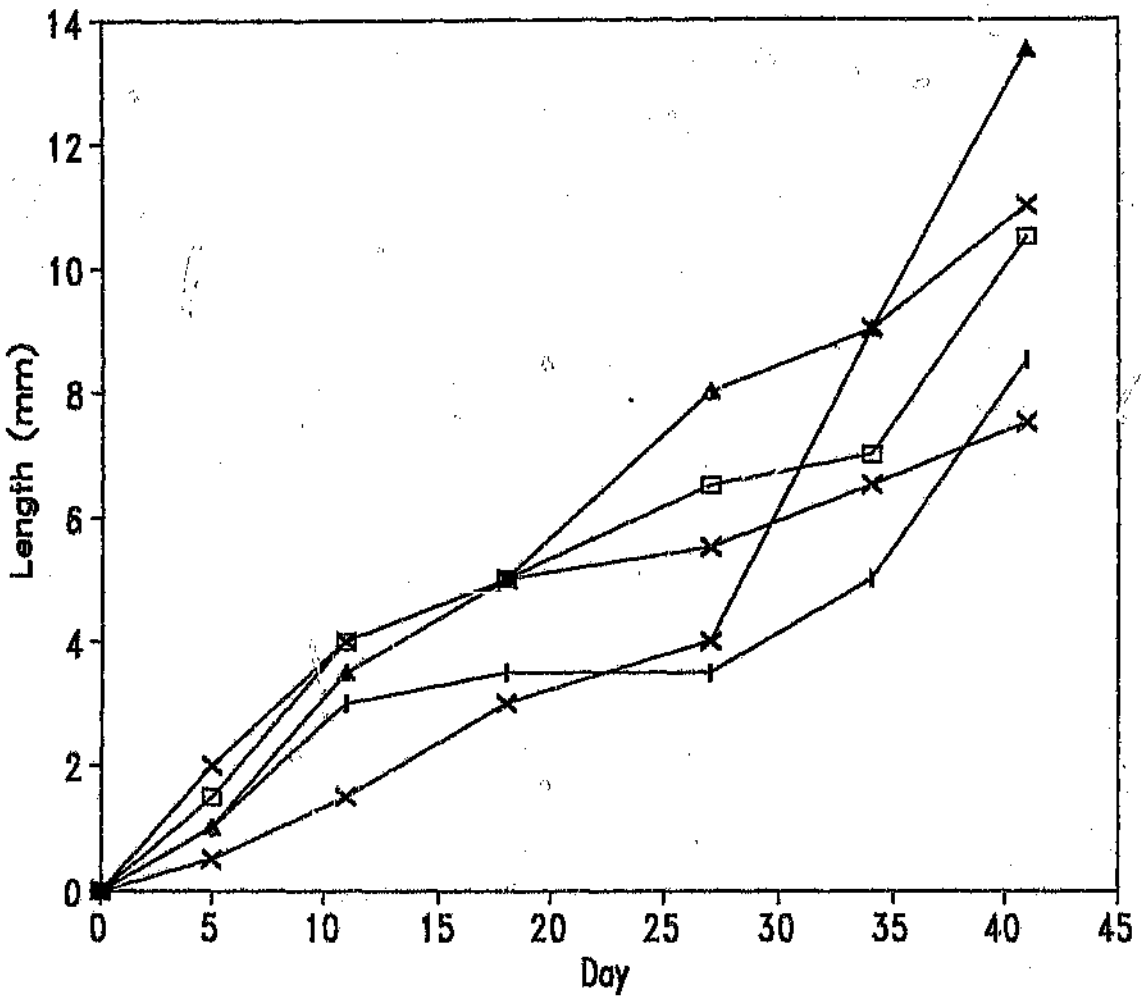


Figure 55: Graph indicating the increase in length (mm) of five excised apical tips.



Figure 56: Silhouette of a specimen of Dictyopteris longifolia from the field showing peculiar regeneration of the tip region (Scale 1cm = 0.5cm).

F) Large sections of dichotomising laminae, having both ends removed with a straight cut, were also cultured and these exhibited regeneration from the apical cut edge only (Pl. 21, C & D; Fig. 8, F). The laminae regenerated were similar to those from other sections and the process was similar to that described in 3.10.3. No regeneration occurred from the basal cut edge.

G) Complete laminae having the apical tips removed with a V-shaped cut displayed similar regeneration from the cut surface (Pl. 20, I-K; Pl. 21, E; Fig. 8, G).

R ,eneration occurred along the entire cut surface and not only from the midrib region.

H) Complete plants were also kept in culture and each lamina had the apical tip removed with a V-shaped cut. Once new laminae had regenerated, these were once again cut and again regenerated new laminae. Figure 57 is a drawing showing one of these plants with regenerated laminae.

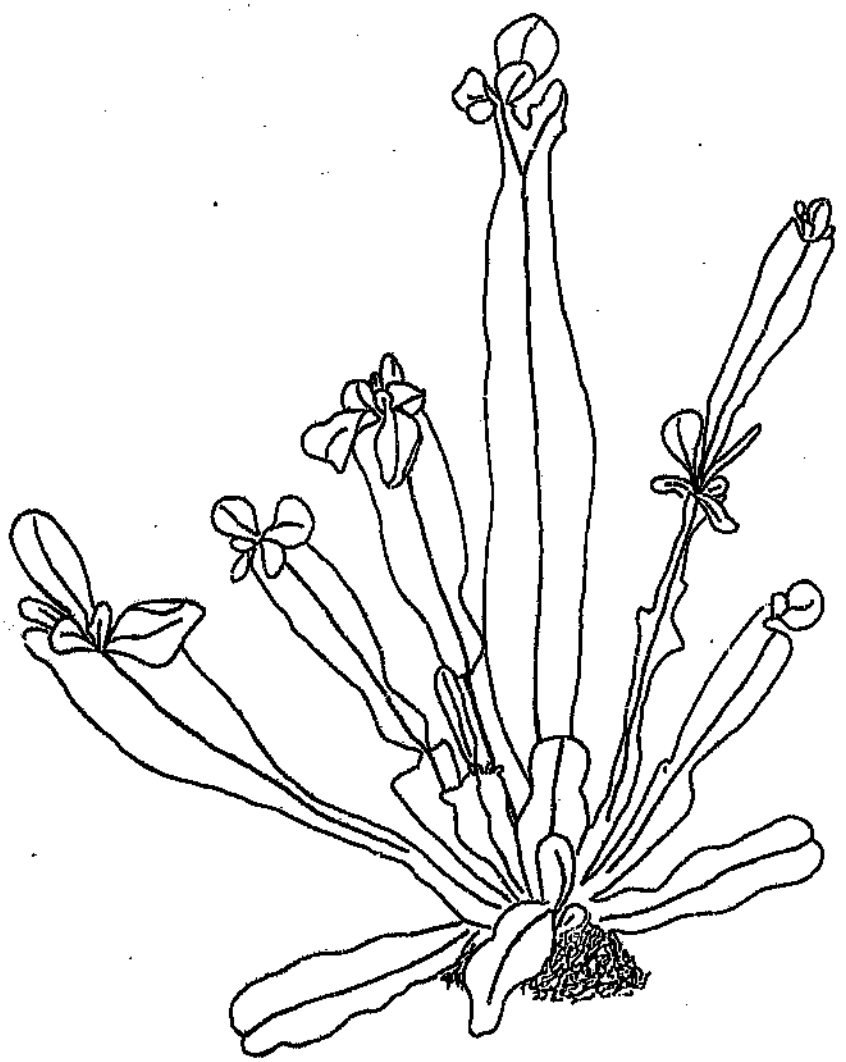


Figure 57: Drawing of <u>Dictyopteris longifolia</u> showing regeneration of new laminae from the damaged laminal tips of the parent plant (Scale 1cm = 2cm).

3.10.3 Process of Regeneration from Injured Laminae

Regeneration of new laminae was observed to occur with a similar sequence of developments (on all sections cultured). Initially there was cytoplasmic concentration in, and protrusion of, a single cell above the rest of the cells on a cut surface (Pl. 22, A & B; Pl. 23, A-D; Pl. 24, A-D; Fig. 58, B). The surrounding damaged cells remained as cell walls only (Pl. 24, A-C; Fig. 58, B & C). The protruding cell then divided into a multicellular thallus (Pl. 22, C-J; Pl. 23, E-S; Pl. 24, E-L; Fig. 58 E & G). The newly regenerated lamina developed in a similar way to other new laminae of the plant, with an apical pit and meristematic cells developing in the apical region (Pl. 22, G-J; Pl. 23, J-M, O). Longitudinal division of the apical meristematic cells can clearly be seen in Plate 23, J. The midrib region also becomes visible (Pl. 22, I & J) and in the more advanced stages of development, the laminae develops basal rhizoidal outgrowths at the point of attachment to the parent material (Pl. 23, M, N, P-S; Pl. 24, L; Fig. 58, L). These outgrowths grow into a fully developed system of rhizoids. The regenerated laminae were never observed to break loose from the parent material and attach, although they had the rhizoidal network for attachment.

3.10.4 Regeneration from the Uncut Surface of a Lamina

In some cases regeneration was observed to occur from the uncut surfaces of laminae. This was observed rarely in the field, where the regenerated laminae developed from the base of the parent lamina near the midrib. There did not seem to be any damage at the point of attachment of the new lamina although, there was occasionally some small holes in the region. Laminal regeneration of this type was observed to occur in culture on sporelings

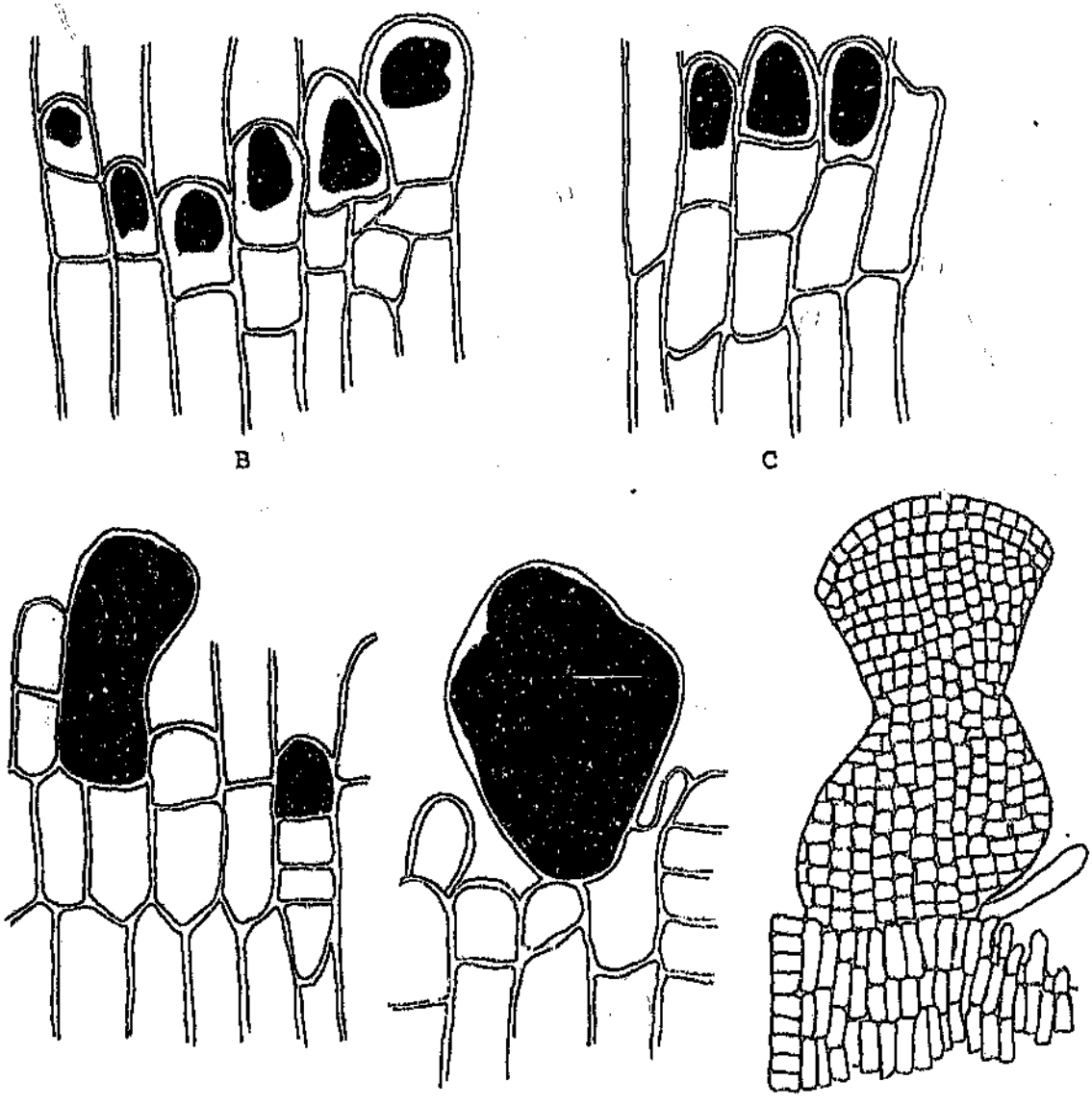


Figure 58: Cross-sections through stages of regeneration of Dictyopteris longifolia (Redrawn from Pl. 24, B, C, E, G & L; Scale 1cm = 140μm, except L where 1cm = 350μm).

(Pl. 25, A), on regenerated laminae which had been removed from the parent material (Pl. 25, B) and from the apical tips of lamina sections damaged in culture (Pl. 25, C). The regenerated laminae reached an advanced stage of development, with the growth of rhizoids occurring (Pl. 25, D). The process of regeneration was similar to that from a cut surface, with a single cell protruding initially (Pl. 25, E-H). This protrusion then divided into a multicellular structure (Pl. 25, I-L) which developed further into a new lamina. The regenerated laminae did not grow very large but, in some cases, developed further thalli and rhizoidal outgrowths from their surfaces (Pl. 25, M-P).

3.10.5 Regeneration from the Holdfast

The holdfast of D. longifolia is perennial and it was observed that when all the laminae are removed by herbivory and/or abrasion, new laminae are produced from the old holdfast (Pl. 26, A). In culture (see Section 2.5.4.4; Fig. 8, H), small holdfast clumps with all the laminae and stipe regions removed, regenerated new laminae (Pl. 26, B-F) after approximately 3 weeks. The new laminae were normal and developed from the holdfast region (Pl. 26, G) in a similar manner to those observed to develop in other regions.

3.10.6 Regeneration from Rhizoid Sections

It has been reported in the literature (Tokida et al., 1953) that members of the Dictyotales, and other brown algae, have been observed to regenerate new laminae from rhizoid sections. After many attempts, small sections of the rhizoids of D. longifolia regenerated new laminae in culture (see Section 2.5.4.5). The attempts using short, unbranched segments (Fig. 8, J) all failed, however, slightly larger clumps including branches were successful

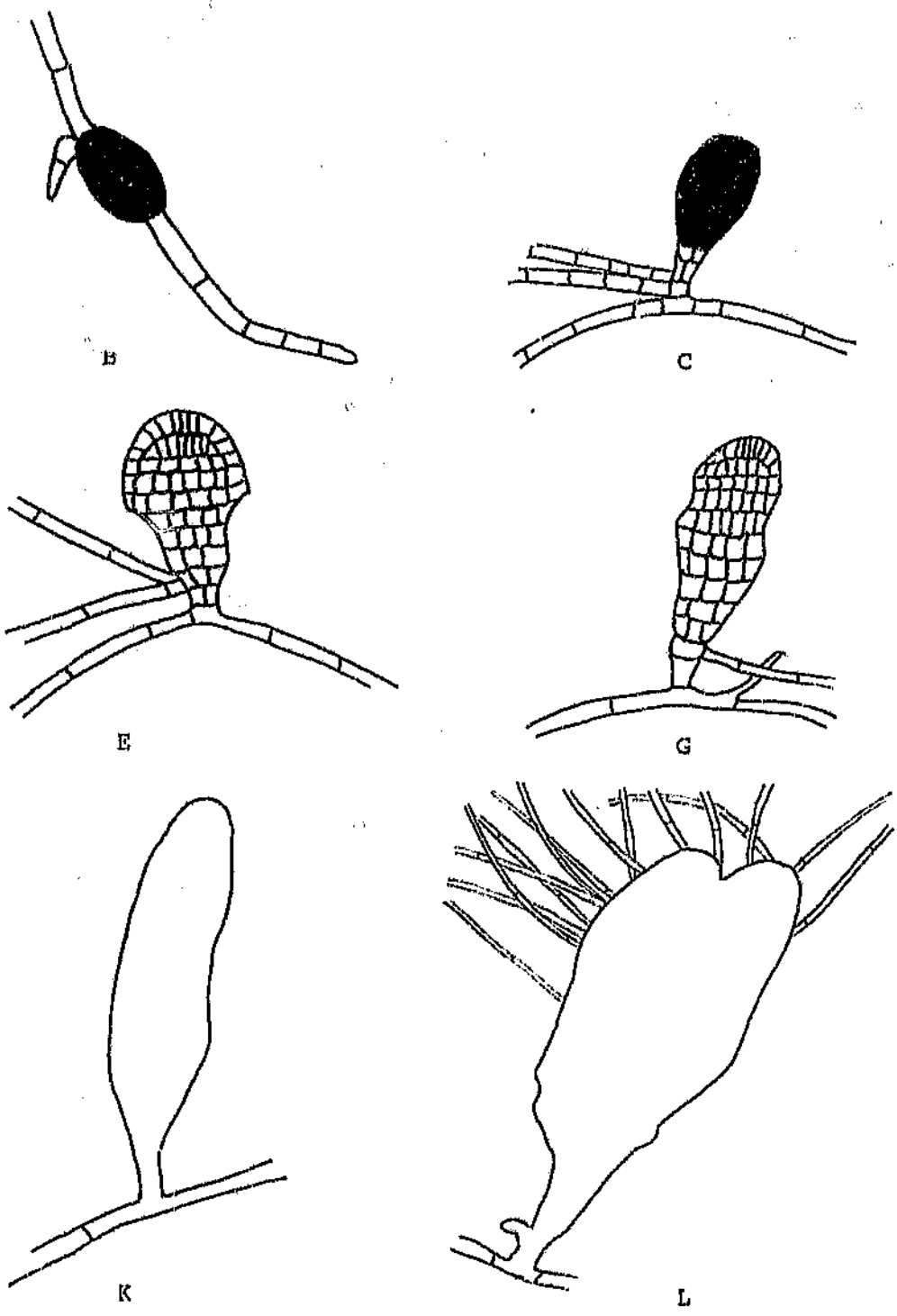


Figure 59: Regeneration of new laminae from sections of rhizoid from Dictyopteris longifolia (Redrawn from Pl. 27, B, C, E, G, J & L; Scale 1cm = 340μm).

(Pl. 27, A; Fig. 8, I). Initially a cell in the rhizoid enlarged and became dense (Pl. 27, B; Fig. 59, B). This cell then divided into a multicellular lamina (Pl. 27, C-P; Fig. 59, C-K) which produced more rhizoids from its basal region. The apical cells developed into a meristematic region (Pl. 27, K-N) and eventually an apical pit formed (Pl. 27, L; Fig. 59, L). There was also some growth of surface hairs in the more advanced laminae (Pl. 27, L; Fig. 59, L). There was no further growth of the laminae although they stayed alive for approximately two months.

The regeneration patterns observed on experimentally damaged sections of D. longifolia are summarised in Figure 67.

3.11 SEXUAL REPRODUCTION

Although the study of sexual reproduction in D. longifolia was not part of the original study design, it was observed to occur in the field and in culture and was thus recorded. The sexual structures observed in this species appear to be similar to those recorded for other members of the Dictyotales. A diagram (Fig. 60) of the structures reported for Dictyota diemensis (Phillips et al., 1991b) has been included to clarify the structure of the oogonia and antheridia observed in D. longifolia.

3.11.1 Antheridia

The presence of antheridia was fairly commonly observed in the field, on herbarium specimens and on sections in culture (see Section 2.5.5), especially in the summer months. The structures are characterised by a

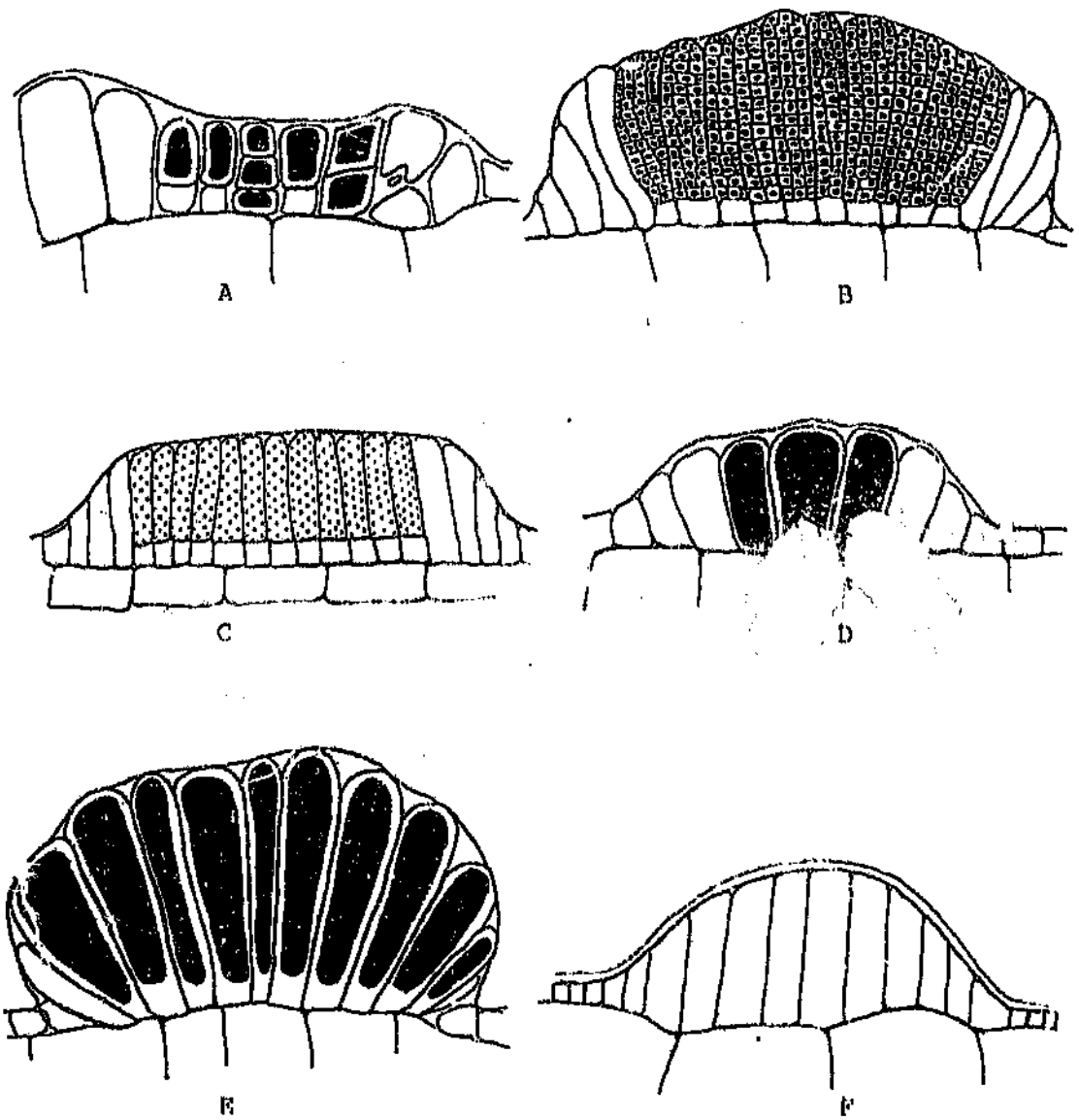


Figure 60: Antheridia and oogonia (Redrawn from Phillips *et al.*, 1991b; *Dictyota diemensis*); Pl. 28, H & L). Early (A) and late (B) stages of antheridial formation in *D. diemensis* and (C) the stage of formation observed in *D. longifolia* (redrawm from Pl. 28, H). Early (D) and late (E) stages of oogonial development in *D. diemensis* and the stage of formation observed in *D. longifolia* (F; redrawn from Pl. 28, L; Scale 1cm = 90µm for C and 40µm for F).

"pock-marked" lamina appearance. The surface on either side of the midrib was observed to be covered by an irregular arrangement of lighter areas (Pl. 28, A-C). The early stages of antheridial formation, were most frequently seen (Pl. 28, D & E). A pit lined by dividing cells was observed on the surface of the lamina. A later stage of development was also observed. The pits became shallower with the division of cells into antheridia (Pl. 28, F & G). The most developed stage observed, was just prior to sperm release. The antheridia were observed to be swollen above the surface of the lamina and the definite area of denser material, indicating the sperm cells, could be seen (Pl. 28, H & I; Fig. 60, C). The antheridia were observed on both surfaces of the lamina.

3.11.2 Oogonia

The oogonia were less frequently observed. The structures could be identified by circular, darkened areas spaced randomly and fairly far apart on the lamina (Pl. 28, J). The structures were only observed on the dorsal side of the lamina (Pl. 28, K). Only a very early stage of development was observed. This was characterised by a raised area in which longitudinal divisions could be observed (Pl. 28, L; Fig. 60, F).

3.12 TETRASPOROGENESIS AND MORPHOGENESIS

A study of tetrasporogenesis and morphogenesis of released tetraspores, was not included in the original study design. However, tetrasporangia in different stages of development were observed to occur abundantly on plants in the field, as well as on segments of the thallus in culture (segments were the width of the lamina and about 1cm long; Section 2.5.6). Development of

tetraspores on the surface of the laminae, and germination and growth of the spores into sporelings, was observed and recorded.

3.12.1 Development of the Tetraspores

Tetrasporogenesis occurred after 28 days (beginning in mid-June) in culture (Section 2.5.6). Tetrasporangia developed within sori on the surface of the laminal sections. Sori were scattered over both sides of the laminal wings (Pl. 29, A-E; Pl. 30, A & B) but not on the midrib (Pl. 29, B - midrib is on the right hand side). A single spore mother cell was observed to begin development below the surface of the lamina (Pl. 31, A; Fig. 62, A). Development was first observed to occur with a concentration of cell contents in the spore mother cell and a gradual bulging towards the exterior of the lamina (Pl. 29, F; Pl. 30, C & D; Pl. 31, B; Fig. 61, F). The protruding tetrasporangium was observed to have a thick cuticle (approximately 30 μm thick) covering the exterior surface (Pl. 31, C; Fig. 62, C). Once the tetrasporangium (site of meiosis) had completed protrusion, it was observed to undergo division into four tetrahedrally arranged tetraspores (Pl. 29, G-J; Pl. 30, E-H; Fig. 61, H-J). A single stalk cell was produced at the base of each sporangium (Pl. 31, D-H; Fig. 62, G) and the tetraspores were released from the sporangia, leaving the empty sporangial casings on the laminal surface (Pl. 30, I-K; Pl. 31, L-O; Fig. 62, N). In some cases, the four released spores began germination without separating (Pl. 29, K & L; Pl. 31, K; Fig. 61, K & L). In other instances, the spores began germination whilst still attached to the sporangia (Pl. 30, L-S; Pl. 31, I & J). Lack of water movement under experimental conditions may account for the *in situ* development observed, as the germination of tetraspores, attached to the sporangium or to one another, was not been observed in the field.

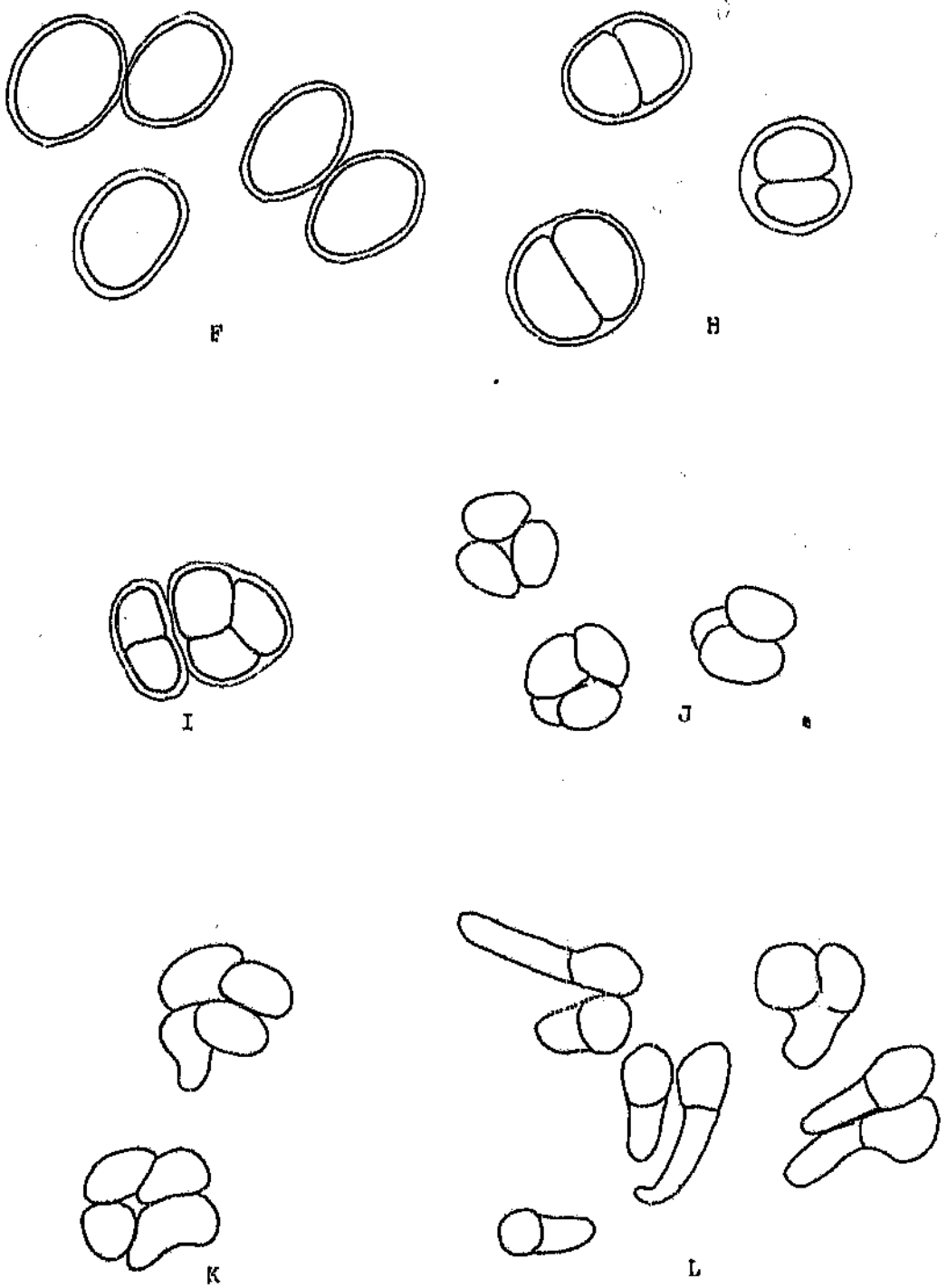


Figure 61: Early stages of spore development and germination in Dictyopteris longifolia (Redrawn from Pl. 29, F, H-L; Scale 1cm = 105μm).

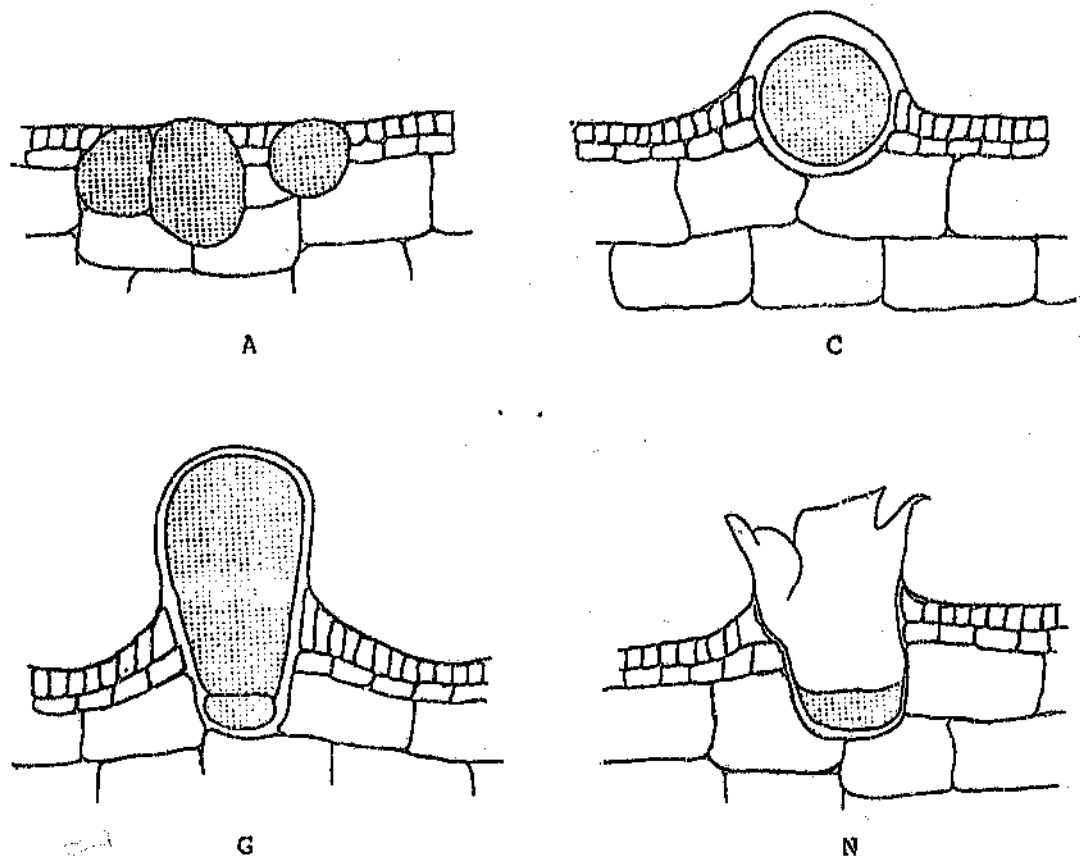


Figure 62: Detail of sections through different stages of tetraspore development in Dictyopteris longifolia (Redrawn from Plate 31, A, C, G & N; Scale 1cm = 110μm).

However this phenomenon may explain the clumped appearance observed in the field.

3.12.2 Morphogenesis

Morphogenesis of individual tetraspores was observed (Section 2.5.6) to begin with an initial elongation of one side of the spore (Pl. 32, D-F; Fig. 63, D-F), before

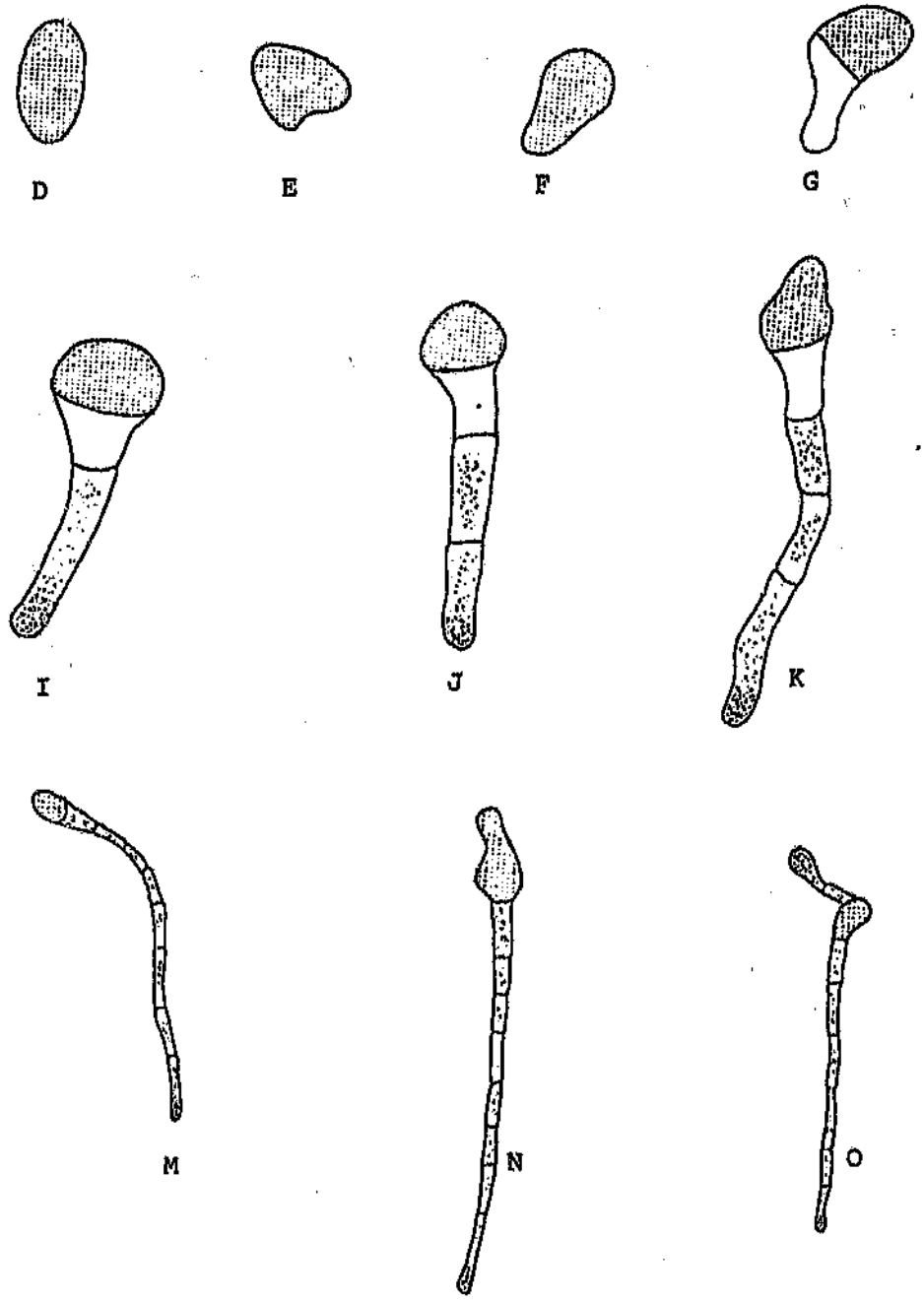


Figure 63: Detail of germinating spores in <u>Dictyopteris longifolia</u> (Redrawn from Pl. 32, D-G, I-K & M-O; Scale 1cm = 120μm).

the first division occurred and polarity was established (Pl. 32, G; Fig. 63, G). Protrusion of the wall at one end of the cell could clearly be seen when the cell was labelled with calcofluor before the onset of germination (Pl. 32, A). The areas of new wall development, ie the protruding end, were less heavily labelled after three days of growth due to the synthesis of new wall material in the region (Pl. 32, B & C). Once the first division had occurred, the spore was polarised into a rhizoidal and a thalloid pole. Growth continued with rapid elongation and division of cells in the rhizoid (Pl. 32, I-N; Fig. 63, G-N). In some spores, a second rhizoid was observed to develop prior to (Pl. 32, O-P; Fig. 63, O), or during (Pl. 33, A; Fig. 64, A) thallus development. Occasionally two well-developed rhizoids were observed with little thallus development having occurred (Pl. 33, B & C; Fig. 64, B). The developing thalli underwent cell division to become multicellular (Pl. 33, D & E) and eventually became well established with apical, meristematic cells (Pl. 33, F & H). Development of the sporeling continued until the lamina was large and well developed with an apical pit, a midrib and many basal rhizoids (Pl. 33, H-K; Fig. 64, J & K). None of the sporelings maintained in culture were observed to develop any further than a single lamina with rhizoids (Pl. 33, K).

Some peculiarities of sporeling development were observed, especially in the culture kept at 20°C (from day 9). Amongst these peculiarities were sporelings having short rhizoids but well developed thalli (Pl. 34, A), as well as those with strangely shaped thalli (Pl. 34, J & K). The most common aberrance was a highly branched, aseptate, "jigsaw puzzle" shaped rhizoid tip (Pl. 34, B-F & H & I; Fig. 70, C), which developed instead of the normal rounded, growing tip (Pl. 34, G).

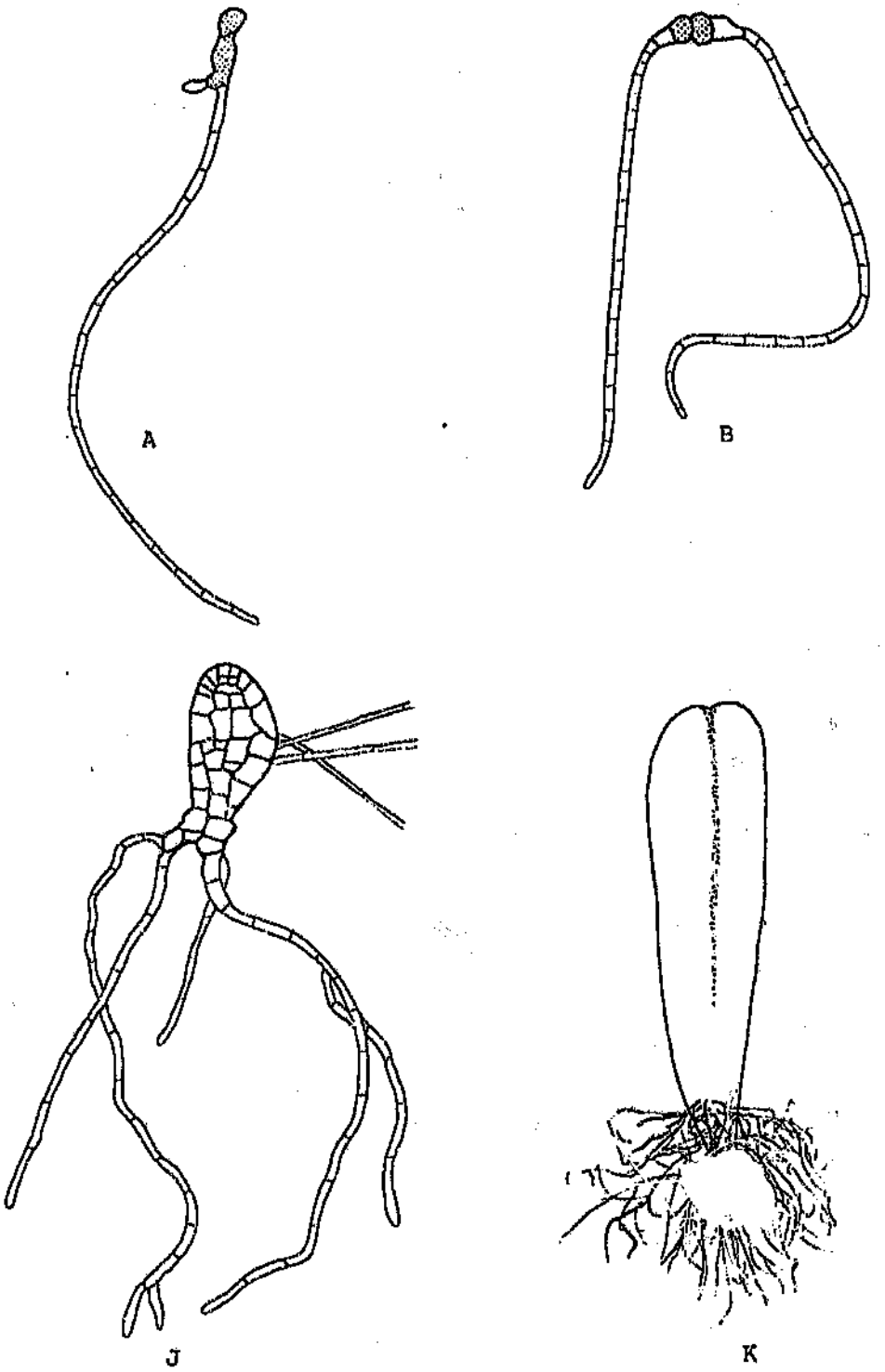


Figure 64: Detail of advanced stages of spore germination and sporeling development in Dictyopteris longifolia (Redrawn from Pl. 33, A, B, J & K; Scale 1cm = 180μm except for K where 1cm = 600μm).

This phenomenon was rare in cultures at temperatures other than 20°C (ie at 10°, 15°, 30° and 35°C).

3.12.3 Growth Rates under Different Temperatures.

Growth and development of tetraspores was observed to differ under different temperatures (10°C, 15°C, 20°C, 25°C, 30°C and 35°C were tested). The optimum temperature for the development of both the rhizoids and the thalli, was observed to be from 20°C to 25°C, at 70$\mu Em^{-2}s^{-1}$. Figures 65 and 66 are graphs of the mean growth rates of the thalli and rhizoids (respectively) of 30 individuals at each temperature The graphs show that there was an initial rapid elongation of the primary rhizoid (in particular in the 20°C and 25°C cultures) up until day 9. After this there was a decrease in the elongation rates under both treatments. Following the initial slight elongation (up to day 3), growth of the primary rhizoid stopped in all the other cultures (ie at 10°, 15°, 30° and 35°C). The thalli elongated at a much slower rate than the rhizoids, but the individuals at 20°C and 25°C still had the greatest growth. There was either very slight, or no growth at all, of the thalli at the other temperatures (ie at 10°, 15°, 30° and 35°C). There was no development of either rhizoids or thalli at 35°C.

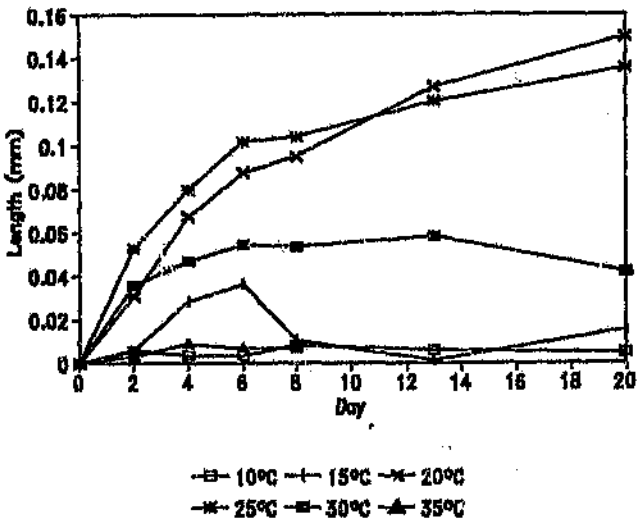


Figure 65: Sporeling thallus elongation rates with respect to temperature.

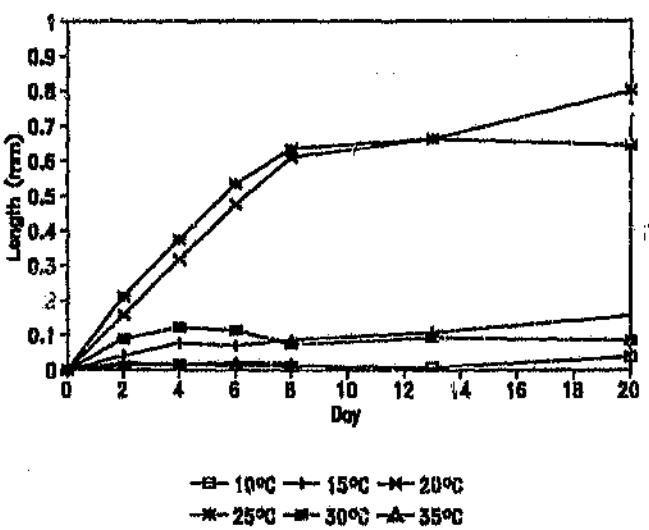


Figure 66: Sporeling rhizoid elongation rates with respect to temperature.

4 DISCUSSION

4.1 EXPERIMENTAL ORGANISM

4.1.1 External Morphology

The alga used in this study is commonly known as Dictyopteris longifolia and was observed to grow in a range of habitats from calm rock pools to highly wave exposed areas at Palm Beach, Natal. It is composed of a number of flat, strap-shaped laminae with up to 8 dichotomies per lamina (although many short laminae lacked dichotomies completely). The laminae are golden brown, becoming greenish when removed from the water and black when dried. D. longifolia laminae were observed to measure from a few centimetres to over 60cm in length, and 0.5-1.5cm in width (the width is similar for the entire length of the lamina). The plant is an erect tuft with the laminae attached to the substratum by means of a mat of entangled rhizoids (Pl. 4, A; Fig. 1) which are produced from the base of the lamina, "stipe" and holdfast region (Pl. 4, I-L). The rhizoids are multicellular, trichothallic and branched, with rounded tips (Pl. 4, E-H). The basal wing tissue was frequently observed to degenerate (particularly towards winter) leaving only the midriff. There is a prominent (0.5-1mm thick), unveined midriff, down the centre of the lamina. The midriff decreases in prominence near the apex (Pl. 5, C) of the lamina and becomes more cylindrical in the basal region, where the wings are abraded away and rhizoids are produced (Pl. 5, E & F; Figs 51 & 52). The apex of the lamina is rounded. However, during the latter part of the study period, a greater number of more acutely rounded tips, were observed. The latter shaped laminal tips were also observed on regenerated laminae in culture (Pl. 21, F). The temporal differences in

abundance of the different shaped apical tips, in some populations, could be due to a difference in response of the gametophyte and sporophyte to environmental conditions, although D. longifolia is reported to be isomorphic (as are all Dictyotales; Lobban & Wynne, 1981). There are, however, reports of temporal and spatial differences in gametophyte and sporophyte dominance in the Dictyotales (Fritsch, 1945; Phillips, 1988), and the possibility that there could be morphological differences in the response of the phases to environmental conditions, should not be ruled out. Katsaros and Galatis (1988) report that the meristoderm cells in the basal portions of the lamina of Dictyopteris membranacea develop outwards, either as rhizoids or as adventitious branches. Although these branches were not observed in D. longifolia, it is interesting to note that the apical tips of adventitious branches in D. membranacea appear to be more acute, whilst those of the rest of the plant are smoothly convex with the apical initials in a small depression. The possible reason for the difference in shape in this species, is reported to be a higher rate of asymmetrical divisions in the first stages of development, leading to an acutely shaped tip (Katsaros & Galatis, 1988). There is a pit containing the meristematic initials in the apex of the lamina of D. longifolia (Pl. 7, A-M; Fig. 50). The margins of the lamina are entire and the surface is smooth, except for the occasional tuft of colourless, trichothallic hairs (Pl. 16, A-P; Fig. 53).

The midrib of the lamina of D. longifolia is composed of approximately fourteen layers of cells covered by a single layer of epidermal cells (on both surfaces; Pl. 10, A-D). The wing is comprised of approximately five layers of cells in mature laminae (Pl. 9, H-I) and two in immature laminae (Pl. 9, G; covered by epidermis). The mature wings have marginal bulges composed of

approximately ten layers of cells with smaller cells in the exterior region of the bulge (Pl. 9, A-F; Fig. 52).

The antheridial sori are irregularly shaped, light coloured patches scattered over both surfaces of the wings of the laminae (Pl. 28, A-C). In cross section, the sori appear as raised regions (Pl. 28, H & I). The detailed structure of the antheridia was not, however, studied. The oogonia appeared as darkened, raised areas similar in appearance to the tetrasporangia. However, only very early stages of development were observed (Pl. 28, J-L).

The tetrasporangia were observed to occur in sori which appeared as small, dark spots scattered over both surfaces of the wing, but not on the midrib (Pl. 29, A-C). The sporangia covered a large percentage of the laminal surface. The approximate diameter of the mature tetrasporangium is 60μm. The sporangia are initially spherical in shape and become more ovoid when mature. There is a single, rectangular stalk cell at the base of the sporangium and this cell becomes flatter as the sporangium develops (Pl. 31, F). The surrounding epidermal cells extend up the sides of the sporangium and there appears to be a colourless cuticle covering the structure (Pl. 31, C).

4.1.2 Nomenclature

The identification and description of the species which is commonly referred to as Dictyopteris longifolia (Simons, 1976; Branch & Branch, 1981; Seagrief, 1984), has been under some debate. Isaac (1956) reports a species from the Mozambique Coast which resembles Haliseris dichotoma (Suhr) Kütz., as described by Kützing in Tabulae Phycologicae IX Tab 57(i). Levring changed the name Haliseris dichotoma (Suhr) Kütz. to Dictyopteris

dichotoma (Suhr) Levring in 1938. Material identified as Dictyopteris dichotoma (Suhr) Levring, was also reported to resemble the material collected from Mozambique (Isaac, 1956). Stephenson (1947) however, reported that Papenfuss was convinced that the material collected on the southern African coast was not Suhr's species D. dichotoma and was describing it as a new species to be known as Dictyopteris longifolia. Unfortunately, Professor Papenfuss died before formally publishing this name. The description was never completed and, although the species is commonly known as D. longifolia, it is in fact Dictyopteris longifolia Papenfuss (in ed.).

After examining material of D. ligulata (Suhr) O.C. Schmidt, Papenfuss suggested that this species was conspecific with his new species, D. longifolia. In 1963, Chihara (under Professor Papenfuss' supervision) initiated a comparison of D. ligulata and the potentially new species. Chihara (1963) appears to be convinced that the new species is not D. ligulata. Although the sporangial distribution of the two are similar, there are a number of other differences which led Chihara to believe that the material was indeed a new species which he suggested should be named Dictyopteris longifolia Papenfuss (et Chihara). He does, however, suggest that the material figured by Kützing was similar to the material being studied, except that the former had veinlets and the latter not. As only a single specimen of D. ligulata was obtained by Suhr, it has been suggested that the species is rare whereas D. longifolia, which was frequently collected, is a more common species.

The comparison of D. ligulata and the new material being described, clearly indicates that these are two different species. It is also clear from Chihara's notes (1963) that the material he described is similar to the material used in this study, and commonly known as D. longifolia.

Table 3: Comparison of D. ligulata (Suhr), the alga described by Chihara (both from Chihara's notes) and the alga used in this study.

D. ligulata	Chihara description	Alga from this study
laterally issued branches	dichotomously branched (1-5) on 1 plane	dichotomously branched (1-5, 8 rare) in 1 plane
sharply acute apex	obtuse or retuse apex	rounded or slightly acute apex
spindle shaped laminae	strap-shaped, tapering to base and briefly to tip	strap-shaped tapering to base and briefly to tip
unknown thallus structure	4-5 layers medullary cells surrounded by epidermis (mature)	4-6 layers wing cells surrounded by epidermis (mature)
tetrasporangia scattered over lamina	tetrasporangia scattered over lamina	tetrasporangia scattered over lamina
antheridial distribution unknown	antheridia in patches (microscopically)	antheridia in patches

There is still a possibility however, that the new species is similar to D. dichotoma (Suhr) Levring. Unfortunately samples of the latter species could not be obtained to compare it to the species in this study, however, Papenfuss seemed convinced that his new material was not D. dichotoma.

4.2 DISTRIBUTION

The map indicating the collection and observation points of Dictyopteris longifolia, which was compiled from literature studies, herbarium specimens, personal observation and personal communication (Fig. 9), indicates that the species appears to be restricted to intertidal regions in warmer waters. The distribution extends down the east coast of the subcontinent from Mozambique to Cape Agulhas. Although it has been determined that D. longifolia does not occur on the West coast, the extent of the distribution up the east coast has not been established. Chihara (1963) reported that Papenfuss collected specimens of the species from the coast of East Africa, however, the exact location was not specified. From the reports on the herbarium specimens and personal observation, it appears that the species is able to survive conditions varying from calm pools to wave exposed areas in the intertidal zone. Clayton (1981) reports that members of the Dictyotales are common in both hemispheres, in warmer temperate to tropical waters. This suggests that the order is ancient and was widespread before the splitting of the continents. Other species of Dictyopteris are reported in, amongst others, southern Australia (D. acrostichoides (J. Agardh) Boergesen and D. muelleri; Phillips, 1988), Japan (D. divaricata; Tokida et al., 1953), California (D. undulata Holmes; Benson, 1986) and Greece (D. membranacea; Katsaros & Galatis, 1988).

4.3 WATER MOVEMENT

The intertidal region is defined as the region regularly covered and uncovered by the tides (Dawes, 1981). Water movement is probably the single most important factor influencing adaptation to intertidal life. The movement

of water results in a number of different stresses which act on the intertidal organism. For example, the hydrodynamic force of the water, ie drag can be extremely strong and the intertidal organism has to be able to withstand this force to survive (Carrington, 1990). Charters et al. (1969) report that the forces experienced by intertidal plants (due to water) are greater than those experienced by terrestrial plants (due to wind). Despite the stresses that are experienced in the intertidal zone, the biota in this region is extremely diverse (Denny, 1988). Water motion also affects growth in plants by constantly renewing the supply of nutrients, allowing greater growth to occur (Neushul, 1972; Kain, 1977). Nutrient supply is increased by reduction of the thickness of the boundary layer due to increased water movement, and the resulting reduction in resistance to nutrient diffusion (Dring, 1982; Gerard & Mann, 1979). The reduction in boundary layer allows gaseous exchange potential to increase. Increased water movement also enables waste products to be removed, temperature to be kept constant by mixing, organisms to be kept clear of sediment (Neushul, 1972; Denny, 1988; Gerard & Mann, 1979) and competition and herbivory to be limited (Gerard & Mann, 1979). Water motion causes severe abrasion of laminae (by sand abrasion and whipping), makes establishment of new seaweeds difficult (Dring, 1982) and reduces the light penetration (due to increased turbidity and reflection off tne surface). There are many conflicting reports on the different effects of water motion on the growth of plants. Burrows (1955) and Norton et al. (1981) suggest that growth decreases with an increase in wave action, due to the decrease in light penetration (increase in reflection off turbulence). Gerard & Mann (1979) report an increase in the productivity of "Kombu" (Laminaria spp.) with an increase in water motion (due to increased nutrient and gas supply). However, the latter authors did report that the

growth of plants in extremely violent conditions, is inhibited. Plants in highly wave exposed areas have to make a compromise between the conflicting demands of increasing thallus surface area to receive enough sunlight, gas and nutrients, and being able to withstand the mechanical forces of drag (Jones, 1959; Charters et al., 1969; Gerard & Mann, 1979). Numerous seaweeds achieve this by being highly flexible, spreading out in the water to increase light reception during calm periods and clumping together to reduce drag on the holdfast, ie going in the direction of flow and becoming streamlined) during increased wave motion (Charters et al., 1969; Neushul, 1972; Carrington, 1990). It is obvious that there are many "trade-offs" in the structure and function of algae living in wave exposed areas. In Laminaria longicruris, for example, the laminae become narrow and thick to reduce drag, and thus experience a reduction in photosynthetic area and the area available for the production of reproductive structures (Gerard & Mann, 1979).

The degree of wave exposure is also reported to affect aspects of population dynamics such as the distribution of a species. For example, the abundance of the holdfasts of Turbinaria ornata (Turner) J. Agardh increases with an increase in water movement (Payri, 1984). Dring (1982) reports that the breaking waves experienced during storms cause a great deal of dislodgement in macroalgae and may be a significant source of mortality. The size and age structure of the population may thus differ considerably following periods of exceptionally high wave exposure (Carrington, 1990). Wave action affects the zonation of the shore by increasing the height at which growth can occur up the shore through increased splash and spray (Chapman & Chapman, 1973). The effect of wave exposure on a population is important in commercially utilised species, where some species increase in productivity in

exposed areas and others show a decrease (Druehl, 1981b). Water motion is obviously an important factor influencing the form and function of individuals and the dynamics of populations.

4.3.1 Wave Action

All the techniques that were used to measure water movement, wave strength and number in this study, indicate that the sites subjectively ranked as the highest wave action site (H+) and the slightly lower high wave action site (H), were correctly ranked in this order. The other sites were either not measured, could not be statistically analyzed or showed no difference in wave strength due to the lack of waves at low tide (eg the Lifesaver technique). Although Dring (1982) reports that dynamometer readings correlate well with subjective ranking, Palumbi (1984) points out that the measurement of wave strength using the dynamometer has a possible flaw in that the strength of the strongest wave in the observation period is measured. This might be of unusual strength and thus would give an unreasonably high measurement of wave action for an area. The drogue of the dynamometer also has a slow response time and has to travel 180^{o} from the backwash of one, to the forward flow of the next wave (Denny, 1988). There is also the possibility that there may be some effect from the attachment structure, and the drag coefficient of the drogue is not taken into account.

4.3.2 Water Motion

The technique which involves the use of attached plaster blocks (Munnik, 1987), is believed to be the most useful of the methods used in this study. Unfortunately it was not repeated, and could thus not be statistically tested, as in some of the sites only a single block was recovered

after a period of about 12 hours exposure to water motion. The problem with this method, as discussed in the results section (Section 3.3.2) is that, in order to get a true representation of the differences in water motion between the different sites, the blocks need to be put out in one low tide and retrieved at a high tide (ie over a full tidal cycle). In some of the more wave exposed sites this would be highly dangerous. There is the added problem that the blocks are worn down by abrasion (due to sand and the laminae of other plants) as well as water movement, thus a reduction in weight is not solely a measurement of water movement.

The graph of the weight loss from the plaster blocks (Fig. 13) indicates that the highest wave action site (H+) and the slightly lower high wave action site (H) had the highest degree of weight loss (68.94 (±0)% and 61.87 (±11.04)%, respectively). The lowest wave action site (L1) had however, a similar degree of weight loss (58.09 (±6.20)%). One of the blocks in the latter site did appear to have lost a large chip of plaster, which may have fallen out due to a fault in the structure of the block and would have caused a misleadingly high percentage weight loss. The one intermediate site (I) had the lowest degree of weight loss (22.49 (±0)%). This site experienced intermittent, heavy sand inundation, but was fairly sand free when the blocks were laid. However, when the blocks were retrieved, the site was inundated and the blocks were buried which would have caused a decrease in weight loss due to the lack of water movement over the block. The plants in this site did not become abraded as early as the plants in the other sites (Fig. 17). The lack of degeneration could have been due to the periodic inundation which reduced sand abrasion of the laminae and decreased the effects of desiccation and wave exposure. The burial and subsequent lack of water movement over the blocks is thought to have been the

cause of the low degree of weight loss. The other sites (L2, L+ and I+) all appear to have had an intermediate and similar degree of weight loss (42.44 (±3.82)%, 46.14 (±11.66)% and 46.47 (±14.41)%, respectively), indicating a similar and lower (than H and H+) degree of water movement over the blocks. The high, intermediate wave exposure site (I+) showed a surprisingly low degree of weight loss. This is believed to be due to the pool being much deeper than the other sites. It was also backed by deep sea (Fig. 3, C), and thus the sand content of the water was very low (Section 3.4), leading to a low loss in mass due to sand abrasion.

The PCA (Fig. 14) shows that the plaster block method is not correlated with the rest of the wave action measurement techniques. This is thought to be due to the fact that the former method measured water motion over a tidal cycle and the other three methods did not, ie the plaster blocks measured wave exposure over high and low tides, whilst the other methods only measured over the low tide.

The structure and size of the block is believed to be important, as the shape of the block may affect the degree and speed of weight loss by affecting the turbulence around the blocks; and the plaster consistency is believed to affect the ability to dissolve. If this technique was to be used for further studies, a control study would have to be performed to determine the effect of shape (and other factors) on weight loss. The effect of temperate on dissolution rate has been reported by a number of researchers (Muus, 1968; Gerard & Mann, 1979; Denny, 1988). A calibration would thus have to be performed to allow future studies to use this method in different seasons, (ie different temperatures).

From the methods (excluding the plaster block method), that were used, it would appear that the H+ site, does indeed have the highest degree of wave exposure, with the H site having the second highest degree. The correct wave exposure ranking of all the sites used in this study cannot be quantified because the measurements (except the plaster blocks) could not be taken when all the sites were experiencing wave exposure. It must also be remembered that the dissolution methods were measuring abrasion as well as water movement.

The study and measurement of wave exposure and strength has been performed using a number of methods, each differing in the aspect of wave action that is measured (Norton et al., 1981; Dring, 1982). It is thus difficult to compare similar studies, ie ecological studies, which are based on wave exposure but which measure it in different ways. Despite the large variety of methods which have been suggested in various intertidal studies, it is difficult to find a method which measures an aspect of wave exposure correctly, is cheap and easy to construct, can be left unattended on the shore and is suitable for a small scale study such as that described in this thesis (Lobban et al., 1985). Some of the numerous methods of wave exposure measurement are discussed below.

Subjective expression of the degree of exposure is the most common method of dividing the coast into different regions (Cousens, 1985; Cheshire & Hallam, 1988). It is, however, a highly unreliable method which varies considerably with the observer, tide and weather (Lewis, 1964; Field, 1968; Norton et al., 1981), although there are reports of other methods correlating closely with the subjective method (Dring, 1982). It is impossible to compare different areas which have been subjectively ranked by different people (Dring, 1982). However, the

majority of studies continue to use subjective ranking as a basis for ecological comparisons.

Lewis (1964) suggests a biological exposure scale because no single method can measure all the different aspects of wave action at once (Dring, 1982). This uses the presence or absence of certain species, eg Fucus distichus (L.) Emend. Powell and Alaria in areas of extreme exposure, and long Ascophyllum plants in areas of shelter; as well as the extent or width of the zones and their position relative to the tidal levels. This method can be refined by the addition of numerical abundances of different species. Features of a single species may also be used, eg width of the laminae of Laminaria longipes Bory (Palmisano & Sheng, 1977). The problem with this method is that wave exposure may not be the only factor which affects species distribution, eg differences in slope and shading may also influence it. Other problems include the possibility that a species may be more tolerant at the limits of its distribution, the scale can only be used in the range inhabited by the species used for that particular scale, the results may differ according to growing season and the number of levels of exposure may differ with observer (Dring, 1982). Dring (1982) suggests the use of the entire biological character of the shore to determine the degree of exposure. He lists five degrees of exposure and the relevant species composition for each, for the British coastline. The advantage of a biological method is that all the different aspects of exposure are included, ie impact of the waves, drag caused by the waves, wetting effects of the spray, sediment and loose sand transport, and nutrient availability (Lobban et al., 1985). Other biological exposure indices include the structural wave exposure scale which uses features such as the tenacity of a limpet, or the strength or rate of coral breakage (both of which increase with an increase in exposure).

Disadvantages of using features such as these, include the fact that moving limpets are less strongly attached and damaged coral is more easily broken. There is the added problem that the species used for the index may not be found in all the sites (Denny, 1988).

Exposure indices are also used by different researchers. Baardseth (1970; in Lobban et al., 1985) and Dring (1982) use the number of 9^{o} compass sectors of unimpeded fetch, at a distance of at least 7.5 km from the shore. This method shows a reasonable correlation with the dynamometer (Dring, 1982). Dring (1982) reports the formation an exposure index using the percentage of days on which the wind blows directly onto the shore. This method relies on the relation of wave action to fetch and does not take other factors involved in the modification or generation of waves, into account. McEachreon and Thomas (1987) developed an exposure index which used the local weather data and included it into the formula suggested by Thomas (1986) with the final product being:

$$\text{Exposure index} = \log 10 \Sigma W[1+\log 10(F/[CS+.1FS]$$

(McEachreon & Thomas, 1987)

W = wind energy
F = fetch (km) over open water
CS = close shore distance or extent of proximal water (km) less than 6m deep, and within the sector
FS = far shore water or extent of water (km) less than 6m deep and within the sector, but separated from the shore by points greater than 6m deep

The main disadvantage of this method is that both the measurements and the calculations are difficult to obtain. Weather data and hydrographic charts are needed for each site, and if the sites are close together (such

as in this study), these factors would not differ to a great degree. The advantages are that it includes wind velocity, arc of exposure for the shore, and the distribution of shallow water both near and off shore. The method could be improved by adding the slope of the shore to the formula.

The relative wave action of an area, as water motion or net flow, has been measured in a number of ways. These methods use the relative rates of dissolution of moulded objects to determine differences in water motion (Dring, 1982). The objects are weighed before and after exposure. Plaster of paris balls were used by Gerard and Mann (1979; Munnik, 1987) and "clod cards" made of the same substance were used by Doty (1971). Concrete blocks were used in a similar test performed by Craik (1980; in Lobban et al., 1985). Martell (1989, pers. comm.) suggests the use of boiled sweets known as "Lifesavers". Druehl (1981b) uses cylinders because "clod cards" and balls cause turbulence which lead to biased erosion. When the diameter loss of the mid-section of a cylinder is measured, the dissolution measured is due to laminar flow alone. Gerard and Mann (1979) added latex to the plaster of paris to decrease the dissolution rate and to thus extend the period of use of the structure, thus allowing it to be used in long-term studies. These researchers report no correlation with wave exposure when the latex was added but, in the structures lacking the latex there was an increase in dissolution rate with an increase in water movement. The variability however, was great. Martell (pers. comm.) showed an increase in the dissolution rate of Lifesaver sweets with increased velocity in a calibrated water flume. A problem with the dissolution methods is that the rate of dissolution differs disproportionately with a difference in temperature. This means that care must be taken to ensure that the temperature of calibration is similar to the

temperature most frequently experienced in the field. Another disadvantage is that dissolution is not only due to the effects of wave action, but also the effects of abrasion due to suspended solids and neighbouring plants (Koehl & Wainwright, 1981). Similar plaster devices have been used to measure the abrasion caused by kelp plants which sweep the substratum (Koehl & Wainwright, 1981).

Dawes (1981) uses a method following that of Jones and Demetropoulos (1968), which involves the construction of a mechanical dynamometer consisting of a spring, gauge, and drogue. The latter part of the construction may be a fishing float (Palumbi, 1984), wooden disc (Druehl, 1981a) or a toilet float (this study). Although this method may give varying results, it is used in the commercial Kombu farms in Japan (Druehl, 1981b). The waves place a drag on the drogue and this force is transferred to the gauge. The strength of the individual waves (impact), as kg per cm^2 (cross-sectional area of the drogue), in the tidal and subtidal areas can be measured. The dynamometer is reported to correlate well with the results of the subjective ranking, eg forces of 2-20N have been measured (Dring, 1982, Palumbi, 1984). Palumbi (1984) uses a similar structure which is smaller, inexpensive and can easily be transported. The structure consists of a drogue (fishing float) which is attached to a cable tie and elastics. The wave causes the cable tie head to move along the tie until the force of the stretched elastics is equal to the strength of the wave (Fig. 4). The force is measured with a spring balance and equals the maximum wave strength (over the cross-sectional area of the drogue) that the device has experienced in the allotted time period. The disadvantages of this method are that measurements cannot be made in areas where the water movement is very slight, and the current and the backwash are also measured. The longer that the device remains in the water, the more the

chance of it experiencing an unusually large wave and thus having an misleadingly high reading. Different size drogues and elastics may be used in different wave action areas, however, inter-site measurements should be made with the same equipment to reduce variation due to differences in the drag coefficient. Both dynamometer methods experience the disadvantages that the structures are only accessible at low tide in high wave exposure areas, and respond slowly. The latter problem depends on the length of the string attached to the drogue. If the string is long then it only becomes fully stretched once the wave has passed, whilst a short string would be stretched out rapidly. The drogue and string have to swing through 180^{0} from the direction of flow of the wave, to that of the backwash (Denny, 1988). There are also the problems of the drag coefficient and wake which are not considered (Vogel, 1981).

Charters et al. (1969) developed a method to measure current velocity called a "fish-pole tensimeter" which consists of a spring, scale and pointer attached to the end of an aluminium pole which has a double roller at the tip. A hollow plastic ball filled with seawater (to give it a neutral buoyancy) is attached to the pointer and spring with a line. The rod is erected perpendicular to the main direction of surge on a frame attached to the substratum. The ball is dragged back and forth by the waves and backwash, and the strength of the movement is measured off the scale. The readings are calibrated by taking the readings off the scale under known loads, and determining the drag force of the ball. The disadvantages of this method are that there is friction of the tip roller, there are differences of calibration at the maximum and minimum extension of the spring, the sphere causes drag which should be taken into account, and the construction is cumbersome and difficult to move. The structure also measures backwash and current. Current

movement can also be measured using the "Lagrangian method" which involves a drogue or marked orange (has a neutral density). This measures the course of water movement over time by recording the movement of the floating object. It is useful when measuring the movement of drift material, but has the disadvantage of being useless when there is turbulent wave action (Koehl & Wainwright, 1985).

Other methods of measuring aspects of wave exposure are less commonly used. These include measurements of surge intensity, which was determined by an observer floating at a specific point and observing the maximum lateral displacement caused by single swell in a 1 minute period. This measurement was found to correlate well with wind speed (Foster, 1987). Some researchers even use the percentage of experimental equipment that is lost during the period of the experiment, as a measure of the relative differences in wave exposure between different sites (Palumbi, 1984)! Another method is to count the number of waves which break over a site in a certain time period. This is also unreliable as it does not give an indication of the relative strength of the waves and cannot be used high up the shore at low tide. The position of the tide when the waves are counted, also affects the measurement. Koehl & Wainwright (1985) report the use of the deflection of a tethered sphere which was attached over a large plastic protractor. The problem with this is that the turbulence around the ball causes it to sink and move around, thus decreasing the accuracy of measurements.

The various methods which are described above, are all fairly simple, inexpensive methods. There are however, a number of mechanical devices which have been used to determine differences in wave action and water motion. These are more accurate but also prohibitively expensive

for a small scale study. Druehl and Green (1970; in Lobban et al., 1985) suggest a "surf sensor" which is attached to a strip chart. The number of times that the area is wetted, is recorded and the device functions on the basis of electrical conductivity. This is therefore a measurement of wave number and gives no indication of wave strength or direction. An electromagnetic flowmeter was used by Koehl and Wainwright (1977) to measure the water velocity in kelp beds. The advantages of this method are that the response is very fast, there are no moving parts to go wrong and any movement of water in a horizontal direction is measured by the device (Koehl & Wainwright, 1981). The major problems with this method are the high price of the equipment and the fact that it cannot be left unattended at the study site. Denny (1982; in Palumbi, 1984), uses an intertidal wave telemetry system to continuously monitor the waves using radio transmission. Denny (1983) then went on to develop a mechanical version of this device that measures the maximum wave force and direction over a tidal cycle. The disadvantage of this is that the sites require substantial preparation and thus is it is not appropriate for measuring a number of sites at the same time. However, the method does measure the direction of the waves, which is a factor lacking in other methods.

A "turbulometer" was designed by Field (1968) and gives the average reading of the amount of water that flows over a surface during the period of measurement. The method can be used to compare different sites. The device is a "Savonious-type current meter" composed of a rotor which is turned by the water movement, and is attached to a counter which reads the number of rotations. The device is however, subject to fouling and has a slow reaction time. The total water movement is not really a useful measurement. A more useful measurement can be obtained when the rate of flow is at its strongest, ie at the time

when the waves are having their greatest effect on the organisms. For this reason, Field (1968) took the mean of the highest 10 readings in a 5 minute interval. The readings had to be repeated at the other sites in as short a time as possible to cut down on variation due to differences in the tide or weather. The problem with this is that to compare the measurements of different sites at a particular time may not give typical results for those sites and it would thus be better to leave the device to record over an entire cycle. This method is also expensive. Pressure-sensing devices can also be used. These determine orbital velocities of the water using data of wave height and period. They may be obtained commercially but the disadvantage is the high price of the equipment (Koehl & Wainwright, 1985). Another instrument that may be used is the "wave rider" which is a buoy attached to a mooring. This floats on the surface and sends a radio signal to a station on the shore. It is also a prohibitively expensive piece of equipment (Koehl & Wainwright, 1985). The vector-measuring current meter is commercially available and expensive piece of equipment. It measures only the current water motion and filters out the motion due to wave action (Koehl & Wainwright, 1985). The "Eulerian" method measures the net movement past a stationary point using an electromagnetic flow meter or a propeller device. This is applicable to the movement of water past a plant, but the equipment is expensive (Koehl & Wainwright, 1985).

There are thus many methods of measuring water movement, all of which have both advantages and disadvantages. A researcher must take care, when choosing a method, that the necessary information is available or easily obtainable. A important factor that must be considered is which aspect of water movement is required, ie general water movement, strength of individual waves or back wash, movement due to currents or the tides.

4.4 SAND CONTENT

The sand and particulate matter content of the water is another important feature of the intertidal environment, which affects organisms in the zone considerably. It not only causes abrasion and regulates the epiphyte and sessile herbivore populations, but also alters the amount of light reaching the plants (Neushul, 1972; Denny, 1988).

It was initially presumed that the sand and particulate matter content of the water would be correlated with the degree of water motion experienced, however, from a PCA (Fig. 14) of the different water motion measurements and the features of sand that were measured, it appears that there is no correlation between these two factors. The results displayed in Figure 15 can be explained by the position of the sites and the condition of the surrounding areas. The highest wave action site (H+; 0.101 (±0.044) g/100ml) and the intermediate gully (I; 0.088 (±0.033) g/100ml) had the highest sand and particulate matter content. The former is composed of a rocky reef backed on the seaward side by a shallow sandy basin (Pl. 3, A). At low tide (when the samples were taken) the waves were breaking over the basin or on the back of the reef. The sand from the basin was thus put into suspension in the breakers, and thrown over the site. The latter site (I) is composed of a sandy gully bordered by steep rocky sides and running perpendicular to the breakers (Pl. 3, B). Incoming waves wash over a fairly wide stretch of sand before entering the gully. The water entering the gully became turbulent and not only brought sand from the beach behind the gully, but also from the bottom as it washed through. The higher intermediate wave exposure site (I+; 0.044 (±0.004) g/100ml) and the lower of the two high wave action sites (H; 0.047 (±0.029) g/100ml), had the

lowest sand content. These results can also be explained by the position of the sites. The first of the two (I+) is a high pool, backed on the seaward side by very deep water (Pl. 3, C). Waves breaking over the seaward wall of the pool did not contain a great deal of sand and the pool was rarely observed to become inundated by sand. The H site, is a shallow site but it is backed on the seaward side by a large rock outcrop (Pl. 3, B). The waves break fairly far back and then wash over a large area before reaching the site, thus most of the suspended sand is deposited before reaching the study site. The remaining three sites (L1; 0.057 (±0.022) g/100ml, L2; 0.062 (±0.003) g/100ml and L+; 0.072 (±0.006) g/100ml) are the lowest wave exposure sites and have a similar but slightly higher sand content than the latter two sites (I+ and H). The low wave exposure sites are all fairly large and undisturbed pools. They are far back on the shore and raised above the beach (Pl. 3, G-E). The slightly higher measurements may be due to the fact that waves breaking into the pools at high tide wash over a large stretch of sand and thus contain large quantities of suspended sand. This may take a long time to settle (through fairly deep water) and would thus explain the high levels of sand in the water. An alternative reason may be that no distinction was made between sand and other particulate matter. In these calm pools, there was regularly a high degree of organic debris in suspension. Although this organic matter would not cause as much abrasion as sand, it would still cause some degree of abrasion and would affect light penetration. It must be noted that water samples were not taken from all the sites on all the trips. On some occasions, the water in all the sites was more turbid than at other times. There would thus be a bias against those sites not measured during extremely turbid periods.

Intertidal species which experience high degrees of sand scouring must have some strengthening tissue to withstand sand abrasion. Flimsy species living in sand scoured areas would regularly be destroyed. An abrasion study involving various intertidal algae from Palm Beach, indicated that D. longifolia was abraded less than other species (Savage, in prep.). Tough species which are able to withstand scouring provide epiphytic algae with hosts which remain attached (Oates, 1989). D. longifolia at Palm Beach was observed to act as a host for a number of epiphytic red and brown algal species (Section 3.9.8.3).

4.5 SAND DEPOSITION

The effects of sand burial on intertidal organisms has been investigated by a number of researchers (Littler et al., 1983; Williams et al., 1985). Inundation by sand affects the degree of abrasion, the degree of competition, the amount of light, the gemination of spores, the amount of gas and nutrients, the temperature of the microenvironments (Foote & Kadlec, 1988) and the epiphytic and herbivore composition experienced by an intertidal organism (Mathieson, 1982a; Littler et al., 1983; D'Antonio, 1986). There are various reports on the seasonality of sand deposition with Littler et al. (1983) reporting an increase in sand deposition during winter due to increased wave activity, and Mathieson (1982a) reporting a decrease due to winter storms (washes sand away). There are other studies that report seasonal fluctuations in the level of sedimentation, due to the seasonal changes in water movement (Littler et al., 1983; Williams et al., 1985).

The movement of sand into, and out of, the study areas at Palm Beach was observed to be considerable (Pl. 6, A-L). It appears that the degree of sand inundation at Palm

Beach varies over a short period of time (from one tide to the next a site can become completely inundated), although there may also be seasonal variation as well (this was not investigated in this study). Sites very close to each other can experience differing degrees of sand inundation, and the amount of sand in the area completely changes the depth, nature and shape of pools. An example of this was the intermediate site (I) which was very close geographically to the low wave exposure site (L2), however, the former site was regularly heavily inundated with sand while the latter rarely filled up. Due to the considerable differences in the degree of sand inundation (especially in the intermediate gully (I)) observed over the initial part of the study period, it was decided to include some measurement of the sand deposition in the study. The technique used in this study was potentially useful, however, when the bricks were put into place numerous problems were encountered. Firstly, the bricks were extremely heavy and unmanageable and the sites were relatively far apart and inaccessible. This, and the number of bricks lost, made repetition of the experiment impractical. A number of the bricks were washed away completely (four out of seven bricks were lost on the first or second attempt), moved a considerably distance from the original site or irretrievably buried beneath a large amount of sand. Unfortunately, the number of measurements obtained from some of the sites prohibited an extensive statistical analysis of the results however, Figure 16 shows the mean mass of sand captured for each of those sites in which the traps were retrieved. It does appear that the low wave action site (L1) has the lowest amount of sand deposition (300.88 (±10.859)g, while the intermediate gully site (I; 347.03 (±8.869)g and the highest wave action site (H+; 354.66 (±22.84)g) had the highest amount of sand deposition. These results correlate with the results obtained in the sand content study,

suggesting that the brick method did work in those sites where the bricks were retrieved. However, there are several improvements which could be made to make the method more successful. Firstly, the blocks could be attached to the substratum in some way, heavier blocks could be used or permanent cement traps could be installed. The effects of the pipes and any eddy movements caused by them, on sand deposition, would also have to be investigated. The measurements in this study needed to be repeated in each site over a number of tides, as there was considerable variation in sand deposition from day to day. Another possible solution would be to use a method suggested by Daly and Mathieson (1977) which entails measuring the fluctuations of the substratum height between two known points.

Clayton (pers. comm.) reports that many of the Dictyotales found in southern Australia, appear to prefer areas of high sand deposition and scour. The reason for this is not known however, from the observations made in the sandy, intermediate gully (I) in this study, D. longifolia also appears to thrive and was far healthier when frequently inundated with sand. This may be due to protection from herbivores, sand scouring, sun bleaching or wave damage provided by complete sand cover. Intertidal organisms which are subject to severe sand abrasion and frequent burial, are reported to have powerful recovery and regeneration abilities (Daly & Mathieson, 1977). There are reports that the brown alga Phaeostrophion irregulare is only found in areas of high sand fluctuations and may be covered for periods of four to six months. This plant grows and reproduces when the sand subsides (Mathieson, 1982a). Spores of the species remain viable for long periods of time. The respiration rate of P. irregulare, when inundated, is reported to be very low, and thus the photosynthetic surplus allows survival of the individual (Mathieson, 1982b). However,

not all species of algae thrive when inundated. In a study performed on the green alga Caulerpa, it was found that daily burial resulted in a reduction in elongation and growth and an increase in plant death and decomposition (Williams et al., 1985). Increased sedimentation is also said to reduce plant growth rates and the density of plants in some species.

Sand inundation is obviously a very important feature of intertidal life and something that should be studied further with reference to the degree of epiphytism, herbivory and abrasion displayed. It would be interesting to determine if the most violent storms and periods of wave action correlate with the major decrease in laminal length that was measured in plants from most of the sites. This would indicate a seasonal increase in degradation rather than a change in rate of regeneration (Santelices, 1977).

4.6 MEAN MAXIMUM LAMINAL LENGTH OF THE POPULATION

The graphs displayed in Figure 17 indicate that the mean size of the plants in a single population, fluctuates seasonally. There are reports that the chance of death due to removal is increased in areas of high wave exposure (Santelices et al., 1981), and this may lead to variation in mean population size during seasonal increases in wave exposure. An attempt to tag individual plants with cable ties, as described for Laminaria (Klinger & DeWreede, 1988), failed and was thought to increase the chances of removal by waves by obstructing the natural movement of the plants. Armstrong (1987) also reports that there are more surface flaws on Hedophyllum sessile (C. Agardh) Setchell. laminae from high wave exposure areas and that this results in large lamina removal due to stress concentration, especially during

periods of particularly high wave exposure. The removal of large laminae, under extreme wave exposure would reduce the drag and stop the entire plant from being dislodged. This may be the reason for the removal of laminae from D. longifolia plants in the high wave activity sites (H+ and H). As far as possible, individual plants of D. longifolia were remeasured for this study, over the time period however, some were lost during the year. The holdfasts of D. longifolia appear to be perennial with annual foliage, although Benson (1986) reports that the holdfasts of Dictyopteris undulata are frequently detached and are thus considered to be annual. The length of the longest laminae of mapped individuals of D. longifolia were measured to give the mean maximum population size. A similar study was performed by Benson (1986) on D. undulata, in which the mean maximum height of the population was determined by measuring the maximum length of individuals. This author reported that the mean maximum length was affected by depth. It was not ascertained however, whether depth had an effect on D. longifolia, eg I+ was distinguished from the other sites in that it was a fairly deep pool. The laminae of D. longifolia in this study reached a maximum size in approximately March and then underwent a sharp decrease during the early winter months. The decrease was due to abrasion and herbivorous effects on the long laminae. It could also have been caused by an increase in mortality due to storms, as the removal of large individuals during a storm would severely affect the size distribution of the population (Carrington, 1990). Longer laminae are also thrashed against the rocks more during storms than short plants, and are therefore abraded more (Dring, 1982). Kilar and Hanisak (1989) report that different patterns in development and senescence cause seasonal changes in the ratios of laminal measurements. The mean laminal length of D. longifolia in this study appeared to remain constant over the winter months and it is believed

that this is due to the lack of growth or further abrasion of the already established small laminae over this period. After September, when warmer conditions were being experienced, the new and regenerated laminae developing from the holdfast, were observed to resume elongation and growth. It must be noted that the study only started in March and that the mean size decreased from this measurement. The mid-summer measurements, may thus have been higher than the March measurements. Unfortunately, without the timing and size of the highest measurements, a prediction of the growth rates from September cannot be made. The results are displayed in I of Figure 17 show the mean size of the population of plants found in the sandy, intermediate wave action gully (I). This graph appears to have a reverse curve to those results from the other sites. Measurements in this site only began in April and from here there was an increase in size until September when the plants began to die back and decrease in length. It is believed that the plants in this site were protected from abrasion and herbivory by being totally inundated by sand for long periods of time. The protection of plants by total sand cover was also reported for Phaeostrophion irregulare (Mathieson, 1982b). The plants in I also appeared to be relatively free of epiphytic organisms. Possibly the decrease in size from September was due to natural senescence of old laminae, or due to a prolonged period of a low degree of sand inundation, and the subsequent abrasion of the laminae. There were numerous new laminae growing from the base of the holdfasts of individuals in the intermediate site (I), at the same time as growth was observed in the plants from the other sites. It is surprising that plants frequently inundated to such a degree can survive, never mind flourish.

It appears from the various studies reported, that seasonality is particularly common in large brown

seaweeds (Duggins & Dethier, 1985; Druehl & Wheeler, 1986). These authors report that Hedophyllum plants reach a peak size in summer and are then reduced to tatters in winter due to the winter storms. There are similar reports of seasonal degeneration in Laminaria longipes (Palmisano & Sheng, 1977). It has also been reported that there is a seasonal change in the length of the laminae of members of the Dictyotales and other brown algae, with the long laminae being abraded back (Norton et al., 1981; King & Farrant, 1987). These authors report that the length of members of Dictyopteris acrostichoides from Australia varies seasonally and new growth occurs in Autumn when the water is the warmest. A similar report of seasonal growth and die back has been reported for another member of the Dictyotales, Glossophora kunthii (C. Agardh) J. Agardh (Malbràn & Hoffmann, 1990). Seasonal changes in the mean size of Laminaria populations have been correlated with seasonal changes in the chemical composition of seawater (Black & Dewar, 1949). This seasonal differentiation in length indicates the danger of measuring a parameter such as this at a single time of year, eg if the lengths of individuals of D. longifolia populations were measured only once during the study period, highly conflicting conclusions would have been drawn. There are reports that the growth rates of Ascophyllum nodosum are greatest in intermediate wave exposure areas (Cousens, 1982; Cheshire & Hallam, 1988) and Durvillaea potatorum is reported to have a maximum internodal length at intermediate wave exposure, possibly due to the gradients of factors which influence growth reaching an overall optimum in the intermediate areas, ie no extreme conditions present (Cheshire & Hallam, 1988). D. longifolia individuals in the intermediate wave exposure site (I) are longest at certain times of the year however, a study involving another season would have to be completed to determine whether this pattern occurs regularly.

4.7 MORPHOMETRY

Marine macroalgae have frequently been reported to display variation in morphology with variation in environmental conditions (Lobban & Wynne, 1981; Dring, 1982). Cheshire and Hallam (1988) report that there is a correlation between the differences in morphology and water motion because wave exposure affects the physiology, phenotypic expression and genotypic differentiation of populations of the same species, living under different environmental conditions. The studies which have been performed on this subject include aspects of the holdfast (de Paula, 1982; in Cheshire & Hallam, 1988), lamina (McEacheron & Thomas, 1987) and stipe (Chapman, 1973). The size of a plant is dependant (amongst other factors) on nutrient availability and is thus affected by wave action. The latter determines the nutrient supply due to mixing (Denny, 1988). Although the differences in morphology are usually related to differences in wave activity, they may also be affected by changes in light penetration and temperature (which are, in turn, also affected by wave motion; Gerard & Mann, 1979). Many algae adopt a crustose alternate phase to withstand sand scour and wave exposure, whilst others (such as D. longifolia) become thick and leathery with thick cell walls and can thus grow to a large size (Littler et al., 1983). There are reports that changes in morphological features such as length, width of the laminae and length of the stipe cavity occur in association with changes in environmental features, and that this causes taxonomic problems (Mann, 1971). The morphometric study included in this thesis involved a comparison of morphological features of D. longifolia plants from different wave exposure sites. It must be noted, however, that not all the measurements were performed in all the sites throughout the year, and thus

mean values include plants at different stages of development. This may have led to misleading results.

4.7.1 Features of the Holdfast

An increase in wave exposure places a greater stress on the holdfasts of intertidal algae which have to remain in place to allow the plant to complete its life cycle. There are reports of a greater biomass, abundance and density of holdfasts in higher wave action areas (Payri, 1984). In the case of flexible plants, the laminae spread out to reduce the stress on the holdfast in calm water, and then clump together and surge in one direction to reduce drag when experiencing the force of wave action (Cheshire & Hallam, 1988). This results in the holdfast experiencing a sudden jerk in one direction. Different aspects of the morphology of the holdfast of D. longifolia were measured.

4.7.1.1 Diameter of Holdfast

It has been reported that the holdfasts of Sargassum cymosum increase in size with an increase in wave exposure (de Paula & de Oliveira, 1982). Denny (1988) also discusses the necessity for increased adhesion and the resulting increase in holdfast size of plants growing in highly wave exposed areas. It has also been reported that the diameter of the holdfast increases with an increase in wave action.

The results from the present study largely support the reports that there is an increase in holdfast size with an increase in wave exposure. The lowest wave exposure sites (L1, L2 and L+; 15.8 (±4.42)mm, 15.7 (±2.8)mm and 12.95 (±2.75)mm, respectively) have the smallest holdfast diameter and the highest wave exposure sites (H and H+; 23.23 (±5.29m) and 21.85 (±7.77)mm) have the

largest holdfasts (Fig. 18). It would be expected (based on the subjective site ranking) that H+ would have the largest mean holdfast diameter due to the higher wave exposure, however, the slightly lower wave exposure site (H) has a significantly ($p<0.001$) larger mean holdfast diameter. This could be due to the large number of juvenile plants that were observed in the H+ site (particularly at the end of the study period). The larger number of juvenile plants in this site, is believed to be due to the high degree of production of reproductive structures (particularly tetrasporangia) which was observed in this population. The latter observation was probably due to the increased laminal surface available for reproductive structure production, as well as the increased nutrient and gas supply. The H+ population was larger and much denser than the other populations studied, and thus sporelings could easily have been caught amongst the other plants. The large clumps of plants that were observed in this site did make identification of single holdfasts difficult, and there could have thus been a bias to choose the more easily identifiable and smaller holdfasts.

The scatter diagram (Fig. 19) of the holdfast diameter versus the lamina length for L1 and H+ over the entire study period, indicates that there are five groups of plants. There is a group composed of small plants with small holdfasts (from L1 and H+; holdfast diameter 5-28.5mm, lamina length 4-132mm) which are believed to be all the plants from L1 and the juvenile plants of H+. The group consisting of plants with longer laminae and small holdfasts (H+ only; holdfast diameter 6-19mm, lamina length 170-230mm) are thought to be older juvenile plants, the medium sized plants with medium holdfasts (H+ only; holdfast diameter 19-36mm, lamina length 305-375mm) are believed to be older plants and the plants with long laminae and large holdfasts (H+ only; holdfast diameter

52.5-65.5mm, lamina length 477-535mm) are believed to be mature plants at the peak of the growing season (of the study period). The group of plants having large holdfasts and short laminae (H+; holdfast diameter 28.5-32.5mm, lamina length 39-102mm) are plants which had lost their long laminae and were regenerating new laminae (at the end of the season). It must be remembered that plants in all stages of development, from the entire study period, are included in this diagram. Tovey and Moss (1978) report that there is enlargement of the holdfast area with an increase in laminal number and size in Laminaria, it is clear, however, that there are seasonal changes in laminal length of D. longifolia (Section 4.6) and thus this relationship would be difficult to identify.

4.7.1.2 Holdfast Area

It has been reported that the area of holdfasts experiencing a high degree of wave action is greater than those in calmer areas. Moss (1950) reports that members of Fucus vesiculosus populations living in sheltered areas have less holdfast area in contact with the substratum than individuals from more wave exposed sites. This is due to the presence of proliferations growing under the holdfast and reducing the area of attachment. Members of the some species are reported to lack holdfasts in salt marshes which do not experience water motion (Moss, 1950). There are reports that Macrocystis pyrifera (L.) C. Agardh from sheltered areas has no basal meristem or holdfast (Gerard & Kirkman, 1984) indicating the reduced necessity for attachment in calm areas.

The results of the measurement of D. longifolia holdfast area, in relation to the degree of wave exposure, indicates that there is a direct relationship between the holdfast area and the degree of wave exposure, ie holdfast area increases significantly ($p<0.001$) between

low and high wave exposure (as ranked subjectively; Fig. 20; L+, 0.00013 (4.78 x $10^{-5}m^2$); H+ 0.000516 (3.6 x $10^{-4}m^2$)). This indicates that an increase in holdfast area in contact with the substratum is necessary to allow D. longifolia to survive in high wave exposure areas.

4.7.1.3 Holdfast Mass

Holdfast biomass of populations of Sargassum cymosum and Turbinaria ornata is reported to increase with an increase in wave action (de Paula & de Oliveira, 1982; Payri, 1984). There is a problem in determining the mass of holdfasts, in that those attachment organs consisting of rhizoids retain a large amount of sand due to the adherance of the rhizoids to the sand particles (Tovey & Moss, 1978). The sand is thus included in the mass measurements as removal of the sand particles is impossible.

The holdfast mass measurements (Fig. 21 & Fig. 22; of wet and dry mass, respectively) also show correlation with exposure, with the low wave exposure sites (L+, 0.372 (±0.206)g wet) having the lightest holdfasts and the high wave exposure sites the heaviest (H 3.843 (±1.68)g wet; H+, 5.547 (±6.29)g wet). This is due to the greater area of holdfast (Section 4.7.1.2) having a greater mass (ie a greater amount of structural tissue) but also containing a greater volume of sand. Although living drift material of D. longifolia was regularly observed, it was not determined whether this was ripped up or whether it came from floating material in sheltered areas. The holdfast size of the drift material was also not measured. It was determined, however, that mature plants do not need attachment for survival in sheltered areas as, detached plants survived and grew in tanks for many months without reattaching (Section 4.10.2). These plants did, however, remain upright.

4.7.2 Features of the Lamina

There are many conflicting reports on the effect of wave exposure on macroalgal laminal morphology. Some researchers report that, to overcome the harsh environment of wave exposed areas, plants become smaller and narrower (Denny, 1988), whilst other reports suggest that the plants growing in more wave exposed areas flourish and grow larger due to the increase in nutrient and gas availability. Russell (1978) reports that the changes in aspects such as laminal length, width and shape are commonly found to be associated with environmental changes in brown algae, and this has led to a great deal of confusion in the taxonomy of members of the group. It is not only the size of the laminae which may be affected by the wave exposure, the shape and structure of the laminae are also important. Long, smooth, flexible strap-shaped laminae such as those in D. longifolia are thought to be optimal in highly wave exposed areas as they are able to move in the direction of flow rapidly (Norton et al., 1981). Bending over also takes the laminae closer to the substratum and into areas of lower water velocity (Charters et al., 1969).

4.7.2.1 Laminal Length

There are conflicting reports about whether plants living in more wave exposed environments are longer or shorter. Ascophyllum nodosum and Turbinaria ornata (Russell, 1978; McEacheron & Thomas, 1987; Payri, 1984) are reported to be shorter in more wave exposed areas. Durvillaea potatorum is reported to be short, stunted and highly branched (due to continuous regenerative recovery from damage to the tips) in high wave exposure areas, but to have a maximum internodal length at intermediate wave exposure (Cheshire & Hallam, 1988). The latter observation is thought to be due to this region being

intermediate of all the gradients affecting growth (advantageous and disadvantageous), ie no extreme conditions exist in this region (Norton et al., 1981). Neushul (1972) reported long, thin individuals in sheltered areas where the plants respond to the decrease in nutrients by increasing the absorptive surface. Schiel and Choat (1981) report that individuals of dense, monospecific algal stands found in areas of higher exposure, tend to be larger in size. A similar report suggests that individuals of Laminaria setchelli in more wave exposed areas are taller and thicker than individuals of a similar age in less wave exposed areas, presumably due to the increase in nutrient availability (Klinger & DeWreede, 1988). De Paula & de Oliveira (1982) report that Sargassum cymosum populations in sheltered areas are longer but of a lower density than those in wave exposed areas. Many members of the Dictyotales have seasonal changes in laminal length with the longest length not occurring at the peak of biomass production rate, due to the long laminae being degraded badly (King & Farrant, 1987). Long laminae are exposed to different degrees of water motion, light and nutrients at the tip and the base (Dawes, 1981) which may cause differences in grow rates of different regions. It appears that the wave exposure has different effects on different species, indicating the importance of intensive growth studies to determine optimal conditions for the growth of commercial seaweed.

From the graph of the mean values of laminal length for D. longifolia over the entire year (Fig. 23), it appears that there is an increase in laminal length with an increase in wave exposure (according to the subjective ranking; L1, 46.19 (±9.49)mm ($p<0.001$); H+, 118.29 (±79.22)mm) probably due to the increase in nutrient and gas availability. It must be remembered that the measurements of D. longifolia were taken over the entire

year and that H+ was abraded the most and thus the laminal length was reduced more than the other sites. To get a mean maximum laminal length, measurements would have to be taken throughout the year and the measurements at peak growth compared. However, as the study was not performed over a complete year, the period when the greatest length was attained, could not be determined. This is a constraint of the study and the data should be interpreted accordingly. The seasonal changes in laminal length in the different sites are shown in Figure 17.

4.7.2.2 Laminal Width

There are reports of various other aspects of laminal morphology changing with variation in the degree of wave exposure experienced, eg laminal width and thickness. The laminal width of Ascophyllum nodosum in areas of higher wave exposure is reported to be less than that in sheltered areas (McEacheron & Thomas, 1987), Laminaria hyparborea shows an increase in thickness due an increase in nutrient supply (Kain, 1977) and Laminaria longipes experiences a decrease in width (Kain, 1977) with an increase in water movement (Palmisano & Sheng, 1977). The latter authors report that this decrease in width is so pronounced that they used L. longipes as an exposure indicator and attribute the strap-like laminal shape to a method of reducing resistance. Russell (1978) reports that there is no correlation between the width and length of laminae of Fucus vesiculosus from areas of different wave exposure.

Although the mean laminal width of D. longifolia from all the sites in this study, are not significantly ($p>0.05$) different (except L1 which has a significantly lower mean laminal width; 8,21 (±1.25)mm ($p<0.001$)), there does seem to be a trend in laminal width in relation to wave exposure, ie there is an increase in laminal width with

an increase in wave exposure. Once again, it must be remembered that the mean laminal widths from the whole year are plotted on a graph (Fig. 24), but that the number of plants from each season included in the mean, differed for each site. The width of the three longest lamina of each individual were measured and thus plants experiencing high degrees of abrasion and growth of new lamina, eg H+ would have a lower mean laminal width than plants where the mature laminae were still intact. The ideal situation would be to measure the mean width when the laminae were at their longest, ie peak of the growing season. However, to do this the seasonal patterns of growth would need to be determined.

The scatter diagram of laminal length versus laminal width for plants from L1 and H+ over the whole year (Fig. 25), indicates three groups of plants. There is a group of short, narrow plants from both sites (lamina width 2-14mm, lamina length 4-170mm), which appears to be the entire population of L1 and what is assumed to be young juveniles of H+. There is a group of intermediate plants with fairly long, wide plants from H+ which are assumed to be older juvenile plants (lamina width 14-21.33mm, lamina length 38-235mm). The last group of plants are long and wide and are from H+ only (lamina width 15.6-19.6mm, lamina length 351-535mm). This group is assumed to be composed of adult plants. The latter two groups could possibly be the sporophyte and the gametophyte which, although D. longifolia is reported to be isomorphic, may respond differently to the different conditions. A genetic study would have to be performed to determine this. It is important to note that the measurements were taken over the entire year and thus different stages were included together. There is a similar grouping if the March results are studied (Fig. 26) however, the short narrow group (L1;lamina width 3.3-12.3mm, lamina length 29-132mm) is composed of only L1

plants. As the width of the three longest laminae were measured, this indicates the presence of long laminae on all the mature plants from the H+ site, ie the group with long, wide laminae (H+; lamina width 16.6-19.6mm, lamina length 425-535mm) are mature plants from H+. The group of plants made up of shorter, wide H+ plants is believed to be young laminae which are wider at this time of the year (increased growth of the plants) than young laminae from the rest of the study period (H+; lamina width 14-19.66mm, lamina length 52-351mm). If we look at the October readings only (Fig. 27), all the plants are much shorter as they have been abraded and have only begun to regenerate (lamina width 2-17mm, lamina length 4-102mm), ie the new laminae are in the process of being produced.

4.7.2.3 Laminal Surface Area

Klinger and DeWreede (1988) report that the area of Laminaria laminae, increases with an increase in wave exposure and they attribute these differences to the increase in nutrient supply in wave exposed areas. The drag experienced by an organism is reported to be proportional to the laminal area of the object which moves in the direction of flow (Vogel, 1981; Denny, 1988), thus plants in more wave exposed sites should, theoretically, have smaller laminae so as to decrease the drag. However, the total laminal area of individuals of D. longifolia appears to increase with an increase in wave exposure (Fig. 28), with H+ having a significantly higher ($P<0.001$; 0.020989 ($\pm$0.029)m^2) mean laminal surface area than the other sites (L1 and L+ have the lowest area values of 0.002345 ($\pm$0.001)m^2 and 0.003653 ($\pm$0.0007)m^2, respectively). This may be due to the fact that there were a greater number of laminae on the plants in H+ (Section 4.7.2.6). The mean laminal length (Section 4.7.2.1) and width (Section 4.7.2.2) of D. longifolia from H+ are also greater than those of the

other sites. Presumably the increased area is due to greater growth caused by an increased nutrient and gas supply, due to the higher degree of wave exposure.

4.7.2.4 Mass of Laminae

The mass of the laminae of an individual is another feature of algal morphology which is reported to change with a change in the degree of wave exposure. Payri (1984) reports that there is a decrease in mass of Turbinaria ornata with an increase in wave exposure. Cheshire and Hallam (1988) report changes in the morphology, but not in biomass, of Durvillaea potatorum in differing areas of wave activity. It has also been reported that dry mass of laminae of Fucus plants growing in sheltered areas is greater than that in wave exposed areas (where plants are abraded by sand), whilst there is no significant difference in the wet mass of laminae from different areas (Schonbeck & Norton, 1979). The difference between the wet and dry mass results is attributed to differences in the relative amounts of strengthening and photosynthetic tissue (Schonbeck & Norton, 1979). Mabeau and Kloareg (1987) studied a range of brown algae and reported that 35-45% of the dry thallus mass is composed of cell wall material and that this percentage is related to zonation and desiccation resistance.

The study of laminal mass in D. longifolia seems to indicate that mass is directly related to wave exposure and that there is a significant ($p<0.001$ between most of the values) increase in laminal mass (wet and dry) with an increase in wave exposure (Fig. 29; L1 0.583 (±0.285)g wet; H+, 9.133 (±12.81)g wet). This is probably due to an increase in laminal area in the higher exposure areas (due to the increase in nutrient and gas supply), but may also be due to an increase in

strengthening tissue. A further study would have to be performed to determine the percentage of wet laminal mass composed of structural tissue.

4.7.2.5 Number of Dichotomies per Lamina

Laminae dichotomy number is another factor of morphology which may change with a change in wave exposure. There is reported to be an increase in digitation of Saccorhiza, Durvillaea potatorum and Ascophyllum nodosum living in more wave exposed areas (Norton, 1969; Cheshire & Hallam, 1988; McEacheron & Thomas, 1987). However, there are also reports of a decrease in the number of branches in Pelvetia (Russell, 1978) and Turbinaria ornata (Payri, 1984), whilst Cheshire and Hallam (1988) report that there is an decrease in digitation but an increase in laminal number in Durvillaea potatorum from more exposed areas. Kilar and McLachlan (1986) report that Acanthophora spicifera (Vahl) Borg. has small plants with fewer branches in wave exposed areas.

It appears from Figure 30, that the number of dichotomies per lamina in D. longifolia increases with an increase in wave exposure (as ranked subjectively). The number of dichotomies may be related to the laminal length and possibly there is a minimum laminal length at which dichotomies are formed. If this was the case, it may explain why the dichotomy numbers in the sheltered pools (L1 and L+) were so low (0.267 (±0.12) and 0.956 (±0.073); respectively), ie the laminae did not reach the minimum length for dichotomy production while in the highest wave exposure sites (H and H+; 1.738 (±1.22) and 1.672 (±1.24)) the dichotomy number was significantly higher ($p<0.001$). The mean measurements from March (Fig. 31) indicate that the highest wave action site H+ had the greatest number of dichotomies (3.652 (±1.15)). It also had the greatest mean laminal length (Section 4.6). In

October, when the plants of H+ were abraded back (more than any of the other sites) and the holdfasts had only just begun to produce new laminae, the H+ site had the second lowest mean dichotomy number (Fig. 32; 0.535 (±0.677)). In both these months the low wave exposure site (L1) had the lowest dichotomy number (March and October; 0.176 (±0.512) and 0.186 (±0.389) respectively). The suggestion that the number of dichotomies present is related to the laminal length, is supported by the scatter diagram (Fig. 33) of the laminal length versus the number of dichotomies for L1 and H+ for the entire year, which shows that there is an increase in dichotomy number with an increase in laminal length in both the L1 and H+ sites.

The site having low laminal length (L1) has the greatest percentage (57.97 (±30.61)%; $p<0.001$) of laminae without dichotomies, while the other sites have lower percentages of laminae without dichotomies (Fig. 17). The site with the lowest percentage of laminae lacking dichotomies is H 16.20 (±10.72)%) which may be explained by the higher number of long laminae at certain times of the year. If the dichotomy number is directly related to the laminal length, then the dichotomy number will be related to the amount of abrasion and wave exposure that the plant experiences (as this decreases the mean laminal length).

4.7.2.6 Number of Laminae per Individual

The number of laminae per plant (greater and less than 5mm) was another aspect of morphology that was measured for D. longifolia. The low wave action sites L2 and L+ had the greatest number of small (less than 5mm) laminae per plant (Fig. 35), whilst the rest of the sites had similar numbers of small laminae. This could be explained by the observation that even at the peak of the growing

season, the plants in the sheltered pools had a large proportion of laminae that were less than 5mm in length.

The mean number of laminae greater than 5mm, show a surprising trend. It appears that the L+ and H+ sites have the lowest number of longer laminae (12.4 (±2.8) and 12.68 (±8.59)). This can be explained, in the case of the L+ site, by the low wave exposure and reduced plant size (although L1 and L2 show significantly higher values than L+; 16.84 (±9.23) and 18.55 (±4.75), respectively). In the case of H+, it must be remembered that the plants of this site were highly abraded (more than any of the other sites) and for a large proportion of the study period were composed of new lamina or short abraded sections of lamina. The mean laminal number per plant is another morphological measurement which would probably be most meaningful if it was performed at the peak of the growing season. The unexpectedly high number of laminae longer than 5mm from the intermediate wave exposure site (I+; 23.23 (±4.97)), could possibly be explained by the depth of the water in this site. There was also comparatively little sand in suspension in the water of this site (Section 4.4), and thus the abrasion was less than in the other sites. The plants in this site were also only measured near the end of the study period when regeneration had begun. Even during the initial part of the study of the plants of this site, very little abrasion or degradation of the lamina was observed.

The results of the morphometric and structural studies are summarised and compared in Section 4.13.

4.8 STRUCTURAL PROPERTIES

4.8.1 Tensile Strength

Intertidal organisms such as macrophytic algae have to be able to withstand the violent jerks caused by currents and waves. These organisms have evolved two alternative forms to enable them to withstand these forces. The first of these is to remain rigid and withstand the forces of moving water. Alternatively, the organisms can be flexible and withstand the forces by reducing the area in contact with the waves and "flowing" in the same direction as the water movement. In the latter case, the organisms require less strengthening tissue (Denny, 1988). Flexible algae must also be able to extend and stretch without breaking under stress (Denny, 1988). There are two phases of extension under a strain such as the drag caused by water. The first is within the elastic limits, ie the stretch before breakage, and the second is greater than the first and leads to breakage (Delf, 1932). The breaking stress is reported to be the stress which "just exceeds the greatest longitudinal stress which can be borne per unit area without rupture" (Delf, 1932). The period of recovery between stresses, ie waves or storms is also of importance. Delf (1932) tested the extensions and breaking strains of the stipes of various brown algae such as Ascophyllum, Fucus and Laminaria. There are however, other factors besides plant structure, which may affect the tensile strength or breaking strain of algal thalli. Kraemer (1990) reports in the red alga Iridaea, there is a significant increase in the tensile strength of the laminae with a water loss of up to 50%, thereafter the tensile strength decreased. Thus the tensile strength may be altered by the environmental conditions experienced by the alga

Tensile strength of the lamina is a feature frequently used in the study of land plants including grasses (Evans, 1964), in relation to factors such as palatability. It was initially believed that the tensile strength of D. longifolia laminae would be related to the wave exposure experienced by the plant. The method that was used in this study involved the construction of a tensilimeter (Section 2.4.7.1) which was effective but could only be used when the laminae being measured were of a reasonable length (5cm or more). To standardise the measurements, the length of lamina put into the machine was kept at 5cm but, for a majority of the plants, the laminae were less than this for most of the year. This resulted in a low number of measurements for some of the sites. The sections of lamina also needed to be free of any damage, epiphytes or parasites. The clamps did cause some damage to the plant. In some cases the lamina broke at the clamp however, these results were discarded. The measurement of the tensile strength indicated that there was a high degree of elasticity in the laminae which elongated a great deal before breaking. Possibly the measurement of the degree that the lamina can stretch before breaking (ie elasticity), would be a useful indication of how much drag the plant can be exposed to before the laminae are broken. Unfortunately, measurements of tensile strength were only taken when sufficient material was available. This resulted in the mean tensile strength for the study being obtained from different numbers of measurements for each site (from different times of the year). The results of mean tensile strength must be viewed with this in mind, ie at certain times of the year only immature laminae were available whilst at other times 5mm sections of mature laminae were used. A more useful comparison would have been the tensile strength of laminae measured at the peak of the growing season when all the laminae were at a maximum size.

Delf (1932) had a similar problem and reports that young laminae of Laminaria have a much lower breaking stress than older laminae. From the graph of the mean tensile strength for the year (Fig. 37), it appears that there is no relationship between the degree of wave action and the tensile strength, other than that the highest wave exposure site (H+) has the highest tensile strength (524.87 (±86.13) dynes/mm) and the lowest wave exposure site (L1) the lowest tensile strength (349.95 (±14.22) dynes/mm). In March (Fig. 38), the laminae of all the plants were fully developed, and the highest wave action site (H+) has a significantly higher tensile strength than the other sites (509.78 (±234.47) dynes/mm). Unfortunately, only the L1, H and H+ sites were measured at this time of the year. It must be noted however, that not all the sites were measured in all the months (only October had all the site measurements). The October measurements also lacked a trend, although the highest wave action site (H+; (669.69 (±234.26) dynes/mm) had the highest mean tensile strength (Fig. 39). This would seem to indicate that even when the lamina are small (newly regenerated from the holdfast), extremely high wave exposure may induce an increased tensile strength. At the same time, the low wave exposure site (L1; 334.80 (±99.32) dynes/mm) has the lowest tensile strength. The apparent lack of relationship between tensile strength and wave exposure in D. longifolia is surprising considering the studies which conclude that there is a relationship between the two. This could however, be due to the uneven spread of measurements over the year. Delf (1932) reported that there are no differences in the breaking strain of two species of Fucus from sheltered and wave exposed sites, however, Armstrong (1987) reports stronger tissue resulting in a higher tensile strength of Hedophyllum sessile from areas of higher wave activity.

Similar tests of elasticity and tensile strength have been reported for Nereocystis luetkeana (Mertens) Postels and Ruprecht (Koehl & Wainwright, 1985). There is also a report that there is an increase in breaking strength with an increase in wave exposure in Ascophyllum nodosum (McEacheron & Thomas, 1987). The latter study described similar problems to those experienced in this study, ie desiccation of the plant material prior to breakage and damage by the equipment. Koehl and Wainwright (1977) report that N. luetkeana survives wave exposure by having high elasticity rather than tensile strength. It is possible that D. longifolia has a similar method of coping with drag and other stresses of water movement. The latter authors report that the stretch is due to the cellulose fibrils in the walls of the central cortical cells.

From the PCA (Fig. 43) of the morphological and structural aspects of the lamina and holdfast, it appears that tensile strength is fairly closely correlated with aspects of the lamina such as laminal width. It is surprising that the tensile strength is closer to laminal succulence than sclerophylly, as the latter is a measurement of strength (strengthening tissue). However, there were some problems experienced with the measurement of laminal sclerophylly and succulence (Section 4.8.3) which may have caused misleading results.

The tensile strength measurements are included in the structural and morphological summary (Section 4.13).

4.8.2 Attachment Strength

The attachment strength of the holdfast to the substratum is obviously an important feature of the ability of intertidal algae to survive under harsh conditions. It was initially presumed that the mean attachment strength

would be directly related to the degree of wave action being experienced. There were a few problems experienced with the technique used to measure the attachment strength of D. longifolia in this study. The clamps that were used did cause some damage to the laminae and, as the method defined attachment strength as the force needed to remove the plant from the rock or to break the laminae (whichever came first; Carter, 1986), the measurements obtained in many of the cases could have been lower than the true forces required to remove the alga from the rock. Another problem was that some of the plants were so firmly attached that the clamps slipped off and thus a cable tie was used. The cable tie also caused damage to the plant and may have affected the results. There are other reports that the device used to hold a holdfast during attachment strength measurements, weakens the plant and leads to misleading results (Lobban et al., 1985). Very small plants could not be fastened into the clamp and this caused a size bias. A similar problem with small sized plants was described by McEacheron and Thomas (1987). A further problem with the method used in this study, was that different numbers of laminae and different combinations of lamina size were included into the clamp. This may have affected the results (when attachment strength equals the breakage of the laminae). For example, if a greater number of laminae or if more large, mature laminae were included in the clamp, the attachment strength measurement would be greater than if there only immature or few laminae included.

As mentioned in Section 3.8.2, the attachment strengths were only measured in September and October (Fig. 40). The H+ and H sites had by far the largest populations of D. longifolia and at this time of the year, a large number of the plants in the populations were juvenile individuals and were thus not firmly attached. This may

account for the low attachment strengths measurements in these sites (H+ and H; 10.63 (±1.95) Newtons and 9.82 (±4.14) Newtons, respectively). This suggestion is supported by the fact that the September attachment strengths (Fig. 41) were lower than those for October (Fig. 42) when juvenile plants were larger and more firmly attached. The area of the holdfast should also be included in the measurement and this would, perhaps account for the removal of juvenile plants from some of the sites. The intermediate wave exposure sites (I and I+) had the highest attachment strength (14.50 (±7.97) Newtons and 14.61 (±1.28) Newtons, respectively) which may be explained by the decrease in abrasion to the holdfast due to the sand inundation (in I), and reduced sand suspended content (in I+). The attachment strength of the individuals from the low wave exposure site (L1) is by far the lowest of the sites (7.07 (±2.07) Newtons), and this may be due to the small holdfast size throughout the year (Section 4.7.1.1, and also due to the fact that the plants were often attached to soft sandstone with a high degree of sand inclusion in the holdfast material. Lobban et al. (1985) report that the substratum does influence the attachment strength. Tovey and Moss (1978) report that the rhizoids of the holdfast of Laminaria digitata (Huds.) Lamour. attach by growing into all the irregularities on the substratum and thus fitting the substratum perfectly. Grains of loose sand are also picked up the adhesive rhizoids. There are also reports of the gaps between the rhizoids and the substratum being filled with mucilage which is thought to be some form of adhesive compound (Tovey & Moss, 1978; Cheshire & Hallam, 1985). A smooth substratum is thus not optimal for adhesion and would result in easy removal of the plant. The other sites in this study show no particular trend with relation to wave movement and this may be due to a

lack of trend, or to the results being affected by the problems discussed above.

Attachment strength measurements performed on Ascophyllum nodosum were measured by attaching a grommet to the stipe below the first internode. The force needed to break the stipe at or above the holdfast was measured using a spring balance (McEacheron & Thomas, 1987). However, this method was a measurement of the tensile strength of the stipe rather than the attachment strength of the plant (similar to the method used in this study. Despite this, the latter authors report an increase in strength of attachment organs from highly wave exposed shores when compared to sheltered shores.

The PCA of the various aspects of structural and morphometric measurements (Fig. 43) indicates, surprisingly, that there is some correlation between the attachment strength and laminar measurements, but little correlation between the attachment strength and the holdfast measurements. As mentioned in Section 3.8.2, the definition of the method used to measure attachment strength resulted in the force measured often being the tensile strength of the laminae to which the clamp was attached, and not force needed to remove the holdfast. Considering this, it is not surprising that the attachment strength is correlated to the tensile strength and the features of the lamina such as its width, sclerophylly and succulence; and not correlated at all with the features of the holdfast. As mentioned previously, the inclusion of some aspect of holdfast area would perhaps have given a more accurate measurement.

The attachment strength measurements are included in the structural and morphological summary (Section 4.13).

4.8.3 Sclerophylly and Succulence

Wilson (1965) showed that leaf strength in the rye grass Lolium was an indicator of cellulose content. Although brown seaweeds do contain cellulose in the cell walls, alginic acid is also a major component in the walls. Variations in the type of alginic acid can be related to the morphology and environmental factors. For example, the stipe and laminae of Durvillaea potatorum bend, whilst the holdfast does not. These areas have different ratios of alginic acid to other material (Cheshire & Hallam, 1985). "Tough" algae are reported to be more resistant to herbivores, abrasion and wave shearing forces, and to compete with more delicate species for light and space (by the whiplash effect; Dayton, 1975; in Littler et al., 1983; Littler et al., 1983). Surprisingly, the tissue strength of desiccated Iridaea (Rhodophyta) is reported to not be out of the range hydrated tissue strength (Kraemer, 1990).

4.8.3.1 Lamina Sclerophylly

There appears to be no trend in the lamina sclerophylly (amount dry matter per area) with respect to wave action (Fig. 44). This result is surprising considering that laminae in wave exposed areas could only survive if they were able to withstand abrasion and drag, and were "tough". However, laminae of D. longifolia may survive wave forces by having high elastic properties or rapid regeneration rates, rather than expending energy on strengthening tissue. The lowest wave exposure site (L1) did have the lowest sclerophylly values ($p<0.001$; 33.61 ($\pm$4.34) g/m^2) indicating that these plants had less strengthening tissue than the plants from the other sites and are thus "flimsy". The sclerophylly values for the other sites show little trend with respect to wave exposure (according to the subjective ranking). The

results of this section are included in the summary of morphological and structural features (Section 4.13).

4.8.3.2 Holdfast Sclerophylly

The holdfast sclerophylly values show a definite relationship with the degree of wave exposure. There appears to be an increase in holdfast sclerophylly of D. longifolia, with an increase in wave exposure (as subjectively ranked; Fig. 45). These results support the suggestion that holdfasts in more wave exposed sites must have greater strength and adherence to allow the plants to remain attached to the substratum (L1, 1344.99 (±432.35) g/m^2; H+, 5085.762 (±3291.85) g/m^2). It must be remembered however, that the holdfasts retained a great deal of sand and, as mass is part of the sclerophylly calculations, this retention must have affected the sclerophylly measurements.

4.8.3.3 Lamina Succulence

Mean water content per lamina area (succulence values) also lacks any real trend in relation to wave exposure (Fig. 46). These results can be explained, to some degree, as the rate of desiccation is reported to be related to the water content of the plant (Dromgoole, 1981). The plants in the low wave exposure sites (L1 and L2; 231.82 (±15.86) g/m^2 and 316.98 (±15.86) g/m^2) and the intermediate wave exposure site (I+; 343.86 (±77.17) g/m^2) may have lower lamina water content as they were never observed to suffer exposure to the atmosphere. All these sites consist of deep pools that were never observed to dry up completely. The two high wave exposure sites (H and H+; 423.14 (±37.32) g/m^2 and 422.28 (±98.83) g/m^2) were frequently observed to experience exposure to the air for long periods of time (a few hours at low tide). The plants in

these sites would require a greater lamina water content to overcome desiccation. The intermediate site (I; 570.69 (±100.67) g/m^2) has the highest lamina succulence values ($p<0.001$) which could be explained by the fact that the plants in this site were frequently left out on the sand with no water or splash to keep them moist (as plants in the H and H+ sites had). The plants in this site (I) were also inundated by sand more regularly than those in the other sites. The reason for the high succulence values of the low wave exposure site (L+; 520.83 (±77.8) g/m^2) are not known, as this is a fairly deep pool that was never observed to dry up.

4.8.3.4 Holdfast Succulence

The holdfast succulence in D. longifolia appears to be fairly closely related to the wave exposure (Fig. 47). The low wave exposure sites (L+ and L1; 2253.64 (±538.5) g/m^2 and 2779.84 (±538.5) g/m^2) have the lowest mean succulence values which could be expected considering that plants in these sites were never observed to be exposed to air. The two highest wave exposure sites (H and H+; 5674.93 (±456.99) g/m^2 and 7974.56 (±4693.25) g/m^2) had the highest holdfast succulence values, which could be explained by the fact that the holdfasts in these sites are frequently uncovered and are thus required to retain water to survive. It is interesting to note that the holdfast succulence values for the intermediate wave exposure site (I) are fairly low (3109.02 (±20.38) g/m^2), whilst the lamina succulence values are high. The reason for this is not known, however, it must be remembered once again, that again the sand retention of the holdfasts may have affected the results obtained.

From the Principle Component Analysis (Fig. 43) of various features of the lamina and holdfast of D.

longifolia, it appears that the features of lamina strength, sclerophylly, succulence and size are closely correlated with each other. The features of the holdfast (including sclerophylly and succulence) are not related to the lamina traits but are correlated with each other. Attachment strength was presumed to be related to the features of the holdfast because a larger holdfast area should mean better attachment. However, due to the definition of the method, the attachment strength was measured as the breaking force of the lamina in many of the firmly attached plants.

From the results obtained, and considering the problems in holdfast measurement (due to the inclusion of sand), in the measurement of sclerophylly and succulence in D. longifolia, it does not appear that these attributes are as useful in the determination of the effect of the environmental conditions on macroalgae, as they are in terrestrial studies. However, there is a possibility that the attributes may provide useful inter-species comparisons, and further investigation should be performed before sclerophylly and succulence are rejected as unimportant in aquatic studies.

The sclerophylly and succulence results are included in the structural summary (Section 4.13).

4.8.4 Desiccation and Rehydration

Intertidal organisms may be transferred from an aquatic to a terrestrial environment during the tidal cycle. Emersion changes the temperature (and thus metabolism), water content and exposure to light of these organisms (Dring, 1982). The degree of desiccation is therefore, another factor which affects the growth and distribution of intertidal algae. Zonation on rocky shores is reported

to be determined, to a certain degree, by the tolerance of the species to different levels of desiccation (Dromgoole, 1981; Dring, 1982). In this study, the plants in the wave-swept populations (H and H+) were exposed to the atmosphere at low spring tide, whereas in the pools (L1, L2, L+ and I+) the plants were never exposed to the atmosphere, and would thus be expected to have different tolerances. The rate of desiccation is related to the ratio between the evaporating surface and the volume and, to a lesser extent, the water content of the plant (Dromgoole, 1981). Larger plants have smaller surface area to volume ratios which means that less water is lost. It also means, however, that there is more drag in wave exposed areas and that the plants may be removed before reaching reproductive maturity (Denny, 1988). It has been reported that the thickness of the cell walls and the presence of muc 'age is not of great importance (Dromgoole, 1981), although Chapman and Chapman (1973) report that thicker cell walls are frequently found in algae experiencing higher degrees of desiccation. The presence of alginic acid in the walls is also reported to reduce desiccation in fucoids (Berard Therriault & Cardinal, 1973; in Dromgoole, 1981). An increase in air temperature is reported to decrease desiccation resistance in Padina japonica (Allender, 1977), indicating that desiccation may vary seasonally. This is supported by the report that resistance to desiccation in Fucus spiralis Linnaeus and Pelvetia sp. reaches a maximum in summer and a minimum in winter, and that the percentage dry matter content of the tissue is correlated with both the changes in resistance and the season (Schonbeck & Norton, 1979). Plants are reported to either tolerate or avoid desiccation. Examples of tolerance include reports that Pelvetia canaliculata is able to recover after being exposed to the air for a few days during neap tide, and Fucus distichus has greater photosynthetic activity when initially emerged than when

submerged (Dring, 1982). However, continued emergence reduces the photosynthesis of this species. There are suggestions that the position on the shore determines whether photosynthesis is greater when emerged or submerged (Quadir et al., 1979; Oates & Murray, 1983). Desiccation for four hours during the day, causes death of Ascophyllum nodosum, whilst exposure during the night has no effect (Rheault & Rythor, 1983). This indicates the importance of the time of day (and temperature) at which the emersion occurs, ie emersion at midday does more harm than at night, dusk or dawn (Chapman & Chapman, 1973). The morphology and growth phase of the plant is also reported to affect the desiccation resistance (Zanevald, 1937; in Allender, 1977). The gametophyte of Padina japonica is reported to have a higher emersion tolerance than the sporophyte (Allender, 1977). It was observed that many of the intertidal algae (including D. longifolia) having plants with a number of lamina, are not as badly desiccated as plants with less laminae. This is due, in part, to the protection of some laminae by those lying above them. Similarly very dense populations are more resistant to desiccation due to the potential protection from neighbours, ie aggregation of laminae, whilst single plants have less protection unless they are surrounded by plants of another species. Palmisano and Sheng (1977) report that large clumps of seaweed and kelp protect each other from desiccation and also slow down waves, thus reducing the effect of wave action. Plants lying on sand are also able to retain water longer due to the water retention potential of the sand (Isaac, 1933), and there are reports that plants buried under 10cm of sand experience the same temperature as that in the subtidal region (Johnson, 1963). Cheshire and Hallam (1988) report that there is physical erosion of the tips of Durvillaea potatorum plants which have been exposed to desiccation, and Norton et al. (1981) suggest that the erosion of algal lamina tips due to desiccation may

result in a considerable decrease in growth. Erosion following desiccation may be one of the major factors leading to the degeneration of the plants in the H+ and H sites, which were the only plants that were exposed to the air for any period of time (except I which was covered by sand for long periods of time). The much denser populations in these two sites, and the larger plants (over 60cm for large periods of the year) may, however, have led to desiccation resistance. Unfortunately, the lethal level of desiccation was not measured in this study, however, this would make an interesting study.

From the results obtained for the desiccation curves of D. longifolia from the different sites (Fig. 48, A & B), it appears that the pattern of desiccation is similar for plants from all the sites however, the plants from the more frequently wave exposed sites (I, H and H+) experienced a greater percentage of desiccation over the allotted time period. This is probably explained by the larger laminal area of plants from these areas. Another study performed on intertidal algae from Palm Beach, showed that although D. longifolia rapidly lost water in the initial stages of desiccation experiments, it recovered rapidly and completely suggesting a high level of lethal desiccation (Savage, in prep.). It would have been interesting to compare the lethal desiccation level of plants from the different sites, some of which were never exposed (L1, L2, L+ and I), and others that were regularly exposed to desiccation (I+, H and H+).

The percentage rehydration after oven drying (Fig. 49), indicates that only the intermediate site (I; 77.82 (±4.88)% had a significantly higher percentage rehydration ($p<0.001$), whilst all the other sites had similar values (H+; 63.94 (±5.15)%. The lowest wave activity site L1 did however, have the lowest percentage

rehydration and only recovered 49.92 (±8.82)% of the original mass. This could be explained by the fact that the former site (I) was frequently inundated by sand or completely dried out. The plants in this region would thus need to be able to rehydrate completely after desiccation. Although the high wave exposure sites (H and H+) did suffer emergence, there was the occasional wave or splash which kept the plants moist. The intermediate site (I) however, was observed to suffer periods of up to few hours, without any water movement or spray. It has been suggested that water loss or desiccation reduces the survival of thalli in wave swept environments because the biomechanical features which allow the plant to survive are affected by desiccation, eg lamina strength may be affected (Kraemer, 1990).

The aspects of desiccation and rehydration measured for D. longifolia are included in the structural summary (Section 4.13).

4.9 ANATOMICAL STUDIES

There are numerous studies involving different aspects of cell anatomy in members of the Dictyotales and other brown algae. Few of these report any anatomical difference between plants growing in wave exposed sites and those from more sheltered areas. Kristensen (1968; in Cheshire & Hallam, 1988) does however, report that the cell walls of fucoids from areas of high wave activity are thicker than walls of plants from more sheltered sites. A detailed anatomical comparison of D. longifolia from different wave activity areas was originally planned for this study however, due to the difficulty experienced in the preparation of material for TEM, the detailed anatomical section of the study was terminated. Fixation and infiltration problems are commonly experienced during

the preparation of brown algae for TEM (Hallam & Luff, 1988). This is reported to be due to the presence of thick walls, physodes and phenols which disrupt the infiltration process. The anatomical study which was performed on D. longifolia is a general description of the cell types and arrangement using information from light, Scanning and occasional Transmission Electron microscope photographs. An anatomical comparison involving cell wall thickness, ratios of cell types and the sizes, and ultrastructure of the cells of plants from different wave exposure regions would, however, be an interesting study.

4.9.1 Apical tip

Members of the Dictyotales are characterised by an apical meristematic region. The meristematic cells divide longitudinally and transversely and are reported to give rise to the other meristems, as well as the midrib initials in Dictyopteris (Katsaros & Galatis, 1988). These authors report that the longitudinally dividing cells become the central, apical cells and are fully meristematic, whilst the transversely dividing cells undergo further division before playing a role in the expansion of the wings. The organelles in the apical cells of D. membranacea are reported to be highly polarised (Katsaros & Galatis, 1988). Dictyopteris is distinguished from the other members of the Dictyotales by the marginal, apical row of four to five (rarely more) large, meristematic cells which divide into a thin lamina and a prominent midrib (Johnson, 1889; Fritsch, 1965; Allender & Kraft, 1983). The sunken apical tip containing the elongated meristematic cells, such as that observed in D. longifolia (Pl. 7, A-M), is reported for other species of Dictyopteris. However, the pit in D. membranacea does not appear to be as deep as that in D. longifolia (Katsaros & Galatis, 1988). The tips of the

newly dichotomised branches or the tips of new laminae of D. longifolia do not have a pit (Pl. 7, C) but the elongated, "sausage shaped", longitudinally dividing, apical cells are visible at the laminal tips (Pl. 7, D-E). It appears that two of these cells initiate the formation of the dichotomy (Pl. 7, L & M) and the midrib (Katsaros & Galatis, 1988).

There appear to be two layers lining the pit (a thin, fibrous, inner layer and a thicker, outer layer). The outer layer appears to be mucilaginous in nature and is thickest (up to 100μm) at the base of the pit and tapers outwards, whilst the inner layer is much thinner (30μm at the widest point) and tapers only slightly (Pl. 8, A-D; Fig. 50). It is thought that these two layers form a protective coat or layer over the sensitive meristematic cells. An extensive literature search was performed, but no similar report was found. The composition of the layers was not investigated however, if a larger range of staining techniques had been used, the composition may have been determined.

4.9.2 Wing Structure

The mature wing of D. longifolia has characteristic bulges at the margins (Pl. 9, A-F; Fig. 51, B; Fig. 52, A). This thickened margin with a cluster of small cells at the outer edge, has also been described for Dictyopteris nigricans Womersley (Womersley, 1987) and D. delicatula (Allender & Kraft, 1983), but not for all the species of Dictyopteris. The thickened area increases with maturity and young laminae may have only slight thickening (Pl. 9, D; Fig. 51, A), whilst in older laminae the bulge may consist of a number of layers of cells (Pl. 9, E & F; Fig. 52, A). In the basal regions of the laminae of D. longifolia, the wing bulges and (in the most basal regions) the entire wing may be removed.

Katsaros and Galatis (1988) report a similar reduction of the wings at the base of the laminae of D. membranacea. However, these authors suggest that this reduction is not due to tissue degradation and abrasion, but rather due to an increase in the rate of asymmetrical divisions during the initial stages of thallus development. The cells in the marginal bulge are dissimilar to those in other areas of the wing in that they are much smaller (25μm) and more tightly packed (Pl. 9, F). There are approximately 13 of these cells across the bulge. The entire lamina is covered by a single layer of epidermal cells (on both surfaces). The remainder of the wing is composed of a number of parallel layers of large (50-75μm), irregularly shaped, thin walled (1.5μm) cells which divide in different directions. In young laminae there may be only two layers of wing cells (Pl. 9, G; Fig. 52, B) whilst in more mature laminae there are a few layers (Pl. 9, H-J & K; Fig. 52, C). Katsaros and Galatis (1988) report the presence of marginal apical initials that give rise to the tissue of the wing. The latter authors report that at different distances from the apical initials, the derivative cells start dividing and result in a two layered wing such as that observed in D. longifolia (Pl. 9, G).

4.9.3 Midrib

The midrib is the thickened region (0.5-1mm thick) running down the centre of the lamina of D. longifolia, and is characteristic of the genus. It appears to be initiated by the meristematic cells of the apical region and is not as thick in the apical region and in newly formed laminae (Pl. 10, A-C; Fig. 51, B; Fig. 52, E). The cells in the less prominent midrib (500μm thick) are smaller and have thinner walls than those in the more mature regions (Pl. 10, E). The epidermal cells are also smaller and less prominent in the immature midrib. The

more mature regions (approximately 1mm thick) of the midrib are found nearer to the base of the lamina as growth occurs from the apical tip. Although the apical cells may be responsible for longitudinal growth, there must be some meristematic activity that accounts for the thickening of the midrib towards the more mature regions. There does seem to be some division in the epidermal cells of the midrib, and in more mature regions the epidermis becomes the meristoderm and produces the rhizoids (Pl. 10, F-J; Fig. 51; C; Fig. 52, F). However, this is not very clear from the photographs taken in this study. There is a report of a superficial meristem which is involved in increasing the thickness of the midrib (in D. membranacea; Katsaros & Galatis, 1988). In the more mature regions of D. longifolia, the cells are large (30μm) with thick walls (4μm; Pl. 11, A-J). Katsaros and Galatis (1988) also report that the walls of the midrib cells of D. membranacea are very thick. The walls of the cells in D. longifolia appear to be composed of layers of material (Pl. 11, K & L). A similar report of thick walls composed of what appears to be fibrillar material, has been reported for Fucus and other brown algae (McCully, 1965). The cell walls of another Dictyotalean alga Dictyota dichotoma is also reported to be multilayered (Evans & Holligan, 1972).

There are approximately 14 layers of cells across the midrib. It is believed that the cells of the midrib are thick walled (4μm thick; Pl. 11, B-L) for extra strength because the midrib is often the only part of the laminae that remains once the wings have been abraded away (Chapman & Chapman, 1973). The structure and thickness of the midrib is similar from the mature region to the holdfast. In the basal region of the lamina there may be some production of rhizoids from the epidermal meristem (meristoderm) of the midrib (Pl. 10, F-M). The wings of the basal region of the lamina may degenerate leaving

little tissue surrounding the midrib. The midrib appears to get narrower (6 cells across; 200μm thick) nearer the base of the lamina and into the holdfast. This may be due to prolific division of the outer cells of the midrib to produce rhizoids (hence the smaller size of the cells on the periphery). Although in some brown algae the "stalk" at the base of the lamina is called the stipe, in this species this region is believed to be caused by the abrasion of the laminae wings and was thus determined by the degree of abrasion experienced, ie at certain times of the year the entire lamina was reduced to midrib and would have thus, by other definitions, have been called the stipe. The remains of the midrib at the lamina base was thus not considered as a stipe, but was included as part of the lamina. At the base of the lamina, just before the midrib enters the holdfast, the midrib was observed to become cylindrical in cross-section (from being fairly flattened). A similar observation was reported for D. membranacea and it has been suggested that this change is due to the activity of the meristoderm in this region (Katsaros & Galatis, 1988). There appears to be a core of midrib cells (approximately 200μm wide) in the centre of the holdfast (Pl. 10, N & O; Fig. 51, F; Fig. 52, H).

The cells of the midrib throughout the lamina of D. longifolia appear to be square or brick-shaped in cross section and smaller (30μm wide) than those of the wing, with thick walls (4μm). The composition of the different wall layers in D. longifolia was not determined. The cells are elongated in longitudinal section (approximately 65μm long; Pl. 12, A-E) with pores in the longitudinal walls (Pl. 12, F & G).

Large, more complex seaweeds, such as some members of the Phaeophyceae which may grow up to a size of 30m (eg Macrocystis; Manley, 1981), require some form of

transport other than the simple diffusion of material between the cells of the plant (Schmitz & Srivastava, 1974; Buggeln, 1983). The conducting systems of the brown algae are believed to be a parallel evolution to those in green plants, without there being any connection between the two groups (Schmitz & Lobban, 1976). The process, and aspects of the anatomical features of substance transport in brown algae, has been the subject of numerous studies entailing observations of dye and radioisotope transport at speeds exceeding those possible by diffusion alone (Parker, 1965; Buggeln, 1983). The transport of both organic and inorganic material over long distances, in big and fast growing brown species, eg Nereocystis (grows 6-13cm per day), is highly efficient. It is also believed that some type of transport occurs in smaller, less advanced species, but this has not yet been shown (Diouris & Floc'h, 1984). Seaweeds, unlike terrestrial plants, are able to absorb and accumulate nutrients from the water, through all parts of the thallus (Floc'h, 1982). Translocation (long distance transport) of absorbed substances, eg phosphorus (Floc'h & Penot, 1978), nitrogen (Davison & Stewart, 1983) and C-labelled materials (Lüning et al., 1972); as well as photosynthates, have been reported.

The theory that material is transferred from areas of high (source), to areas of low availability (sink) in seaweeds, is supported by the observation that there may be a greater dry mass in the growing tip, meristematic regions, and unfurled laminae of the plants than can be explained by the photosynthetic capabilities of these regions alone. In more mature parts of the thallus, the opposite is true, ie there is a greater carbon fixation than what is needed for growth. Thus, it has been suggested that there is transport from the areas of excess which are usually mature, to areas of deficiency which are usually growing (Schmitz & Lobban, 1976;

Buggeln, 1983). In the case of plants growing under a canopy, the areas in the light act as the source and the photosynthates are transported to areas where there is reduced illumination (Schmitz, 1981). The direction of the movement may also change if the sink is removed, eg the growing tip is destroyed. Material applied in the middle may move bidirectionally (Buggeln, 1983) and there is also reported to be lateral movement in the wings (Diouris & Floc'h, 1984). Schmitz and Kühn (1982) suggested that prior to long distance transport in the medulla, there must be transport across the parenchyma cells of the cortex in what is believed to be a symplastic process. Photosynthesis occurs mainly in the outer layer of the cortex cells, and then the photosynthates are transferred across the cortex to the medulla in the centre of the plant for transport (Schmitz & Kühn, 1982). There may also be a change in direction during different seasons, ie if the growing tip changes or the reproductive structures develop and become new sinks (Schmitz, 1981). The transport from a new region to an old is not believed to occur and, in the non-growing season, the transport from the mature fronds is believed to be to the holdfast for storage (Schmitz & Lobban, 1976; Lobban, 1978). The midrib has been identified as the pathway for movement in some Fucalean species, as its removal prevents transport (Diouris & Floc'h, 1984).

Translocation occurs in both light and dark conditions, but light and temperature affect the velocity and possibly also direction, of the movement (Parker, 1965; Buggeln, 1983). There is difficulty in measuring translocation velocity due to the fact that the velocity may vary with species, plant, thallus region and environmental condition (Schmitz, 1981; Buggeln, 1983). The diameter of the pores in the sieve plate also affects the velocity. The translocation rate is a more frequently used aspect of movement. It is defined as the movement of

dry material per unit time, divided by the cross sectional area of the transporting channel (Schmitz, 1981).

In the large, more complex members of the brown algae, eg Laminariales there may be a highly specialised cell organisation with different cells having different functions (Schmitz, 1981). Studies on the anatomy of various advanced members of the brown algae, eg Laminaria (Schmitz & Srivastava, 1974) and Macrocystis (Parker, 1965), have related the presence of "hyphae" or sieve elements in the medulla to the transport of substances in thallus of the seaweed (Sideman & Scheirer, 1977; Buggeln, 1983). The transporting cells found in the medullary region are not organised into bundles such as in higher plants, but rather form a reticular system (Schmitz & Lobban, 1976); although Buggeln (1983) reported a fairly regular system of tubes. The sieve tubes of algae differ from those of higher plants in that there are no companion cells and no central vacuoles (Lee, 1980). The tubes may become trumpet shaped due to passive stretching caused by growth. The names "sieve tube" or "sieve element", relate to the presence of a sieve plate with pores traversed by protoplasmic strands, which separate the cells across their transverse walls (Fritsch, 1945; Bisulputra, 1966; Lee, 1980). The pores of the cortical cells are only found in thin regions of the wall, whereas, in the sieve elements, the pores are found evenly all over the sieve plate (Sideman & Scheirer, 1977). Transport is reported to cease in the older elements which may die and undergo callose deposition in the pores (Fritsch, 1945; Schmitz, 1981). The pores of algae are reported to be less advanced than those found in the higher plants due to the lack of internal components (La Claire, 1981). The pores do however, maintain the cytoplasmic continuity between the cells, eg Dawes et al. (1961; in Bisalputra, 1966) report